A STUDY IN THE TORNOCERATIDAE: THE SUCCESSION OF *TORNOCERAS* AND RELATED GENERA IN THE NORTH AMERICAN DEVONIAN

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The species of *Tornoceras*, *Parodiceras*, *Epitornoceras* and *Aulatornoceras* in North America are described. The study provides an independent stratigraphical goniatite zonation, particularly for the New York State Devonian, and it also provides an analysis of allomorphis in *Tornoceras*. A discussion on the protoconch apparatus and the significance of the metamorphosis at the nepionic constriction in *Tornoceras* is given.

For the *Tornoceras* stock descriptions are provided where possible of the ontogeny from protoconch to adult of species at eleven successive stratigraphical levels, and faunas at other levels are also described. Thus the successional ontogenies shed light on the phylogeny of the stock. Faunas at each level may be morphologically defined, but few consistently maintained evolutionary trends have been observed. Shell form seems particularly subject to independent, and probably phenotypic variation. Through the equivalents of the Middle Devonian to the lower Frasnian, protoconch width appears to increase progressively. Similarly the suture becomes more undulating, particularly with regard to the steepness of the ventrad face of the lateral lobe. Later species show reversion to early characters in these respects.

The origin of *Tornoceras* from *Parodiceras* is argued, and it is considered that *Tornoceras* gave rise to all later members of the Tornoceratidae. A new subgenus, *Linguatornoceras*, is erected for Frasnian and lower Famennian tornoceratids with small lingulate lateral lobes. Seven new species and subspecies are described.

I. Introduction

Tornoceras is the longest-ranging goniatite genus in the North American Devonian and it occurs from equivalents of the lowest Givetian to the lower Famennian. Pyritic or marcasitic assemblages, mostly referred in the past to *T. uniangulare*, occur at many levels, especially in New York and adjacent states. Such material is admirably suited for ontogenetic and phylogenetic studies. This work on the Tornoceratidae was commenced primarily in order to investigate the significance of factors of successional ontogeny and variation in the evolution of a closely related goniatite group. It has proved possible to elucidate details of the ontogeny at many levels from the protoconch onwards, and quantitative studies of the development of the shell form have been made wherever possible. This study in *Tornoceras* is thus an analysis of allomorphosis in a closely related goniatite stock. Emphasis has been laid on the means of distinguishing successive time assemblages, whilst the differences found at one horizon have been more freely interpreted as due to the natural variation of interbreeding populations.

Historically the American faunas are of great interest in studies of the Tornoceratidae. In 1842 Conrad described from the Leicester pyrite of New York the species *Goniatites uniangulare*, which was made the type-species of *Tornoceras* by Hyatt in 1884. James Hall in his *Palaeontology of New York* (1879) figured many examples of the group, and Beecher in 1890 gave the first detailed account of the ontogeny of the genus based on material probably from the Alden Marcasite. In his description of the Naples fauna Clarke (1898) described and named several species and described the ontogeny (in part) of forms from the Cashaqua Shale preserved as barytic shell replacements. The youngest occurrence of the genus in the United States at the level of the European *delphinus* Zone (House 1962) was recorded first by Raymond (1909) from the Three Forks Shale Formation of Montana. Younger records from the Exshaw Shale (Miller 1938, p. 166) are misidentifications (Schindewolf 1959). Most of the American records up to 1938 have been summarized, with full bibliography, by A. K. Miller in his monograph of the Devonian ammonoids of America published in 1938. Some new records and a revised correlation of the American succession with the European Devonian sequence have been made elsewhere by the author (House 1962).

This study was commenced during 1958/59 whilst the author was a Commonwealth Fund Fellow in the United States and he is much indebted for support then to that organization. Professor J. W. Wells has been especially helpful in the provision of specimens and in discussion, and Professor G. M. Ehlers helped in the provision of Canadian specimens. The curators of the museums mentioned, especially Mr Clinton Kilfoyle of the New York State Museum, have been very helpful. Most of the specimens have been photographed by Mr G. Dresser and the work has been aided by a grant from the Department of Scientific and Industrial Research.

II. The Stratigraphical distribution of genera

(1) *General statement*

Tornoceras is first seen in America in rocks a little above the Cherry Valley Limestone of New York, which appears to correlate with the lowest Givetian of the European sequence (House 1962, p. 254). *Parodiceras*, the probable ancestor, occurs in the Cherry Valley Limestone. Identifications of *Tornoceras* at earlier horizons (Miller 1938, p. 147, 153; Oliver 1956, p. 404) refer to *Foordites* or generically indeterminate goniatites.

Throughout the Hamilton Group of New York and its equivalents, *Tornoceras* is perhaps the commonest goniatite, and it continues to appear, but less conspicuously, throughout the Frasnian equivalents and into the Candaway Group. The youngest records are from the Three Forks Shale, which may be correlated with the *Platyclymenia* Stufe of the European lower Famennian.

The occurrences will now be discussed briefly in stratigraphical order. The stratigraphic terminology used is based largely upon the work of Cooper (1930, 1942) and the units mentioned belong to the New York State succession unless otherwise stated. The horizons of the faunas studied, and their inferred phylogenetic relation, are shown on an accompanying diagram (figure 1).

(2) *Middle Devonian*

(*a*) *Marcellus formation*

Tornoceras has been recorded from the Union Springs Shale, but until solid specimens showing the suture are found, these specimens should be regarded as indeterminable. The Cherry Valley Limestone was the source for the types of *Parodiceras discoideum* (Hall). Precisely where the true *Tornoceras* enters above this level is uncertain since only crushed specimens have been seen from the Chittenango and Cardiff Shales.

(*b*) *Skaneateles formation*

Crushed *Tornocerae* are very abundant at certain horizons in the Levanna Shale but solid specimens are rare. The material subsequently described comes mainly from the equivalent Arkona Shale of Ontario where *T. arkonense* sp.nov. occurs in the lower part and *T. mesopleuron* sp.nov. in the upper part. Closely allied forms of both these species occur in the Silica Shale of N.W. Ohio and *T. arkonense* occurs in the Plum Brook Shale of N. Ohio.

(*c*) *Ludlowville formation*

A few specimens of *Tornoceras* from the Centerfield Limestone have been examined but they have proved insufficient for critical description. A rich fauna occurs in the Ledyard Shale and *T. uniangulare aldenense* subsp.nov. is here described from the Alden Marcasite horizon (Fisher 1951) and this was almost certainly the source of the specimens which Beecher used for his ontogenetical study of 1890. A rich fauna of closely comparable type occurs in the Widder Shale of Ontario together with an unnamed new species. From an horizon of concretions in the upper Ledyard Shale a few feet below the overlying King

Ferry Shale on Cayuga Lake, Professor J. W. Wells has assembled a large collection of a *Tornoceras* with ribbing on the early whorls and this species is described here as *T. amuletum* sp.nov. The stratigraphical relation of this fauna to that of the Alden Marcasite is uncertain.

