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II. THE TRILOBITES OF THE SEYDIŞEHIR FORMATION (ORDOVICIAN)

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BY

WILLIAM THORNTON DEAN

Geological Survey of Canada

Pp. 1–24 ; 5 *Plates*, 3 *Text-figures*

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THE LOWER PALAEOZOIC STRATIGRAPHY AND FAUNAS OF THE TAURUS MOUNTAINS NEAR BEYŞEHİR, TURKEY. II. THE TRILOBITES OF THE SEYDİŞEHİR FORMATION (ORDOVICIAN)

By W. T. DEAN

CONTENTS

SYNOPSIS

Trilobites from the upper half of the Seydişehir Formation near Beyşehir are described. Almost all are represented only by disarticulated fragments but the following genera are identified : *Geragnostus, Ampyx ?, Colpocoryphe, Neseuretus, Symphysurus, Paramegalaspis, Megistaspis, Ptychopyge* and *Taihungshania*. Three new species are described : *Geragnostus lycaonicus, Neseuretus sexangulus* and *Symphysurus blumenthali*. The assemblage is of Lower Arenig age and mostly of Tethyan type, but some genera from the highest strata exhibit Balto-Scandinavian affinities.

I. INTRODUCTION & ACKNOWLEDGMENTS

THE present paper is the first of a series describing the Lower Palaeozoic trilobites of that area of Turkey which lies between Beyşehir and Seydişehir (see Fig. 1), some 100 kilometres south-west of Konya. An earlier paper (Dean & Monod, 1970) introduced the reader to the succession of Cambrian and Ordovician strata there and gave a series of sketch-maps showing the position of fossil localities and their stratigraphical position, if known.

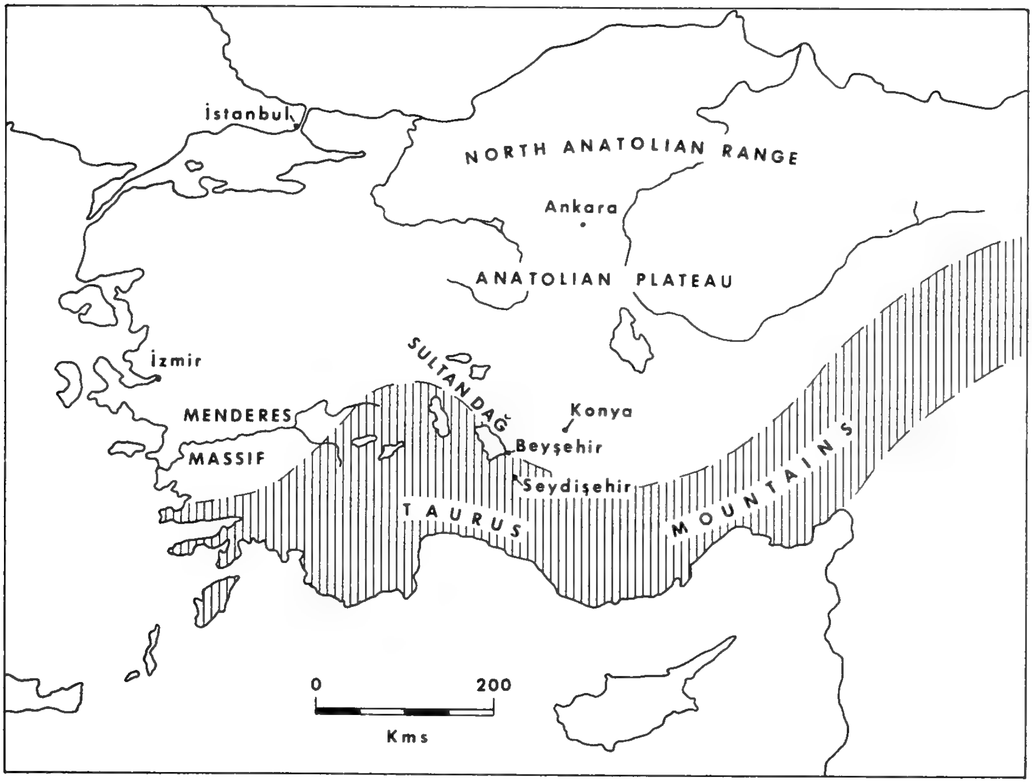

FIG. 1. Outline map of Turkey showing the location of the Beyşehir-Seydişehir district in relation to the Taurus Mountains (vertical shading) and other major structural units.

The Seydişehir Formation, at least part of which is Lower Ordovician in age, forms by far the largest Lower Palaeozoic outcrops of the region (see Fig. 2), and comprises the Seydişehir Shales, silty shales more than 1000 metres thick with occasional resistant bands of brown-weathering, sandy limestone, followed by 20 metres of coarser beds, the Upper Greywackes. The rocks, often tectonically deformed, are largely barren, but at some localities, all of which represent levels in the upper half of the Seydişehir Formation, the harder bands have yielded fossils. The latter include graptolites which indicate an Arenig age, possibly both the Extensus and Hirundo

Zones of that series, together with a few brachiopods and molluscs, and the trilobites described in the following pages. The trilobite remains are almost always broken and comprise about fifty fragments, mostly pygidia and librigenae, in addition to the specimens now described ; they are difficult to determine specifically, but at least eleven genera have been collected. Fossils were found for the first time in the Seydişehir Shales by M. Olivier Monod, who not only placed his material at my disposal but also introduced me to the geology of the Beyşehir region during a visit in the

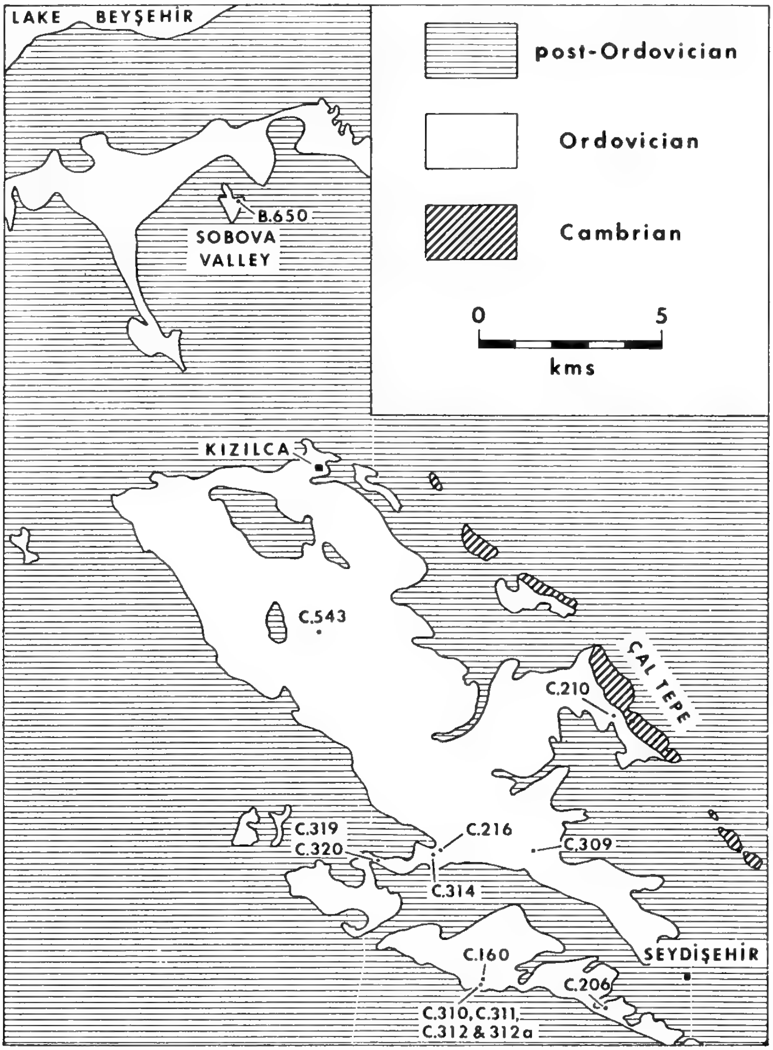

FIG. 2. Sketch-map showing the situation of fossil localities in the Seydişehir Formation of the district between Beyşehir and Seydişehir.

summer of 1968. I am much indebted to him for his co-operation and to Prof. H. B. Whittington who has kindly read and criticized the manuscript.

II. SYSTEMATIC DESCRIPTIONS

The terminology employed here is essentially that proposed by Harrington, Moore & Stubblefield in the Treatise on Invertebrate Paleontology (*in* Moore 1959 : O 117–O 126), though that describing *Geragnostus* follows Whittington (1963 : 28).

Family **AGNOSTIDAE** M'Coy 1849

Genus ***GERAGNOSTUS*** Howell, 1935

Type species. *Agnostus sidenbladhi* Linnarsson, 1869.

Geragnostus lycaonicus sp. nov.

Pl. 1, figs. 1, 3, 4, 7, 8

Diagnosis. Species of *Geragnostus* distinguished particularly by strongly convex pygidium with axis about five-sixths of total length. Anterior part of axis formed by two well-defined axial rings with median lobes joined to form a longitudinal lobe; remainder of axis scarcely defined, but with median tubercle near elliptical tip.

Holotype. BM. It.7992 (Pl. 1, figs. 3, 4, 8).

Paratypes. BM. It.7991 (Pl. 1, fig. 1) ; It.7993 (Pl. 1, fig. 7).

Locality and horizon. Sobova Valley, locality B.650, in the highest beds of the Seydişehir Shales, about 33 metres from the top of the Sobova Formation.

Description. The cranidium has an elongated, semielliptical glabella that occupies two-thirds the length and half the basal breadth of the cranidium and is bounded by broad, shallow axial furrows. The glabella carries a small tubercle slightly in front of centre and in-line with a pair of slight indentations in the sides of the glabella. One specimen (Pl. 1, fig. 1) shows these indentations linked to the median tubercle by shallow furrows which form a chevron, apex directed forwards, but it is not clear whether they are primary structures because similar furrows, almost certainly the result of crushing, diverge forwards from the median tubercle. The hindmost portion of the cranidium is imperfectly preserved but there are traces of a pair of subtriangular occipital lobes comparable with those found in other species of *Geragnostus*. Though incomplete, an otherwise broad border becomes slightly narrower posterolaterally and is delimited by a broad border furrow.

The pygidium is strongly arched both longitudinally and transversely, has a maximum breadth slightly greater than the median length and is semiellipitical in plan. The anterior margin (excluding the articulating half-ring, which is missing) is transversely straight medially but then runs backwards slightly to the articulating facets ; these are bounded by furrows that coalesce with the lateral border furrow, which in turn delimits a narrow border. As far as can be seen, there are no posterolateral border spines, but this part of the exoskeleton is imperfectly preserved. The frontal breadth of the axis is equal to half, its median length about five-sixths, that of the pygidium. The frontal two-fifths of the axis is composed of two unequal axial rings, the anterior of which is slightly the smaller. The median quarter or so of this part of the axis is occupied by a longitudinal structure, formed by the fusion of the median lobes of the axial rings, and the posterior half was probably produced dorsally to form a blunt spine, judging by the broken surface remaining. The ring furrows curve forwards gently at inner and outer ends, and both they and the axial furrows are deep and broad. The remainder of the axis is poorly defined and the axial furrows are scarcely discernible, though they can be seen to curve gently to the semielliptical tip, just in front of which is a small median tubercle (see Pl. 1, fig. 8). The posterior portion of the axis carries traces of a number of small pits like those on the pygidium of *Glyptagnostus* as described and figured by Öpik (1961, text-figs 15, 16) who termed them muscle spots. Apparently similar structures behind the pygidial axis of *Galbagnostus* have been described as muscle pits by Whittington (1965 : 308).

Discussion. The cephalon of the new species has no obviously distinctive features to separate it from approximately contemporaneous members of *Geragnostus*, such as *G. occitanus* Howell (1935 : 231 ; see also Dean 1966 : 274) from the lower Arenig Series of southern France. The latter species has a distinctive pygidial axis in which the anterior, segmented portion is relatively much larger than that of *G. lycaonicus*. The axial furrows of the pygidium of *G. occitanus* display considerable variation and may become completely effaced. There is insufficient material of the new species to test for such variation, but similar effacement of the axial furrows affects only the posterior half of the pygidial axis of *G. lycaonicus*. In this respect it resembles *G. tullbergi* (Novák), from the Llanvirn Series of Bohemia (see Dean 1966 : 273) but the latter species may be readily distinguished by its narrower, slightly shorter axis with a proportionately smaller segmented portion of the axis. *G. tullbergi* was made the type species of *Geragnostella* Kobayashi 1939, to which *G. lycaonicus* would at one time have been assigned, but this genus has since been placed in the synonymy of *Geragnostus*.

The pygidium of *G. lycaonicus* shares some features—the form of the axial rings, the small median tubercle, and the undefined posterior portion of the axis—with that of *G. ? explanatus* Tjernvik (1956 : 193, pl. 1, figs. 13, 14), from the Lower Arenig of Sweden, but the Swedish species is distinguished by its wider border.

Family **RAPHIOPHORIDAE** Angelin, 1854

Genus ***AMPYX*** Dalman, 1827

Type species. *Ampyx nasutus* Dalman, 1827.

Ampyx ? sp.

Pl. 1, fig. 5

Figured specimen. BM. It.8658.

Locality and horizon. Locality C.543, 4·5 kms south of Kızılca, and in the upper half of the Seydişehir Shales.

Description. A small, poorly-preserved cranidium approximately 5 mm wide is the only representative of the Raphiophoridae yet known from the Seydişehir Shales. The fixigenae are convex, almost quadrant-shaped in plan, and the narrow (*exsag.*) posterior border, separated from the fixigenae by a deep, broad (*exsag.*) posterior border furrow, curves gently forwards abaxially. There is a faint suggestion of wrinkle-like ornamentation on the test of the left fixigena. The glabella is broken but the remains of the external mould suggest that it was relatively short and extended only a little way in front of the fixigenae.

Although detailed comparison of such inadequate material is not possible, perhaps the closest raphiophorid is *Ampyx ? villebruni* Thoral (1935 : 307) from the Arenig Series of St. Chinian, southern France. In an earlier paper (Dean, 1966 : 281) it was suggested that the affinities of Thoral's species lie with *Ampyxina*, and the same may be true of the Turkish specimen.

Family **CALYMENIDAE** Edwards, 1843

Subfamily **COLPOCORYPHINAE** Hupé, 1955

Genus ***COLPOCORYPHE*** Novák *in* Perner, 1918

Type species. *Calymene arago* Rouault, 1849.

Colpocoryphe sp.

Pl. 1, figs. 2, 9, 10

Figured specimens. BM. It.7994 (Pl. 1, figs. 2, 5), It.7995 (Pl. 1, figs. 9, 10).

Locality and horizon. Sobova Valley, locality B.650, in the highest strata of the Seydisehir Shales, and about 33 metres below the summit of the Seydişehir Formation.

Description. Two incomplete cranidia were found, both of which exhibit the bifid, ventrally-directed prolongations of the anterior border which have been interpreted as vincular structures (Dean, 1966 : 308 ; 1966a : 135). The more completely-preserved glabella has straight sides which converge forwards at about 30 degrees ; the anterior margin of the frontal glabellar lobe is slightly concave forwards, whilst the posterior margin of the glabella is transversely straight. There are three pairs of glabellar lobes ; the 1p and 2p pairs are almost equisized in Pl. 1, fig. 2, but those of Pl. 1, fig. 10 are markedly unequal and perhaps less distorted. The 3p lobes and frontal glabellar lobe are of approximately equal length and about two-thirds the size of the 1p and 2p lobes. Small, incomplete palpebral lobes are positioned opposite the 2p furrows and the anterior part of the 1p lobes.

Only one other species of *Colpocoryphe* of Arenig age is known, *C. thorali* Dean (1966 : 304) from the Extensus Zone of southern France. The latter differs from the Turkish form in having a bell-shaped glabellar outline that is slightly constricted in front of the 2p glabellar lobes, a conspicuously longer frontal glabellar lobe, and less well-defined 2p and 3p glabellar furrows.

Subfamily **SYMHOMALONOTINAE** Kobayashi 1960

Genus ***NESEURETUS*** Hicks, 1872

TYPE SPECIES. *Neseuretus ramseyensis* Hicks, 1872.

Neseuretus sexangulus sp. nov.

Pl. 1, figs. 6, 11, 12

DIAGNOSIS. *Neseuretus* with hexagonal glabellar outline, the sides parallel as far as 2p glabellar furrows but then converging forwards strongly to transversely straight frontal glabellar lobe. 1p and 2p glabellar furrows well developed ; traces only of 3p furrows. Swollen anterior border about one-fifth length of cranidium. Eyes set well forwards, opposite 3p glabellar lobes. Posterior portions of fixigenae relatively large.

HOLOTYPE. BM. It.7996.

LOCALITIES AND HORIZONS. The holotype is from locality C.216, about 8 kms north-west of Seydişehir. A fragmentary cranidium at locality C.312, 6 kms west of Seydişehir, may represent the same species but is too poorly preserved for certain identification. Both localities are in the upper half of the Seydişehir Shales.

DESCRIPTION. The distinctive cranidium is preserved as an internal mould. Although the fixigenae are slightly distorted, it is calculated that the median length of the specimen is approximately three-fifths of the maximum breadth, measured across the genal angles. The glabella, excluding occipital ring, is roughly hexagonal in outline, almost as long as wide, with subparallel sides extending forwards as far as the 2p glabellar furrows. In lateral view the glabella is of low convexity, and when viewed anteriorly the dorsal surface appears slightly flattened (see Pl. 1, fig. 11). The median third of the posterior margin of the glabella is transversely straight, set slightly in front of the outer thirds which form gentle curves, concave forwards, around the bases of the 1p glabellar lobes. The anterolateral margins are almost straight and converge forwards at about 75 degrees so that the anterior margin, which has a slight median indentation, is equal to half the glabellar breadth. The main portion of the glabella, behind the convergent anterolateral margins, is divided into two pairs of glabellar lobes by deep glabellar furrows. The 1p lobes are slightly the largest and occupy one-third of the total glabellar length; they have the "cat's ear" outline found commonly in calymenaceids and are delimited anteriorly by deep, conspicuous 1p glabellar furrows that run inwards and back, expanding slightly at their inner ends but terminating so as to leave an unfurrowed median band one-third the breadth of the glabella. The 2p lobes are parallel-sided, bounded anteriorly by straight 2p glabellar furrows which diverge forwards at about 130 degrees. The 2p furrows end adaxially in-line with the 1p furrows, whilst abaxially they become markedly shallow immediately before intersecting the axial furrows. The glabella in front of the 2p furrows forms an almost continuous structure, with only a pair of faint indentations to suggest the position of 3p glabellar furrows. The axial furrows are subparallel, deep and narrow as far forwards as the 2p glabellar furrows, where they become slightly broader and shallower. The median third of the occipital ring is parallel-sided, and the corresponding portion of the occipital furrow is shallow, but abaxially the furrow becomes conspicuously deeper and curves forwards around the bases of the 1p glabellar lobes. At the same time the occipital ring narrows markedly and ends in a poorly-defined pair of occipital lobes, the tips of which extend forwards adjacent to the basal part of the 1p lobes. The anterior border, although slightly damaged, is evidently characteristic for the genus, swollen medially, separated from the glabella by a broad, shallow furrow and from the fixigenae by still broader furrows. The eye lobes are small, sited well forwards opposite the 3p lobes and at a distance outside the axial furrows equal to one-third the breadth of the glabella. The proportion of the fixigenae behind the eyes is thus relatively large for the genus. The remainder of the exoskeleton is unknown.

DISCUSSION. Whittard (1960 : 138 *et seq.*) has described the type and other species of *Neseuretus* from the Shelve Inlier of Shropshire and various parts of Wales. All, save one atypical species which should probably be excluded from the genus, are of Arenig age. In each case the combined anterior border and preglabellar furrow are appreciably longer than those of the Turkish species, and the latter differs also in the marked convergence of the axial furrows in front of the 2p glabellar furrows. *Neseuretus arenosus* Dean (1966 : 313) from the lower Arenig Series of southern France has generally similar glabellar proportions but is distinguished by the less angular outline of the front of the glabella, the smaller fixigenae, and the apparently less convex anterior border. The type species of *Neseuretus*, *N. ramseyensis* Hicks from the Lower Arenig of Wales (see Bates, 1969 : 22) has a more rounded glabellar outline and less distinct glabellar furrows than the Turkish species. *N. parvifrons* (M'Coy), also of Arenig age in Wales (Bates, 1969 : 26 ; Whittington, 1966 : 500), is distinguished by having a larger anterior border, and a glabellar outline that is more evenly convergent forwards. In both these species the posterior halves of the fixigenae are conspicuously smaller than those of *N. sexangulus*.

Neseuretus ? sp.

Pl. 2, fig. 9

A single fragmentary pygidium, preserved as an internal mould, has the anterior margin strongly convex forwards, whilst the posterolateral margins are straight, and diverge forwards at about 130 degrees. The left and sole surviving side-lobe is smooth for the most part but has two pleural ribs and a trace of a third rib in addition to the articulating facet and anterior half-rib. The ribs are delimited by shallow pleural furrows which cross only two-thirds of the side-lobe so as to leave a broad, smooth border. The axis extends to within a short distance of the pygidial tip and is infundibular in plan, with a marked break in outline behind the third axial ring.

There are five well-defined axial rings and a sixth less well defined, followed by a small terminal piece with semielliptical tip. The ring furrows are transversely straight and, apart from the first two, do not quite attain the broad, shallow axial furrows.

A similar axial outline has been described by Whittard (1960 : 142, 146) for *Neseuretus grandior* and *N. brevisulcus*, both from the Extensus Zone of the Arenig Series in the Shelve Inlier. In each case, however, the pygidial axis is parallel-sided behind the seventh axial ring, compared with the third ring in the Turkish form. The relative smoothness of the side-lobes, though it does not exclude the specimen from *Neseuretus*, is perhaps more suggestive of *Colpocoryphe*, but lack of the characteristic vincular furrows argues against such an identification. For the present I prefer to assign the pygidium questionably to *Neseuretus*.

FIGURED SPECIMEN. BM. It.8001.

LOCALITY AND HORIZON. Sobova Valley, locality B.650, in the highest portion of the Seydişehir Shales.

? Family **CHEIRURIDAE** Salter 1864

Cheirurid ? gen. et sp. indet.

Pl. 2, figs. 2, 5

FIGURED SPECIMEN. BM. It.8000.

LOCALITY AND HORIZON. Loc. C.160, about 5·5 kms west of Seydişehir, in the upper half of the Seydişehir Shales.

DESCRIPTION. A single, incomplete, poorly-preserved glabella of unusual type, with a fragment of the anterior border, is the only available, if doubtful, evidence for cheirurid trilobites in the Seydişehir Shales. The glabella is of inflated form, elliptical in plan, with breadth just over four-fifths of the maximum length. In lateral view the glabellar outline is tumid, strongly arched-down frontally, and there is evidence of at least two pairs, with a suggestion of a third pair, of glabellar furrows, preserved as narrow, lightly-impressed lines on the internal mould. Glabellar furrows interpreted as the 1p pair arch adaxially backwards towards, though they do not reach, the occipital furrow, whilst the 2p furrows are more transverse, only gently curved. The pairs of glabellar lobes so delimited are of large size, each about three-tenths of the length of the glabella. The axial furrows were evidently broad and deep, overhung on their adaxial sides by the tumid glabella. Traces of the anterior border show it was small and narrow, separated from the glabella by a furrow comparable in depth and breadth with the axial furrows. Only a fragment of the anterior branch of the facial suture remains, and meets the anterior margin of the cranidium at an obtuse angle.

It is difficult to assign such fragmentary material to a family with any degree of certainty, but the swollen glabella, the course taken by the glabellar furrows and the form of the outer portion of the anterior border suggest the Cheiruridae. Cranidia of this type are unusual in the Arenig Series but some comparison may be made with forms such as *Pseudosphaerexochus* (*Pateraspis*) *inflatus* Poulsen (1965 : 104, pl. 9, esp. figs. 1–4), from the Skelbro Limestone of Bornholm. This unusually early representative of the genus differs from the Turkish specimen in having a glabella that is less tumid in cross-section, a slightly larger anterior border, and more deeply-incised glabellar furrows. However, it shares enough features, such as the swollen glabella, conspicuously arched in lateral view and elliptical in plan, the position and direction of the glabellar furrows, and the shape of the anterior border, to suggest a possible affinity.

Family **NILEIDAE** Angelin, 1854

Genus ***SYMPHYSURUS*** Goldfuss, 1843

TYPE SPECIES. *Asaphus palpebrosus* Dalman, 1827.

Symphysurus blumenthali sp. nov.

Pl. 2, figs. 1, 3, 4, 6–8, 10 ; Pl. 3, figs. 5, 6, 10

DIAGNOSIS. *Symphysurus* with large, strongly convex glabella about four-fifths as broad as long, expanding slightly at front. Median tubercle developed. Large palpebral lobes situated just behind centre, each equal to two-fifths of glabellar length. Pygidium about twice as broad as long, with posterior margin strongly curved. Straight-sided axis clearly visible only on internal mould.

HOLOTYPE. BM. It.7997 (Pl. 2, figs. 1, 7, 10).

PARATYPES. BM. It.7998 (Pl. 2, fig. 3) ; It.7999 (Pl 2, figs. 4, 6, 8).

LOCALITY AND HORIZON. All the type material is from locality B.650 in the Sobova Valley. The specimens were collected from a thin band of weathered sandy limestone about 33 metres below the summit of the Seydişehir Formation.

DESCRIPTION. The exoskeleton is known only from disarticulated cranidia and pygidia. The cranidium is strongly convex both longitudinally and transversely, with projected length about two-thirds of the breadth. The glabella is large, occupies just over half the maximum basal breadth of the cranidium, and its sides are subparallel as far as the front of the palpebral lobes, beyond which the breadth expands by about one-quarter. Owing to its marked convexity, the front of the glabella appears rounded in plan, but when viewed anteriorly the margin of the frontal glabellar lobe is seen to be only slightly convex sagittally (see Pl. 2, fig. 7). The shallow axial furrows diverge forwards gently from the back of the cranidium until just in front of the posterior border furrow, where they become subparallel as far as the front of the palpebral lobes ; they then deepen and flex gently around the frontal glabellar lobe. Deep, slot-like anterior pits are sited in the axial furrows just in front of the palpebral lobes. There is no anterior border. A conspicuous tubercle is situated well behind the centre of the glabella. The occipital ring is not differentiated anteriorly from the glabella but its posterior margin projects backwards in a broad curve, with a small notch, marking the position of the axial furrows, situated at either end, beyond which the straight posterior margins of the posterior border run slightly back abaxially. The eyes and librigenae have not been found, but large, elongated, semielliptical palpebral lobes, which lack palpebral furrows, are sited immediately outside the axial furrows. When the cranidium is viewed laterally in its presumed life attitude, the flat upper surface of the palpebral lobes is declined forwards at about 40 degrees. When the cranidium is viewed with the palpebral lobes horizontal, the latter appear equal to two-fifths of the glabellar length, with one-fifth of the latter behind them. The anterior branches of the facial suture run parallel to, and immediately outside, the anterolateral margins of the frontal glabellar lobe and then turn adaxially through slightly more than a right-angle so as to meet frontally in an unbroken gentle curve. The posterior branches run outwards and slightly backwards from the rear of the eyes in almost straight lines, so that the posterior portions of the fixigenae are small and triangular.

The hypostoma and thorax are not known.

The pygidium is about twice as broad as long. The anterior margin arches forwards gently while the posterior margin forms a stronger, parabolic curve, so that the two curves meet at almost a right-angle. In both side and posterior views the pygidium appears moderately convex, with the top of the axis almost continuous with that of the side-lobes. The front of the axis has a breadth equal to one-third of the maximum breadth of the pygidium. The axial furrows are straight, converging backwards gently, and both they and the ring furrows are almost obsolete on the external surface of the test. On the internal mould the axial furrows appear deeper and at least three axial rings are visible, together with a small articulating half-ring, but it was not possible to examine the tip of the axis. The side-lobes have a pair of large articulating facets, just behind each of which is a broad (*exsag.*), shallow pleural furrow, visible only on the internal mould.

The surface of the glabella is ornamented with numerous thin, anastomosing ridges which form a Bertillon pattern and are subparallel to the margins of the frontal glabellar lobe. The surface of the pygidium is smooth.

A pygidium (Pl. 3, fig. 6) from the type locality has the axis better.defined than that of *S. blumenthali*, but is slightly crushed ; its specific position is in doubt, and it is termed merely *Symphysurus* sp. Likewise a fragmentary specimen (Pl. 3, figs. 5, 10) that shows the doublure ornamented by subparallel terrace-lines, but is too incomplete for determination. Another pygidium of *Symphysurus* (Pl. 4, fig. 2) from the Seydişehir Shales at locality C.312 has the appropriate outline and proportions for *S. blumenthali*. but the axis appears to be better-segmented and there are traces of more pleural ribs.

DISCUSSION. A modern diagnosis and modified illustration of the type species of *Symphysurus*, *Asaphus palpebrosus* Dalman 1827, have been published more recently by Poulsen (*in* Moore 1959 : O 358, Fig. 267, 8). They show that the Swedish species differs from *S. blumenthali* in having a relatively shorter glabella with axial furrows that are more divergent forwards, and eyes set farther forwards, so that the posterior portions of the fixigenae are proportionately larger. The pygidium of *S. palpebrosus* has a more rounded outline and an axis that is better defined and perhaps shorter, though this feature is hard to assess.

The pygidium of *S. blumenthali* appears to be very close to that of *S. angustatus* (Sars & Boeck) from the late Tremadoc and early Arenig Series of Norway and Sweden (Tjernvik 1956 : 211, pl. 2, figs. 24, 25). As far as can be judged from illustrations, both have an axis that is well defined on the internal mould but obsolete on the outer surface of the test. The cephalon of *S. angustatus* is less tumid and has a more straight-sided glabella that is relatively narrower. The slight carination of the glabella of *S. angustatus* is of dubious significance. The trilobite from the early Ordovician of the Montagne Noire, south-western France, described originally by Bergeron (1895 : 478, pl. 5, figs. 6–8) as *Aeglina sicardi* is clearly a *Symphysurus* and is sometimes cited as a variety of *S. angustatus*. The glabella is slightly shorter than that of *S. blumenthali*, the median tubercle and palpebral lobes are sited farther back, and the front of the glabella is more convex in plan. The pygidium attributed by Bergeron to the species is much longer than any of those considered above, with a wide, concave border and long, narrow axis ; probably it does not belong to the genus.

Family **ASAPHIDAE** Burmeister, 1843

Trilobites of generalized asaphid type are represented by locally abundant fragments in the resistant, thin bands of sandy limestone in the Seydişehir Shales. Such remains invariably pose problems of identification, particularly when the hypostoma is lacking. Consequently it has rarely proved possible to give more than a tentative generic assignment to the material.

Genus ***PARAMEGALASPIS*** Thoral *in* Jaanusson, 1956

TYPE SPECIES. *Megalaspis* (*Paramegalaspis*) *immarginata* Thoral, 1935.

Paramegalaspis sp.

Pl. 5, figs. 5, 8. 9, 11

FIGURED SPECIMENS. BM. It.8016 (Pl. 5, fig. 8) ; It.8019 (Pl. 5, fig. 11) ; It.8020 (Pl. 5, fig. 5) ; It.8021 (Pl. 5, fig. 9).

LOCALITIES AND HORIZONS. It.8021 is from locality C.314, in the upper half of the Seydişehir Shales, about 8 kms north-west of Seydişehir. The other three specimens are from locality B.650, in the highest beds of the Seydişehir Shales in the Sobova Valley, south of Beyşehir.

DESCRIPTION. A single incomplete cranidium (Pl. 5, fig. 9) has the median length rather more than three-quarters of the basal breadth. The glabella is poorly defined but as far as can be seen the breadth is about five-eighths of the median length. The front of the glabella is almost semicircular and the sides are parallel except behind the palpebral lobes, where they are slightly digergent posteriorly. The anterior portion of the cranidium—frontal area of Harrington, Moore & Stubblefield *in* Moore 1959 : O 120—shows no distinct differentiation into preglabellar field and anterior border, but the marginal area corresponding to the anterior border is slightly flattened, separated from the glabella by a broad (*sag.*), gently depressed area which corresponds to the preglabellar field. The occipital ring is almost indiscernible, although faint traces occur near the axial furrow, and there is a small median tubercle on the glabella in a position estimated to be immediately in front of the obsolete occipital furrow. There are traces of a narrow (*sag.*) doublure along the posterior margin of the occipital ring, and an apodeme is visible at the end of the right axial furrow. The eyes are positioned opposite the centre, and have a length (*exsag.*) equal to one-quarter, of the combined glabella and occipital ring. The flattened palpebral lobes are sub-semicircular in plan with no palpebral furrows, although the internal mould suggests a marginal thickening of the test. The anterior branches of the facial suture arch forwards and out from the eyes until half-way to the margin, at which point they are in-line abaxially with the centres of the palpebral lobes ; they then curve forwards and strongly inwards to meet at a blunted obtuse angle. The posterior branches run outwards and slightly back from the eyes in a very gentle curve, concave forwards, for a distance equal to nearly half the breadth of the glabella, and then turn backwards sharply to cut the posterior margin at almost a right-angle. The posterior area of each fixigena so formed is small, sub-triangular in plan, and carries a slightly curved posterior border furrow which runs parallel to the posterior margin and widens (*exsag.*) a little abaxially.

An almost complete left librigena (Pl. 5, fig. 8) from the same locality as the above cranidium shows the facial suture following a generally similar course, though the anterior branch appears straighter in front of the eye, perhaps due to crushing. The anterolateral margin is straight for the most part but becomes curved both frontally and, more strongly, near the genal angle, which is produced to form a moderately-long, slim spine, directed backwards and slightly outwards. A hypostoma preserved as an internal mould (Pl. 5, fig. 11) shows the characteristics of the genus and may be compared with one illustrated as *Paramegalaspis* sp. from the Lower Arenig Series of the Montagne Noire, southern France (Dean 1966 : 326, pl. 18, fig. 9). A pygidium (Pl. 5, fig. 5) preserved as an internal mould and exhibiting a uniformly narrow doublure has generally similar proportions to material illustrated from the Arenig Series of the Montagne Noire, for example *Paramegalaspis* cf. *frequens* Thoral (Dean 1966, pl. 18, figs. 2, 10, 13). The pleural ribs of the Turkish specimen appear to be slightly less well defined but further comparison is difficult with so little material.

DISCUSSION. According to the Treatise on Invertebrate Paleontology (Jaanusson *in* Moore 1959 : O 349) *Paramegalaspis* has no border on either cephalon or pygidium ; the frontal area is 0·2 to 0·25 of the cephalic length ; librigenal spines are present ; and the pygidium has a flattened axis and a narrow doublure. Material from the type area in southern France has been shown to exhibit a small amount of cephalic variation so that the anterior border may be moderately well defined (Dean 1966 : 326) or almost obsolete, as is the case for the Turkish cranidium now figured. Jaanusson (*loc. cit.*) claimed *Dolerasaphus*, type species *D. laevis* Harrington & Leanza (1957 : 157), as a synonym of *Paramegalaspis*, but the illustrations of *D. laevis* show that it, like the Turkish cranidium now described, has a frontal area which occupies slightly less than the 0·2 to 0·25 of the cephalic length stipulated in the Treatise. Such small differences are probably not valid at generic level, particularly when one is dealing with compressed specimens, and *Dolerasaphus* shows no other significant differences from *Paramegalaspis* as generally interpreted, though the hypostoma has not yet been described.

Genus ***MEGISTASPIS*** Jaanusson 1956

TYPE SPECIES. *Trilobites limbatus* Boeck, 1838.

Megistaspis sp.

Pl. 3, fig. 8 ? ; Pl. 4, fig, 5 ; Pl. 5 figs. 1 ?, 3, 4, 6, 10

FIGURED SPECIMENS. BM. It.8007 (Pl. 3, fig. 8); It.8013 (Pl. 4, fig. 5) ; It.8014 (Pl. 5, fig. 1) ; It.8015 (Pl. 5, figs. 3, 4, 6) ; It. 8017 (Pl. 5, fig. 10).

LOCALITIES AND HORIZONS. In the area north-west of Seydişehir the genus was collected at localities C.310, 312 and, most commonly, C.314, all of them in the upper half of the Seydişehir Shales. It was found less commonly in the highest part of the shales at B.650, in the Sobova Valley. Fragments referred questionably to the genus were obtained at localities C.319 and C.320 in the Upper Greywackes.

DESCRIPTION. Several fragmentary pygidia have been collected which correspond to the generic diagnosis given by Jaanusson (*in* Moore 1959 : O 347). The largest pygidium (Pl. 5, fig. 10) is parabolic in plan, gently convex both longitudinally and transversely, with median length about five-sixths of the maximum breadth as measured across the anterolateral angles. The front of the axis of this specimen is more than one-third of the maximum breadth of the pygidium, and the sides are straight, converging backwards at approximately 25 degrees to the indistinct tip. The whole axis, excluding the small articulating half-ring, occupies four-fifths of the pygidial length. The axial furrows are broad, shallow and for the most part poorly defined on the outer surface, so that the distinction between axis and side-lobes is not clear except frontally. The side-lobes are of low convexity, with large facets cutting obliquely across the abaxial halves of the anterior half-ribs. There is almost no trace of other furrows and the pygidium is bounded by a broad (*tr.*) border which becomes still broader (*sag.*) between the axis and the tip of the pygidium.

The above remarks apply only to the largest pygidium, and one of the best-preserved smaller specimens (Pl. 5, figs. 3, 4, 6) shows slight differences. For example the length is about nine-tenths of the maximum breadth, though such proportions have been affected to a certain degree by compression, particularly in the large specimen noted above. Certainly the axis and side-lobes of the smaller pygidium show more evidence of segmentation, and some of the pleural ribs have traces of interpleural furrows (see also specimen It.8014, Pl. 5, fig. 1). The doublure appears to correspond in size to the smooth border. This pygidium (It.8015) is preserved as an internal mould and a partly-exfoliated smaller specimen (Pl. 4, fig. 5) is of particular interest as it demonstrates the lack of furrows on the outer surface of the test, while the internal mould shows evidence of ten axial rings and at least seven pairs of pleural ribs.

No corresponding cranidium has yet been found, but an incomplete right librigena (Pl. 3, fig. 8) is questionably referred to *Megistaspis*?. The genal angle is produced to form a short, sharp spine and part of the test is missing so as to reveal the narrow doublure. A fragment of another right librigena (Pl. 5, figs. 2, 7) represents one of the largest trilobite remains found in the Seydişehir Shales. It is unusually deep anteriorly and the ventral side shows conspicuous ridge-like structures running at right angles to the margin. The incomplete anterior branch of the facial suture suggests *Megistaspis* rather than any of the other asaphid genera found in the area, but the material is insufficient for certain identification.

Megistaspis (*Megistaspidella*) of Jaanusson (1956 : 71 ; *in* Moore 1959 : 348, Fig. 259, 3) has a broadly similar pygidium but the tip is slightly more pointed and the side-lobes and axis are smooth, except for two axial rings. The type species, *Entomostracites extenuatus* Wahlenberg 1821, was figured also by Schmidt (1906, pl. 7, figs. 1, 2a, 3a) whose illustrations of the pygidium show it to be very like the Turkish specimens, though the border is more concave and wider near the bluntly pointed tip.

Genus *PTYCHOPYGE* Angelin, 1854

TYPE SPECIES. *Asaphus angustifrons* Dalman, 1827.

Ptychopyge sp.

Pl. 4, figs. 7, 8 ?

In 1964 Balashova erected a new subfamily Ptychopyginae and included therein the type genus and three new genera, *Metaptychopyge*, *Paraptychopyge* and *Pseudoptychopyge*. The present scanty material from the Seydişehir Shales does not lend itself to such detailed treatment and the specimens are referred merely to *Ptychopyge* sensu lato.

An isolated hypostoma (Pl. 4, fig. 7) from locality C.310 lacks the anterior wings but the maximum breadth, measured across centre, is three-quarters of the median length. The median body is moderately convex, occupies slightly more than three-quarters of the median length of the hypostoma, and is an elongated ellipse in plan, two-thirds as broad as long. It is divided into two unequal lobes by a median furrow which becomes almost effaced medially, runs in a gentle curve, convex forwards, and forms deep notches at either end. The crescentic posterior lobe so formed occupies about one quarter of the length (*sag.*) of the median body. The front of the hypostoma is incompletely preserved, but the lateral border starts opposite the middle of the anterior half of the median body, and the lateral margins are gently convex abaxially. The lateral border is continuous with the posterior border, but the latter is broader (*exsag.*), slightly flattened, and has a short, narrow median notch. The border is separated from the median body by a broad, shallow border furrow. The overall appearance is similar to that of the hypostoma of *Ptychopyge angustifrons* (Dalman) (see Jaanusson *in* Moore 1959 : O 339, Fig. 250, 2c) but differs in having a narrower lateral border, whilst the posterior lobe of the median body is slightly longer and better differentiated. One may also compare the hypostoma of *Ptychopyge lesnikovae* Balashova (1964, pl. 1, fig. 6) but the latter has a slightly larger, more pointed median notch and the posterior lobe of the median body is almost continuous with both the anterior lobe and the posterior border.

The pygidium from locality C.312*a* questionably assigned to *Ptychopyge* (Pl. 4, fig. 8) is subparabolic in plan, has a low convexity and a maximum breadth rather more than one and a half times the median length. The axis has a frontal breadth equal to two-sevenths that the pygidium and extends back for more than four-fifths of the pygidial length; in plan it has a slightly infundibular appearance owing to the converging of the sides at about 30 degrees for half the length, followed by their running parallel to the rounded tip. There are four rings on the anterior half, followed by two faint additional rings, and the rest of the axis is smooth. Outside the broad, shallow axial furrows are flattened side-lobes which merge imperceptibly with a smooth, concave border that widens posteriorly. The inner portion of the side-lobes is lightly furrowed with five pairs of ribs in addition to the anterior half-rib ; each rib, in turn, carries a faint interpleural furrow which divides it into anterior and posterior half-ribs, the latter slightly the larger. The furrowing of the pleural ribs is a feature not usually found in *Ptychopyge*, though it can occur in related genera as shown by the internal mould of a pygidium of *Metaptychopyge truncata* Nieszkowski sp. (Balashova 1964, pl. 8, fig. 7), the external surface of which exhibits smooth ribs.

Asaphid gen. et sp. undetermined

Pl. 3, figs. 1, 2, 4, 7, 9, 11 ; Pl. 4, figs. 1, 3, 4, 6, 9

FIGURED SPECIMENS. BM. It.8002 (Pl. 3, figs. 1, 9, 11), It.8003 (Pl. 3, figs. 2, 4, 7), It.8008 (Pl. 4, figs. 1, 3, 4), It.8010 (Pl. 4, figs. 6, 9).

LOCALITIES AND HORIZONS. Localities C.310 and C.312*a*, both 6 kms west of Seydişehir and in the upper half of the Seydişehir Shales ; also locality B.650 in the Sobova Valley, where it forms part of the highest Seydişehir Shales.

DESCRIPTION. Certain asaphid fragments exhibit characters which exclude them from the other genera so far recorded from the Beyşehir region but are inadequate for generic assignment. No undistorted cranidium has been found, but a well-preserved left librigena (Pl. 3, figs. 1, 9, 11) gives useful information regarding the course of the facial suture and the position of the eye. The palpebral lobe is semicircular in outline, positioned relatively far forwards so that the projected length of the cephalon in front of the eye is 0·34 of the estimated median length. The length of the eye is 0.28 that of the cephalon. From this and other specimens the facial suture is seen to be of isoteliform type, with the anterior branches meeting frontally at an obtuse angle. There is a weakly-developed, low anterior border, bounded by a shallow furrow which curves evenly backwards abaxially to meet the lateral margins immediately in front of the conspicuous, broadly-rounded genal angles. Pl. 4, figs. 6, 9 shows another left librigena of apparently the same type but with part of the test removed to reveal the doublure, which is narrow, dorsally concave, except at its inner margin where it becomes slightly reflexed, and ornamented with closely-spaced, subparallel terrace-lines.

No corresponding cranidium has been found well preserved. Pl. 3, fig. 4 shows the glabella and occipital ring to be continuous, bounded by broad, shallow, almost parallel axial furrows. The dorsally flattened palpebral lobes are slightly inclined abaxially, and are situated close to the sides of the glabella. Traces of a shallow furrow circumscribing the front of the glabella suggest the presence of an anterior border.

Only six segments of the thorax have been found preserved (Pl. 4, figs. 1, 3, 4) and are of asaphid type, with a broad, flattened axis occupying more than one-third of the breadth. The conjoined cephalon resembles the material already noted but the front is distorted by crushing.

Discussion. The material agrees in most respects with specimens attributed to *Paramegalaspis*, as well as the type species of its subjective synonym *Dolerasaphus*. The latter (Harrington & Leanza 1957 : 157) was stated to have no anterior border, but was founded on only a single specimen. As noted earlier, this feature has been described as slightly variable in *Paramegalaspis* and consequently the anterior border alone should not exclude the Turkish specimen from the genus. However, a conspicuous feature of the present material is its possession of broadly-rounded genal angles, a character found in such genera as *Asaphus*, in which the glabellar lobation is quite different, and *Asaphus* (*Neosaphus*), the type species of which has the eyes set much farther back (Jaanusson in Moore 1959 : O 336), though other species attributed to the latter subgenus may have the eyes set farther forwards and possess librigenal spines (see Jaanusson 1953). Rounded genal angles have not been reported from *Paramegalaspis* or similar forms, but crushing and the fragmentary nature of the material from the Seydişehir Formation preclude more detailed comparison, and in the circumstances I prefer not to make a definite generic assignment.

Family **TAIHUNGSHANIIDAE** Sun, 1931

Genus ***TAIHUNGSHANIA*** Sun, 1931

Type species. *T. shui* Sun, 1931.

Taihungshania sp.

Pl. 3, fig. 3

Figured specimen. BM. It.8004.

Locality and specimen. Locality C.543, 4·5 kms south of Kızılca and in the upper half of the Seydişehir Shales.

Description. The genus is represented in the Beyşehir region by a single incomplete pygidium which lacks both the posterior part of the axis and the posterior margin, but is estimated to have been approximately three-quarters as long as wide. The axis has straight sides, bounded by shallow axial furrows which converge backwards at about fifteen degrees. Only the anterior half of the axis is preserved, on which there are six axial rings of uniform width (*sag.*), separated by shallow, transversely straight ring furrows. The right side-lobe only is preserved and has six well-defined ribs and traces of two further ribs. The anterior half-rib is transversely straight for about one-third of its length (*tr.*) as far as a well-defined fulcrum, but then turns back through about forty-five degrees and is bounded anterolaterally by a large facet. From front to rear of the pygidium the ribs become progressively more strongly directed backwards, each rib being parallel-sided for half its length (*tr.*) but then turning backwards and tapering before dying-out. The angle through which the ribs turn backwards becomes progressively less from front to rear of the pygidium, and those of the fifth pair are almost straight. The first three ribs extend across about three-quarters of the breadth of the side-lobe and then almost die out towards the pygidial margin. Although, according to Jaanusson (*in* Moore 1959 : 356), there is no pygidial border in *Taihungshania*, nevertheless the specimen shows what appears to be a true, almost smooth border which becomes broader towards the tip of the pygidium. The pygidium of the type species *T. shui* Sun (1931, pl. 2, figs. 1a, b) appears to be generally similar, though with more pleural ribs, and the supposed absence of a border may be more apparent than real owing to the state of preservation. The portion of the border in-line with the third rib is slightly swollen and the margin there is produced backwards to form a spine which is only partially preserved. Most of the surface of the test is smooth, but that of the axial rings and the posterior bands of the ribs is pitted. Similar pitting occurs also in the first two pleural furrows.

DISCUSSION. In the Montagne Noire, southern France, *Taihungshania* [*Miquelina*] *miqueli* (Bergeron) has been used as an index fossil for part of the Extensus Zone of the Arenig and has been recorded from China by Sheng (1958 : 192). The pygidium of *T. miqueli* was refigured by Dean (1966, pl. 16, figs. 3, 4), and differs from that of the present specimen in having a narrower axis and a greater number of ribs, as well as a narrower border upon which the pleural furrows are slightly more impressed. *Taihungshania landayranensis* (Thoral), also from the Lower Arenig of the Montagne Noire (Dean, 1966 : 331–332, pl. 16, fig. 7), has a number of ribs broadly comparable with that of the Turkish specimen but relatively smaller side-lobes.

III. AGE AND RELATIONSHIPS OF THE TRILOBITES

A generalized section through the Seydişehir Formation is given below (Fig. 3) together with the estimated stratigraphic levels of the principal localities known at present in the Seydişhir–Sobova region (see Fig. 1). It must be emphasized that in strata of this type, which have undergone a considerable amount of folding, the horizons given can be no more than approximations.

The trilobites of the Seydişehir Formation, although relatively sparse, show unmistakable evidence of belonging, at least in part, to what has been termed variously the Calymenid—Trinucleid Province or the *Selenopeltis*—Fauna (Whittington 1966a). These names are sometimes difficult to apply owing to lack of the eponymous trilobite groups and I prefer to use the term Tethyan Province or Fauna (Dean 1967). Geographically the Tethyan faunal province has been shown to have extended westwards from the Mediterranean to encompass the Anglo-Welsh area, south-east Newfoundland and Florida, if not still farther. To the east it extended at least as far as south-west China during Arenig times and probably beyond, into Australia.

The trilobite families and genera characteristic of the Mediterranean part of the Tethyan region during the early Ordovician are Asaphidae (*Paramegalaspis, Plesiomegalaspis*), Colpocoryphidae (*Colopocoryphe*), Synhomalonotidae (*Neseuretus*) [these two families are sometimes regarded as subfamilies of the Calymenidae], Taihungshaniidae (*Taihungshania*) and Trinucleidae (*Myttonia, Hanchungolithus*). Of these the trinucleids, so useful in Ordovician stratigraphy, have unfortunately not yet been found in the higher Seydişehir Shales, but all the other families and most of the genera are present, though never in large numbers. Other genera are present

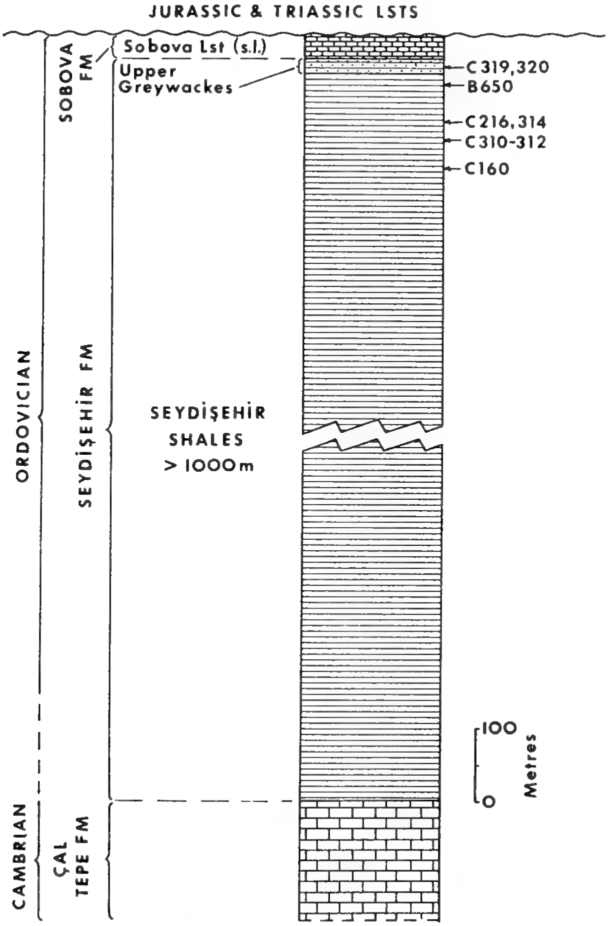

FIG. 3. Composite stratigraphical column for the Ordovician and adjacent rocks of the Beyşehir-Seydişehir district, showing the approximate horizons of fossil localities in the Seydişehir Shales and Upper Greywackes. C.309 and C.543 have been omitted owing to even greater uncertainty regarding their horizon, though it is undoubtedly in the upper half of the Seydişehir Shales.

which, as noted later, support Whittington's (1966a) contention that the boundaries between Ordovician faunal provinces are sometimes difficult to draw. The few graptolites found at C.206 and C.310 (see Fig. 2) indicate an Arenig age (Toghill *in* Dean & Monod, 1970) and supplement the evidence provided by the trilobites.

In a previous paper (Dean & Monod 1970) preliminary lists of trilobite identifications were given for the known fossiliferous localities in the Seydişehir Formation. The foregoing descriptions enable a series of revised faunal lists to be compiled, as follows:

Locality B.650.	Asaphid gen. et sp. undetermined, *Colpocoryphe* sp., *Geragnostus lycaonicus* sp. nov., *Megistaspis* ? sp., *Neseuretus* ? sp., *Paramegalaspis* sp., *Symphysurus blumenthali* sp. nov., *Symphysurus* sp.
Locality C.160.	Cheirurid ? gen. et sp. indet., *Paramegalaspis* ? sp.
Locality C.216.	*Neseuretus sexangulus* sp. nov., *Paramegalaspis* sp.
Locality C.309.	*Paramegalaspis* sp.
Locality C.310.	Asaphid gen, et sp. undetermined, *Megistaspis* ? sp., *Ptychopyge* sp.
Locality C.311.	*Paramegalaspis* sp.
Locality C.312.	*Megistaspis* sp., *Neseuretus* ? sp., *Paramegalaspis* sp., *Symphysurus* sp.
Locality C.312a.	Asaphid gen. et sp. undetermined, *Paramegalaspis* sp., *Ptychopyge* ? sp.
Locality C.314.	Asaphid gen. et sp. undetermined, *Megistaspis* sp., *Paramegalaspis* sp.
Localities C.319 & C.320.	Asaphid fragments, possibly *Megistaspis* sp.
Locality C.543.	*Ampyx* ? sp., *Taihungshania* sp.

Upper Cambrian and Tremadoc strata have not been found in this region, and the nature of the Cambrian—Ordovician boundary is not yet known. Certainly there are some hundreds of metres of clastic sediments lying between undoubted Middle Cambrian and Arenig strata, but so far there is no evidence for their age. The lower half, at least, of the Seydişehir Shales has not yet yielded identifiable fossils and the lowest fossiliferous horizon, at locality C.210, produced only unidentifiable fragments of uncertain affinities. Probably the oldest trilobites collected from the shales are from the upper part of the succession at C.160, where the Tethyan genus *Paramegalaspis* is accompanied by a cheirurid which, though unidentifiable, nevertheless represents a group that is more Baltic than Tethyan in aspect, a suggestion that receives some support from the few brachiopods at the same locality.

The small sample from C.543 is of particular interest as it includes the only specimen of *Taihungshania* yet known from the Seydişehir Shales. Although the latter is not identical with any of the species described from southern France or south-west China, it is accompanied here by a small raphiophorid apparently allied to *Ampyx* ? *villebruni*, described by Thoral from the Arenig Series of the Montagne Noire.

One of the youngest trilobite faunas, and also the most prolific, from the Seydişehir

Formation was collected at B.650 in the Sobova Valley, about 33 metres below the base of the overlying Sobova Limestone. *Colpocoryphe* and *Neseuretus* are typical Tethyan elements, and both genera had a long vertical range there, from Lower Arenig to Caradoc Series. *Colpocoryphe* is essentially a western Tethyan form, extending westwards to Florida and eastwards to Turkey but *Neseuretus* is more widespread in an easterly direction and is well known from the Lower Ordovician of south-west China. The *Geragnostus* present belongs to a group of species found particularly in the Arenig and Llanvirn of the Mediterranean region and Bohemia. At least three asaphid genera are present, and although *Paramegalaspis* is again of Tethyan type, *Megistaspis* and *Symphysurus* are northern European forms. The presence of *Symphysurus* at this point in the succession foreshadows the even greater abundance of the genus, together with additional Baltic elements, in the Sobova Limestone, and suggests at least a temporary break in the relatively uniform Tethyan Lower Arenig faunas, accompanied by the establishment of new faunal links with the Baltic region and Scandinavia.

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W. T. DEAN, D.Sc., Ph.D.
GEOLOGICAL SURVEY OF CANADA
601 BOOTH STREET
OTTAWA, 4, CANADA

EXPLANATION OF PLATES

All the material illustrated was sprayed lightly with ammonium chloride before photographing. Specimens preserved as internal moulds were painted with a black opaque before spraying ; casts of black latex were made from external moulds. The specimens carry numbers with the prefix It. and are housed in the British Museum (Natural History), London. Photographs by the writer.

PLATE 1

Geragnostus lycaonicus sp. nov.

Seydişehir Formation, Seydişehir Shales, locality B.650, Sobova Valley.

FIG. 1. Plan of internal mould of incomplete cranidium. Paratype. It.7991. × 8.

FIGS. 3, 4, 8. Posterior, left lateral and plan views of internal mould of pygidium. Note median tubercle on tip of ill-defined axis. Holotype. It.7992. × 10.

FIG. 7. Latex cast of incomplete cranidium. Paratype. It.7993. × 10.

Colpocoryphe sp.

Seydişehir Formation, Seydişehir Shales, locality B.650, Sobova Valley.

FIG. 2. Plan view of internal mould of cranidium. It.7994. × 7.

FIGS. 9, 10. Left anterolateral and plan views of internal mould of incomplete cranidium. It.7995. × 7.

Ampyx ? sp.

Seydişehir Formation, Seydişehir Shales, locality C.543, 4·5 kms south of Kızılca.

FIG. 5. Plan view of damaged cranidium with centre of glabella missing. It.8658. × 5.

Neseuretus sexangulus sp. nov.

Seydişehir Formation, Seydişehir Shales, locality C.216, 8 kms north-west of Seydişehir.

FIGS. 6, 11, 12. Right lateral, anterior and plan views of internal mould of crandium. Holotype. It.7996. × 5.

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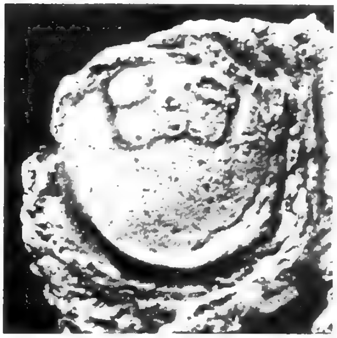

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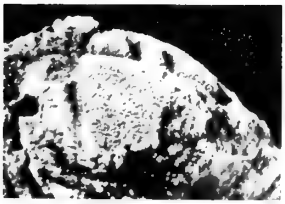

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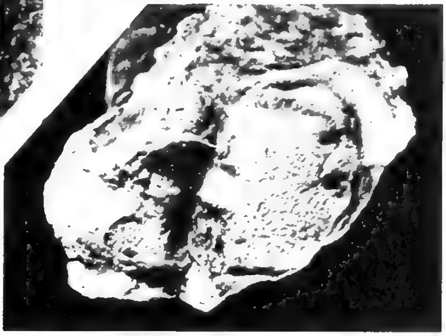

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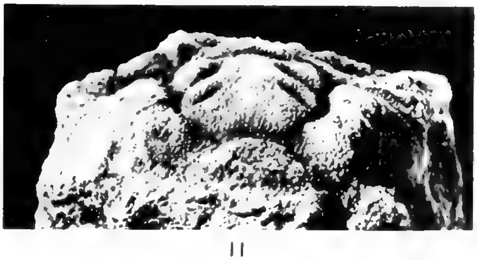

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PLATE 2

Symphysurus blumenthali sp. nov.

Seydişehir Formation, Seydişehir Shales, locality B.650, Sobova Valley.

FIGS. 1, 7, 10. Plan, anterior and right lateral views of partially exfoliated cranidium. Holotype. It.7997. × 3·5.

FIG. 3. Partly exfoliated pygidium. Note the axial furrows, which are strongly developed only on the internal mould. Paratype. It.7998. × 3·5.

FIGS. 4, 6, 8. Left lateral, plan and posterior views of pygidium. Paratype. It.7999. × 2.

Cheirurid? gen. et sp. indet.

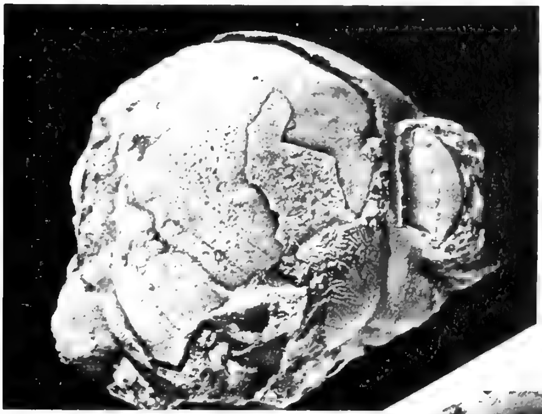
Seydişehir Formation, Seydişehir Shales, locality C.160, 6 kms west of Seydişehir.

FIGS. 2, 5. Anterior and right lateral views of internal mould of incomplete cranidium. It.8000. × 3·5.

Neseuretus? sp.

Seydişehir Formation, Seydişehir Shales, locality B.650, Sobova Valley.

FIG. 9. Internal mould of incomplete, small pygidium. It.8001. × 5.



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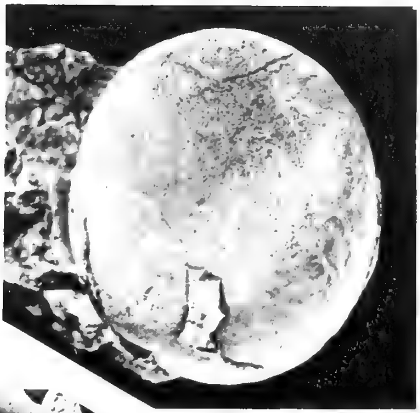

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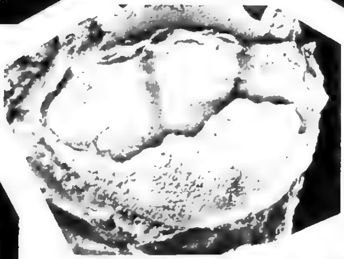

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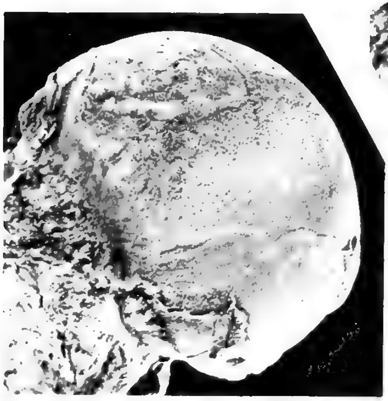

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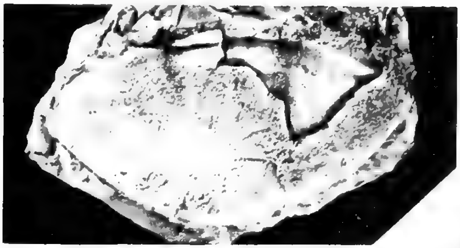

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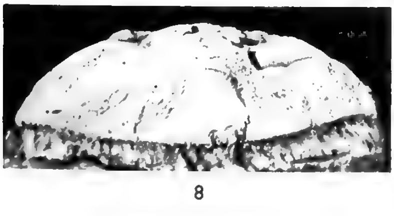

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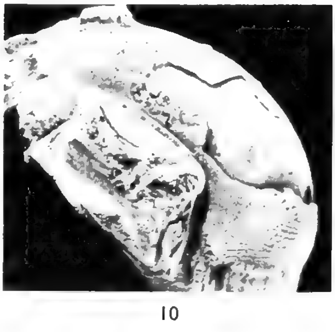

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PLATE 3

Asaphid gen. et sp. undet.

Seydişehir Formation, Seydişehir Shales, locality C.312a, 6 kms west of Seydişehir.

FIGS. 1, 9, 11. Plan, anterior and left lateral views of internal mould of left librigena BM. It.8002. × 4.

Seydişehir Formation, Seydişehir Shales, locality B.650, Sobova Valley.

FIGS. 2, 4, 7. Left lateral, plan and anterior views of slightly distorted internal mould of cranidium. BM. It.8003. × 2·5.

Taihungshania sp.

Seydişehir Formation, Seydişehir Shales, locality C.543, 4·5 kms south of Kızılca.

FIG. 3. Plan view of incomplete pygidium. BM. It.8004. × 3.

Symphysurus sp.

Seydişehir Formation, Seydişehir Shales, locality B.650, Sobova Valley.

FIGS. 5, 10. Posterior and plan views of damaged pygidium showing impression of ventral surface of doublure. BM. It.8005. × 3.

FIG. 6. Plan view of small pygidium. BM. It.8006. × 3.

Megistaspis ? sp.

Seydişehir Formation, Seydişehir Shales, locality C.310, 6 kms west of Seydişehir.

FIG. 8. Plan view of largely exfoliated right librigena. Note genal spine and inner margin of doublure. BM. It.8007. × 2.


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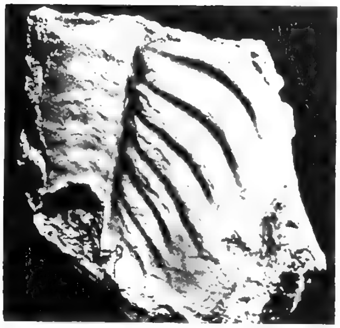
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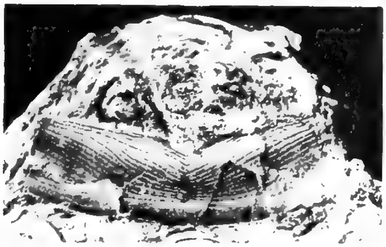
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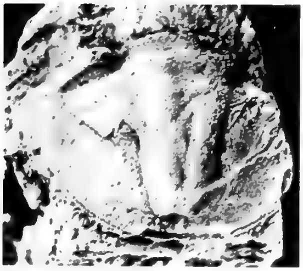
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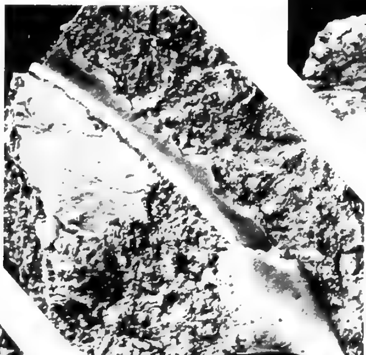
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PLATE 4

Asaphid gen. et sp. undet.

Seydişehir Formation, Seydişehir Shales, locality B.650, Sobova Valley.

FIGS. 1, 3, 4. Plan, left lateral and anterior views of internal mould of cephalon and first six thoracic segments. BM. It.8008. × 2·5.

Seydişehir Formation, Seydişehir Shales, locality C.310, 6 kms west of Seydişehir.

FIGS. 6, 9. Plan and left anterolateral views of incomplete left librigena with part of doublure exposed. BM. It.8010. × 4.

Symphysurus sp.

Seydişehir Formation, Seydişehir Shales, locality C.312, 6 kms west of Seydişehir.

FIG. 2. Ventral side of incomplete pygidium showing doublure ornamented with terrace-lines. BM. It.8009. × 1·5.

Megistaspis sp.

Seydişehir Formation, Seydişehir Shales, locality C.312, 6 kms west of Seydişehir.

FIG. 5. Partly exfoliated small pygidium. Note lack of furrows on external surface. BM. It.8013. × 4.

Ptychopyge sp.

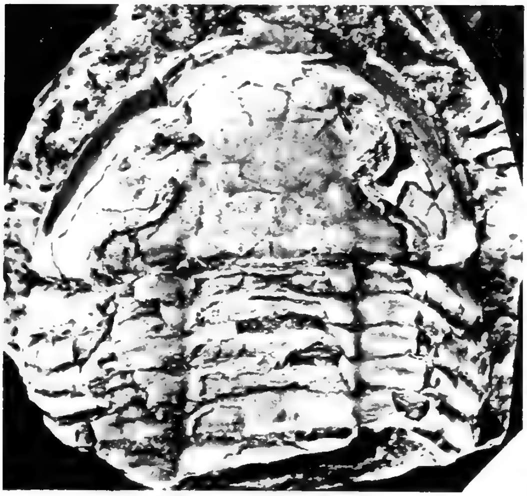
Seydişehir Formation, Seydişehir Shales, locality C.310, 6 kms west of Seydişehir.

FIG. 7. Internal mould of hypostoma. BM. It.8011. × 6.

Ptychopyge ? sp.

Seydişehir Formation, Seydişehir Shales, locality C.312a, 6 kms west of Seydişehir.

FIG. 8. Plan view of small pygidium. BM. It.8012. × 4.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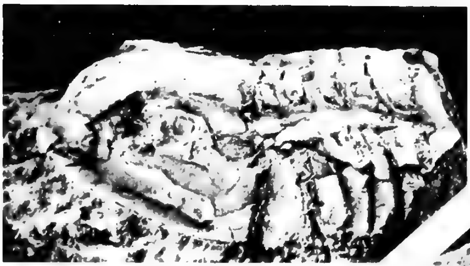
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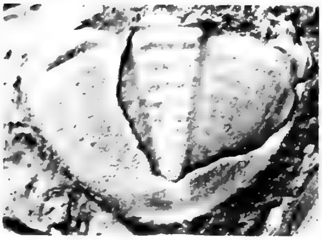
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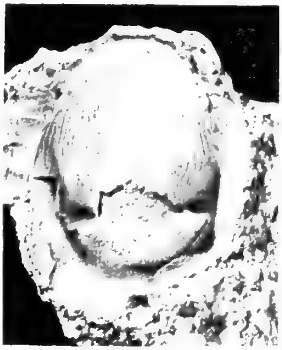
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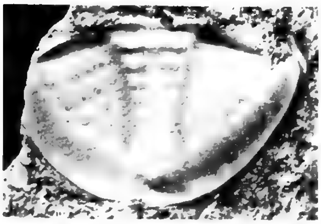
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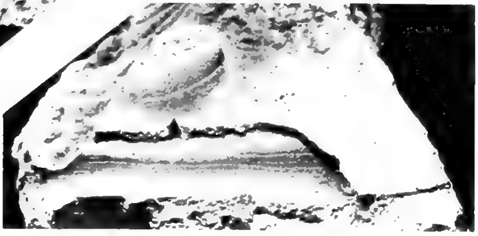
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PLATE 5

Megistaspis sp.

Seydişehir Formation, Seydiçehir Shales, locality B.650, Sobova Valley.

FIG. 1. Internal mould of incomplete pygidium. BM. It.8014. × 2·5.

Seydişehir Formation, Seydişehir Shales, locality C.314, 8 kms north-west of Seydişehir.

FIGS. 3, 4, 6. Internal mould of pygidium. BM. It.8015. × 2.

FIG. 10. Internal mould of large pygidium. BM. It.8017. × 1·5.

Asaphid gen. et sp. indet.

Seydişehir Formation, Seydişehir Shales, locality C.314, 8 kms north-west of Seydişehir.

FIGS. 2, 7. Partly exfoliated fragment of large right librigena. BM. It.8018. × 2.

Paramegalaspis sp.

Seydişehir Formation, Seydişehir Shales, locality B.650, Sobova Valley.

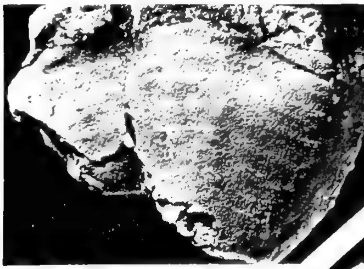
FIG. 5. Internal mould of pygidium showing doublure. BM. It.8020. × 3.

FIG. 8. Internal mould of left librigena. BM. It.8016. × 2.

FIG. 11. Internal mould of hypostoma. BM. It.8019. × 6.

Seydişehir Formation, Seydişehir Shales, locality C.314, 8 kms north-west of Seydişehir.

FIG. 9. Internal mould of almost complete cranidium. BM. It.8021. × 5.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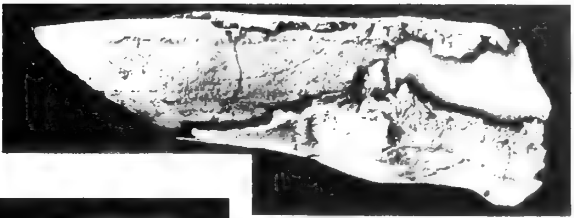
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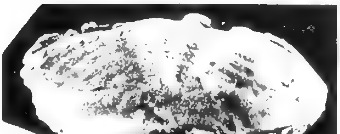
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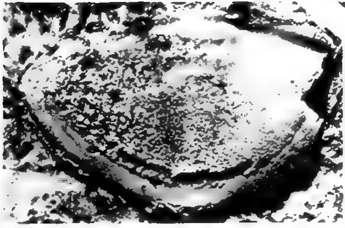
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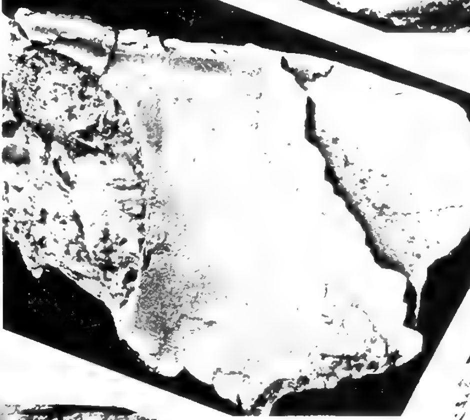
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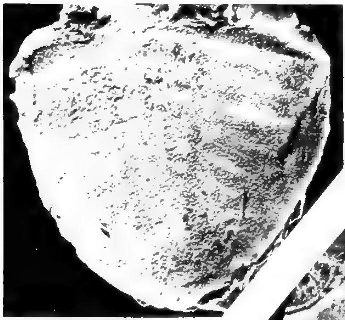
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LOWER CRETACEOUS AMMONITES FROM NORTH-EAST ENGLAND: THE HAUTERIVIAN GENUS *SIMBIRSKITES*

P. F. RAWSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 20 No. 2
LONDON: 1971

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BY
PETER FRANKLIN RAWSON
(Queen Mary College, London)

Pp. 25–86; 12 *Plates*; 10 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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LOWER CRETACEOUS AMMONITES FROM NORTH-EAST ENGLAND: THE HAUTERIVIAN GENUS *SIMBIRSKITES*

By P. F. RAWSON

CONTENTS

SYNOPSIS

Simbirskites (with four subgenera, *Simbirskites* s.s., *Speetoniceras*, *Milanowskia* and *Craspedodiscus*) occurs in Beds C7–LB5 of the Speeton Clay of Filey Bay, Yorkshire, and in the Lower Tealby Clay and Tealby Limestone of Lincolnshire. The stratigraphy of these beds is outlined and 21 species of *Simbirskites* occurring therein are described. 2 species, *S.* (*C.*) *juddi* and *S.* (*C.*) *variabilis*, are new, 14 are referred to or compared with previously described species, and 5 are left under open nomenclature. The occurrence of the ammonite genera *Aegocrioceras*, *Crioceratites*, *Paracrioceras*, *Protaconeceras*, *Spitidiscus*, *Hypophylloceras* and *Lytoceras* in the *Simbirskites* beds is reviewed. As a result of careful bed-by-bed collecting of the ammonite fauna the *Simbirskites* beds of the Speeton Clay have been divided into five zones, all defined by species of *Simbirskites*. This new zonation replaces earlier schemes proposed by Spath (1924) and Chernova (1951). The faunal succession now established allows a detailed comparison to be made with the equivalent beds in Russia and north Germany. The problem of correlating the Hauterivian-Barremian boundary of the standard Tethyan sequence with the north European succession is briefly discussed with reference to the well-known occurrence in the northern Caucasus and Crimea of a mixed Boreal (*Simbirskites*)—Tethyan fauna.

I. INTRODUCTION

Simbirskites occurs in the Hauterivian beds of the Boreal Province and is a useful zonal form in Russia, north Germany and north-east England. The ammonite fauna of the Russian Simbirskitid Beds consists almost exclusively of species of this genus, whereas the corresponding beds in Germany and England yield a more varied fauna with crioceratitid ammonites common at some horizons. Hence different zonal schemes have evolved, the German (Koenen 1902, Stolley 1925) and north-west European (Spath 1924) zonations utilizing a combination of *Simbirskites* and crioceratitid and holcodiscid ammonites as zonal forms while the Russian scheme (Pavlow 1901, Chernova 1951) relies exclusively on *Simbirskites*. The differences between the various zonations obscure the close similarity that exists between the *Simbirskites* faunas of the three areas.

The first species of *Simbirskites* to be described were the Speeton Clay "*Ammonites*" *speetonensis* (Young and Bird 1828) and "*A.*" *concinnus*, "*A.*" *marginatus* and "*A.*" *venustus* (Phillips 1829), but most of the early descriptive work was published in Germany (e.g. Roemer 1841, Neumayr and Uhlig 1881, Weerth 1884) and Russia (e.g. Trautschold 1865, Lahusen 1874, M. Pavlow 1886, A. P. Pavlow 1901). Many of the German type and figured specimens have subsequently been lost or destroyed.

The English fauna has never been described in detail, though *Simbirskites* is quite common in the Speeton Clay (beds C7–LB5) of Yorkshire and also occurs in the Lower Tealby Clay and Tealby Limestone of Lincolnshire. A few species have been figured by Pavlow (1889), Pavlow *in* Pavlow and Lamplugh (1892) and Danford (1906), and individual records have been discussed by Judd (1867, 1868, 1870) and Lamplugh (1889, 1896). The standard reference on the Speeton ammonite sequence is Spath's (1924) exhaustive faunal list which recorded over 20 *Simbirskites* species.

The present review of the English fauna is based on material collected bed by bed by the author, supplemented where necessary by museum material. Most of the museum specimens are poorly localized and reference is made therefore only to particularly important specimens. The author's collection has been divided between the British Museum (Natural History) and the Department of Geology, University of Hull.

This paper forms part of a study commenced during the tenure of an N.E.R.C. Research Studentship in the University of Hull (1963–66) and continued during the tenure of an N.E.R.C. Post-Doctoral Fellowship at Queen Mary College, University of London (1966–67). Field work in Germany was assisted by a grant from the British Council under the Younger Research Workers Interchange Scheme (1965) and an award from the Daniel Pidgeon Fund of the Geological Society of London (1969). I gratefully acknowledge an award from the Central Research Fund of the University of London.

Among many colleagues who have assisted me are Dr. R. Casey (I.G.S.), Professor D. T. Donovan (University College, London), Professor V. V. Drushchitz (Moscow), Dr. B. N. Fletcher (I.G.S.), Dr. C. Forbes (Sedgwick Museum, Cambridge), Dr. M. K. Howarth (British Museum), Dr. E. Kemper (Hannover), Professor J. F. Kirkaldy (Queen Mary College), Dr. J. W. Neale (Hull), Mr. E. F. Owen and Mr. D. Phillips (British Museum), Dr. J. Remane and Dr. S. Ritzkowski (Göttingen), Dr. Fr. Schmid (Hannover), Mr. G. F. Wilmot (York Museum), Mr. C. J. Wood (I.G.S.) and Mr. C. W. Wright (London). Dr. F. A. Middlemiss (Queen Mary College) kindly read the initial manuscript.

II. STRATIGRAPHY

(a) *The Speeton Clay*

The type-locality of the Speeton Clay is a 1·2 kilometre ($\frac{3}{4}$ mile) coastal section along the southern part of Filey Bay, Yorkshire (Text-fig. 1). Here the clay crops out in low cliffs, where the succession is frequently obscured by slipped or rain-washed material. Hence the section often appears as "a wild and tumbled slope of clay in which at first sight it is hopeless to make out any order" (Blake 1891 : 138). Occasionally, however, the sea reaches the cliff face and cleans parts of the section, or sand may be removed from the beach in the intertidal zone to give continuous exposures of the underlying clays. Such transient exposures allow one to build up a composite picture of the Speeton succession, though some parts are still poorly known.

Leckenby (1859) and Judd (1868) made the first serious attempts to subdivide the Speeton Clay, but the classic description, and the one upon which all subsequent work has been based, is that of Lamplugh (1889). On the basis of the belemnite sequence Lamplugh recognized four major divisions, labelled A–D from the top

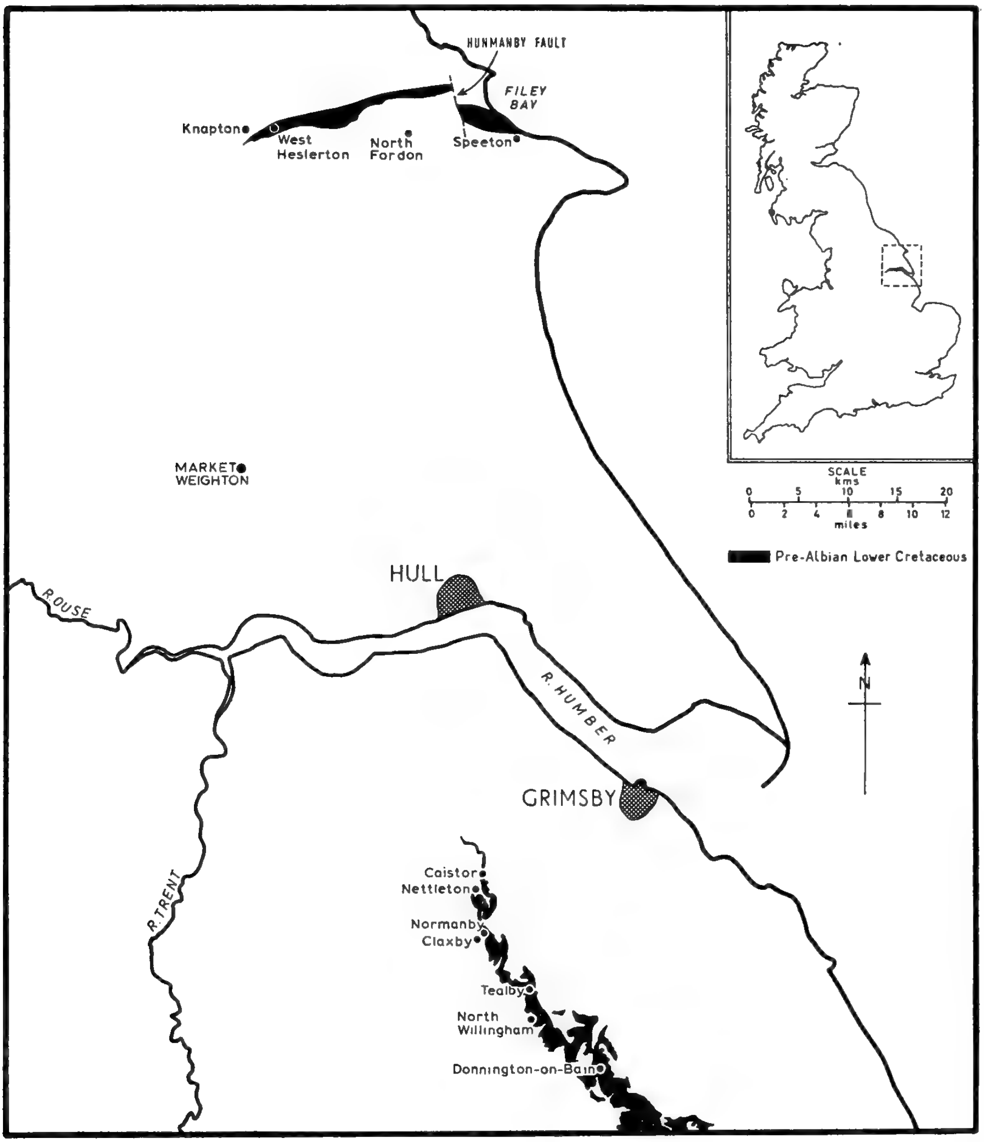

FIG. 1. Map showing the distribution of pre-Albian Lower Cretaceous rocks in East Yorkshire and North Lincolnshire, and the localities mentioned in the text.

downward (the reverse of the normal stratigraphical procedure). A fifth division, bed E, is a 100 mm (4 inch) thick seam of phosphatic nodules, the "Coprolite Bed", which rests on Upper Kimmeridge Clay.

Lamplugh further divided each of his major divisions; thus the B Beds were divided into Upper B, the Cement Beds and Lower B, and the C Beds into C1 to C11. These subdivisions provided the framework for a more detailed subdivision (based on lithological changes) of the Lower B Beds by Kaye (1964) and of the C Beds by Fletcher (1969). *Simbirskites* first appears in C7H (the lowest subdivision of bed C7) and the last known specimens are from LB5E, only 0·61 metres (2′) above the base of Lower B. All the author's specimens have been localized according to Fletcher's and Kaye's bed numbers. The succession below is essentially that of Fletcher and Kaye,, with only minor amendments, and their bed numbers are followed throughout.

SUCCESSION:

		metres	ft.	in.
LB5D	Dark, often shaly, pyritic clay with 75 mm (3″) mottled band (light mottles in dark clay) at top	0·91	3	0
LB5E	Dark, highly glauconitic mottled clay	0·46	1	6
LB6	Pale blue clay, weathering brown, with occasional "potato stone" nodules. Top 75 mm (3″) mottled (dark mottles in light clay)	0·51	1	9
C1A	Dark, glauconitic clay with conspicuous pale mottling	0·13		5
C1B	Pale grey clay mottled by large, dark, glauconitic streaks	0·10		4
C2A	Dark grey glauconitic clay with large pyrite crystals	0·30	1	0
C2B	Pale grey clay, darker in lowest 75–100 mm (3–4″). Band of small (25–50 mm), brown-weathering calcareous nodules at base	0·30	1	0
C2C	Medium grey clay becoming paler downwards	0·76	2	6
C2D	Dark, gritty, glauconitic clay with pale streaks. Stands out as a thin but prominent dark band among the lighter clays above and below	0·10		4
C2E	Pale grey clay; brown-weathering streak with occasional calcareous nodules in upper part	0·46	1	6
C2F	Medium grey clay. Boundary between this and C3 is gradational	0·61	2	0
C3	(The "*Echinospatangus* Bed" of Lamplugh) Pale grey clay with a conspicuous layer of sparsely scattered, brown-weathering calcareous nodules (up to 150 mm diameter) 0·9 m (3′) above the base	2·44	8	0

SUCCESSION:

		metres	ft.	in.
C4A	Thin limestone band, pale grey-green when fresh but weathering a pale reddish-purple; forms a good marker horizon for the top of C4	0·07		3
C4B	Dark, glauconitic clay	0·76	2	6
C4C	Pale clay with small phosphatic nodules	0·61	2	0
	Mottled bed; light mottles in dark glauconitic clay	0·15		6
	Pale clay	0·15		6
C4D	Thin, greenish-yellow impure limestone. Very similar to bed C4A	0·07		3
C4E	Dark grey glauconitic clay	0·30	1	0
C4F	Pale grey clay	0·46	1	6
C4G	Dark grey clay, mottled at top (large pale streaks in dark clay)	0·46	1	6
C4H	Brown weathering silty clay with occasional round calcareous nodules (up to 150 mm in diameter)	0·23		9
C4I	Dark, shaly clays	3·05	10	0
C4J	Brown-weathering silty clay with small, slightly flattened brown calcareous nodules at base	0·23		9
C4K	Dark grey clays, glauconitic in middle	2·70	9	0
C4L	Brown weathering silty band, without nodules but patchily indurated. Large *Simbirskites (Craspedodiscus) gottschei* and *Aegocrioceras* cf. *seeleyi*	0·23		9
C5A	Dark grey clays with thin mottled band at top	1·52	5	0
C5B	Olive grey clay with large, light coloured mottles at base	0·46	1	6
C5C	Dark grey clay with occasional small brown nodules	0·91	3	0
C5D	Dark grey clay with pyrite; finely mottled bed near top	0·76	2	6
C5E	Pale green, slightly glauconitic clay with occasional nodules	0·23		9
C5F	Dark grey clays with large pale mottles near top; bed of small nodules in middle	0·91	3	0
C5G	Brown-weathering silty clay, partially indurated, and with widely scattered, large calcareous nodules	0·23		9
C5H	Medium grey clay	0·76	2	6
C5I	Pale grey clay	0·15		6
C5J	Olive grey clay, mottled in part (light mottles in darker clay)	0·46	1	6

SUCCESSION:		metres	ft.	in.
C5K	Dark grey clay with some pyrite; occasional small brown nodules	1·70	5	6
C5L	Brown-weathering silty clay, partially indurated and with widely scattered calcareous nodules	0·23		9
C6	Dark grey shaly clays with 75 mm (3″) mottled bed at top (large and small pale grey mottles in dark clay). Occasional brown nodules in upper portion. Small *Simbirskites* (*Milanowskia*) *concinnus* common in lowest 0·61 m (2′)	4·55	15	0
C7A	Brown-weathering, silty indurated clays with large calcareous nodules. Large *Crioceratites* common	0·30	1	0
C7B	Pale grey clay	0·30	1	0
C7C	Dark grey clay with large mottling (pale mottles in dark clay) at top	0·38	1	3
C7D	Pale grey clay with a little glauconite	0·30	1	0
C7E	Black clay; large pale grey mottles at top. Glauconite abundant in upper part of clay, decreasing downward and absent at base	0·38	1	3
C7F	Pale grey clay with abundant flattened impressions of *Simbirskites* (*Speetoniceras*) sp..	0·15		6
	Pale grey silty clay, weathering brown and locally indurated. Contains rounded phosphatized nodules (up to 150 mm diameter) and larger, more irregular calcareous concretions. Body chambers of *Aegocrioceras* common	0·23		9
C7G	Pale grey clay, mottled in part. *Aegocrioceras bicarinatum* common	0·53	1	9
C7H	Dark grey clay with abundant glauconite. Small *Simbirskites* (*Speetoniceras*) *inversum* and crushed *Thracia phillipsi* common.	0·30	1	0
C8	Pale grey clay with large (up to 100 mm diameter) nodules	0·23		9
	Dark grey clay with bed of small (20 mm), brown-weathering nodules in middle. *Endemoceras regale*	1·80	6	0

Beds C8, C7 and the base of C6 are well exposed in the southern part of Middle Cliff, while the high C Beds (C4B to C1) and Lower B are seen in the cliff and adjacent parts of the foreshore at Black Cliff slip (opposite a breakwater at TA 151763) and also along a low cliff immediately north of Speeton Beck (for all localities on this section see map in Kaye 1964, figs 5 and 6). C4, C5 and most of C6 are seen only on temporary beach exposures; C4 and C5 in particular are rarely clearly exposed, but from occasional observation and from published records both appear to be sparsely fossiliferous.

Although the succession is essentially argillaceous it is by no means monotonous; well-marked nodule bands, alternating pale and dark clays, gritty glauconitic beds, and bioturbated horizons (the "mottled beds") provide a series of useful marker horizons. In particular the brown-weathering, silty clays of C4H, C4J, C4L, C5G, C5L, and C7A are more resistant to erosion than the surrounding clays and stand out as slight but noticeable scars on beach exposures.

The Speeton Clay crops out inland along the southern edge of the Vale of Pickering, at the foot of the wold scarp, finally disappearing in the vicinity of Knapton (Text-fig. 1). The C and Lower B beds have never been exposed but have been proved in boreholes at North Fordon (Neale 1960 : 203) and West Heslerton (Neale and Sarjeant 1962 : 439).

(b) *The Tealby Beds*

The Lower Cretaceous deposits of the Lincolnshire–North Norfolk basin consist of a series of shallow-water ironstones, sandstones, limestones and clays. They thin southward towards the London Platform and northward towards the Market Weighton Upwarp, both of which were landmasses in pre-Albian Lower Cretaceous times.

The Tealby Beds, which form the middle part of the Lincolnshire succession, are subdivided into the Lower Tealby Clay, the Tealby Limestone and the Upper Tealby Clay. Ammonites are rare, but *Simbirskites* occurs in the Lower Tealby Clay and the Tealby Limestone. At present, the only good exposures of these beds occur at Nettleton, in north Lincolnshire, where they have been exposed during the quarrying of the underlying Claxby Ironstone. The correlation between the Lower Cretaceous succession here and the Speeton Clay has been summarized in Penny and Rawson (1969 : 212, table 1). The Lower Tealby Clay was formerly well exposed in the brick-yard next to Donnington-on-Bain station and the Tealby Limestone in numerous shallow pits around Tealby, Normanby and North Willingham.

1. *The Lower Tealby Clay*

The Lower Tealby Clay is generally a fairly uniform, stiff blue-grey clay with phosphatic nodules and prominent glauconitic streaks. *Hibolites jaculoides*, index belemnite of the C Beds of the Speeton Clay, occurs throughout, and this and rare ammonites together indicate a correlation with beds C1 to C7. There appears to have been a break in deposition between the Claxby Ironstone and the Lower Tealby Clay, for the former yields ammonites and belemnites typical of the upper D Beds of the Speeton Clay. The *regale* zone (C8–C11) is unrepresented in Lincolnshire, a faunal break first commented on by Lamplugh (1896 : 203).

Above the ironstone quarries in Nettleton Valley (TF 118985) the Lower Tealby Clay is about 12 metres (about 40 feet) thick. Partially phosphatized nodules in the basal 0·61 metres (2 feet) have yielded fragments of *Aegocrioceras* cf. *bicarinatum* (Young and Bird), a species common just above the base of C7 (C7G) at Speeton. The only *Simbirskites* from this locality have been found loose on tip heaps; they include a specimen close to *S.* (*M.*) *polivnensis* (p. 69), a crushed specimen of the *S.* (*M.*) *concinnus* group, and a whorl fragment of *S.* (*S.*) cf. *virgifer*, though the last may have come from the Tealby Limestone.

Elsewhere, *Simbirskites* has only been recorded from the old brick-pit at Donnington-on-Bain, where the record of *"Ammonites" speetonensis* (including "vars." *venustus* and *concinnus*) (Ussher, Jukes-Brown and Strahan 1888 : 97) suggests the *speetonensis* zone. *"Crioceras duvalii"* (probably a *Crioceratites* of the *wermbteri* group) indicates a similar or slightly earlier (top *inversum* zone) horizon, while Lamplugh's (1896 : 207) record of *"Olcostephanus* (*Simbirskites*) *umbonatus"* (figured by Pavlow (1892), and discussed below under *S.* (*S.*) *yorkshirensis*) from the same pit suggests that a higher horizon (early *variabilis* zone) is also represented.

2. *The Tealby Limestone*

The Tealby Limestone consists of a series of thin, impure arenaceous limestones interbedded with oolitic clays. It reaches its maximum thickness of 6 metres (20′) in Nettleton Valley, and forms a prominent scarp feature from Caistor to Donnington-on-Bain. Further south the individual limestones become thinner and softer and no longer form a noticeable ridge, until in south-east Lincolnshire the Tealby Limestone is virtually indistinguishable from the Lower and Upper Tealby Clays.

Belemnites (*Oxyteuthis pugio* and allies) indicate a correlation with the B Beds of the Speeton Clay, and the rare ammonites suggest a correlation with the lower part of Lower B; the only ammonite common to both beds is *Simbirskites* (*Craspedodiscus*) *discofalcatus* which occurs in Bed LB6 at Speeton. The ammonites described below (*S.* (*C.*) *juddi*, *S.* (*C.*) *discofalcatus* and *S.* (?*C.*) sp. b) were collected in the last century at a time when the numerous shallow pits between Normanby and North Willingham and around Tealby were being worked by hand. Details of some of the exposures have been given in Judd (1867 : 244) and Lamplugh (1896 : 209). Although the present exposures in Nettleton Valley are good the limestone is now removed mechanically and the workmen very rarely collect ammonites. A single, poorly preserved, indeterminate *S.* (*Craspedodiscus*) has been collected by the author.

Spath's (1924 : 79, 82) anomalous record of *S.* aff. *toensbergensis* (Weerth) and *S.* aff. *fasciatofalcatus* (Lahusen) from the Claxby Ironstone of Claxby led him to tentatively correlate the upper part of the ironstone with C4 of the Speeton Clay. The two specimens are in the Sedgwick Museum, numbers B11122 and B11123 respectively; their preservation shows that the former (an indeterminate species) came from the Tealby Limestone or Lower Tealby Clay and the latter (discussed below as *S.* (*C.*) *discofalcatus*) from the Tealby Limestone.

III. THE ASSOCIATED AMMONITE FAUNA

Representatives of five other ammonite families, the Crioceratitidae, Holcodiscidae, Oppeliidae, Phylloceratidae and Lytoceratidae are associated with *Simbirskites* in beds C7–LB5 of the Speeton Clay; only the Crioceratitidae are common. The rare oppeliid genus *Protaconeceras* is represented by an undescribed species from C4 (Casey 1954 : 270) and the holcodiscid *Spitidiscus rotula* (Sowerby) occurs in the lower part of C5 (C5L). A related form, *S. inflatiformis* Spath, occurs in the nodule bed at the top of C8. A whorl fragment (author's colln., BM. C.75852) of the phylloceratid *Hypophylloceras* cf. *perlobatum* (Sayn), previously known from Speeton by a single specimen from C8 (Rawson 1966 : 455), has been found about 0·60 metres (approximately 2 feet) above the base of C6. From slightly higher in C6 (about 1·8 metres above the base)Whitehouse and Brighton (1924 : 360) recorded *Lytoceras* cf. *subfimbriatum* (d'Orb.).

The Crioceratitidae first appear in bed C7G, just above the base of C7, and occur through the overlying Upper Hauterivian and Barremian beds of the Speeton section. Numerous species of *Aegocrioceras* occur in bed C7 (Spath 1924, Rawson 1970) and *Crioceratites* is common in C7A and lower C6. Higher in the C Beds section crioceratitids are rare; large body chamber fragments of *Aegocrioceras* cf. *seeleyi* (Neumayr and Uhlig) occur in C4L and two small, septate whorl fragments of *Paracrioceras statheri* Spath have been collected in bed C2C.

In Lincolnshire, *Aegocrioceras* and *Crioceratites* occur in the Lower Tealby Clay (p. 35) and poorly preserved crioceratitids in the Tealby Limestone. A single *Lytoceras* aff. *vogdti* Karakasch is recorded from the latter bed (Spath 1924 : 79).

IV. SYSTEMATIC DESCRIPTIONS

Morphological terms used in the systematic descriptions are defined in the ammonoid volume of the "Treatise on Invertebrate Paleontology" (1957 : R. C. Moore, editor). Detailed ontogenetic studies of sutural development are beyond the scope of this paper, and for the purposes of general morphological description of representative suture lines the relatively simple terminology used in the "Treatise" (Moore 1957 : L96, fig. 141) has been followed.

Dimensions are given in millimetres, as follows: diameter; oblique whorl height, whorl thickness, width of umbilicus.

The oblique whorl height is measured from the mid-line of the venter to the umbilical seam, and the whorl thickness has been measured on the ribs and not between.

The specific descriptions are based on 227 specimens from Speeton and Lincolnshire, together with a limited number of foreign specimens (12 German and 5 Russian) which are referred to for comparative purposes. The 244 specimens are distributed among 23 discrete taxa, as follows:

	Speeton	Lincolnshire	Germany	Russia
S. (*Sp.*) *subbipliciforme*	7	–	–	–
S. (*Sp.*) *inversum*	29	–	–	2

	Speeton	Lincolnshire	Germany	Russia
S. (*Sp.*) cf. *versicolor*	2	–	–	–
S. (*Sp.*) sp.	1	–	–	–
S. (*M.*) *concinnus*	66	–	1	–
S. (*M.*) *speetonensis*	22	–	–	1
S. (*M.*) sp.	3	–	1	–
S. (*M.*) *staffi*	2	–	2	–
S. (*M.*) *lippiacus* and *S.* (*M.*) cf. *lippiacus*	4	–	2	–
S. (*C.*) *gottschei*	8	–	2	–
S. (*C.*) cf. *kayseri*	3	–	1	–
S. (*C.*) *variabilis*	12	–	–	–
S. (*C.*) *discofalcatus* and *S.* (*C.*) cf. *discofalcatus*	6	7	–	1
S. (*C.*) *phillipsi*	–	–	2	–
S. (*C.*) sp. (*phillipsi* group)	3	–	–	–
S. (*C.*) *juddi*	–	2	–	–
S. (?*C.*) sp. a	14	–	–	–
S. (?*C.*) sp. b.	–	1	–	–
S. (*S.*) *umbonatus*	–	–	–	1
S. (*S.*) *marginatus*	13	–	–	–
S. (*S.*) *yorkshirensis* and *S.* (*S.*) cf. *yorkshirensis*	5	1	–	–
S. (*S.*) *decheni* group	15	–	1	–
S. (*S.*) cf. *virgifer*	–	1	–	–
	215	12	12	5

In addition, reference is made at the end of this section to a number of specimens which are too inadequately preserved for accurate determination.

Abbreviations: BM. = British Museum (Natural History); GSM. = Geological Survey Museum; Göttingen = Geologisches-Palaeontologisches Institut, Georg-August-Universität, Göttingen; NLfB = Niedersächsisches Landesamt für Bodenforschung, Hannover; HU. Rn. = Rawson collection, University of Hull; SM. = Sedgwick Museum, Cambridge; YM. = Yorkshire Museum, York.

Suborder AMMONITINA Hyatt, 1889

Superfamily **PERISPHINCTACEAE** Steinmann, 1890

Family **OLCOSTEPHANIDAE** Haug, 1910

Subfamily **SIMBIRSKITINAE** Spath, 1924

Three genera, *Speetoniceras*, *Simbirskites* and *Craspedodiscus* were included in the subfamily by Wright (1957 : L349). *Speetoniceras*, *Craspedodiscus* and *Milanowskia*

(Chernova 1952) are here regarded as subgenera of *Simbirskites*, so that the subfamily now consists of *Simbirskites*, divided into four subgenera, and the provincial north American genera *Hertleinites* Imlay 1958 and *Hollisites* Imlay 1957.

The Simbirskitinae are a widespread and important group in the later Hauterivian beds of the Boreal Province, and are the last surviving members of the Middle Jurassic to Lower Cretaceous superfamily Perisphinctaceae, dying out at the end of the Hauterivian.

Genus ***SIMBIRSKITES*** Pavlow 1892

Type species: *Ammonites decheni* Roemer 1841, by original designation.

Diagnosis: Ornament consists of short, sharp primary ribs branching into a varying number of secondary ribs; in most species there is a prominent tubercle at the point of branching in at least the earlier growth-stages. Other secondary ribs may branch from earlier ones higher on the whorl-flank, or may be intercalated. The ribs curve forwards on crossing the venter.

The external suture consists of five trifid lobes, a ventral, a lateral, and three auxilliaries, separated by bifid saddles; none of the incisions within these major elements is deep. The suture is inverse (ascendent) i.e. if a radial line is drawn from venter to umbilical edge, the saddles are seen to ascend towards the aperture on approaching the umbilicus.

Discussion: *Simbirskites* is a very variable genus, embracing evolute, coronate forms to involute, compressed forms. Within individual species there are often considerable changes in whorl proportions, rib pattern and rib density with growth. The genus was first proposed for "olcostephanids" of the *O. decheni* group, and subsequently (Pavlow 1901 : 67) divided into three groups, the Perisphinctoidea (group of *S. versicolor*), the Umbonati (group of *S. umbonatus* and *S. decheni*) and the Discofalcati (group of *S. discofalcatus*). Spath later divided *Simbirskites* into three genera, *Simbirskites* s.s. "restricted to the original coronate forms of the *decheni* group" (Spath 1924 : 87), *Speetoniceras*, proposed for the perisphinctoid early forms and therefore equivalent to Pavlow's Perisphinctoidea, and *Craspedodiscus*, proposed for the discoidal forms. The last genus included many of Pavlow's Discofalcati, though Spath included some of these in *Simbirskites*. In fact, Spath was inconsistent (Chernova 1952 : 46) in restricting *Simbirskites* to the coronate forms and then including in it *S. speetonensis* and *S. progredicus* which are moderately compressed species of Pavlow's Discofalcati group.

Wright (1957 : L350) followed Spath in regarding *Speetoniceras*, *Simbirskites* and *Craspedodiscus* as separate genera, placing two other genera, *Thysanotoceras* Whitehouse 1927 and *Stoicoceras* Whitehouse 1927, in synonomy with *Simbirskites*. *Thysanotoceras* was proposed for Weerth's (1884 : 12, pl. 2, fig. 5–6) *A. picteti*, and "includes the group with prominent bundling of costae in groups of four at the tubercle" (Whitehouse 1927 : 109). The genus is here regarded as a junior subjective synonym of *Simbirskites* s.s. *Stoicoceras* was not defined, but was proposed for *A. teutoburgensis* Weerth (1884 : 20, pl. 5, fig. 1). This species is difficult to interpret, but appears to be a neocomitid.

Roman (1938 : 393) regarded *Speetoniceras* and *Craspedodiscus* as subgenera of *Simbirskites*, as did Bähr (unpublished dissertation)[1].

Chernova's (1952) major work on *Simbirskites* included detailed ontogenetic studies, from which she concluded that *Speetoniceras* and *Simbirskites* are separate genera. In the former genus Chernova included Pavlow's Perisphinctoidea and Discofalcati, and in the latter his Umbonati plus *S. coronatiformis* (M. Pavlow) and *S. pavlovae* Chernova (*nomen novum* for *S. elatus* M. Pavlow *non* Trautschold), which were originally included in the Perisphinctoidea. Chernova divided *Speetoniceras* into three subgenera, *Speetoniceras sensu stricto, Craspedodiscus* and a new subgenus, *Milanowskia*. *Simbirskites* remained undivided.

According to Chernova (1952 : 53) *Simbirskites* is more inflated than *Speetoniceras sensu* Chernova, though the earliest *Simbirskites* and contemporary *Speetoniceras s.s.* are very similar in the adult stage. In addition, she suggested that the sculpture in the two genera developed differently; in *Simbirskites* the tubercles normally appear first, followed by the primary ribs and lastly the secondaries, whereas in *Speetoniceras* the primary ribs appear first and are followed by the secondary ribs and then the tubercles. However, Chernova shows that in the two earliest (*versicolor* zone) species of *Simbirskites* (*S. coronatiformis* and *S. pavlovae*) the primary ribs appear before the tubercles (as in contemporary *Speetoniceras*). There thus seems no merit in placing any major phylogenetic significance on the order of appearance of each of these features. Furthermore, in practice it can be very difficult to decide which feature does appear first.

Chernova (1952 : 54) further assumed an independent origin for the two genera, deriving *Simbirskites sensu* Chernova from *Polyptychites* of the *gravesiformis* group (i.e. the forms separated by Pavlow (1913) as *Euryptychites*) and *Speetoniceras sensu* Chernova from another (undescribed) group of *Polyptychites* or from *Tollia*. On the available evidence it is more reasonable to derive *Simbirskites sensu* Chernova (the group here included in the restricted subgenus *Simbirskites*) from *S.* (*Speetoniceras*) *versicolor*, with *S.* (*S.*) *pavlovae* and *S.* (*S.*) *coronatiformis*, the two earliest Russian *Simbirskites* s.s., as connecting links (see page 64).

It is impossible to draw sharp boundaries between *Craspedodiscus*, *Milanowskia*, *Simbirskites* s.s. and *Speetoniceras*, and all four are here regarded as subgenera of *Simbirskites*. In certain species the inner whorls have previously been placed in one genus and the outer whorls in another. Although the evolutionary relationship between some species appears clear, the complex *Simbirskites* lineages have by no means been unravelled completely and Chernova's (1951 : figs 1 and 2) detailed lineages are of doubtful value. At present, therefore, the division of *Simbirskites* into four subgenera is based as far as possible on phylogenetic studies, but as our knowledge of the interrelationships between various species increases the boundaries

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[1] Bähr, H. H., 1964. "Die Gattung *Simbirskites* (Ammonoidea) im Ober-Hauterive Nordwestdeutschlands". Unpublished dissertation, Technischen-Hohschule, Braunschweig. Referred to throughout this paper as "Bähr, unpublished dissertation".

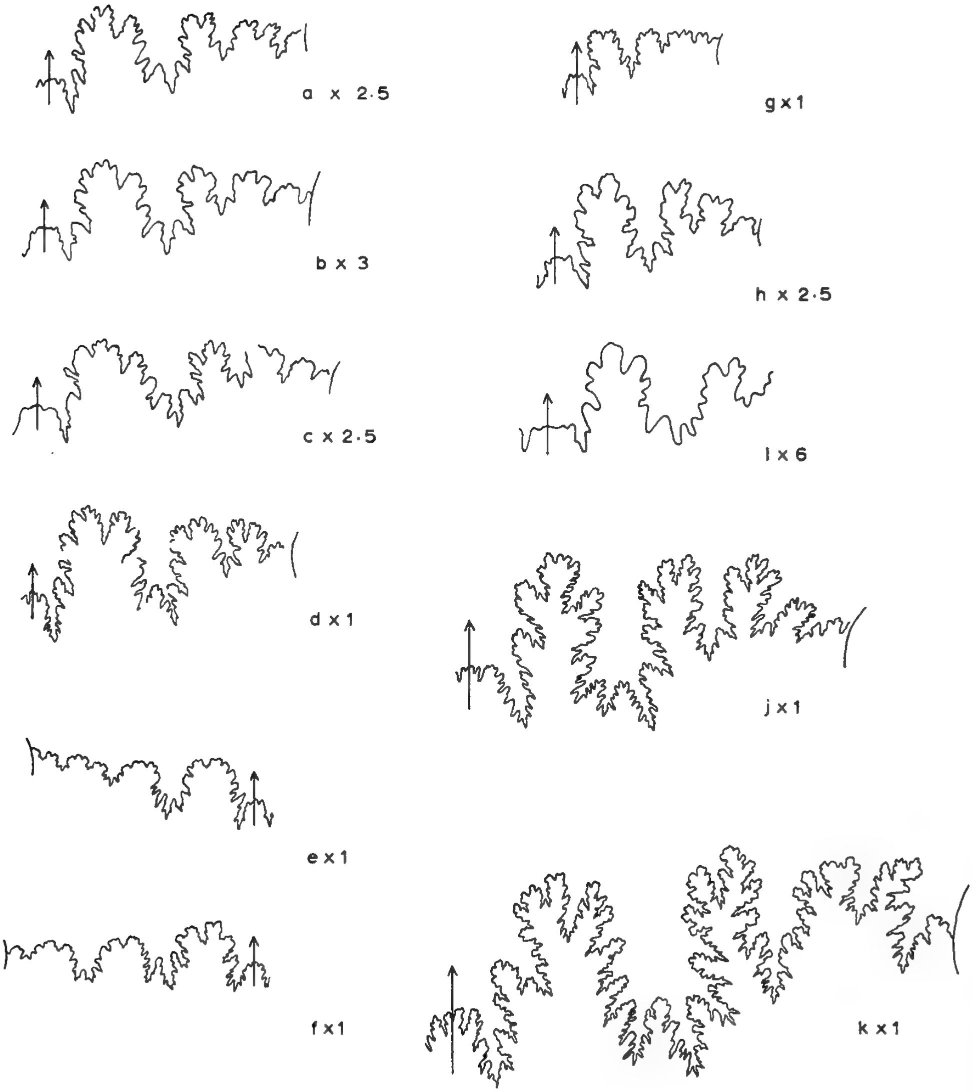

Fig. 2. Suture lines of *Simbirskites*. a–f sutures with relatively broad elements, g–k sutures with narrower, deeper elements. a. *S.* (*S.*) cf. *decheni* var. a, at 21 mm diameter (BM. C.75887). b. *S.* (*M.*) *concinnus*, at 20 mm diameter (HU. Rn.397). c. *S.* (*M.*) *staffi*, at 34 mm. diameter (NLfB Kp.37). d. *S.* (*Sp.*) *inversum*, at 85 mm. diameter (BM. C.4). e. *S.* (*S.*) *kowalewskii*. f. *S.* (*S.*) *umbonatiformis*. g. *S.* (*S.*) *decheni*. h. *S.* (*S.*) *yorkshirensis*, at 17 mm. diameter (BM. C.75885). i. *S.* (*S.*) *marginatus*, at 9·5 mm diameter (holotype, YM. tablet 414). j. *S.* (*M.*) *progredicus*. k. *S.* (*S.*) *umbonatus*.

figures a–d, h, i, original; figures e–g, j, k, redrawn from Pavlow (1901).

between the subgenera, and possibly the number of subgenera recognized, will doubtless require adjustment.

An outstanding problem, which can only be resolved after a detailed study of sutural ontogeny of the Russian, German and English forms, is the significance of the relative length and breadth of the elements of the suture. Both Pavlow (1901) and Chernova (1952) recognized that in some species of *Simbirskites* the saddles are broad and only slightly subdivided at all growth stages, while in other species they are narrow and longer and become more strongly subdivided with growth (Text-fig. 2). Pavlow (1901) regarded these sutural differences as the main feature distinguishing *S.* (*S.*) *umbonatiformis* from *S.* (*S.*) *umbonatus* and *S.* (*S.*) *kowalewskii* from *S.* (*S.*) *decheni*. This variation has not been observed in *Speetoniceras* (with broad saddles) and *Craspedodiscus* (with narrow saddles) but is recorded in *Milanowskia* and *Simbirskites s.s.* Observation of the limited amount of suitable Speeton material suggests that there may be a time significance, the earlier species having the broader saddles and later species the narrower saddles.

Simbirskites probably evolved in the Boreal Ocean from one of the late Valanginian polyptychitids; the time break between these and the earliest *Simbirskites* (*Speetoniceras*) is represented in the Russian successions by a stratigraphical break and in north-west Europe by beds with *Endemoceras*, an endemic boreal neocomitid genus derived from a tethyan ancestral stock.

Numerous species of *Simbirskites* have been described from the Russian Platform, north Germany, Heligoland and Speeton. Unfortunately, it is a particularly difficult genus to study; Pavlow (1901 : 66) has discussed the taxonomic difficulties caused by the considerable morphological changes which often occurred during growth. Failure to recognize these changes, or inadequate type material, has resulted in a proliferation of specific names and there are probably far more names available than there are species of *Simbirskites*.

Comparisons between the *Simbirskites* species of the various parts of the Boreal Province are further complicated by differences in size of the preserved specimens. At Speeton, most specimens are septate inner whorls rarely more than 25 mm in diameter, whereas many of the Russian species described by Lahusen (1874), M. Pavlow (1886) and A. P. Pavlow (1901) and the north German species of Neumayr and Uhlig (1881) were described from much larger specimens. The numerous species described by Weerth (1884) from the Teutoburger Wald and by Koenen (1904) from Heligoland were based upon small and medium-sized specimens directly comparable with the Speeton forms.

Outside the Anglo-German and Russian Platform regions, *Simbirskites* is rare. It has recently been recorded from Spitzbergen (see Parker 1967 : 502). From the Northern Richardson Mountains in the North-West Territories of Canada, Jeletzky (1964 : 58, pl. 15, fig. 2) has figured a poorly preserved, apparently simbirskitid, ammonite as *S.* cf. *kleini* (Neumayr and Uhlig). More definite records of *Simbirskites* are the species figured by Imlay (1960) from California and Oregon.

The description of an Australian species, *Simbirskites morvenae* (Whitehouse 1927 : 111), was based on material in an old collection in Queensland Museum labelled "Victoria Downs, Morven". The record has not been substantiated by further collecting and Whitehouse (1946) subsequently questioned the provenance of the specimens as they closely resemble comparable German individuals in preservation. There is no other evidence for marine Hauterivian strata in the area.

Spath (1924 : 82, 87) included the Mexican and Himalayan "*Simbirskites*" described by Burckhardt (1912) and Uhlig (1910) respectively in the Upper Jurassic genus *Grayiceras*. Leanza's (1958) Argentinian *Simbirskites* have been misidentified generically. In lateral view *S. auracanus* Leanza is similar to *S. decheni* and *S. quadripartitus* Leanza resembles *S. kleini*, but all four of Leanza's species differ from *Simbirskites* in that the ribs extend straight across the venter instead of curving forwards. Leanza's species appear closer to *Rogersites*; the recorded stratigraphical horizon (late Valanginian) would agree with this.

Simbirskites occurs, very rarely, in the south of France; unfortunately the specimen from Barrême in the Astier collection (BM. 73463) referred to as "comparable to forms of C6" (Spath 1924 : 82) is too poorly preserved to be identified.

Subgenus ***SPEETONICERAS*** Spath 1924

TYPE SPECIES: *Sp. subbipliciforme* Spath 1924, by original designation.

DIAGNOSIS: A perisphinctoid subgenus of *Simbirskites* with a moderately evolute to evolute shell, rounded to coronate whorl section, and strongly biplicate ribbing. The suture has relatively broad, only slightly subdivided saddles and lobes at all growth stages.

DISCUSSION: Following Spath (1924 : 87), the subgenus *Speetoniceras* is here retained for the early perisphinctoid species of *Simbirskites*, i.e. Pavlow's (1901 : 67) "Perisphinctoidea, ou groupe de *Simbirskites versicolor*". Chernova (1952 : 50) also included within the subgenus the German group of *S. inverselobatus* (Neumayr and Uhlig).

Chernova (1952 : 50) states that all *Speetoniceras* species reach maturity at about 90 mm diameter and grow to as much as 500–600 mm diameter; within this growth-range the general form and sculpture of each species remains constant. Most of the large Russian specimens were originally included in *Sp. versicolor* (Trautschold), but after studying the ontogeny of the various forms M. Pavlow (1886) distinguished three species, *Sp. inversum*, *Sp. subinversum* and *Sp. versicolor*. There is a gradation between the three, *Sp. versicolor* having the most inflated inner whorls with strong tubercles and coarse ribbing, while at the other extreme *Sp. inversum* has the least inflated inner whorls with feeble tubercules and finer ribbing. With growth these differences diminish so that the outer whorls of the three species are virtually identical and can best be separated by sutural differences. The sutures of *Sp. inversum* were described as strongly inverse, those of *Sp. subinversum* less so, and those of *Sp. versicolor* only slightly inverse. The stratigraphical ranges of these three species in the Volga section reflect the morphological gradation; *Sp. versicolor* appears first, followed by *Sp. subinversum* and then by *Sp. inversum* (Chernova 1951 : 52–53. Text-fig. 10 here).

Although large specimens of *Speetoniceras* are common in Russia, the Speeton material consists almost entirely of septate inner whorls of less than 30 mm diameter, so that it is difficult to compare specimens from the two areas.

Speetoniceras is not known from north Germany, but has been recorded from Spitzbergen (Parker 1967 : 502) and from Oregon (Imlay 1960 : 213).

Simbirskites (Speetoniceras) subbipliciforme (Spath)

(Pl. 1, figs 2, 5)

1906 *Olcostephanus* (*Simbirskites*) ?sp. Danford: pl. 12, fig. 3.
1924 *Speetoniceras subbipliciforme* (= "?sp." Danford, pl. 12, fig. 3) Spath: 76.

TYPE: The holotype, refigured here, pl. 1, fig. 2; GSM. 17930, Danford collection, from "C7–8" of the Speeton Clay.

MATERIAL: Six septate nuclei; author's collection BM. C.75620–21; HU. Rn. 26, Rn. 230, Rn. 1102; GSM. 17913. Speeton Clay, bed C7H (BM. C.75620–21 and Rn. 1102; horizon of others unrecorded).

DESCRIPTION: Known only from septate inner whorls, the largest being 28·7 mm in diameter. Shell evolute, whorl section rounded. Ribs strong, gently prorsiradiate; rib pattern regular, the short primary ribs normally bifurcating at a subdued swelling about a third of the distance over the whorl flank. Rarely, a primary rib remains unbranched. The secondary ribs curve forwards on crossing the rounded venter.

DIMENSIONS OF FIGURED SPECIMENS:

GSM. 17930 (holotype). 28·0; 10·2, 10·6, 11·2. 18 pr., approx. 34 sec. ribs.
BM. C.75620. 21·4: at 20·7; 7·5, 8·0, 8·0. 19 pr., approx. 36 sec. ribs.

DISCUSSION: *S.* (*Sp.*) *subbipliciforme* has not previously been described; the specific name was introduced by Spath (1924) as a *nomen novum* for Danford's (1906) figured "*Olcostephanus* (*Simbirskites*) ?sp.". The species differs from the inner whorls of other *Speetoniceras* in being more evolute, less inflated, and more coarsely ribbed; the secondary ribs curve forwards more strongly over the venter than in other species. It is approached only by the more coarsely ribbed varieties of *S.* (*Sp.*) *inversum,* which differ in being less evolute and a little more inflated.

DISTRIBUTION: Speeton Clay, *inversum* zone, Speeton.

Simbirskites (Speetoniceras) inversum (M. Pavlow)

(Pl. 1, figs 1, 3, 4, 6, 7, 9; Pl. 2, fig. 1; Text-figs 2d, 3–5)

?1865 *Ammonites versicolor* Trautschold: pl. 2, fig. 3 (non fig. 4).
1886 *Ammonites* (*Olcostephanus*) *inversus* M. Pavlow: 36, pl. 1, figs 4, 5; pl. 2, fig. 1.
1892 *Olcostephanus* (*Simbirskites*) *inversus* (M. Pavlow) Pavlow: 508, pl. 18, fig. 14.

?1892 *Olcostephanus* (*Simbirskites*) aff. *inversus* (M. Pavlow); Pavlow: pl. 15, fig. 3.
1892 *Olcostephanus* (*Simbirskites*) *subinversus* M. Pavlow; Pavlow: 507, pl. 18, fig. 12 (?fig. 13).
1906 *Olcostephanus* (*Simbirskites*) *subinversus* (M. Pavlow); Danford: 110, pl. 12, fig. 4.
?1907 *Simbirskites inversus* (M. Pavlow) Karakasch: 129, pl. 13, fig. 4a, 4b (interior).
1924 *Speetoniceras inversum* (M. Pavlow) Spath: 76.
1924 *Speetoniceras subinversum* (M. Pavlow) Spath: 76.
1960 *Speetoniceras inversum* (M. Pavlow); Drushchitz and Kudryavtseva: 273, pl. 17, fig. 2.

TYPE: M. Pavlow's figured syntypes are in the Geological Reconnaissance Institute, Moscow; the original of Pavlow's plate 1 figure 5, is here selected as lectotype.

MATERIAL: 29 septate inner whorls from bed C7H (common) and C7G (rare) of the Speeton Clay. Author's collection, BM. C.75622–46 (25 specimens) and HU. Rn. 147, Rn. 690, Rn. 708, and Rn. 937 (4 specimens). 2 specimens from Simbirsk, Russia, BM. C.4 (Damon collection) and Kabanov collection, number 1364. There is additional material from Speeton in all the collections examined.

DESCRIPTION (of specimens up to 30 mm diameter): Shell moderately evolute, flanks and venter rounded, whorl section sub-circular. Primary ribs extend almost half-way over the whorl-flank, where they bifurcate at a subdued tubercle; very rarely a primary rib either remains single or trifurcates. The secondary ribs curve gently forwards over the venter. There are 20–28 (usually 21–25) primary ribs and 40–55 secondary ribs per whorl at 16–32 mm diameter (Text-fig. 4).

The shell is smooth to 7–8 mm diameter, when primary and secondary ribs appear practically simultaneously; one individual (BM. C.75643) remains smooth for another half-whorl, to about 12 mm diameter.

The suture-line (Text-fig. 2d, 3) is inverse with broad, only slightly subdivided saddles.

DIMENSIONS OF FIGURED SPECIMENS:

BM. C.75626. 20·5; 8·7, 8·0, 7·0. 23 pr., 46 sec. ribs.
BM. C.75624. 24·8; 10·3, 10·0, 8·5. 27 pr., 49 sec. ribs.
BM. C.75623. 27·2; 11·6, 12·8, 8·4. 25 pr., 50 sec. ribs.
BM. C.75625. 29·6; 11·4, 11·2, 11·0. 23 pr., 46 sec. ribs.
BM. C.75627. 31·2; 12·0, 13·0, 11·2. 27 pr., 50 sec. ribs.
BM. C.75622. 35·4; 13·7, 14·1, 13·4. 21 pr., 41 sec. ribs.
Kabanov colln. 1359. 78·5; 27·5, 27·2, 33·0. 32 pr., 64 sec. ribs.

DISCUSSION: This species is represented at Speeton by small, septate specimens up to 32 mm diameter; they are slightly less inflated than the smallest of Pavlow's syntypes (1886 : pl. 1, fig. 5), a plaster cast of which has been made available by Professor Drushchitz. However, Chernova (1952 : fig. 3) illustrated the whorl section of a Russian individual of 30 mm diameter, and this compares closely with whorl sections of Speeton specimens of similar diameter. M. Pavlow described the inner whorls of *S.* (*Sp.*) *inversum* as rounded, with feeble tubercles at the point of bifurcation of the ribs; at a later growth-stage the tubercles disappear and the whorl flanks flatten. Large specimens, comparable in size to the typical Russian forms, are virtually unknown at Speeton, but the two large whorl fragments from Speeton figured by Pavlow (1892) as *S.* (*Sp.*) aff. *inversum* and *S.* (*Sp.*) *subinversum* may belong to *S.* (*Sp.*) *inversum.* A large Russian specimen is figured here (Pl. 1, fig. 4) for comparison.

The small Speeton specimens of *S.* (*Sp.*) *inversum* exhibit variation in general whorl proportions (Text-fig. 5), rib density (Text-fig. 4) and degree of inversion of the suture-line (Text-fig. 3). A. P. Pavlow (1892 : pl. 18, figs 12 and 14) figured two Speeton specimens as two different species, *S.* (*Sp.*) *inversum* and *S.* (*Sp.*) *subinversum*, separating them mainly according to the degree of inversion of the suture.

FIG. 3. *Simbirskites* (*Speetoniceras*) *inversum*: variation in degree of inversion of suture lines of 5 specimens from Bed C7H, Speeton. a. BM. C.75640 at 20·5 mm diameter; b. HU. Rn.937 at 18·2 mm diameter. c. BM. C.75645 at 25·0 mm diameter; d. BM. C.75625 at 28·6 mm diameter. e. BM. C.75627 at 30·2 mm diameter. All × 2.

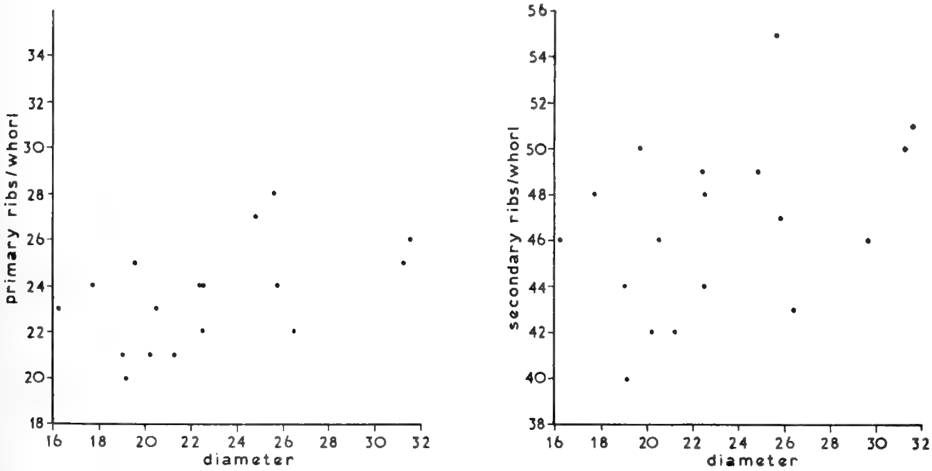

FIG. 4. Variation in density of primary and secondary ribs per whorl in 18 specimens of *Simbirskites* (*Speetoniceras*) *inversum* from Bed C7H, Speeton.

The difference between them is small and both fit into the range of variation of *S.* (*Sp.*) *inversum.* Danford's (1906) and Spath's (1924) records of *S.* (*Sp.*) *subinversum* from the Speeton Clay are apparently based on A. P. Pavlow's interpretation of the species.

S. (*Sp.*) *agnessense* Imlay differs from *S.* (*Sp.*) *inversum* in having more involute and more finely-ribbed inner whorls.

DISTRIBUTION: Speeton Clay, *inversum* zone, Speeton; *inversum* and *pavlovae* subzones of the *versicolor* zone, Russia.

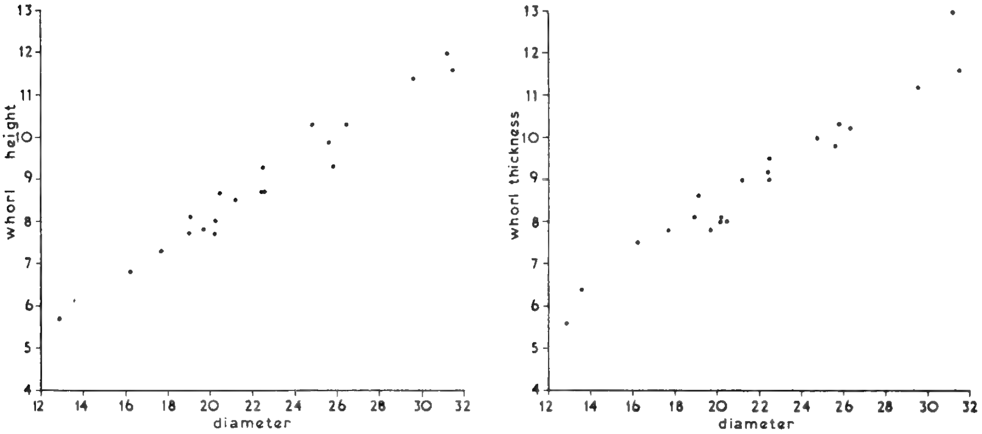

FIG. 5. Variation in whorl-proportions of 21 specimens of *Simbirskites* (*Speetoniceras*) *inversum* from Bed C7H, Speeton.

Simbirskites (Speetoniceras) cf. ***versicolor*** (Trautschold)

(Pl. 1, fig. 8)

cf. 1865 *Ammonites versicolor* Trautschold: pl. 2, figs 3, 4.
cf. 1886 *Ammonites* (*Olcostephanus*) *versicolor* Trautschold; M. Pavlow: 30, pl. 1, figs 1–3.

MATERIAL: One septate specimen (author's collection, BM. C.75647) and one whorl fragment (HU. Rn. 84) from the C Beds of the Speeton Clay (exact horizon unknown).

DESCRIPTION: Shell moderately evolute, inflated, whorl section almost coronate. Coarsely ribbed, the short, sharp primary ribs branching into two, rarely three, secondary ribs at a prominent tubercle about a third of the way over the whorl flank. The secondary ribs curve gently forwards over the broadly rounded venter.

DIMENSIONS OF FIGURED SPECIMEN:

BM. C.75647. 30·4; 11·5, 14·6, 12·5. 20 pr., 44 sec. ribs.

Discussion: The inner whorls of *S.* (*Sp.*) *versicolor* figured by M. Pavlow (1886) are similar to the Speeton specimens in degree of inflation, but the tubercle is higher on the flanks. However, Chernova's (1952 : fig. 3) diagrammatic cross-section at 30 mm diameter is very close to that of the Speeton example; the Speeton specimens are therefore provisionally referred to *S.* (*Sp.*) *versicolor*. They are considerably more inflated than the inner whorls of *S.* (*Sp.*) *inversum*.

The Speeton specimen(s) on which Spath's (1924 : 76) record of *S.* (*Sp.*) *versicolor* was based has not been traced.

Distribution: Speeton Clay; exact horizon not known. *Versicolor* zone, Russia.

Simbirskites (Speetoniceras) sp.

(Pl. 1, fig. 10)

Discussion: A small, partly crushed specimen (author's collection, BM. C.75648), 20·3 mm in diameter, appears close to *S.* (*Sp.*) *inversum* in general features but is more finely ribbed, having 30 primary and approximately 60 secondary ribs on the last whorl. The specimen came from the pale blue clay just above the hard stone band of C7F, the highest horizon from which *Speetoniceras* has so far been recorded at Speeton. A number of similar but completely crushed forms were found in the same bed but disintegrated on exposure.

Subgenus ***MILANOWSKIA*** Chernova, 1952

Type species: *Ammonites speetonensis* Young and Bird 1828, by original designation.

Diagnosis: Shell moderately evolute to slightly involute, usually moderately compressed though the earliest whorls may be more inflated, resembling those of *Speetoniceras*. Short primary ribs normally branch at a subdued tubercle into 2–5 secondary ribs; other secondaries may appear higher on the whorl flank.

Both types of *Simbirskites* suture occur in *Milanowskia*.

Discussion: Species of *Milanowskia* grew to large diameters, but the two commonest and best-known Speeton species, *S.* (*M.*) *concinnus* and *S.* (*M.*) *speetonensis*, are known only from septate inner whorls. *S.* (*M.*) *concinnus* is intermediate in form between the earlier *S.* (*Sp.*) *inversum* and the later *S.* (*M.*) *speetonensis*, but the relationship between other species is less clear. The origin of *S.* (*M.*) *staffi* and related forms from north Germany is particularly problematic, and this group was separated from *Milanowskia* by Bähr (unpublished dissertation) as a new subgenus.

Among the species of *Milanowskia* described here the earlier forms (*concinnus*, *speetonensis*, *staffi*, and *S.* (*M.*) sp.) have a suture with relatively broad, only slightly subdivided saddles, while the later *S.* (*M.*) *lippiacus* and *S.* (*M.*) cf. *lippiacus* have the narrower, longer, more strongly subdivided saddles typical of Chernova's (1952 : 50) *progredicus* group of *Milanowskia*.

Simbirskites (Milanowskia) concinnus (Phillips)

(Pl. 2, figs 2–6, 8; Pl. 12, fig. 11; Text-figs 2b, 6)

1829 *Ammonites concinnus* Phillips: 123, pl. 2, fig. 47.
1835 *Ammonites concinnus* Phillips; Phillips: 94, pl. 2, fig. 47.
1875 *Ammonites concinnus* Phillips; Phillips: 264, pl. 2, fig. 47.
1889 *Olcostephanus speetonensis concinnus* (Phillips) Pavlow: pl. 3, fig. 7.
1892 *Olcostephanus (Simbirskites) concinnus* (Phillips); Pavlow: 501, pl. 18, fig. 16.
1892 *Olcostephanus (Simbirskites) progrediens* (Lahusen); Pavlow: 504, pl. 18, fig. 15.
1906 *Olcostephanus (Simbirskites) concinnus* (Phillips); Danford: 110, pl. 12, fig. 2.
1924 *Simbirskites? concinnus* (Phillips) Spath: 76.
1924 *Simbirskites progredicus* (Pavlow 1892 *non auct.*) Spath: 77.
1951 *Speetoniceras (Milanowskia) lahuseni* Chernova: 63.
1962 *Simbirskites concinnus* (Phillips); Howarth: 130, pl. 19, fig. 6.

TYPE: The holotype, originally in the Yorkshire Museum, York, has decomposed (Melmore 1947 : 235); the specimen figured by Pavlow (1892 : pl. 18, fig. 16) was designated neotype and refigured by Howarth (1962 : pl. 19, fig. 6). BM. C.4651.

MATERIAL: 65 septate inner whorls from the Speeton Clay; 62 from 0·3–0·9 metres above the base of bed C6 (author's collection, BM. C.75649–75709, C.75893); BM C.34953 (Lamplugh collection), HU. Rn. 397 and GSM. 30582 from C6. One specimen (author's collection, BM. C.75711) from the *capricornu* zone of Sarstedt, near Hannover. There is additional Speeton material in all the examined collections.

DESCRIPTION: Known only from septate inner whorls (up to 33·5 mm diameter). Shell moderately evolute with sub-circular whorl section and rounded flanks and venter. Sharp primary ribs branch a third of the way over the whorl flank at a feeble, radially elongate tubercle, into two or three secondary ribs. There are 18–25 (usually 19–22) primary ribs and 45–65 (usually 50–60) secondary ribs per whorl at diameters of 20–25 mm. The ribs are gently prorsiradiate, curving forwards over the venter. The shell is smooth to about 8 mm diameter when the primary and secondary ribs appear practically simultaneously.

The suture-line (Text-fig. 2b) is inverse, with broad, only slightly subdivided saddles.

DIMENSIONS OF FIGURED SPECIMENS:

BM. C.75695. 17·5; 8·5, 8·0, 4·3.
BM. C.75893. 20·4; 8·8, 9·7, 6·0. 20 pr., approx. 48 sec. ribs.
BM. C.75706. 24·2; 10·5, 10·8, 7·4. 24 pr., 60 sec. ribs.
BM. C.75708. 25·8; 11·0, 10·7, 7·8. 23 pr., 58 sec. ribs.
BM. C.75711. 30·6; at 24·3; 10·3, 10·0, 7·1. 18 pr., approx. 46 sec. ribs.
GSM. 30582. 33·5; 13·6, 12·8, 11·5. 22 pr., 55 sec. ribs.

DISCUSSION: The variation in the dimensions of this species is shown in Text-fig. 6; most of the specimens are less than 20 mm in diameter and the earliest part of the last preserved whorl is still smooth, so that few rib counts can be made. The proportion of bifurcating to trifurcating ribs varies; at one extreme only about one third of the primary ribs trifurcate while at the other extreme every primary rib trifurcates. The neotype is a coarsely ribbed individual; at 27 mm diameter there

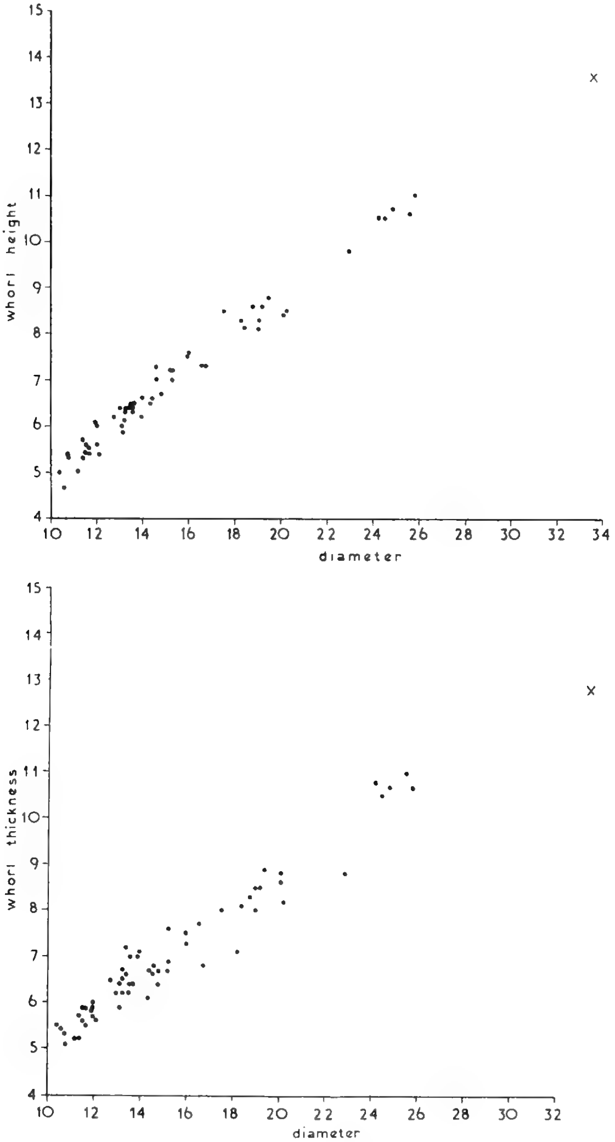

FIG. 6. Variation in whorl-proportions of 63 specimens of *Simbirskites* (*Milanowskia*) *concinnus*, 62 specimens from Bed C6 (0·3–0·9 metres above base) and 1 specimen (GSM.30582, indicated by a X) from the C Beds, Speeton.

are 18 primary ribs and only about 46 secondary ribs. There is every range of variation between this and a finely ribbed, slightly less inflated specimen of S. (*M.*) *concinnus* figured by Pavlow (1892 : pl. 18, fig. 15) as "*Olcostephanus* (*Simbirskites*) *progrediens* (Lahusen)". Pavlow recorded this from C4 but Spath listed "*S. progrediens* (Pavlow, 1892 non auct.)" from C6. Pavlow's specimen (BM. C.34953) has 22 primary ribs and approximately 65 secondary ribs at 23 mm diameter, and compares closely with other finely-ribbed specimens of S. (*M.*) *concinnus* from low C6. Pavlow's specimen is the holotype of S. (*M.*) *lahuseni* Chernova (1951 : 63), which was proposed as a *nomen novum* for S. *progrediens* (Pavlow 1892 *non* Lahusen). S. (*M.*) *lahuseni* is here regarded as a junior subjective synonym of S. (*M.*) *concinnus*.

S. (*M.*) *concinnus* is close to *Speetoniceras*; the more coarsely ribbed specimens differ from the small Speeton examples of S. (*Sp.*) *inversum* only in the possession of trifurcating as well as bifurcating ribs. It has clearly evolved from S. (*Sp.*) *inversum*, and in turn gives rise to S. (*M.*) *speetonensis*.

S. (*M.*) *concinnus* resembles some of the varieties of S. cf. *decheni*, but is less inflated. It is more inflated and more evolute than S. (*M.*) *speetonensis*.

S. (*M.*) *concinnus* occurs in north Germany, but from the limited material available the German specimens appear to be more coarsely ribbed with fewer secondary ribs than the Speeton forms. A German specimen from the upper part of the *capricornu* zone, Sarstedt, is figured here (pl. 2, fig. 5).

DISTRIBUTION: Speeton Clay *speetonensis* zone, *concinnus* subzone; Lower Tealby Clay of Donnington-on-Bain, Lincolnshire (p. 35); upper part of *capricornu* zone, north Germany; *decheni* zone, *speetonensis* subzone, Russia.

Simbirskites (Milanowskia) speetonensis (Young and Bird)

(Pl. 2, figs 7, 9–11, 15; Pl. 11, fig. 4)

1828 *Ammonites spetonensis* (sic) Young and Bird: 265, pl. 12, fig. 5.
1829 *Ammonites venustus* Phillips: 123, pl. 2, fig. 48.
1835 *Ammonites venustus* Phillips; Phillips: 94, pl. 2, fig. 48.
1874 *Ammonites fasciatofalcatus* Lahusen: pl. 7, fig. 1.
1875 *Ammonites venustus* Phillips; Philips: 264, pl. 2, fig. 48.
1889 *Ammonites speetonensis* Young and Bird; Lamplugh 613 (*pars*).
1889 *Olcostephanus speetonensis venustus* (Phillips) Pavlow: 59, pl. 3, fig. 6.
1889 *Olcostephanus fasciatofalcatus* (Lahusen) Pavlow: 117, pl. 3, fig. 8.
1892 *Olcostephanus* (*Simbirskites*) *speetonensis* (Young & Bird) Pavlow: 500, pl. 18 (11), fig. 7.
1901 *Simbirskites speetonensis* (Young and Bird) Pavlow: 76, pl. 4, fig. 1, pl. 7, fig. 4.
1906 *Olcostephanus* (*Simbirskites*) *payeri* (Toula); Danford: pl. 12, fig. 1.
1924 *Simbirskites venustus* (Phillips); Spath; 77.
1924 *Simbirskites speetonensis* (Young and Bird); Spath: 77.
1952 *Speetoniceras* (*Milanowskia*) *speetonensis* (Young and Bird) Chernova: 50.
?1960 *Speetoniceras speetonensis* (Young and Bird); Drushchitz and Kudryavtseva: 274, pl. 19, fig. 1.
1962 *Simbirskites speetonensis* (Young and Bird); Howarth: 131, pl. 19, fig. 2.
1962 *Simbirskites venustus* (Phillips); Howarth: 131, pl. 19, fig. 3.

TYPE: BM. C.34951 (Lamplugh collection), figured by Pavlow (1892 : pl. 18, fig. 7), was designated neotype and refigured by Howarth (1962 : 131, pl. 19, fig. 2). Bed C6, Speeton.

MATERIAL: 21 septate inner whorls from Speeton; 17 (author's collection, BM. C.75835–51) from the upper part of Bed C6; GSM. 17919 (Danford collection) from C6; YM. tablet 419 (holotype of *Ammonites venustus* Phillips); Neale collection 1701 from C6; Wrights' collection 18670. One specimen from Ulyanovsk (Simbirsk) (Göttingen, Orig. Nr. 609–1). There is additional material in all the collections examined.

DESCRIPTION: (of specimens up to 25 mm diameter): Shell slightly to moderately involute, slightly inflated to moderately compressed. Whorl flanks gently rounded in the slightly inflated forms, almost flat in the more compressed varieties. Ribs gently prorsiradiate; at first the short primary ribs branch at a subdued tubercle about a third of the way over the whorl flank into two or three secondary ribs, then above about 20 mm diameter a third or fourth secondary rib is normally intercalated. The ribs curve forwards over the rounded venter. There are 20–30 primary ribs per whorl at 20–25 mm diameter; in the specimens with fine primary ribbing only three secondary ribs are usually associated with each primary.

The suture has relatively broad elements.

DIMENSIONS OF FIGURED SPECIMENS:

BM. C.75847. 18·7; 8·5, 7·5, 5·3. 26 pr., approx. 61 sec. ribs.
GSM. 17919. 20·8; 9·0, 8·0, 6·2. 26 pr., approx. 66 sec. ribs.
Wright's colln. 18670. 21·3; 10·0, 8·1, 5·0. 30 pr., approx. 70 sec. ribs.
BM. C.75850. 21·7; 9·9, 8·0, 6·2. 22 pr., approx. 64 sec. ribs.
HU. Neale colln. 1701. 22·5; 10·5, 8·5, 5·7. 25 pr., approx. 64 sec. ribs.

