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EARLIEST CARBONIFEROUS GONIATITE RECOVERY AFTER THE HANGENBERG EVENT

by

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(2 figures and 5 plates)

ABSTRACT.- Following the extinction of most goniatites and clymeniids below the new Devonian/Carboniferous boundary, only prionoceratids survived to give rise to new groups. Comments are made on the faunas known around the boundary in Europe and North America. Juvenile goniatite faunas are known in the earliest Carboniferous in many parts of the world. In the Stockum Limetone faunas these include evolute early stages with or without constrictions which have recently, but not convincingly, been referred to *Acutimitoceras.* Also there are costate early stages and forms with sulcate margins referred to *Sulcimitoceras.* The relation of these early stages to more normal adult stages is a fascinating puzzle awaiting solution. Illustrations and brief descriptions of these forms are given. Early stages also occur at similar levels in the Montagne Noire, Ireland, Missouri and in the Exshaw Shale of Canada and these occurrences are reviewed. Attention is drawn to how evolutionary novelty, following the extinctions at the Hangenberg Event, shows first as variety in early stages and the initiation of new stocks of Prionoceratidae and then of quite new groups, including the Voehringeritinae, Karagandoceratidae, *Qiannanites* Group, Prolecanitidae and Prodromitidae.

KEY WORDS.- Ammonoids, goniatites, extinction, event, evolution, Devonian/Carboniferous, Hangenberg Event, paedomorphism.

1.- INTRODUCTION

Attention has recently been drawn to the fact that after certain extinction events in the Devonian, especially after the Taghanic and Kellwasser Events, evolution showed itself by the initiation of novelty in the earliest whorls through changes of shell form, growth line pattern, and sutural ontogeny (House, 1985; Becker, 1986). This paper concerns similar changes following the Hangenberg Event which terminated many Devonian ammonoid groups. This also has a bearing on the defintion, using goniatites, of the level for the Devonian/Carboniferous boundary.

The 1935 definition for the Devonian/Carboniferous boundary was made on the basis of the entry of the goniatite *Gattendorfia* in the Hangenberg Kalk of the Oberrödinghausen railway cutting in the Hönnetal, Germany (Jongmans & Gothan, 1937). This was documented in detail by Schindewolf (1937) and later by Vöhringer (1960). The abrupt extinction of most clymeniids and many goniatite groups by the early Hangenberg Schiefer below and the continuance of prionoceratids was recognised. The 1937 boundary was defined by the entry of new forms of prionoceratid, characterised by *Gattendorfia,* in which the adult shell was subevolute or evolute, rather than involute, and in which the umbilical lobe had migrated from the umbilical seam into the low ventral flanks.

For reasons which need not be recounted here, but partly due to the great rarity internationally of occurrences of *Gattendorfia* at that time, a need arose for a more precisely defined Devonian/Carboniferous boundary by IUGS and the acceptance by the IUGS Executive Committee in annual meeting,

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held at Sao Paulo, in January 1991, of a Global Stratotype Section and Point at La Serre in the Montagne Noire. This GSSP had been chosen on the basis of a refined definition by Flajs & Feist (1988) within the conodont *praesulcata-sulcata* lineage which the Working Group had decided was best used as the basis for the new GSSP. But the Devonian/Carboniferous boundary is now defined, not by conodonts, nor by any other faunal group, but by the physical boundary at the base of bed 89 in the La Serre section.

These decisions have left the question of how the Devonian/Carboniferous boundary may be defined using other groups, and particularly the ammonoids, to a large extent unresolved. In 1960 Vöhringer and later Weyer (1977) demonstrated that several species of the earliest Tournaisian prionoceratids had open *umbilici* in the early whorls and Korn (1981) favoured the name *Acutimitoceras* for these. In 1984 Price & House published a review of ammonoids near the Devonian/Carboniferous boundary and the view was taken that the most distinctive novelty close to the *praesulcata/sulcata* boundary was shown by a transitional fauna, known especially from the Stockum Limestone, in which the early stages of Prionoceratidae, but not the later, were evolute. These were also referred to the genus *Acutimitoceras* Librovitch although no demonstration was possible that the Stockum early stages bore very much relation to the adult oxyconic forms on which Librovitch based the genus. *Acutimitoceras* has now become been widely used for almost any prionoceratid in the earliest Carboniferous which is open umbilicate in the early stages following descriptions of faunas by Korn (1984) and Kusina (1985). It is here recommended that the definition of *Acutimitoceras* revert to the precise limits given by Librovitch, and some suggestions on a more satisfactory classification are given.

2.- AMMONOID EXTINCTION AND LATER DIVERSIFICATION AROUND THE DEVONIAN/CARBONIFEROUS BOUNDARY

Goniatite groups which become extinct in the upper part of the *Wocklumeria* Stufe and top of the Wocklum Kalk include the Tornoceratidae, Posttornoceratidae and Sporadoceratidae : these are lost within the *praesulcata* conodont Zone (Fig. 1). Vöhringer (1960) thought that only two groups survived the new Devonian/Carboniferous boundary and pass into the Carboniferous. These he referred to as the *varicosum* and *lineare* stocks. It is now known that the *prorsum* Group was initiated below the boundary and evidence comes from the Louisiana Limestone of Missouri, the Upper Hangenberg Shale of Germany (Paproth & Streel, 1970; Becker *et al.,* 1984; Korn, 1991) and this will be discussed below. The clymeniid ammonoids are almost lost completely within the Middle *praesulcata* conodont Zone, and extinctions include the families Cyrtoclymeniidae, Cymaclymeniidae, Clymeniidae, Gonioclymeniidae, Woclumeriidae and the Parawocklumeriidae with other groups were lost a little earlier (Fig. 1). Korn (1988) has suggested that *Wocklumeria* rather than *Cymaclymenia* may be the last clymeniid known above the Wocklum Schichten but he later indicated that they co-occured (Korn, 1989) and now appears to revert to the view that *Cymaclymenia* is, indeed, the last clymenid (Korn, 1989, 1991). It is recorded as occurring with Gen. nov. *A. prorsum,* both in the extremely thin section at Müssenberg (Korn, 1990) and at Drewer, the section which seems to have the best ammonoid succession over the Hangenberg Event.

Apart from the possible short-term survival of *Cymaclymenia,* only one ammonoid family, the Prionoceratidae, survives the Devonian/Carboniferous boundary. The distinction of this family is taken to date from Hyatt (1884, p. 328) who used the term Prionocerae. This gives priority for the family name Prionoceratidae (nom. transl. Bogoslovsky, 1971, p. 180) rather than Imitoceratidae (Ruzhencev, 1950).

This paper is concerned primarily with radiation in the Prionoceratidae after the Hangenberg Event and how this may be used to enable goniatite definition of the new Devonian/Carboniferous boundary. The prionoceratid radiation was the first step in goniatite recovery. Later, new groups of Tornoceratina appear, including the Karagandoceratidae, Voeringeritinae, *Qiannites* Group and, later, the Goniatitidae. The Prolecanitina also appears and, at some unspecified level, the enigmatic Prodromitidae. The rise of these new goniatite stocks has been documented by Vöhringer (1960) and Korn (1981, 1984) has described relevant faunas. Evolutionary aspects have been dealt with in a series of excellent papers by Weyer (1965, 1972, 1976, 1977, 1987, 1988) and Bartsch & Weyer (1985).