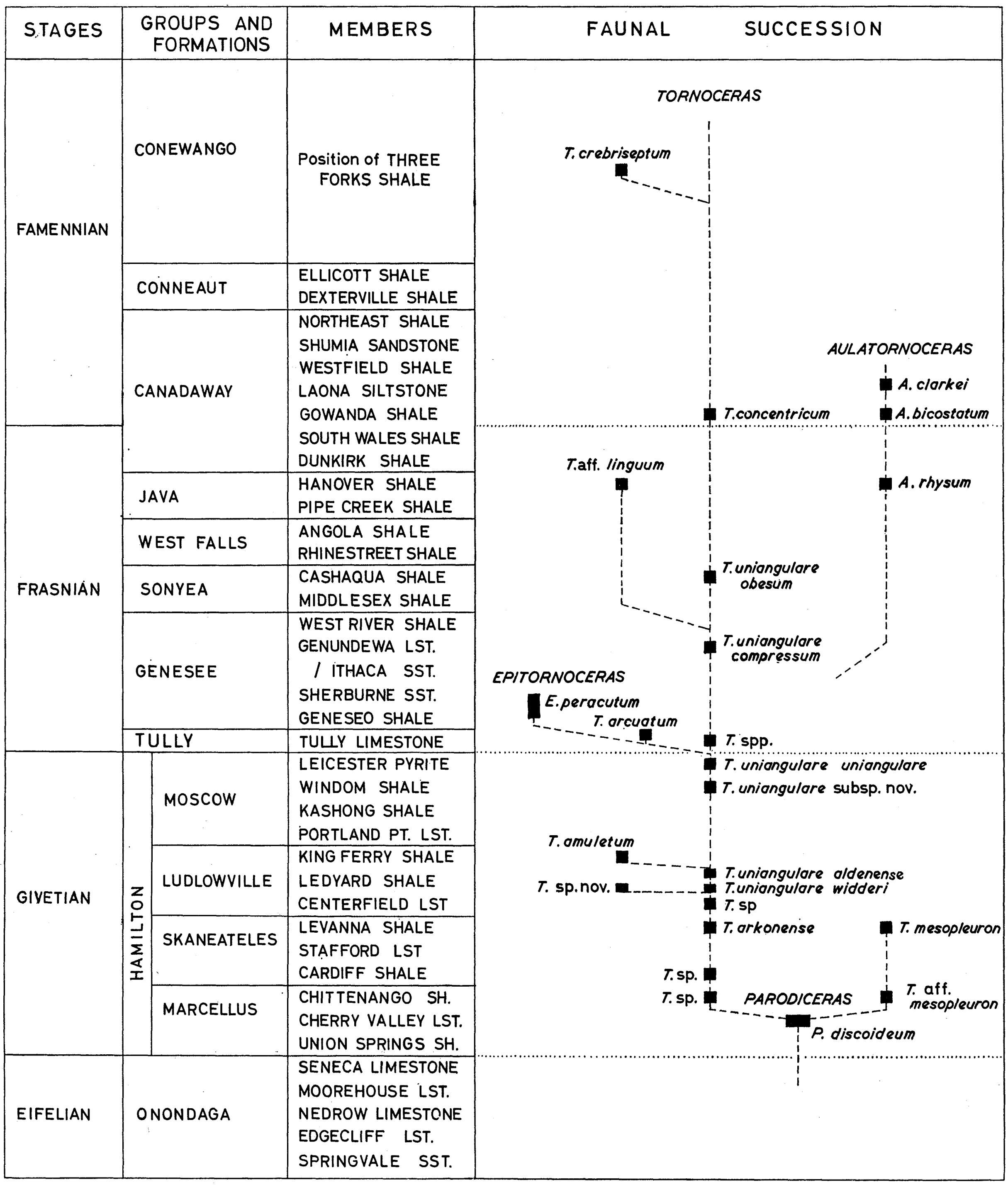

Figure 1. Diagram showing the Devonian succession of New York and the stratigraphical position and morphological relations of the faunas of *Tornoceras*, *Epitornoceras* and *Aulatornoceras* which have been studied.

(*d*) *Moscow formation*

Poorly preserved *Tornoceras* occur quite commonly in the Windom Shale, but it has not yet proved possible to assemble a sufficient number for a critical analysis of the fauna. In the western part of New York State the Leicester Pyrite horizon ('Tully Pyrite'), at the top of the Windom Shale, yielded the types of *T. uniangulare* (Conrad). The relations of this horizon to the Tully Limestone farther east have been a cause of past dispute. As the earlier name 'Tully Pyrite' implies, it was at first thought to be a lateral equivalent of the Tully Limestone (Loomis 1903), but later Cooper & Williams (1935) correlated it, on faunal grounds, with the *Vitulina* Zone which lies immediately below the Tully Limestone farther east. This correlation has recently been challenged by de Witt & Colton (1959, p. 2818) who consider the 'Tully Pyrite' is the equivalent of a pyrite and marcasite level found above a reduced Tully Limestone on the east side of Canandaigua Lake. The evidence of *Tornoceras* upholds the view of Copper & Williams (1935, p. 795), for Professor Wells has located the true *T. uniangulare* in a pyritic horizon immediately below the Tully Limestone at Grove's Creek Quarry, Seneca County. Correlations have been confused in the past by the failure to recognize that pyritic or marcasitic horizons occur both below and above the Tully Limestone. The faunal evidence shows that the 'Tully Pyrite' is the equivalent of the lower of these. The upper, and much younger, demonstrated to the author by Professor Wells at Gorham, has yielded immature *Tornoceras*, but that horizon is Upper Devonian.

(3) *Upper Devonian*

(*e*) *Tully formation*

Tornoceras is quite common in the Tully Limestone at several levels and Dr Rousseau Flower has a description of the forms in manuscript (one of which is figured here, figures 80, 81, plate 9). Apart from a new species to be described by Dr Flower the fauna is interesting in showing a form comparable with *T. arcuatum* sp.nov., a new species described here from the Squaw Bay Limestone of N. Michigan. This may be taken to confirm the evidence provided by *Pharciceras amplexum* that the Tully should be referred to the basal Frasnian (House 1962, p. 256), for in Michigan *T. arcuatum* occurs with *Koenenites*, a genus, like *Pharciceras*, unknown outside the basal Frasnian in Europe. Specimens of *Tornoceras* sp. occur in the Antrim Shale of Michigan (specimens in M.M.P.* from the Huron Portland Cement Co. quarry at Paxton and from about 1·1 miles north of Norwood, Charleroix Co.).

(*f*) *Genesee group*

For this and the subsequent Frasnian formations the terminology of Rickard (1964) is used. Indeterminate immature *Tornoceras* occur in the pyrite level at the base of the Geneseo Shale at Gorham as has already been mentioned. From the top of the Geneseo Shale at Hubbard's Quarry, Seneca County, Professor Wells has collected an *Epitornocerus* cf. *peracutum* which is 240 mm in diameter (C.U.M.L. 40105), the largest American tornoceratid seen. The true *E. peracutum* (Hall) came from the Sherburne or Lower Ithaca member in the Cayuga Lake area, and a specimen determinable as *E.* aff. *peracutum* was figured by Harris (1899, pl. 6, fig. 35) from the Ithaca member.

* For list of abbreviations see p. 128.

Tornoceras is exceptionally abundant in the Genundewa Limestone. All specimens appear to be conspecific, and the somewhat inappropriate name *T. compressum* (Clarke) (here regarded as a subspecies of *T. uniangulare*) has priority for them. The genus also occurs in the West River Shale on Eighteen Mile Creek (C.U.P.L. 40104), but only a single immature specimen has been examined.