DISCUSSION: Small, septate specimens of *S.* (*M.*) *speetonensis* are moderately common in the upper half of Bed C6 at Speeton; the largest known Speeton example (the neotype) is only 34 mm in diameter. They vary in whorl proportions and ribbing, and the "typical" compressed, moderately involute forms with flattened flanks (e.g. the neotype and BM. C.75850) are rare. The commonest forms are less involute and slightly inflated, with rounded flanks. In museum collections these are often labelled as *S. venustus* (Phillips), though Howarth (1962) has shown that Phillips' holotype is almost identical at similar diameter to the neotype of *S.* (*M.*) *speetonensis*, of which it is a junior subjective synonym.

Some of the more evolute, slightly inflated varieties of *S.* (*M.*) *speetonensis* have moderately coarse ribbing and approach the more finely ribbed varieties of *S.* (*M.*) *concinnus*. They are still not as inflated or as coarsely ribbed as the latter species but are clearly derived from it. These forms occur in the lower part of the range of *S.* (*M.*) *speetonensis* and the more "typical" forms near the top.

The specimen figured by Danford (1906 : pl. 12, fig. 1) as *S. payeri* (Toula) is refigured here (pl. 2, fig. 15) as a finely ribbed variety of *S.* (*M.*) *speetonensis*.

A more advanced growth stage of this species was described from Russia (Lahusen 1874) as *Ammonites fasciatofalcatus*. Pavlow (1892, 1901) subsequently included Lahusen's species in synonomy with *S.* (*M.*) *speetonensis* and refigured (Pavlow 1901 : pl. 4, fig. 1) Lahusen's holotype, illustrating the opposite flank to that shown in Lahusen's original figure. Pavlow's illustration shows the inner whorls to be very close to the neotype of *S.* (*M.*) *speetonensis*, and the similarity is emphasized by another Russian specimen which Pavlow presented to the Göttingen collections (609–1). Both flanks of the Göttingen specimen are figured here. The outer whorl (Plate 11, fig. 4b) is identical to Lahusen's *S. fasciatofalcatus* while the earlier whorls (Plate 11, fig. 4a) are the same as those of *S.* (*M.*) *speetonensis*.

The Russian examples of *S.* (*M.*) *speetonensis* thus show that above about 40 mm diameter the number of secondary ribs usually decreases to three per primary, and these branch from a small, mid-lateral tubercle. The whorls are slightly involute with flattened flanks. This morphology persists to at least 100 mm diameter (Pavlow 1901 : pl. 7, fig. 4). No examples of this morphological stage have yet been found at Speeton.

Septate nuclei of a form close to *S.* (*M.*) *speetonensis* occur in the lower part of the German *seeleyi* zone (p. 76).

DISTRIBUTION: *Speetonensis* subzone of the *speetonensis* zone, Speeton; *speetonensis* subzone, *decheni* zone, Russia; *seeleyi* zone, Germany (*S.* (*M.*) ?*speetonensis*).

Simbirskites (Milanowskia) sp. (= ***S. progredicus*** Danford *non* Lahusen)

(Pl. 2, figs 12, 13)

Non 1874 *Ammonites progredicus* Lahusen: pl. 6, fig. 3.
?1902 *Simbirskites elatus* Trautschold; Koenen: pl. 6, figs 10–12.
1906 *Olcostephanus* (*Simbirskites*) *progrediens* (*sic*) Lahusen; Danford: pl. 12, fig. 5.

MATERIAL: Three, two septate specimens in the Danford collection, GSM. 21556 and 17923 (the latter figured by Danford) and part of the body chamber and inner whorls of a third specimen in the author's collection, BM. C.75714. All from the Speeton Clay C Beds, exact horizon unknown.

DESCRIPTION: Shell slightly involute, moderately compressed, whorl section oval, broadest in the lower third of the whorl and narrowing towards the rounded venter. Ribs gently prorsiradiate, curving forwards over the venter; short, sharp primary ribs branch at a small, well-developed tubercle about a third of the way over the whorl flank into three, or rarely two, secondary ribs.

DIMENSIONS OF FIGURED SPECIMEN:

GSM. 17923. 26·9; 11·6, 10·3, 8·4. 20 pr., 59 sec. ribs.

DISCUSSION: GSM. 17923 was figured by Danford as *S. progredicus* (Lahusen)e although the two species are close in rib pattern the flanks of *S. progredicus* converg;

conspicuously towards the narrowly rounded venter at all growth stages (Pavlow 1901 : pl. 2, figs 4, 5) while those of *S.* (*M.*) sp. are flatter. The Speeton ammonite which Pavlow (1892 : pl. 18, fig. 15) figured as *S. progredicus* is more inflated and belongs to *S.* (*M.*) *concinnus* (p. 50). A specimen in the Göttingen collection, figured by Koenen (1902) as *S. elatus* (Trautschold), is close to *S.* (*M.*) sp. in general proportions but has more bifurcating primary ribs. A septate nucleus from Speeton in the Neale collection (S1726) is slightly more involute than *S.* (*M.*) sp. and the tubercles at the points of branching of the ribs are less well developed.

S. (*M.*) sp. is more compressed than *S.* (*M.*) *concinnus* and more coarsely ribbed than *S.* (*M.*) *speetonensis*. It differs from both in having more clearly developed tubercles at the points of branching of the ribs.

Danford recorded his figured specimen from C6, and his other specimen (GSM. 21556) from "C upper".

Simbirskites (Milanowskia) staffi Wedekind

(Pl. 2, figs 14, 16; Pl. 3, figs 1, 4; Text-fig. 2c)

1910 *Simbirskites staffi* Wedekind: 96, pl. 4, fig. 3.

TYPE: The holotype, in the Geologisches-Paläontologisches Institut, Göttingen, is from the *capricornu* Zone at Ihme, near Hannover.

MATERIAL: Two: author's collection BM. C.75712 from C6, 0·6 metres above the base, and BM. C.75713 (loose on cliff face, Speeton).

DESCRIPTION: The septate inner whorls of one individual and a whorl fragment of another are the only known Speeton representatives of this species. Whorls evolute, moderately compressed, with almost flat flanks and a narrow, well-rounded venter. Umbilicus shallow, broad, occupying almost a third of the diameter. Ribs slightly prorsiradiate; the primaries are short, extending about a third of the way over the whorl flank where they bifurcate at a small, radially elongated tubercle. A third secondary rib frequently appears higher on the flank, branching from the anterior side of the posterior rib of the original pair so that a virgatome pattern develops. The secondary ribs curve strongly forwards over the venter.

DIMENSIONS OF FIGURED SPECIMENS:

BM. C.38369.	42·0; 15·0, 11·7, 16·6.	22 pr., 60 sec. ribs.
NLfB Kp.37.	34·4; 12·9, 11·2, 12·9.	22 pr., 58 sec. ribs.
BM. C.75712.	27·2; 10·6, 8·7, 9·9.	
BM. C.75713.	27·8: at 26·0; 9·6, 8·3, 9·9.	20 pr., 58 sec. ribs.

DISCUSSION: Two German specimens of *S.* (*M.*) *staffi* are figured here for comparison with the Speeton specimens. The latter are slightly more evolute than the holotype but fit well into the range of variation of a series of specimens in the

Göttingen collections. The holotype has 18 primary ribs at a diameter of 28 mm.

S. (*M.*) *staffi* differs from species of the *S.* (*M.*) *speetonensis* group in its virgotome rib pattern. It is close to two Heligoland species described by Koenen (1904) a *S. paucilobus* and *S. triplicatus*, but is more evolute. *S. virgifer* (Neumayr and Uhlig) approaches *S.* (*M.*) *staffi* in rib pattern, but the holotype is a large individual not directly comparable with the much smaller examples of *S.* (*M.*) *staffi*. Koenen (1904 : pl. 21, fig. 2) figured a small specimen which he assigned to *S. virgifer* but which may not be conspecific with Neumayr and Uhlig's species; it appears close to *S.* (*M.*) *staffi* but is more involute.

Although not previously recorded from Speeton, *S.* (*M.*) *staffi* is one of the commonest German *Simbirskites*; it is found associated with rare *S.* (*M.*) *concinnus* immediately above the beds with abundant *Aegocrioceras* spp. The only accurately localized Speeton specimen (BM. C.75712) was found in the identical stratigraphical position associated with numerous *S.* (*M.*) *concinnus*.

DISTRIBUTION: Speeton Clay, *concinnus* subzone, Speeton. Upper part of the *capricornu* zone and lower part of the *hildesiense* zone, north Germany.

Simbirskites (Milanowskia) lippiacus (Weerth)

(Pl. 3, figs 2, 5)

1884 *Ammonites* (*Olcostephanus*) *lippiacus* Weerth: 13, pl. 3, fig. 3, pl. 5, fig. 3.
1902 *Simbirskites lippiacus* Weerth; Koenen: 160, 416, pl. 37, fig. 3.

TYPES: The syntypes, originally at Detmold, are believed lost.

MATERIAL: Two specimens from Tönsberg, near Oerlinghausen; Weerth Collection, Göttingen, Orig. Nr. 457–125, 609–2.

DESCRIPTION: Shell slightly evolute, moderately compressed with flattened flanks and narrowly rounded venter. Primary ribs strong, gently prorsiradiate, terminating a third of the way over the flank at a tubercle, from which arise two or three secondary ribs. Some secondaries branch at varying positions higher on the flank and other, long secondaries may be intercalated about half-way over the flank. 5–7 secondaries are associated with each primary. The secondaries curve strongly forward over the venter.

DIMENSIONS OF FIGURED SPECIMENS:

Göttingen. Orig. Nr. 457–125. 92·8: at 86·0; 35·6, —, 24·9.
Göttingen. Orig. Nr. 609–2. 44·2: at 40·5; 17·0, 12·2, 10·9.

DISCUSSION: Weerth's type specimens are believed lost and the species has not been refigured, so that the two Göttingen topotypes are important for the interpretation of the species. The larger of the two (457–125) was discussed, and its suture figured, by Koenen (1902 : 160, pl. 37, fig. 3). It appears slightly more evolute than the larger of the two syntypes (Weerth 1884 : pl. 3, fig. 3) but, as Koenen noted, the figure is inaccurate in this respect, for Weerth's description and dimensions indicate a slightly more evolute shell than is shown in his figure.

A neotype for this species will not be selected until the loss of the syntypes is definitely established.

The species is not definitely known from Speeton, but four whorl fragments are described below as *S.* cf. *lippiacus*.

Simbirskites (Milanowskia) cf. ***lippiacus*** (Weerth)

(Pl. 3, fig. 3)

Material: 4 whorl fragments: BM. C.75715–16 (author's collection) from the stone band in Bed C2E, Speeton; BM. C.72643 (Lamplugh collection); GSM. 17542 (Danford collection) "Upper C".

Discussion: The material is too fragmentary to be definitely referred to *S.* (*M.*) *lippiacus*; three of the specimens are similar in general proportions though possibly slightly less compressed, and the primary ribs only extend about a quarter of the way over the flank. The fourth (BM. C.72643) is more involute and more inflated than the Göttingen specimens.

Subgenus ***CRASPEDODISCUS*** Spath 1924

Type species: *Ammonites discofalcatus* Lahusen 1874, SD Wright 1957, L350.

Diagnosis: A subgenus of *Simbirskites* with compressed, involute, finely ribbed whorls in at least one growth-stage. Early *Craspedodiscus* (*gottschei* group) become more compressed and more evolute with growth, while later *Craspedodiscus* (*discofalcatus* group) become more compressed and more involute with growth, becoming oxycone in the adult stage.

The suture has long, narrow saddles and lobes which become strongly subdivided during growth.

Discussion: The boundary between this subgenus and *Milanowskia* is an arbitrary one and is here drawn where the whorls in at least one growth-stage are compressed and involute. *Craspedodiscus* includes at least two separate radiations, probably from *Milanowskia*, an earlier *kayseri-gottschei* group, with rather evolute, almost preisphinctoid outer whorls, and a later *discofalcatus-juddi* group with an oxycone adult stage. *S.* (*C.*) *variabilis* probably represents a third offshoot from *Milanowskia*. Until the ontogeny of some of these species is known in greater detail and their relationship to the various species of *Milanowskia* more clearly understood, it is inadvisable to split the group into more subgenera.

Simbirskites (Craspedodiscus) gottschei (Koenen)

(Pl. 4, figs 2, 4, 5; Pl. 5, fig. 1)

1892 *Olcostephanus* (*Simbirskites*) *discofalcatus* Lahusen; Pavlow: 505, pl. 18 (11), fig. 2.
1904 *Craspedites gottschei* Koenen: 32, pl. 1, figs. 3, 4.
1910 *Simbirskites extremus* Wedekind: 97, pl. 4, fig 4.
1924 *Craspedodiscus gottschei* (Koenen) Spath: 77.

TYPE: The original of Koenen 1904, pl. 1, fig. 3, in the Göttingen collection, is designated lectotype.

MATERIAL: Eight specimens; BM. C.75717–19 (author's collection) from bed C4L, Speeton, BM. C.34958, BM. C.4704, BM. C.27673, and GSM. 21555 (Danford collection, "C4") and Wrights' collection 24375 (probably C4).

DESCRIPTION: Inner whorls involute, compressed, with a narrowly arched venter. Primary ribs gently prorsiradiate, extending slightly more than half-way over the whorl flank. There are 21–26 primary ribs per whorl at 35–45 mm diameter; three or four secondaries are associated with each primary, but there is no definite point of branching and the ribs are frequently weakened on mid-flank. At first, all the secondary ribs either branch from the primary or are intercalated a little more than half-way over the flank, but above 25–30 mm diameter very occasional primary ribs branch, or a long secondary is intercalated, low on the whorl-flank. These longer secondary ribs may branch again later.

The outer whorls (above 150 mm diameter) are evolute and less compressed; whorls of intermediate size (70–150 mm) have not been found. On the outer whorls there are four to six broad, shallow, oblique constrictions. Primary ribs branch about half-way over the whorl into a bundle of three or four secondary ribs, though the point of branching is usually obscure. Some secondaries are intercalated; the secondaries curve gently forwards across the rounded venter. Both primary and secondary ribs are strongly prorsiradiate.

The suture-line has moderately narrow, elongate elements.

DIMENSIONS OF FIGURED SPECIMENS:

BM. C.75717. 40·3: at 32·1; 15·9, —, 6·0.
BM. C.4704. 40·9: at 39·2; 18·9, 14·0, 8·8. 23 pr., approx. 74 sec. ribs.
Wrights' colln. 24375. 184: at 165·5; 55, 35·5, 68.
at 43·7 there are 26 pr. and approx. 93 sec. ribs.

DISCUSSION: The holotype of *S.* (*C.*) *extremus* Wedekind (Göttingen collection) is almost identical in rib pattern and general proportions to the lectotype of *S.* (*C.*) *gottschei*, differing only in being more coarsely ribbed; it is here regarded as a junior subjective synonym of *S.* (*C.*) *gottschei*. There is some variation in the rib density of the inner whorls of the Speeton specimens; hence BM. C.75718 and Wrights' specimen closely resemble the lectotype of *S.* (*C.*) *gottschei* while BM. C.75717 is close to the holotype of *S.* (*C.*) *extremus*. Both BM. C.75717 and C.75718 came from bed C4L.

BM. C.34958 was figured by Pavlow (1892) as *S.* (*C.*) *discofalcatus* and was later (Pavlow 1901 : 79) reidentified as *S.* (*C.*) *phillipsi*; this and a smaller specimen (BM. C.4704; pl. 4, fig. 2) are here regarded as inflated varieties of *S.* (*C.*) *gottschei*.

The outer whorls of *S.* (*C.*) *gottschei* have not been figured before; the excellent specimen in the Wrights' collection has just over three quarters of an evolute outer whorl preserved, of which slightly more than half the whorl is body chamber. The last sutures are not conspicuously crowded, and in the absence of any noticeable uncoiling of the body chamber the specimen cannot definitely be regarded as adult. A second, crushed specimen (BM. C.75718) has three quarters of a whorl of incomplete body chamber preserved. The outer whorls are close to those of *S.* (*C.*) *kayseri* (Neumayr and Uhlig). The inner whorls of the latter differ from those of *S.* (*C.*) *gottschei* only in having fewer secondary ribs per primary, and stronger, more clearly defined primary ribs (Bähr, unpublished dissertation).

DISTRIBUTION: *gottschei* zone, Speeton; *seeleyi* and possibly *tenuis* zones, Germany; *decheni* zone, *speetonensis* and *discofalcatus* subzones, Russia.

Simbirskites (Craspedodiscus) cf. ***kayseri*** (Neumayr and Uhlig)

cf. 1881 *Perisphinctes kayseri* Neumayr and Uhlig: 146, pl. 19, fig. 1.

MATERIAL: Two septate inner whorls in the Neale collection, S. 1730 and S. 1682, and a third specimen in the British Museum, C. 4705.

DISCUSSION: The three specimens resemble the inner whorls of the more compressed varieties of *S.* (*C.*) *gottschei*, differing in having only two or three secondary ribs associated with each primary; they are identical to a specimen of similar size which Bähr (unpublished dissertation) figured as the inner whorls of the large *S.* (*C.*) *kayseri* (Neumayr and Uhlig).

In north Germany this species appears low in the *seeleyi* zone (Bähr, unpublished dissertation) and apparently gave rise to *S.* (*C.*) *gottschei*.

Simbirskites (Craspedodiscus) variabilis sp. nov.

(Pl. 4, figs 1, 3, 6; Pl. 5, figs 3, 4)

1906 *Olcostephanus* (*Simbirskites*) *decheni* Roemer; Danford: pl. 12, fig. 7.
1924 *Simbirskites* aff. *toensbergensis* (Weerth) (= "*decheni*" Danford *non* Roemer); Spath: 77.
1924 *Simbirskites trifurcatus* (Bean MS.); Spath: 77.
?1967 ?*Simbirskites toensbergensis* (Weerth); Kemper: 126, pl. 11, figs 3, 4.

DIAGNOSIS: Shell compressed; inner whorls involute, with short primary ribs ending at a small tubercle. Four to six secondary ribs are associated with each primary. Outer whorl slightly evolute, with more regular rib pattern; number of secondary ribs reduced to three per primary.

TYPE SERIES: Holotype: HU. Rn. 700, from Bed LB6 of the Speeton Clay, Speeton; Paratypes: 11 specimens, 9 in the author's collection, BM. C.75853–61; Neale collection 1901; BM. C.4649. LB6, C2B (base) and C2C, Speeton.

DESCRIPTION: Shell compressed, inner whorls involute up to 40–50 mm diameter, becoming slightly evolute on the outer whorl (body chamber). Earliest whorls (Pl. 5, fig. 3), up to 18 mm diameter, slightly inflated with short, widely spaced primary ribs which end at a small, sharp tubercle. Four or five secondary ribs are associated with each primary; some of these join the tubercle and the others are intercalated at about the same level. Above about 18 mm diameter a sixth rib may appear and the mode of branching becomes rather irregular (Pl. 4, figs 3c, 6; Pl. 5, fig. 4); two or three secondary ribs branch from the tubercle, another rib may be intercalated at about the same level, and one of the secondaries may branch again a little higher on the flank.

The number of primary ribs increases with growth, from 9 at 14 mm diameter to 16 at 35 mm diameter and about 25 at 80 mm diameter. Above about 50 mm diameter the number of secondary ribs per primary decreases to three (rarely, two or four) (Pl. 4, figs 1, 3a). Of these, two branch from the tubercle and a third branches from one of the original pair slightly higher on the whorl. Less commonly, one secondary rib is intercalated instead of joining the tubercle.

In individuals from C2 some secondary ribs branch again close to the venter; this may happen in both inner and outer whorls.

DIMENSIONS OF FIGURED SPECIMENS:

BM. C.4649. 79·9; 29·2, 19·1, 27·0. 24 pr., 80 sec. ribs (estimated).
BM. C.75853. 28·7; 14·6, 8·8, 6·0. 14 pr., approx. 60 sec. ribs.
BM. C.75857. 14·0; 6·8, 6·2, 3·6.

DISCUSSION: This species has previously been recorded as *S. trifurcatus* Bean MS., and a specimen in Bean's collection (BM. C.4649) bearing his label "*Am. trifurcatus*" is the original of Spath's record of this manuscript name. It consists of one whorl of body chamber with trifurcating ribs. Spath recorded the specimen from C4, probably because the matrix invites comparison with some of the siltstone bands on this part of the Speeton section; it is much more likely that Bean obtained it from LB6, where the holotype and one of the paratypes were collected. The preservation of the specimen and its associated matrix supports this view. There are two varieties of this species; in specimens from bed C2 some secondary ribs branch again near the venter, a feature which has not been noted in the specimens from LB6 or in Bean's specimen.

The species is known from early whorls and from body chamber fragments with associated external moulds of the inner whorls; by placing body chamber against mould it has proved possible to make latex casts showing the form of the penultimate whorl (Pl. 4, fig. 3c, Pl. 5, fig. 4). There is no definite evidence that any of the specimens are adult; the modification of the ribbing and change in tightness of coiling of the shell is a recurring feature in *Simbirskites* and frequently occurs well before the adult stage is reached.

The earliest whorls of this species are similar to those of *S.* (*S.*) *yorkshirensis* but are less inflated with less prominent tubercles. Whorls of intermediate size (20–50 mm diameter) differ from the inner whorls of *S.* (*C.*) *discofalcatus* in being more compressed with a less regular rib-pattern. *S.* (*C.*) *gottschei* is less compressed, the secondary ribs appear higher on the whorl flank, and there are no tubercles. The outer whorl of *S.* (*C.*) *variabilis* is close to Russian examples of *S.* (*M.*) *speetonensis* of similar diameter, but the inner whorls are more compressed, and more involute, and have a less regular rib pattern with slightly more secondary ribs per primary, than Speeton and Russian examples of *S.* (*M.*) *speetonensis* of comparable size.

Danford's (1906) figured *S. decheni* has decomposed, but a plaster cast (GSM. 17920) shows that it can be referred to *S.* (*C.*) *variabilis*.

The derived specimens from Alstätte which Kemper (1967) figured as ?*S. toensbergensis* may belong to *S.* (*C.*) *variabilis*, though the outer whorl has more numerous secondary ribs per primary than in the Speeton species.

DISTRIBUTION: Speeton Clay, *variabilis* zone, Speeton.

Simbirskites (Craspedodiscus) discofalcatus (Lahusen)

(Pl. 7, fig. 1; Pl. 8, fig. 1; Pl. 9, figs 1, 2; Pl. 11, figs 2, 3, 5)

1874 *Ammonites discofalcatus* Lahusen: 67, pl. 7, figs 2–4.
1890 *Olcostephanus discofalcatus* (Lahusen) Pavlow: 2, pl. 6, fig. 1.
1901 *Simbirskites discofalcatus* (Lahusen) Pavlow: 78, pl. 6, fig. 1; pl. 7, fig. 2 (*non* 3).
cf. 1906 *Olcostephanus* (*Simbirskites*) *discofalcatus* (Lahusen); Danford: pl. 12, fig. 8.
1924 *Craspedodiscus discofalcatus* (Lahusen) Spath: 77–79.
1924 *Simbirskites* aff. *fasciatofalcatus* (Lahusen); Spath 1924 : 79.
1960 *Craspedodiscus discofalcatus* (Lahusen); Drushchitz and Kudryavtseva: 274, pl. 19, fig. 2, ?fig. 3.

TYPE: Following Bähr (unpublished dissertation) the original of Lahusen's pl. 7, fig. 2–3, is proposed as lectotype: Mining Museum, Leningrad Mining Institute, catalogue number. $\frac{19}{48}$.

MATERIAL: 2 specimens and 2 whorl fragments from the Speeton Clay: GSM. 21493 (Danford collection, "B. Base") and York Museum (no number); GSM. 17543 and 21494 (Danford collection; whorl fragments). 7 specimens from the Tealby Limestone: GSM. 30883 (Judd collection) and BM. C.19993 (P. F. Kendall collection) from North Willingham, BM. C.73376–78 (J. E. Lee collection) and BM. C.25183 from Normanby, and SM. B11123 from Claxby (erroneously recorded from the Claxby Ironstone).

In addition, 2 Speeton specimens (GSM. 17922 (Danford collection) and BM. C.72641 (Lamplugh collection)) are figured here as *S.* (*C.*) cf. *discofalcatus*.

Description (of specimens more than 100 mm in diameter): Shell compressed, involute, with narrowly rounded venter. Whorl broadest near the umbilical edge; umbilicus moderately shallow, umbilical wall fairly steep. Rib pattern irregular; 4 or 5 secondary ribs are associated with each primary, but their point of origin is usually obscure. Some arise from a primary rib about a third of the way over the whorl, others are intercalated either in the middle or on the outer part of the whorl. There are 19–23 primary ribs and 100–120 secondary ribs per whorl at about 120 mm diameter.

The strength of the ribs gradually diminishes with growth (Plate 7), until at diameters above 150–200 mm the shell becomes almost smooth, ornamented only by feeble rib-folds or striae (Plate 8).

The suture has long, narrow, strongly divided saddles and lobes.

Dimensions of figured specimens:

BM. C.5. 101: at 86·7; 43·3, 22·2, 17 (approx.). Approx. 22 pr. ribs at 101 mm diam.
BM. C.73376. 122·4: at 115·3; 57·8, 30·3, 18·2. 20 pr., approx. 112 sec. at 122 mm diam.
BM. C.73377. 212·5; 109·5, 47 (approx.), 26·0. 24 pr. ribs.
BM. C.19993. 234·0; 119·5, 52·5, 29·0.

Discussion: Only two specimens (GSM. 21493 and SM. B11123) show the inner whorls, and they are poorly preserved. At small diameters (less than 45 mm) the inflation of the whorl is similar to that of some species of *Milanowskia*, but with growth S. (*C.*) *discofalcatus* becomes proportionately more compressed; Pavlow (1901 : 79) has discussed in detail the changes in whorl proportions and ornamentation with growth. A small, slightly distorted specimen of 25 mm diameter figured by Danford (1906 : pl. 12, fig. 8) is refigured here (Pl. 11, fig. 2), together with a similar individual in the Lamplugh collection (BM. C.72641), as S. (*C.*) cf. *discofalcatus*. Some even smaller, closely related forms which may be the earliest whorls of S. (*C.*) *discofalcatus* are described below as S. (?*C.*) sp. a.

Of the Speeton specimens definitely referred to S. (*C.*) *discofalcatus*, one (GSM. 21493) is recorded as "B. Base" and the horizon of the others is not accurately recorded. Lamplugh's small S. (*C.*) cf. *discofalcatus* is from C3. The species is more common in the Tealby Limestone of Lincolnshire, where large individuals of 100–240 mm diameter occur. These closely match the typical Russian forms; a Russian specimen from Ulyanovsk (Simbirsk) (Damon collection, BM. C.5) is figured here (Pl. 11, fig. 5) for comparison.

The Speeton specimen which Pavlow (1892 : 505, pl. 18, fig. 2) figured as S. (*C.*) *discofalcatus* belongs to S. (*C.*) *gottschei* (Koenen).

Distribution: *variabilis* zone, Speeton and Lincolnshire; *marginatus* zone (S. (*C.*) cf. *discofalcatus*), Speeton; *tenuis*? and *strombecki* zones, north Germany; *decheni* zone, *discofalcatus* and *umbonatus* subzones, Russia.

Simbirskites (Craspedodiscus) phillipsi (Roemer)

(Pl. 9, fig. 3)

1841 *Ammonites phillipsii* Roemer: 85.

Discussion: *S.* (*C.*) *phillipsi*, was first described, though not figured, by Roemer (1841 : 85), who suggested that Phillips' (1829 : 123; 1835 : 94) record of *Am. lamberti*? from the Speeton Clay referred to this species. Roemer described *Am. phillipsi* as involute, disc-shaped, with an almost carinate venter, and with ribs which bifurcate at a small tubercle near mid-flank, one of the pair bifurcating again later on the whorl flank. The primary ribs number 24–30 on the last whorl. The size of the specimen was not indicated, though "4–5 whorls", were recorded which suggests that it may have been fairly large. The original is now lost.

The lack of a figure or a good original definition of the species has led to considerable variation in its interpretation. Neumayr and Uhlig (1881 : 33, pl. 15, fig. 7) were the first to figure the species, their figured specimen probably being smaller than Roemer's original. They state that in their figured, incomplete example, there are 24 to 30 primary ribs, which split into 2 or 3 secondaries somewhat under half-way over the whorl, occasional ribs bifurcating again later on the whorl. The venter is described as narrow and strongly rounded; the figure shows that the venter is probably more rounded than in the specimen described by Roemer, but this may be a reflection of difference in size rather than of any specific difference. Neumayr and Uhlig's specimen may well belong to Roemer's species, but unfortunately this specimen too is lost.

Weerth (1884 : 17, pl. 4, figs 2, 3) next described and figured a large individual (102 mm in diameter) from the Teutoburger Wald. This agrees with Roemer's original description in density of primary ribbing (25 ribs on the last whorl) and in having a very narrow, almost keeled venter. Weerth, however, stated that about a third of the way over the whorl the primary ribs branch into three or four secondary ribs, which in turn frequently bifurcate later, whereas Roemer only recorded two secondary ribs, one of which later bifurcates.

Weerth's original is believed lost, but in the Weerth collection at Göttingen there are two Tönsburg (Teutoburger Wald) specimens (Orig. Nr. 457–124, 457–123) referred to by Koenen (1902 : 157), the larger of which (Orig. Nr. 457–124) is almost identical in size, general proportions and rib-pattern to Weerth's figured specimen. This specimen is figured here (Pl. 9, fig. 3) as *S.* (*C.*) *phillipsi* (Roemer *sensu* Weerth).

Dimensions:

110 (approx.); 58 (approx.), 25·8, 15·0.

It is close to *S.* (*C.*) *discofalcatus* in general proportions but has more numerous primary and secondary ribs and a slightly narrower umbilicus.

Pavlow (1901 : 79) included the more inflated Speeton specimen which he had previously (1892 : pl. 18, fig. 2) figured as *S.* (*C.*) *discofalcatus*, in *S.* (*C.*) *phillipsi*, and suggested that the latter differed from *S.* (*C.*) *discofalcatus* in having more numerous primary ribs and a broader venter. In fact, the descriptions reviewed above suggest that the German forms described as *S.* (*C.*) *phillipsi* have as sharp a venter as that of *S.* (*C.*) *discofalcatus* but are more finely ribbed (25–30 primaries per whorl instead of 19–22). The Speeton form figured by Pavlow is here included in *S.* (*C.*) *gottschei* (p. 56).

In view of the difficulty surrounding the interpretation of *S.* (*C.*) *phillipsi* it is a very unsatisfactory zonal index, though Koenen (1902) and Spath (1924) both recognized a *phillipsi* zone.

Simbirskites (Craspedodiscus) sp. ***(phillipsi*** group***)***

(Pl. 5, fig. 2)

?1904 *Simbirskites phillipsi* (Roemer); Koenen: pl. 1, fig. 6.

MATERIAL: Three; one small whorl fragment from the base of C2B (author's collection, BM. C.75881) and latex casts from 2 external moulds on a nodule from the base of C2B (author's collection, BM. C.75882–3).

The rib-pattern of these three specimens is close to that of the German individuals described above as *S.* (*C.*) *phillipsi* (Roemer *sensu* Weerth), but because of their much smaller size they cannot definitely be referred to that species.

The inner whorls of *S.* (*C.*) *discofalcatus* and *S.* (*C.*) *variabilis* have fewer primary ribs and a higher number of secondaries per primary. *S.* (*C.*) *juddi* has a similar rib-pattern to that of *S.* (*C.*) sp. (*phillipsi* group) but has a narrower umbilicus.

The Heligoland specimen figured by Koenen (1904) as *S. phillipsi* is probably conspecific with the Speeton specimens.

Simbirskites (Craspedodiscus) juddi sp. nov.

(Pl. 10, figs 1, 2)

1867 *Ammonites clypeiformis* d'Orbigny; Judd: 246.
1924 *Craspedodiscus clypeiformis* (Judd *non* d'Orbigny); Spath: 79, 87.

DIAGNOSIS: A compressed, involute, oxycone *Craspedodiscus* with very narrow umbilicus, acute venter and fine, dense, primary and secondary ribs.

TYPE SERIES: Holotype: GSM. 31059 (Judd collection) from the Tealby Limestone of Tealby. Paratype: BM. C.73375 (J. E. Lee collection), Tealby Limestone, Normanby.

DESCRIPTION: Shell compressed, involute, oxycone, umbilicus very narrow. Ribs fine, dense, branching irregularly; primary ribs branch about half way over the flank into two or three secondaries, and additional secondaries are intercalated close to the venter. The ribs curve forwards over the acute venter.

DIMENSIONS OF FIGURED SPECIMENS:
GSM. 31059 (holotype). 153: at 145; 78, 29·5, 14.
BM. C.73375 (paratype). 107·5, 59, 27·5, 9.

Discussion: The rib pattern can only be seen clearly on part of the holotype, and changes of rib-pattern with growth have not been observed. Despite the indifferent preservation of the type material, *S.* (*C.*) *juddi* is readily distinguished from *S.* (*C.*) *phillipsi* (Roemer *sensu* Weerth) and *S.* (*C.*) *discofalcatus* (Lahusen) by the greater compression of the shell and greater degree of involution with consequently narrower umbilicus. It is further distinguished from *S.* (*C.*) *discofalcatus* by its denser primary and secondary ribbing.

S. (*C.*) *juddi* was recorded by Judd (1867 : 246) as *Ammonites clypeiformis* d'Orb, and the holotype is a specimen from Tealby presented to the Geological Survey by Judd in 1867. This is almost certainly the same specimen which Pavlow (1901 : 80, footnote) referred to as close to *S.* (*C.*) *discofalcatus* but even more discoidal; Pavlow provisionally identified it as "*Ammonites discus*".

Lamplugh's (1896 : 210) reference to "*Ammonites clypeiformis*" probably embraces both *S.* (*C.*) *juddi* and *S.* (*C.*) *discofalcatus*.

Stratigraphical information on the relative position within the Tealby Limestone of *S.* (*C.*) *discofalcatus* and *S.* (*C.*) *juddi* is lacking, and Spath's (1924) recognition of a *clypeiformis* (Judd *non* d'Orb.) zone above a *discofalcatus* zone is presumably based on his suggestion (Spath 1924 : 87) that *S.* (*C.*) *clypeiformis* Judd *non* d'Orb. is the final, oxycone stage of the *Craspedodiscus* group.

Distribution: Upper part of the *variabilis* zone, Tealby Limestone, Lincolnshire.

Simbirskites (?Craspedodiscus) sp. a

(Pl. 11, fig. 1)

Material: 14 septate nuclei (10 in author's collection BM. C.75862–71; 4 in Neale collection) from C3, Speeton.

Description: Known from septate inner whorls only; the largest specimen is only about 20 mm in diameter, and in none are details of the ribbing preserved above 15 mm diameter. Shell involute, moderately compressed, venter narrowly rounded. Primary ribs extend nearly half-way over the whorl, where they swell slightly and branch into secondaries. Three or four, sometimes five, secondaries are associated with each primary, of which two or three branch from the primary and one or two are intercalated close to the point of branching. Ribs prorsiradiate, curving strongly forwards near to and over the venter.

Dimensions of figured specimen:

BM. C.75862. 13·6: 7·0, 6·1, 3·0. 19 pr. ribs.

Discussion: This species is common in C3 at Speeton, from which bed Lamplugh (1889 : 596) recorded it as "the fine-ribbed variety of *Amm. speetonensis*". The specimens are too small to be identified with certainty but appear close to the earliest whorls of *S.* (*C.*) *discofalcatus* as described by Pavlow (1901 : 79). They have more numerous secondary ribs per primary than the early whorls of *S.* (*M.*) *speetonensis*.

Simbirskites (?Craspedodiscus) sp. b

(Pl. 6, fig. 1)

1868 *Ammonites bipinnatus* Williamson MS.; Judd: 246 (pars).

A large Tealby Limestone ammonite (GSM. 47071, presented by Judd and labelled "*Ammonites bipinnatus*") has the following dimensions:

205: at 198; 76·5, —, 62.

It is slightly involute with gently curved flanks and narrowly arched venter. Primary ribs bifurcate about a third of the way over the whorl flank, and one or both secondaries may branch again nearer the venter. Occasionally a secondary is intercalated in mid-flank. The suture has long, narrow, strongly divided saddles and lobes.

The specimen is probably an original of Judd's (1868 : 246) record of *A. bipinnatus*. However, the record of this species from the "Ancyloceras beds" of the Speeton Clay (associated with "*Ancyloceras duvalii*" in Judd's fig. 4) probably refers to *S.* (*C.*) *gottschei*, the outer whorls of which are close to the present specimen but are more evolute with shallow constrictions. The stratigraphical horizon would agree; although it is difficult to correlate the "Ancyloceras beds" with Lamplugh's succession they may correspond with bed C4, at the base of which *S.* (*C.*) *gottschei* and *Aegocrioceras* cf. *seeleyi* (the "*A. duvalii*" of Judd's record?) occur.

Subgenus ***SIMBIRSKITES SENSU STRICTO***

DIAGNOSIS: Shell inflated to coronate; short primary ribs normally end at prominent tubercles, from which arise 2–4 secondary ribs. Both types of suture occur.

DISCUSSION: *S.* (*S.*) *pavlovae* and *S.* (*S.*) *coronatiformis*, the two earliest known *Simbirskites s.s.*, occur in the upper part of the Russian *versicolor* zone and it has already been suggested (p. 39) that they may be connecting links between *S.* (*Speetoniceras*) *versicolor* and later *Simbirskites s.s.* The inner whorls of both species differ from those of *S.* (*Sp.*) *versicolor* and allies in being more inflated with more numerous secondary ribs (3–4) per primary. With growth the number of secondary ribs decreases to two per primary and the whorl becomes less coronate, so that adult specimens closely resemble contemporaneous *Speetoniceras* (Chernova 1952 : 53). Thus both morphologically and stratigraphically they lie between *S.* (*Sp.*) *versicolor* with bifid ribbing and inflated inner whorls, and later *Simbirskites s.s.* which remain inflated or coronate with 3–4 secondary ribs throughout growth.

Simbirskites s.s. appears to have evolved along a separate line from the *Milanowskia–Craspedodiscus* groups, though evolutionary relationships are still far from clear and there may be connections between these three subgenera.

Simbirskites s.s. is rare at Speeton, being represented by a few small, septate nuclei belonging to three species; large specimens are common in Russia, and the most typical form and sculpture is seen in specimens of 50–90 mm diameter (Chernova 1952 : 47). Above this diameter the sculpture usually weakens.

Simbirskites (Simbirskites) umbonatus (Lahusen)

(Pl. 12, fig. 15; Text-fig. 2k)

1874 *Ammonites umbonatus* Lahusen: 33, pl. 5, fig. 2; pl. 6, fig. 1 (*non* 2).
1884 *Ammonites picteti* Weerth: 12, pl. 2, fig. 6 (?*non* fig. 5).
1901 *Simbirskites umbonatus* (Lahusen) Pavlow: 71, pl. 5, figs 1, 2.

DISCUSSION: *S.* (*S.*) *umbonatus* is a coronate species in which strong primary ribs branch at a prominent tubercle into three or four secondaries; a Russian specimen in which each rib trifurcates is figured here, and has the following dimensions:

78·7: 28·7, 37·6, 31·7. 25 primary ribs, approx. 75 secondary ribs.

The specimen (BM. C.17, Damon collection) is from Ulyanovsk (formerly Simbirsk).

Although *S.* (*S.*) *umbonatus* is well known in Russia and is a subzonal index in the Russian *decheni* zone, it has not been found at Speeton; the specimens recorded by Pavlow (1892 : 503, pl. 18 (11), figs 3, 8) belong to the less inflated *S.* (*S.*) *yorkshirensis* Chernova. The small specimens described here as *S.* (*S.*) *marginatus* (Phillips) may be the inner whorls of *S.* (*S.*) *umbonatus*; their relationship is discussed below.

Simbirskites (Simbirskites) marginatus (Phillips)

(Pl. 12, figs 13, 14; Text-fig. 2i)

1829 *Ammonites marginatus* Phillips: 123, pl. 2, fig. 41.
1835 *Ammonites marginatus* Phillips; Phillips: 95, pl. 2, fig. 41.
1868 *Ammonites marginatus* Phillips; Judd: 247.
1875 *Ammonites marginatus* Phillips; Phillips: 264, pl. 2, fig. 41.
1889 *Ammonites marginatus* Phillips; Lamplugh; 614.
1924 *Simbirskites marginatus* (Phillips) Spath: 77.
1962 *Ammonites marginatus* Phillips; Howarth: 132.

TYPE: The holotype (from the Speeton Clay of Speeton), formerly believed lost (Howarth 1962 : 132), is in the Yorkshire Museum, tablet 414. It is refigured here (Pl. 12, fig. 13).

MATERIAL: 12 specimens: BM. C.75872–79 (author's collection) from C3 and BM. C.75880 from C2F, Speeton. BM. C.34955–6 and YM. tablet 414A from Speeton, exact horizon not known.

DESCRIPTION: Known from early whorls (up to 15 mm diameter) only. Shell inflated, whorl-section sub-coronate to coronate. Umbilical wall bears feeble rib-folds which terminate just above the umbilical edge in prominent tubercles, 11 or 12 per whorl. From these arise four or five secondary ribs, of which one is usually intercalated. The secondaries curve gently forwards over the broad ventral region. The tubercles appear at a very early growth-stage (3·5–4·0 mm diameter) and the ribs slightly later (7 mm diameter).

The external suture (Text-fig. 2i) has relatively narrow elements, even at only 9·5 mm diameter.

DIMENSIONS OF FIGURED SPECIMENS:

YM. tablet 414 (holotype). 11·3; 5·1, 7·3, 3·6. 12 tubercles.
BM. C.75874. 12·0; 6·2, 9·4, 3·7. 12 tubercles.

DISCUSSION: Although known only from small specimens, this species is sufficiently well-marked to have long been recognized as distinctive of part of the Upper C Beds, "occurring most frequently in the lower part of the *Echinospatangus*-bed [C3], though nowhere abundant" (Lamplugh 1889 : 614). It occurs scattered throughout C3 and is a useful index fossil for this part of the succession.

S. (*S.*) *marginatus* may be conspecific with the Russian *S.* (*S.*) *umbonatus* (Lahusen), for the holotype closely matches a Russian individual of 15 mm diameter figured by Pavlow (1901 : pl. 5, fig. 2) as the early whorls of *S.* (*S.*) *umbonatus*. In the absence of larger Speeton specimens closer comparison is not possible. The comparison between the two species is further complicated by Chernova's (1951 : 55) view that Pavlow's figured specimens of *S.* (*S.*) *umbonatus* are not conspecific with Lahusen's originals. Chernova renamed Pavlow's specimens as *S.* (*S.*) *pavlovi* nom. nov., though it is doubtful whether they are really a distinct species.

S. (*S.*) *marginatus* differs from the more inflated varieties of the *S.* (*S.*) *decheni* group in having sharper tubercles and finer ribbing.

Because of the small size of the holotype and Phillips' sketchy figure, the specific name "*marginatus*" caused confusion for later workers; Roemer (1841 : 86) apparently applied it to a species of *Polyptychites*, a practice definitely followed by Neumayr and Uhlig (1881 : 157) and Koenen (1902 : 127; 1909 : 25).

DISTRIBUTION: Speeton Clay, *marginatus* zone, Speeton.

Simbirskites (Simbirskites) yorkshirensis Chernova

(Pl. 12, figs 2, 5, 7)

1892 *Olcostephanus* (*Simbirskites*) *umbonatus* (Lahusen); Pavlow: 504, pl. 18 (11), figs 3, 8.
1924 *Simbirskites* aff. *toensbergensis* (Weerth); Spath: 77.
1951 *Simbirskites iorkshirensis* (sic) Chernova: 63.

TYPE: Chernova introduced *S. yorkshirensis* as a *nomen novum* for *S.* (*S.*) *umbonatus* Pavlow (1892) *non* Lahusen; of the two syntypes, the original of Pavlow's plate 18 (11) fig. 8, is here selected lectotype. BM. C.34962, from the upper C Beds, Speeton.

MATERIAL: Four small septate specimens from the Speeton Clay; BM. C.75884 (author's collection) from bed C2C, BM. C.75885–6 (author's collection) from the upper C Beds, and Wrights' collection 24284.

DESCRIPTION: Shell slightly inflated with ellipsoid whorl section, broadest near the umbilical edge; venter arched. Short, straight primary ribs extend about a third of the distance over the flank, ending in a prominent mid-lateral tubercle. There are 10–12 tubercles per whorl at diameters of 14–21 mm. Four, or rarely three, secondary ribs are associated with each tubercle, of which one is usually intercalated while the others join the tubercle. Ribs nearly straight on the flanks, secondaries curving forwards over the venter.

DIMENSIONS OF FIGURED SPECIMENS:

Wrights' colln. 24284. 21·1; 9·6, 9·0, 6·4. 12 pr., 49 sec. ribs.
BM. C.75885. 18·7; 9·1, 8·6, 5·0. 12 pr., 46 sec. ribs.

DISCUSSION: Pavlow's other figured specimen (BM. C.34982) from the Lower Tealby Clay of Donnington-on-Bain, Lincolnshire, is considerably larger than the Speeton examples and can only provisionally be attached to *S. yorkshirensis*. Pavlow (1892 : 504) regarded his figured *S. umbonatus* as intermediate in character between *S. umbonatus* (Lahusen) and *S. toensbergensis* (Weerth), and later (1901 : 72) referred the Speeton specimens to *S. toensbergensis* instead. Three specimens of the latter species were figured by Weerth (1884 : pl. 4, figs 4–6) of which one (fig. 5) is of comparable diameter to the Speeton *S. yorkshirensis* and differs only in having slightly more numerous secondary ribs (four or five to each primary). The two are clearly closely related, but Weerth's species requires modern revision.

S. (S.) yorkshirensis differs from the inner whorls of *S. (S.)* cf. *decheni* in being more compressed with stronger tubercles.

DISTRIBUTION: Speeton Clay *variabilis* zone, Speeton. Lower Tealby Clay of Donnington-on-Bain, Lincolnshire (*S. (S.)* cf. *yorkshirensis*). *Decheni* zone, *umbonatus* subzone, Russia.

The ***Simbirskites (Simbirskites) decheni*** (Roemer) group

(Pl. 11, fig. 6; Pl. 12, figs 1, 3, 4, 6, 8–10)

DISCUSSION: Although *S. (S.) decheni* is a difficult species to interpret it is extensively quoted in the Russian, German and English literature and is the index fossil of the Russian *decheni* zone. The German type-specimen, from the "Quader" of the Teutoburger Wald, is lost and Roemer's (1841 : pl. 13, fig. 1) figure is poor; it is therefore difficult to decide whether two specimens from the Osning Sandstone of Tönsberg (Teutoburger Wald) figured by Weerth (1884 : pl. 1, fig. 3; pl. 2, fig. 1) are conspecific with Roemer's original. Most Russian workers have followed Pavlow's (1901) interpretation of the species, as did Wedekind (1910 : 94) in Germany. Pavlow (1901 : 69) had conserved the specific name for those Russian forms which (following Lahusen 1874) were commonly referred to *S. (S.) decheni*, whilst showing that Roemer's original description also corresponded in part to two other Russian species, *S. elatus* and *S. pseudobarboti*. Pavlow therefore attributed authorship of the Russian *S. (S.) decheni* to Lahusen.

The species clearly requires stabilization by the erection of a neotype, but this cannot be attempted until a satisfactory German specimen becomes available. The various English, German and Russian forms which have been figured as *S. (S.) decheni* are closely related and may well be conspecific. At Speeton the *S. (S.) decheni* group is represented by rare septate inner whorls which exhibit some variation in shell proportions and rib density; most can be compared closely with small specimens previously figured as *S. (S.) decheni*.

Two varieties occur in the lowest 0·61 metres (2 feet) of C6 (*concinnus* subzone). At comparable growth-stages, BM. C.75887–9 (author's collection) and BM. C.75568 (collected from the C Beds by Mr. D. Ward) closely match the Speeton specimen figured by Pavlow (1892 : pl. 18, fig. 5 only; this specimen was later (Pavlow 1901 : 68) referred to *S. elatus* (Trautschold)). Four specimens are figured here (Pl. 12, figs 1, 3, 4, 10) as *S.* (*S.*) cf. *decheni* (Roemer) var. a. They show only a feeble swelling where the primary ribs branch, and differ from *S.* (*M.*) *concinnus* only in being slightly more inflated.

The second variety from low C6 (figured here, Pl. 12, figs 8, 9 as *S.* (*S.*) cf. *decheni* (Roemer) var. b) is more inflated with more clearly developed tubercles; there is a small specimen in the author's collection (BM. C.75890; pl. 12, fig. 9) and a larger individual (probably C6) in the Wrights' collection (17593; pl. 12, fig. 8).

A larger, strongly tuberculate specimen from Middle C, figured by Pavlow (1892 : pl. 18, fig. 4), is close to a German specimen from Ihme figured by Wedekind (1910 : pl. 4, fig. 1) and to another Ihme specimen figured here (Pl. 11, fig. 5) as *S.* (*S.*) *decheni* (Roemer) *sensu* Wedekind. It is also close to the Russian individuals figured by Pavlow (1901 : pl. 1, figs 4–6). Some partly crushed, coarsely ribbed whorl fragments from C4 (author's collection, BM. C.75891–2 from Bed C4I and Wrights' collection 24578–80, 24697) probably belong to the same variety or to a closely related, slightly more compressed form in the Lamplugh collection (BM. C.72632) figured here (Pl. 12, fig. 6) as *S.* (*S.*) cf. *decheni* var. c.

DIMENSIONS OF FIGURED SPECIMENS:

BM. C.75888. 14·4; 6·8, 8·0, 4·0.
BM. C.75568. 16·4; 7·5, 9·3, 4·5. 15 pr. ribs.
BM. C.75889. 16·0; 7·2, 8·6, 4·7. 15 pr. ribs.
BM. C.75887. 21·9; 10·0, 12·0, 6·7. 18 pr., approx. 50 sec. ribs.
BM. C.75890. 14·2; 7·0, 9·3, 3·0.
Wrights' colln. 17593. 23·1; 9·7, 13·6, 7·9. 16 pr., approx. 52 sec. ribs.
BM. C.14419. 34·3; 13·4, 17·0, 12·3. 18 pr., approx. 42 sec. ribs.

Until more material becomes available it will be impossible to make an adequate study of the German and English forms or to ascertain the relationship between these and the forms figured by Weerth (1884) as *S.* cf. *inverselobatus* (Neumayr and Uhlig) and *S. nodocinctus* (Weerth).

Simbirskites (Simbirskites) cf. ***virgifer*** (Neumayr and Uhlig)

(Pl. 12, fig. 12)

cf. 1881 *Olcostephanus virgifer* Neumayr and Uhlig: 160, pl. 33, fig. 1.

DISCUSSION: A single whorl fragment (HU. Rn. 923, collected by Mr. D. Sowter) from the Lower Tealby Clay or Tealby Limestone of Nettleton is close to the holotype of *S.* (*S.*) *virgifer* in rib-pattern and general proportions. The primary ribs of the Nettleton specimen branch at a slight swelling into two secondary ribs; a third usually branches from the anterior side of the posterior rib of the original pair.

Simbirskites spp.

In addition to the species described above, there are a number of specimens in the author's collection and in museum collections which are too inadequately preserved for description; none of them can be definitely named but they indicate the presence of several otherwise unrecorded species.

A specimen from the Lower Tealby Clay of Nettleton (Wrights' collection 21711) and a similar individual from Speeton (Yorkshire Museum) appear close to *S.* (*M.*) *polivnensis* Pavlow (1901 : 77, pl. 7, figs 5–6). Several tuberculate fragments from C2C and C2E (author's collection) belong to the *yorkshirensis-toensbergensis* group, and two other whorl fragments from C2C and C2E (author's collection) appear close to Weerth's poorly known *Simbirskites arminius*.

Some very compressed nuclei from C5? (Wrights' collection) appear to be an undescribed species of *Craspedodiscus*, and C2E yields large, smooth *Craspedodiscus* fragments.

A large, indifferently preserved specimen from the Tealby Limestone of Nettleton (BM. C.74671, presented by Mr. A. Eborn) has a smooth septate outer whorl and sharply ribbed earlier whorls. The whorl section and ribbing of the penultimate whorl show that the specimen can be provisionally identified as *S.* (*M.*) cf. *progredicus* (Lahusen).

Spath (1924) recorded several species not described here. His record of *S.* (*Sp.*) *subinversum* (Pavlow) is believed to be based on A. P. Pavlow's misidentification of that species (p. 46). The originals of *S. triplicatus* Koenen from C6 and *S. progredicus* (Lahusen) from C3 and C1 have not been traced. The *S.* (*C.*) *carinatus* (Koenen) from B Base is probably a whorl fragment of *S.* (*C.*) *discofalcatus*. The records of *S.* (*C.*) *barbotanus* (Lahusen) and *S.* (*C.*) *phillipsi* (Roemer) Weerth sp. from the Tealby Limestone have not been confirmed.

V. ZONATION OF THE *Simbirskites* BEDS OF THE SPEETON CLAY

The four belemnite zones which Lamplugh (1889) distinguished in the Speeton Clay are large units and are therefore only of limited use in correlation. The replacement within the *Simbirskites* beds of *Hibolites jaculoides* by *Oxyteuthis* marks the C/B Beds boundary; the same faunal change occurs in Lincolnshire at the Lower Tealby Clay/Tealby Limestone junction (p. 35) and in north Germany within the *rarocinctum* zone.

Judd (1867) relied mainly on the ammonite sequence to subdivide the Speeton Clay, and was the first author to utilize a *Simbirskites* ("*Am. speetonensis*") as a zonal form. Unfortunately, although some of Judd's zones are easy to recognize others cannot be satisfactorily correlated with Lamplugh's better known lithological subdivisions. Pavlow (1892 : 559) later distinguished two ammonite zones in the Speeton Clay *Simbirskites* beds, a lower *S.* (*Sp.*) *subinversum* zone (C7–C6) and an upper *S.* (*S.*) *decheni–S.* (*M.*) *speetonensis* zone (C6–C1); he equated the former with the Russian *versicolor* zone and the latter with the *decheni* zone.

In 1924, Spath published a detailed zonation for the north-west European Lower Cretaceous, and for the Speeton succession this appeared to be a great advance on previous schemes. Unfortunately Spath's zonation is based upon a hypothetical ammonite succession, the zonal forms being drawn from both Speeton and North Germany, and some only occurring in one area or the other (cf. Casey's (1961 : 494) criticism of Spath's zonation of the Aptian and Lower Albian).

Spath's subdivision of the *Simbirskites* beds is:

Zone	Bed (Speeton)	
Paracrioceras rarocinctum	Lower B (pars)	
S. (*C.*) *clypeiforme*	Not represented at Speeton	(Tealby Limestone of Lincolnshire)
S. (*C.*) *discofalcatus*		
S. (*M.*) *progredicus*	C1–3	
S. (*C.*) *phillipsi*	C4	
Spitidiscus rotula	C5	
S. (*M.*) *speetonensis*	C6	
Aegocrioceras capitanei	C7	
Aegocrioceras capricornu		
———— (unnamed gap)		

Of the zonal species, *Aegocrioceras capricornu* and *S.* (*C.*) *phillipsi* are difficult to interpret, while *A. capitanei* is an undescribed and indeterminate species known from a manuscript name only (Rawson 1970 : 591). Spath's record of *S.* (*M.*) *progredicus* has not been confirmed, and the relative position of the *discofalcatus* and *clypeiforme* (=*S.* (*C.*) *juddi*) zones is not known (see p. 63).

Chernova (1951 : 61) severely criticized Spath's zonation because his divisions were guided by Lamplugh's lithological divisions rather than by "the principle of detailed investigation of the group or groups of the most changeable forms (in this case the ammonites), which to us seems the basic principle of biostratigraphy" (translated from the Russian). Because Spath's zones were not based on the appearance of new species Chernova rezoned the *Simbirskites* beds of the Speeton Clay using the species ranges given by Spath, supplemented by reference to earlier published information. Her scheme, which utilises simbirskitid ammonites only, is as follows:

Zone	Bed
S. (*S.*) *yorkshirensis* and *S.* (*C.*) *discofalcatus*	C2—Base of Lower B
S. (*M.*) *progredicus*	Upper part of C4 to C3
S. (*M.*) *speetonensis*	Upper part of C6 to lower part of C4
S. (*Sp.*) *versicolor* and *S.* (*Sp.*) *subinversum*	Upper part of C8 to lower part of C6.

Although this is an improvement on Spath's scheme, the published information on the vertical distribution of the *Simbirskites* species is inaccurate, as Chernova realized, and thus her zonal boundaries are of little value. Again, most of the zonal species are extremely rare. The zonation of the equivalent beds in Germany is inadequate (p. 75) and is based mainly on crioceratitid ammonites, so that it is impracticable to apply the German scheme to the Speeton Clay. The Russian zonation is based upon *Simbirskites*, but some of the zonal forms are not recorded from Speeton.

A new zonation for the Speeton sequence is therefore proposed here (Text-fig. 7); the only index species used by Spath or Chernova which has been retained in the new scheme is *S.* (*M.*) *speetonensis*. It must be stressed that in the beds above C6 ammonites are rare, and the proposed zonation for this part of the succession is tentative. In C6 and C7 ammonites are relatively common, so that here the zonation is more firmly established.

Although it is not apparent from Spath's (1924 : 76) faunal list, detailed collecting has shown a major change in the generic composition of the fauna at the C8/C7 boundary, i.e. at the base of the *Simbirskites* beds. The neocomitids (*Endemoceras*[2] and *Acanthodiscus*) and *Olcostephanus* die out at the top of C8 while the first *Simbirskites* and crioceratitids appear low in C7. Only the rare Tethyan forms *Spitidiscus* and *Hypophylloceras* cross the boundary.

BED	PAVLOW 1892	SPATH 1924	CHERNOVA 1951	ZONATION PROPOSED HERE	
LOWER B (pars)		Paracrioceras rarocinctum		Paracrioceras rarocinctum	LB4
				?	LB5
				C. variabilis	LB6
C1	S. decheni and M. speetonensis	M. progredicus	S. yorkshirensis and C. discofalcatus		C1
C2					C2
C3			M. progredicus	S. marginatus	C3
C4		C. phillipsi		C. gottschei	C4
C5		Spitidiscus rotula	M. speetonensis	M. speetonensis M. speetonensis subzone	C5
C6		M. speetonensis		M concinnus subzone	C6
C7	Sp. subinversum	Aegocrioceras capitanei Aegocrioceras capricornu	Sp. versicolor and Sp. subinversum	Sp. inversum	C7
C8	Endemoceras regale (C8 - C11)	Subastieria sulcosa		Endemoceras regale (C8 - C11)	C8

FIG. 7. Zonal schemes proposed for the *Simbirskites* beds of the Speeton Clay.

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[2] The genus *Endemoceras* (type species *Hoplites amblygonius* Neumayr & Uhlig) was proposed by Thiermann (1963) for a group of boreal neocomitids previously included in *Lyticoceras* Hyatt. *Lyticoceras* (type species *Am. cryptoceras* d'Orb.) is regarded as a junior subjective synonym of *Leopoldia*.

The *regale* zone

INDEX SPECIES: *Endemoceras regale* (Pavlow)

The index species occurs throughout C10, C9 and C8; other species include *Acanthodiscus* spp. (C9 and C8), *Olcostephanus subfilosus* Spath (C8), *Subastieria sulcosa* (Pavlow) (C9A), *Parastieria peltoceroides* (Pavlow) (C9A, C9C) and *Spitidiscus inflatiformis* Spath (top nodule band of C8).

The *inversum* zone

INDEX SPECIES: *Simbirskites* (*Speetoniceras*) *inversum* (M. Pavlow)

The zone spans the whole of C7 and is 2·9 metres (9·5 feet) thick. The index species appears at the base of the zone, being common in bed C7H and rare in C7G. Rare *S.* (*Sp.*) *subbipliciforme* (Spath) occur in C7H and large, indeterminate *S.* (*Speetoniceras*) fragments in the nodule band of C7F. Small, flattened *S.* (*Sp.*) sp. (p. 47) occur in the pale blue clay of C7F just above the nodule band.

The heteromorph genus *Aegocrioceras* appears in abundance in C7G and from here to the top of the *inversum* zone is the dominant element of the fauna. *Crioceratites* first appears at the top of the zone, in bed C7A.

The *speetonensis* zone

INDEX SPECIES: *Simbirskites* (*Milanowskia*) *speetonensis* (Young and Bird).

ZONE	*INVERSUM*					*SPEETONENSIS*			*GOTTSCHEI*					*MARGINATUS*				*VARIABILIS*						
BED / SPECIES	C7H	C7G	C7F	C7E	C7D-A	C6		C5L-A	C4L	C4K	C4J	C4I	C4H-A	C3	C2F	C2E	C2D	C2C	C2B	C2A	C1B	C1A	LB6	LB5E
						lower	upper																	
Sp. subbipliciforme	×																							
Sp. inversum	×	×																						
Sp sp.			×																					
Sp indet.			×																					
M concinnus						×																		
M. staffi						×																		
M speetonensis							×																	
*M.*cf. *lippiacus*																×								
C. gottschei									×															
C. sp. a														×										
C. variabilis																		×	×				×	
*C.*sp. (*phillipsi* group)																			×					
C discofalcatus																							×	
S. decheni group						×						×												
S. marginatus														×	×									
S yorkshirensis																		×						

FIG. 8. Distribution of species of *Simbirskites* in the Speeton Clay.

Includes beds C6 and C5, and is approximately 12·9 metres (42·2 feet) thick.

Both Spath (1924) and Chernova (1951) recognized a *speetonensis* zone, though with different upper and lower limits (Text-fig. 7).

The base of the zone is drawn at the base of C6, where there is an important change in the ammonite fauna. The abundant *Aegocrioceras* of the *inversum* zone die out, and there is a change in the subgeneric composition of the *Simbirskites* fauna, species of *Milanowskia* and *Simbirskites* s.s. replacing *Speetoniceras*. From this level upward *Simbirskites* becomes the dominant ammonite of the C Beds fauna. Two subzones are recognized, a *concinnus* subzone below and a *speetonensis* subzone above, *S.* (*M.*) *concinnus* being limited to the lower part of C6 and *S.* (*M.*) *speetonensis* to the upper. C5 has not yielded identifiable *Simbirskites* and can only provisionally be included in the *speetonensis* subzone.

Fragments of septate inner whorls of the *Crioceratites beani* group occur in the *concinnus* subzone and *S.* (*M.*) *staffi* and *S.* (*S.*) cf. *decheni* in the basal part of the subzone. Rare *Spitidiscus rotula* (Sowerby) occur in bed C5L (*speetonensis* subzone).

The *gottschei* zone

INDEX SPECIES: *Simbirskites* (*Craspedodiscus*) *gottschei* (Koenen).

Includes all the subdivisions of bed C4, and is approximately 9·5 metres (31·2 feet) thick. The index species occurs in the basal bed, C4L, and from this level upward *Simbirskites* occurs spasmodically through the rest of the C Beds and extends into the base of Lower B. Large *Aegocrioceras* cf. *seeleyi* (Neumayr and Uhlig) are associated with *S.* (*C.*) *gottschei* in C4L. Although *Simbirskites* is rare higher in C4, crushed *S.* cf. *decheni* occur in C4I (p. 68) and large, flattened *Simbirskites* of the *kleini* group have been seen high in C4.

The *marginatus* zone

INDEX SPECIES: *Simbirskites* (*Simbirskites*) *marginatus* (Phillips).

The zone includes bed C3 and beds C2F–C2D, and is 3·6 metres (11·8 feet) thick. The index species occurs throughout C3, appearing at the very base of this bed, and a single specimen is known from C2F. Associated with it in C3 are the small specimens described above (p. 63) as *S.* (*C?*) sp. a. Beds C2D and C2E are provisionally included in this zone: C2E yields *S.* (*M.*) cf. *lippiacus* (Weerth) and indeterminate fragments of the *yorkshirensis-toensbergensis* group (p. 69), together with poorly preserved fragments of a large, indeterminate *Simbirskites* with smooth outer whorls (p. 69).

The *variabilis* zone

INDEX SPECIES: *Simbirskites* (*Craspedodiscus*) *variabilis* sp. nov.

The base of the zone is drawn at the base of C2C where the index species first appears. *S.* (*C.*) *variabilis* is the commonest ammonite of the zone, occurring in C2C, the nodules at the base of C2B, and in LB6. Rare *S.* (*S.*) *yorkshirensis* Chernova and *Paracrioceras statheri* Spath occur in C2C and *S.* (*C.*) sp. (*phillipsi* group) (p. 62) in the nodules at the base of C2B. Some larger whorl fragments of the *yorkshirensis-toensbergensis* group occur in C2C. A single *S.* (*C.*) *discofalcatus* is recorded from LB6 and two indeterminate *Simbirskites* nuclei have been found in LB5E. *S.* (*C.*) *discofalcatus*, *S.* (*C.*) *juddi* and *S.* (?*C.*) sp. b occur in the Tealby Limestone of Lincolnshire, which is correlated with the upper part of the *variabilis* zone.

The *rarocinctum* and *fissicostatum* zones

Ammonites are rare above Bed LB6 and the only common forms are large, crushed and indeterminate crioceratitids which usually decompose on exposure. The few determinable specimens are conspecific with German forms and the German zonal divisions can provisionally be adopted for this part of the Speeton succession. Kaye (1964 : 349) recorded *Paracrioceras strombecki* from Bed LB3 and considered it likely that beds LB4–6 were also of *strombecki* zone age. Kaye's record is doubtful; the occurrence of *S.* (*C.*) *discofalcatus* in the German *strombecki* zone (p. 76) suggests that this zone should be equated with part of the *Simbirskites* beds (Text-fig. 9). My own collecting has yielded several fragmentary *Hoplocrioceras fissicostatum* (Roemer *sensu* Neumayr and Uhlig) in Bed LB3, thus equating this part of the succession with the German *fissicostatum* zone. Beds LB4–LB5D are provisionally included in the *rarocinctum* zone, though identifiable ammonites have not yet been found here.

VI. CORRELATION WITH OTHER AREAS

(a) *North Germany*

The marine Lower Cretaceous strata of the Lower Saxony Basin overly non-marine Wealden Beds; invasion of the sea commenced early in the Lower Valanginian (German "Mittel Valendis"). From then to the upper Cretaceous there was continuous deposition of sediments, dark grey, often shaley clays with bands of ferruginous concretions being laid down in the central part of the basin while shallower-water, marginal facies beds were deposited along the extremities (Thiermann and Arnold 1964 : 692). Sandstones, usually interdigitating with clays, occur around the south-western margin (Bentheim embayment: Kemper 1963) and along the Teutoburger Wald and Eggegebirge. Further east, fringing the northern foothills of the Hartz, occur the important iron ores of the Saltzgitter region.

Simbirskites is well represented in German museum collections though there are few localities from which it can still be collected. The large specimens figured by Neumayr and Uhlig (1881) came from the ironstones of Saltzgitter while the fauna described by Weerth (1884) was collected from the sparsely fossiliferous Osning Sandstone of the Detmold region (Teutoburger Wald). The most prolific collecting locality was the brick-pit at Ihme, 8 kilometres south-west of Hannover (Wedekind 1910). The best modern section is the Moorberg brick-pit at Sarstedt, 17 kilometres south-south-east of Hannover, where the Hauterivian and Barremian are well exposed. Here the clays were deposited in relatively shallow water in the region of a salt stock. They are lighter in colour and less shaley than their equivalents in the central region of the Lower Saxony Basin, but are lithologically very similar to the equivalent horizons at Speeton.

The *Simbirskites* described by Neumayr and Uhlig (1881) and Weerth (1884) have remained difficult to interpret, and few species were figured in Koenen's (1902) monograph on the north German Lower Cretaceous ammonites. The latter author did, however, describe numerous crioceratitid species from the later Hauterivian and early Barremian strata, and the zonal schemes for this part of the German Lower Cretaceous have consequently relied largely on crioceratitids (e.g. Koenen 1902; Stolley 1925). The zonation currently in general use (e.g. Bartenstein and Bettenstaedt 1962; Bähr, unpublished dissertation) is summarized in Text-fig. 9. This zonation is inadequate, for many of the zonal species are extremely rare and difficult to interpret.

The pattern of ammonite distribution in the later Hauterivian strata is similar to that at Speeton, in that crioceratitids become rare above the beds with abundant *Aegocrioceras* while *Simbirskites* decreases in numbers upwards but usually dominates the fauna. From Bähr's unpublished work and from my detailed collecting in the lower part of the *Simbirskites* beds at Sarstedt it is apparent that the *Simbirskites* zones proposed here for the Speeton succession could usefully be adopted, with modification to allow for local variation, for the north German succession. Many of the species ranges discussed below have been obtained from Bähr's unpublished dissertation.

The *capricornu* zone

Index species: *Aegocrioceras capricornu* (Roemer).

The *capricornu* zone overlies the *Endemoceras noricum* zone, the fauna of the *regale* zone of Speeton and the *Speetoniceras* fauna of the base of the *inversum* zone being unrepresented in north Germany. This is believed to be due to a failure in preservation rather than to a stratigraphical break.

Aegocrioceras is abundant in the lower part of the *capricornu* zone, and rare body chamber fragments of large *Crioceratites* of the *wermbteri* group appear in the middle of the zone (author's collection, from Sarstedt). Abundant *Simbirskites* appear a few centimetres above this level and almost completely replace *Aegocrioceras*. Exactly the same faunal sequence is seen at Speeton, where *Aegocrioceras* is abundant through most of the *inversum* zone (C7), is joined by *Crioceratites* cf. *wermbteri* (Koenen) in the top bed of the zone (C7A) and is replaced by abundant *Simbirskites* a few centimetres higher in the succession, at the base of the *speetonensis* zone (base C6). The same species, *S.* (*M.*) *concinnus*, *S.* (*M.*) *staffi* and *S.* (*S.*) cf. *decheni*, appear in both areas, replacing identical *Aegocrioceras* assemblages, but there is a significant difference in the relative abundance of the *Simbirskites* species; at Speeton *S.* (*M.*) *concinnus* is common and *S.* (*M.*) *staffi* extremely rare, while the inverse relationship holds in Germany.

The *hildesiense* zone

Index species: *Crioceratites hildesiense* (Koenen).

The index species is rare; its first appearance defines the base of the zone. *S.* (*M.*) *staffi* extends into the lower part of the zone and *S.* (*S.*) of the *decheni* group occur throughout. The zone can be correlated with some part of the *speetonensis* zone of Speeton.

The *seeleyi* zone

INDEX SPECIES: *Aegocrioceras seeleyi* (Neumayr and Uhlig)

A. seeleyi is common at the base of the zone (Bähr, unpublished dissertation); about 2 metres above the base in the southern part of the Moorberg pit, Sarstedt, there is a rich *Simbirskites* horizon, from which I have collected numerous septate inner whorls of an undescribed species (=*S.* sp. nov. of Wedekind (1910 : pl. 4, fig. 2) and *S. ihmensis* Bähr MS.), a form close to *S. speetonensis* (=*S. speetonensis venustus* of Bähr) and *S. decheni* (Roemer) *sensu* Wedekind. None of the species can be matched exactly with any well-localized Speeton forms (a single *S. decheni sensu* Wedekind is known from "Middle C" (p. 68)) but the assemblage probably correlates with the higher part of the *speetonensis* zone.

S. (*C.*) *gottschei* appears higher in the *seeleyi* zone; this is found associated with *A.* cf. *seeleyi* at the base of the *gottschei* zone at Speeton.

Bähr also recorded *S. virgifer* (Neumayr and Uhlig) and *S. paucilobus* Koenen from the *seeleyi* zone; neither species is recorded from Speeton though *S.* cf. *virgifer* occurs at Nettleton.

The *tenuis* zone

INDEX SPECIES: *Simbirskites* (*Craspedodiscus*) *tenuis* Koenen.

The only German zone defined by a simbirskitid is based on a very rare species originally described from about 6 specimens; Bähr did not find a single specimen and was unable to separate the *tenuis* from the underlying *seeleyi* zone. *S.* (*C.*) *discofalcatus* first appears at about this level.

The *strombecki* zone

INDEX SPECIES: *Paracrioceras strombecki* (Koenen).

The index species is not common, and according to Bähr it extends up into the lower part of the *fissicostatum* zone. *Simbirskites* is rare, but *S.* (*C.*) *discofalcatus* occurs.

The *rarocinctum* zone

INDEX SPECIES: *Paracrioceras rarocinctum* (Koenen).

The zonal species is very rare and *Simbirskites* was not recorded by Bähr. The belemnite *Oxyteuthis*, typical of the Speeton B Beds, is first recorded from this zone.

The *fissicostatum* zone

INDEX SPECIES: *Hoplocrioceras fissicostatum* (Roemer).

The index species is difficult to interpret (compare the considerably different figures in Neumayr and Uhlig 1881 : pl. 56, fig. 1, and Koenen 1902 : pl. 22, figs 1,

2) but is recorded from Sarstedt by Bähr; *H. fissicostatum* (Roemer *sensu* Neumayr and Uhlig) occurs in LB3 at Speeton.

The correlation between Speeton and north Germany suggested by these records is summarized in Text-fig. 9; much of the correlation can only be regarded as tentative, pending further detailed collecting in both areas.

Lower Cretaceous clays with *Simbirskites* occur off the coast of Heligoland, and specimens picked up off the beach were described by Koenen (1904).

(b) *Russia*

Thick, sandy clays of Hauterivian and Barremian age are widespread through the middle Volga region and the Moscow syncline. They have been divided into the Simbirskitid Beds below and the Belemnite Series above, the former yielding an extensive *Simbirskites* fauna and the latter a belemnite-lamellibranch fauna. Early work on the Simbirskitid Beds culminated in Pavlow's (1901) extensive review of the stratigraphy and *Simbirskites* fauna. The Simbirskitid Beds were divided into a *versicolor* zone below and a *decheni* zone above, each of which has subsequently (Chernova 1951) been divided into three subzones. Chernova reviewed earlier

SPEETON		GERMANY	RUSSIA		TETHYS	STAGE
			SUBZONE	ZONE		
LB3 — ? —	*fissicostatum*	*fissicostatum*	BELEMNITE SERIES with *Oxyteuthis brunsvicensis* (*pars*)			BARREMIAN (*pars*)
LB4-LB5D — ? —	*rarocinctum* (no ammonites recorded)	*rarocinctum* — ? —				
LB5E-C2C	*variabilis*	*strombecki* — ? —	*umbonatus*	*decheni*	*angulicostata*	HAUTERIVIAN (*pars*)
C2D-C3	*marginatus*	*tenuis* — ? —				
C4	*gottschei*	*seeleyi* — ? —	*discofalcatus* — ? —		*sayni*	
C5-C6	*speetonensis*	*hildesiense* — ? —	*speetonensis*			
C7	*inversum*	*capricornu*	*pavlovae* — ? — *inversum*	*versicolor*	*duvalii*	
C8-C11	*regale*	FAUNAL BREAK	*versicolor* — ? — NO DEPOSITS	— ? —	— ? — *radiatus* (*pars*)	

FIG. 9. Comparison between the Speeton zones and their German, Russian and Tethyan equivalents. ? indicates that the correlation with the Speeton zones is only approximate.

evidence showing that the *Endemoceras* fauna of the earliest Hauterivian beds of western Europe is absent over most of Russia, the Simbirskitid Beds resting on an eroded Valanginian surface in the Middle Volga region and transgressing over various horizons of the Valanginian or late Jurassic in the Moscow synclise.

The classic sequence in the Simbirskitid Beds and Belemnite Series is a 7 km section along the right bank of the Volga, from the village of Polivny to Ulyanovsk (formerly Simbirsk). Here, Chernova (1951 : 52–55) recognized the following faunal sequence in the Simbirskitid Beds:

The *versicolor* zone

The zone is typified by species of the subgenus *Speetoniceras*, which dies out at the top of the zone.

a. *versicolor* subzone

S. (*Sp.*) *versicolor* occurs sporadically in the lower part of the subzone and becomes abundant higher up, where *S.* (*Sp.*) *subinversum* and *S.* (*S.*) *coronatiformis* appear.

b. *inversum* subzone

The species of the *versicolor* subzone are joined by *S.* (*Sp.*) *inversum*.

c. *pavlovae* subzone

In the lower part of the subzone the species of the *inversum* subzone still occur, together with *S. pavlovae* Chernova (*nomen novum* for *S. elatus* M. Pavlow *non* Trautschold). In the upper part of the subzone *S.* (*S.*) *coronatiformis* disappears and *S.* (*Sp.*) *versicolor* and *S.* (*Sp.*) *inversum* are rare.

The *decheni* zone

a. *speetonensis* subzone

The base of the subzone is marked by a major faunal break; all the species of the *versicolor* zone disappear and are replaced by species of the subgenera *Simbirskites* s.s., *Milanowskia* and *Craspedodiscus*.

b. *discofalcatus* subzone

Most species of the *speetonensis* subzone disappear but the subzone is characterized by large numbers of *S.* (*C.*) *discofalcatus*, *S.* (*M.*) *progredicus*, *S.* (*M.*) *polivnensis*, *S.* (*S.*) *umbonatiformis* and *S.* (*S.*) *pseudobarboti*.

c. *umbonatus* subzone

Characterized by *S.* (*S.*) *umbonatus* and *S.* (*S.*) *pavlovi* Chernova (*nomen novum* for *S. umbonatus* Pavlow 1901 *non* Lahusen). Ammonites are restricted to the lower part of the subzone.

The distribution of *Simbirskites* in the Ulyanovsk section is summarized in Text-fig. 10, compiled from Chernova's (1951 : table 5; pp. 52–55) published work.

The boundary between the *versicolor* and *decheni* zones correlates with the *inversum*/*speetonensis* zonal boundary at Speeton. The Russian *inversum* subzone is represented in the lower part of the Speeton Clay *inversum* zone while the *pavlovae* subzone probably correlates with the upper part of the zone. The relative position of the Russian *versicolor* subzone is more difficult to decide; there is either a faunal break at this level at Speeton (i.e. between the *regale* and *inversum* zones) or the *versicolor* subzone is represented by part of the *regale* zone. The latter is regarded as more likely (Text-fig. 9); *Speetoniceras* probably arose in the northern seas and migrated into the Speeton seas at a later date, replacing the neocomitid fauna.

The Russian *decheni* zone is equated with the *speetonensis* to *variabilis* zones, but

SPECIES \ ZONE	*VERSICOLOR*			*DECHENI*		
SUBZONE	*VERSI-COLOR*	*INVER-SUM*	*PAVL-OVAE*	*SPEET-ONENSIS*	*DISCOF-ALCATUS*	*UMBON-ATUS*
Sp. versicolor	×	×	×			
Sp. subinversum	×	×	×			
Sp. coronatiformis	×	×	×			
Sp. inversum	-	×	×			
S. pavlovae	-	-	×			
C. phillipsi	-	-	-	×	×	
C. gottschei	-	-	-	×	×	
C. barboti	-	-	-	×	×	×
M. speetonensis	-	-	-	×		
M. concinnus	-	-	-	×		
M. lahuseni	-	-	-	×		
S. elatus	-	-	-	×		
S. decheni	-	-	-	×	×	
S. kowalewskii	-	-	-	×		
C. discofalcatus	-	-	-	-	×	×
M. progredicus	-	-	-	-	×	×
M. polivnensis	-	-	-	-	×	
S. umbonatiformis	-	-	-	-	×	
S. pseudobarboti	-	-	-	-	×	
S. umbonatus	-	-	-	-	-	×
S. yorkshirensis	-	-	-	-	-	×
S. pavlovi	-	-	-	-	-	×

FIG. 10. Distribution of species of *Simbirskites* in the Ulyanovsk (= Simbirsk) section (after Chernova 1951).

the relative position of the higher two subzones of the *decheni* zone is more difficult to establish. At this horizon there are few species in common between the two areas, though this difference may be more apparent than real, the probable similarity between the two faunas being obscured by taxonomic separation due to size differences between the large Russian forms and the small, rare Speeton individuals.

The *umbonatus* subzone is equated with the *marginatus* and *variabilis* zones at Speeton; *S.* (*S.*) *yorkshirensis* and *S.* (*C.*) *discofalcatus* are common to both areas, while the Speeton *S.* (*S.*) *marginatus* is close to (and possibly conspecific with) *S.* (*S.*) *umbonatus* and *S.* (*S.*) *pavlowi*.

This implies that the Russian *discofalcatus* subzone should be correlated with the upper part of the *gottschei* zone, i.e. with upper C4. However, *S.* (*C.*) *discofalcatus* occurs only at a much higher horizon in England—at the base of Lower B and in the Tealby Limestone of north Lincolnshire. A single, crushed *S.* (*C.*) cf. *discofalcatus* (Pl. 11, fig. 3) is known from C3 at Speeton, and this earlier record will be strengthened if the nuclei described here as *S.* (?*C.*) sp. a do eventually prove to be the earliest whorls of *S.* (*C.*) *discofalcatus*. On the other hand, *S.* (*C.*) *gottschei* occurs in the *discofalcatus* subzone in Russia. In Germany, *S.* (*C.*) *discofalcatus* probably occurs in both the *tenuis* and *strombecki* zones, and thus has a similar range to the Russian forms. If the correlations outlined above are correct, then *S.* (*C.*) *discofalcatus* should also occur in upper C4 at Speeton.

VII. THE HAUTERIVIAN-BARREMIAN BOUNDARY IN NORTH-WEST EUROPE

Faunal separation in the European Lower Cretaceous reached its peak in Hauterivian and Barremian times, the ammonite faunas of the Boreal and Tethyan Provinces being almost mutually exclusive. *Simbirskites* and, in Germany and England, crioceratitids dominated the Boreal seas during late Lower Hauterivian and Upper Hauterivian times; *Simbirskites* is represented in southern Europe by only a few stray specimens, and the Tethyan crioceratitids are specifically distinct from northern forms.

Hence direct correlation between the two provinces can only be attempted on evidence from the northern Caucasus and Crimea, where elements of the two faunas intermingle. Chernova (1951), after discussing evidence from earlier Russian works (especially Karakasch 1907), concluded that the two *Simbirskites* zones recognized in the Simbirskitid Beds of the Volga Region can be traced over the Crimea and Northern Caucasus. She equated the lower, *versicolor* zone with the *Crioceratites duvali* zone of Tethys, and the upper, *decheni* zone with the Tethyan *Subsaynella sayni* and *Pseudothurmannia angulicostata* zones. Subsequent work by Drushchitz and Kudryavtseva (1960) supports this correlation.

Chernova followed Haug (1910) in drawing the Hauterivian/Barremian boundary at the base of the *sayni* zone of the standard Tethyan sequence, and hence included the Russian *decheni* zone in the Barremian, a practice independently followed by other Russian workers. It is this which accounts for the records in Russian literature of *Simbirskites* in the Barremian. The Lyons Colloquium (Rat 1963 : Debelmas and Thieuloy 1965: Busnardo 1965) recommends that Kilian's (1910) interpretation be followed, in which the *sayni* and *angulicostata* zones are included in the Hauterivian, and the base of the Barremian is drawn at the base of the overlying *Nicklesia pulchella* zone. In Russia, Drushchitz (1962, 1964) now follows Kilian's scheme, and therefore includes the *decheni* zone in the Hauterivian. Following this correlation, the Speeton equivalents of the *decheni* zone, i.e. the *speetonensis-variabilis* zones (beds C6–LB5E) should be included in the Hauterivian, and the Hauterivian/Barremian boundary is provisionally drawn between the *variabilis* and *rarocinctum* zones. Chernova (1951 : 66) equated the top of the *decheni* zone with the *rarocinctum* or possible *fissicostatum* zone of north Germany, and Bähr provisionally drew the Hauterivian/Barremian boundary through the German *rarocinctum* zone. The same boundary is adopted here (Text-fig. 9) though German workers have customarily drawn it lower, at the base of the *strombecki* zone.

At present, the base of the Barremian in England and Germany cannot be more accurately defined; the Barremian ammonite faunas of north-west Europe consist almost exclusively of crioceratitids, specifically distinct from the rich crioceratitid faunas of the Tethyan Barremian (Sarkar 1955: Thomel 1964). In the Caucasus and Crimea the Lower Barremian faunas are essentially Tethyan, though in the Nalchik sequence of the Caucasus *Paracrioceras denckmanni* (Koenen) is recorded in association with *Costidiscus recticostatus* and other Lower Barremian Tethyan ammonites, overlying beds with *Pseudothurmannia angulicostata* and *Simbirskites* (*Craspedodiscus*) spp. (Chernova 1951 : 74). If the identification is correct it provides a useful cross-check, for *P. denckmanni* is the index fossil for the zone above the *fissicostatum* zone in north Germany.

Thus all the available evidence shows that *Simbirskites*, the last representative of the Perisphinctaceae, is a useful zonal form in the north European Hauterivian and dies out at the end of the Hauterivian.

VIII. ZUSAMMENFASSUNG

Die Ammonitengattung *Simbirskites* charakterisiert Schichten des Hauteriviums der borealen Provinz und stellt brauchbare Zonen-Leitfossilien in Rußland, Norddeutschland und NE-England. Sie tritt in England in der C7–LB5-Folge des Speeton Tons (Yorkshire) sowie im Unteren Tealby Ton und im Tealby Kalkstein (Lincolnshire) auf. Die Stratigraphie dieser Schichtenfolge wird hier erläutert. Dabei werden 21 *Simbirskites*-Arten beschrieben. Zwei davon sind neu: *S.* (*C.*) *juddi* und *S.* (*C.*) *variabilis*. Vierzehn werden bekannten Arten zugeordnet oder mit ihnen verglichen und fünf in offener Nomenklatur behandelt. Einige der Arten wurden zuerst aus Rußland oder Norddeutschland beschrieben. Von den deutschen Arten werden Topotypen des nur wenig bekannten *S.* (*M.*) *lippiacus*

(Weerth) aus dem Osningsandstein vom Tönsberg abgebildet. Ferner wird die problematische Interpretation von *S.* (*C.*) *phillipsi* (Roemer) und *S.* (*S.*) *decheni* (Roemer) ausführlich diskutiert.

Als Ergebnis einer sorgfältigen, horizontierten Absammlung der Speeton-Folge ist eine Unterteilung der Simbirskiten-Schichten in Yorkshire nach *Simbirskites*-Arten in fünf Zonen möglich. Weiterhin erlaubt die bei Speeton ermittelte Faunenfolge einen detaillierten Vergleich dieser Schichten mit den entsprechenden Ablagerungen in Norddeutschland und Rußland. Der in Norddeutschland zur Zeit üblichen Zonengliederung, die auf Arbeiten von Koenen und Stolley zurückgeht, liegen in erster Linie crioceratitische Ammoniten zu Grunde. Die meisten dieser vermeintlichen Zonenleitfossilien sind aber sehr selten. Vertreter der Gattung *Simbirskites* sind dagegen häufiger, so daß es empfehlenswert erscheint, *Simbirskites*-Arten als Leitfossilien auch in Norddeutschland heranzuziehen. Vermutlich kann die bei Speeton ermittelte Gliederung mit geringen Einschränkungen auch in Norddeutschland verwendet werden. Die russischen Simbirskiten-Schichten sind in eine Serie von Zonen und Subzonen gegliedert worden (Pavlow 1901, Chernova 1951), die enge Vergleiche mit der Schichtenfolge Yorkshires gestatten.

Das Auftreten von gemischten Faunen aus borealen und Tethys-Elementen im Nordkaukasus und auf der Krim erlaubt die Anknüpfung der borealen Zonenfolge an die Standard-Gliederung des Hauteriviums im Tethys-Raum (Text-fig. 9). Dabei ergibt sich, daß die Grenze Hauterivium/Barremium innerhalb der *rarocinctum*-Zone Norddeutschlands (Bähr, unveröffentlichte Dissertation) und an der Basis der *rarocinctum*-Zone von Speeton verläuft.

I thank Dr. E. Kemper for this translation.

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ADDENDUM

Since this paper was written, two points have been drawn to my attention. In June 1970 Dr. Kemper informed me that renewed search at Detmold, by members of the Geologisches Landesamt Nordrhein-Westfalen, has successfully resulted in the discovery of Weerth's collection, hitherto believed lost. Dr. Kemper has subsequently (on 10 November 1970) seen the collection and recognized several type specimens of *Simbirskites*, though the majority appear to be lost. The collection does, however, include other specimens which were apparently collected after Weerth's paper was published in 1884.

In a recent paper by Hiltermann and Kemper (1969) the occurrence of *Simbirskites* in the Heligoland Hauterivian is reviewed. Four species are figured: *Simbirskites (Speetoniceras) versicolor* (Trautschold), *S.* (*Sp.*) cf. *inversum* (M. Pavlow), *S.* (*Cras-*

pedodiscus) juv. sp., and *S.* (*C.*) *carinatus* Koenen. The two figured *Speetoniceras* closely resemble Speeton examples of the same species. The figured *S.* (*C.*) *carinatus* are similar in lateral view to the Speeton form which I figure (Pl. 5, fig. 2) as *S.* (*C.*) sp. (*phillipsi* group). Hiltermann and Kemper (p. 22, footnote) consider it possible that *S.* (*C.*) *carinatus* could be the juvenile stage of *S.* (*C.*) *phillipsi* (Roemer).

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PLATES

The photographs are by Mr. B. Samuels, of Queen Mary College, except Plate 1 figure 4 by the author.

All specimens have been coated with ammonium chloride.

The figures are natural size, unless otherwise stated.

PLATE 1

FIG. 1. ***Simbirskites (Speetoniceras) inversum*** (M. Pavlow). Bed C7, Speeton, collected by Mr. R. G. Clements. BM. C.75622.

FIG. 2. ***Simbirskites (Speetoniceras) subbipliciforme*** (Spath). Holotype. "Bed C7 or C8," Speeton. Danford collection, GSM. 17930.

FIG. 3. ***Simbirskites (Speetoniceras) inversum*** (M. Pavlow). Bed C7H, Speeton. BM. C.75625.

FIG. 4. ***Simbirskites (Speetoniceras) inversum*** (M. Pavlow). *Versicolor* zone, Ulyanovsk (Simbirsk), Russia. Kabanov collection, 1364.

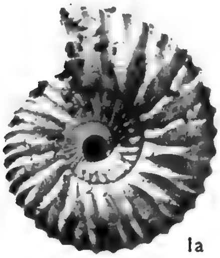
FIG. 5. ***Simbirskites (Speetoniceras) subbipliciforme*** (Spath). Bed C7H, Speeton. BM. C.75620.

FIGS 6, 7. ***Simbirskites (Speetoniceras) inversum*** (M. Pavlow). Fig. 6. Bed C7H, Speeton. BM. C.75626. Fig. 7. Bed C7G, Speeton. BM. C.75623.

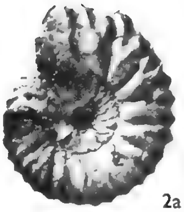
FIG. 8. ***Simbirskites (Speetoniceras)*** cf. ***versicolor*** (Trautschold). Lower C Beds, Speeton. BM. C.75647.

FIG. 9. ***Simbirskites (Speetoniceras) inversum*** (M. Pavlow). Bed C7H, Speeton. BM. C.75627.

FIG. 10. ***Simbirskites (Speetoniceras)*** sp. Bed C7F, pale blue clay just above the *Aegocrioceras* nodule band. BM. C.75648.


1a


1b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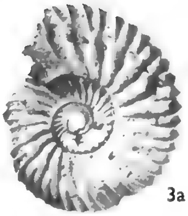
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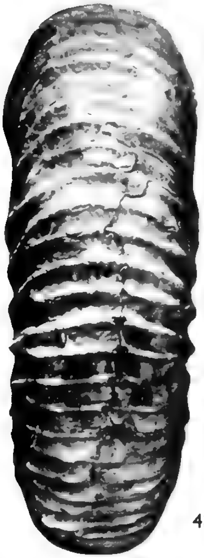
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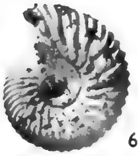
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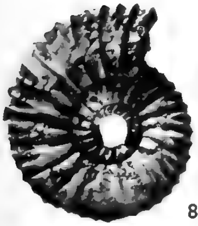
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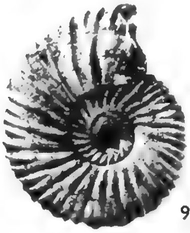
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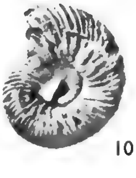
10

PLATE 2

FIG. 1. ***Simbirskites (Speetoniceras) inversum*** (M. Pavlow). Bed C7H, Speeton. BM. C.75624.

FIGS 2–6. ***Simbirskites (Milanowskia) concinnus*** (Phillips). Figs 2, 3. Bed C6, Speeton, approx. 0·76 metres above base, BM. C.75708 and C.75706. Fig. 4. Bed C6 Speeton, GSM.30582. Fig. 5. Upper part of the *capricornu* zone, Sarstedt, north Germany. BM. C.75711. Fig. 6. Partly crushed specimen from Bed C6, Speeton, BM. C.75852.

FIG. 7. ***Simbirskites (Milanowskia) speetonensis*** (Young & Bird). Bed C6, Speeton, approx. 1·5 metres below top. BM. C.75847.

FIG. 8. ***Simbirskites (Milanowskia) concinnus*** (Phillips). Bed C6, Speeton, approx. 0·6 metres above base. BM. C.75695.

FIGS 9—11. ***Simbirskites (Milanowskia) speetonensis*** (Young & Bird). Fig. 9. Mid C, Speeton, Wrights' colln. 18670. Fig. 10. C6 Speeton, 5 cm below top, BM. C.75850. Fig. 11. C6, Speeton, HU. Neale colln. 1701.

FIGS 12, 13. ***Simbirskites (Milanowskia)*** sp. Fig. 12. "C6", Speeton, Danford collection, GSM. 17923 (figd Danford 1906 as *S. progredicus*). Fig. 13. C Beds, Speeton, BM. C.75714.

FIG. 14. ***Simbirskites (Milanowskia) staffi*** Wedekind. Upper part of *capricornu* zone, Fümmelse, near Wolfenbüttel, north Germany. BM. C.38369.

FIG. 15. ***Simbirskites (Milanowskia) speetonensis*** (Young & Bird). C Beds, Speeton. Danford colln., GSM. 17919 (figd Danford 1906 as *S. payeri*).

FIG. 16. ***Simbirskites (Milanowskia) staffi*** Wedekind. C Beds, Speeton (found loose on cliff face). BM. C.75713, collected by Mr. R. Hinton.


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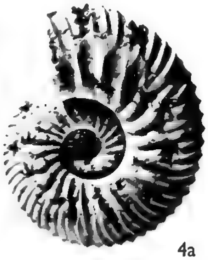
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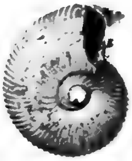
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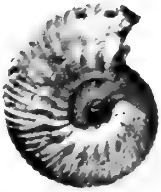
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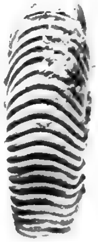
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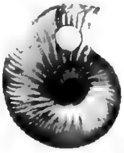
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PLATE 3

FIG. 1. ***Simbirskites (Milanowskia) staffi*** Wedekind. Upper *capricornu* zone? Stöcken, near Hannover. NLfB. Orig. Nr. Kp.37.

FIG. 2. ***Simbirskites (Milanowskia) lippiacus*** (Weerth). Topotype, Osning Sandstone, Tönsberg, near Oerlinghausen, north Germany. Göttingen, (Weerth collection). Orig. nr. 609–2.

FIG. 3. ***Simbirskites (Milanowskia)*** cf. ***lippiacus*** (Weerth). Upper C Beds, Speeton. Danford colln., GSM. 17542.

FIG. 4. ***Simbirskites (Milanowskia) staffi*** Wedekind. Bed C6, Speeton, 0·6 metres above base. BM. C.75712.

FIG. 5. ***Simbirskites (Milanowskia) lippiacus*** (Weerth). Topotype, Osning Sandstone, Tönsberg, near Oerlinghausen, north Germany. Göttingen, (Weerth colln.). Orig. nr. 457–125.

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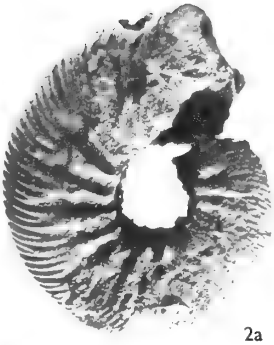

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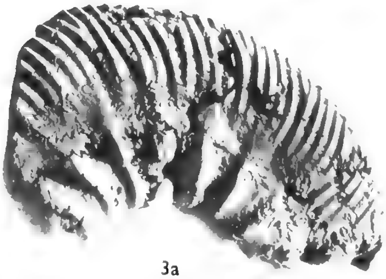

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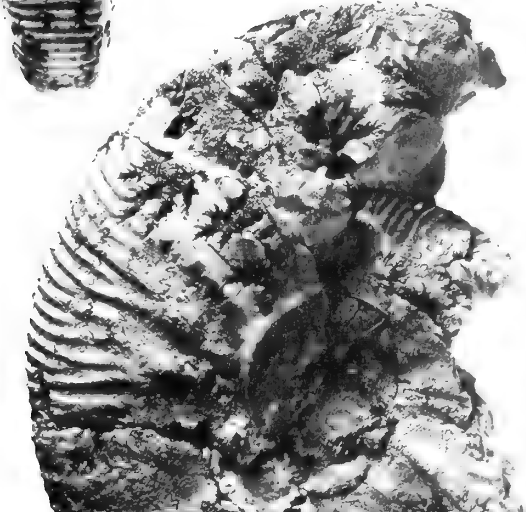

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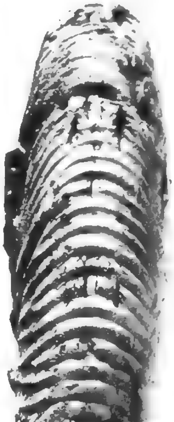


5b

PLATE 4

FIG. 1. ***Simbirskites (Craspedodiscus) variabilis*** sp. nov. Paratype. Speeton Clay, Bean colln., BM. C.4649.

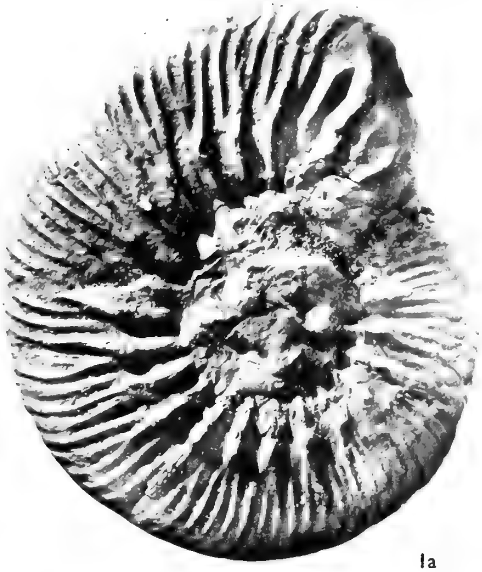
FIG. 2. ***Simbirskites (Craspedodiscus) gottschei*** (Koenen). C Beds, Speeton. BM. C.4704.

FIG. 3. ***Simbirskites (Craspedodiscus) variabilis*** sp. nov. Holotype. Bed LB6, Speeton. a, b natural mould of body chamber, c latex cast of earlier whorls of same specimen. HU. Rn.700.

FIG. 4. ***Simbirskites (Craspedodiscus) gottschei*** (Koenen). C4 (?), Speeton. Inner whorls (× 1) of specimen figured on Plate 5, fig. 1. Wrights' colln. 24375.

FIG. 5. ***Simbirskites (Craspedodiscus) gottschei*** (Koenen). Bed C4L, Speeton. BM. C.75717.

FIG. 6. ***Simbirskites (Craspedodiscus) variabilis*** sp. nov. Paratype. Bed C2C, Speeton. BM. C.75853.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4b


3a


3b


4a


5a


5b


6a


6b


3c

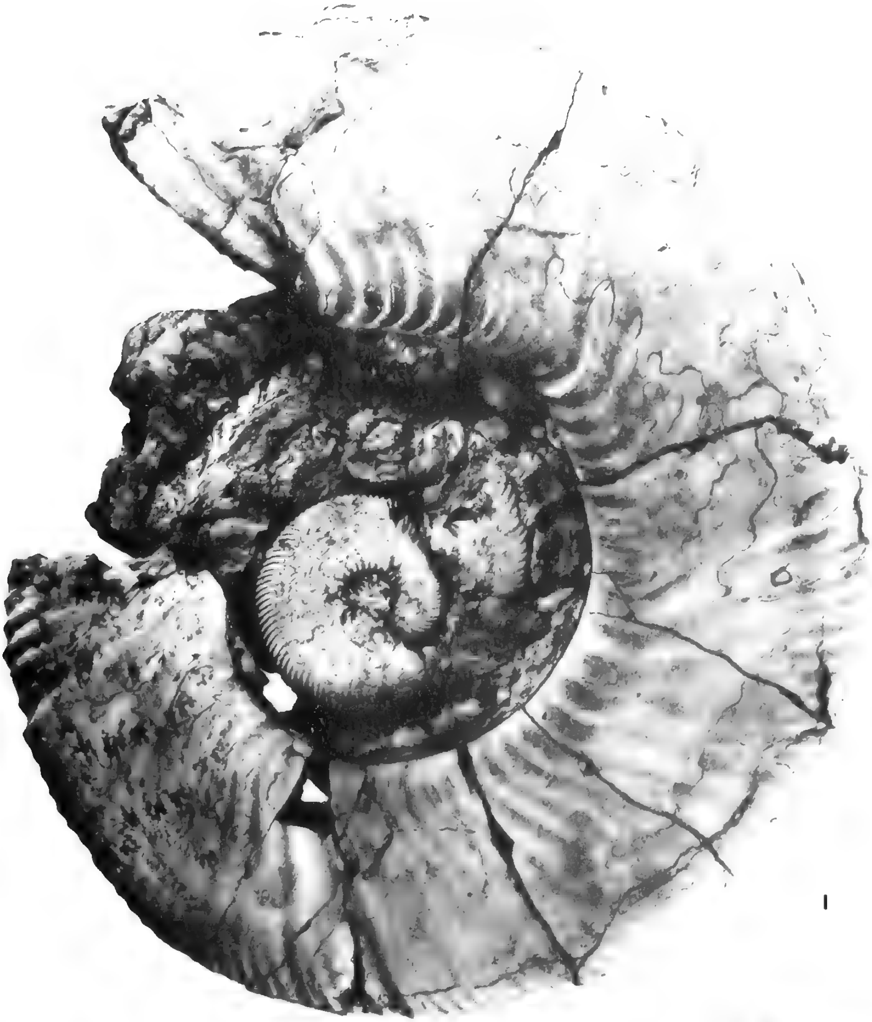
PLATE 5

FIG. 1. ***Simbirskites (Craspedodiscus) gottschei*** (Koenen). Bed C4 (?), Speeton. Body chamber and septate inner whorls (see plate 4, fig. 4). Wrights' colln. 24375, ×0·75.

FIG. 2. ***Simbirskites (Craspedodiscus)*** sp. ***(phillipsi*** group). Bed C2B (base), Speeton. Latex cast from external mould. BM. C.75882.

FIG. 3. ***Simbirskites (Craspedodiscus) variabilis*** sp. nov. Paratype. Bed C2C, Speeton. BM. C.75857. × 2.

FIG. 4. ***Simbirskites (Craspedodiscus) variabilis*** sp. nov. Paratype. Bed LB6, Speeton. Latex cast of penultimate whorl of a specimen in the Neale collection (Hull University), no. 1901.



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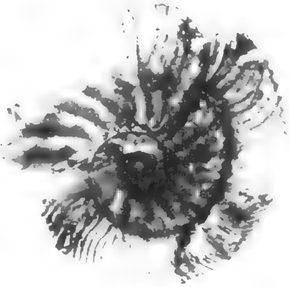
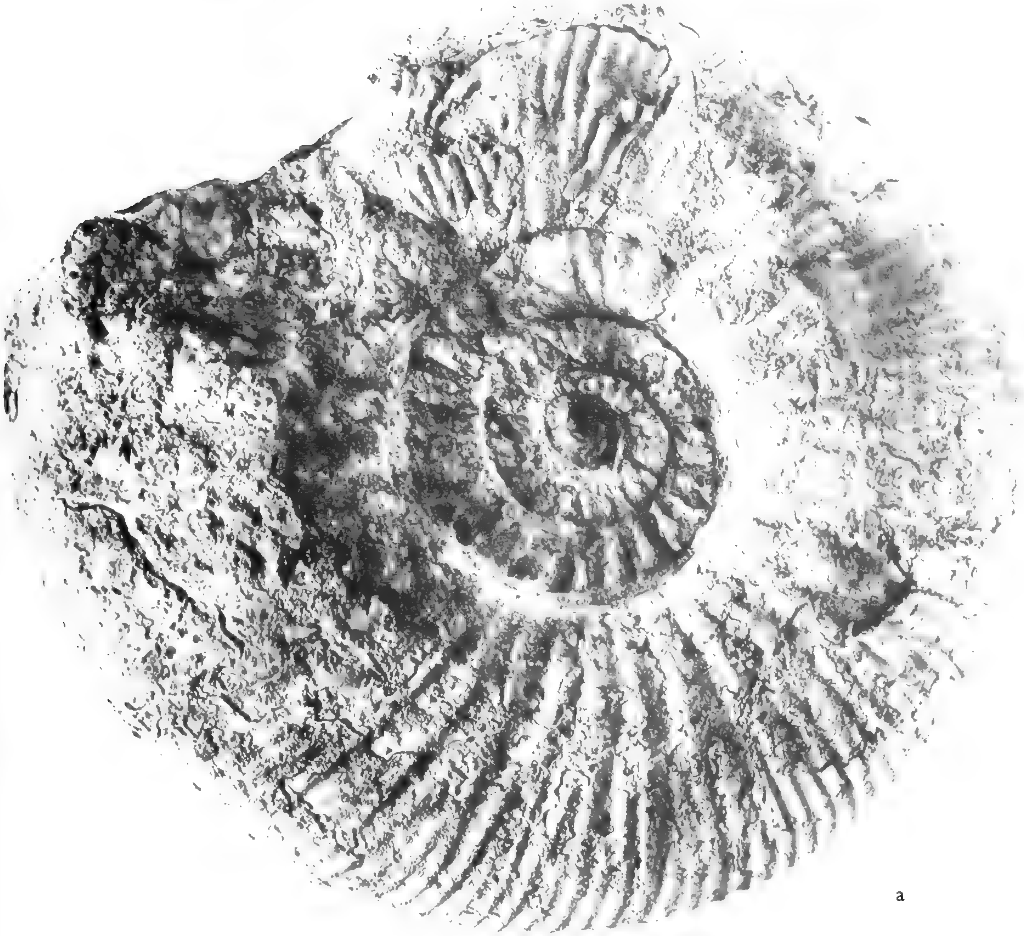


4

PLATE 6

Simbirskites (?Craspedodiscus) sp. b. Tealby Limestone, North Lincolnshire (Tealby?). GSM.47071, presented by J. W. Judd, 1867. × 0·7.

b



a

PLATE 7

Simbirskites (Craspedodiscus) discofalcatus (Lahusen). Tealby Limestone, Normanby. BM. C.73377, presented by J. E. Lee, 1885. × 0·64.


b

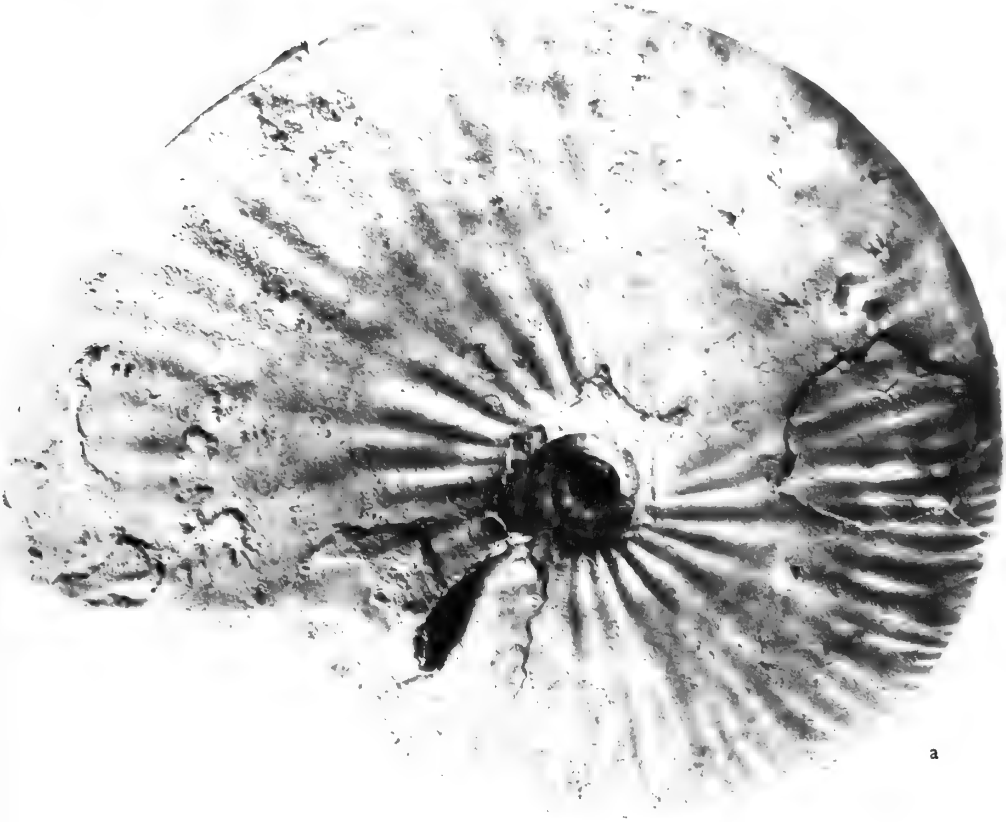

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PLATE 8

Simbirskites (Craspedodiscus) discofalcatus (Lahusen). Tealby Limestone, North Willingham. BM. C. 19993, presented by P. F. Kendall, 1919. × 0·62.

b

a

PLATE 9

FIG. 1. ***Simbirskites (Craspedodiscus) discofalcatus*** (Lahusen). Tealby Limestone, Normanby. BM. C.73376, presented by J. E. Lee, 1885. × 0·72.

FIG. 2. ***Simbirskites (Craspedodiscus) discofalcatus*** (Lahusen). Speeton Clay, Speeton. York Museum, labelled "*Ammonites yo*? Kimmeridge Clay, Speeton". × 0·72.

FIG. 3. ***Simbirskites (Craspedodiscus) phillipsi*** (Roemer *sensu* Weerth). Osning Sandstone, Tönsberg, near Oerlinghausen, north Germany. Göttingen, Orig. nr. 457–124 presented by O. Weerth, 1897. × 0·72.


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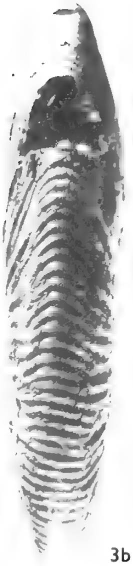
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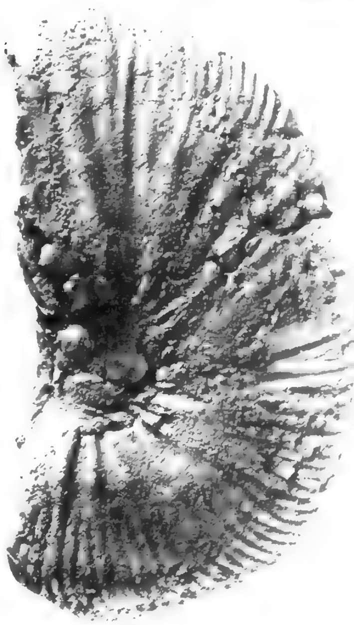
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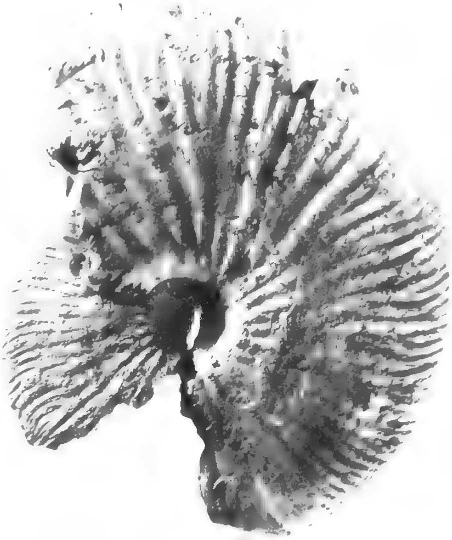
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PLATE 10

FIG. 1. ***Simbirskites (Craspedodiscus) juddi*** sp. nov. Holotype. Tealby Limestone, Tealby. GSM. 31059, presented by J. W. Judd, 1867. × 0·75.

FIG. 2. ***Simbirskites (Craspedodiscus) juddi*** sp. nov. Paratype. Tealby Limestone, Normanby. BM. C.73375, presented by J. E. Lee, 1885. × 0·75.

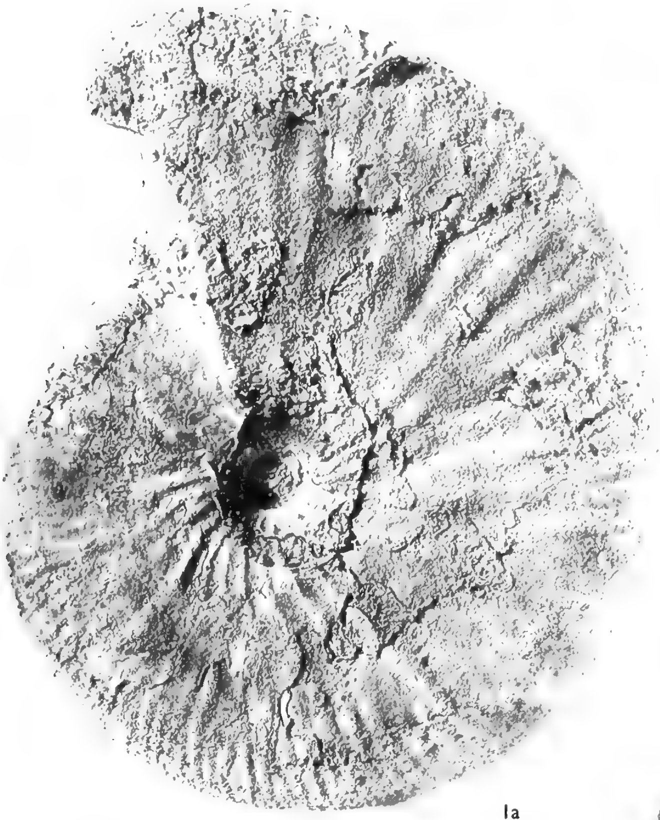

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PLATE 11

FIG. 1. ***Simbirskites (?Craspedodiscus)*** sp. a. Bed C3, Speeton. BM. C. 75862 × **2.**

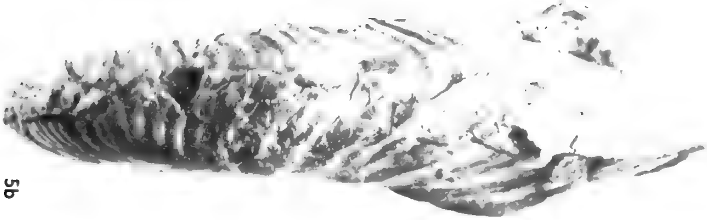
FIG. 2. ***Simbirskites (Craspedodiscus)*** cf. ***discofalcatus*** (Lahusen). Speeton, originally figd. by Danford (1906). GSM. 17922.

FIG. 3. ***Simbirskites (Craspedodiscus)*** cf. ***discofalcatus*** (Lahusen). Bed C3, Speeton. BM. C.72641 (Lamplugh colln.).

FIG. 4. ***Simbirskites (Milanowskia) speetonensis*** (Young & Bird). *Decheni* zone, Ulyanovsk (formerly Simbirsk), Russia. Göttingen, Orig. nr. 609–1, presented by A. P. Pavlow, 1902.

FIG. 5. ***Simbirskites (Craspedodiscus) discofalcatus*** (Lahusen). *Decheni* zone, Ulyanovsk (formerly Simbirsk), Russia. BM. C.5 (Damon colln.).

FIG. 6. ***Simbirskites (Simbirskites) decheni*** (Roemer) *sensu* Wedekind. "*Simbirskites* zone" (upper *capricornu* zone?), Ihme, near Hannover, north Germany. BM. C.14419.



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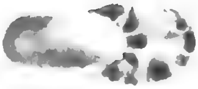

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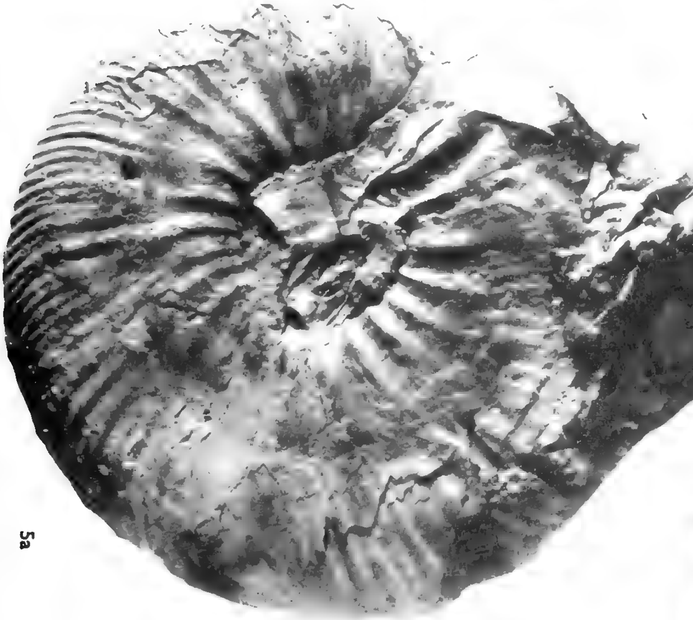

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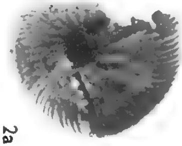

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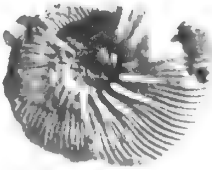

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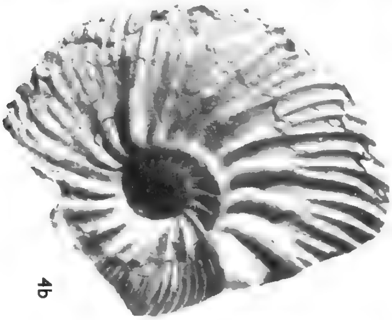

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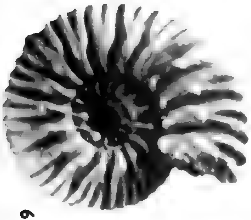

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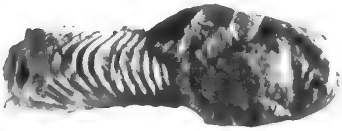


4c

PLATE 12

FIG. 1. **Simbirskites (Simbirskites)** cf. **decheni** (Roemer) var. a. Bed C6, Speeton, approx. 0·76 metres above base. BM. C.75887.

FIG. 2. **Simbirskites (Simbirskites) yorkshirensis** Chernova. Upper C Beds, Speeton, collected by Mr. M. Thompson. BM. C.75885.

FIG. 3. **Simbirskites (Simbirskites)** cf. **decheni** (Roemer) var. a. C Beds, Speeton, collected by Mr. D. Ward. BM. C.75568.

FIG. 4. **Simbirskites (Simbirskites)** cf. **decheni** (Roemer) var. a. Bed C6, Speeton, approx. 0·76 metres above base. BM. C.75889.

FIG. 5. **Simbirskites (Simbirskites) yorkshirensis** Chernova. Upper C Beds (C4 ?), Speeton. Wrights' colln., 24284.

FIG. 6. **Simbirskites (Simbirskites)** cf. **decheni** (Roemer) var. c. C Beds, Speeton. BM. C.72632 (Lamplugh colln.).

FIG. 7. **Simbirskites (Simbirskites) yorkshirensis** Chernova. Bed C2C, Speeton. BM. C.75884.

FIGS 8, 9. **Simbirskites (Simbirskites)** cf. **decheni** (Roemer) var. b. Fig. 8. probably C6, Speeton, Wrights' colln. 17593. Fig. 9. C6, Speeton, 0·76 metres above base, BM. C.75890. × 2.

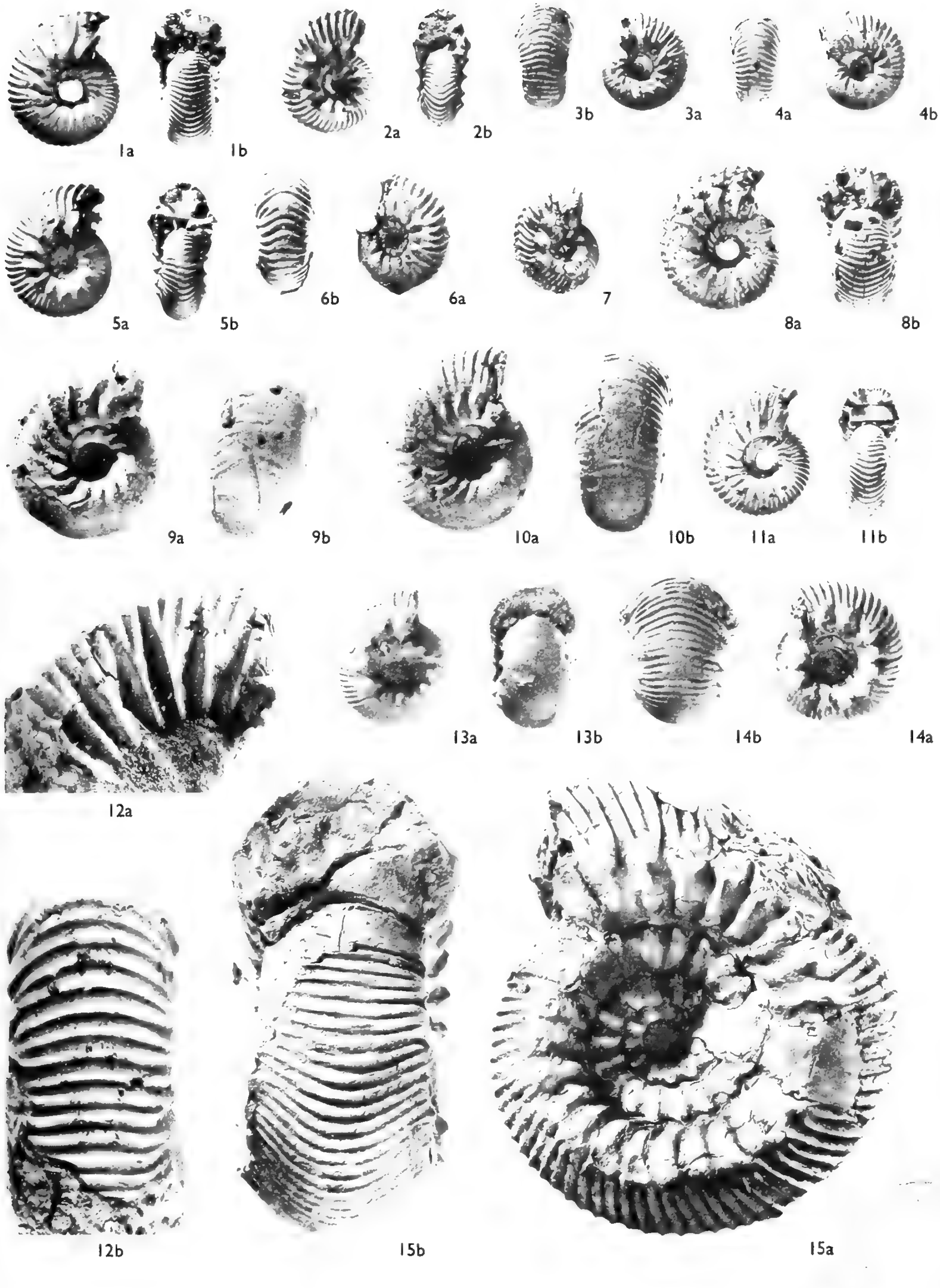
FIG. 10. **Simbirskites (Simbirskites)** cf. **decheni** (Roemer) var. a. Bed C6, Speeton, 0·76 metres above base. BM. C.75888. × 2.

FIG. 11. **Simbirskites (Milanowskia) concinnus** (Phillips). Bed C6, Speeton, 0·76 metres above base. BM. C. 75893.

FIG. 12. **Simbirskites (Simbirskites)** cf. **virgifer** (Neumayr & Uhlig). Lower Tealby Clay or Tealby Limestone, Nettleton. HU. Rn.923, collected by Mr. D. Sowter.

FIGS 13, 14. **Simbirskites (Simbirskites) marginatus** (Phillips). Fig. 13. Holotype, Speeton Clay Speeton, YM. tablet 414. Fig. 14. Bed C3 (upper part), Speeton. BM. C.75874. Both figs × 2.

FIG. 15. **Simbirskites (Simbirskites) umbonatus** (Lahusen). *Decheni* zone, Ulyanovsk (formerly Simbirsk), Russia. BM. C.17 (Damon colln.).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W. A. CLEMENS
AND
J. R. E. MILLS

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GEOLOGY Vol. 20 No. 3
LONDON : 1971

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AND

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Pp. 87–113; 4 *Plates*; 3 *Text-figures*

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REVIEW OF *PERAMUS TENUIROSTRIS* OWEN (EUPANTOTHERIA, MAMMALIA)

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CONTENTS

SYNOPSIS

Review of *Peramus tenuirostris* Owen (Eupantotheria, Peramuridae) was occasioned by the discovery of a fragmentary maxilla, B.M.(N.H.) M21887, containing part of the hitherto undescribed upper dentition. M^2 and M^3 of this fossil have large paracones and metacones, small stylocones, and lingual cingula but lack distinct protocones. M^1 lacks a stylocone and the metacone does not have the typical tribosphenic functions. A lingual cingulum is not developed. The four premolars are two-rooted and have trenchant crowns. M^4, the terminal molar, was destroyed during fossilization. G. G. Simpson's (1928) catalogue and description of the mandible of *Peramus* are revised.

Peramus probably is a descendant of the Rhaetic mammal *Kuehneotherium*, but *Amphitherium* is not one of the members of this lineage. *Aegialodon* from the English Wealden could be a descendant of *Peramus*. *Pappotherium* and *Holoclemensia* from the Albian, Trinity Sands of North America probably include a peramurid other than *Peramus* in their late Jurassic ancestry.

I. INTRODUCTION AND ACKNOWLEDGMENTS

The entire sample of *Peramus tenuirostris* Owen, family Peramuridae, is now preserved in the collections of the Department of Palaeontology, British Museum (Natural History). All these fossils are part of the S. H. Beckles collection from Purbeckian strata exposed at Durlston Bay, Dorset. Since publication of G. G. Simpson's catalogue (1928) the sample has been significantly augmented in both size and scientific value. In this paper his catalogue is brought up to date, two specimens of *Peramus tenuirostris* that recently have been thoroughly prepared are described, and some interpretations of dental function and phylogenetic relationships of the genus are presented.

Several years ago while studying the collections of Purbeckian reptiles in the British Museum (Natural History), Dr. Robert Hoffstetter (1967) found four partially prepared fossils from the Mammal Bed that he suspected to be mammalian remains. Additional preparation verified his suspicions. One of these is a mandible, M21885, containing an incisor, a larger tooth of caniniform morphology, and fragments of postcanine teeth. This fossil, which was formerly catalogued under number 48255, is certainly part of the lower jaw of a mammal, but a more specific identification cannot be made. Three mammalian fossils were found in a group of specimens numbered 48407. One, M21886, is a fragment of mandible containing two molars that is now identified as *Amblotherium* sp. The second, M21887, is the fragment of maxilla of *Peramus tenuirostris* described subsequently. The third, M21888, is a fragmentary mandible of *P. tenuirostris* that has been described elsewhere (Mills 1964).

The research reported here reflects the encouragement and help of a large number of colleagues. Dr. Errol I. White, former Keeper of the Department of Palaeontology, and Dr. A. J. Sutcliffe initially suggested that the sample of *Peramus tenuirostris* be restudied and made the material available. They and Dr. H. W. Ball, Keeper of Palaeontology, have supported this study in a variety of significant ways. Their contributions are gratefully acknowledged.

As the specimens of *Peramus* were prepared and became available for study, they have been seen by many palaeontologists. A paper including a description of M21888 has been published (Mills 1964). Drs. K. A. Kermack and J. R. E. Mills started to prepare a report on the maxilla, M21887, but the press of other responsibilities kept it from completion. When a Natural Science Foundation Postdoctoral Fellowship made it possible for W. A. Clemens to return to England, he was invited to take part in the study. Dr. Kermack withdrew, however he not only made his preliminary notes and photographs available, but also Prof. M. Abercrombie and he provided research facilities in the Department of Zoology, University College, London.

The conclusions presented here embody the results of interchanges of ideas with many other palaeontologists. Although not committing them to the interpretations given subsequently, we wish to acknowledge the valuable, long discussions with Prof. P. M. Butler, Prof. A. W. Crompton, Dr. K. A. Kermack, Dr. B. Krebs, Prof. A. W. Kühne and Mrs. Frances Mussett that have played an important part in their formation.

The fossils described here were skilfully released from the rock by Mr. Arthur Rixon whose deft preparation has added greatly to the value of the collections of *Peramus* and other British Mesozoic mammals. Text-fig. 1 and the plates are the work of Mr. A. J. Lee. The cost of preparation of these illustrations was met through a grant from the Museum of Paleontology, University of California, Berkeley.

II. TAXONOMY AND MATERIAL

The synonymies of *Peramus tenuirostris* Owen given by Simpson (1928, p. 121) have not been modified. The following additions are made to his catalogue of material (*ibid.*, pp. 121–122):

47742.	None [Holotype].
47739.	Removed from rock and cleaned by A. Rixon in 1968; redescribed here.
47744.	Removed from rock and cleaned by A. Rixon in 1962; described by J. R. E. Mills (1964).
47751.	None.
47754.	None.
47799.	None.
48404.	Removed from rock and cleaned by A. Rixon in 1962; described by J. R. E. Mills (1964).
M21887.	Left maxilla with eight fragmentary postcanine teeth. Removed from rock and cleaned by A. Rixon in 1961; described here.
M21888.	Right mandible with M_3, trigonid of M_4 and fragments of P_3 through M_2. Removed from rock and cleaned by A. Rixon in 1962; described by J. R. E. Mills (1964).

As far as can be determined from the records all these fossils came from the Mammal Bed, one of the units of the Purbeck beds exposed in the cliffs at Durlston (=Durdlestone) Bay. The Mammal Bed is stratigraphically below the Cinder Bed and part of the Lulworth Beds (Casey, 1963). Problems of determination of the age of the Lulworth Beds have been reviewed by Dodson *et al.* (1964). Because the Purbeckian mammals have long been described as being of late Jurassic age and a change in terminology to reflect the disparity of standards has no apparent value in the context of this paper, the Boreal standard for the Jurassic–Cretaceous boundary and a late Jurassic age for the Purbeckian mammals are employed. Purbeckian is used in the sense suggested in the report by Ager (1963), ". . . not a stage but a facies, predominantly fresh-water and continental . . .".

III. DESCRIPTIONS AND INTRAGENERIC COMPARISONS

a. *Maxilla*, B.M.(N.H.) M21887

In addition to lateral displacement, the fossil (Pls 1 and 2) was distorted by pressure from a posterior direction that crushed or severely damaged the distal three molars. A groove along its dorsal edge above these molars (Pl. 1, fig. 1) might mark the course of a maxilla-jugal suture. Otherwise no clear evidence of bones other than the maxilla was found in M21887. An anteroposteriorly elongated trench dorsal to P^4 and M^1 probably marks the course of a collapsed infraorbital canal with its foramen dorsal to P^3 and P^4.

Eight teeth in various states of preservation are present. Part of the root of a tooth immediately mesial to the first preserved premolar (Pl. 1, fig. 1) shows these teeth were not separated by a long diastem. The lingual and distal sides of the alveolus of this more mesial tooth and the fragment of its root suggest the tooth was large, single-rooted, and caniniform. Curvature of the maxilla and absence of evidence of alveoli suggests the dentition lacked additional distal elements. Thus the fossil probably contains the remains of the entire postcanine dentition. The postcanine dental formula proposed by Simpson (1928) for the lower dentition of *Peramus*, four premolars and four molars, is adopted here.

All premolars are two rooted and their crowns have a basic trenchant morphology. The crown of P^1 is broken from its roots and displaced buccally. Its apex is slightly in advance of the center of the crown. No evidence of basal accessory cusps or cingula was found.

The crown of P^2 is displaced buccally and slightly mesially to overlap the distal end of P^1. Unlike P^1, the fracture is closer to the apex of the crown and cuts across the region where basal cusps or cingula would be expected. Probably a small posterior basal cusp was present and its remains are not now clearly distinguishable among the fragments along the zone of fracture. However, the step on the distal margin of P^2 might only be an artifact of mesial displacement of the crown. Otherwise no evidence signals the presence of basal cusps or cingula. P^2 has the appearance of being slightly smaller than P^1 but damage at the crown's base prevents accurate measurement of comparable dimensions.

The position of their roots suggests P^{1-2} were not separated by a diastem. A major fracture zone crosses the fossil posterior to P^2. Movement associated with this fracturing displaced the anterior part of the maxilla posteroventrally with a slight rotation and depression of its anterior end. Before distortion P^2 and P^3 were separated by a small diastem of about the same length as that separating P^3 and P^4.

Although the mode of preservation has muted textural and colour differences between enamel and dentine, the absence of a vitreous surface layer, discernable on other teeth, indicates that enamel has been lost from large parts of the dorsal two-thirds of the crown of P^3. At least a small, posterior basal cusp was present. The roots of P^3, which form an angle of approximately 45 degrees, appear to be much more widely divergent than those of the other premolars. Perhaps the tooth here designated P^3 is a deciduous premolar.

The bone forming the surface of the diastem between P^3 and P^4 is deeply pocketed (Pl. 1, fig. 2). The palatal process of the maxilla is broken and distorted in this region. The pit might be an artifact, but this appears unlikely.

In length and height of crown P^4 is distinctly larger than the other premolars. A nearly horizontal fracture cuts the mesial half of the crown near its base. Loss of enamel along this fracture accentuates the anterior basal cingulum (Pls 1 and 2). The apex of the main cusp is slightly in advance of the midpoint of the crown. Its mesial surface lacks a vertical ridge. Distally a prominent ridge extends from the apex toward the disto-lingual basal cusp. They are separated by only a small notch. Buccal to this ridge the surface of the main cusp is either flat or slightly depressed. A second distal basal cusp of slightly smaller size and more mesial position is situated buccal to the first. A small cingulum extends forward a short distance mesially from the disto-lingual basal cusp. Otherwise the tooth lacks lingual or labial basal cingula.

M^1 is two rooted, the distal root is larger and slightly wider transversely. A high paracone, which is now fractured and displaced at two levels, dominates the crown.

Low on its distal surface is a second major cusp. Identification of this cusp is discussed subsequently (p. 103). M^1 has been moved lingually and mesially, and its mesio-buccal corner damaged. What remains indicates only one small cusp was present. Certainly this part of the crown did not overlap the buccal side of the distal end of P^4. The crest along the mesial edge of the paracone might not have reached the mesio-buccal cusp. Irregularities of the crown's damaged surface suggest the crest was deflected disto-buccally. If it was, this disposition of the crest suggests the mesiobuccal cusp is a parastyle and not a stylocone.

On the lingual surface of M^1, just ventral to the alveolar margin, are vestiges of a narrow cingulum. Mesio-lingually it is represented by a relatively broad shelf carrying two distinct cusps of which the more lingual is also the more dorsally placed. Distally, across the middle of the crown, the cingulum is virtually obsolete being represented only by a line marking an abrupt change in the slope of the lingual surface. On this line are two isolated cusplike expansions. On the most distal quarter of the crown the cingulum again becomes distinct. In this region it curves ventrally to reach a small cusp which lies adjacent to the large cusp at the distal end of the crown. Mesio-bucally from the latter are two stylar cusps. The stylar shelf is continued mesially by a narrow cingulum.

Most of the parastylar region of M^2 is missing, however enough remains to show it was large and overlapped the distal end of M^1. Several approximately horizontal fractures pass through the crown of M^2 but little displacement occurred along most of them. The crown of M^3, acting as a wedge, was driven dorsal to that of M^2 pushing it ventrally and rotating its base distally. Distal displacement appears to be minor and the angle of the embrasure between M^1 and M^2 not greatly distorted. In contrast, the distal lobe of the stylar shelf of M^2 was crushed against the crown of M^3.

From the high paracone of M^2 a ridge sweeps mesio-buccally to a small cusp, the stylocone, immediately adjacent to the missing parastylar region (Pl. 1, fig. 2, and Pl. 2, fig. 2). Two small cuspules are present on what remains of the buccal edge of the anterior lobe of the stylar shelf. The small stylocone is undamaged by post mortem fracturing and can only have been slightly blunted by wear. A short ridge extends mesially from its base. Directly mesial to the ridge linking the stylocone and paracone the crown is gently rounded, not a vertical wall.

Dorsally, near the lingual base of the crown, three cuspules are imperfectly linked to form a cingulum-like ledge (Pl. 2). The metacone of M^2 is high on the side of the paracone. Their common base is separated from the distal lobe of the stylar shelf by a diagonal linear depression, now the locus of a major fracture. Mesial to the paracone of M^3 the crown of M^2 is heavily crushed. The shards remaining are sufficient to be the residue of a cusp the size of that in the comparable position on M^3. Buccal to this crushed area part of the crown of M^2 remains intact but displaced. From a small cusp near the disto-buccal corner a ridge extends toward the crushed area. A groove mesio-buccal to this cusp separates it from what appears to be the remains of one or two smaller cusps. M^2 is supported by three roots of approximately equal size.

Part of the parastylar region of M^3 is also missing but, in comparison to M^2, the fracture is more vertically oriented and situated farther buccally. It cuts through a cusp, possibly the parastyle, on the buccal side of the crown. A ridge from the stylocone extends disto-buccally toward the edge of the crown but reaches neither the parastylar cusp nor the more distal, small marginal stylar cusps. Relative to this section of the crown the paracone and metacone are displaced mesially. These cusps do not differ in size or position from those of M^2. Although now offset, a low ridge, paracrista, connected the paracone and stylocone.

On the lingual surface of the crown a short, narrow cingulum shows no evidence of subdivision into cusps (Pl. 2). This part of the tooth suffered some damage and is partly obscured by the remains of M^4. Clearly both mesially and lingually no pieces of the crown of M^3 are missing and, except for possible slight distortion or post mortem abrasion, the original shape of the crown and its lingual cingulum is preserved. Distolingually some enamel is missing. Loss of these chips carried away that part of the distal limb of the cingulum not covered by M^4. The curvature of adjacent enamel surfaces does not suggest, but cannot rule out, greater transverse width of the distal part of the lingual cingulum. Probably three roots are present, but they are not clearly visible.

Like M^2, a fracture follows the depression between the common base of paracone and metacone of M^3 and the distal lobe of the stylar shelf, but the latter area is not as heavily damaged. Three cusps are present on this lobe. The most lingual is the highest and largest. Although its apex is higher than the buccal cusp, the middle cusp in the row has the smallest volume.

M^4 bore the brunt of the distorting pressure and its crown is now crushed against M^3. Remains of alveoli prove that at least part of the material is derived from an upper molar. No evidence suggests the presence of parts of a lower molar, but the possibility cannot be ruled out.

The mass of dental material now covering part of the disto-lingual surface of M^3 could be the remains of the major lingual cusp of M^4. The buccal mass of M^4 is not as crushed but was rotated clockwise through approximately 90 degrees. It includes part of the parastylar region carrying the bases of two cusps of subequal size followed distally by two smaller cusps. M^4 was supported by at least a buccal root under the parastylar region and a second lingual root. No indication of a third root was found.

At the time of its death the animal from which M21887 is derived had not lived long enough to heavily wear its dentition. Only one or two surfaces that are clearly the result of wear could be found, for example flat areas on the crests of the ridges radiating from the stylocone of M^2. Planar areas on the disto-lingual surface of the paracones and mesio-lingual surface of the metacones of M^2 and M^3 might be wear facets, but the evidence is not conclusive. Admittedly evidence of wear may now be obscured by a combination of the small size of the fossil, imperfections in preservation of the surfaces of the teeth, and the necessary coat of preservative.

b. *Mandible*, B.M.(N.H.) 47739

The two distal, single-rooted incisors are represented by the broken root of the more mesial and the alveolus of the distal (Text-fig. 1). Dimensions of both alveoli are approximately: length = 0·4 mm., width = 0·3 mm. Although the tip of the dentary is missing, the curvature of what remains suggests the presence of an additional one or two, if not more incisors in the complete dentition. Before burial the canine was lost. The oval aperture of its alveolus has a length of 1·0 mm. and a maximum width of 0·3 mm. Although its alveolus is slightly constricted medially, the canine was probably supported by a single root.

The distal margin of the crown of P_1 is slightly concave and slopes down to the single posterior basal cusp. Probably P_1, like P_2 and P_3, lacked an anterior basal cusp, but this area of the crown is damaged. There is no indication of a lingual or buccal basal cingulum. All premolars are two rooted (Pls 3 and 4).

Other than its slightly larger overall size and relatively larger posterior accessory cusp, P_2 is very similar to P_1. On the buccal side of the dentary a mental foramen is present below and slightly in advance of the anterior root of P_2. P_3 illustrates the mesio-distal trends for gradual increase in premolar size and increase in relative size of the posterior basal cusp.

P_4 is distinctly larger and higher than P_3. It also differs in the presence of a small anterior basal cusp just lingual to the midline of the crown. From the apex of the main cusp a crest on its lingual side curves buccally onto the damaged dorsal surface of the talonid-like posterior basal cusp. What remains suggests this crest extended directly to the apex of a single cusp. There is no evidence of a metaconid or distinct talonid basin on either side of the crest.

M_1 is neither as long nor as high as P_4. Its largest cusp, the protoconid, has a flat lingual and convex buccal surface. Two small cusps are present on the mesial end of the crown. The smaller is situated just in front of and in line with the lingual side of the protoconid. A larger cusp (anterior cusp of Mills 1964), its apex now missing, was present directly lingual to it. Possibly a third cusp was present buccal to the first at a point where a small, oval scar indicates a flake of enamel was chipped away (Pl. 4, fig. 1). M_1 lacks a large, projecting metaconid of the kind found on the following molars. However, the distal slope of its protoconid is drawn out into a blade. Buccal and lingual grooves on the crown vaguely demark the bodies of the protoconid and metaconid. The tip of the metaconid is now broken away but the fracture surface indicates that it had a small, separate apex. The crest along the distal edge of the metaconid is separated by a notch from the crest of the talonid cusp. Apparently there was only one talonid cusp set slightly lingual to the midline, but its apex is missing and the possibility of the presence of two, very closely approximated cusps cannot be excluded. Lingually and buccally from this crest the crown falls away gradually toward the nearly vertical sides of the talonid. An entoconid is lacking. Slight bevelling of the buccal side of the talonid is probably the first stage in development of a wear facet resulting from contact with the paracone. No evidence of wear was found on the lingual side of the talonid. A mental foramen is present beneath and between the adjacent roots of P_4 and M_1.

Unlike M_1, M_2 has a high, three-cusped trigonid. Its protoconid is distinctly higher than the paraconid. The latter is closer to the midline than the larger and more lingually situated metaconid. The edge of the crown extends mesially to contact the back of M_1. Enamel is missing from both the lingual and buccal sides of the mesial end of the trigonid. Basal cusps serially homologous to those of M_3

and M_4 might have been present. A prominent crista sweeps down from the metaconid to a low point at the base of the hypoconid distal to the embrasure that received the paracone. This crest forms a prominent vertical "lip" on the back of the trigonid (Mills 1964). The surface of the embrasure between protoconid and hypoconid was scarred during early preparation and, if any existed, clear traces of wear cannot now be recognized. At the end of the crown, distal and lingual to the hypoconid, is a much smaller and lower hypoconulid. A very shallow trough starting between these cusps and paralleling the crista obliqua, descends linguomesially across the lingual face of the talonid. A small cusp is present in the position of an entoconid.

M_2 and M_3 were probably very similar in size and morphology, the major differences now distinguishing them appear to be the result of post mortem damage. M_3 has two prominent anterior basal cusps; the lingual is awl-like and directed mesiodorsally. The buccal anterior basal cusp, now slightly blunted, is in a more ventral position and merges with an expansion extending toward the buccal base of the protoconid. The hypoconulid of M_3, which is situated between the anterior basal cusps of M_4, is slightly larger and extends farther distally than that of M_2.

The trigonid of M_4 does not exhibit any significant differences from that of M_3. Its buccal anterior basal cusp is better preserved and clearly illustrates union with the expansion across the base of the protoconid. In contrast, the talonid of M_4 most closely resembles that of M_1 in its narrower, ridge-like morphology and presence of only one major cusp. Unlike M_1, a small entoconid is present and the talonid crest is directed posterobuccally.