3.- NOTES ON GENERIC TERMINOLOGY

Comment on generic goniatite terminology is required on forms included within the Prionoceratidae, the only group to survive the Hangenberg Event. There is such a bewildering range of shell forms, growth line and constriction patterns and, to some extent sutural form that difficulty is inevitable and many of the type specimens of critical species have not been redescribed. Terminology will not be

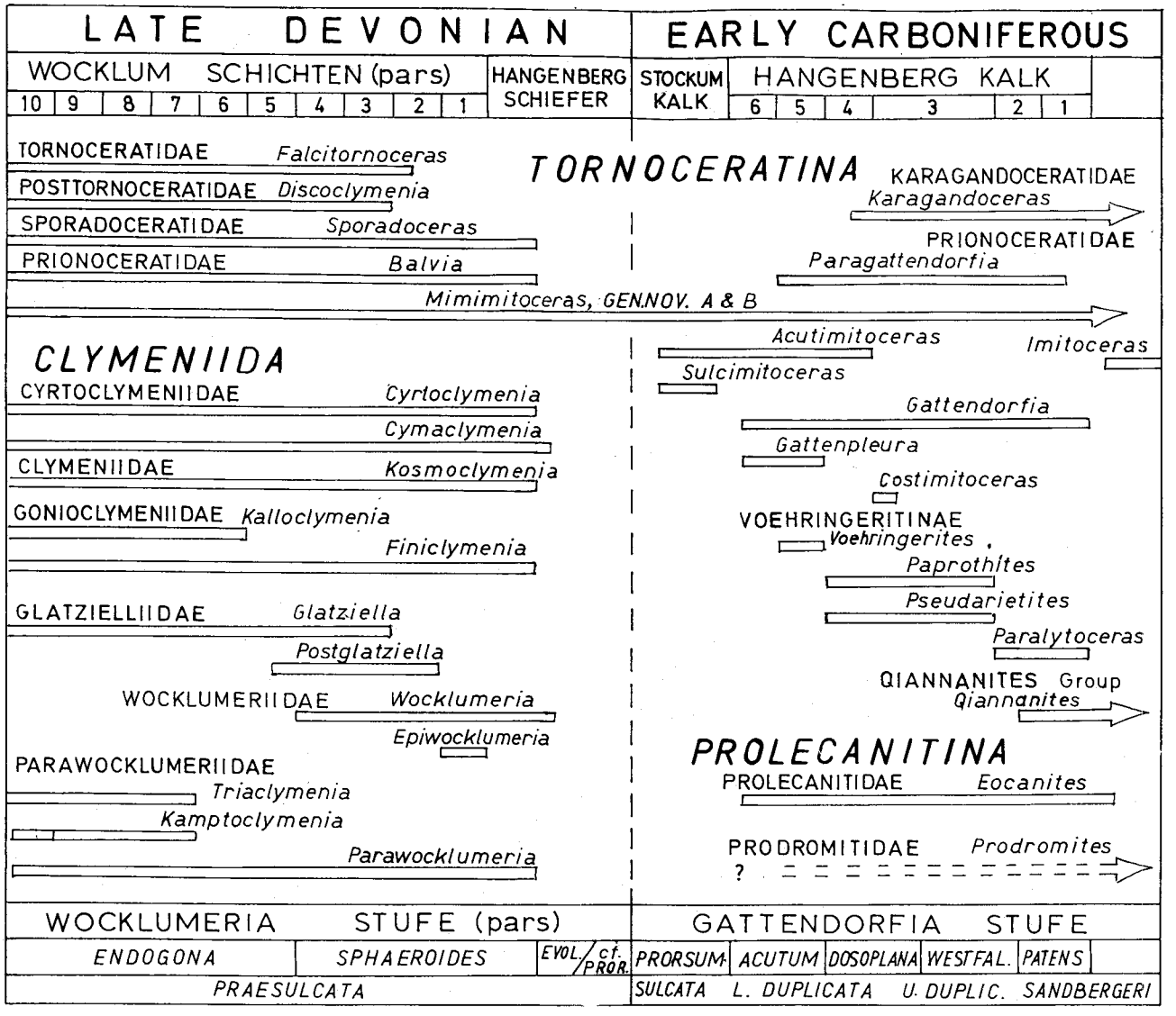

Fig. 1.- Diagram showing ranges of ammonoid genera near the Devonian-Carboniferous boundary. Data mainly from Schindewolf (1937) and Vöhringer (1960) and modified from Price & House (1984) in the light of more recent work and the comments of Dr R.T. Becker.

stabilised until this is done and neotypes designated where necessary. Further, when rich faunas at one level have been described, as by Korn 1984 from the Stockum Limestone, and Kusina (1985) from the River Chabldak, one has the feeling that the many new species do not take into account the variability in a natural population of ammonoids of the sort made famous by the work of Reeside & Cobban (1960). The other problem relates to the environmental change associated with the Hangenberg Event. As seen in Europe and North America the sedimentological and hypoxic conditions almost certainly led to the representation in surviving groups of forms which were more low oxygen tolerant or dwellers in deeper or colder waters than represented in beds above and below the "event" and hence likely to be poorly known. Thus we may never have a complete time-series of Prionoceratidae through the period from the late Devonian to early Carboniferous.

Within such a framework taxonomic decisions are better taken slowly, which is why rather open nomenclature is used here and no generic or subgeneric names are proposed. An account of the many relevant genera was given by Miller & Collinson (1950) and they explained why the genera *Brancoceras* and *Aganides* cannot appropriately be used. There are several generic and subgeneric groups represented in boundary faunas which need separate comment.

3.1.- *PRIONOCERAS*

Prionoceras Hyatt (1884, p. 324) has to be interpreted by the type-species designated by Hyatt which is *Goniatites divisus* (Münster, 1832, p. 24, pl. 4, figs. 6a-d). It is a small goniatite showing three convex constrictions in the last whorl which disappear approaching the venter. I was not satisfied that any specimen in the Münster collection at Munich corresponded with the figured specimen. Other species showing this character are *Prion. frechi* (Wedekind, 1913), *Prion. sulcatum* (Münster) and *Prion. medium* (Wedekind, 1913); none are known in the latest Devonian. If restricted to forms close to its type species, *Prionoceras* is restricted to the Famennian.

3.2.- *IMITOCERAS*

It has been recommended that *Imitoceras* be restricted to forms like its type species which are large goniatites, with a swelling of the ventral lobe, the lateral flanks of which are rather parallel sided, with convex growth lines, and which do not have conspicuous constrictions (Price & House, 1984): this would restrict the genus to the Tournaisian. In an attempt to discover and give some nomenclatorial value to earliest Carboniferous goniatite markers this recommendation has several advantages.

3.3.- *ACUTIMITOCERAS*

This genus was proposed by Librovitch (1957, p. 263) with the type species *Imitoceras acutum* Schindewolf (1923, p. 338, text-figs. 4e.$_{1,2}$, pl. 15, figs. 3, 4). It is an oxyconic species described from Gattendorf; the smaller of the two photographs shows growth lines or a constriction which is rectilinear on the flanks. This change in growth line pattern is distinctive of most prionoceratids at the Devonian/Carboniferous boundary. *Acutimitoceras* has become widely used for any prionoceratid which show an open umbilicus in the early whorls but this feature has not been demonstrated in the type material, but is inferred from collections from Thuringia (Weyer, 1965) and the Rheish Slate Mountains (Vöhringer, 1960). The early stages of very few late Famennian prionoceratids have been described and the supposition that this is a newly-appearing character may be misleading. It seems unwise to continue to use this genus so widely that it has become a useless carpet-bag. It too should be restricted to rather laterally compressed, oxyconic forms conforming to the type species but possibly including *Acut. carinatum* (Schmidt) and *Acut. wangyuensis* Sun (1964) and others with similar form currently in open nomenclature.