(*g*) *Sonyea group*

The main collection which has been studied is a barytized suite from the Cashaqua Shale made by Clarke from various localities, but probably only one horizon, between Shurtleff's Gully and Honeoye Lake. Professor Wells has investigated the horizon of this barytic fauna and informs the author that it lies about 6 ft. below the top of the formation at Shurtleff's Gully. Clarke gave the varietal name *obesum* to a tornoceratid from this level. Most of Clarke's specimens labelled as from the 'Naples group' probably belong to the Sonyea.

(*h*) *West Falls group*

The only occurrence of note in this formation is a specimen of *T.* (*L.*) aff. *linguum* (G. & F. Sandberger) from Gibson's Glen, Wyoming Co., probably from the Gardeau Flags. Further collecting would be desirable here.

(*i*) *Java group*

From the Hanover Shale comes the type specimen of *Aulatornoceras rhysum*, but few specimens of this species are known.

(*j*) *Canadaway group*

The type material of *Aulatornoceras bicostatum* is thought to have come from the Gowanda Shale and *T. concentricum* sp.nov. occurs at the same level together with *Cheiloceras amblylobum*, which is taken to indicate a correlation with the lowest European Famennian zone, that of *C. curvispina* (House 1962). This complete fauna is only known at Corell's Point on the shore of Lake Erie.

At the top of the Gowanda Shale, or from the Laona Siltstone or Westfield Shale at Forestville, New York, come the type-specimens of *Aulatornoceras clarkei* (Miller), formerly referred to *Manticoceras*.

No higher tornoceratids are known in New York State, and the only higher occurrences in the United States are those of the Three Forks Shale of Montana where *T. crebriseptum* occurs, which is to be correlated with some level within the Conewango group of New York.

(*k*) *Conneaut group*

From this group at Nile, Allegany Co. N.Y. comes the type specimen of '*T.*' *edwinhalli* Clarke (N.Y.S.M. 4090). The specimen is crushed and poorly preserved in a micaceous flaggy siltstone. The generic assignment is doubtful. It is almost certainly not a *Tornoceras* but could be a *Prolobites* or a worn *Cheiloceras*.

III. Material and techniques

(1) *Modes of occurrence*

In the America Devonian *Tornoceras* is commonest in shales and mudstones, rarer in limestones and exceptionally rare in siltstones and absent from coarser clastic rocks.

Most shales yield goniatites and they may be exceptionally abundant at certain levels, especially in dark to black shales where pelecypods, brachiopods and trilobites are uncommon. But in shales specimens are usually crushed and therefore more easily overlooked and less easily collected than from the rarer pyritic or marcasitic horizons. Mudstones and concretions are commonly barren but certain horizons in the Cashaqua and Hanover Shales are very rich in them.

The more argillaceous limestones, such as the Tully or Cherry Valley Limestones, commonly provide goniatites. But marly limestones rich in corals and brachiopods rarely yield them, and few are known from the major limestone marker beds such as the Centerfield and Stafford Limestones. They can be exceptionally abundant, however, in limestones rich in *Styliolina*, as, for example, the Genundewa and Squaw Bay Limestones.

(2) *Modes of preservation*

Specimens may be preserved in several different ways and this has provided a significant problem in this study and, will always be a problem in determining specimens. It is therefore useful to summarize the preservation types, and the limits of information which may be gleaned from each.

(*a*) *Crushed flat on shale bedding plane*

In these cases the growth lines and ornament are well preserved but as the suture lines, if seen, are usually distorted, it is rarely possible to elucidate ontogenies or shell form.

(*b*) *Uncrushed specimens in mudstones or limestones*

These preserve shell form and surface ornament and, when exfoliated, sutures can be traced. It is usually very difficult to break specimens down to study the protoconch and particularly difficult to trace sutures at the early diameters, for they are usually concealed by recrystallized shell.

(*c*) *Uncrushed specimens with shell replaced by barytes* (*Cashaqua Shale fauna*)

By treatment with 15% dilute acetic acid fragile specimens may be obtained showing exquisite details of the shell and especially the wrinkle layer (figure 72, plate 8). But sutures are rarely visible and specimens cannot be broken down to show sutural ontogeny although all growth series may be represented in the residues. Further, all dimensions refer to the outside of the shell.

(*d*) *Uncrushed specimens preserved as internal moulds in iron pyrites, marcasite or haematite*

These have formed the main basis for this study since specimens can be readily broken down to show the early ontogeny. But only inner shell features are seen on the moulds and the outer shell ornament and wrinkle layer structures are not preserved. Dimensions refer to the inner shell surface only. Commonly the protoconch and part of the subsequent whorl is preserved in calcite. Hence it is not safe to use acids to facilitate breakdown of specimens.

(3) *Techniques*

Sutures of larger specimens have been prepared by tracing with indian ink on a 'Sellotape' or 'Scotch tape' peel on which a median radial line has been drawn through the suture being copied. This method is too inaccurate for specimens less than about 30 mm in diameter. For all smaller diameters an eyepiece micrometer grid mounted in a binocular microscope with a turret of objectives has been used. Whenever possible a radial whorl section has first been prepared by copying the sections seen on the grid directly on to graph paper. This is best done when a complete septum is exposed. This serves to give an accurate perimeter for the projection of the suture and the position of the umbilical seam, and distinctive marks on the specimen may be marked on it. In the final stages the proportions may be checked by independent resections of parts of the suture.

Early stages have been extracted by mechanical breakdown using vice clamps, small hammers and needles sharpened to chisel edge. For the innermost whorls it is necessary for fractures to be made whilst the specimen is viewed through a binocular microscope, and the specimens were set in Plasticine to avoid loss of splinters. Measurements have been made using a corrected eyepiece micrometer for small specimens and vernier calipers for larger specimens. Specimens have been prepared for photography with a sublimate of ammonium chloride.

IV. The early stages of *Tornoceras*

Study of the earliest stages of *Tornoceras* have led to general conclusions on the early stages of ammonoids which will be first considered. In the systematic section which follows references to the form of the earliest stages will draw attention to the distinctive features of particular species and subspecies.

(*a*) *The protoconch and nepionic whorl*

The larval or nepionic stage of *Tornoceras* comprises the protoconch and rather more than the first whorl. The end of this stage is marked by a constriction and a sudden change in the growth-line pattern. These may be taken to mark the close of the nepionic stage and the onset of adolescence.

The protoconch of American specimens of *Tornoceras* ranges in size from 0·75 to 1·1 mm in maximum diameter, and from 0·7 to 1·2 mm in maximum width. The form varies from subglobular to barrel-shaped. The first whorl arises from the protoconch from a crescentic or reniform proseptal area and the first whorl is tightly wrapped about the protoconch forming an imperforate umbilicus but with only a slight degree of involution. The protoconch is separated from the first whorl, or larval body chamber, by the apicadly concave proseptum. The proseptum differs fundamentally in form from the first true septum and later septa in that the ventral prosuture is rectilinear, or nearly so, and the dorsal prosuture forms a broad, shallow saddle. Neither of these features recurs subsequently. Through the proseptum passes the siphuncle, and it may lie close to the ventral margin, in which case a deep siphuncular lobe is formed; or it may lie as much as one-third the way across the proseptum, in which case the ventral prosuture is little disturbed.