Mesially (Text-fig. 1) the masseteric fossa terminates in a distinct pocket. Ventrolaterally the concave floor of this fossa continues onto the convex side of the horizontal ramus without interruption by a pocket or a ridge. On the lingual side of the dentary the slope of the dorsal surface of the symphysis is continued posteriorly along the horizontal ramus to the level of M_1 by a line reflecting a change in curvature of the ramus. Slightly posterior to the level of M_4 a well defined groove begins and extends to the posterior end of the specimen. This groove first lies beneath the anterior part of the pterygoid fossa and then merges with it. The fragments of bone preserved in 47739 give no evidence of a dental foramen. Also there is no evidence clearly suggesting the presence of a coronoid.

TABLE 1

Measurements, B.M.(N.H.) 47739, in millimetres

	Length	Width
P_1	·52	·24
P_2	·66	·27
P_3	ca. ·7	—
P_4	·96	·36
M_1	·93	·40
M_2	1·0	·51
M_3	1·0	·47
M_4	·91	·47

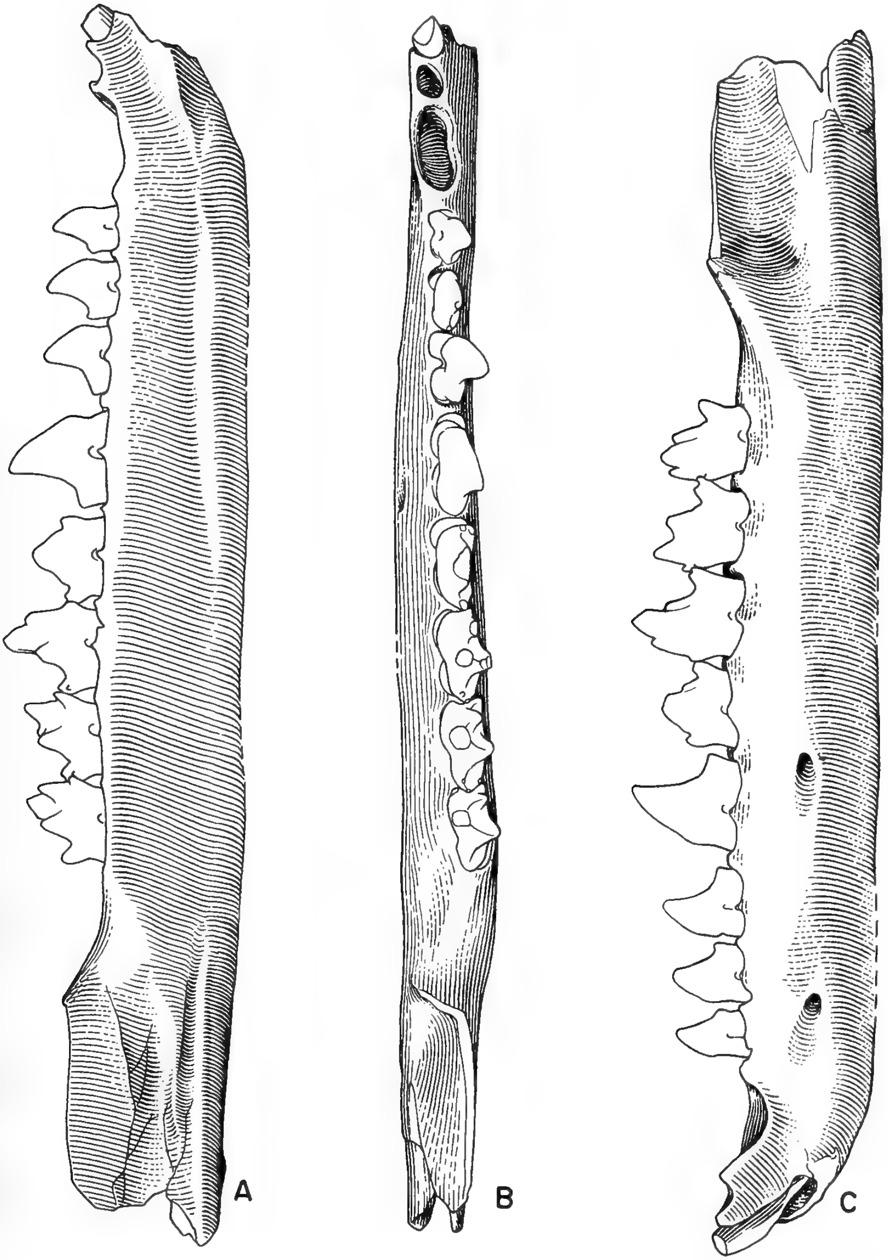

FIG. 1. *Peramus tenuirostris* Owen. × 13. Mandible, B.M.(N.H.) 47739, with fragment of root of an incisor (I3?), alveoli of distal incisor and canine, P_{1-4} and M_{1-4} (teeth outlined, see pls 3 and 4) in A, lingual view, B, occlusal view, and C, labial view.

c. *Other Mandibles,* Excepting B.M.(N.H.) 47799 and 48404

The presence of at least four lower incisors is demonstrated by 47744 in which three incisors are represented by alveoli and a fourth (probably I_2), a procumbent peg-shaped tooth, is preserved (note Mills 1964, p. 118). Probably only four lower incisors were present but none of the available mandibles clearly rules out the presence of additional teeth anteriorly.

Although slightly constricted medially the canine alveolus of 47739 (Text-fig. 1) is clearly one that housed a single-rooted tooth. Mills (1964, p. 118), on the basis of the morphology of M21888 and 47744 thought the canine of *Peramus* was two rooted. The canine region of 47744 is crushed and fragments of bone are missing from one side of the ramus. The parts preserved suggest the tooth was either two-rooted or had a single root with a deep vertical medial constriction.

Reinterpretation of M21888 in light of comparisons with 47739 results in identifications of the teeth preserved differing from those published earlier (Mills 1964). The most distal preserved molar, only its trigonid remains, is probably M_4. M_3 is the most complete molar preserved in the jaw. M_2 and M_1 are represented by the bases of their crowns and talonid regions. P_4 is similarly damaged but more of the crown of P_3, which is the most mesial tooth in M21888, is preserved. By this interpretation the posterior mental foramen of M21888, like 47739, lies beneath and slightly anterior to the mesial half of M_1.

None of the anterior premolars, P_1 through P_3, preserved in these mandibles have a distinct anterior basal cusp. Some show a slight swelling on their mesio-buccal slope, the region of the "antero-buccal ledge" in the terminology of Butler (1939). The P_3 of M21888 was mistakenly thought to be a geminated tooth (Mills 1964, p. 119). Comparisons with the subsequently cleaned 47739 indicate abnormal development did not take place.

P_4 of M21888 has lost its main cusp but the posterior basal cusp remains. The curvature of the fracture surface indicates a small cusp might have been present lingual and mesial to the posterior basal cusp. P_4's of both 47744 and 47754 are damaged. What remains of their crowns does not differ from that of 47739.

M_1 of the holotype, 47742, closely resembles the first molar of 47739. It differs in lacking the pronounced flattening of the lingual side of the protoconid. Also only one prominent anterior basal cusp is present slightly lingual to the midline of the crown, but a basal mesial cingulum continues across the crown to the buccal side. The talonid is broad and dominated by a single cusp. Because of a covering of matrix, presence or absence of an entoconid cannot be determined.

In comparison to the adjacent teeth, M_1 of 47744 is relatively small. The area mesial to its protoconid is broken and distortion may be masked by a thick layer of preservative. Its talonid is short (mesio-distally), narrow and unicuspid. The metaconid is not well defined. Like the M_1 of 47742 the protoconid lacks the flattening of its lingual surface found in 47739.

The first molars of 47751 and M21888 are damaged. As far as can be determined M_1 of 47751 does not differ significantly from that of 47739 except in the presence of a minute entoconid. M_1 of M21888 is larger, relative to the adjacent teeth, than that of 47739. The lingual anterior basal cusp and the buccally directed cingulum of M21888 resemble those of 47742. The distal face of the protoconid is broad and expanded buccally, thus resembling the posterior molars more than is the case in 47739. A small cusp on the distal face of the trigonid might be the metaconid but it could be a posterior accessory cusp comparable to those found on the molars of 47799 and 48404.

Recognizing the points of difference, probably reflecting individual variation, the M_1's of 47739, 47742, 47744, 47751, and M21888 conform to a morphological pattern that clearly distinguishes them from the more distal molars. If present, the metaconid is only a small projection on the distal slope of the protoconid. None of the M_1's have a paraconid, although one of the anterior basal cusps might be its remnant or precursor. Excepting the minute entoconids present on some M_1's, their talonids are unicuspid. The crest of the talonid is directed distally or distolingually and lacks a prominent buccal expansion.

The mesial end of M_2 of 47739 is damaged and presence of anterior basal cusps cannot be verified. Morphology of M_2's of 47742, 47744, 47751, and M21888 indicates that two anterior basal cusps can be present. These are situated on either side of the midline; the intervening depression received the distal end of M_1. The lingual basal cusp (anterior cusp, Mills 1964) is larger and in a more dorsal position than the buccal (antero-buccal ledge, *ibid.*). Mills (*ibid.*) has described the variation in structure of the trigonid of M_2 and the "lipping" produced by the high ridge extending down the distal face of the trigonid.

The talonid of M_2 of M21888 is damaged but certainly its hypoconid did not project as far buccally as that of 47739. A wear facet on the anterior buccal basal cusp of M_3 of M21888 is aligned with the wear facet produced by the paracone of M^2 on the talonid of M_2. Perhaps in this animal a re-entrant to receive a metacone was not present. To the extent that they are preserved and prepared the talonids of the M_2's of 47742, 47744, and 47751 do not differ significantly from that of 47739. The crest along the distal face of their trigonids extends posterobuccally to a hypoconid and then turns posterolingually to reach a smaller hypoconulid thus producing a small but distinct buccal salient. A minute entoconid is present on at least some M_2's.

M_3's preserved in 47742, 47751 and M21888 do not differ significantly from that of 47739. On all the talonid is dominated by the hypoconulid and slightly higher, buccally salient hypoconid. Mills (1964, p. 120) has described the few differences between M_2 and M_3. The talonid of M_4 of 47742 is relatively shorter (mesiodistally) than that of M_4 of 47739. Although partly obscured by rock, it also appears to be dominated by a single cusp.

Krebs (1969) called attention to the presence of a rudimentary coronoid on the lower jaws of certain dryolestid and paurodont eupantotheres. Traces of a coronoid or a coronoid-dentary suture are not apparent on 47739. However, small triangular, rugose areas near the anteroventral corners of the pterygoid fossae of 47751 and 47754 might indicate the presence of coronoids in these individuals of *Peramus*.

d. *Mandibles*, B.M.(N.H.) 47799 and 48404

These two mandibles are described separately for they consistently differ from the others in one character of molar morphology. On all the molars preserved in 47799 and 48404 a small cusp is present near the base of the trigonid on the crest linking the metaconid and a talonid cusp. This cusp is always mesial to the lowest point on the crest and either at the head or just distal to the base of the groove that received the paracone. It is designated the posterior accessory cusp (Mills 1964). None of the molars in the other mandibles of *Peramus*, with the possible exception of the M_1 of M21888, have a posterior accessory cusp.

In comparison to the last premolar of 47739, P_4 of 48404 has a shorter (mesiodistally) posterior basal cusp that is not enlarged into a talonid-like spur, and a larger conical, mesially projecting anterior basal cusp. The protoconid of M_1 exhibits the same lingual flattening found in 47739. Its posterior accessory cusp is low on the slope of the protoconid and set off by a distinct notch from the major distal talonid cusp. A small entoconid is present. Thus, like the first molars of the other group of jaws, the talonid lacks a prominent buccal projection.

The major differences between M_2 and M_3 of 48404 and 47739 are associated with the presence of the posterior accessory cusp on the molars of 48404. On M_2 the cusp is situated low at the base of the trigonid; breakage and distortion of the crown make it appear to be a talonid cusp. Hypoconid and hypoconulid are not so well separated as in 47739 but form a prominent buccal projection mesial and dorsal to the anterior basal cusp of M_3. An entoconid might have been present, but this area is damaged and now covered with preservative. M_3 of 48404 is closely comparable to the M_2. The differences have been described by Mills (*ibid.*).

As now preserved and illustrated by Mills (1964, fig. 1) the talonid of M_4 of 48404 appears to differ significantly from that of 47739, which is essentially unicuspid. On 48404 the distal is the highest talonid cusp. A ridge projecting buccally links it with the posterior accessory cusp, but this ridge is always lower than the apices of these two cusps and might be the result of breakage. A hypoconid could have been present and lost after death. If it was not present the talonid of M_4 would have a structure more closely comparable to the talonid of M_1 than those of M_2 and M_3. M_3 and M_4 are preserved in 47799 and clearly show the presence of posterior accessory cusps on both molars. Although in need of further preparation what is now exposed shows the talonid of M_4 had only one major cusp distal to and separated by a notch from the posterior accessory cusp.

47799 is the only mandible of *Peramus* in which the posteriorly placed dental foramen, the angular process and the base of the condylar process are now preserved. The angle was preserved in the type specimen 47742 and figured by Owen (1871). A small rugose area at the anterior end of the pterygoid fossa might mark the position of a coronoid bone.

e. *Intrageneric Variation*

Noting what appeared to be a relatively wide range in variation in size of the teeth in the mandibles referred to *Peramus tenuirostris*, Simpson (1928, p. 124) concluded two species might be represented. If this proved correct, he suggested 47742 and 48404 would be members of the species with a dentition of larger size. Another suggestion based on considerations of size and various other morphological characters, was that 47742 and M21888 represented a species distinct from *Peramus tenuirostris* but no formal changes in nomenclature were proposed (Mills 1964). Further preparation of the fossils and additional material has given a slightly better appreciation of variation in size within the sample that in itself does not indicate the presence of two species.

Most other aspects of dental morphology do not clearly indicate heterogeneity of the sample. The exception is the presence or absence of a posterior accessory cusp. It is present on the molars of 48404 (M_{1-4}) and 47799 (M_{3-4}). A posterior accessory cusp might be present on the M_1 of M21888 but the cusp in question is minute and could be the metaconid or a curious individual variation. The talonids of M_2 and M_3 of M21888 are damaged, but if present and as large as those of 48404, some indication of the posterior accessory cusp should be preserved. It is not. Thus the sample can be clearly subdivided on the basis of presence or absence of a posterior accessory cusp, which might indicate taxonomic heterogeneity. Considering the small number of available fossils, we choose to note and describe the variation but not suggest changes in nomenclature.

IV. OCCLUSION AND FUNCTIONAL INTERPRETATIONS

Through the introductory and descriptive sections it has been assumed that M21887 is a maxilla of *Peramus tenuirostris*, a species typified on a mandible. This assumption is justified on the following evidence: M21887, the type, and all other specimens of *P. tenuirostris* came from the Purbeckian Mammal Bed at Durlston Bay. The maxilla is of the proper size to be referable to *P. tenuirostris* and, like the mandible, carries eight postcanine teeth. The upper and lower postcanine teeth exhibit the same pattern of differentiation. The mesial three are clearly premolariform. M^2, M^3, and probably M^4, like M_2 through M_4 are molariform. In both upper and lower dentitions the last premolar is larger than the immediately adjacent premolar and molar and has basal cusps not found on the other premolars. Although molariform, the first molars differ from the others primarily in the absence or small size of primary cusps of the trigon and trigonid. Finally, it will be shown here that when restored the dentition of M21887 is a functional counterpart of the kind of lower dentition on which *P. tenuirostris* was typified.

Because of the lack of extensive wear on the molars of M21887, small size of the fossil, and need to maintain a coat of preservative over fractured areas, wear facets cannot be clearly delimited. This attempt to deduce the functional pattern of the dentition depends primarily on considerations of molar morphology and comparisons with other mammals rather than facets and other direct evidence of wear.

When considered in the context of the work by Crompton and Hiiemäe (1969) on *Didelphis* and studies of various primitive mammals, the morphology of the dentition of *Peramus* suggests that mastication was affected almost entirely by orthal movement of the mandible. A lingual component was introduced during the final stage of jaw closure when the protoconid and parastylar region and/or paracone and buccal wall of the talonid came into contact. The mandibular symphysis of *Peramus* was not fused. The dentition probably was anisognathic and during mastication the animal can be assumed to have alternately employed the right or left side of the dentition.

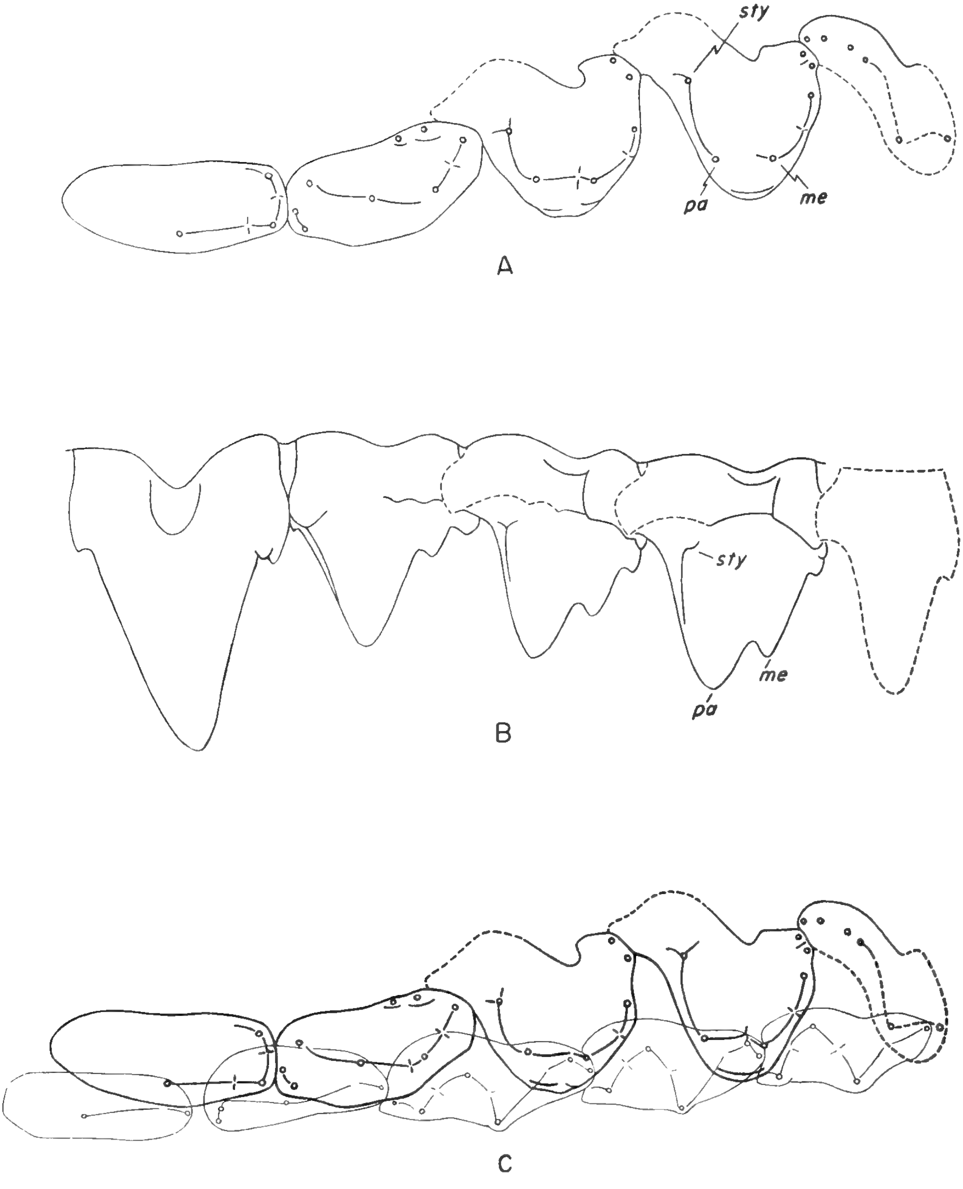

FIG. 2. *Peramus tenuirostris* Owen. Restorations of dentition. P^4 and M^{1-4} in A, occlusal view, and B, labial view. Occlusal relationships of distal premolars and molars near completion of jaw closure in C. (*sty* stylocone; *pa* paracone; *me* metacone.)

No evidence suggests the occlusal pattern of the antemolar dentition differed significantly from the basic therian pattern. The lower canine no doubt occluded just mesial to the upper and the mesial lower premolars lay between the uppers making only limited, marginal contact during mastication.

Although now slightly shifted in position, M^1 having been driven mesially and lingually relative to P^4, clearly these teeth of M21887 were not separated by a deep triangular embrasure like those between adjacent molars (Text-fig. 2). Correlated with the lack of an embrasure is the basically single-cusp morphology of the trigonid of M_1. During the early phase of closure its protoconid was probably received in the valley between the paracone and mesio-lingual cusps of M^1, which in M21887 appears to show traces of wear. When the dentition was fully occluded the protoconid of M_1 appears to have lain distolingual to the point of contact of P^4 and M^1.

The distal crest of the protoconid of M_1 and the crest of its talonid usually form an almost straight line. A buccal salient has not been observed. The paracone of M^1 was received in the groove on the buccal side of M_1 that delimits the talonid and the anterior unit of the crown. A wear facet on the mesial side of this groove is evident on one fossil (facet B, Mills 1964). Apparently the distal crest of the protoconid of M_1, including the metaconid where present, and the mesial crest of the paracone of M^1 formed a functional unit.

The apex of the metacone of a tribosphenic molar is at the junction of two shearing crests. The mesial crest, extending to the base of the paracone, occludes with the crest on the distal slope of the hypoconid. The distal crest forms part of the metastylar blade that occludes with the blade formed by the crest linking the paraconid and protoconid of the distal lower molar.

On M^1 of M21887, between the paracone and the cusp at the disto-buccal corner of its crown, is a large cusp. Its apex is higher than that of the disto-buccal cusp but lower than that of the paracone. In comparison with the paracone the disparity in height is much greater than that of the closely approximated paracone and metacone of M^2 or M^3. The lingual surface of the crown of M^1 just distal to the paracone is not recessed nor are there any traces of wear. The crest linking the distal cusp in question and the disto-buccal cusp of M^1 is blunted and appears to have functioned as a shearing blade acting in conjunction with the crest linking paraconid and protoconid of M_2. The narrow disto-lingual cingulum on M^1 served to deflect food that otherwise would have been driven directly into the gingiva.

Determination of the homologies of the cusp distal to the paracone of M^1 is open to question. The unicuspid talonid of M_1 lacks a hypoconid or other buccal projection. Thus the typical tribosphenic pattern of shear between the distal crest of the hypoconid and mesial crest of the metacone is lacking in the M^1_1 of *Peramus*. This hypoconid-metacone shear pattern is also lacking in *Kuehneotherium*. In this Rhaetic mammal the paraconid, which towered over the talonid of the preceding lower molar, moved upwards to lie between the paracone and "c-cusp" or "metacone" of the upper molar. The talonid of *Kuehneotherium* lower molars is small and usually lacks a buccal salient. Two hypotheses can be offered for the pattern of evolution of tribosphenic molars from those of *Kuehneotherium*. One proposes that in the descendants of *Kuehneotherium* the origin and enlargement of the hypoconid was coupled with elongation of the talonid, and enlargement and lingual shift of the "c-cusp". Shearing between trigonid and "c-cusp" was limited to the distal face of the latter. The mesial face of the "c-cusp" supported a crest which came to shear against the distal crest of the hypoconid. It follows that the "c-cusp" of *Kuenheotherium* is the precursor of the metacone of tribosphenic molars. Crompton (pers. comm.) has informed us that some lower molars of *Kuehneotherium* have a short buccal salient and on a few upper molars he has observed a small wear facet high on the distal crest of the paracone well removed from the "c-cusp". These observations suggest a second working hypothesis. Origin of the hypoconid and metacone were correlated, the latter arising as the high point of an angulation of the distal crest of the paracone mesial to the "c-cusp". Thus the metacone of tribosphenic molars would be a new cusp and the "c-cusp" might be homologous to the cusp found on the metastylar blade of some primitive tribosphenic molars, the penultimate molar of *Pappotherium* for example.

Because of the inadequacies of the fossil record a decision on the homologies of the cusps distal to the paracone of M^1 of *Peramus* will also reflect a choice between the following alternatives: M^1_1 of *Peramus* are phylogenetically derived from molars that had a hypoconid-metacone shear like that of M^2_2. Or, the ancestors of *Peramus* lacked M^1_1 with a hypoconid-metacone shear and in *Peramus* these teeth are somewhat modified molars of the *Kuehneotherium* functional pattern.

The cusp of M^1 of *Peramus* situated between the paracone and disto-buccal cusp performed a function akin to that of the metacone of a tribosphenic molar in that it was at one end of a buccally directed shearing blade. However, it did not support a mesial crest that sheared against a crest of the hypoconid. Because it did not fully perform the functions of a primitive tribosphenic metacone we prefer not to apply this name. Also the authors cannot agree on whether the "c-cusp" of *Kuehneotherium* can or should be considered the phylogenetic precursor of the distal cusp of the M^1 of *Peramus* or the metacone of tribosphenic molars. We conclude, however, that most probably the ancestors of *Peramus* lacked M^1_1 with a hypoconid-metacone shear (p. 108).

If common features of the occlusal patterns of mammals with tribosphenic dentitions and *Kuehneotherium* can be used to interpret the occlusion of *Peramus*, the stylocone of M^2 and the ridge extending mesially from it should be just buccal to the point where the protoconid of M_2 first contacted the upper molar during closure of the jaws. Because of the curvature of the side of M^2 further closure of the jaws would have required a transverse movement in order to allow the protoconid to slide up the lingual side of the parastylar region. The small size of the stylocone and the ridges radiating mesially and lingually (buccal end of the paracrista) from it and the convexity of the mesial side of the crown of M^2 in this region suggest little shearing occurred here until the protoconid started to slide lingually and dorsally. This moved the crest linking the apex of the protoconid and the base of the metaconid transversely across the nearly vertical segment of the mesial crest (lingual end of the paracrista) of the paracone. The existence of a transverse component of movement is also indicated by the orientation of wear scratches on the M_1 of 47744 (Mills 1964, p. 121).

The metacone of M^2 is situated high on the slope of the paracone. On the lingual surface of the crown a pronounced groove separating the two is directed toward the distal end of the lingual cingulum. This groove received the hypoconid of M_2. Wear facets (facet D) on several M_2's of *Peramus* (Mills 1964, p. 121) demonstrate that shearing occurred between the distal crest of the hypoconid and mesial crest of the metacone. The "lipping" (Mills *ibid.*) produced by the crest on the distal side of the metaconid helped form a long, well-defined groove on the lower molar that received the paracone. As the lower molars were moved dorsally, shearing occurred between the distal crest of the paracone and mesial crest of the hypoconid (note facet C, Mills *ibid.*). Thus, unlike M^1, M^2 exhibits the occlusal pattern of the paracone, metacone, and hypoconid found in tribosphenic molars.

Indications of wear have been found on the lingual surfaces of the talonid and on the crest linking metaconid and hypoconid of several molars of *Peramus* (Mills 1964). None are clearly the result of tooth on tooth contact. If M21887 is a maxilla of *Peramus* and there was not gross individual variation, the molars of *Peramus* lack protocones or other projections that could have produced wear on the lingual surface of the talonid. The top of the talonid crest might have been worn by contact with the lingual cingulum of the opposing molar, possibly acting as a stop to prevent overclosure. The evidence of wear on the lingual side of the talonid is probably the result of abrasion by food.

Because of crushing and distortion, the relative positions of M^2 and M^3 cannot be accurately determined. The distal margin of M^2 has been restored using M^3 as a model. As the relative position of these molars is reconstructed here, the two most disto-buccal cusps are treated as parts of the stylar shelf not directly involved in providing shearing surfaces. The large unnamed cusp between the disto-buccal cusps and the metacone of M^2 was situated mesio-lingual to the point where the protoconid of M_3 contacted the parastylar region of M^3. Shearing might have occurred between the buccal margin of this unnamed cusp of M^2 and the lingual margin of the protoconid of M_3 as the latter was moved lingually and dorsally. The existence of this shearing mechanism is highly speculative.

During closure of the jaws once the trigonids moved lingually and were in position to slip deep into the embrasures between the upper molars, the crest between the paraconid and protoconid of M_3 was positioned to move across the crest between the unnamed cusp and metacone of M^2. This is the typical occlusal relationship found between the metastylar blade and trigonid of tribosphenic molars.

M^3 of *Peramus* appears to have had the same occlusal pattern as M^2:

1. In *Kuehneotherium* an important shearing mechanism involves the entire crest of the ridge linking stylocone and paracone (paracrista) and all of the protoconid-metaconid crest on the distal edge of the talonid. Because of the small size of the stylocone, low buccal end of the paracrista, and convexity of the mesial margin of the crown adjacent to the parastylar region, shearing in this part of the crown of *Peramus* was limited to action between the bucco-mesial margin of the paracone and disto-lingual margin of the protoconid. Although the shearing mechanism was restricted to employ only parts of the crests utilized in *Kuehneotherium*, it does not appear to have been diminished in importance.

2. Functions of the distal crest of the paracone, mesial crest of the metacone, and crests of the hypoconid are those typical of tribosphenic molars.

3. The basal lingual cingulum on the upper molars acted to deflect food away from the gingiva. It might have made contact with the crest of the talonid and served as a stop to prevent overclosure. Evidence of wear on the lingual side of the talonid of the opposing molar is probably the result of abrasion by food, not tooth on tooth contact.

4. A metastylar blade, which functioned with the paraconid-protoconid crest, was formed between the metacone and the unnamed cusp on the distal margin of the crown. The buccal margin of the latter cusp might have been a continuation of the metastylar blade and acted with the lingual edge of the protoconid to produce a shear.

Only the parastylar region of M^4 of M21887 is preserved. It suggests the parastylar regions of M^2 and M^3 could have been large buccal extensions of their crowns each carrying several cusps. On all M_4's of *Peramus* the talonids are essentially unicuspid, but unlike M_1, their crests are directed disto-buccally and form distinct salients. This hypoconid-like projection suggests both a paracone and a much smaller metacone were present on M^4.

The occlusal pattern of *Peramus* exhibits several important differences from those found in mammals with tribosphenic molars. M^2 and M^3 differ in absence of the shearing surfaces associated with the protocone. The small size of the stylocone and paracrista suggest little shearing was effected in this area. Additionally, M^1 and M_1 lacked the interaction of the shearing crests of the paracone, metacone and hypoconid.

V. PHYLOGENETIC RELATIONSHIPS

a. Comparison with *Amphitherium*

Amphitherium prevostii is known from four mandibles discovered in the Stonesfield Slate, a Bathonian (middle Jurassic) unit within the Great Oolite. Maxillae or isolated upper teeth of the species have not yet been found. In most recent studies of Mesozoic mammals *Amphitherium* is classified with the therian mammals and treated as a member or representative of the stock ancestral to *Peramus*, dryolestids, paurodonts*, and mammals with tribosphenic dentitions.

Making use of the morphology and pattern of wear of the lower molars an attempt to reconstruct the upper molars of *Amphitherium* has been made (Text-fig 3, from Mills 1964, p. 125–7). The lower molariform teeth have a basically triangular occlusal outline. The uppers must have had a similar outline but of opposite orientation. When a dentition of this reversed triangular pattern is brought into occlusion the margins of the gingiva at the apices of the embrasures could be damaged by food impacted by the opposing molars. On the lower molars the projecting spur

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*The recent study by W. G. Kühne (1968) clearly shows that the concept and content of the Paurodontidae needs thorough review in light of new material from the Jurassic of Portugal. Without attempting to revise the family, for the sake of convenience we choose to employ the Paurodontidae for *Paurodon*, several genera from the Kimmeridgian of Portugal yet to be formally named, *Archaeotrigon*, *Tathiodon*, *Araeodon*, *Pelicopsis*, *Mathacolestes*, and, possibly *Brancatherulum*.

of the talonid protects this part of the gingival margin. No doubt a salient parastylar region with a similar function is present on the upper molars of *Amphitherium.*

The pattern of wear of the trigonids of *Amphitherium* (facets A and B, Mills *Ibid.*) resembles that found on M_2 through M_4 of *Peramus.* A large wear facet (facet C, which is not clearly delimited from facet B on the distal slope of the trigonid) was developed on the bucco-mesial side of the single-cusped talonid. The crest of the talonid is directed disto-buccally and slightly overlaps the trigonid of the following molar. One of the authors (Mills) has re-examined the specimens of *Amphitherium* with improved equipment and finds that the talonid was situated against and largely under the trigonid of the succeeding molar. Where it appears otherwise, this is due to post-mortem displacement. A wear facet along the oblique crest of the talonid (facet F) was interpreted (Mills *ibid.*) to be the result of contact with a lingual cingulum on the upper molar. Evidence from *Peramus,* and other mammals, now indicates contact with a lingual cingulum might have contributed to the wear, but probably facet F is the product of abrasion by food.

As reconstructed (Mills *ibid.*) the upper molars of *Amphitherium* are shown with a prominent lingual cingulum and the metacone situated very near the disto-buccal corner of the crown. These two features of the reconstruction can be modified on the basis of information derived from *Peramus.* Wear on the crest of the talonid (facet F) of *Amphitherium* can be primarily or entirely accounted for through abrasion by food. Probably a lingual cingulum protecting the gingiva is present on the upper molars of *Amphitherium* but it need not be larger than those of *Peramus* or *Kuehneotherium.*

If the apex of the metacone on an *Amphitherium* molar is lower than that of the paracone, and the magnitude of transverse movement slightly greater than previously estimated, the metacone could have been in a much more lingual position than shown in the earlier reconstruction and still produced the facet on the distal end of the talonid (facet D). The wear facet on the distal face of the trigonid (facet B) is larger than that on the mesial (facet A), a relationship similar to that in *Peramus.* This suggests the stylocone and paracrista of *Amphitherium* molars are as small as those of *Peramus.* Thus, within the limits of the available evidence, the upper molars of *Amphitherium* can be reconstructed in a form not greatly different from that of M^2 or M^3 of *Peramus.*

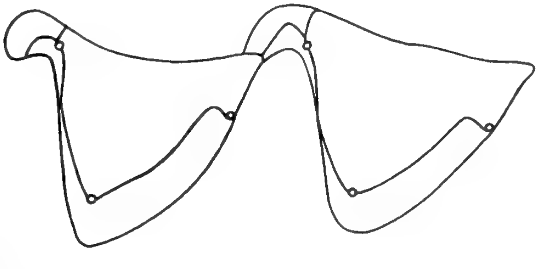

FIG. 3. *Amphitherium prevosti* (H. v. Meyer). Earlier restoration of upper molars (redrawn from Mills 1964, fig. 4B) in occlusal view.

In spite of the possibility of these similarities in upper molar structure and resemblances in the morphology of the lower molars, several features of the dentition of *Amphitherium* suggest it is not directly ancestral to *Peramus*. Like *Amphitherium*, the first molars of paurodonts, dryolestids, and the late Jurassic and younger symmetrodonts do not differ greatly from the second. Usually there are some differences in size—the first molar being smaller—and proportions; but these are not of the magnitude of the differences found between the first and second molars of *Peramus*. We assume that *Kuehneotherium* from the Rhaetic is either a member or representative of the therian radical (Mills 1964; K. A. Kermack *et al.* 1965; D. M. Kermack *et al.* 1968). Information on the morphological differences of its first two molars is not yet available. However, the uniqueness of the degree of morphological difference between the first and second molars of *Peramus* among the probable descendants of *Kuehneotherium* warrants a working hypothesis that this magnitude of difference is not a primitive trait of therians.

M^1 of *Peramus*, except for the small size or absence of the stylocone, closely resembles upper molars of *Kuehneotherium* (note Kermack *et al.*, 1968, Fig. 1). The trigonid of M_1 of *Peramus* does not resemble those of any of the described molars of *Kuehneotherium* but is derivable from them through near or complete loss of the paraconid and metaconid. These changes could reflect a reduction of fully molariform teeth through a pattern of change akin to that involved in the evolution of carnassials in Cenozoic carnivores (Mills *ibid.*, p. 127). In the absence of a hypoconid or buccal salient the M_1 talonid of *Peramus* resembles those of most lower molars of *Kuehneotherium*, not *Amphitherium*. Thus the first molars of *Peramus* are most easily derived from those of a *Kuehneotherium*-type without involving the acquisition and subsequent reduction of the talonid structure found in all molars of *Amphitherium*.

Relative sizes of the distal premolar and mesial molar of *Kuehneotherium* are not certainly known, however, judging from the isolated teeth described by Kermack *et al.* (1968, Fig. 7), the distal premolar could have had a higher crown. The last premolar of the English, late Jurassic symmetrodont *Spalacotherium* is higher than the mesial molar but in at least the lower dentition of *Tinodon* from North America they are of equal height. Among American, late Jurassic dryolestids (Simpson 1929, p. 62) and paurodonts greater crown height of the distal lower and possibly upper premolars appears universal. Of the English representatives of these families *Amblotherium pusillum* contradicts the pattern. Its last lower premolar is higher than the first lower molar, but the inverse proportion characterizes the upper dentition. This evidence suggests another hypothesis: probably greater crown height of the distal premolar relative to the first molar is a primitive therian trait. If so, *Amphitherium* in which the crown of the first molar slightly overtops that of the distal premolar, can be regarded as having diverged from the primitive condition while the lineage leading to *Peramus* did not.

Thus, the simplest interpretation of phylogenetic relationships taking morphology of the distal premolars and mesial molars into account, is that *Amphitherium* and *Peramus* are representatives of disparate lineages. In order to reflect this interpretation we now follow Kermack *et al.* 1968, and others, in removing *Peramus* from the Amphitheriidae and allocating it to a separate family, Peramuridae Kretzoi.

b. Comparisons with Late Jurassic mammals

The work of W. G. Kühne and his associates has produced samples of at least two major Kimmeridgian local faunas from Portugal, here referred to by the names of the principal localities, Guimarota and Porto Pinheiro. Descriptions of these local faunas are just beginning to be published (note Kühne 1968 and refs.; and Krusat 1969), but already several specimens giving evidence pertinent to the ancestry of *Peramus* have been described.

Kühne (1968, p. 121) briefly commented on a mandible containing only P_2 from Guimarota that he identified "cf. *Peramus*". In addition from Guimarota he recovered two isolated lower molars of the size expected for teeth of cf. *Peramus*. Kühne (*ibid.*) comments on the "striking similarity" of these teeth to *Kuehneotherium* and points out several close similarities to *Amphitherium*.

One of us (Clemens) had the opportunity to study these fossils. With a more extensive knowledge of the morphology of *Peramus* it now appears less probable that cf. *Peramus* is part of its ancestry. The gross structure of their dentaries is similar, especially in the size and salient nature of the angular process. However, P_2 of cf. *Peramus* has two small cusps distal to the main cusp while only one is present in *Peramus* and *Amphitherium*. The trigonids of the isolated molars from Guimarota allocated to cf. *Peramus* do not differ significantly from those of M_2 to M_4 of *Peramus*. However, the talonid is unicuspid and "not provided with ridges". Thus it is more closely comparable to the talonids of *Kuehneotherium* and *Amphitherium* than the three or two-cusped, slightly basined talonids of M_2 to M_4 of *Peramus*.

Another fossil pertinent to consideration of the ancestry of *Peramus* is a molar of an as yet unnamed mammal from Porto Pinheiro described by Krusat (1969). The trigonid of this tooth resembles the trigonids of M_2 to M_4 of *Peramus* as well as those of the molars of *Amphitherium* and *Kuehneotherium*. In contrast, the talonid is quite unlike those of any of these mammals. It is large and deeply indented on the labial side. A J-shaped ridge carrying three cusps, originates from the distal slope of the metaconid and forms the lingual and distal margins of this indentation.

Krusat (*ibid.*) rightly points out the uniqueness of the talonid structure of the Porto Pinheiro tooth among molars of Jurassic therians. Only in *Peramus* do some molars also have a three-cusped talonid, but they are incipiently basined and have a distinct crista obliqua. The cusp in the position of a hypoconid at the end of the J-shaped crest on the Porto Pinheiro tooth is by far the lowest of the talonid cusps. Probably this mammal lacked the hypoconid-metacone shear found in some molars of *Peramus* and those of the full tribosphenic type.

It can be hypothesized that in the Porto Pinheiro mammal the paracone supported two long shearing surfaces meeting at a slightly obtuse angle at its apex. Enlargement of the talonid could reflect selection for increase in the size of the paracone and emphasis on this shearing mechanism. The proliferation of talonid cusps might be associated with elaboration of the mechanisms for interlocking adjacent teeth and protection of the gingiva. In any event, if the described tooth is typical of the lower molars of this Porto Pinheiro mammal, it seems unlikely that it is part of the ancestry of *Peramus* in which the evolution of a crista obliqua and lingual basin must have occurred concomitant with enlargement of the talonid.

Brancatherulum tendagurense is based on an endentulous mandible found in the Tendaguru area of Tanzania in the late Jurassic, Upper Saurian Bed. Simpson (1929) suggested *Brancatherulum* is closely allied to *Peramus*. Kühne (1968) noted these two genera are members of a group of eupantotheres including *Amphitherium*, *Archaeotrigon*, and the Kimmeridgian cf. *Peramus* that have a docodontlike angular process of the mandible. Unfortunately the dentition of *Brancatherulum* is unknown and the phylogenetic relationships of the genus remain obscure.

c. Ancestry of *Peramus*, summary

Kuehneotherium from the Rhaetic is considered to be ancestral to or representative of the radical of therian mammals.

Amphitherium from the Bathonian exhibits a grade in evolution of the lower and, we infer, upper molars that probably characterized ancestors of *Peramus*. However, comparison of their distal premolars and mesial molars suggests *Peramus* was not derived from *Amphitherium*. Recently Henkel and Krebs (1969) have adduced evidence suggesting that dryolestids also are not direct descendants of *Amphitherium*. These interpretations suggest, not unexpectedly, that the available collection of Bathonian mammals is a poor sample of eupantotherian diversity at that time.

None of the Kimmeridgian mammals so far described provides compelling evidence for inclusion in the ancestry of *Peramus*. The molars allocated to cf. *Peramus* by Kühne (1968) are more closely comparable to those of *Amphitherium* or *Kuehneotherium*, particularly in structure of the talonid. Cf. *Peramus* could be ancestral to *Peramus* but we feel this conclusion should be treated as one of several working hypotheses until more material becomes available.

Although passing through the evolutionary grade of dental evolution represented by *Amphitherium*, apparently the lineage linking *Kuehneotherium* or a closely related Rhaetic mammal and *Peramus* has yet to be found.

d. Possible descendants of *Peramus*

Most early Cretaceous therians are members of the Spalacotheriidae or Dryolestidae, families established in or before the late Jurassic and certainly not descendants of *Peramus*. The few early Cretaceous mammals that might be derived from *Peramus* are: *Aegialodon* from the English Wealden, the therians of eutherian-metatherian grade from the Trinity Sands including *Pappotherium* and *Holoclemensia*, and *Endotherium*, a poorly known Asian mammal.

Aegialodon is based on an isolated tribosphenic molar from the Cliff End bone bed, a unit of the Wealden, Hastings Beds. In many characters it closely resembles M_2 and M_3 of *Peramus* but there are some distinguishing features. The relative difference in height of trigonid and talonid appears to be less in *Aegialodon*. In both the paraconid is higher than the metaconid but the latter cusp has a slightly more mesial position, relative to the protoconid, in *Aegialodon*. Like at least M_3 and M_4 of *Peramus*, lingual and labial anterior basal cusps (mesial cuspule and mesial ridge respectively of Kermack *et al.* 1965) are present on the molar of *Aegialodon*.

The talonid of *Aegialodon* carries a relatively larger and better delimited basin than that of *Peramus*. We do not agree with Kermack *et al.* (p. 542, 1965) and Krusat's (1969) suggestions that the crista obliqua of *Aegialodon* is a product of abrasion and Krusat's (*ibid.*) further contention that the structure is not homologous with the ridge linking metaconid and hypoconid found on the molars of various Trinity Sands' therians. Although it was probably accentuated by development of adjacent wear facets, the crista obliqua of *Aegialodon* rises slightly above the lingual talonid facet in a fashion suggesting its eminence is not solely the product of wear.

In *Peramus* the hypoconids of M_2 and M_3 are situated at the apices of distinct buccal salients and are as large or larger than the hypoconulids. A hypoconid-metacone shear was functional. A buccal salient is present on the talonid of *Aegialodon* but two, closely approximated cusps smaller than the hypoconulid are present in the position of the hypoconid. The entoconid of *Aegialodon* is larger and in a more mesial position than that of *Peramus*. Also the talonid basin of *Aegialodon* is larger and is worn in a manner that Kermack *et al.* (1965) thought to be indicative of the presence of a small protocone on the occluding upper molar.

If a lineage derived from *Peramus* was characterized by selection favouring evolution of a protocone, then *Aegialodon* could be its Wealden descendant. Small size and subdivision of the hypoconid is unexpected but the wear facets demonstrate a hypoconid-metacone shear was functional. Although permissive, the evidence supporting the hypothesis that *Aegialodon* is derived from *Peramus* is not compelling.

The Albian therians *Pappotherium* and *Holoclemensia* probably are not descendants of *Peramus* if the hypothesis that *Kuehneotherium* is representative of the therian radical is correct. Upper molars of *Pappotherium* have a large stylocone linked to the paracone by a high ridge, the paracrista. A similar pattern pertains in *Kuehneotherium*. In *Peramus*, however, the labial end of the paracrista is very low and the stylocone minute. An evolutionary pattern involving reduction of paracrista and stylocone and then, subsequently, their enlargement seems unlikely. Although smaller than that of *Pappotherium*, the stylocone of *Holoclemensia* is much larger than that of *Peramus*.

On upper molars of both *Pappotherium* and *Holoclemensia* the protocone and parastyle are linked by a cingulum across the mesial face of the paracone. This cingulum, and the protocone, are probably homologous to part of the mesially continuous lingual cingulum of upper molars of *Kuehneotherium*. In *Peramus* this cingulum is reduced to a short ledge lingual to the paracone and metacone and not continuous across the mesial face of the paracone. Thus, both the small size of the stylocone and lingual cingulum of *Peramus* suggest it is not ancestral to either *Pappotherium* or *Holoclemensia*.

Little can be said about the possibility of direct phylogenetic relationships between the enigmatic Asian *Endotherium* and *Peramus*. In grade of evolution the lower molars of *Endotherium* more closely resemble those of *Pappotherium* than those of *Peramus*. No features of *Endotherium* rule out its descent from *Peramus*, but no evidence strongly suggests this was the case.

In summary, we hypothesize that in the late Jurassic probably there were several peramurid genera. *Brancatherulum* from Africa and cf. *Peramus* from Guimarota could be members of this family. *Aegialodon*, and possibly *Endotherium*, might be descendants of *Peramus*. Although *Peramus* probably is not their direct ancestor, possibly *Pappotherium* and *Holoclemensia* are descendants of a peramurid having a large stylocone and mesially complete lingual cingulum.

VI. SUMMARY AND CONCLUSIONS

Peramus tenuirostris Owen is represented in the fossil record by only a few fragmentary mandibles and a maxilla. All are from the Purbeckian Mammal Bed, part of the Late Jurassic (Boreal standard) Lulworth Beds of England, and are now in the collection of the British Museum (Natural History).

The dental formula of *Peramus* is $I^{?}_{4}$, C^{1}_{1}, P^{4}_{4}, M^{4}_{4}. Presence of more than four incisors cannot be excluded. In some individuals the large lower canines are supported by deeply scored but probably undivided roots. Of the four premolariform teeth the last, most distal, is distinctly the largest. Neither P^4 nor P_4 is molariform.

M_1, although molariform, is distinguishable from the following molars through absence of a distinct paraconid, small size or absence of a metaconid, and absence of a hypoconid or other buccal projection on the talonid. Likewise M^1 differs from M^{2-3} in its lesser width of crown, relative to length; absence of a cusp with all the functions of a tribosphenic metacone; and lack of a prominent anterior lobe of the stylar shelf.

M_{2-3} are fully molariform tribosphenic molars with three-cusped, imperfectly basined talonids. M^{2-3} have a broad stylar shelf; small stylocone; high, closely approximated paracone and metacone; and narrow lingual cingulum. Unless great individual variation occurred, the upper molars probably lacked a distinct protocone. The morphology of M^4 is unknown. The trigonid of M_4 resembles that of M_3 but the talonid of the last molar is essentially a buccally deflected blade carrying a small entoconid.

All specimens of *Peramus* are allocated to *P. tenuirostris*. The only character suggesting the presence of two species is the regular development of a small cusp, the posterior accessory cusp, on the crista obliqua of the molars of some individuals.

The morphology of its dentition, especially the tribosphenic-like molars, and mandible demonstrate the therian affinities of *Peramus*. We assume that *Kuehneotherium* from the Rhaetic is a member or representative of the therian radical. Also *Pappotherium* and *Holoclemensia* from the Albian are assumed to be representative of therians of eutherian-metatherian grade.

Amphitherium from the Bathonian (Middle Jurassic) has been suggested to be phylogenetically intermediate between *Kuehneotherium* and *Peramus*. The morphologic differences of their distal premolars and mesial molars are interpreted as indicating *Amphitherium* is not directly ancestral to *Peramus*.

Of the Kimmeridgian mammals described by Kühne (1968) "cf. *Peramus*" might be ancestral to *Peramus*, but the evidence is not compelling. If the isolated tooth from Porto Pinheiro described by Krusat (1969) is a typical lower molar of a Kimmeridgian mammal, it is unlikely this mammal is part of the ancestry of *Peramus* in which evolution of the crista obliqua, lingual talonid basin, and encircling cusps must have occurred concomitant with enlargement of the talonid.

Kuehneotherium, *Pappotherium*, and *Holoclemensia* have upper molars with a large stylocone linked to the paracone by a high paracrista and a continuous basal cingulum across the mesial face of the crown. In *Peramus* the stylocone is greatly reduced and the cingulum interrupted. Although Cretaceous eutherians and metatherians probably had a peramurid ancestor, *Peramus* is not a member of this lineage.

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PLATE 1

Peramus tenuirostris Owen

B.M.(N.H.) M21887

FIG. 1. Labial view, left maxilla with P^{1-4} and M^{1-4}. ×25.

FIG. 2. Occlusal view. Heavily damaged lingual section of M^4 outlined but not shaded. ×25.

1

2

PLATE 2

Peramus tenuirostris Owen

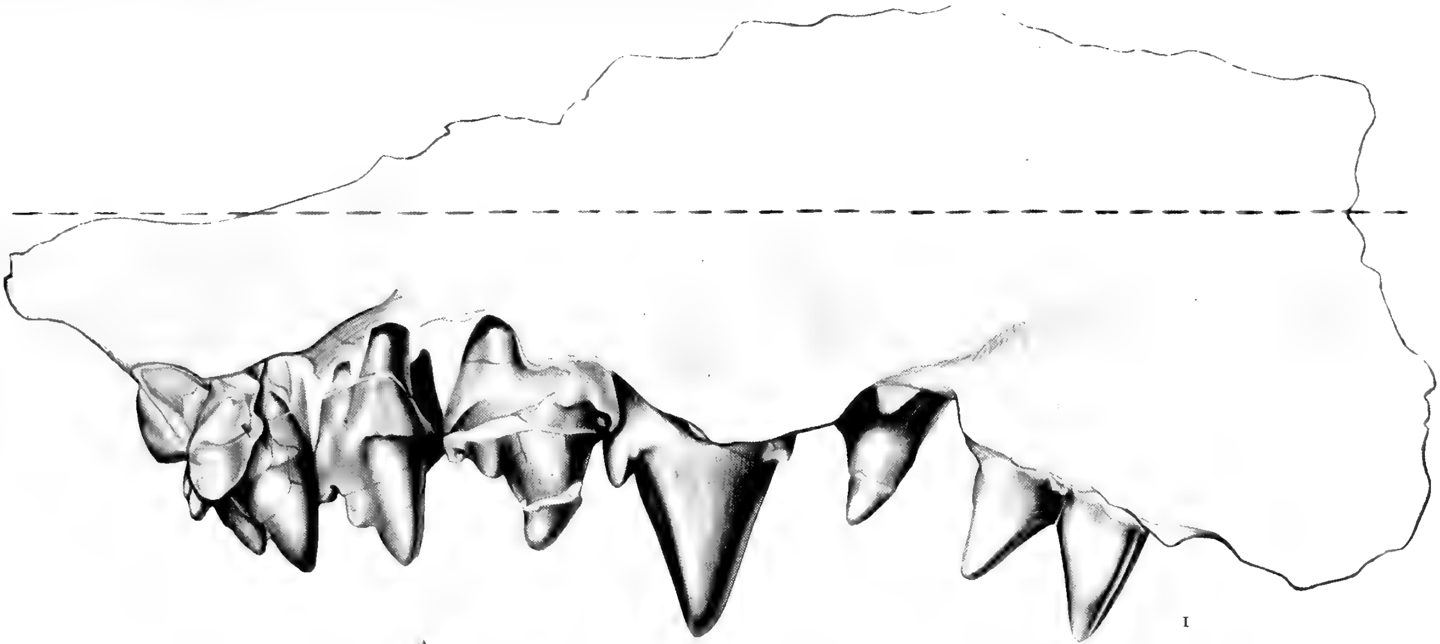
B.M.(N.H.) M21887

FIG. 1. Lingual view, left maxilla with P^{1-4} and M^{1-4}. × 25.

FIG. 2. Oblique view across labial fragment of M^4, and crowns of M^3 and M^2. × 25.

FIG. 3. Cross-section through base of crown of M^2 to show development of lingual cingulum. × 25.

FIG. 4. Cross-section through base of crown of M^3 to show development of lingual cingulum. × 25.



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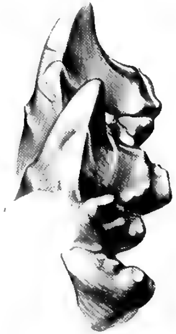

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PLATE 3

Peramus tenuirostris Owen

B.M.(N.H.) 47739

FIG. 1. Occlusal view of canine alveolus, P_{1-4} and M_{1-4}. ×25.
FIG. 2. Lingual view with outline of mandibular ramus. ×25.

1

2

PLATE 4

Peramus tenuirostris Owen

B.M.(N.H.) 47739

FIG. 1. Labial view of a section of mandibular ramus containing canine alveolus, P_{1-4} and M_{1-4}. ×25.

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C. P. HUGHES

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BY

CHRISTOPHER PAUL HUGHES

Pp. 115-182; 16 *Plates*, 13 *Text-figures*

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THE ORDOVICIAN TRILOBITE FAUNAS OF THE BUILTH-LLANDRINDOD INLIER, CENTRAL WALES. PART II.

By CHRISTOPHER PAUL HUGHES

CONTENTS

SYNOPSIS

This paper is the second in a series of four dealing with the Ordovician trilobite faunas of the Builth-Llandrindod Inlier. Those described belong to eight genera and seventeen species, of which four are new. They comprise three subfamilies of the family Trinucleidae. The Marrolithinae is a new subfamily.

I. TERMINOLOGY

THE terminology adopted here is that in standard use for trinucleids, with the addition of the following two terms. The term 'arc' is used instead of 'concentric row' as previously proposed (Hughes 1970), and the term 'inter-radial ridge' is used for the ridges separating adjacent rows of pits on the fringe.

II. DEFINITION OF MEASUREMENTS

As in part I of this study (Hughes 1969), the single orientation method of measurement proposed by Shaw (1957) has been followed. In those measurements involving distances between, or to, furrows, the measurements have been taken from the deepest (dorsoventrally) point in the furrow. All measurements are taken from internal moulds except where specifically stated to the contrary.

Measurements taken on trinucleids (see Text-fig. 1).

A	preoccipital cephalic length—measured in the sagittal line from the occipital furrow to the anterior margin of the cephalon.
A_1	cephalic length—measured in the sagittal line from the posterior margin of the occipital ring to the anterior margin of the cephalon. If an occipital spine is present, then the measurement is taken from the posterior tip of the spine.
B	glabellar length—measured in the sagittal line from the occipital furrow to the anterior of the glabella.
B_1	the distance between the posterior lateral glabellar furrows and the anterior of the glabella, as projected onto the sagittal line.
B_2	the distance between the median lateral glabellar furrows and the anterior of the glabella, as projected onto the sagittal line.

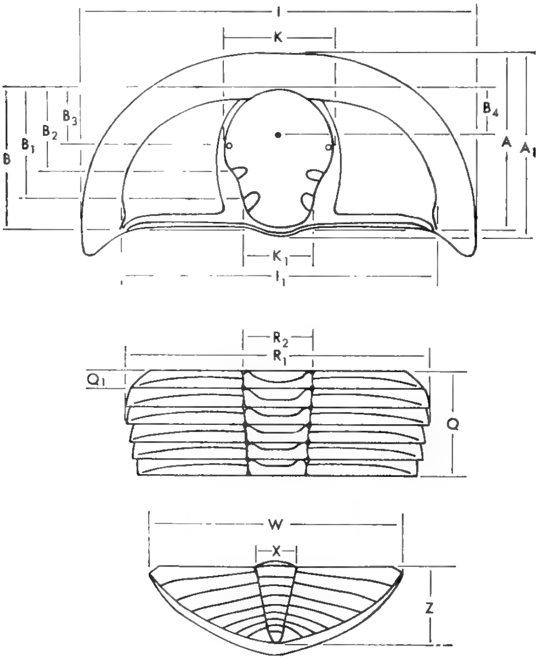

FIG. 1. Diagram showing the measurements taken on trinucleids.

B_3	the distance between the anterior lateral glabellar furrows and the anterior of the glabella, as projected onto the sagittal line.
B_4	the distance between the median glabellar node and the anterior of the glabella, measured in the sagittal line.
I	cephalic width—measured in a transverse direction along the posterior margin of the cephalon.
I_1	maximum cephalic width excluding fringe—measured in a transverse direction.
K	maximum glabellar width—measured in a transverse direction between the axial furrows.
K_1	posterior glabellar width—measured in a transverse direction across the occiput.
R_1	maximum thoracic width—measured in a transverse direction.
R_2	anterior thoracic axial width—measured in a transverse direction along the anterior thoracic margin between the axial furrows.
Q	thoracic length—measured in the sagittal line.
Q_1	anterior thoracic segment length—measured in the sagittal line.
W	maximum pygidial width—measured in a transverse direction.
X	anterior pygidial axial width—measured in a transverse direction.
Z	pygidial length—measured in the sagittal line between the articulating furrow and the inner margin of the posterior border.

III. SYSTEMATIC DESCRIPTIONS

Family **TRINUCLEIDAE** Hawle & Corda, 1847

In this study the need for the revision of the subfamilial classification of the trinucleids became apparent and this question is to be dealt with fully elsewhere. For convenience of reference and comparison diagnoses of the subfamilies and genera described in this paper are given below. The subfamily Marrolithinae nov. is here erected for those genera thought to be closely related to *Marrolithus*, but placed in the Cryptolithinae by Whittington (*in* Moore 1959), i.e. *Marrolithus, Cryptolithoides, Marrolithoides, Protolloydolithus, Reuscholithus, Telaeomarrolithus* together with *Costonia.*

Subfamily **TRINUCLEINAE** Hawle & Corda, 1847

DIAGNOSIS. Cephalon semi-circular; glabella with three pairs of lateral glabellar furrows; pseudofrontal lobe generally prominent; alae may be developed; occipital spine absent; eye tubercles and ridges absent. Fringe with pits of upper lamella sunk into radial sulci; variable number of arcs present external to the girder.

Genus ***TRINUCLEUS*** Murchison, 1839

DIAGNOSIS. Trinucleinids having one E arc and variable number of I arcs; glabella clavate with prominent pseudofrontal lobe. Pygidium much broader than long, generally with furrowed pleural fields.

Genus *ANEBOLITHUS* Hughes & Wright, 1970

DIAGNOSIS. Trinucleinids with no E arcs, I_1 and I_2 complete I_3 variably developed. Glabella pyriform with pseudofrontal lobe; median glabellar node present. Pygidium much wider than long, anterior part of pleural fields faintly furrowed.

Genus *BERGAMIA* Whittard, 1955

DIAGNOSIS. Trinucleinids having E_1 fully and E_2 variably developed; up to six I arcs present laterally; glabella clavate with prominent pseudofrontal lobe; median glabellar node present. Pygidium short, pleural fields furrowed.

Subfamily **CRYPTOLITHINAE** Angelin, 1854

DIAGNOSIS. Cephalon generally semi-circular; glabella clavate to carinate; up to three weakly developed lateral glabellar furrows; occipital node generally present though may be small, absent in *Eirelithus*; alae, eye tubercles and ridges generally absent in adult form. Fringe with one arc external to girder in early genera, more arcs present in later forms; except in early genera, pits generally arranged radially; concentric ridges between arcs on upper lamella common.

Genus *CRYPTOLITHUS* Green, 1832

DIAGNOSIS. Cryptolithinid with E_1 and up to three I arcs continuous medially, variable number of further I arcs developed laterally; pits of upper lamella arranged radially medially but may be irregular laterally due to adventitious pits; E_1 and I_1 pits generally larger than the remainder; concentric ridges between arcs on upper lamella common. Glabella clavate with three pairs of weak lateral glabellar furrows. Pygidium wider than long; pleural fields generally furrowed.

Genus *BETTONIA* Whittard, 1956

DIAGNOSIS. As for *Cryptolithus* except that a variable number of adventitious pits may be developed medially and posterolaterally external to E_1.

Subfamily **MARROLITHINAE** subfam. nov.

DIAGNOSIS. Cephalon generally with angulate margin anterolaterally; glabella pyriform, rarely with swollen pseudofrontal lobe; occipital spine may or may not be developed. Fringe typically swollen anterolaterally except in early genera; one arc developed external to the girder except in later genera in which two are developed; pits may or may not be radially arranged, if so may be set in sulci.

Genus *MARROLITHUS* Bancroft, 1929

Diagnosis. Marrolithinid with one E and a variable number of I arcs; fringe sharply angulated anterolaterally with variable inflation and pit enlargement. Glabella pyriform with one to three pairs of generally weakly developed lateral glabellar furrows. Pygidium wider than long, pleural fields usually weakly furrowed or smooth.

Genus *PROTOLLOYDOLITHUS* Williams, 1948

Diagnosis. Marrolithinid with regular E_1 and I_1 arcs and numerous smaller irregularly arranged pits internal to I_1; E_1 and I_1 separated by a sharp ridge on upper lamella; anterolateral corners rounded; no swelling or inflation of pits. Glabella elongate with three pairs of weak lateral glabellar furrows; short preglabellar field developed. Pygidium wider than long, pleural fields generally strongly furrowed.

Genus *TELAEOMARROLITHUS* Williams, 1948

Diagnosis. Marrolithinid with only one complete E arc but up to eleven I arcs present anterolaterally; occasional pits of E_2 may be developed anterolaterally; anterolateral corner angulate; lower lamella may be inflated anterolaterally with pits of E_1 enlarged; upper lamella with pits in sulci except in inner regions laterally. Glabella pyriform with weakly developed pseudofrontal lobe; three pairs of lateral glabellar furrows developed.

Subfamily **TRINUCLEINAE** Hawle and Corda, 1847

Genus *TRINUCLEUS* Murchison, 1839

1927 *Botriodes* Stetson.
1950 *Edgellia* Shaw *in* Shaw and Stubblefield.

Diagnosis. See above (page 119).

Type Species. *Trinucleus fimbriatus* Murchison 1839.

Distribution. Arenig to basal Caradoc of the British Isles, Norway and Sweden; Middle Ordovician of Russia. Type species from the basal Caradoc of Wales.

Discussion. There has been considerable debate, both in the early part of the century and again in the 1950's, over the validity of the generic name *Trinucleus* Murchison 1839 and its type species. The early discussion, conducted chiefly by Foerste (1910: 10) and Raymond (1913: 4; 1913*a*: 26–30) centred around whether *Cryptolithus* Green 1832 should have priority over *Trinucleus*. Subsequent work however, has shown the two genera to be distinct. Shaw *in* Shaw and Stubblefield (1950: 624), like Raymond (1913: 4), considered *'Trinucleus' caractaci* Murchison to be the type-species of *Trinucleus* and erected *Edgellia* for what became, as a result of his selection, the generically unplaced *fimbriatus*. However they had overlooked the selection by Vogdes (1890: 84) of *T. fimbriatus* as the type-species of *Trinucleus*. In March 1958 the ICZN opinion 505 was published validating *Trinucleus* Murchison 1839 *non* Link 1807, with *Trinucleus fimbriatus* Murchison 1839 as type species.

Størmer (1930: 13) showed the genus *Botrioides* Stetson, 1927 to be synonymous with *Trinucleus* Murchison.

Trinucleus fimbriatus Murchison, 1839

(Pl. 1, figs 1–9; Pl. 2, figs 1–14; Pl. 3, fig. 1; Text-figs 2, 3)

1839 *Trinucleus fimbriatus* Murchison: 660, pl. 23, figs 2a, b.
1851 *Tretaspis fimbriatus* (Murchison); Sedgwick and M'Coy: *pars*, 146, *non* pl. 1E, figs 16, 16a.
1853 *Tretaspis fimbriatus* (Murchison); Salter: 3, 5, 8.
1890 *Trinucleus fimbriatus* Murchison; Vogdes: 84.
1912 *Trinucleus fimbriatus* Murchison; Reed: 349, 351–352, 385, 390, pl. 18, fig. 10, pl. 19, figs 2, 2a.
1913 *Trinucleus fimbriatus* Murchison; Raymond: 4.
1913*a* *Trinucleus fimbriatus* Murchison; Raymond: 28–30.
1914 *Trinucleus fimbriatus* Murchison; Reed: *pars*, 350–352, 354, pl. 28, fig. 2, *non* figs 1, 3.
1925 *Trinucleus fimbriatus* Murchison; Raymond: 19–21.
1927 *Trinucleus fimbriatus* Murchison; Stetson: 87–88, 96, fig. 5.
1930 *Trinucleus fimbriatus* Murchison; Størmer: 14, 30, 36, 75.
1940 *Trinucleus fimbriatus* Murchison; Elles: *pars*, 415–419, 421, 424, 432, pl. 30, fig. 6.
1940 *Trinucleus fimbriatus* mut. *ultimus* Elles: 416–419, 421, 424–425, 432, pl. 30, figs 7, 8.
1940 *Trinucleoides salteri* Elles: 428, pl. 30, fig. 9.
1941 *Trinucleus fimbriatus* Murchison; Whittington: 22, 23, 26.
1941 *Trinucleoides salteri* Elles; Lamont: 443–444.
1948 *Trinucleus fimbriatus* Murchison; Williams: 85.
1948 *Trinucleus fimbriatus* Murchison; Lamont: 376–379, fig. A.
1950 *Edgellia fimbriatus* (Murchison); Shaw *in* Shaw and Stubblefield: 624–625.
1956 *Trinucleus fimbriatus* Murchison; Stubblefield and Whittington: 49–54.
1956 *Trinucleus fimbriatus* Murchison; Whittard: 45, 46, 48, 65, pl. 6, fig. 4.

DIAGNOSIS. *Trinucleus* with arcs I_{1-5} generally developed; E_1 and I_1 pits larger than remainder; I_5 rarely present medially; inter-radial ridges angulate. Pygidium triangular with between six and nine axial rings; pleural fields generally with six ribs. It should be noted that the figure of the species given in Moore (1959: fig. 323.5) is incorrect both in the distribution of the pits on the fringe and in the characters of the pygidium.

LECTOTYPE. GSM Geol. Soc. Coll. 6836a. (Pl. 2, fig. 2). External mould of cranidium.

DIMENSIONS. Although the lectotype is poorly preserved the following approximate measurements give some indication of its dimensions.

A	I
8·0	20·0

Both measurements in mm. For explanation of symbols see Text-fig. 1.

TYPE LOCALITY AND HORIZON. Dark shales in the Gwern-yfed-fâch quarry half a mile south-east of Builth Road station of basal Caradoc age (*gracilis* Zone).

OTHER FIGURED MATERIAL. It. 2719 (Pl. 2, fig. 4); It. 2720 (Pl. 2, fig. 13); It. 2721 (Pl. 2, fig. 6); It. 2722 (Pl. 1, fig. 6); It. 2723 (Pl. 2, fig. 14); It. 2724 (Pl. 2, fig. 3); It. 2725 (Pl. 2, fig. 8); It. 2726 (Pl. 1, fig. 3); It. 2727 (Pl. 1, fig. 9); It. 2728 (Pl. 2, fig. 5); It. 2729 (Pl. 1, fig. 8); It. 2730 (Pl. 1, fig. 7, Pl. 2, fig. 12); It. 2731 (Pl. 2, fig. 1); It. 2732 (Pl. 1, fig. 5); It. 2733 (Pl. 1, fig. 2); It. 2734 (Pl. 2, fig. 11); It. 2735 (Pl. 1, fig. 4); It. 8798 (Pl. 2, figs 9, 10); BM 59499 (Pl. 2, fig. 7); GSM 35356 (Pl. 3, fig. 1); Wattison Collection, H.12 (Pl. 1, fig. 1).

DISTRIBUTION. Known with certainty only from the basal Caradoc of the Builth-Llandrindod region. It may also be present in South Wales but none of the records of the species in the Geological Survey Memoirs for South Wales has been confirmed to date.

DESCRIPTION. The complete individual is roundly rectangular being slightly wider than long, excluding the genal spines.

The cephalon is semi-elliptical and approximately twice as wide as long; large individuals are relatively wider; small ones relatively narrower. Discounting the fringe, the maximum width measured across the genal regions is always slightly over twice the glabellar length, with the larger individuals relatively narrower.

The glabella is clavate, strongly convex and elevated above the genal regions, consisting of a swollen pseudofrontal lobe occupying the anterior two-thirds of the glabella, with a narrow stalk-like posterior portion. In profile it is convex in front and on top, sloping uniformly down to the posterior. Three pairs of lateral glabellar furrows are present. The anterior pair occur as small pit-like depressions on the side of the glabella, slightly posterior to the mid-point of the pseudofrontal lobe (Pl. 1, fig. 3). The median pair, marking the rear of the pseudofrontal lobe, consists of elongated (*tr.*) pits. The posterior furrows are again elongate (*tr.*) pits directed anteromedially. Both the median and posterior pairs of glabellar furrows are placed on the side of the glabella some distance inside the axial furrows (Pl. 1, fig. 4). Lateral and slightly posterior to the posterior lateral glabellar furrows there is commonly a small pit-like depression of uncertain significance, which may represent the outer end of the posterior lateral glabellar furrow (Pl. 1, fig. 3). The base of the glabella (Pl. 1, fig. 7), behind the posterior lateral glabellar furrows, is slightly swollen to form an occiput which is a little less than half the width of the pseudofrontal lobe, and is bounded posteriorly by the occipital furrow. A small median glabellar node is usually present on the external surface of the glabella approximately opposite the anterior pair of lateral glabellar furrows. Medially the dorsal surface of the glabella bears a coarse reticulation, which may also be present, though much finer, on the frontal slope and sides of the glabella (Pl. 1, fig. 7).

The occipital ring is short (*sag.*), convex posteriorly and with no occipital spine. Deep elongate pits are developed at the lateral ends of the occipital furrow, which is relatively shallow medially. The posterior margin is rounded.

Anteriorly the axial furrows are deep and narrow with prominent fossulae near their anterior extremities (Pl. 1, fig. 4). Posteriorly the furrows closely follow the margin of the glabella to about the position of the anterior pair of lateral glabellar furrows; posterior to this the furrows converge slightly and become much wider and shallower (Pl. 1, fig. 4).

The genal regions are roundly triangular, the outer margin is strongly convex, the inner margin slightly concave, and the posterior margin more or less straight. The genae are moderately convex, the outer margin being very steep and the inner regions sloping more gently posteromedially. Externally they are covered with a strong reticulate pattern of raised ridges, which is most coarsely developed along a broad band lying between the genal angles and the anterior fossulae (Pl. 1, fig. 7). At the genal angles the raised ridges tend to coalesce to form a ridge which cuts across the posterior border furrow to the posterior margin, thus isolating the posterior border furrow from the fringe. No eye tubercle or eye ridges are developed. The posterior border furrow is straight, wide and shallow, terminating in a shallow lateral pit slightly lateral to the fulcrum (Pl. 1, fig. 7). The posterior margin is rounded.

The internal surface of the glabella and the genal regions may show a faint impression of the external reticulate pattern. The lateral pits, and lateral glabellar furrows form raised platforms internally, those of the anterior lateral glabellar furrows commonly being poorly developed; the fossulae form small apodemes. The median glabellar node is rarely discernable on the inside of the glabella. Small apodemes are present ventrally, immediately posterior to the lateral extremities of the occipital ring.

The hypostoma is not known.

In most specimens the fringe has almost certainly undergone some degree of flattening, but it seems most likely that the fringe possessed a gently convex genal roll becoming concave towards the brim. The fringe is of almost uniform width, expanding only slightly towards the genal angles. Six arcs of pits are generally developed, namely E_1 and I_{1-5} (Pl. 1, fig. 4); pits of I_6 present occasionally. The pits are arranged in deep radial sulci separated by angulate ridges, the pits of E_1 and I_1 being larger than the remainder. The radial arrangement of the pits is remarkably persistent, breaking down only at the genal angles.

As has already been shown (Hughes, 1970) half-fringe statistics may safely be used in trinucleid studies without reference to the size of individuals, providing that no early meraspides or protaspides are included. The number of pits in the E_1 and I_1 arcs is generally the same on account of the good radial arrangement and ranges from 18–24 (half-fringe) with a mode of about 21 (see Tables 1, 4 for full details). The number of radial rows developed varies between 12 and 20 (half-fringe) with a mode of 17 (see Table 6). Generally arcs I_{1-4} are present frontally with I_5 commencing by row 3 or 4 (see Tables 2, 5).

Slight deformities in the radial pattern of pits are not uncommon. These are usually due to the fusing or bifurcation of an inter-radial ridge giving rise to an incomplete row of pits. Rarely two rows, partial or complete, occur within a single sulcus, and a further type of irregularity is occasionally seen in the development of an oversize pit in I_2 or I_3.

Contrary to Reed's belief (1912: 385) the pits of the lower lamella do correspond to those of the upper lamella. On the lower lamella shallow sulci are developed however only along the anterior part of the fringe, internal to the girder. The inner part of the lower lamella is convex dorsally and the outer part more or less flat, but directed upwards and outwards from the girder. Commonly the girder is found flattened, obscuring the inner part of the lower lamella and giving a false picture of the pit distribution and shape of the lower lamella. The girder is strong, smooth and merges at the genal angles with the genal spines. These spines are nearly straight, diverge slightly to the rear, have a slight keel on the dorsal side and probably extend for a short distance posterior of the pygidium.

The precise course of the facial suture has not been traced, but by analogy with other trinucleids it is almost certainly marginal, becoming dorsal only at the genal angles, thus leaving the genal spines attached to the lower lamella. Lamont (1948: 376) states that on a specimen from the Llanfawr Quarries 'a semi-circular anterior facial suture appears to be present and to run just outside the anterior pits and forward into the fringe so as to enclose a number of pits in the innermost concentric row'. However of the three hundred and fifty cranidia examined from this locality none shows any sign of such a suture. Many do however possess cracks in roughly this position and it is thought that Lamont's 'suture' may well be one of these.

The thorax consists of six segments and is rectangular, being about two and a half times wider than long. The axis, which occupies about one-fifth of the total width, tapers very slightly and is moderately convex. Dorsally the axial furrows are

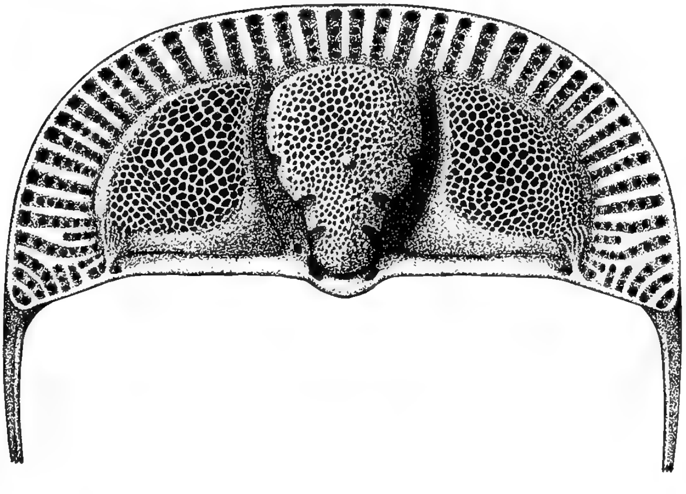

FIG. 2. Reconstruction of the cephalon of *Trinucleus fimbriatus* Murchison in dorsal view. *c.* × 7.

poorly developed, being identified essentially as the line of junction between the convex surface of the axis and the flat surface of the pleurae. Ventrally the furrow is represented by a ridge which appears as a slight depression on internal moulds. The swollen posterior portion of the axis of each segment is separated from the articulating half ring by a wide, shallow articulating furrow, which is deepened laterally into elongate (*tr.*) pits which correspond with strong apodemes on the ventral surface. The anterior segment, however, has no articulating half ring developed, but anterior to the normal pair of apodemes a second pair of weakly developed apodemes is present. Small articulatory sockets and processes are developed in the axial furrows, anteriorly and posteriorly respectively, of each thoracic segment, except for the anterior segment which only has the posterior processes. The pleural regions are flat, bluntly terminated, and deflected ventrally and slightly posteriorly at the fulcrum. They are divided into two roughly equal parts by a transversely directed pleural furrow, which is deflected to the posterior at its distal end. The pleurae of the anterior segment are obliquely truncated; the facets being relatively large.

The triangular pygidium is between three and four and a half times wider than long. In general the smaller individuals are relatively wider than the larger. The anterior margin, excluding the articulating half ring, is straight except for the lateral extremities which are deflected slightly to the posterior at a point corresponding to the fulcrum of the posterior thoracic segment. The posterior margin is defined by a slightly raised marginal rim marking the upper limit of the steeply declined posterior border which has, on the external surface, faint, closely spaced terrace lines. The axis is convex, clearly differentiated, and segmented. There may be from six to nine axial rings present, plus a small terminal piece, there being a slight positive correlation between the size of the pygidium and the number of axial rings developed (see Table 9). Anteriorly the axis occupies between about one-fifth and one-seventh of the width of the pygidium and tapers to about one-half this width. The axial furrows are slightly more prominent on the internal moulds than on external moulds, indicating some slight thickening of the exoskeleton along the line of the furrow. Only the anterior axial ring bears apodemes. The pleural fields are gently undulate and are crossed by straight furrows which become progressively more and more posteriorly directed. Each field possesses an anterior border, usually five or six ribs (rarely four or seven, see Table 10), and a small triangular terminal area. Occasional specimens show differing numbers of ribs on the two pleural fields.

The species shows the usual discoidal enrollment characteristic in the trinucleids, with the posterior margin of the pygidium in contact with the inner margin of the lower lamella. Since no articulating half ring is developed on the anterior thoracic segment it is possible that the flexure of the thorax was accommodated between the first and second, and second and third segments to avoid the production of an unprotected lenticular area between the occipital ring and the axis of the anterior thoracic segment (see Whittington, 1941*a*: 510). Enrolled specimens tend to be too flattened to indicate the relative amounts of flexure between the various segments.

However the first segment generally retains the same orientation as the cephalon, while segments two–six are folded underneath. This suggests that slightly more than half the flexure at least was accommodated by the first two segments; thus on compaction the second segment became inverted with the more posterior thoracic segments and the pygidium (Pl. 2, fig. 6).

ONTOGENY. Only one complete meraspis is known, of degree five, but it is reasonable to suppose that isolated cranidia and pygidia smaller than this are also likely to be meraspides. As Barrande (1852: 265) and Whittington (1940: 254; 1959: 447) have recorded, the later meraspides of trinucleids are very similar to the holaspis form; the meraspides of *T. fimbriatus* follow this pattern. Even the smallest specimen (pre-occipital length, A = 2·2 mm, genal width, I_1 = 4·6 mm) shows, as far as can be determined, very little difference from holaspides (Pl. 2, fig. 14).

The cephalon in the degree five meraspis (A = 5·3 mm, I_1 = 13·5 mm) (Pl. 2, fig. 8) differs from mature individuals in that the fringe barely reaches posterior of the posterior margin of the cephalon, the posterior margin of the fringe being directed only slightly to the posterior from the genal angle. This is also seen in a slightly larger specimen (A = 5·7 mm) but a further specimen of the same size shows the typical holaspis form. Thus a pre-occipital length of 5·7 mm may mark the approximate upper size limit of meraspides.

Two specimens (A = 3·5 mm, 5·0 mm) have the posterior margin of the fringe directed transversely and in the smallest specimen known (A = 2·2 mm, I_1 = 4·6 mm) the posterior margin is directed forwards from the genal angles (Text-fig. 3). Further, in these tiny specimens, the anterior lateral glabellar furrows are poorly developed.

All the pygidia which are thought to be of meraspides are very like those of holaspides. Following the general growth pattern found in the holaspides they tend to be relatively wider than the larger individuals. Counts of axial rings and ribs are difficult to make due to their poor definition towards the posterior, but there appears to be six or seven axial rings and about five ribs.

BIOMETRICAL DATA. The following fringe data and bivariate analyses indicate the characteristics of the major features of the dorsal exoskeleton. They also show that there are no significant differences between the sample from the middle quarry, Llanfawr, and the sample from the type locality.

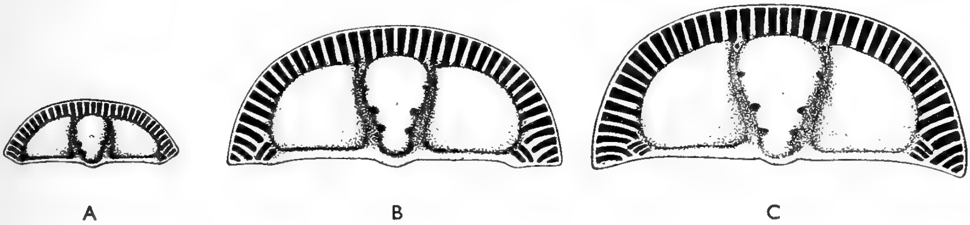

FIG. 3. Diagram illustrating the change in the posterolateral outline of the fringe in meraspides of *Trinucleus fimbriatus* Murchison with increase in size. *c.* × 4. A based on It. 2723 (Pl. 2, fig. 14); B on It. 2732 (Pl. 1, fig. 5); C on It. 2725 (Pl. 2, fig. 8).

Although ideally it is considered that the best measurements of size (length, width) of the cephalon would be the cephalic length (A_1) and the cephalic width (I), it is found, due to slight flattening of the fringe that the glabellar length (B) and the maximum genal width (I_1) give a more useful indication of size. A general qualitative study of the thorax, combined with the small amount of quantitative data available, indicates that it shows little variation, as is believed the case in most trinucleids. Insufficient data, however, are available to determine if the ratio length to width varies with the overall size of the individual. The sample of pygidia from the middle quarry Llanfawr may include a few specimens of *Telaeomarrolithus intermedius* sp. nov. (see page 174) or even *Marrolithus* sp. (see page 168). The effect of any such specimens will, however, be very small since it has proved impossible on qualitative and quantitative grounds to separate differing types of trinucleid pygidia at this locality. Also *T. intermedius* is very much rarer than *T. fimbriatus*, and *Marrolithus* sp. is extremely rare indeed.

Although it is demonstrated below that the sample from Gwern-yfed-fâch does not differ significantly from the much larger sample from Llanfawr, the data from the two samples are not combined, so that further samples may be compared directly with that from the type locality if required.

Fringe Data (half-fringe).

Sample from type locality (Gwern-yfed-fâch).

TABLE 1

Number of pits	21	22	23	24
E_1 arc: Number of specimens	2	—	—	1
I_1 arc: Number of specimens	1	—	—	1

Table giving the frequency distribution of the number of pits in the E_1 and I_1 arcs (half-fringe) for *Trinucleus fimbriatus* Murchison from the type locality.

TABLE 2

	row				Number of Specimens
	1	2	3	4	
I_4	100%	—	—	—	5
I_5	33⅓%	16⅔%	33⅓%	16⅔%	6
I_6	—	—	—	100%	1

Table showing the percentage of specimens in which a particular inner I arc commences in a given row for *Trinucleus fimbriatus* Murchison from the type locality.

TABLE 3

Number of rows	16	17	18	19
Number of specimens	1	1	4	1

Table giving the frequency distribution of the number of rows developed (half-fringe) for *Trinucleus fimbriatus* Murchison from the type locality.

Sample from Middle quarry, Llanfawr, Llandrindod.

TABLE 4

E_1 arc

Number of pits	18	18½	19	19½	20	20½	21	21½	22	22½	23	23½	24
No. of specimens	4	3	4	7	15	9	21	7	5	6	1	2	2

mean = 20·69; var. = 1·7650; n = 86

I_1 arc

Number of pits	18	18½	19	19½	20	20½	21	21½	22	22½	23	23½	24
No. of specimens	3	2	5	10	15	8	20	8	5	4	2	2	1

mean = 20·64; var. = 1·5856; n = 85

Table giving the frequency distributions of the number of pits in the E_1 and I_1 arcs (half-fringe) for *Trinucleus fimbriatus* Murchison from the Middle quarry, Llanfawr. Pits occurring on the sagittal line are counted as half pits.

TABLE 5

	row				Number of Specimens
	1	2	3	4	
I_4	96 %	4 %	—	—	26
I_5	25 %	25 %	16⅔ %	33⅓ %	12
I_6	—	—	—	—	—

Table showing the percentage of specimens in which a particular inner I arc commences in a given row for *Trinucleus fimbriatus* Murchison from the Middle quarry, Llanfawr.

TABLE 6

No. of rows	12½	13	13½	14	14½	15	15½	16	16½	17	17½	18	18½	19	19½	20	20½
No. of specimens	1	—	—	—	1	3	7	14	6	15	3	9	4	—	3	2	2

mean = 16·95; var. = 2·1678; n = 70

Table giving the frequency distribution of the number of rows developed (half-fringe) for *Trinucleus fimbriatus* Murchison from the Middle quarry, Llanfawr. Rows situated along the sagittal line are counted as a half row.

Comparison of the number of pits in the E_1 and I_1 arcs and also the number of radial rows present for the two samples show no significant differences. The data for the commencement of the inner arcs is also very similar in the two samples; in both virtually all specimens have the I_4 arc continuous medially, and 50 % of specimens in both cases show I_5 developed at or before radial row 2 and only rare cases of I_6 commencing before row 5. It is thus seen that regarding the major characteristics, the fringe pit distribution is essentially the same in both samples.

Table 7 gives the bivariate statistics for various parameters for both samples. Comparison where possible shows there to be no significant differences between the two samples.

TABLE 7

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
I_1 : A	10·95	31·3967	5·85	10·8633	0·999	1·000	1·09	0·0001	—	—	4
I_1 : B	10·95	31·3967	4·42	5·4892	0·997	0·998	1·03	0·0025	0·42	0·00048	4
B : K	4·74	4·6130	3·50	3·1900	0·989	0·991	1·11	0·0075	0·83	0·00491	5
W : Z	11·48	4·6670	3·90	1·2600	0·979	0·982	1·51	0·0270	—	—	5
X : Z	1·80	0·4089	3·81	2·8188	0·977	0·980	1·22	0·0074	—	—	10
I : A_1	19·27	8·8740	9·18	1·3069	0·933	0·934	0·81	0·0076	—	—	13
I_1 : A	13·55	5·9093	7·84	2·4620	0·955	0·956	1·11	0·0022	—	—	51
I_1 : B	13·81	5·8768	6·02	1·3653	0·938	0·939	1·10	0·0019	—	—	77
A : B	7·83	2·2687	5·90	1·2516	0·983	0·984	0·99	0·0003	0·74	0·00015	122
B : B_1	6·08	1·2710	4·88	0·7859	0·977	0·978	0·98	0·0002	0·79	0·00017	168
B : B_2	6·05	1·2872	3·91	0·5840	0·967	0·967	1·04	0·0004	—	—	176
B : B_3	6·09	1·0410	2·75	0·2487	0·923	0·924	1·08	0·0012	—	—	140
B : K	6·03	1·2344	4·46	0·7819	0·926	0·927	1·08	0·0009	—	—	177
K : K_1	4·46	0·8236	1·87	0·1194	0·879	0·881	0·91	0·0013	—	—	144
W : Z	11·37	3·1960	3·37	0·4882	0·949	0·950	1·31	0·0016	—	—	104
W : X	11·43	3·2768	2·09	0·1903	0·916	0·918	1·31	0·0028	—	—	98
X : Z	2·10	0·1606	3·48	0·4381	0·860	0·862	1·00	0·0017	1·65	0·00487	148

Bivariate statistics for *Trinucleus fimbriatus* Murchison. Upper part of Table for sample from the type locality (Gwern-yfed-fâch); lower part for the sample from the middle quarry Llanfawr. All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 8

	R_1	R_2	Q	Q_1
It. 2725 (meraspis 5)	9·4	1·9	3·0	—
H 22	14·0	—	5·8	1·0
NMW. 68.376. G186	16·8	—	6·9	1·2
NMW. 68.376. G187	12·8	—	—	0·9
NMW. 68.376. G188	14·5	3·1	5·8	1·0

Thoracic measurements for *Trinucleus fimbriatus* Murchison from the middle quarry, Llanfawr. No data available for the type locality. All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 9

maximum pygidial width in mm		7·0–11·0	11·1–17·0
Number of	6–7	—	—
axial rings	8–9	4	1
maximum pygidial width in mm		7·0–11·0	11·1–17·0
Number of	6–7	11	4
axial rings	8–9	17	35

2 × 2 tables showing relationship between pygidial size (as measured by width) and number of axial rings, for *Trinucleus fimbriatus* Murchison. Upper part of table for type locality (Gwern-yfed-fâch); lower part for the middle quarry, Llanfawr sample.

TABLE 10

Number of ribs on pleural fields	4	5	6	7	8
Number of specimens	—	2	1	3	—

Number of ribs on pleural fields	4	5	6	7	8
Number of specimens	4	13	109	5	—

Mean = 5·88; var. = 0·2465; n = 131

Frequency distribution for the number of pleural ribs developed on the pygidium of *Trinucleus fimbriatus* Murchison. Upper part of table for type locality sample (Gwern-yfed-fâch); lower part for the middle quarry Llanfawr sample.

It may be seen from the above Tables that quantitatively there are no significant differences between the two samples and thus the data from the larger, though non-topotypic sample may be reasonably taken as characterising the species, until such time as more complete data becomes available from the type locality.

DISCUSSION. A difficulty encountered in redescribing this species is the generally poor preservation, particularly of the fringe pits at the type locality, Gwern-yfed-fâch. However it has been shown above that the form found at the middle quarry, Llanfawr appears not to differ significantly from that found at the type locality, and the redescription above has been based mainly on the more satisfactory Llanfawr sample.

Elles (1940: 424–425) in describing two new mutations of *T. fimbriatus*, though on pp. 416, 417 recording *T. fimbriatus* from Gwern-y-fed Quarry and not from Pencerrig Lake, considered (p. 425) Pencerrig Lake to be the type locality of *T. fimbriatus* Murchison. There is, however, no doubt that the lectotype came from Gwern-yfed-fâch. Although her descriptions were brief she did infer that the fringe of *T. fimbriatus* mut. *ultimus* is wider than in the typical form and also that the pits show better radial arrangements at the genal angle. Although she records both the typical form and the *ultimus* mutation as occurring at Llanfawr, no confirmation has been found for the existence of two varieties at this locality, and all would appear to belong to her *ultimus* form. However, it has been shown above that the Llanfawr form does not differ from the form occurring at the type locality of *T. fimbriatus* (Gwern-yfed-fâch); thus Elles's mutation *ultimus* must be considered as a synonym of *T. fimbriatus* s.s. The present study has also shown that Elles's *T. fimbriatus* s.s. and mutation *primus* from Pen-cerig Lake quarry, although dorsally bearing some similarity to *T. fimbriatus*, possess a lower lamella which clearly shows that two E arcs are present and both are here assigned to the genus *Bergamia* Whittard, 1955.

T. acutofinalis Whittard, 1956 is readily distinguished by having only three arcs developed internal to the girder; it also differs in that all the pits are of equal size, and the inter-radial ridges are rounded. *T. foveolatus* (Angelin, 1854) and *T. foveolatus* var. *intermedius* Størmer, 1930 differ from *T. fimbriatus* in being much smaller and in having a median ridge developed on the glabella posterior of the median glabellar node, and also lateral eye tubercles; further the fringe in *T. foveolatus* does not extend behind the posterior margin of the cephalon. *T. bronni* Sars and Boeck *in* Boeck, 1838, is distinguished by its short stubby pygidium with few axial rings and pleural ribs. This last species is very similar to *Bergamia*, particularly in the characters of the pygidium, although Størmer's figures (1930, Pl. 2, figs 2, 5, 6, 7) show only one E arc and so, for the present at least, it seems better to retain this species in the genus *Trinucleus*. *Trinucleus abruptus* sp. nov. (see below) may be easily distinguished by the anterior deflection of the posterior border of the cephalon at the fulcrum, the smaller number of pits in each arc on the fringe and its relatively narrower pygidium with fewer ribs.

Trinucleoides salteri Elles, 1940 is here considered as a junior synonym of *Trinucleus fimbriatus* Murchison. The single known specimen in the Wyatt-Edgell Collection (GSM 35356, Pl. 3, fig. 1) is almost certainly from the basal Caradoc at Gwern-yfed-fâch and is associated with *Trinucleus fimbriatus* and *Cnemidopyge bisecta* (Elles) and not with *Lloydolithus* as claimed by Lamont (1941: 441). Owing to the lower lamella being slightly displaced and pushed up through the upper lamella in places, Elles was misled into believing that the arcs of pits were separated into two series and that tubercles were present laterally. The surface of the glabella and genae is poorly preserved and no trace of any caecae or other surface markings exists. The elongate alae and prominent occipital ring are thought to be accentuated due to distortion on preservation, and the groove between the fringe and left gena to be due to a pygidium folded back beneath the cephalon.

Trinucleus abruptus sp. nov.

(Pl. 3, figs 2–4, 6, 7; Text-fig. 4)

1940 *Trinucleus chamberlaini* Elles: *pars*, pl. 29, fig. 13.
1940 *Trinucleus* cf. *foveolatus* Angelin; Elles: 425, pl. 31, figs 1–2a.

DIAGNOSIS. *Trinucleus* with six arcs of pits developed, most probably being E_1, I_{1-5}; fringe of approximately uniform width with posterior border bent forwards external to fulcrum; inter-radial ridges rounded; small median glabellar node; no eye tubercles. Pygidium triangular with segmented axis and faintly ribbed pleural fields.

TYPE MATERIAL. Holotype. BM In 36920 (Pl. 3, fig. 7). Internal mould of nearly complete specimen.

Paratypes. BM. In 36921 (Pl. 3, fig. 2) Internal mould of complete specimen. BM 59200 External mould of nearly complete specimen. It. 2736 (Pl. 3, fig. 3) Internal mould of nearly complete specimen. It. 2737 Internal mould of pygidium. It. 2738 (Pl. 3, fig. 6) External mould of cephalon. OUM B179 (Pl. 3, fig. 4) Internal mould of nearly complete specimen.

DIMENSIONS.

	A	B	B_1	B_2	B_3	I	I_1	K	K_1
Holotype	7·4	6·0	5·2	4·2	3·0	18·8	14·2	5·2	2·0
In 36921	8·2	7·0	5·7	4·5	3·4	20·3	15·9	5·8	2·3
BM 59200	6·3	5·5	4·5	3·6	2·5	15·3	12·5	4·8	1·8
It. 2736	—	5·8	4·6	3·5	2·1	—	*c.* 14·0	5·0	1·9
It. 2738	—	*c.* 4·2	—	—	—	*c.* 13·5	*c.* 11·1	—	—
OUM B179	*c.* 8·0	*c.* 6·6	—	—	—	18·8	14·6	5·5	*c.* 2·5

	R_1	Q	W	X	Z	No. of axial rings	No. of ribs Left	Right
Holotype	13·8	—	12·5	—	—	—	—	—
In 36921	15·2	6·0	14·1	2·6	4·4	6+	3	2+
BM 59200	11·6	4·8	10·8	2·3	3·8	8+	3+	3+
It. 2736	*c.* 15·0	—	—	*c.* 2·5	*c.* 4·1	6+	4+	4+
It. 2737	—	—	—	2·7	4·3	7+	3+	—
OUM B179	16·0	5·2	12·9	2·5	4·0	9	3	2

All measurements in mm. For explanation of symbols see Text-fig. 1. Measurements on BM 59200 were taken from a latex impression.

TYPE LOCALITY AND HORIZON. The original label affixed to the holotype (figured Elles, 1940, pl. 31, figs 1, 1*a* as *T.* cf. *foveolatus* Angelin) states 'Trinucleus ornatus Sternb. Llandeilo Flags Gwernyfydd. Griffith Davies Coll.' The lithology is, however, completely different from that found at Gwern-yfed-fâch, Nr. Builth, but is very like that found at the small quarries 600 yds east of Upper Gilwern, and the presence of similar specimens at this locality suggests it to be the true locality for the holotype, and also paratypes In. 36921, BM 59200. The evidence of the hand specimen is supported by thin sections taken from the holotype slab and Upper Gilwern material. Of the other paratypes, It. 2736 is from the small quarries 600 yds east of Upper Gilwern and OUM B179 is almost certainly from this locality also; It. 2737, It. 2738 are from the cliff section on the left bank of the Howey Brook half a mile east-south-east of Carregwiber.

DISTRIBUTION. Apart from the two localities from which the type material is drawn, the species is also known from the exposures in the left bank of the track from Bwlch Llŵyn to Hendy Bank, 100 yds south-east of Bwlch Ilŵyn. All these localities are confined to the upper part of the Lower Llanvirn. At present the species is known only from the Builth inlier.

DESCRIPTION. Excluding the genal spines, the complete exoskeleton is oval in outline, but with the maximum cephalic width approximately equal to the total sagittal length.

The elliptical cephalon is about two and a half times as wide as long. The glabella is clavate in plan, strongly convex, extending slightly onto the fringe; three pairs of lateral glabellar furrows developed, the median pair marking the posterior of the prominent pseudofrontal lobe. In profile the glabella is strongly convex anteriorly, levelling off medially and sloping gently down to the posterior. The anterior pair of lateral glabellar furrows, situated just anterior of the mid-point of the glabella, consist of small, weakly developed pit-like depressions in the side of the glabella. The median furrows are more strongly developed and are situated at about two-thirds the distance along the glabella from the anterior. The posterior furrows are well developed, slightly elongate sagittally and mark the front of the weakly developed occiput, near the rear of the glabella. Small crescentic alae are present, though poorly developed. A small median glabellar node is present on the external surface of the glabella situated approximately level with the median pair of lateral glabellar furrows. Medially the external surface of the glabella is covered with small closely spaced pits which may also be present on the sides of the glabella (Pl. 3, fig. 6).

The occipital ring is short (*sag.*), posteriorly convex, transversely arched and overlaps the anterior part of the axis of the first thoracic segment. The occipital furrow is wide and shallow with occipital pits being only weakly developed at the lateral extremities. No occipital spine is present.

Anteriorly the axial furrows are deep and narrow, becoming somewhat wider to the posterior. No anterior fossulae have been observed, but by analogy with other trinucleids it seems likely that they are developed.

The genal regions are transversely semi-oval, the outer margin being strongly convex, the inner margin strongly concave and the posterior margin more or less straight medially, curving forwards at the lateral extremities. The genae are moderately elevated with the outer parts sloping steeply down to the fringe. Externally they are, like the glabella, covered with small pits. Specimen It. 2738 (Pl. 3, fig. 6) shows, on the external surface, a single, unbranched genal caeca extending obliquely from the anterior lateral glabellar furrows to just outside the lateral pits. No eye tubercles or ridges are developed.

The posterior border furrow is moderately deep and narrow axially, becoming wider laterally and terminating in a shallow lateral pit. The posterior margin is straight medially, but is deflected forwards through about 40° at the fulcral processes (Pl. 3, fig. 7).

Internally the lateral glabellar furrows and lateral pits form variably raised platforms. The small median glabellar node is not evident on the inside of the glabella.

The hypostoma is not known.

The fringe is about 1·5 mm in width narrowing to about 1·0 mm in front of the glabella. The upper lamella is gently convex, turning abruptly upwards at the edge to form a prominent rim. The marginal band is declined steeply downwards. Six arcs of pits are developed, the pits of the outer arc being larger than the remainder. The arcs present are probably E_1, I_{1-5} but as the lower lamella is not known there is no way of being certain of this at present. The pits are arranged in shallow radial sulci separated by low, rounded ridges. The radial pattern is persistent, breaking down only at the genal angles. The holotype is the only specimen known showing the individual pits at all clearly; there being nineteen pits in E_1 on the left half-fringe and about eighteen on the right half. The number of pits in the anteromedian rows cannot be determined but five I arcs are present by row 9 on either side of the fringe and continue to the genal angles. Irregularities in the pit distribution occur, the holotype showing two ridges fusing between row 13 and row 14 on the left half of the fringe, and between row 8 and row 9 on the right side (Pl. 3, fig. 7). The paratype OUM B179 (Pl. 3, fig. 4) possesses about 43 pits in the E_1 arc, of which about 21 are situated on the left half-fringe. The preservation of the inner portion of the fringe however does not allow determination of the number of arcs developed.

The facial suture is marginal, being near the bottom of the marginal band anteriorly and tending obliquely across it laterally to be just below the marginal rim at the posterolateral corners, whence it follows the posterior border of the fringe inwards towards the fulcral processes (Pl. 3, fig. 7). The genal spines are known on a single specimen, It. 2736, in which the left spine extends behind the pygidium for about six mm.

The thorax is rectangular in shape, being about two and a half times wider than long. The six segments conform to the usual trinucleid pattern and require no further detailed account. The axial furrows are however better developed dorsally than in the type species.

The triangular pygidium is about three times as wide as long. The posterior margin is defined by a very small raised rim marking the upper limit of the steeply declined posterior border. The convex, clearly differentiated axis may have at least nine rings present, although they are only well developed anteriorly. Up to three faint ribs may be present on the pleural fields in addition to the anterior border (Pl. 3, fig. 4).

Biometrical data. Although relatively few specimens of this species are available, some bivariate analyses have been possible, as detailed below. No

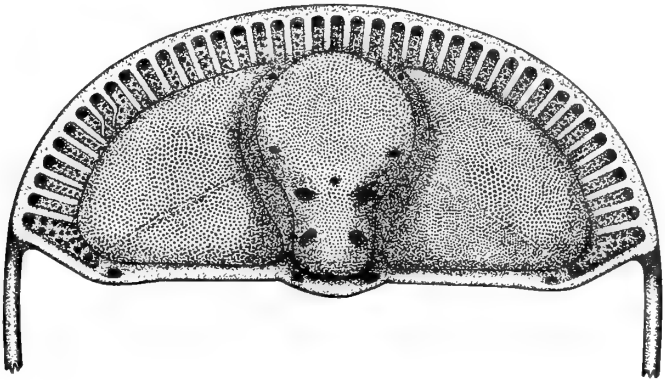

Fig. 4. Reconstruction of the cephalon of *Trinucleus abruptus* sp, nov. in dorsal view. *c.* × 5.

data apart from the few mentioned above in the description are available for the pit distribution or for the pygidial segmentation. All data refer to specimens from, or inferred to be from, the small quarries 600 yds east of Upper Gilwern, unless otherwise stated.

Table 11

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
I_1 : A	14·15	1·9367	7·30	0·6067	0·993	0·993	1·08	0·0078	0·56	0·00209	4
K : K_1	5·18	0·1217	2·00	0·0280	0·959	0·960	1·24	0·0305	0·48	0·00457	6
W : Z	10·74	5·3780	3·58	0·4920	0·967	0·968	0·91	0·0173	0·30	0·00196	5
X : Z	2·20	0·1500	3·58	0·4920	0·985	0·985	1·11	0·0122	1·81	0·03324	5

Bivariate statistics for *Trinucleus abruptus* sp. nov. from the small quarries 600 yds east of Upper Gilwern. All measurements in mm. For explanation of symbols see Text-fig. 1.

Table 12

	B	B_1	B_2	B_3
It. 2736	5·8	4·6	3·5	2·1
In. 36920	6·0	5·2	4·2	3·0
In. 36921	7·0	5·7	4·5	3·4
BM 59200	6·2	5·0	4·1	—
It. 8603	5·5	4·5	3·6	2·5
BU 273	6·4	5·4	4·0	—

Data for the position of the lateral glabellar furrows for *Trinucleus abruptus* sp. nov. Specimen BU 273 from the cliff section in the Howey Brook. All measurements in mm. For explanation of symbols see Text-fig. 1.

Table 13

	R_1	Q	R/Q
In. 36921	15·2	6·0	2·5
BM 59200	12·7	4·8	2·6
It. 8603	11·6	4·8	2·4
It. 8801	9·7	4·1	2·4

Thoracic measurements for *Trinucleus abruptus* sp. nov. All measurements in mm. Measurements for It. 8801 taken from external mould. For explanation of symbols see Text-fig. 1.

Discussion. Although the position of the girder is not known, this species is placed in the genus *Trinucleus* Murchison on the assumption that the outer arc, with the larger pits, represents an E_1 arc. This generic placing is supported by the general *Trinucleus*-like glabella and also by the close similarity between this species and *Trinucleus acutofinalis* Whittard, 1956.

Elles (1940: 425) compared this trilobite with *Trinucleus foveolatus* Angelin, 1854. Apart from the difference in size noted by Elles, the present species differs in fringe shape, lack of eye tubercles, and also in the external surface 'ornament'. In addition the small median glabellar node is more pronounced on the external surface of *T. abruptus*, whereas in *T. foveolatus* it is apparently more prominent on the internal moulds. *T. abruptus* may be distinguished from the somewhat younger, but closely related *T. acutofinalis* by the presence of at least six arcs of pits, and also by the lateral continuation of the sharp upper external rim of the upper lamella. The pygidia of the two species may be separated on the higher number of axial rings and pleural ribs in *T. acutofinalis*. *T. fimbriatus* is readily distinguished by the presence of genal prolongations to the fringe, and a relatively wider pygidium with more ribs. *Trinucleus bronni* Sars and Boeck *in* Boeck, 1838 is distinguished by having only two to four arcs of pits developed and also in possessing lateral eye tubercles.

Although very little information is available, it would appear from the holotype that the same kind of irregularities in the pit distribution as found in *T. fimbriatus* are also present in *T. abruptus*.

A single lower lamella, here described as *Anebolithus* sp. (p. 139, Pl. 4, figs. 3, 5) having no E arcs developed, is known from the type locality of *T. abruptus*, but it differs in outline, particularly at the genal angles. However until such time as a lower lamella is discovered in place in *T. abruptus* there remains the possibility that this species may be better placed in *Anebolithus* Hughes and Wright, 1970.

***Trinucleus* cf. *acutofinalis* Whittard**

(Pl. 3, fig. 5; Pl. 4, figs 4, 7, 8)

FIGURED MATERIAL. It. 2739 (Pl. 3, fig. 5) Internal and external moulds of anterior thoracic segment. It. 2741 (Pl. 4, fig. 4) Internal mould of pygidium and part of thorax. It. 2742 (Pl. 4, fig. 8) Internal and external moulds of damaged cranidium. It. 2743 (Pl. 4, fig. 7) Internal and external moulds of nearly complete specimen.

LOCALITY AND HORIZON. All the figured specimens are from the ashy mudstones and sandstones at the top of the Cwm-Amliw Ash (*Didymograptus murchisoni* Zone) exposed in the stream section about 200 yds south-west of Wern Ddu Barn. Specimens It. 2739–2742 being from the left bank, and specimen It. 2743 from the right bank. These are the only two localities from which the species is known.

DESCRIPTION. The cephalon is slightly over two and a half times as wide as long. Anteriorly the margin is only slightly curved, but becomes more strongly so laterally. The posterior margin is straight axially but is deflected forwards at the fulcrum. The glabella is typically trinucleinid with a swollen anterior portion; details of the lateral glabellar furrows are not known. No indication of any median glabellar node is preserved. The external surface of the genal regions is covered with numerous small pits (Pl. 4, fig. 7). A single genal caeca is developed commencing opposite the mid-point of the glabella and directed obliquely to the genal angle. No eye tubercles or ridges appear to be present. The fringe is narrow and has a prominent marginal rim anteriorly and laterally. Details of the pit distribution are poorly known but it seems probable that four arcs of pits are developed, the inner one or two arcs being absent anteromedially due to the slight encroachment of the glabella onto the fringe. The pits are sunk into radial sulci, there being between seventeen and twenty rows on each half-fringe. Posterolaterally, inter-radial rows with pits of the inner two arcs may be developed (Pl. 4, fig. 8). The position of the girder is not indicated on the upper lamella, though it is possible that the outer arc is external to the girder due to the slightly larger size of the pits.

The thorax appears to conform to the usual trinucleid pattern. As in *T. acutofinalis* and *T. abruptus* sp. nov., the pleural termination of the anterior thoracic segment is markedly oblique (Pl. 3, fig. 5).

The triangular pygidium is nearly three times as wide as long. At least four axial rings and two pleural ribs are developed. Posteriorly the preservation deteriorates, and it is impossible to ascertain if these are the total number of rings and ribs developed.

DISCUSSION. This species is important, for apart from a few incomplete specimens occurring near the base of the Lower *Didymograptus murchisoni* shales, this is the only trinucleid known from the Upper Llanvirn of Builth. Obvious similarities exist between this form and *T. acutofinalis* Whittard from the Betton beds of the Shelve region (Upper part of *D. murchisoni* Zone) with regard to the general outline and fringe details. The marginal rim however, does not diminish laterally and the pygidium has fewer axial rings and pleural ribs than *T. acutofinalis.* In these latter features *T.* cf. *acutofinalis* is more like *T. abruptus* from the upper part of the Lower Llanvirn. However, owing to the probable development of only three I arcs it is thought that these Builth specimens are most closely related to *T. acutofinalis.*

The attitude of the exoskeleton of specimen It. 2743 (Pl. 4, fig. 7) is of interest as the thorax and pygidium are sagittally concave dorsally in a manner akin to, though more pronounced than, the specimen of *Tretaspis seticornis* (Hisinger, 1840) figured by Størmer (1930, fig. 47).

Genus ***ANEBOLITHUS*** Hughes and Wright, 1970

DIAGNOSIS. See page 120.

TYPE SPECIES. *Incaia simplicior* Whittard, 1966.

DISTRIBUTION. Lower Arenig and Lower Llanvirn of the Welsh Borderland.

DISCUSSION. The genus has recently been discussed together with *Incaia* in Hughes and Wright, 1970, and no further discussion is necessary.

Anebolithus sp.

(Pl. 4, figs 3, 5)

FIGURED SPECIMEN. It. 2744 Internal and external moulds of lower lamella.

HORIZON AND LOCALITY. Uppermost part of the Lower Llanvirn (Subzone *D. speciosus*) from the small quarries 600 yds east of Upper Gilwern.

DESCRIPTION. A single specimen is known of a lower lamella apparently having no pits developed external to the girder. It is 14 mm in width at the posterolateral extremities; the estimated cephalic length being about 6·5 mm. The seemingly smooth girder is well developed and nearly semicircular in outline. Traces of two or three arcs of pits internal of the girder are visible with radially arranged pits on most of the convex genal roll. Long outwardly curved genal spines are present extending about 12·5 mm from the posterolateral extremities of the girder, their maximum separation being 16·5 mm which occurs at approximately one-third of their total length as measured from the anterior.

DISCUSSION. Unless the absence of pits external to the girder is due to imperfect preservation it seems that this single specimen is best placed in *Anebolithus* Hughes and Wright, 1970. Its outline, particularly near the genal angles appears to preclude it from being the lower lamella of *T. abruptus*. With only the lower lamella, no adequate comparison can be made with the only other known species of the genus. However it is noteworthy that the Builth specimen is larger and is more smoothly rounded anteriorly than is the case in *A. simplicior* (Whittard, 1966) from the Lower Arenig at Shelve.

Genus ***BERGAMIA*** Whittard, 1955

1966 *Cochliorrhoe* Whittard.

DIAGNOSIS. See page 120.

TYPE SPECIES. *Bergamia rhodesi* Whittard, 1955.

DISTRIBUTION. The genus is known from the British Isles where it is recorded from beds ranging from the Arenig to basal Caradoc, and from the Llandeilo (Dobrotivá Formation) of Czechoslovakia. The genus may also be present in the Upper Llanvirn (4aα) of Norway (Bruton, pers. comm.).

DISCUSSION. In erecting *Bergamia* in 1955 Whittard defined his genus as typically bearing E_1, E_2 and I_1 arcs, fully developed. In 1966, following the discovery of forms apparently lacking between three and five pits of the E_2 arc anteromedially, he erected the genus *Cochliorrhoe* to accommodate forms with E_2 only partially developed. However, the type species of *Bergamia, B. rhodesi* Whittard, has an E_2 pit lacking posterolaterally and might therefore be placed within *Cochliorrhoe* if his diagnosis were strictly followed. It is now known that *Bergamia whittardi* sp. nov. (see p. 146), in common with other trinucleids shows some variation in the total number of pits developed in each arc and in particular in the E_2 arc which is only well developed anterolaterally. In both *Bergamia* and *Cochliorrhoe* the E_2 arc may first appear as twin-pits within the E_1 arc, and from the fringe formulae listed by Whittard (1966: 279–280) it appears that the essential difference between his two genera was that in *Cochliorrhoe* two separate arcs cannot be distinguished, possessing either twinned or distinctly separate pits, until between rows three and five. Although it has been the practice in recent years to base the trinucleid genera on the particular arcs developed, it is thought that the partial development of the E_2 arc does not warrant generic status and it is proposed to consider *Cochliorrhoe* Whittard, 1966 as a junior synonym of *Bergamia* Whittard, 1955.

Bergamia is closely related to *Lordshillia* Whittard, 1966, *Stapeleyella* Whittard, 1955 and *Anebolithus* Hughes and Wright, 1970, but it may be readily distinguished by the presence of the E_2 arc partially or fully developed. *Bergamia* also shows some similarities to *Tretaspis* M'Coy, 1849, but differs in that it has no lists developed between the I arcs of the upper lamella, or eye ridges or tubercles on the genal regions as are typical of *Tretaspis*.

The occurrence of *Bergamia prima* (Elles) and *Bergamia whittardi* sp. nov. is of interest as it is the first record of the genus from the Llandeilo of Britain, it being known previously only from the Llandeilo (Dobrotivá Formation) of Czechoslovakia (Přibyl and Vaněk, 1969). (It is considered by the present author that '*Tretaspis*' *praecedens* Klouček, 1916 was correctly placed in the genus *Bergamia* by Přibyl and Vaněk.) Other previous British occurrences are from the Arenig of South Wales and Shropshire, Lower Llanvirn of Anglesey and from the basal Caradoc of south-east Ireland.

Bergamia prima (Elles)

(Pl. 4, figs 1, 2, 6; Pl. 5, figs 1–6; Pl. 6, figs 1–6, 8; Text-fig. 5)

1940 *Trinucleus fimbriatus* mut. *primus* Elles: *pars*, 410–412, 421, 424, pl. 30, figs 1–3 *non* 4, 5 which are *B. whittardi*.

DIAGNOSIS. *Bergamia* with about twenty to twenty-three pits developed in E_1 and E_2 arcs on each half-fringe; pits of E arcs very close together particularly anterolaterally. Pygidium short, with five or six axial rings and three or four pleural ribs.

TYPE MATERIAL. Holotype. BU 257 (Pl. 4, fig. 6; Pl. 5, figs 1, 2) (Chamberlain Collection) Internal and external moulds of nearly complete specimen.

Paratypes. BU 258 (Chamberlain Collection) Internal mould of incomplete specimen. BU 259 (Chamberlain Collection) External mould of cephalon.

DIMENSIONS.

	A	B	B_1	B_2	B_3	B_4	I_1	K	K_1
Holotype	—	*c.* 5·4	*c.* 4·4	*c.* 3·3	*c.* 2·1	*c.* 2·1	*c.* 12·2	4·4	2·2
BU 258	*c.* 7·0	—	—	—	—	—	—	—	—
BU 259	—	*c.* 6·6	—	—	—	—	*c.* 12·5	*c.* 5·0	—

	R_1	Q	Q_1	W	X	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
Holotype	12·8	5·0	1·0	9·8	2·3	2·5	5	4	4

All measurements in mm. For explanation of symbols see Text-fig. 1.

TYPE LOCALITY AND HORIZON. The type specimens are all from the shales assigned to the Zone of *G. teretiusculus* exposed in the old quarry 350 yds west of Maesgwynne.

OTHER FIGURED MATERIAL. It. 2745 (Pl. 4, figs 1, 2); It. 2746 (Pl. 5, figs 3, 4); It. 2747 (Pl. 6, figs 2, 3); It. 2748 (Pl. 6, fig. 5); It. 2749 (Pl. 5, fig. 6); It. 2750 (Pl. 6 figs 1, 4); It. 2751 (Pl. 6, fig. 6); It. 2752 (Pl. 6, fig. 8); It. 2753 (Pl. 5, fig. 5).

DISTRIBUTION. The species is known only from the Builth region, being recorded with certainty only at the type locality and the stream section 15 yds south-west of the type locality.

DESCRIPTION. Excluding the genal spines, complete specimens are approximately circular in outline.

The semicircular cephalon varies between two and two and a half times as wide as long, excluding the steeply declined fringe. The strongly convex, clavate glabella is elevated well above the genae, overhanging and obscuring the fringe anteriorly. The swollen pseudofrontal lobe is just over one-half of the glabellar length and bears a median node, generally discernible on both internal and external moulds, situated somewhat variably, but generally immediately behind the anterior of the three pairs of lateral glabellar furrows. These furrows occur at about two-fifths of the distance along the glabella from the anterior, and consist of small pit-like depressions in the side of the glabella. The median furrows, marking the posterior of the pseudofrontal lobe, are elongate (*tr.*) pits which extend about half the distance to the sagittal line. The posterior furrows are also elongate (*tr.*) pit-like structures directed anteromedially. Both the median and posterior pairs of lateral glabellar furrows are situated well inside the axial furrows and alae are developed (Pl. 5, figs. 5, 6). A similar depression to that described in *Trinucleus fimbriatus* occurs laterally and slightly posteriorly to the posterior pair of lateral glabellar furrows (Pl. 5, fig. 2). The occiput is generally slightly less than half as wide as the pseudofrontal lobe. A coarse reticulate pattern is developed over the entire external surface of the glabella.

The occipital ring is very short (*sag.*), transversely convex and has no occipital spine. The occipital furrow is shallow medially deepening laterally forming elongate (*tr.*) occipital pits.

Anteriorly the axial furrows are deep and narrow. Posteriorly they converge slightly and become wider and shallower; the alae being situated between the furrows and the glabella. Anterior fossulae are usually poorly preserved.

The genal regions are quadrant-shaped, moderately tumid, with the outer margin declined steeply, and possess a reticulate pattern which becomes less pronounced peripherally on the steep outer margins and posteromedian portions of the genae. No eye ridges or tubercles occur. The posterior border furrow is straight, wide and rather shallow; lateral pits well developed though rarely well preserved (Pl. 6, fig. 4).

The internal surface of the glabella and genae is smooth. The lateral glabellar furrows form raised platforms internally, and small apodemes, corresponding to the anterior fossulae, are present.

The hypostoma is not known.

Although commonly distorted, the fringe probably possessed a steep, nearly vertical genal roll, which flattened out towards the brim. The narrow fringe widens somewhat at the genal angles. Owing to poor preservation, there is very little information concerning the distribution of pits on the fringe. All pits are small and appear to be of approximately equal size. They are arranged in shallow radial sulci separated by low rounded ridges (Pl. 5, fig. 6). The E_1 and E_2 arcs are continuous medially and contain between twenty and twenty-three pits on each half-fringe; at the posterolateral extremity only the E_1 arc is developed. The number of arcs present internal to the girder is uncertain, but probably does not exceed two anteromedially, with up to four present posterolaterally (Pl. 5, fig. 4; Pl. 6, figs 1, 2).

The lower lamella is nearly flat medially, but laterally the girder forms a strong ridge separating an almost flat outer part from a steeply inclined inner region. The E_1 and E_2 are sunken into short sulci and are very close together; at the anterolateral corners they merge into little more than a single arc of twin pits (Pl. 4, fig. 1; Pl. 5, fig. 3; Pl. 6, fig. 3). The girder is apparently smooth and well formed except anteromedially. Posterolaterally it merges with the base of the genal spine. Medially some irregularities may occur with pits of the E_2 arc being absent (Pl. 6, figs 2, 3).

The genal spines are approximately straight, diverging slightly to the rear and with a low dorsal keel; they extend well behind the pygidium (Pl. 4, fig. 6). The entire course of the facial suture has not been traced, but laterally it is marginal, situated high on the marginal band, and becomes dorsal at the genal angle.

The thorax consists of six segments and conforms to the general trinucleid type. It is not more than about two and a half times as wide as long, and narrows slightly to the rear. The distal extremities of the pleurae are deflected posteriorly and ventrally, the amount of deflection becoming progressively greater posteriorly. A strong pleural ridge divides the pleurae into a small posterior and a larger anterior band. A small median node is present on the anterior portion of the axis of each segment (Pl. 4, fig. 6).

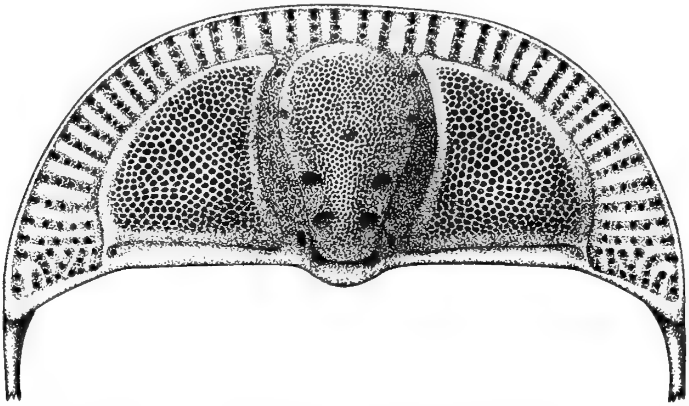

FIG. 5. Reconstruction of the cephalon of *Bergamia prima* (Elles) in dorsal view. *c.* × 7.

The triangular pygidium is slightly less than four times as wide as long. Excluding the articulating half ring, the anterior margin is straight except for the posteriorly directed lateral extremities. The posterior and lateral margins are marked by a low ridge at the upper limits of the steeply declined border region, with closely spaced terrace lines developed on the external surface. The axis is convex, clearly differentiated and segmented, with between three and six axial rings plus a small terminal piece. The axis continues posteriorly as a convex protuberance on the border region (Pl. 5, fig. 5). Anteriorly the axis occupies about one-fifth of the width of the pygidium, tapering posteriorly to about half this width. As is usual in the trinucleids the axial furrows are slightly more prominent on internal than external moulds. The pleural fields are flat and each has an anterior border, usually three or four ribs (rarely two), and a small triangular terminal area. The furrows separating the ribs are straight, sub-parallel and directed slightly to the posterior.

The species exhibits discoidal enrollment as is normal in the trinucleids (Pl. 6, fig. 8).

ONTOGENY. Of the two small specimens known from the stream section 15 yds south-west of the type locality, the larger has a maximum genal width of 4·6 mm and is assocated with four slightly disarticulated thoracic segments and a pygidium, and may thus represent a meraspid degree four. Apart from their size, the specimens are similar to larger individuals, except that the glabella and genal regions are more highly convex (Pl. 6, fig. 5).

DIMENSIONS.

	A	A_1	B	B_1	B_2	B_3	B_4	I_1	K	K_1
It. 2748	2·6	2·4	2·2	1·8	1·4	—	11·1	4·6	1·4	0·7

All measurements in mm. For explanation of symbols see Text-fig. 1.

BIOMETRICAL DATA. Various analyses were undertaken on the major features of the dorsal exoskeleton. Since data for the type locality sample is rather scant, data is also given for the total sample from the inlier.

TABLE 14

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
B : K	5·14	0·9730	4·10	0·5850	0·974	0·975	0·97	0·0158	0·78	0·01020	5
I_1 : B	9·38	7·4444	4·17	1·5625	0·976	0·977	1·03	0·0069	0·46	0·00141	9
A : B	4·70	2·0850	4·26	2·1630	0·997	0·998	1·12	0·0020	—	—	5
B : B_1	4·29	1·8958	3·33	1·1106	0·984	0·985	0·99	0·0026	0·77	0·00164	13
B : B_2	4·49	1·7961	2·84	0·7334	0·985	0·986	1·01	0·0024	0·64	0·00102	14
B : B_3	3·66	1·4330	1·50	0·1650	0·997	0·998	0·83	0·0008	0·34	0·00020	5
B : K	4·23	1·4450	3·35	1·1507	0·978	0·979	1·12	0·0037	—	—	16
K : K_1	3·42	1·4976	1·50	0·2560	0·983	0·984	0·95	0·0031	0·41	0·00062	11
W : X	6·40	3·9950	1·24	0·2480	0·974	0·977	1·27	0·0238	0·25	0·00104	5
X : Z	1·46	0·1776	1·79	0·1774	0·824	0·830	0·82	0·0191	1·00	0·02909	13

Bivariate statistics for *Bergamia prima* (Elles). Upper part of table for the type locality sample; lower part for the total sample from the inlier. All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 15

	B	B_1	B_2
It. 2750	5·7	4·3	3·6
It. 2753	5·5	—	3·2
It. 8805	5·0	—	3·2
It. 8803	6·2	4·7	3·8
It. 8804	6·0	4·9	3·9

Data for the position of the lateral glabellar furrows for *Bergamia prima* (Elles) from the type locality. Data are insufficient to give meaningful bivariate statistics. All measurements in mm. Measurements for It. 8805 taken from external mould. For explanations of symbols see Text-fig. 1.

TABLE 16

	R_1	Q
BU 257	12·8	5·0
It. 2753	11·3	5·1
NMW 68.376.G189	7·0	3·1
NMW 68.376.G190	9·8	4·0

Thoracic measurements for *Bergamia prima* (Elles). First two specimens from the type locality. All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 17

	W	X	Z
BU 257	9·8	2·3	2·5
It. 2753	8·5	1·7	2·3
NMW 68.376.G191	—	1·9	2·2
It. 8802	—	1·1	1·5
NMW 68.376.G192	—	1·9	2·4

Pygidial measurements for *Bergamia prima* (Elles), from the type locality. All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 18

Number of axial rings	3	4	5	6
Number of specimens	—	—	3	1
n = 4				
Number of axial rings	3	4	5	6
Number of specimens	1	7	12	1
n = 21				

Frequency distributions for the number of pygidial axial rings developed in *Bergamia prima* (Elles). Upper part of table for the type locality sample; lower part for the total sample from the inlier.

TABLE 19

Number of pleural ribs	2	3	4
Number of specimens	—	6	2
n = 8			
Number of pleural ribs	2	3	4
Number of specimens	1	13	14
n = 28			

Frequency distributions for the number of pygidial pleural ribs developed in *Bergamia prima* (Elles). Upper part of table for the type locality sample; lower part for the total sample from the inlier.

DISCUSSION. Owing to the poor preservation of the fringe on much of the material available, Elles (1940: 424) erroneously believed this species to occur at Pencerrig Quarry, and to be conspecific with a form from Pencerrig Lake quarry which she considered as a mutuational form of *Trinucleus fimbriatus* Murchison, 1839. The presence of the two arcs of pits external to the girder clearly separates this species from *T. fimbriatus* and indicates its relationship to the genus *Bergamia* Whittard, 1955. The superficially similar form occurring at Pen-cerig Lake quarry is here referred to *Bergamia whittardi* sp. nov., and may be distinguished from *Bergamia prima* by the E_2 arc being present only anteriorly.

Bergamia rhodesi Whittard, 1955 is similar to *B. prima*, but with apparently slightly fewer pits in each arc. However, the data at present available are insufficient to determine the amount of variation of the number of pits in each arc for either of these two forms. Subsequent collecting may well show them to be synonymous, in which case *B. prima* (Elles) would take priority. *B. prima* is easily distinguished from *B. praecedens*, (Klouček) by the smaller number of pits along the posterior margin of the fringe, the closeness of the E_1 and E_2 arcs and the differing surface sculpture on the glabella. *B. prima* is distinguished from *B. inquilium* (Whittard, 1966) and *B. matura* Whittard, 1966, which are thought to represent but a single species, by its greater number of pits in the E arcs and the median development of the I_2 arc. *'Trinucleus' gibbsi* Murchison, 1859, *'Trinucleus' sedgwicki* Salter, 1866 and *'Trinucleus' etheridgei* Hicks, 1875 were provisionally placed by Whittard in *Bergamia*. *B. gibbsi* may be distinguished by its apparent lack of pits internal to the girder lateral to row 8. *B.? sedgwicki* appears to be similar to *B. prima* in general shape and in the presence laterally of three arcs internal to the girder, but differs in having fewer pits in the E_1 and I_1 arcs. *B.? etheridgei* is here considered as a *nomen dubium* (see Whittard, 1955: 35), on account of the poor preservation of the type specimens. Preliminary studies on *'Trinucleus' hibernicus* Reed, 1895 from the Tramore Limestone Series support Whittard's (1955: 31) view that the species is best placed in *Bergamia*, as E_2 arc is fully developed, excepting for two or three pits at the posterolateral extremities of the arc, while one arc occurs internal to the girder. It is easily distinguished from *B. prima* by this single I arc, further, the separation of the two E arcs is greater in *B. hibernicus*. The specimens referred to *Bergamia* (?) sp. by Bates (1968: 184–185, pl. 13, figs 3, 4, 9, 13) from the

Lower Llanvirn of Anglesey are clearly referable to this genus though insufficient detail is known to allow proper comparisons with other known species.

Bergamia whittardi sp. nov.

(Pl. 6, fig. 7; Pl. 7, figs 1–12; Pl. 8, figs 1–9, 11; Pl. 9, figs 1, 2; Text-figs 6, 7)

1851 *Tretaspis fimbriatus* (Murchison); Sedgwick and M'Coy: *pars*, 146, pl. 1E, figs 16, 16a.
1914 *Trinucleus fimbriatus* Murchison; Reed: *pars*, 350–352, 354, pl. 28, figs 1, 3, *non* fig. 2.
1940 *Trinucleus fimbriatus* mut. *primus* Elles: *pars*, 410–412, 421, 424, pl. 30, figs 4, 5.

DIAGNOSIS. *Bergamia* with up to fourteen pits present anteromedially in E_2 arc (full-fringe), E_1 arc fully developed with about twenty-six to thirty pits (half-fringe); I_{1-5} arcs developed laterally.

TYPE MATERIAL. Holotype. BU 260a (Chamberlain Collection) (Pl. 7, fig. 6) (figured as *Trinucleus fimbriatus* mut. *primus* by Elles, 1940, pl. 30, fig. 5) Mould of dorsal surface of incomplete lower lamella.

Paratypes. It. 2754 (Pl. 7, fig. 12) Internal mould of nearly complete specimen. It. 2755 (Pl. 8, fig. 3) External mould of nearly complete specimen. It. 2756 (Pl. 7, fig. 7) Fragment of mould of dorsal surface of lower lamella. It. 2757 (Pl. 8, fig. 7) Internal mould of cephalon. It. 2758 (Pl. 7, fig. 10) Internal mould of nearly complete specimen. It. 2759 (Pl. 7, fig. 3) Fragment of mould of dorsal surface of lower lamella. It. 2760 (Pl. 8, fig. 1) Internal mould of nearly complete specimen. Wattison Collection H14 (Pl. 8, fig. 9) Internal mould of damaged cephalon.

DIMENSIONS.

	A	A_1	B	B_1	B_2	B_3	B_4	I_1	K	K_1
It. 2754	—	—	5·7	4·5	3·8	2·6	—	10·5	3·4	1·6
It. 2755	—	2·6	2·0	1·6	1·2	—	1·0	—	1·5	—
It. 2758	—	—	2·3	1·9	1·4	0·9	—	5·7	2·1	1·8
Wattison Coll. H14	*c.* 8·0	—	—	5·1	4·0	2·9	3·0	*c.* 15·0	4·8	—

						No. of	No. of ribs	
	R_1	Q	W	Z	W	axial rings	Left	Right
It. 2755	4·5	1·9	3·6	0·7	0·8	3+	3	3
It. 2757	—	—	10·3	3·1	2·7	6	4	4
It. 2758	*c.* 5·7	2·5	4·7	0·8	1·2	4+?	3	3

All measurements in mm. For explanation of symbols see Text-fig. 1.

Fringe data for holotype. Left half-fringe: E_1 1–*c.* 27; E_2 1–*c.* 7; I_1 1–*c.* 21; I_2 1–*c.* 19; I_3 1–*c.* 19; I_4 11–*c.* 19; I_5 17–*c.* 19. Auxiliary pit: xvi, xvii, xviii present in I_{3-5}. Number of radial rows *c.* 19.

TYPE LOCALITY AND HORIZON. The holotype and all the paratypes are from the small quarry at the south-western end of Pen-cerig Lake in shales of the uppermost

Llandeilo, with the exception of paratype It. 2760 which is from shales of Llandeilo age from the stream section 120 yds south-east of Tre coed.

OTHER FIGURED MATERIAL. It. 2761 (Pl. 7, fig. 9); It. 2762 (Pl. 7, fig. 1); It. 2763 (Pl. 8, fig. 11); It. 2765 (Pl. 9, fig. 1); It. 2766 (Pl. 7, fig. 8); It. 2767 (Pl. 9, fig. 2); It. 2768 (Pl. 8, fig. 4); It. 2769 (Pl. 8, fig. 8); It. 2770 (Pl. 8, fig. 5); It. 2771 (Pl. 7, fig. 5); It. 2772 (Pl. 7, fig. 2); It. 2773 (Pl. 6, fig. 7); It. 2774 (Pl. 8, fig. 6); It. 2775 (Pl. 8, fig. 2); It. 2776 (Pl. 7, fig. 4); It. 2778 (Pl. 7, fig. 11).

DISTRIBUTION. The species has only been recorded from the Llandeilo of the Builth region. It is extremely abundant in the Pen-cerig Lake quarry and is also known from the Dulas Brook as well as the other locality from which the type material is drawn.

DESCRIPTION. Excluding the genal spines, complete specimens are generally subcircular to oval in outline (Pl. 7, fig. 10; Pl. 8, fig. 2).

The cephalon is semicircular and, excluding the fringe, varies between two, and two and a half times as wide as long. The clavate glabella, its furrows and the occipital ring are similar to those of *Bergamia prima*. The median glabellar node is typically not well developed on internal moulds, while axial furrows and alae are again very similar in the two species.

The genal regions are quadrant-shaped, less tumid than in *B. prima* and have a strong reticulate pattern which is most coarsely developed along a diagonal band from the genal angles to the antero-median corner of each genae. No eye ridges or tubercles are present. The posterior border furrows are wide, shallow and more or less straight, terminating in clearly developed lateral pits. Rarely, traces of the

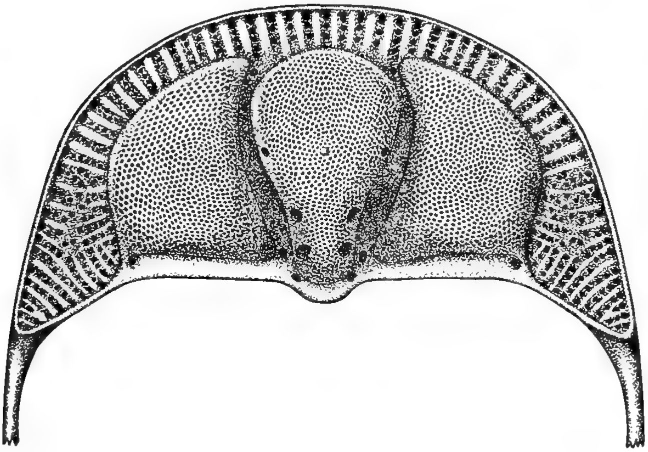

FIG. 6. Reconstruction of the cephalon of *Bergamia whittardi* sp. nov. in dorsal view. *c.* × 10.

reticulate pattern are present in internal moulds (Pl. 8, fig. 9). Internal platforms reflecting the lateral glabellar furrows are present as in *B. prima.*

The hypostoma is not known.

The preservation of the fringe varies considerably. In the majority of specimens the fringe is fairly flat, commonly showing signs of cracking around its inner margin (Pl. 8, fig. 9). In a few specimens, however, the genal roll is steeply inclined as in *B. prima.* Although much of the flattening of the fringe may be attributed to preservation in shale, it is considered that the initial inclination of the fringe of *B. whittardi* may not have been so great as in *B. prima.* The pits are arranged in shallow radial sulci which are separated by low rounded ridges. The pits of the E_1 and I_1 arcs are larger than the rest, which are small and subequal in size. Dorsally the pits of the anteromedially developed E_2 arc are very close to those of the E_1 arc and give the impression of twin-pits; ventrally the pits, although closely spaced, are separated and represent two distinct arcs (Pl. 7, figs 3, 6, 7).

Insufficient data are available to allow a full statistical description of the pit distribution on the fringe, but the following observations may be made. The number of pits in the E_1 and I_1 arcs varies between about twenty-four and thirty. The development of the E_2 arc anteromedially appears to vary, but at least seven pits are present on the half-fringe of the holotype. Specimen It. 2754 suggests, however, that the pits of the E_2 arc are not always present in all the anteromedian rows. Only a single specimen, It. 2754, shows the arc internal to the girder at all clearly (Pl. 7, fig. 12). On the left half-fringe of this specimen arcs I_1 and I_2 are present medially with I_3 appearing at row four, I_4 at row nine and I_5 at row twelve. The genal flanges are large and consist of an outer fimbriate zone incorporating the pits of the E_1, I_1 and I_2 arcs, and an inner fimbriate zone with four or five pits in each row developed along the margin of the genae and along the posterior border. Up to about twelve rows of pits may be present in this inner zone. The central triangular area between the two fimbriate zones has its pits irregularly positioned (Pl. 7, fig. 12). The genal flange has up to seven or eight E_1 pits on its posterior extension from the cephalon.

The facial suture is marginal medially where it is situated very high on the marginal band becoming dorsal at the genal angles. The girder merges posterolaterally with the base of the genal spines. Only the anterior portions of the genal spines are known and are gently curved in a smooth arc continuous with the lateral cephalic margins.

The thorax is typically trinucleid and is very similar to that of *B. prima.* The extremities of the pleurae are however slightly less strongly deflected posteriorly (Pl. 7, fig. 1).

The triangular pygidium is about four times as wide as long, with the anterolateral corners deflected slightly posteriorly as noted in the thoracic segments. The number of axial rings ranges from five to seven, with two to four pleural ribs. In all other features the pygidium is very similar to that of *B. prima.*

ONTOGENY. The only certain meraspis is of degree four and has the posterior margin of the fringe directed anterolaterally from the genal angle in a similar manner to that found in the meraspis of *Trinucleus fimbriatus*. On the other hand, the smallest certain holaspis has well-developed genal flanges extending posterior to the cephalon (Pl. 7, fig. 11; Pl. 9, fig. 1). It seems reasonable to assume that other small isolated cephala with the posterior border of the fringe directed either anterolaterally or transversely are also late meraspides. The degree four meraspis is about 4 mm in length and is very like the holaspid form apart from the number of segments and the anterolaterally directed posterior margin of the fringe. The genae rise fairly steeply from the axial furrows, leaving the posterior part of the axial furrows and the alae rather sunken. Collections also include a single isolated cranidium which is slightly smaller, but otherwise similar; this is also presumed to be of degree 4. An impression of an enrolled individual of similar size, is too poorly preserved to reveal its stage of development (Pl. 6, fig. 7). Four slightly larger isolated cephala have a posterior margin to the fringe which becomes directed progressively less anterolaterally, until in the largest individual it is directed transversely (Text-fig. 7). This last form may be a degree five meraspis, but until more specimens showing the number of thoracic segments are available no definite assignment can be made.

A single tiny isolated pygidium (maximum width approximately 2·4 mm), though poorly preserved, shows a segmented axis and ribbed pleural fields (Pl. 7, fig. 2). This pygidium is slightly smaller than that of the degree four meraspis and may thus represent an earlier meraspis degree.

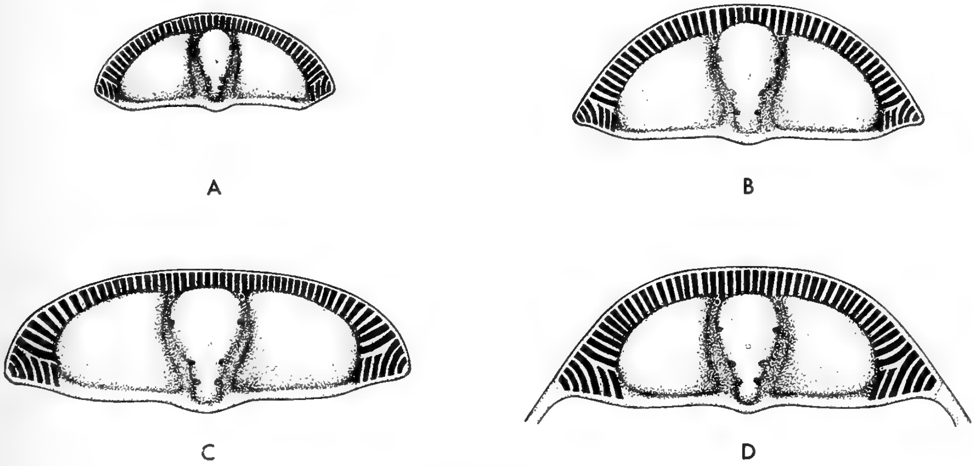

FIG. 7. Diagram illustrating the change in the posterolateral outline of the fringe in meraspides of *Bergamia whittardi* sp. nov. with increase in size. *c.* × 7. A based on It. 2763 (Pl. 8, fig. 11); B on It. 2765 (Pl. 9, fig. 1); C on It. 2768 (Pl. 8, fig. 4); D on It. 2775 (Pl. 8, fig. 2).

TABLE 20

	A_1	B	I_1	K	W	Z	Degree
It. 2772	—	—	—	—	—	0·5	?
It. 2763	—	*c.* 1·2	3·0	0·8	—	—	?
It. 2773	—	*c.* 1·2	*c.* 2·8	—	—	—	?
It. 2765	*c.* 2·0	*c.* 1·6	—	—	*c.* 3·0	0·5	4
It. 2768	1·8	1·5	3·7	1·0	—	—	?
It. 2775	1·8	*c.* 1·5	3·0	0·8	—	—	?
It. 2774	1·9	1·5	3·2	0·8	—	—	?
It. 2778	1·7	1·5	3·8	1·3	—	—	holaspis

Dimensions of meraspides and the smallest known holaspis of *Bergamia whittardi* sp. nov. All measurements in mm. For explanation of symbols see Text-fig. 1.

BIOMETRICAL DATA. A number of bivariate analyses were undertaken and the results given below. As the majority of data available are from the type locality sample (Pen-cerig Lake quarry), the data given are restricted to this sample.

TABLE 21

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
I_1 : A	6·42	5·2870	3·42	1·2620	0·990	0·991	0·92	0·0053	0·49	0·00160	5
I_1 : B	6·48	5·9209	2·89	1·4622	0·971	0·974	1·11	0·0032	—	—	22
A : B	3·38	1·0177	2·82	0·7017	0·997	0·997	1·00	0·0015	0·83	0·00110	6
B : B_1	4·13	2·9090	3·27	1·8140	0·994	0·995	1·00	0·0009	0·79	0·00063	13
B : B_2	4·35	2·4918	2·75	1·0118	0·990	0·991	1·01	0·0019	0·64	0·00082	12
B : B_3	4·30	2·3720	1·82	0·3737	0·988	0·989	0·94	0·0050	0·40	0·00095	6
B : B_4	4·22	3·1370	2·14	0·6280	0·968	0·971	0·89	0·0152	0·45	0·00417	5
B : K	3·20	2·1153	2·22	1·2703	0·973	0·976	1·11	0·0022	—	—	29
W : Z	6·56	6·9538	1·63	0·5246	0·979	0·981	1·10	0·0056	0·27	0·00039	10
W : X	6·56	6·9538	1·28	0·3173	0·985	0·987	1·09	0·0039	0·21	0·00017	10
X : Z	1·39	0·3341	1·79	0·5974	0·981	0·982	1·04	0·0034	1·34	0·00613	13

Bivariate statistics for *Bergamia whittardi* sp. nov. from the type locality. All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 22

	R_1	Q
It. 2755	4·5	1·9
It. 2762	8·5	2·5
It. 2758	*c.* 5·7	2·5

Details of thoracic measurements for *Bergamia whittardi* sp. nov. from the type locality. All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 23

Number of pleural ribs	3	4
Number of specimens	2	12

n = 14

Frequency distribution for the number of pleural ribs developed in *Bergamia whittardi* sp. nov., from the type locality.

TABLE 24

Number of axial rings		5	6 or 7
Length of	0·19–1·9 mm	5	2
pygidial axis	2·0–2·7 mm	5	4

Details of the number of axial rings developed in *Bergamia whittardi* sp. nov. from the type locality sample.

The figures in Table 24 above suggest that for the type locality sample there is possibly a correlation between the size and the number of axial rings developed ($P = 0{\cdot}06$). This is confirmed by the data for the total known sample of the species where $P < 0{\cdot}05$.