3.4.- *SULCIMITOCERAS*

This genus was proposed by Kusina (1985) for a single specimen (refigured here, text-fig. 2) of 8 mm diameter in which the distinctive feature is the presence of an internal ventral groove seen throughout the last whorl. Inner whorls from the Stockum Limestone also showing ventral grooves on the internal moulds but not on the outside of the shell are here also referred to *Sulcimitoceras*.

3.5.- *MIMIMITOCERAS*

This genus was erected by Korn with *Mim. trizonatum* as type species (Korn, 1991, p. 606, text-fig. 1). The small specimens were from the lower *subarmata* Zone. This groups would appear to include *Mim. varicosum* which is the second group which Vöhringer (1960) recognised ascontinuing from the Devonian into the Carboniferous. The group differs from the Gen. nov. B in that the constrictions show on the external shell indicating that they are formed by a fold in the shell, rather than as an internal thickening, and therefore best not considered true constrictions. The species *varicosum* is due to Schindewolf (1923, p. 405, text-fig. 13b) who in 1952 (text-fig. 14, fig. 3a) showed how there were discordances between the course of the growth lines and the constrictions. Indeed, *trizonatum* might reasonable be considered a young specimen of *varicosum* or, at best, a subspecies of it; Korn in his description of *trizonatum* did not comment on its relationships. There are other, and later forms in which there are up to eight radial shell grooves. An original specimen of *Goniatites quadripartitum* (Münster *nom. nud.*, Gümbel, 1962, p. 317) (House, 1978; *et al.*, 1986, Fig. 7(14)) does not show the shell relations so cannot be assigned here with certainty.

3.6.- GEN. NOV. A, *PRORSUM* GROUP (SCHMIDT, 1925)

This group is recognised to appear at the new Devonian/Carboniferous boundary or very slightly earlier if those referred to below from the top of the Hangenberg Schiefer belong here. As shown by Korn (1984) these are open umbilicate in the early whorls. In this rather small group periodic constrictions show dominantly on the inside of the shell and often only on the outside of the shell as constrictions strengthening from the flanks to the mid venter. The group

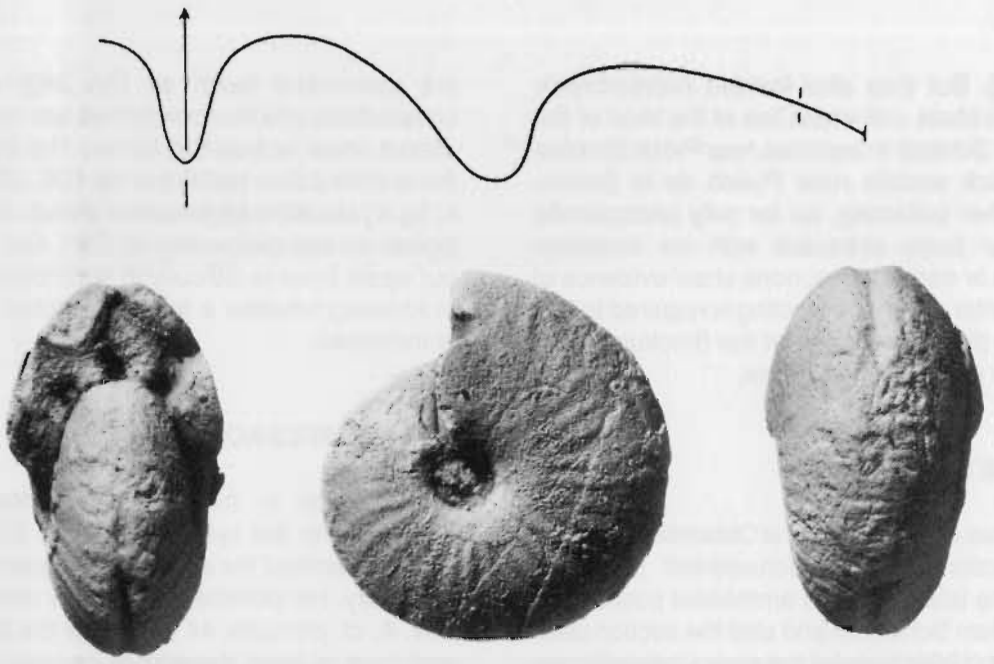

Fig. 2.- The holotype of *Sulcimitoceras yatskovi* Kusina from the River Chabldak, Aktybinskaya Oblast. Specimen loose but thought to come from the *acutimitoceras* Beds. Maximum diameter 8 mm.

shows the development of biconvex growth lines with which the constrictions correspond. Specimens from Stockum thought to represent early stages of this group are described below.

3.7.- GEN. NOV. B, *LINEARE* GROUP

This is one of two groups which Vöhringer (1960) recognised as continuing from the Devonian into the Carboniferous. The original of *Goniatites linearis* Münster (1832, p. II, pl. 2, figs. 5a-c, 6c) has been examined at the Bayerischen Staatsmuseum, Munich. This shows a well-rounded, laterally compressed form with about four constrictions in the last whorl which do not show on testate portions and which are rather deep close to the umbilicus and then extend slightly prorsiradiately to the venter where there is thought to be a shallow sinus. Although indicated by Münster, the ventral lobe does not show a swelling and the sigmoidal lateral lobe is terminally pinched.

3.8.- GEN. NOV. C, *"INFRACARBONICUS"* SCHMIDT (1925) *NON* PAECKELMANN (1913)

One concept of a generalised prionoceratid is illustrated here (Pl. 4, figs. 8,9) by one of Schmidt's specimens of *Aganides infracarbonicus* Paeckelmann (1913), but Paeckelmann's original drawings show a different form with constructions. In Schmidt's specimen the growth lines are simply convex with no trace or rectilinearity or biconvexity. It appears also to show no constrictions. As Schmidt (1925, pl. 19, fig. 4) illustrated it has an unswollen ventral lobe and a slight umbilical sinus. Schmidt had material of this form from Stockum but recent descriptions of that fauna do not mention it. This "classic" type may need generic separation but it is thought to be related to the *prorsum* Group; it seems to be the form described by Korn (1984) as *kleinerae.*

3.9.- GEN. NOV. D.

This refers to the strongly ribbed inner whorls found at Stockum which it is thought Schmidt (1925) refered to *Agan. ornatissimus.*

4.- REVIEW OF FAUNAS IN EUROPE AND NORTH AMERICA

Comments will now be made about faunas at number of localities close to the newly defined Devonian/Carboniferous boundary.

4.1.- MONTAGNE NOIRE

Very few and only poorly preserved ammonoids were found by Feist and Flajs in their collecting at the new Devonian/Global Stratotype Section and Point (GSSP) at La Serre, near Cabrières in southern France. The writer gave determinations which are included in the published accounts (Feist & Flajs

(Eds), 1987). But they also located micromorphic faunas in the shale unit which lies at the level of the Hangenberg Schiefer in trenches near Pic de Bissous and in a track section near Puech de la Suque. Despite further collecting, so far only protoconchs have so far been extracted with no complete ammonitella or early stages; none show evidence of a sulcate venter. Further collecting is required to see whether the distinctive forms of the Stockum fauna occur which are described below.

4.2.- HÖNNETAL

The famous railways cutting at Obberrödinghausen has the section used by Schindewolf (1937) to document the late Devonian ammonoid succession of the Wocklum Schichten and also the section used by Vöhringer (1960) to detail the early Carboniferous faunas of the Hangenberg Kalk. The intervening Hangenberg Schiefer (6 m) was known to have *Cymaclymenia* near the very base but Paproth & Streel (1970) documented the occurrence of prionoceratids in the upper part of the shale and comments on the fauna here are made later. Bed 6, the lowest bed of the Hangenberg Kalk, showed the entry of *Gattendorfia subinvoluta* which would formerly have defined the Devonian/Carboniferous boundary but Walliser (*in* Paproth & Streel, 1982, 1983) reported that the basal 10 cms of Bed 6 lacks *Gattendorfia* but details of what goniatites were present was not given. This section is the one Walliser (1984) has used to illustrate facies changes at the Hangenberg Event which he draws at the base of the Hangenberg Schiefer and before the final clymeniid extinction.