Evidence of the structures within the protoconch have been observed in some specimens, especially those used by Beecher, and the reconstruction given here (figure 2 *A*) illustrates the protoconch apparatus. The siphon passes back from the proseptum into a balloon-like caecum and is attached to the opposite side of it, the point of attachment forming a marked indentation of the caecum. The caecum may lie closely against the ventral wall of the protoconch forming a caecal area or, more usually, scarcely touch the protoconch wall at all. A small prosiphon has been observed to pass towards the caecum from the mid-line of the protoconch wall opposite the proseptum. No trace of a cicatrix has been seen in any protoconch.

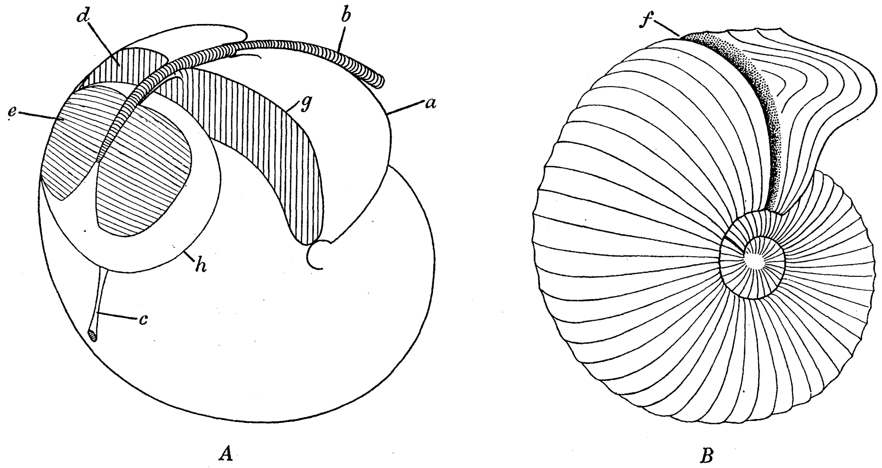

FIGURE 2. Diagrams illustrating the early stages of *Tornoceras*. *A*, the protoconch and first chamber drawn in oblique view showing the protoconch apparatus (approximately × 50). *B*, the nepionic whorl, showing the nepionic constriction and the sudden commencement of the adult-type growth lines. Drawn in oblique view (approximately × 25). Abbreviations: *a*, the first suture; *b*, siphon; *c*, prosiphon; *d*, proseptum; *e*, caecal area; *f*, nepionic constriction; *g*, prosuture, *h*, caecum.

The shell surface of the protoconch and first whorl is ornamented by convex evenly spaced raised lirae (figure 2*B*). At a little over one complete whorl from the protoconch is the nepionic constriction. This constriction is formed by a thickening of the shell, and is most readily discerned on the inner surface of the shell, but it may form a shallow groove on the outside of the shell. At the constriction, or perhaps a little later, the pattern of the growth lines change markedly (figure 2*B*) and the convex lirae give place to biconvex lirae which show a prominent ventro-lateral salient and a deeper, narrower ventral sinus: this pattern continues through adolescence to the adult with only little modification.

It seems probable that the formation of the nepionic constriction and the formation of the proseptum coincided, for the constriction precedes the onset of the adolescent growth pattern, and the proseptum is followed by true septa which differ fundamentally from it. This would allow for a nepionic body chamber of about one whorl in length, and this length is found in *Tornoceras* at all later stages of ontogeny. In younger Palaeozoic and Mesozoic Ammonoidea several writers have claimed that the prosepta may be distinguished from the true septa since they are continuous in structure with the material of the shell wall, whereas true septa are cemented to the shell wall (Miller & Unklesbay 1943;

Grandjean 1910; Arkell *in* Moore 1957), but it has not been possible to demonstrate this in *Tornoceras*. In *Tornoceras* there seem to be serious grounds for believing this could not be the case, for it would imply that the protoconch wall and proseptum were either laid down externally or from a structure left within the protoconch, both hypotheses which seem improbable. Further, the ornament on the protoconch itself (figure 94, plate 10) is identical with that on the first whorl and the later pattern, and hence was formed by shell secreting glands of similar type.

The significance and function of the protoconch apparatus may now be considered. Caecal and prosiphonal structures have been described for numerous post-Devonian ammonoids, for example from the Carboniferous (Schindewolf 1939), Permian (Böhmers 1936; Bogoslovskaya 1959), Jurassic and Cretaceous (Grandjean 1910) and most authors have commented on the similarity with the living *Spirula* (Munier-Chalmas 1873). The structures in the Alden Marcasite specimens of *Tornoceras* show distinctive characters in four respects. First, the caecum is somewhat larger and more inflated. Second, the siphon can be demonstrated to pass through the caecum and to meet an invagination of the caecal wall. Third, the caecum in some instances forms a caecal area against the wall of the protoconch, but usually this does not occur. Finally, it is clear from the foregoing that at least in some specimens of *Tornoceras* the caecum is not merely a swollen termination of the siphuncle (Schindewolf 1933) but a distinct structure. Attention should be drawn, however, to more typical protoconch structures in *Tornoceras* figured by Bogoslovski (in Orlov 1962, pl. 2, figs. 1, 2).

As the prosiphon is attached to the protoconch wall and the shape of the caecum may be modified to form a flattened area against the protoconch wall it is clear that the protoconch apparatus was formed after the wall of the protoconch and, as has already been pointed out, the apparatus must have preceded the formation of the proseptum. It has been shown that at the time of formation of the proseptum the body chamber probably extended to a little over one whorl beyond the protoconch and that its formation is marked by an apertural constriction. It is to be inferred, therefore, that the pause in growth probably represented by these changes marks also a change in the body organization. Whereas in the adolescent and mature stages a septum is always present in the posterior part of the body chamber, in the early nepionic stage this would not be so. It may be suggested that the protoconch apparatus partly served the function of anchoring the soft parts to the protoconch before septa were introduced and before the usual aponeurotic attachment was established. With the formation of the proseptum and subsequent septa a different mode of body anchorage was achieved. Blake (*in* Tate & Blake 1876, p. 263) suggested that pressure during septal growth may be responsible for the forward projection of the sutural elements in ammonites, and this has been invoked to explain the forward projection of the proseptum in latisellate and angustisellate protoconchs. But there is no such projection in the proseptum of *Tornoceras*; indeed, in some species a slight mid-ventral lobe is formed. Nevertheless, a similar tension to that envisaged by Blake may be responsible for the observed caecal invagination. Following recent work on septal formation in *Nautilus*, however, an absorptive function after proseptal deposition is a possible purpose for the caecum.

Swinnerton & Trueman (1918, p. 50) have suggested that a change of the ammonoid akin to metamorphism may take place between the formation of the proseptum and the first true septum. In *Tornoceras* it would appear that a greater change occurs between the earliest state with caecal attachment and the later aponeurotic form of attachment. The differences seen between proseptum and later septa may be interpreted as a reflexion of the transitionary nature of prosepta. From the viewpoint of terminology it is convenient to follow earlier usage and take the formation of the proseptum as marking the end of the larval stage. There is no support for Ruzhencev's claim (1960, p. 614) that the first septum and prosuture were formed within the egg capsule, but probably hatching occurred after the constriction was formed.