DISCUSSION. *Bergamia whittardi,* although closely related to *B. prima* (Elles) may be readily distinguished from that and all other species assigned to *Bergamia* by the incomplete E_2 arc being developed only anteromedially. It also differs from *B. prima* in having a slightly higher number of axial rings developed on the pygidium. *B. inquilium* (Whittard, 1966) is similar in having an incomplete E_2 arc, but in this species it is only developed in the posterolateral regions. *B. praecedens* may also be distinguished by the greater separation of E_1 and E_2 and by the surface sculpture.

Trinucleinid gen. et sp. indet.

(Pl. 8, fig. 10; Pl. 9, figs 3, 7)

FIGURED MATERIAL. It. 2779 (Pl. 8, fig. 10) Internal and external moulds of pygidium and posterior part of thorax. It. 2780 (Pl. 9, figs 3, 7) Internal and external moulds of nearly entire specimen.

LOCALITY AND HORIZON. Both specimens occur in the Lower *Didymograptus murchisoni* shales. Specimen It. 2779 being from the pale ashy shales in the track exposures about sixty yards south-west of Bwlch-y-cefn and It. 2780 from the darker shales of the main tributary to the Howey Brook.

DESCRIPTION. The complete specimen is about 14 mm long, and excluding the fringe, is approximately 12 mm wide (Pl. 9, figs 3, 7). Very little detail is preserved of the cephalon. The glabella however appears to expand anteriorly as is typical of the trinucleinae. Long curved genal spines extend posteriorly of the pygidium.

The thorax appears to be typically trinucleid.

The pygidium is triangular in outline, just under four times as wide as long. Faint traces of segmentation are visible on the axis and one very weakly developed rib may be present on the pleural fields.

Discussion. These two specimens are worthy of note owing to the extreme rarity of trinucleid remains in the Lower *Didymograptus murchisoni* shales of the Builth region. The only others known are three fragments of a cryptolithinid. The two specimens described above are here considered as belonging to the same form owing to the similarity of the pygidia and their similar stratigraphical age. Until more complete and better preserved material is available no real comparisons can be made with other forms, though it is noted that *T.* cf. *acutofinalis* occurs at Builth only a little higher in the succession at the top of the Cwm-Amliw Ash.

Subfamily **CRYPTOLITHINAE** Angelin, 1854

Genus ***CRYPTOLITHUS*** Green, 1832

Diagnosis. See page 120.

Type species. *Cryptolithus tessellatus* Green.

Distribution. The genus is recorded with certainty in the British Isles from the uppermost Llanvirn to Upper Caradoc. In N. America the genus does not appear until the Upper Caradoc (Barnveld of Fisher, 1962). The genus is present in the Caradoc and Ashgill of Czechoslovakia (Přibyl and Vaněk, 1969) and may also be present in the Caradoc of South-eastern Turkey (Dean, 1967).

Discussion. With the inclusion of all the cryptolithinids of the Lower Llanvirn of the Builth district in *Bettonia*, the earliest known representative of *Cryptolithus* is from the passage beds at the top of the Betton Beds (top of *D. murchisoni* Zone) in the Shelve region. There is thus a possibility that *Cryptolithus* may have developed from *Bettonia* by the loss of the frontal adventitious pits. The N. American species possess a smaller number of arcs internal to the girder than is typical of the British species and it is thought that further studies may reveal the existence of two or more genera at present placed within *Cryptolithus*.

Cryptolithus instabilis sp. nov.

(Pl. 9, figs 4–6, 8; Pl. 10, figs 1–8; Pl. 11, figs 5, 12; Text-fig. 8)

Diagnosis. *Cryptolithus* with about thirty pits in the E_1 and I_1 arcs on each half-fringe; I_{1-3} continuous medially; I_4 generally appearing at row three or four; I_5 and I_6 commencing at approximately row eight and twelve. Irregularities in pit arrangement common, particularly in inner I arcs.

Type material. Holotype. It. 2792 (Pl. 10, fig. 1) Internal mould of cranidium. Paratypes. It. 2793 (Pl. 9, fig. 4) Mould of ventral surface of lower lamella. It. 2794 (Pl. 9, fig. 5) Internal mould of cranidium with thorax and pygidium folded beneath cephalon. It. 2795 (Pl. 11, fig. 5) Internal mould of pygidium. It. 2796 (Pl. 10, fig. 3) Internal mould of nearly complete specimen. It. 2797 (Pl. 10, fig. 4) Internal and external moulds of damaged cranidium. It. 2798 (Pl. 10, fig. 2) Internal mould of damaged cranidium. It. 2799 (Pl. 10, fig. 6) Internal mould of damaged cephalon. It. 2800 (Pl. 11, fig. 12) Ventral surface of part of lower lamella. It. 2801 (Pl. 10, fig. 5) Internal mould of damaged cranidium. It. 2802 (Pl. 9, fig. 6) Internal mould of nearly complete specimen. It. 2803 (Pl. 10, fig. 7) Internal mould of nearly complete specimen.

Dimensions of type and figured material.

	A	A_1	B	I	I_1	K	K_1
Holotype	6·6	—	5·3	13·6	11·0	3·0	1·2
It. 2793	—	—	—	*c.* 12·5	—	—	—
It. 2794	—	—	*c.* 6·1	—	*c.* 11·2	—	—
It. 2796	*c.* 7·5	—	*c.* 6·1	—	12·5	—	—
It. 2797	*c.* 5·7	—	*c.* 4·7	—	—	—	—
It. 2798	7·9	—	6·4	—	12·5	3·5	—
It. 2799	8·8	—	6·8	—	—	3·0	—
It. 2801	6·1	6·7	—	—	—	3·1	—
It. 2802	—	—	4·0	—	—	—	1·4
It. 2803	7·2	—	5·4	—	12·2	3·0	1·5
It. 2804	8·2	—	6·5	17·5	12·5	3·6	1·7
It. 2805	6·2	—	5·0	—	9·7	2·7	—

				No. of	No. of ribs	
	W	X	Z	axial rings	Left	Right
It. 2795	9·8	1·6	2·8	10+	5	5
It. 2802	8·0	1·4	2·0	—	5	5

All measurements in mm. For explanation of symbols see Text-fig. 1. Note B – glabellar length, is measured from the anterior of the pre-glabellar field.

Type locality and horizon. The holotype and paratypes It. 2793–2799 are from the Llandeilo shales exposed in the left bank of the Dulas Brook, 60 yds north of spot height 727, 150 yds south-west of the old quarry 350 yds west of Maesgwynne. Paratypes It. 2800–2803 are from shales of similar age exposed at the easterly end of the stream section 160 yds south-east of Tre coed.

Other figured material. It. 2804 (Pl. 10, fig. 8); It. 2805 (Pl. 9, fig. 8).

Distribution. The species is known with certainty only from the two localities yielding the type specimens, although it is probably present in the stream section

15 yds south-west of the quarry at Maesgwynne, and in the lane leading to Newmead, but preservation at these latter localities is not good enough to allow positive identification.

Description. Excluding the fringe and genal spines, complete individuals are roundly rectangular in outline, being slightly longer than wide.

The cephalon is approximately semicircular with no marked angulation anterolaterally. The clavate, convex glabella commonly has a low median ridge extending behind a small median glabellar node. Three pairs of lateral glabellar furrows are present, generally taking the form of shallow, oval depressions on the sides of the glabella (Pl. 9, fig. 6). In some cases, however, the furrows appear much deeper, but this is attributed to distortion (Pl. 10, fig. 2). Suggestions of weakly developed alae are present in a few specimens (Pl. 10, fig. 3). Anteriorly the glabella is truncated rather squarely by a shallow preglabellar furrow separating the glabella from a narrow ribbon-shaped preglabellar field.

The occipital furrow is shallow and broad medially, deepening laterally into deep occipital pits. The occipital ring consists of little more than an expanded base to a well developed occipital spine.

Anteriorly the axial furrows are deep and narrow, with well developed fossulae, which are bounded anteriorly by a ridge linking the genal regions and the preglabellar field, thus terminating the axial furrows behind the fringe. The furrows are gently curved and become shallower and wider to the posterior.

The genal regions are quadrant-shaped and only gently convex. Some specimens show traces of two thin simple genal caecae on the external surface of the genae (Pl. 10, figs 6, 7). The external surface of both the genae and glabella is covered with numerous small pits (Pl. 10, fig. 4). No eye tubercles or ridges are developed. The posterior border furrow is straight, wide and shallow; lateral pits appear not to be developed.

Internally the lateral glabellar furrows are developed as slightly raised areas, while apodemes correspond to the anterior fossulae. No trace of the median glabellar node or median ridge has been detected on internal moulds.

Full details of the fringe are not known due to the lack of really well-preserved material. In general character, the fringe is of typical cryptolithid-type with a strong I_{1-2} ridge on the upper lamella; slightly larger E_1 and I_1 pits and a basic radial arrangement of the pits of all arcs. A characteristic feature of the species is the frequent irregularities of pit distribution.

There are between twenty-seven and thirty pits in the E_1 and I_1 arcs on each half-fringe, the total number of which, as far as can be ascertained from the limited amount of material available, is not dependent on the size of the individual. Posterolaterally, auxilliary pits are commonly developed in the E_1 arc (Pl. 10, fig. 1). The inner arcs are not well known, but anteriorly all the pits show a basic radial arrangement; laterally this radial pattern is lost due to the development of auxiliary pits in the inner arcs. The development of these extra pits appears to follow no set pattern, nor is their arrangement typically symmetrical. In general the arcs I_{1-3} are continuous anteriorly, though in about one-fifth of the specimens the I_3 arc is absent in row 1. I_4 generally commences at row 3, but in a few cases it appears in row 2, 4 or 5 (see Table 25). Laterally arcs I_5 and I_6 commence at about row 8 and 12 respectively.

The genal flanges are well developed, extending a short distance behind the posterior margin of the cephalon. Between sixty and seventy irregularly placed pits are developed on each flange. In many specimens the inner portion of the ridge separating rows five and six is markedly swollen causing some distortion in the general radial pattern present anteriorly (Pl. 10, figs 1, 7). On the lower lamella the girder is only slightly more strongly developed than the pseudogirders separating the various I arcs. The pseudogirders and girder bear terrace lines on the outer surface. Two specimens, It. 2804 (Pl. 10, fig. 8) and It. 2805 (Pl. 9, fig. 8) are provisionally included in this species although they show slight differences in that they have a single pit of the E_1 arc situated on the sagittal line. It. 2804 also shows considerable amount of irregularity in the development of the inner I arcs, particularly laterally. The marginal facial suture is only rarely observed (Pl. 10, figs 2, 8). The proximal end of the genal spines are directed more or less posteriorly, the distal ends being unknown.

The thorax is rectangular and of typical trinucleid morphology.

The triangular pygidium is about three times as wide as long. The convex axis has at least ten axial rings, whilst the pleural fields are gently undulate with a narrow border, five or six ribs and a small terminal area. The ribs are directed somewhat posteriorly, this deflection being increased distally. The number of ribs developed is not related to the pygidial length (see Table 27).

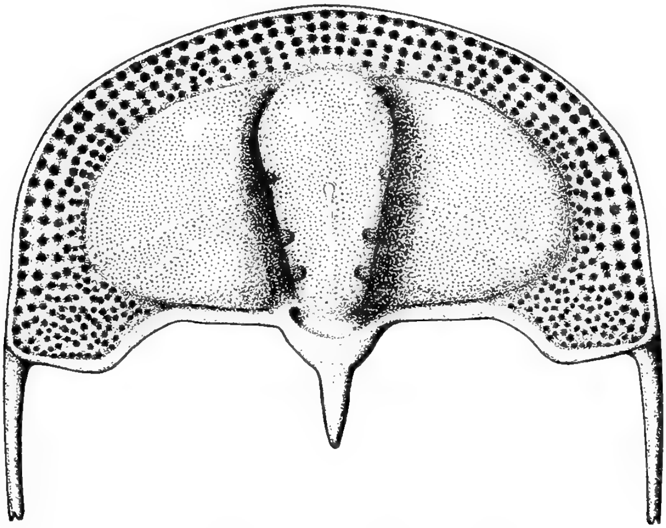

FIG. 8. Reconstruction of the cephalon of *Cryptolithus instabilis* sp. nov. in dorsal view. *c.* × 6.

Biometrical data.

Table 25

	Commencing row of arc I_4							
left half-fringe	3	3	4	4	3	3	3	—
right half-fringe	2	3	4	—	3	3	—	5

Details of the row in which I_4 arc commences in eight specimens of *Cryptolithus instabilis* sp. nov.

Table 26

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
I_1 : A	10·92	6·3644	6·33	3·3800	0·917	0·920	1·25	0·0341	0·73	0·01208	9
I_1 : B	11·60	5·1727	5·75	1·8191	0·917	0·919	1·19	0·0221	0·59	0·00560	12
A : B	7·17	1·9635	5·78	1·3603	0·966	0·967	1·03	0·0054	0·83	0·00356	15
B : K	5·79	1·2942	3·07	0·3391	0·902	0·903	0·97	0·0096	0·51	0·00272	20
W : Z	9·48	4·0836	2·82	0·5776	0·927	0·930	1·26	0·0237	0·38	0·00220	11
W : X	9·86	3·7754	1·57	0·1861	0·918	0·921	1·38	0·0290	—	—	12
X : Z	1·57	0·1451	3·04	0·4482	0·853	0·856	0·91	0·0110	1·76	0·04207	22

Bivariate statistics for *Cryptolithus instabilis* sp. nov. for the total sample from the inlier. All measurements in mm. For explanation of symbols see Text-fig. 1. Note that B – 'Glabellar length' is here taken from the anterior of the preglabellar field.

Table 27

Number of ribs		5	6
Pygidial length	2·4–3·0	2	2
in mm	3·1–3·9	4	1

n = 9

Details of the number of ribs developed on the pygidium of *Cryptolithus instabilis* sp. nov. for the total sample.

Discussion. The species, erroneously recorded as *Trinucleus* (*Cryptolithus*) *lloydi* (Murchison, 1839) by Elles (1940), is closely related to the Llandeilian cryptolithinids from the Shelve area. From *Cryptolithus inopinatus* Whittard, 1958 it is easily distinguished by the absence of the I_4 arc medially and the delayed appearance of pits of the I_5 arc to about row eight. *Cryptolithus intertextus* Whittard, 1958 differs in that the radial arrangement of the pits is rapidly lost laterally due to the intercalation of interradial rows in the arcs I_{2-4}. Also, as in *C. inopinatus*, there are fewer pits of the I_4 arc absent medially than in *C. instabilis*, while the cephalon of *C. intertextus* is relatively longer (*sag.*). Of all the Shelve cryptolithinids, *C. radiatilis* Whittard is perhaps the most closely related to *C. instabilis*, although it may be distinguished by the appearance of the I_4 arc in row one or two and by its apparent lack of the I_6 arc. Furthermore *C. radiatilis* appears not to attain the dimensions reached by *C. instabilis*, and the outline of the cephalon is less rounded. *C. abductus* Přibyl and Vaněk, 1969, which was considered closely related morphologically to *C. radiatilis* by Přibyl and Vaněk, presumably chiefly on account of its well-developed radial arrangement of pits which persists to the posterior margin of the fringe, is readily distinguished by the presence of E_2 arc, lack of arcs I_{5-6} and fewer pits in each arc.

Cryptolithus sp. A

(Pl. 11, figs 1, 4, 6)

Figured material. It. 2806 (Pl. 11, fig. 1) Mould of part of dorsal surface of lower lamella. It. 2807 (Pl. 11, fig. 4) Internal mould of pygidium. It. 2808 (Pl. 11, fig. 6) External mould of part of thorax.

Locality and horizon. Near the base of the Lower *Didymograptus murchisoni* shales on the right bank of the stream flowing north-west from the pass above Bwlch-y-cefn, about 100 yds downstream from the waterfall.

Description. The three figured specimens are the only trinucleid fragments known from the locality and are assumed to belong to a single species. The fragment of the lower lamella reveals that the E_1 and I_{1-3} arcs are present, as is a strong girder and a well-developed pseudogirder between I_1 and I_2; both girder and pseudogirder bear terrace lines. Approximately twenty-five pits are present in the E_1 arc on the left half-fringe (right in ventral view), but the preservation does not allow an accurate count. The pits of the genal flange are smaller than the others. Long gently curved genal spines are developed. Although the preservation is rather poor, the thorax is seemingly typically trinucleid. The pygidium is triangular in outline being three and a half times as wide as long. At least six ribs are developed on the pleural fields and seven axial rings are clearly visible on the axis.

Discussion. If these specimens are correctly placed in *Cryptolithus* then they are of particular interest for they are probably slightly older than the previous oldest known member of the genus recorded from strata below the top of the Upper Llanvirn of the Shelve region by Whittard (1958, pp. 71 ff.).

? ***Cryptolithus*** sp. B

(Pl. 11, figs 2, 7)

Figured specimen. It. 2809 Fragment of lower lamella.

Locality and horizon. Stream section east of Wellfield Lodge, east of the main road, immediately above the point where the stream is piped under the road; shales assigned to the *G. teretiusculus* Zone.

Description. A single fragment of a lower lamella shows only the E_1, I_1 and I_2 arcs. The I_1 and I_2 arcs are separated by a strong pseudogirder which is only slightly less prominent than the girder; both girder and pseudogirder bear terrace lines. A unique feature seen in this specimen is the arrangement of the pits in the I_1 arc (Pl. 11, fig. 7), where laterally alternate pits have been pushed outwards as if by overcrowding. The genal flange is irregularly pitted with pits slightly smaller than those in the arcs.

Discussion. A further specimen of ?*Cryptolithus* is known from shales from the other side of the road, and while it is quite possible that this is conspecific with ?*Cryptolithus* sp. B, it is here described separately as ?*Cryptolithus* sp. C until more material is available.

?***Cryptolithus*** sp. C

(Pl. 11, figs 3, 8)

Figured specimen. It. 2810 External mould of fragment of cephalon.

Locality and horizon. Stream section at Wellfield Lodge immediately downstream of the point where the stream emerges after being piped under the road; shales assigned to the *G. teretiusculus* Zone.

Description. A single fragmentary specimen is of note in that of the arcs apparently internal to the girder, only the I_1 and I_2 arcs are continuous medially. The I_3 arc does not commence until row three; I_4 beginning at about row eight or nine. In this respect it is not unlike *Bettonia chamberlaini* (Elles) from the Llanvirn, although no adventitious pits are present medially.

Until the position of the girder is definitely known it is impossible to place this form generically with any certainty. Further the lack of any frontal adventitious pits suggests it belongs to *Cryptolithus*, their absence does not necessarily preclude it from *Bettonia*.

Discussion. Two further trinucleids are known from this locality; one, It. 2830 appears to have some affinity to *Bettonia superstes* Whittard, the other is too poorly preserved to be generically placed.

Genus ***BETTONIA*** Whittard, 1956

Diagnosis. See page 120.

Type species. *Trinucleus chamberlaini* Elles, 1940.

Distribution. Known from the upper beds of the Lower Llanvirn *D. bifidus* Zone; *D. speciosus* subzone) and the Llandeilo (*G. teretiusculus* Zone) of the Builth region; from the Weston and the Betton Beds (*D. murchisoni* Zone) and possibly also from the Meadowtown Beds (*G. teretiusculus* Zone) of the Shelve area.

Discussion. Whittard originally erected this genus to accommodate five or six poorly known species which were superficially similar to *Cryptolithus* Green, 1832, but differed in that they possessed a varying number of adventitious pits external to the E_1 arc. In the description of his type species, *Bettonia frontalis* Whittard, 1956, he acknowledged that it was very like *'Trinucleus'* (*Cryptolithus*) *gibbosus* Elles, 1940, from Builth and that differences, if any, were only likely to be found in the number and arrangements of the adventitious pits. He referred both *T.* (*C.*) *gibbosus* and *T. chamberlaini* to *Bettonia.*

The study of a large amount of material from the type locality of *Bettonia chamberlaini* (Elles, 1940) and *B. gibbosa* has shown these two species to be identical. Furthermore, the population exhibits considerable variation both in arrangement and number of pits in the E_1 and I_1 arcs frontally and in the number of adventitious pits developed which ranges from 0–10 (see Text-fig. 10), which covers a greater range than that exhibited by all five of Whittard's original species with the exception of *Bettonia superstes.* The variation found in the anteromedian distribution of the pits of the E_1 and I_1 arcs in *B. chamberlaini* together with *B. frontalis, B. irregularis* Whittard and *B. paucipuncta* Whittard may be considered as a basically simple radial pattern in which one or more pits may become slightly displaced (see Text-figs 10, 11). In view of the variation now known to be present within a single population of *Bettonia, B. frontalis, B. irregularis, B. paucipuncta* together with *B. gibbosa* are here considered as junior synonyms of *Bettonia chamberlaini* (Elles, 1940).

The occurrence within the sample of the population of *B. chamberlaini* of individuals with no adventitious pits, and others with one or two pits only on one half of the fringe raises the question of the validity of the genus *Bettonia* as distinct from *Cryptolithus.* Further doubt is raised by the similarity, apart from the frontal adventitious pits, between *Cryptolithus intertextus* Whittard, 1958, and *Bettonia superstes* Whittard, 1956. However, until more samples are available ,the genus *Bettonia* is provisionally retained for forms in which the majority of individuals have adventitious pits developed, whilst *Cryptolithus* rarely, if ever, has them. *Cryptolithus* sp. Whittard (1956: 68, pl. 9, fig. 16) is considered to belong to *B. chamberlaini.* It is thought that *B. superstes* might be better considered as being conspecific with *C. intertextus,* if this is so it would then leave *B. chamberlaini* as the sole representative of the genus *Bettonia.*

Bettonia chamberlaini (Elles)

(Pl. 11, figs 9–11, 13–15; Pl. 12, figs 1–7; Pl. 13, figs 1–8; Pl. 14, figs 1–5, 8–10; Text-figs 9–11)

1940 *Trinucleus chamberlaini* Elles: 423–424, pl. 29, figs 10–12, *non* fig. 13 which is *T. abruptus.*
1940 *Trinucleus* (*Cryptolithus*) *gibbosus* Elles: 425–426, pl. 31, figs 3–9.
1941 *'Trinucleus' chamberlaini* Elles; Whittington: 26.
1941 *'Trinucleus'* (*Cryptolithus*) *gibbosus* Elles; Whittington: 26.
1941 *Cryptolithus? chamberlaini* (Elles); Lamont: 449.
1941 *Cryptolithus gibbosus* Elles; Lamont: 464.
1956 *Bettonia frontalis* Whittard: 67–68, pl. 9, fig. 7.
1956 *Bettonia chamberlaini* (Elles); Whittard: 67, 69, pl. 9, figs 13, 14.
1956 *Bettonia gibbosa* (Elles); Whittard: 67–70, pl. 9, fig. 8.
1956 *Cryptolithus* sp. Whittard: 68, pl. 9, fig. 16.

1956 *Bettonia paucipuncta* Whittard: 68–69, pl. 9, figs 9–11.
1956 *Bettonia irregularis* Whittard: 69–70, pl. 9, fig. 12.
1966 *Bettonia frontalis* Whittard; Whittard: 280–281, pl. 49, figs 1–4.

DIAGNOSIS. *Bettonia* with nil to ten frontal adventitious pits external to E_1 arc, with rare development of pits external to E_1 posterolaterally. Arcs E_1, I_{1-2} continuous with about twenty pits in E_1 and I_1, and fifteen in I_2, on each half-fringe; I_3 generally appears in row two or three and contains about fourteen pits; I_4 commencing between row four and twelve, consists of a variable number of small pits adjacent to genae. Median pit in E_1 always present though commonly displaced; auxiliary pits in E_1 commonly developed, but rare in other arcs. Pygidium triangular; axial rings exceed in number the weakly developed ribs.

TYPE MATERIAL. Holotype. BU 261a (Chamberlain Collection) (Pl. 12, fig. 5) Internal mould of nearly complete specimen.

Paratypes. BU 262 (Chamberlain Collection) (Pl. 13, fig. 4) Internal mould of cranidium, pygidium and part of thorax. BU 263 (Chamberlain Collection) (Pl. 12, fig. 1) Internal mould of damaged nearly complete specimen.

DIMENSIONS.

	A	B	B_1	B_2	I_1	K	K_1
Holotype	*c.* 5·8	*c.* 4·6	3·8	3·0	—	3·3	—
BU 262	*c.* 7·5	*c.* 5·9	4·7	3·6	10·0	3·0	1·8
BU 263	—	3·8	—	—	—	2·0	—

	W	X	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
Holotype	8·2	1·6	2·3	?	—	—
BU 263	*c.* 6·2	1·3	1·6	?	trace	trace

All measurements in mm. For explanation of symbols see Text-fig. 1.

Fringe Data. Paratype BU 262

Numbers of pits in various arcs

	E_1	I_1	I_2	I_3	I_4
Left half-fringe	22	18	16	14	10+?
Right half-fringe	22+	16+	16	13	10

E_1, I_{1-2} are continuous; I_3 commences at row two; I_4 at row three. Five anterior adventitious pits are developed. Auxiliary pits e_1 xiii, and xiv are present on both left and right half-fringes. Fifteen radial rows are developed on the left half-fringe and at least fourteen on the right.

Only a fragment of the fringe is preserved in the holotype and no data are available. Fringe details are not available in the second paratype.

TYPE LOCALITY AND HORIZON. All three type specimens are from the shales of Lower Llanvirn age in the cliff section on the left bank of the Howey Brook, half a mile east-south-east of Carregwiber.

OTHER FIGURED MATERIAL. It. 2811 (Pl. 14, fig. 10); It. 2812 (Pl. 11, fig. 15; Pl. 14, fig. 1); It. 2813 (Pl. 12, fig. 7); It. 2814 (Pl. 12, fig. 6); It. 2815 (Pl. 11, fig. 10); It. 2816 (Pl. 11, fig. 14); It. 2817 (Pl. 12, fig. 2); It. 2818 (Pl. 12, fig. 4); It. 2819 (Pl. 13, fig. 3); It. 2820 (Pl. 13, fig. 7); It. 2821 (Pl. 13, fig. 6); It. 2822 (Pl. 14, fig. 2); It. 2823 (Pl. 13, fig. 8); It. 2825 (Pl. 11, fig. 11); It. 2826 (Pl. 11, fig. 9); It. 2827 (Pl. 11, fig. 13); It. 2828 (Pl. 14, fig. 4); It. 2829 (Pl. 14, fig. 5); GSM 86785 (Pl. 12, fig. 3); GSM 86786A (Pl. 14, fig. 8); GSM 86789 (Pl. 14, fig. 3); SM A 10082 (Pl. 13, fig. 5); BU 261b (Pl. 13, fig. 1); BU 264 (Pl. 13, fig. 2); BU 368 (Pl. 14, fig. 9).

DISTRIBUTION. The species is known from the upper beds of the Lower Llanvirn (*D. speciosus* Subzone) of the Builth region; and from the Betton and the Weston Beds (*D. murchisoni* Zone) of the Shelve area. In the Builth region it is very abundant at the type locality and relatively common at the small quarries 600 yds east of Upper Gilwen; it also occurs at various other localities at the same horizon in the Builth inlier.

DESCRIPTION. Excluding the genal spines and the fringe, complete specimens are roundly quadrate in outline.

The cephalic outline varies between semicircular and subrectangular, with the anterolateral angulation being variably developed. Excluding the occipital spine, the cephalon is generally about twice as wide as long.

The pyriform glabella is strongly convex and elevated well above the genal regions. In undeformed specimens it is generally about twice as long as wide. Three pairs of short lateral glabellar furrows typically take the form of rather indistinct shallow depressions on the near vertical sides of the glabella. The anterior pair occur at about two-fifths, the median pair at three-fifths and the posterior pair at about four-fifths along the glabella, measured from the anterior. Rarely a small median glabellar node is preserved in internal moulds (Pl. 13, fig. 7); apparently no such node is developed on the dorsal surface (Pl. 12, fig. 4). Commonly external moulds fail to show any surface markings, however, a few well-preserved specimens, particularly small holaspides, show a coarse reticulation on the glabella, and a slightly less coarse development on the genae (Pl. 12, fig. 4; Pl. 14, fig. 4).

The occipital ring forms an expanded base to the well-developed occipital spine (Pl. 12, fig. 4). The occipital furrow deepens laterally to form deep occipital pits which are directed anterolaterally.

The axial furrows, deep anteriorly with well-developed anterior fossulae, follow the lateral margins of the glabella closely becoming wider posteriorly. Alae are not developed.

The genae are quadrant-shaped with the inner margin gently concave and the posterior margin directed slightly anteriorly. They are moderately convex with fairly steeply sloping outer regions. Occasional specimens (BU 262, Pl. 13, fig. 4) show two faint caecae directed posterolaterally across the gena from about the mid-point of the inner margin towards the genal angle. The posterior border furrow is straight, broad and fairly shallow and has no lateral pit.

Internally the lateral glabellar furrows form poorly developed raised platforms. A small apodeme corresponds to each of the anterior fossulae.

The hypostoma is not known.

In spite of commonly developed cracks on the fringe of many specimens, particularly around the margins of the genae, it seems that the genal roll was moderately steeply declined, and the brim relatively flat; the change in curvature of the upper lamella probably being located along the strong ridge between I_1 and I_2. The fringe is of constant width with a short tongue extending behind the genae, lateral to the fulcrum. Five arcs of pits, E_1, I_{1-4}, are developed. The pits of the various arcs are arranged essentially radially, except near the genal angles, with the pits of E_1 and I_1 being larger than the remainder. The E_1, I_{1-2} arcs are continuous; I_3 arc generally commences at either row two or three and I_4 appears somewhat variably between row four and twelve. Generally about fifteen radial rows are developed on each half-fringe, with the anterolateral angulation occurring, if present, at about row twelve. Anteromedially the rows of pits diverge slightly and a median pit is present in the E_1 arc. Variations in the pattern of pits are common, and are caused by the displacement of one or more pits; they may all be referred to the basic pattern however (see Text-figs 10, 11). The number of anterior adventitious pits external to E_1 varies from nil to ten, and they are rarely distributed symmetrically with respect to the sagittal line. Rarely adventitious pits are also located

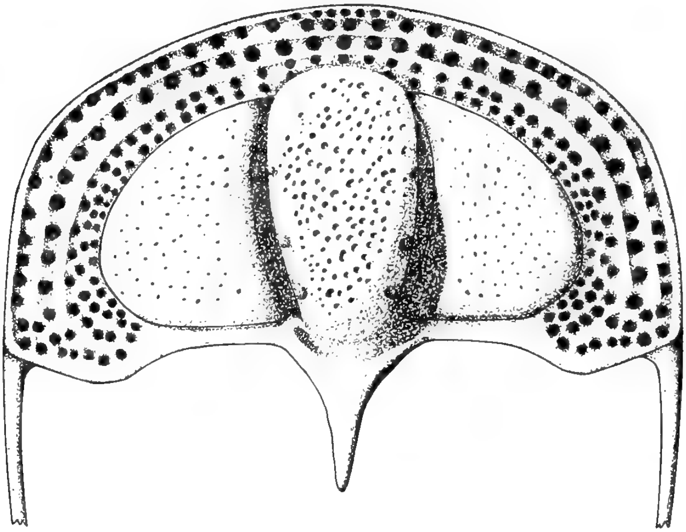

FIG. 9. Reconstruction of the cephalon of *Bettonia chamberlaini* (Elles) in dorsal view. c. × 8.

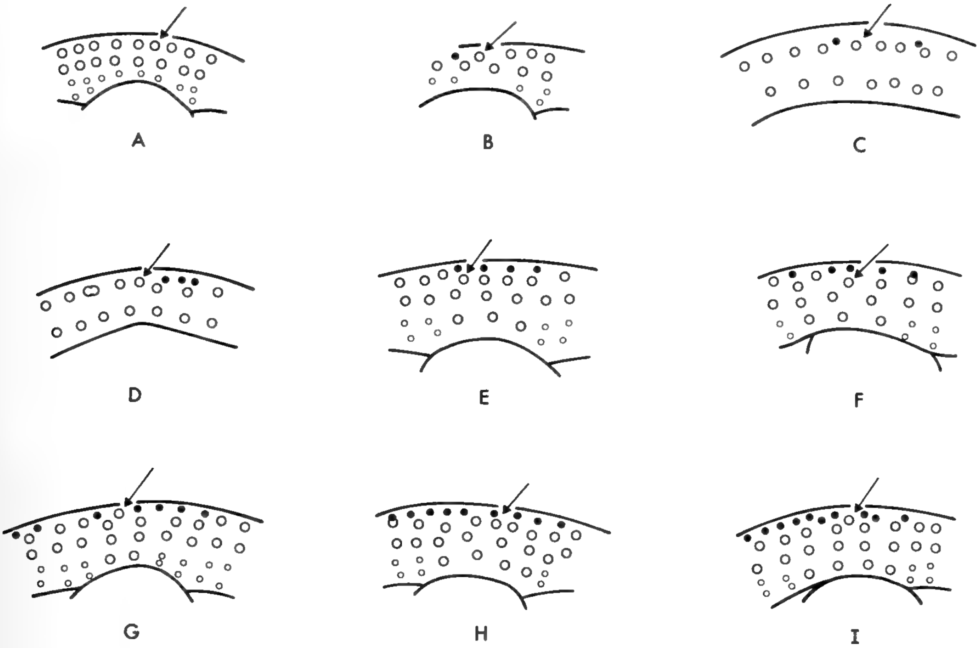

FIG. 10. Diagram illustrating the variation in numbers and distribution of pits in the anteromedian portion of the fringe in *Bettonia chamberlaini* (Elles) from the type locality. The diagrams are arranged showing a progressive increase in the number of anterior adventitious pits (shown as solid circles) present external to the E_1 arc. The median pit of the E_1 arc, at times displaced laterally, is arrowed. All diagrams × 7. A—It. 2820 (Pl. 13, fig. 7); B—BU 261a (Pl. 12, fig. 5); C—It. 2821 (Pl. 13, fig. 6); D—BU 261b (Pl. 13, fig. 1); E—It. 2813 (Pl. 12, fig. 7); F—BU 264 (Pl. 13, fig. 2); G—BU 262 (Pl. 13, fig. 4); H—It. 2817 (Pl. 12, fig. 2); I—It. 2819 (Pl. 13, fig. 3).

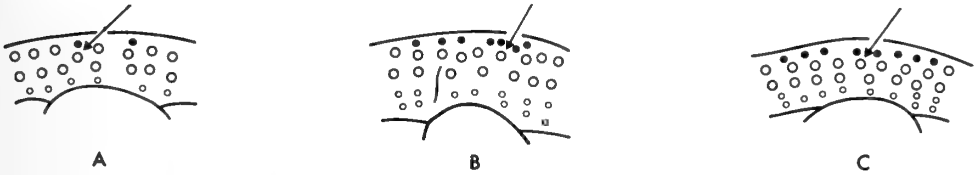

FIG. 11. Diagram illustrating the variation in numbers and distribution of pits in the anteromedian portion of the fringe in the type specimens of Whittard's species *Bettonia paucipuncta*, *Bettonia irregularis* and *Bettonia frontalis* from Shropshire. Anterior adventitious pits shown as solid circles. The median pit of the E_1 arc, at times displaced laterally, is arrowed. Note that all these distributions fall within the variation shown in Fig. 10 for the type locality sample of *Bettonia chamberlaini* (Elles). All diagrams × 7. A—GSM 86786A *B. 'paucipuncta'* (Pl. 14, fig. 8); B—GSM 86789 *B. 'irregularis'* (Pl. 14, fig. 3); C—GSM 86785 *B. 'frontalis'* (Pl. 12, fig. 3).

posterolaterally external to E_1 (Pl. 12, fig. 2); auxiliary pits are common in the E_1 arc, much less frequent in I_1 and rare in the other arcs. The auxiliary pits are rarely symmetrically distributed. The genal flanges lack a radial pit arrangement and although some variation is found, the arrangement is typically like that of Text-fig. 9. Occasional abnormalities of pit distribution usually take the form of a slight distortion of the radial pattern. One individual (Pl. 14, fig. 2) however has an E_1 pit missing laterally on both halves of the fringe.

The pit distribution on the lower lamella corresponds with that of the upper lamella. A strong, apparently smooth girder merges posterolaterally with the base of the genal spines; the ridge between I_1 and I_2 is represented ventrally by a pseudogirder, which may be as strongly developed as the girder, and shows faint traces of terrace lines (Pl. 14, fig. 1).

No correlation exists between the size of individuals and the number of pits present in any arc, or the number of anterior adventitious pits present; neither is there any correlation between size and the number of radial rows developed, nor in the commencement of the I_2 and I_3 arcs (for full fringe data see pages 165–6).

The genal spines are long, slender and gently incurved, extending some way behind the pygidium.

The suture line is not seen in the Builth material, but is clearly visible on GSM 86786A (Pl. 14, fig. 8), from Shelve (the original holotype of *B. paucipuncta*), where it passes round the declined marginal band and continues along the posterior margin of the cephalon, disappearing near the fulcrum.

The thorax is of normal trinucleid pattern and requires no detailed description. It is about two and a half times as wide as long, the maximum width occurring at the third segment. The axis occupies about two-fifths of the total thoracic width anteriorly, tapering slightly to the rear.

The triangular pygidium is about two and three-quarter times as wide as long, with a straight anterior margin, (excluding the articulating half-ring), and steeply declined smooth posterior and lateral borders. The inner margin of the posterior border is defined by a low narrow rim. The moderately convex tapering axis occupies slightly less than one-fifth of the anterior width of the pygidium. Traces of axial rings are seen in some specimens and up to eight are known. The axial furrows converge slightly, and become weaker to the posterior. The flat pleural fields have an anterior border and one, or possibly two, very weakly developed ribs.

Ontogeny. Although several specimens smaller than the smallest certain holaspis are known, the preservation is such that the number of thoracic segments developed cannot be precisely determined. All these small specimens, whether they are meraspides or small holaspides, resemble adult specimens except in size.

Biometrical data. Although the species is extremely abundant at the type locality, the specimens are so closely packed together that they overlap and crush one another thus making measurements impossible on the majority of specimens. However some data are available for a moderately sized sample and these are given below in Tables 28–35.

TABLE 28

No. of pits	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
E_1 arc	—	—	—	—	—	—	—	1	3	—	2	7	4	—	—	1
			(mean = 20·61; var. = 3·6630; n = 18)													
I_1 arc	—	—	—	—	—	—	1	—	3	6	3	—	2	1	—	—
			(mean = 19·44; var. = 3·0624; n = 16)													
I_2 arc	—	—	—	—	—	5	2	1	—	—	—	—	—	—	—	—
							(n = 8)									
I_3 arc	—	—	2	2	2	—	2	—	—	—	—	—	—	—	—	—
							(n = 8)									
I_4 arc	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—
						(n = 3)										

Frequency distributions for the number of pits developed in arc E_1 for *Bettonia chamberlaini* (Elles) from the type locality.

TABLE 29

Row in which I_3 first appears	2	3	4	5	
Number of specimens	18	7	2	1	(n = 28)

Frequency distribution for the commencement of arc I_3 in *Bettonia chamberlaini* (Elles) from the type locality. Arcs E_1, I_{1-2} are continuous anteromedially.

TABLE 30

Row in which I_4 first appears	4	5	6	7	8	9	10	11	12	
Number of specimens	1	1	—	1	1	1	1	—	1	(n = 7)

Frequency distribution for the commencement of arc I_4 in *Bettonia chamberlaini* (Elles) from the type locality.

TABLE 31

Row	10	11	12	13	rounded outline
Number of specimens	2	2	5	4	4

Frequency distribution for the position of the anterolateral angulation where present in *Bettonia chamberlaini* (Elles) from the type locality sample.

TABLE 32

Number of pits	0	1	2	3	4	5	6	7	8	9	10	
Number of specimens	2	1	1	1	1	4	1	1	1	—	1	(n = 14)

Frequency distribution for the number of anterior adventitious pits developed in *Bettonia chamberlaini* (Elles) from the type locality sample.

TABLE 33

Number of radial rows	14	15	16	17	
Number of specimens	2	4	1	1	(n = 8)

Frequency distribution for the number of radial rows developed in *Bettonia chamberlaini* (Elles) from the type locality sample.

In all the above fringe data the half-fringe is taken as that part of the fringe to the left or right of the median pit in the E_1 arc. In half-fringe counts on the E_1 arc the median pit is not included. In some specimens a small error may be introduced by the incorrect determination of the median pit. Such errors are small and tend to cancel out in the overall data from the sample.

TABLE 34

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
I_1 : A	8·16	1·9346	5·74	1·2082	0·889	0·890	1·12	0·0096	0·79	0·00486	29
I_1 : B	8·17	2·5038	4·44	0·8664	0·886	0·888	1·08	0·0045	0·59	0·00136	57
A : B	5·76	1·1479	4·53	0·7179	0·977	0·977	1·00	0·0013	0·79	0·00081	38
B : B_1	4·71	0·5007	3·76	0·3888	0·895	0·896	1·10	0·0199	0·88	0·01286	14
B : B_2	4·74	0·6365	2·96	0·2265	0·962	0·963	0·95	0·0074	0·60	0·00292	11
B : K	4·34	0·9990	2·35	0·3134	0·881	0·884	1·03	0·0036	0·56	0·00108	67
K : K_1	2·49	0·2807	1·44	0·0885	0·765	0·769	0·97	0·0099	0·56	0·00335	41
W : Z	6·41	1·9128	1·78	0·1689	0·864	0·866	1·07	0·0178	0·30	0·00140	18
W : X	6·41	1·9128	1·23	0·0835	0·905	0·908	1·08	0·0129	0·21	0·00049	18
X : Z	1·23	0·0704	1·78	0·1654	0·887	0·889	1·06	0·0112	1·53	0·02390	23

Bivariate statistics for *Bettonia chamberlaini* (Elles) for the type locality sample.

TABLE 35

Specimen	A	B	B_3	I	R_1	Q
SM A10084	6·1	—	—	11·5	—	—
NMW 68.376.G193	6·2	—	—	11·1	—	—
NMW 68.376.G194	3·9	—	—	8·2	—	—
NMW 68.376.G195	—	5·5	2·2	12·9	—	—
NMW 68.376.G196	—	4·3	1·8	—	—	—
BU 369	7·5	6·0	2·5	—	—	—
BU 368	—	—	—	—	8·0	3·3
NMW 68.376.G197	—	—	—	—	6·3	2·5
NMW 68.376.G198	—	—	—	—	5·0	2·0

Details of the length and width measurements for the cephalon and thorax, and for the position of the anterior pair of lateral glabellar furrows for *Bettonia chamberlaini* (Elles) from the type locality sample.

No data are available for the number of pygidial axial rings and pleural ribs above that given in the description above.

DISCUSSION. See discussion of genus (page 158).

Bettonia aff. ***superstes*** Whittard

(Pl. 14, fig. 11)

FIGURED SPECIMEN. It. 2830 Internal mould of damaged cranidium with three thoracic segments.

LOCALITY AND HORIZON. Stream section at Wellfield Lodge immediately downstream of the point where the stream emerges after being piped under the road; shales assigned to *G. teretiusculus* Zone.

DESCRIPTION. A single specimen is known from the Llandeilo of the Builth district which shows affinity to *Bettonia superstes*. Although the fringe is damaged anteriorly three adventitious pits can be seen and assuming symmetrical distribution, it is calculated that about eight such pits would be present on the complete fringe; posterolaterally however no adventitious pits are developed. A prominent ridge separates the E_1 and I_1 arcs, whose pits are slightly larger than the rest, from the inner arcs. About twenty-eight pits are developed in the E_1 arc on the right half-fringe. Medially the arcs I_{1-3} are continuous, with I_4 appearing at about row eight. Laterally the pits of the arcs I_{2-4} lose their radial arrangement due to the intercalation of auxiliary pits. The glabella and genal regions appear to be identical to those of other *Bettonia* and require no description.

The thoracic segments are not well preserved but appear to be of the normal trinucleid type. The pygidium is not known.

DISCUSSION. The general features of this specimen are very similar to *B. superstes*. The fringe however differs in that there are no posterolateral adventitious pits, probably fewer anterior adventitious pits and slightly more pits in the E_1 arc in the Builth specimen. However in view of the amount of variation now known to be present in *Bettonia chamberlaini* (Elles), it is considered undesirable to attempt a definite specific assignment until such time as details of the variation of *B. superstes* are known.

Subfamily **MARROLITHINAE** Nov.

DIAGNOSIS. See page 120.

Genus ***MARROLITHUS*** Bancroft, 1929

DIAGNOSIS. See page 121.

TYPE SPECIES. *Trinucleus ornatus* var. *favus* Salter, 1848.

DISTRIBUTION. The genus is recorded with certainty only from the Anglo-Welsh region and the Armorican Massif. In the Armorican Massif it is represented by

M. bureaui (Oehlert, 1895), from the *M. bureaui* beds of the May syncline, possibly of Lower Llandeilo age (see Whittard, 1956: 54). *M. bureaui* has also been recorded from Portugal (Delgado, 1908: 58, 80) and Spain (Born, 1926: 202, 204). The occurrence of *Marrolithus* in the Builth district is of interest as it is the first record of the genus, albeit only as a rarity, from this part of the Anglo-Welsh area. The distribution now includes south-west Wales, and the Builth, Shelve, and Berwyn regions of the Anglo-Welsh faunal province; with *M. ultimus* Bancroft having been transferred to *Costonia* (Whittard, 1956: 50), the genus is no longer recognized from the South Shropshire outcrops east of the Longmynd.

Marrolithus sp.

(Pl. 14, figs 6, 7)

FIGURED SPECIMEN. It. 2781 Internal mould of cephalon.

LOCALITY AND HORIZON. From the *N. gracilis* shales of the middle quarry, Llanfawr, Llandrindod.

DESCRIPTION. The solitary cephalon is an internal mould with the lower lamella. The cephalon is 12·3 mm wide medially and 4·9 mm long sagittally. The slightly convex anterior margin meets the concave lateral margins at about 90° and forms protuberant anterolateral angles. The posterior margin is more or less straight. The glabella is clavate, encroaching slightly onto the fringe, shows slight traces of reticulation, and has one pair of very shallow pit-like lateral glabellar furrows situated posteriorly. The axial furrows are fairly wide, but there are no traces of alae. Anterior fossulae are present. The short occipital ring bears no trace of a spine. The straight, open posterior border furrows terminate in very shallow lateral pits. The genal regions are semi-elliptical, flatly convex and smooth; eye ridges and tubercles are absent. The base of the genal spines is inclined at about 45° to the axial direction.

The fringe is poorly preserved anteriorly so that a precise fringe count cannot be made. The fringe terminates level with the posterior cephalic margin, with a short tongue extending behind the genal regions; it is narrowest anteromedially (0·8 mm) and widest (radially) at the anterolaterial corners (3·0 mm), located at about row 18. The following arcs and pits are developed:

E_1, I_1 continuous (E_1 with about 40 pits); I_2 ?continuous; I_3, I_4 both commence slightly lateral to the axial furrows and continue to the genal angles; I_5 has about eight pits and I_6 about four pits, situated at the anterolateral corners.

The swollen areas consist of nine I_1 pits (approximately row 11–19), eight I_2 pits (approximately row 12–19) and four I_3 pits (approximately row 15–18). All the pits on the swollen area are enlarged as are the pits of E_1 in rows 14–19 (approximately) and I_1 row 20. The increase in pit size along the anterior margin is gradual, but the decrease posteriorly along the lateral margin is more rapid. The girder is best developed anteriorly, becoming less marked anterolaterally and laterally to reappear as a ventral ridge at the base of the genal spines.

The thorax and pygidium are unknown.

Discussion. The species seems to be most closely related to *M. inornatus* Whittard, 1956. The traces of reticulation on the internal mould suggests that the external surface of the exoskeleton may have been more strongly reticulated; this might distinguish the species from *M. inornatus.* The Builth specimen appears to differ in having a slightly larger swollen area, more markedly protuberant anterolateral corners, and also in that the glabella encroaches slightly onto the flange, though this latter feature may be as a result of compression. As the variation in these characters is unknown the importance of such slight differences cannot yet be assessed. Until more is known, it is preferred to leave this specimen unassigned specifically.

Genus ***PROTOLLOYDOLITHUS*** Williams, 1948

Diagnosis. See page 121.

Type species. *Trinucleus ramsayi* Hicks, 1875.

Distribution. The genus is known only from the Anglo-Welsh regions, being present in the Arenig of South Wales and Shelve and the Llandeilo of the Builth area.

Discussion. The genus is here considered as the most primitive member of the Marrolithinae. Lu and later Dean (1966: 281–283) showed that *'Trinucleus' primitivus* Born, 1921, placed in *Protolloydolithus* by Whittard (1956), should be transferred to *Hanchungolithus* Lu, 1954, the genus is represented by only three species. The occurrence of *Protolloydolithus reticulatus* (Elles, 1940) at Builth is of interest because of its relatively high (Llandeilo) stratigraphic horizon; the other two species are confined to the Lower Llanvirn.

Protolloydolithus reticulatus (Elles)

(Pl. 15, figs 1, 5–9, 11; Pl. 16, fig. 2; Text-fig. 12)

1940 *Trinucleoides reticulatus* Elles: 427, pl. 29, figs 6–9.
1941 *'Trinucleoides' reticulatus* Elles; Lamont: 443.
1941 *Trinucleoides reticulatus* Elles; Whittington: 26.
1956 *Protolloydolithus reticulatus* (Elles); Whittard: 41.

Diagnosis. *Protolloydolithus* with between about forty and fifty pits in entire E_1 arc; genal prolongations moderately developed; genae with fine reticulations and caecae. Pygidium about three and a half times as wide as long, with between five and seven pleural ribs and up to sixteen axial rings.

TYPE MATERIAL. Holotype. BM I 7216 (Pl. 15, fig. 1) Internal mould of almost complete specimen.

Paratypes. BM I 7328 (Pl. 15, fig. 11) Internal and external moulds of damaged cephalon. It. 8604 (Pl. 15, fig. 7) Internal and external moulds of nearly complete thorax and pygidium.

DIMENSIONS.

	B	I_1	Q	Q_1	R_1
Holotype	*c.* 6·5	*c.* 15·0	4·5	0·9	13·0
I 7328	*c.* 6·0	*c.* 15·0	—	—	—

	W	X	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
Holotype	*c.* 12·0	*c.* 1·8	3·5	11+	6	—
It. 8604	*c.* 11·0	*c.* 1·8	*c.* 3·5	—	6	—

All measurements in mm. For explanation of symbols see Text-fig. 1.

TYPE LOCALITY AND HORIZON. It is almost certain that the holotype and the paratypes come from the stream section in shales of Llandeilo age to the east of Bach-y-graig, Llandrindod. The label accompanying the holotype gives the locality as 'Cym-y-rhain Dingle on stream behind Pump House, Llandrindod Wells, Radnorshire'. Labels with the paratypes give the locality variously as 'Stream E. of Hillside' and 'Llandrindod Wells'. All new specimens collected are from the left bank of the stream section east of Bach-y-graig 65 yds east of the point where the footpath enters the wood at the western end of the section.

OTHER FIGURED MATERIAL. It. 2782 (Pl. 15, fig. 6; Pl. 16, fig. 2); It. 2783 (Pl. 15, fig. 8); It. 2784 (Pl. 15, fig. 5); NMW 15.207.G3 (Pl. 15, fig. 9).

DISTRIBUTION. The species is not known outside the type locality.

DESCRIPTION. Excluding the genal prolongations and spines, complete specimens are subcircular, with a semicircular cephalon.

The moderately convex glabella possesses a pseudofrontal lobe which extends for two-thirds of the glabellar length. The glabella is traversed anteriorly by a weakly developed furrow delimiting a small triangular preglabellar field that encroaches a short distance onto the fringe. Three pairs of pit-like lateral glabellar furrows are developed on the sides of the glabella. The anterior pair, which are the smallest, are situated at about two-fifths the distance along the glabella from the anterior. The median and posterior pairs are somewhat larger and deeper and occur at about two-thirds and four-fifths of the glabellar length respectively. Alae extend posteriorly from just behind the anterior pair of lateral glabellar furrows. Lateral, and subparallel to the posterior part of each ala a low elongate swelling of uncertain significance is present in the floor of the axial furrows, which are wide at the posterior. The presence of this swelling in several specimens suggests it to be an original feature of the exoskeleton, and not due to any *post mortem* distortion. Medially, the external surface of the glabella is pitted, with a low median glabellar node near the front.

The occipital ring is short (*sag.*) slightly convex posteriorly, and bears no occipital spine. The occipital furrow is extremely shallow medially, deepening laterally to form shallow occipital pits.

Anteriorly the axial furrows follow the lateral margins of the pseudofrontal lobe until opposite the anterior pair of lateral glabellar furrows; posteriorly from this point the straight furrows become wider and shallower. Poorly developed pits mark the site of the anterior fossulae.

Internally the lateral glabellar furrows form small raised platforms.

The genal regions are quadrant-shaped, with the inner margin slightly concave. The genae are only slightly convex, but with a moderately steeply declined outer margin. The exterior surface is covered with a fine reticulate pattern of raised ridges distributed over the genae in the normal trinucleid manner. Two fine genal caecae, originating approximately level with the anterior of the alae also cross this area posteriorly. The presence of only one caeca in some specimens is considered to be a reflection of imperfect preservation.

The posterior border is sharply upturned behind the straight, shallow, though clearly developed posterior border furrow. It is highest at the fulcrum where it

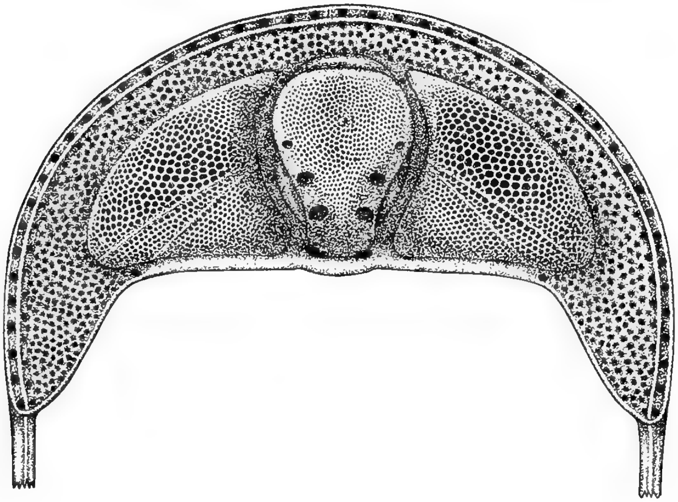

FIG. 12. Reconstruction of the cephalon of *Protolloydolithus reticulatus* (Elles) in dorsal view. *c.* × 5.

turns abruptly posterolaterally. The crest of the border appears to bear a few parallel terrace lines.

Observations on the poorly preserved fringe show that an orderly E_1 arc is developed together with several internal arcs; of the latter only I_1 arc is orderly arranged. The E_1 arc has between nineteen and twenty-six pits developed on each half-fringe and is separated from the I_1 arc on the upper lamella by a sharp, high ridge with the I_1 pits situated on its inner slope. At least five irregularly arranged I arcs internal to I_1 are present anteriorly and show some tendency to radial arrangement medially. Laterally the number of pits increases and the distribution becomes entirely haphazard. The pits of these inner arcs are smaller than those of the E_1 and I_1 arcs. Moderately large genal prolongations are developed and about seven or eight pits of the E_1 arc lie behind the posterior margin of the cephalon. The pitted area extends medially as far as the fulcrum. Little is known of the lower lamella but there is no reason to suspect any discordance between the pits of the two lamellae. The strongly developed girder merges posteriorly into the genal spines.

Although the genal spines are not preserved in their entirety they probably extend some way behind the pygidium.

The suture is not seen, but it seems most likely that the suture is marginal, becoming dorsal at the genal angles as in other trinucleids.

As pointed out by Lamont (1941: 443) and Whittard (1956: 41), the thorax has only six segments and not seven as recorded by Elles (1940: 427). In outline it is rectangular, about three times as wide as long, the convex (*tr.*) axial rings contrasting with the flat pleural regions. The articulating furrows are narrow and deeper laterally than medially. The pleurae are crossed by a shallow oblique pleural furrow which extends into the posteriorly deflected, blunt terminations. The fulcral processes on the anterior edge are proportionately nearer the axial furrows than in most other trinculeid genera.

The roundly triangular pygidium is about three and a half times as wide as long. The axis tapers gently and has at least sixteen axial rings developed which are poorly defined posteriorly. The tubercles mentioned by Whittard (1956: 41) on the axial rings have not been observed. The pleural fields have a narrow (*sag.*) anterior border and a triangular terminal area together with six, or less commonly five or seven, ribs. These widen distally to become progressively more posteriorly directed. The strongly declined posterolateral border bears terrace lines. Although relatively few data are available, there appears to be no correlation between the size of the pygidium and the number of ribs (see Table 38). No examples of the asymmetrical development of the ribs on the two halves of the pygidium are known.

ONTOGENY. A single poorly preserved specimen most probably represents a meraspis degree three or four (Pl. 15, fig. 8). It appears similar to the holaspid form apart from the number of thoracic segments and overall size. A further small cephalon (width approximately 5·0 mm) probably referable to this species, shows a slightly carinate glabella.

BIOMETRICAL DATA. Because of poor preservation very few data are available for this species; such data as are available are given in Tables 36–38 below.

TABLE 36

Spec. No.	A	A_1	B	B_1	B_2	B_3	I	I_1	K	K_1
It. 2783	—	*c.* 1·2	—	—	—	—	*c.* 3·5	—	—	—
It. 2784	—	—	*c.* 3·8	—	—	—	—	*c.* 8·5	—	—
NMW 15.207.G3	—	—	6·0	5·0	4·2	—	17·4	13·2	3·5	—
It. 8809	—	—	5·4	4·2	3·4	—	—	*c.* 12·0	—	—
NMW 68.376.G200	6·9	7·3	5·7	4·5	3·5	2·3	—	—	4·2	1·8
It. 8807	6·4	—	4·9	—	—	—	—	10·5	3·0	—

Details of measurements made on *Protolloydolithus reticulatus* (Elles). All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 37

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	9·66	3·7862	2·79	0·3114	0·937	0·938	0·99	0·0236	0·29	0·00200	7
W : X	9·66	3·7862	1·39	0·1214	0·936	0·937	1·24	0·0373	0·18	0·00080	7
X : Z	1·39	0·1214	2·79	0·3114	0·924	0·927	0·80	0·0181	1·60	0·07463	7

Bivariate statistics for the pygidium of *Protolloydolithus reticulatus* (Elles). All measurements in mm. For explanation of symbols see Text-fig. 1.

TABLE 38

		No. of pleural ribs	
Spec. No.	Pygidial length	Left	Right
NMW 68.376.G201	1·8	7	7
It. 2784	2·2	5	5
NMW 68.376.G202	2·2	7	7
It. 8806	2·2	7	7
NMW 68.376.G203	2·6	—	6
NMW 68.376.G204	3·0	6	6
NMW 68.376.G200	3·3	6	6
It. 8808	3·3	6	6
NMW 15.207.G3	3·3	6	6

Table showing the lack of correlation between the number of pleural ribs developed and pygidial length in *Protolloydolithus reticulatus* (Elles).

DISCUSSION. Elles's original placing of this species in the genus *Trinucleoides* Raymond, 1917 cannot be upheld, for whilst the well-developed alae of *P. reticulatus* bear some resemblance to the lateral lobes of *Trinuceoides reussi* (Barrande, 1872), the structure of the fringe in the two species is completely different.

Protolloydolithus ramsayi (Hicks, 1875) is similar to *P. reticulatus* but may be distinguished by its smaller genal prolongations, less well developed alae, probable higher number (six–eight) of arcs internal to I_1 and its relatively wider pygidium. The only other species referred to the genus, *P. neintianus* Whittard, 1956, is readily separated on the narrowness of the fringe anteriorly and the unfurrowed pleural fields of the pygidium.

Morphologically the species shows no new features apart from the possible development of terrace lines along the crest of the posterior cephalic border which is a structure apparently previously unrecognized in the trinucleids.

Genus ***TELAEOMARROLITHUS*** Williams, 1948

DIAGNOSIS. See page 121.

TYPE SPECIES. *Trinucleus radiatus* Murchison, 1839.

DISTRIBUTION. The genus is restricted to the basal Caradoc (*N. gracilis* Zone) of the Anglo-Welsh faunal province, being represented in the Llandeilo, Builth and Shelve regions.

DISCUSSION. Williams (1948: 85) considered *Telaeomarrolithus* to have been derived from the marrolithids by the collapse of the swollen area. The occurrence at Builth of *T. intermedius* sp. nov. with a slightly swollen area ventrally and expanded pits in the E_1 arc of the lower lamella gives support to Williams' belief that *Telaeomarrolithus* is more closely related to the marrolithids than to *Trinucleus*. However, the presence of expanded pits solely in the E_1 arc, a feature not found in any other marrolithinid, suggests that it may not be derived directly from *Marrolithus favus* (Salter, 1848) as suggested by Williams, or indeed from any marrolithinid known at present.

Telaeomarrolithus intermedius sp. nov.

(Pl. 15, figs 2–4, 10; Pl. 16, figs 1, 4–9; Text-fig. 13)

DIAGNOSIS. *Telaeomarrolithus* with about thirty-eight to forty-four pits in E_1 arc, of which five or six at anterolateral corners are markedly expanded on the lower lamella; occasional pits external to the girder but internal of E_1 developed anterolaterally; maximum of about seven pits in anterolateral rows; four in median rows.

TYPE MATERIAL. Holotype. It. 2785 (Pl. 16, figs 1, 5) Internal and external moulds of cephalon.

Paratypes. It. 2789 (Pl. 16, fig. 4) Internal mould of cephalon. It. 2788 (Pl. 16, fig. 8) Internal and external moulds of possibly enrolled specimen showing part of thorax. It. 2786 (Pl. 16, fig. 6) Internal mould of small cranidium. It. 2787 (Pl. 16, fig. 9) Internal mould of damaged cranidium. It. 8606 (Pl. 15, fig. 4) Mould of lower lamella. It. 8799 (Pl. 15, fig. 2) Internal mould of damaged cranidium. It. 8800 (Pl. 15, fig. 3) External mould of cephalon. BM In. 48533 (Pl. 15, fig. 10) Internal mould of cranidium. USNM 160108 (Pl. 16, fig. 7) External mould of disarticulated entire specimen.

DIMENSIONS.

	A	A_1	B	B_1	B_2	B_3	B_4
It. 2785	8·5	9·1	6·7	5·2	4·1	c. 2·7	2·9
It. 2786	3·8	4·1	2·9	—	—	—	—
It. 2787	6·4	6·7	4·8	3·9	3·0	2·1	—
It. 2789	—	—	6·6	5·4	4·2	3·0	—
It. 2790	c. 9·1	c. 9·6	c. 7·0	—	4·5	3·1	—
In. 48533	7·8	8·2	5·9	4·3	3·6	2·5	—

	I	I_1	K	K_1
It. 2785	—	c. 13·5	4·5	3·0
It. 2786	—	6·9	2·1	1·0
It. 2787	—	—	3·3	1·8
It. 2789	c. 17·5	—	—	—
It. 2790	—	—	4·7	—
In. 48533	17·3	13·2	4·0	1·9

All measurements in mm. For explanation of symbols see Text-fig. 1.

Fringe Data

	Number of pits in E_1 arc		Number of expanded pits in E_1 arc		Presence of Row O
	Left	Right	Left	Right	
It. 2785	19½	19½	—	—	present
It. 2789	—	c. 20	—	—	?
It. 2790	—	19	—	5	?
In. 48533	20½	21½	6	5	present

	Max. Number of I arcs		Number of I arcs medially		Position of anterolateral angulation	
	Left	Right	Left	Right	Left	Right
It. 2785	—	—	—	—	row 12	row 11
It. 2788	—	?6	—	—	—	—
It. 2789	—	?6	—	4	—	c. row 12
It. 2790	—	?6	—	?3	—	row 11–12
In. 48533	—	?5	4	4	row 12	row 13

TYPE LOCALITY AND HORIZON. *N. gracilis* shales exposed in the middle quarry, Llanfawr, Llandrindod.

DISTRIBUTION. The species is known only from the type locality.

DESCRIPTION. The cephalon is about twice as wide as long, excluding the genal spines. The lateral margins are straight and slightly divergent anteriorly; anterior margin arched forwards medially; anterolateral corners angulate.

The glabella is convex, with the pseudofrontal lobe occupying the anterior three-fifths; it is of moderately convex profile anteriorly and gives the impression of encroaching onto the fringe in compressed specimens. The poorly preserved anterior lateral glabellar furrows are weakly developed. The median pair, delimiting the posterior of the pseudofrontal lobe, are better developed and consist of elongate (*tr.*), rather shallow pits. The posterior pair are again elongate pits, but are directed slightly anteromedially. A small median glabellar node is situated about half-way along the glabella. A coarse reticulate pattern is developed medially on the glabella. Alae extend posteriorly from the rear of the pseudofrontal lobe. A weakly developed occiput is present.

The occipital ring is short (*sag.*) consisting of little more than a median continuation of the low ridge forming the posterior margin of the genal regions. The occipital furrow is shallow; no occipital spine is developed.

The shallow axial furrows are most clearly defined anteriorly where a pair of anterior fossulae are developed.

The genal regions are quadrant-shaped and apart from the steeply declined outer margin are only slightly convex. Traces of a course reticulation are present distributed in the typical trinucleid manner. In some specimens a small lateral eye tubercle appears to be developed on each gena, close to the axial furrows and slightly anterior of the median lateral glabellar furrows, although eye ridges are lacking (Pl. 16, fig. 4). The posterior margin is upturned to form a low ridge-like border

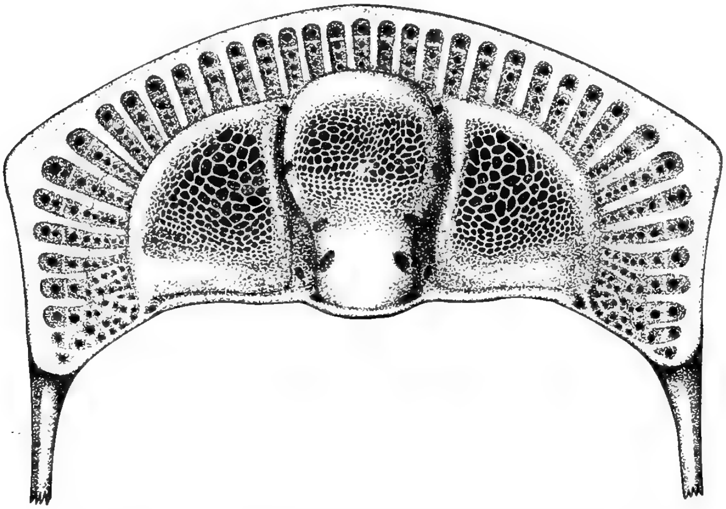

FIG. 13. Reconstruction of the cephalon of *Telaeomarrolithus intermedius* sp. nov. in dorsal view. *c.* × 5.

separated from the genae by a straight, shallow posterior border furrow which terminates in a small lateral pit.

Internally the lateral glabellar furrows form raised platforms; the anterior fossulae and the lateral pits having corresponding apodemes. Internal traces of the reticulation on the median glabellar node are only rarely seen (Pl. 16, fig. 1).

The upper lamella of the fringe is widest anterolaterally, and narrowest medially. Between about nineteen and twenty-two radial rows are present on each half-fringe. The pits of the E_1 and I_1 arcs are larger than those of the other I arcs, and anterolaterally the pits of E_1 tend to be slightly enlarged. A few specimens show pits of two E arcs developed in up to four radial rows at the anterolateral corners (Pl. 15, figs 2, 10). Traces of such pits have only been detected on one lower lamella in which they appear to be developed internal to E_1 on the outer steep sides of the swolled area. The significance of these pits, and their apparent absence in some specimens is not known. Arcs I_{1-3} appear to be present medially, I_4 appearing in row two or three. At least six I arcs are developed anterolaterally. The radial arrangement of the pits only breaks up at the genal angles where moderate genal prolongations are developed with three or four pits of the E_1 and I_1 arcs located behind the posterior margin of the genal regions. Laterally the fringe is differentiated into two regions, the outer being characterized by more strongly developed ridges between the radial rows. Only the pits of the E_1 and I_1 arcs lie in the outer zone, the arcs becoming more widely separated at the anterolateral corners.

The inner part of the lower lamella is steeply declined to the very strongly developed, smooth girder; the outer part being reflected sharply dorsally from the girder. The pit distribution corresponds to that of the upper lamella, but in addition four or five pits in the E_1 arc are generally markedly expanded at the anterolateral corners which occurs at about row twelve. In addition low, weakly developed ridges are present laterally between the various I arcs. From the material available it appears that either a row of pits or a ridge may lie along the sagittal line.

The girder merges posterolaterally with the long, slightly divergent genal spines. On one paratype (It. 2789) of cephalic width approximately 17·5 mm, the genal spines are about 14·5 mm long.

The course of the suture is not seen, but is presumably marginal, becoming dorsal only at the genal angles and may be non-functional (see discussion).

The thorax is typically trinucleid and requires no further description.

The sole known pygidium (Pl. 16, fig. 7) is triangular in outline being about three and a half times as wide as long. Its overall morphology is extremely similar to that of the pygidium of *Trinucleus fimbriatus* and isolated pygidia cannot be distinguished. At least five pleural ribs and six axial rings are developed. The steeply declined posterior border bears terrace lines on the external surface.

Biometrical data. In view of the small number of measurements possible, full details are given. In addition to those already given for the type of specimens, further measurements are given in Table 39. Since very few exact pit counts could be made, no further statistical data can be given for the pit distribution on the fringe above that given in the description.

TABLE 39

Spec. No.	A	A_1	B	B_1	B_2	B_3	B_4	I_1	K	K_1
NMW 68.376.G205	5·9	6·2	4·2	3·2	2·5	—	—	8·5	2·8	1·3
NMW 68.376.G206	—	7·1	—	—	—	—	—	—	—	—
NMW 68.376.G207	—	—	5·5	4·3	3·5	—	—	12·5	3·4	1·9
It. 2791	8·5	8·9	6·4	—	—	—	3·5	12·7	—	2·4
It. 8605	5·0	5·3	3·8	—	—	—	—	8·5	—	—

Details of measurements made on the cephalon of *Telaeomarrolithus intermedius* sp. nov. in addition to those made on the type material. All measurements in mm. For explanation of symbols see Text-fig. 1.

DISCUSSION. Only thirty specimens of this new species are known from the middle quarry, Lanfawr and it is thus relatively rare compared with the majority of species at that locality.

The morphological features developed in this species make generic placing a little difficult. Dorsally the cephalic exoskeleton shows strong similarities to *Trinucleus fimbriatus* with its well developed radial sulci and anteriorly swollen glabella. However the presence of two distinct areas on the fringe laterally, the angulate outline and the presence of markedly swollen pits in the E_1 arc on the lower lamella are thought to indicate that the species is best placed in *Telaeomarrolithus*. The new species is easily distinguished from the type species by its expanded pits on the lower lamella, the presence of two pits external to the girder in the anterolateral rows, the smaller number of pits in each arc, and the smaller number of I arcs represented anterolaterally. *Telaeomarrolithus* sp. indet. described by Whittard (1956: pl. 9, fig. 6) is too poorly preserved for any proper comparison, although the rather rounded anterolateral angles are more like those of *T. radiatus* than that of *T. intermedius*.

About two-thirds of the internal moulds of *T. intermedius* have the impression of the ventral surface of the lower lamella preserved, indicating that the lower lamella was still attached to the cephalic exoskeleton. This type of preservation is only rarely found in specimens of *Trinucleus fimbriatus* from the same locality. In view of this, and that the trilobite exoskeletons are generally disarticulated, it seems possible that the marginal suture of *T. intermedius* was no longer functional. It is interesting to note that the four specimens of *T. radiatus* referred to by Williams (1948: 83) together with a further specimen from Llandeilo all show the same mode of preservation and it may be that an ankylosed marginal suture is characteristic of *Telaeomarrolithus*.

Telaeomarrolithus radiatus (Murchison)

(Pl. 16, fig. 3)

1839 *Trinucleus radiatus* Murchison 660, pl. 23, figs 3a, 3b.
1948 *Telaeomarrolithus radiatus* (Murchison); Williams: 83, text-fig. 11, pl. 6, fig. 10.

TYPE MATERIAL. Syntypes. GSM Geol. Soc. Coll. 6836; GSM Geol. Soc. Coll. 6837.

Discussion. Murchison's localities for *Trinucleus radiatus* read, 'Trilobite Dingle, Welsh Pool, Caradoc and Meifod Hills etc.', (Murchison, 1839: 660), but there is some doubt as to the locality of the figured syntypes, for the original label gives the locality as 'Llandeilo Flags, Builth'. However the lithology of the syntypes does not match anything known from the Builth region, but is similar to that of Williams's specimens from Crûg, near Llandeilo. It thus seems more probable that the types come from the Llandeilo, rather than the Builth area. This is supported by the fact that no other specimens of *T. radiatus* are known from the Builth region and it is thus proposed to remove *T. radiatus* from the faunal lists of the region.

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EXPLANATION OF PLATES

Most of the trilobites figured are in collections of the British Museum (Natural History) and their numbers are prefixed BM, I., In., or It. Other specimens are in collections in the following institutions: Birmingham University (BU), Institute of Geological Sciences, London (GSM), National Museum of Wales, Cardiff (NMW), Oxford University Museum (OUM), Sedgwick Museum, Cambridge (SM), United States National Museum, Washington D.C. (USNM) and the private collections of Mr J. T. Wattison (H). All specimens were whitened with ammonium chloride before photographing. All photographs are by the author and none is retouched.

PLATE 1

Trinucleus fimbriatus Murchison p. 122

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.

G.R. SO.066617.

FIG. 1. Latex impression from internal mould showing general characteristics of dorsal exoskeleton. Wattison Collection H.22 × 3.

FIG. 2. Latex impression from external mould showing faint terrace lines on posterior border. It. 2733. × 5.

FIG. 3. Internal mould of cranidium showing a depression lateral to the posterior lateral glabellar furrow. It. 2726. × 5.

FIG. 4. Internal mould of cranidium showing the pits of the inner I arcs anteromedially. It. 2735. × 4. (Specimen donated by Radnorshire County Museum, Llandrindod Wells.)

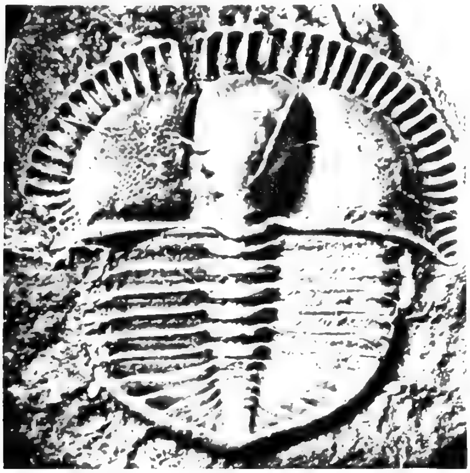
FIG. 5. Latex impression from external mould of meraspis ?degree 4 cranidium showing posterolateral outline of fringe (see also Text-fig. 3). It. 2732. × 5.

FIG. 6. Internal mould of cranidium showing irregularities in the fringe. It. 2722. × 2·5.

FIG. 7 Latex impression from external mould of cranidium showing surface sculpture It. 2730. × 4.

FIG. 8. Internal mould of cranidium showing irregularities in the pit distribution on the left side. It. 2729. × 3.

FIG. 9. Internal mould of cranidium showing the fusion of two ridges on the fringe. It. 2727. × 3.



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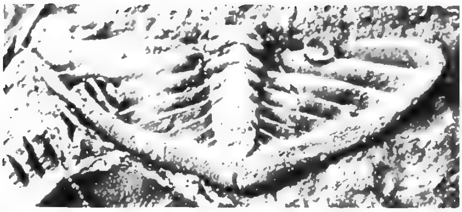

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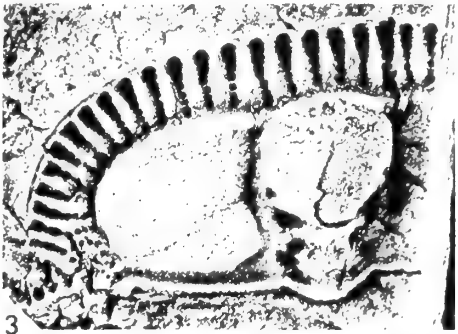

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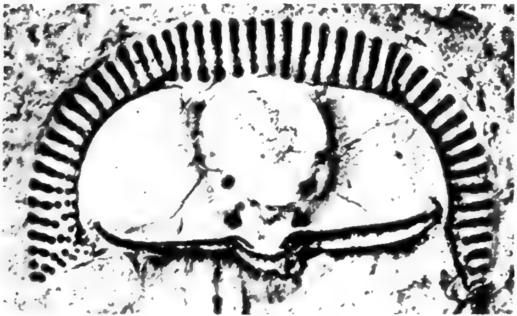

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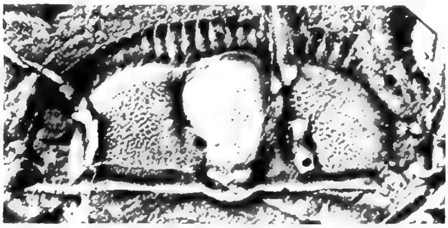

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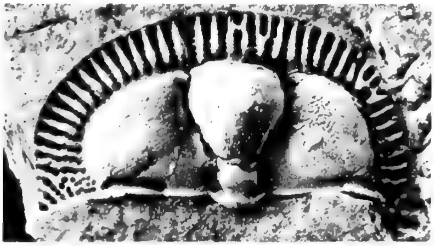

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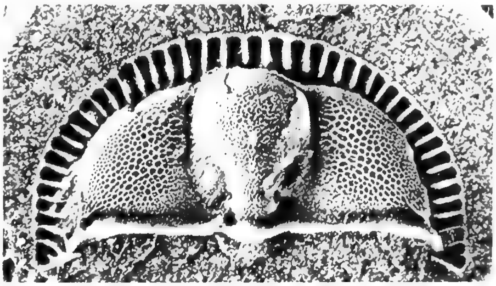

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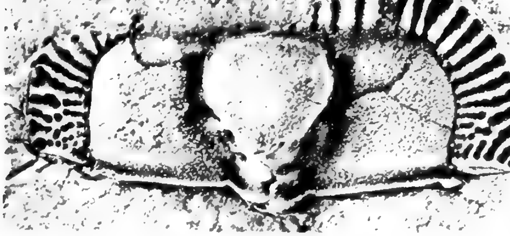

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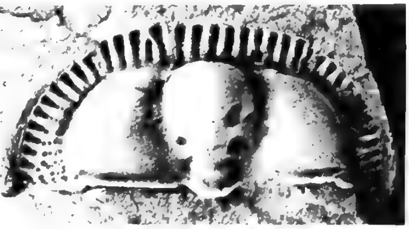

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PLATE 2

Trinucleus fimbriatus Murchison p. 122

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 1. Internal mould of lower lamella. It. 2731 × 2.

FIG. 3. Internal mould of ?meraspis cranidium showing irregularities in the fringe. It. 2724. × 4.

FIG. 4. Internal mould of small holaspis. It. 2719. × 3.

FIG. 5. Internal mould of lower lamella with genal spines. It. 2728. × 2·5.

FIG. 6. Enrolled specimen showing five thoracic segments folded over and the posterior pygidial margin fitting against the inner margin of the fringe. It. 2721. × 3.

FIG. 8. Internal mould of meraspis degree 5 (see also Text-fig. 3). It. 2725. × 3·5.

FIGS 9, 10. Dorsal and oblique lateral views of internal mould of complete specimen. It. 8798. × 1·5.

FIG. 11. Internal mould of anterior thoracic segment showing the lack of articulating half ring. It. 2734. × 4.

FIG. 12. Enlargement of part of Pl. 1, fig. 7. Latex impression from external mould of cranidium showing median glabellar node. It. 2730. × 10.

FIG. 13. Internal mould of cranidium showing occipital ring and furrows, fulcral processes and lateral pits. It. 2720. × 2·5.

FIG. 14. Internal mould of small meraspis showing outline of fringe posterolaterally (see also Text-fig. 3). It. 2723 × 8.

Basal Caradoc, quarry at Gwern-yfed-fâch, half a mile south-east
of Builth Road station
G.R. SO.030526.

FIG. 2. Lectotype. Latex impression from external mould of cranidium. GSM Geol. Soc. Coll. 6836a. × 2·5.

FIG. 7. Internal mould of cephalon showing external mould of lower lamella. BM 59499. × 3.


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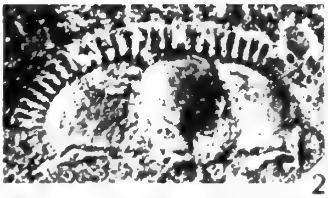
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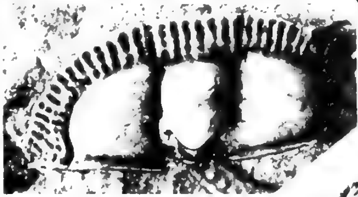
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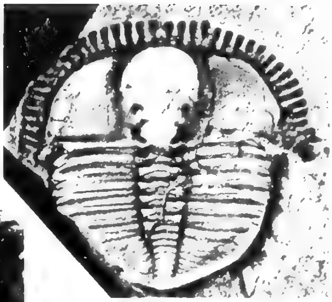
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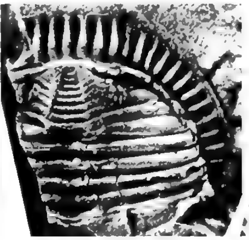
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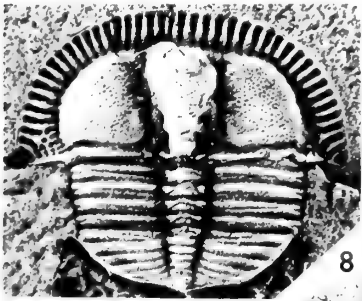
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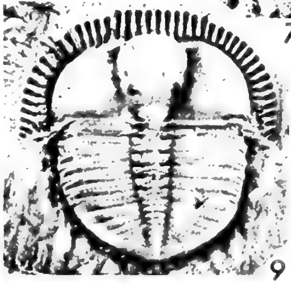
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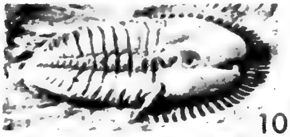
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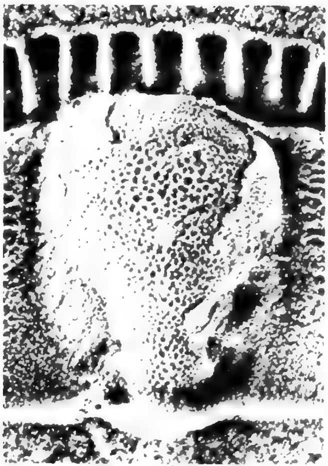
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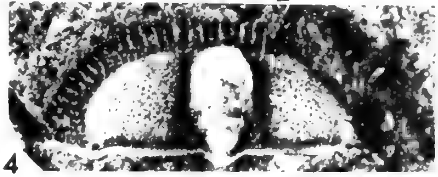
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PLATE 3

Trinucleus fimbriatus Murchison p. 122

Basal Caradoc, quarry at Gwern-yfed-fâch, half a mile
south-east of Builth Road station.
G.R. SO.030526.

FIG. 1. Internal mould of cephalon with displaced lower lamella showing through upper lamella. GSM 35356. × 3. (Figured as *Trinucleoides salteri*, Elles, 1940, pl. 30, fig. 9.)

Trinucleus abruptus sp. nov. p. 132

Lower Llanvirn, small quarries 600 yards east of
Upper Gilwern. G.R. SO.092582.

FIG. 2. Paratype. Internal mould of virtually complete specimen. BM 36921. × 2·5. (Figured as *Trinucleus* cf. *foveolatus* Angelin; Elles, 1940, pl. 31, figs 1, 1a.)

FIG. 3. Paratype. Internal mould showing left genal spine. It. 2736. × 3.

FIG. 4. Paratype. Internal mould of nearly complete specimen. OUM B.179. × 2·5.

FIG. 7. Holotype. Internal mould of nearly complete specimen. BM 36920. × 4. (Figured as *Trinucleus* cf. *foveolatus* Angelin; Elles, 1940, pl. 31, figs 2, 2a.)

Lower Llanvirn, cliff section on left bank of Howey Brook
half a mile east-south-east of Carregwiber.
G.R. SO.089582.

FIG. 6. Paratype. Latex impression from external mould of cranidium showing small median glabellar node and fine reticulate sculpture. It. 2738. × 6.

Trinucleus cf. ***acutofinalis*** Whittard p. 137

Upper Llanvirn, in left bank of stream 200 yards south-west of
Wern-Ddu Barn. G.R. SO.080610.

FIG. 5. External mould of anterior thoracic segment. It. 2739. × 5.


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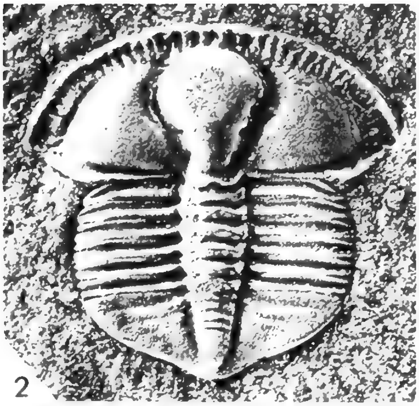
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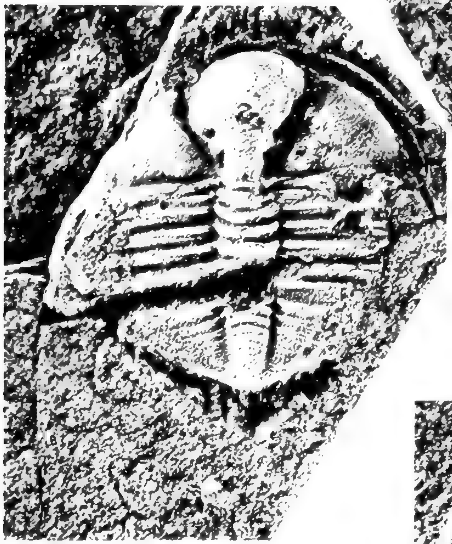
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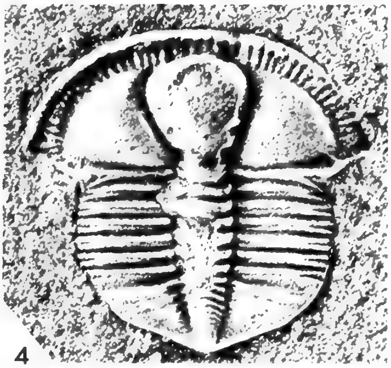
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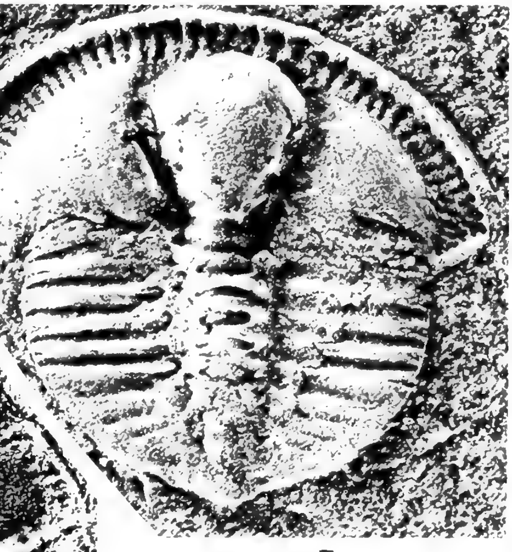
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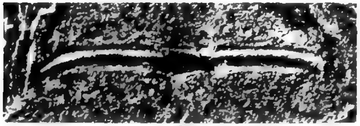
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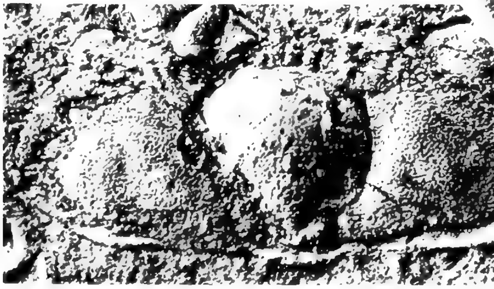
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PLATE 4

Bergamia prima (Elles) p. 140

Llandeilo, stream section 15 yards south-west of the old quarry
350 yards west of Maesgwynne. G.R. SO.059566.

FIGS 1, 2. Internal mould of lower lamella showing the two arcs of pits external to the girder. It. 2745. Fig. 1. × 10; Fig. 2. × 4.

Llandeilo, old quarry 350 yards west of Maesgwynne.
G.R. SO.059566.

FIG. 6. Holotype. Latex impression from external mould. BU 257. × 4·5. (Figured as *Trinucleus fimbriatus* mut. *primus*, Elles, 1940, pl. 30, fig. 1, upper specimen.)

Anebolithus sp. p. 139

Lower Llanvirn, small quarries 600 yards east of Upper Gilwern.
G.R. SO.092582.

FIGS 3, 5. Internal and external moulds of lower lamella. It. 2744. × 3.

Trinucleus cf. **acutofinalis** Whittard p. 137

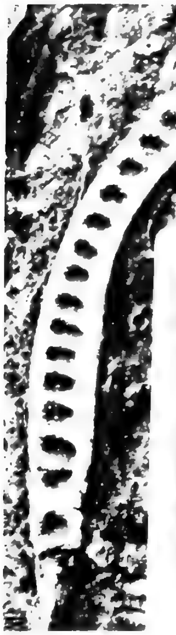
Upper Llanvirn, in left bank of stream 200 yards south-west of
Wern-Ddu Barn. G.R. SO.080610.

FIG. 4. Internal mould of pygidium and part of thorax. It. 2741. × 5.

FIG. 8. Latex impression from external mould of cranidium showing the fringe pits. It. 2742. × 5.

Upper Llanvirn, in right bank of stream 200 yards south-west of
Wern-Ddu Barn. G.R. SO.080610.

FIG. 7. Latex impression from external mould of nearly complete specimen. It. 2743. × 7.



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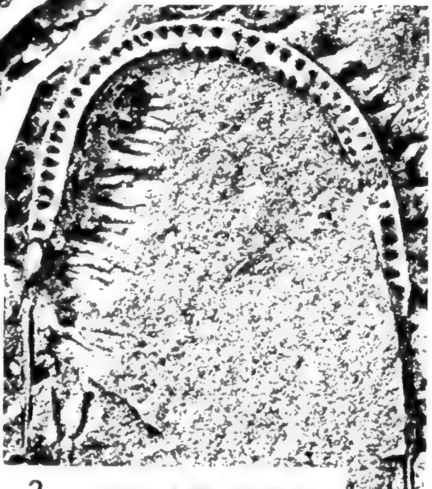

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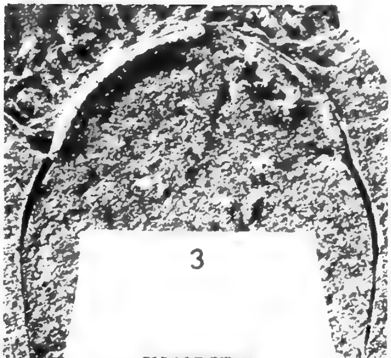

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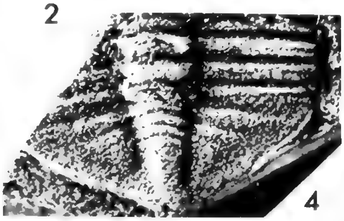

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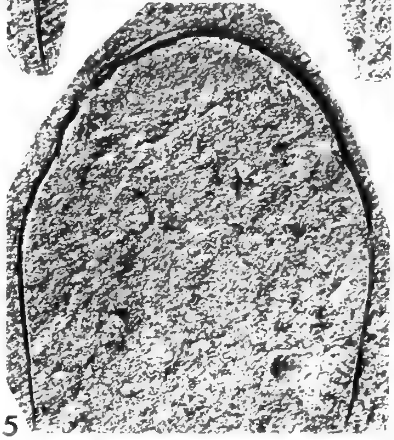

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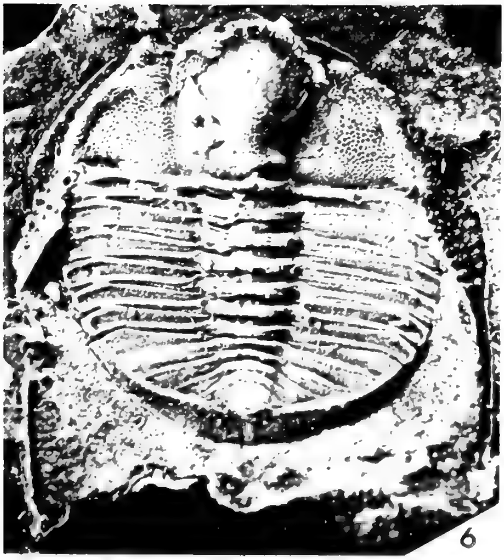

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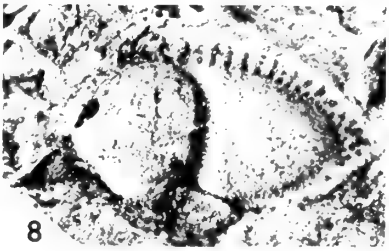

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PLATE 5

Bergamia prima (Elles) p. 140

Llandeilo, old quarry 350 yards west of Maesgwynne.
G.R. SO.059566.

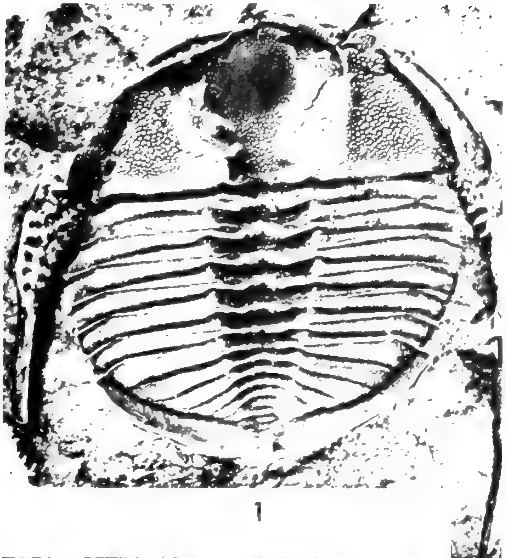
FIGS 1, 2. Holotype. External and internal moulds of nearly complete specimen. BU 257. × 4. (Figured as *Trinucleus fimbriatus* mut. *primus*, Elles, 1940, pl. 30, fig. 1, lower specimen.)

FIG. 5. Internal mould of complete specimen showing median glabellar node. It. 2753. × 3·5.

Llandeilo, stream section 15 yards south-west of the old quarry
350 yards west of Maesgwynne.
G.R. SO.059566.

FIGS 3, 4. Internal mould of lower lamella showing the two arcs of pits external to the girder. It. 2746. Fig. 3. × 10; Fig. 4. × 4.

FIG. 6. Internal mould of complete specimen. It. 2749. × 3.



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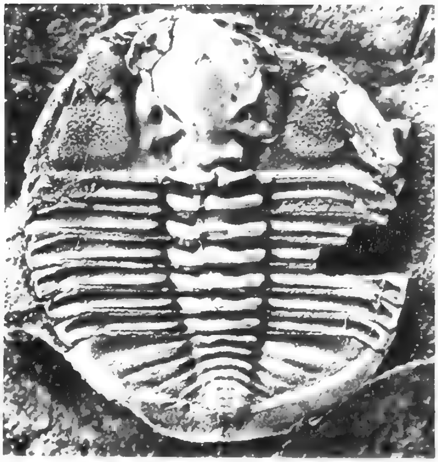

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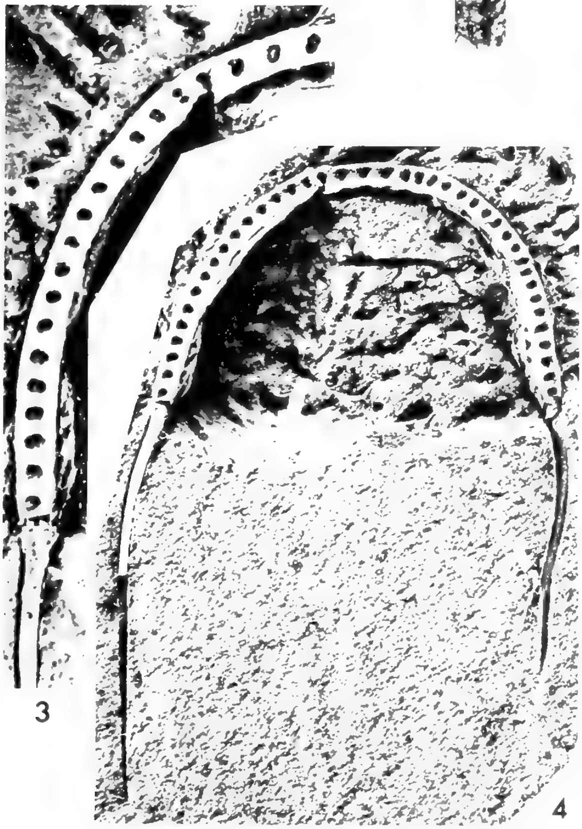

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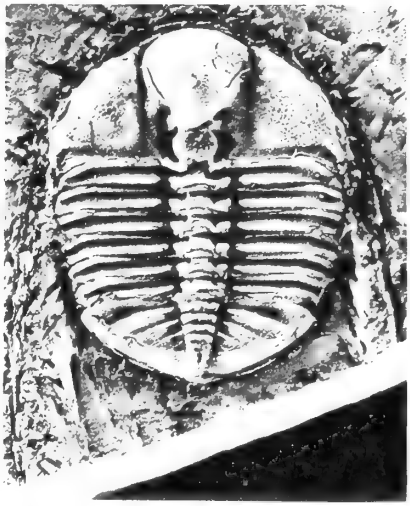

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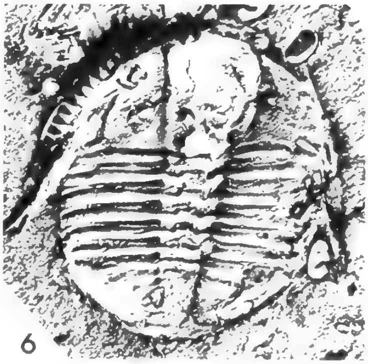

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PLATE 6

Bergamia prima (Elles) p. 140

Llandeilo, old quarry 350 yards west of Maesgwynne.
G.R. SO.059566.

FIGS 1, 4. Oblique and dorsal views of specimen showing an external mould of the lower lamella. It. 2750. Fig. 1. × 5; Fig. 4. × 3·5.

FIG. 6. Latex impression from external mould of anterior thoracic segment. It. 2751. × 5.

FIG. 8. Enrolled specimen showing internal mould of thorax and pygidium and external mould of one gena. It. 2752. × 6.

Llandeilo, stream section 15 yards south-west of the old quarry
350 yards west of Maesgwynne.
G.R. SO.059566.

FIGS 2, 3. Internal mould of lower lamella showing the E_1 and E_2 arcs being barely more than twin pits anterolaterally. It. 2747. Fig. 2. × 5; Fig. 3. × 10

FIG. 5. Internal mould of meraspis ?degree 4. It. 2748. × 10.

Bergamia whittardi sp. nov. p. 146

Uppermost Llandeilo, small quarry at south-western end of
Pen-cerig Lake. G.R. SO.043541.

FIG. 7. Enrolled ?meraspis. It. 2773. × 10.

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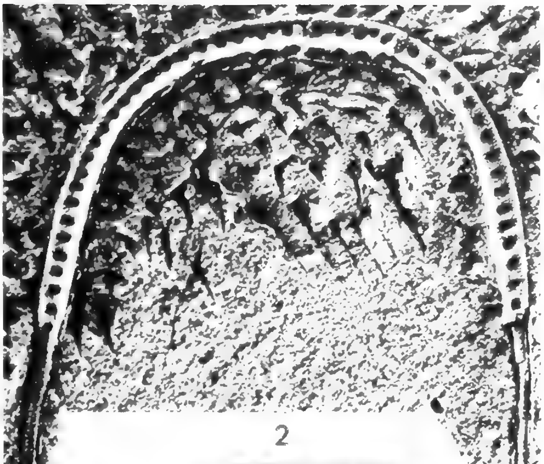

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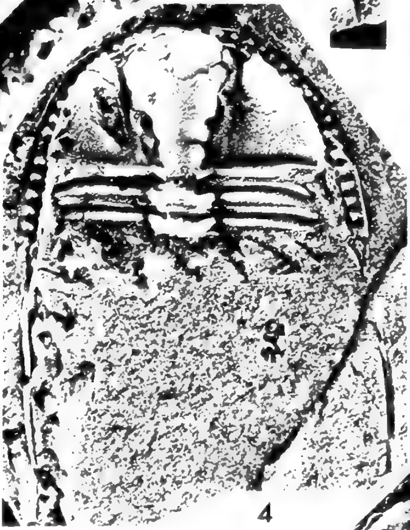

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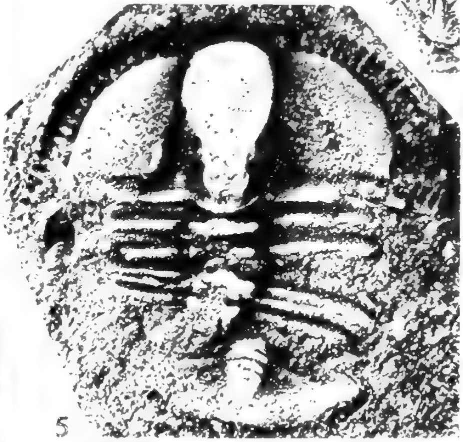

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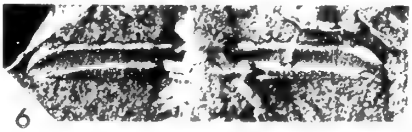

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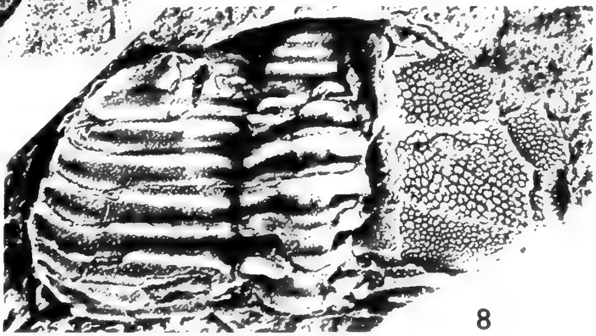

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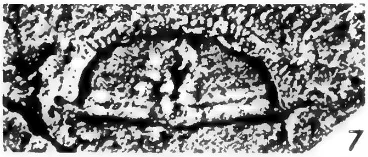

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PLATE 7

Bergamia whittardi sp. nov. p. 146

Uppermost Llandeilo, small quarry at south-western end of
Pen-cerig Lake. G.R. SO.043541.

FIG. 1. Internal mould of thorax showing lack of articulating half ring on anterior segment. It. 2762. × 6.

FIG. 2. Internal mould of transitory pygidium. It. 2772. × 15.

FIG. 3. Paratype. Internal mould of part of lower lamella showing incomplete E_2 arc. It. 2759. × 5.

FIG. 4. Internal mould of ?meraspis cephalon. It. 2776. × 10.

FIG. 5. Latex cast from external mould of lower lamella showing the pit distribution on the genal flange. It. 2771. × 8.

FIG. 6. Holotype. Internal mould of part of lower lamella, showing E_2 arc developed anteriorly. BU 260a. × 8. (Figured as *Trinucleus fimbriatus* mut. *primus*, Elles, 1940 pl. 30, fig. 5.)

FIG. 7. Paratype. Internal mould of part of lower lamella showing incomplete E_2 arc. It. 2756. × 6.

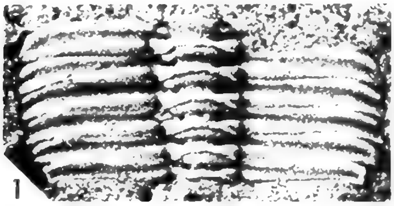
FIG. 8. Internal mould of transitory pygidium. It. 2766. × 12.

FIG. 9. Internal mould showing upper and lower lamellae. It. 2761. × 6.

FIG. 10. Paratype. Internal mould of nearly complete specimen. It. 2758. × 8.

FIG. 11. Internal mould of small holaspis. It. 2778. × 10.

FIG. 12. Paratype. Internal mould of cranidium showing pit distribution and surface sculpture. It. 2754. × 5.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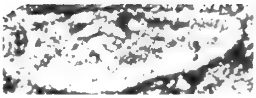
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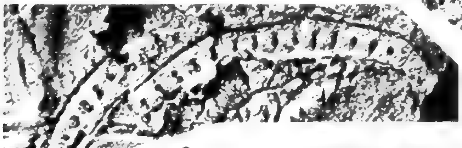
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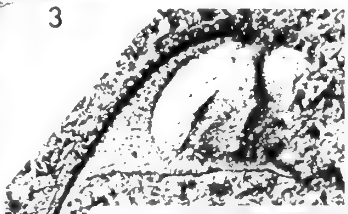
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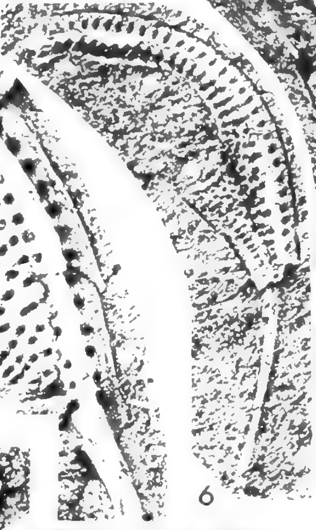
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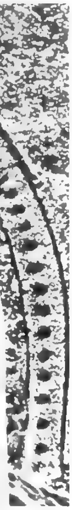
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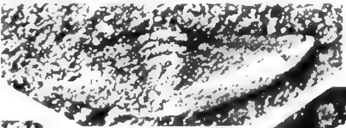
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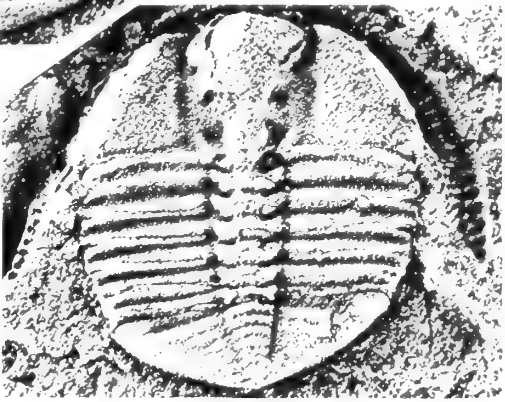
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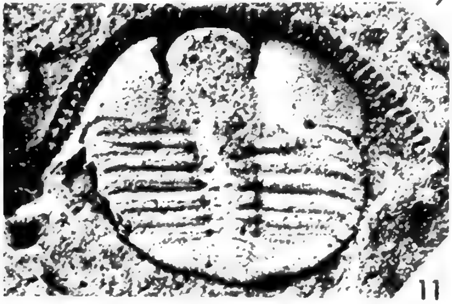
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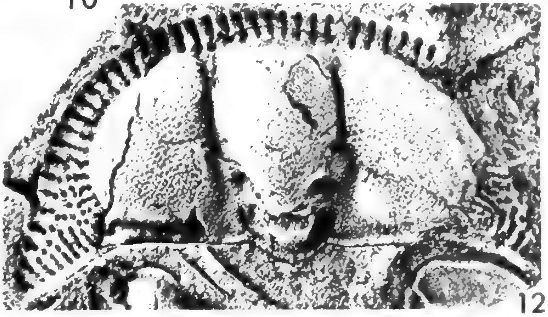
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PLATE 8

Bergamia whittardi sp. nov. p. 146

Llandeilo, 120 yards south-east of Tre coed on left bank of stream.
G.R. SO.054552.

FIG. 1. Paratype. Internal mould showing parts of the upper and lower lamellae. It. 2760. × 6.

Uppermost Llandeilo, small quarry at south-western end of
Pen-cerig Lake. G.R. SO.043541.

FIG. 2. Internal mould of meraspis cephalon (see also Text-fig. 7). It. 2775. × 10.

FIG. 3. Paratype. Latex impression from external mould of small holaspis. It. 2755. × 10.

FIG. 4. Internal mould of meraspis cranidium (see also Text-fig. 7). It. 2768. × 10.

FIG. 5. Enrolled specimen. It. 2770. × 7.

FIG. 6. Internal mould of meraspis cephalon. It. 2774. × 10.

FIG. 7. Paratype. Internal mould of pygidium. It. 2757. × 6.

FIG. 8. External mould of pygidium showing terrace lines on posterior border. It. 2769. × 10.

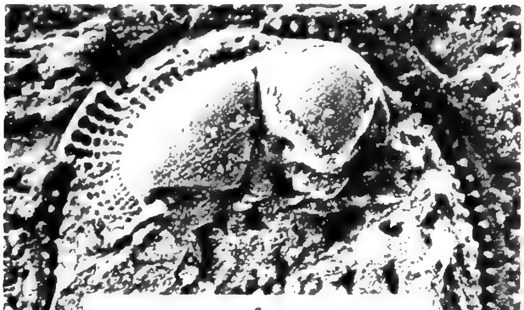
FIG. 9. Paratype. Internal mould of cranidium. Wattison Collection H.14. × 5.

FIG. 11. External mould of meraspis cephalon (see also Text-fig. 7). It. 2763. × 10.

Trinucleinid gen. et sp. indet. p. 151

Upper Llanvirn, track 60 yards south-west of Bwlch-y-cefn.
G.R. SO.120610.

FIG. 10. External mould of part of thorax and pygidium. It. 2779. × 5.



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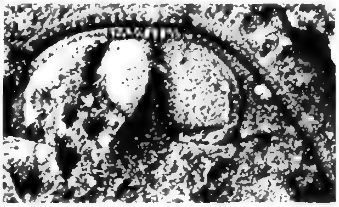

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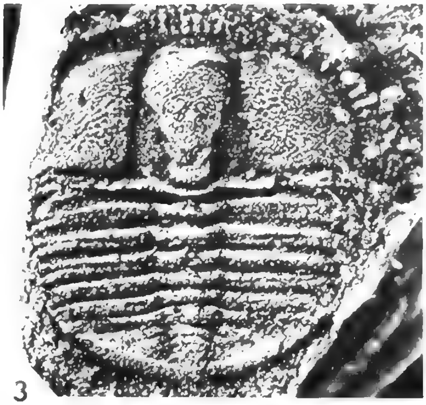

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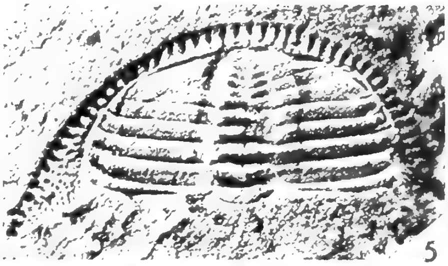

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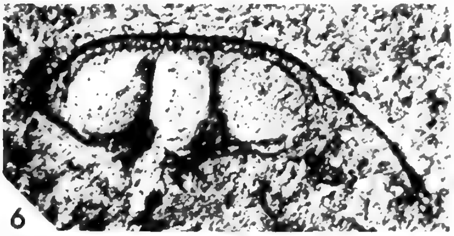

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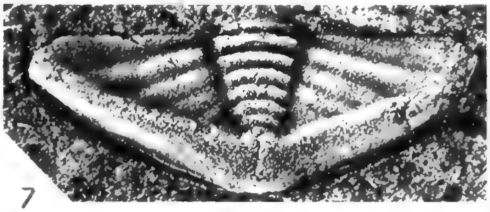

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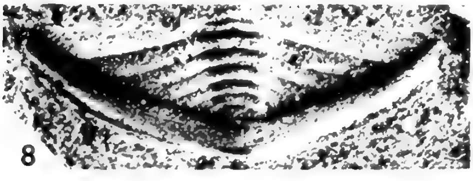

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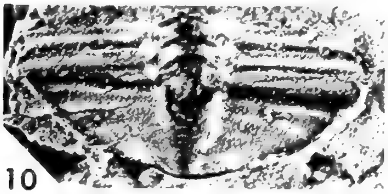

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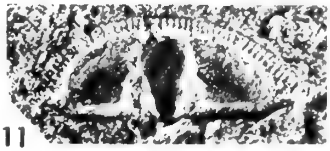

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PLATE 9

Bergamia whittardi sp. nov. p. 146

Uppermost Llandeilo, small quarry at south-western end of
Pen-cerig Lake. SO.043541.

FIG. 1. External mould of meraspis degree 4 (see also Text-fig. 7). It. 2765. × 12.

FIG. 2. Internal mould of pygidium showing extension of axis onto posterior border. It. 2767. × 8.

Trinucleinid gen. et. sp. indet. p. 151

Upper Llanvirn, in left bank of tributary to Howey Brook,
35 yards below lowest waterfall.
G.R. SO.092591.

FIGS 3, 7. Internal and external moulds of poorly preserved specimen. It. 2780. × 4.

Cryptolithus instabilis sp. nov. p. 152

Llandeilo, left bank of Dulas Brook, 150 yards south-west of
the old quarry west of Maesgwynne.
G.R. SO.058564.

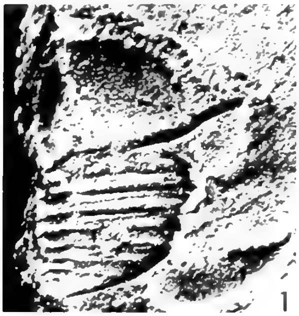
FIG. 4. Paratype. External mould of lower lamella. It. 2793. × 5.

FIG. 5. Paratype. Enrolled specimen. It. 2794. × 3.

FIG. 8. Internal mould of cranidium showing a single pit developed medially. It. 2805. × 6.

Llandeilo, 160 yards south-east of Tre coed on
left bank of stream. G.R. SO.054552.

FIG. 6. Paratype. Internal mould showing occipital spine extending to fourth thoracic segment. It. 2802. × 5.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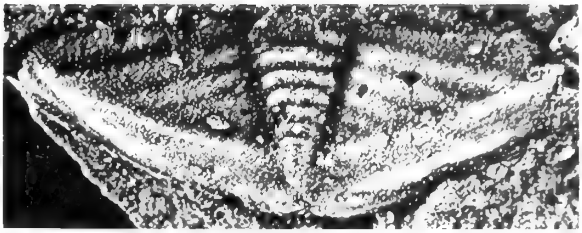
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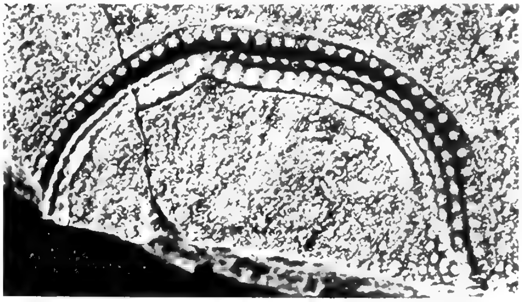
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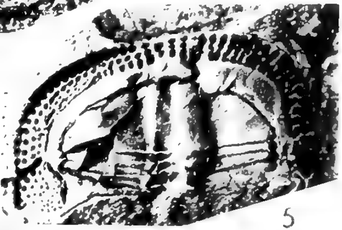
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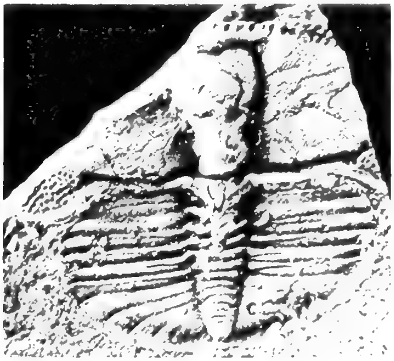
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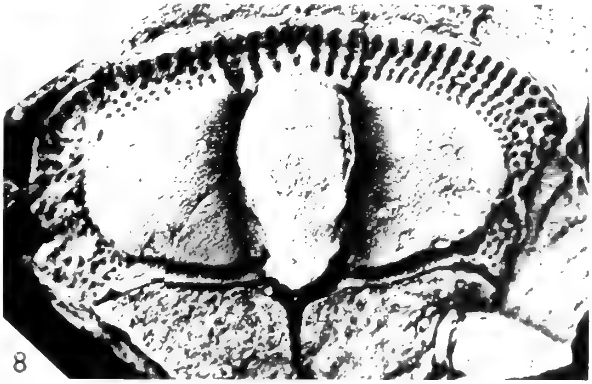
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PLATE 10

Cryptolithus instabilis sp. nov. p. 152

Llandeilo, left bank of Dulas Brook, 150 yards south-west of the
old quarry west of Maesgwynne. G.R. SO.058564.

FIG. 1. Holotype. Internal mould of cranidium. It. 2792. × 4.

FIG. 2. Paratype. Internal mould of cranidium showing only three pits in the median row and well developed lateral glabellar furrows. It. 2798. × 3.

FIG. 3. Paratype. Internal mould showing lower lamella and weakly developed alae. It. 2796. × 4.

FIG. 4. Paratype. Latex impression from external mould showing sculpture on the glabella and gena, and presence of median glabellar ridge. It. 2797. × 8.

FIG. 6. Paratype. Internal mould showing pit distribution. It. 2799. × 3·5.

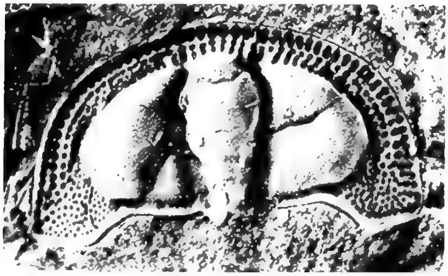
Llandeilo, 160 yards south-east of Tre coed on left bank of stream.
G.R. SO.054552.

FIG. 5. Paratype. Dorsal surface showing sculpture and genal caecae. It. 2801. × 5.

FIG. 7. Paratype. Internal mould with some exoskeleton adhering. It. 2803. × 3·5.

Llandeilo, stream section 15 yards south-west of the
old quarry 350 yards west of Maesgwynne. G.R. SO.059566.

FIG. 8. Dorsal surface of cranidium showing irregularities in lateral distribution of I arcs and also a single pit developed medially. It. 2804. × 4.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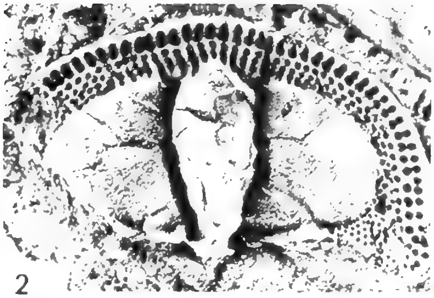
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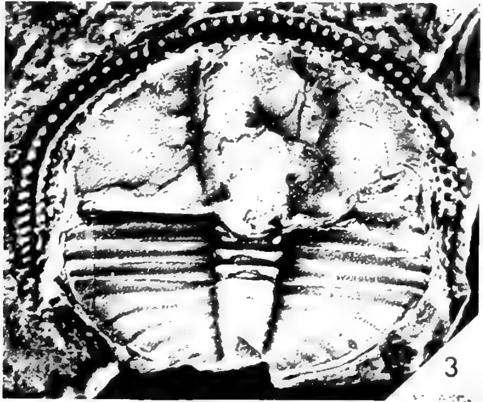
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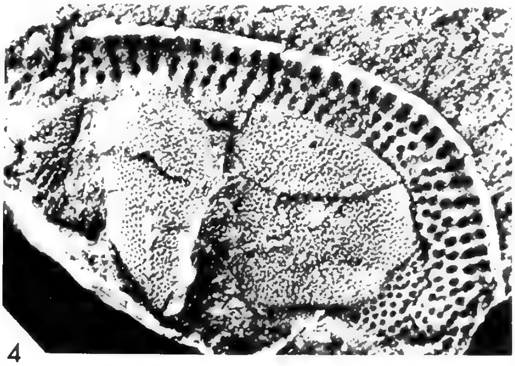
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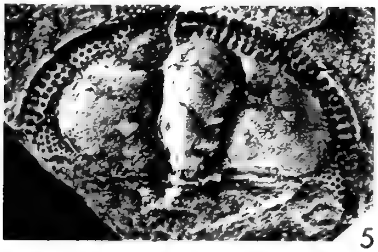
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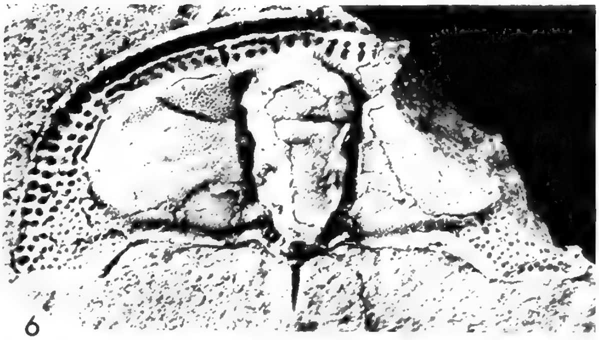
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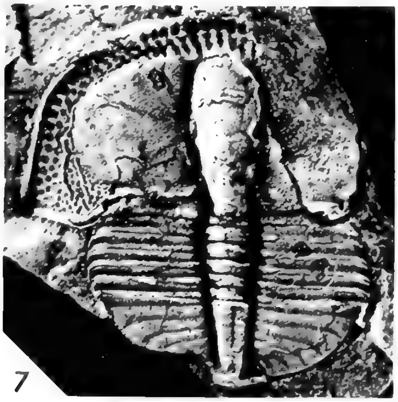
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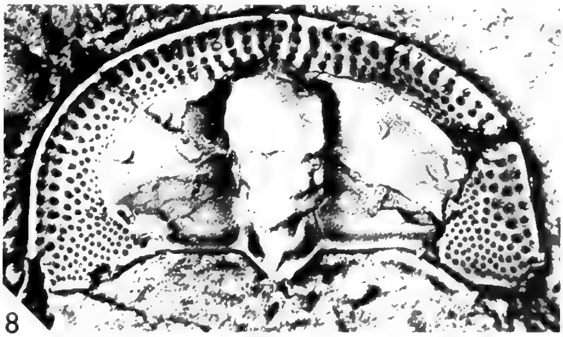
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PLATE 11

Cryptolithus sp. A p. 157

Upper Llanvirn, right bank of stream 100 yards below
waterfall in pass north-east of Bwlch-y-cefn.
G.R. SO.123612.

FIG. 1. Internal mould of lower lamella. It. 2806. × 3.
FIG. 4. Internal mould of pygidium. It. 2807. × 10.
FIG. 6. External mould of part of thorax. It. 2808. × 5.

?**Cryptolithus** sp. B p. 157

Llandeilo, stream section at Wellfield Lodge immediately above
where the stream is piped under the road.
G.R. SO.044528.

FIGS 2, 7. External and internal moulds of fragment of lower lamella. It. 2809. × 5.

?**Cryptolithus** sp. C p. 158

Llandeilo, stream section at Wellfield Lodge immediately
below where the stream is piped under the road.
G.R. SO.044528.

FIGS 3, 8. External mould and latex impression of fragment of cephalon. It. 2810. × 5.

Cryptolithus instabilis sp. nov. p. 152

Llandeilo, left bank of Dulas Brook, 150 yards south-west of
the old quarry west of Maesgwynne.
G.R. SO.058564.

FIG. 5. Paratype. Internal mould of pygidium. It. 2795. × 5.

Llandeilo, 160 yards south-east of Tre coed on left bank of stream.
G.R. SO.054552.

FIG. 12. Paratype. Internal mould of fragment of lower lamella showing proximal part of genal spine. It. 2800. × 3.

Bettonia chamberlaini (Elles) p. 159

Lower Llanvirn, cliff section on left bank of Howey Brook
half a mile east-south-east of Carregwiber.
G.R. SO.089582.

FIG. 9. Internal mould of small holaspis. It. 2826. × 10.
FIG. 10. Internal mould of meraspis ?degree 5. It. 2815. × 10.
FIG. 11. Internal mould of fragment of lower lamella. It. 2825. × 2·5.
FIG. 13. External mould of ?transitory pygidium. It. 2827. × 10.
FIG. 15. Latex impression from external mould of lower lamella. It. 2812. × 4.

Lower Llanvirn, small quarries 600 yards east of Upper Gilwern.
G.R. SO.092582.

FIG. 14. Enrolled specimen. It. 2816. × 4.


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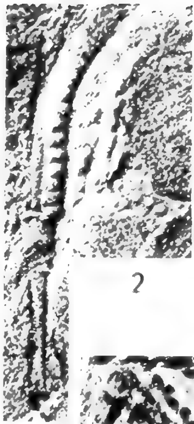
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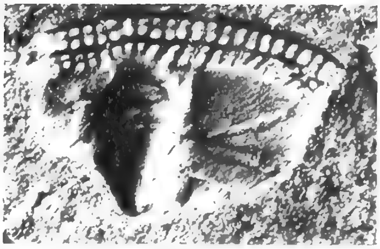
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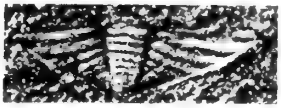
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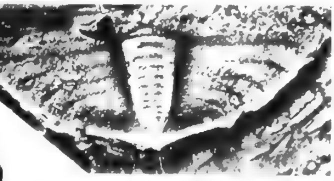
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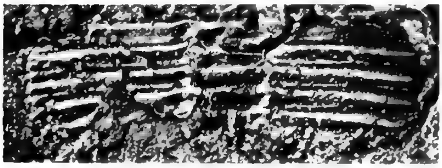
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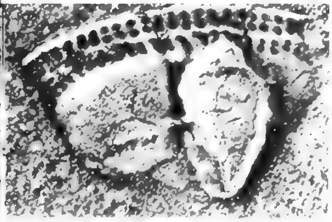
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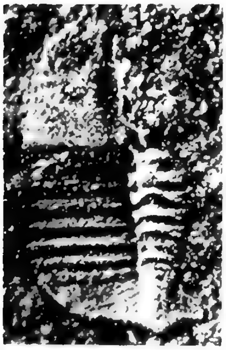
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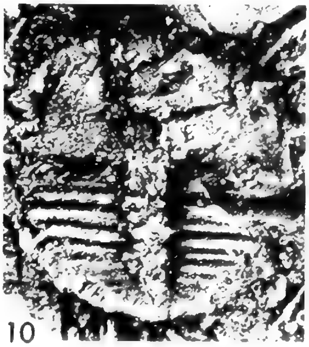
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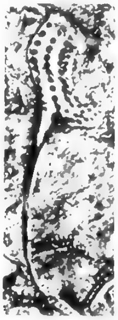
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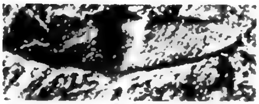
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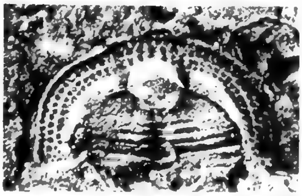
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PLATE 12

Bettonia chamberlaini (Elles) p. 159

Lower Llanvirn, cliff section on left bank of Howey Brook
half a mile east-south-east of Carregwiber.
G.R. SO.089582.

FIG. 1. Paratype. Internal mould of small holaspis. BU 263. × 6.

FIG. 2. Internal mould of cranidium (see also Text-fig. 10). It. 2817. × 5.

FIG. 4. Latex impression from external mould of cranidium showing occipital spine and surface sculpture It. 2818. × 7.

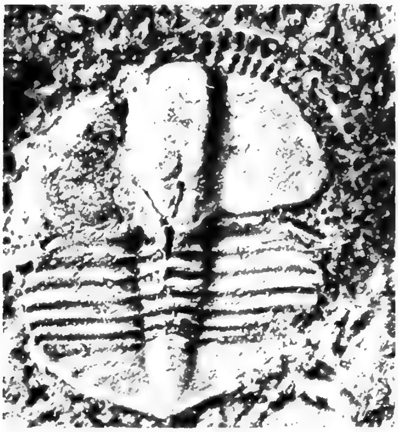
FIG. 5. Holotype. Internal mould of nearly complete specimen with damaged fringe (see also Text-fig. 10). BU 261a. × 4.

FIG. 6. Internal mould of small holaspis. It. 2814. × 8.

FIG. 7. Latex impression from external mould showing adventitious pits and sculpture on gena (see also Text-fig. 10). It. 2813. × 5.

Upper Llanvirn, about 15 yards below confluence of
Holywell and Whitehouse Brooks, Rorrington, Shropshire.

FIG. 3. Internal mould of cranidium (see also Text-fig. 11). GSM 86785. × 5. (Figured as holotype of *Bettonia frontalis*, Whittard, 1956, pl. 9, fig. 7.)



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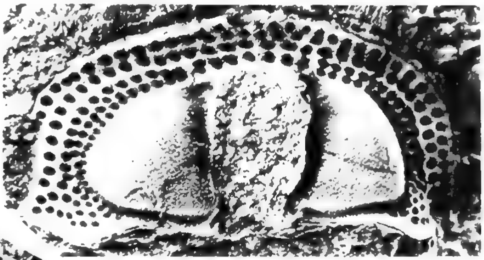

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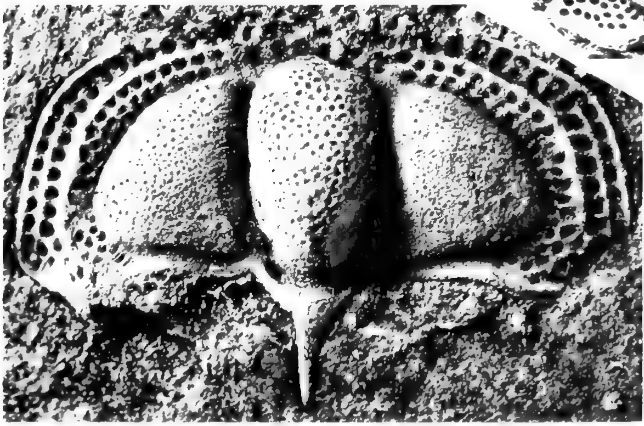

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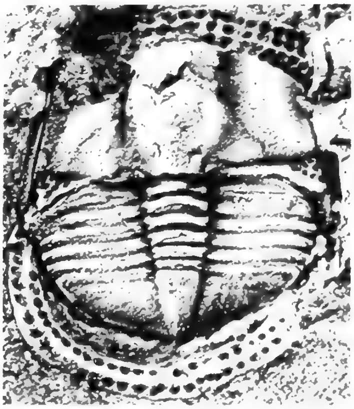

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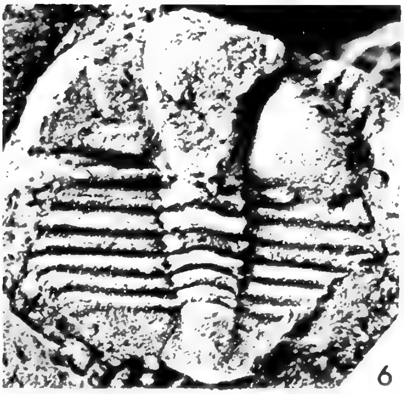

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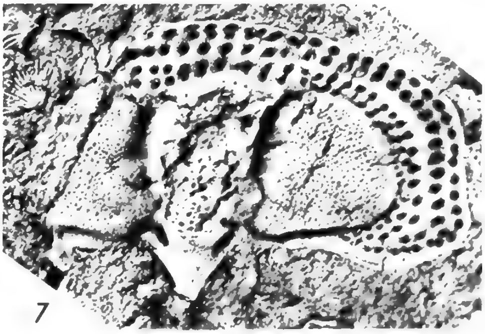

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PLATE 13

Bettonia chamberlaini (Elles) p. 159

Lower Llanvirn, cliff section on left bank of Howey Brook
half a mile east-south-east of Carregwiber.
G.R. SO.089582.

FIG. 1. Internal mould of lower lamella (see also Text-fig. 10). BU 261b. × 5.

FIG. 2. Internal mould of cranidium (see also Text-fig. 10). BU 264. × 5.

FIG. 3. Internal mould of damaged cranidium (see also Text-fig. 10). It. 2819. × 5.

FIG. 4. Paratype. Internal mould of damaged specimen (see also Text-fig. 10). BU 262. × 4.

FIG. 5. Internal mould of cranidium. SM A10,082. × 4. (Figured as holotype of *Trinucleus* (*Cryptolithus*) *gibbosus*, Elles, 1940, pl. 31, fig. 3.)

FIG. 6. Internal mould of lower lamella (see also Text-fig. 10). It. 2821. × 4.

FIG 7. Internal mould of cranidium showing small median glabellar node, and no adventitious pits external to E_1 (see also Text-fig. 10). It. 2820. × 5.

FIG. 8. Internal mould of nearly complete specimen. It. 2823. × 5.


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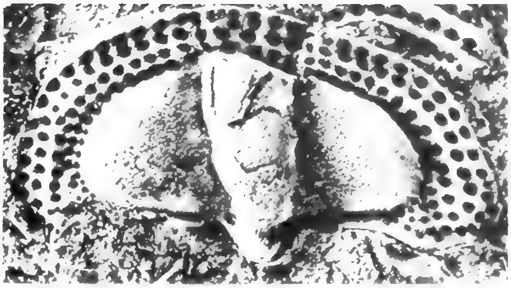
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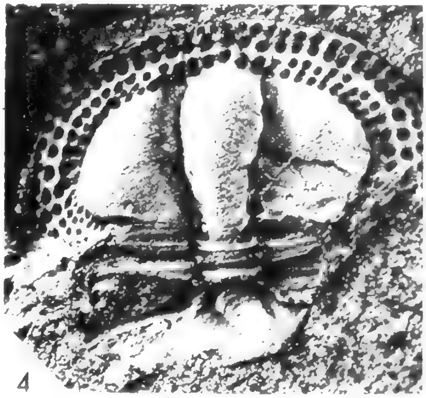
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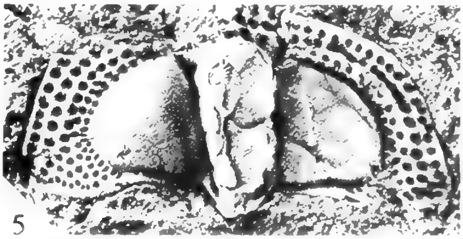
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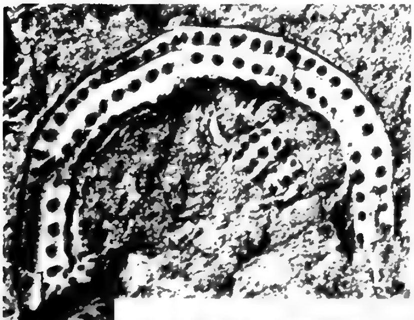
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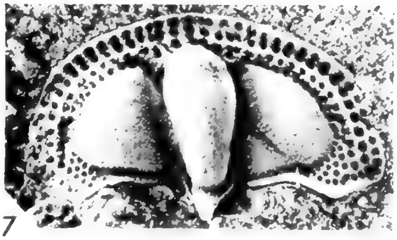
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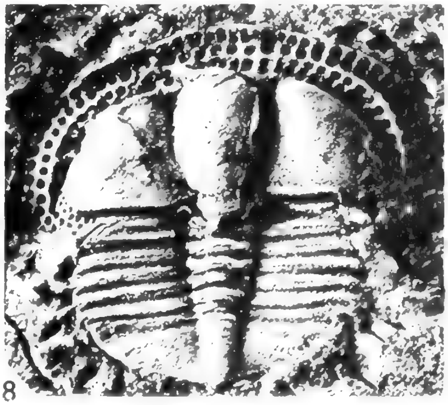
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PLATE 14

Bettonia chamberlaini (Elles) p. 159

Lower Llanvirn, cliff section on left bank of Howey Brook
half a mile east-south-east of Carregwiber.
G.R. SO.089582.

FIG. 1. Enlargement of part of Pl. 11, fig. 15 showing terrace lines on the pseudogirder. It. 2812. × 15.

FIG. 2. Internal mould of cranidium showing symmetrical absence of an E_1 pit laterally. It. 2822. × 5.

FIG. 4. Latex impression from external mould of small cranidium showing coarse reticulation on glabella and gena. It. 2828. × 10.

FIG. 5. Internal mould of meraspis ?degree 5. It. 2829. × 8.

FIG. 9. Internal mould of thorax and pygidium. BU 368. × 6.

Upper Llanvirn, about 15 yards below confluence of
Holywell and Whitehouse Brooks, Rorrington, Shropshire.

FIG. 3. Internal mould of cranidium (see also Text-fig. 11). GSM 86789. × 5. (Figured as holotype of *Bettonia irregularis*, Whittard, 1956, pl. 9, fig. 12.)

Upper Llanvirn, lane leading to Lyde, 170 yards south-east of
Mincop, Shropshire.

FIG. 8. Latex impression from external mould of cephalon (see also Text-fig. 11). GSM 86786A. × 5. (Figured as holotype of *Bettonia paucipuncta*, Whittard, 1956, pl. 9, fig. 9.)

Lower Llanvirn, small quarries 600 yards east of
Upper Gilwern. G.R. SO.092582.

FIG. 10. Internal mould of complete specimen (see also Text-fig. 10). It. 2811. × 5.

Marrolithus sp. p. 168

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIGS 6, 7. Latex impression and internal mould of cephalon with mould of ventral surface of lower lamella. It. 2781. × 3·5.

Bettonia aff. ***superstes*** Whittard p. 167

Llandeilo, stream section at Wellfield Lodge immediately
below where the stream is piped under the road.
G.R. SO.044528.

FIG. 11. Internal mould of cranidium and anterior thoracic segments. It. 2830. × 4.


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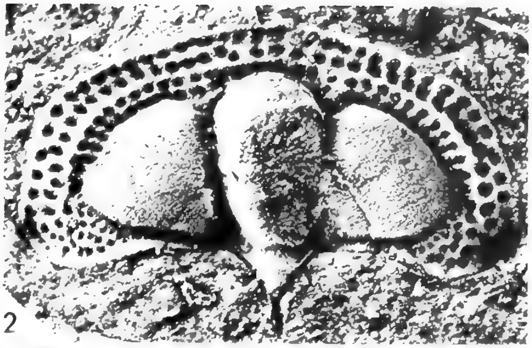
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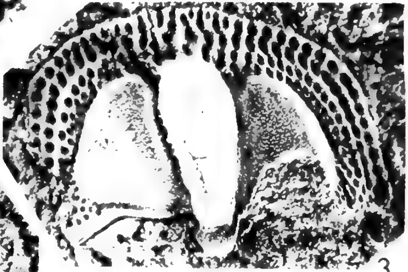
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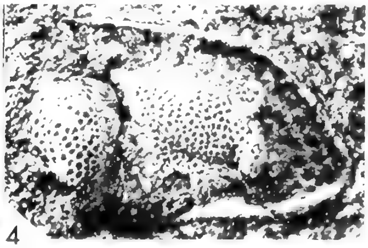
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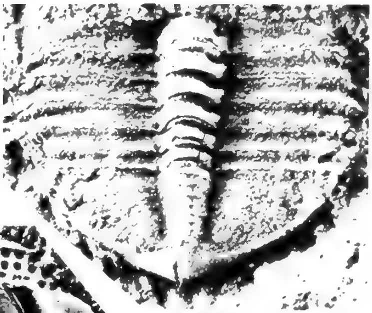
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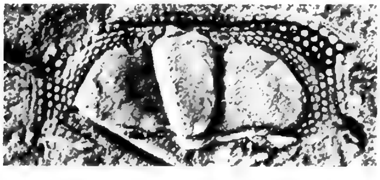
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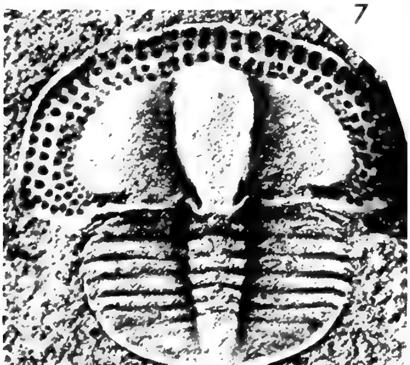
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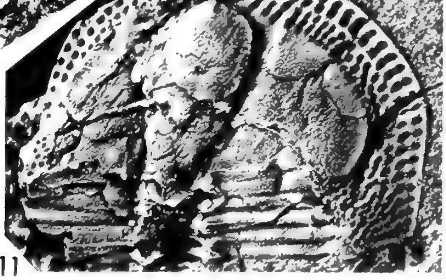
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PLATE 15

Protolloydolithus reticulatus (Elles) p. 169

Llandeilo, stream section east of Bach-y-graig, exact locality unknown.

FIG. 1. Holotype. Internal mould. I. 7216. × 3. (Figured as *Trinucleoides reticulatus*, Elles, 1940, pl. 29, fig. 6.)

FIG. 7. Paratype. Internal mould of thorax and pygidium. It. 8604. × 4. (Figured as *Trinucleoides reticulatus*, Elles, 1940, pl. 29, fig. 8.)

FIG. 9. Latex impression from external mould of complete specimen showing general features. NMW 15.207.G3. × 3.

FIG. 11. Paratype. Internal mould of cranidium. I. 7328. × 3. (Figured as *Trinucleoides reticulatus*, Elles, 1940, pl. 29, fig. 7.)

Llandeilo, left bank of stream section east of Bach-y-graig,
45 yards east of the point where the footpath enters the
wood at the western end of the section. G.R. SO.071610.

FIG. 5. Internal mould of nearly complete specimen showing right genal spine. It. 2784. × 4.

FIG. 6. Latex impression from external mould showing faint terrace lines along the crest of the posterior border. It. 2782. × 10.

FIG. 8. Internal mould of poorly preserved meraspis. It. 2783. × 15.

Telaeomarrolithus intermedius sp. nov. p. 174

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 2. Paratype. Internal mould of damaged cranidium showing two E arcs anterolaterally. It. 8799. × 5.

FIG. 3. Paratype. Latex impression from external mould of cephalon showing surface sculpture and median glabellar node. It. 8800. × 3.

FIG. 4. Paratype. Internal mould of lower lamella showing expansion of pits at anterolateral corners. It. 8606. × 4.

FIG. 10. Paratype. Internal mould of cranidium showing two E arcs developed at anterolateral corners. In. 48533. × 4.


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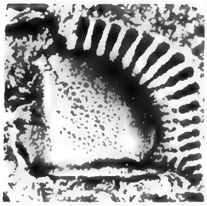
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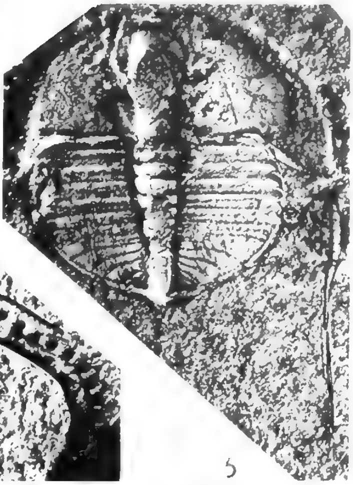
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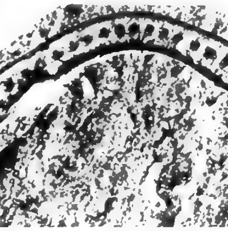
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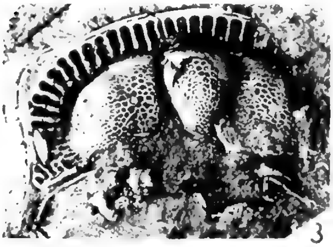
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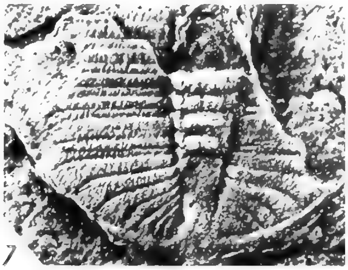
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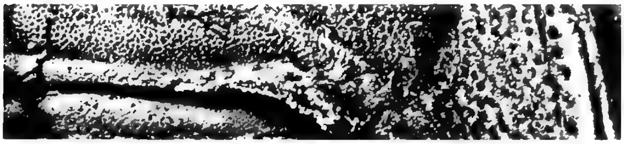
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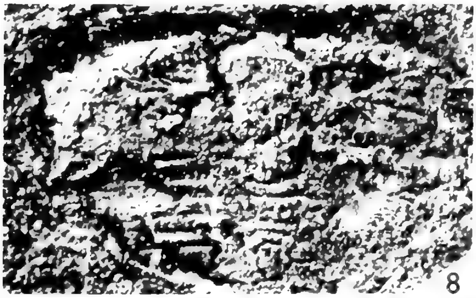
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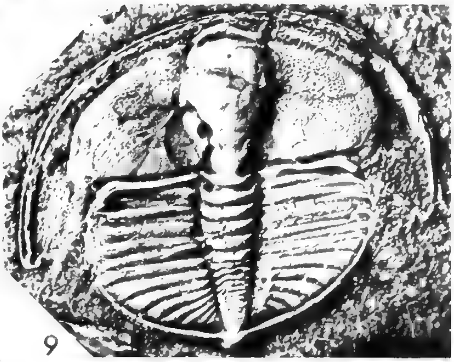
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PLATE 16

Telaeomarrolithus intermedius sp. nov. p. 174

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 1. Holotype. Internal mould of cephalon showing lower lamella. It. 2785. × 3.

FIG. 4. Paratype. Internal mould showing posteriorly divergent genal spines. It. 2789. × 3.