I am indebted to Eva Paproth for illustrations of the goniatites referred to in Paproth & Streel (1970). Several levels are involved and all the material is crushed. From 2.1-2.5 m below the top of the Hangenberg Schiefer is a small form (De 267) with constrictions which are emphasised towards the venter but weaken actually on the ventral mid-line; this may be referred to ? Gen. nov. A aff. *prorsum* Group; there is uncertainty as to whether a true constriction (with internal shell thickening only) is shown. There is a fauna from 1.5-2 m below the top which includes a specimen (De 259) with a closed umbilicus, with growth lines well and regularly developed which are rectilinear across the flanks and with about four constructions, following the course of the growth lines across the flanks; this may belong to the *Mim.* cf. *varicosum* Group; also from the level is a specimen (De. 258, figured Pl. 4, figs. 3,4) which shows a disturbed constriction emphasised on the venter but also seen laterally which may be referred to Gen. nov. A aff. *prorsum* Group. In the top of 0.5 m are specimens (such as De. 240) which show constrictions and the growth lines are retriradiate and almost linear across the flanks. The highest specimens from 0.5cm below the top (DE. 234, figuredPl. 4, fig. 6) show the slight lateral growth-line sinus and typical ventral deepening of Gen. nov. A *prorsum,* but again there is difficulty in such crushed material in knowing whether a true constriction or shell fold is indicated.

4.3.- HASSELBACHTAL

A section in the Hasselbach Valley, was a candidate for the system boundary GSSP. Becker (1988) described the ammonoid sequence across the boundary. He identified forms now referred to Gen. nov. A, cf. *prorsum,* 44 cm below the top of Bed 85 and from a level thought to correspond with the Stockum Limestone, a prionoceratid *indet.* (globose species). Dr Becker informs me that he now has pyritized juveniles from the top of Bed 85, immediately below the entry of *Siphonodella sulcata* (LN spore biozone).

4.4.- STOCKUM

Stockum, Germany, provided a fauna described by Schmidt (1924) from limestone lenses from beside a forest track near Arnsberg. The beds yielded him 100 small specimens he named *Agan. infracarbonicus* Paeckelmann, 30 he named *Agan. ornatissimus* (de Koninck), perhaps 50 specimens named *Agan. carinatus* Schmidt n. sp., and about 35 specimens he named *Agan.* cf. *sciotense* Miller & Faber; these forms Schmidt later named *prorsum* (Schmidt 1925 *pro* Schmidt 1924, Taf. 8, figs. 6,6a). All his figured specimens of these were from Stockum. The juveniles were from weathered limestone. It is the same locality and weathered limestone but only from the trackside section, which provided the juveniles described here, which were collected by D. Korn, J.D Price and myself.

Two trenches have been dug in trees a short distance from the track (Alberti *et al.,* 1974) and this has provided goniatites which were described by Korn (1984) under the genus name *Acutimitoceras* as *intermedium* (Schindewolf), *subbilobatum* (Münster), *carinatum* (Schmidt), and *prorsum* (Schmidt) and he described the new species *kleinerae, stockumensis,* and *caeseri.* Korn did not recognise Schmidt's *Agan. infracarbonicus,* but Paeckelmann's type specimen of that species is rather depressed and has strong constrictions. To judge from Schmidt's unfigured material, seen in Göttingen (one figured here, Pl. 4,

figs. 8,9), his interpretation of infracarbonicus was close to *kleinerae* (Korn, 1984; Taf. 1, fig. 3a,b) and they are referred to gen. nov. C here. Korn did not comment on the forms identified as *Agan. ornatissimus* by Schmidt, but strongly ribbed juveniles in my collections seem to be the forms to which he was referring. Dieter Korn has kindly sent me examples of his described species but I have not been successful in dissecting out early whorls from them nor relating them convincingly with the descriptions given below which concern the early stages only. These offer considerable scope for a more thorough examination of this micromorphic assemblage and it is hoped someone else will do this. The assemblage described here shows the extraordinary differentiation of these prionoceratid juveniles following the Hangenberg Event.

4.4.1.- *Sulcimitoceras* aff. *yatskovi* Kusina.

A number of inner whorls from the trackside exposure show the development of strong concavities and grooves on the venter of the internal moulds at diameters of 2-4 mm (Pl. 3, figs. 1-7). Although Korn (1984) gave cross sections and statistics for the early stages of a large number of specimens of the species he described it is noticeable that he neither illustrated nor commented on this character. It may be that there are slight age differences, and hence faunal differences, between discrete limestone lenses. Some specimens (Pl. 3, fig. 3) show that the grooves are internal and that the constrictions indicate a lateral sinus which is a character shown also in the single type specimen (Kusina 1985, p. 46, pl. 3, figs. 10a,b,c refigured here, text-fig. 2). But the Stockum material available does not shown ribbing, but it may not reach sufficient diameters to do so. Ventral grooves occur in a number of Devonian genera, as in *Archoceras, Prochorites* and *Maternoceras* but these all show in the external mould. The type material is from the River Chabldack, Aktyubinskaya Oblast, from levels referred to the *Acutimitoceras* Beds. Dr Kusina has informed me that the specimen was not in place. The whole fauna described by Kusina is similar to that described by Korn (1984) and the possibility of synonomy among newly described species needs attention.

4.4.2.- Gen. nov. A, *prorsum*

In the collection of inner whorls there is some variability in the development of constrictions but there is one group in which they are developed early and which form a series of specimens which can be matched with Schmidt's species *prorsum;* The subspecies of *prorsum, convexum,* described by Vöhringer (1960, p. 139, pl. 2, fig. 5) from Bed 6 of the Hangenberg Kalk seems specifically distinct. The new juveniles (Pl. 1, fig. 8 upper right) show that the ammonitella was about 1.2 mm in diameter with the nepionic constriction hardly showing on the outside of the shell. The adventitious lobe develops very early (Pl. 1, fig. 9, lower right). After two to three whorls (Pl. 2, figs. 4-9) the emphasis of the constrictions ventrally is clear and they number about four per whorl and the forward projection in the outher flanks associated with the ventro-lateral salient is already apparent. Older specimens (Pl. 4, figs. 1,11, 12) show the characteristic development of slight biconvexity and the emphasis of constrictions towards the venter.

4.4.3.- Gen. nov. D.

Very distinctive specimens are present from the trackside locality which show ribbed inner whorls (Pl. 1, figs. 1-6, pl. 2, figs. 1-3). These may represent the forms recognize by Schmidt (1924) under the name *Agan. ornatissimus.* They show biconvexity of growth lines and open umbilici which characterises prionoceratids of the earliest Carboniferous confirming that a close relationship exists between them. Some (Pl. 1, fig. 1) show there are constrictions, at a frequency of about four per whorl. The outer whorls of specimens referred to the *Mim. varicosum* groups show similar characters and show a similar growth line pattern, and some show the rather irregular shell growth pattern of these inner whorls. A complete link with adult forms is required.

The big interest of the juveniles lies in their discreteness and clear morphological differenciation. From the several hundred specimens available to me I consider these may represent true specific differences demonstrated already in the early stages. In addition to those described there are early stages like Gen. nov. A *prorsum,* as described here, but without constrictions. These may represent early whorls of one of the other species described by Korn (1984).