Accompanying the probable body change at the end of the larval stage is the change from convex to biconvex growth lines. The ventral sinus in the growth lines of ammonoids is usually taken to indicate the position of the hyponome. The fact that a sinus in this position is not present in the nepionic stage suggests that in *Tornoceras* the hyponome may have been rudimentary or absent in the earliest stages. Since the hyponome acts as a major propulsive mechanism in living cephalopods this suggests that larval goniatites were passively planktonic (probably within the egg capsule) and that active nektonic or benthonic existence followed the 'metamorphism' already described. These conclusions support those made from different premises by Deitz (1922).

V. Systematic descriptions

Suborder GONIATITINA Hyatt, 1884

Superfamily Cheilocerataceae Frech, 1897

Family Tornoceratidae Athaber, 1911

(1) Genus **Parodiceras** Hyatt, 1884

Type-species by the original designation of Hyatt (1884, p. 320) *Goniatites discoideus* Hall. This genus was omitted from the recent Treatise (Miller & Furnish *in* Moore 1957), but had previously been regarded as a subgenus of *Tornoceras* (Miller 1938, p. 140 *et seq.*; Glenister 1958, p. 89). Recently Petter (1959, p. 223) has proposed the family Parodiceratidae to include *Parodiceras*, claiming that the genus is very distinct from *Tornoceras*. The present study has shown that *Parodiceras* can be regarded, as its name implies, as an intermediate form linking *Tornoceras* with ancestral anarcestids. *Parodiceras* shows the distinctive wrinkle-layer pattern which is characteristic of *Tornoceras*. In view of the primitive form of the genus it seems advisable to regard it as generically distinct from *Tornoceras*, but separation at a higher taxonomic level would be unwarranted.

(*a*) ***Parodiceras discoideum*** (Hall), figures 29, 30, 34, plate 5; figure 46, plate 6; figure 3*A*, *B*.

Goniatites discoideus Hall (1860, pp. 97–98, text-figs. 3–5 not text-fig. 6).

G. discoideus Hall (1876, pl. 71, figs. 4–6, 8, 9 not figs. 1–3, 7, 10–13; pl. 74, fig. 3 not fig. 4).

G. discoideus Hall (1879, pl. 71, figs. 4–6, 8, 9 not figs. 1–3, 7, 10–13; pl. 74, fig. 3 not fig. 4).

Tornoceras (*Parodiceras*) *discoideum* Miller (1938, p. 144, pl. 32, figs. 11–16).

Miller (*supra cit.*) has given a redescription of the original types which need not be repeated here. More detailed dimensions of the paratypes are as follows:

	D (mm)	*WW* (mm)	*WH* (mm)	*UW* (mm)	*BC* (°)	*Wh* (mm)
N.Y.S.M. 4055(= 12440/2) figured Hall (1879), pl. 71, fig. 4; pl. 74, fig. 3), the holotype	24·0	11·2	13·8	0	—	—
N.Y.S.M. 4057 figured Hall (1879, pl. 71, figs. 8, 9)	45·4	16·8	27·0	0	300+	—
N.Y.S.M. 4056 figured Hall (1879, pl. 71, figs. 5, 6)	23·4	10·8	14·3	0	360+	7·5

Remarks

The published figures suggest that the sutural elements became more subdued in the adult (see Hall's figures of N.Y.S.M. 4055 and 4057) although the lateral lobe is shallow even in the early stage. But the ventral portion of N.Y.S.M. 4056 as illustrated by Hall is a complete reconstruction. Associated with the true *P. discoideum* in the Cherry Valley Limestone are some specimens with a well-developed lateral lobe even at early diameters. A specimen in the Peabody Museum (figure 3*C*) at 11 mm diameter has a much more prominent lateral lobe than the holotype of *P. discoideum* has at 17 mm diameter (figure 3*B*), and juveniles of similar type are in the C.U.P.L. This form may be specifically distinct and it heralds the *Tornoceras mesopleuron* group which occurs higher in the succession.

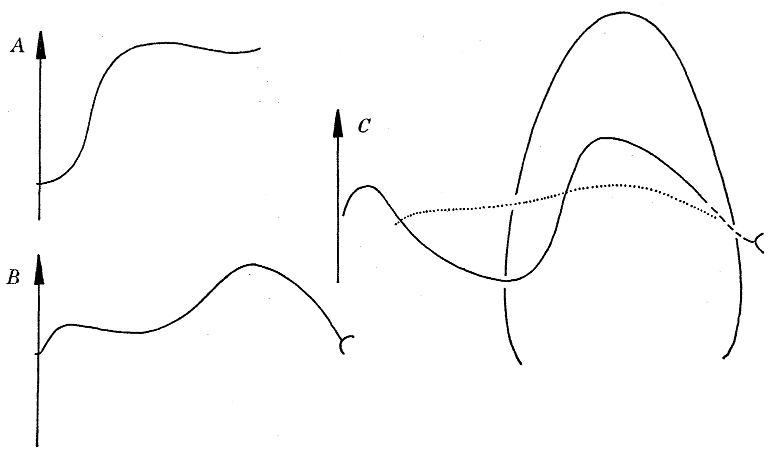

FIGURE 3. Diagrams of tornoceratids from the Cherry Valley Limestone. *A*, *B*. The holotype of *Parodiceras discoideum* (Hall). *A*, growth line at 22 mm diameter. *B*, suture at *ca.* 17 mm diameter. Both N.Y.S.M. 4055 (× 3·3). *C*, *Tornoceras* (*T.*) aff. *mesopleuron* House sp.nov., whorl section, suture and growth line at 11 mm diameter; P.M.Y. 23855 (× 6·7).

The growth lines never form a prominent ventro-lateral salient, but slope gently and concavely back across the outer flanks. Certain lines are more prominent and are raised as lirae (figure 34, plate 5).

Specimens and locality

Limited to the Cherry Valley Limestone. As Miller (1938, p. 147) has pointed out, most of the widespread determinations of this species are incorrect, and refer to

Tornoceras s.s. All specimens are from the Cherry Valley region of Otsego Co., N.Y., and westward to the vicinity of Manlius, Onondaga Co. Specimens examined include N.Y.S.M. 4055–7, P.M.Y. 23855 (referred to *T.* aff. *mesopleuron*) and C.U.P.L. 40123 (three specimens).

(2) Genus *Tornoceras* Hyatt, 1884

Type-species by the original designation of Hyatt (1884, p. 321) is *Goniatites uniangularis* Conrad. This genus has usually been widely interpreted (Miller 1938, pp. 143, 144; Glenister 1958, pp. 89, 90) and *Aulatornoceras* and *Protornoceras* have been regarded as subgenera. Here they are regarded as distinct genera, and *Tornoceras* is restricted to two subgenera, *Tornoceras* s.s. and *Linguatornoceras* subgen.nov. Thus limited the genus ranges from the lowest Givetian to the Famennian *Platyclymenia* Stufe (Schindewolf 1923, p. 367; Müller 1956, p. 48) in Europe. In America the range appears to be identical.