FIG. 5. Holotype. Latex impression from external mould of cephalon showing details of upper lamella and surface sculpture. It. 2785. × 3.

FIG. 6. Paratype. Internal mould of small cephalon. It. 2786. × 6.

FIG. 7. Paratype. Latex impression from external mould of nearly complete specimen. USNM 160108. × 4.

FIG. 8. Paratype. Internal mould of enrolled specimen. It. 2788. × 3.

FIG. 9. Paratype. Internal mould of damaged cranidium. It. 2787. × 5.

Protolloydolithus reticulatus (Elles) p. 169

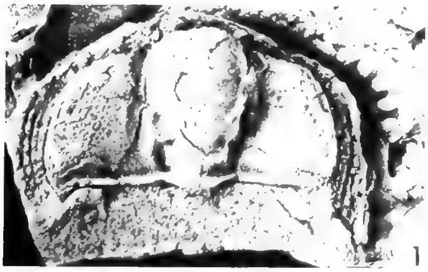
Llandeilo, left bank of stream section east of Bach-y-graig,
45 yards east of the point where the footpath enters the wood at the
western end of the section. G.R. SO.071610.

FIG. 2. Internal mould showing general nature of pit distribution. It. 2782. × 3.

Telaeomarrolithus radiatus (Murchison) p. 178

Basal Caradoc, ?200 yards south-south-east of Crûg, Carmarthenshire.

FIG. 3. Internal mould of cephalon showing lower lamella. GSM Alwyn Williams Coll. 75202. × 2.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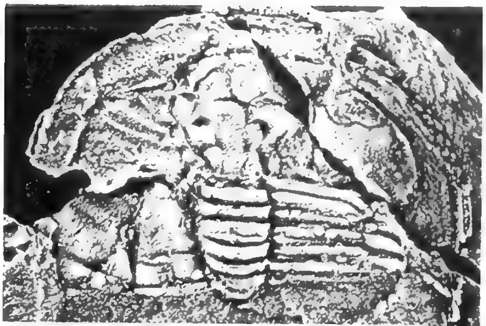
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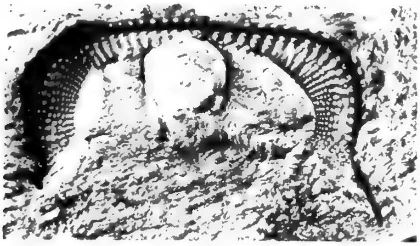
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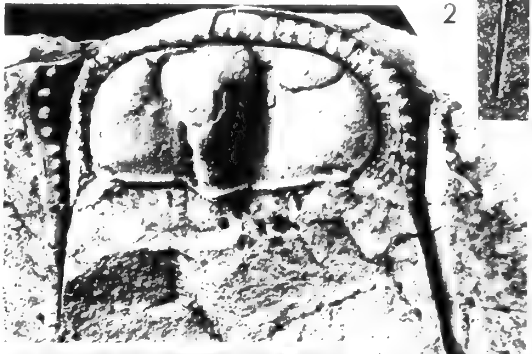
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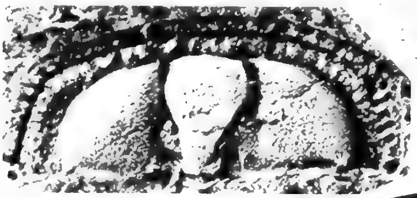
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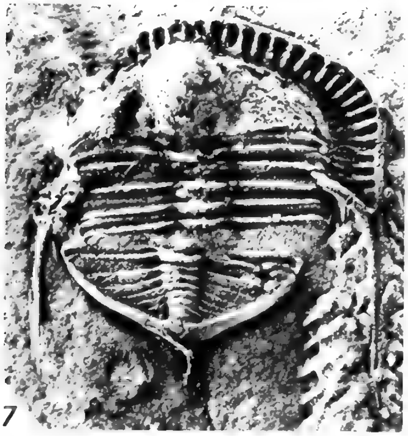
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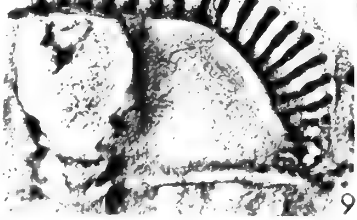
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PALAEOZOIC CORAL FAUNAS FROM VENEZUELA, I. SILURIAN AND PERMO-CARBONIFEROUS CORALS FROM THE MÉRIDA ANDES

C. T. SCRUTTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 20 No. 5
LONDON: 1971

PALAEOZOIC CORAL FAUNAS FROM VENEZUELA, I. SILURIAN AND PERMO-CARBONIFEROUS CORALS FROM THE MÉRIDA ANDES

BY
COLIN THOMAS SCRUTTON
Department of Geology, University of Newcastle upon Tyne

Pp. 183-227; 5 *Plates*, 8 *Text-figures*

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By C. T. SCRUTTON

CONTENTS

SYNOPSIS

Rugose and tabulate corals of Lower Llandovery, Ludlow and Permo-Carboniferous ages are described from localities in the southern part of the Mérida Andes of western Venezuela. The Palaeozoic stratigraphy of the area is briefly reviewed and the ages and relationships of the coral faunas are discussed. The new taxa *Columnaxon angelae* gen. et sp. nov., *Syringaxon arnoldi* sp. nov., *S. suripaense* sp. nov., *Streptelasma shagami* sp. nov., *Leolasma kaljoi* sp. nov. and *Cymatelasma aricaguaense* sp. nov. as well as species of *Lophophyllidium*, *Lophamplexus*, *Tryplasma*, *Coenites*, *Cystihalysites* and *Acanthohalysites* are described. Observations are made on the concepts of some genera and families, particularly *Syringaxon* and the Lindstroemiidae.

I. INTRODUCTION

THE rugose and tabulate corals described in this paper come from localities in the southern part of the Mérida Andes of western Venezuela (Text-fig. 1). The bulk of the material was collected by H. C. Arnold (then Compañia Shell de Venezuela) during 1960–61 but additional material from R. Shagam (University of Pennsylvania) and G. R. Pierce and W. R. Smith (both Creole Petroleum Corporation) has been included. Faunas of three different ages are present; Lower Llandovery, Ludlow and Permo-Carboniferous (?Pennsylvanian), the latter two with some North American affinities. Sixteen species are described belonging to twelve genera; six species and one genus are new. Discounting preliminary reports all the genera except *Lophophyllidium* are recorded for the first time from South America. The material is housed in the Department of Palaeontology, British Museum (Natural History).

II. ACKNOWLEDGEMENTS

The author is grateful to Professor A. J. Boucot (Oregon State University), Dr J. G. Johnson (Oregon State University), Dr R. Shagam (University of Pennsylvania), Dr H. C. Arnold, Jr (Nederlandse Aardolie Maatschappij) and Dr J. M. Bowen (Shell International Petroleum Corporation) for discussion relating to the stratigraphy and age of the faunas from the Mérida Andes. Acknowledgement is also due to Compañia Shell de Venezuela and the Creole Petroleum Corporation for permission to describe this material which they have presented to the British Museum (Natural History).

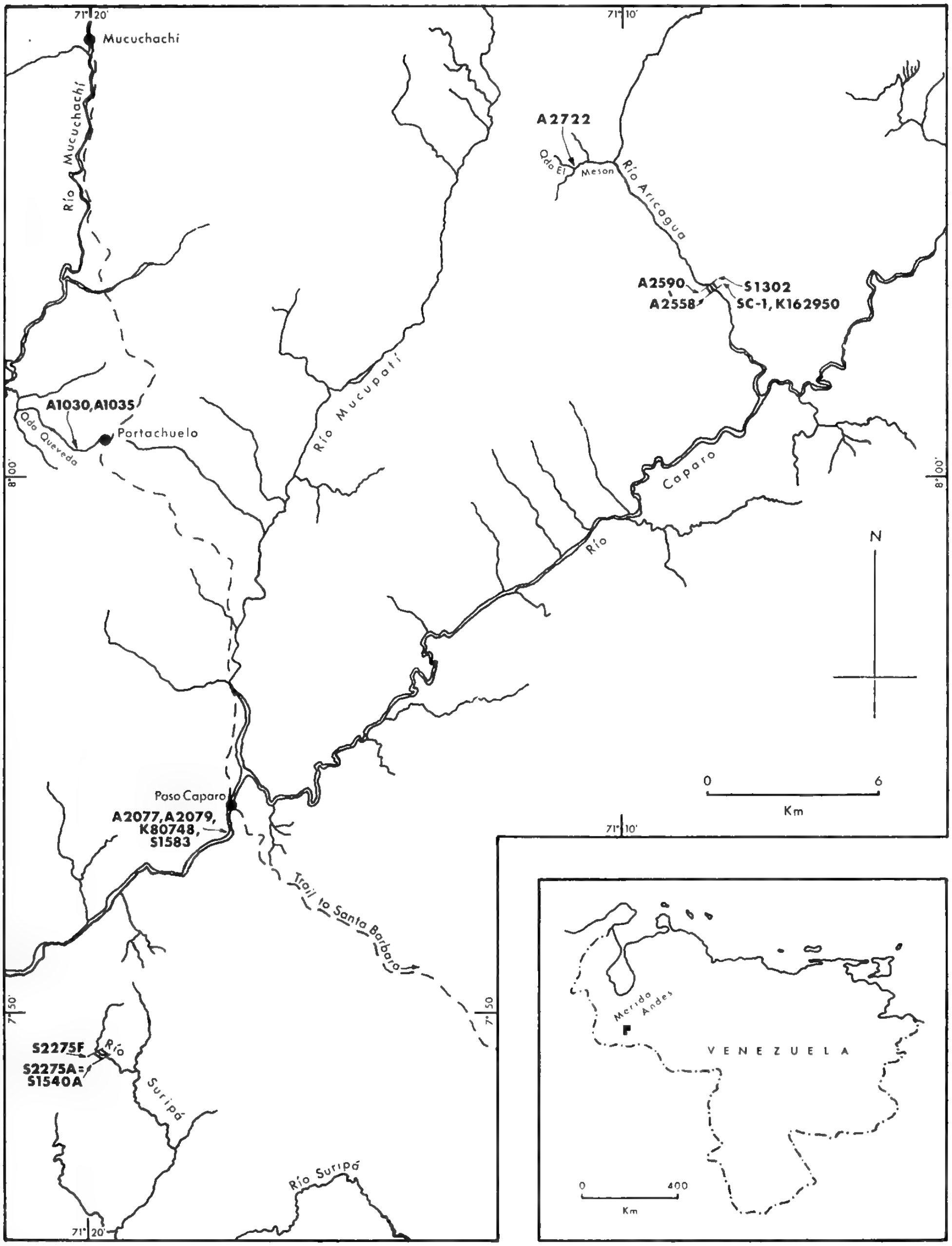

FIG. 1. Sample locations in the southern Mérida Andes. The area covered by the large scale map is indicated in the inset. For further explanation see Appendix.

Dr P. K. Sutherland (University of Oklahoma), and Dr W. J. Sando (United States Geological Survey) have kindly read and commented on the systematic section of the manuscript.

R. F. Wise and P. J. Green (both of the British Museum (Natural History)) respectively prepared thin sections and photographed material for this paper.

III. PALAEOZOIC STRATIGRAPHY OF THE SOUTHERN MÉRIDA ANDES

A review of the known Palaeozoic stratigraphy of the Mérida Andes was published by Cia. Shell de Venezuela & Creole Petroleum Corporation, 1964 (hereafter Shell and Creole, 1964). Their particular object was to demonstrate that the Devonian age assigned to the Mucuchachí Group by Pierce *et al.* (1961 : 352) was based on faunal misidentifications. The re-examination of the original material and of further collections made by H. C. Arnold shew faunas of Middle Ordovician, Silurian and Permo-Carboniferous age to be present in beds assigned to this group, but no

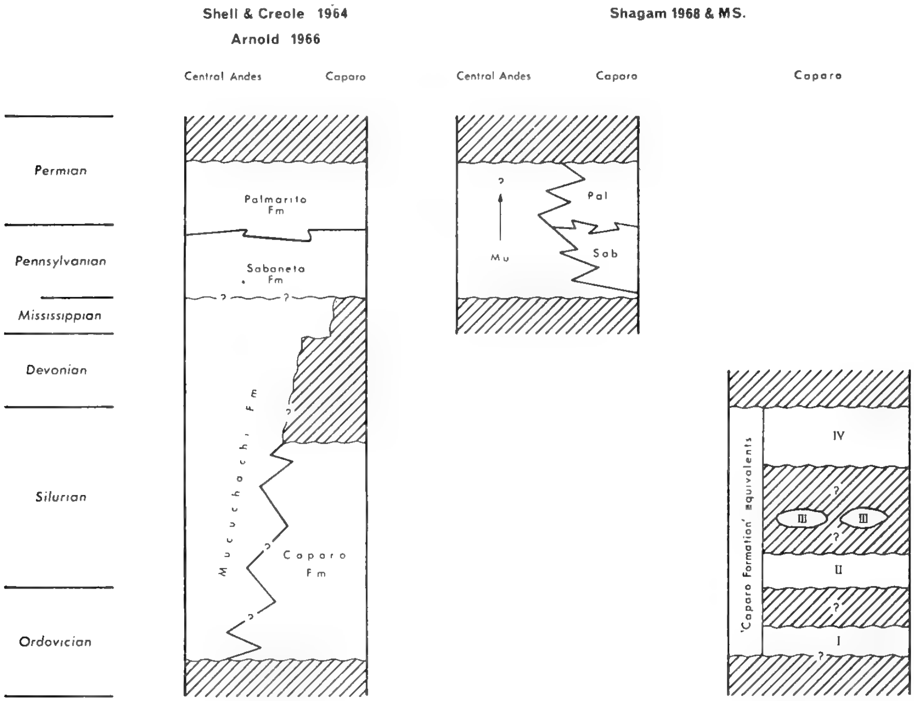

FIG. 2. Alternative interpretations of the Palaeozoic successions in the Mérida Andes, Venezuela. Pal = Palmarito Formation; Sab = Sabaneta Formation; Mu = Muchuchachí Formation. For comments see text.

evidence whatsoever of a Devonian fauna. They also shew that the Caparo Formation, previously considered Middle Ordovician (Schuchert 1935 : 692) and to underlie the Mucuchachí Group, contained faunas of Middle Ordovician to Upper Silurian age.

Pierce (1960 : 222; Pierce *et al.* 1961 : 350, 352) had recognized three formations in the Mucuchachí Group, the Remolino Formation, Libertad Formation and Río Momboy Formation in order of increasing age. Shell & Creole (1964 : 76), however, claimed that this division, based on erroneous palaeontological information, was inapplicable and unrecognizable in the field. They reassigned the Remolino Formation and part of the Libertad Formation to the Caparo Formation on field and faunal evidence. Thus, in their scheme, all known faunas of Middle Ordovician to Upper Silurian age occur in rocks assigned to the Caparo Formation and the only faunal evidence remaining for the restructured Mucuchachí Formation occurs 'high in the formation' (Shell & Creole 1964 : 83) and indicates a Permo-Carboniferous age.

Two possible interpretations of the spatial relationships of the Mucuchachí Formation were put forward (Text-fig. 2). H. C. Arnold considered the Caparo and the lower part of the Mucuchachí Formations to be distinct facies contemporaneously deposited in the same basin, whereas W. R. Smith related the Mucuchachí to the younger Palaeozoic sedimentary cycle including the Sabaneta and Palmarito Formations. Smith further thought that the older and younger Palaeozoic cycles were operative in geographically distinct basins. The latter viewpoint is also held by Shagam (pers. comm.) who postulates the lateral equivalence of the Mucuchachí and Sabaneta facies.

Shagam (1968 : 171) reported large limestone blocks containing a fauna of late Llandovery age embedded in supposed Wenlock—Ludlow shales in the Caparo area. This limestone, which presumably represents a fourth faunal horizon in Shell & Creole's so-called "Caparo Formation", is not yet known in its autochthonous situation. Shagam stressed the uncertainty surrounding much of the Lower Palaeozoic succession and expressed doubt as to its homogeneity. He postulated tectonic episodes between each of the four faunas so far recognized in this stratigraphical complex. To avoid the introduction of new stratigraphic units in this paper, which is primarily concerned with the coral palaeontology, the four faunal horizons in the Lower Palaeozoic rocks of the Caparo area are referred to by the roman numerals I (oldest) to IV (see Text-fig. 2).

In the Upper Palaeozoic sequence, the Palmarito Formation rests conformably on the Sabaneta Formation. The terrestrial red beds of the latter have yielded spores indicating a possible Permian age for most of the Sabaneta Formation according to Shell & Creole (1964 : 83) and Arnold (1966 : 2371) although the lower part may belong to the Carboniferous. The succeeding Palmarito is marine and richly fossiliferous but even so, the age of the formation is not precisely fixed. The macrofauna was considered by Pierce *et al.* (1961 : 357) to indicate a Pennsylvanian to Permian age, probably early Permian according to Arnold (1966 : 2378). Arnold (*op. cit.*), however, also reported preliminary ostracod identifications from the Palmarito of Quebrada Queveda as including many species comparable with Pennsylvanian ostracods of the U.S.A. In addition, the two corals described here from the Palmarito section of Quebrada Queveda both compare best with North American Pennsylvanian species. Thus the present faunal and floral evidence suggests that the Palmarito marine transgression began in Pennsylvanian times and was not completed in the area until the Permian. Clearly however, detailed studies of the Upper Palaeozoic sequences and their biota are needed here to determine more precisely the relationships of the various sedimentary units, both vertically and laterally.

IV. AGES AND RELATIONSHIPS OF THE CORAL FAUNAS

Very few systematic descriptions of Palaeozoic corals from South America have been published. The only previous work on Venezuelan material known to the writer is that of Weisbord (1926 : 224) which was revised by Wells (1943 : 95). This is all of Devonian age and will be referred to in more detail in a later paper dealing with faunas from the Sierra de Perijá. Other systematic work on South American Palaeozoic corals has been published by Douglas (1920 : 44), Knod (1908 : 561), Kozlowski (1923 : 97), Meyer (1914 : 601, 624) and Thomas (1905 : 267) but this only amounts to descriptions of about a dozen species. Mostly the same corals are also referred to in various fossil lists.

Almost all the genera and species described here, therefore, are either new or are recorded from South America for the first time. Three distinct coral faunas are present, two from the "Caparo Formation" equivalents of Lower Llandovery (Caparo II) and Ludlow (Caparo IV) ages respectively and one from the Palmarito Formation of Permo-Carboniferous (?Pennsylvanian) age.

(a) *"Caparo Formation" equivalents.*

(i) *Caparo II—Lower Llandovery.* A small collection of corals comes from a section on the Río Caparo approximately 900 m downstream from the Paso Caparo, the locality 2 of Shell & Creole (1964, tab. 1). Shell & Creole list two faunas from this locality, one probably middle Ordovician in age and the other early Llandovery. The corals, *Streptelasma shagami* sp. nov., *Leolasma kaljoi* sp. nov. and *Streptelasma* sp., are not sufficiently sensitive to indicate an age within these limits. *Leolasma,* it is true, has previously only been recorded from the upper Middle and lower Upper Ordovician of the Baltic and China but the range of the genus is felt to be far from adequately known. Ordovician and Silurian streptelasmids from North America are in need of extensive revision and no useful comparisons can be made there. On the other hand, brachiopods from the same samples as the corals are dated Lower Llandovery by J. G. Johnson (pers. comm.).

The corals described here are the *Streptelasma* spp., identified by H. D. Thomas and dated as Ordovician by him, which are listed by Shell & Creole (1964, table 1) under locality 2 as probably Ordovician.

(ii) *Caparo IV—Ludlow.* Several of the specimens described here were collected from a section on the Río Aricagua, the locality 7 of Shell & Creole (1964, table 1). Again, two faunas are listed, one collected by H. C. Arnold for Shell and dated Niagaran and the other collected by Creole and dated late Llandovery to Ludlow. Nearly all the corals are in five samples from the very detailed collections made by Arnold and appear to represent a single faunal suite. One specimen in the Creole collection and three specimens collected by R. Shagam from the same locality can be approximately equated with Arnold's samples (see Appendix) and also clearly belong to the same suite. The fauna contains *Syringaxon arnoldi* sp. nov., *Columnaxon angelae* gen. et sp. nov., *Cymatelasma aricaguaense* sp. nov. and *Cystihalysites brownsportensis* (Amsden). The presence of the latter suggests a younger Niagaran (Wenlock or early Ludlow) age, but unfortunately the new species are of no assistance and the genera are too long ranging to refine this age further. Brachiopods from the same samples as the corals indicate either Ludlow or Llandovery to Ludlow ages according to J. G. Johnson (pers. comm.). The homogeneity of the coral fauna suggests all the samples involved to be closely similar in age and thus a Ludlow horizon is indicated.

The fauna has one species in common with North American Silurian faunas. The genus *Cymatelasma*, however, has only previously been recorded from the Silurian of England, and the new genus and species make no contribution to an assessment of the faunal affinities.

A second fauna, also probably of Ludlow age, was collected by R. Shagam from a section on the Río Suripá. The corals are *Syringaxon suripaense* sp. nov., *Tryplasma* sp. cf. *T. nordica* Stumm, *Tryplasma* sp., *Coenites* sp., *Cystihalysites brownsportensis* and *Acanthohalysites* sp. Again a Wenlock or early Ludlow age is suggested by the presence of *C. brownsportensis*: *Tryplasma nordica* is also of Wenlock or Ludlow age. J. G. Johnson (pers. comm.) describes brachiopods from the same samples as probably Ludlow in age. The corals show some North American affinities but, more interestingly, *C. brownsportensis* is the only species in common between the Río Suripá and Río Aricagua faunas. This may be the result of small sample sizes, ecological variation or a slight difference in age between the two outcrops; it is not possible to decide which factor or combination of factors is responsible on the available evidence.

(b) *Palmarito Formation.*

Only four specimens from two localities are available from this formation. Two samples from the Portachuelo section (Qda. Queveda) yielded *Lophophyllidium pelaeum* (Jeffords) and *L.* sp. cf. *L. wewokanum* Jeffords. One sample from the Qda. El Mesón included *Lophophyllidium* sp. and *Lophamplexus* sp. *L. pelaeum* and *L. wewokanum* are both North American species of Pennsylvanian age whilst the *Lophophyllidium* sp. from the Qda. El Mesón is most similar to a North American species also of Pennsylvanian age. Thus there is some evidence here that the parts of the Palmarito Formation represented by these samples is Pennsylvanian rather than Lower Permian in age.

V. SYSTEMATIC DESCRIPTIONS

The terminology used in the following descriptions is that proposed by Smith (1945 : 4–9) and Moore, Hill & Wells (1956) unless otherwise indicated.

The sample number is given in brackets after the British Museum (Natural History), Department of Palaeontology registered number for each specimen. Sample numbers prefixed 'A' are from H. C. Arnold's collection, 'S' from R. Shagam's collection and 'K' from the collections of the Creole Petroleum Corporation. All available locality details for the samples are given in the Appendix. Comments on the locality and horizon of specimens in this section of the paper refer to broad units only (i.e. Río Aricagua section; Silurian, Ludlow) and reference should be made to the sample numbers in the Appendix for details.

Order RUGOSA Edwards & Haime 1850

Suborder STREPTELASMATINA Wedekind 1927

Superfamily **CYATHAXONIICAE** Edwards & Haime 1850

Family **LINDSTROEMIIDAE** Počta 1902

1902 Lindstroemiidae Počta : 181.
1962 Laccophyllidae; Philip : 170.
1965 Lindstroemiidae; Federowski : 336.
1965 Amplexocariniidae; Federowski : 350.
1965 Lindstroemiidae; Kullmann : 63, *pars*.
1967b Lindstroemiidae; Pedder : 110.
1967b Amplexocariniidae; Pedder : 124.
1968 Laccophyllidae; Goryanov : 90.

TYPE GENUS. *Lindstroemia* Nicholson & Thomson 1876 : 150.

DIAGNOSIS. Small solitary corals. Major septa fused at axis in early ontogeny to form a pseudocolumella. In some forms this persists in the mature stages, in others the septa are withdrawn to form a perfect or imperfect axial tube by the deflection, or by the thickening and lateral contiguity, of their axial ends. Minor septa contratingent when present, becoming free in the calice. Minor septa flanking counter septum accelerated; the remainder cyclically inserted in late ontogeny. Tabulae tent-shaped to box-shaped. Dissepiments developed in a few forms.

DISCUSSION. The type species of *Lindstroemia*, *L. columnaris* Nicholson & Thomson (1876 : 150) from the Devonian of North America, is imperfectly known and the type material cannot be traced. Nevertheless, as Pedder (1967b : 110) remarked, Nicholson & Etheridge (1878, text-figs 4b, 4b′ on p. 84) provided figures of the interior of *Lindstroemia columnaris* which justify the family concept and indeed caused Stumm (1949 : 7, 8) to suggest that *Lindstroemia* might prove to be a senior synonym of *Stereolasma* Simpson (1900 : 205).

The general characters of the corals assigned to this family have recently been discussed by Glinski (1963 : 323, 331), Fedorowski (1965) and Kullmann (1965 : 64

et seq.). Glinski (1963 : 331 *et seq.*) demonstrated the close relationship of *Svringaxon* to *Metriophyllum*, bringing these two genera together in the same family but distinguishing them at the subfamily level by the development of horizontal carinae in the Metriophyllinae. Pedder (1967b : 110), however, suggested that these carinae evolved independently in different lineages.

Fedorowski (1965 : 336, 342) recognized the subfamilies Metriophyllinae and Syringaxoninae based mainly on differences in the ontogeny of the aulos in those genera possessing one. He claimed that members of the Syringaxoninae form the earliest stages of the axial tube by the deflection of the axial ends of the major septa, as opposed to a slight withdrawal of the septa from the axis, without deflection, which produces the aulos in the Metriophyllinae. This account was apparently based in part on the ontogeny of specimens of *Syringaxon bohemica bohemica* (Barrande) from Poland. In the only other member of the Syringaxoninae described by Fedorowski (1965 : 344), *Stewartophyllum polonicum* (Sobolew), the ontogeny illustrated does not show a stage in which the aulos is formed by deflected septal ends, although he mentions other material belonging to this species which does. The writer has examined the sections cut by Butler to describe the ontogeny of *Syringaxon siluriense* (Butler 1935 : 120) and these also show no sign of such a stage in the development of the aulos.

The writer believes that the precise form of the axial ends of the septa in these corals is largely a function of aulos diameter, septal number and thickness and possibly the amount of sclerenchyme available to coat the axial structure. Septa remain straight throughout ontogeny in those corals where increase in aulos size is accompanied by a concomitant increase in the thickness of the septal ends as is shown by *Syringaxon siluriense* (BM(NH) R25891, R29444, R30165) and the specimen of *Stewartophyllum polonicum* figured by Fedorowski (1965, fig. 1D). In corals where increasing size of the axial structure is not matched by septal thickening, a tube is formed by deflecting the septal ends, as in the early stages of *Syringaxon bohemica bohemica* as figured by Fedorowski and such corals as '*Barrandeophyllum*' *perplexum* Počta (see Prantl 1938, pl. 3, fig. 16). Interpreted thus, no great significance is attached to the presence or absence of septal deflection in the construction of the aulos in the Lindstroemiidae.

Kullmann (1965 : 64) accepted Glinski's subfamilial division and diagnosed the Lindstroemiinae as exhibiting both cyclic and serial insertion of minor septa: he including the genus *Petraia* Münster in the subfamily. This he based on a reappraisal of the septal insertion in *Syringaxon* as illustrated by *S. siluriense* and two new species, *S. pinguis* and *S. postsiluriense*. The minor septa flanking the counter septum are inserted early in ontogeny, after the insertion of 14 major septa in *S. siluriense* (Butler 1935 : 121) and after 10 major septa in *S. pinguis* (Kullmann 1965, fig. 5). In the former, the rest of the minor septa are inserted in a normal cyclic manner when the number of major septa has reached 18, the average mature septal number in the species being about 20. Similarly, in *S. pinguis*, there are 14 major septa present before the rest of the minor septa are inserted more or less simultaneously, this being the average septal number in maturity. Butler (1935 : 122) regarded this basically as cyclic insertion of the minor septa, noting the early insertion of the two counter lateral minors and pointing out its occurrence in some other unrelated corals. Kullmann (1965 : 67) on the other hand, claimed that the situation in *Syringaxon* was homologous with that in *Petraia* in which minor septa are inserted serially with the metasepta from the earliest ontogenetic stages. The writer feels that Kullmann has considerably overstressed the significance of the early insertion of the counter lateral minor septa and that Butler's interpretation is the more reasonable. *Petraia* is excluded from the family Lindstroemiidae here.

Pedder's (1967b : 110) understanding of the Lindstroemiidae is essentially that accepted here. Fedorowski's (1965 : 350) removal of *Amplexocarinia* Soshkina to a new family, the Amplexocariniidae (followed by Pedder 1967b : 124), has been noted but the structure of the type species, *A. muralis* Soshkina, has yet to be clearly demonstrated. Otherwise both septa and tabulae appear to be involved in the formation of the aulos in species of *Amplexocarinia*, very like the development of this structure in such species as *Syringaxon memorabilis* Prantl (1938 : 30, pl. 1, figs 7, 8; pl. 2, figs 11, 12). Prantl described the aulos in *S. memorabilis* as formed by the bending of the axial ends of the major septa with only slight thickening, and unless the figure is misleading (pl. 3, fig. 11), the tabulae are developed with striking similarity to those illustrated in *A. tortuosa* by Fedorowski (1965, pl. 4, fig. 6). *Amplexocarinia* is retained in the Lindstroemiidae here.

Genus ***SYRINGAXON*** Lindström 1882

1882 *Syringaxon* Lindström : 20.
1900 *Laccophyllum* Simpson : 201.
1902 *Nicholsonia* Počta : 184.
1902 *Barrandeophyllum* Počta : 190.
1902 *Alleynia* Počta : [vi].
1928 *Laccophyllum*; Grabau : 82.
1928 *Alleynia*; Grabau : 84.
1928 *Barrandeophyllum*; Grabau : 87.
1935 *Syringaxon*; Butler : 117.
1938 *Syringaxon*; Prantl : 21.
1938 *Barrandeophyllum*; Prantl : 34.
1945 *Syringaxon*; Smith : 58.
1949 *Syringaxon*; Stumm : 10.
1949 *Barrandeophyllum*; Stumm : 10.
1951 *Syringaxon*; Schouppé : 207.
1954 *Syringaxon*; Schouppé : 395.
1956 *Syringaxon*; Flügel : 33.
1962 *Syringaxon*; Flügel & Free : 224.
1963 *Syringaxon*; Glinski : 331.
1965 *Syringaxon*; Sutherland : 34.
1965 *Syringaxon*; Fedorowski : 343.
1965 *Syringaxon*; Kullmann : 65.
1965 *Barrandeophyllum*; Kullmann : 87.
1968 *Syringaxon*; Goryanov : 91.
1968 *Barrandeophyllum*; Goryanov : 96.

TYPE SPECIES. *Cyathaxonia siluriensis* M'Coy 1850 : 281; 1851 : 36, pl. 1C, figs 11, 11a. High Bannisdale Slates or lowermost Kirkby Moor Flags (*vide* R. B. Rickards), Silurian, Ludlow, *leintwardinensis* zone; Underbarrow, near Kendal, Westmorland (see Pl. 1, fig. 6).

DIAGNOSIS. Small simple, conical or cylindrical corals. A more or less perfect axial tube is formed in the late neanic and ephebic stages by the thickening and lateral contiguity or sideways deflection of the axial ends of the major septa. Minor septa usually developed, contratingent becoming free in the calice. No horizontal carinae but peripheral septal nodes present in some species. Tabulae horizontal in the axial tube and steeply sloping downwards to the periphery outside it; no dissepiments.

DISCUSSION. Recent interpretations of *Syringaxon* have been based on Butler's (1935) paper in which he described in detail material he assigned to the type species, *S. siluriense*. Sutherland (1970) has now redescribed the holotype of *S. siluriense* (figured here on Pl. 1, fig. 6) which is clearly congeneric and almost certainly conspecific with Butler's material. Butler (1935 : 118) thought that both *Laccophyllum* Simpson and *Alleynia* Počta appeared to be synonyms of *Syringaxon* but he did not finally commit himself. Subsequently Prantl (1938 : 21) advocated the synonymy of *Alleynia* with *Syringaxon* on the basis of a comparison of the septal development in the two type species and Smith (1945 : 58, pl. 1, fig. 18) figured a syntype of *Laccophyllum acuminatum*, the type species of *Laccophyllum*, which is undoubtedly congeneric with *Syringaxon siluriense*.

Opinions have differed on the relationship between *Syringaxon* and *Barrandeophyllum*. Prantl (1938 : 34) reviewed earlier concepts of *Barrandeophyllum* and himself considered it worthy of generic status, distinguished from *Syringaxon* by the irregularity of its aulos, usually elliptical in section, by a sparing development of dissepiments and limited additional sclerenchyme. Prantl's dissepiments are actually the peripheral tabulae. Stumm (1949 : 10), Hill (1956 : 258) and Kullmann (1965 : 87) also consider the two genera distinct essentially on the same grounds. In addition, Stumm refers to a tendency in *Barrandeophyllum* for the diameter of the aulos to increase more rapidly with growth whilst Kullmann mentions the larger size and septal number and more numerous tabulae usually found in species of *Barrandeophyllum*.

Weissermel (1939 : 356; 1941 : 170), Schouppé (1951 : 207; 1954 : 396) and Flügel (1956 : 33) have all favoured a subgeneric relationship. Schouppé claimed the presence of 'dissepimental interconnexions' between the septa in *Barrandeophyllum* as taxonomically significant but Flügel & Free (1962 : 231) quite rightly point out that these are merely sections of tabulae which tend to be more numerous in species assigned to *Barrandeophyllum* than in those assigned to *Syringaxon*.

Only Wang (1950 : 204) and Flügel & Free (1962 : 224 *et seq.*) have placed *Barrandeophyllum* in synonymy with *Syringaxon*. Flügel & Free expressed reservations, however, and recorded (1962 : 231, footnote 2) an apparent difference between the septal microstructure developed in a specimen of *B. bohemicum* and that in their species of *Syringaxon*. This is considered here in all probability to be due to the effects of recrystallization in the latter material.

Thus all characters that have been quoted as distinguishing *Barrandeophyllum* from *Syringaxon* have either been misinterpreted or are of a quantitative nature. There appears to be no basic structural divergence to warrant separation at the generic level. Differences in size, growth-form and degree of perfection in the formation of the aulos are here considered to be of specific significance only and *Barrandeophyllum* is therefore placed in synonymy with *Syringaxon*.

Syringaxon arnoldi sp. nov.

(Pl. 1, figs 1–5; Text-fig. 3)

DERIVATION OF NAME. After the collector, Dr H. C. Arnold, Jr of Nederlandse Aardolie Maatschappij.

DIAGNOSIS. *Syringaxon*, 4·1 to 5·1 mm diameter with 15 to 18 major septa at base of calice. Minor septa contratingent; counter-lateral minor septa equal in length to counter septum, others half radius in length. Aulos wide but with narrow axial tube largely infilled in pre-ephebic stages. Tabulae sparse within aulos and rare outside it.

HOLOTYPE. R46740 (A2558). Río Aricagua section; Silurian, Ludlow.

PARATYPES. R46741–2 (A2561), R46743–4 (A2582), R46745 (K162950). Same locality and horizon as holotype.

DESCRIPTION. Small, conico-cylindrical corals up to 6 mm in diameter and 10 mm in length. Epitheca with strong inter-septal ridges.

In cross-section, uncrushed corals are circular with a longitudinally corrugated epitheca and a peripheral stereozone 0·3 to 0·4 mm thick. At the base of the calice, the major septa extend almost to the axis where their thickened, club shaped ends are more or less laterally contiguous and invested in sclerenchyme to form a regular, thick walled aulos 1·4 to 1·7 mm in diameter. There is no deflection of the septal ends in the aulos which has a maximum internal diameter of 0·8 mm. The major septa are waisted between the aulos and the outer wall, thinning to 0·15 mm or less across with the cardinal septum almost invariably thinner than the other major septa. The minor septa are contratingent and usually reach half the coral radius in length: the counter-lateral minor septa are equal in length to the counter septum.

Above the calice base, the aulos degenerates first on the cardinal side and lastly on the counter side. The major septa begin to withdraw peripherally and the minor septa become free at their axial ends 0·5 mm above the first breach in the aulos: 2 mm above the base of the calice, the septa are reduced to ridges up to 0·5 mm in length and virtually inseparable into major and minor series.

In longitudinal section, the aulos is largely infilled in pre-ephebic stages, leaving scattered axial bowl or funnel shaped voids capped by shallowly depressed tabulae in the neanic stage. Between the aulos and the peripheral stereozone, one tabula sloping axially and upwards was seen in the region of the counter septum in the holotype (Pl. 1, fig. 2). On the cardinal side, three arched plates are present at the periphery but their form towards the aulos is obscured by septa in the plane of section. Signs of tabulae are extremely rare in the paratypes.

At the base of the calice, the corals vary in diameter between 4·1 and 5·1 mm with 15 to 18 major septa. Septal ratios vary between 3·3 and 3·7. The measurements are plotted in Text-fig. 3.

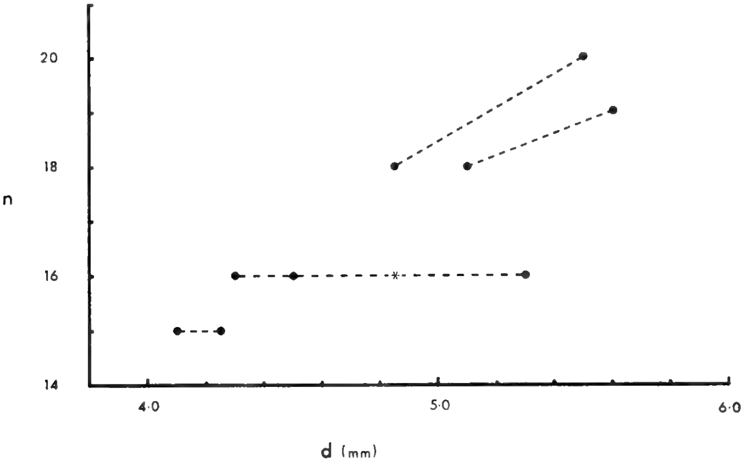

FIG. 3. Number of major septa plotted against diameter for specimens of *Syringaxon arnoldi*. The holotype is indicated by an asterisk. The dashed lines join points representing different sections of the same specimen.

DISCUSSION. *Syringaxon arnoldi* is easily distinguished from the North American species *S. acuminatum* (Simpson) by the much larger thin walled aulos, thin septa and well developed tabulae in the latter. *S. adaense* Sutherland (1965 : 34) from the Henryhouse Formation of Oklahoma is also clearly distinct, through its extremely short minor septa in particular. *Syringaxon arnoldi* resembles most closely the German Eifelian species *S. wedekindi* Glinski (1963 : 331, fig. 5) although it is difficult from the cursory description and drawing to make a proper comparison. *S. wedekindi* apparently has a septal ratio of 2·7, considerably less than that for *S. arnoldi*, and the detailed septal shape, with a strong peripheral expansion, is distinctive.

Syringaxon suripaense sp. nov.

(Pl. 1, figs 7, 8; Text-fig. 4c)

DERIVATION OF NAME. After the type locality on the Río Suripá.

DIAGNOSIS. *Syringaxon*, 5·0 to 5·7 mm in diameter with 18 to 19 major septa at base of calice. Minor septa contratingent; counter-lateral minor septa equal counter septum, others half radius or slightly more in length. Nodes present on major and minor septa close to periphery. Aulos medium to thin walled, may be irregular in shape.

Holotype. R46746 (S2275D). Río Suripá section; Silurian, Ludlow.

Paratype. R46747 (S2275D). Same locality and horizon as holotype.

Description. Two fragments of small solitary corals embedded in grey mudstone. External shape unknown.

In cross-section, the corals are subcircular with a strongly longitudinally corrugated epitheca reflecting pronounced interseptal ridges. The peripheral stereozone is 0·2 mm thick. The major septa are thin, about 0·15 mm across, and reach within a short distance of the axis at the base of the calice. The axial ends of the septa have a pronounced club-shaped thickening bringing them into lateral contact to form a medium to thin walled aulos. There is little additional material reinforcing the structure. The aulos may be regular or irregular in shape and has an internal diameter of about 0·8 mm. The minor septa are the same thickness as the major septa and contratingent with them. They may reach 0·6 of the radius in length except for the counter-lateral minor septa which are equal in length to the counter septum. Both major and minor septa develop irregular rounded or sharp edged nodes (Knoten of Kullmann 1965), 0·5 mm from the epitheca, which may double or treble the normal septal thickness. The nodes partially close the space between adjacent major septa to produce a keyhole appearance at the peripheral end of the gap (see particularly Pl. 1, fig. 7 and Text-fig. 4c).

No longitudinal sections of the species are available. Signs of tabulae between the major septa in cross-section are extremely rare although sections of horizontal elements appear more commonly between the major septa and their contratingent minors.

Coral diameters at the base of the calice are 5·0 mm with 18 major septa and 5·7 mm with 19 major septa. Septal ratios are 2·8 and 3·0.

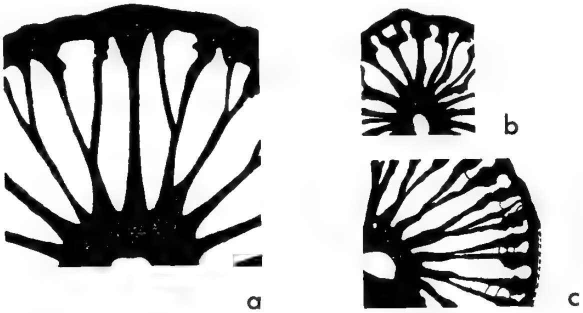

Fig. 4. The development of septal nodes in species of *Syringaxon*; a. *S. cantabricum*, b. *S. parvum*, c. *S. suripaense*. Figs 4a and 4b after Kullmann (1965, text-figs 7d, e). All × 8.

DISCUSSION. The development of septal nodes distinguishes *S. suripaense* from all syringaxoniids but two species assigned to *Barrandeophyllum* by Kullmann (1965 : 88, 91), *B. cantabricum* and *B. parvum* from the Emsian of North Spain (see Text-fig. 4). *B. cantabricum*, however, is a much larger species, reaching 13 mm in diameter. The septal nodes take a slightly different form from those of the Venezuelan material and the counter-lateral minor septa are significantly shorter than the counter septum. *B. parvum*, on the other hand, is more similar to *S. suripaense* although somewhat smaller and distinguished by a very small aulos.

Genus ***COLUMNAXON*** nov.

DERIVATION OF NAME. Descriptive of the axial columella characteristic of the genus.

DIAGNOSIS. Very small, simple, conico-cylindrical corals. Aulos present in early ontogeny. In ephebic stage, counter septum forms a columella against which other major septa abut to form a solid axial column. In the calice, major septa withdraw, the counter septum last, to leave a free columella. Minor septa contratingent at calice base, free in calice; counter-laterals accelerated. Tabulae simple, sloping down from axial structure to periphery and flat within aulos of early ontogeny.

TYPE SPECIES. *Columnaxon angelae* sp. nov.

DISCUSSION. *Columnaxon* is essentially *Syringaxon* in which, in the ephebic stage, the counter septum grows into the aulos and dilates to close the axial tube. This columella formed by the counter septum persists into the calice and becomes isolated by the withdrawal of the major septa, finally severing contact with the counter septum to form a free standing boss or spine.

This structural modification of *Syringaxon* is interesting as the result is strongly homoeomorphic with the Carboniferous genus *Cyathaxonia*. The columella in *Cyathaxonia*, however, is formed independently of the major septa and not as a dilation of the axial end of the counter septum as in *Columnaxon*. Also, minor septa in *Cyathaxonia* are inserted alternately with the major septa. In *Columnaxon* the septal insertion is not known but is thought to be the same as in *Syringaxon* which is, with the exception of the accelerated counter-lateral minors, cyclic. *Columnaxon* also shows a gross homoeomorphy with *Lophophyllidium*. The latter genus, however, lacks the strongly accelerated counter-lateral minor septa of *Columnaxon* and possesses a weak cardinal septum in a distinct fossula.

Columnaxon angelae sp. nov.

(Pl. 1, figs 9–12; Text-fig. 5)

DIAGNOSIS. *Columnaxon* 9 mm long, 5·5 mm maximum diameter with 16 major septa.

Holotype. R46748 (A2579). Río Aricagua section; Silurian, Ludlow.

Additional material. R46749 (SC1), R46750 (S1302). Same locality and horizon as holotype.

Description. Small, straight, conico-cylindrical coral, 9 mm long and 5·5 mm maximum diameter. There are 16 major septa.

In cross-section, the coral is circular with a longitudinally corrugated epitheca reflecting strong interseptal ridges. A peripheral stereozone 0·5 mm thick is developed. Midway to the axis, the counter and cardinal septa are about 0·1 mm thick and the other major septa about 0·2 mm thick. The septa expand gradually towards the periphery. In the sub-calicular sections, all major septa except the counter reach 0·85 of the radius in length. Their axial ends are dilated and in lateral contact, forming, with a little additional sclerenchyme, a strong periaxial wall. The counter septum, however, extends through the wall to the axis with a considerably expanded, club shaped end about 0·5 mm across which more or less completely blocks the axial tube (see Text-fig. 5g). Evidence from the longitudinal section suggests that in early ontogeny a more normal aulos may be present and that the counter septum does not grow into the axis until the late neanic or early ephebic stage (see Pl. 1, fig. 9).

In the sub-calicular section the minor septa are about half the radius in length and contratingent. The counter-lateral minors, however, are very nearly as long, three-quarters of the radius, as the major septa (excepting the counter), although notably thinner.

At the base of the calice, the major septa withdraw from the axis first in the cardinal area and last in the counter area (Text-fig. 5). Minor septa also become free standing first adjacent to the cardinal septum and progressively later towards the counter. The counter-lateral minor septa are an exception and detach from the counter at about the same level as the minor septa in the alar area become free.

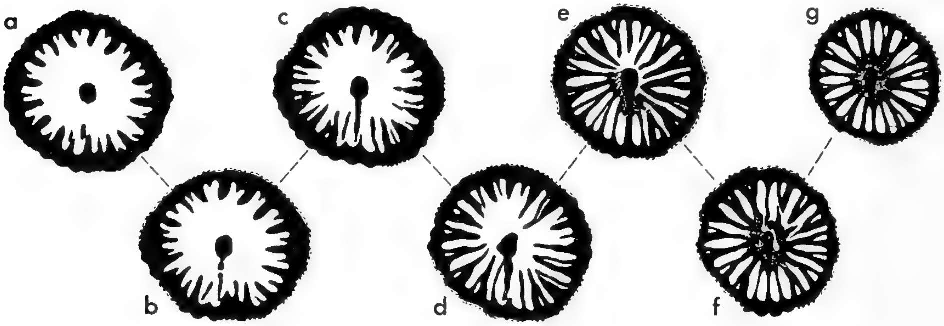

Fig. 5. Late stage development in the holotype of *Columnaxon angelae*. Spacing of cross-sections: a (R46748a)—0·6 mm—b (R46748b)—0·6 mm—c (R46748c)—0·6 mm—d (R46748d)—1·2 mm—e (R46748f)—1·8 mm—f (R46758i)—1·2 mm—g (R46748k). All × 4.

The counter septum becomes uniformly thin from the periphery to the sharply defined quadrate columella slightly elongated in the counter-cardinal plane and 0·75 × 0·6 mm in section. Finally, the counter septum withdraws very rapidly leaving the columella, now 0·7 × 0·5 mm, isolated in the axis. It is not known how much higher in the calice the columella extends.

In the longitudinal section (Pl. 1, fig. 9), the axial column is solid and about 1·6 mm wide in the distal (late neanic—early ephebic) 0·7 mm. Below this, however, a bowl-shaped void is capped by a flat, slightly inclined tabula indicating that an aulos is open at this stage of ontogeny. The column decreases in width proximally and a very fine axial canal, in which traces of tabulae can be seen, is present in the lower 1·5 mm preserved: the tip of the coral has been eroded. The interseptal spaces outside the axial structure appear to be poorly partitioned. Traces of two, or possibly three tabulae are visible on the counter side, concave up peripherally and apparently directed axially and upwards to the core, although towards the centre a septum in the plane of section obscures them.

Discussion. This description is based on the holotype alone as the two other specimens of *Columnaxon* available cannot be confidently assigned to the same species. R46749, 3·8 mm in diameter with 15 major septa, may represent a slightly earlier ontogenetic stage than any seen in the holotype with the aulos only partially infilled by the counter septum. It has, however, rather distinctive axial thickening of the major septa. R46750, on the other hand, is a calicular section 3·7 mm in diameter with 14 major septa. It has a thin (0·2–0·25 mm) peripheral stereozone which is highly crenulate and a very elongate columella 1 × 0·3 mm in section. The holotype at a comparable stage of development is 5·3 mm in diameter with 16 major septa. These may be variants of the same species or taxonomically distinct and a decision is best left until additional material allows specific variation to be assessed.

Family **LOPHOPHYLLIDIIDAE** Moore & Jeffords 1945

Genus ***LOPHOPHYLLIDIUM*** Grabau 1928

1928 *Lophophyllidium* Grabau : 98.
1928 *Sinophyllum* Grabau : 99.
1941 *Lophophyllidium*; Moore & Jeffords : 78.
1942 *Lophophyllidium*; Jeffords : 211.
1945 *Lophophyllidium*; Moore & Jeffords : 93.
1947 *Lophophyllidium*; Jeffords : 15, 21.
1947 *Stereostylus* Jeffords : 16, 38.
1953 *Lophophyllidium*; Formichev : 180.
1953 *Agarikophyllum* Formichev : 196.
1955 *Lophophyllidium*; Minato : 151.
1961 *Lophophyllidium*; Fontaine : 77.
1961 *Sinophyllum*; Fontaine : 79.
1961 *Khmerophyllum* Fontaine : 81.
1961 *Stereostylus*; Fontaine : 83.
1962 *Lophophyllidium*; Ross & Ross : 1181.

1962 *Stereostylus*; Ross & Ross : 1185.
1964 *Lophophyllidium*; Rowett & Sutherland : 25.
1966 *Stereostylus*; Bebout : 1.

TYPE SPECIES (original designation). *Cyathaxonia prolifera* McChesney 1860 : 75 and 1865, pl. 2, figs 1–3. Upper Pennsylvanian, 8 miles south of Springfield, Illinois, U.S.A.

DIAGNOSIS. Solitary corals possessing a columella formed by the expansion of the axial end of the counter septum from which it may separate in the ephebic stage. Major septa except cardinal long and usually rhopaloid. Tabulae tent-shaped; no dissepiments.

DISCUSSION. The lophophyllidid corals were extensively reviewed by Moore & Jeffords (1941, 1945) and Jeffords (1942, 1947). The writer follows Duncan (1962 : 65) and Rowett & Sutherland (1964 : 25) in considering slight structural differences in the columella and the degree of thickening of the skeletal elements in these corals not to be of generic significance. Thus, in agreement with them, *Stereostylus* is placed in synonymy with *Lophophyllidium*. The subgenus *Agarikophyllum* Formichev (1963) and the genus *Khmerophyllum* Fontaine (1961) have also been erected on supposedly significant modifications of columella structure. In both cases, however, generic differentiation from *Lophophyllidium* is thought not to be warranted.

Lophophyllidium has been recorded several times previously from South America —from the Permian of Bolivia (see Ahlfeld & Braniša 1960 : 100) and from the Carboniferous of Peru by Douglas (1920 : 44). It has unfortunately not proved possible to compare the present material with these earlier records.

Lophophyllidium pelaeum (Jeffords 1947)

(Pl. 1, figs 13–15)

1947 *Stereostylus pelaeus* Jeffords : 48, fig. 7, pl. 16, figs 1–8, pl. 20, figs 1 and 7.
1966 *Stereostylus brushensis* Bebout : 3, pl. 2, figs 1–3.

MATERIAL. R46751 (A1030). Qda. Queveda section; Permo-Carboniferous (?Pennsylvanian).

DESCRIPTION. Small conical coral, outer form uncertain but epitheca with strong septal grooves.

In the late neanic stage, the peripheral stereozone averages 0·5 mm thick. The major septa are slim, 0·2–0·25 mm across at their narrowest, and usually very slightly rhopaloid, their axial ends fused about two prominent alar fossulae (Pl. 1, fig. 13). The counter septum is not clearly distinguished but comparable in length with adjacent septa. The cardinal septum is slightly shorter than its adjacent septa but no pronounced cardinal fossula is present. In septal formula is $C3A10K9A4C$ at a diameter of 10 mm. Minor septa may be present as rudimentary swellings between some of the major septa. Tabulae are intercepted quite frequently.

In the ephebic stage (Pl. 1, fig. 14), the peripheral stereozone is thinner, 0·3–0·5 mm thick. All septa except the counter are variably withdrawn from the axis. The cardinal septum is very short, 1·5 mm in length, tapering to a point in a narrow, key-hole shaped cardinal fossula. Other major septa are 0·15 mm thick, weakly rhopaloid and vary in length between two-thirds and almost the full radius. The counter septum extends to the axis with a rhopaloid end, no clear cut column being formed. The septal formula is not clear; there are 31 major septa at a mean diameter of 12 mm. Minor septa are developed only in the counter quadrants, increasing in length towards the counter septum. Only one tabula is cut in this section and shows strong axial displacement in the cardinal fossula.

The longitudinal section is cut slightly off centre and septa obscure some of the details. The tabulae are thin, largely complete, well spaced and slope steeply axially and upwards in the peripheral areas.

Discussion. The Venezuelan specimen agrees very closely with *Stereostylus pelaeus* Jeffords from the Missourian (Upper Pennsylvanian) of Oklahoma and Kansas. *S. brushensis* Bebout is slightly smaller than *S. pelaeus* but otherwise does not appear to differ significantly from that species. *S. bruhsensis* is recorded from the Conemaugh of Ohio which is correlated with the Missourian of the mid-continental U.S.A.

Lophophyllidium sp. cf. ***L. wewokanum*** Jeffords 1947

(Pl. 1, figs 16–18)

cf. 1947 *Lophophyllidium wewokanum* Jeffords : 24, figs 5, 6; pl. 4, figs 4–7; pl. 7, fig. 5; pl. 10, figs 4–5; pl. 11, fig. 3.

?cf. 1947 *Lophophyllidium plummeri* Jeffords : 33, figs 1, 5–6; pl. 5, fig. 4; pl. 7, figs 2, 6, 7; pl. 10, figs 2, 3; pl. 11, figs 1, 2, 5, 6.

Material. R46752 (A1035). Qda. Queveda section; Permo-Carboniferous (?Pennsylvanian).

Description. Conical coral of 15 mm maximum mean diameter with strong septal grooves.

The peripheral stereozone is largely beekitized but about 0·8 mm thick. In the section immediately below the calice (Pl. 1, fig. 18), the septa are moderately thick, 0·3–0·4 mm across at their mid point, expanding slightly to the periphery and rhopaloid. Apart from the cardinal septum, the major septa are slightly variable in length around 0·7 of the radius. The counter, counter-lateral and alar septa may just touch the columella which is large, oval to quadrate and measures 2·6 × 2·4 in cross-section. There is a discontinuity between the counter septum and the columella. The cardinal septum is very short, less than half the radius, in a quadrate fossula formed by the slightly pinnate arrangement of the cardinal quadrant septa. The septal formula is $C5A7K7A4C$ at a diameter of 12 mm. Minor septa are not apparently developed at this level. Tabulae appear widely spaced, regularly concentric except in the cardinal fossula where they are displaced axially. The microstructure is obscure, many septa showing a chevron pattern which is probably the result of recrystallization.

In the base of the calice, the columella is oval and smaller, 2·6 × 2·1 mm, with its long axis in the counter-cardinal plane. Its reduction in size is continued quite rapidly as at a low level in the calice, with the major septa still two-thirds the radius in length and with the counter septum still abutting the columella, its dimensions are 2·5 × 1·75 mm (Pl. 1, fig. 16). Minor septa begin to appear at the base of the calice but remain as little more than low ridges. The cardinal septum shortens and projects only 1 mm from the wall in the base of the calice. The number of major septa increases from 27 at a diameter of 12 mm just below the calice to 29 at a mean diameter of 13·5 mm in the calice itself.

The longitudinal section is dominated by the broad axial columella. The tabulae are thin, mostly complete, generally flat and steeply sloping axially and upwards towards the columella, flattening out in the axial area. They are often crested in part by septal material. On the cardinal side, what appear to be growth-lines in a septum partly in the plane of section are broadly trough shaped between the periphery and columella.

Discussion. The Venezuelan specimen has features in common with *Lophophyllidium wewokanum* Jeffords from the Desmoinesian of Oklahoma and *Lophophyllidium plummeri* Jeffords from the Virgilian of Texas. In fact, it would appear that Jeffords (1947 : 34) only distinguished these two species on the basis of their stratigraphical separation and a purely morphological distinction between them would be very difficult to maintain. The present specimen differs from them in a number of small points such as the quadrate cardinal fossula, the diminution of the columella in the lower calice whilst still contiguous with the counter septum and the weaker minor septa. Both *L. wewokanum* and *L. plummeri* have triangular fossulae and large isolated columellae in the lower calice, and *L. plummeri* has quite well developed minor septa.

Lophophyllidium sp.

(Pl. 2, figs 1, 2)

Material. R46753 (A2722). Qda. El Mesón section. Permo-Carboniferous (?Pennsylvanian).

Description. Corallite shape is unknown but the epitheca develops shallow septal grooves.

At the base of the calice (Pl. 2, fig. 1), the peripheral stereozone is 0·4 mm thick. The major septa are slim, expanding slightly towards the periphery and weakly rhopaloid. They are withdrawn from the axis, the alars about 0·6 of the radius in length, and the other major septa shorter and slightly variable in length. The cardinal septum and the two flanking major septa are very short with tapering axial ends leaving a rather wide cardinal fossula. The counter septum extends towards the axis with a slim spindle shaped dilatation. The thin axial end then joins the columella at one side and appears to be partly wrapped round it. The columella is slim and oval, 2·3 × 1·2 mm in section, elongated in the counter-cardinal plane. The septal formula is *C6A7K7A7C* at a diameter of 12 mm. Minor septa are very short and thorn-like. The tabulae appear widely spaced.

A section in the calice, with 32 major septa at a diameter of 13 mm, shows a strong isolated columella 2·2 × 0·9 mm in section with the major septa, including the counter, smoothly tapered and half the radius or slightly less in length. The cardinal septum is reduced to one-fifth the radius with the two flanking major septa slightly longer. The minor septa are short but evenly developed.

No longitudinal section is available.

Discussion. This specimen compares most closely with *Lophophyllidium elongatum* Jeffords (1942 : 234, pl. 4, figs 1–3) from the Missourian (Upper Pennsylvanian) of Oklahoma. There seem to be too many distinctions in detail, however, for the Venezuelan specimen to be assigned to this species. *L. elongatum* varies between 10·3 and 19 mm in diameter with 28 to 30 major septa accelerated in the counter quadrants, with very long major septa in the base of the calice and a narrow triangular fossula. The specimen described here has a higher septal ratio and lacks the acceleration of the counter quadrant normally so characteristic of the lophophyllidiids. Also, the major septa are shorter than in *L. elongatum* and the two septa flanking the cardinal septum are noticeably reduced in length.

Genus ***LOPHAMPLEXUS*** Moore & Jeffords 1941

1941 *Lophamplexus* Moore & Jeffords : 90.
1945 *Lophamplexus*; Moore & Jeffords : 120.
1947 *Lophamplexus*; Jeffords : 62.

Type species (original designation). *Lophamplexus eliasi* Moore & Jeffords 1941 : 91, pl. 3, figs 2, 3; pl. 8, fig. 1. Lower Permian (Wolfcampian); Grand Summit, Cowley County, Kansas, U.S.A.

Diagnosis. Solitary corals, possessing a columella formed by the expansion of the axial end of the counter septum in early stages, which becomes discontinuous or is lacking in maturity. Major septa much shortened and cardinal fossula indistinct in mature stages. Minor septa may be weakly developed. Tabulae simple tent-shaped or flat-topped domes; no dissepiments.

Discussion. *Lophamplexus* does not appear to have been recorded before outside North America where it is known from the Pennsylvanian and Lower Permian.

Lophamplexus sp.

(Pl. 2, figs 3–6)

Material. R46754 (A2722). Qda. El Mesón section. Permo-Carboniferous (?Pennsylvanian).

Description. Slim, conical coral with very weak septal grooves.

In the late neanic stage (Pl. 2, fig. 3), the major septa are slim and taper gently to meet at the axis in the counter quadrants, with the counter septum itself slightly rhopaloid. In the cardinal quadrants, the septa are variably withdrawn from the axis leaving a large cardinal fossula in which the cardinal septum is slightly longer than the flanking septa. The tabulae appear quite closely spaced. The diameter is about 9 mm with 27 major septa.

In the early ephebic stage (Pl. 2, fig. 4), the peripheral stereozone is 0·4–0·5 mm thick. The major septa are very variable in length, between one-third and two-thirds the radius. The counter septum, however, extends to the axis and is weakly rhopaloid. The cardinal septum which is half the radius in length is flanked by very short major septa. Traces of minor septa are present between most major septa and are particularly well developed either side of the cardinal septum. Tabulae appear closely spaced at the periphery but leave a clear axial area. The diameter is 10 mm with 27 major septa.

In higher sections (Pl. 2, fig. 5) the counter septum also withdraws from the axis, leaving an axial area one third to one half the diameter across free of septa. Several major septa, including the counter septum may develop rhopaloid ends. At the base of the calice the diameter is 11 mm with 30 major septa.

The longitudinal section is cut from the proximal part of the corallite and shows a strong axial core which appears to involve several septa in the plane of section. The tabulae are strong, generally complete and slope steeply axially and upwards flattening slightly near the axis.

Discussion. This specimen cannot be assigned to a described species of *Lophamplexus* at the moment and may prove to be a new species. Further material is required, however, to furnish information not available from the present specimen and to determine if certain characters, such as the relatively long cardinal septum, are consistently maintained.

Superfamily **ZAPHRENTICAE** Edwards & Haime 1850

Family **STREPTELASMATIDAE** Nicholson 1889

1956 Streptelasmatinae; Hill : 268, *pars*.
1965 Streptelasmatidae; Kullmann : 139.
1969 Streptelasmatidae; Neuman : 7.

Type genus. *Streptelasma* Hall 1847 : 17.

Diagnosis. Solitary corals with a narrow peripheral stereozone. Axial ends of major septa either lobed or discontinuous and usually involved in a loose axial structure, or amplexoid in ephebic stages. Cardinal fossula may or may not be distinguished. Tabulae generally complete; arched. No dissepiments.

Discussion. Ivanovskii (1965 : 57) has divided the Streptelasmatinae of Hill (1956 : 268) among three families mainly on the basis of the development of stereoplasm and septal thickening in early ontogeny. Whilst these factors have in some cases played a part in the diagnosis of streptelasmatid genera, divisions at family level are more soundly based on major structural modifications which are considered to have phylogenetic significance. Skeletal thickening alone in the streptelasmatids does not appear to be of fundamental taxonomic importance and Ivanovskii's scheme cuts across more natural relationships. For example, *Streptelasma*, *Crassilasma* and *Dinophyllum* are all placed in separate families despite their basic structural similarities; similarly *Leolasma* and *Kenophyllum.*

Kullmann (1965 : 140), on the other hand, recognized two groups within the Streptelasmatinae of Hill. He separated off the genus *Heterophrentis* and allied forms as a new subfamily, the Heterophrentinae, in which a strong cardinal fossula is developed and the axial structure of lobed septal ends is lost through the withdrawal of the septa from the axis in the ephebic stage. Neuman's (1969) work, however, suggests that both features are quite variable within streptelasmatid genera and the value of Kullmann's classification is regarded as questionable.

Of the Streptelasmatinae of Hill, *Ditoecholasma* has been placed in a new family by Sutherland (1965 : 35) and *Palaeophyllum* has been shown to belong to the Stauriidae (Hill 1961).

Genus ***STREPTELASMA*** Hall 1847

1847 *Streptelasma* Hall : 17.
?1930 *Streptelasma*; Smith : 311, *pars.*
1937 *Streptelasma*; Cox : 2, *pars.*
1958b *Brachyelasma*; Kaljo : 102.
1960 *Brachyelasma*; Pestana : 868.
1963b *Streptelasma*; Stumm : 25, *pars.*
1963 *Brachyelasma*; Ivanovskii : 42, *cum syn.*
1965 *Brachyelasma*; Ivanovskii : 62, 104.
1969 *Streptelasma*; Neuman : 8, *cum syn.*

DIAGNOSIS. Solitary corals with a narrow peripheral stereozone and interseptal loculi present throughout ontogeny. Septa of two orders, the minor very short, the major usually extending more or less to the axis where the septal ends are irregularly twisted to form a weak axial structure. Major septa may be amplexoid in the ephebic stage. Tabulae complete and incomplete arched plates.

TYPE SPECIES (see Roemer 1861 : 19). *S. corniculum* Hall 1847 : 69, pl. 25, figs 1a–d. Trenton Limestone, Ordovician (Champlainian); Middleville, New York, U.S.A.

DISCUSSION. Neuman (1969 : 10) has recently chosen and described a lectotype for *Streptelasma corniculum.* He showed that the type species of *Streptelasma* is congeneric with *Dybowskia prima* Wedekind (1927 : 18, pl. 1, figs 10, 11) (= *Brachyelasma primum*), the type species of *Brachyelasma*, and that the group of species up until then referred to *Streptelasma* required a new generic name. Neuman (1969 : 28) has erected the genus *Helicelasma* for these species.

Neuman (1969 : 9, fig. 3) recognized two groups of species within the genus *Streptelasma* thus emended, one characterized by amplexoid septa in the late neanic and ephebic stages, the other characterized by the persistence of loosely intertwined major septa in the axial region up to the immediately subcalicular level of the corallite. Both the type species of *Streptelasma* and its junior subjective synonym *Brachyelasma* fall into the ampleximorph group. Although Neuman claimed that intermediates exist between these two groups, he gave no details of these. In general, the two groups of species appear to be so well distinguished that the writer considers that separation at the subgeneric level may well prove to be justified.

Neuman (1969 : 7–8) also commented on the various subgeneric relationships previously suggested between these and other Ordovician members of the Streptelasmatidae. In particular, he regarded *Streptelasma* as emended and *Helicelasma* as warranting full separate generic status and this is followed here.

Streptelasma sensu Neuman is best known from the (?) Middle and Upper Ordovician to Llandovery of Scandinavia, the Baltic region and the U.S.S.R. The genus has also been recorded, usually as *Brachyelasma*, from the Upper Ordovician of Ireland (Kaljo & Klaamann 1965 : 421) and the Middle and Upper Ordovician of North America (Hall 1847 : 17; Pestana 1960 : 868).

Streptelasma shagami sp. nov.

(Pl. 2, figs 7–10; Text-fig. 6)

DERIVATION OF NAME. After the collector of the type material, Dr R. Shagam (University of Pennsylvania).

DIAGNOSIS. Conical corals reaching 26 mm diameter with 41 major septa. Skeletal elements unthickened throughout ontogeny and little stereoplasm developed. Major septa slim with some intermingling at the axis. Cardinal septum short in neanic stage, equal in length to other major septa in ephebic stage; weak fossula. Minor septa 2–4 mm long in basal calice. Tabulae well spaced, strongly arched in axis with flat or shallowly depressed crests.

HOLOTYPE. R46755 (S1583). Río Caparo, near the Paso Caparo; Silurian, Lower Llandovery.

PARATYPES. R46756–9 (S1583), R46760 (K80748). Same locality and horizon as holotype.

DESCRIPTION. Incomplete conical corals embedded in matrix. Early ontogenetic stages unthickened. The peripheral stereozone is thin and highly longitudinally corrugated. The major septa are strongly pinnate, the longer septa meeting at the axis, the shorter ones leaning against the longer.

In the later neanic stages (Pl. 2, fig. 7), the peripheral stereozone is 0·5 mm or less in thickness. The septa are usually sinuous, occasionally straight, and variable in length although all reach or nearly reach the axis. They may be uniformly thick, about 0·25 mm, or slightly rhopaloid. There is some intermingling of the axial ends of the septa and they may fuse in groups of three or four: they may also be lightly invested with sclerenchyme in the axial area. The cardinal septum is shorter than the other majors, about a half the radius in length, in a poorly developed long narrow fossula. Rudimentary minor septa appear in the stereozone between most major septa. Horizontal elements are sporadic in the planes of section.

At the base of the calice (Pl. 2, figs 8, 10), the strongly grooved peripheral stereozone may reach 1 mm, and the septa 0·3–0·35 mm in thickness. Characteristically, the cardinal septum increases in length to equal the other major septa, although a weak fossula may still be detected—in the holotype (Pl. 2, fig. 8), the septa adjacent to the cardinal septum are shortened. Also, the counter septum shortens slightly and may only be a third of the radius in length. There is a slight withdrawal of the other major septa from the axis. Minor septa are short but well developed, < 2 mm long in the holotype but may reach 4 mm in the larger specimens. Traces of tabulae are scattered.

In longitudinal section (Pl. 2, fig. 9), tabulae are well developed, thin, complete or incomplete large curved plates. They are arranged as axial flat-topped or shallowly depressed domes sloping steeply downwards peripherally and developing narrow troughs against the wall in some instances. The arrangement in the axial area is obscured by septal traces. The tabulae are spaced 2–3 mm vertically apart. There are no dissepiments.

Ephebic stage sections of specimens in the type series show a great range in sizes from 11·8 to 26·3 mm mean diameter in calicular sections. Mature septal ratios range from 2·55 to 1·56 with increasing mean size. The data are shown graphically in Text-fig. 6.

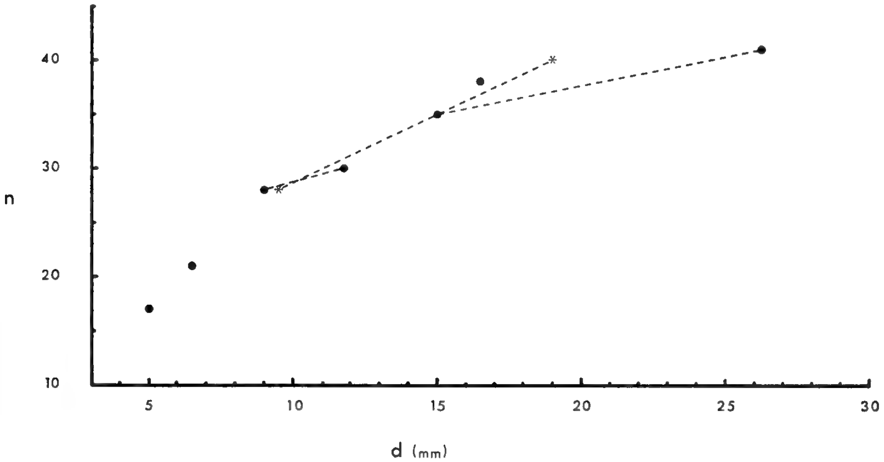

FIG. 6. Number of major septa plotted against diameter for specimens of *Streptelasma shagami*. The holotype is indicated by asterisks. The dashed lines join points representing different sections of the same specimen.

Discussion. *Streptelasma shagami* has some similarity to *S. poulseni* Cox (1937 : 9) from the Richmondian (Ordovician) of Greenland. The Venezuelan species, however, is distinguished by its more strongly arched tabulae and a lower septal ratio.

Streptelasma sp.

(Pl. 2, figs 11, 12)

Material. R46761 (A2077). Río Caparo, near the Paso Caparo; Silurian, Lower Llandovery.

Description. The specimen is an incomplete conical coral, partly decorticated. In cross-section, the peripheral stereozone is 0·7 mm thick with well developed septal grooves. The major septa are short and thin, tapering gradually towards the axis. They are slightly less than half the radius in length. Only half of the corallite is seen in cross-section and in this neither a fossula nor any of the primary septa can be identified. The minor septa are very thin and variable in length, apparently extending axially as crests on the tabulae with a maximum axial extension of 2 mm. Tabulae are intersected, widely spaced, in the peripheral area.

In longitudinal section, the tabulae are thin and mainly incomplete. They are shallowly depressed across the axis and strongly domed in the peripheral area where subsidiary vesicular elements may occur. There is evidence of septal development on the crests of the tabulae. At the periphery, the plates may curve up slightly against the stereozone to form a small trough. In the axis, the spacing is somewhat irregular, averaging 7 tabulae in 10 mm.

There are an estimated 42 major septa at a diameter of 24 mm.

Discussion. Despite the limits of the material, which preclude specific identification, this specimen can be confidently assigned to the genus *Streptelasma.*

Genus ***LEOLASMA*** Kaljo 1956

1956 *Leolasma* Kaljo : 36.
1965 *Leolasma*; Ivanovskii : 59.

Diagnosis. Solitary conical corals. Septa of two orders, the major extending to the axis and dilated to completely close the lumen in early ontogeny. In mature stages, the major septa are dilated peripherally to form, with the minor septa, a moderately wide stereozone. Their axial ends are rhopaloid and fuse to form a more or less compact axial boss. Cardinal fossula narrow. Tabulae sparsely developed or absent.

Type species (by original designation). *Leolasma reimani* Kaljo 1956 : 36, pl. 9, figs 3–5. Upper Ordovician, Vazalemmaskii horizon; Rakvere, Estonia.

Discussion. In his original diagnosis, Kaljo (1956 : 36) remarks that tabulae are absent and does not mention a cardinal fossula. Ivanovskii (1965 : 59), however, mentions sparse tabulae in his diagnosis for *Leolasma* and from published illustrations of *L. reimani* (Kaljo 1956, pl. 9, fig. 5; Ivanovskii 1965, pl. 2, figs 1a, b) a narrow cardinal fossula similar to that in the Venezuelan material appears to be present.

Leolasma appears to be very close to the genus *Kenophyllum* Dybowski which was revised by Kaljo (1958a : 22). Kaljo diagnosed *Kenophyllum* as lacking tabulae and, from his illustration of the type species *K. subcylindricum*, sclerenchyme is involved with the septa in the formation of the axial structure. Thus the present material compares more closely with *Leolasma* than *Kenophyllum* although the slight differences between the two may prove not to be of generic significance.

Leolasma is known from the upper Middle and lower Upper Ordovician of the Baltic area and China and is recorded here from the Lower Llandovery of the Mérida Andes.

Leolasma kaljoi sp. nov.

(Pl. 2, fig. 13; Pl. 3, figs 1–8; Text-fig. 7)

Derivation of name. After Dr D. L. Kaljo (Institute of Geology, Academy of Sciences of the Estonian S.S.R.).

Diagnosis. *Leolasma* with peripheral stereozone one quarter to one-third the radius. Cardinal fossula well developed with cardinal septum shortening rapidly in subcalicular stages. Tabulae simple, flat plates sloping axially and upwards, developed only in the ephebic stage: earlier stages completely infilled by laterally contiguous septa.

Holotype. R46762 (A2077). Río Caparo near the Paso Caparo; Silurian, Lower Llandovery.

Paratypes. R46763–7 (A2077), R46768 (A2079), R46769–75 (S1583). Same locality and horizon as holotype.

Description. Straight, conical corals reaching at least 30 mm high with a calice about 10 mm deep with steep sides and a shallow bowl shaped floor.

In the early stages (Pl. 3, fig. 6), the lumen is completely infilled by major septa reaching the axis, laterally contiguous along their whole length and alternating in the peripheral third to quarter of the radius with slim wedge shaped minor septa. The arrangement of the major septa varies between radial and slightly pinnate and a counter clockwise axial vortex may develop in some specimens.

The septa first separate in the cardinal fossula leaving a narrow elongate cavity bisected by a thin cardinal septum (Pl. 3, fig. 1). Subsequent spaces appear between major septa immediately on the axial side of the minor septa (Pl. 3, fig. 2). The major septa thin rapidly in their mid-length leaving a wide peripheral stereozone usually between a quarter and a third the radius wide, equivalent to the length of the minor septa, and an axial column of fused septal ends (Pl. 3, fig. 3). The septa in the axis are straight or a slight vortex may persist from earlier stages. Between the first separation of the septa and the base of the calice, the cardinal septum shortens rapidly and the axial column decreases in diameter and finally breaks up with the separation of the rhopaloid axial ends of the septa (Pl. 3, fig. 4). In the holotype, the cardinal septum decreases in length from 5 mm to 2·3 mm in 1·54 mm vertical growth and the major septa begin rapid withdrawal from the axis in the base of the calice about 3·5 mm above the level at which only a small cardinal fossula is open. In the calice, the peripheral stereozone is about one-third the radius in thickness except in the cardinal fossula where it is strongly notched. The cardinal septum is extremely short. The septal microstructure shows the water-jet pattern of divergent fibres typical of uniserial monacanthine trabeculae and is very well preserved in some specimens (Pl. 2, fig. 13).

Longitudinal sections are filled by septal tissue in which the trabeculae are directed axially and upwards at angles varying about 70° to the wall. Signs of tabulae are seen in one section only (Pl. 3, fig. 8) where complete flat plates 0·8 mm apart slope axially and upwards at about 30°.

Specimens range in size up to 17 mm in diameter with 38 major septa. Data are presented graphically in Text-fig. 7. Septal ratios range from 2·22 to 3·18 in mature sections.

DISCUSSION. *Leolasma kaljoi* is distinguished from *L. reimani* Kaljo by the development of tabulae and the possession of a much stronger cardinal fossula. Otherwise, the two species appear to be very similar.

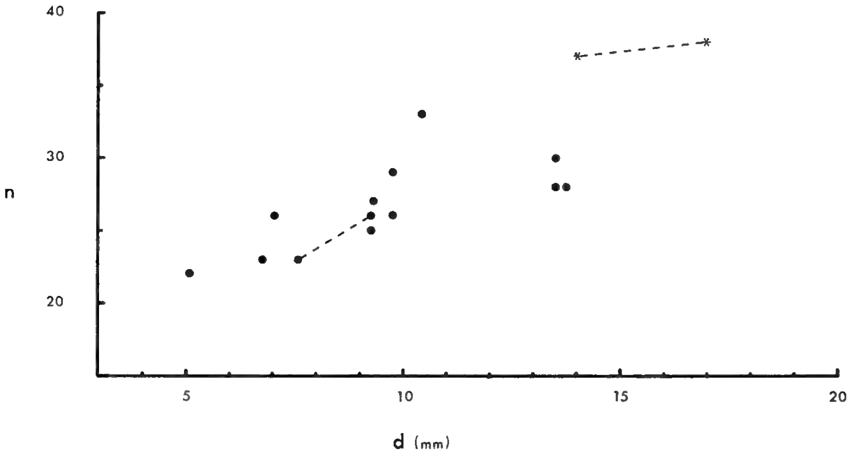

FIG. 7. Number of major septa plotted against diameter for specimens of *Leolasma kaljoi*. The holotype is indicated by asterisks. The dashed lines join points representing different sections of the same specimen.

Suborder COLUMNARIINA Rominger 1876

Family **SPONGOPHYLLIDAE** Dybowski 1873

1964 Spongophyllidae; Pedder : 436.

Discussion. The writer follows Pedder and others in considering the family Ptenophyllidae Wedekind 1923 as synonymous with the Spongophyllidae.

Genus ***CYMATELASMA*** Hill & Butler 1936

1936 *Cymatelasma* Hill & Butler : 516.

Type species. *Cymatelasma corniculum* Hill & Butler 1936 : 518, pl. 16, figs 2–8. Woolhope Limestone, Silurian, Wenlock; road cutting south of Stony Hill Farm, Woolhope, Herefordshire.

Diagnosis. Simple rugose corals with marked septal dilatation in early stages, usually reducing during ontogeny to a peripheral stereozone in the adult. The septa are waved parallel to their upper edges and carinae may develop along the crests of the waves. In the ephebic stage, the major septa are unequal in length and distinctively arranged in pinnate groups. Tabulae complete or incomplete: tabularium inversely conical or bowl-shaped. No dissepiments.

Discussion. Since Hill & Butler (1936) erected the genus and four species of *Cymatelasma* from beds of Llandovery to Ludlow age in the Welsh Borderland and the English Midlands, the genus appears to have been unused. Only passing comments on the genus are known to the writer.

Wang (1950 : 216), with no explanation, reassigned Hill & Butler's original species to *Pycnactis* (the type species), *Dinophyllum* and *Spongophylloides*. This dispersion seems completely unjustified as the genus from Hill & Butler's thorough descriptions appears to be a well defined homogeneous unit readily distinguished through septal structure, symmetry and lack of dissepiments from *Pycnactis* and *Dinophyllum*.

Cymatelasma is, however, most closely related to *Spongophylloides* and the species *Spongophylloides cockei* Sutherland (1965 : 16) includes in its range of variation specimens in which the dissepimentarium is almost completely replaced by a septal stereozone. Sutherland (*op. cit.*), in a useful comparison of the two genera, points out that they are distinguished only by the development of lonsdaleoid dissepiments in *Spongophylloides* and that *S. cockei* appears to show a continuous gradation between the two generic types. At present there is still some value in regarding the two genera as distinct and the Venezuelan species can be unequivocally assigned to *Cymatelasma*. If, however, *Spongophylloides pusillus* and *Cymatelasma carinatum* from the English Wenlock Limestone do prove to be a single variable species, a possibility suggested by Sutherland (*op. cit.*), then the status of *Cymatelasma* may need to be reconsidered.

Pedder (1967a : 3) remarked on the resemblances between *Cymatelasma, Enterolasma* and young individuals of *Lyrielasma*. *Lyrielasma* and *Cymatelasma* are undoubtedly closely related, the former genus differing essentially through the development of a dissepimentarium in later ontogeny, its exclusively (or nearly so) fasciculate growth form and a less consistently developed pinnate septal symmetry. It is possible that *Lyrielasma* is descended from *Cymatelasma* but the present known distribution patterns of the two genera do not encourage this suggestion.

The type species of *Enterolasma, E. strictum,* has never been adequately described and understanding of the genus is based chiefly on various accounts of *E. waynense* (Safford). *Cymatelasma* and *E. waynense* are superficially similar but the latter lacks a distinctive pinnate septal symmetry and possesses an arched tabularium similar to that in streptelasmatids.

The diagnosis given for *Cymatelasma* here is slightly modified from that given by Hill & Butler to take account of the new species. The South American record suggests that the distribution of *Cymatelasma* is far from adequately known and representatives of the genus are likely to be found in the Silurian of North America.

Cymatelasma aricaguaense sp. nov.

(Pl. 3, figs 9–15; Pl. 4, fig. 1; Text-fig. 8)

DERIVATION OF NAME. After the type locality on the Río Aricagua.

DIAGNOSIS. Ceratoid *Cymatelasma*. Major septa 36 at diameters of 11 to 14·5 mm, characteristically pinnate, lobed but not fused at their axial ends and bearing carinae sloping slightly axially and downwards. Tabulae incomplete; tabularium bowl-shaped.

HOLOTYPE. R46776 (A2558). Río Aricagua section; Silurian, Ludlow.

PARATYPES. R46777–78 (A2558), R46779 (A2561), R46780 (A2562), R46781 (SC1). Same locality and horizon as holotype.

DESCRIPTION. Incomplete ceratoid corals with very weak septal grooves.

The peripheral stereozone is usually 1·5 to 2 mm but may reach 4 mm in thickness. Septa of two orders, the majors extending into the axial area but characteristically arranged and variable in length. The cardinal and counter septa are longest and almost join at the axis. The alar and the mid metasepta in the counter quadrants also nearly reach the axis, with the other septa shorter and arranged in pinnate groups in the six segments thus formed (Pl. 3, figs 9, 11, 12). The major septa are moderately thin, generally tapering slightly towards the axis but with small irregularities in thickness along their length. The sides of the septa bear small scattered thorny projections which are the sections of carinae sloping gently into the axis. The axial ends of the septa are usually lobed, often with thorns on the lobes, but they do not intermingle and only rarely do adjacent septa fuse. The swellings are usually larger on the axial ends of the cardinal and counter septa. The minor septa are variable in length but never project more than 0·5 mm beyond the peripheral stereozone. In late neanic–early ephebic sections, only rudimentary minor septa deep in the stereozone are present between some of the major septa (Pl. 3, fig. 12).

In longitudinal section, the stereozone is evenly developed from a minimum observed corallum diameter of 4 mm. Trabeculae are directed axially and upwards at 20–30° to the horizontal, becoming steeper towards the axis. The tabulae are mainly large incomplete curved plates, sloping into the axis steeply at the periphery but apparently with a flatter axial series. Their distribution is confused by the many septal traces and sections of the carinae. The lobed axial ends of the septa appear as a poorly defined spongy axial 'column'. In sections at right angles to their length, the septa appear strongly zigzagged with the carinae developed on the crests. On the sides of the septa the carinae are occasionally discontinuous along their length. They are otherwise regularly developed with an average vertical spacing of 0·5 mm and slope very gently into the axis.

The largest specimen is 14·5 mm in diameter with 36 major septa; the complete data are shown in Text-fig. 8. The septal ratio varies between 2·48 and 3·3 in maturity.

Discussion. *Cymatelasma aricaguaense* is immediately distinguished from all the species described by Hill & Butler through the possession of incomplete tabulae. Otherwise the Venezuelan species is most similar to *C. carinatum* Hill & Butler, although lacking the accelerated counter lateral minor septa of the latter. *C. aricaguaense* also has the characteristic septal symmetry more prominently developed than in *C. carinatum.*

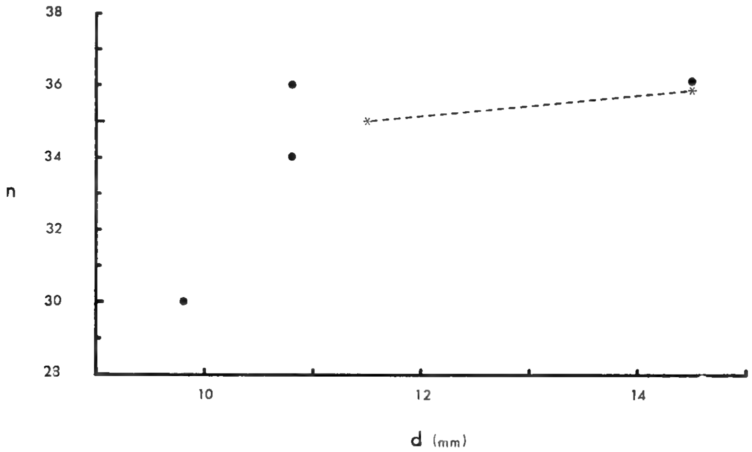

Fig. 8. Number of major septa plotted against diameter for specimens of *Cymatelasma aricaguaense*. The dashed line joins asterisks representing different sections of the holotype.

Suborder CYSTIPHYLLINA Nicholson 1889

Family **TRYPLASMATIDAE** Etheridge 1907

Genus ***TRYPLASMA*** Lonsdale 1845

1845 *Tryplasma* Lonsdale : 613.
1904 *Aphyllostylus* Whiteaves : 113.
1950 *Tryplasma*; Schouppé : 80.
1956 *Tryplasma*; Stearn : 91.
1961 *Tryplasma*; Strusz : 343.
1963a *Tryplasma*; Stumm : 4.
1963 *Tryplasma*; Oliver : 13 *cum syn.*
1964 *Tryplasma*; Stumm : 50.
1965 *Tryplasma*; Sutherland : 30.
1966 *Holacanthia* Sytova : 208.
1969 *Cantrillia*; Ivanovskii : 29, *pars.*
1969 *Holocanthia*; Ivanovskii : 31.
1969 *Tryplasma*; Ivanovskii : 33.
1969 *Rhabdacanthia* Ivanovskii : 45.
1969 *Wenlockia*; Ivanovskii : 52, *pars.*

TYPE SPECIES (by subsequent designation of Etheridge 1907 : 42). *T. aequabile* Lonsdale (1845 : 613, 633, pl. A, figs 7, 7a); Silurian, River Kakva, east side of northern Urals, U.S.S.R.

DIAGNOSIS. Solitary and fasciculate rugose corals with acanthine septa and a narrow peripheral stereozone. Tabulae usually complete; no dissepiments.

DISCUSSION. Ivanovskii (1969) has recently presented a comprehensive review of the Tryplasmatidae in which he advocated a series of generic divisions based on growth form and trabecular type. These two characters, however, appear in most cases in the tryplasmatids to be of doubtful genetic significance. The separation of solitary and fasciculate forms in the absence of other structural modifications seems inadvisable, particularly as species such as *T. malvernense* Hill show both growth forms. Further, the distinction between trabecular types is, at least to some extent, a function of preservation and holacanths may well be the recrystallized remains of original monacanthine or rhabdacanthine trabeculae. In both species of *Tryplasma* described here, rhabdacanths can be recognized in the septa where the microstructure is slightly better preserved although most trabeculae show varying degrees of alteration towards a holacanthine state. For these reasons, the genus *Tryplasma* is maintained here in the sense of earlier workers and the genera *Holacanthia* Sytova and *Rhabdacanthia* Ivanovskii are not recognized.

Tryplasma sp. cf. ***T. nordica*** Stumm 1963

(Pl. 4, figs 2–4)

cf. 1963a *Tryplasma nordica* Stumm : 4, pl. 2, figs 14–16.
cf. 1963 *Tryplasma nordica* Stumm; Oliver : 13, pl. 7, figs 1–7.

MATERIAL. R46782–4 (S1540A). Río Suripá section; Silurian, Ludlow.

Description. Cylindrical fragments of a *Tryplasma* with neither calice nor proximal end preserved nor any indication of increase.

The coral is subcircular in cross-section with a longitudinally corrugated epitheca reflecting septal grooves on the exterior. Diameters range between 5 and 5·5 mm with 22 major septa. The septa are discrete acanthine rhabdacanths, where the microstructure is preserved, embedded in lamellar calcite which forms a thin peripheral stereozone 0·3 mm thick (Pl. 4, fig. 4). Major and minor septa may be distinguished. Their appearance in cross-section is variable and occasionally the plane of section may fail to cut some or all of a ring of spines. The longest major septum seen was 0·7 mm long, the minor septa reaching up to half this length. Discontinuity or lobing of septa in cross-section due to the interception of two rhabdacanths in vertical series was occasionally seen.

In longitudinal section, the rhabdacanths are arranged on average 0·2 mm apart in regular vertical rows. The septa project into the lumen at a slightly variable but very low angle. The tabulae are usually complete and flat, although they may be slightly upturned peripherally. Occasionally incomplete tabulae slope steeply down into the axis. The tabulae are wide and irregularly spaced, averaging 1 mm apart. Dissepiments are not developed.

Discussion. The specimens agree more closely with the *T. nordica* from the Silurian (Wenlock or Ludlow) of Quebec described and figured by Oliver (1963) than with any other species of *Tryplasma*, particularly among those from North America. *T. nordica* is, however, larger with relatively, a somewhat lower septal number (48 to 60 septa of both orders in corals of 7·0 to 10·5 mm diameter according to Oliver) compared to the present material. The septa of the former are also longer and the tabulae more U-shaped. From Stumm's (1963a) description, the type specimens of *T. nordica* from the Silurian of Maine are less comparable to the Venezuelan specimens than Oliver's material.

Tryplasma sp.

(Pl. 4, figs 5–9)

Material. R46785 (S1540A). Río Suripá section; Silurian, Ludlow.

Description. Several small cylindrical corallites, well spaced and subparallel in a mudstone matrix, probably all belonging to one fasciculate colony.

The corallites are circular to subcircular, varying between 2·3 and 4·5 mm and averaging 2·8 mm in diameter. There are 19 major septa in a corallite 2·3 mm in diameter and about 28 in one 4·5 mm in diameter. The septa are acanthine rhabdacanths where details of microstructure can be observed. Their appearance in cross-section is highly variable and sometimes only one or two spines may be sectioned. They are set in lamellar calcite forming a peripheral stereozone 0·2–0·4 mm thick. Both major and minor septa may be distinguished, the latter reaching half the length of the former. The longest major septum seen in cross-section was 1 mm measured from the periphery.

In longitudinal section, the rhabdacanths project into the lumen with an elevation of 40°—there is little variation. One rhabdacanth measured 0·2 mm in diameter (Pl. 4, fig. 7). The septal spines are arranged 0·35 mm apart in vertical series. Tabulae are complete and flat or very slightly domed, their spacing varying between 0·4 and 1·7 mm. Dissepiments are not developed.

One instance of axial increase was seen in longitudinal section (Pl. 4, fig. 9). Only two daughter corallites were sectioned although more could be present out of the plane of section. In another corallite, a hysterocorallite was seen developing against the wall of the parent (Pl. 4, fig. 8). Whether this is a case of increase or an extreme form of rejuvenescence is uncertain.

Discussion. Among the several described species of *Tryplasma* which are fasciculate and have corallites of small diameter, *T. gracilis* (Whiteaves) and *T. lonsdalei* Etheridge appear to be the most similar to the present material. *T. gracilis* was redescribed by Stearn (1956 : 91, pl. 6, figs 1, 8) on weathered out but unsectioned topotype and other material from the Upper Ordovician Stonewall Formation of Southern Manitoba. It agrees with the specimens described here in size and growth form, including an apparent lack of connecting processes in the colony, but further comparison is difficult in the absence of sections of *T. gracilis*. Etheridge (1907) described several species of *Tryplasma* which have points in common with the Venezuelan material. Of these, the closest is *T. lonsdalei* var. *minor* Etheridge (1907 : 81, pl. 16, figs 3, 4; pl. 24, fig. 9; pl. 25, figs 6, 7; pl. 26, fig. 11), which has only slightly larger corallites and a comparable septal ratio to the Venezuelan material but differs from it by possessing connecting processes, slightly longer septa and more regular tabulae. Both Hill (1940 : 406) and Strusz (1961 : 343) agree in not differentiating Etheridge's varieties of *T. lonsdalei* and Hill describes rhabdacanthine septa in the species. In Australia, *T. lonsdalei* ranges in age from the Lower Devonian down to the Lower Silurian or Upper Ordovician.

At the present time, it is not possible to assign the Venezuelan coral to either *T. gracilis* or *T. lonsdalei* with confidence. A definite identification must await the collection of further material and more complete information on *T. gracilis*.

Order TABULATA Edwards & Haime 1850

Suborder FAVOSITINA Sokolov 1962

Family **COENITIDAE** Sardeson 1896

Genus ***COENITES*** Eichwald 1829

1829 *Coenites* Eichwald : 179.
1939 *Coenites;* Lecompte : 62.
1964 *Coenites;* Chudinova : 47.

Type species (see Miller 1897 : 727). *C. juniperinus* Eichwald 1829 : 179. Drift specimen, Lithuania (a neotype for *C. juniperinus* has been described from the Yagarakhuskii horizon (Wenlock); Saaremaa, Estonia by Klaamann 1964 : 116).

Diagnosis. Branching, laminar or finely zoned massive colonies. Corallites small and short, their walls thin proximally but much thickened distally, opening obliquely at the surface of the colony. Calices cresentic. Tabulae few and mural pores rare. Septa occasionally represented by three processes in the calice.

Coenites sp.

(Pl. 4, figs 10, 11)

Material. R46786 (S2275F). Río Suripá section. Silurian. Ludlow.

Description. A thin laminar encrusting colony 1·5 mm thick consisting of a single expansion which splits into two levels in one area.

Corallites about 0·1 mm across the short axis in longitudinal section, inclined at a low angle to the colony base and curving up slightly to meet the surface of the colony at an angle of 30–40°. Corallite walls thicken gradually from base to surface of the colony where they may reach 0·1 mm or slightly more in thickness. Mural pores are infrequent and about 0·05 mm diameter. The tabulae are flat, complete, variably spaced 0·25 mm or more apart.

The calices are gently curved, parallel sided slits with rounded ends 0·075 mm across and about 0·5 mm long. Septa are apparently not developed.

Discussion. This specimen may be referable to *Coenites laminatus* Hall (1852 : 143, pl. 39, figs 6a–d) which is widely recorded in rocks of Silurian age in North America. Unfortunately a modern description and adequate illustrations of the species are not available for a proper comparison to be made.

Suborder HALYSITINA Sokolov 1962

Family **HALYSITIDAE** Edwards and Haime 1850

Genus ***CYSTIHALYSITES*** Chernyshev 1941

1941 *Cystihalysites* Chernyshev : 70.
1962 *Cystihalysites*; Norford : 34.
1964 *Cystihalysites*; Sutton : 452, *cum syn.*

Type species. *Cystihalysites mirabilis* Chernyshev 1941 : 70, pl. 2, figs 5–7; pl. 3, figs 1–6. Upper Silurian; middle course of the Khandyga River, E. Verkhoyan'ya, U.S.S.R.

Diagnosis. Colonies formed of chains of long dimorphic corallites which divide and anastomose to form fenestrules. Autocorallites rounded or elliptical, sometimes developing septal spines and separated by rectangular mesocorallites. Tabulae of autocorallites usually complete, occasionally with vesicles on the corallite walls.

Tabulae of mesocorallites strongly arched or incomplete and vesicular. Autocorallites and mesocorallites separated by a true wall or peripheral faces of mesocorallite tabulae. Increase interstitial and peripheral. (After Sutton 1964 : 453).

Discussion. Nothing need be added here to the useful review of the genus given by Sutton (1964 : 452).

Cystihalysites brownsportensis (Amsden) 1949

(Pl. 5, figs 1–4)

1949 *Halysites catenularia brownsportensis* Amsden : 94, pl. 18, figs 1–3.
1955 *Halysites brownsportensis* Amsden; Buehler : 65, pl. 9, figs 4–6; pl. 10, fig. 6.
1957 *Cystihalysites brownsportensis* (Amsden) Hamada : 403, text-figs 1 (8), 2c.
1962 *Halysites brownsportensis* Amsden; Jull, text-fig. 1d.

Diagnosis. *Cystihalysites* with oval autocorallites 2 × 1·5 mm to 2·4 × 2 mm, developing short septal spines. Mesocorallites large, up to 1·5 mm long parallel to chain, containing small thin walled highly vesicular tabulae.

Material. R46787 (A2558), Río Aricagua section. R46788 (S2275F), Río Suripá section. Both Silurian, Ludlow.

Description. Damaged colonies, the largest piece 80 × 50 mm in area, composed of chains of dimorphic corallites. Crushing has broken the chains down to unbranched units up to 7 autocorallites in length. All signs of budding are extremely rare, suggesting large lacunae.

Autocorallites oval, internally smooth or weakly scalloped in cross-section. Internal diameters vary between 1·2 × 1·8 mm and 1·3 × 2·3 mm; external diameters 1·5 × 2 mm to 2·0 × 2·4 mm. Short septal spines are rarely seen (Pl. 5, fig. 3). The mesocorallites are large and square, 0·5 × 0·5 mm internally, or rectangular with the long axis, which may reach 1·5 mm internally, parallel to the chain. Auto- and mesocorallites are contained within a common wall varying between 0·15 and 0·3 mm thick and are separated by a thin partition 0·05 to 0·1 mm thick. There are no balken. Cross-sections of tabulae in the autocorallites are strongly curved and may even be circular. In the mesocorallites a thin walled network of vesicular tissue of about 0·2 mm diameter mesh and two to three ranks in width is developed. The autocorallites are spaced 2·7 to 3·9 mm centre to centre along the chains.

In longitudinal section the tabulae of the autocorallites are regularly developed, complete, arched, flat or saucer-shaped with few subsidiary plates. From colony to colony between 9 (rarely as few as 6) and 13 tabulae develop in 5 mm vertical growth. Traces of septal spines may be seen in subcentral sections developed in regular series 0·25 mm apart vertically. The mesocorallites are filled with thin walled, highly vesicular tabulae, usually 4 or 5 in 1 mm vertical growth and up to 6 ranks along the length of the chain in well developed mesocorallites. The wall separating auto- and mesocorallites is apparently formed by the thickened outer faces of the peripheral mesocorallite tabulae.

Discussion. Apart from possessing very slightly larger autocorallites, the Venezuelan specimens agree in every respect with Amsden's and Buehler's figures and description of *Halysites brownsportensis*. This species is recorded from the Niagaran (Wenlock and Ludlow) of North America.

Genus ***ACANTHOHALYSITES*** Hamada 1957

1957 *Acanthohalysites* Hamada : 404.
1961 *Acanthohalysites*; Strusz : 353.

Type species. *Halysites australis* Etheridge 1898 : 78, pl. 17, figs 1–8. Silurian; Bell River, Wellington, N.S.W., Australia.

Diagnosis. Dimorphic Halysitidae with septal spines developed in the autocorallites. Lacunae larger than autocorallites. Mesocorallites with non-cystose tabulae.

Discussion. *Acanthohalysites* and *Cystihalysites* are distinguished only through the development of cystose tabulae in the mesocorallites of species of *Cystihalysites*; Hamada (1957 : 397) was unaware of the septal spines developed in that genus.

Acanthohalysites sp.

(Pl. 5, figs 5, 6)

Material. R46789 (S1540A). Río Suripá section; Silurian, Ludlow.

Description. Fragmental dimorphic chains 1·5 to 1·9 mm across up to 7 autocorallites in length unbranched. Shape and size of lacunae unknown.

The autocorallites are subcircular to strongly oval in cross-section with maximum internal dimensions of 1·8 × 1·3 mm. The internal face is often clearly scalloped and occasionally septal spines are seen well developed. The longest spine projects 0·25 mm into the lumen. In other autocorallite sections, spots of tissue in the lumen probably represent the tips of septal spines. Autocorallites and mesocorallites are enclosed by a common wall 0·2 to 0·3 mm thick within which they are separated by partitions also 0·2 to 0·3 mm thick. The mesocorallite lumen is very small, rectangular or circular, or it may be closed completely: its maximum size is about 0·45 × 0·25 mm, elongated across the width of the chain. The distance centre to centre between autocorallites along the chain is 2·2 to 2·6 mm.

In longitudinal section, the autocorallites contain complete, flat to saucer-shaped tabulae regularly spaced 13 to 15 in 5 mm vertical growth. Incomplete tabulae are extremely rare. In a subcentral section, regular series of septal spines are seen 0·15 to 0·25 mm apart vertically (Pl. 5, fig. 5, upper half of central corallite). The mesocorallites are very narrow and may be intermittently closed. The tabulae appear to be flat or saucer-shaped but their spacing is indeterminate.

DISCUSSION. The Venezuelan specimen does not appear to be referable to an established species of *Acanthohalysites* but its indifferent preservation and fragmentary nature makes the erection of a new species undesirable.

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VII. APPENDIX—LOCATION OF SAMPLES

The following is the most accurate information available to the writer on the location of samples referred to in this paper. All the localities are in the southern Mérida Andes, western Venezuela. Sample numbers are prefixed 'A' for H. C. Arnold's collection, 'S' for R. Shagam's collection and 'K' for the collections of the Creole Petroleum Corporation. Location of the samples is also shown in Text-fig. 1.

Samples A1030, A1035 (Palmarito Formation, Permo-Carboniferous).

Section on the Quebrada Queveda (a tributary of the Río Mucuchachí) approximately 0·7 km due west of Portachuelo, Mérida State. A1030 is stratigraphically 0·5 m above the base of the Upper Palmarito limestone and A1035 is 45·5 m (including a break in the succession of 44 m which may conceal a fault) below the base of that limestone.

Samples A2077, A2079, S1583, K80748 (Caparo II, Lower Llandovery).

Section 10 to 15 m thick on the south bank of the Río Caparo at a pronounced bend in the river approximately 900 m downstream of the Paso Caparo, Mérida State. Locality 2 of Shell & Creole (1964, table 1).

Samples A2558–A2582, S1302, SC1, K162950 (Caparo IV, Ludlow).

Upper part of the Silurian section on the Río Aricagua, outcropping between approximately 4·1 km and 4·3 km upstream (measured direct) from the confluence of the Río Aricagua and the Río Caparo, Mérida State. Locality 7 of Shell & Creole (1964, table 1).

The equivalence between Arnold's collecting points (to which the measurements refer) and those of Shagam and Creole in the following table is approximate only.

Stratigraphic thickness in metres above base of Silurian outcrop:—

335		top of section	
			S1302
314	A2582		
308	A2579		
240·5	A2562	≙	SC1 K162950
237	A2561		
231	A2558		
0		base of section	

Sample 2722 (*Palmarito Formation, Permo-Carboniferous*).

213 m above the base of the Palmarito Formation in the Quebrada El Mesón, approximately 1·5 km west (measured direct) of its confluence with the Río Aricagua, Mérida State.

Samples S1540A, S2275D, S2275F (*Caparo IV, Ludlow*).

Upper part of a section approximately 550 m thick measured from the stratigraphic base at the major elbow in the upper reaches of the Río Suripá (see Text-fig. 1) downstream to a point, about 200 m above a tributary entering from the west, where the stratigraphically highest sample was collected (S1540A), Barinas State. Samples S2275D and S2275F are approximately 100–150 m below sample S1540A in the sequence.

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PLATE 1

Syringaxon arnoldi sp. nov.

FIG. 1. Cross-section (peel). R46740c (taken from holotype). × 6.

FIG. 2. Longitudinal section in counter-cardinal plane; C on right (slide). R46740h (cut from holotype). × 6.

FIG. 3. Cross-section (slide). R46741a. × 6.

FIG. 4. Longitudinal section in counter-cardinal plane; C on left (slide). R46742h. × 6.

FIG. 5. Cross-section (peel). R467459. × 6.

All Río Aricagua section; Silurian, Ludlow.

Syringaxon siluriense (M'Coy)

FIG. 6. Cross-section (slide). A5468b (cut from holotype, Sedgwick Museum, Cambridge). Underbarrow, near Kendal, Westmorland, England; high Bannisdale Slates or lowermost Kirkby Moor Flags, Silurian, Ludlow, *leintwardinensis* zone. × 6.

Syringaxon suripaense sp. nov.

FIG. 7. Cross-section (slide). R46746a (cut from holotype). × 6.

FIG. 8. Cross-section (slide). R46747a. × 6.

Both Río Suripá section; Silurian, Ludlow.

Columnaxon angelae gen. et sp. nov.

FIG. 9. Longitudinal section in counter-cardinal plane; C on left (slide). R46748p (cut from holotype). × 6.

FIG. 10. Cross-section (peel). R46750b. × 6.

FIG. 11. Longitudinal section in counter-cardinal plane; C on left (slide). R46750e. × 6.

FIG. 12. Cross-section (slide). R46749a. × 6.

All Río Aricagua section; Silurian, Ludlow.

Lophophyllidium pelaeum (Jeffords)

FIG. 13. Cross-section (peel). R46751b. × 3.

FIG. 14. Cross-section (slide). R46751a. × 3.

FIG. 15. Longitudinal section (slide). R46751c. × 3.

Quebrada Queveda; Permo-Carboniferous (?Pennsylvanian).

Lophophyllidium sp. cf. ***L. wewokanum*** Jeffords

FIG. 16. Cross-section (peel). R46752a. × 3.

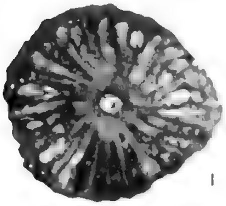
FIG. 17. Longitudinal section in counter-cardinal plane; C on right (slide). R46752e. × 3.

FIG. 18. Cross-section (slide). R46752c. × 3.

Quebrada Queveda section; Permo-Carboniferous (?Pennsylvanian).

All cross-sections orientated with the cardinal septum at top centre.

PLATE 1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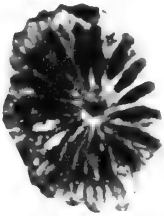
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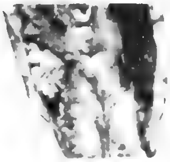
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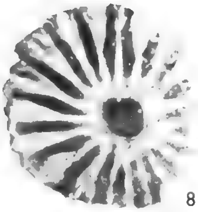
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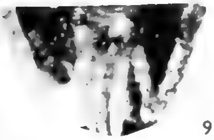
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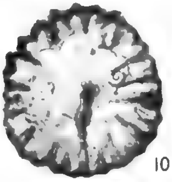
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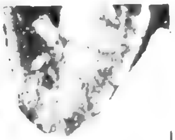
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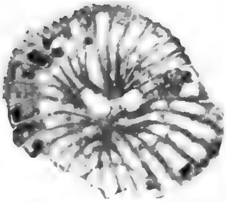
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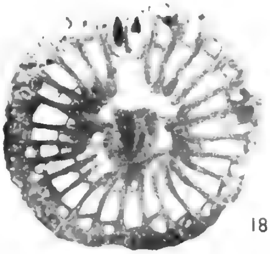
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PLATE 2

Lophophyllidium sp.

FIG. 1. Cross-section (slide). R46753b. × 3.
FIG. 2. Cross-section (peel). R46753a. × 3.
Quebrada El Mesón section; Permo-Carboniferous (?Pennsylvanian).

Lophamplexus sp.

FIG. 3. Cross-section (peel). R46754a. × 3.
FIG. 4. Cross-section (slide). R46754b. × 3.
FIG. 5. Cross-section (peel). R46754c. × 3.
FIG. 6. Longitudinal section in counter-cardinal plane; C on right (slide). R46754h. × 3.
Quebrada El Mesón section; Permo-Carboniferous (?Pennsylvanian).

Streptelasma shagami sp. nov.

FIG. 7. Cross-section (slide). R46755b (cut from holotype). × 2.
FIG. 8. Cross-section (slide). R46755a (cut from holotype). × 2.
FIG. 9. Longitudinal section in counter-cardinal plane; C on left (slide). R46755c (cut from holotype). × 2.
FIG. 10. Cross-section (slide). R46756a. × 1·5.
Both Río Caparo, near the Paso Caparo; Silurian, Lower Llandovery.

Streptelasma sp.

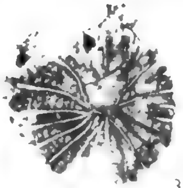
FIG. 11. Cross-section (slide). R46761a. × 2.
FIG. 12. Longitudinal section (slide). R46761c. × 2.
Río Caparo, near the Paso Caparo; Silurian, Lower Llandovery.

Leolasma kaljoi sp. nov.

FIG. 13. Cross-section (slide). R46762a (cut from holotype). × 6.
Río Caparo, near the Paso Caparo; Silurian, Lower Llandovery.

All cross-sections orientated with the cardinal septum at top centre.


1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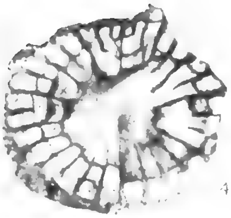
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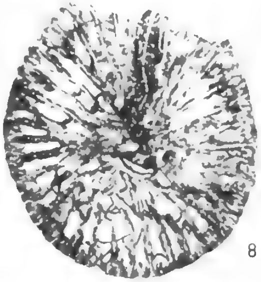
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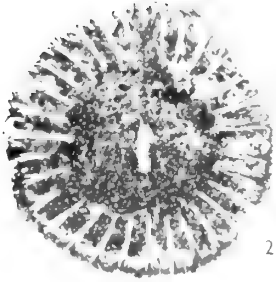
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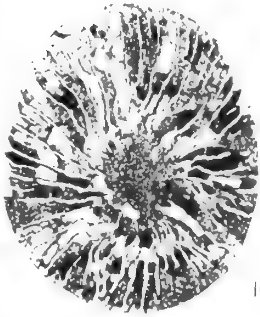
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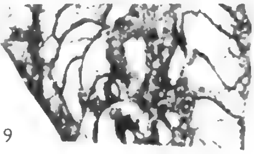
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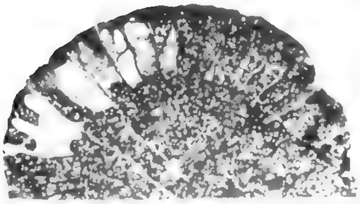
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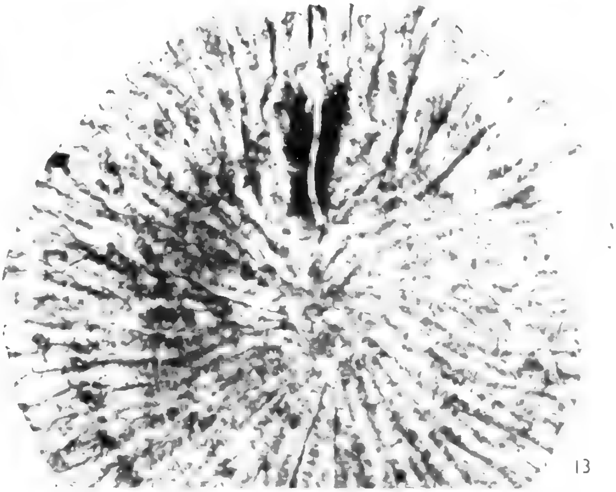
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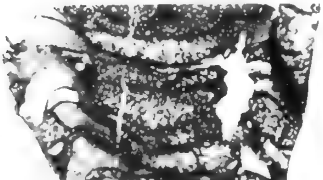
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PLATE 3

Leolasma kaljoi sp. nov.

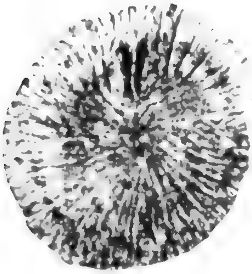
FIG. 1 (slide) and FIGS 2–4 (peels). Serial cross-sections in base of calice. Fig. 1 (R46762a)—1·40 mm—Fig. 2 (R46762d)—1·34 mm—Fig. 3 (R46762e)—1·32 mm—Fig. 4 (R46762g). Cut from holotype. × 2·5.

FIG. 5. Cross-section (slide). R46775a. × 2·5.
FIG. 6. Cross-section (slide). R46766a. × 2·5.
FIG. 7. Cross-section (slide). R46771a. × 2·5.
FIG. 8. Longitudinal section (slide). R46766b. × 3.
All Río Caparo, near the Paso Caparo; Silurian, Lower Llandovery.

Cymatelasma aricaguaense sp. nov.

FIG. 9. Cross-section (slide). R46778a. × 3.
FIG. 10. Cross-section (slide). R46776a (cut from holotype). × 3.
FIG. 11. Cross-section (slide). R46776b (cut from holotype). × 3.
FIG. 12. Cross-section (slide). R46781a. × 3.
FIG. 13. Longitudinal section (slide). R46779b. × 3.
FIG. 14. Longitudinal section (slide). R46778c. × 3.
FIG. 15. Longitudinal section (slide). R46776c (cut from holotype). × 3.
All Río Aricagua section; Silurian, Ludlow.

All cross-sections orientated with the cardinal septum at top centre.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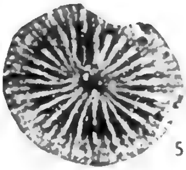
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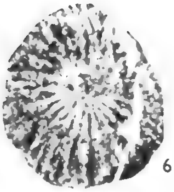
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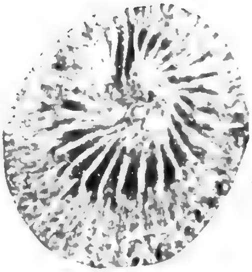
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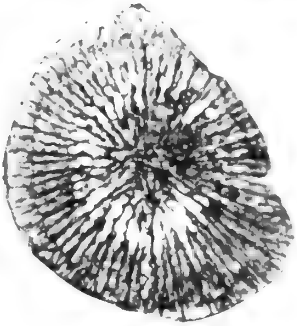
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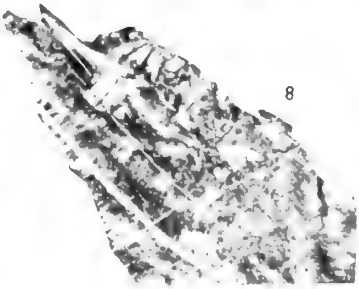
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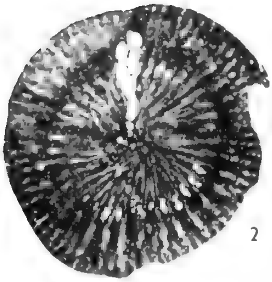
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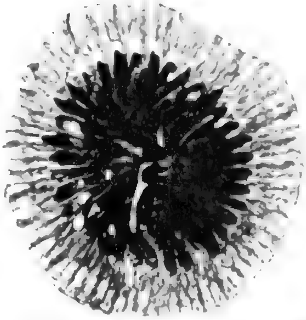
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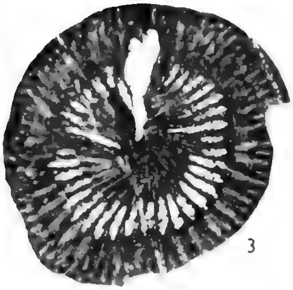
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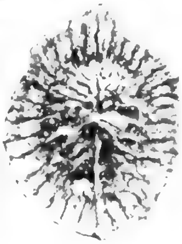
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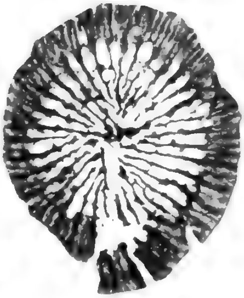
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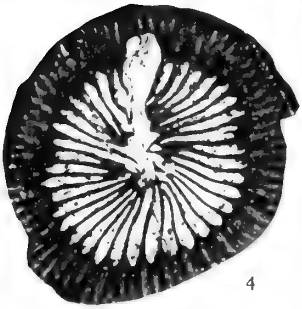
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PLATE 4

Cymatelasma aricaguaense sp. nov.

Fig. 1. Cross-section (slide). R46776b (cut from holotype). × 8.
Río Aricagua section; Silurian, Ludlow.

Tryplasma sp. cf. *T. nordica* Stumm

Fig. 2. Cross-section (slide). R46782a. × 5.
Fig. 3. Longitudinal section (slide). R46783a. × 5.
Fig. 4. Longitudinal section (slide). R46784g. × 16.
Río Suripá section; Silurian, Ludlow.

Tryplasma sp.

Figs 5, 6. Cross-sections (slides). R46785c. × 5.
Fig. 7. Longitudinal section (slide). R46785a. × 40.
Fig. 8. Oblique sections (slide). R46785b. × 5.
Fig. 9. Longitudinal and oblique sections (slide). R46785a. × 5.
Río Suripá section; Silurian, Ludlow.

Coenites sp.

Fig. 10. Cross-section (slide). R46786a. × 10.
Fig. 11. Longitudinal section (slide). R46786b. × 10.
Río Suripá section; Silurian, Ludlow.


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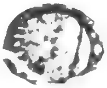
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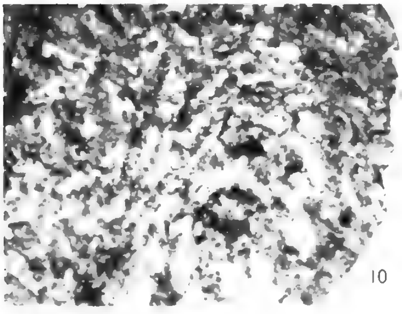
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PLATE 5

Cystihalysites brownsportensis (Amsden)

FIG. 1. Cross- and longitudinal sections (slide). R46788c. × 4.
FIG. 2. Cross-sections (slide). R46788a. × 4.
FIG. 3. Cross-section (slide). R46788a. × 9.
FIG. 4. Longitudinal section (slide). R46788b. × 4.
Río Suripá section; Silurian, Ludlow.

Acanthohalysites sp.

FIG. 5. Longitudinal section (slide). R46789f. × 4.
FIG. 6. Cross-sections (slide). R46789a. × 4.
Río Suripá section; Silurian, Ludlow.


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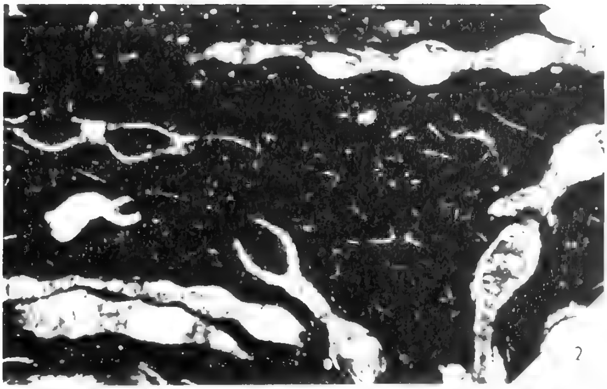
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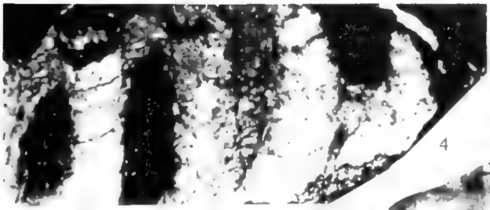
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THE EARLIEST GOATS AND OTHER ANTELOPES FROM THE SAMOS *HIPPARION* FAUNA

A. W. GENTRY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 20 No. 6
LONDON : 1971

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BY

ALAN WILLIAM GENTRY

Pp. 229–296; 6 *Plates*, 16 *Text-figures*

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THE EARLIEST GOATS AND OTHER ANTELOPES FROM THE SAMOS *HIPPARION* FAUNA

By A. W. GENTRY

CONTENTS

SYNOPSIS

Lower Pliocene antelopes belonging to *Palaeoryx*, *Protoryx* and *Pachytragus* and hitherto taken as Hippotragini, are revised and placed in the Caprinae. The species of *Protragelaphus*, *Prostrepsiceros* and *Palaeoreas* are likewise revised; the last two genera have normally been classified as Tragelaphini, but *Prostrepsiceros* should join *Protragelaphus* in the Antilopini and *Palaeoreas* is in the Ovibovini. Hippotragini and Tragelaphini are almost totally African, Caprinae and Ovibovini almost all Eurasian, and those Antilopini to which *Prostrepsiceros* and *Protragelaphus* are related are also Eurasian. Thus the Samos fossil fauna contains no antelopes related to living African species; it is more properly seen as a stage in the evolution of Eurasian bovid faunas.

I. INTRODUCTION

Towards the end of the nineteenth century Major (1888, 1891a, 1891b, 1894) collected fossil mammals on the Aegean island of Samos very close to the mainland of Turkey, and recognized a later Tertiary fauna similar to that already known from Pikermi in Attica. Much of his collection passed to the Geology Department of Lausanne University, some was purchased by the British Museum (Natural History) in 1889 and 1890, and more pieces went to other museums. Before the First World War collectors provided material for geological institutes in Munich, Münster in Westphalia and Stuttgart, and for the museum in Vienna, and in 1924 Brown collected for the American Museum of Natural History, New York. His field notebook contains meagre details of the quarries which he excavated, and their positions were shown on a small map in Brown (1927 : 19). Quarry 1 was in the Adriano district on land owned by the Soufoulis family; this quarry was near former German excavations and about 1½ miles north of Mytlini; quarry 2 was in the Potamies district on land owned by Trifon Balidakis; quarry 3 was in the Megalosvrakos district on land owned by Trifon Balidakis, but no Bovidae are known from this quarry; quarry 4 was in the Potamies district on land owned by Dr Gliarmis; quarry 5 was in the Limitzis district on land owned by the widow Soumena; quarry 6 was in the Tholoramo or Vigles district on waste land.

Despite all this collecting, there is little information on the geology of the fossiliferous deposits. Stefani (*in* Stefani, Major and Barbey, 1892) acknowledged accounts of some earlier travellers, and noted two basins of Tertiary lacustrine or marshy deposits, that of Mytilini occupying a large part of the island east of Ambelos, and that of Karlovassi farther west. Brown (1927) gave a summary of the deposits. Schlosser (1904 : 112) noted from the matrix on the fossils that different associations of bovid species occurred in different compositions of the sediments. Abel (1922 : 143) considered that the Samos fauna had been catastrophically annihilated in volcanic eruptions, but that the absence of associations of the skeletal parts indicated postmortem stream transport.

J. A. Van Couvering (pers. comm.) writes as follows. 'Tertiary sediments of the Mytilini district consist of well-bedded volcanic sediments—siltstones, sandstones, and volcanic pebble breccias—interlayered with freshwater algal limestones and marble cobble conglomerates (Van Couvering & Miller, 1970). The only authigenic minerals within the sequence are calcite (in the limestones and locally as cement in the sediments) and silica, which appears only in a thin-layered cherty limestone formation near the top of the sequence. No soil horizons appear to have been developed in the sequence, and no angular unconformities can be detected, indicating that deposition was more or less continuous. The sequence is one which seems most likely to have developed in a slowly subsiding intermontane basin surrounded by upfaulted marble basement and traversed by low-gradient streams carrying mostly fine-grained volcanic detritus from the nearby active Cappadocian pyroclastic province to the east (Westerveld 1957). The basin floor was periodically submerged in shallow lakes, probably after activity on the faults to the west and northeast which now show downthrow towards the basin, and the water in the lakes and in the subsurface was high in dissolved carbonate from the basement. The zeolites and authigenic feldspar which might have formed in a more arid, alkaline environment from the volcanic detritus (Hay 1966) are absent, which suggests that the steppe climate of the Samos fauna was more like that of the temperate zone grasslands than the African savannah. The fossils occur in a variety of volcanic sediment types (Schlosser 1904) in the main horizon at Adrianó (Soufoulis farm), but not in association with primary ash falls accounting for the deaths of the animals. Suggestions that the algal limestones formed in a Pontian "Aegan lake" (Spratt 1846) or that the alluvial beds are part of the valley fill in an ancient course of the Maeander or Menderes River (Brown 1927) are unsupported by the geological evidence.'

A group of antelopes which is more abundant at Samos than at any other site is that of *Palaeoryx* and *Pachytragus*, and I shall here reconsider their classification. A second group in the Samos fauna which will be similarly treated contains the spiral-horned *Protragelaphus*, *Prostrepsiceros* and *Palaeoreas*. Two other lower Pliocene sites broadly contemporaneous with Samos will be referred to, those of Maragha in northern Persia (see Pohlig 1886 and Mecquenem 1908) and Pikermi in Greece (Woodward 1901). Pikermi has material of *Protoryx*, a relative of *Palaeoryx* and *Pachytragus*, and Maragha has a diversity of spiral-horned antelopes. However, it is the presence of so many complete skulls, crania and dentitions of bovids and the large number of species in the Samos deposits, which give that fauna its decisive importance. Adequate discussion of these antelopes involves referring to other fossil genera, and necessitates giving opinions about their classification. Nevertheless my revision covers only species of the above six genera occurring at Samos, Pikermi and Maragha. During this study I have had access to previously published material in European museums and to unpublished material in New York. The initials BM(NH) indicate material in the British Museum (Natural History) in London, and AMNH in the American Museum of Natural History, New York. Measurements are always expressed in millimetres.

II. SYSTEMATICS OF *PALAEORYX*, *PROTORYX* AND *PACHYTRAGUS*

The first of the *Palaeoryx* group to be discovered was the large *Antilope pallasi* Wagner (1857 : 149) from Pikermi, of which the type specimen is still in Munich. Gaudry founded the generic name *Palaeoryx* for this species although he actually intended the name as a subgenus. He likened the fossil particularly to *Oryx* among living antelopes and since then it has always been considered a member of the Hippotragini. Schlosser (1904 : 38 and 43) added two more species from Samos, *P. majori* and *P. ingens*, the latter based only on teeth, and Andree (1926 : 161) added *P. laticeps*. Some other species formerly supposed to belong to *Palaeoryx*, particularly the fine later Pliocene skulls of '*Palaeoryx*' *boodon* and '*Palaeoryx*' *cordieri* in Paris have been placed in a separate boselaphine or bovine genus *Parabos* by Arambourg and Piveteau (1929a : 144), and others may belong to *Leptobos* (Pilgrim and Hopwood 1928 : 74).

Major (1891a : 608–609) founded the genus *Protoryx* for some antelopes from Samos similar to *Palaeoryx*, but having more compressed horn cores and sometimes a longer cranium. He considered *Protoryx* to have more striking resemblances to Hippotragini than did *Palaeoryx*. He referred to the new genus a Pikermi cranium figured but not named by Gaudry (1865 : 289, pl. 52 fig. 1 'Antilope d'espèce indéterminée') and a skull from Maragha, BM(NH) M.3841 which was not figured. Four species were named as occurring at Samos, *P. carolinae*, *P. longiceps*, *P. gaudryi* and *P. hippolyte*, none of which were given diagnoses or figures. *P. carolinae* is the only one he cited as occurring at Pikermi, and for this reason Pilgrim and Hopwood (1928) later selected *P. carolinae* as the name for Gaudry's illustrated cranium.

Schlosser (1904 : 45) corrected the generic diagnosis in which Major had mistakenly referred to the braincase being very little angled on the face, referred three Samos skulls to *P. carolinae* Major (Schlosser 1904 : 45, pl. 9 figs 1, 4, 8) and a frontlet to *P.* cf. *carolinae,* founded a second species *P. hentscheli* on teeth only, and suggested that another new genus and species of his, *Pseudotragus capricornis,* might include material of Major's *nomina nuda Protoryx gaudryi* and *P. hippolyte.* He founded a new genus and species *Pachytragus crassicornis* differing from *Protoryx* by having an anterior keel on the horn cores, rather divergent horn cores in anterior view, the braincase still more strongly angled on the face axis, and wide orbital rims. He also (1904 : 87) established a subfamily Pseudotraginae to include *Protoryx, Pseudotragus* and *Pachytragus* along with *Eotragus* (=*Eocerus*), *Protragocerus, Miotragocerus*[1] and *Neotragocerus.* His definition of the new subfamily (1904 : 85) included the characters of strongly compressed goat-like horns and a long narrow face, and *Palaeoryx* remained a hippotragine.

Andree (1926) referred new material to *Protoryx carolinae,* founded a new species *P. crassicornis,* a new variety *laticeps* of *P. carolinae,* and a new variety *tenuicornis* of *P. hentscheli* Schlosser. He founded a new species of *Pachytragus*—*P. schlosseri,* referred a skull to *Pseudotragus capricornis* Schlosser, and founded a new species *longicornis* of *Pseudotragus.* Finally he referred one fossil skull to *Hippotragus* as the new species *H. kopassi.* He followed Schlosser's consignment of the genera into Pseudotraginae and Hippotraginae.

Pilgrim & Hopwood (1928 : 27, 30) selected *P. carolinae* as the type species of *Protoryx* with Gaudry's skull in Paris as holotype. They added to *P. carolinae* two Pikermi skulls, BM(NH) M.10839 and M.11415, and one from Samos, M.4198, as well as two Lausanne skulls, 298 and 362, which Major (1894 : 28, 30) had labelled '*P. gaudryi*'. They reduced *P. crassicornis* Andree to a variety of *P. carolinae,* but raised his variety *laticeps* of *P. carolinae* to species level, assigning to it Lausanne skulls 28 and 201 and the maxilla 580 and Schlosser's (1904 : 48) frontlet of *P.* cf. *carolinae.* They considered that Schlosser's and Andree's records of *P. carolinae* were not conspecific with Gaudry's type skull or the other material they had just assigned themselves to this species, and used for it Major's name *P. longiceps* with the Lausanne skull 22 as holotype and the Maragha skull BM(NH) M.3841 as paratype. Finally they took a skull in Lausanne, 30, labelled *P. hippolyte* as the type of a new variety of Schlosser's *Pseudotragus capricornis.*

Bohlin (1936 : 17, 18) transferred the two London skulls M.10839 and M.11415 from *Protoryx carolinae* to the related genus *Palaeoryx,* suggested confining the specific name *carolinae* to the actual Paris specimen and using *P. gaudryi* as the name for

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[1] I thank Q. B. Hendey for telling me of a paper by Kretzoi (1968) in which it is pointed out that the familiar generic names *Tragocerus* Gaudry 1861 and *Microtragus* Andree 1926 for fossil antelopes are definitely preoccupied by beetles. Kretzoi proposed the new name *Sporadotragus* in place of *Microtragus.* For *Tragocerus* the next available name seems to be *Miotragocerus* Stromer. This name was published in 1928; *Graecoryx,* which I believe could have been applied to the same genus, was published by Pilgrim and Hopwood at some date close to 28th June 1928. This was the date at which the copy of their book in the Palaeontology Library of the British Museum (Natural History) was accessioned. In this paper I shall use *Miotragocerus* in place of the junior homonym *Tragocerus.*

Samos '*P. carolinae*', i.e. the Lausanne skulls 298 and 362. He thought the London Samos skull M.4198 was not a *Protoryx*, but he assigned to *Protoryx* many specimens previously put elsewhere: Andree's specimens of Schlosser's *Pseudotragus capricornis*, of *Pseudotragus longicornis*, *Pachytragus schlosseri* and *Hippotragus kopassi*, and Pilgrim and Hopwood's *Pseudotragus capricornis* var. *hippolyte*. There was no skull from Pikermi which agreed with any of the Samos *Protoryx*, and this threatened a nomenclatorial revision since the type cranium of *Protoryx carolinae* was a Pikermi fossil. None the less he continued to use the genus *Protoryx* for Samos specimens, although he considered that they represented a group which, like *Chilotherium* Ringström and *Samotherium* Major, never spread as far as Pikermi. He attempted no revision at the species level, but did propose that *Palaeoryx* could not be in a separate family (=tribe of Simpson's 1945 classification) from *Protoryx*. From this it seemed to follow that they would all pass into the Hippotragini, and that the group 'Pseudotraginae' in which they were wrongly linked with *Eotragus*, *Protragocerus*, *Miotragocerus* and *Neotragocerus* would be abolished. Already in his work on Chinese lower Pliocene Bovidae Bohlin (1935c : 119) had doubtfully referred the two genera, with some related Chinese forms, to Hippotragini. Neither Pilgrim (1939 : 26–27) nor Gentry (1967 : 266) challenged this view, but Sokolov (*in* Orlov 1968 : 537) had doubts. It is now the purpose of this paper to interpret *Pachytragus* and possibly *Protoryx* as members of the tribe Caprini, and *Palaeoryx* as an ovibovine. Although I do not place all three genera in one tribe, there is no doubt that in the lower Pliocene time level they were closely related.

Palaeoryx, *Protoryx* and *Pachytragus* differ from the contemporaneous and commonly fossilized boselaphine *Miotragocerus* by not having a stepped anterior keel, by having horn cores less strongly compressed medio-laterally, a braincase more strongly angled on the face axis and without temporal ridges on its dorsal surface, a higher infraorbital foramen, a wider mastoid exposure of the periotic, and smaller foramina ovalia.

Skull characters shared by *Palaeoryx*, *Protoryx* and *Pachytragus* are horn cores without transverse ridges or torsion; the postcornual fossa, lying postero-laterally to the horn core base, is shallow or altogether absent; the braincase top is at an angle to the line of the face axis; the parieto-frontals suture has only a slight anteriorly directed indentation centrally or none at all; temporal lines are not developed as strong ridges and do not approach one another very closely; the supraorbital pits are small; the preorbital fossa is large and shallow and sometimes has an upper rim; the back edge of the infraorbital foramen is fairly high over P^{2-3} or P^3; the median indentation at the back of the palate is level with the lateral ones or passes slightly anterior to them; the mastoid exposure of the periotic has a moderate or large area; posteriorly the ventral edge of the auditory bulla may pass downwards where it meets the front of the paraoccipital process; there are no goat folds (anterior transverse flanges) on the lower molars; the lateral lobes of the lower molars are not drawn out transversely. These characters could be considered for inclusion in the definition of any tribe or subfamily to which the three genera belong.

Genus *PALAEORYX* Gaudry

1861a *Palaeoryx* Gaudry : 241.
1861b *Palaeoryx* Gaudry : 393.

TYPE SPECIES. *Antilope pallasi* Wagner, 1857 : 149, pl. 9, fig. 21.

GENERIC DIAGNOSIS. As for the species.

Palaeoryx pallasi (Wagner)

1857 *Antilope pallasi* Wagner : 149, pl. 9 fig. 21.
1861a *Palaeoryx pallasi* Gaudry : 241.
1861b *Palaeoryx speciosus* Gaudry : 393, pl. 9 figs 1–3.
1865 *Palaeoryx pallasi* Gaudry : 271, pl. 47 figs 1–5.
1894 *Palaeoryx rotundicornis* [nom. nud.] Major : 24.
1904 *Palaeoryx majori* Schlosser : 38, pl. 7 figs 1–5.
1926 *Palaeoryx laticeps* Andree : 161, pl. 13 figs 4, 4a, 6.
1928 *Palaeoryx woodwardi* Pilgrim & Hopwood : 77, pl. 6 fig. 1.
1928 *Palaeoryx woodwardi* var. *columnatus* Pilgrim & Hopwood : 78.

LECTOTYPE. The cranium at Munich figured by Wagner, and designated by Pilgrim & Hopwood (1928 : 75). It has survived the Second World War.

LOCALITIES. Pikermi, Samos.

AGE. Lower Pliocene.

DIAGNOSIS. Moderate to large sized antelopes with a low and wide skull; horn cores are of short to moderate length, little compressed medio-laterally, without keels, set fairly obliquely in side view and widely apart, moderately divergent in anterior view, tips reapproaching slightly; braincase is short and wide; orbital rims are moderately projecting; frontals between the horn bases are a little higher than the orbital rims; mid-frontals suture is not raised; mid-frontals and parieto-frontals sutures are not usually complicated; sides of braincase are generally parallel, but sometimes widening anteriorly or posteriorly; supraorbital pits are set widely apart; ethmoidal fissure is present; zygomatic arch is deep at its anterior end where it passes beneath the orbit; back edge of tooth row is slightly anterior to the level of the front of the orbit.

Occipital surface faces almost uniformly backwards; the median vertical occipital ridge is well marked and the hollows on either side of it moderately so; the anterior tuberosities of the basioccipital are set rather widely apart; basioccipital usually has some indication of a central longitudinal groove; foramina ovalia are moderately sized; auditory bulla is small to moderate sized and moderately inflated.

Brachyodont cheek teeth; enamel may be somewhat rugose; basal (or accessory) pillars are moderate-sized to small on lower molars and small to absent on uppers; there are indentations into the back edge of the rear central cavities of the upper molars; the rear of the front medial lobe and the front of the rear medial lobe on the upper molars fuse only relatively late in wear; styles are not very prominent on upper molars or premolars; ribs between parastyle and mesostyle of upper molars are sometimes strong; premolar row is long with scarcely reduced front premolars.

REMARKS. *Previously named specimens.* The horn cores of the lectotype diverge rather less than is normal in the species, and this was partly the reason for founding some of the synonymous species names. However some other fossils have previously been referred to *Palaeoryx pallasi*. These are a skull from Pikermi now in Paris which was figured by Gaudry (1865 : 271, pl. 47 fig. 1); a Lausanne specimen, 198, from Samos with part of its left horn core and most of the braincase; a Münster skull referred to by Andree (1926 : 160, pl. 15 fig. 7) with rather a narrow cranium and small horn cores, probably a female; a cranium from Pikermi in the Vienna museum labelled *P. pallasi*; and a Pikermi skull and cranium, BM(NH) M. 10831 and M.11426, referred to *P. pallasi* by Pilgrim & Hopwood (1928 : 76). M.11426 has its horn core perhaps badly stuck on but certainly curving strongly backwards, and it is M.10831 which indicates the presence of an ethmoidal fissure in this species. The skull of *P. pallasi* from Maragha (Mecquenem 1924 : 31, pl. 4 fig. 1) is really a *Miotragocerus* as noticed by Bohlin (1936 : 14), and there is no other convincing evidence of *Palaeoryx pallasi* from Maragha. I have not seen the two Stuttgart skulls mentioned by Andree (1926 : 160, pl. 12 fig. 8) as possibly females of *P. pallasi*.

The Lausanne skull, 200, of *Palaeoryx rotundicornis* Major has already been referred by Pilgrim & Hopwood (1928 : 75) to *P. pallasi*. A Lausanne cranium with horn core bases, 29, was also taken as *P. rotundicornis* by Major (1894 : 18), but is also *P. pallasi*. The anterior tuberosities of the basioccipital of 29 are rather wider apart than in 200.

The cranium of *P. majori* Schlosser (1904, pl. 7 figs 5, 5a, 5b) in Munich has fairly straight, very divergent horn cores which show considerable inward curvature at the tips. According to the diagnosis the orbits are situated entirely beneath the horn cores, but this character is difficult to use in bovids with such obliquely inserted horns, and I could not see that any difference existed between this species and the lectotype of *P. pallasi*. The horn core characters, larger braincase, rounded orbits, and supposedly smaller primitive teeth do not justify a separate specific name. Andree (1926 : 161) placed a Samos cranium in Vienna, 1911.v.9, in *P. majori*, and this too can be taken as *P. pallasi*. Schlosser (1904 : 43, pl. 8 figs 3–5) also founded a species *Palaeoryx ingens* on teeth, but I would not be certain that they even belong to *Palaeoryx* (see also p. 239). The holotype of Andree's *P. laticeps* is a cranium with a low wide braincase, horn cores rather strongly curved backwards, thick and robust. These, and other linked characters given in his diagnosis essentially amount to a wide skull and backward horn core curvature, and are insufficient to carry the specimen beyond a likely range of variation for *P. pallasi*.

P. woodwardi, BM(NH) M.10832, was alleged by Pilgrim & Hopwood to differ from *P. pallasi* in its more divergent and narrower horn cores, which with the frontals are smaller relative to the rest of the skull. The horn cores certainly are small but all that this and other invoked characters demonstrate is a less robust skull which is possibly of a female. It is true that there are no basal pillars on the upper molars, but teeth assigned by Schlosser (1904, pl. 7 fig. 1) to *P. majori* have a small basal pillar only on M^2. The greater divergence of the horn cores in this species agrees with those called *laticeps* and *majori*, but there is not the inward curvature of the tips. The variety *columnatus* of *P. woodwardi* was based on a Lausanne skull 199 and a London palate M.11416. The palate was noted to be too wide for *Protoryx carolinae* [but was mistakenly assigned to that species on another page (Pilgrim & Hopwood 1928 : 30)]. Basal pillars are present on all molars, as in most upper molars of *Palaeoryx pallasi*, and the supposed hypsodonty and weak development of mesostyles are insufficient to separate it from *P. pallasi*. The preserved right horn core of 199 is very narrow, widely divergent with little inward curving at the tip, and set obliquely.

Palaeoryx pallasi is not represented by skulls, crania or frontlets in the Samos collection of the American Museum of Natural History.

Infraspecific variation

I have not found differences between the Samos and Pikermi representatives of this species, but there is a fair amount of individual variation. Thus the Vienna specimen from Samos shows a flattening of the lateral surface of the horn cores. The mid-frontals sutures are complicated in the London and Vienna skulls from Pikermi but less so in Lausanne skulls 29 and 200 from Samos; the frontals-parietal suture has almost no central indentation in the Lausanne skulls but more in others. The braincase widens anteriorly in the Munich skull from Samos and in BM(NH) M.10831 from Pikermi, but in Lausanne 200 and the Münster specimen figured by Andree (1926, pl. 13 figs 4, 6) it widens slightly posteriorly, and in BM(NH) M.10832 and both Vienna skulls its sides are nearly parallel. The back edge of the infraorbital foramen is high over the middle or back of P^3 in M.10831 and Lausanne skulls 199 and 200, but over the P^{2-3} junction in the Paris example. The Münster specimen shown in Andree (1926, pl. 15 fig. 7) has the median indentation at the back of the palate behind the level of the lateral ones. The occipital median ridge and flanking hollows are quite strongly developed in Lausanne skull 198. In 29 the strong median ridge gives the appearance of the occipital surface facing two ways. The basioccipital has a central longitudinal groove in most pieces but not in Lausanne 29 (Pl. 1 fig. 2) and 200. Moderately sized foramina ovalia may be seen in Lausanne 198 and BM(NH) M.10831, and larger ones in the Münster skull figured by Andree (1926, pl. 13 figs 4, 6). The downturning of the lower edge of the auditory bulla into the paraoccipital process is seen in Lausanne 29 (Pl. 1 fig. 1) and in the Münster skull figured by Andree (1926, pl. 13 figs 4, 6). Both specimens have quite small auditory bullae, that of 29 perhaps more inflated than in the Münster specimen. The bulla of the other Münster skull (Andree 1926, pl. 15 fig. 7) is slightly larger and the back does not pass down into the paraoccipital process.

Some mean skull measurements of *Palaeoryx pallasi*, together with ranges, standard deviations and coefficients of variation are shown on Table 2 p. 258. With individuals coming from both Pikermi and Samos and with the possibility of female animals having been included, there are high coefficients of variation.

Tooth characters

The upper teeth of *Palaeoryx pallasi* are known from the London skulls M.10831 and M.10832, the Paris skull illustrated by Gaudry (1865, pl. 47 fig. 1), the Lausanne skulls 199 and 200, and from the skull in Münster illustrated by Andree (1926, pl. 15 fig. 7). They are distinguished from teeth of the similarly sized Samos ovibovine *Criotherium argalioides* Major by the latter's rounded medial lobes of the upper molars and premolars, massive P^2, relatively long and narrow upper molars, lower premolars with transversely-running rather than diagonal front and back edges, the somewhat rounded outline of worn lateral lobes of the lower molars, not very outbowed medial walls of the lower molars, their straighter central cavities, and the small basal pillars set away from the main body of the tooth.

They are more difficult to distinguish from *Miotragocerus*. Even their great size is not decisive, since a larger species of *Miotragocerus* than *M. amalthea* is known from Samos and Maragha (p. 243 below). This animal, which is quite definitely not a *Palaeoryx* by the lack of bending of its braincase, its temporal ridges, its horn cores being medio-laterally compressed at least in their higher parts, fails to show even the distinctive large P^2 of the smaller *Miotragocerus* species.