4.5.- IRELAND

From just east of the Old Head of Kinsale, Matthews (1983) described goniatites from the Castle Slate Member Formation. Many are small pyritic specimens and Matthews hopes of describing them and their succession in detail were sadly terminated by his early death. His described fauna was made available to me through the kindness of Dr J.R. Nudds. Matthews (1983, fig. 1,3,4) illustrated constricted juvenile goniatites with constrictions similar

to those assigned here to Gen. nov. *A. prorsum*, but dogmatism is not possible. More helpful is a larger fragment (Matthews, 1983, figs. 1,6), reillustrated here (pl. 4, fig. 7), which shows slightly biconvex growth-lines and a constriction-like groove increasing in depth from the flanks to the venter. He assigned this to *Imitoceras* cf. *prorsum,* a determination modified here to gen. nov. *A.* cf. *prorsum.* However, the question arises, as with the Hasselbachtal form, whether shell dissolution and compression has led to the expression of true constrictions on the outside of the shell which would not have been apparent in life, or whether the structure is a shell fold. The assignment to the earliest Carboniferous is thus based on the palynological evidence of Naylor and Higgs (1980) rather than the goniatite evidence.

4.6.- EXSHAW SHALE

The Devonian/Carboniferous boundary in Canada falls within the black Exshaw Shale on Jura Creek which forms perhaps the most accessible locality and it lies 32 km southeast of Banff, and north of Exshaw and the Bow River and east of the entrance to the Banff National Park (Richards *et al.,* 1991). Miller (1938, pl. 35, figs. 1-3) figured three specimens said to come from the adjacent Exshaw Creek as *Tornoceras* cf. *uniangulare* (Conrad) but Crickmay (1952) gave a better determination as *Aganides discoidale* Smith indicating a Carboniferous prionoceratid. I have had the opportunity to visit Jura Creek on three occasions and goniatites are commonest in the basal 0.6 m of the Upper Exshaw Formation, 13.4-14.2 m above the base of the measured section (Richards *et al., 1991, p. 60, Fig. 31),from rather silty limestones which Richards* et al. (1991) refer to the base of the Siltstone Member. From my own collecting, and a joint examination with Dr. R.T. Becker of faunas held in the Institute of Sedimentary and Petroleum Geology at Calgary, several different forms seem represented.

4.6.1.- Gen. nov. A, aff. *discoidale* (Smith)

From the 0.6 m bed are large specimens (GSC 102960) with no constrictions with delicate growth lines as figured by Miller (1938, pl. 35, fig. 2) and which develop a shallow sinus on the flanks giving a biconvexity which probably misled Miller, who did not see a suture, into assigning it to *Tornoceras.* The true *discoidale* does not show biconvexity. All specimens are crushed and the whorl section is not determinable but growth lines patterns of this type are figured by Korn (1981, p. 522, fig. 4e) from the very condensed section at Müssenberg as *Acutimitoceras carinatum* (Schmidt). The holotype of Schmidt (1925, pl. 19, fig. 3), from Balve, shows only convex growth lines, but that may be a feature of earlier growth stages.

4.6.2.- Gen. nov. B, cf. *quadripartitum* (Schindewolf)

A single fragment collected loose, but thought to be from the same level (GSC 102956), is similar to the preceding, but shows evidence of rather more than four weak radiating constrictions per whorl. As usual there is no evidence of whorl section, House *et al.* (1986) illustrated a specimen from the Münster collection in Munich as *Prionoceras quadripartitum* (Münster) which is probably from the upper Famennian which,in the absence of any evidence of the constriction type in *quadripartitum* cannot dogmatically be placed but is presumed to be of the *lineare* type.

4.6.3.- Gen. nov. A, cf. *prorsum*

Also present are forms (GSC 102961) with convex growth lines and constrictions, about four per whorl, which begin on the outer flanks and become deepest on the venter, a form characteristic of Gen. nov. A, *prorsum* (Schmidt 1925, p. 534, fig. 3) the only specimen of which figured by Schmidt was small and from Stockum and the constrictions start lower on the flanks.

4.6.4.- Form X

From an overlying bed, 14.2-14.5 m is a form (GSC 102962) with about four biconvex constrictions per whorl of *prorsum* type but apparently with a wider open umbilicus than in that species.

4.6.5.- Form Y

From ca. 14.4 m is a larger fragment (GSC 102963) with about nine crude rugations on the outer flanks and venter which increase in intensity towards the venter as in the *prorsum* group. Again there is uncertainty as to whether these represent true constrictions.

4.6.6.- ? *Pseudarietites*

There is another form collected by Dr Becker in 1987 from the basal 0.6 m of the Upper Exshaw Formation on Jura Creek which is poorly preserved

but appears to be open umbilicate and with rursiradiate ribbing. It might be a ? *Pseudarietites* (GSC 102959).

In 1959 Schindewolf published a paper on adolescent ammonoids from the Exshaw Shale based on a pyritic microfauna obtained from the Brazeau River which defines the eastern boundary of Jasper National Park, Alberta at the same locality where Pamenter (1956) has previously given an account of *Imitoceras;* It cannot be assumed that these are from the same level as the Jura Creek fauna and it seems to me that it is younger. I am indebted to Prof. G.E.C. Westermann for sending to me material held at McMaster University but collections which may be held by the Shell Oil Co. have not been examined.

4.6.7.- Prionoceratidae

In the Exshaw Shale fauna from the Brazeau River Schindewolf tentatively recognized two species of *Imitoceras*; both showed ribbing. One showed a bell-shaped lateral (adventitious) lobe, weak ribbing which was rectiradiate over the flanks, and four constrictions in the last whorl seen (at 14 mm diameter) which divided the last whorl.

4.6.8.- Prionoceratid ammonitellas *indet.*

This refers to indeterminable protoconchs and ammonitellas referred to by Schindewolf as *Imitoceras* sp.

4.6.9.- Prodromitidae indet.

Forms which develop very early subdivision of the ventral lobe were so identified by Schindewolf (1959, pl. 121, figs. 3,4). Another specimen has been subject to stereoscan study and is figured here (Pl. 5, figs. 6-9). This shows that not only is the ventral lobe divided early but so is the dorsal lobe. Further, the tight coiling indicates that the protoconch must be approaching a spindle-shaped. These are all factors which rule out a relation to the Gephuroceratidae (Work *et al.,* 1988). There is also a fragment, now disintegrated (Pl. 5, fig. 5) which showed either sutures or fractures on the flanks, but if the former, of a type characteristic of *Prodromites,* the later ontogeny of which was elucidated by Miller & Collinson (1951, p. 482-486) and Work *et al.* (1988).

4.6.10.- Prolecanitidae indet.

Schindewolf recognized prolecanitids in his fauna, but none have been seen by me. He illustrated a sutural ontogeny (Schindewolf, 1959, text-fig. 2); the specimens are not adult enough to be dogmatic about a generic assignment but they may refer to *Protocanites* and his figured specimen from Fernie would support this assignment.

It appears to me that the Brazeau River fauna from anoxic shales, and presumably also that at Fernie, represent a different faunal level to that on Jura Creek, and the prodromitids and prolecanitids in it suggest it is younger in age.

4.7.- OHIO

Goniatite faunas from around the Devonian/ Carboniferous boundary in northern Ohio were described by House *et al.* (1986). Some forms were identified as *Prionoceras quadripartitum* Münster's specimens of that species was illustrated but it does not show the nature of the constrictions since it is an internal mould. A specimen figured from 1.3 m above the base of the Bedford Shale on Brandywine Creek (House *et al.* 1986, fig. 4, 17-19) shows the discordance of constrictions and growth lines, and slight lateral biconvexity of the growth lines of *Mimimitoceras varicosum* and the specimen is best assigned with it (Pl. 4, fig. 5).