Linguatornoceras subgen.nov. is here proposed with *Goniatites retrorsus* var. *lingua* (G. & F. Sandberger 1852, p. 109, pl. 10, fig. 20.) from Büdesheim as type-species. The subgenus includes those tornoceratids characteristic of the mid-Frasnian to lowest Famennian which have small, tongue-shaped lateral lobes and flat-topped ventro-lateral saddles. There are several undescribed species. *Tornoceras haugi* Frech (1902, p. 47, pl. 3 (2), fig. 20) also belongs here.

Attention may be drawn to the work of Makowski (1962) who gives evidence that lower Famennian forms of *Tornoceras* are dimorphic, the macroconch reaching about twice the size of the microconch but showing little other difference. Work on the American forms does not confirm or deny this hypothesis and few sections have been cut along the plane of coiling to elucidate the number of whorls, a factor which Makowski finds most important. Certainly, if the large specimens which occur in faunas in which most specimens are generally small do represent macroconchs, then in both *T. arkonense* and *T. uniangulare aldenense* the microconchs outnumber the macroconchs by a factor of between 10 and 20.

(*b*) *Tornoceras* (*Tornoceras*) *arkonense* sp.nov., figures 28, 35, plate 5; figure 4*A* to *P*.

Material

Fifty-three internal pyritic moulds from the Arkona Shale of southern Ontario. Holotype selected as M.M.P. 38500. Due to the great possibility of contamination at the most celebrated localities, Hill no. 4, Rock Glen and Hungry Hollow, great care has been taken in the selection of material for this study. The description which follows would have been impossible were it not for the generous efforts of Dr G. M. Ehlers who spent several days searching for material from localities where contamination from the Widder Shale is highly improbable.

Description

	dimensions		
specimen	*D* (mm)	*WW* (mm)	*WH* (mm)
M.M.P. 38500 (holotype)	18·4	7·3	10·0
M.M.P. 38470 (paratype)	8·4	4·4	5·0

Protconch sub-barrel shaped, transversly elongate and oblate in lateral view (figure 4*J* to *L*). Transverse width 0·82 mm (M.M.P. 38477) to 0·85 mm (M.M.P. 38486), maximum diameter 0·8 mm (M.M.P. 38485). Proseptum adorally concave, composed of two areas almost at right angles, the outer (ventral) with siphuncle opening 0·1 mm from the venter, about one-quarter of way across the outer area: the inner area (dorsal) crescentic and forming a shallow groove. The width and height of the first whorl increase slowly from the protoconch. At 1·3 mm diameter (about three-quarters of a whorl) the width is 1·0 mm (WW/WH = 200% in M.M.P. 38486), the whorl section is crescentic with rounded umbilical shoulders; the umbilicus is open and imperforate. The relative changes in the subsequent shell proportions are shown on the accompanying diagram (figure 17*A*).

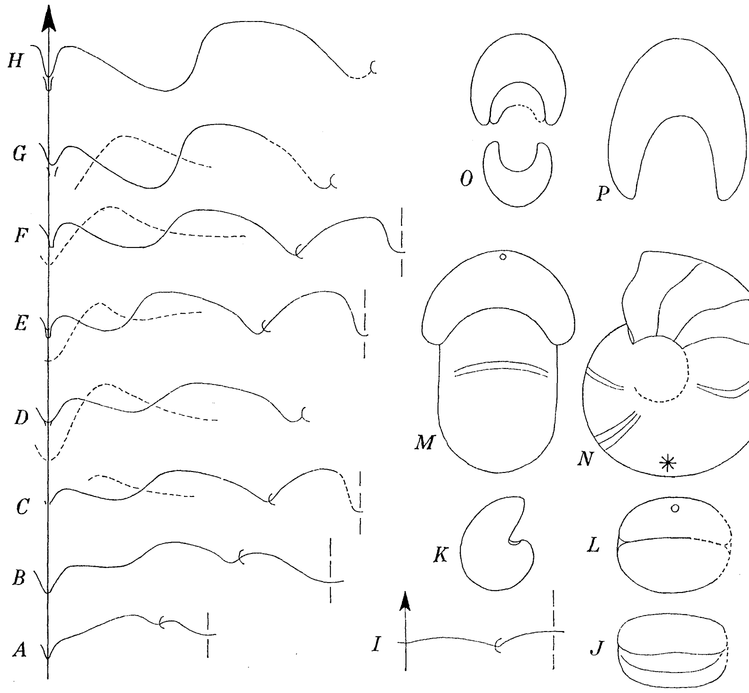

FIGURE 4. Diagrams illustrating the ontogeny of *Tornoceras* (*T.*) *arkonense* House sp.nov. from the Arkona Shale of southern Ontario. *A*, suture at 1·3 mm diameter; M.M.P. 38486 (× 16·7). *B*, suture at 2·25 mm diameter; M.M.P. 38486 (× 16·3). *C*, suture and growth line at 4·8 mm diameter; M.M.P. 38474 (× 8·3). *D*, suture and growth line at 5·6 mm diameter; M.M.P. 38473 (× 8·3). *E*, suture and growth line at 8·4 mm diameter; M.M.P. 38470 (× 4·2). *F*, suture and growth line at 11·2 mm diameter; M.M.P. 38502 (× 4). *G*, suture and growth line at 19·9 mm diameter; M.M.P. 38500 (× 2·7), reversed for comparison. *H*, suture at 29 mm diameter; M.M.P. 38498 (× 2). *I* to *L*, prosuture and protoconch; M.M.P. 38485 (× 16·3). *M*, *N* early whorls at 2·2 mm diameter based on M.M.P. 38477, showing the form of the growth lines before and after the nepionic constriction (the site of which is marked with an asterisk) (× 13·6). *O*, median section through the early whorls at 5·5 mm diameter; M.M.P. 38476 (× 4). *P*, whorl section at 8·4 mm diameter; M.M.P. 38470 (× 4·2).

No trace of ornament has been seen on the internal moulds of the protoconch. By 1·5 mm diameter, growth lines take the form of convex lirae (figure 4*H*, *I*) which pass convexly back across the flanks to form a very broad and shallow sinus on the venter. These have a frequency of five per 0·5 mm on the venter at 1·3 mm diameter. At 1·5 mm diameter (on M.M.P. 38477) biconvex growth lines suddenly appear accompanied by traces of a slight radial constriction. Thereafter growth lines form biconvex lirae, with a V-shaped ventral sinus (figure 4*D* to *G*), a protecting ventro-lateral salient passing convexly backward to the umbilical seam. This pattern continues to the outer whorls. Later whorls also show weakly developed spiral striae on the internal moulds.