Individual dentitions

Even complete upper or lower dentitions are very difficult to identify unless they are attached to complete skulls or associated with horn cores. The palate which Roth & Wagner (1855 : 452, pl. 14 fig. 1) described as *Antilope speciosa* may belong to *P. pallasi* or to some other species. It is not identifiable from the illustration, although Gaudry (1861a : 240; 1861b : 393) took it as the same species as *P. pallasi*.

In the Munich collection the upper dentition figured by Schlosser (1904, pl. 7 fig. 1) as *Palaeoryx majori* can perhaps be assigned to *P. pallasi*. The late joining up of the back of the front lobe of M^2 can be seen, and the incipient bilobing of P^3 is slightly less than it appears on the drawing. By the relative sizes of individual premolars this is slightly more likely to be *Palaeoryx* than a large *Miotragocerus*. The deciduous premolars and lower molar shown in pl. 7 figs 2 and 3 could be *P. pallasi*, but I would not identify them thus with certainty. The lower dentition of pl. 7 figs 4, 4a is more likely to belong to a *Miotragocerus* by the large size of its P_2 and the shallowness of the ramus. The Munich teeth assigned by Schlosser (1904, pl. 8 figs 3, 4, 5) to *Palaeoryx ingens*, supposedly differed from *P. pallasi* by their large size and molars with more angular crescents. The generic attribution is doubtful, but if it were correct there would be no reason to separate the teeth from *P. pallasi*. The basal pillars on the lower molars stand clear of the body of the tooth.

A large palate from Pikermi in London, BM(NH) M.11416, was figured by Pilgrim & Hopwood (1928, pl. 5 fig. 1, 1a) as *Palaeoryx woodwardi* var. *columnatus*, and is very large, as much so as AMNH 20587. As with the above specimens there is the difficulty of deciding whether it might be referable to a large *Miotragocerus* species.

A possible specimen of *Palaeoryx pallasi* teeth in New York is AMNH 20587 from quarry 5. It is a large palate in which the permanent premolars are just coming into wear. The molars have strong ribs between their parastyles and mesostyles such as exist in the *Palaeoryx pallasi* skull BM(NH) M.10831 and tapered and pointed medial lobes, the premolars are narrower than in *Criotherium*, there are no basal pillars, there are indentations into the rear central cavities of the M^2s; in no molars are the medial lobes joined to one another or to the lateral side of the tooth in its centre, and the infraorbital foramen is above the back of P^3. The P^4s are somewhat twisted in their sockets, a distortion also seen in the next palate below. The brachyodonty can be assessed from the measurements: height of mesostyle on little worn M^3 from the base of the enamel = 20·3 and length = 26·4 at the occlusal surface and 29·7 as the maximum at a lower level.

AMNH 20751 is another palate from quarry 4, with rather more worn teeth than the above. The left P^2 is absent (present in life), the left P^4 is twisted in its socket, and some molars are damaged. It is a smaller palate than 20587, P^2 may be relatively smaller and P^3 is certainly smaller than in 20587. Other characters are narrow and pointed medial lobes, no basal pillars, strong ribs between parastyle and mesostyle, no spurs into central cavities (at this stage of wear), mesostyles less marked (again at this state of wear), infraorbital foramen above back of P^3.

AMNH 20643 from quarry 1 is a very damaged palate; all teeth except the right P^2 have survived but only the left P^2 and right M^3 are undamaged. The teeth are well worn although the molars still have their central cavities. The basal pillars are small, and the left M^2 shows what was probably a strong rib between parastyle and mesostyle.

AMNH 86627 from quarry 1 is a palate in middle wear with all its teeth except the left P^2, but slight damage to some teeth. It is a little smaller than the previously mentioned fossils, and does not have strong ribs between parastyle and mesostyle. There are very small basal pillars on M^2 and M^3.

AMNH 86465 a left P^3–M^3 and 86570 a left upper molar from quarry 1 could also belong to *Palaeoryx pallasi*.

A number of fossils in Lausanne may belong to *P. pallasi*: a right rather worn maxilla, 519, a worn left mandible 411 with P_2–P_4 and the anterior part of the medial wall of P_4 closed, a left mandible 888 with P_3–M_1, a left mandible fragment 1095 with a broken M_1 and $M_2 + M_3$, and a right mandible fragment 1264 with M_2 and M_3. However the identity of the mandibles is not certain, and lower tooth characters were not included in the diagnosis of *Palaeoryx pallasi*.

There are also dentitions in the Münster collection which could belong to *P. pallasi*.

COMPARISONS. Bohlin (1935c : 138, text-figs 119–126) refers to *Palaeoryx sinensis* and *Palaeoryx* sp. from the Chinese lower Pliocene. He wrote that *P. sinensis* was so close to *P. majori* (here included in *P. pallasi*) that it could be the same species. The same would probably apply to *Palaeoryx longicephalus* Sokolov (1955 : 219, fig. 2) from the upper Miocene or lower Pliocene of Novocherkassk. We may conclude that the single species *P. pallasi* or a superspecies of which it was part was widespread in the lower Pliocene. *Sinoryx bombifrons* Teilhard de Chardin & Trassaert (1938, pl. 1 fig. 5, text-figs 37, 38) could also belong here; the pictures of it much resemble a crushed cranium of *Palaeoryx pallasi*, 1122, in Lausanne, except that its tooth row may be placed too posteriorly. *Palaeoryx athanasiui* Simionescu (1922 : 452; 1930 : 121, 145, text-figs 60–66, pl. 4 figs 2, 3, pl. 5 fig. 1) from the Romanian site of Mălușteni of Plaisancian age is later than other *Palaeoryx*. Its tooth row is also rather too posterior for it to be satisfactory as *Palaeoryx*, although its small central incisors support the idea of it as some kind of caprine.

Genus ***PROTORYX*** Major

1891a *Protoryx* Major : 609.
1892 *Protoryx* Major *in* Stefani, Major & Barbey : 94.

Type species. *Protoryx carolinae* Major, 1891a : 608.

Generic diagnosis. The type species is the only one here included in the genus. It is known only from Pikermi.

Protoryx carolinae Major

1865 Antilope d'espèce indéterminée. Gaudry : 289, pl. 52 fig. 1.
1891a *Protoryx carolinae* Major : 608.
1928 *Protoryx carolinae* Major. Pilgrim & Hopwood : 30, pl. 3 figs 1, 3.

Holotype. The cranium from Pikermi in Paris figured by Gaudry.

Locality. Pikermi.

Age. Lower Pliocene.

Diagnosis. Differs from *Palaeoryx pallasi* in its slightly smaller size. The skull is high and narrow rather than low and wide; horn cores are long, somewhat compressed in the medio-lateral plane, with a tendency to a flattened lateral surface, widest posteriorly, without keels, more uprightly inserted in side view than in *Palaeoryx pallasi* and appearing to insert less posteriorly, set closer together at their bases, not very divergent in anterior view, strongly curving backwards, horn core tips scarcely reapproach; sides of the braincase are more or less parallel; the braincase is narrow in dorsal view; orbital rims project moderately; the frontals are a little higher between the horn bases than are the orbital rims; the mid-frontals suture is not very raised; the mid-frontals and parieto-frontals sutures are not very complicated; supraorbital pits are set widely apart; the large ethmoidal fissure is not narrow (BM(NH) M.11415); zygomatic arch is deep anteriorly (BM(NH) M.11415); tooth row may be less anteriorly placed than in *Palaeoryx pallasi*; each half of the occipital surface tends to face partly laterally as well as backwards; basioccipital is narrow perhaps with a less clear central longitudinal groove than in *Palaeoryx pallasi*; moderately large auditory bulla. Tooth characters as in *Palaeoryx pallasi*.

REMARKS. The differences of *Protoryx carolinae* from *Palaeoryx pallasi* very largely amount to a narrower skull (Text-fig. 1) and associated features such as narrower, more uprightly inserted and backwardly curved horn cores. Otherwise, and particularly in its tooth characters, there is very little difference. The holotype cranium and left horn core in Paris and two skulls in London are all from Pikermi. The Paris specimen shows clearly that the frontals, including the horn pedicel, are hollowed, and is not preserved sufficiently far anteriorly to show the supraorbital pits.

Pilgrim & Hopwood (1928 : 32) provisionally assigned to *P. carolinae* a Samos skull with mandibles, atlas and axis vertebrae, BM(NH) M.4198. Bohlin (1936 : 3) rejected this identification, and I follow him. The braincase of this skull is hardly

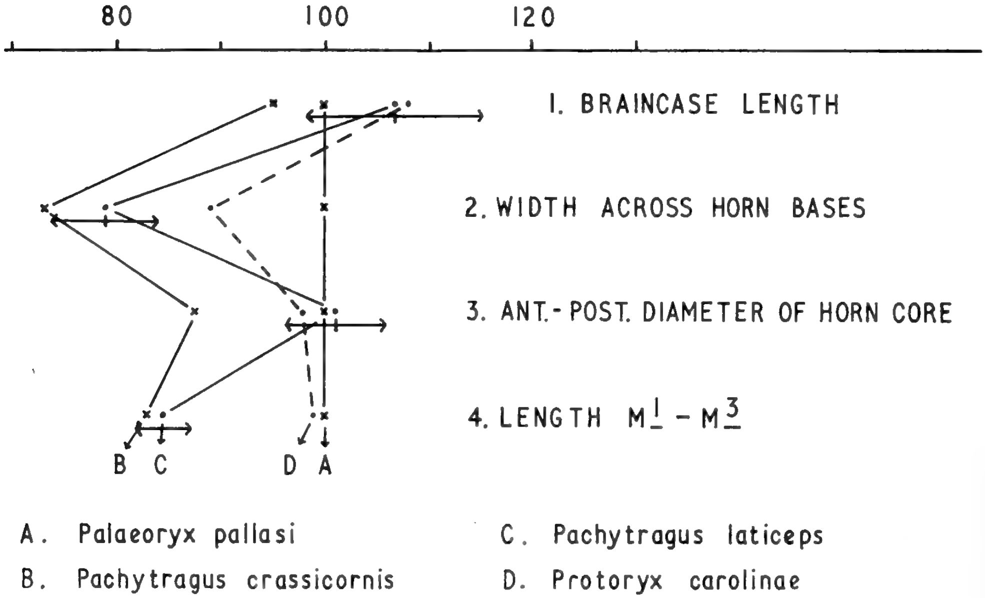

FIG. 1. Percentage diagram of the means of four measurements on skulls belonging to the *Palaeoryx-Pachytragus* group of antelopes. *Palaeoryx pallasi* has been used for the standard line at 100%; the mean readings for other species are expressed as percentages of the mean reading in *P. pallasi*. Both Pikermi and Samos specimens contribute to the readings for *P. pallasi*, and tooth measurements were taken only from identified skulls. The maximum numbers of readings for each species were: *P. pallasi* 11, *Protoryx carolinae* 3, *Pachytragus laticeps* 25, *P. crassicornis* 13, but the full number of readings was not available for every measurement. Horizontal lines show the extent of the standard deviations for *P. laticeps*. Note the slightly smaller size and narrow skull of *Protoryx carolinae* compared with *Palaeoryx pallasi*, the rather large horns in *Pachytragus laticeps* compared with *Protoryx carolinae*, and that the teeth of *Pachytragus crassicornis* are only a little smaller than in *P. laticeps*.

at all angled on the face axis, and I believe that it belongs to the Boselaphini. Along with a number of other skulls in various collections from Samos and Maragha, it is likely to be a species related to *Miotragocerus amalthea* but somewhat larger. *Prodamaliscus gracilidens* Schlosser (1904 : 29, pl. 4 fig. 6, pl. 6 fig. 4) may also have been this species, but the specimen was probably destroyed during the Second World War. Pilgrim & Hopwood (1928 : 30) had *P. carolinae* at Samos on the basis of Lausanne skulls 298 and 362, but Bohlin (1936 : 4) has already pointed out that 362 is a *Miotragocerus*, and I accept neither skull as *P. carolinae* (see p. 250 below). The Pikermi mandibles in London referred by Pilgrim & Hopwood (1928 : 32) to *P. carolinae* could well be of that species, but I would not be certain of the identification.

COMPARISONS. It is interesting that *Protoryx carolinae* shows some similarities to ?*Protoryx planifrons* from the Chinese lower Pliocene of Kansu described by Bohlin (1935c : 119, text-figs 88–91, pl. 15 fig. 5). It is not likely, so far as I can see, that ?*P. shansiensis* Bohlin (1935c : 123, text-figs 92–94) or ?*Protoryx* sp. (Bohlin 1935c : 125, text-figs 95, 96) are distinct species from ?*P. planifrons*. This Chinese species agrees with *Palaeoryx pallasi* and with *Protoryx carolinae* in being a large antelope, its supraorbital pits set widely apart, the parieto-frontals and mid-frontals sutures not very complicated, possibly a deep zygomatic arch anteriorly, the molar teeth not very hypsodont, with basal pillars and long premolar rows. In addition it resembles *P. carolinae* in the fairly upright horn core insertions, the relative height of the skull, and in the greatest width of the horn core section lying posteriorly, but a central longitudinal groove on the basioccipital and perhaps the divergence of the horn cores take it closer to *Palaeoryx*. With its especially massive horn cores and notably small supraorbital pits it must represent an East Asian development of the *Protoryx* stock unparalleled at more western sites. The skull M.1295 in Uppsala of ?*Protoryx shansiensis* has a thick parietal bone and an extremely small and narrow ethmoidal fissure.

There is no reason to suppose that the antelopes referred in the same paper to *Prosinotragus* and *Sinotragus* (Bohlin 1935c : 130, 133) are other than a more extreme development from the same ancestry as *Protoryx planifrons*. Their horn cores have become very short and thick, compressed with an anterior keel above, with a clockwise torsion in the right horn core, a short braincase much angled on the face, wide nasals, a quadrangular basioccipital, small foramina ovalia, and small to moderately inflated auditory bullae, but still a large preorbital fossa and rather unadvanced teeth. It is interesting that clockwise torsion in the right horn core has developed in this stock as well as in the smaller *Oioceros*. *Protoryx carolinae* could be an ancestor or a western ancestral-like member of this group. In this case the ultimate nomenclatorial procedure would be to extend the name *Protoryx* to the whole Chinese group, and not to sink a monospecific *Protoryx carolinae* in *Palaeoryx*.

Paraprotoryx founded by Bohlin (1935c : 126, figs 97–104) for other Chinese specimens with a fairly well rounded horn core section, is probably related to *Protoryx*.

Genus ***PACHYTRAGUS*** Schlosser

1904 *Pachytragus* Schlosser : 56.

Type species. *Pachytragus crassicornis* Schlosser, 1904 : 56.

Generic Diagnosis. Smaller than *Palaeoryx* or *Protoryx*; skulls are fairly narrow; horn cores are moderately long to long, medio-laterally compressed, more uprightly inserted even than in *Protoryx* and appearing to rise more directly above the orbits than in *Palaeoryx*, set closer together, little divergent, the widest part of their transverse section lying mid-way along their antero-posterior diameter, hollowed close to their bases; frontals are higher between the horn bases than in *Palaeoryx* or *Protoryx*; mid-frontals suture is rather raised; mid-frontals and parieto-frontals sutures are quite complicated; braincase has parallel sides or widens anteriorly; supraorbital pits are less small and less widely spaced than in *Protoryx carolinae*; nasals are long, domed and have a narrowly drawn out back suture; ethmoidal fissure is long and narrow; zygomatic arch has not deepened anteriorly; occipital surface is in two planes with each half facing partly laterally as well as backwards; basioccipital is narrow; foramina ovalia are small to moderate; auditory bullae are moderate to large; the ventral edge of the bulla may pass downwards posteriorly on to the front edge of the paraoccipital process, instead of rising to make the join.

The teeth are more hypsodont than in *Palaeoryx pallasi* or *Protoryx carolinae*; their enamel is only slightly rugose; basal pillars are very small or absent on upper molars and small on lower molars; there is no late joining of the medial lobes of the upper molars; the upper molars have a strong mesostyle with a tendency for the lateral wall behind to acquire a concave section; the rib between parastyle and mesostyle is not strong; medial walls of lower molars are little outbowed between the stylids; premolar row is short; styles are fairly strong on upper premolars; hypoconid of P_4 is quite pointed so that the lateral wall in front of it appears indented; metaconid of P_4 is rather bulbous in middle wear; paraconid of P_4 is not joined with the metaconid to close the anterior part of the medial wall; P^2 smaller than in *Palaeoryx pallasi* and *Protoryx carolinae*.

Contained species: *Pachytragus crassicornis* Schlosser, the type species.
Pachytragus laticeps (Andree).

Remarks. The most important difference of *Pachytragus* from the antelopes previously considered, and the one which principally justifies its generic rank and indicates the origin of a new adaptive zone (definition of Simpson 1953 : 201) is its advanced teeth. The diagnostic features of these teeth are illustrated in Text-fig. 5. A more stable support for the horn cores of *Pachytragus* is perhaps indicated by the decline of the anteriorly deepened zygomatic arch. *Pachytragus* as conceived here contains many specimens formerly placed in *Protoryx*.

Pachytragus laticeps (Andree)

1891a *Protoryx carolinae* (in part) Major : 608.
1891a *Protoryx longiceps* [nom, nud.] Major : 608.

1891a *Protoryx gaudryi* [nom. nud.] Major : 608.
1891a *Protoryx hippolyte* [nom. nud.] Major : 608.
1904 *Protoryx carolinae* Major. Schlosser : 45, pl. 9 fig. 8.
1904 *Protoryx* cf. *carolinae* Schlosser : 48.
1924 *Protoryx carolinae* Mecquenem : 33, pl. 5 figs 3, 4.
1926 *Protoryx carolinae* Andree : 151, pl. 12 figs 3, 3a, 4.
1926 *Protoryx carolinae* var. *laticeps* Andree : 153, pl. 12 figs 5, 9.
1926 *Protoryx hentscheli* Schlosser. Andree : 154, pl. 12 fig. 2, pl. 13 fig. 9.
1926 *Protoryx hentscheli* var. *tenuicornis* Andree : 155, pl. 12 fig. 6, pl. 13 fig. 2.
1926 *Protoryx crassicornis* Andree : 156, pl. 12 fig. 1, pl. 13 fig. 8.
1926 *Hippotragus kopassi* Andree : 158, pl. 15 figs 8, 10.
1928 *Protoryx longiceps* Pilgrim & Hopwood : 34, pl. 3 figs 2, 2a, pl. 5 figs 2, 2a.
1928 *Protoryx carolinae* var. *crassicornis* Andree. Pilgrim & Hopwood : 33.
1928 *Pseudotragus capricornis* var. *hippolyte* Pilgrim & Hopwood : 40.
1928 *Protoryx laticeps* Andree. Pilgrim & Hopwood : 36, pl. 4 figs 1–3.

HOLOTYPE. The skull in Münster figured by Andree (1926, pl. 12 figs 5, 9).

LOCALITIES. Samos, Maragha.

AGE. Lower Pliocene.

DIAGNOSIS. Horn cores are relatively larger than in *Protoryx carolinae*, moderately long, compressed medio-laterally, without keels, strongly curved backwards, sometimes more strongly bent back at the tips than lower down; orbital rims are narrow to moderately wide; braincase is sometimes long; median occipital ridge and its flanking hollows are frequently only poorly marked; the basioccipital has a central longitudinal groove.

REMARKS. The smaller size and relatively larger horn cores of *Pachytragus laticeps* than *Protoryx carolinae* can be seen in Text-fig. 1. The increased horn size must be linked with other differences from *Palaeoryx* and *Protoryx*, for instance that the horn cores have acquired more upright insertions and a more curved course in profile, thereby distributing their increased weight equally over each side of the occipital condyle-atlas pivot.

The illustrated paratype of this species is the Maragha skull BM(NH) M.3841. The Paris skull of *Pachytragus* from Maragha (Mecquenem 1924 : 33, pl. 5 figs 3, 4) also belongs here; its horn cores diverge about as much as in the holotype but are shorter. The back of the nasals is narrow, there is a long and narrow ethmoidal fissure, and the preorbital fossa lacks an upper rim.

Long-brained and short-brained varieties

In some examples, for which Pilgrim & Hopwood (1928 : 34) used Major's name *Protoryx longiceps*, the horn cores are larger, more medio-laterally compressed, less divergent and with tips which do not reapproach, the width across the top of the skull in the region of the horn bases is smaller, the braincase longer, the occipital surface higher and the median occipital ridge and its flanking hollows less marked. This is a more extreme change from the putative *Palaeoryx* or *Protoryx*-like ancestors. In the graphs of Text-figs 2–4 I have indicated by a separate symbol the specimens assigned by Pilgrim & Hopwood to the name *longiceps* as well as others which seemed to fit the criteria just mentioned. It can be seen that there is only imperfect separation from other *Pachytragus laticeps* in horn core compression, braincase length and relative narrowness across supraorbital pits and horn bases. It is probable that temporally or geographically separate natural populations have contributed to the *P. laticeps* material as it exists in museum collections today.

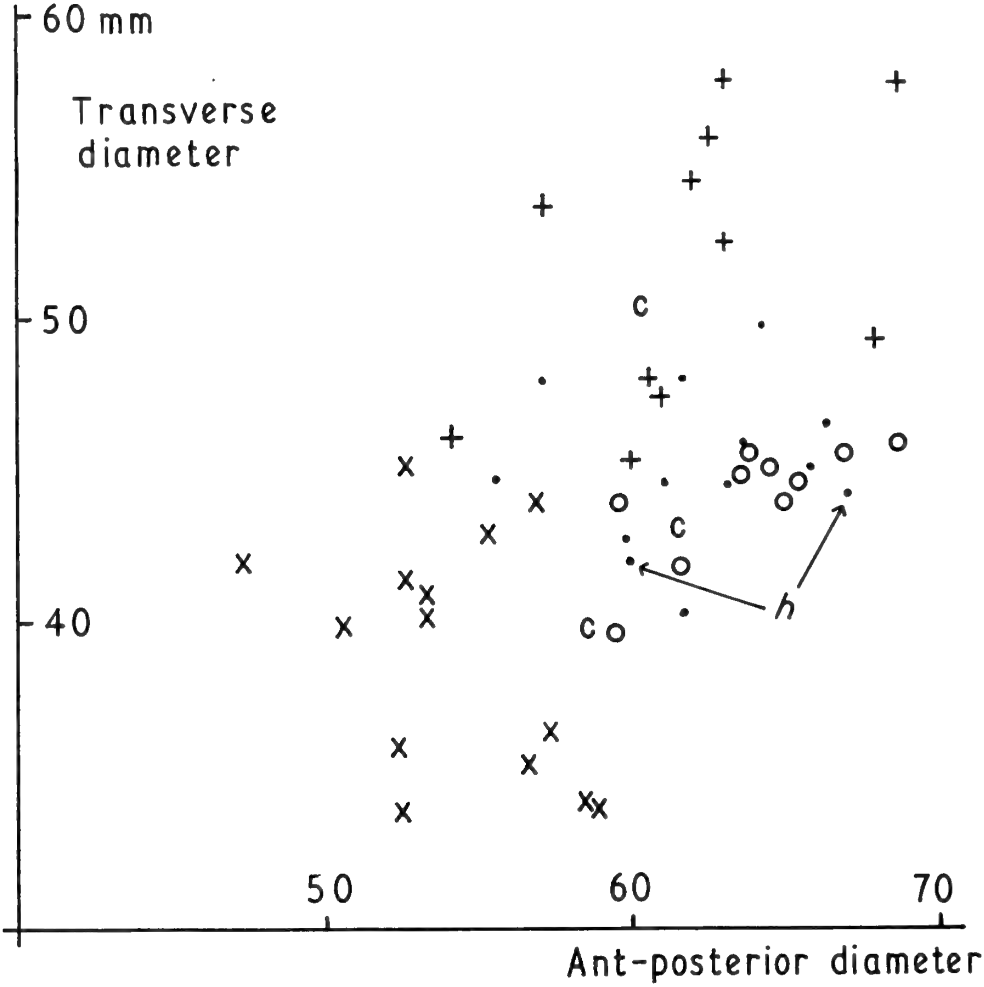

FIG. 2. Graph of horn core compression. The readings were taken at the base of the horn cores immediately above the pedicel. *Palaeoryx pallasi* has large and little compressed horn cores, those of other species are more medio-laterally compressed, and in *Pachytragus crassicornis* they are also smaller. + = *Palaeoryx pallasi*, c = *Protoryx carolinae*, · = *Pachytragus laticeps*, o = longer crania of *P. laticeps*, x = *P. crassicornis*, *h* = two Lausanne specimens of '*Protoryx* '*hippolyte*.

It is impossible to sort out the members of these original populations, and it would be unwise to assume that only two such populations have been sampled, one for each extreme of the range of variation. For this reason I shall not use the trivial name *longiceps* as a trinomial.

The means of some skull measurements, and their ranges, standard deviations and coefficients of variation for *Pachytragus laticeps* are shown in Table 2 on p. 258. Despite the inclusion of the long-brained individuals of this species, the coefficients of variation are generally less high than in the smaller sample of *Pachytragus crassicornis*.

The cranium with horn cores at Lausanne, 22, was that which Pilgrim & Hopwood (1928 : 28) believed Major had intended to be the holotype of *Protoryx longiceps*. The tips of its horn cores are not sharply bent backwards, the frontals above the left orbit are hollowed, the mid-frontals suture is not raised, the sides of the braincase are parallel or even widening anteriorly, the large mastoids are visible, the anterior tuberosities of the basioccipital are not large and flank a central longitudinal groove

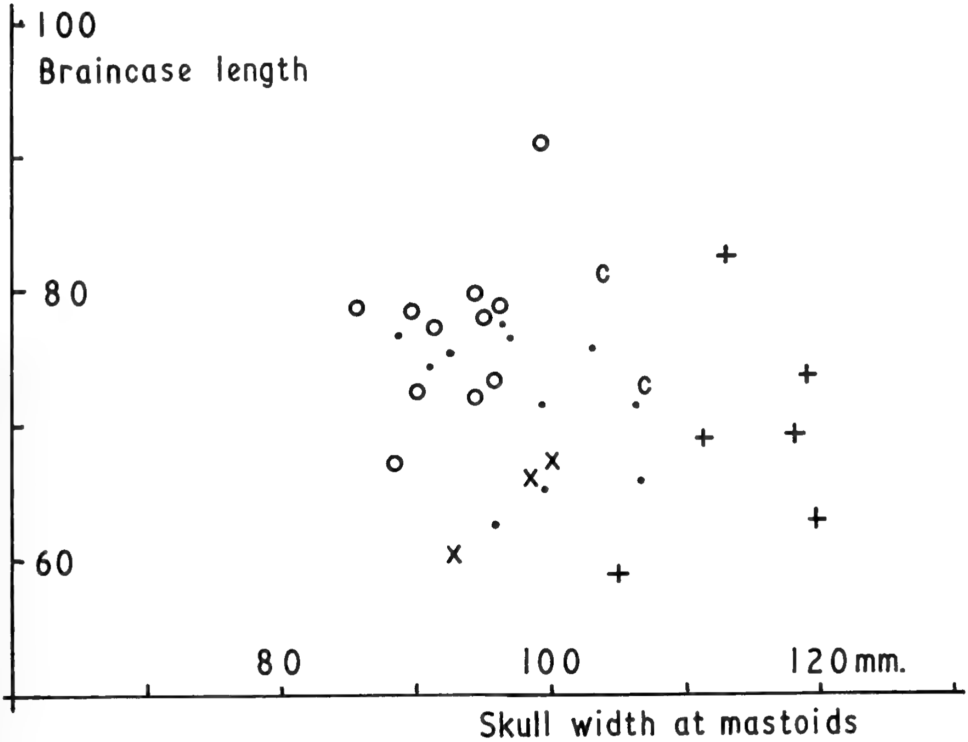

FIG. 3. Graph of braincase length against skull width across the mastoids. This graph indicates the size and relative narrowness of the cranium. Braincase length is measured from the mid-dorsal point of the parieto-frontals suture to the top of the occipital surface. Symbols as in Text-fig. 2.

(Pl. 2 figs 1, 2). The median vertical ridge on the occipital is not marked, but the left and right sides of the bone face partly laterally. The Lausanne cranium 26 is very similar except for the more localized raising of its frontals between the horn bases.

Protoryx carolinae of Schlosser (1904 : 45) is a long-brained *Pachytragus laticeps*. The braincase is parallel sided and there is a large mastoid. The face fragment used in his pl. 9 fig. 8 cannot be fitted to the cranium; in fact a part of the posterior end of the face is not shown in the illustration.

Examples of long-brained *P. laticeps* in the American Museum of Natural History are as follows. 20612 from quarry 1 is a cranium with lower parts of the horn cores in which the apparent length of the braincase may have been increased by the use of plaster. 20621 also from quarry 1 is a cranium with lower part of the right and almost complete left horn core; it is the only New York specimen with an auditory bulla and the bulla shows the downward connection to the front of the para-occipital process. It also has small to moderate-sized foramina ovalia. 20645 from quarry 1 is a cranium with horn cores. 20649 from quarry 1 is a frontlet with lower parts of horn cores. 20690 from quarry 1 is a cranium with well preserved horn cores showing abrupt bending back of the tips. 22783 from block H in quarry 1 is a cranium with the right horn core and part of the left; the left one was sectioned approximately 20 mm above the pedicel top and showed spongy central parts (Pl. 2 fig. 4). 23037 from quarry 4 is a cranium with complete horn cores, bent

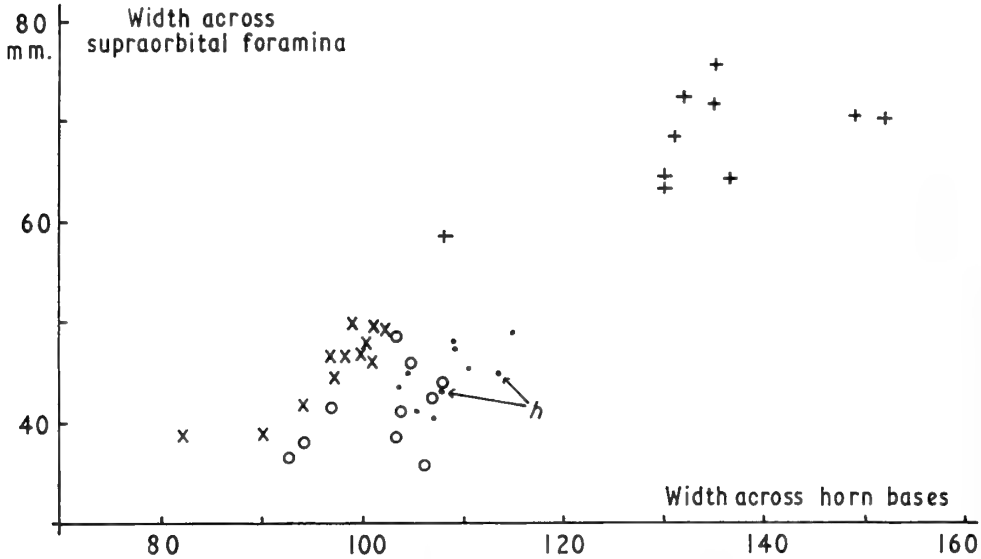

Fig. 4. Width across supraorbital foramina compared with width across narrowest part of lateral walls of horn pedicels. Symbols as in Text-fig. 2. Among *Pachytragus* it is *P. crassicornis* which has the widest separation of supraorbital foramina, and is closest to later goats.

back at their tips. 23038 from quarry 1 is a cranium with the lower parts of its horn cores. The right one was sectioned at about 10 mm above the pedicel top and showed a clear central hollowing (Pl. 2 fig. 3).

The Lausanne cranium 20453 has rather a long braincase, and also has a hollowing at the base of its left horn core.

Andree's *Hippotragus kopassi* in Münster is also rather long-brained. It has a narrow ethmoidal fissure, parallel sides of its braincase, small foramina ovalia, the ventral edge of its auditory bulla rises posteriorly where it meets the paraoccipital process, and it has preserved its dentition and rather high face. Andree (1926 : 158, 159) used this skull to show the closeness of *Hippotragus* to his *Protoryx* group of the Pseudotraginae (=*Pachytragus* as used in this paper). The narrow and high face, strong bending of the braincase on the face, and the high insertions of the large transversely compressed horn cores impressed him as distinctive characters, but it did not appear to me that any substantial difference existed between this skull and other *Pachytragus laticeps*.

The holotype cranium of *Pachytragus laticeps* does not have a particularly long braincase. It has parallel sides of its braincase, and the ventral edge of the left auditory bulla descends to meet the front edge of the paraoccipital process.

A well preserved *P. laticeps* skull on public exhibition in the Natural History Museum in Basle is an excellent example of the shorter-brained form of this species. Its horn cores approach having an anterior keel in the middle of their course. Although the M^1s have already lost their central cavities, there are indications of transverse ridges across the dentine of the molars' occlusal surfaces, which suggests use of the cheek teeth in a way similar to goats and sheep.

The shorter-brained Lausanne cranium 201 (Pilgrim & Hopwood 1928, pl. 4 figs 1, 1a) is a *P. laticeps*, but the lack of a central longitudinal groove on its basioccipital makes it more like the species to be described next. Its occipital surface is lower and wider than in the long-brained Lausanne cranium 22, and the sides of its braincase are parallel. A Lausanne frontlet 28 (Pilgrim & Hopwood 1928, pl. 4 fig. 2) has no anterior keels and rather diverging horn cores, and is probably from a shorter-brained *P. laticeps*.

I have not seen the material of *Protoryx* cf. *carolinae* of Schlosser (1904 : 48), but I include it with the shorter-brained *Pachytragus laticeps*, following his description and Pilgrim & Hopwood's (1928 : 36) placing.

The shorter-brained Münster skull which Andree (1926 : 156, pl. 12 fig. 1, pl. 13 fig. 8) called *Protoryx crassicornis* shows quite compressed horn cores with large bases, a high face, a braincase widening slightly anteriorly, moderate-sized foramina ovalia, and a moderately-developed median occipital ridge and flanking hollows. The illustration in front view shows reapproaching horn core tips, now lost. The differences which Andree noted from other skulls here included in *Pachytragus laticeps*, valid as they may be between individuals, do not carry the skull beyond the morphological range within which it could be considered conspecific. There was certainly no reason for Pilgrim & Hopwood (1928 : 33) to link this skull with *Protoryx carolinae* which they had principally built around Pikermi specimens, for this skull is smaller, its horn cores insert more uprightly, and the teeth are like those of other Samos skulls. Andree's own text (1926 : 156) emphasizes this point about the teeth.

Shorter-brained *Pachytragus laticeps* in the American Museum of Natural History are the following. As with the long-brained variety, none come from quarry 5. 20674 from quarry 1 is a cranium with left horn core strongly bent back at its tip and with the lower part of the right horn core. 20691 from quarry 1 is a cranium with the lower parts of both horn cores. 20707 from block E in quarry 1 is a partly cleaned skull without the front of its face. Both its horn cores are broken at the level of the top of the pedicel and hollowed internally. The long narrow ethmoidal fissures and back part of the nasals are visible. 20770 from 100 yards west of Mytilini village is a cranium with horn core bases. 20777 from 100 yards west of the same village is a rather small left horn core with an inwardly deflected tip. 22857 from quarry 4 is a cranium with horn cores. 86580 is a frontlet with horn cores, and it is labelled 'block Y' but without a quarry number. 86583 of unknown quarry is a damaged cranium with horn cores broken at their bases and clearly hollowed.

I have not been able to assign all *P. laticeps* to the shorter or longer brained varieties. Doubtful specimens in New York are 20609 from quarry 1 which is a face without premaxillae or the right nasal but showing the lachrymal and jugal sutures, 20598 from quarry 1 a cranium with horn core bases, 20673 from quarry 1 the base of a right horn core and a left horn core with skull fragments, 20778 and 20779 two frontlets with horn core bases from 100 yards west of Mytilini, and 86450 a frontlet with horn cores. The Lausanne frontlet 27 is another doubtful specimen.

Other skulls and crania

The Lausanne cranium 298 is interesting; it was labelled as *Protoryx gaudryi* by Major and referred to *P. carolinae* by Pilgrim & Hopwood (1928 : 30). It is considerably damaged and has been repaired with glue and plaster; it agrees with the species to be described next in its keels and diverging horn cores, but is rather large and has a wide shallow longitudinal groove on its basioccipital. No measurements could be taken because of the damage.

The other Lausanne cranium, 362, which they also referred to *P. carolinae* belongs to *Miotragocerus* as shown by its temporal ridges with rugose surface in between, the occipital surface in one plane only, the horizontal top edge of the occipital in rear view, rather narrow mastoids, and large foramina ovalia.

The most difficult specimen to assess at Lausanne is the cranium, 30, of '*Protoryx hippolyte*' (Pl. 3 figs 1, 2), referred to as a variety of Schlosser's *Pseudotragus capricornis* by Pilgrim & Hopwood (1928 : 40). However it is too large to belong to that species, does not show the relatively very large horn cores of the presumed male skull, and the supraorbital pits are set closer together. At first sight it appears that the braincase is little bent on the face axis but this is probably due to distortion, the back of the braincase having been pushed forwards against the horn bases. There is strong medio-lateral compression of the horn cores, their divergence increases evenly towards the tips, and they appear rather uprightly inserted in side view. Their appearance of having been short and having had an anterior keel may result from damage caused by weathering. The *Pachytragus* skull in Basle shows that the angle of the parietal to the occipital surface here is not too small for *P. laticeps*. The occipital surface is low and wide as in most *P. laticeps*, and it has a weak median ridge without hollows on either side. The front of the basioccipital is missing but there was a well marked central longitudinal groove. From these characters and its size this specimen can be provisionally included in *P. laticeps*.

Another Lausanne specimen, the frontlet 31, much resembles the cranium just discussed.

Protoryx hentscheli was founded by Schlosser (1904 : 49) on teeth of *Pachytragus*. The syntypes in Munich were supposed to differ from teeth of '*Protoryx carolinae*' (=*Pachytragus laticeps* as used here) by weaker styles and ribs on the molars, smaller premolars, the anterior position of the vertical indentation on the lateral side of P_3 and P_4, the weaker indentation on the medial lobes of P^2 and P^3, and the weaker development of medial cusps on P_3 and P_4. These, and other differences mentioned by Pilgrim & Hopwood (1928 : 38) seem valid only between individuals. It is impossible to assign the teeth specifically; that they belong to *Pachytragus* is all I would be prepared to say. The name *Protoryx hentscheli* was subsequently extended by Andree to a nearly complete skull, and the name *P. hentscheli* var. *tenuicornis* to a cranium, both in Münster. The nearly complete skull is very interesting in that it shows some characters divergent from other *Pachytragus*: frontals only a little raised between horn bases, rather a low face, the tooth row set rather anteriorly; all this recalls *Palaeoryx pallasi*. Otherwise it appears to be an example of the normal fairly short brained *P. laticeps* with horn cores diverging in the middle of their course and reapproaching towards the tips. The cranium of var. *tenuicornis* agrees with the above skull in what characters are available, and its broken left horn core shows a hollowed pedicel. Although these skulls are an apparently primitive variation of *Pachytragus laticeps*, I do not consider them worth naming, and certainly there is no case for applying to them Schlosser's specific name *hentscheli*, based on indeterminate teeth. They illustrate what an early form of *Pachytragus* could have been like. I have retained these two pieces within *P. laticeps*, and have not supposed that they belong to an actual ancestral species. They suggest that *Pachytragus* could derive from *Palaeoryx* or a *Palaeoryx*-like ancestor, perhaps some antelope not dissimilar to *Protoryx carolinae*.

A skull from Salonica assigned to *Protoryx carolinae* by Arambourg & Piveteau (1929b : 105, pl. 7 fig. 6, 6a) probably belongs to this species. Its closely inserted horn cores are without keels, the brain widens anteriorly in dorsal view, temporal lines are wide posteriorly, the nasals are narrowly drawn out posteriorly and have no lateral flanges anteriorly, and large premaxillae rise with even width to a definite contact with the nasals. These characters at the front of the face are probably common to the whole genus *Pachytragus*, if not to *Palaeoryx* and *Protoryx* as well.

A female skull

In the New York collection is a *Pachytragus* skull with small horn cores, 20687 from quarry 1 (Pl. 3, fig. 3). It is presumably a female. It is complete except for premaxillae, most of the nasals, a part of the left postorbital bar, and the right postorbital bar and zygomatic arch. The horn cores are of very small basal diameter (30·2 × 22·0, right), somewhat medio-laterally compressed, set rather obliquely and with a concave front edge in profile, inserted close together and diverging little in anterior view. Connected with the smallness of the horn cores is the strong slope of the orbital rims. The preorbital fossa is only shallow (they are normally smaller in females), neither supraorbital pits nor infraorbital foramina are visible, the frontals between the horn bases are hardly higher than the orbital rims, the maxilla is deep above the tooth row, and the occipital surface is clearly in two planes. The skull's provenance in quarry 1 would seem to rule out its assignation to *P. crassicornis*. An awkward question is why there are no other female skulls in any Samos collections. A left horn core AMNH 20777 is very like a horn core of *P. laticeps* and is an alternative candidate for representing females among the fossils. Its basal diameters are about 49 × 38 mm.

Tooth characters and individual dentitions

The teeth of *Pachytragus laticeps* may easily be told from those of *Palaeoryx pallasi* and *Protoryx carolinae* by their smaller size and advanced morphology. Smaller size distinguishes them from the unnamed large *Miotragocerus* represented by AMNH 23036, BM(NH) M.4198 and other specimens, and their advanced characters from all *Miotragocerus*. Teeth of *Miotragocerus* are less hypsodont, they retain larger basal pillars (*a*) and a later joining together of the medial lobes of the upper molars (*b*), the mesostyle on the upper molars is less marked (*c*), the medial walls of the lower molars are more outbowed between the stylids (*d*), the premolar row is longer and anterior premolars larger, hypoconid of P_4 is not pointed (*e*), metaconid of P_4 is less bulbous but has a large backwardly turned medial flange (*f*), and the paraconid of P_4 is larger relative to the parastylid (*g*). The characters indicated by letters (*a*) to (*g*) are illustrated in Text-fig. 5, and a *Pachytragus* palate is photographed in Pl. 4 fig. 2.

Very many upper and lower dentitions of *Pachytragus* are known, and I will comment only on previously misidentified specimens. The teeth shown by Schlosser (1904, pl. 9) may all be taken as belonging to either this species or the next. The teeth of pl. 9 figs 2, 3, 5, 6 and 7 had been used to establish the species *Protoryx hentscheli*, supposedly having weaker ribs and styles, rounded inner lobes, a large metastyle on M^3, a triangular rear lobe of M_3, and rugose enamel. These characters, in so far as they are detectable at all, are inadequate to remove the teeth from assignation to *Pachytragus laticeps* or to the next species. Since it is doubtful which of the two they belong to, I have not listed *P. hentscheli* as of Schlosser (1904) among the synonyms of *P. laticeps*. Skulls which Andree later assigned to *P. hentscheli* have been included in *P. laticeps*.

The right upper dentition 578 in Lausanne, listed by Major (1894 : 35) as '*Protoryx* sp.' is really a *Miotragocerus*.

Pachytragus crassicornis Schlosser

1904 *Pachytragus crassicornis* Schlosser : 56, pl. 11 fig. 11.
1926 *Palaeoryx* cf. *stützeli* Andree : 162, pl. 14 figs 1–3.
1926 *Pseudotragus longicornis* Andree : 147, pl. 10 figs 2, 3.
1926 *Pseudotragus capricornis* Schlosser. Andree : pl. 13 fig. 7.
1926 *Pachytragus schlosseri* Andree : 148, pl. 12 fig. 7, pl. 13 fig. 3.

LECTOTYPE. The frontlet described and figured by Schlosser (1904 : 56, pl. 11 fig. 11) was designated by Pilgrim & Hopwood (1928 : 43). *Pachytragus crassicornis* is the type species of its genus.

LOCALITY. Samos.

AGE. Lower Pliocene.

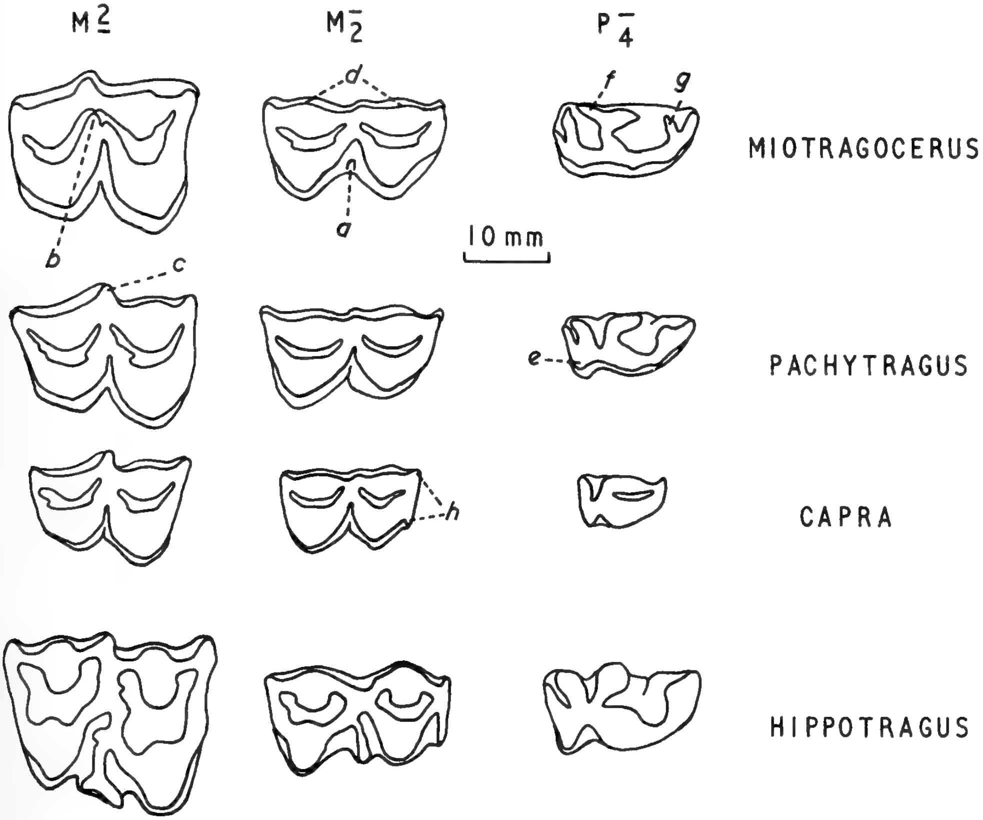

FIG. 5. Occlusal views of cheek teeth of the right side, their anterior edges being towards the right. Explanation in text, p. 252, and *h* = goat fold.

DIAGNOSIS. Smaller than *Pachytragus laticeps*; horn cores are slightly smaller and shorter, often more medio-laterally compressed, with an anterior keel, insertions less upright than in *P. laticeps* but more than in *Protoryx carolinae,* divergence greater and increasing toward the tips instead of tending to reapproach at the tips, less curved backwards in side view; orbital rims are rather wide; braincase top is fairly long and set at a steeper angle to the occipital surface; tooth row set more posteriorly than in *Palaeoryx pallasi*; median occipital ridge is often prominent and with deeper flanking hollows; basioccipital has fairly localized anterior tuberosities and thus little development of a central longitudinal groove; teeth are no smaller than in *P. laticeps* despite the overall size reduction.

REMARKS. By its smaller overall skull size unaccompanied by any substantial diminution of tooth size *P. crassicornis* is evidently adapted to a harsher environment than *P. laticeps.* It differs additionally from that species by its shorter less backwardly curved horn cores with anterior keels, and the tooth row is now definitely placed rather posteriorly. Profile views of this species in comparison with others are shown in Text-fig. 6, anterior views of horn cores in Text-fig. 7, and sections across horn cores in Text-fig. 8.

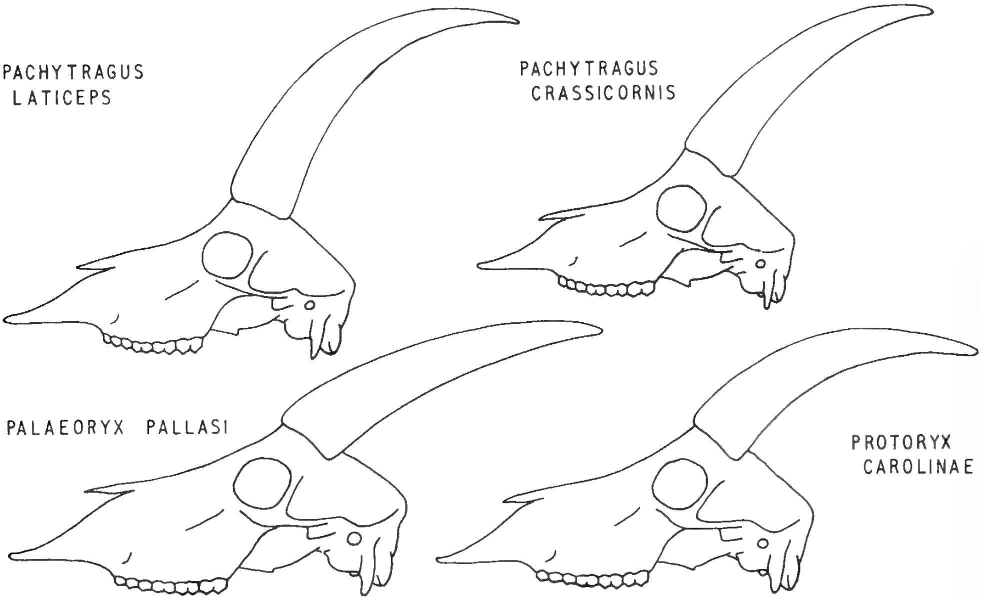

FIG. 6. Reconstructions of side views of skulls of *Palaeoryx*, *Protoryx* and *Pachytragus*. The figures are in scale with one another. Notice the inclination and curvature of the horn cores and deep anterior part of the zygomatic bars in *Palaeoryx pallasi* and *Protoryx carolinae*; the anterior positioning of the tooth row in *Palaeoryx pallasi*; that the teeth of *Pachytragus crassicornis* have not diminished below the size of those of *P. laticeps*; and the differing inclinations and curvatures of their horn cores.

The lectotype of *Pachytragus crassicornis* Schlosser (1904 : 56, pl. 11 fig. 11) shows strong bending of the braincase on the face axis (the appearance of this being exaggerated by distortion), the orbital rims would have been wide when complete, and the upper parts of the right horn core are sufficiently preserved to show the anterior keel.

Individual skulls and crania

The following specimens in the American Museum of Natural History are all from Brown's quarry 5 with one exception. 20567 is part of a skull with braincase, right horn core, part of the right side of the face, the right P^3 to M^3 and the left P^4 to M^3. 20568 is a more or less complete skull lacking only the front of its face; it has the left P^2 to M^3 and the right P^3 to M^3, and a long and thin ethmoidal fissure. 20569 (Pl. 4 fig. 1) is most of a skull lacking parts of the right orbit, nasals, premaxillae and parts of the basioccipital; it has the right P^3 to M^3 and left P^2 to M^3. 20579 is another more or less complete skull, lacking only nasals and premaxillae; it is probably the best preserved skull of the species in existence. The ethmoidal fissures are long and thin, and the teeth present are the right P^2 to M^3 and the left M^1 to M^3. 20708 is from quarry 1 but agrees better with *P. crassicornis* than with *P. laticeps*; it is a cranium without the right horn core or parts of the lower occipital surface. 22938 is a cranium with both horn cores intact. 22939 is a cranium with both horn cores. 22940 and 22943 are frontlets with most of the right horn core and part of the left. 22948 is a damaged cranium with a somewhat distorted right

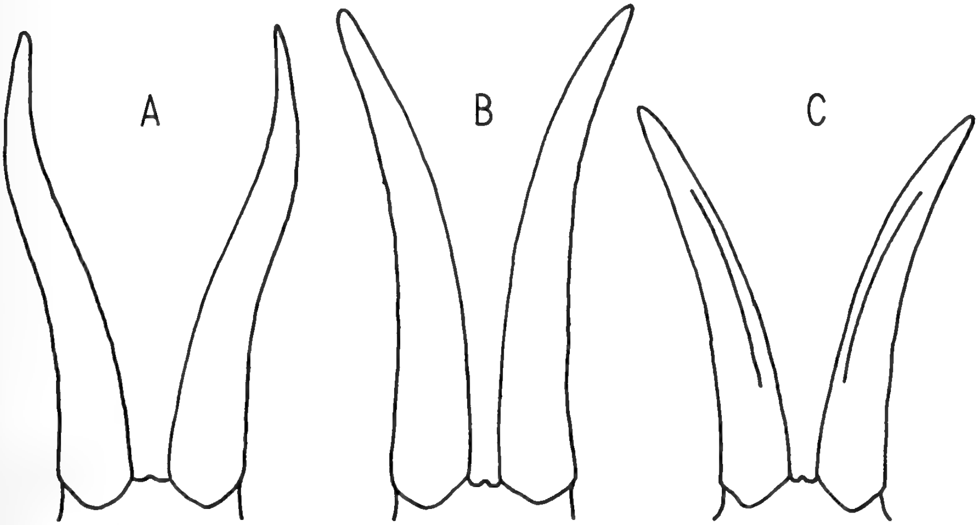

FIG. 7. Anterior view of the horn cores of (*A*) *Pachytragus laticeps*, (*B*) long-brained variety of *P. laticeps*, (*C*) *P. crassicornis*. The figures are in scale with one another. Notice in (*B*) compared with (*A*) that the horn cores are larger, less divergent, and with tips which do not reapproach. *P. crassicornis* has anterior keels.

horn core and part of the left one. 22949 is a cranium with horn cores on which part of the left preorbital fossa is visible.

A number of other named specimens in European museums can best be placed in this species, although their inclusion widens the range of variation within the species. As with the long-brained examples of *P. laticeps*, no conception of what was happening to the species in time can be hoped for without more geological knowledge of the Samos deposits. The first of these specimens is the skull of *Pseudotragus capricornis* in Münster described by Andree (1926 : 146, pl. 13 fig. 7) but not conspecific with the skull for which Schlosser (1904 : 51, pl. 10 figs 7, 8) had first used the name. Andree's specimen shows short medio-laterally compressed horn cores diverging from one another and with anterior keels, the braincase probably widening anteriorly, but the basioccipital not clearly with less developed longitudinal ridges behind the anterior tuberosities than in *Pachytragus laticeps*. There is a slight tendency towards transverse wear ridges across the dentine of the upper molars as in goats and sheep. I have not seen the Stuttgart skull fragment which Andree refers to (1926 : 146) under this name, but the Münster one differs from *Pseudotragus capricornis* by its greater size, anterior keel, and relatively larger teeth and face.

The almost complete skull of *Pachytragus schlosseri* Andree (1926 : 148, pl. 13 fig. 3) is in Vienna and is certainly rather small. It has been much restored with

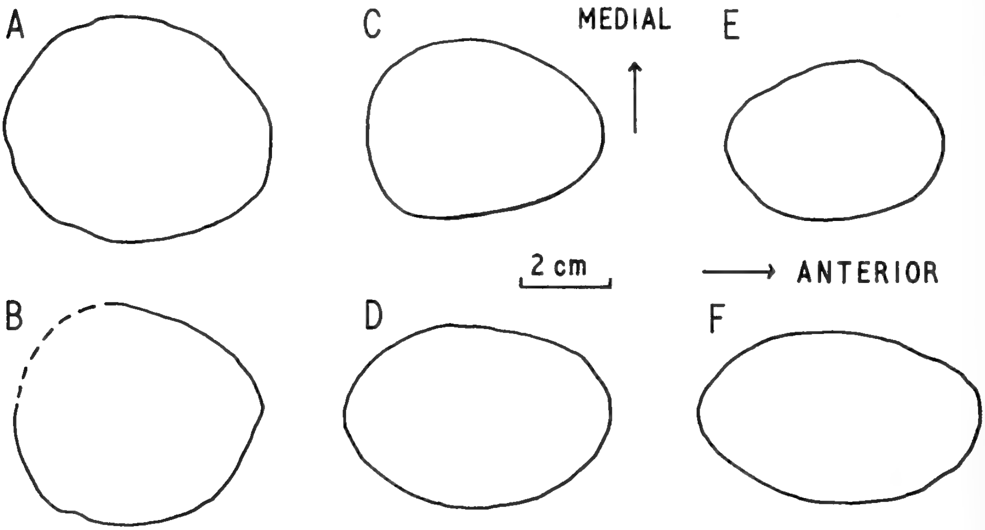

FIG. 8. Sections of right horn cores taken at a distance above the pedicel top equal to half the antero-posterior diameter at the base of the horn core. A = *Palaeoryx pallasi* from Samos figured by Schlosser (1904, pl. 7 fig. 5); B = *Megalovis latifrons*, a left horn core (Se 1483) in Basle reversed for this drawing; C = *Protoryx carolinae* BM(NH) M.11415; D = *Pachytragus laticeps*, a skull in Basle; E = *P. crassicornis* AMNH 22938 reversed for this drawing; F = the long brained variety of *P. laticeps* AMNH 23037.

plaster on the alisphenoid flanges, the right zygomatic bar, the top of the postorbital bars, and the top of the occipital surface. It is the restoration of the top of the postorbital bars which has given a wrong impression of narrow orbital rims. Also in the dentition picture (Andree 1926, pl. 14 fig. 4) the large metastyle of M^2 should have been shown as the parastyle of M^3. The horn cores are somewhat compressed, their triangular cross section as shown by Andree does not extend much above their base, they are quite strongly divergent in anterior view, there is a small ethmoidal fissure, the small and shallow preorbital fossa has a trace of an upper rim, the infraorbital foramen is high above the front of P^3 on the left and the back of P^3 on the right, and the median indentation at the back of the palate is behind the level of the lateral ones. The skull is probably closer to this species than to *P. laticeps* by its rather small size, latero-medial compression of horn cores without reapproach of the tips, and the quite strong divergence of the horn cores. But the horn cores lack keels, and the condition of the occipital surface cannot be clearly seen.

The cranium in Münster assigned to *P. schlosseri* by Andree (1926, pl. 12 fig. 7) is similarly difficult to assign. It has no anterior keel on the horn cores, but it does have divergent short horn cores, and the frontals between the horn cores are well raised. The braincase probably widened anteriorly.

Pseudotragus longicornis of Andree (1926, pl. 10 figs 2, 3) is in Vienna. The lateral surface of its horn cores is somewhat flattened, the back of the nasals is just a little in front of the level of the front of the orbits, the moderate sized preorbital fossa has a slight upper rim, the infraorbital foramen is above the front of P^3. It is like *Pachytragus crassicornis* in its small size, strong medio-lateral compression higher up its horn cores with which is linked the tendency to an anterior keel, and the shape of the anterior tuberosities of the basioccipital with barely any central longitudinal groove. The lesser divergence of the horn cores, and their backward

TABLE I

	Antero-posterior diameter of horn core	Latero-medial diameter of horn core	Minimum width across lateral sides of horn pedicels	Width across lateral edges of supraorbital foramina	Length M^1–M^3	Length P^2–P^4
Pseudotragus capricornis (Andree pl. 13 fig. 7)	52·6	33·7	—	39·8	55·1	—
Pachytragus schlosseri (Andree pl. 13 fig. 3)	47·3	42·0	101·4	49·7	56·6	39·3
Pachytragus schlosseri (Andree pl. 12 fig. 7)	56·8	43·9	98·3	46·4	—	—
Pseudotragus longicornis (Andree pl. 10 figs 2, 3)	52·7	45·2	97·0	c.46·5	53·5	38·1
Palaeoryx cf. *stützeli* (Andree pl. 14 figs 1, 3)	55·3	43·0	97·3	c.44·3	—	—

curvature are more like *P. laticeps*, but in the width of its orbital rims and the hollowings of the occipital surface the Vienna animal is intermediate.

The frontlet in Vienna which Andree assigned to *Palaeoryx* cf. *stützeli* agrees well with his specimens of '*Pseudotragus longicornis*' and '*Pachytragus schlosseri*'. It is not conspecific with the example of *Palaeoryx stützeli* Schlosser (1904, pl. 8 fig. 6) in Munich which is a *Sporadotragus*; this specimen is of a larger animal, it lacks the anterior surface on its horn cores and has less extreme bending down of the face on the braincase. The orbital rims are moderately to strongly projecting, the lateral surface of the horn cores is a little flattened, and there is possibly an approach to having a keel higher up on the right, but it is too damaged to be certain.

Those skulls described by Andree which I believe to be *Pachytragus crassicornis* have the following measurements shown in Table 1 on p. 257, which I made myself and used in the Text-figures.

Some skull measurements for *Pachytragus crassicornis* are shown in Table 2 below. Coefficients of variation are rather high in comparison with the low numbers of measured individuals; this is because of the difficult skulls just discussed.

TABLE 2

	Number measured	Mean	Range	Standard deviation	Coefficient of variation
Antero-posterior diameter of horn core at base	10	62·3	54·2–68·7	4·08	6·55
	23	62·9	57·0–68·9	2·99	4·75
	13	54·1	47·3–58·7	3·34	6·17
Latero-medial diameter of horn core at base	10	51·6	45·3–57·9	4·90	7·55
	24	44·5	35·4–49·8	3·34	7·52
	13	38·7	33·5–45·2	4·02	10·40
Minimum width across lateral surfaces of horn pedicels	11	133·5	108·2–152·0	11·33	8·49
	21	105·6	94·4–123·6	6·71	6·36
	10	97·7	82·2–102·5	5·95	6·09
Width across lateral edges of supraorbital pits	10	68·1	58·6–75·9	5·23	7·68
	21	43·0	36·5–49·0	3·73	8·77
	13	45·6	38·6–49·8	3·56	7·80
Braincase length from back of frontals to top of occipital	10	69·5	59·2–82·8	7·13	10·26
	17	75·5	65·3–91·2	5·89	7·81
	6	66·8	60·1–75·3	5·13	7·69
Skull width across mastoids behind auditory meatus	6	114·3	105·0–119·8	5·72	5·01
	22	95·4	85·8–106·8	5·60	5·87
	5	93·5	85·7–100·3	6·10	6·52
Length M^1–M^3	6	67·6	61·9–69·9	3·00	4·44
	18	57·6	54·4–61·0	1·84	3·19
	15	56·8	53·5–60·6	2·12	3·74
Length P^2–P^4	4	50·1	46·2–52·6	—	5·62
	9	38·0	35·1–41·9	2·13	5·60
	9	37·2	34·0–39·3	1·60	4·29

For each measurement the top line shows the readings for *Palaeoryx pallasi*, the middle line for *Pachytragus laticeps*, and the last line for *P. crassicornis*.

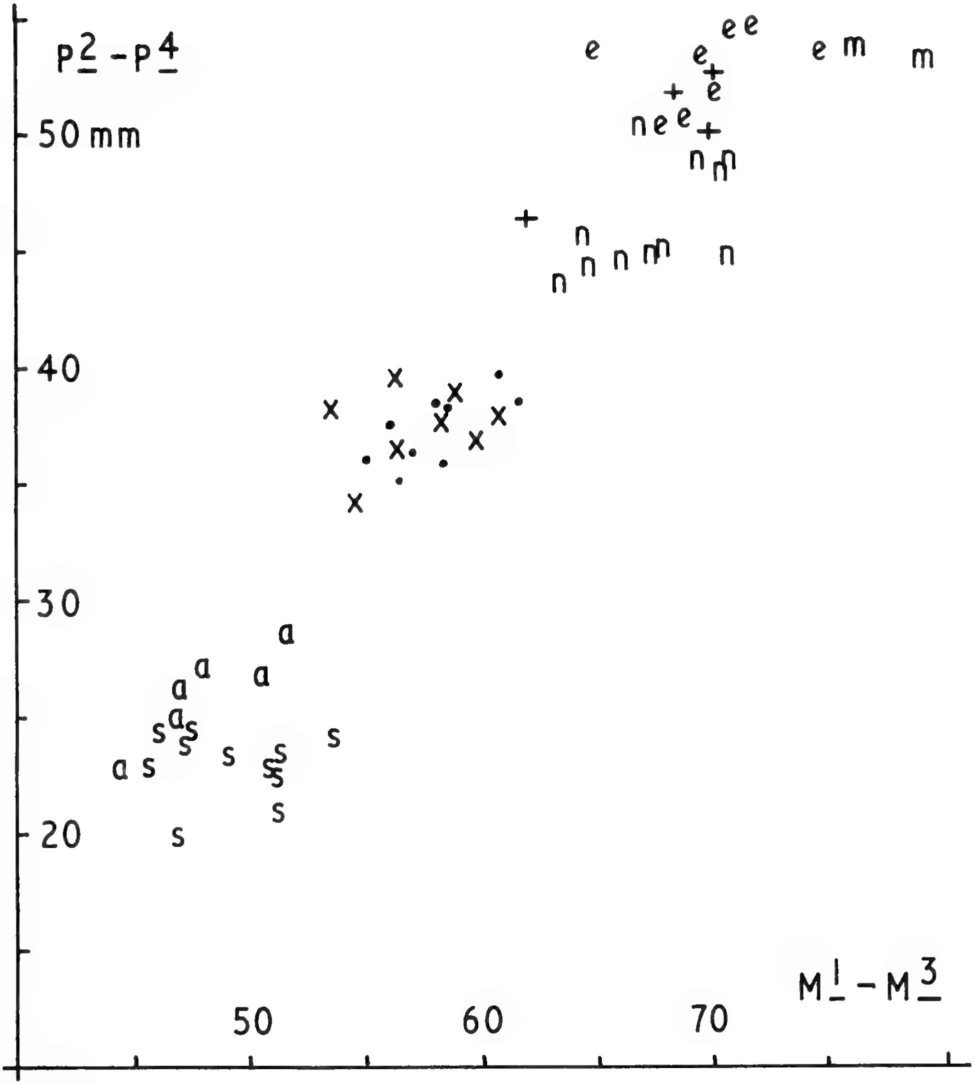

FIG. 9. Graph of the length of the upper premolar row plotted against length of upper molar row. Symbols as in Text-fig. 2 except that no separate symbol is used for the long brained *Pachytragus laticeps*, e = *Hippotragus equinus*, n = *H. niger*, s = *Capra sibirica*, a = *C. aegagrus*, and m = *Megalovis latifrons*. Tooth measurements were taken on identified skulls, and in addition one *Pachytragus* dentition from Brown's quarry 5 in New York was taken as *P. crassicornis* and four from quarries 1 and 4 as *P. laticeps*. Notice that the two *Pachytragus* species have the same size and proportions despite the smaller overall size of *P. crassicornis*. *Megalovis latifrons* has a slightly shorter premolar row than does *Palaeoryx pallasi*.

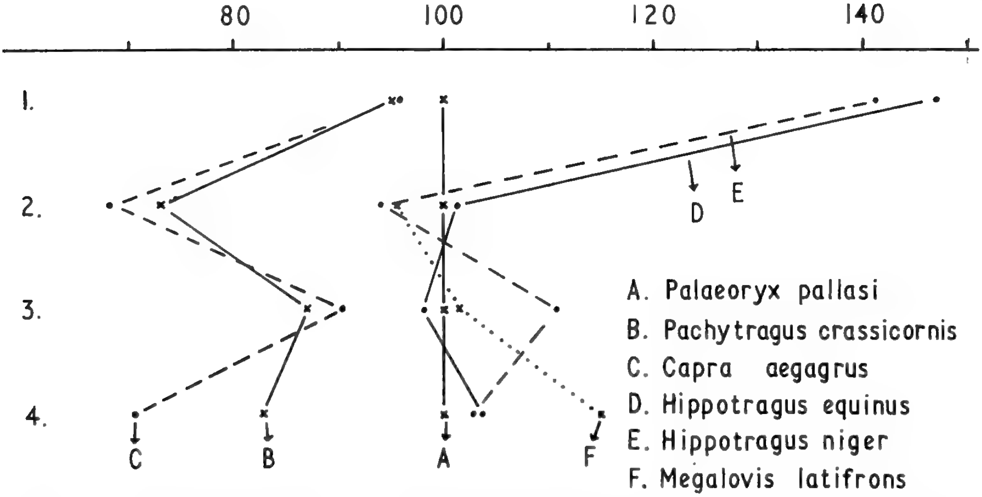

FIG. 10. Percentage diagram to compare some mean skull measurements of *Palaeoryx pallasi* (the standard line at 100%) and *Pachytragus crassicornis* with males of some living Bovidae: *Capra aegagrus* (10 individuals), *Hippotragus equinus* (10), and *H. niger* (12). Three measurements of *Megalovis latifrons* from Senèze are also shown, based on only one reading for separation of horn cores and two for the other two measurements. The measurements numbered 1 to 4 on the left of the diagram are the same as in Text-fig. 1. *Capra aegagrus* may differ from *Pachytragus crassicornis* by its more closely inserted but large horn cores, and has small teeth. The two *Hippotragus* species are rather more different from *Pachytragus crassicornis*, *H. niger* being slightly smaller but with larger horn cores.

Dentitions

The teeth which Schlosser (1904, pl. 11 figs 2, 4, 5) put in *Pachytragus crassicornis* may be taken as *Pachytragus* of some species although those of figs 2 and 5 are rather scrappy, but the teeth of pl. 11 figs 1 and 3 which he also placed in *P. crassicornis* are more likely to be of *Miotragocerus*. The teeth of pl. 8 figs 1 and 2 assigned to *Palaeoryx stützeli* are also of *Miotragocerus*.

COMPARISONS. Teilhard de Chardin and Trassaert (1938 : 41) described from the lower or perhaps later Pliocene of China an antelope called ?*Protoryx yushensis* which from the figures appears to match *Pachytragus crassicornis* in its short braincase widening anteriorly in dorsal view, and keels on the horn cores. The horn cores are rather short (as in Lausanne skull remains 30 and 31). In anterior view the horn cores diverge more than in the Samos skulls. The Chinese skull may well be a closely related species.

Of the two Samos species of *Pachytragus* it is *P. laticeps* which must be the more primitive on the basis of horn cores without anterior keels, the orbital rims being only moderately wide alongside the horn core insertions, and the less developed median occipital ridge and its poorer flanking hollows.

III. SYSTEMATICS OF SPIRAL HORNED ANTELOPES

Clearly spiralled horns occur among living antelopes as follows.

Tragelaphini	all species	Africa	horns in males only, except in *Taurotragus* and one species of *Tragelaphus*
Hippotragini	*Addax nasomaculatus*	Sahara desert	horns in both sexes
Antilopini	*Antilope cervicapra*	India	horns in males only
Caprini	*Capra caucasica*	Caucasus	horns in both sexes
	C. falconeri	India	horns in both sexes
	Ammotragus lervia	North Africa	horns in both sexes
	Pseudois nayaur	Central Asia	horns in both sexes
	Ovis ammon	Eurasia	horns sometimes in males only, but many populations with horned females as well
	O. canadensis	Siberia, N. America	horns in both sexes

It is apparent that several independent evolutions of spiralled horns have taken place.

The first fossil antelope with spiral horn cores to be described was *Antilope lindermayeri* from Pikermi by Wagner (1848 : 367), later transferred by Gaudry (1865 : 290) to *Palaeoreas.* Wagner (1857 : 154) described another spiral horned antelope from Pikermi, *Antilope rothi,* which Gaillard (1902 : 93) took as the type species for his genus *Oioceros.* Pikermi had two more spiral horned antelopes to yield, both of them already present in Gaudry's material assigned to *Palaeoreas lindermayeri.* These were *Protragelaphus skouzesi* Dames (1883 : 97) and *Helicoceras rotundicornis* Weithofer (1888 : 288) the latter's generic name subsequently becoming *Helicotragus.*

As the only species of its genus, *Palaeoreas lindermayeri* has had a simple history. Gaudry (1861) named the genus in accordance with his belief that it was an early tragelaphine, and since then it has not been moved from that tribe. *Prostrepsiceros* has had a more complicated history. Major (1891a : 609) took as his genotype the species *Tragelaphus*? *houtumschindleri* then newly described by Rodler & Weithofer (1890 : 768) from Maragha. He referred Samos specimens to a new species *P. woodwardi* and to *Prostrepsiceros*? sp. Schlosser (1904 : 31) named a similar specimen from Samos *Protragelaphus zitteli,* considering it closely related to Dames's *P. skouzesi.* Pilgrim & Hopwood (1928 : 84, 89, 91) regarded Major's *Prostrepsiceros woodwardi* as a *nomen nudum* and themselves assigned to it a holotype. They added a third species, *P. mecquenemi*, to the genus for Mecquenem's (1924 : 37) Maragha material in Paris, which he had assigned to *P. houtumschindleri*. They assigned *Protragelaphus zitteli* Schlosser to a new genus, *Hemistrepsiceros*, and in this species they also placed Major's *Prostrepsiceros*? sp.

Ozansoy (1965) referred some Turkish fossils to new species of *Palaeoreas* and *Helicotragus*, but they come from later Plaisancian deposits than other species of those genera, and it is difficult to relate them convincingly to the older species.

Prostrepsiceros and *Hemistrepsiceros* have been regarded as members of the Tragelaphini, but Pilgrim & Hopwood (1928 : 20) assigned *Helicotragus* to the Antilopini, and Pilgrim (1939 : 129, 135) thought that *Protragelaphus skouzesi* should go there as well. The purpose of the second part of this paper is to transfer *Prostrepsiceros* to the Antilopini and *Palaeoreas* to the Ovibovini, and to revise the Samos, Pikermi and Maragha species of these genera. I shall also discuss *Protragelaphus skouzesi* which I accept as an antilopine. I have already briefly referred to these questions (Gentry 1968 : 874).

The two genera *Prostrepsiceros* and *Protragelaphus* share the following skull characters, which can be taken as a kernel for defining any suprageneric grouping to which they and their relatives may belong. They have an open spiralling of the horn core or a twisting of its axis which is anticlockwise from the base upwards on the right side, no transverse ridges on the horn cores nor a flattened lateral surface, little divergence of the horn cores, complicated mid-frontals and parieto-frontal sutures, temporal lines wide apart on the top of the braincase, braincase sides parallel or widening slightly posteriorly in dorsal view, a preorbital fossa, a moderate area of exposure of the mastoid, the ventral edge of the auditory bulla not descending posteriorly to meet the front of the paraoccipital process, fairly hypsodont cheek teeth, and quite short premolar rows.

Although both genera are known at Pikermi and Samos, it is the more complete remains in the Paris collection from Maragha which are the most important for their interpretation.

Genus ***PROSTREPSICEROS*** Major

1891a *Prostrepsiceros* Major : 609.
1903 *Helicotragus* Palmer : 873.
1928 *Hemistrepsiceros* Pilgrim & Hopwood : 94.

Type species. *Tragelaphus*? *houtumschindleri* Rodler & Weithofer.

Generic diagnosis. Small to moderate sized antelopes; horn cores are moderately long, with keels or traces of keels, no deep longitudinal grooving, inserted above the orbits and rather obliquely in side view, moderately wide apart at their insertions in anterior view and rather openly spiralled; postcornual groove is fairly shallow or moderately deep; frontals are not hollowed internally.

Orbital rims project; frontals between horn bases are only marginally higher than orbital rims; supraorbital pits are moderate-sized; preorbital fossa is moderate to large.

Nuchal crests are poor to moderate; median vertical occipital ridge and flanking hollows are poor to moderate; anterior tuberosities on the basioccipital are moderately sized with some development of longitudinal ridges behind them; anterior tuberosities are close together, hence a central longitudinal groove is seen anteriorly; auditory bulla is large and inflated.

Teeth are known from only one of the two contained species.

Prostrepsiceros houtumschindleri (Rodler & Weithofer)

1890 *Tragelaphus? houtum-schindleri* Rodler & Weithofer : 768, pl. 6 fig. 2.
1891a *Prostrepsiceros woodwardi* [nom. nud.] Major : 608.
1891a *Prostrepsiceros* sp. Major : 608.
1904 *Protragelaphus zitteli* Schlosser : 31, pl. 6 figs 2, 3, 5, 12.
1924 *Tragelaphus houtum schindleri* Mecquenem : 37, pl. 5 figs 5, 7; pl. 6 figs 5, 7.
1928 *Prostrepsiceros woodwardi* Pilgrim & Hopwood : 91, pl. 7 figs 1, 1a, 1b.
1928 *Prostrepsiceros mecquenemi* Pilgrim & Hopwood : 92.
1928 *Hemistrepsiceros zitteli* (Schlosser). Pilgrim & Hopwood : 94.

HOLOTYPE. A frontlet from Maragha in the Natural History Museum, Vienna, numbered 1886.XXVIII.6.

LOCALITIES. Samos and Maragha.

AGE. Lower Pliocene.

DIAGNOSIS. Horn cores are robust, with some latero-medial compression, medial surface less convex than lateral one (Maragha), strong posterior keel descending to a postero-lateral insertion or posterior keel absent, another keel descending to an anterior or antero-medial insertion and strong in those without a posterior keel, and poor to moderate divergence; braincase is strongly angled on the face.

The remaining characters are known in Maragha specimens only: nasals are fairly long with transverse doming and small lateral and central flanges anteriorly; ethmoidal fissure is moderate-sized and narrow; premaxillae rise with even width and have a short contact on the nasals.

Teeth are fairly hypsodont; basal pillars are absent on upper molars but sometimes present on lowers; there are no indentations into back edges of rear central cavities of upper molars; medial lobes of upper molars do not join to one another and to lateral side of tooth until quite late after eruption; styles and ribs on upper molars are poor; lower molars have goat folds; P_4 has a medial opening between paraconid and metaconid; metaconid of P_4 is directed backwards; lateral wall of P_4 is indented in front of the hypoconid.

REMARKS. *Material from Maragha. P. houtumschindleri* is represented in Vienna by the damaged type frontlet with left horn core, a left horn core 1886.XXVIII.9, and two other horn cores, 1886.XXVIII.8, from Maragha. There are many Maragha specimens in Paris including the skull figured by Mecquenem (1925, pl. 5 fig. 5 for its teeth and pl. 6 fig. 7) which lacks the distal parts of its horn cores and the braincase, a second skull also lacking its braincase (Pl. 5 fig. 1), a skull with M^2 and M^3 on both sides but lacking the left side and back of the braincase and the face above the tooth row, a cranium with right horn core on which the front of the basioccipital is missing, and many other dentitions and horn cores.

The original illustration of this species by Rodler and Weithofer (1890, pl. 6 fig. 2) was probably constructed from both the type frontlet and the better preserved left horn core, 1886.XXVIII.9. The divergence of the horn cores on the holotype exceeds that on most of the Paris examples, although the Paris specimen with the most completely preserved cranium does have a similarly pronounced divergence.

A second variety from Samos

From Samos there is a skull BM(NH) M.4192 (Pl. 5 fig. 3), a frontlet with left horn core, M.4210, and part of a right horn core, M.4213; a frontlet with horn cores from Brown's quarry 6, AMNH 20575 and a left horn core from quarry 5, AMNH 20576; a frontlet figured by Schlosser (1904, pl. 6 fig. 5) in Munich; and a frontlet, 1911 Samos V 130, in Vienna. Schlosser's specimen does not have so compressed a section in its upper parts as the others, and shows that any tendency to a posterior keel is confined to near the horn core tip. In these Samos examples which have hitherto been placed in the species *woodwardi* and *zitteli*, the horn cores have an anterior keel but no posterior keel. They are a distinct variety from the Maragha specimens, but I take them as conspecific by their robust, little divergent, keeled horn cores and by the braincase top being so angled on the face axis.

Dentitions

The two mandibles figured as *P. houtumschindleri* by Mecquenem (1924, pl. 5 fig. 7 and pl. 6 fig. 5) agree in size with the upper dentitions attached to skulls. They show small back lobes on the M_3s, very small or absent basal pillars on the molars of one and moderate to small basal pillars on the other, goat folds on the molars, the anterior part of the medial wall of P_4 is not closed, metaconid of P_4 is directed backwards, the lateral wall of P_4 is indented just in front of the hypoconid, and the horizontal ramus is not very deep. Large numbers of lower partial dentitions of this size are present in the Maragha collections in Paris, and even though some may belong to other species it is very likely that many belong to the same species as the most numerous horn core type. The most likely alternative identity for some of these mandibles is *Oioceros rothi*, which is present at Maragha but less numerous than *Prostrepsiceros houtumschindleri*. The only indication of the size of the teeth in this species is provided by the skull of Mecquenem (1924, pl. 7 fig. 7). It is not certain that this skull is of *O. rothi*, but by its basioccipital morphology it is certainly not a *Prostrepsiceros*. Its tooth row (Mecquenem pl. 6 fig. 4) is slightly smaller than those of the skulls of *P. houtumschindleri*, but suggests that there would be a considerable size overlap between dentitions of the two species. There is no perceptible morphological variation among the mandibles of this size range as they are preserved, and it would not be surprising if *O. rothi* had very similar teeth to *P. houtumschindleri*.

The supposed *P. rotundicornis* mandible from Maragha (Mecquenem 1924, pl. 7 fig. 5) is smaller than the mandibles among which some may be accepted as *P. houtumschindleri*, its molars have no goat folds, the basal pillars range in size from moderate on M_1 and M_2 to slightly smaller on M_3, and the back lobe of M_3 is quite large and possesses a central cavity. This and other similar mandibles are not *P. houtumschindleri*, but they might belong to the species which Mecquenem (1924 : 30) called *Gazella deperdita* (see p. 284 footnote and Gentry 1970 : 273).

The specific name of this species was wrongly spelled by Pilgrim & Hopwood (1928) as *houtum-schlindleri* with two 'l's.

Prostrepsiceros rotundicornis (Weithofer)

1865 *Palaeoreas lindermayeri* (in part) Gaudry : 292, pl. 52 fig. 5.
1888 *Helicoceras rotundicorne* Weithofer : 288, pl. 18 figs 1–4.
1889 *Helicophora rotundicornis* (Weit.). Weithofer : 79.
1903 *Helicotragus rotundicornis* (Weit.). Palmer : 873.
1908 *Antidorcas? gaudryi* Mecquenem : 52.
1924 *Helicophora rotundicornis* Mecquenem : 39, pl. 7 fig. 1.
1926 *Helicoceras fraasii* Andree : 163, pl. 11 fig. 4; pl. 15 fig. 1.
1928 *Helicotragus fraasii* (Andree). Pilgrim & Hopwood : 23.

LECTOTYPE. The Pikermi specimen figured by Weithofer (1888, pl. 18 figs 1, 2) in the Natural History Museum at Vienna was chosen by Pilgrim & Hopwood (1928 : 21).

LOCALITIES. Pikermi, Samos, Maragha.

AGE. Lower Pliocene.

DIAGNOSIS. Horn cores are less massive than in Maragha examples of *P. houtumschindleri*, with some degree of antero-posterior compression; posterior keel

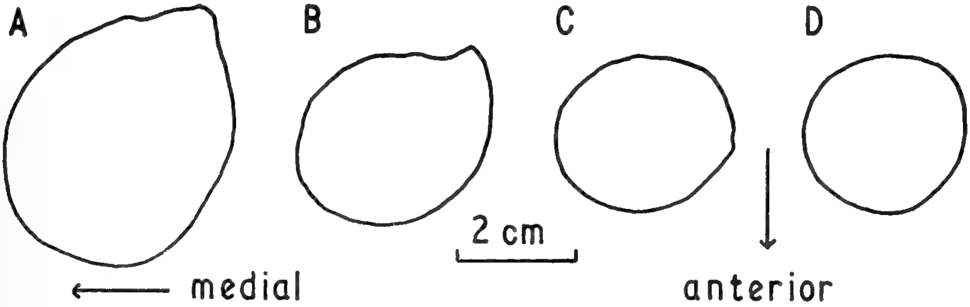

FIG. 11. Sections of left horn cores from Maragha taken at a distance above the pedicel top equal to half the antero-posterior diameter at the base of the horn core. A = *Protragelaphus skouzesi* (Mecquenem 1924, pl. 6 fig. 6); B = *Prostrepsiceros houtumschindleri* (Mecquenem 1924, pl. 6 fig. 7); C = *P. rotundicornis* (Mecquenem 1924, pl. 7 fig. 1); D = *Antilope cervicapra*, BM(NH) 32.12.11.8.

is absent; a trace of an anterior keel is present and descends to an antero-medial or medial insertion; braincase is not strongly angled on the axis of the face.

REMARKS. *The Pikermi variety.* The last species existed in two well marked varieties at Maragha and Samos but was absent from Pikermi; this one also exists in two clear varieties, but one occurs at both Maragha and Samos, and the other at Pikermi. *P. rotundicornis* is less completely preserved than *P. houtumschindleri* but the following specimens are known. In London there is the Pikermi material listed by Pilgrim & Hopwood (1928 : 23), among which the incomplete skull M.11437 was figured by them (pl. 1 figs 2, 2a). There are also horn cores from Pikermi in Paris. The Pikermi material shows not very great divergence of the horn cores, not exceeding that of most of the *P. houtumschindleri* material, the horn cores are inserted rather obliquely at the base, and the basal part of the horn core before any outward swing begins is short. The skull M.11437 has a trace of a posterior keel at its base.

A second variety from Maragha and Samos

Maragha examples of this species are represented possibly by two single horn cores numbered 1886.XXVIII.8 in Vienna and by many specimens in Paris among which the more important are the frontlet figured by Mecquenem (1924, pl. 7 fig. 1), a cranium with the left horn core and part of the left preorbital fossa (Pl. 5 fig. 2), two further frontlets, and a frontlet possessing only the left horn core. The Maragha specimens of this species have horn cores inserted more uprightly, and a long basal part followed by a strong outward swing. It is interesting that there is a cranium with horn cores from Samos which agrees with the Maragha variety of *P. rotundicornis*.

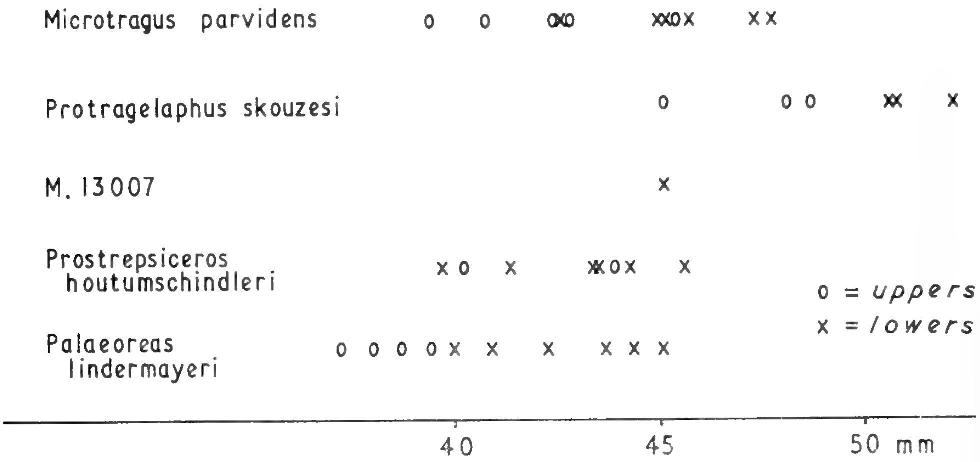

FIG. 12. Lengths of upper and lower molar rows of some antelopes. The uppers are from identified skulls only; the lowers of *Palaeoreas lindermayeri* and *Protragelaphus skouzesi* are fairly easily recognizable; the *Sporadotragus* (=*Microtragus*) *parvidens* is only doubtfully identified. The *Prostrepsiceros houtumschindleri* is from Maragha only, and the *Palaeoreas lindermayeri* from Pikermi only.

It was figured by Andree (1926, pl. 11 fig. 4 and pl. 15 fig. 1), and I have seen at Münster a cast of the original specimen kept at Stuttgart. The horn core on the left side is sufficiently near complete to show that its divergence as a whole does not exceed that in other *Prostrepsiceros* despite the outward swing above the basal part. The braincase of this specimen appears to be angled on the face rather more than in the Pikermi M.11437 or in the Maragha specimen figured here, but it is less angled than in *P. houtumschindleri*.

Major (1894 : 25) listed two Samos horn cores in Lausanne, 204 and 205, as *Helicophora rotundicornis*, but I believe that they are more likely to belong to *Oioceros wegneri* Andree (1926 : 170, pl. 15 figs 3, 6).

The Pikermi examples of this species are the ones which have been called *rotundicornis* in the past, while the Maragha ones and the Samos example have been called *fraasi*.

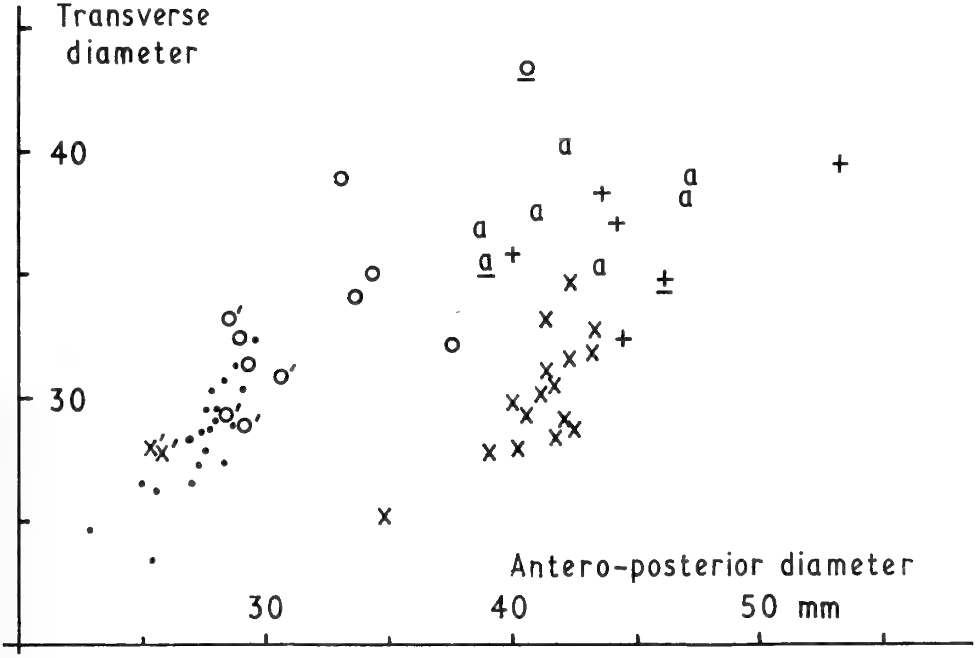

FIG. 13. Graph of horn core compression. x = *Prostrepsiceros houtumschindleri* from Maragha, x′ = *P. houtumschindleri* from Samos, o = *P. rotundicornis* from Maragha, o′ = *P. rotundicornis* from Pikermi, + = *Protragelaphus skouzesi*, a = *Palaeoreas lindermayeri* (including a̲ the Samos specimen in Lausanne), · = *Antilope cervicapra*. o̲ and ± are the casts in Münster of *Prostrepsiceros rotundicornis* and *Protragelaphus skouzesi* from Samos. The Samos *Prostrepsiceros houtumschindleri* and the Pikermi *P. rotundicornis* are closest to *Antilope* but the Maragha *P. rotundicornis* is rather larger. *Protragelaphus skouzesi* and Maragha *Prostrepsiceros houtumschindleri* are more mediolaterally compressed than the others.

Both varieties of *P. rotundicornis* differ from *P. houtumschindleri* by less massively built horn cores, keels absent or nearly absent, an 'anterior' keel in so far as one is ever present perhaps descends to a medial rather than to an antero-medial insertion, the horn cores are not more compressed higher up than lower down, the braincase is less angled on the face axis (Pl. 5 fig. 2), and the supraorbital pits are perhaps smaller.

On the percentage diagram (Text-fig. 14) *Prostrepsiceros rotundicornis* from both Pikermi and Maragha has horn cores more like those of *Antilope cervicapra* than has the Maragha *P. houtumschindleri*; the horn cores of the Pikermi *P. rotundicornis* are also small enough to approach the size of those of *Antilope cervicapra.*

Dentitions

The only example of a mandible I have been able to find which might belong to this species is BM(NH) M.13007, a left mandible from Pikermi with P_3 to M_3 in an early stage of wear (Pl. 6 fig. 2). It had been assigned to *Palaeoreas lindermayeri* (Pilgrim & Hopwood 1928 : 87). There is a small back lobe of M_3; basal pillars are of small to moderate size on M_1, small on M_2 and absent on M_3; there are goat folds on the molars; the metaconid of P_4 is directed backwards and there is quite a deep indentation on the lateral wall in front of the hypoconid. All these characters cause M.13007 to resemble the slightly smaller *Prostrepsiceros houtumschindleri* mandibles from Maragha, but the ramus may be slightly deeper below the tooth row. The teeth are slightly larger than in a number of *Palaeoreas lindermayeri* mandibles from Pikermi, the molars have larger goat folds, and P_3 is relatively

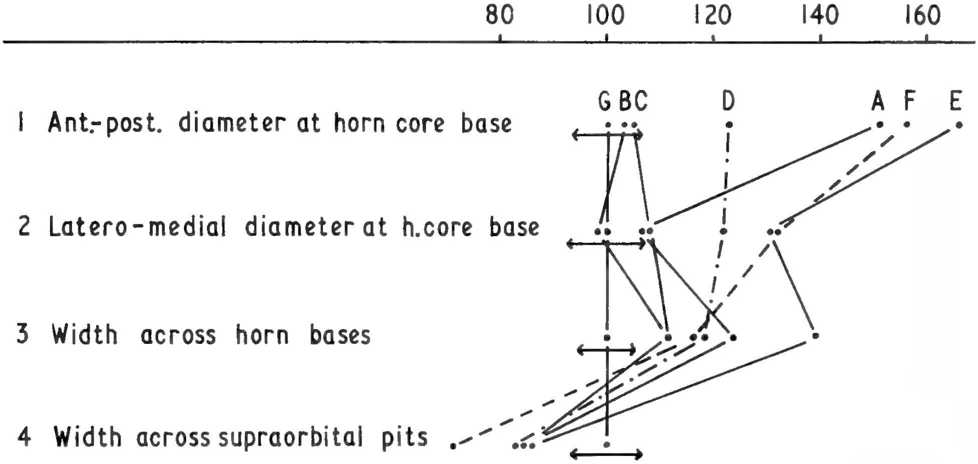

Fig. 14. Percentage diagram for some skull measurements of spiral-horned antelopes, based on Table 3 in the text. The standard line at 100% is the mean of 20 male *Antilope cervicapra*, and means of the other species are expressed as percentages of their values in *A. cervicapra*. Horizontal lines show the extent of standard deviations in *A. cervicapra*. The capital letters, A to G, indicate the species concerned as on Table 3, p. 274.

smaller. The complete premolar row would have been relatively longer than in *Protragelaphus skouzesi*, which in any case has larger teeth. M.13007 is not small enough to belong to a gazelle or probably to *Oioceros rothi* (see discussion on p. 264), but it would be the right size for *Sporadotragus parvidens*. Other mandibles which I have tentatively assigned to *S. parvidens* in my notes, e.g. BM(NH) M.13009, M.13011 and M.4184; AMNH 22778 and 86415, differ only in less or no development of goat folds, so M.13007 cannot be definitely taken as *Prostrepsiceros rotundicornis*. My expectation would have been to find a smaller tooth row in this last species. The right M_1 and M_2 of an immature Samos antelope illustrated by Schlosser (1904, pl. 13 fig. 12), agree with M.13007.

Genus **PROTRAGELAPHUS** Dames

1883 *Protragelaphus* Dames : 97.

TYPE SPECIES. *Protragelaphus skouzesi* Dames.

GENERIC DIAGNOSIS. As for the species, which is the only one in the genus.

Protragelaphus skouzesi Dames

1857 *Antilope lindermayeri* (in part) Wagner : 155, pl. 7 fig. 18.
1865 *Palaeoreas lindermayeri* (in part) Gaudry : 291, pl. 53 fig. 4.
1883 *Protragelaphus skouzesi* Dames : 97.

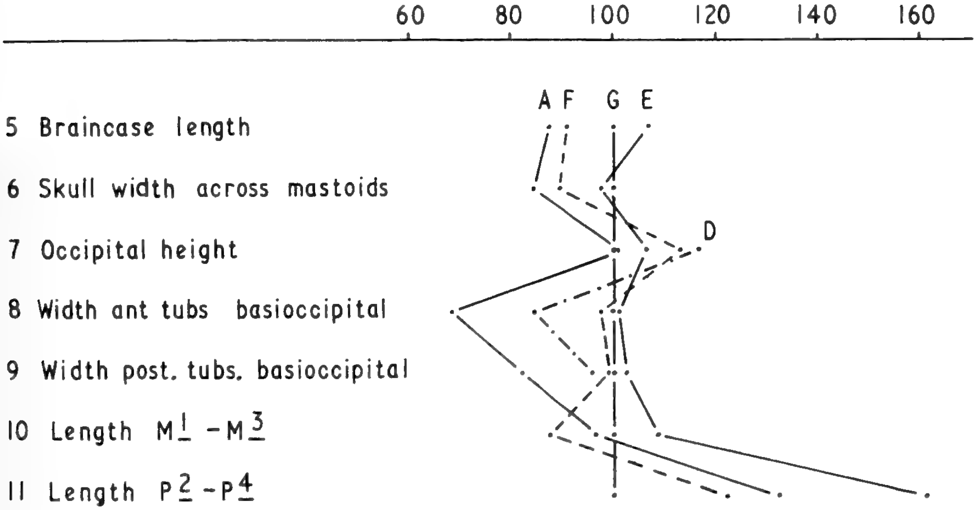

FIG. 15. Percentage diagram for further skull measurements of spiral-horned antelopes. Explanation under Text-fig. 14. The braincase length was measured from the mid-frontals' suture at the level of the supraorbital pits to the occipital top. Standard deviations for *Antilope cervicapra* could not be shown on this diagram, and have been listed after Table 3 in the text, p. 275.

Holotype. The Berlin frontlet described but not figured by Dames. Pilgrim & Hopwood (1928 : 88) take Wagner's figure as being of the paratype. Gaudry's figure is a right mandible which is the size of this species, and was so taken by Pilgrim & Hopwood.

Localities. Pikermi, Samos and Maragha.

Age. Lower Pliocene.

Diagnosis. Moderate sized antelopes (larger than *Prostrepsiceros*); skull is fairly low and wide; horn cores are long, not medio-laterally compressed but the posterior keel adds to the antero-posterior diameter, with a strong posterior keel descending to a postero-lateral insertion but no anterior keel, inserted a little behind the orbits and rather obliquely in side view, inserted moderately wide apart in anterior view, moderately diverging, and the axis itself is twisted and lacks the open spiralling of *Prostrepsiceros*; postcornual fossa is usually moderate or large sized; frontals are hollowed; orbital rims slope rather than project strongly; braincase top is short and strongly angled on face axis; frontals are slightly higher between the horn bases than the level of the orbital rims; frontals surface is convex in front of the horn bases; mid-frontals suture may be raised; parieto-frontals suture is indented; supraorbital pits are smaller than in *Prostrepsiceros* and moderately wide apart; nasals are fairly long; suture at back of nasals is narrowly drawn out as a V-shape; preorbital fossa is moderate to large sized; infraorbital foramen is above the front half of P^3; premaxillae may rise with an even width to a short contact with the nasals; median palatal indentation is level with or behind lateral ones; nuchal crests are poor to moderate; occipital surface is more nearly in one plane facing backwards than in *Prostrepsiceros*; median occipital ridge and flanking hollows are poorly marked; anterior tuberosities of the basioccipital are wider apart than in *Prostrepsiceros*; anterior tuberosities are small with poor longitudinal ridges behind.

Teeth are fairly hypsodont; the enamel is only slightly rugose; basal pillars are very small on upper molars and small to moderate on the lowers, decreasing backwards; rear central cavities of upper molars have indented back edges; medial lobes of upper molars remain unfused to one another fairly late in wear; styles and ribs are poor; goat folds on lower molars are poor or non-existent; premolar row is short; metaconid of P_4 may join the paraconid and close the anterior part of the medial wall; the lateral wall of P_4 is indented in front of the hypoconid; P_3 is shorter relative to P_4 than in *Palaeoreas*.

Remarks. The more important fossils of *Protragelaphus skouzesi* which I have seen are the paratype skull from Pikermi in Munich, two skulls in Paris from Maragha one of which was figured by Mecquenem (1924, pl. 6 fig. 6 and pl. 5 fig. 2), a cranium in London, M.10840, from Pikermi, a frontlet from Samos in Stuttgart, and a fontlet from Maragha in Vienna. There are other Maragha horn cores in Paris. I have not seen the holotype, nor the cranium in Göttingen figured by Weithofer (1888, pl. 17 figs 4–6).

The Stuttgart specimen figured by Andree (1926, pl. 15 figs 4, 5) is the only decisive evidence for this species from Samos; I did not see the original but was able to see a plaster cast in Münster. The twisting of the keels on this Samos specimen is rather tight and the keel stronger than in other specimens; at its base the keel connects by a ridge with the back of the orbit. The London cranium has the back part of the braincase stuck to the front, and it is possible that the braincase appears to slope too little on the face axis on this specimen.

There is a palate from Maragha in Paris which seems to belong to this species, and in addition I would assign to it these dentitions and teeth: mandibular pieces BM(NH) M.13021 and M.13022 (Pl. 6 fig. 2) from Pikermi, AMNH 86478 from Samos, 618 and 661 from Samos in Lausanne, and the Paris mandible figured by Mecquenem (1924, pl. 6 fig. 1) from Maragha. These pieces show that the teeth of this species are large among the smaller antelopes of lower Pliocene times but smaller than the common Samos genus *Pachytragus*.

COMPARISONS. *Protragelaphus skouzesi* differs from *Prostrepsiceros* as a whole by its greater size; more posterior horn insertions; a twisting of the horn core axis rather than an open spiralling; the combination of strong posterior keel on the horn cores and no anterior keel is not found in any known *Prostrepsiceros* population (Text-fig. 11); higher frontals between the horn bases; hollowed frontals with a convex surface in front of the horn bases; orbital rims projecting little; smaller supraorbital pits; occipital surface more definitely in one backwardly-facing plane; and wider anterior tuberosities on the basioccipital with less of a longitudinal central groove between them.

It differs additionally from *P. houtumschindleri* in not having any medio-lateral compression of its horn cores (Text-fig. 13); a narrowly drawn out suture at the back of its nasals; upper molars with spurs often projecting into the back edges of the rear central cavities; no goat folds on its lower molars; and a tendency for paraconid-metaconid fusion to close the anterior part of the medial wall of P_4. The Maragha mandible figured by Mecquenem (1924, pl. 6 fig. 1) has a completely fused paraconid and metaconid on its P_4. It differs additionally from *P. rotundicornis* by its braincase being more strongly angled on the facial axis, and by the horn cores being more obliquely inserted than in Maragha and Samos specimens.

On the percentage diagram (Text-figs 14 and 15) *Protragelaphus skouzesi* is quite similar to the smaller *Prostrepsiceros houtumschindleri*, the latter having relatively narrower anterior tuberosities of its basioccipital. One can visualize the common ancestor of this pair not too far in the past.

Genus **PALAEOREAS** Gaudry

1861a *Palaeoreas* Gaudry : 299.
1861b *Palaeoreas* Gaudry : 395.

TYPE SPECIES. *Antilope lindermayeri* Wagner.

GENERIC DIAGNOSIS. There is only one species within the genus, so the generic diagnosis is as for that species.

Palaeoreas lindermayeri (Wagner)

1848 *Antilope lindermayeri* Wagner : 367, pl. 12 fig. 5.
1861a *Palaeoreas lindermayeri* Gaudry : 299.
1861b *Palaeoreas lindermayeri* Gaudry : 395.
1865 *Palaeoreas lindermayeri* Gaudry : 290, pl. 52 fig. 4; pl. 53 figs 1–3; pl. 54; pl. 55.

HOLOTYPE. Base of a right horn core in the Palaeontological Institute, Munich, no. 530. The antero-posterior diameter at the base of this horn core is 42·1 and the latero-medial diameter 40·2 mm.

LOCALITIES. Pikermi and Samos.

AGE. Lower Pliocene.

DIAGNOSIS. Small to moderate sized antelopes; horn cores are moderately long and massive (more massive than in *Prostrepsiceros houtumschindleri*), not mediolaterally compressed, often with deep fairly irregular longitudinal grooving, with a posterior keel which is sometimes strong and a weaker anterior keel, the posterior keel descending to a postero-lateral position, horn cores inserted above the orbits, set fairly obliquely in side view, close together in anterior view and poorly divergent, and the axis itself twisted anticlockwise from the base up on the right side but without open spiralling; there is an elongated very deep postcornual fossa. Orbital rims project moderately; mid-frontals and parieto-frontals sutures are not visible; temporal lines on braincase roof probably do not approach closely posteriorly; braincase may widen posteriorly; large supraorbital pits; mid-frontals suture is raised as an incipient ridge in front of the horn bases; there is another localized raising of the mid-frontals suture behind the horn bases; the ethmoidal fissure is long and narrow; preorbital fossa is extensive and moderately deep; face is low in side view; infraorbital foramen is above the back part of P^2; the premaxillae rise with an even width to a short contact on the nasals.

Occipital surface is low and its dorsal edge is not evenly rounded; the median vertical occipital ridge is strong with large shallow flanking hollows; mastoids are moderate to large; basioccipital is long with a central longitudinal groove weaker in the centre than at either end; nuchal crests are moderately strong; auditory bulla is inflated and moderate to large, and its ventral edge does not descend posteriorly to meet the front of the paraoccipital process.

The teeth are fairly hypsodont (but perhaps less than in *Prostrepsiceros* and *Protragelaphus*); basal pillars are small or absent on the upper molars and slightly larger on the lowers; there are not usually indentations in the back edge of the rear central cavities on the upper molars; medial lobes of the upper molars remain unfused with one another until fairly late in wear; styles on upper molars are moderate sized and a rib between parastyle and mesostyle is often fairly strong; there is a tendency to goat folds on the lower molars; front and back edges of P_3 and P_4 are set transversely: anterior medial wall of P_4 is not closed; the metaconid on P_4 is not directed backwards; there is no valley in front of the hypoconid on the lateral wall of P_4; P_3 has a strong entostylid behind the entoconid; and P_3 is fairly large in relation to P_4.

REMARKS. There is a face with horn cores M.10843, several frontlets, and many horn cores of this species in London, all Pikermi. There are three skulls, and many other horn cores from Pikermi in the Paris collection. Three frontlets, 23, 24 and 25 (Pl. 6 fig. 1) in Lausanne are the only known occurrence of the species from Samos. In the London collection I assign the following mandibular pieces to this species: the four numbered M.11505, M.13008, M.13012, M.15828 (Pl. 6 fig. 2) and M.15829. Pilgrim & Hopwood (1928 : 23, 70) had assigned M.11505 and M.13012 differently, but they did have M.13008 as *P. lindermayeri*. Of the other dentitions which they assigned to *P. lindermayeri*, I believe M.13007 has a P_3 too small in relation to P_4 for assignation to *Palaeoreas lindermayeri* (see p. 268), and the others I would not care to identify.

In the Paris collection from Pikermi is a fine small palate with M^1–M^3 measuring 39·4 mm long, M^2 13·9 mm, and P^2–P^4 28·3 mm long. The rear median indentation passes further forwards than the lateral ones, ribs are strong between parastyle and mesostyle on the molars, M^1 alone has a very small basal pillar, and the medial lobes of the molars are still not joined to the lateral sides of the teeth. I have taken this as *P. lindermayeri*, as it agrees with other dentitions on the Paris and London skulls in its strong ribs.

The species is thus very common at Pikermi, but rare at Samos. It has been recorded from other sites, but I would not accept most of these records based as they are on doubtful dentitions. However Schlosser (1921 : 44) recorded a horn core from Veles in Macedonia. It is principally from the London skull and the series of more or less complete ones in Paris that the diagnosis has been constructed. It is unfortunate that some weathering or rolling has taken place on these skulls, so that the details of structure are often missing. On one of the two Paris skulls in which they are present the nasals are transversely domed and on the other they are not. Nor could I be certain about the level of the median indentation at the back of the palate.

The Samos skull in Münster which was named *Oioceros wegneri* by Andree (1926 : 170, pl. 15 figs 3, 6) has many resemblances to *Palaeoreas lindermayeri*, for example no horn core compression, deep longitudinal grooving on the horn cores, the great height of the frontals between the horn bases, a localized raising of the mid-frontals suture anterior to the horn bases, and a long narrow ethmoidal fissure. Such similarities are surprising when it is realized that the torsion of the horn cores is in the reverse direction from *P. lindermayeri*. The only other clear differences of *O. wegneri* from *P. lindermayeri* are that the torsion is stronger, the spiralling more open, the keel descends to a lateral insertion, and the braincase is shorter with a more steeply inclined roof. I have considered *Oioceros* as quite unrelated to *Palaeoreas, Protragelaphus* or *Prostrepsiceros*.

COMPARISONS. *Palaeoreas lindermayeri* is the most distinctive of the lower Pliocene spiral horned antelopes. It differs from *Prostrepsiceros* and *Protragelaphus* by its more massive horn cores, horn cores sometimes with deep irregular longitudinal grooving, a stronger posterior keel than in all except the Maragha *P. houtumschindleri*, horn cores not very compressed antero-posteriorly or medio-laterally (Text-fig. 13), a deeper postcornual fossa, braincase more strongly bent on the face axis, frontals higher between the horn bases, the mid-frontals and parieto-frontals sutures not visible, larger supraorbital pits closer together, perhaps a larger ethmoidal fissure, stronger median vertical occipital ridge and thus more of a tendency for the occipital surface to face partly laterally as well as posteriorly, perhaps a slightly larger mastoid, basioccipital larger, basioccipital with less localized anterior tuberosities and as large a central longitudinal groove as the strongest ones in *P. houtumschindleri*, and probably a stronger rib between parastyle and mesostyle on the upper molars.

TABLE 3

	A	B	C	D	E	F	G
Antero-posterior diameter at base of horn core	41·3 (11)	28·3 (3)	28·6 (3)	33·5 (5)	45·4 (5)	42·7 (7)	27·3 (20)
Latero-medial diameter at base of horn core	30·3 (11)	27·8 (2)	30·5 (3)	34·5 (5)	37·1 (5)	37·3 (5)	28·3 (20)
Minimum width across lateral edges of horn pedicels	92·2 (9)	82·9 (3)	82·7 (3)	87·9 (3)	103·7 (5)	86·5 (5)	74·4 (20)
Width across lateral edges of supraorbital pits	40·2 (8)	40·3 (2)	40·4 (2)	39·4 (3)	41·7 (4)	34·0 (5)	47·6 (19)
Braincase length from level of supraorbital pits to occiput	89·9 (1)	—	—	—	109·4 (1)	93·5 (4)	102·4 (20)
Skull width across mastoids behind exterior auditory meatus	69·0 (1)	—	—	—	79·8 (2)	73·3 (4)	81·7 (17)
Occipital height from top of foramen magnum	27·1 (1)	—	—	31·3 (1)	28·7 (2)	30·5 (6)	26·9 (19)
Width across anterior tuberosities of basioccipital	15·5 (1)	—	—	19·2 (1)	22·8 (3)	22·2 (4)	22·7 (17)
Width across posterior tuberosities of basioccipital	23·8 (1)	—	—	27·8 (1)	29·7 (2)	28·9 (4)	29·0 (15)
Length M^1–M^3	42·0 (2)	—	—	—	47·3 (2)	38·3 (4)	43·6 (16)
Length P^2–P^4	27·2 (1)	—	—	—	33·2 (1)	25·2 (3)	20·6 (12)

A = *Prostrepsiceros houtumschindleri* from Maragha only.
B = ,, ,, from Samos only.
C = ,, *rotundicornis* from Pikermi only.
D = ,, ,, from Maragha only.
E = *Protragelaphus skouzesi* from Pikermi and Maragha.
F = *Palaeoreas lindermayeri* from Pikermi only.
G = *Antilope cervicapra*, males of the living blackbuck.

It differs additionally from *Prostrepsiceros* by its horn cores with a twisted axis instead of more open spiralling and perhaps by smaller auditory bullae, and from *P. houtumschindleri* by less strong goat folds on its lower molars, transversely set front and back edges of P_3 and P_4, the metaconid on P_4 is not directed backwards, no indentation on the lateral wall of P_4 in front of the hypoconid, a larger P_3 and P_3 with a strong entostylid. It differs additionally from *Protragelaphus skouzesi* by less divergent horn cores, more projecting orbital rims, the back of the nasals less narrowly drawn out, the transverse front and back edges of P_3 and P_4, no closing of the anterior part of the medial wall of P_4, no indentation on the lateral wall of P_4 anterior to the hypoconid, the large size and strong entostylid of P_3.

On the percentage diagram (Text-figs 14 and 15) *Palaeoreas lindermayeri* has large horn cores and a fairly large back part of the skull (characters 5–9 inclusive) compared with the size of the tooth row; the massiveness of the back of the skull presumably being linked with the size of the horn cores.

Table 3 shows the means of some skull measurements of spiral horned antelopes used in Text-figs. 14 and 15 and the figures in brackets are the size of the sample. Standard deviations for the sample of *Antilope cervicapra*, listed in the same order as the measurements, are: 1·78, 2·21, 4·14, 3·27, 3·46, 3·85, 2·26, 1·82, 1·67, 2·26 and 1·34.

IV. TRIBAL CLASSIFICATION

The Palaeoryx, Protoryx and Pachytragus group

Comparison with Hippotragini

The tribe Hippotragini includes the following living species:

Hippotragus equinus (Desmarest 1804) the roan,
Hippotragus niger (Harris 1838) the sable antelope,
Oryx gazella (Linnaeus 1758) the gemsbok and beisa,
Oryx dammah (Cretzschmar 1826) the scimitar oryx,
Oryx leucoryx (Pallas 1777) the Arabian oryx,
Addax nasomaculatus (Blainville 1816) the addax.

They are medium to large-sized stocky antelopes with large horn cores in both sexes, hypsodont cheek teeth with basal pillars on the molars, and little reduction of premolars. *Hippotragus* has a long braincase and medio-laterally compressed horn cores strongly curved backwards, *Oryx* has a shorter braincase and little-compressed straight horn cores, and *Addax* has a shorter braincase and spiralled horn cores.

The older authors gave but few reasons why they regarded *Palaeoryx*, *Protoryx* and *Pachytragus* as Hippotragini. Gaudry (1861a : 241; 1861b : 394) in writing of *Palaeoryx* mentions the form, proportions and insertion of the horn cores, position of the supraorbital pits and lack of wide orbital rims as resembling modern *Oryx*, although its teeth were certainly very different. Major (1891a : 608) in founding

Protoryx writes of a more decided hippotragine aspect than even *Palaeoryx* possessed —horn cores bigger relative to skull size, brachyodont teeth, and in some species a short parietal. The reference to brachyodonty as a resemblance is puzzling. Apart from that, it seems that the little compressed and obliquely inserted horn cores of *Palaeoryx* cause it to resemble *Oryx*, and that *Protoryx* with its more compressed and uprightly inserted horn cores can be regarded as not unlike *Hippotragus*.

So far this is not very convincing, and the only other resemblances of the fossils to Hippotragini lie in characters which can reasonably be supposed to be primitive. Thus the fossils have no keels on the horn cores (except in *Pachytragus crassicornis*), the extent to which the frontals are raised between the horn bases is about the same, there are no transverse ridges on the front of the horn cores, the horns are inserted above the back of the orbits, the horn cores of *Protoryx carolinae* and *Pachytragus laticeps* diverge about as much as in *Hippotragus*, the horn cores have a simple course without torsion, postcornual fossae are small or absent, the orbital rims have about the same width, the supraorbital pits are small, an ethmoidal fissure is present, the infraorbital foramen above the tooth row is in about the same position, the palatal foramina are at about the same antero-posterior level, the mastoids are large, the anterior tuberosities of the basioccipital are set about as widely apart, and the degree of hypsodonty in *Pachytragus* approaches that of Hippotragini.

Two other possible resemblances to the Hippotragini need further discussion; these are the solid horn cores of the fossils and the dimensions of their braincases. The fossil horn cores are mostly solid, but traces of a basal hollowing have been found (see p. 248). Hippotragini also have solid horn cores, but in them the central lowest parts are at most only slightly spongy in texture, and I have found no sign of the development of hollowing. A collection in Cape Town of the large extinct *Hippotragus gigas* Leakey from the Elandsfontein Pleistocene site confirms this. Hollowing of the frontals extends to the top of the horn pedicels, above which the horn core itself is not hollowed. A very large East African frontlet of the same species in Nairobi (figured by Leakey 1965, pls 89, 90) has the frontal hollowing extending about 35 mm above the external indication of the pedicel top, but this hollowing is clearly demarcated from the horn core substance above. A male roan antelope in the National Museum, Nairobi was sectioned 20 mm above the top of its horn pedicel and at that level it was solid. So the hollowing in the fossil AMNH 23038 (see p. 249) already exceeds that in *Hippotragus*, and even the extreme sponginess of AMNH 22783 would not be expected in *Hippotragus*. It is therefore difficult to derive the totally solid condition of living *Hippotragus* from that of the fossils in which hollowing has already been initiated.

Braincase lengths of the fossils can be matched with one or other of the Hippotragini. Thus *Palaeoryx pallasi* agrees with *Oryx*, *Protoryx carolinae* and longer-brained *Pachytragus* with *Hippotragus equinus*, and other *Pachytragus* with *Hippotragus niger*. This is in line with the supposed connection of *Palaeoryx* with *Oryx*, and of *Protoryx* and *Pachytragus* with *Hippotragus*. However the resemblance ends here. The bending down of the braincase on the facial axis is less in either species of *Hippotragus* than in *Protoryx* and *Pachytragus*, and braincases of *Hippo-*

tragus are wider than in the fossils. With the differences in inclination and proportion, it is difficult to see that the length of the braincases can indicate any real connection of the fossils with Hippotragini.

Turning to the differences of the fossils from Hippotragini, we find that the most important ones concern the teeth. Hippotragini retain basal pillars on their molars, and have strong outbowed labial ribs between the styles on their upper molars. *Hippotragus* itself has evolved large basal pillars, complicated central cavities on its upper molars, goat folds on its lower molars, and relatively large premolars (Text-fig. 5). It is obvious that the teeth of the two *Pachytragus* species are not evolving in this direction. Even if one could discuss a possible hippotragine relationship for *Palaeoryx* or *Protoryx*, one could certainly not do so for *Pachytragus*.

Finally in comparing the Samos fossils with modern Hippotragini, one should mention that there are two fossil hippotragines from the Pinjor stage of the Siwalik Hills in India and Pakistan (perhaps of early Pleistocene age) which are substantially different from living Hippotragini but do not suggest a derivation from *Protoryx* or *Pachytragus*. These two fossils are *Sivatragus bohlini* (Pilgrim 1939 : 80, pl. 2 figs 3–6, text-fig. 6) and *Sivoryx sivalensis* (=*Antilope sivalensis* of Lydekker 1878 : 154, pl. 25 figs 1, 2) which I take to include *S. cautleyi* (Pilgrim 1939 : 74); both are represented in the British Museum (Natural History). Neither have the frontals between the horn bases raised above the level of the orbital rims; *Sivatragus bohlini* shows boselaphine-like characters in the braincase being little angled on the line of the (absent) face and in its fairly marked temporal lines behind the horn bases, and is further unlike the Samos and Pikermi antelopes in its braincase being definitely wider posteriorly than anteriorly; *Sivoryx sivalensis* has rather a low and wide skull and its upper molar teeth have basal pillars and are without such marked mesostyles as *Pachytragus*. Derivation of *S. sivalensis* from *Palaeoryx pallasi* could not be ruled out on morphological grounds, but *P. pallasi* is too large to be a likely ancestor.

I conclude from all the above evidence that *Palaeoryx*, *Protoryx* and *Pachytragus* cannot be placed in the Hippotragini.

Comparison with the Caprini

Most of the primitive skull characters in which the fossils resemble Hippotragini are also resemblances to Caprini, and particularly to goats (*Capra* Linnaeus 1758) within the Caprini. Caprini are wholly Palaearctic except only for *Capra walie* Rueppell 1835 which has reached a part of the Ethiopian highlands and *Ovis canadensis* Shaw 1804 which has spread into America.[2] If the Samos antelopes should turn out to be caprines, the supposed African affinities of that fauna would be much diminished. It is therefore of interest to look for further caprine resemblances in the fossils.

The delimitation of the species of goats and their very near relatives (*Capra*,

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[2] *Oreamnos americanus* (Blainville 1816), the Rocky Mountain goat, is also in North America, but Simpson (1945 : 162) places *Oreamnos* in the tribe Rupicaprini of the subfamily Caprinae.

Hemitragus, Ammotragus, Pseudois) adopted by Ellerman and Morrison-Scott (1951 : 403–410) and the arrangements of more recent authors are clearly unsatisfactory in their various ways. Many of the named forms can interbreed to produce fertile offspring (Gray 1954 : 70), and striking differences of male horns probably have little taxonomic value. This has been Payne's (1968) point of view, and although I do not follow him to all his conclusions, it seems unlikely that we could find separate ancestors for most or all of the 'species' of *Capra* very far back in the geological record. In this paper I shall use the specific names of Ellerman and Morrison-Scott within the genera *Hemitragus, Ammotragus* and *Pseudois*, and within *Capra* the following names: *C. aegagrus* Erxleben 1777 for goats with an anterior keel on their horn cores, *C. ibex* Linnaeus 1758 for the European ibex, *C. sibirica* (Pallas 1776) for Siberian ibexes, *C. caucasica* Güldenstaedt & Pallas 1783 for the Caucasian turs, and *C. falconeri* (Wagner 1839) for the spirally horned markhors.

There are a number of characters in which the Samos fossils, especially *Pachytragus*, are similar to goats, and taken together these characters indicate convincingly a relationship of the fossils to goats. These characters are as follows.

An anterior keel exists on the horn cores of *Pachytragus crassicornis*, the most advanced of the fossils, and on those of *Capra* and *Hemitragus*. In AMNH 22938 and AMNH 22939 the keel descends to an antero-medial insertion; this would allow for the later development of an antero-lateral longitudinal swelling such as can be seen in many *Capra aegagrus*. The beginning of such a swelling may be present in AMNH 20708. This swelling could so easily develop into the broad anterior surface of ibex horn cores, that one doubts whether ibexes necessarily had different ancestors from *C. aegagrus* as far back as the lower Pliocene.

The cranium AMNH 23037 of *Pachytragus laticeps* has horn cores completely preserved to their tips, and in profile their course is not an even arc with a large radius of curvature like *Hippotragus* but they become more sharply curved towards their tips; such a curvature resembles that in the male horns of living goats and ibexes. Other examples of *Pachytragus* fail to show this so well, but it does occur in the *Pachytragus laticeps* cranium 201 in Lausanne, and in AMNH 20674 and 20690.

Extensively hollowed horn cores are characteristic of the living Bovini and Caprini, but in other bovid tribes hollowing is confined to the frontals and horn pedicels. Traces of hollowing near the bases of the horn cores have been noted in *Pachytragus* (page 248), and this would be appropriate in ancestors or relatives of later Caprini.

The bending down of the braincase on the axis of the face in *Protoryx* and *Pachytragus* is a character also found in goats.

In some *Pachytragus* (and *Palaeoryx*) individuals a tendency exists for the widest part of the braincase to lie anteriorly. It appears in the Lausanne skull 30 which is probably a *Pachytragus laticeps*, in the Münster skull of *P. crassicornis* figured by Andree (1926, pl. 13 fig. 7), in a number of the New York *Pachytragus* skulls, and in the *Pachytragus* skull from Salonica figured by Arambourg & Piveteau (1929, pl. 7 figs 6, 6a). It can also be seen in the *Palaeoryx pallasi* skull BM(NH) M.10831 and in the Munich example of the same species from Samos, but two other *P. pallasi* braincases widen posteriorly. In Hippotragini the sides of the braincase are either parallel or widen posteriorly, but in living Caprini they are parallel or widen anteriorly.

On Text-fig. 4 it can be seen that the supraorbital foramina have become wider apart, relative to the distance across the horn bases, in *Pachytragus crassicornis* than in *P. laticeps*, and this character would link *P. crassicornis* more closely with *Capra.*

The ethmoidal fissure is not only present in both species of *Pachytragus*, but is also long and narrow as in *Capra, Hemitragus* and *Ammotragus*; it is less wide than in Hippotragini.

The *Pachytragus* face of AMNH 20609 has a jugal which is not unlike that of *Capra*, but is without the two unequally-sized lobes of a *Hippotragus.* It does not show any antero-ventral expansion and smoothly rounded overall course of the front suture like many individuals of caprine species.

The foramina ovalia are small to moderately sized in the fossils as in Caprini instead of moderate to large as in Hippotragini.

In the type skull and in the cranium AMNH 20621 of *Pachytragus laticeps* and in the Lausanne cranium 29 (Pl. 1 fig. 1) and Münster cranium (Andree 1926, pl. 13 figs 4, 6) of *Palaeoryx pallasi*, the auditory bullae have survived, and it can be seen that the posterior part of their ventral edges turn downwards to meet the front of the paraoccipital processes as in the caprines *Hemitragus, Pseudois, Ammotragus* and many *Capra.* I took this to be a resemblance of the fossils to Caprini (Gentry 1968 : 874), and although this was correct I have since found that the character occurs frequently in the sable antelope.

The diminution of basal pillars on the cheek teeth of *Pachytragus laticeps* and *P. crassicornis* foreshadows their almost total absence in the teeth of living Caprini; the central cavities of the upper molars have an uncomplicated outline; in *P. laticeps* and *crassicornis* the mesostyle is frequently prominent on the upper molars and is followed by a concave lateral wall behind as in Caprini. Finally the short premolar row (Text-fig. 9, already shorter in *P. laticeps* and *P. crassicornis* than in *Hippotragus*) and somewhat reduced P^2 in the fossils foreshadow later Caprini. Such teeth can convincingly be seen as an intermediate stage in the evolution of modern caprine teeth from the fairly generalized original condition of bovid teeth such as is seen in *Palaeoryx pallasi* and *Protoryx carolinae.*

An extremely interesting character to know would be the size of the central incisor teeth in *Palaeoryx, Protoryx* and *Pachytragus*, for they are small in all Caprini (as in most Eurasiatic antelopes) but larger in Hippotragini (as in most African antelopes). The mandible AMNH 23073 had I_1s perhaps only slightly bigger than the more lateral incisors and canine like Caprini, but clear evidence from an unworn dentition is required. A mandibular symphysis in Münster of an unknown Samos antelope of the size of *Pachytragus* has rather small I_1s.

Text-fig. 10 shows the relative proportions of some skull measurements in the fossils and living antelopes. The sable antelope has larger horn cores than the roan and both have rather long braincases, the last character being exaggerated on the diagram because of the relative shortness of the braincase in *Palaeoryx pallasi*, here used as a standard. *Capra* and *Pachytragus crassicornis* have similar proportions of the cranium, but *Capra* has very large horn cores and small teeth.

It is difficult to interpret the evolutionary history of *Pachytragus*, not least because of the lack of precise details about the vertical distribution of its species. It is known only that *P. crassicornis* in the New York collection is confined to Brown's quarry 5, while quarries 1 and 4 contain the less advanced *P. laticeps*. The supposition that quarry 5 might be later than the other quarries depends on the morphological interpretation of the two species of *Pachytragus*; Sondaar (1968 : 68) has mentioned a time difference between the quarries but without specifying whether quarry 5 was the later. Except for the relative smallness of the teeth in *Capra*, there seems no reason why *Pachytragus crassicornis* should not be the actual ancestor of goats. A more detailed knowledge of later Pliocene faunas is desirable before asserting this more definitely.

Tossunnoria pseudibex Bohlin (1937 : 37, pl. 4 fig. 3, pl. 5 figs 1–3, text-figs 66–68, 70b, 71–74), a caprine from the lower Pliocene of north eastern Tibet, has been linked with the ancestry of goats. It has large very strongly compressed horn cores inserted at a high angle to one another so that their bases diverge backwards. Its braincase widens posteriorly. I am prepared to relate it to *Pachytragus* among its contemporaries, and very tentatively to *Hemitragus* among its successors. Its horn cores are more advanced or specialized than in *Pachytragus*.

Differences of the Samos fossils from living Caprini

A number of advanced characters of later Caprini are absent in the lower Pliocene fossils: the extreme enlarging of male horn cores and the linked raising of the level of the frontals between the horn bases, the frequently posterior setting of the palatal foramina, and the very wide anterior tuberosities of the basioccipital. The primitive state of these characters in the fossils were previously noted as similarities to Hippotragini; such resemblances may simply result from the acquisition of some specializations in Caprini later than the earlier Pliocene. Other later caprine characters not met with in these fossils are the very wide projection of the lower rim of the orbits (less pronounced in *Ovis ammon* and *Ammotragus lervia* than in other living Caprini), the tendency to antero-ventral expansion of the jugal and an evenly curved course of its front suture which is most apparent in *Pseudois*, *Ammotragus* and *Hemitragus*, the small angle of the lower jaw, the fusion of the metaconid and paraconid on P_4, the presence of goat folds on lower molars, and high transverse crests across little worn and unworn upper molars. The crests across the upper molars are detectable on dentine as well as enamel and must result from rigidly fixed transverse occlusal movements. Possible initial traces of such wear are visible on the *Pachytragus laticeps* and *P. crassicornis* specimens in Münster figured by Andree (1926, pl. 12 fig. 2 and pl. 13 fig. 7).

Among these characters by which modern goats differ from *Pachytragus*, the large horn cores with extensive hollowings, raised frontals, and wide basioccipital suggest that the method of intraspecific fighting used by *Capra* (see Schaffer 1968) had not yet evolved. It may be mentioned that although the sparse and inadequately identified antelope limb bones from Samos have not been studied in this paper, there are no extremely shortened goat-like metapodials in any museum collection to suggest that even *Pachytragus crassicornis* had entered areas of precipitous rocky slopes.

If we consider other skull characters than those in which the fossils are less advanced than all living genera of Caprini, we find that *Pachytragus* is still not very close to *Ovis*, the latter genus differing strongly in its broad-fronted divergent curled horn cores and no ethmoidal fissure.[3] *Pseudois* differs by its non-compressed divergent horn cores often with deep longitudinal grooving in mature animals, the short braincase very strongly angled on the face, the generally advanced outline of the jugal, no preorbital fossa or ethmoidal fissure, and small mastoid. *Ammotragus* differs by its non-compressed divergent horn cores, the generally advanced outline of its jugal, no preorbital fossa and no ethmoidal fissure. *Hemitragus* differs by its short horn cores, long dorsal parts of its orbital rims, often an expanded jugal, and no preorbital fossa. *Capra aegagrus* differs in the absence of a preorbital fossa, and it is this form from which *Pachytragus*, especially *P. crassicornis*, is least remote; *Capra falconeri* has a large posterior keel and strongly twisted horn cores, most ibexes have broad-fronted horn cores (the prominent knobs on the sheaths are not present on the cores), and *Capra caucasica* has horn cores rather more reminiscent of *Ammotragus* or *Pseudois*.

The position of Palaeoryx pallasi

The similarities noted between the Samos fossils and living goats have principally concerned *Pachytragus* and especially *P. crassicornis*. Little positive sign of a connection between *Palaeoryx pallasi* and goats can be seen. Although *P. pallasi* cannot satisfactorily be taken as in the Caprini, it does have some similarities to later members of other tribes of Caprinae, for example the living East Asian *Capricornis* Ogilby. The resemblance to *Capricornis* is at least as great as to the hippotragine *Oryx*. More interesting are its similarities to *Megalovis latifrons* from the Villafranchian of Senèze, France (Schaub 1923 : 292, fig. 5; 1943 : 281, figs 5 and 6). Some fossils assigned to *Pliotragus* (=*Deperetia*) *ardeus* are very probably conspecific with *M. latifrons*, e.g. the cranium illustrated by Schaub (1923, fig. 3) and the skull from the Villafranchian of Olténie in Romania illustrated by Bolomey (1965, figs 1–3). It is even possible that this species includes the original maxilla of *Antilope ardea* Depéret (1884, pl. 8 fig. 3) in which case nomenclatorial alteration

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[3] It may be more difficult in the future to determine the ancestry of sheep than of goats. *Sivacapra* Pilgrim (1939 : 49) from the Pinjor stage of the Siwaliks has torsion of its horn cores which is clockwise on the right side and it is a possible relative of sheep. It has resemblances both to *Sinotragus* mentioned on p. 243 above and to *Samotragus crassicornis* Sickenberg (1936) from Samos, which in its turn is like *Oioceros wegneri* Andree (1926 : 170, pl. 15 figs 3, 6). Yet it is impossible to link *Sinotragus* with *Oioceros* if the former's relationship to *Protoryx* and *Palaeoryx* (p. 243) is accepted, so one is faced with two caprine stocks having clockwise torsion of their horn cores. The assignation of individual fossils becomes difficult, and we also have to find out whether sheep descend from either stock or from some other form such as *Sporadotragus* (see p. 283 below).

of *M. latifrons* to *M. ardea* would be needed. Villalta & Crusafont Pairo's (1955 : 431, figs 1–3) *Hesperoceras merlae* from Villaroya must be at least a close relative of *M. latifrons*. Bolomey's skull in particular suggests a connection with *Palaeoryx pallasi*, with which it shares or from which it could easily have derived the following characters: large size (both species are large among their contemporaries), short to moderately long horn cores, little compression of the horn cores (Text-fig. 8), horn cores strongly divergent and inserted behind the level of the orbits, braincase angled on the axis of the face, short braincase, small supraorbital pits set widely apart, and the back of the tooth row lying just anteriorly to the level of the front of the orbits. Text-fig. 10 shows that a couple of measurable *Megalovis latifrons* have rather larger horn cores and tooth rows than in *Palaeoryx pallasi*. Other Villafranchian skull pieces I examined in Paris and Basle show further characters in common with *Palaeoryx pallasi*: not very complicated mid-frontals and parieto-frontals sutures, a large mastoid, and a wide basioccipital. However, the teeth of these Pleistocene fossils are more advanced than in *P. pallasi*, and the relative length of the premolar row a little reduced (Text-fig. 9).

Accepting *Pachytragus* as a definite member of the Caprini, one can either place *Palaeoryx* and *Protoryx* with it as close relatives or separate them, placing *Palaeoryx* in the same tribe as *Megalovis*. The correct tribal position for *Megalovis* has been a problem, some authors relating it to sheep and others to the Ovibovini (Guérin 1965 : 12). Unlike Schaub (1923) I take it as an ovibovine. It agrees with the Ovibovini (discussed further on page 289) or at least with the living *Ovibos* and *Budorcas* in its large size, dorso-ventral compression of the horn cores, their insertion behind the orbits and very wide divergence, presence of a ridge from the base of the horn core to the top back of the orbit, short braincase, well projecting orbital rims, not a complicated mid-frontals suture, small supraorbital pits which are set widely apart, infraorbital foramen placed as far posteriorly as above the back of P^3, an indication of concavities postero-laterally to the anterior tuberosities of the basioccipital, small auditory bulla, absence of basal pillars on the molar teeth, upper molars rather long relative to width, upper molars with fairly strong styles and rounded medial lobes, P^2 remaining large, mandible not markedly deep below the molars, and paraconid of P_4 fused to the metaconid. In addition the quite sharp upstanding ridges on the posterior tuberosities of the basioccipital and the central longitudinal groove constricted between the anterior tuberosities are like *Budorcas*. There seems to be no reason to link *Megalovis* with sheep which have horn cores inserted above the orbits, emerging without much divergence, and with a marked spiral course. I suggest that *Megalovis* is an ovibovine and that *Palaeoryx* too be placed in that tribe. This opinion is tentative, and I have not seen the *Megalovis* skull from Olténie, but I believe it is better to have a definite and possibly interim classification than one with an unworkable proportion of queried assignations. In the same manner I shall take *Protoryx* and its Asian relatives as Caprini, although there is hardly any balance of probabilities taking them closer to that tribe than to Ovibovini. With *Palaeoryx* no longer related to *Oryx*, the evidence for rather dry steppe conditions at Pikermi, if not also at Samos, is diminished. An ancestor of *Oryx* could be visualized with a tendency to inhabit the rather dry areas favoured by the living species, but we do not know what habitats might have held an ancestor of *Megalovis latifrons.*

Other related lower Pliocene fossils

The foregoing revision has been concerned only with species of *Palaeoryx, Protoryx* and *Pachytragus* occurring at Samos, Pikermi and Maragha. *Paraprotoryx, Prosinotragus, Sinotragus* and *Sinoryx* have been mentioned in the comparisons, and there are other Eurasian Pliocene bovids which should probably be removed from the Hippotragini, namely *Pseudotragus, Leptotragus, Olonbulukia* and *Sporadotragus.*

Pseudotragus capricornis founded by Schlosser (1904 : 51) on Samos material is represented by the type skull in Munich (Schlosser 1904, pl. 10 fig. 7) by a poorly preserved skull in New York (AMNH 20577), by the London skull BM(NH) M.4193, and by some dentitions in Munich (Schlosser 1904, pl. 10 figs 1–3, 5, 6). The Munich examples are in a different matrix from the other bovids (Schlosser 1904 : 112–113), hence there is a good likelihood that the teeth are correctly referred; the New York specimen is from Brown's quarry 6 in which, like quarry 2, *Pachytragus* is not represented. *Leptotragus* was founded by Bohlin (1936 : 8, figs 2, 3) for a second smaller skull referred by Schlosser (1904 : 51, pl. 10 fig. 8) to *Pseudotragus capricornis,* the supposed generic difference being based on its straighter and narrower horn cores, larger orbits situated more anteriorly, horn cores set more obliquely and having an anterior keel. It seems unlikely that *Leptotragus pseudotragoides* can be separated specifically from *Pseudotragus capricornis,* but I was not able to check the specimen in Munich which was probably destroyed in the Second World War. *Pseudotragus* in Schlosser's original sense is smaller than *Pachytragus,* and has relatively very large, strongly compressed horn cores, well projecting orbital rims, a long premolar row and a relatively large P^2. It resembles Caprini in the rather small size of the face relative to the cranium and in the braincase being strongly angled on the face.

Olonbulukia tsaidamensis Bohlin (1937 : 30, pl. 2 figs 10, 11, pl. 3 fig. 1) is based on a cranium from the supposed lower Pliocene of Tsaidam in China. It is about the size of *Pachytragus* or *Pseudotragus,* has horn cores strongly compressed lateromedially, with an anterior keel, little divergent and curved backwards in side view. There is a postcornual fossa and the braincase would have been somewhat angled on the missing face. *Olonbulukia* shows no clear sign of tribal affinities in itself, but it can continue to be tentatively taken as an Asian relative of *Pachytragus* and *Protoryx.*

Sporadotragus Kretzoi (1968) is the corrected name for *Microtragus* Andree (see p. 234). It is again smaller than *Protoryx.* It differs from *Pseudotragus* by having less compressed horn cores, frontals very strongly raised between the horn bases, horn cores frequently with an anterior surface, and narrower orbital rims. The middle two of the preceding characters, along with the rather small face (Pikermi) and widening of the anterior parts of the braincase (Pikermi) are decidedly caprine-like and the clear upper and lower rims of the preorbital fossa recall sheep in particular.

I suggest that *Pseudotragus* (including *Leptotragus*) and *Sporadotragus* be transferred to the Caprini, while *Olonbulukia* be regarded as ?Caprini.

The skull of *Tragoreas oryxoides* Schlosser (1904 : 34, pl. 6 figs 1 and 9) is from a small antelope with strongly compressed and obliquely inserted horn cores, frontals less raised between the horn bases than in *Pseudotragus*, no upraised mid-frontals suture, a preorbital fossa without an upper rim, a fairly large P^2, and an apparently undistorted brain top which is scarcely angled on the face axis. It could be related to *Miotragocerus* on the basis of these characters, although smaller than the smallest species of that genus, *M. valenciennesi* Gaudry (1865 : 288). No feature of its morphology suggests membership of the Hippotragini, but only the strongly compressed horn core would go against such an assignation. Doubtful placing in the Boselaphini seems a better solution to the problem, since it would not be satisfactory to use this unique and puzzling specimen as the only basis for the presence of Hippotragini at Samos.[4]

Ancestors for the Palaeoryx group

Nothing certain is known of the ancestors of *Palaeoryx*, *Protoryx* or *Pachytragus*. Earlier representatives of the boselaphine genus *Miotragocerus* than the Samos, Pikermi and Maragha species are known from the Sarmatian of the Vienna Basin (Thenius 1959 : 87) and the Chinji of India and Pakistan, and the related genera *Protragocerus* and *Eotragus* also occur at such early time levels. But the record for pre-Pannonian Caprini includes only *Oioceros* from Tung Gur, Fort Ternan and Prebreza, ?*Pseudotragus potwaricus* (Pilgrim) from the Siwaliks and Fort Ternan and its possible relative ?*Gazella stehlini* from Europe. (See Gentry (1970) for discussion and references to these occurrences.) The only bovid which is a possible candidate for ancestry of *Palaeoryx*, *Protoryx* or *Pachytragus* is *Damalavus boroccoi*, known as a cranium and other horn cores and teeth from the Miocene of Oued Hammam (=Bou Hanifia) in Algeria. It was described by Arambourg (1959 : 120,

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[4] Bohlin (1935c : 107, pl. 13 figs 7–14, pl. 14 figs 1–6) described two fine skulls of *Tragoreas lagreli* from the Chinese lower Pliocene which he later suggested should be renamed *T. altidens* (Bohlin 1941 : 107). They had somewhat compressed horn cores set very closely together, very deep postcornual fossae, the front of the braincase at a high level relative to the face, but the back part bent downwards. Should *Tragoreas* become unavailable as a generic assignation for this species, it could be referred to *Pseudotragus* or to *Dorcadoryx* Teilhard de Chardin & Trassaert (1938 : 32), possibly as a separate species from their *D. triquetricornis*. A number of horn cores in the Paris collection from Maragha may be close to '*Tragoreas*' *altidens*; they are short and thick, there is a very deep postcornual fossa, wide orbital rims, and a braincase much angled on the face. A frontlet has been illustrated (Mecquenem 1924, pl. 3 fig. 3), and all of the Maragha specimens are larger than the *Gazella deperdita* from the type locality, Mount Léberon, to which they were referred. (Another Maragha frontlet of this supposed gazelle in Vienna had previously been named by Rodler & Weithofer (1890 : 767, pl. 5 fig. 1 and pl. 6 fig. 1) as *Gazella capricornis*, changed to *G. rodleri* by Pilgrim & Hopwood (1928 : 16), and later said by Pilgrim (1939 : 45) to be possibly an *Oioceros*. In the absence of well marked torsion of its horn cores there is no reason to assign it to *Oioceros*.) A frontlet from the Nagri stage of the Siwalik Hills in Pakistan which Pilgrim (1939 : 86, pl. 2 figs 1, 2) called gen. indet. (cf. *Tragoreas*) *potwaricus* and the same species from the Fort Ternan upper Miocene in Kenya are unlikely to be linked with *Tragoreas oryxoides* or with '*Tragoreas*' *altidens*; I have written elsewhere that a relationship to *Pseudotragus* is just possible (Gentry 1970 : 288).

pl. 18 figs 4, 4a) as an alcelaphine, and the type specimen does resemble a *Damaliscus*, but with a long braincase and short more obliquely inserted horn cores. It is alternatively possible that this ancient antelope could be an ancestor of *Palaeoryx* (this may have been Arambourg's (1954 : 297) first opinion of it when he wrote of a *Palaeoryx* at the site). It is large for its geological age but smaller than *P. pallasi*, the horn cores are only moderately long, slightly curved backwards and obliquely inserted in side view, without keels and with perhaps a slight lessening of divergence towards their tips. The cranium has been transversely crushed, as Arambourg noted; its horn cores may have been slightly more divergent in anterior view, and their insertions a little wider than actually appears. There is a shallow postcornual fossa, small supraorbital pits, the frontals between the horn bases are hardly higher than the orbital rims, the braincase is moderately long and not very strongly bent on the face axis (this is a difference from *Palaeoryx*, but one which is probable in its putative ancestor), mid-frontals and fronto-parietal sutures are fairly complicated, and there are no temporal ridges—only temporal lines which do not approach very closely posteriorly. This absence of temporal ridges might remove it from candidature for boselaphine ancestry. Measurements on this specimen, comparable with those taken on *Palaeoryx* and *Protoryx* are: antero-posterior and transverse diameter of horn core 40·2 and 32·8 mm.

A left M_3 which Monsieur Arambourg showed me in Paris appeared to be a companion piece to the right M_3 assigned to *Tragocerus* (now *Miotragocerus*) and shown in pl. 17 figs 4, 4a of his work and was of a size to go with *Damalavus*. It was 22·0 mm long at its occlusal surface, and the height of its medial wall between front and central lobes was 10·2 mm.

As to the age of Oued Hammam, Arambourg (1959 : 10) thought it was Tortonian. Cooke (1968 : 249) believed it could be later, and I agree (Gentry 1970 : 312). It would be of much zoogeographical interest if the affinities of *Damalavus* could be definitely decided, but I was unable to do this when I saw the material in Paris.