4.8.- MISSOURI

There is a goniatite fauna described by Williams (1943) from the Louisiana Limestone of Missouri which includes forms clearly related to those under discussion here which were described under the names *Aganides compressus* Moore, *Protocanites louisianus* (Rowley) and *Prolec.* sp.

The specimen figured as *Agan. compressus* shows about five constrictions which are rectilinear across the flanks (Williams, 1943, pl. 9, figs. 52-53) and curve apicad over the venter and it differs from the *varicosum* and *quadripartitum* groups in that the ventral lobe is drawn as being swollen. The original of Moore (1928, p. 283, pl. 13, figs. 7,8) is from a similar level but he does refer to a sigmoidal course of the constrictions, which suggests a difference. Williams (1943, p. 108) compared his form with *Agan. discoidalis* Smith from the Chouteau Shale and Branson *et al.* (1938, pl. 25, fig. 1) assigned a

specimen from the Hannibal Shale which is probably a prionoceratid but too poorly preserved for assignment.

Many years ago I was able to examine the smaller of Williams' specimens in the U.S. Geological Survey in Washington although it had collection numbers of the University of Missouri. Some of the specimens had been referred to *Prolecanites louisianensis.* It was concluded (House, 1962, p. 263, fig. 5A-E) that these were open umbilicate imitoceratids and it was left open whether they represent the inner, more evolute whorls of *Imitoceras* (and hence possibly Devonian), or whether the adult is also evolute so that the specimens belong to *Gattendorfia* or a related genus (and hence probably Carboniferous). This uncertainty is still present but emphasised by our lack of knowledge of the early whorls of Devonian prionoceratids but conodont evidence places the source level in the Upper *praesulcata* Zone. Miller & Collinson (1951, p. 479) commented on the difficulty of assigning *Gon. louisianensis* (Rowley, 1895, p. 221, text-figs. 15-19) although Schmidt (1925, p. 511) assigned it to *?Protocanites*. Rowley's original figure appears to show three constrictions in the last, septate, whorl which was only about 6 mm in diameter and does not show clearly the extra umbilical lobes which would lead to an assignment in the prolecanitids. It seems better assigned to Gen. nov. A, *prorsum* Group.Judging by Weller's description he may well also have had *Eocanites* in his fauna. Also among Weller's material was a small elongate and spindle-shaped protoconch, reminiscent of the specimens among Schindewolf's material from the Exshaw Shale. Also there is an early whorl close to that figured by Schindewolf (1959, pl. 120, figs. 1-3) with a projecting prosuture ventrad.

5.- CONCLUSIONS

This discussion has been related to Prionoceratidae which occur near the new Devonian/ Carboniferous boundary. Stocks which became extinct may well have been those of shallower and equable environments. Those that survived may have been deeper-water, colder-water or hypoxia-tolerant groups. Characters of boundary forms which are referred to Prionoceratidae which may prove to be diagnostic are; firstly, the entry of forms which develop slightly biconvex growth lines, and secondly of forms which develop significantly open umbilici in the early whorls. These are referred to Gen. nov. Groups A-C in this paper. New forms which enter in the Stockum Limestone and earliest Carboniferous, *Sulcimitoceras,* which develops ventral grooves on the internal surface of the shell. At later levels within Hangenberg Kalk equivalents, as documented by others, new groups of Tornoceratina appear, including the Voehringeritinae, *Qiannanites* Group and Karagandoceratidae. The Prolecanitina also appear and at some unspecified level the enigmatic Prodromitidae. The recovery following extinctions at the Hangenberg Event is gradual, and it is noticeable that for most of the novel characters, these can be recognised in the earliest stages of growth, witnessing to the importance of larval and juvenile strategies, both for survival, recovery and diversification of the Ammonoidea following an extinction event when the group very nearly disappeared.

6.- ABBREVIATIONS

The following abbreviations are used for collection numbers. GSC, Geological Survey ofCanada, Calgary. MRH, the author's collection. MU, McMaster University, Geology department collections. NMNH, National Museum of Natural History, Washington, D.C., TCD, Trinity College, Dublin.

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PLATE 1

Immature goniatites from the Stockum Limestone. All from the trakside exposure of Schmidt (1924).

Figs. 1-6. ? Gen. nov. D, sp. juv. 1-3, MRH. 1388, X 24. 4-6, MRH. 1389, X 22.

Fig. 7. Gen nov. C, Aff. *kleinerae* (Korn), X 25.

Figs. 8-9. Gen. nov. A. *prorsum* (Schmidt) sp. juv. MRH. 1274a,b, X 20.

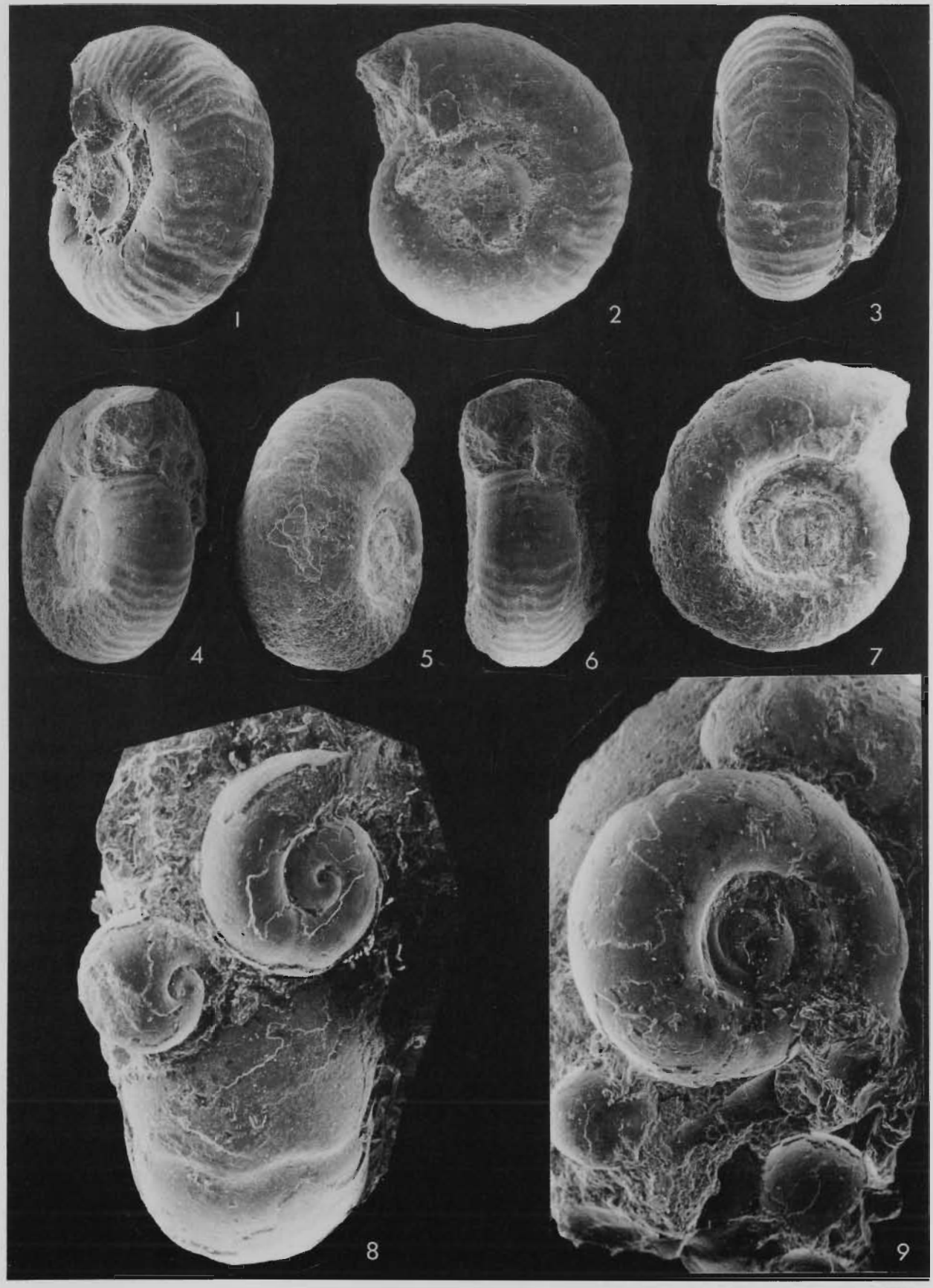
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PLATE 2

Immature goniatites from the Stockum Limestone. All from the trackside exposure of Schmidt (1924).