The prosuture has only been well seen in one specimen (M.M.P. 38485, figure 4*I*), in which it appears to form a shallow lobe. On the lateral areas there is a very shallow saddle and the true lateral lobe centres on the umbilical seam. The development of the sutures is illustrated in the accompanying diagrams (figure 4*A* to *H*). The adventitious lobe is formed between 1·3 and 2·0 mm diameter. The ventral lobe, which remains V-shaped throughout ontogeny, is very narrow at the largest diameters seen (29 mm in M.M.P. 38498, figure 4*H*). Arching of the latero-umbilical saddle develops slowly and the ventrad face only starts to become significantly steep above 15 mm diameter. Septal frequency shows considerable variation as the following figures indicate:

specimen	*D* (mm)	septal frequency
M.M.P. 38474	4·8	16
M.M.P. 38473	5·6	17
M.M.P. 38490	5·8	9
M.M.P. 38484	6·3	12
M.M.P. 38470	8·4	15
M.M.P. 38471	8·5	14
M.M.P. 38502	11·2	14
M.M.P. 38503	20·4	17

Slight displacement of the ventral lobe is not uncommon (figure 4*F*, *G*).

Remarks

This species can also be distinguished among specimens from the Plum Brook Shale of north western Ohio, the Silica Shale of northern Ohio and the Pompey Shale of New York. A specimen has been figured as *Tornoceras uniangulare* by Stumm (1942, pl. 81, fig. 46) from the Plum Brook Shale at Plum Brook, 2 miles N.E. of Point Station. This specimen (O.C. 6072) has a diameter of 17·3 mm and the last whorl has sixteen septa (these details are taken from the published figure). The figure agrees with specimens from the Arkona Shale in the moderate steepness of the ventrad face of the umbilico-lateral saddle and the relatively few camerae per whorl.

Specimens of *Tornoceras* from the Silica Shale fall into two groups, one of which is comparable with *T. arkonense*. Typical dimensions are:

specimen	*D* (mm)	*WW* (mm)	*WH* (mm)	*S* (mm)
U.S.N.M. 137685	13·6	5·9	8·1	9
U.S.N.M. 137686	15·7	—	—	?12

These specimens show both the moderate slope of the ventrad face of the umbilico-lateral saddle and also the relative infrequency of the septa which is typical of *T. uniangulare arkonense*. Both these specimens are from the Silica Shale of a quarry 2½ miles S.W. of Sylvania, Ohio. One specimen from the Skaneateles Formation of New York (U.S.N.M. 137720) from the Pompey Shales at Delphi Falls belongs to this species, and a specimen showing growth lines from Pratt's Falls (C.U.P.L. 40013, figure 27, plate 5) may belong here.

These records confirm the correlation of the Arkona Shale with the Silica Shale, Plum Brook Shale and Skaneateles Formation as given by Cooper (1942).

Comparison

Comparison with the tornoceratids of the *uniangulare* group found above the Centerfield equivalents will be given after the description of *T. uniangulare widderi*.

Specimens and locality

All specimens come from the Arkona district of southern Ontario and are from the Arkona Shale with the possible exception of M.M.P. 38502, 3, from a horizon well below the Hungry Hollow Limestone. Specimens include M.M.P. 38470–38486 and 38487 (nine specimens) from a locality just downstream of a broken dam on the east side of the Ausable River, $\frac{1}{8}$ mile S. of the junction of Rock Glen and the Ausable River, $1\frac{1}{4}$ miles N.E. of Arkona, Ontario: M.M.P. 38488–38490 from the same locality collected by Dr I. G. Reinmann: M.M.P. 38496–38498 and 38499 (five specimens) from the same locality collected by Mr and Mrs E. P. Wright: U.S.N.M. 137706–137713 from the same locality: M.M.P. 38500 (two specimens) and 38501 from a locality on the banks of the Ausable River near Hill no. 4, and $\frac{1}{3}$ mile downstream from the mouth of Hill no. 4 Creek and about $2\frac{1}{3}$ miles N. and $\frac{3}{4}$ mile E. of Arkona, collected by Dr and Mrs Ehlers and Mr and Mrs Wright. These localities near river level lie about 19 to 20 ft. or more below the Hungry Hollow Limestone. At Rock Glen the level of the Ausable River is 39 ft. below the Hungry Hollow Limestone (Stauffer 1915). Also M.M.P. 38502, 3 from the Tileyard about $1\frac{1}{2}$ mile N. of Thedford, Ontario, collected by Mr C. Southworth.

(*c*) ***Tornoceras* (*Tornoceras*) *mesopleuron*** sp.nov. Flower MS., figures, 32, 33, plate 5; figure 5*A*, *B*, *D*.

Material

Seven specimens from the Thedford region of Ontario. Although better specimens are known, the manuscript holotype of Flower is retained (M.M.P. 38504).

Description

specimen	dimensions *D* (mm)	*WH* (mm)	*WH* (mm)	*UW* (mm)	*Wh* (mm)	*S* (mm)
M.M.P. 38504 (holotype)	—	14·0	26·0	—	*ca.* 5·0	—
	—	20·0	*ca.* 30·0	—	—	—
M.M.P. 38504	44·8	15·9	26·8	*ca.* 0	—	13($\frac{1}{2}$)
M.M.P. 34466	45·3	16·4	26·8	*ca.* 1·0	—	*ca.* 23
U.S.N.M. 137714	28·3	*ca.* 11·6	17·6	—	—	10($\frac{1}{2}$)

Shell form involute, laterally compressed in adult with umbilicus closed or nearly so. Whorl section (figure 5*A*) compressed with maximum width close to the umbilical shoulder and flanks sloping flatly to the well-rounded venter. Complete body chamber not seen. Several specimens show orad approximation of the septa at about 40 to 46 mm diameter.

Surface growth lines not seen. One specimen shows dorsal wrinkle layer striae sloping spirally back from the umbilicus across the flanks at a low angle as typical for the genus (M.M.P. 38504).

Ventral lobe narrowly V-shaped (figure 5*B*, *D*) with rounded ventro-lateral saddle and asymmetric lateral lobe. Latero-umbilical saddle distinctive and highly arched with steeper ventral face. Dorsal suture not seen. Septa typically close together, numbering about 20 to 26 per whorl.

Remarks

This species is distinguished by the highly arched and characteristic latero-umbilical saddle, the flatter flanks and greater sutural frequency from species occurring in the lower Arkona Shale and the Widder Shale above.

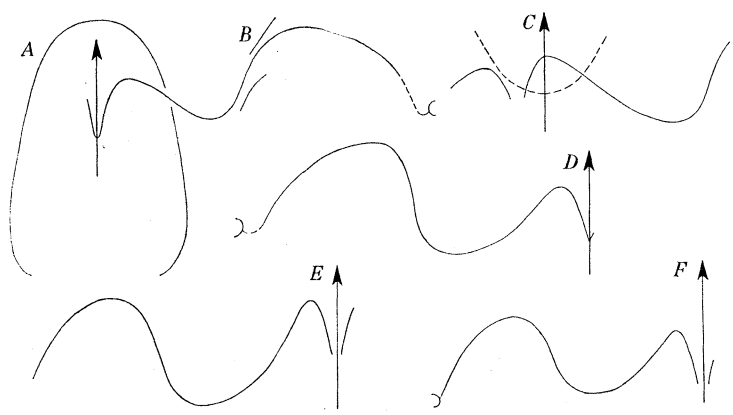

FIGURE 5. Suture diagrams of *Tornoceras* (*T.*) *mesopleuron* House sp.nov. and related goniatites. *A*, *B*, *D*, *T.* (*T.*) *mesopleuron* sp.nov. *A*, *B*, suture and whorl section based on the holotype, in the collection of Professor R. Flower (× 1·3). *D*, suture at 25 mm diameter based on U.S.N.M. 137684 (× 3·3). *C*, *E*, *F*, *T.* (*T.*) aff. *mesopleuron* sp.nov. *C*, suture and growth line in the ventral region at 23·5 mm diameter. U.S.N.M. 137717 (× 2·7). *E*, suture at 21 mm diameter. U.S.N.M. 137718 (× 2·7). *F*, suture at 21 mm diameter. U.S.N.M. 137719 (× 2·7).