Spiral horned antelopes

Comparison with Tragelaphini

Prostrepsiceros and *Palaeoreas* have always been taken as Tragelaphini although Pilgrim (1939 : 129, 135) moved *Protragelaphus* to the Antilopini. The living Tragelaphini are a fairly homogeneous group of browsing African antelopes found in habitats ranging from montane moorlands to forest but generally where there is at least some bush. They are mostly large sized. Their skulls have keeled and spiralled horn cores with anticlockwise torsion on the right side, which is their major resemblance to the Eurasian Pliocene fossils. Otherwise they show quite a distinctive pattern of skull characters which is not at all foreshadowed in the fossils. These are that a postcornual fossa is absent, horn cores tend to insert behind the orbits, the dorsal part of the orbital rims slopes from the horn bases and projects very little, the frontals between the horn bases are a little raised above the level of the orbital rims, the mid-frontals and parieto-frontal sutures disappear in adult males, the braincase sometimes widens posteriorly, a perforation in the side of the braincase is often seen behind the postorbital bar, the orbital surface of the lachrymal is at a wide angle to its facial surface, the supraorbital foramina are in lengthened narrow pits, a preorbital fossa is absent, the infraorbital foramen is placed anteriorly and rather low, the premaxillae narrow anteriorly to a blunt point, the occipital surface has a flat top edge and straight sides, the mastoids are small, the basioccipital is long with anterior tuberosities in front of the foramina ovalia and it has a transverse constriction centrally, and P_4 often has a fused paraconid and metaconid.

Tragelaphini retain as probably primitive characters a braincase which is little angled on the face axis, long nasals, an ethmoidal fissure, brachyodont cheek teeth, medial lobes of the upper molars which do not fuse with one another until late in wear, lower molars without goat folds, and long premolar rows with large front premolars. The extinct *Tragelaphus nakuae* Arambourg (1941 : 343; 1947 : 418) from Omo in southern Ethiopia is appreciably more primitive than living tragelaphines in its projecting orbital rims, supraorbital pits not elongated antero-posteriorly, and an occipital surface which is perhaps less squared in outline.

The resemblances of *Prostrepsiceros*, *Protragelaphus* and *Palaeoreas* to Tragelaphini lie almost entirely in primitive characters, and none of them are evolving towards the sort of morphology seen in living tragelaphines. Sometimes they may show resemblances, as for example in the long basioccipital of *Palaeoreas lindermayeri*, but such resemblances are few and apparently fortuitous. In the past Tragelaphini have been linked with the Boselaphini and Bovini, which is a position I support (Gentry 1970 : 316), and it would certainly be awkward to accommodate in the same overall group the small spiral horned genera from Samos.

Comparison with the Indian blackbuck

I would rather put *Prostrepsiceros* and *Protragelaphus* into the same group as the living Indian blackbuck, *Antilope cervicapra* (Linnaeus 1758). Whereas Tragelaphini tend to be larger antelopes, the blackbuck is a fairly small bovid like most of the fossils. This and its lack of the specialized features of Tragelaphini make it quite a strong contender for relationship to the fossils. Its fairly long horn cores, their spiralling with anticlockwise torsion on the right side, their inclination in side view, width across the insertions and the amount of divergence are all about the same as in *Prostrepsiceros* and *Protragelaphus*.

It agrees with both the *Prostrepsiceros* species in its horn cores being inserted above the orbits, frontals not being raised between the level of the horn bases, and in the moderate projection of the orbital rims, but these characters amount only to a lack of the more specialized conditions found in *Protragelaphus*. Going down to species level, one finds that some facial and dental characters of *P. houtumschindleri* agree with *A. cervicapra*. The small central and lateral flanges anteriorly on the nasals (Pl. 5 fig. 1) and the premaxillae rising with even width to a contact on the nasals give *P. houtumschindleri* quite a striking resemblance to the blackbuck. The near absence of basal pillars on the molars (complete absence in the blackbuck), poor styles and ribs on the upper molars, lower molars with goat folds (slightly less marked in the blackbuck), no paraconid-metaconid fusion on P_4, and the indented lateral wall of P_4 in front of the hypoconid are additional resemblances. It is quite possible that such resemblances would also be found in the unknown face and dentition of *P. rotundicornis*. With *P. rotundicornis* in particular the blackbuck agrees in the absence of keels, no medio-lateral compression of its horn cores, and the poor degree of bending of the braincase on the face axis.

Antilope cervicapra is practically devoid of keels and this obviously gives it more resemblance to *P. rotundicornis* than to any other of the fossil species. There are occasional examples of *A. cervicapra* in which a vestige of an anterior keel exists, e.g. BM(NH) 27.2.14.41, 27.2.14.50 and 32.12.11.8, and this keel descends to a medial rather than to an antero-medial insertion, which is also like *P. rotundicornis*. Finally, although the horn cores of *P. rotundicornis* are neither so slender nor spiralled so closely to the central axis as in *A. cervicapra*, they are less massive than in the other fossils (Text-figs 11, 13, 14) and thus approach the living form more closely. These characters all make *P. rotundicornis* the best choice as the species to which *A. cervicapra* could be related. However the more important conclusion is that the group of *Prostrepsiceros* and *Protragelaphus* as a whole is related to the blackbuck and not to tragelaphines.

A. cervicapra differs from *Prostrepsiceros* by its very large supraorbital pits, smaller preorbital fossa, wide anterior tuberosities of the basioccipital (Text-fig. 15), and very large mastoid. Face and dental characters differing from *P. houtumschindleri* are the shorter and wider nasals, very small or absent ethmoidal fissure, more hypsodont teeth, occasional presence of indentations into the back edge of the rear central cavities on the upper molars, earlier fusion of the medial lobes of the upper molars, less backwardly inclined metaconid of P_4, and absent P_2. The percentage diagrams (Text-figs 14 and 15) show that *A. cervicapra* has supraorbital pits fairly wide apart, a relatively wide and low braincase, and a short premolar row. There is no reason to suppose that any of these characters are primitive and could preclude the blackbuck from descent from or relationship to the fossil genus. However they are probably sufficient to retain *Prostrepsiceros* as a separate genus from *Antilope*.

A. cervicapra differs rather more from the larger *Protragelaphus skouzesi*. Apart from characters in which it is advanced, it has a less low and wide skull, horn cores less massive at the base, no posterior keel on the horn cores and less open spiralling, horn cores not inserted so posteriorly, more strongly projecting orbital rims, braincase less angled on the face axis, frontals not hollowed, flatter nasals, the median indentation at the back of the palate passing forward of the lateral ones, palatine foramina close together, goat folds on the lower molars, and no paraconid-metaconid fusion on P_4. It can scarcely have descended from *P. skouzesi*.

A. cervicapra differs still more strongly from *Palaeoreas lindermayeri*, which accords with my conclusion that the latter can best be classified as a small ovibovine. The differences are less massive horn cores at the base, no deep irregular longitudinal grooving, horn cores less thick, no posterior keel nor a weak anterior one, some spiralling of the horn cores rather than a mere twisting of their axis, not such a deep post cornual groove, orbital rims strongly projecting, braincase not strongly angled, longer braincase, frontals low between the horn bases, no raising of the mid-frontals suture, infraorbital foramen high over P^3, a less strong median ridge on the occiput, poor styles and ribs on the upper molars, the lateral wall of P_4 indented in front of the hypoconid, P_3 relatively smaller, and the front and back edges of P_3 and P_4 not set transversely.

Phylogeny of spiral horned Antilopini

On the question of phylogeny, not a lot can be said, particularly in the absence of detailed time correlations of the sites where the varieties of horn core types occur. It is possible to conceive that the Maragha and Samos forms of *P. rotundicornis* are later than that in Pikermi, in so far as they are more gracile and therefore remote from *P. houtumschindleri*. However this conclusion is the more doubtful by the fact that the Pikermi form of *Sporadotragus* appears more advanced than at Samos. Bearing in mind the possibility of a time span at Samos, it is as well to follow the speculation no further. On the whole *P. rotundicornis* shows more signs of ancestry to *A. cervicapra* than any other of the Pliocene species, and it is a pity that it is less completely known than *P. houtumschindleri* or *Protragelaphus skouzesi*.

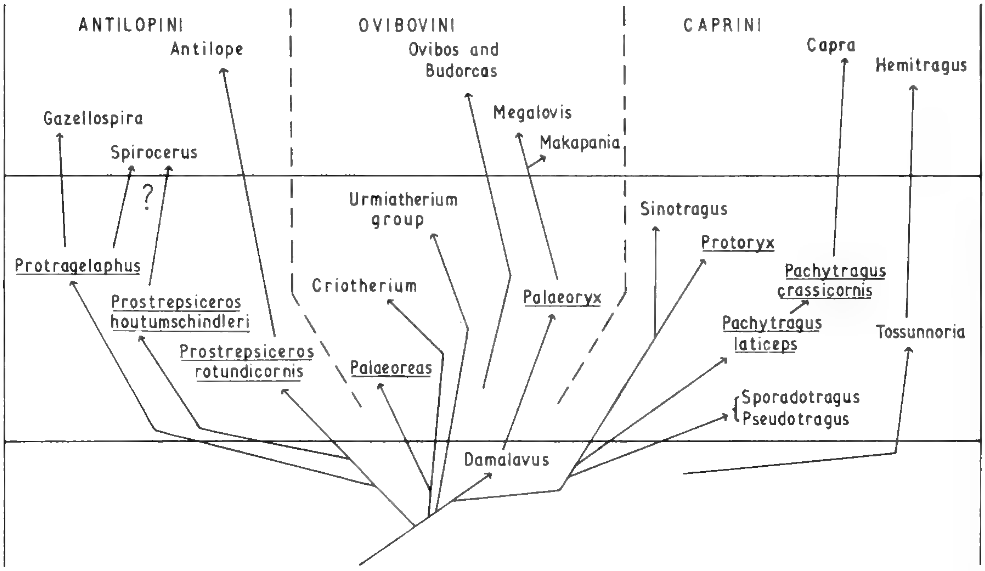

FIG. 16. Possible relationships of bovids mentioned in this paper. Names of species and genera which have been dealt with at length are underlined. The middle horizontal band contains forms known from Samos and other sites of broadly the same age. The upper band is for later forms, and the lower one is for a pre-Samos time level. Precise origins are not shown for *Spirocerus*, *Ovibos* and *Tossunnoria*.

It is certainly possible and very plausible to link *Protragelaphus skouzesi* with the similar European Villafranchian *Gazellospira torticornis* (Aymard), which Pilgrim & Schaub (1939) have already classified as an antilopine.

It would be interesting, were the material accessible, to assess the relationships of these European and West Asian spiral-horned antelopes with those of the Pliocene and Pleistocene of China. It is likely that there is a Pliocene species in China, *Antilospira licenti*, succeeded by the Pleistocene *Spirocerus wongi* (see Teilhard de Chardin & Piveteau (1930), Teilhard de Chardin & Young (1931), and Teilhard de Chardin & Trassaert (1938) for these Chinese antelopes, remembering that many of their specific names are likely to be synonyms. *Spirocerus wongi* dates from 1930, but is itself quite likely to be a synonym of the Russian *S. kiakhtensis* (Pavlow) 1910). It is tempting to see *S. wongi* as an eastern form of the same species or superspecies as *Gazellospira torticornis*, but *S. wongi* possesses an anterior keel and sometimes a weaker posterior one whereas *G. torticornis*, in common with the earlier *Protragelaphus skouzesi*, has a strong posterior keel and no anterior one. One wonders if *S. wongi* descends from the earlier *Antilospira licenti* and if that in its turn is related to *Prostrepsiceros houtumschindleri* or to *Protragelaphus skouzesi*, but I can write nothing useful about this.

A possible ancestor of the Pliocene spiral-horned antelopes is *Sivoreas eremita* (Pilgrim 1939 : 131, pl. 4 figs 1, 1a) from the Chinji stage of the Siwalik Hills (Gentry 1970 : 259). It has horn cores more medio-laterally compressed than in the lower Pliocene antelopes; anterior and posterior keels on the horn cores, the anterior one descending to an anterior rather than to an antero-medial or medial insertion; torsion of the horn cores and a narrow transverse ridge across the frontals between the horn bases. Much doubt surrounds the rather inadequate remains.

The living blackbuck is almost exclusively a grazer, and has some physiological adaptation to scarcity of water. In its undisturbed state it was an animal of flat plains and open woodlands, moving in big herds over areas of short grass. Its ecology was similar to that of a gazelle, although competition with *Gazella bennetti* was avoided. One can probably assume that *Prostrepsiceros* showed a tendency to inhabit the harsher environments, but this may not have applied to *Protragelaphus*.

The position of Palaeoreas lindermayeri

I had earlier written (Gentry 1968 : 874) that *Palaeoreas lindermayeri* should be placed in the Antilopini, along with *Prostrepsiceros* and *Protragelaphus*. However the comparisons on p. 273 have shown that it is very distinct from those Antilopini. I now think that although it is less phenetically remote from them than is any other ovibovine, there is a slight preference for assigning it to the Ovibovini because of characters it shares with the much larger *Criotherium argalioides*.

Besides the living muskox, *Ovibos moschatus* (Zimmermann), and takin, *Budorcas taxicolor* Hodgson, and their immediate Pleistocene relatives such as the fossil muskoxen of Europe, the early Chinese muskox *Boopsis sinensis* Teilhard de Chardin, and the early takin *Lyrocerus satan* Teilhard de Chardin & Trassaert, this tribe contains a number of other extinct genera and species. These are:

Urmiatherium polaki Rodler 1889 from Maragha,
Urmiatherium intermedium Schlosser 1903 from the Chinese lower Pliocene,
Plesiaddax depereti Schlosser 1903 from the Chinese lower Pliocene; (Bohlin (1935c) first assigned skulls to Schlosser's names for the last two species, which had been based on teeth),
Tsaidamotherium hedini Bohlin 1935a from the lower Pliocene of Tsaidam in western China,
Parurmiatherium rugosifrons Sickenberg 1933 from Samos,
Criotherium argalioides Major 1891a, 1892 from Samos.

In addition I have already referred the European Villafranchian *Megalovis latifrons* and its synonyms or relatives to the Ovibovini (see p. 282), and I also believe that the extinct *Makapania broomi* Wells & Cooke 1956 from the Transvaal is related to *Megalovis latifrons* (Gentry, in press). I shall not here enter into the complicated questions of a revision of this whole group. The Maragha and Chinese species of *Urmiatherium* appear to be very close to *Plesiaddax depereti* and the smaller *Parurmiatherium rugosifrons*, and all have specialized horn cores, a condition carried still further in *Tsaidamotherium*. All the Villafranchian and later ovibovines have a rather less extreme horn core morphology, and, as I have noted above, some of them may descend from *Palaeoryx pallasi*. *Criotherium*, known only from Samos, stands by itself with spiralled horn cores, but I am not ready to dispute Schlosser's (1904 : 27) and Bohlin's (1935b) opinions of its ovibovine affinities, chiefly because of dental similarities and its basioccipital morphology with strong paired longitudinal ridges and the trace of an enlargement of the posterior tuberosities. However it should be noted that the teeth of *Criotherium* are less advanced than those of *Urmiatherium* in retaining basal pillars on the lower molars, less rounded lateral lobes on the lower molars, and a longer premolar row. Also *Criotherium's* horn cores, fairly large preorbital fossa, fairly unenlarged occipital condyles, and basioccipital morphology are definitely less extremely specialized than in *Urmiatherium*. It is to *Criotherium* that I would now relate *Palaeoreas*.

It must be admitted that *Palaeoreas lindermayeri* differs from Ovibovini in many characters. It has its own specializations of a very deep postcornual groove, large supraorbital pits, and a long basioccipital. It also lacks quite a number of the specializations of later Ovibovini. It does not have a long face with anteriorly placed upper tooth row, the ethmoidal fissure is still present, the preorbital fossa is rather large, the infraorbital foramen is in a forward position instead of above P^3 or further back, the nasals are not parallel or almost parallel with the upper tooth row, the occipital condyles are not unusually massive nor are the posterior tuberosities of the basioccipital enlarged, the upper molars do not have rounded medial lobes, the lower molars do not have rounded and transversely narrow lateral lobes, they also do not have little outbowed medial walls or straight central cavities, and the cervical vertebrae lack enlarged centra. Some of these specializations, particularly those of the cervical vertebrae, condyles and basioccipital could be unnecessary in *P. lindermayeri* because of its smaller size.

In comparison with *Criotherium argalioides* the horn cores of *P. lindermayeri* are inserted less far behind the orbits, the braincase is longer and less angled on the face axis, basal pillars are slightly larger on its lower molars and sometimes present on its uppers, and there is sometimes a strong rib between parastyle and mesostyle on the upper molars. In all these characters the smaller form lacks the specializations of the larger, which is a frequent situation between related pairs of species of differing size.

In fact *Palaeoreas lindermayeri* can be regarded as a small and less specialized version of *Criotherium argalioides*. It shows the following strong agreements with that species:

The horn cores have a strong postero-lateral keel and a weaker anterior one.

There is deep irregular longitudinal grooving on some horn cores.

The axis of the horn cores is twisted, and twisted in the same direction as in *Criotherium*, and there is no open spiralling.

There is a localized raising of the mid-frontals suture forward of the horn bases and just behind the nasals. (This elevated suture is also to be seen in *Sporadotragus*.)

The central cavities of the upper molars remain joined to one another until fairly late in wear.

The left mandible BM(NH) M.15828 assigned to *Palaeoreas lindermayeri* has its P_3 and P_4 with transverse front and back edges (Pl. 6 fig. 2).

There is no valley in the lateral wall of P_4 in front of the hypoconid.

P_3 is fairly large in M.15828 in relation to P_4.

Some of the differences of *Palaeoreas lindermayeri* from all or various of the other spiral-horned antelopes considered in this paper also cause it to approach *Criotherium argalioides*. Such features are:

The rather massive horn cores of *Palaeoreas*. Their massiveness gives them an appearance of relative shortness.

The small divergence of the horn cores in anterior view.

The stronger angling of the braincase on the face axis.

The higher level of the frontals between the horn bases.

The usual disappearance of signs of the mid-frontals and parieto-frontals suture in adults.

The smaller separation of the supraorbital pits from one another.

A central longitudinal groove on the basioccipital.

The metaconid of P_4 not being directed backwards.

For these reasons it seems marginally better to place *Palaeoreas* in the Ovibovini than in the Antilopini, the resemblances to *Criotherium* being sufficiently strong to suggest not too remote a common ancestry. A count of skull character differences gave the result that *Palaeoreas lindermayeri* had 22 differences from *Protragelaphus skouzesi*, 15 from *Prostrepsiceros houtumschindleri* and 17 from *Criotherium argalioides*; this quantifies the problem and is an indication of how marginal the classification of *Palaeoreas lindermayeri* must be.

If it is accepted that *Palaeoreas* is an ovibovine, then it and *Criotherium* are the only members of the tribe with spiralled horn cores of any length. However this is probably not a severe isolating feature, because vestiges of spiralling remain in *Parurmiatherium*, and *Budorcas* and *Ovibos* have at least slight torsion. I don't think it would be advantageous to split them from other Ovibovini.

V. CONCLUSIONS

In a previous paper (Gentry 1970) I have described how the antelopes of the Fort Ternan upper Miocene site in Kenya, dated to 14 million years B.P., were closely related to Eurasian antelopes of the Vindobonian and equivalent time levels. They could be satisfactorily included in the tribes Boselaphini and Caprini, tribes which later became largely Eurasian in their distribution. It was just possible that some signs of ancestry to later African antelopes could be seen at Fort Ternan, but this was rather tentative, and the origin and development of African antelopes remains more undocumented than that of Eurasian ones. It is clear that some antelope groups confined to Africa by the historical period were also in northern India during the Quaternary and at least the later Tertiary. Work on such important African sites as Baringo, Kanapoi and Lothagam (Kenya) and Langebaanweg (Cape Province, South Africa) may throw more light on the history of African antelopes. This present paper on Samos has been intended to remove one source for confusion in deciphering this history. *Palaeoryx*, *Protoryx* and *Pachytragus* are not hippotragines and *Prostrepsiceros* and *Palaeoreas* are not tragelaphines. The only Samos antelope which at present looks as if it could be even remotely connected with the ancestry of any later African form is the unique skull of *Tragoreas oryxoides* (see above p. 284). In fact there are no firm grounds for detecting any African affinities among the Samos antelopes. They are more properly seen as an earlier stage in the evolution of Eurasian bovid faunas, and date from a time younger than the Fort Ternan fauna when regional differentiation must have been becoming more marked. I have discussed the historical zoogeography of antelopes at greater length in my Fort Ternan paper (Gentry 1970 : 310–317).

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VII. SUMMARY

This paper considers the classification, phylogeny and aspects of the zoogeography of two groups of antelopes prominent in the lower Pliocene fauna of Samos, and also known from the rich sites of Pikermi in Greece and Maragha in Iran.

Antelopes hitherto referred to a number of species of *Palaeoryx*, *Protoryx* and *Pachytragus* can be arranged in the following species:

Palaeoryx pallasi (Wagner) from Samos and Pikermi,
Protoryx carolinae Major from Pikermi,
Pachytragus laticeps (Andree) from Samos and Maragha,
Pachytragus crassicornis Schlosser from Samos.

Both *Pachytragus* species, and particularly the more advanced *P. crassicornis*, have affinities with the living goats (Caprini, *Capra*). *Protoryx carolinae* and *Palaeoryx pallasi* are related to *Pachytragus*, and none of these species belong to the African tribe Hippotragini, which is where they have been placed in Simpson's (1945) and other classifications of mammals, following work in the years between the two World Wars. *Protoryx carolinae* can be linked with Chinese lower Pliocene fossils and tentatively placed in the Caprini, while *Palaeoryx pallasi* could well be related to the Villafranchian ovibovine *Megalovis latifrons*. I suggest that *Palaeoryx* itself be placed in the Ovibovini.

Spiral-horned antelopes with anticlockwise torsion on the right side can be arranged in four species:

Prostrepsiceros houtumschindleri (Rodler & Weithofer) from Maragha and Samos,
Prostrepsiceros rotundicornis (Weithofer) from all three sites,
Protragelaphus skouzesi Dames from all three sites,
Palaeoreas lindermayeri (Wagner) from Pikermi and Samos.

Prostrepsiceros and *Protragelaphus* can both be taken as Antilopini, and are related more or less closely to the Indian blackbuck, *Antilope cervicapra*. *Palaeoreas lindermayeri* is best classified as a small and primitive ovibovine related to *Criotherium argalioides* of the Samos fauna. None of the spiral-horned antelopes from Pikermi, Samos or Maragha can be placed in the African tribe Tragelaphini. Bovids from these three sites can be seen as a stage in the evolution of those occurring later in Eurasia, and show no signs of relationship with African antelopes.

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PLATE 1

Palaeoryx pallasi

(Scales represent 20 mm)

FIG. 1. Lateral view of Lausanne cranium, 29, to show the ventral edge of the auditory bulla descending posteriorly to the front of the paraoccipital process. This is indicated by the arrow.

FIG. 2. Ventral view of the same cranium. The anterior tuberosities of the basioccipital are localized and without longitudinal ridges to the rear.

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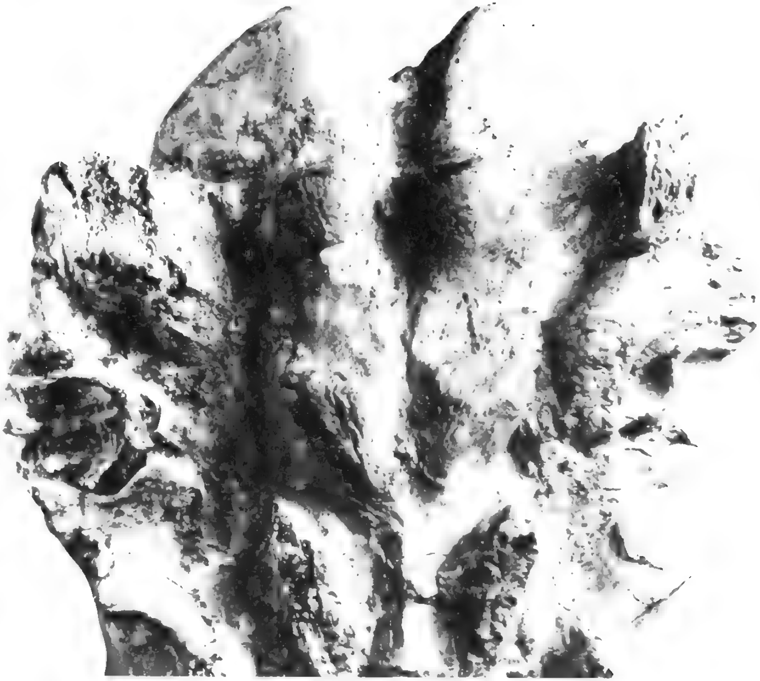

PLATE 2

Pachytragus laticeps

(Scale represents 10 mm)

FIG. 1. Posterior view of Lausanne cranium, 22, to show the shape of the occipital surface, the median vertical ridge and the large mastoids.

FIG. 2. Ventral view of the same cranium. The basioccipital has longitudinal ridges flanking a central groove.

FIG. 3. Section across right horn core, AMNH 23038, about 10 mm above the top of the pedicel. This view is looking towards the tip of the horn core from below, with the anterior edge towards the top of the page and the lateral side to the left.

FIG. 4. Section across left horn core, AMNH 22783, about 20 mm above the top of the pedicel. The horn core is oriented as in fig. 3, except that the lateral side is to the right.

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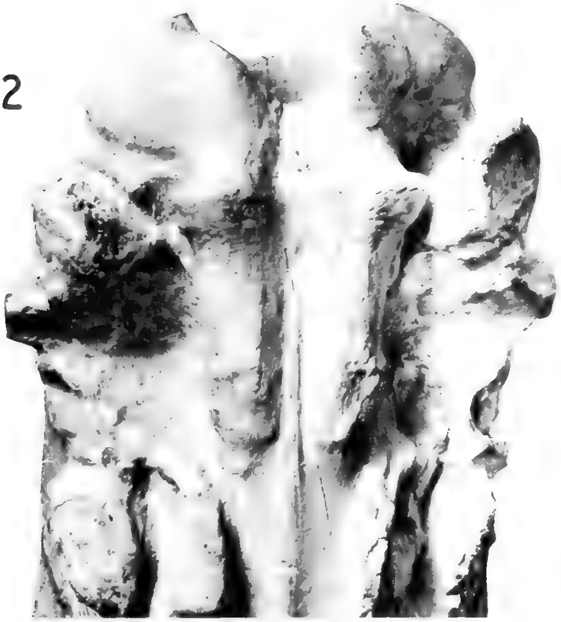

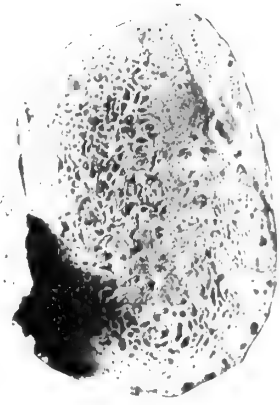

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PLATE 3

Pachytragus laticeps

(Scales represent 50 mm)

FIG. 1. Anterior view of Lausanne cranium, 30.

FIG. 2. Lateral view of the same cranium.

FIG. 3. Lateral view of the female skull, AMNH 20687, from quarry 1, Samos.

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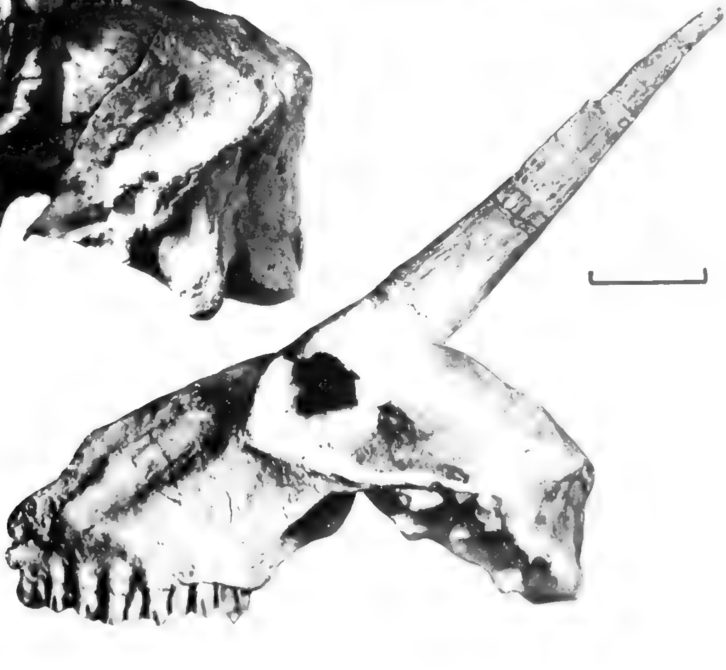

PLATE 4

Pachytragus crassicornis

(Scales represent 50 mm)

FIG. 1. Lateral view of skull, AMNH 20569, from quarry 5, Samos.

FIG. 2. Palate, AMNH 22981, from quarry 5. It is definitely of *Pachytragus*, and by its provenance is assumed to belong to *P. crassicornis*.

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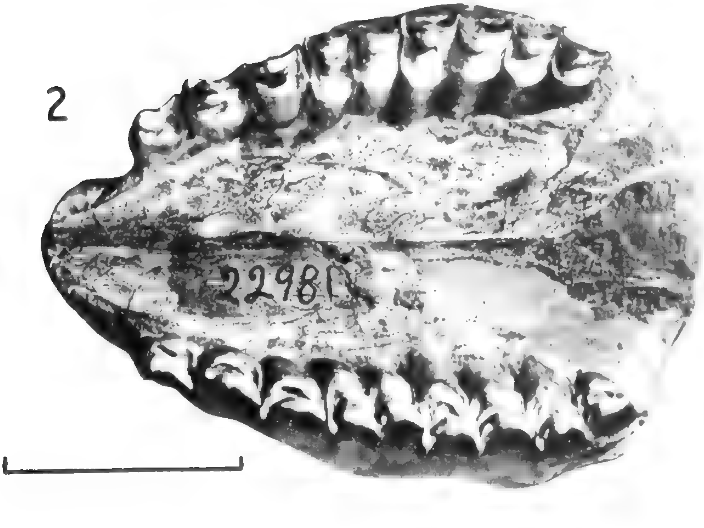

PLATE 5

(Scales represent 20 mm)

FIG. 1. Anterior view of a previously unfigured skull of ***Prostrepsiceros houtumschindleri*** from Maragha and now in Paris. Notice the anterior keel and divergence of the horn cores, and the small central and lateral flanges at the front of the nasals.

FIG. 2. Lateral view of a cranium of ***P. rotundicornis*** from Maragha and now in Paris.

FIG. 3. Lateral view of a skull of ***P. houtumschindleri*,** BM(NH) M.4192, from Samos. Notice the inclination of the braincase roof and of the horn core insertions in comparison with the cranium in fig. 2.

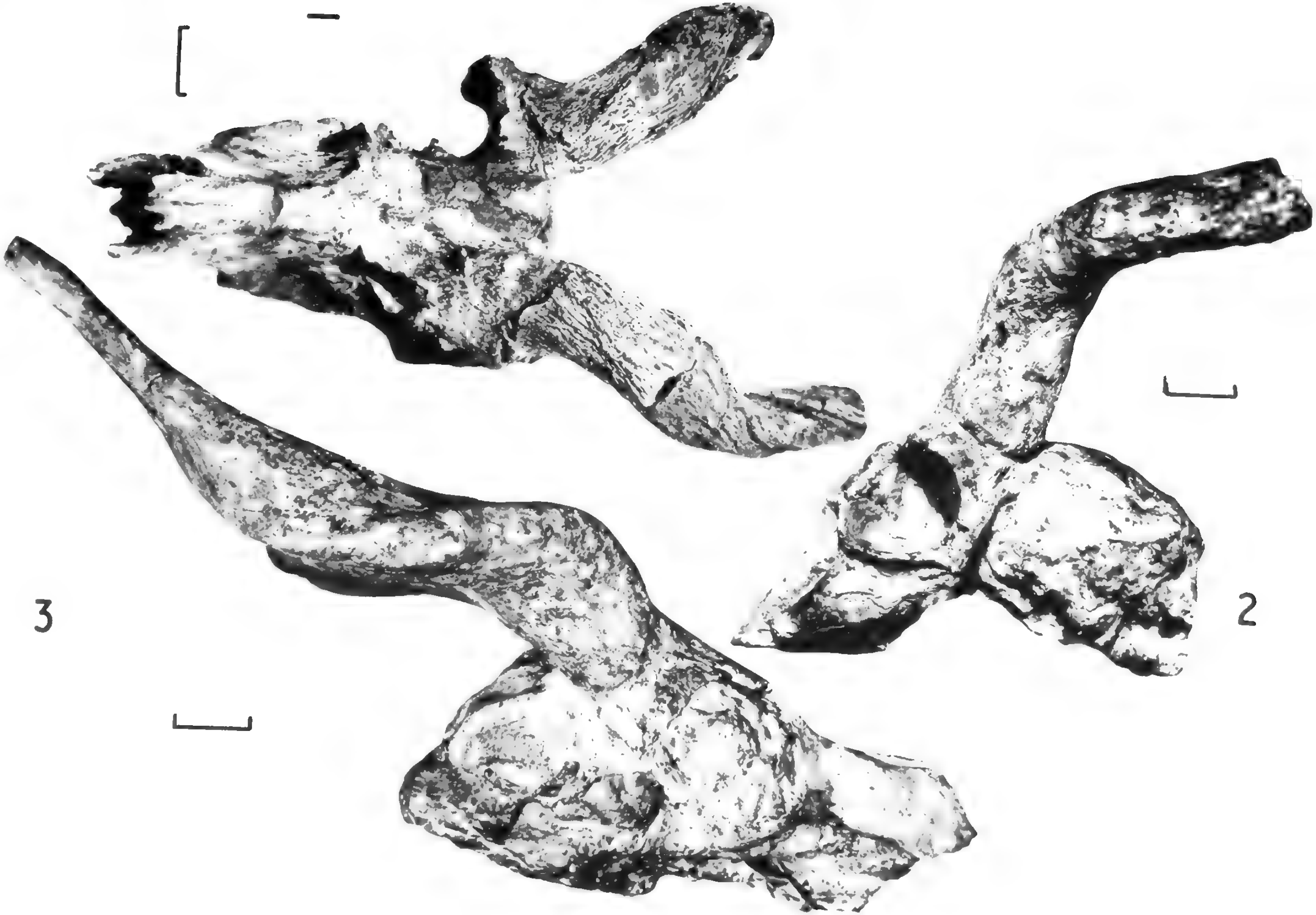

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PLATE 6

(Scales represent 20 mm)

FIG. 1. Anterior view of Lausanne frontlet, 25, ***Palaeoreas lindermayeri*** from Samos.

FIG. 2. Three lower dentitions from Pikermi. From above they are BM(NH) M.15828, left, of ***Palaeoreas lindermayeri***; M.13022, right, of ***Protragelaphus skouzesi***; M.13007, left, thought to be of ***Prostrepsiceros rotundicornis***.

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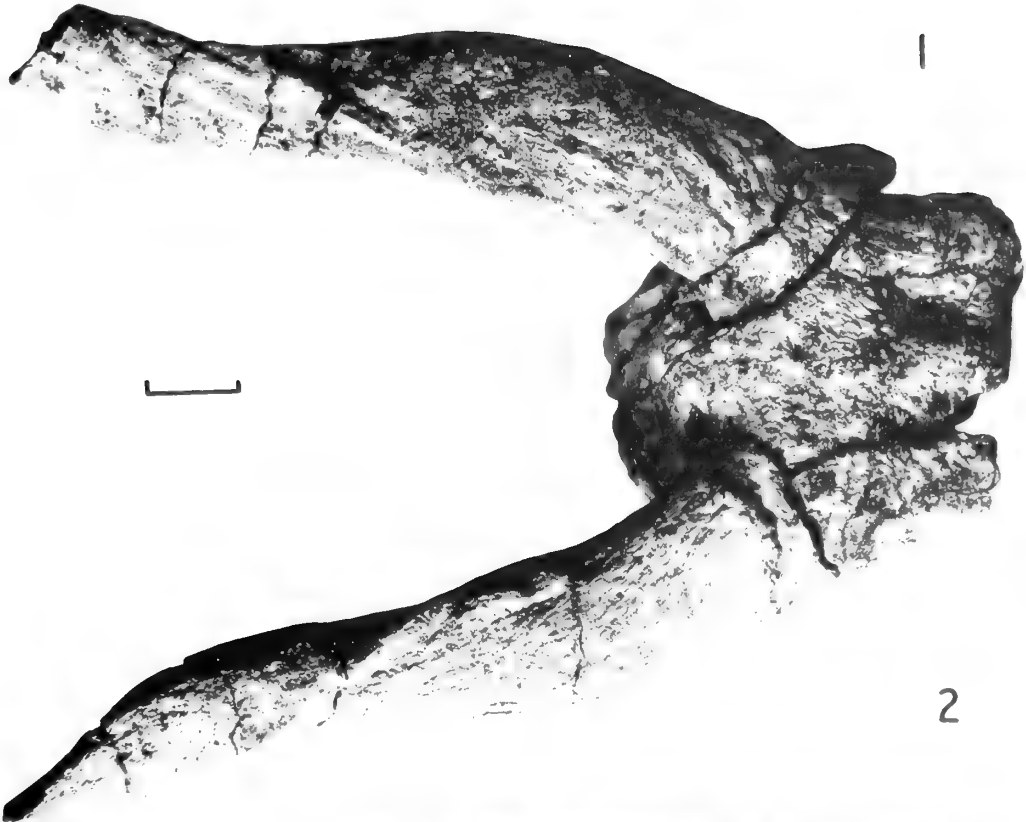

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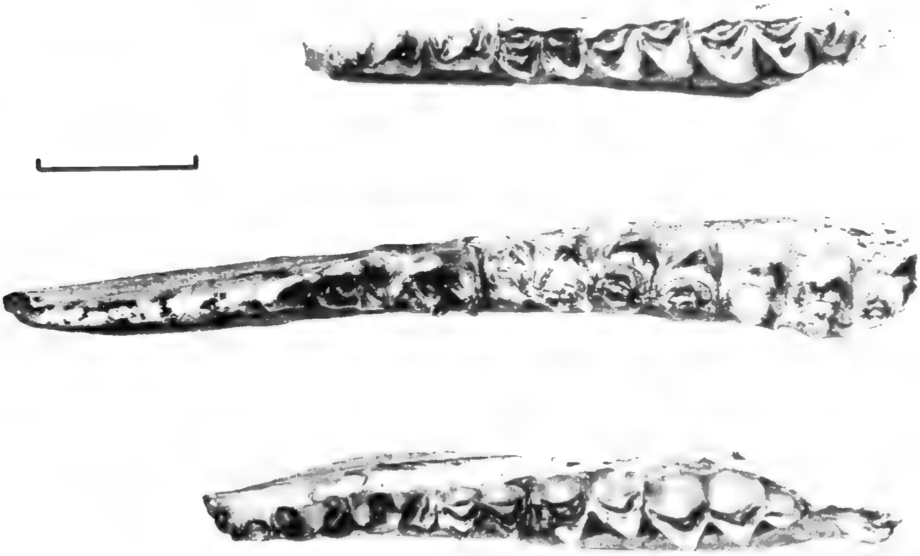

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BY

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Pp. 297–380; 11 *Plates;* 6 *Text-figures*

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By A. N. FATMI

CONTENTS

ABSTRACT

The stratigraphy of the Jurassic and Lower Cretaceous formations and Jurassic ammonites from Hazara, Kala Chitta, Nizampur, Western Kohat (Samana Range) and the Trans Indus Ranges in Northern Pakistan are described.

A provisional zonal scheme is proposed and correlation is suggested with Spiti, Cutch, Madagascar, Mediterranean Province, Middle East, and East Africa. Failure to recognize certain ammonite zones in the area may be explained by non-deposition, slow deposition, unfavourable facies, failure of collection or some combination of these factors.

Middle Callovian, Upper Oxfordian and Lower Kimmeridgian ammonites from the Trans Indus Range, Upper Oxfordian–Tithonian ammonites from Nizampur, Lower Toarcian ammonites from Kala Chitta and Lower Tithonian ammonites from northern areas of Hazara are recorded and described for the first time. In addition, a definite Aptian ammonite fauna is recognized in parts of Western Kohat and the Kala Chitta Range.

The faunal studies indicate that the Jurassic passes into the Cretaceous without a break in most areas of northern West Pakistan. The major stratigraphical breaks are Pre-Toarcian, Intra-Jurassic (pre-Upper Oxfordian, pre-Kimmeridgian or pre-Tithonian) and intra-Cretaceous (post-Lower–Middle Albian).

I. INTRODUCTION

Existing knowledge of the Jurassic–Cretaceous biostratigraphy in general, and of the ammonite faunas in particular, of the northern areas of Pakistan (fig. 1) is very imperfect. In the majority of cases the faunal descriptions are based on collections which lack adequate biostratigraphical control. The geological information available in more recent published literature (Davies 1930; Cotter 1933; Spath 1930, 1934, 1939; Arkell 1956; Pascoe 1959; Krishnan 1960), though it gives the impression of the presence in the area of various Jurassic–Cretaceous stages, does not clearly relate them to the rock succession and little attempt has been made to correlate them in different parts of the country.

This state of confusion may be judged by the following remarks of Arkell (1956: 393) on the Jurassic rocks of the Salt Range, "Very little palaeontological classification of these (Jurassic) rocks is yet possible, though ammonites occur. Callovian is indicated by Golden Oolite . . . . It was also found in working the fauna of the condensed and transgressive Valanginian beds that they contain a number of derived Upper Jurassic ammonite fragments which indicate the former presence of Middle Spiti Shales. Old records by Oppel of ammonites . . . suggest the presence of Upper Oxfordian also". Spath similarly (1939; 131, 152) recognized Callovian and Tithonian ammonite fragments from the Salt Range and its Trans Indus extension, but considered the Tithonian fauna to be derived, and doubtfully pointed out the Callovian ammonites to have come from the limestone below the "Belemnite Beds".

Encouraged by the known occurrences of ammonites in the area, a detailed study of selected Jurassic and Lower Cretaceous sections in northern Pakistan (figs 1, 3) was carried out during 1963–1966. In this paper the biostratigraphy of the Jurassic and Lower Cretaceous rocks and the systematic descriptions of Jurassic ammonites from Hazara, Kala Chitta, Nizampur, Samana Range (Western Kohat) and Trans Indus Ranges are presented. A tentative correlation of the various Jurassic and Cretaceous formations of northern West Pakistan is also offered. This work forms part of a Ph.D. thesis submitted to the University of Wales in 1968. The ammonites of Lower Cretaceous age will be described in a separate publication.

The Mesozoic rocks of northern West Pakistan (figs 2, 3) are exposed in the hill ranges bordering the Kohat district to the north (Samana and adjoining ranges) and extending eastward into Nizampur and the Kala Chitta Range. Further east of

Kala Chitta the outcrops take a north easterly swing and are exposed in Hazara Ranges (Margala and Murree Hills) lying between Abbottabad and Islamabad. These northerly placed Mesozoic out-crops are separated by a belt of Tertiary and Quarternary deposits from the southern outcrops of Western Salt Range and Trans Indus Ranges (Surghar, Maidan and Khisor Ranges including Shaikh Budin Hills). In the eastern and north-eastern limits the Mesozoic rocks of northern areas are separated from that of Himalaya (Spiti) by a belt of Tertiary and Quarternary

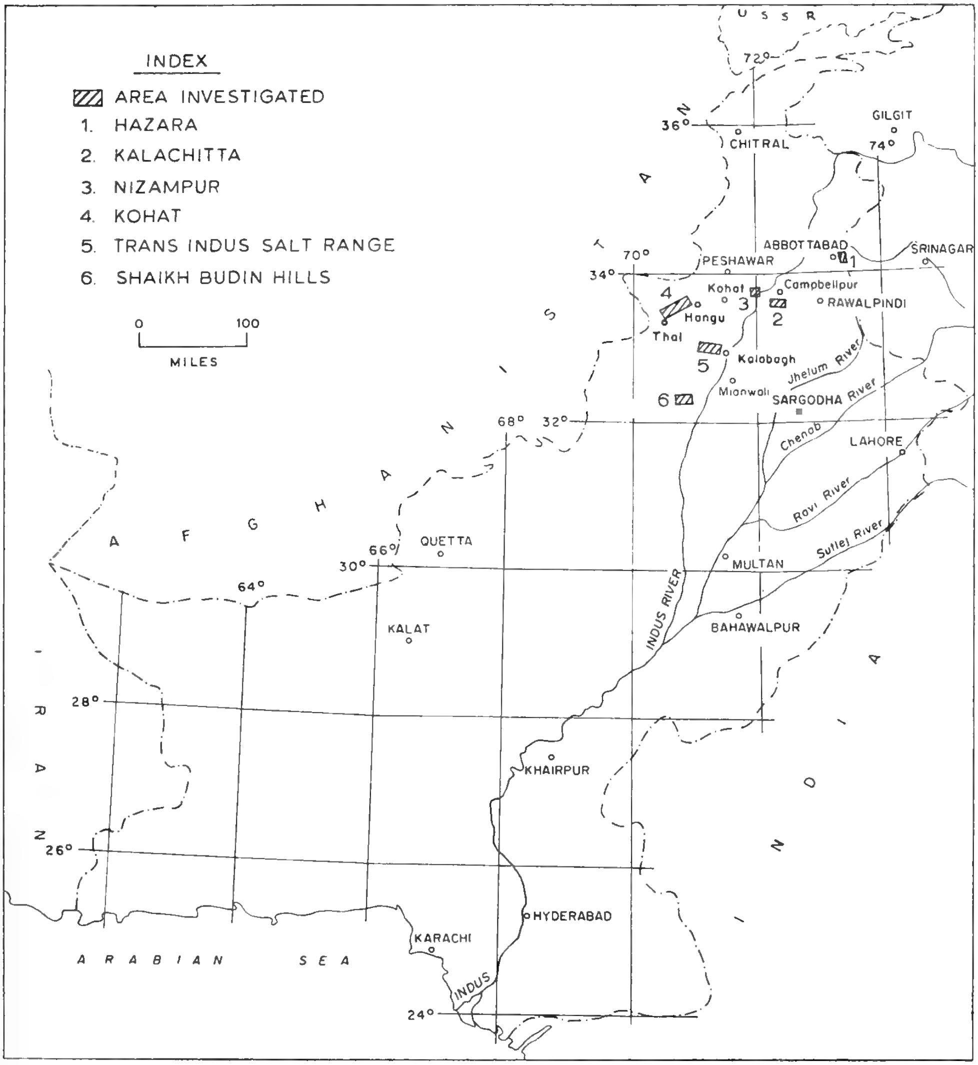
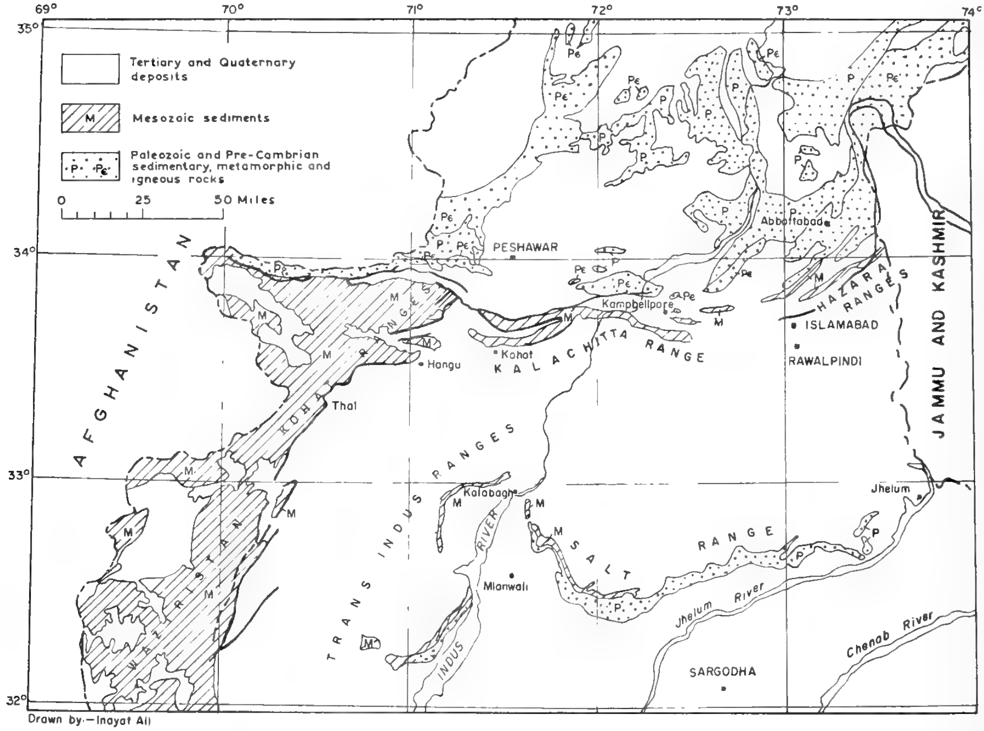


FIG. 1. Index map of West Pakistan showing areas investigated.

deposits while in the western limits the Tertiary and Quarternary deposits of D.I. Khan district separate it from the Mesozoics of Sulaiman Range and its northerly extension is Waziristan and Kurram Agency.

The area investigated falls between Lat. 32° N and 34° 30′ N and Long. 71° E and 73° 30′ E. Bordering it in the north are the high Karakoram-Hindukash mountain ranges with a complex geological history and with rocks belonging to a complex igneous and metamorphic suite of doubtful Precambrian to Tertiary age. On the southern boundary of the area, the Salt Range and Trans Indus Ranges with Precambrian to Tertiary rocks give place to the alluvial plain of River Indus through which protrudes near Chiniot and Shahkot (Kerana Hills), the reminiscent of the Precambrian metamorphic rocks of the Indian Shield.

The majority of the ammonites are preserved as internal moulds in a ferruginous, phosphatic, glauconitic, sandy, calcareous matrix, and much less commonly they have recrystallised or original shell matter preserved. The Callovian and Lower Jurassic ammonites are preserved in limestone. The Lower Jurassic (Toarcian) ammonites have abundant comminuted molluscan debris, are often fragmentary, and are unevenly distributed along the outcrop. The Callovian ammonites are better preserved and more complete.



Drawn by—Inayat Ali

FIG. 2. Geological map of parts of West Pakistan showing Mesozoic outcrops.

The Upper Oxfordian ammonites occur in condensed sandy, glauconitic, nodular marls (less than a foot in thickness) at the base of the Chichali Formation. They are commonly fragmentary and worn, though abundant, in certain parts of the outcrop, but irregular in their distribution. The specimens from the Trans Indus Ranges show a better preservation than those from the Kala Chitta and Nizampur (Mazari Tang). The ammonites are associated with bivalves, gastropods, brachiopods and belemnites.

The Lower Kimmeridgian ammonites are preserved in calcareous, ferruginous, phosphatic nodules and are not very common. They are located in the lower 10 to 15 feet of the Chichali Formation ("Belemnite beds") in the Trans Indus Ranges and in the basal 2 to 3 feet of the Chichali Formation (= "Spiti Shales") in parts of Hazara and Kala Chitta.

The Tithonian ammonites are more commonly distributed in the succeeding beds of the lower member of the Chichali Formation in the Trans Indus Ranges. In parts of Hazara they occur in the basal part of the Lumshiwal Formation (="Giumal sandstone") and show better preservation than that of the Trans Indus Ranges. Associated with ammonites are abundant belemnites, less commonly bivalves (*Trigonia* sp., *Gryphaea* sp.), brachiopods and reptilian remains.

This paper presents the results of the research work on Mesozoic Stratigraphy and Palaeontology of northern areas of West Pakistan carried out for a Ph.D. thesis at the University College, Swansea, University of Wales during 1967–68. Many colleagues and friends in and outside Pakistan have been of great assistance in providing helpful suggestions and criticisms. I am particularly indebted to Prof. F. H. T. Rhodes and Dr. J. C. W. Cope of University College, Swansea for their supervision, guidance and critical review of the work. For this paper I am deeply indebted to Dr M. K. Howarth who guided me in its presentation and has critically reviewed the fauna. Assistance of Dr. M. K. Howarth and the staff of the British Museum in reorganizing some of the illustrations and re-photographing the specimens for presentation in this paper is gratefully acknowledged. Special thanks are due to Dr J. H. Callomon of University College, London for his helpful criticism of the research work. Dr R. Casey, Mr N. J. Morris and Prof. D. V. Ager are thanked for their guidance and identification of some ammonites, bivalves and brachiopods respectively.

Financial assistance to carry out the research at the University College of Swansea from the Government of Pakistan and the Senate of the University College, Swansea is gratefully acknowledged.

The systematic descriptions mostly carry the standard morphological terms as defined in the Treatise on Invertebrate Palaeontology (1957: (L) Mollusca-4). The standard dimensions (diameter, whorl height, whorl thickness, umbilical diameter) are given in millimeters and as percentage of diameter. The measurements were made over the ornamentation unless specified in the text.

II. HISTORY OF PREVIOUS RESEARCH

The presence of Jurassic and Cretaceous rocks in northern West Pakistan was first recognized in the late 19th century (Waagen 1875; Wynne 1878; 1880, Griesbach

1891; Middlemiss 1896), but it was many years later that a more detailed Mesozoic succession was established by the field studies of Davies (1930) in the Samana Range, Cotter (1933) in the Kala Chitta Range, Spath (1939) and Gee (1945) in the Salt Range and its Trans Indus extension (Trans Indus Ranges).

The ammonite collections of Gee, Cotter, Davies and such other workers as Wynne and Fleming were described by Spath in a series of monographs (1930, 1934, 1939).

Spath based his palaeontological conclusions on the stratigraphical information provided by other workers. His interpretation of the fauna, though fairly accurate, lacks in many instances a proper biostratigraphical control. Four of his observations, mentioned below, have been found to require reassessment in the light of the present work.

1. Spath and others (Arkell, Pascoe, Krishnan) suggested a break in sedimentation at the Jurassic–Cretaceous boundary. Although Spath mentioned Upper Jurassic ammonites in the basal "Belemnite Beds", he considered them to be derived. The present study shows that there is no break of sedimentation at the Jurassic–Cretaceous boundary.

2. Spath (1930 : 65–66) suggested the absence of Aptian transgression (which reached Persia and Cutch) from most of the areas of northern West Pakistan. The present discovery of Aptian ammonites in Kohat-Nizampur area indicates sea connections with Cutch and Persia via Baluchistan in at least the western half of the area examined.

3. Spath (1939 : 132) believed the lowermost Neocomian (Berriasian and Lower Valanginian) to be absent in the main Salt Range (implying the western part) and the Tithonian and rest of the Upper Jurassic down to Callovain to be absent from the Trans Indus Ranges. In the present study, it was found that Berriasian and Lower Valanginian ammonites occur in the western Salt Range and that a definite Upper Oxfordian–Lower Kimmeridgian–Tithonian and Berriasian succession is present in the Trans Indus Ranges.

4. Spath (1939 : 131) postulated the continuity of "Spiti Shale" facies of Spiti, Himalaya in the Hazara, Kala Chitta, Waziristan and Baluchistan regions and the subsequent denudation and erosion of the Upper Jurassic sediments prior to Berriasian transgression. The present study indicates that the Upper Oxfordian–Lower Kimmeridgian transgression connected Cutch with Spiti through parts of the area under discussion. The major transgression, however, took place in the Tithonian and effected all the area extending to Baluchistan in the west.

The more important contributions to the Mesozoic stratigraphy and palaeontology of individual areas may be summarized as follows:

Hazara. Rather fragmentary information exists in literature on the area (Waagen and Wynne 1872; Middlemiss 1896; Wadia 1926; Arkell 1956; Pascoe 1959; Krishnan 1960). Waagen and Wynne and later Middlemiss recognized the following Himalayan (Spiti) succession:

3.	"Giumal Sandstone"	Cretaceous
2.	"Spiti Shales"	Jurassic
1.	"Kioto Limestone"	Mainly Triassic

The "Kioto Limestone" of Hazara is the most confusing unit being relatively poor in ammonites and other well-preserved fossils. It has been referred to the Upper Triassic by Middlemiss (1896), Wadia (1926 : 155), Pascoe (1959 : 897) and to the Upper Triassic–Lower Jurassic by Cotter (1933), Arkell (1956) and Krishnan (1960). The Upper Triassic age was suggested on the reported occurrence of fragmentary mollusca, identified as *Megalodon, Dicerocardium, Chemnitzia* (Pascoe: 898). More recently Davies and Gardezi (1965) recorded *Bouleiceras* (identified by Dr Howarth of the British Museum) of Lower Jurassic age (Lower Toarcian) from the lower part of the "Kioto Limestone" in parts of Hazara (Bagnotar).

The "Spiti Shales" in Hazara are reported to contain *Belemnopsis gerardi* (Oppel) and *Virgatosphinctes frequens* (Oppel).

Spath (1933 : 804) recorded the Berriasian ammonites *Neocosmocarms octagonides* (Uhlig) and *Neocosmoceras subradiatus* (Uhlig) from Murree Hills in Hazara and correctly thought them to have come from below the Albian ammonite beds and above the *Virgatosphinctes frequens* (Oppel) horizon in the Guimal Sandstone (Pascoe 1959 : 1186) near Kathwal. A similar Lower Tithonian ammonite fauna from this area is described here.

From the upper part of the "Giumal Sandstone" Spath (1930) described Middle Albian ammonites such as *Lyelliceras lyelli* (d'Orbigny), *Douvilleiceras* aff. *monile* (J. Sowerby), and *Oxytropidoceras* aff. *roissyanum* (d'Orbigny). He correlated the Hazara Albian ammonite bed with that of Kala Chitta and Kohat (Samana Range) and pointed out the abundance of *Lyelliceras* in Hazara and that of *Douvilleiceras* in the Samana Range.

Middlemiss (1896) and Wadia (1926) compared the Jurassic rocks of northern Hazara with the "Spiti Shales" of Himalaya (Spiti) and the more arenaceous facies of southern Hazara with the Jurassic of the Salt Range. It is, however, not evident which arenaceous rocks they implied in the correlation.

Kala Chitta Range. Cotter (1933) carried out the first detailed survey of the Kala Chitta Range. His fossil collections were studied and monographed by Spath (1934—Cephalopoda), Cox (1935—Bivalves and Gastropoda) and Muir Wood (1937—Brachiopoda). Cotter recognized the following Mesozoic succession.

"Shales north of Kawaghar".		(uncertain age ? Palaeocene)
"Giumal" limestone, sandstone and sandy limestone	Undifferentiated .	Upper Oxfordian to Albian
"Kiota Limestone"		Upper Triassic to Liassic.

Cox (1935) identified *Indopecten* sp. of Upper Triassic age and *Lima gigantea* (Sowerby), *Eopecten velata* (Goldfuss), *Plicatula spinosa* (Schloth) of Lower Jurassic age from the "Kioto Limestone, but no precise stratigraphic position of these fossils was given. He further identified the Middle Jurassic bivalves *Corbula lyrata* (Sowerby), *Protocardia grandidieri* (Newton), *Eomiodon indicus* Cox from the gray rubbly limestone, and placed them doubtfully in the upper part of the "Kioto Limestone". Cox compared the fauna with the Kuar Bet Beds of Cutch and regarded it as Bajocian, but with the reassessment of the fauna of Kuar Bet Beds the age of the beds was changed to Upper Bathonian (Arkell 1956 : 391, 400).

Spath (1933 : 803) briefly mentioned some Lower Triassic ammonites submitted to him in Wynne's Punjab collections from "Central Kala Chitta Pahar" (Kala Chitta Range), but without any precise location or stratigraphic position. In the present work the stratigraphy of the "Kioto Limestone" is redefined on the basis of newly found fossil horizons and changes in lithology. The limestone is divided into five distinct formations. The lower three Triassic formations are separated with a marked disconformity from the overlying Lower and Middle Jurassic formations.

From the ammonite collections of Cotter marked "basal Giumal", Spath (1934) identified a typical Upper Oxfordian (Transverserium Zone) and Tithonian assemblage including species of *Perisphinctes*, *Mayaites polyphemus* (Waagen), *Blanfordiceras*, *Aulacosphinctes*, *Himalayites* etc. Cox (1935) identified *Exoygra fourtaui* Stefanini, *Gryphaea balli* (Stefanini) and *Ctenostreon proboscideum* (J. Sowerby). Although he assigned an Upper Oxfordian age to the assemblage, he mentioned rightly that *Gryphaea balli* is abundantly distributed in the basal Kimmeridgian of British Somaliland, and the present study shows that this species occurs in beds of Lower Kimmeridgian and younger age.

From the upper part of "Giumal" Spath identified *Oxytropidoceras* and Cox *Neithea attockensis* Cox, *Exogyra arduennensis* (d'Orbigny) and assigned a Middle Albian age. Cox also identified *Trigonia ventricosa* Krauss from the "Giumal Sandstone" and assigned a Neocomian age.

Summarizing the geological information on the Attock district (Kala Chitta Range), Arkell (1956 : 400) stated "the Spiti Shales in turn are overlapped by Giumal Sandstone, which takes on a shelly facies and incorporates at the base, or rests on condensed representatives of, certain Oxfordian horizons which belong low down in the Spiti Shales". Similar views were expressed by Cotter (1933) who contended that the "Spiti Shales" may not have been deposited in the area. The present study indicates that the "Spiti Shales" and the "Giumal Sandstone" renamed in accordance with the Stratigraphic Code of Pakistan as the Chichali and Lumshiwal Formations respectively are distinct and recognizable units which show lateral variations in lithology and thickness, but are persistent in the area investigated.

Nizampur. Excepting for some general remarks regarding the presence of Jurassic and Cretaceous rocks (Griesbach 1891; Pascoe 1959 : 1314, 1169) there is no published information on the fauna of this area.

Kohat district. L. M. Davies (1930) was the first to define the Mesozoic succession in the Samana Range and assign more precise ages based on his own observations and identification of the fossils by Cox (1930—gastropods and bivalves), Muir-Wood (1930—brachiopods), Currie (1930—echinoids) and Spath (1930—ammonites). Davies established the following sequence in the Samana Range.

7.	"Upper Lithographic Limestone"	Upper Cretaceous
6.	"Variegated Series"	
5.	"Lower Lithographic Limestone"	
4.	"Main Sandstone Series"	Lower Cretaceous
3.	"Belemnite Bed"	Neocomian
2.	Samana Suk Limestone	Uppet Jurassic
1.	"Lowest Samana Beds"	Lower-Middle Jurassic

From the upper part of Unit 1 Muir-Wood identified *Rhynchonelloidea arcuta* (Quenstedt) and the horizon was assigned a probable Upper Bathonian and possible Lower Callovian age.

From the upper part of the Samana Suk Limestone (Unit 2) Davies recorded traces of ammonites, belemnites and fragmentary crinoids (*Pentacrinus* sp.) and considered the age to be Upper Jurassic.

From Unit 3 ("Belemnite Bed") Davies reported abundant belemnites, but no ammonites from the Samana Range. He did collect one ammonite from the Khadimakh hill (Kadamak of Davies), which was identified by Spath as *Olcostephanus* (*O.*) aff. *astierianus* (d'Orbigny) and assigned a Lower Hauterivian age. It is from this formation that a fairly representative Berriasian–Valanginian ammonite fauna was collected during the present survey.

From the uppermost bed of Unit 4 ("Main Sandstone Series") poorly preserved gastropods, bivalves, echinoids, brachiopods and ammonites have been monographed. Amongst the ammonites Spath described *Douvilleiceras mammillatum* (Schlotheim), *Cleoniceras daviesi* Spath and *Brancoceras indicum* Spath etc. A Middle Albian age was assigned to the formation.

No fossils were recorded from Units 5 to 7. The present work indicates that the Unit 6 ("Variegated Series" of Davies) is not present in the area and the Upper and Lower Lithographic Limestone units follow each other conformably and are distinguishable as members of a formation. The limestone contains abundant small Foraminifera (*Globotruncana* sp.) and rarely ammonites (in the basal part).

Trans Indus Salt Ranges. Waagen (1875) compared the Jurassic rocks of the Salt Range with that of Cutch, and Wynne (1880) further pointed out the similarity of the "Golden Oolite" (Callovian) of Khera Hill of Cutch with similar rocks on either side of the River Indus. The strata that Wynne referred to as "Golden Oolite", a name also quoted in later literature (Arkell 1956 : 393), occur in a sandy, ferruginous formation (Pascoe 1959 : 1158), the "Variegated Series" of Gee (1945). Their stratigraphic position is much below the presently established Callovian beds in the uppermost part of the overlying "Baroch Limestone".

The most substantial contribution to the geology of the Salt Range and its Trans Indus extension could be attributed to E. R. Gee (1945) who divided the Jurassic and Cretaceous rocks as follows:

4.	"Lumshiwal Sandstone"	Cretaceous
3.	"Belemnite Beds"	Lower Cretaceous-Jurassic
2.	"Baroch Limestone"	Jurassic
1.	"Variegated Stage"	Jurassic

No precise ammonite horizons were reported from either the "Variegated Stage" or the "Baroch Limestone", but Spath (1933 : 802) recorded *Subkossmatia flemingi* (Fleming's collections) from the "Calcareous strata below the coal shales with belemnites" near Kalabagh. Spath also identified some fragmentary ammonites as *Hubertoceras* sp., *Obtusicostites* sp. and *Kinkeliniceras* sp. marked by the collectors "from the Belemnite Beds of Miranwal nala, Makerwal". He (1939 : 121) correctly thought their position to be below the "Belemnite Beds" in the Jurassic limestone. Spath (1933 : 802) mentioned some unlabelled ammonites housed in the British

Museum, which he considered to have come from the Chichali Hills in the Trans Indus Salt Ranges. He identified them as *Indocephalites transitotious* Spath, *Pleurocephalites habyensis* Spath and *Kamptokephalites magnumbilicatus* (Waagen). Because of their golden matrix. Spath first thought them to have come from Cutch. Krishnan (1960 : 419) placed the above mentioned ammonites in the limestone above the "Variegated Series" without reference to their locality. If the occurrence of the Lower Callovian ammonites from the Chichali Hills is correctly reported, they must be very rare as no such ammonites were detected in the Chichali Hills during the present survey.

A confusing account of some Upper Jurassic ammonites and belemnites (considered derived) is represented in the literature (Arkell 1956 : 393; Pascoe 1959 : 1159–1160; Spath 1933 : 802; 1939 : 162). These ammonites are believed to have come from the "Belemnite Beds" of Neocomian age. Pascoe (1959) reviewing the Jurassic rocks of the Salt Range and the Trans Indus Ranges, pointed out correctly the presence in these areas of Bathonian, Callovian and Tithonian (mentioned only from Sokun in the Main Salt Range). He, however, contended that several ammonite found in the overlying Cretaceous beds ("Belemnite Beds") appeared to have been derived from the Spiti Shales. Arkell (1956 : 393) similarly pointed out the overstepping of the Neocomian "Belemnite Beds" on the underlying Jurassic. The views expressed by Arkell, Pascoe and Krishnan are presumably based on Spath's analysis of the faunas who contended (1939 : 132) "there is no evidence that the Infra-Valanginian (Berriasian) and Lower Valanginian were ever represented in the Salt Range proper where the Middle and Upper Valanginian may rest upon the Tithonian. Conversely the Lower Valanginian must have been comparatively well developed in the west (Trans Indus Ranges) where, however, the Tithonian is completely absent in addition to the rest of the Upper Jurassic down to Callovian".

An Upper Oxfordian–Kimmeridgian–Tithonian–Berriasian–Valanginian ammonite sequence has been established in the "Belemnite Beds" by the present field investigations. These beds rest disconformably on the Middle Callovian ammonite bed of the "Baroch Limestone". The Jurassic–Cretaceous boundary is transitional and not disconformable as previously thought.

Shaikh Budin Hills. Lower Jurassic ammonites (*Bouleiceras* sp.) and Callovian brachiopods have been reported from this area (Pascoe 1959 : 1160–61). From a green glauconitic sandstone (possibly "Belemnite Beds") Sahani (1939) identified Oxfordian and Kimmeridgian brachiopods (*Zelleria* sp., *Kingena* sp.). Spath (1939 : 136) recorded *Hibolithes subfusiformis* (Raspail), *Cymatoceras* sp. and crioceratid fragments and concluded the presence of "Belemnite Beds" in the area. C. W. Wright (unpublished oil company report) identified *Blanfordiceras acuticostatum* (Uhlig) and *Virgatosphinctes communis* Spath from the basal part of the "black zone" ("Belemnite Beds"). Similar Tithonian ammonites were collected and are described here.

III. GENERAL SEQUENCE

The Mesozoic rocks of the area comprise of the following formations. The oldest is underlain disconformably (Para-conformity of Teichert and Kummel, 1966) by

Permian Chhiddru Formation and the youngest overlain disconformably by Palaeocene Hangu Formation or Dhak Pass Formation.

8.	Kawaghar Formation	Upper Cretaceous
		Disconformity
7.	Lumshiwal Formation	Upper Jurassic to mainly Lower Cretaceous
6.	Chichali Formation	Upper Jurassic to Lower Cretaceous
5.	Samana Suk Limestone	Middle Jurassic
		Disconformity
4.	Datta Formation	Lower Jurassic
		Disconformity
3.	Kingriali Formation	? Upper Triassic
2.	Tredian Formation/ Chak Jabbi Limestone	? Middle Triassic
1.	Mianwali Formation	Lower Triassic

Mianwali Formation: The name Mianwali was used by Gee (in Pascoe, 1959 : 852) and formalized by Kummel (1966 : 373–374) as a formation for rocks referred to previously (Waagen 1875; Wynne 1878) as "Ceratite Limestone", "Ceratite Marls", "Ceratite Sandstone" and "Bivalve Beds". The formation is marine consisting of limestone, marls, with subordinate sandstone and dolomite. Kummel (1966) divided the formation into three members (Kathwai, Mittiwali and Narmia). The formation is 350–600 feet thick in the Salt Range and Trans Indus Ranges and 130 feet thick (base not exposed) in the Kala Chitta Range.

Tredian Formation/Chak Jabbi Limestone: The name Tedian was introduced by Gee (written communication to the Stratigraphic Committee of Pakistan) for rocks referred to earlier by him (1945) as Kingriali Sandstone in Salt Range and Trans Indus Ranges. It consists of shale (lower part) and sandstone (upper part). The thickness is 130–207 feet. In Kala Chitta the equivalent rocks which immediately overlie the Mianwali Formation are sublithographic, medium bedded, unfossiliferous limestone named here as Chak Jabbi Limestone. The thickness is 110 feet. No Tredian Formation lithology is developed in Kala Chitta.

Kingriali Formation: Overlying the Tredian Formation of the Salt Range and Trans Indus Ranges and the Chak Jabbi Limestone of Kala Chitta are the massive to thick bedded dolomite and dolomitic limestone of the Kingriali Formation, (the "Kingriali dolomite" of Gee, 1945). The unit is 300–350 feet thick and is probably present in Hazara and parts of Kohat.

Jurassic and Lower Cretaceous Formations: These comprise of clastic and carbonate rocks of marine to non-marine origin and are overlain and underlain disconformably by Upper Cretaceous and Triassic formations respectively. A disconformity between the Middle and Upper Jurassic is also present (Chapter IV).

Kawaghar Formation: The name Kawaghar is here adopted (after Day of Attock Oil Company) for rocks referred to previously as "Lithographic Limestone" in unpublished Geological Survey of Pakistan and Oil Companies reports. The formation is typically a lithographic to sublithographic grey limestone with subordinate marls and shale in Western Kohat and Hazara. In Eastern Kohat, Nizampur and northern

Kala Chitta, the lithology is mainly dark marls and calcareous shale with subordinate limestone. The thickness varies from 147 to 420 feet. The formation is missing in southern Kala Chitta, Salt Range and Trans Indus Ranges.

IV. STRATIGRAPHY OF THE JURASSIC AND LOWER CRETACEOUS ROCKS OF THE AREA

The ammonites described in this publication were collected from the following four formations which are over and underlain disconformably by Upper Cretaceous and Triassic rocks (fig. 4).

4.	Lumshiwal Formation 32–687 ft	Upper Jurassic to mainly Lower Cretaceous
3.	Chichali Formation 30–213 ft	Upper Jurassic to Neocomian
	Disconformity	
2.	Samana Suk Limestone 220–1087 ft	Middle Jurassic
1.	Datta Formation 60–1300 + ft	Lower to Middle Jurassic

These formations have large aerial extent. They show significant lateral facies changes and, in most areas, the lithological boundaries transgress time planes (fig. 5).

Datta Formation

The name Datta Formation was introduced by Danilchik (1961) from the Datta nala in the Trans Indus Salt Ranges for the "Variegated Stage" of Gee (1945). The name is here adopted for similar rocks (fig. 4) in western Kohat ("Lower Samana Beds" of Davies 1930), Kala Chitta Range ("Ferruginous Beds in the Kioto Limestone" of Cotter 1933, "Red Clay Zone" and "Sumbal Panni Clay" of Oil Company Geologists), and Hazara ("Maira Formation" of R. G. Davies and Gardezi 1965).

Trans Indus Ranges

This area forms the type locality of the Datta Formation. The lithology consists of variegated sandstone and shale with some argillaceous limestone interbeds in the upper part, and coaly, carbonaceous, ferruginous and fireclay beds in the lower part. It rests with a disconformity on the ?Upper Triassic Kingriali Formation and is transitional with the overlying Samana Suk Limestone.

The thickness ranges from 500 feet in Nammal Gorge to 700 feet in Datta nala (Danilchik and Shah (1967) and over 1300 feet in the Shaikh Budin Hills (Gee 1945; Habib Abbas and Bhuyan 1966, unpublished report). It thins out east of Nammal Gorge and is thick towards the west and south west in the Trans Indus Ranges.

Fauna and Age: Pascoe (1959 : 1160) has recorded *Bouleiceras* sp. from Shaikh Budin Hills (without any stratigraphic position or locality). Spath (1933 : 802) identified *Indocephalites* aff. *transitorious* Spath and *Kamtokephalites* cf. *magnumbilicatus* (Waagen) which he thought to have come from the Chichali hills in the Surghar Range.

Commenting on this fauna Spath (1933 : 802) said "on account of their matrix I have up to now taken them to be from Kachh (India). The preservation in

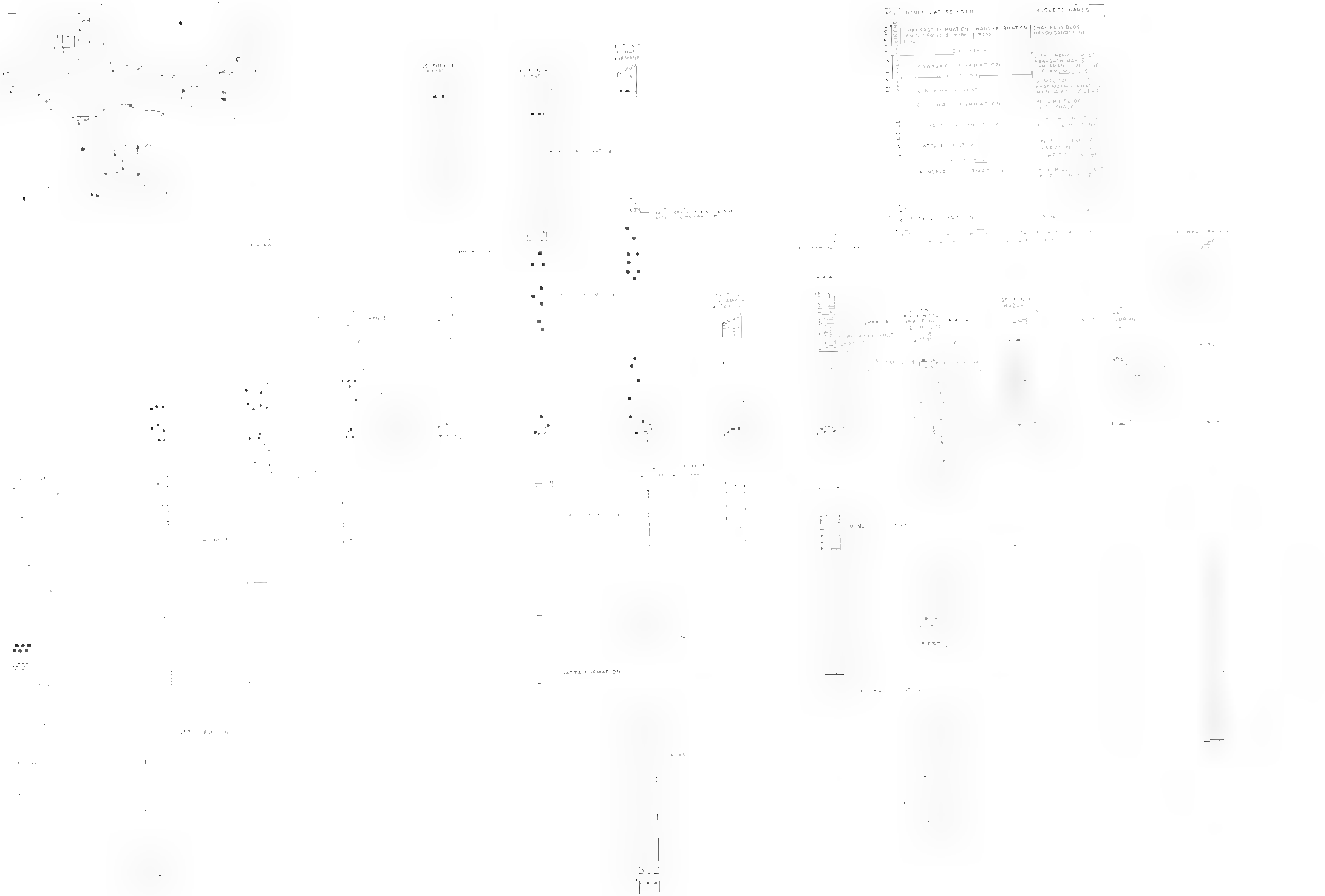


Fig. 3. Lithological sections of the Mesozoic rocks of Hazara, Kala Chitta, Nizampur, Kohat, Trans Indus Ranges including Shaikh Budin Hills, West Pakistan

the characteristic yellow and crimson matrix of the ferruginous 'macrocephalus' beds is identical with that of certain undoubted Kachh examples". The same fauna has been listed by Krishnan (1960 : 410) and Pascoe (1959 : 1160) from the limestone which overlie the "Variegated stage" in the Trans Indus Ranges. Spath (1933) further pointed out the similarity of "golden oolite" of Cutch with the "golden oolite" referred by Wynne (1878 : 101; 1880 : 46–47) from the Salt Range and the Trans Indus Extension. Wynne's so-called "golden oolite" occurs in the upper part of the Datta Formation (Pascoe 1959 : 1158). If the *Bouleiceras* and other ammonites are correctly reported the Datta Formation in this area is Lower to Middle Jurassic in age and may be correlated with Western Kohat.

In the present Survey, no Lower Callovian ammonites were found in the Chichali hills (mentioned by Spath 1933), and this occurrence may still be regarded doubtful until their correct stratigraphic position or occurrence is established by future work.

Kala Chitta–Nizampur area: In the Kala Chitta Range a rather confused name of "Kioto Limestone" was used by Cotter (1933) for the limestone below the "Giumal and Spiti" sequence. An Upper Triassic to Liassic age was assigned by Cotter. The upper age limit was later extended to Upper Bathonian on the basis of the similarity of bivalves with the Kaur Bet Beds of Cutch (Arkell) 1956 : 400. During the present study it was found that the "Kioto Limestone" of Cotter consists of five distinct formations, and the Triassic–Jurassic contact is disconformable. The five divisions are as follows (fig. 4: Section 4).

5.	Samana Suk Limestone	620 ft Middle Jurassic
4.	Datta Formation	61 ft Lower Jurassic

Disconformity

3.	Kingriali Formation, dolomite, dolomitic limestone, massive, thick bedded, brown to greyish brown	300 ft ? Upper Triassic
2.	Chak Jabbi Limestone, grey, medium bedded, lithographic to sublithographic limestone, unfossiliferous, slightly dolomitized in beds and equivalent to Tredian Formation ("Kingriali Sandstone") of the Salt Range.	110 ft ? Middle Triassic
1.	Mianwali Formation, thin bedded limestone, calcareous shale and marls, green, grey, argillaceous with abundant ammonites	130 + ft Lower Triassic (base not exposed)

The Triassic sequence: The Lower Triassic Mianwali Formation is exposed in the faulted outcrops north of Chak Jabbi Rest House (43 C/6) and in the core of the anticline one mile east south east of Bagh (43 C/1).

The ammonites (to be studied and described) include *Owenites*, *Anokashmirites*, *Subvishnuites*, *Xenoceltites*, *Xenodiscoides*, *Koninckites*, *Kymatites* and *Paranorites*.

The ammonites are typically Scythian and represent a mixed Himalayan and Salt Range assemblage.

The Mianwali Formation is overlian by Chak Jabbi Limestone in Kala Chitta which stratigraphically hold the same position as the Tredian Formation in Salt Range and Trans Indus Ranges. The formation is well exposed in Bagh and Chak Jabbi outcrops. It is overlain by the thick cliff-forming, brown weathering Kingriali Formation.

Overlying the Triassic Kingriali Formation with a marked disconformity (best seen in the Chakdalla section) is the Datta Formation of Kala Chitta Range. In a measured section near Chakdalla (43 C/6), the Datta Formation is 61 feet thick and can be divided into three members. The upper member (19 ft) is red clays and thin bedded limestone. The middle member (22 ft) is grey, nodular marly limestone with *Bouleiceras* and other fossils. The lower member consists of red and white quartzose and hematitic sandstone with (locally) fire clay horizons. As compared to the Salt Range, Trans Indus Ranges and Western Kohat, the thickness is much reduced in the Kala Chitta Range.

Fauna and Age: The fauna from the middle member consists of *Bouleiceras nitescens* Thevenin, *Bouleiceras chakdallaense* sp. nov., *Spiriferina* sp. *Vela ta velata* (Goldfuss), *Pecten* sp. (similar to *Indopectan* sp. figured by Cox 1935 from this area), *Lima* (*Plagiostoma*) *gigantea* J. Sowerby and indeterminate corals and gastropods. The age of the middle member is Lower Toarcian and the age of the formation in the Kala Chitta area is Lower Jurassic (mainly Toarcian).

Western Kohat (*Samana Range*)

The Datta Formation in Western Kohat shows a significant facies change, and consists of thin to medium bedded, grey to brownish grey limestone with interbedded sandstone, calcareous sandstone, sandy, oolitic limestone and shale. In a measured section north east of Shinawari, on the western end of the Samana Range, the thickness is over 1300 feet, the base being faulted against Tertiary shale. The upper contact is gradational with the overlying Samana Suk Limestone (fig. 4, section 7).

The Datta Formation is not exposed in the Khadimakh section, but north of Darsamand 500 to 600 feet crops out in the core of an anticline. In the Tribal Hills north and east of the Samana Range and Shinawari a greater thickness seems to be developed, but due to inaccessibility of this area it has not yet been studied. As correctly pointed out by Davies (1930) the possibility of Triassic rocks in the Tribal Hills to the north and east of the Samana Range cannot be ruled out.

The Datta Formation of Western Kohat is of shallow-water marine origin as contrasted to the mixed marine (upper) and continental (lower) type in the Salt Range Trans Indus Ranges, Kala Chitta and Hazara. The lithology is more closely comparable with rocks of Lower and Middle Jurassic age of the Sulaiman province (Baluchistan and Kurram).

Fauna and Age: In the upper part, rhynchonellid brachiopods occur which were also recorded by Davies (1930) and identified by Muir Wood (1930 : 26) as *Rhyn-*

chonelloidea arenata (Quenstedt) of Upper Bathonian or Lower Callovian age. The presence of *Spiriferina* sp., *Velata* sp. and indeterminate ammonite fragments (oxyconic with complicated suture) in the lower beds indicates a Lower Jurassic age similar to the bivalves and brachiopods of the Toarcian beds of the Kala Chitta Range. The age of the Datta Formation in Western Kohat may, therefore, be considered like that of the Trans Indus Ranges as Lower to Middle Jurassic (Pre Callovian).

Hazara

The present investigation does not cover a detailed stratigraphic study of the Datta Formation in Hazara. In one measured section, north of Kalapani, of the "Kioto Limestone" (treated here under Samana Suk Limestone), the Datta Formation lithology is not developed, partly due to intensive folding and faulting, and partly due to non-deposition (fig. 6). In the Galdanian area, north west of Kalapani (43 F/7) Calkins and Matin (1968 : 15) recorded "Red Beds" with hematitic shale, sandstone and limestone ("Galdanian formation") underlying conformably their "Daulatmar limestone" (Samana Suk Limestone) and overlying a dolomitic limestone unit ("Abbottabad formation"). These "Red Beds" are considered Lower Jurassic in age and possibly represent the Datta Formation (similar to the Red Beds of Kala Chitta). The underlying dolomitic limestone is similar to the Kingriali Formation of ?Upper Triassic age. These correlations are tentative, based on the present study of the Kala Chitta Range and the similarity of the so-called "Kioto Limestone" of Hazara with that of Kala Chitta (Cotter 1933).

Davies and Gardezi (1965) found *Bouleiceras* sp. in a section near Bagnotar (43 F/8), Hazara, in the middle part of the "Maira formation", (=Datta Formation) which overlies "Hazara slates" disconformably and underlie their "Jurassic limestone" (=Samana Suk Limestone). The thickness varies from 100 to 120 feet (1965 : 25). The lithology shows a strong similarity with that of Kala Chitta Range.

Fauna and Age: The presence of *Bouleiceras* in the Bagnotar area of Hazara and the strong similarity of this section with Kala Chitta indicate a Lower Jurassic (mainly Toarcian) age of the formation which rest disconformably on Precambrian, Paleozoic or Triassic rocks (figs 4, 5), and is not developed in parts of Hazara (e.g. Kalapani section).

Samana Suk Limestone

The name Samana Suk was introduced by L. M. Davies (1930) from the peak of this name in the Samana Range, Western Kohat. The name is here adopted for similar limestones of the Kala Chitta Range (part of "Kioto Limestone" of Cotter 1933), the Salt and Trans Indus Ranges ("Baroch Limestone" of Gee 1945) and Hazara (part of "Kioto limestone" of Middlemiss 1896; "Jurassic limestone" of Davies and Gardezi 1965; "Daulatmar limestone" of Calkins and Matin 1968).

Western Kohat (Samana Range)

In the type area the Samana Suk consists of grey, medium grey to dark grey, thick to medium bedded limestone with oolitic, calcareous shale and marl interbeds.

The thickness varies from 615 feet in the Samana Range (western outcrops near Shinawari) to 562 feet in the Darsamand section.

The formation is gradational with the underlying Datta Formation, and is overlain disconformably by the Chichali Formation.

Fauna and Age: The fossils are mostly comminuted shells (bivalves, gastropods and brachiopods). About 3 feet below the top belemnites (*Belemnopsis* cf. *grantana*) were obtained from a shale parting on the south flank of the Samana anticline. The top uneven surface of the limestone, which weathers rusty brown, has sectioned belemnites, molluscan casts and crinoidal remains. On the basis of *Belemnopsis granata* (d'Orbigny), which is similar to the figured specimen of Spath (1924, pl. III, fig. 3) from Cutch, the upper age limit of the formation is dated as Middle Callovian, and the formation may range in age from Middle to Lower Callovian.

Trans Indus Ranges

The Samana Suk Limestone is similar in lithology to the type locality, except the bedding is thinner and the colour is lighter grey. The formation is 220 feet in the Chichali section. It thins out towards the east in the Salt Range, but thickens to 450 feet in Baroch nala towards the west. Further south, in the Shaikh Budin Hills, Krishnan (1960 : 419) recorded 800 feet of the limestone.

The uppermost 2 to 3 feet of the formation is richly fossiliferous in ammonites, particularly in the area west of Chichali Pass (Datta, Punnu, Lunda, Mallakhel, Makerwal), and has yielded the Middle Callovian ammonites described in the present work. In the sections east of the Chichali Pass no ammonites were detected in this horizon, but Spath (1928 : 205) has recorded *Subkossmatia flemingi* from north of Kalabagh.

Fauna and Age: The ammonites include *Reineckeia anceps* (Reincecke), *R.* sp. indet. *R.* cf. *torulosus* (Spath), *Choffatia* sp. indet., *Hubertoceras* sp. indet., *Obtusicostites buckmani* Spath and *Obstuicostites* sp. indet.

Among the non-ammonite fauna, rhynchonellid and terebratulid brachiopods, bivalves and gastropods occur quite commonly. The Bivalves include *Homomya* cf. *gibbosa* Sowerby, *Pecten* sp., *Arctostrea* sp. and *Tellurimya tellaris* (Lamarck). Among the rhynchonellids *Somalirhynchia nobelis* (J. De C. Sowerby) is the most abundant species in some sections.

The upper age limit of the formation is Middle Callovian and the formation may extend in age from Middle to Lower Callovian (Middle Jurassic).

Kala Chitta Nizampur area

The Samana Suk Limestone in this area (upper part of the "Kioto Limestone" of Cotter 1933) consists of thin to medium bedded limestone with thicker interbeds.

CRETACEOUS

JURASSIC

TRIASSIC

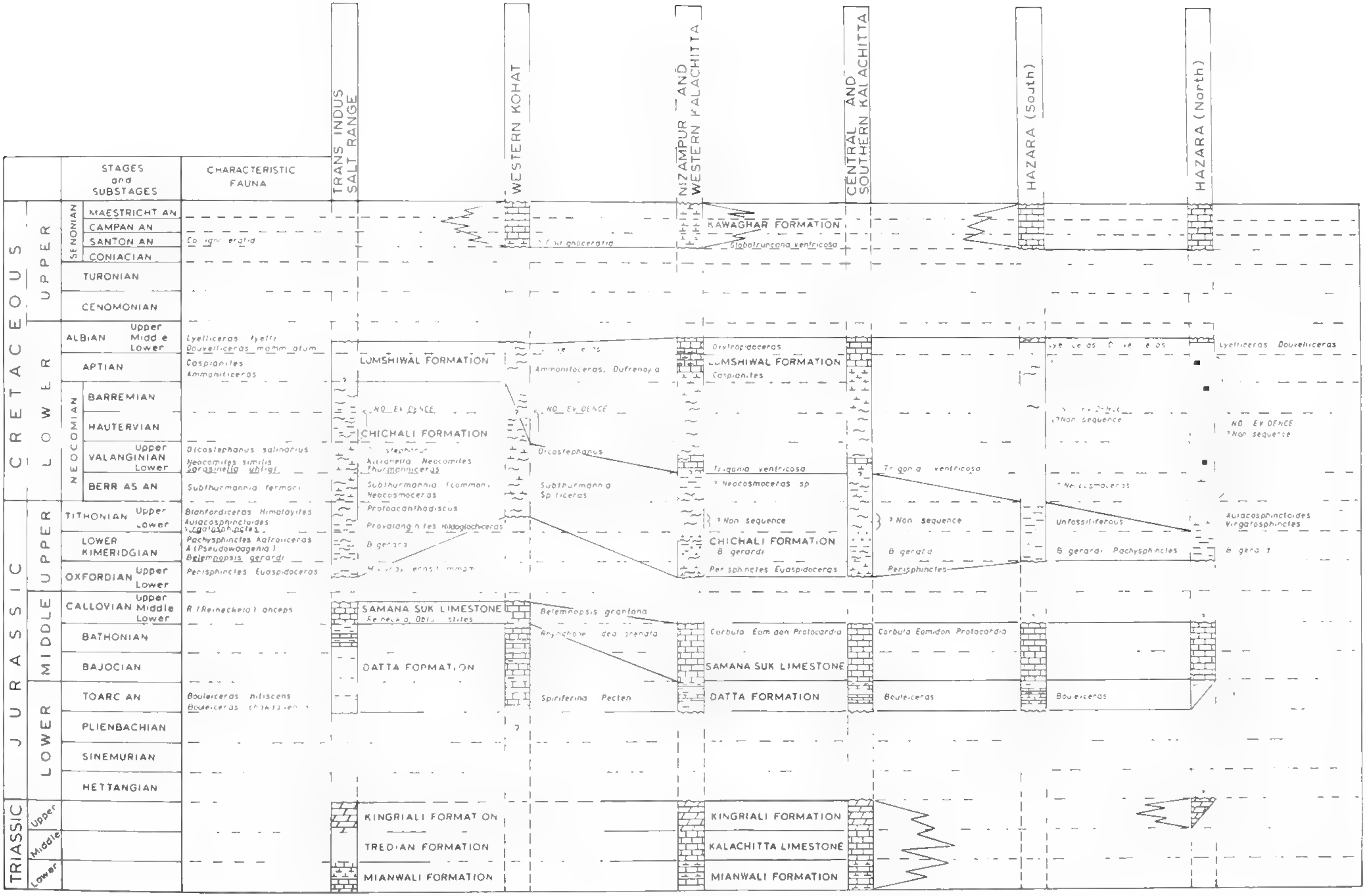


FIG. 4 Biostratigraphical correlation of the Mesozoic formations of northern West Pakistan.

The limestone weathers to grey-brown and has subordinate nodular marl and calcareous shale intercalations. The succession is gradational to the underlying Datta Formation and is disconformably overlain by the Chichali Formation.

Nearly 10 feet above the basal shelly limestone occurs a distinct yellow brown to dark rusty brown ferruginous coarse oolitic bed of 2 to 5 feet in thickness. This ferruginous oolite bed is developed in the western half of Kala Chitta (West of Chak Jabbi), while in the eastern section, it is represented by calcareous oolites only.

The upper 1 or 2 feet of the Samana Suk Limestone are nodular, marly and have yielded bivalves.

The thickness in a measured section near Chakdalla is 620 feet. In the Gandab section of Nizampur, the thickness increases to 800 feet.

Fauna and Age: The bivalves in the top bed of the formation include *Protocardia grandidieri* (Newton), *Eomiodon indicus* Cox and *Corbula lyrata* J. de C. Sowerby. The bivalves are the same as described by Cox (1935) from the "Kioto Limestone" of this area. They are also similar to the one occurring in the Kuar Bet Beds of Cutch, which have been assigned an Upper Bathonian age (Arkell 1956 : 391, 400).

The upper age limit of the Samana Suk Limestone in Kala Chitta is Upper Bathonian, and as the formation overlies the known Toarcian Datta Formation of this area conformably, the lower age limit may extend to Bajocian.

It is worth mentioning that nearly 60 to 70 miles further west in the Samana Range, and 50 to 60 miles south west in the Trans Indus Ranges, the Samana Suk Limestone is Callovian.

Hazara

In the Hazara area the formation was studied only in one section, situated 1½ miles north of Kalapani (43 F/8). The lithology comprises thick to medium bedded (with thin beds) grey, brownish grey limestone, poorly fossiliferous, with interbeds of oolitic dolomitized limestone, nodular marl and calcareous shale. It is disconformably overlain by dark shale of the Chichali Formation ("Spiti Shales"), and disconformably underlain by quartzites and slates of doubtful Palaeozoic age. The basal 3 feet of the limestone is conglomeratic with quartz pebbles.

The thickness is 1087 feet in the section north of Kalapani.

From the Bagnotar area to the south R. G. Davies and Gardezi (1965 : 25) reported over 1200 feet of similar limestone overlying their "Maira Formation" (=Datta Formation with *Bouleiceras*). Calkins and Matin (1968) from the Galdanian area recorded thick, grey limestone ("Daulatmar Limestone") overlying their "Galdanian formation" (=Datta Formation). This limestone probably represents the Samana Suk Limestone.

Fauna and Age: The Samana Suk Limestone of Hazara is poor in identifiable fossils. No ammonites occur. Its stratigraphic position above the Lower Jurassic *Bouleiceras*-bearing Datta Formation, lithological similarity with that of the Kala Chitta area and its disconformable contact with the overlying Upper Jurassic Chichali Formation, suggest a Middle Jurassic age similar to the Kala Chitta Range.

Chichali Formation

The name Chichali Formation was introduced by Danilchik (1961) and Danilchik and Shah (1967) from the Chichali pass in the Trans Indus Ranges for rocks previously described as "Belemnite Beds" (Spath 1939; Gee 1945). The name is here adopted (fig. 4) for similar rocks which disconformably overlie the Samana Suk Limestone in Kala Chitta ("Spiti Shales" of Middlemiss 1896) and Shaikh Budin Hills ("Black Zone" of oil company geologists).

Trans Indus Ranges

The lithology in the Trans Indus Ranges, which includes the type locality, consists of dark green, greenish brown, dark bluish grey (lower part), soft glauconitic sandstone and sandy shale, with subordinate nodular, calcareous, phosphatic strata. Some portions of the formation (the Middle member in Makerwal area and the Upper member in Chichali–Kalabagh area) are sufficiently rich in glauconite and/or chamosite to provide low grade iron ore.

The thickness ranges from 150 feet in the eastern section of Kalabagh to 180 feet in the Chichali Pass and 185 feet in the western sections of Makerwal and Baroch Nala. From the Shaikh Budin Hills, Abbas and Bhuyan reported (unpublished) a maximum thickness of 159 feet.

The formation is divisible into three members. The basal bed of the lower member (less than a foot in thickness) is calcareous, glauconitic and sandy, with Upper Oxfordian ammonites and belemnites. These are succeeded by dark grey silty, sandy, glauconitic shale (10–15 ft), which contains some calcareous, phosphatic, or ferruginous nodules with Lower Kimmeridgian ammonites and abundant belemnites (including *Belemnopsis gerardi*). The shale becomes gradually more sandy and greenish in colour in the succeeding 20 to 30 feet and has yielded Lower Tithonian ammonites and abundant *Hibolithes* but no *Belemnopsis*. The rest of the lower member passes into a dark green, glauconitic sandstone weathering into soft sands with Upper Tithonian ammonites. In the uppermost 2 to 3 feet the first basal Cretaceous ammonites (*Subthurmannia*) appear, and it is this part which is considered transitional from the Jurassic to the Cretaceous. The thickness of the lower member ranges from 70 to 75 feet in the Makerwal–Lunda–Punnu Mines sections, to 110 feet to the east in Chichali Pass and Kalabagh sections.

The middle member is a massive, calcareous, glauconitic sandstone, weathering rusty brown to greenish brown (dark green when fresh). It has abundant belemnites and common ammonites. The lower 3 to 4 feet of the member has Berriasian ammonites and the rest Valanginian. In the uppermost 2 to 3 feet Upper Valanginian ammonites (*Olcostephanus*) are commonly distributed. The thickness ranges from 35 to 45 feet in the Makerwal–Punnu Lunda Mines sections to 25 to 30 feet in the Kalabagh and Chichali Pass sections. The middle member thins towards the east, and in the Shaikh Budin Hills a maximum of 40 feet has been reported.

The upper member consists of greenish or reddish brown, massive, sandy shale and sandstone which are glauconitic and chamositic but are devoid of ammonites. In the Chichali Pass and western sections about 3 to 5 feet below the top contact with the Lumshiwal Formation some *Hibolithes* and *Gryphaea* occur. In the rest of the member even belemnites, which are abundantly distributed in the lower and middle members, are absent. The upper contact with the Lumshiwal Formation in the sections west of the Chichali Pass appears to be transitional. In the sections at and east of the Chichali Pass, the upper contact with the Lumshiwal Formation is marked by a red ferruginous sandstone bed and is sharp. The thickness of the upper member is 10 feet in Kalabagh, 40 feet in the Chichali Pass, 60 feet in the Makerwal–Lunda–Punnu Mines and 80 feet in the Shaikh Budin Hills. The upper member shows a marked thinning towards the east (Main Salt Range).

Fauna and Age: The Upper Oxfordian fauna includes *P.* (*Kranaosphinctes*) sp. indet., *P.* (*Dichotomosphinctes*) cf. *rotoides* Ronchadze, *P.* (?*Dichotomosphinctes*) sp. indet., *Mayaites* cf. *waageni* (Uhlig), and *Belemnopsis gerardi* (Oppel).

The Lower Kimmeridgian is represented by *Aspidoceras* (*Aspidoceras*) sp. indet., *A.* (*Pseudowaagenia*) sp. indet., *Physodoceras* (*Simaspidoceras*) sp. indet., *Laevaptychus*, *Ptychophylloceras ptychoicum* (Quenstedt), *Katroliceras* cf. *pottingeri* (J. de C. Sowerby), *Pachysphinctes robustus* Spath, *Hibolithes* sp., *Belemnopsis gerardi* and *Hybonoticeras* sp. indet. The non-cephalopod fauna consists of *Gryphaea* sp., some rhynchonellid and terebratulid brachiopods.

The Lower Tithonian is represented by *Aulacosphinctoides* sp., *Virgatosphinctes* sp., *Hildoglochioceras* sp. indet., *Proniceras indicum* Spath, *Provalanginites rhodesi* gen. nov. sp. nov., *Provalanginites howarthi* sp. nov., *Holcophylloceras silesiacum* (Oppel). The Upper Tithonian fauna includes *Blanfordiceras* cf. *wallichi* (Grey), *Himalayites* cf. *hyphaisis* (Blanford), *Himalayites* sp. indet., *Pterolytoceras exoticum* (Oppel), *Spiticeras multiforme* Djanelidze, *Ptroacanthodiscus* cf. *michaelis* (Uhlig), *Protacanthodiscus* sp. indet., and *Aulacosphinctes spitiensis* (Uhlig).

This Upper Oxfordian to Tithonian fauna occurs in the lower member of the Chichali Formation. In the upper 2 feet, however, *Subthurmannia* appears, and extends into the basal 3 to 4 feet of the middle member. The Jurassic–Cretaceous boundary is placed at the first appearance of the genus *Subthurmannia.*

The Berriasian is represented by *Protacanthodiscus* sp., *Subthurmannia fermori* Spath (abundant), *S. lissonioides* Spath and other *Subthurmannia* spp., *Neocosmoceras subradiatus* (Uhlig), *Neocosmoceras* cf. *spitiensis* (Uhlig), and *Spiticeras* (*Negreliceras*) aff. *subnegreli Djanelidze.*

The Lower Valanginian (Middle member of the Chichali Formation) is represented by *Thurmanniceras* sp., *Sarasinella uhligi* Spath, *Sarasinella spinosa* (Uhlig), *Neocomites* (*Neocomites*) sp. nov., *N.* (*Neocomites*) cf. *teschensis* (Uhlig), *N.* (*Neocomites*) *pycnoptychus* (Uhlig), *N.* (*Calliptychoceras*) spp. nov., *N.* (*Parandiceras*) cf. *rota* (Spath), *N.* (*Parandiceras*) *theodorii*, (Oppel), *N.* (*Parandiceras*) aff. *indicus* (Uhlig), *N.* (*Odontodiscoceras*) *similis* Spath, and its subspecies, *Uhligites* sp. indet. *Kilianella asistica* Spath, *K. besairei* Spath, *Kilianella* sp. nov., *Neohoploceras* (*Neohoploceras*) sp. indet. and *Neohoploceras baumbergeri* Spath.

The Upper Valanginian is represented in the uppermost 2 to 3 feet of the middle member by *Olcostephanus* (*Olcostephanus*) *salinarius* and its 5 subspecies (most common), *O.* (*O.*) *sakavalensis* (Besairie), *O.* (*O.*) cf. *filosa* (Baumberger), *O.* (*O.*) *sublaevis* Spath, *O.* (*O.*) *fascigerus* Spath, *O.* (*O.*) sp. nov., *O.* (*O.*) aff. *geei* Spath, *O.* (*Rogersites*) *schenki* (Oppel), *O.* (*R.*) sp. nov., *Leopoldia* sp., *Distoloceras* sp. and *Lyticoceras* sp. nov.

No ammonites occur in the upper member excepting for some poorly preserved *Gryphaea* and *Hibolithes* in the upper part.

The ammonite fauna indicates an Upper Oxfordian to Valanginian age of the lower and middle members. The upper Member may represent the rest of the Neocomian (Hauterivian–Barremian).

Western Kohat (*Samana–Darsamand–Khadimakh sections*)

The lithology is very similar to the type section of the Trans Indus Ranges except that the thickness is much attenuated (50–60 ft). In the Samana–Darsamand area, the formation is divisible into three members, but in the Khadimakh section only two fold division (corresponding to lower and middle members of the Samana section) is possible. The upper member in Khadimakh is not separable from the overlying Lumshiwal Formation of similar lithology (fig. 4).

The formation rests disconformably on the Samana Suk Limestone, and is followed by the glauconitic (in Khadimakh) or quartzose sandstone of the Lumshiwal Formation.

Fauna and Age (fig. 5): The ammonites in the lower member include ?*Protacanthodiscus* sp., *Berriasella* sp., *Spiticeras* (*Spiticeras*) aff. *greisbachi* (Uhlig), *S.* (*S.*) cf. *mojsvari* (Uhlig), *Neocosmoceras octagonum* (Blanford) and *Subthurmannia* aff. *boissieri* (Pictet). These are followed in the basal part of the middle member by *Subthurmannia fermori* Spath, *S.* aff. *pseudopunctata* Spath, *S. lissonioides* Spath, *Pterolytoceras* aff. *exoticum* (Oppel), *Pterolytoceras* sp. indet., *Thurmanniceras* sp. and *Neolissoceras grasianum* (d'Orbigny). Succeeding these faunas in the middle member are *Neocomites* sp., *Kilianella* sp. nov. and *Kilianella leptosma* (Uhlig). This is followed, in the upper 2 to 3 feet of the middle member by *O.* (*O.*) *salinarius* Spath, *O.* (*O.*) *radiatus* Spath, *O.* (*O.*) cf. *sublaevis* Spath, *O.* (*O.*) sp. nov., *O.* (*O.*) *pachycyclus* Spath and *Lyticoceras* sp. indet.

The upper member is barren of fossils. The age of the Chichali Formation is Upper Tithonian to Neocomian.

Kala Chitta–Nizampur area

The Chichali Formation of this area is broadly comparable in lithology with the Trans Indus Ranges and the Samana Range, but it also shows some peculiarities which require separate treatment.

In the outcrops of Western Kala Chitta (Bagh, Sujhanda sections) and south east of Nizampur (Wuch Khawr and Gandab sections) the formation is 80 to 90 feet thick and consists of two members. The Upper Member is a dark pyritic silty shale, and is not developed in the outcrops of central Kala Chitta (Chakdalla–Jhallar sections) where the formation is 30 to 40 feet thick and consists of dark green or grey glauconitic sandstone and sandy shale with a nodular calcareous bed at the base.

In the sections north–north west of Jhallar, central Kala Chitta Range, the formation consists of the following:

Upper part	Greenish sandy shale, glauconitic with *Hibolithes* sp., *Gryphaea* sp. annelids, overlain by light brown calcareous sandstone of the Lumshiwal Formation 20 to 15 feet.
Lower part	Dark green, glauconitic, soft sandstone, with phosphatic and calcareous nodules, containing the following fossil horizons: 20 to 15 feet
d.	near the top, *Neocosmoceras subradiatus* (Uhlig) and *Gryphaea* aff. *balli* (Stefanini).
c.	major portion of the unit; abundant *Hibolithes* sp., *Gryphaea* cf. *balli* (Stefanini), and less commonly *Himalayites* sp., and *Blanfordiceras* sp. towards the base.
b.	belemnite shingle (up to 1 ft) consisting of nodular (calcareous, ferruginous) glauconitic silty sands, with abundant *Belemnopsis gerardi* (Oppel) and *Hibolithes* sp., and some gastropods and bivalves.
a.	sandy glauconitic, calcareous, rubbly bed (up to $1\frac{1}{2}$ ft), with abundant poorly preserved perisphinctid ammonites, brachiopods, bivalves, gastropods, belemnites; overlies disconformably the Samana Suk Limestone.

Fauna and Age (fig. 5): The lithology and fossil beds indicate that, though the formation ranges in age from Upper Oxfordian to Lower Neocomian, it is much condensed and is full of non-sequences.

The Upper Oxfordian fauna (unit a) includes *Prosophinctes* (?) *virguloides* Waagen, *P.* (*P.*) sp. indet., *P.* (*Arisphinctes*) *orientalis* Siemiradzki, *P.* (?*Dichotomosphinctes*) sp. indet. *Euaspidoceras* cf. *wagurense* (Spath), *Euaspidoceras* sp. indet., and the bivalves and gastropods include *Ctenostreon proboscideum* (J. Sowerby) and *Pleurotomaria* sp.

There is no evidence from the ammonites of the presence of Lower Tithonian, but the abundance of *Belemnopsis gerardi*, rare fragmentary perisphinctid ammonites and *Gryphaea* cf. *balli* (Stefanini) in the condensed horizon (unit b), indicate the presence of Lower Kimmeridgian. The Lower Tithonian is probably missing because of non-sequences in Kala Chitta. The Upper Tithonian is represented by *Himalayites* cf. *depressus* Uhlig, *Blanfordiceras* sp. indet and *Aulacosphinites* sp. indet. and *Gryphaea* cf. *balli* (Stefanini). *Gryphaea* is also commonly distributed in the glauconitic sands (unit c) in beds which overlie *Blanfordiceras*. It may be pointed out that the *Blanfordiceras* specimens are limonitic and occur towards the base of unit c.

The Berriasian is indicated by the presence of fragmentary specimens of *Neocosmoceras* cf. *subradiatus* (Uhlig).

Because of the presence of *Trigonia ventricosa* (Krauss) in the basal beds of the overlying Lumshiwal Formation, which in Cutch and South Africa (Arkell 1956 : 387) is found in the Valanginian, the upper age limit of the Chichali Formation in Kala Chitta may be Lower Valanginian.

Hazara

In Hazara the Chichali Formation shows a distinct facies change from the dark "Spiti shales" type exposed in the outcrops north of Haro River (investigated west of Jabrian and in Kathwal–Kalapani sections) to the Kala Chitta type dark green glauconitic sandstone facies exposed south of Haro River (investigated north of Jabrian Rest House and extending to the south west in the Margala Hills).

The "Spiti Shales" facies is represented by black or dark grey shale with some ferruginous, sandy and silty concretions. The shales are unfossiliferous, except in the lowermost part where some belemnites (*Belemnopsis* sp.) and fragmentary perisphinctid ammonites occur. The formation rests disconformably on the Samana Suk Limestone ("Kioto limestone"), and is followed without any apparent break, but with change of lithology, by the Lumshiwal Formation ("Giumal sandstone").

The thickness in the section north northwest of Kalapani is 213 feet and thins out to 134 feet to the south in a roadside section near Jhamiri village.

The green glauconitic sandy facies of the Chichali Formation is 110 feet thick in a measured section north of Jabrian Rest House on the Haro River (north bank).

Fauna and Age: The formation is poor in ammonites and other fossils. The occurrence of *Belemnopsis gerardi* (Oppel) and poorly preserved, phosphatized fragmentary perisphinctid (?*Pachysphinctes* sp.) ammonites in the basal part indicate a Lower Kimmeridgian age for the base. It appears that the condensed Upper Oxfordian bed developed in Kala Chitta and the Trans Indus Ranges is missing from this area. *Belemnopsis gerardi* (Oppel) occurs both in the Upper Oxfordian and Lower Kimmeridgian beds of the Trans Indus and Kala Chitta Ranges. Unless more definite evidence of Upper Oxfordian age (based on ammonites) is obtained by future investigations of other outcrops, a Lower Kimmeridgian age is favoured here for the base of the formation.

The upper age limit of the Chichali Formation in Hazara is still less definite, mainly because of the paucity of fossils. In the Kalapani–Kathwal sections Lower Tithonian ammonites occur in the basal part of the overlying Lumshiwal Formation ("Giumal Sandstone") indicating mainly a Lower Kimmeridgian age of the Chichali Formation in these sections.

In the sections of Haro River, no fossil evidence could be obtained from the upper part of the formation, but Spath (1933) and Pascoe (1959) have reported *Neocosmoceras subradiatus* (Uhlig) and *Neocosmoceras octagonides* (Uhlig) from the overlying "Giumal sandstone" in outcrops 10 to 15 miles north east of the examined localities (Murree–Abbottabad Road). This suggests that the upper age limit of the Chichali Formation in the Haro River sections (Jabrian) may be Tithonian and the formation may extend from Lower Kimmeridgian to Tithonian.

Lumshiwal Formation

The name Lumshiwal was introduced by E. R. Gee (1945) for a white or light coloured sandstone overlying the Chichali Formation ("Belemnite Beds") and overlain disconformably by the Lower Tertiary coal beds in the Trans Indus Ranges. The name Lumshiwal Formation is here adopted for similar rocks previously called the "Main Sandstone Series" (Davies 1930) in the Samana Range, and "Giumal sandstone" in Kala Chitta (Cotter 1933) and Hazara (Middlemiss 1896).

The formation exhibits a great variability of lithology and thickness in different parts of the area investigated (fig. 4). It is mainly quartzose sandstone in the Trans Indus Ranges, quartzose, and glauconitic sandstone in western Kohat and parts of Hazara and a mixed quartzose, glauconitic or calcareous sandstone and limestone in Nizampur, Kala Chitta, and southern Hazara.

The thickness is 330 feet in the Trans Indus Ranges, but it thins out eastward and is absent in the main Salt Range. It is 670 feet in western Kohat, 220 feet in Nizampur, 180 feet north of the Haro River and 32 feet in the Kalapani–Kathwal sections of northern Hazara.

The upper age limit of the formation is Lower–Middle Albian in Kohat, Kala Chitta, Hazara and doubtfully so in the Trans Indus Ranges. The lower age limit is more variable. It is regarded doubtfully Aptian in Trans Indus Ranges and more definitely in Western Kohat, Upper Neocomian in Nizampur and Kala Chitta, doubtfully Lower Neocomian in the Haro River sections and Lower Tithonian in Kathwal–Kalapani sections of Hazara (fig. 5).

The formation is overlain disconformably by the Kawaghar Formation of Upper Cretaceous age in Kohat, Nizampur, northern half of Kala Chitta and Hazara. In the Trans Indus Ranges and southern half of Kala Chitta, no Upper Cretaceous rocks are developed, for Lower Tertiary sandy marls and limestone lie disconformably on the Lumshiwal Formation.

Trans Indus Ranges

The lithology consists of fine to medium and some times coarse, light grey or white, quartzose sandstone. The sandstone is massive and current bedded, cliff-forming and in the upper part commonly includes carbonaceous matter. The basal 5 to 10 feet is silty glauconitic shale or siltstone, and contains poorly preserved *Gryphaea* sp. and *Hibolithes* sp. in Baroch Nala outcrops. In the eastern sections of Chichali and Kalabagh no such fauna occurs. The lower contact with the Chichali Formation in the sections west of Chichali Pass is transitional, while towards the east, it is sharp. The upper contact with the Lower Tertiary coal beds is disconformable.

The thickness is 330 feet in the Makerwal area, 125 feet in the Chichali Pass and is practically missing in the Kalabagh section.

Age and Fauna: The formation is unfossiliferous except for some *Gryphaea* in the western sections of the Trans Indus Ranges. Its transitional contact with the underlying Neocomian beds and lithological similarity with the Kohat sections suggest an ?Aptian to Mid-Albian age.

Western Kohat

In the Samana Range section, the formation (641 ft) is divisible into three members. The upper member is a green to reddish brown glauconitic and ferruginous sandstone with a hard (2–6 ft) calcareous sandstone containing abundant fossils including ammonites near the top. The middle member (187 ft) is a light coloured coarse to medium grained current-bedded, massive, quartzose sandstone. The lower member (250 ft) is a thin to medium-bedded, quartzose sandstone with decomposed pyrite and some silty clay partings in the middle part.

In the Darsamand section, the lithology is similar to that of the Samana Range except the thickness is reduced to 550 feet. In Khadimak section no quartzose sandstone is developed. The formation (thickness 670 ft) is represented by dark green to greenish grey glauconitic sandstone and sandy shale with some calcareous and phosphatic interbeds.

Fauna and Age: The topmost hard, dark rusty weathering, calcareous sandstone bed in the Samana and Darsamand sections contains ammonites and other fossil casts. The most common ammonite is *Douvilleiceras mammillatum* (Schlotheim). Other ammonites genera include *Oxytropidoceras*, *Desmoceras*, *Cleoniceras*, *Brancoceras*, and *Lemuroceras*. In addition, poorly preserved brachiopods, bivalves and echinoids occur, which have been figured by Muir Wood, Cox and Currie (1930). The upper age limit in Western Kohat is Lower Albian (Mammillatum Zone). From the Khadimakh section nearly 200 feet below the Mammillatum zone, Aptian ammonites were located. These include *Caspianites* sp. nov. cf. *C. wassillewsky* (Renngarten), "*Ammonitoceras*" sp. cf. *pavlowi* (Vassillievsky), Pseudosaynellid (?*Ailoceras*), Deshayesitids (?Gen. nov. aff. *Dufrenoyia*) (identified by Dr R. Casey of the Institute of Geological Sciences, London).

As no ammonites and other fossils occur in the lower most part, no positive age assignment is possible. From the stratigraphic position above the known Neocomian ammonite—bearing rocks of the Chichali Formation, the lower age limit is very probably Aptian and may extend in some sections (Khadimakh) to Upper Neocomian.

Kala Chitta Nizampur area

When compared with Western Kohat and the Trans Indus Ranges, the Lumshiwal Formation in this area shows a significant facies change and consists of limestone and marl in the upper part and glauconitic and quartzose sandstone in the lower part (fig. 4). The thickness is 155 feet in Wuch khawr section of Nizampur, 190 feet in Western Kala Chitta (south of Sujhanda) and 172 feet in Central Kala Chitta (north northwest of Jhaffar).

The lithology in Wuchkhawr section is as follows:

d. limestone and nodular marls, medium bedded with comminuted shells (bivalves, gastropods) and with a 2 feet hard, nodular, brownish, phosphatic, glauconitic, limestone bed near the top, echinoids and some ammonites (*Oxytorpidoceras* sp.) in the lower part. 40 feet

c. grey to green marly limestone, nodular, thin bedded with echinoids ammonite; Douvilleiceralids and nautiloids in the middle part. 52 feet

b. grey to green, fine silty sandstone, thin bedded, glauconitic, phosphatic, of calcareous towards the top. 36 feet

a. a-3 Coarse glauconitic sandstone
a-2 limestone, sandy, glauconitic with bivalves (*Trigonia* sp.)
a-1 light grey to grey, quartzose sandstone, glauconitic in the upper part with *Trigonia* sp.

Fauna and Age: The lowermost unit (a) in all the sections has yielded *Trigonia* spp., including *Trigonia ventricosa* (Krauss). The uppermost unit (d) is generally poor in recognizable fossils but contain *Oxytropidoceras* sp. and *Neithea attockensis* Cox. Unit c contain Large Douvilleiceralids (Gen. nov.).

The age of the formation may, therefore, range from Upper Neocomian to Lower ?Middle Albian.

Hazara

In Hazara, the Lumshiwal Formation, like the Chichali Formation, shows a significant facies change in the sections lying north and south of the Haro River. In the Jabrian section on the north bank of the Haro River (near Forest Rest House) the lithology is mixed sandstone and limestone similar to the Kala Chitta Range, while in the section further north the formation is mainly sandstone comparable with the "Giumal sandstone" of Spiti. The thickness is 32 feet in Kathwal and 177 feet in the section north of Jabrian Rest House. In the Kathwal–Kalapani sections the formation is mainly quartzose and ferruginous glauconitic sandstone with Lower–Middle Albian fossils in the top calcareous rusty beds and Lower Tithonian fossils from the lowest 6 to 7 feet of the formation.

Fauna and Age: The uppermost 2 to 4 feet of the Lumshiwal Formation in the Kathwal and north of Haro River sections (Jabrian) has yielded Lower–Middle Albian ammonites and other poorly preserved bivalves and gastropods. The ammonites include *Lyelliceras* (abundant), *Oxytropidoceras, Mojsisoviczia, Dipoloceras, Hamites* and *Douvilleiceras*.

From the basal 6 to 7 feet of the highly condensed sequence of the Lumshiwal Formation in Kathwal–Kalapani sections Lower Tithonian ammonites (fig. 5) occur which are described in the present work. These include *Aulacosphinctiodes hazaraensis* sp. nov., *Aulacosphinctoides uhligi* Spath, *Aulacosphinctiodes* sp. indet., *Virgatosphinctes densiplicatus* (Waagen) *Virgatosphinctes frequens* (Oppel). The bivalves include *Trigonia* sp. (small form).

The age of the Lumshiwal Formation is from Lower Tithonian to Lower–Middle Albian in the northern sections (Kathwal–Kalapani) and probably Berriasian to Middle Albian in the Haro River sections. The Berriasian age in the latter areas is considered likely because in the adjoining sections of Murree–Abbottabad Road *Neocosmoceras* has been reported (Pascoe 1959; Spath 1933) to occur in the "Giumal sandstone" (Lumshiwal Formation). The formation in this area appears to be full of non-sequences and represents a highly condensed deposit.

V. FOSSIL LOCALITIES (Text-figs 1–2)

1. *Hazara*

Lower Tithonian and Albian ammonites and other fossils occur in the basal and upper most beds of the Lumshiwal Formation respectively in the Kathwal (lat. 34° 11′ 45″; long. 73° 19′) and Kalapani (lat. 34° 13′; long. 73° 10′ 30″) sections of northern Hazara (fig. 2; 1–2). The underlying Chichali Formation in this area has a few belemnites (*Belemnopsis* sp.) in the basal 2 to 3 feet.

In the section north of Jabrian (lat. 33° 54′ 30″; long. 73° 10′ 30″) in southern Hazara (fig. 2; 3–4), Albian ammonites are commonly distributed in the uppermost 5 feet of the Lumshiwal Formation. One mile south of Jabrian (fig. 2; 5), some Upper Jurassic fragmentary perisphinctid ammonites and belemnites (*Belemnopsis* sp.) occur in the basal 2 to 3 feet of the Chichali Formation.

2. *Kala Chitta Range*

Lower Triassic ammonites are found ½ a mile north of Chak Jabbi Rest House in central Kala Chitta and 1½ miles east of Bagh (lat. 33° 45′ 30″; long. 72° 13′) in Western Kala Chitta (fig. 2, 8).

Lower Jurassic (Toarcian) ammonites occur in the middle part of Datta Formation north of Chak Dalla village (lat. 33° 38′ 50″; long. 72° 23′ 25″) in central Kala Chitta (fig. 2; 6).

Upper Bathonian bivalves in the uppermost beds of Samana Suk Limestone and Upper Jurassic ammonites, belemnites and other fossils in the basal 2 to 3 feet of the Chichali Formation occur in the outcrops of central and Western Kala Chitta Range (fig. 2; 6). The best exposures are found north northwest of Jhallar (lat. 33° 38′ 45″; long. 72° 19′ 15″).

3. *Nizampur*

In the Wuch Khawr section (lat. 33° 46′; long. 72° 2′ 30″), 2 miles south east of Nizampur (fig. 2; 9), Albian and Aptian ammonites and other fossils occur in the upper and middle part and Neocomian bivalves in the basal 10 to 15 feet of the Lumshiwal Formation. In the Mazari Tang section (fig. 2; 10) southwest of Nizampur (lat. 33° 44′; long. 71° 57′ 30″) Upper Jurassic ammonites are distributed in the basal 2 to 3 feet of the Chichali Formation.

4. *Kohat*

The Albian ammonites and other fossils are commonly distributed in the upper 4 to 6 feet of the Lumshiwal Formation in the Samana Range (fig. 2; 11–14), north of Darsamand (fig. 2; 15–17) and north of Thal (fig. 2; 18–18) in Khadimakh Hill. In the Khadimakh section Aptian ammonites and other fossils occur 200 feet below the top Albian fossiliferous bed of the Lumshiwal Formation, while the upper dark rusty brown sandstone members of the Chichali Formation in this section has yielded Berriasian to Valanginian ammonites. In the section west northwest of Darsamand village, rare Upper Cretaceous ammonites occur in the basal 3 feet of the Kawaghar Formation.

5. *Trans Indus Ranges*

The bulk of the ammonites described in the paper comes from the Surghar and Maidan Ranges located between Kalabagh (lat. 32° 59 ′; long. 71° 32′ 30 ″) and Makerwal (lat. 32° 56′ 30″; long. 71° 9′) in Mianwali district (fig. 2; 21–27). The Middle Callovian ammonites occur in the outcrops of Samana Suk Limestone (upper bed) between west of Chichali Pass and Makerwal (Datta, Lunda and Punnu mines sections; Baroch nala section). The Upper Jurassic and Neocomian ammonites are distributed in the lower and middle members of Chichali Formation exposed in Maidan and Surghar Ranges and extend eastward in western Salt Range and southward in Shaikh–Budin Hills.

6. *Shaikh Budin Hills*

The Tithonian ammonites were collected from the lower member of Chichali Formation, 2 miles east and west of Shaikh Budin Village (lat. 32° 18′; long. 70° 49′ 45″) in Dera Ismail Khan district (fig. 2; 28–30).

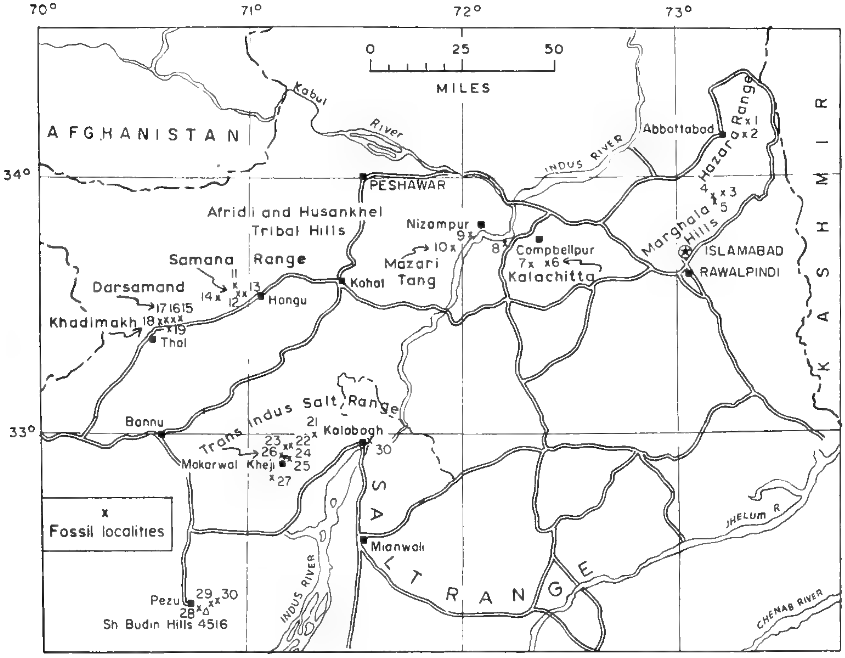


FIG. 5. Fossil locality map of Hazara, Kala Chitta, Kohat, Trans Indus Ranges including Shaikh Budin Hills, West Pakistan.

VI. SYSTEMATIC DESCRIPTIONS

Class *CEPHALOPODA*
Sub-class *AMMONOIDEA*
Order PHYLLOCERATIDA
Superfamily **PHYLLOCERATACEAE**
Family **PHYLLOCERATIDAE** Zittel 1884
Sub-family **CALLIPHYLLOCERATINAE** Spath 1927
Genus ***HOLCOPHYLLOCERAS*** Spath 1927
Holcopyhlloceras silesiacum (Oppel)

(Plate 1)

1865 *Ammonites silesiacus* Oppel: 550
1868 *Phylloceras silesiacum* (Oppel) Zittel: 62, pl. 5, figs 1–7

MATERIAL. One specimen, C.76546.

HORIZON. 20 feet above the base of Chichali Formation, Lower Tithonian.

DESCRIPTION. The specimen is a wholly septate internal mould, 280 mm in diameter. The whorl section is elliptical, much higher than wide, and the umbilicus is very narrow. There are 10 to 12 constrictions per whorl on the internal mould, which are conspicuous near the venter, but weak towards the umbilicus. They are prorsiradiate on the lower half of the whorl side, then bend backwards to become rursiradiate on the upper part of the whorl.

DIMENSIONS. C.76546–280: 165 (59), 95 (34), 30 (11).

REMARKS. The specimen is comparable with Spath's figure (1927; pl. VI, fig. 2b) of *H.* aff. *polyolcum* (Benecke) from the Kimmeridgian beds of Cutch, but the style of constrictions and suture line are different. Spath's figured specimen has a less elevated whorl section.

LOCALITY. Chichali Pass, Trans Indus Ranges.

Genus *PTYCHOPHYLLOCERAS* Spath 1927
Ptychophylloceras ptychoicum (Quenstedt)

(Plate 2, figs 1a, b)

1847 *Ammonites ptychoicus* Quenstedt: 219, pl. 17, fig. 12.
1875 *Phylloceras ptychoicum* (Quenstedt) Waagen: 30, pl. VII, figs 2a–c.
1927 *Ptychophylloceras ptychoicum* (Quenstedt); Spath: 46 (see for synonymy).

MATERIAL. One specimen, C.76547.

HORIZON. Lower part of lower member (about 10 feet above the base) of the Chichali Formation, Lower Kimmeridgian.

DESCRIPTION. The specimen is involute, inflated, wholly septate and about

66 mm in diameter. The whorl section has sub-parallel whorl sides and a broadly arched venter, and the umbilicus is very narrow. There are 6 labial ridges per half whorl at 66 mm diameter, which are well developed on the venter and ventral shoulder, but fade out on the whorl sides, and are not seen on the inner whorl.

DIMENSIONS. C.76547–66: 38 (58), 32 (48), —.

REMARKS. This specimen is very similar to Waagen's figure from the Katrol Beds of Cutch; from *P. tithonicum* Spath (1927, : 48, pl. V, fig. 9) it is distinguished by its more compressed whorl section.

LOCALITY. Punnu Mines, Trans Indus Ranges.

Order LYTOCERATIDA
Superfamily **LYTOCERATACEAE**
Family **LYTOCERATIDAE** Neumayr 1875
Sub-family **LYTOCERATINAE** Neumayr 1875
Genus ***PTEROLYTOCERAS*** Spath 1927
Pterolytoceras exoticum (Oppel)

(Plate 2, figs 2a, b)

1863 *Ammonites exoticus* Oppel: 278, pl.76, figs 5a–c.
1903 *Lytoceras exoticum* (Oppel) Uhlig: 114, pl. I, figs 3a–d, 4a–c (see also for synonymy).
1939 *Pterolytoceras exoticum* (Oppel); Spath: 7 (see for discussion).

MATERIAL. One specimen and two doubtful fragments C.76548–50.

HORIZON. Near the base of the middle and upper part of the lower member of the Chichali Formation, Upper Tithonian–Berriasian.

DESCRIPTION. The complete specimen is very evolute, the outer whorl hardly touching the inner one, and is 91 mm in diameter. Nearly half of the outer whorl is body-chamber. The whorl section is sub-circular, wider than high. The ornamentation consists of very fine, ridge-like, crinkled costae, which are distant on septate whorls, but closer on the body-chamber; they are rectiradiate or gently prorsiradiate on the whorl side and venter. Between them are finer and denser ribs or lirae. The shell is thin and internal moulds are smooth.

DIMENSIONS. C.76548–90: 32 (36), 34 (38), 40 (44).
C.76548–64: 22 (34), 25 (39), 28·5 (45).

REMARKS. These specimens resemble closely in ornamentation and dimensions Uhlig's figure from Chidamu, Spiti area, but they have slightly more inflated shells with a greater whorl height and whorl thickness at comparative diameters.

The two poorly preserved fragmentary specimens from the Samana Range are wholly septate.

LOCALITIES. Chichali Pass (C.76548), Trans Indus Ranges, and south of Fort Lockhart, Samana Range (C.76549–50).

Pterolytoceras sp. indet.

(Plate 2, figs 3a, b)

Material. Three specimens, C.76551–3.

Horizon. Basal part of the middle member and upper part of the lower member of the Chichali Formation, one fragment from the lower part of the rusty brown sandstone member of the Chichali Formation at Khadimakh; Upper Tithonian–Berriasian.

Description. The figured specimen is a smooth, wholly septate internal mould of approximately 180 mm in diameter. The whorl section is sub-oval near the aperture, higher than wide, but half a whorl before it is sub-circular, slightly wider than high. The umbilicus is wide, the umbilical wall is steep and the umbilical edge is rounded.

Dimensions. C.76551–180: 64 (35), 60 (33), 80 (44) (all approx.).

Remarks. One of these specimens occurs in the same bed as *P. exoticum* (Oppel) described above. The overall whorl shape and suture line compare favourably with *P. exoticum* (Oppel), which on Uhlig's figured specimen from the Spiti area (1910: pl. I, fig. 3a, b) has a complete body chamber with dorsal extensions at the apertural end at about 80·0 mm diameter, and occupies nearly half of the outer whorl.

In its large size, the figured specimen may be compared with *Hemilytoceras rex* (Waagen) (1875 : 36, pl. VII, fig. 1). Waagen's species has similar whorl proportions (at 660 mm: 220 (36), 200 (33), 230 (39)), but shows different ornamentation. The whorl section, however, is very similar.

Localities. South west of Malla Khel, Trans Indus Ranges; South of Fort Lockhart, Samana Range; Khadimakh.

Order AMMONITIDA

Superfamily **HILDOCERATACEAE**

Family **HILDOCERATIDAE** Hyatt 1867

Subfamily **BOULEICERATINAE** Arkell 1950

Genus ***BOULEICERAS*** Thevenin 1906

Bouleiceras nitescens Thevenin

(Plate 3, figs 1a, b, 3a, b)

1906 *Bouleiceras nitescens* Thevenin: 171, figs 1–3.
1908 *Bouleiceras nitescens* Thevenin: 13, pl. 11, figs 6 (lectotype designated by Arkell 1952), 11.
1952 *Bouleiceras nitescens* Thevenin; Arkell, p. 261.

Material. Three specimens, C.76554–6.

Horizon. Middle member of Datta Formation, Lower Toarcian.

Description. The larger fragmentary septate specimen (C.76555) is smooth, and has a rectangular whorl section which is much higher (75 mm) than wide (51 mm).

The whorl sides are flat and parallel. The venter is unicarinate and fairly broad. The suture line includes a three to four pronged asymmetrical, fairly deep, first lateral lobe.

The smaller specimen (C.76554) is more typical of the species. It is evolute, of roughly 58 mm diameter, and has a sub-rectangular whorl section, higher (21 mm) than wide (?18 mm). The whorl sides are sub-parallel, and gradually convergent towards a rather broad unicarinate-bisulcate venter. The inner whorl (up to a diameter of approximately 43 mm) has two rows of strong, sharp spine-like tubercles on the ventral and umbilical shoulders. The outer whorl has rounded, smooth rursiradiate ribs which curve forwards obliquely and are weakly tuberculate at the umbilical edge. Some ribs bifurcate at the umbilical edge.

REMARKS. The larger septate fragment has a similar suture-line to Arkell's figured specimen of *B.* sp. indet. from Jebel Tuwaiq (1952 : 263, fig. 5 (1); pl. xv, fig. 1). In its large size and partly in suture it is comparable with Thevenin's (1908: pl. ii, fig. 11) of *B. nitescens*. The smaller specimen is very similar to the lectotype designated by Arkell (Thevenin 1908 : pl. II, fig. 6).

The specimen figured by Arkell (1952: 260, fig. 4) from Jebel Tuwaiq, Arabia, as *B. nitescens* has a more compressed and comparatively much higher than wide whorl section, which is convergent to a narrow, keeled venter. The ventral shoulders are not as distinct as in the lectotype or the Kala Chitta specimen. It appears that Arabian forms are closer in whorl section to Thevenin's (1908) pl. ii, figs 8 and 10, which Arkell (1952) designated as *B. elegans* Arkell (with weaker tubercles).

LOCALITY. Chakdalla, Kala Chitta Range.

Bouleiceras chakdallaense sp. nov.

(Plate 3, figs 2a, b, 4)

DIAGNOSIS. Evolute, whorl section sub-rectangular, slightly wider than high on inner whorl, and higher than wide on outer whorl. Venter unicarinate-bisulcate. Shell with two rows of thick bullate tubercles.

HOLOTYPE. C.76557.

MATERIAL. Two septate fragmentary specimens, C.76557–8.

HORIZON. Middle member of Datta Formation, Lower Toarcian.

DESCRIPTION. Both specimens are wholly septate, and up to 92 mm in diameter. The whorl section is sub-rectangular with sub-parallel whorl sides and a unicarinate-bisulcate venter. There are two rows of prominent bullae at the umbilical and ventral shoulders which become thick and blunt on the outer whorl. The suture line consists of two or three pronged first lateral lobes and rounded saddles.

DIMENSIONS. C.76557–92: 30 (33), 30 (33), 44(48).
C.76557–64: 19 (30), 22 (34), 30 (47).

REMARKS. The strong tumid tubercles of this species are comparable with those of *B. tumidum* Arkell (1952 : 261; also Thevenin 1908 : pl. II, fig. 9, lectotype), but it differs distinctly in whorl section, evolution and the persistence of two rows or tubercles at a larger diameter.

LOCALITY. Chakdalla, Kala Chitta Range.

Bouleiceras sp. indet.

MATERIAL. Three specimens, C.76559–61.

HORIZON. Middle member of Datta Formation, Lower Toarcian.

DESCRIPTION. The larger fragmentary specimen (C.76561) has a smooth, septate, fairly compressed and involute shell. The whorl section is much higher than wide. The whorl sides are convergent towards a rather narrow unicarinate venter.

REMARKS. The specimen resembles, in side view and suture line, Arkell's figure of *B. nitescens* Thevenin from Jebel Tuwaiq (Arkell 1952 : 260, fig. 4). In its tall compressed whorl section, the specimen may also be compared with *B. elegans* Arkell (Thevenin : 1890, pl. II, figs 8 and 10). It is also comparable with *B.* aff. *nitescens* Thevenin from Hazara (Davies and Gardezi 1965).

LOCALITY. Chakdalla, Kala Chitta Range.

Superfamily **HAPLOCERATACEAE**

Family **HAPLOCERATIDAE** Zittal 1884

Genus ***HILDOGLOCHICERAS*** Spath 1924

Hildoglochiceras sp. indet.

(Plate 3, fig. 5)

MATERIAL. One specimen, C.76562.

HORIZON. 20 feet above the base of Chichali Formation, Lower Tithonian.

DESCRIPTION. The whorl section is much compressed with whorl sides converging towards a bluntly keeled venter. There is a spiral furrow at the middle of whorl side which first appears at about 18 mm diameter and becomes distinct and fairly deep at diameters greater than 28·5 mm. In cross section the ventral side of the furrow is shallow, but the umbilical side is deep and steeply inclined. The inner whorls are smooth, but at 22 mm diameter weak, crescent-shaped rursiradiate ribs appear on the ventral side of the spiral furrow.

DIMENSIONS. C.76562–28·5: 12 (42), 6 (21), 8·5 (30).

Remarks. The specimen differs from *Hildoglochiceras latistrigatum* (Uhlig) (1903 : 27, pl. II, fig. 4; pl. III, fig. 5) in being more compressed, having a higher whorl section, showing earlier appearance of crescent-shaped costae, and lacking a distinct spiral furrow on the earlier whorls. In the earlier appearance of costae and the later appearance of the spiral furrow it is more like specimens of *Hildoglochiceras kobelli* (Oppel) figured by Uhlig (1903 : 25, pl. LVII, figs 3a–b, 4a–d) and Waagen (1875 : 72, pl. XIII, figs 11–12) from middle Katrol sandstone of Cutch. It differs, however, in being more compressed and in having a shallower spiral furrow. Spath (1939 : 124, pl. XVIII, figs 8a, b) figured a specimen from the Trans Indus Ranges as *Hildoglochiceras* sp. indet. (group of *H. propinoum* Waagen) but considered it to be worn and probably derived. The present form differs from Spath's species in whorl shape and ornamentation. The external mould is attached to the whorl side of an *Aulacosphinctoides* (group of *A. uhligi* Spath) and suggests a close association of the two genera.

Locality. West of Makerwal, Trans Indus Ranges.

Superfamily **STEPHANOCERATACEAE**

Family **MAYAITIDAE** Spath 1928

Genus ***MAYAITES*** Spath 1924

Mayaites cf. ***waageni*** (Uhlig) sp. indet.

(Plate 3, figs 6a, b, 7a, b)

1910 *Macrocephalites waageni* Uhlig: 270, pl. LXXVII, figs 1–3.
1933 *Mayaites waageni* (Uhlig); Spath: p. 804.

Material. Two specimens, C.76563–4.

Horizon. Basal 3 inches of Chichali Formation, Upper Oxfordian.

Description. The specimens are involute, septate, and 30 and 51 mm in maximum diameter respectively. The whorl section is subcircular, slightly wider than high on the inner whorls, but higher than wide at larger diameters. The umbilicus is narrow and deep. The ribs are strong and gently sinuous, and three secondary ribs intervene between each primary rib. There are 16 to 17 primary ribs at 30 mm diameter on C.76563 and 18 to 19 at 24 mm diameter on C.76564.

Dimensions. C.76563–30: 15 (50), 15·5 (52), 7·5 (25);
C.76563–24: 11 (46), 12 (50), 6 (25).
C.76564–51: 20·5 (40), 20 (39), ?15·5 (30);
C.76564–24: 11 (46), 11·5 (48), 7 (29).

Remarks. In size, ornamentation and involution the specimen compares favourably with *M. waageni* (Uhlig) and is less close to *M. kitcheni* (Uhlig) from the Upper Oxfordian of Spiti. It differs in being less inflated, more evolute and in having a narrower, less elevated whorl section.

Locality. Punnu Mines, Trans Indus Salt Ranges.

Superfamily **PERISPHINCTACEAE**

Family **REINECKEIIDAE** Hyatt 1900

Genus ***REINECKEIA*** Bayle 1878

Reineckeia anceps (Reinecke)

(Plate 4, figs 1a, b, 2a, b, 3a, b)

1818 *Nautilus anceps* Reinecke: 82, pl. VII, fig. 61.
1846 *Ammonites anceps* (Reinecke); d'Orbigny: 462, pl. 166.
1876 *Reineckeia anceps* (Reinecke); Bayle: pl. LVI, figs 1?, 2, 3.
1881 *Reineckeia anceps* (Reinecke); Steinmann: 284
1928 *Reineckeia anceps* (Reinecke); Spath: 255, pl. XLIV, fig. 6a–c (see for discussion).

MATERIAL. Seven specimens, C.76565–71.

HORIZON. Upper one foot of Samana Suk Limestone, Middle Callovian.

DESCRIPTION. The specimen C.76565 is evolute, septate and 50 mm in diameter. The whorl section is cadiconic, much depressed, with a broadly arched venter and a mid-ventral groove. The umbilicus is wide and shallow, and the umbilical wall is rounded. There are two to three oblique, deep constrictions on all visible whorls. Weak primary ribs on the umbilical wall terminate at strong conical tubercles on the side of the whorl. Three or four secondary ribs issue from each tubercle and cross the venter with interruption at the shallow mid-ventral sulcus. Occasional ribs are intercalated and not joined to tubercles. The rib preceding a constriction is weakly tuberculate, while the rib following the constriction on the apertural side is non-tuberculate.

There are 14 or 15 tubercules on the outer whorl of C.76565. Specimen C.76568 differs in being less evolute, having four constrictions on its last whorl, a narrow ventral groove and greater number of tubercles at a comparative diameter.

DIMENSIONS. C.76565–48: 13 (27), 22 (46), 24 (50).
C.76568–60: 16 (27), 24 (40), 22 (37).

REMARKS. The specimen C.76565 compares very closely in ornamentation and depressed whorl section, to the inner whorls of the specimens figured by d'Orbigny and Bayle. It is similar in whorl shape and ornamentation to the small septate specimen figured by Spath (1928) from Neidlingen, Wurttemburg.

LOCALITIES. Lunda Mines (C.76565–69) and Punnu Mines (C.76570–71), Trans Indus Ranges.

Reineckeia cf. ***torulosus*** (Spath)

(Plate 4, figs 4a, b)

1933 *Reineckeites torulosus* Spath: 679, pl. CXXVII, figs 5, 6, 11; pl. CXXVIII, figs 1, 8.

MATERIAL. Four specimens C.76572–5.

HORIZON. Upper one foot of Samana Suk Limestone, Middle Callovian.

DESCRIPTION. The shell is evolute, septate and approximately 113 mm diameter. The whorl section is oval, higher than wide, with subtabulate, grooved venter. The umbilicus is wide and the umbilical wall is steeply inclined. Weak ribs on the umbilical wall are surmounted by radially elongate tubercles on the lower third of whorl side. Three or four straight, prorsiradiate ribs issue from each tubercle and are interrupted along the mid-venter.

DIMENSIONS. C.76572–?113: 44·5 (39), 26 (32), 44 (39).

REMARKS. The species was described by Spath (1933) from the Anceps Beds of Cutch. It is placed here in *Reineckeia* because of its prominent lateral tubercles and bundles of 3 or 4 secondary ribs.

LOCALITIES. West of Makerwal (C.76572), and Lunda Mines (C.76573–5), Trans Indus Ranges.

Reineckeia sp. indet.

MATERIAL. Five specimens, C.76576–80.

HORIZON. Upper 2 feet of Samana Suk Limestone, Middle Callovian.

DESCRIPTION. The specimen C.76576 is worn, evolute and approximately 120 mm in diameter. The worl section is rounded with equal height and thickness. The umbilicus is wide and the umbilical wall is steep. Some constrictions are present.

Distant, rectiradiate ribs are surmounted by tubercles on the lower third of the whorl side. 4 or 5 rectiradiate to slightly prorsiradiate ribs issue from each tubercle and are interrupted at the mid-venter.