Figs. 1-3. ? Gen. nov. D, sp. juv. MRH, 1102, X 21.

Figs. 4-9. Gen. nov. A, *prorsum* (Schmidt). 4-6, MRH, 1394, X 20.7. 7-9, MRH. 1392, X 26.


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PLATE 3

Immature goniatites from the Stockum Limestone. All from the trackside exposure of Schmidt (1924).

Figs. 1-7. *Sulcimitoceras* aff. *yatskovi* (Kusina). 1,2, MRH 1273, X 21. 3,6, MRH 1396a, X 25. 4,5, MRH 1396b, X 25.

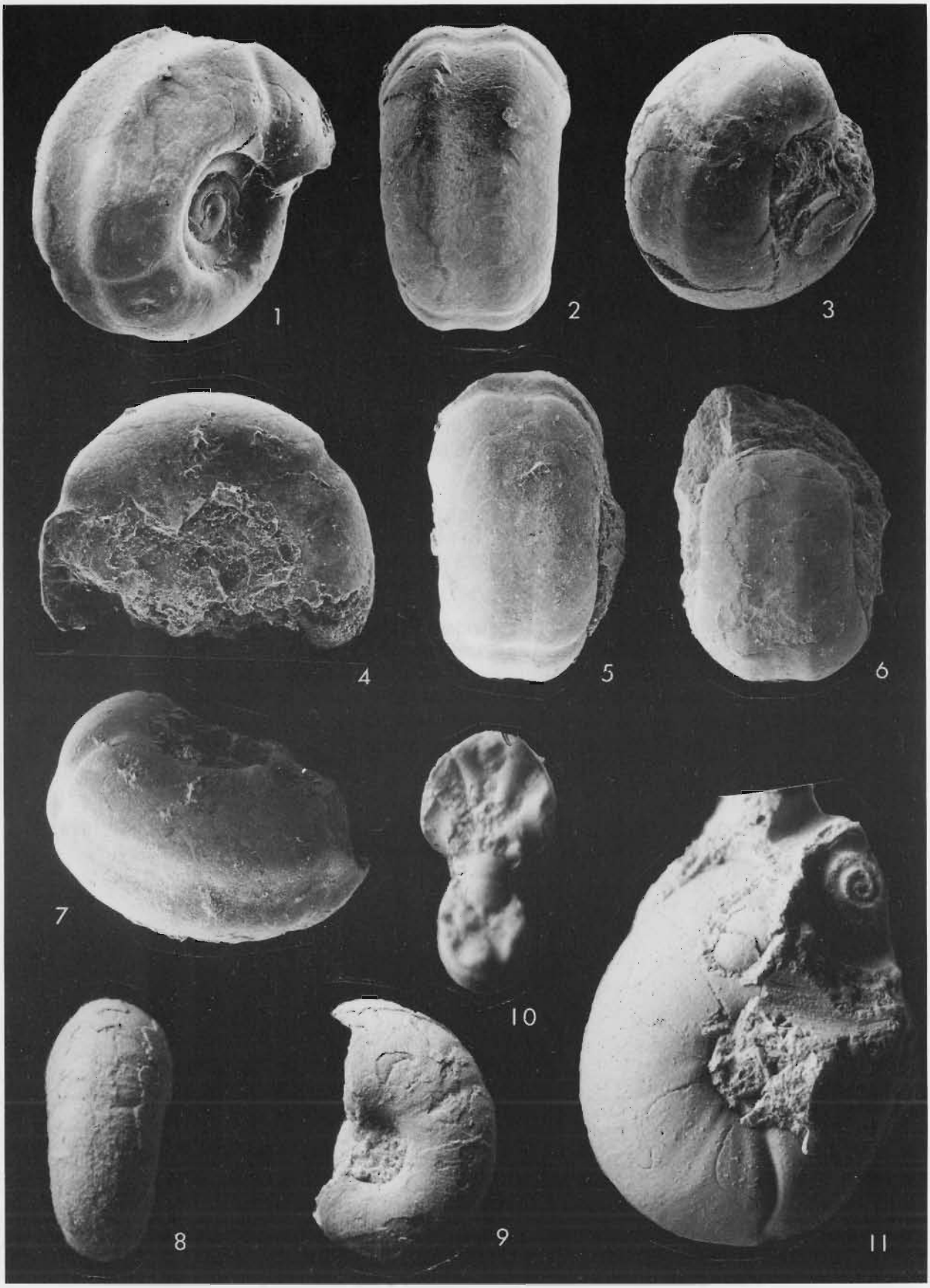
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PLATE 4

Goniatites from Stockum, Oberrödinghausen and Ireland.

Figs. 1,2,10,11. Gen. nov. A, *prorsum* (Schmidt). From the Stockum trackside section of Schmidt (1924). 1, MRH D 2363, X 10. 2, MRH D. 2364, X 10. 11, MRH 1285, X 5.

Figs. 3, 4, 6. Gen. nov. A, aff. *prorsum* (Schmidt), Paproth collection from the Oberrödinghausen railwaty cutting. 3,4, from 1.5-2.0 m below the top of the Hangenberg Schiefer, De 258, 3, X 3, 4, X 5. 6, from 0-0.5 m below, De 234, X 5.

Fig. 5. *Mimimitoceras varicosum* (Schindewolf) Group. Specimen from 1.3 m above the base of the Bedford Shale on Brandywine Creek, northern Ohio (House *et al.* 1986), NMNH 240515, X 1.0.

Fig. 7. ? Gen. nov. A, *prorsum* Group. Specimen figured by Matthews 1983) from the Old Head of Kinsale, Ireland. TCD 17817, X 4.

Figs. 8, 9. Gen. nov. C,*kleinerae* (Korn). From the Stockum trackside locality of Schmidt (1924). From the Schmidt Collection, Göttingen, photographed in 1960. Ca. X 4.

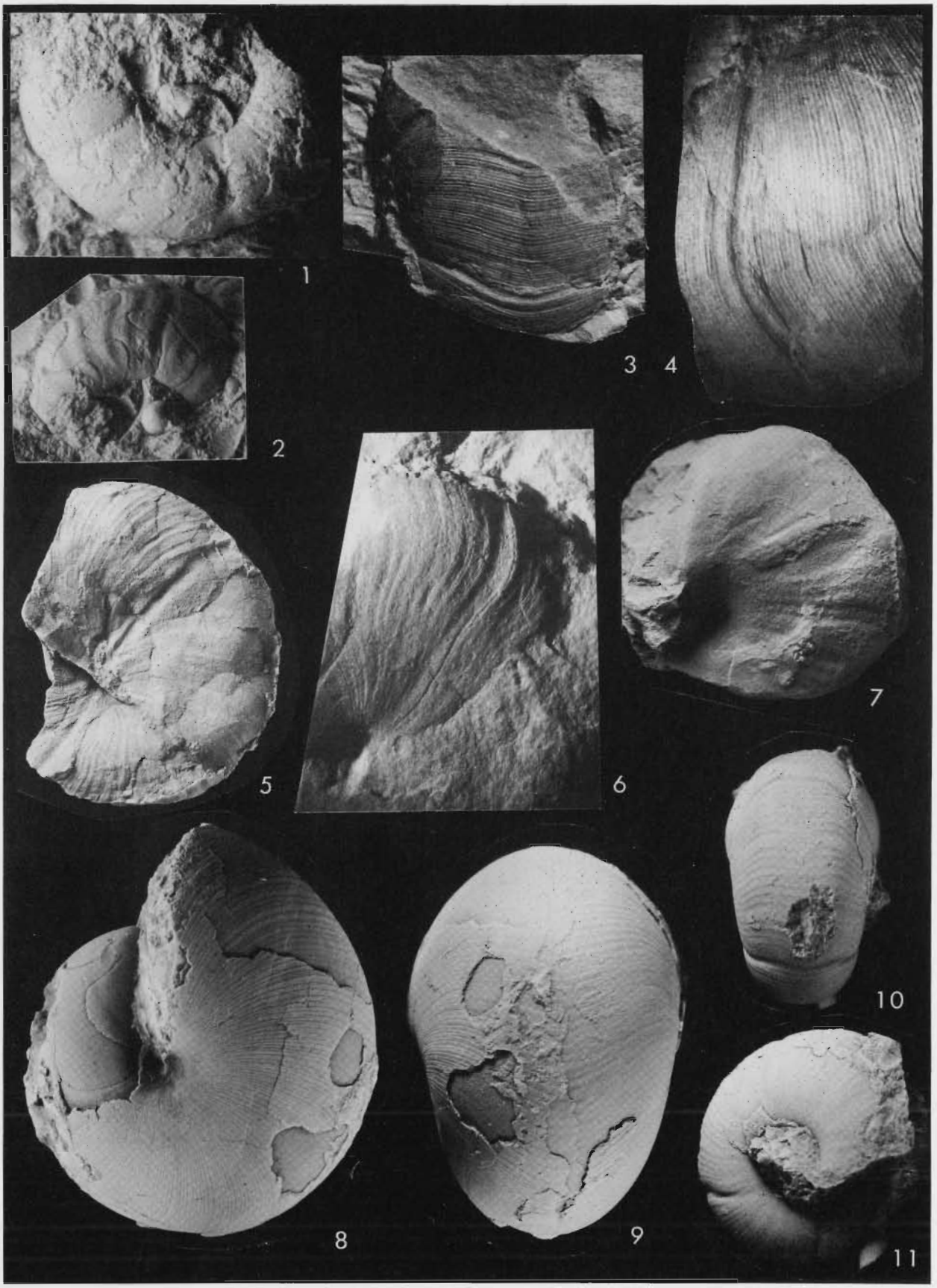
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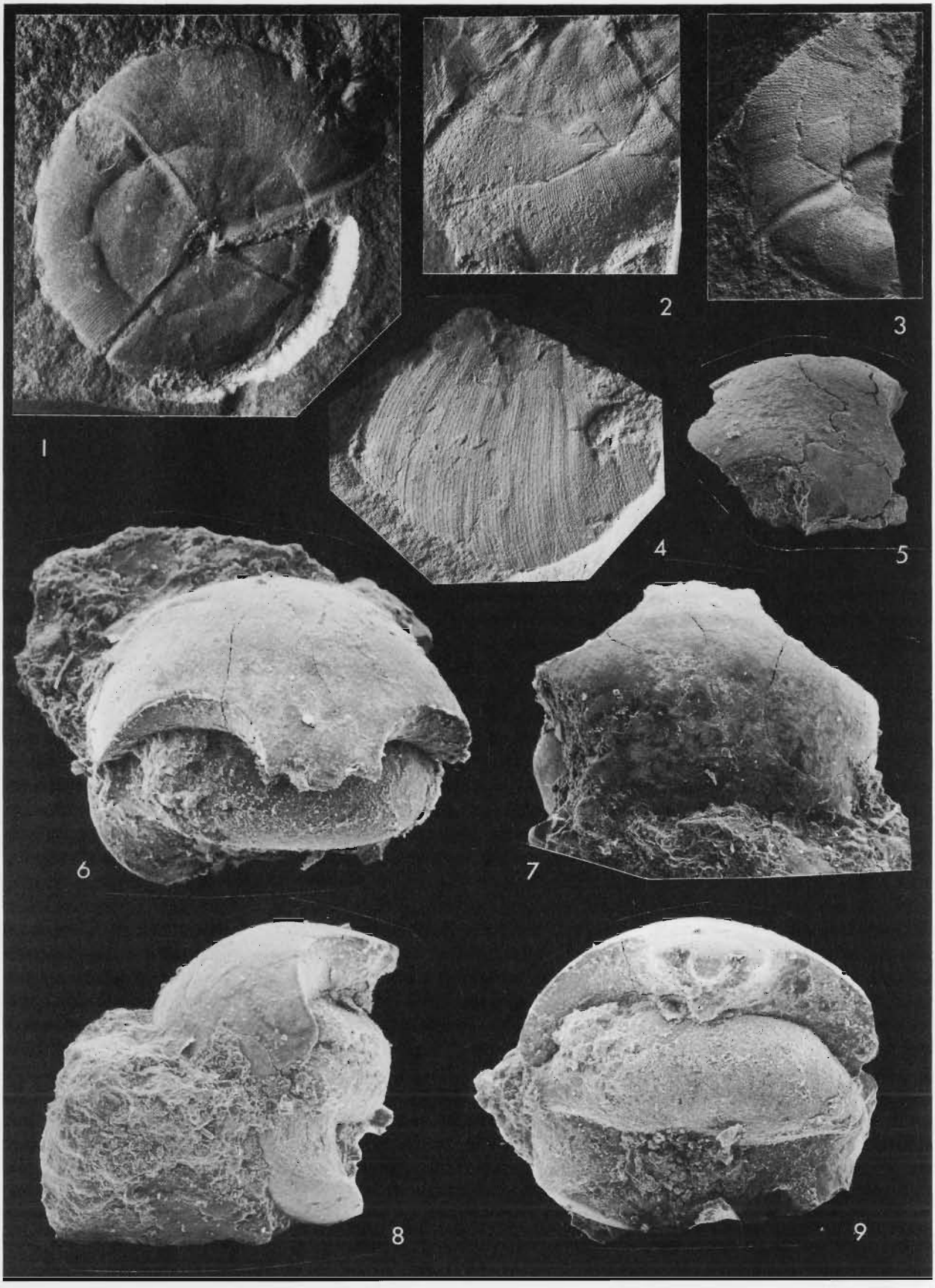
PLANCHE 5

Goniatites from the Exshaw Shale, western Canada

Figs. 1-4. Gen. nov. B, cf. *quadripartitum* (Schindewolf). 1, specimen in the Iowa Geology Department collections, X 2. 2-5, specimenscollected by the author and Dr R.T. Becker from the base of the Upper Member of the Exshaw Formation on Jura Creek. 2, GSC 102956, X 2. 3, GSC 102957, X 2. 4, GSC 102958, X 2.

Figs. 5-9. Prodromitidae examined by Schindewolf and in the collections of McMaster University. 5, specimen showing divided lobe of *Prodromites,* which subsequently disintegrated. 6-7, protoconch and earliest whorls, X 50.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