REMARKS. In its smooth venter, evolute shell, and rounded whorl section, C.76576 is comparable with *Reineckeia brancoi* Steinmann (1881 : 285, text-figure 4), but differs in ornamentation. In *R. brancoi* there are frequently non-tuberculate trifurcating and bifurcating ribs along with tuberculate bundled ribs. The specimen C.76578 has coarse ribs which resemble *R. arthritica* (J. de C. Sowerby) as figured by Spath (1928, pl : XXXIII, figs 2a–b) from Cutch.

LOCALITIES. Lunda Mines (C.76576–7), and south of Malla Khel (C.76578–80), Trans Indus Ranges.

Family **PERISPHINCTIDAE** Steinmann 1890

Sub-family **PROPLANULITINAE** Buckman 1921

Genus ***OBTUSICOSTITES*** Buckman 1921

Obtusicostites buckmani Spath

(Plate 4, figs. 5a, b; Plate 5, figs 1a, b, 2a, b)

1875 *Perisphinctes obtusicostata* Waagen: 147, pl. XXXVIII, figs 3a, b only.

1931 *Obtusicostites buckmani* Spath: 300, pl. LIII, figs 3a–b (paratype); pl. LXII, fig. 8 (see for synonymy).

MATERIAL. Four specimens, C.76581–4.

HORIZON. Uppermost 1½ feet of Samana Suk Limestone, Middle Callovian.

Description. The specimen C.76584 may be a microconch for it shows the beginning of body chamber and uncoiling of the last whorl at the apertural end at 75 mm diameter. The other two specimens are septate, and C.76583, of 135 mm diameter, appears may be a macroconch. The whorl section is rounded and slightly wider than high. The umbilical wall is smooth and almost vertical, and the umbilical edge is rounded. The ribs are strong, rectiradiate to gently prorsiradiate, and bifurcate or trifurcate at about the middle of the whorl side. The rib counts are as follows:

C.76581—15 primary ribs at 66 mm diameter.
C.76583—23 primary ribs at 135 mm diameter, 20 at 98 mm.
C.76584—15 or 16 primary ribs at 75 mm diameter.

Dimensions. C.76581– 52: 20 (38), 24 (46), 19 (37).
C.76583–120: 46 (38), 42 (35), 42 (35).
C.76584– 73: 27 (37), 29 (40), 27 (37).

Remarks. C.76581 closely resembles the holotype figured by Waagen (1875, pl. XXXVIII, fig. 3). The specimen C.76583 resembles, in ornamentation and dimensions, Spath's paratype (1931 : pl. LIII, figs 3a–b) from Upper Anceps–Lower Athleta Beds of Cutch. The species differs from *O. obtusicosta* (Waagen) in having longer and less strong and blunt, nontuberculate primary ribs and the persistence of strong secondary ribs on the body chamber.

Locality. Punnu Mines, Trans Indus Ranges.

Obtusicostites sp. indet.

Material. Seven specimens, C.76585–91.

Horizon. Upper 2 feet of Samana Suk Limestone, Middle Callovian.

Remarks. The fragments C.76585–6 and C.76588 show coarse primary ribs branching into two to four secondary ribs low on the whorl side. In ribbing and whorl section, C.76585–6 are like *O. buckmani* Spath and *O. ushas* Spath (1931: pl. LIII, fig. 1a–b; pl. LVI, fig. 1). C.76588 also resembles *O. buckmani* Spath, but its blunt primary ribs splitting into 3 to 4 secondary ribs are like those of *O. obtusicosta* (Waagen) (1875 : pl. XXXVIII, figs 1a–b). C.76591 is crushed but shows coarse primary ribs (19 to 20 per whorl at 94 mm diameter) dividing into 3 secondary ribs near the middle of whorl side. The approximate dimensions are: 94 mm: 39 (41), 27 (29), 30 (32). This specimen may also belong to *O. buckmani* Spath though the straight secondary ribs resemble *O. devi* Spath (1931: pl. LIV, figs 1a–b) and *O. waageni* Spath (1931: pl. LIII, figs 2a–b) from Cutch.

Localities. Lunda Mines (C.76585–90), and Datta Mines (C.76591), Trans Indus Ranges.

Genus *HUBERTOCERAS* Spath 1930

Hubertoceras sp. indet.

(Plate 5, figs 3, 4a, b, 5a, b, 6)

MATERIAL. Three incomplete body chamber specimens and 10 fragments, C.76592–C.76604.

HORIZON. Upper 2 feet of Samana Suk Limestone, Middle Callovian.

DESCRIPTION. The four figured specimens and most of the fragments are body chambers, and C.76597 shows a lateral lappet. Moderately strong rectiradiate to gently prorsiradiate primary ribs bifurcate or rarely trifurcate in the upper third of the whorl side. Occasionally the secondary ribs are intercalatory and the primary ribs simple. The whorl section is oval and higher than wide, with a rounded venter. The umbilicus is rather narrow and the umbilical wall is steep.

DIMENSIONS. C.76592–41: 16·5 (40), 14 (34), 12·5 (30).
C.76595–42: 16 (38), 14 (33), 15 (36).
C.76597–57: 22 (39), 14 (25), 20·5 (30).

REMARKS. Spath (1931) described and figured a number of *Hubertoceras* species and their variants from Lower Athleta and Anceps Beds of Cutch. In view of the poor preservation and fragmentary nature of the Trans Indus specimens, it is not possible to assign them to any of the species of Waagen and Spath from Cutch. The Trans Indus species show some variations in ribbing, whorl thickness and involution but are generally more involute and smaller in size than the Cutch forms. They are from one locality and horizon.

The figured specimen C.76595 (Plate 5, figs 5a, b) can be compared in whorl section and ornamentation with *H. dhosaense* (Waagen) (Spath 1931: 319), but differs in having additional intercalatory ribs and in being more involute. The specimen C.76597 (Plate 5, fig. 6) compares favourably in compressed whorl section with *H. mutanus* (Waagen) (Spath 1931: 318), but differs in details of ornamentation.

LOCALITY. Lunda Mines, Trans Indus Ranges.

Sub-family **PSEUDOPERISPHINCTINAE** Schindewolf 1925

Genus *CHOFFATIA* Siemiradzki 1898

Choffatia sp. indet.

MATERIAL. Three fragments, C.76605–7.

HORIZON. Upper 2 feet of Samana Suk Limestone, Middle Callovian.

DESCRIPTION. The specimen C.76605 is evolute and wholly septate, with a whorl height of 33 mm and whorl thickness of 27 mm. The primary ribs are long, rectiradiate or gently prorsiradiate, and bifurcate near the ventral shoulder. Occasionally there is one short intercalatory rib between the bifurcating ribs. The secondary ribs are weak and interupted on the mid-venter. C.76607 has more convex whorl sides and coarser, distant primary ribs.

REMARKS. The poor preservation does not allow close comparison with any species of the genus. C.76605 is comparable in ornamentation and whorl section with *C. sakuntla* Spath (1931: 351, pl. LXIII figs 4a–b), but has a more evolute shell. C.76607 show some resemblance in coarse, blunt primary ribs with *C. cobra* (Waagen).

LOCALITY. South south west of Malla Khel (Baroch nala), Trans Indus Ranges.

Sub-family **PERISPHINCTINAE** Steinmann 1890

Genus ***PHOSOSPHINCTES*** Schindewolf 1925

Prosophinctes (?) ***virguloides*** (Waagen)

(Plate 6, figs 1, 2a, b)

1875 *Perisphinctes virguloides* Waagen: 203, pl. XLIX, figs 1a–b.
1925 *Perisphinctes virguloides* Waagen; Spath: 122.
1931 *Prososphintes virguloides* (Waagen); Spath: 441, pl. LXX, fig. 3; pl. XC, fig. 4 (see for synonymy).
1932 *Perisphinctes virguloides* Waagen; Lanquine: 635.
1934 *Prososphinctes virguloides* (Waagen); Spath: 12, pl. I, figs 3, 4a–b, 6 (holotype); pl. II, figs 3, 4a–b; pl. IV, figs 5a–b; pl. V, fig. 7.

MATERIAL. Twelve specimens, C.76608–19.

HORIZON. Basal one foot of Chichali Formation, Upper Oxfordian.

DESCRIPTION. The specimens are wholly septate and up to 88 mm in diameter. The whorl section is oval, with flat sides. Shallow constrictions parallel to the rib direction can be seen on the 88 mm diameter specimen but are absent on the other specimens. Long primary ribs bifurcate at the ventro-lateral shoulder; there are 28 primary ribs per half whorl at 88 mm diameter on C.76609, and 53 or 54 on C.76608 at 81 mm diameter.

DIMENSIONS. C.76608–81: 25 (31), —, 39 (48).
C.76609–88: 28 (32), 24·5 (28), 36·5 (41).

REMARKS. This species was placed in the genus *Perisphinctes* by Spath (1925), Dietrich (1925 : 19) and Lanquine (1932 : 635). Later, Spath (1931 : 441; 1934 : 12) put it into *Prososphinctes* and assigned to it an Upper Oxfordian to Lower Kimmeridgian age in Cutch, and an Upper Oxfordian, Transversarium Zone, age in Kala Chitta. Spath (1934: pl. I, fig. 6) refigured Waagen's holotype, which shows strong and sharp prorsiradiate ribs with pronounced forward projection on venter. The specimen figured here is Pl. 6, fig. 1, from Mazari Tang, Nizampur, is very similar in ornamentation and dimensions to the holotype.

Spath (1934 : pl. II, fig. 4) figured another specimen from Kala Chitta which is more involute, and considered it to be the best example of the species. The incomplete specimen figured here in Pl. 6, fig. 2, also from Mazari Tang, is similar, and differs from the holotype in being more involute and in having a greater whorl height.

P. virguloides is doubtfully referred to the genus *Prososphinctes*, for it shows strong sharp ribbing, has weak or no constrictions, and occurs in the Upper Oxfordian, Transversarius Zone of Kala Chitta and Mazari Tang. *Prososphinctes* is regarded by Arkell (1957) as Lower Oxfordian in age, and the type species, *Perisphinctes mazuricus* Bukowski, 1887, has weak, dense ribs, prominent constrictions and less distinct bifurcation. Arkell (1937 : 1) also did not agree with Spath's inclusion of *P. virguloides* in *Prososphinctes*.

LOCALITY. Mazari Tang, Nizampur, and north north-west of Jhallar, Kala Chitta.

Genus *PERISPHINCTES* Waagen 1869

Perisphinctes sp. indet.

(Plate 6, figs 3a, b)

MATERIAL. Two specimens C.76622–3, from Mazari Tang and two, C.76620–1 from Trans Indus Ranges.

HORIZON. Basal bed of Chichali Formation, Upper Oxfordian.

DESCRIPTION. The inner whorls of specimen C.76622 from Mazari Tang are similar to those of C.76620 from Trans Indus Ranges. The whorls are depressed and the dense prorsiradiate ribs bifurcate on the upper part of the whorl then cross the venter with slight forward arching. Some ribs are simple. Distinct constrictions are present. The outer whorl of C.76622 has distant coarse ribs.

DIMENSIONS. C.76620–35: 9·5 (27), 11 (31), 11·3 (32).

REMARKS. In the dense prorsiradiate ribbing and presence of constrictions, the Mazari Tang specimen, C.76622, compares favourably with the holotype of *Perisphinctes jelskii* (Siemiradzki) (Spath, 1934: 6, pl. V, figs 6a–b) and with other specimens from the Transversarium Zone of the Attock district figured by Spath (1934: 6, pl. IV, figs 2–4).

LOCALITIES. Mazari Tang, Nizampur (C.76622–3); north of Kalabagh, Trans Indus Ranges (C.76620–1).

Subgenus *KRANAOSPHINCTES* Buckman 1921

Perisphinctes (Kranaosphinctes) sp. indet.

(Plate 6, figs 4a, b)

MATERIAL. Four specimens, C.76624–27.

HORIZON. Basal bed of Chichali Formation, Upper Oxfordian.

DESCRIPTION. The figured specimen, C.76624, is very evolute, wholly septate and 100 mm diameter. The whorl section is rounded, slightly wider than high, and the whorl sides are nearly flat. Two constrictions (one deep) are seen on the outer whorl. The strong, straight, prorsiradiate ribs are moderately distant, and bifurcate high on the whorl side near the ventral shoulder. There are a few intercalated secondary ribs on the final third of the last whorl and a very few ribs remain simple throughout. The ribs are much reduced, or almost effaced, at the middle of the venter. C.76624 has about 48 primary ribs at 100 mm diameter.

Dimensions. C.76624–100: 24, 25, 59.

Remarks. The species is similar in its evolute whorls, ornamentation and rib density to the inner whorl of *P.* (*K.*) *cymatophorous* (Buckman) figured by Arkell (1939: pl. XXXVII, figs 3a–b), but differs in dimensions. In dimensions, rib density and whorl section it also compares with *P.* (*K.*) *trifidus* (J. Sowerby) as figured by Arkell (1939 : pl. XXXVI, fig. 2a–b), but shows more irregular trifurcation of the ribs.

Localities. Chichali Pass (C.76624), north of Kalabagh (C.76625), Trans Indus Ranges; north north west of Jhallar (C.76626–7), Kala Chitta Range.

Subgenus ***ARISPHINCTES*** Buckman 1924

Perisphinctes (Arisphinctes) orientalis Siemiradzki

1875 *Perisphinctes plicatilis* (J. Sowerby); Waagen: 189, pl. LI, figs 2a–b; pl. LII, fig. 3
1891 *Perisphinctes orientalis* Siemiradzki: 289.
1931 *Perisphinctes orientalis* Siemiradzki; Spath: 416, pl. LXIX, fig. 1; pl. LXXII, fig. 2; pl. LXXIV, figs 3a–b (see for synonymy).
1934 *Perisphinctes orientalis* Siemiradzki; Spath: 4, pl. IV, figs 1a–b.

Material. One specimen, C.76627.

Horizon. Basal one foot of Chichali Formation, Upper Oxfordian.

Description. The shell is evolute, wholly septate and 190 mm diameter. The whorl section is rounded quadrate, higher than wide, but depressed on the inner whorls. The ribs are moderately dense on the inner whorls, becoming gradually more distant and coarse on the outer whorl. They are prorsiradiate, bifurcate near the ventral shoulder and are gently arched forwards on the venter. There are occasional short intercalatory ribs. Near the aperture, the ribs fade out on the mid-venter and many are simple. There are about 47 ribs at 190 mm diameter. Some shallow constrictions occur especially on the inner whorls.

Dimensions. 190: 52 (27), ?46 (24), 102 (54).

Remarks. This is a worn incomplete specimen, very similar in ornamentation, rib density and whorl section to the Kala Chitta and Cutch specimens figured by Spath, but differs in dimensions and in having a higher than wide whorl section at comparative diameters.

Locality. Mazari Tang, Nizampur.

Subgenus *DICHOTOMOSPHINCTES* Buckman 1926

Perisphinctes (Dichotomosphinctes) cf. *rotoides* Ronchadze

(Plate 7, figs 1a, b, 2)

1917 *Perisphinctes rotoides* Ronchadze: 11, pl. I, fig. 8.
1938 *Perisphinctes* (*Dichotomosphinctes*) *rotoides* Ronchadze; Arkell: 90, pl. XVI, figs 1–7.

MATERIAL. Five fragments, C.76629–33.

HORIZON. Basal 4 inches of Chichali Formation, Upper Oxfordian.

DESCRIPTION. These are septate fragments with evolute, quadrate whorls, the whorl section being higher (20·5 mm) than thick (18·5 mm). Strong rectiradiate or slightly prorsiradiate ribs are separated by wider interspaces. They bifurcate high on the whorl side near the ventral shoulder and are straight or slightly arched forwards across the venter. Occasional simple ribs occur. There are prominent deep constrictions parallel to the ribs.

REMARKS. These Trans Indus fragmentary specimens compare well in ornamentation, whorl section, evolute shell and in the presence of deep constriction with Arkell's figures of *P.* (*D.*) *rotoides* from the Plicatilus Zone of England. They also compare with *P.* (*D.*) *antecedens* Salfield as figured by Arkell (1938 : pl. XVI, fig. 8).

LOCALITY. Chichali Pass, Trans Indus Ranges.

Perisphinctes (?Dichotomosphinctes) sp. indet.

(Plate 7, fig. 3a, b)

MATERIAL. Two fragments, C.76634–35, from Trans Indus Ranges, and C.76636 from the Kala Chitta Range.

HORIZON. Basal 3 inches (Trans Indus Ranges) or basal one foot of Chichali Formation Upper Oxfordian.

REMARKS. These fragmentary specimens indicate the presence of one or more species of *Dichotomosphinctes* in the collections. They have dense, prorsiradiate ribs which bifurcate high on whorl side close to the ventral shoulder, and cross the venter with slight forward arching. At small diameters, the whorl height is less than whorl thickness, but the outer whorl is more compressed. Spath (1934: 11, pl. III, figs 5a–b; pl. VI, figs 3a–c) figured specimens from Kala Chitta similar to C. 76636 as *P.* (*Dicholomosphinctes*) aff. *grossouvrei* (Siemiradzki). The Trans Indus specimens are somewhat different, and resemble *P.* (*D.*) *Jacki* Spath (1931: pl. LXXIII, fig. 6) and *P.* (*D.*) *subhelenae* Spath (1931: pl. CI, figs 2, 4a–b) in ribbing and whorl section.

LOCALITIES. Chichali Pass, C.76634, and Punnu Mines, C.76635, Trans Indus Range; north north west of Jhallar, C.76636, Kala Chitta Range.

Sub-family **VIRGATOSPHINCTINAE** Spath 1923

Genus ***KATROLICERAS*** Spath 1924

Katroliceras cf. ***pottingeri*** (J. de C. Sowerby)

(Plate 7, figs 4a, b)

1840 *Ammonites pottingeri* J. de C. Sowerby: 719, pl. LXI, fig. 10.
1931 *Katroliceras pottingeri* (J. de C. Sowerby); Spath: 505, pl. LXXXIII, fig. 4; pl. XCV, figs 6, 7; pl. XCVIII, fig. 4; pl. CII, figs 5a–d (see for synonymy).

MATERIAL. One fragment, C.76637.

HORIZON. 6 to 7 feet above the base of Chichali Formation, Lower Kimmeridgian.

DESCRIPTION. The specimen is septate, and has a sub-coronate whorl section, with a broad, gently arched venter. The whorl height is 44 mm, the thickness approximately 60 mm. Distant, massive ribs are separated by broad interspaces. They branch near the umbilical shoulder into about three ribs which cross the venter with forward arching. There is a swelling at the point of branching. Occasionally one of the ventral ribs is intercalated.

REMARKS. This specimen closely resembles, in ribbing and whorl section the example *K. pottingeri* (J. de C. Sowerby), from the Middle Katrol beds of Cutch, figured by Spath (pl. CII, figs 5a–b; pl. LXXXIII, fig. 4). It also resembles the very closely allied species, *K. pingue* Spath (1933: pl. LXXXII, figs 1a–b) from a similar horizon in Cutch.

LOCALITY. Punnu Mines, Trans Indus Ranges.

Katroliceras sp. indet.

MATERIAL. Three specimens, C.76638–40.

HORIZON. 5 to 7 feet above the base of Chichali Formation, Lower Kimmeridgian.

REMARKS. The specimens are small and septate with the following dimensions:
C.76639–25: 8·5 (34), 12 (48), 12·5 (50).
C.76638–20·5: 7 (34), 10 (49), 9 (44).

They may represent the inner whorls of forms like *K. depressum* Spath (1931: 515, pl. LXXXIX, figs 4a–b) or *K. zitteli* Spath (1931: 513, pl. LXXXVII, figs 6a–b). It is possible that the species is the inner whorls of *Pachysphinctes* which also has a depressed whorl section and similar ornamentation at a comparative diameter.

LOCALITIES. Datta Mines (C.76638) and north of Kalabagh (C.76639–40), Trans Indus Ranges.

Genus ***PACHYSPHINCTES*** Dietrich 1925

Pachysphinctes robustus Spath

(Plate 7, figs 5a, b)

1931 *Pachysphinctes robustus* Spath: 491, pl. LXXXIV, fig. 5; pl. XCIII, figs 10a–b.

MATERIAL. Three specimens, C.76641–3.

HORIZON. 5 to 7 feet above the base of Chichali Formation, Lower Kimmeridgian.

DESCRIPTION. These are evolute, septate fragments up to 135 mm diameter. The whorl section is sub-quadrate, wider than high, with greatest thickness on the lower third of the whorl side. The strong, rectiradiate or gently prorsiradiate ribs are separated by deep interspaces two to three times as wide on the outer whorl, but inner whorls are more densely ribbed. They bifurcate high on the whorl side at a small blunt tubercle. Occasionally ribs remain simple (about 2 per half whorl), and a few indistinct trifurcating ribs appear near the aperture. The ribs are arched forwards on the venter and weaken along the siphonal line.

DIMENSIONS. C.76641–135: 40 (30), 42 (31), 68 (50).

REMARKS. The figured specimen is similar in whorl section, dimensions and ornamentation to Spath's holotype from Cutch. The other fragments are comparable to *P. robustus* Spath, and also to the allied species *P. major* Spath (1931 : 489) and *P. bathyplocus* (Waagen) (Spath 1931 : 493) in whorl section and ornamentation. *P. robustus* Spath is very closely allied in ornamentation and whorl section to *P. major* Spath.

LOCALITIES. Punnu Mines (C.76641–3), Trans Indus Ranges.

Genus ***AULACOSPHINCTOIDES*** Spath, 1923

Aulacosphinctoides hazaraensis sp. nov.

(Plate 8, figs 1a, b, 2a, b)

DIAGNOSIS. Evolute, depressed whorls, with distant, prorsiradiate coarse ribs that bifurcate and occasionally trifurcate just ventral of the middle of the whorl side. Slight mid-ventral depression. 3 or 4 well marked constrictions per whorl.

MATERIAL. Two specimens, C.76644—the holotype, and C.76645—the paratype.

HORIZON. Basal bed of Lumshiwal Formation ("Giumal Sandstone"), Lower Tithonian.

DESCRIPTION. The holotype consists of a complete body chamber, probably of an immature specimen, two-thirds of a whorl long and 83 mm maximum diameter. The mouth-border is flared especially on the venter, and is preceded by a constriction, and there is a constriction at the beginning of the body chamber. The paratype consists of half a specimen, 63 mm diameter, showing parts of 3 whorls. The final third of the outer whorl is body chamber. In both specimens, the whorl section is rounded and depressed, and there is a slight mid-ventral depression. The ribs are almost straight prorsiradiate and strong; the holotype has 17 or 18 ribs per half whorl at 83 mm diameter, the paratype 17 ribs per half whorl at 63 mm. On the outer third of the whorl, the ribs bifurcate or sometimes trifurcate on the outer whorls, then pass straight across the venter and are partly interrupted at the mid-ventral depression. There are 3 or 4 deep constrictions per whorl parallel to the ribs.

DIMENSIONS. C.76644–75: 25 (33), 32·5 (43), 43·5 (46).
C.76645–62: 20·5 (33), 26 (42), 27 (44).

REMARKS. Uhlig (1910) described a number of *Aulacosphinctoides* species from the Himalayas. This new species compares well with *A. infundibulus* (Uhlig) (1910 : pl. LXVI, fig. 3; pl. LXXII, figs 1–4) and *A. hundesianus* (Uhlig) (1910: pl. LXXI, fig. 3; pl. LXXII, fig. 2; pl. LXVI, fig. 4) in ribbing, whorl section and dimensions, but differs in having coarser, less dense and more commonly trifurcating ribs on the outer whorl at comparative sizes. In the presence of frequent and fairly prominent constrictions, it is close to *A. hundesianus* (Uhlig), but differs in ornamentation details. *A. infundibulus* (Uhlig) has 41 to 44 ribs at 83 mm diameter, while the new species (which has a complete body-chamber at 83 mm) has about 34 to 36 primary ribs. *A. hundesianus* (Uhlig) has about 46 to 48 primary ribs at the same size.

LOCALITY. Kathwal, Hazara.

Aulacosphinctoides uhligi Spath

(Plate 8, figs 3a, b)

1910 *Perisphinctes* (*Aulacosphinctes*) *torquatus* (J. de C. Sowerby); Uhlig: 368, pl. LXIX, figs 2a–d; pl. LXXI, figs 1a–d, 2a–c.
1923 *Aulacosphinctoides uhligi* Spath: 299.
1939 *Aulacosphinctoides* aff. *uhligi* Spath: 120, pl. XV, figs 8a–b.

MATERIAL. Two specimens, C.76646–7.

HORIZON. Two feet above the base of Lumshiwal Formation ("Giumal Sandstone") in Hazara and 20 feet above the base of Chichali Formation in the Trans Indus Ranges, Lower Tithonian.

DESCRIPTION. The shell is evolute, septate and 62 mm in diameter. The whorl section is rounded, sub-circular on the outer whorl, but depressed and with flatter whorl sides on the inner whorls. The ribs are prorsiradiate and bifurcate at the middle or slightly higher on the whorl side. On the inner whorls, the bifurcation point is higher, near the ventral shoulder. There are 23 ribs per half whorl at 62 mm diameter, and slightly more on the inner whorls. There are two oblique constrictions on the outer whorl, and the one at the apertural end appears to mark the beginning of the body chamber. The constrictions cut across several secondary ribs immediately preceding them. The rib following a constriction is simple.

DIMENSIONS. C.76646–62: 20 (32), 22·5 (36), 29·5 (48).
C.76646–21: 7 (33), 12 (57), 10 (47).

REMARKS. The figured specimen compares well in ornamentation and dimensions with the type specimens of *A. uhligi* Spath (1923 : 299; 1933 : 476) which were figured by Uhlig (1910: 368, pl. 69, fig. 2; pl. 71, figs 1, 2). In the Himalayas it is quite common at various localities. The change from depressed inner to elevated outer whorls, and the change of the bifurcation point from the ventral shoulder on the inner whorl to lower on the side of the outer whorl, compares well with Uhlig's illustrations. It differs, however, in having a smaller number of primary ribs. It is distinguished from *A. infundibulus* (Uhlig) by its straight, prorsiradiate ribs, bifurcating higher on the whorl side and more compressed whorl section. It is like *A. willisi* (Uhlig 1910: pl. LXXIII, figs 1a–c) in ornamentation, but differs in whorl section and other details. The fragmentary specimen described by Spath (1939) from the Trans Indus Ranges as *A.* aff. *uhligi* Spath is also similar.

LOCALITIES. Kathwal, Hazara, and a doubtful fragment from the Trans Indus Salt Ranges.

Aulacosphinctoides sp. indet.

(Plate 8, figs 4a, b)

MATERIAL. Four specimens, C.76648–51.

HORIZON. One foot above the base of Lumshiwal Formation ("Giumal sandstone"), Hazara, and 20 feet above the base of Chichali Formation, Trans Indus Ranges, Lower Tithonian.

DESCRIPTION. The figured specimen has a maximum diameter of 78 mm; slightly more than half of the outer whorl is body chamber, the last septum occurring at 57 mm diameter. The whorl section is well rounded and depressed, and has a shallow mid-ventral groove. The ribs are prorsiradiate, bifurcating high on the whorl side, then pass straight across the venter, but are weakened along the siphonal line. On the last whorl trifurcating ribs are dominant, but near the aperture the ribbing becomes irregular and simple. There are 35 ribs at 57 mm diameter. There are two oblique, moderately deep constrictions on the septate whorls, which cut across the ribs preceding them. The rib following a constriction is simple.

DIMENSIONS. C.76648–57: 28 (35), 25 (44), 22·5 (39).

REMARKS. In whorl section, straight ribs and deep constrictions, this species resembles *Aulacosphinctoides willisi* (Uhlig 1910: pl. LXV, figs 3c–d; pl. LXXIII, figs 1a–c), but differs in having frequent trifurcating ribs on the outer whorl. Uhlig's species is based on a mature adult specimen of 84 mm diameter, which has a lappet, but on the body chamber only two out of 22 to 23 primary ribs trifurcate, the rest bifurcate. Contrary to this, in the present specimens more than 75% of the ribs trifurcate on the outer half whorl. In the trifurcating ribs it resembles *A. hazaraensis* sp. nov., but is more involute, has finer straight ribs and a deeper umbilicus. The three other specimens (C.46649–51) of *Aulacosphinctoides* are indeterminate due to poor preservation. They have very evolute shells, depressed whorl sections and dense, fine ribs.

LOCALITIES. Kathwal (C.76648), Hazara; Chichali Pass (C.76649), Shaikh Budin Hills, (C.76650–51), Trans Indus Ranges.

Genus ***VIRGATOSPHINCTES*** Uhlig 1910

Virgatosphinctes denseplicatus (Waagen)

(Plate 8, figs 5a, b)

1875 *Perisphinctes denseplicatus* Waagen: 201, pl. XLVI, figs 3a–b; pl. LV, fig. 1a–b.
1910 *Perisphinctes* (*Virgatosphinctes*) *denseplicatus* Waagen; Uhlig: 313, pl. LIII, figs 3a–d; pl. LIV, figs 1a–c; pl. LV, figs 1a–d, 2a–d, 3a–d; pl. LVI, figs 1a–c.
1933 *Virgatosphinctes densplicatus* (Waagen); Spath: 532, pl. LXXVII, figs 3a–c; pl. XC, fig. 1; pl. XCVI, figs 3a–b; pl. CII, fig. 4 (see for synonymy).

MATERIAL. Two specimens, C.76652–3.

HORIZON. Basal part of Lumshiwal Formation ("Giumal sandstone"), Hazara, and 20 feet above the base of Chichali Formation, Trans Indus Ranges, Lower Tithonian.

DESCRIPTION. The figured specimen is wholly septate and 57 mm diameter. The outer whorl embraces half to two-thirds of the previous whorl. The whorl section is rounded and slightly wider than high. The sharp, dense ribs are prorsiradiate, bifurcate near the middle of the whorl side, and cross the venter arched slightly forwards. There are a few shallow constrictions parallel to the ribs, and they are followed by a simple rib. The rib density is 50 at 57 mm diameter.

DIMENSIONS. C.76652–57: 22 (39), 23·5 (41), 21 (37).

REMARKS. This specimen has ribbing typical of *V. denseplicatus* (Waagen) and compares closely with Spath's figure of an evolute form of the species *V. rotunda* Spath (1933: pl. CII, fig. 4) from the lower Umia group of Cutch and with Uhlig's figure of the inner whorls of *V. denseplicatus* (Waagen) from Spiti area (Uhlig 1910: pl. LIII, figs 3a–c; pl. LXV, figs 2a–d). It differs primarily in having slightly less dense ribbing than Uhlig and Spaths' specimens.

LOCALITIES. Kathwal, Hazara (C.76652), west of Makerwal, Trans Indus Ranges (C.76653).

Virgatosphinctes frequens (Oppel)

(Plate 9, fig. 1a, b)

1865 *Ammonites frequens* Oppel: 295, pl. 87.
1910 *Perisphinctes* (*Virgatosphinctes*) *frequens* (Oppel), Uhlig: 325, pl. LXIII, figs 1a–c, 3a–c; pl. LXXXV, figs 1a–c; pl. LXXV A, figs 1a–c (see for synonymy).

MATERIAL. Three specimens, C.76654–6.

HORIZON. Lower 2 to 3 feet of Lumshiwal Formation, Giumal sandstone, Lower Tithonian.

DESCRIPTION. The figured specimen is evolute and 98 mm in diameter. The whorl section is oval with sides that converge towards a rather narrow venter. The ribs are prorsiradiate, moderately distant on the outer whorl, but more dense on the inner whorls. They bifurcate or trifurcate near the middle of whorl side, then the fine secondary ribs recurve to cross the ventral shoulder and the venter radially. There are 56 or 57 primary ribs at 98 mm diameter.

DIMENSIONS. C.76654–98: 33 (34), 31 (32), 42 (43).

REMARKS. The figured specimen resembles strongly, in ornamentation, Oppel's holotype and other specimens figured by Uhlig (1910) from the Spiti area. It differs in being more evolute and in having a less inflated and elevated whorl section. It has almost identical dimensions to *Virgatosphinctes subfrequens* Uhlig (1910: 327, pl. XLIX, figs 1a–d; pl. LXI, figs 1a–d). One of the two fragmentary specimens, C.76655, is more inflated and appears to be closer in dimensions to Oppel's holotype. *V. frequens* was recorded from different localities in Hazara by Middlemiss (1896 : 33–34) and Spath (1933 : 804). It is the most abundant *Virgatosphinctes* in northern Hazara and occurs in association with *Aulacosphinctoides*. One fragment from 20 feet above the base of Chichali Formation in the Makerwal area is doubtfully assigned to this species and is also associated with *Aulacosphinctoides*. Arkell (1956 : 407) similarly pointed out the close association of these two genera in the Middle Spiti shales of Himalaya.

LOCALITIES. Kathwal–Kalapani (C.76654–5), Hazara, one fragment from Makerwal, Trans Indus Ranges (C.76656).

Virgatosphinctes sp. indet.

MATERIAL. One specimen, C.76657.

HORIZON. 2 feet above the base of Lumshiwal Formation ("Giumal sandstone"), Lower Tithonian.

REMARKS. The specimen has strong, sharp and dense ribs which cross the venter transversely. The ribs usually bifurcate from the middle of whorl side, but a few trifurcate and there are occasional simple ribs on the inner whorls. It has part of the body chamber on which the ribs trifurcate in a virgatome fashion and are more distant. Dimensions are: 72: 28 (39), 29 (40), 23·5 (33). It is comparable with *V. subquadratus* Uhlig (1910: pl. LXVIII, figs 1a–c) and *V. indistinctus* Uhlig (1910: pl. LXVI, figs 2a–b) in whorl section and ornamentation, but is more involute and has denser ribs.

LOCALITY. Kathwal, Hazara.

Family **ASPIDOCERATIDAE** Zittel 1895

Sub-family **ASPIDOCERATINAE** Zittel 1895

Genus ***EUASPIDOCERAS*** Spath 1931

Euaspidoceras cf. ***wagurense*** (Spath)

1931 *Neaspidoceras wagurense* Spath: 614, pl. CXX, figs 7a–d (see for synonymy).

MATERIAL. One fragment, C.76658.

HORIZON. Basal one foot of Chichali Formation, Upper Oxfordian.

Description. The specimen is evolute with a sub-rectangular whorl section; whorl height 42 mm and thickness 39 mm at the aperture. The whorl sides converge gradually towards a broad sub-tabulate venter. Two rows of tubercles at the umbilical edge and ventral shoulder are connected by weak, blunt ribs. The umbilical tubercles extend rursiradially on the umbilical wall. The tubercles on the ventral shoulder are obliquely elongated.

Remarks. The specimen is poorly preserved, but closely resembles, in ornamentation and whorl section Spath's figure of a specimen from the Kantcote sandstone (Bimammatum Zone) of Cutch. It may also be compared with *E. varians* Spath (1931: pl. CV, figs 7a–b ; pl. CX, figs 1a–b) from the same horizon in Cutch, but differs in having a less compressed whorl section and arched whorl sides.

Locality. Mazari Tang, Nizampur.

Genus ***ASPIDOCERAS*** Zittel 1868

Sub-genus ***ASPIDOCERAS*** Zittel 1868

Aspidoceras (Aspidoceras) sp. indet.

Material. One specimen, C.76659.

Horizon. 5 to 7 feet above the base of the Chichali Formation, Lower Kimmeridgian.

Description. The specimen is involute, probably septate, and approximately 56 mm diameter. It has a subcircular whorl section, wider than high. There is a distinct row of tubercles near the umbilical shoulder, and a suggestion of an indistinct row of outer tubercles on the side of the inner whorl. There are no ribs.

Dimensions. C.76659–56: 25 (45), 30·5 (54), 61 (29).

Remarks. In inflated shell and weak outer row of tubercles, the species may be compared with *A.* (*A.*) *iphiceroides* (Waagen) (Spath, 1931: 635, pl. CXXIII, figs 8a–b). In dimensions it is similar to a small example from Mombasa described by Spath as *A.* (*A.*) *mombasense* (Spath 1931 : 636). The whorl section is very similar to a form from Cutch figured by Spath (1931: pl. CXXII, fig. 9) as *A.* (*Aspidoceras*) sp. indet.

Locality. Punnu Mines, Trans Indus Ranges.

Sub-genus ***PSEUDOWAAGENIA*** Spath 1931

Aspidoceras (Pseudowaagenia) sp. indet.

(Plate 9, figs 2a, b)

Material. One specimen, C.76660.

Horizon. One foot above the base of Chichali Formation, Lower Kimmeridgian.

Description. The shell is half involute, septate, and 36 mm diameter. The whorl section is oval and higher than wide. There are no ribs. There are 15 to 16 small, rounded tubercles at the umbilical shoulder at 36 mm diameter.

Dimensions. C.76660–36: 16 (44), 15 (42), 10 (28).

Remarks. The suture line of this specimen is very similar to that of *Pseudowaagenia hyanaldi* (Neumayr) and *Pseudowaagenia micropla* (Oppel) as figured by Spath (1933: pl. CXVIII, fig. 11; pl. CXXII, fig. 30) from Cutch. Spath (1933: 623, pl. CXXII, figs 3a–c) figured a specimen of *P. micropola* (Oppel) from the lower Katrol beds of Cutch, which had dimensions of 55 mm: 42%, 36%, compared with 55 mm: 40%, 25%, 33%, in Oppel's type. The specimen described here is distinguished from both Neumayr's and Oppel's species in being more involute and more inflated.

Locality. Punnu Mines, Trans Indus Ranges.

Genus ***PHYSODOCERAS*** Hyatt 1900

Sub-genus ***SIMASPIDOCERAS*** Spath 1925

Physodoceras (Simaspidoceras) sp. indet.

Material. One fragment, C.76661.

Horizon. About one foot above the base of Chichali Formation, Lower Kimmeridgian.

Description. This fragment has a rounded, trapezoidal whorl section, with greatest thickness just above the umbilical shoulder, and a broad venter. The umbilicus is narrow. There are weak ribs and weak blunt tubercles near the umbilical shoulder.

Remarks. The weak ribs, umbilical tubercles, broadly rounded venter and squarish whorl section, may be compared with *Simaspidoceras argobbae* Dacque (1905). The suture line also compares well with Dacque's species.

Locality. Punnu Mines, Trans Indus Ranges.

Sub-family **SIMOCERATINAE** Spath 1924

Genus ***HYBONOTICERAS*** Breistroffer 1947

Hybonoticeras sp. indet.

Material. One fragment, C.76662.

Horizon. 5 feet above the base of Chichali Formation, Lower Kimmeridgian.

Description. This is a septate fragment, with a sub-rectangular whorl section and nearly flat whorl sides. There is a deep sulcus in the middle of the venter, bordered by sharp ridges. The ornamentation consists of very weak, distant rectiradiate or gently prorsiradiate ribs. These swell into blunt, thick tubercles at the umbilical shoulder and again on the whorl side near the ventral shoulder. The ventral tubercles tend to be clavate while the umbilical tubercles are obliquely elongated backwards and extend partly on to the umbilical wall.

Remarks. The species is comparable in weak ribs, size, side and ventral views with *Hybonoticeras kachensis* (Spath) from Lower–Middle Katrol beds of Cutch (Spath 1933 : 645, pl. CXXII, fig. 6), and with *H. pressulum* (Neumayr) and *H. ciliatum* Berckhemer and Holder, both figured by Berckhemer and Holder (1959: pl. I, fig. 1; pl. II, fig. 6, pl. 3, fig. 9). The suture line is comparable with a specimen figured by Spath (1933: pl. XCV, fig. 2) as *H.* sp. nov. aff. *hybonata* (Oppel) from Lower Katrol beds of Cutch.

Locality. East of Chichali Pass (Kutch Mines), Trans Indus Ranges.

Family **OLCOSTEPHANIDAE** Haug 1910

Sub-family **SPITICERATINAE** Spath 1924

Genus ***PRONICERAS*** Burckhardt 1919

Proniceras indicum Spath

(Plate 9, figs 3a, b)

1939 *Proniceras indicum* Spath: 34, pl. III, figs 4a–d.

Material. One specimen, C.76663.

Horizon. 25 to 30 feet above the base of Chichali Formation, Lower Tithonian.

Description. This specimen is an almost complete immature of 38 mm diameter. The whorl section is almost circular. The prorsiradiate ribs bifurcate near the middle of the whorl side, and cross the venter as forwardly-directed chevrons, but are weak at the mid-ventral line. There are a few simple ribs on the outer whorl. There are about 50 ribs per whorl at 38 mm diameter. Three moderately deep oblique constrictions per whorl are present on outer and inner whorls. The rib following each constriction is simple.

Dimensions. C.76663–38: 15 (39), 15 (39), 14 (37).

Remarks. The specimen is very similar to Spath's holotype which was based on a fragmentary specimen, 19 mm in diameter, from the Trans Indus Salt Range.

Locality. Chichali Pass, Trans Indus Salt Ranges.

Genus ***SPITICERAS*** Uhlig 1903

Spiticeras multiforme Djanelidze

(Plate 9, figs 4a, b)

1922 *Spiticeras multiforme* Djanelidze: 143, pl. VII, figs 3a–b; pl. XV, figs 1a–c, 2a–c; pl. XX figs 1a–c; pl. XXII, figs 3a–b.

Material. One specimen, C.76664.

HORIZON. 3 feet below the base of the middle member of the Chichali Formation, Upper Tithonian.

DESCRIPTION. This is a wholly septate specimen, of approximately 66 mm diameter. The whorl section is oval with greatest breadth near the umbilicus. There are 16 or 17 prominent, umbilical tubercles on the outer whorl. Prorsiradiate ribs issue from the tubercles in bundles of 4 or 5 and pass over the venter arched forwards. Occasional ribs bifurcate higher up on the side of the whorl, and some ribs are intercalated. The ribs weaken along the mid-ventral line. There are an estimated 105 ribs on the final whorl.

REMARKS. This specimen is almost identical in dimensions and ornamentation with Djanelidze's figure (Pl. VII, figs 3a–b) of a specimen from France. It also compares well with *Spiticeras bilobatus* (Uhlig) and *Spiticeras subbilobatus* (Uhlig) (1910 : 96, 98, pl. X, figs 1a and 2) in ornamentation, side and ventral views. It however, shows more elevated whorl section, denser ribs, less evolute shell and absence of prominent constrictions.

LOCALITY. South west of Malla Khel, Trans Indus Ranges.

Spiticeras sp. indet.

MATERIAL. Two fragments, C.76665–6.

HORIZON. 3 feet below the base of the middle member of the Chichali Formation, Upper Tithonian.

REMARKS. These fragments are characterized by strong forwardly projected ribs on the upper half of the whorl side and acute forward chevrons on the venter. There are prominent radially elongated tubercles at the umbilical shoulder. In ribbing style and strong forward projection of the ribs they compare well with *Spiticeras* aff. *scriptus* (Strachey) (Uhlig, 1910 : 112, pl. XIV, figs 3a–d) from Lochambelkichak, Spiti area. They, however, differ in whorl section, and Uhlig's form has a less acutely rounded venter.

LOCALITY. South west of Mallakhel, Trans Indus Ranges.

Sub-family **PROVALANGINITINAE** nov.

Genus ***PROVALANGINITES*** nov.

TYPE SPECIES. *Provalanginites rhodesi* sp. nov.

DIAGNOSIS. Involute, inflated sphaerocones, with an eccentrically coiled and contracted adult body-chamber of 40–60 mm maximum diameter. Whorl section depressed, semicircular, with an occluded umbilicus on septate whorls and a very narrow eccentric umbilicus on the body-chamber. Adult body-chamber occupies about seven-eighths of a whorl. Ribs moderately dense, simple, or bifurcating and trifurcating from the middle of the whorl side, but fading towards umbilical shoulder. Ribs prorsiradiate on side of whorl and venter. Suture line fairly simple with multifid asymmetric first lateral lobe and retracted suspensive lobe.

REMARKS. The species recalls the sphaerocone–cadicone shells and eccentric coiling of the earlier families Tulitidae (Middle Jurassic) and Oecoptychidae (Middle Callovian to Lower Oxfordian), and the later family Olcostephanidae, especially the type species, *Ammonites nuculeus* Roemer (Koenen 1902 : pl. IV, figs 6–7) of the genus *Valanginites* (Upper Valanginian). The sub-family Provalanginitinae nov. is characterized by sphaeroconic, involute, eccentrically coiled shell, with weak, non-tuberculate ribs. It may include the genus *Valanginites* and range from Tithonian to Valanginian.

In the Trans Indus Ranges the two new species of the genus and sub-family occur in the Tithonian beds of the Chichali Formation.

Provalanginites rhodesi sp. nov.

(Plate 10, figs 1a, b, 3a, b)

DIAGNOSIS. Moderately-sized species, adult body chamber of 45–50 mm diameter. Inner whorls sphaeroconic, body chamber eccentrically coiled, contracted. Ribs simple or bifurcating, smooth near umbilical shoulder, but becoming strong and forwardly arched on venter.

MATERIAL. Three specimens; C.76671, the holotype, and C.76672–73, paratypes.

HORIZON. 20 to 30 feet above the base of the Chichali Formation, Lower Tithonian.

DESCRIPTION. The holotype has most of its body chamber complete, only the final quarter whorl is missing; its maximum diameter is 44 mm. Both paratypes are wholly septate, and of 29 and 25 mm diameter. The septate whorls are depressed sphaerocones with the umbilicus occluded. The venter of the adult body chamber uncoils away from the spiral of the previous whorl, so that the umbilicus opens slightly; the body chamber also contracts markedly towards the aperture. The mouth border is not preserved.

The ribs are fairly dense on inner whorls, but stronger on the body-chamber. They are simple, bifurcating or occasionally trifurcating, and are weak near the umbilicus. They are strongly prorsiradiate, and cross the venter arched forwards. There are an estimated 45–46 ribs per whorl at 44 mm diameter.

DIMENSIONS. C.76671–44: 24 (55), 27 (61), 4·5 (10).
C.76671–34: 18 (53), 27 (79), 2·5 (7).
C.76672–21: 11 (52), 18 (86), 0·0 (0).

REMARKS. The species resembles in eccentric coiling and sphaerocone shell the type species of Callovian genus *Kheraiceras* and the Lower Oxfordian genus *Protophites*, but differs in details of coiling, whorl section and ornamentation.

In eccentric coiling and sphaerocone shell, it resembles more closely *Valanginites nucleus* (Roemer) (Koenen, 1902: pl. IV, figs 6–7) from the Valanginian beds of Europe, but differs in ornamentation details. The genus *Valanginites* is restricted (Wright, 1957) to the Upper Valinginian.

LOCALITIES. Lunda mines (C.76671), and Chichali Pass (C.76672–73), Trans Indus Ranges.

Provalanginites howarthi sp. nov.

(Plate 10, figs 2a, b)

DIAGNOSIS. Larger than *P. rhodesi*, adult body chamber being 52 mm diameter, septate whorls sphaetoconic but more depressed, ribs almost absent on whorl sides and less strong on the venter than in *P. rhodesi*.

MATERIAL. One specimen C.76674, the holotype.

HORIZON. About 25 feet above the base of Chichali Formation, Lower Tithonian.

DESCRIPTION. The single specimen is a complete adult, with a body chamber seven-eighths of a whorl long, which coils eccentrically on the venter, contracts in whorl thickness half way along the body chamber, then flares slightly at the aperture. Some of the mouth border is preserved on the venter. The inner whorls are sphaeroconic and very depressed although only the final part of the last septate whorl can be seen. The sides of the body chamber are smooth, weak ribs being confined to the venter where they arch gently forwards, and appear to fade along the mid-ventral line.

DIMENSIONS. C.76674–52: 23 (44), 32 (62), ?6 (12).

REMARKS. The species differs from *Provalanginites rhodesi* sp. nov. in having weaker ornament, smoother body-chamber, a more depressed whorl section and a broader venter.

LOCALITY. Punnu Mines, Trans Indus Ranges.

Family **BERRIASELLIDAE** Spath 1922

Sub-family **BERRIASELLINAE** Spath 1922

Genus ***BLANFORDICERAS*** Cossman 1907

Blanfordiceras cf. ***wallichi*** (Gray)

(Plate 10, figs 4a, b, 5a, b)

1832 *Ammonites wallichi* Gray: Pl. C, fig. 3.

1910 *Hoplites* (*Blanfordia*) *wallichi* (Gray); Uhlig: 186, pl. XXXI, figs 1a–c, 2; pl. XXIX, figs 1a–b, 2a–b, 3a–c; pl. XXX, figs 1a–c.

1939 *Blanfordiceras* aff. *wallichi* (Gray); Spath: 43, pl. IV, fig. 6; pl. V, figs 1, 9, 10 (see for synonymy).

MATERIAL. Three fragments, C.76675–7.

HORIZON. 10 to 60 feet below the base of the middle member of the Chichali Formation, Upper Tithonian.

DESCRIPTION. The whorl section is sub-quadrate, higher than wide, with a tabulate venter that has a marked sulcus in the middle. Strong, gently sinuous and prorsiradiate ribs, bifurcate near the middle of the whorl side. A few ribs are simple. The ribs are high and sharp on the venter and are interrupted by the sulcus. On the body-chamber, the ribs tend to cross the venter with only slight degeneration along the mid-venter.

REMARKS. These fragmentary specimens broadly resemble the examples of *Blandfordiceras wallichi* (Gray) figured by Uhlig (1910). In the Spiti area the species has been reported from both the upper and middle shales, suggesting a long time range in the Tithonian. In the Trans Indus Ranges, it is found above the *Aulacosphinctoides* horizon, and as high as the *Himalayites* and *Spiticeras* beds.

LOCALITIES. North of Kalabagh, Chichali Pass, Punnu Lunda Mines, and south west of Malla Khel, Trans Indus Ranges.

Blanfordiceras cf. ***latidomus*** (Uhlig)

(Plate 10, figs 6a, b, 7a, b)

1910 *Hoplites* (*Blanfordia*) *latidomus* Uhlig: 196, pl. XXXV, figs 1a–c.
1939 *Blanfordiceras* aff. *latidomus* (Uhlig); Spath: 46, pl. V, figs 12a–b.

MATERIAL. Two specimens, C.76678–9.

HORIZON. About 20 feet below the base of the middle member of the Chichali Formation, Upper Tithonian.

DESCRIPTION. These evolute, wholly septate specimens have sub-quadrate or polygonal whorl sections, with whorl thickness equalling whorl height, and sulcate venters. The ribs are prorsiradiate, sharp, fairly distant, and bifurcate at the middle of the whorl side; the point of bifurcation being marked by a small, sharp tubercle. They are sharp and elevated on the venter and are interrupted by the sulcus. A few ribs remain simple.

DIMENSIONS. C.76678–?47: 16 (34), 17 (36), 18 (38).
C.76679–36: 13 (36), 13 (36), 14 (39).

REMARKS. The specimens resemble, in whorl shape and ornamentation, Uhlig's holotype from Lochambelkichak, Spiti area. They are wholly septate and of smaller size, but all of them show the sharp tuberculation on the middle of the whorl side, and rather straight prorsiradiate ribs.

LOCALITY. Lunda Mines, Trans Indus Ranges.

Blanfordiceras sp. indet.

(Plate 10, figs 8a, b)

MATERIAL. Four fragments, C.76680–83.

HORIZON. 2 to 3 feet above the base of Chichali Formation in Kala Chitta, and

10 to 30 feet below the base of middle member of Chichali Formation in the Trans Indus Ranges, Upper Tithonian.

Remarks. These fragments may belong to one or more species of the genus. Poor preservation does not allow a specific determination. C.76680 has a rounded whorl section, ribs that bifurcate near the middle of whorl side and the point of bifurcation is marked by radially elongated blunt tubercles. The ribs are interrupted at the mid-venter but are without any prominent tuberculation. In ventral view and whorl section it resembles a small inner whorl fragment figured by Spath (1930 : pl. IV, fig. 5; pl. V, fig. 2,; pl. VI, figs 5, 11, 12 and 15) as *Blanfordiceras* cf. *boehmi* (Uhlig). C.76681 has a higher than wide whorl section, sharp fairly distant prorsiradiate ribs, sharp tubercles at the point of bifurcation on whorl side and at the termination of ribs on the grooved venter. The fragment may be compared in ribbing and higher than wide whorl section with *B. acuticosta* (Uhlig 1910 : 301, pl. XXXVIII, figs 2a–c).

Localities. Chichali Pass and Kalabagh, Trans Indus Ranges (C.76682–83), and north north west of Jhallar, Kala Chitta Range (C.76680–81).

Genus ***PROTACANTHODISCUS*** Spath 1923

Protacanthodiscus cf. ***michaelis*** (Uhlig)

(Plate 11, figs 1a, b)

1902 *Hoplites michaelis* Uhlig: 35, pl. VII, figs 1–4.

Material. One fragment, C.76684.

Horizon. 3 feet below the base of the middle member of the Chichali Formation, Upper Tithonian, just below *Subthurmnnia fermori* horizon.

Description. A detached fragment of the body chamber has a rectangular whorl section with a broadly rounded venter, whorl height of 61 mm and breadth of 38 mm. It has only very weak ribs, but prominent umbilical and ventrolateral tubercles and weak lateral ones. The septate part of the specimen (as figured) has a more compressed whorl section, with flat sides and a flat sulcate venter. The ribs are strong and nearly straight, and they branch at the middle of the whorl side at the lateral tubercle. Occasional ribs branch from an umbilical tubercle, and there are frequent non-tuberculate simple ribs. There are prominent umbilical tubercles, smaller mid-lateral tubercles, and all the ribs swell into blunt transverse tubercles at the ventral shoulder and are interrupted at the mid-ventral sulcus.

Dimensions. C.76684–?96: 36 (38), 24 (25), ?38 (40).

Remarks. The specimen compares well with *Hoplites michaelis* Uhlig in whorl section and general ornamentation, but differs in having frequent intercalatory ribs, less frequent bifurcation from the umbilical shoulder, transverse rather than oblique ventral tubercles and greater forward projection of the ribs. It is also similar to forms like *Berriasella chaperi* (Pictet, 1868 : 242, pl. 37, fig. 3; Mazenot, 1939: 80, pl. VIII, figs 5–9, pl. IX, figs 1a–b), *Berriasella aspera* Mazenot (1939: pl. IX, figs 2–3) and *Berriasella malbosi* (Pictet, 1863: 77, pl. XIV, figs 1–2; Mazenot, 1939 : 98, pl. XIII, figs 8a–c; pl. XIV, fig. 1). *B. chaperi* attains a diameter of about 150 mm, and at 63 mm has the following dimensions (Mazenot, 1939 : 81): whorl height 36%, whorl thickness 23%, umbilical width 38%. All these species have prominent tubercles and tabulate venters and are closer to *Protacanthodiscus* than to *Berriasella*.

This specimen has great stratigraphic importance in the area, for it lies just below the zone of *Subthurmannia fermori* and close to the Jurassic/Cretaceous boundary.

LOCALITY. Lunda Mines, Trans Indus Ranges.

?***Protacanthodiscus*** sp. indet.

(Plate 11, figs 4a, b)

1939 *Himalayites*? (Gen. nov.) ?sp. indet. Spath: 66, pl. VII, figs 1a–c.

MATERIAL. One specimen, C.76685.

HORIZON. Five feet below the base of the middle member of the Chichali Formation, Upper Tithonian.

DESCRIPTION. The specimen is wholly septate, with a hexagonal section and a sulcate venter. The ribs are concave forwards, mainly simple, but some bifurcate at the lateral tubercle. At the ventro-lateral edge, they swell into high, thin tubercles which form chevrons along the sides of the ventral sulcus. Prominent, radially elongated tubercles occur sporadically on some simple and all bifurcating ribs at the middle of the whorl side.

REMARKS. This specimen is provisionally placed in the genus *Protacanthodiscus* because of its fairly broad venter, large size and presence of mid-lateral and ventro-lateral tubercles. It differs from the type species and other species of *Protacanthodiscus* in details of ribbing and in having a *Himalayites*-type hexagonal whorl section. In ornamentation and forward projection of ribs near the ventral shoulder, it is closer to *Raimondiceras*, e.g. *R. raimondi* (Arkell and Wright 1957 : 351) and *R. ?salinarium* Spath (1939 : 62, pl. XIV, figs 4, 5), but differs in ventral aspects, whorl section and its less dense ribs. In whorl section and the forward projection of the ribs near the venter, it recalls the Valanginian species *Neohoploceras baumbegeri* Spath (1939: pl. XXII, figs 3a–b). It strongly resembles a form described and figured by Spath from the Trans Indus Ranges as *Himalayites*? (Gen. nov.?) sp. indet. (1939: pl. VII, fig. 1a–c), except that Spath's form is more inflated and has a few trifurcating ribs.

The specimen incorporates the whorl section of *Himalayites*, the tabulate, broad venter of *Protacanthodiscus*, and the forward projection of ribs on the ventral shoulder of *Raimondiceras*. It probably represents a new Tithonian genus, intermediate between *Protacanthodiscus* and *Raimondiceras* which could have given forms like *Kilianella* and *Neohoploceras* during Berriasian and Valanginian times.

LOCALITY. Lunda Mines, Trans Indus Ranges.

Sub-family **HIMALAYITINAE** Spath 1925

Genus ***HIMALAYITES*** Uhlig in Boehm 1904

Himalayites cf. ***depressus*** Uhlig

1910 *Himalayites depressus* Uhlig: 148, pl. XL, figs 2a–c.

Material. One specimen, C.76669.

Horizon. 2½ feet above the base of the Chichali Formation in Mazari Tang section, Nizampur, Upper Tithonian.

Description. The specimen is evolute and roughly 56 mm in diameter. The whorl section is highly depressed, much wider than high with a broad flattish sulcate venter. Strong primary ribs end at large lateral tubercles, from which secondary ribs issue in bundles of 2 to 4, and pass onto the venter as sharp, high ribs. They are interrupted by the mid-ventral sulcus, and there are occasional small ventral tubercles (about 4 per half whorl) at each side of the sulcus.

Remarks. In spite of the poor preservation the specimen resembles closely in whorl section and ornamentation Uhlig's holotype from the Spiti area, except for the occasional tubercles on some ribs near the ventral margin.

Locality. Mazari Tang, Nizampur.

Himalayites middlemissi (Uhlig)

(Plate 9, figs 6a, b)

1910 *Hoplites* (*Blanfordia*) *middlemissi* Uhlig: 197, pl. XXXVII, figs 1a–c.

Material. One specimen, C.76668.

Horizon. 10 feet below the base of the middle member of the Chichali Formation in the Trans Indus Ranges, Upper Tithonian.

Description. The specimen has a much depressed whorl section with a sulcate venter. The coarse primary ribs terminate near the middle of the whorl sides in large knob-like tubercles. From the tubercles bundles of 2 or 3 secondary ribs cross the venter with slight forward arching, and are interrupted at the mid-ventral sulcus. The whorl height is 22 mm, and the whorl thickness over the tubercles is 36·5 and 32 mm between the tubercles.

Remarks. Uhlig (1910) placed the species, established by him from Lochambelkichak, Spiti area, in the genus *Blanfordia*. The prominent lateral tubercles, the depressed whorl section and trifurcating ribs on the outer whorl indicate generic affinities with *Himalayites*.

Locality. Chichali Pass, Trans Indus Ranges.

Himalayites sp. indet.

Material. One specimen, C.76670.

Horizon. 10 feet below the base of the middle member of the Chichali Formation, Upper Tithonian.

Description. This is a large wholly septate half whorl fragment of about 180 mm diameter. At the aperture the whorl height is 62 mm, the thickness about 70 mm. The whorl section is rounded at the apertural end but subquadrate at the smaller end, and the venter has a slight sulcus. The primary ribs are coarse, distant, slightly prorsiradiate and end at a large ventro-lateral tubercle. From the tubercles, 2 or 3 times as many secondary ribs cross the venter with slight forward arching, but fade along the mid-ventral line. There are smaller umbilical tubercles on the ribs.

Remarks. This specimen is comparable with *Himalayites celebrans* (Uhlig 1910 : pl. XXXVI, figs 1a–c) from the Spiti area, in its whorl section, ventral view and partly in ornamentation, but differs in having longer primary ribs, with higher ventro-lateral tubercles and a smaller number of secondary ribs.

Locality. Punnu Mines, Trans Indus Ranges.

Himalayites cf. ***hyphaisis*** (Blanford)

(Plate 9, figs 5a, b)

1863 *Ammonites hyphaisis* Blanford: 132, pl. IV, figs 2, 2a–b.
1910 *Himalayites hyphaisis* (Blanford); Uhlig: 149, pl. XXXVIII, figs 2a–b, 3–ad.
1910 *Himalayites* sp. nov. indet. Uhlig: 150, pl. XXXVIII, figs 5a–d.

Material. One specimen, C.76667.

Horizon. 10 feet below the base of the middle member of the Chichali Formation, Upper Tithonian.

Description. A small, wholly septate half whorl fragment, with a subhexagonal whorl section, and grooved venter. The ribs are moderately distant, and fine simple ribs alternate with heavier ribs that bifurcate at a prominent mid-lateral tubercle.

All the ribs swell into radially elongated weak tubercles at the edge of the mid-ventral groove.

Dimensions. C.76667–28·5: 11 (39), 11 (39), 10 (35).

Remarks. The specimen compares favourably with *H. hyphasis* (Blanford) from Spiti, in ornamentation and whorl shape, but it differs in its less evolute shell, more prominent lateral tubercles, and more elevated whorl section. These differences may partly be due to the larger size of Uhlig's specimens (49 mm and 46·5 mm). In ribbing and prominent lateral tubercles, it is closer to *Himalayites* sp. nov. indet. (Uhlig, 1910 : 150) which in turn is closely allied to *H. hyphasis* (Blanford).

Locality. South west of Malla Khel, Trans Indus Ranges.

Genus *AULACOSPHINCTES* Uhlig 1910

Aulacosqhinctes spitiensis (Uhlig)

(Plate 11, figs 2a, b, 3a, b)

1910 *Perisphinctes* (*Aulacosphinctes*) *spitiensis* Uhlig: 351, pl. XXXIII, figs 1a–c, 3a–c; pl.XLI, figs 1a–c.

Material. Two specimens, C.76686–7.

Horizon. About 2 feet below the base of the middle member of the Chichali Formation, Upper Tithonian.

Description. The larger specimen is evolute, moderately compressed, 72 mm in diameter, and part of the outer whorl is body-chamber. The whorl section is subquadrate, and the venter has a moderately deep groove. The ribs are straight and prorsiradiate, and commonly bifurcate on the upper part of the whorl side. Ribs that bifurcate twice are common on the outer whorl, but only occasional on the inner whorls. The first bifurcating point of these ribs is in the middle or the lower part of the whorl side. There are a few simple ribs, and rarely the ribs branch near the umbilical shoulder and one or both bifurcate again in the middle of the whorl side. The outer whorl has 42 ribs at 72 mm diameter. There are occasional shallow constrictions parallel to the ribs.

Dimensions. C.76687–72: 20 (28), 20·5 (28), 36 (50).

Remarks. These specimens are very similar in dimensions, rib density and multiple ribs to Uhlig's (1910) figured examples of *A. spitiensis* from the Himalayas. *Aulacosphinctes moerikeanus* (Oppel) is a very closely related species, also from the Himalayas (Uhlig, 1910 : 350, pl. XXXIII, fig. 2; pl. XXXVIII, fig. 6), which differs in being slightly more evolute and in having slightly fewer ribs.

Locality. South-west of Shaikh Budin, Shaikh Bud in Hills, Trans Indus Ranges.

APTYCHI

Laevaptychus

Material. Six fragments.

Horizon. 4 to 5 feet above the base of the Chichali Formation, Lower Kimmeridgian.

Description. The shell is moderately broad and thick, covered with fine pores on the convex side and concentric growth line or striae on the concave side (the inside).

Remarks. They are similar to the aptychus figured by Spath (1931: pl. LXXXVI) from the Katrol Beds of Cutch. In the Trans Indus Ranges they occur at the same horizon and locality as *Aspidoceras* (*Aspidoceras*) sp. indet.

Locality. Punnu Mines, Trans Indus Ranges.

VII. CORRELATIONS

a. Jurassic and Cretaceous stages in northern West Pakistan

The condensed nature of fossiliferous beds and the irregular distribution of ammonites in all the sections of northern West Pakistan do not warrant a detailed zonation. The zonal scheme (Fig. 6) adopted here is that of North West Europe for the Lower–Middle Jurassic (inclusive of the Callovian), Central and Southern Europe for the Upper Jurassic, and Western Europe for the Lower Cretaceous (Arkell and Wright 1957).

Jurassic

Lower Toarcian

The earliest marine fossiliferous Jurassic rocks are of Lower Toarcian age and contain a *Bouleiceras* fauna (including *B. nitiscens* Thevenin) which agrees well with that of Madagascar and Jebel Tuwaiq, Saudi Arabia (Arkell 1952, 1956).

Bajocian–Bathonian

No ammonites have been found in rocks of this age.

Callovian

The Callovian ammonites show a strong similarity with Cutch. The dominant genera are *Reineckeia, Obtusicostites, Hubertoceras, Choffatia.* The recognition of *Reineckeia anceps* in the assemblage places the beds in the Anceps Zone of the Middle Callovian.

No ammonites occur in the Lower Callovian beds and most of the Upper Callovian and Lower Oxfordian is missing from the area.

Upper Oxfordian

The Upper Oxfordian ammonites are again closely comparable with those of the "Upper Dhosa Oolite" and "Kantcote Sandstone" of Cutch (Spath 1933). The recognition in the assemblage of *Perisphinctes* (*Kranaosphinctes*) sp. indet., *Perisphinctes* (*Dichotomosphinctes*) cf. *rotoides* Ronchadze, and *Mayaites* cf. *waageni* (Uhlig), from the Trans Indus Ranges, and *Perisphinctes* (*Arisphinctes*) *orientalis* Siemiradzki and *Prososphinctes virguloides* (Waagen) from Kala Chitta–Nizampur area, places the assemblage in the Transversarium Zone. The higher Bimammatum Zone may also be presented in the highly condensed rubbly Upper Oxfordian beds (less than 2 feet thick) of northern West Pakistan. The ammonites are worn and indicate reworking. Spath (1934) placed the Kala Chitta fauna in the Transversarium Zone but pointed out that some species may belong to the Bimammatum Zone.

Lower Kimmeridgian

Above the Upper Oxfordian ammonite bed of the Chichali Formation in the Trans

Indus Range *Aspidoceras* (*Pseudowaagenia*) sp. indet. and *Physodoceras* (*Simaspidoceras*) sp. indet. occur. Five to ten feet above these beds are found *A.* (*Aspidoceras*) sp., *Laevaptychus*, *Pachysphinctes robustus* Spath and *Katroliceras* cf. *pottingeri* (J. de C. Sowerby) followed by *Ptychophylloceras ptychoicum* (Quenstedt) and *Hybonoticeras* sp. The assemblage indicates a Lower Kimmeridgian age. Associated with the ammonites are *Belemnopsis gerardi* (Oppel) which, though occurring in the underlying Upper Oxfordian rocks, does not extend into the overlying Lower Tithonian beds with *Aulacosphinctoides* and *Hildoglochiceras*.

Lower Tithonian

About 5 feet above the higher Kimmeridgian bed *Aulacosphinctoides* (including *A. uhligi* Spath), *Hildoglochiceras* sp. indet. (comparable with *H. kobelli*), *Virgatosphinctes* (*V. frequens*, *V. densiplicatus*) and *Provalanginites* gen. nov. occur followed higher up by *Proniceras indicum* Spath and *Holcophylloceras silesiacum* (Oppel). The first appearance of *Aulacosphinctoides* is taken here as marking of the base of the Tithonian, but the placing of the faunas in the detailed zonal scheme of Arkell (1957) is not yet possible because of the rare occurrence of these genera, uneven distribution in the area and condensed nature of the deposits.

Upper Tithonian

In the Upper Tithonian the commonly occurring genus is *Blanfordiceras* (including *B. wallichi*). The first appearance of *Blanfordiceras* in the area is taken to mark the boundary between the Lower and Upper Tithonian. *Blanfordiceras* is associated higher up with *Himalayites* and *Aulacosphinctes*.

Immediately below the *Subthurmannia* beds (considered here to mark the base of the Cretaceous) *Protacanthodiscus* aff. *michaelis* (Uhlig), *Protacanthodiscus* sp. indet., *Spiticeras multiforme* Djanelidze, *Spiticeras* sp. indet. occur. This assemblage suggests the highest Tithonian (Chaperi Zone).

The Upper Tithonian beds of the Chichali Formation have abundant *Hibolithes* (also abundant in the Lower Tithonian and Kimmeridgian) but are not very rich in ammonites.

Jurassic–Cretaceous Boundary

The Cretaceous boundary is drawn at the first appearance of *Subthurmannia* (including *S. fermori*) in the upper part of the Lower member of the Chichali Formation. The Jurassic–Cretaceous boundary is transitional in most areas, except in parts of Hazara, where non-sequences are present in the succession.

Lower Cretaceous

Berriasian

Subthurmania is the most abundant genus, associated with *Neocosmoceras* (*N.* aff. *spitiensis*) and *Negreliceras*. The assemblage is typically Berriasian and indicates the Boissieri Zone.

The ammonites of Berriasian age are also present in the western part of the Main Salt Range, though they are less abundantly developed. This is in contrast to Spath's suggestion (presumably based on failure of collections) that they are absent from the Salt Range (1939 : 131). In Hazara and Kala Chitta Range their occurrence is rare, and in parts of Hazara they are missing because of non-sequence.

Valanginian

The Valanginian ammonites, though condensed in beds 15 to 20 feet thick and missing in parts of Kala Chitta and Hazara (because of a non-sequence), include three faunal assemblages in the Trans Indus Ranges and Western Kohat. These are (from top to bottom) as follows:—

3. *Olcostephanus* (*Olcostephanus*) *salinarius* Zone, including many species of *O.* (*Olcostephanus*), less commonly *O.* (*Rogersites*), *Distoloceras, Lyticoceras* and *Leopoldia.*
2. *Neocomites* (*Odontodiscoceras*) *similis* Zone, including species of *Neocomites* (*Parandiceras*) such as *N.* (*P.*) *theodorii* (Oppel), *Kilianella* (*K. asiatica* Spath, *K. leptosma* Uhlig, *Kilianella* sp. nov.), *Neocomites* (*Calliptychoceras*) and *Neohoploceras.*
1. *Sarasinella uhligi* Zone. This is a provisional poorly defined zone and includes *Sarasinella subspinosa* (Uhlig), *Thurmanniceras* sp. *Neocomites* (*Neocomites*) sp. nov.

The *Sarasinella uhligi* Zone seems to correspond to the unnamed zone below the Roubaudiana Zone of Wright (1957) or to Gratianopolitense Zone of Spath (1939 : 132).

The *Neocomites* (*Odontodiscoceras*) *similis* Zone is equivalent to the *Kilianella roubaudiana* Zone of Wright and Spath.

The highest *Olcostephanus* (*O.*) *salinarius* Zone corresponds to the Schenki and Verrucosum Zones of Spath (1939). The dominant genus in this zone is *Olcostephanus* (*Olcostephanus*) which is associated with *O.* (*Rogersites*), *Distoloceras, Leopoldia* and *Lyticoceras.*

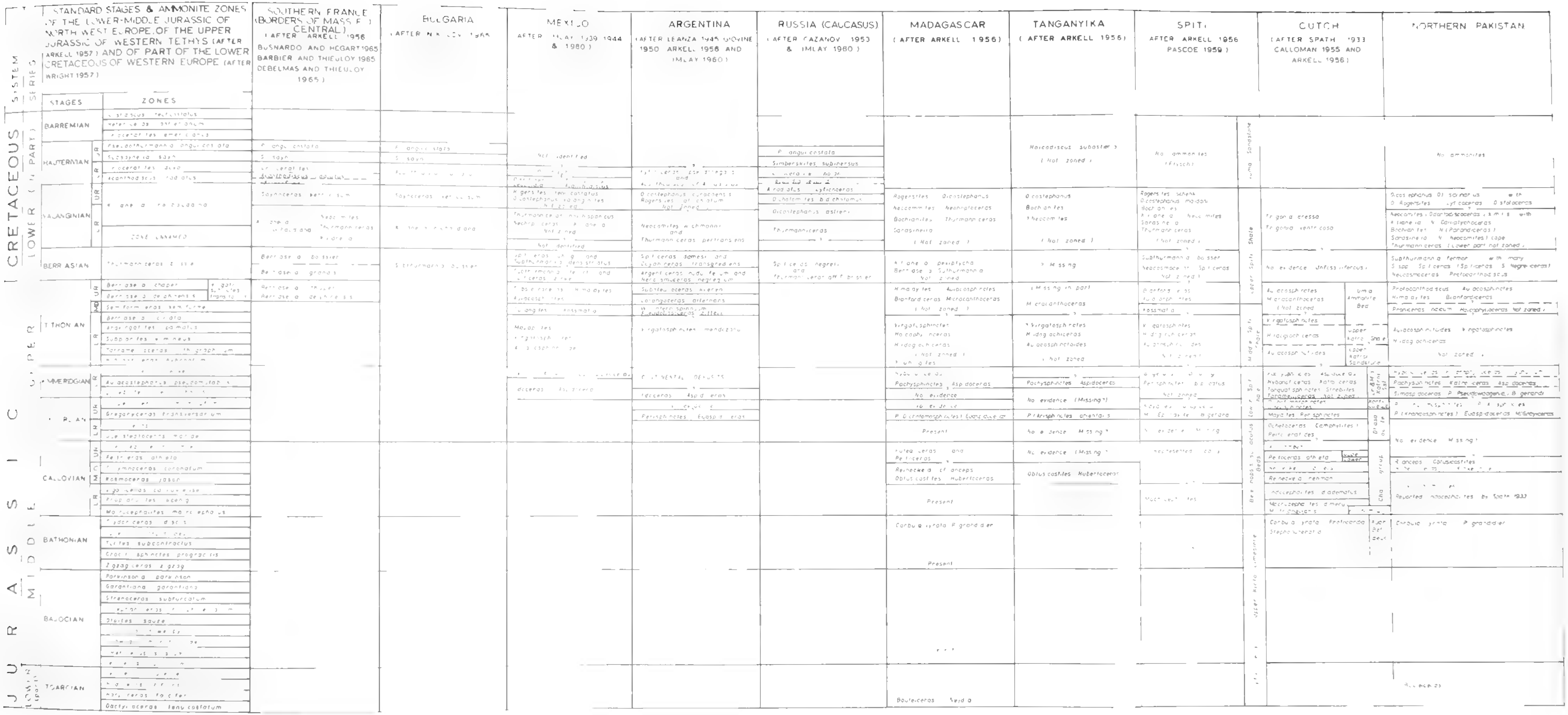
b. Correlations within Pakistan

(i) *Baluchistan*

In Baluchistan ammonites of Lower (Toarcian and doubtful Sinemurian), Middle (Upper Bathonian–Lower Callovian) and Upper Jurassic (Lower Tithonian) age have been recorded (Noetling 1897; Vredenburg 1909; Spath 1933, 1936; Arkell 1956). The main similarities between the ammonite faunas are found in the Lower Toarcian and Tithonian.

The *Bouleiceras* species are similar, but the other recorded Lower Jurassic ammonite genera from Baluchistan do not occur in the Lower Toarcian ammonite bed of Kala Chitta and Hazara. The associated rhynchonellids and *Pecten* sp., however, are closely comparable. A detailed study of the Lower Jurassic sequence

SYSTEM.	SERIES.	STANDAR OF THE L NORTH W JURASSIC ARKELL 1957 CRETACEO WRIGHT 1957 STAGES.	956)	SPITI. (AFTER ARKELL 1956 PASCOE 1959)		CUTCH. (AFTER SPATH 1933, CALLOMAN 1955 AND ARKELL 1956).		NORTHERN PAKISTAN.
CRETACEOUS	LOWER (IN PART).	BARREMIAN		No ammonites (Flysch)	Giumal Sandstone			No ammonites
		HAUTERIVIAN	ia					
		VALANGINIAN		Rogersites schenki Olcostephanus maidani Bochianites Kilianella, Neocomites Sarasinella, Thurmanniceras (Not zoned) ?	Upper Spiti Shale	Trigonia cressa Trigonia ventricosa ?		Olcostephanus (O) salinarius with O (Rogersites), Lyticoceras, Distoloceras ? Neocomites (Odontodiscoceras) similis with Kilianella, N (Calliptychoceras). Bochianites, N (Parandiceras), Sarasinella, N (Neocomites) copei Thurmanniceras (Lower part not zoned)
		BERRIASIAN		Subthurmannia boisseri Neocosmoceras, Spiticeras (Not zoned)		No evidence (Unfossiliferous)		Subthurmannia fermori with many S spp, Spiticeras (Spiticeras), S (Negreliceras), Neocosmoceras, Protocanthodiscus
JURASSIC	UPPER	TITHONIAN		Blanfordiceras Aulacosphinctes		Aulacosphinctes Micracanthoceras (Not zoned)	Umia Ammonite Bed	Protocanthodiscus, Aulacosphinctes Himalayites, Blanfordiceras ?
				Kossmatia ?	Middle Spiti Shale	? Virgatosphinctes		Praniceras indicum, Holcophylloceras (Not zoned) ?
				Virgatosphintes Hildoglochiceras Aulacosphinctoides (Not zoned) ?		Hildoglochiceras	Upper Katrol Shale	Aulacosphinctoides, Virgatosphinctes Hildoglochiceras (Not zoned)
						Aulacosphinctoides ?	? Upper Katrol Sandstone	
		KIMMERIDGIAN	s	B gerardi, B, uhligi "Perisphinctes" biplicatus (Not zoned) ?	Lower Spiti Shale	Pachysphinctes, Aspidoceras Hybonoticeras, Katroliceras Torquatisphinctes, Streblites Taramelliceras (Not zoned)	Lr & Mid Katrol Sst	Hybonoticeras, Ptychophylloceras ptycholcum Pachysphinctes, Katroliceras, Aspidoceras, Simaspidoceras, P (Pseudowaagenia,) B gerardi ?
		OXFORDIAN		Mayaites (Grayiceras) M (Epimayites), B gerardi		Dichotomosphinctes Discosphinctes	Kantcote Sst	P (Dichotomosphinctes), P (Arisphinctes) P (Kranaosphinctes) Euaspidoceras, M(Grayiceras)
						Mayaites, Perisphinctes	Dhasa oolite	
				No evidence ?(Missing)	Belemnopsis sulcacutus Beds	Ochetoceras (Camphylites) Peltoceratides ?		No evidence (Missing) ?
	MIDDLE	CALLOVIAN		? Represented locally		A lamberti	Chari group	
						Peltoceras athleta	Upper Lower	
			as			Reineckeia anceps		R anceps, Obtusicostites, Hubertoceras, Kinkeliniceras
				? Macrocephalites		Reineckeia rehmani		? No ammonites Reported Indocephalites by Spath, 1933
						Indocephalites diadematus		
						Macrocephalites dimerus M triangularis	Patcham Grp	
		BATHONIAN		?	Laptal Series (= Upper Kioto Limestone)	Corbula lyrata, Protocardia Stephonoceratid	Kuar Bet Beds	Corbula lyrata, P grandidieri
		BAJOCIAN		?				
	LOWER (part)	TOARCIAN		Aloclytoceras				Bouleiceras



System	Series	Stages	Zones (Standard stages & ammonite zones of the Lower-Middle Jurassic of North West Europe, of the Upper Jurassic of Western Tethys (after Arkell 1957) and of part of the Lower Cretaceous of Western Europe (after Wright 1957))	Southern France (Borders of Massif Central) (after Arkell 1956, Busnardo and Hegart 1965, Barbier and Thieuloy 1965, Debelmas and Thieuloy 1965)	Bulgaria (after [illegible] 1965)	Mexico (after Imlay 1939, 1944 & 1960)	Argentina (after Leanza 1945, Giovine 1950, Arkell 1956 and Imlay 1960)	Russia (Caucasus) (after Cazanov 1953 & Imlay 1960)	Madagascar (after Arkell 1956)	Tanganyika (after Arkell 1956)	Spiti (after Arkell 1956, Pascoe 1959)	Cutch (after Spath 1933, Calloman 1955 and Arkell 1956)	Northern Pakistan
CRETACEOUS	LOWER (IN PART)	BARREMIAN	[illegible] Heteroceras astierianum [illegible] emericianus							Holcodiscus subastieri ? (Not zoned)	No ammonites (Flysch)		No ammonites
		HAUTERIVIAN	Pseudothurmannia angulicostata Subsaynella sayni Crioceratites duvali Acanthodiscus radiatus	P. angulicostata S. sayni Crioceratites Acanthodiscus radiatus	P. angulicostata S. sayni [illegible]	Not identified	[illegible] and [illegible]	P. angulicostata Simbirskites subinversus [illegible] A. radiatus Lyticoceras					
		VALANGINIAN	Kilianella roubaudiana Zone unnamed	Saynoceras verrucosum Kilianella roubaudiana, Neocomites, Thurmanniceras, Kilianella	Saynoceras verrucosum Kilianella roubaudiana	Rogersites tenuicostatus, Olcostephanus [illegible] (Not zoned) Thurmanniceras [illegible], Neohoploceras, Kilianella (Not zoned) Not identified	Olcostephanus curacoensis, Rogersites cf. [illegible] (Not zoned) Neocomites wichmanni and Thurmanniceras pertransiens	Dichotomites bidichotomus Olcostephanus astieri Thurmanniceras	Rogersites, Olcostephanus, Neocomites, Neohoploceras, Bochianites, Thurmanniceras, Sarasinella (Not zoned)	Olcostephanus, Bochianites, ?Neocomites (Not zoned)	Rogersites schenki, Olcostephanus maidani, Bochianites, Kilianella, Neocomites, Sarasinella, Thurmanniceras (Not zoned)	Trigonia cressa Trigonia ventricosa	Olcostephanus, O. salinarius with O. Rogersites, Lytoceras, O. [illegible] Neocomites, Odontodiscoceras, Kilianella, N. Campylotoxoceras, Bochianites, N. (Parandiceras), Sarasinella, N. (Neocomites), Thurmanniceras (Lower part not zoned)
		BERRIASIAN	Thurmanniceras [illegible]	Berriasella boissieri Berriasella grandis	Subthurmannia boissieri	Spiticeras [illegible] and Subthurmannia densistriatus Subthurmannia [illegible] and [illegible]	Spiticeras damesi and Cuyaniceras transgrediens Argentiniceras noduliferum and Neocosmoceras negreli	Spiticeras negreli and Thurmanniceras aff. T. boissieri	Kilianella pexiptycha, Berriasella, Subthurmannia Not zoned	? Missing	Subthurmannia boissieri, Neocosmoceras, Spiticeras Not zoned	No evidence (Infra-[illegible])	Subthurmannia fermori with many S. spp., Spiticeras (Spiticeras, S. Negreliceras), Neocosmoceras, Protacanthodiscus
JURASSIC	UPPER	TITHONIAN	Berriasella chaperi Berriasella delphinensis (Virgatosphinctes transitorius) Semiformiceras semiforme Berriasella ciliata Anavirgatites palmatus Subplanites vimineus [illegible] lithographicum [illegible]	Berriasella [illegible] Berriasella delphinensis		Proniceras, Himalayites, Aulacosphinctes Durangites, Kossmatia Mazapilites, Virgatosphinctes, Aulacosphinctoides	Substeueroceras koeneni Corongoceras alternans Windhauseniceras internispinosum Pseudolissoceras zitteli Virgatosphinctes mendozanus		Himalayites, Aulacosphinctes, Blanfordiceras, Micracanthoceras (Not zoned) Virgatosphinctes, Haplophylloceras, Hildoglochiceras (Not zoned), ?Durangites	(Missing in part) Micracanthoceras ?Virgatosphinctes, Hildoglochiceras, Aulacosphinctoides (Not zoned)	Blanfordiceras, Aulacosphinctes Kossmatia Virgatosphinctes, Hildoglochiceras, Aulacosphinctoides (Not zoned)	Aulacosphinctes, Micracanthoceras (Not zoned) Virgatosphinctes Hildoglochiceras Aulacosphinctoides Umia Ammonite Bed Upper Katrol Shale Upper Katrol Sandstone	Protacanthodiscus, Aulacosphinctes, Himalayites, Blanfordiceras Proniceras, Neocomites, Haplophylloceras (Not zoned) Aulacosphinctoides, Virgatosphinctes, Hildoglochiceras (Not zoned)
		KIMMERIDGIAN	[illegible] Aulacostephanus pseudomutabilis [illegible]			[illegible] Idoceras, Aspidoceras	Continental deposits Idoceras, Aspidoceras		Hybonoticeras Pachysphinctes, Aspidoceras No evidence	Pachysphinctes, Aspidoceras No evidence (Missing?)	[illegible] Perisphinctes [illegible] Not zoned	[illegible] Hybonoticeras, Katroliceras, Torquatisphinctes, Streblites, Taramelliceras (Not zoned) Lower Katrol	Hybonoticeras [illegible] Pachysphinctes, Katroliceras, Aspidoceras Simosphinctes, Aspidoceras, P. Pseudowaagenia, B. gerardi
		OXFORDIAN	[illegible] Gregoryceras transversarium [illegible] Quenstedtoceras mariae				[illegible] Perisphinctes, Euaspidoceras		No evidence P. Dichotomosphinctes, Euaspidoceras Present	No evidence (Missing?) Perisphinctes orientalis No evidence (Missing?)	[illegible] Mayaites, Epimayaites gerardi No evidence (Missing)	[illegible] Mayaites, Perisphinctes Ochetoceras, Campylites Peltoceratoides	P. [illegible] P. (Kranaosphinctes), Euaspidoceras, Mirosphinctes No evidence (Missing?)
	MIDDLE	CALLOVIAN	[illegible] Peltoceras athleta Erymnoceras coronatum Kosmoceras jason Sigaloceras calloviense Proplanulites koenigi Macrocephalites macrocephalus						[illegible] and Peltoceras Reineckeia cf. anceps, Obtusicostites, Hubertoceras Present	No evidence (Missing?) Obtusicostites, Hubertoceras	Not represented [illegible] Macrocephalites	[illegible] Peltoceras athleta Reineckeia [illegible] Reineckeia rehmanni Indocephalites diadematus Macrocephalites [illegible]	R. anceps, Obtusicostites [illegible] Reported Indocephalites by Spath 1933
		BATHONIAN	Clydoniceras discus [illegible] Tulites subcontractus Gracilisphinctes progracilis Zigzagiceras zigzag						Corbula lyrata, P. grandidieri Present			Corbula lyrata, Protocardia Stephanoceras [illegible]	Corbula lyrata, P. grandidieri
		BAJOCIAN	Parkinsonia parkinsoni Garantiana garantiana Strenoceras subfurcatum [illegible] Otoites sauzei [illegible] [illegible] [illegible] [illegible]						[illegible]				
	LOWER (IN PART)	TOARCIAN	[illegible] [illegible] Harpoceras falcifer Dactylioceras tenuicostatum						Bouleiceras [illegible]				[illegible]

Fig. 6 Correlation of Jurassic and Lower Cretaceous faunas of northern West Pakistan

of Baluchistan should prove of great interest in comparing the supposed Upper Pliensbachian age of the *Bouleiceras* in Spain by Bizon *et al.* (1966), as the sequence in Baluchistan is believed to extend below the Toarcian.

The *Virgatosphinctes* species, *V. denseplicatus* (Waagen) compare well with the *Virgatosphinctes* species, found associated with *Aulacosphinctoides* in Hazara and the Trans Indus Ranges.

The ?Berriasian or Valanginian "Belemnite shales" (Arkell 1956 : 396) apparently succeed Lower Callovian limestone with *Macrocephalites*, and have *Hibolithes* (*H. pistilliformis* and *H. subfusiformis*), which have also been recorded by Spath (1939) from the Salt Range and Trans Indus Ranges. Stevens (1965 : 150), reviewing the belemnites of the Salt Range, confirmed Spath's identification of *H. pistilliformis* and *H. subfusiformis*, but has suggested that "It is likely that the belemnites recorded by Spath from this locality, and all *Belemnopsis* recorded by him from the Salt Range, have been derived from the underlying Upper Jurassic horizon, the belemnite in place being *Hibolithes*". Spath (1939), however, described *Hibolithes* (*H. pistilliformis* and *H. subfusiformis*) associated with the less commonly occurring *Belemnopsis* from Trans Indus and Salt Ranges.

The present investigations indicate that *Hibolithes* occurs in association with *Belemnopsis* and other Upper Jurassic ammonites, and none of the assemblage appears derived. In the major part of the Tithonian *Hibolithes* occurs without association of *Belemnopsis*, but lower down the two species of *Hibolithes* are associated with less commonly *Belemnopsis*. Forms resembling *H. pistilliformis* and *H. subfusiformis* continue in the Berriasian and Valanginian, but are not so well preserved as those in the Kimmeridgian and Lower Tithonian beds of the Chichali Formation ("Belemnite Beds" of Spath). In fact the preservation of the *Hibolithes* monographed by Spath, suggests that they are mostly from the Tithonian and Kimmeridgian beds of the "Belemnite shales" of the Trans Indus and Salt Range. These observations suggest that *H. pistilliformis* and *H. subfusiformis* are either long ranging (Upper Jurassic to Lower Cretaceous) or their identification as such from the Salt Range and the Trans Indus Ranges needs more careful examination. A long range for these species seems to be a more logical conclusion. Their presence in Baluchistan in the "Belemnite shales" may not restrict the age of these beds to Berriasian or Valanginian, but in all probability the "Belemnite shales" of Baluchistan range in age from Tithonian to Neocomian, for Lower Tithonian is indicated by the presence of *Virgatosphinctes* in certain areas of Baluchistan.

c. Correlations with areas outside Pakistan

(i) *Cutch*

The Middle and Upper Jurassic faunas of Cutch show close similarity with those of northern West Pakistan, particularly those of Trans Indus and Kala Chitta Ranges (Fig. 6). The Jurassic and Lower Cretaceous succession of Cutch has been summarized by Spath (1933) and Arkell (1956).

The Upper Bathonian bivalves fauna of Kuar Bet Beds of Cutch can be correlated with a similar fauna from the uppermost beds of the Samana Suk Limestone in Kala Chitta (fig. 6). The faunas of the Macrocephalus and Rehmanni Zones have not been found by the present survey. There is a suggestion of the presence of the Rehmanni Zone in the *Subkossmatia flemingi* Bed north of Kalabagh (reported by Spath 1933, but not found by the present survey), and the *Belemnopsis grantana* Bed of Western Kohat (uppermost part of the Samana Suk Limestone). These faunas suggest that the uppermost part of the Samana Suk Limestone in these areas may be slightly older than the Anceps fauna of the rest of the Trans Indus Ranges (west of Chichali Pass).

The Anceps Zone of Cutch is well represented in commonly occurring genera and species in the uppermost 2 feet of the Samana Suk Limestone of the Trans Indus Ranges (west of Chichali Pass). The major part of the Athleta Zone and Lower Oxfordian are missing from northern West Pakistan. The Upper Dhosa Oolite (Transversarium Zone) and Kancote Sandstone (Bimammatum Zone) faunas may be correlated with a similar assemblage in the condensed bed (less than 2 feet) at the base of the Chichali Formation in the Trans Indus Ranges and the Kala Chitta–Nizampur areas.

The ammonite faunas of the Lower and Middle Katrol Beds compare favourably with those found in the Trans Indus Ranges, except that not all the genera occurring in Cutch (such as *Taramelliceras*, *Glochiceras*, *Streblites*) have been found in Pakistan. These Lower–Middle Katrol Beds have been doubtfully placed by Spath and Arkell in the Middle Kimmeridgian, though both authors have pointed out the presence of Pseudomutabilis and Upper Tenuilobatus Zones in the assemblage.

In the Trans Indus Range it was found that *Aulacosphinctoides* occurs a few feet above the *Pachysphinctes*, *Katroliceras* and *Hybonoticeras* Beds, and the lowest Kimmeridgian beds have *A.* (*Pseudowaagenia*) and *P.* (*Simaspidoceras*), and no *Pachysphinctes*. These two Kimmeridgian horizons are comparable with the Middle and Lower Katrol Beds of Cutch.

The placing of Lower and Middle Katrol Beds in the Middle Kimmeridgian by Spath (1933) and Arkell (1956) presumably was based on the identification of *Hybnoticeras beckeri* in the Lower Katrol Beds. The other elements of the fauna point to a Lower Kimmeridgian age of the assemblage. In Europe and parts of Africa *Pachysphinctes*, *Taramelliceras*, *Torquatisphinctes* and *Katroliceras* have been more typically reported from the Lower Kimmeridgian rather than from the *H. beckeri* Zone. In the Tellian Atlas *Streblites tenuilobatus* occurs in association with *Hybonoticeras* (Arkell 1956 : 273). It is, therefore, likely that the genus *Hybonoticeras* may have appeared earlier in the Kimmeridgian in Cutch and the Trans Indus Ranges, and very likely it does not represent the true Beckeri Zone.

It is interesting to note that more definite evidence of the occurrence of *Aulacosphinctoides* is reported from the next higher horizon, the Upper Katrol Sandstone, which is over 700 feet thick and in main is unfossiliferous. The Trans Indus Kimmeridgian and Tithonian Beds on the other hand are much condensed, but even there a slight unfossiliferous interval occurs between the *Pachysphinctes* Beds and the overlying *Aulacosphinctoides* Beds. It is suggested that the time interval represented by the true Beckeri Zone may be present in the unfossiliferous Upper

Katrol Sandstone of Cutch or the beds above the *Pachysphinctes* horizon in the Trans Indus Ranges.

The Upper Katrol Sandstone, Upper Katrol Shales and the lower part of Umia Ammonite Bed, can be correlated with the Lower Tithonian Beds of the Trans Indus Range and Hazara. There are, however, some differences: in Cutch *Aulacosphinctoides* is reported from the Upper Katrol Shales which has *Hildoglochiceras* and other faunas; it is doubtfully and rarely recorded from the Umia Ammonite Bed which has more typically a good representation of *Virgatosphinctes*.

In the Trans Indus Ranges and especially in Hazara, *Aulacosphinctoides* and *Virgatosphinctes* occur in close association. *Hildoglochiceras* has been found associated with *Aulacosphinctoides* in the Trans Indus Ranges.

In northern West Pakistan the appearance of *Aulacosphinctoides* has proved to be a useful and convenient horizon to mark the base of the Lower Tithonian. The Upper Tithonian/Lower Tithonian boundary is placed at the appearance of *Blanfordiceras*, followed by *Himalayites* and *Aulacosphinctes*. From the Umia Ammonite Bed of Cutch, there is no record of *Himalayites* and *Blanfordiceras* (common in Spiti, Pakistan and Madagascar), but *Aulacosphinctes* is reported, which suggests that part of the Umia Ammonite Bed is Upper Tithonian.

(ii) *Spiti*

The Upper Jurassic, Berriasian and Valanginian faunas of the Spiti Shales (thickness 500 feet) compare favourably with northern West Pakistan (fig. 6). The ammonites were monographed by Uhlig (1903–10) who defined the stratigraphic position of some within the three-fold division of the Spiti shales. Other faunas were placed undefined in the Spiti shales, but many of these are considered by Pascoe (1959 : 1174) to have been collected from the Chidamu Beds (Middle Spiti Shales). The succession is described by Diener (1895), Hayden (1904), Uhlig (1910), Arkell (1956) and Pascoe (1959).

Giumal sandstone (up to 495 ft). This formation is regarded as Middle Neocomian by Arkell (1956) and post Valanginian by Pascoe (1959).

Spiti shales (500 ft), consisting of the following three divisions: Upper Spiti shales (Lochambel Beds), with *Olcostephanus* (*Olcostephanus*), *O.* (*Rogersites*), *Neocomites* (*Calliptychoceras*), *N.* (*Parandiceras*), *N.* (*Odontodiscoceras*), *Kilianella*, *Neocomites*, *Sarasinella*, *Thurmanniceras*, *Subthurmannia*, *Neocosmoceras*, *Spiticeras*, *Blanfordiceras*, *Himalayites* and *Aulacosphinctes*.

Middle Spiti shales. A number of Upper Tithonian and Lower Neocomian genera have been doubtfully listed from these beds (Pascoe 1959 : 1174–75). In addition, more definite forms reported include *Blandforiceras*, *Pterolytoceras exoticum*, *Paraboliceras*, *Kossmatia* and *Uhligites*. This assemblage suggests that at least part of the Middle Spiti Shales is Upper Tithonian. Other ammonites from the Middle Spiti Shales include *Virgatosphinctes*, *Aulacosphinctoides* and *Hildoglochiceras* (stratigraphical position unknown), and *Belemnopsis uhligi* Stevens (=*B. gerardi* of Uhlig).

Lower Spiti shales (Belemnopsis gerardi Beds), with *Belemnopsis gerardi* (Stevens 1965, p. 149 doubts its identification), *Mayaites*, *Grayiceras* and *Epimayites*.

The Lower Spiti shales are regarded as Upper Oxfordian by Uhlig (1910), Spath (1933, 1939), Arkell (1956), Pascoe (1959) and Krishnan (1960), but Stevens (1965 : 149) on the basis of identification of *B. uhligi* (=*B. gerardi* of Uhlig) considers them to be Middle Kimmeridgian. In the present correlation, on the basis of the mayaitid ammonites, these are regarded as Upper Oxfordian to Lower Kimmeridgian.

The Lower Spiti shales can be broadly correlated with the lowest bed of the Chichali Formation of the Trans Indus Range, the basal 2 to 3 feet condensed bed of the Chichali Formation of Kala Chitta and Nizampur areas, and with the whole of the Chichali Formation ("Spiti Shale" facies) of Kalapani–Kathwal sections of Hazara. In Hazara there is no evidence of Upper Oxfordian beds, and it is likely also that in parts of Spiti the Upper Oxfordian mayaitid beds may not have been deposited, and the whole of the Lower Spiti Shales may be Lower Kimmeridgian in age.

The ammonites faunas of the Middle Spiti shales (Chidamu Beds) compare well with those of northern West Pakistan, except that such genera as *Kossmatia* and *Paraboliceras* are not known from Pakistan. The *Aulacosphinctoides* and *Virgatosphinctes* compare closely with those found in the Trans Indus Ranges, Budin Hills and Hazara. In Hazara these two genera occur in the lower part of the "Giumal sandstone" (Lumshiwal Formation) and are not found in the "Spiti shale" facies of the Chichali Formation of the Kathwal–Kalapani sections. This correlation requires caution, for in the vast outcrop of the Spiti shales in the Himalayas the fauna may not be restricted to the same lithological division of the Spiti shales. This presumably accounts for the Lower Tithonian–Valanginian fauna listed by Pascoe (1959 : 1174), who believed most of them to have come mainly from the Middle Spiti shales. It is, therefore, probable that the three divisions of Spiti shales in the Spiti area may be diachronous as in Hazara.

The Upper Spiti shales have a very interesting assemblage which is of upper Tithonian to Valanginian age. The Upper Tithonian can be correlated with a similar fauna from northern West Pakistan, except that *Protacanthodiscus* seems to be not represented in the Spiti shales. The Jurassic/Cretaceous boundary occurs within the Upper Spiti shales without a break similar to that of the Trans Indus Ranges. The Berriasian is indicated by *Subthurmannia boissieri* and *S. surgharensis*. The more common occurrence of *Neocosmoceras* and *Spiticeras* as compared to *Subthurmannia* in Spiti, is contrasted with the abundance of *Subthurmannia* in the Berriasian of the Trans Indus Ranges.

The three Valanginian zones of the Trans Indus Ranges (*O. salinarius*, *N. similis* and *S. uhligi*) are represented in the Valanginian assemblages of the Spiti shales.

The overlying Giumal Sandstone can be broadly correlated with the Lumshiwal Formation of Kala Chitta, with the Upper member of the Chichali Formation, and the Lumshiwal Formation of Western Kohat and the Trans Indus Ranges. In Pakistan, Aptian and Albian ammonites occur, but apparently no ammonites are reported from the "Giumal sandstone" of Spiti.

(iii) *Persia* (*Elburz Mountains*)

In the Elburz Mountains marine succession from Toarcian to Lower Cretaceous is developed, and the Lower and Middle Jurassic rocks have many ammonite horizons. There appears to be a faunal break between the Middle Callovian and Upper Oxfordian, and the Toarcian marine rocks overlie the rest of the continental Lower Jurassic (Arkell 1956).

The *Reineckeia* Beds of Persia (with *R. anceps*) are comparable with those of the Trans Indus Ranges, except that in Persia genera like *Obtusicostites*, *Hubertoceras* have not been reported.

The perisphinctid fauna and associated *Euaspidoceras* of Upper Oxfordian age compare well with that of the Trans Indus Ranges and Kala Chitta.

There is hardly any similarity with the Kimmeridgian faunas, but from the Tithonian *Virgatosphinctes*, *Berriasella* and *Substeueroceras* have been recorded which show the presence of Lower and Upper Tithonian (Spath 1933 : 831).

On the Lower Cretaceous Spath (1939 : 141) commented, "There is only one small suite, submitted to me . . . . which showed a remarkable similarity even in the preservation, to the fauna of the Valanginian marls of the south of France". He further remarked, "there is abundant evidence of the presence of forms like *Berriasella*, *Substeuroceras* and allies in southern and south western Persia and of a complete succession from the uppermost Jurassic into the Lower Cretaceous".

(iv) *Saudi Arabia* (*Jebel Tuwaiq*)

The Jurassic and Cretaceous sequence in Saudi Arabia (Powers, Remirez, Redmond and Elberg 1966) indicates disconformities between Triassic and Lower Toarcian, between Middle Callovian and Oxfordian and within the Lower and Upper Cretaceous which are comparable with Northern Pakistan.

Ammonites are recorded from Toarcian, Middle–Upper Bajocean, Middle Bathonian, Middle Callovian and there is a small perisphinctid assemblage from Oxfordian (Transversarium Zone) and Kimmeridgian (Tenuilobatus Zone). The Jurassic/Lower Cretaceous boundary is considered transitional.

A firm correlation exists with the Lower Toarcian *Bouleiceras* Beds (Marrat Formation) of Jebel Tuwaiq (Arkell 1956 : 300).

(v) *Iraq* (*Kurdistan*)

An interesting Upper Jurassic assemblage was described by Spath (1950) from Kurdistan. The lowest Upper Jurassic fauna (Arkell 1956 : 376) is placed in the Lower Kimmeridgian (Pseudomutabilis Zone) and has the genera *Ataxioceras* and *Aulacostephanus* which are not found in northern West Pakistan.

The next fossiliferous beds (with *Pseudolissoceras*) are separated from the underlying Lower Kimmeridgian by 39 meters of unfossiliferous sediments. The fauna of the *Pseudolissoceras* Beds includes *Pseudolissoceras*, *Proniceras*, *Phanerostephanus* and ?*Glochiceras*, and was placed into the Middle Tithonian by Spath. He (1950 :

100–101) doubtfully assigned two specimens to *Glochiceras*, though one was closely compared with *Hildoglochieras grossicostatum* Imlay, and the other has a pronounced mid-lateral groove and is more evolute than a typical *Glochiceras*. The presence of *Proniceras* in the assemblage suggests its correlation with the *Proniceras indicum* Bed of the Trans Indus Ranges, where it occurs above the *Aulacosphinctoides* and *Virgatosphinctes* horizon. The latter two genera are not known from Kurdistan and it appears that this zone will occupy a position in the 39 meters of unfossiliferous sediments below the *Pseudolissoceras* Beds. The fauna of the Lower Tithonian (lower part) thus seems to be missing from Kurdistan.

The ammonites of higher beds are placed in the Upper Tithonian which include *Substeueroceras*, *Berriasella* and *Paradontoceras*, and can be broadly correlated on the basis of *Berriasella* with northern West Pakistan.

Spath (1950) mentioned that the fauna of the Boissieri Zone of the Lower Cretaceous is present in Kurdistan and thus the Jurassic–Cretaceous boundary appears transitional.

(vi) *Madagascar*

In the northern areas of Madagascar a more complete Jurassic–Lower Cretaceous sequence is developed and the Jurassic–Cretaceous boundary is transitional (Thevenin 1906, 1908; Besairie 1932, 1936, 1946; Collignon 1949; Arkell 1956) Firm correlations with northern West Pakistan can be made in the Lower Toarcian, Upper Bathonian, Middle Callovian, Upper Oxfordian, Lower Kimmeridgian, Tithonian, Berriasian and Valanginian (fig. 6). The rest of the Jurassic ammonite sequence is better developed and more complete in Madagascar than in northern West Pakistan.

The earliest marine Jurassic fauna reported from Madagascar is dated as Lower Toarcian on the basis of *Bouleiceras*, which is associated with *Protogrammoceras*, *Nejdia*, *Speriferina rostrata* and *Pecten*. These beds can be correlated with the *Bouleiceras* Beds of the Datta Formation in Kala Chitta and Hazara.

The next strata that can be correlated are the Upper Bathonian Bivalve Beds of Madagascar with *Corbula lyrate* and *Protocardia grandidieri* also found in the uppermost beds of the Samana Suk Limestone in Kala Chitta.

From the Middle Callovian of Northern and Southern Madagascar, *Obtusicostites*, *Hubertoceras*, *Reineckeia* cf. *anceps* and other ammonite genera have been recorded (Arkell 1956 : 340). This assemblage compares well with that of the Trans Indus Ranges, except that other associated ammonite genera are lacking in northern West Pakistan.

In the Upper Oxfordian of Madagascar a *P.* (*Dichotomosphinctes*) and *Euaspidoceras* fauna of the Transversarium Zone is present, but the higher Bimammatum Zone is believed to be absent. These faunas are comparable with the Upper Oxfordian faunas of the Trans Indus Ranges and Kala Chitta.

The Lower Kimmeridgian succession in Madagascar is probably incomplete, extending to the Pseudomutabilis Zone. The lowest Tenuilobatus Zone is believed to be absent. The fauna includes *Aspidoceras*, *Pachysphinctes*, *Lithacoceras*, *Torquatisphinctes* and *Taramelliceras*. *Aspidoceras* and *Pachysphinctes* are comparable with the similar forms found in the Lower Kimmerdigian succession of the Trans Indus Ranges.

The Tithonian of Madagascar again has some common faunal elements. In the Lower Tithonian *Virgatosphinctes* occurs quite commonly and is associated with *Holcophylloceras*, *Hildoglochiceras kobelli* (Oppel), and other ammonites. This associated is comparable with northern West Pakistan where, *Aulacosphinctoides* also occurs. Apparently no *Aulacosphinctoides* are known from Madagascar.

The Upper Tithonian Beds of Madagascar, with *Aulacosphinctes*, *Blanfordiceras acuticosta* Uhlig and *Himalayites*, can be correlated with a similar assemblage in northern West Pakistan. It is interesting to note that *Blanfordiceras* and *Himalayites* are shared by Madagascar, Northern Pakistan and Spiti, but are not known from Cutch where only *Aulacosphinctes* is reported. The genus *Micracanthoceras* reported from the Upper Tithonian of Madagascar is not known from northern West Pakistan or Spiti.

The Upper Tithonian clays and marls pass into the overlying Neocomian Beds in Madagascar. In the Berriasian Spath (1939 : 137) has listed *Subthurmannia*, which was previously identified as *Berriasella* by Besairie, and associated with this is *Kilianella*. In Pakistan *Kilianella* occurs commonly associated with *Neocomites* rather than *Subthurmannia*.

From the *Rogersites* Beds of Madagascar Spath (1930 : 138) has listed a number of genera and species which are similar to the Valanginian beds of the Chichali Formation of the Trans Indus Ranges. These include *Thurmanniceras*, *Sarasinella*, *Neocomites*, *Neohoploceras*, *Bochianites*, *Olcostephanus* (*Olcostephanus*), *O*. (*Rogersites*), *Distoloceras* and ?*Leopoldia*. *O*. (*Rogersites*) is more abundantly distributed in Madagascar than *O*. (*Olcostephanus*), while in the Trans Indus Ranges *O*. (*Olcostephanus*) occurs more abundantly than *O*. (*Rogersites*). The association of these two genera with *Distoloceras* and *Leopoldia* is very closely comparable with Northern Pakistan.

Neolissoceras grasianum (d'Orbigny), though listed from the Valanginian beds of Madagascar, was found to occur both in the Berriasian and Valanginian beds of the Trans Indus Ranges. The genus *Subthurmannia* is also not so well represented in Madagascar.

(vii) *Tanganyika*

The Middle Callovian and Upper Jurassic fauna of Kilwa–Kiswere Lindi Hinterland (Arkell 1956 : 331) show strong similarity with parts of northern Pakistan. The common genera in the Callovian are *Obtusicostites*, *Hubertoceras* and *Choffatia*. The upper Oxfordian has perisphinctids, myaitids and *Euaspidoceras*.

Dietrich (1925) and Arkell (1956) placed the Kimmeridgian ammonites from the Septarian marls in the Mutabilis and/or Pseudomutabilis Zones (Lower Kimmeridgian). The assemblage includes some common genera such as *Pachysphinctes*, *Aspidoceras* and *Ptychophylloceras*, but others, such as *Streblites*, *Glochiceras*, *Taramelliceras* (known from the Middle and Lower Katrol Sandstone of Cutch) and

Nebrodites (not recorded from Cutch), are not known from Northern Pakistan. On the basis of *Pachysphinctes* and *Aspidoceras*, the Trans Indus Kimmeridgian beds can be correlated with that of Tanganyika.

The *Virgatosphinctes* fauna of the Smeei Beds is comparable with a similar fauna from Northern Pakistan, except that no *Aulacosphinctoides* is reported from the Kiswere–Lindi Hinterland. In the Tendaguru area, however, the Smeei Beds (Arkell 1956 : 335) have yielded *Holcophylloceras*, *Hildoglochiceras* and *Subdichotomoceras*, which compares well with the Upper Katrol *Hildoglochiceras* Beds of Cutch. At a lower level (*Nerinella* Bed), *Haploceras*, ?*Pachysphinctes staffi* (generic affinities strongly doubted by Spath 1933, who regarded it an *Aulacosphinctoides*) and *Subdichotomoceras sparsiplicatum* (Waagen) occur. It appears that the doubtful *Aulacosphinctoides* of the *Nerinella* Beds of Tendaguru occur below the *Hildoglochiceras* Beds, and occupy a position similar to the Upper Katrol Sandstone of Cutch with *Aulacosphinctoides*. In northern Pakistan, *Aulacosphinctoides* is associated with *Hildoglochiceras* and *Virgatosphinctes* and may thus indicate a rather condensed Lower Tithonian sequence in Pakistan.

From the *Trigonia schwartzi* Beds of Tendaguru, which disconformably succeed the Jurassic rocks, *Olcostephanus*, *Bochianites* and a doubtful *Neocomites* are recorded (Spath 1930 : 140) and these compare with similar Valanginian fauna from Pakistan.

(viii) *Jubaland*

Although rocks of Lower Jurassic, Kimmeridgian and Cretaceous ages are known from Jubaland (Arkell 1956 : 317), the best correlation is established with the Lower Toarcian *Bouleiceras* Beds of Didimtu Hill, which overlie, with intervening conglomeratic or gritty beds, the metamorphic basement complex.

The Upper Oxfordian fragmentary perisphinctid (*Kranaosphinctes*), *Dhosaites* and *Euaspidoceras* assemblage can be correlated with that of the Kala Chitta Range.

(ix) *Somaliland*

The Lower Toarcian *Bouleiceras* Beds and the Lower–Middle Kimmeridgian formations of Somaliland are comparable with northern West Pakistan. In the Tithonian a different ammonite assemblage (*Anavirgatites* and *Pseudoinvoluticeras*) is developed (Arkell 1956 : 309). The Kimmeridgian Daghani Shale underlies Tithonian Gawan Limestone and has *Streblites*, *Subdichotomoceras*, *Torquatisphinctes*, *Idoceras* and *Hybonoticeras* in the upper part. Lower down *Idoceras*, *Sutneria*, *Aspidoceras* and *Aptychus latus* occur.

(x) *Southern France (borders of the Massif Central)*

The Upper Jurassic (Tithonian) and Lower Neocomian ammonite faunas of the classic areas of Berrias show close similarity in genera and some similarity in species with northern West Pakistan (fig. 6). There are, however, discrepancies which raise correlation problems.

In the type section of the Upper Tithonian (Ardeche), Neumayr (1871) proposed *Virgatosphinctes* (? an *Aulacosphinctes*) *transitorius* (Oppel) as the zonal index of the Upper Tithonian. Mazenot (1939) used two other indices, *Berriasella chaperi* (Pictet) above and *B. delphinensis* (Kilian) below, with the associated fauna of *Corongoceras*, *Micracanthoceras*, *Proniceras* and *Spiticeras* particularly well developed near Chomerac. Some of the *Berriasella* species of the Upper Tithonian, including *B. chaperi*, are more closely related to *Protacanthodiscus* because of their development of tubercles. The genera shared between Pakistan and France, are *Proracanthodiscus* and *Spiticeras*. The two zones of Mazenot may thus correspond to the *Protacanthodiscus*, *Himalayites*, *Spiticeras* fauna above and the *Blanfordiceras* fauna below.

Proniceras indicum Spath, the only species known from Pakistan, occurs lower down in the sequence, and similarly a number of *Virgatosphinctes* species known from Pakistan occur associated with *Aulacosphinctoides* in the Lower Tithonian. The occurrence of *Proniceras* in France seems to be higher in the Tithonian.

The ammonite succession of the classic type area of Berrias was summarized by Hegart (1965) and Busnardo and Hegart (1965). The dominant Berriasian genus in France is *Berriasella*, while in the Trans Indus Ranges it is *Subthurmannia*. This discrepancy seems to be partly due to non-recognition of the genera *Protacanthodiscus* and *Subthurmannia* by the French authors. A number of species listed by Mazenot (1939) and others under *Berriasella* (*chaperi*, *malbosi*, *paramimouna*, *aspers* etc) seem to be closely related to *Protacanthodiscus*. Similarly *boissieri* has been placed in *Berriasella*, though American and British palaeontologists have put it in *Subthurmannia*. *Boisseri* is closely related to the type species of *Subthurmannia*, (*S. fermori* Spath), and its inclusion in *Subthurmannia* is preferred here.

A comparison with the frequency and range of Tithonian–Berriasian–Valanginian ammonite genera and species in France given by Busnardo and Hegart (1965 : 27, Table VI) leads to the following conclusions:

1. The genus *Berriasella*, though starting in the Lower Tithonian, has a maximum development in the Berriasian and dies out about the beginning of Valanginian. In the Berriasian of northern West Pakistan, *Subthurmannia* is abundantly distributed and only one doubtful *Berriasella* species is recognized.
2. Busnardo and Hegart have shown that *Himalayites* extends from the Upper Tithonian to fairly high in the Berriasian (in Arkell and Wright 1957, the genus is treated as Tithonian). In Pakistan no species of *Himalayites* were found associated with a typical Berriasian assemblage. The genus occurs below the *Subthurmannia* Beds in horizons which have yielded *Protacanthodiscus* and even *Blanfordiceras* and *Spiticeras*, suggesting it to be a good indicator of Upper Tithonian in Pakistan.
3. The range of *Spiticeras* is from the Upper Tithonian to about the middle of the Lower Valanginian, with a maximum development in the Berriasian. In Pakistan *Spiticeras* and *Negreliceras* occur with *Subthurmannia* and *Neocosmoceras* in the Berriasian. It is not found in the Valanginian, and only a few species occur in the Upper Tithonian. *Spiticeras multiforme* Djanelidze,

reported by Hegart (1965) from Boisseri Zone, occurs in the Trans Indus Range 3 feet below the *Subthurmannia* Beds at a horizon which indicates uppermost Tithonian.

4. The range and maximum development of *Thurmanniceras* in the Lower Valanginian is closely comparable with Pakistan.
5. The range and distribution of *Neocosmoceras* in the Berriasian of France is similar to Pakistan.
6. The distribution of *Kilianella* is again comparable with Pakistan except that its occurrence is somewhat higher in the Lower Valanginian of Pakistan.
7. In France, Busnardo and Hegart have shown that the genus *Neocomites* extends from almost the base of the Upper Tithonian to the Valanginian and probably higher. If this is the range of *Neocomites* sensu stricto, it seems to be long ranging in France. No true *Neocomites* (*Neocomites*) has been found in Pakistan below the *Subthurmannia* beds, or in the *Olcostephanus* beds of the Upper Valanginian. It is more typical of the Lower Valanginian of Northern Pakistan.
8. *Olcostephanus* has been shown by the French authors start in the Lower Valanginian, and show a maximum development in the Upper Valanginian and Hauterivian. In Pakistan *O.* (*Olcostephanus*) occurs more abundantly and *O.* (*Rogersites*) less abundantly in the Upper Valanginian condensed beds, and is much less frequently associated with *Leopoldia*, *Lyticoceras*, and *Distoloceras*. The *Olcostephanus* species includes comparable forms like *O.* (*R.*) *atherstoni* (reported from the Upper Valanginian and Lower Hautervian of France) and *O.* (*O.*) *filosus* Baumberger (reported from the Lower Hauterivian of France). Thus there appears to be overlap of the lower zone of Lower Hauterivian of France with the *O.* (*O.*) *salinarius* zone of the present author from the Upper Valanginian of Pakistan. The lower Hauterivian of France, in contrast to Pakistan, shows abundance of *Leopoldia*, *Lyticoceras*, and *Acanthodiscus*. The *Olcostephanus* Beds of Pakistan show rare occurrence of *Leopoldia*, *Lyticoceras* and *Distoloceras* (Upper Valanginian–Hauterivian genera), and thus are regarded here as Upper Valanginian.

To conclude, the Berriasian and Valanginian ammonite faunas of France have many affinities with the faunas of northern West Pakistan, but the range of many genera in France and the association of some do not tally with the noted sequence in Pakistan. No doubt the succession in France is more complete and the fauna is rich in number of species and specimens.

The zone of *B. grandis* is difficult to correlate with the succession in Pakistan where the base of *Subthurmania* has been found to be a convenient and logical horizon to place the base of Cretaceous, and this (Fermori Zone) corresponds well with the Boisseri Zone of France. In a comparable position to the Grandis Zone, *Himalayites hypaisis* (Blanford), *Himalayites* sp., *Protacanthodiscus* spp., *S. multiforme*, *Aulacosphinctes* sp., have been found. If this assemblage is put in the Grandis Zone, the Tithonian and Cretaceous boundary becomes vague and undeterminable in the continuous glauconitic sandy Upper Tithonian–Berriasian sequence of Pakistan.

The present author thus considers the base of the *S. boisseri* (or *S. fermori*) as a most suitable place to draw the Cretaceous–Jurassic boundary, as this zone has been recognized by Imlay (1961) in Mexico, Leanza (1945) in South America, Cazanov (1953) in Russia and has been discussed in more detail by Casey (1963).

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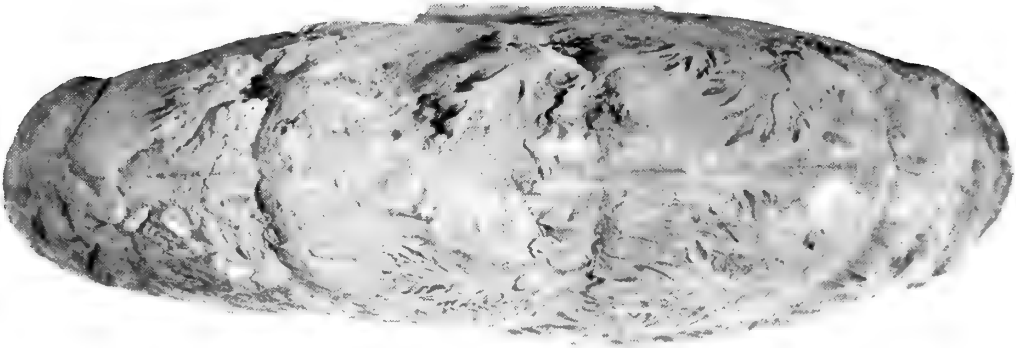
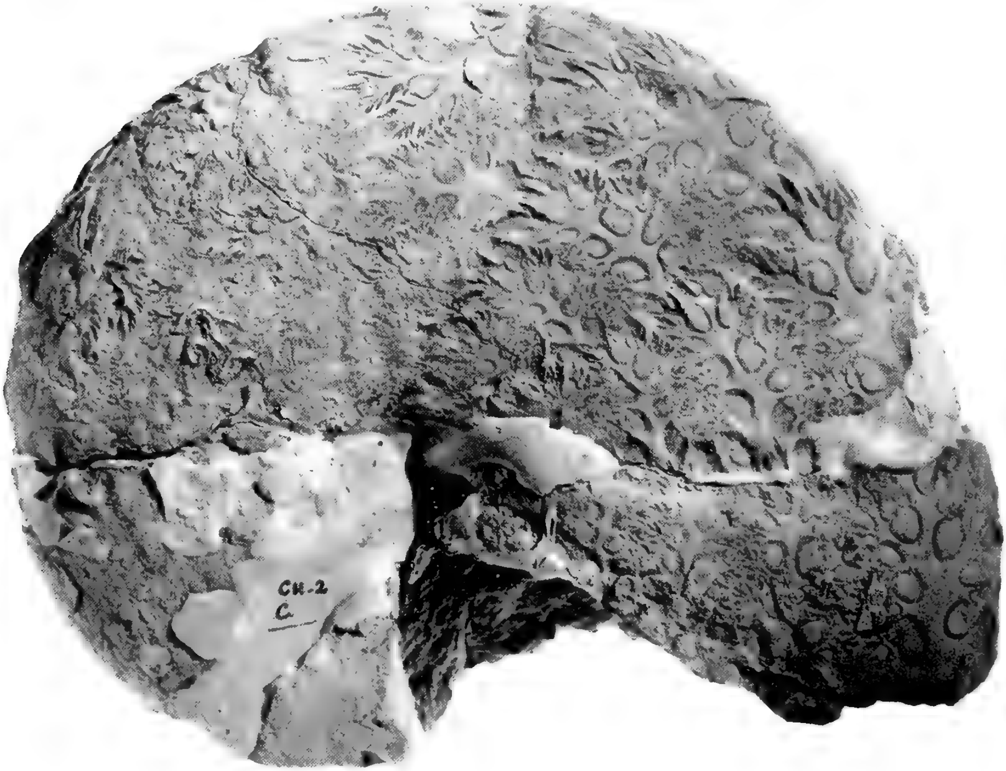
A. N. FATMI, B.Sc., Ph.D.
GEOLOGICAL SURVEY OF PAKISTAN
QUETTA
WEST PAKISTAN

PLATE 1

Holcophylloceras silesiacum (Oppel). 20 ft above base of Chichali Formation. Lower Tithonian. Chichali Pass, Trans Indus Ranges. C.76546, ×0·55.

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C.

PLATE 2

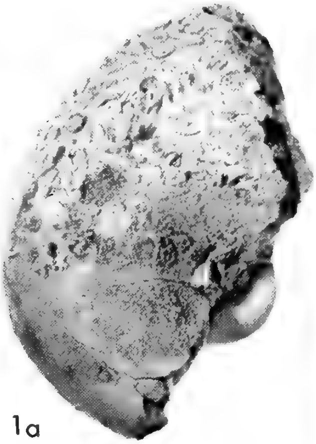
FIGS 1*a*, 1*b*. ***Ptychophylloceras ptychoicum*** (Quenstedt). About 10 ft above base of Chichali Formation. Lower Kimmeridgian. Punnu Mines, Trans Indus Range. C.76547.

FIGS 2*a*, 2*b*. ***Pterolytoceras exoticum*** (Oppel). Lower member of Chichali Formation. Upper Tithonian. Chichali Pass, Trans Indus Ranges. C.76548.

FIGS 3*a*, 3*b*. ***Pterolytoceras*** sp. indet. Lower member of Chichali Formation. Upper Tithonian. S.W. of Mallakhel, Trans Indus Ranges. C.76551, ×0·6.

All figures natural size, except Fig. 3.

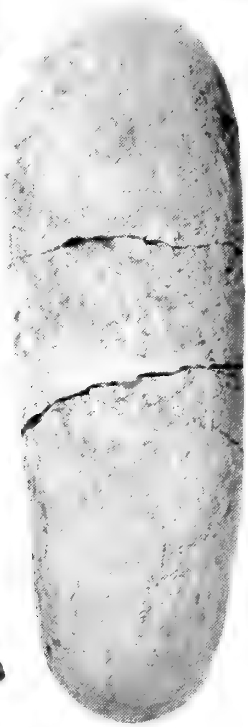
1b



1a

2a

3a



3b

2b

PLATE 3

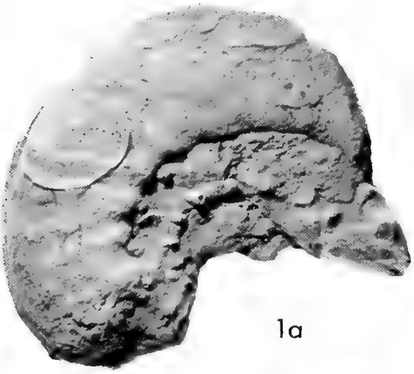
FIGS 1*a*, 1*b*; 3*a*, 3*b*. ***Bouleiceras nitescens*** Thévenin. Middle member of Datta Formation. Lower Toarcian. Chakdalla, Kala Chitta Range. Fig. 1, C.76554. Fig. 3, C.76555, ×0·6.

FIGS 2*a*, 2*b*; 4. ***Bouleiceras chakdallaense*** sp. nov. Middle member of Datta Formation. Lower Toarcian. Chakdalla, Kala Chitta Range. Fig. 2, C.76557, holotype. Fig. 4. C.76558, paratype.

FIG. 5. ***Hildoglochiceras*** sp. indet. 20 ft above base of Chichali Formation. Lower Tithonian. W. of Makerwal, Trans Indus Ranges. C.76562.

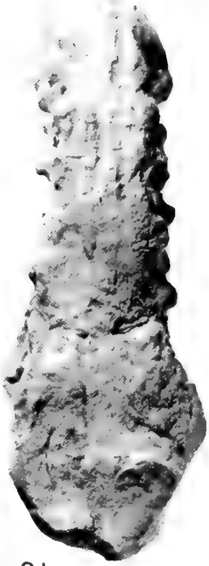
FIGS 6*a*, 6*b*; 7*a*, 7*b*. ***Mayaites*** cf. ***waageni*** (Uhlig). Basal 3 inches of Chichali Formation. Upper Oxfordian. Punnu Mines, Trans Indus Range. C.76563-64.

All figures natural size, except Fig. 3.



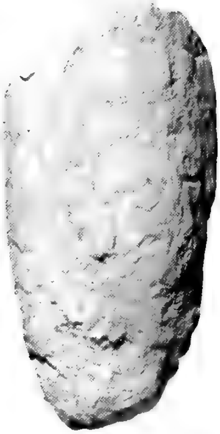
1a

2a

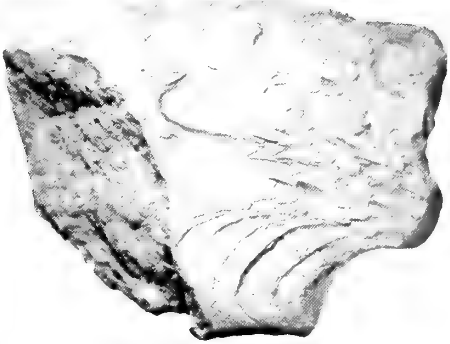


2b

1b

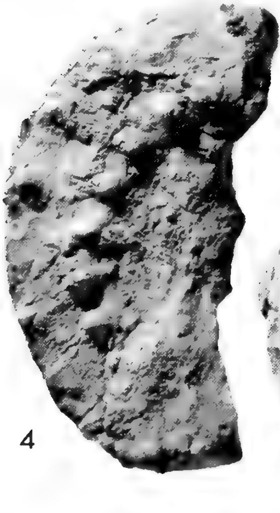


3b



3a

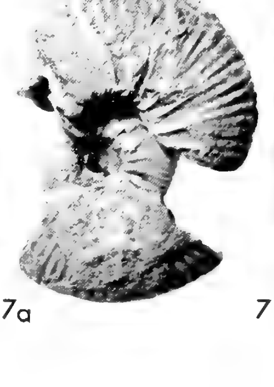
5



4

6b

6a



7a

7b

PLATE 4

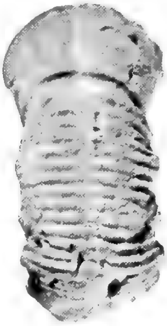
FIGS 1–3. ***Reineckeia anceps*** (Reinecke). Top 1 ft of Samana Suk Limestone. Middle Callovian. Lunda Mines, Trans Indus Ranges. Fig. 1, C.76565. Fig. 2, C.76566. Fig. 3, C.76568.

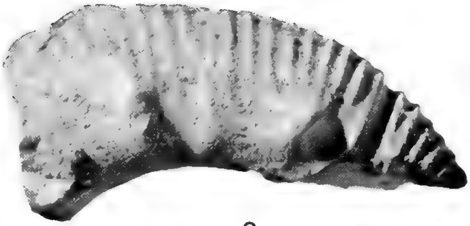
FIGS 4*a*, 4*b*. ***Reineckeia*** cf. ***torulosus*** (Spath). Top 1 ft of Samana Suk Limestone. Middle Callovian. W. of Makerwal, Trans Indus Ranges. C.76572, ×0·75.

FIGS 5*a*, 5*b*. ***Obtusicostites buckmani*** Spath. Top 1½ ft of Samana Suk Limestone. Middle Callovian. Punnu Mines, Trans Indus Range. C.76581.

All figures natural size, except Fig. 4.


1a


1b


2a


2b


3a


3b


4a


4b


5a

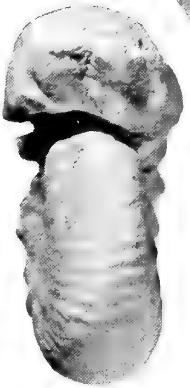
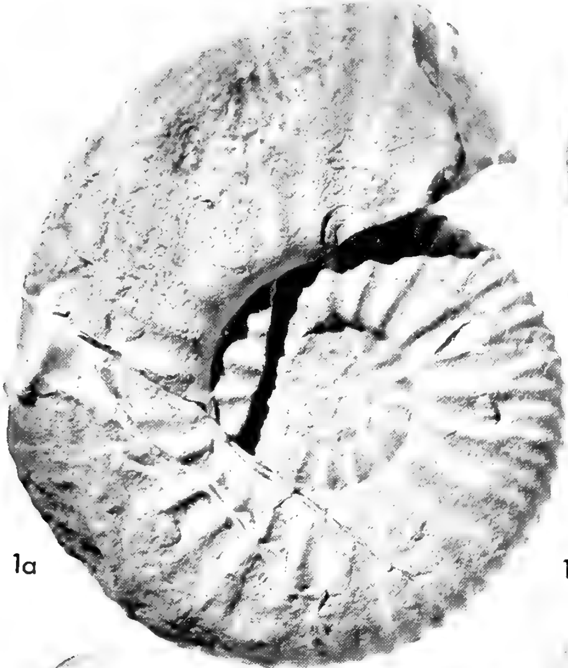

5b

PLATE 5

FIGS 1*a*, 1*b*; 2*a*, 2*b*. ***Obtusicostites buckmani*** Spath. Top 1½ ft of Samana Suk Limestone. Middle Callovian. Punnu Mines, Trans Indus Ranges. Fig. 1, C.76583, ×0·7. Fig. 2, C.76584.

FIGS 3–6. ***Hubertoceras*** sp. indet. Top 2 ft of Samana Suk Limestone. Middle Callovian. Lunda Mines, Trans Indus Range. Fig. 3, C.76592. Fig. 4, C. 76594. Fig. 5, C.76595. Fig. 6, C.76597.

All figures natural size, except Fig. 1.


1a


1b


3


4a


2b


2a


5b


4b


5a


6

PLATE 6

FIGS 1; 2*a*, 2*b*. ***Prososphinctes virguloides*** (Waagen). Basal 1 ft of Chichali Formation. Upper Oxfordian. Mazari Tang, Nizampur. Fig. 1, C.76608. Fig. 2, C.76609.

FIGS 3*a*, 3*b*. ***Perisphinctes*** sp. indet. Basal 3 inches of Chichali Formation. Upper Oxfordian. N. of Kalabagh, Trans Indus Range. C.76620.

FIGS 4*a*, 4*b*. ***Perisphinctes (Kranaosphinctes)*** sp. indet. Basal 3 inches of Chichali Formation. Upper Oxfordian. Chichali Pass, Trans Indus Ranges. C.76624.

All figures natural size.


1


2a


2b


3a


3b


4a


4b

PLATE 7

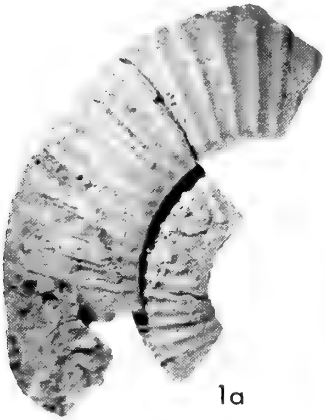
FIGS 1*a*, 1*b*; 2. ***P. (Dichotomosphinctes)*** cf. ***rotoides*** Ronchadzé. Basal 4 inches of Chichali Formation. Upper Oxfordian. Chichali Pass, Trans Indus Ranges. Fig. 1, C.76629. Fig. 2, C.76630.

FIGS 3*a*, 3*b*. ***P. (?Dichotomosphinctes)*** sp. indet. Basal 3 inches of Chichali Formation. Upper Oxfordian. Punnu Mines, Trans Indus Ranges. C.76635.

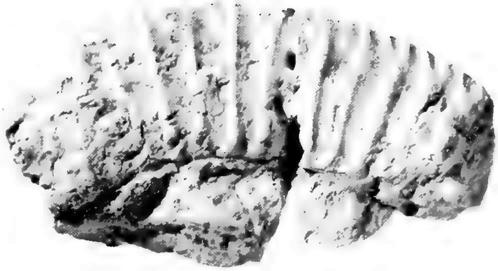
FIGS 4*a*, 4*b*. ***Katroliceras*** cf. ***pottingeri*** (J. de C. Sowerby). Between 6 and 7 ft above base of Chichali Formation. Lower Kimmeridgian Punnu Mines, Trans Indus Ranges. C.76637.

FIGS 5*a*, 5*b*. ***Pachysphinctes robustus*** Spath. Between 5 and 7 ft above base of Chichal Formation. Lower Kimmeridgian. Punnu Mines, Trans Indus Ranges. C.76641, ×0·6.

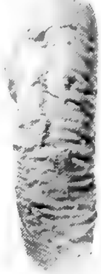
All figures natural size, except Fig. 5.


1a


1b


2


3a


3b


4a


4b


5a

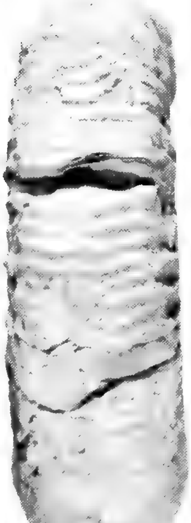

5b

PLATE 8

FIGS 1*a*, 1*b*; 2*a*, 2*b*. ***Aulacosphinctoides hazaraensis*** sp. nov. Basal bed of Lumshiwal Formation. Lower Tithonian. Kathwal, Hazara. Fig. 1, holotype, C.76644. Fig. 2, paratype, C.76645.

FIGS 3*a*, 3*b*. ***Aulacosphinctoides uhligi*** Spath. 2 ft above base of Lumshiwal Formation. Lower Tithonian. Kathwal, Hazara. C.76646

FIGS 4*a*, 4*b*. ***Aulacosphinctoides*** sp. indet. 1 ft above base of Lumshiwal Formation. Lower Tithonian. Kathwal, Hazara. C.76648.

FIGS 5*a*, 5*b*. ***Virgatosphinctes denseplicatus*** (Waagen). Basal bed of Lumshiwal Formation. Lower Tithonian. Kathwal, Hazara. C.76652.

All figures natural size.


1a


1b

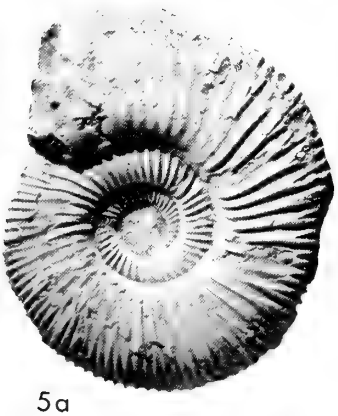

3a


2a


2b


3b


4b


5a


5b

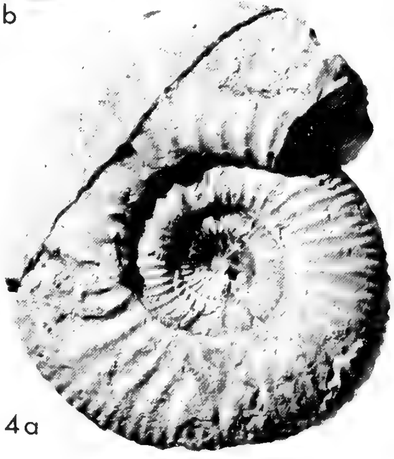

4a

PLATE 9

FIGS 1*a*, 1*b*. ***Virgatosphinctes frequens*** (Oppel). Basal Lumshiwal Formation. Lower Tithonian. Kathwal–Kalapani, Hazara. C.76654.

FIGS 2*a*, 2*b*. ***Aspidoceras (Pseudowaagenia)*** sp. indet. 1 ft above base of Chichali Formation. Lower Kimmeridgian. Punnu Mines, Trans Indus Ranges. C.76660.

FIGS 3*a*, 3*b*. ***Proniceras indicum*** Spath. Between 25 ft and 30 ft above base of Chichali Formation. Lower Tithonian. Chichali Pass, Trans Indus Ranges. C.76663.

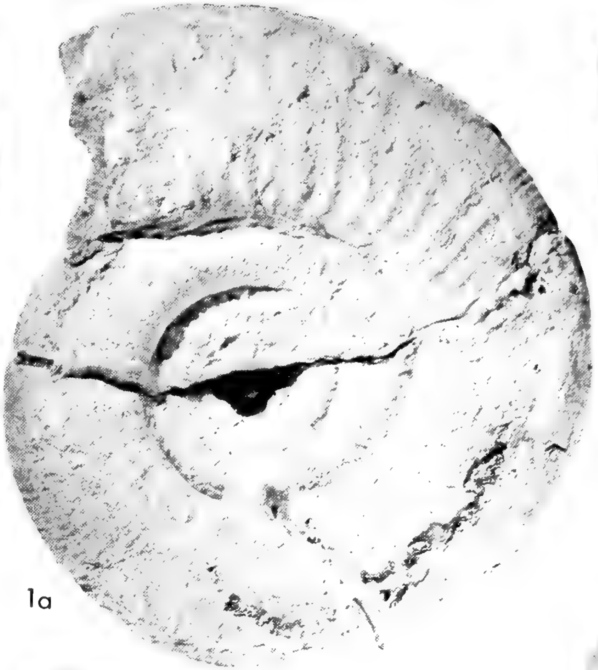
FIGS 4*a*, 4*b*. ***Spiticeras multiforme*** Djanelidze. 3 ft below base of middle member of Chichali Formation. Upper Tithonian. S.W. of Malla Khel, Trans Indus Ranges. C.76664.

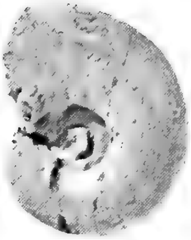
FIGS 5*a*, 5*b*. ***Himalayites*** cf. ***hyphaisis*** (Blanford). 10 ft below base of middle member of Chichali Formation. Upper Tithonian. S.W. of Malla Khel, Trans Indus Ranges. C.76667.

FIGS 6*a*, 6*b*. ***Himalayites middlemissi*** (Uhlig). 10 ft below base of middle member of Chichali Formation. Upper Tithonian. Chichali Pass, Trans Indus Ranges. C.76668.

All figures natural size.

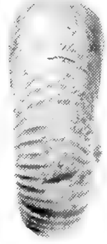

1b

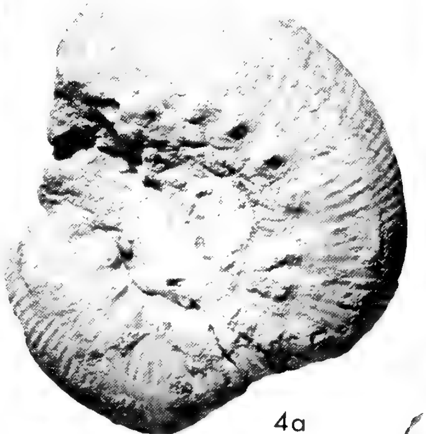

1a

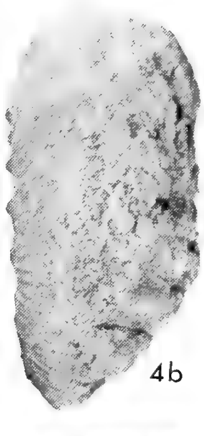

2a


2b


3a

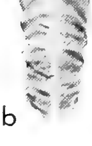

3b


4a


4b


6b


5a


5b


6a

PLATE 10

FIGS 1*a*, 1*b*; 3*a*, 3*b*. ***Provalanginites rhodesi*** sp. nov. 20–30 ft above base of Chichali Formation. Lower Tithonian. Trans Indus Ranges. Fig. 1. Lunda Mines, C.76671, holotype. Fig. 3, Chichali Pass, C.76672, paratype.

FIGS 2*a*, 2*b*. ***Provalanginites howarthi*** sp. nov. 25 ft above base of Chichali Formation. Lower Tithonian. Punnu Mines, Trans Indus Ranges. C.76674, holotype.

FIGS 4*a*, 4*b*; 5*a*, 5*b*. ***Blanfordiceras*** cf. ***wallichi*** (Gray). 10–60 ft below base of middle member of Chichali Formation. Upper Tithonian. Chichali Pass, Trans Indus Ranges. Fig. 4, C.76675. Fig. 5, C.76676.

FIGS 6*a*, 6*b*; 7*a*, 7*b*. ***Blanfordiceras*** cf. ***latidomus*** (Uhlig). 20 ft below base of middle member of Chichali Formation. Upper Tithonian. Lunda Mines, Trans Indus Ranges. Fig. 6, C.76678. Fig. 7, C.76679.

FIGS 8*a*, 8*b*. ***Blanfordiceras*** sp. indet. 2–3 ft above base of Chichali Formation. Upper Tithonian. N.N.W. of Jhallar, Kala Chitta Range. C.76680.

All figures natural size.

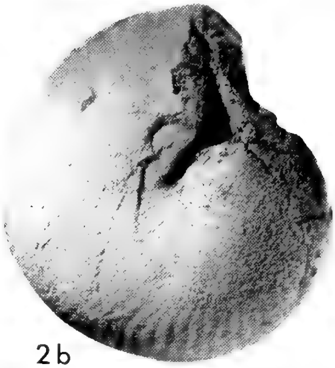

1a

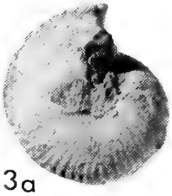

1b


4a


4b


2a


2b


3a

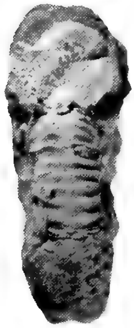

3b

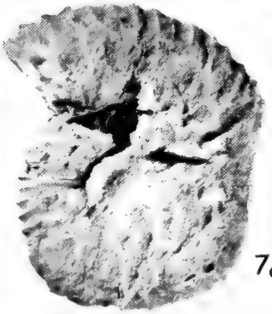

5a


5b


6a


6b


7b


7a


8a


8b

PLATE 11

FIGS 1*a*, 1*b*. ***Protacanthodiscus*** cf. ***michaelis*** (Uhlig). 3 ft below base of middle member of Chichali Formation. Upper Tithonian. Lunda Mines, Trans Indus Ranges. C.76684.

FIGS 2*a*, 2*b*; 3*a*, 3*b*. ***Aulacosphinctes spitiensis*** (Uhlig). 2 ft below base of middle member of Chichali Formation. Upper Tithonian. S.W. of Shaikh Budin Hills, Trans Indus Ranges. Fig. 2, C.76686. Fig. 3, C.76687.

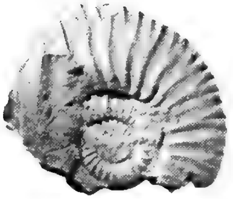
FIGS 4*a*, 4*b*. ?***Protacanthodiscus*** sp. indet. 5 ft below base of middle member of Chichali Formation. Upper Tithonian. Lunda Mines, Trans Indus Ranges. C.76685.

All figures natural size.

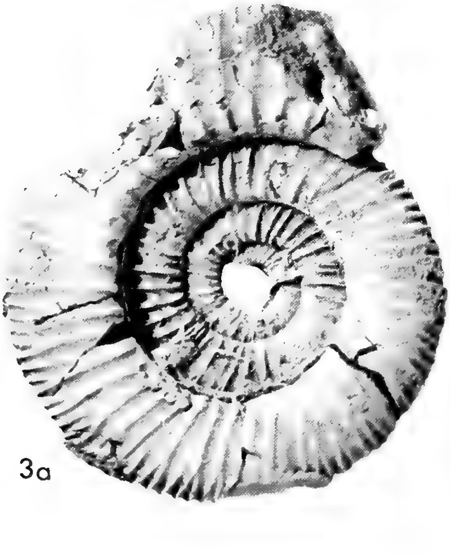

1a


1b


4b


2a


2b


3a


3b


4a

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