The figured specimen (figure 33, plate 5) is encrusted with a bryozoan which Dr Helen Duncan has kindly determined as a *Hederella* of the group of *H. canadensis* (Nicholson) and closest to *H. parvirugosa* Bassler. This encrustation is seen on many specimens from the type locality.

Certain specimens from the Silica Shale in a quarry 2½ miles S.W. of Sylvania, Ohio, show a resemblance to *T. mesopleuron* but differ in that the umbilico-lateral saddle is curiously arched (figure 5*C*, *E*, *F*; figure 24, plate 5). These forms are here referred to *T.* aff. *mesopleuron*. Sufficient material is not available to give a critical analysis of this form. Other specimens of *Tornoceras* found with them (U.S.N.M. 137715; figure 23, plate 5) show sutures comparable with *T. arkonense*, but the umbilico-lateral saddle is more flat-topped.

Specimens and locality

All specimens come from the Arkona Shale and probably from a horizon near the top, for Mrs E. P. Wright, who has collected many specimens, has informed the writer that it has been found 'perhaps 15 ft. below the Hungry Hollow formation' at the tileyard, ½ mile S. of Thedford, Ontario. This locality is the source of the holotype, M.M.P. 38504, also M.M.P. 34466, 33069 and U.S.N.M. 137684. Another specimen, in Dr Rousseau Flower's collection, is from Harrison's Field, Thedford. One specimen in the Stuart Perry collection, M.M.P. 161185, is labelled as from Thedford, Ontario only.

(*d*) ***Tornoceras* (*Tornoceras*) *amuletum*** sp.nov., figures 37 to 45, 47, 49, 50, plate 6; figures 6, 17*C*.

Material

Some thirty-five specimens collected by Professor J. W. Wells from a concretion layer in the upper part of the Ledyard Shale. Holotype selected as C.U.P.L. 40084 (figures 44, 45, plate 6).

Description

	dimensions			
	D (mm)	*WW* (mm)	*WH* (mm)	*UW* (mm)
C.U.P.L. 40088	35·6	12·2	19·5	0
	27·3	9·1	15·5	0
C.U.P.L. 40110	21·8	8·4	11·7	0
C.U.P.L. 40098	4·8	2·2	2·0	*ca.* 0·8
	2·9	1·6	1·33	—

The earliest whorls and protoconch have not been seen. Whorl height equals whorl width at about 5 mm diameter where the whorl section is rotund. At higher diameters the flanks gradually tend to flatten and converge towards a well-rounded venter. The relative change in the proportions of the whorl section is illustrated in figure 17*C*. Ribbing is developed in the early whorls. By 3 mm diameter flat nodes occur on the lower lateral flanks at the position of maximum whorl width. These become more prominent in the next two whorls and gradually form ribs which pass from the umbilical shoulder to the ventro-lateral where they disappear; they follow a subradial course with a slight lateral concavity. At 7·5 mm diameter there are eleven ribs in the preceding whorl. By 11 mm diameter the relative strength of the ribbing decreases and the ribs, after crossing the umbilical shoulder almost radially, are retracted across the lower flanks and fade away towards the venter. Their course precisely follows that of the growth lines. Over the venter the periodicity of the ribbing is emphasized by a strengthening of certain growth lines. At 11 mm diameter there are eight or nine umbilico-lateral ribs in the preceding half-whorl. By 15 mm diameter the ribbing has disappeared. Growth lines at 3 mm diameter pass almost radially across the flanks but with a shallow lateral sinus, and form a projecting ventro-lateral salient and a tongue-shaped ventral sinus. At this diameter the growth lines take the form of raised lirae which number 10 in 0·5 mm on the venter. The lirae are individually beaded along their length when seen from the outside of the shell. At 10 mm diameter the growth lines form a slight umbilico-lateral salient and a shallow lateral sinus, and then project forward to a subacute ventro-lateral salient and back to a deep, V-shaped ventral sinus. By 17 mm diameter the umbilico-lateral salient is more prominent and the whorl course of the growth-line is retracted. At greater diameters the backward deflexion becomes more prominent and at least by 34 mm diameter the ventro-lateral salient is wide and shallow.

Some large specimens show wrinkle-layer striae particularly well laid down on the outer surface of the shell. They follow the typical *Tornoceras* pattern and consist of fine raised lines, anastomosing and not infrequently discontinuous, with a frequency of 5 or 6 per mm in the mid-flanks at 38 mm diameter, and they are rather more closely packed on the umbilical slopes.

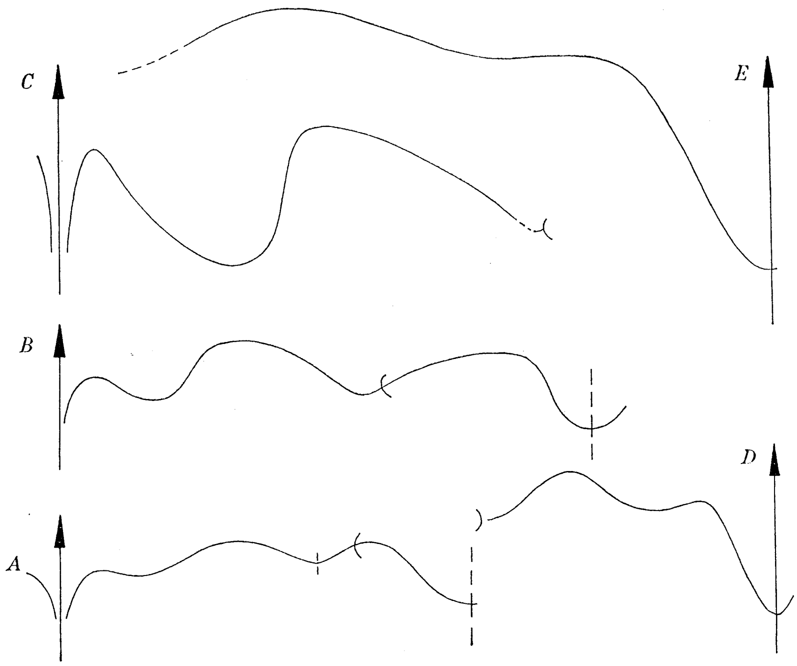

FIGURE 6. Diagrams showing the ontogeny of the suture and growth lines of *Tornoceras* (*T.*) *amuletum* sp.nov. from the Ledyard Shale at Sheldrake, Cayuga Lake, N.Y. *A*, suture at 2·9 mm diameter; C.U.P.L. 40098 (× 20). *B*, suture at 7 mm diameter; C.U.P.L. 40091 (× 10). *C*, suture at 30 mm diameter; C.U.P.L. 40090 (× 3·3). *D*, growth line at 17 mm diameter; C.U.P.L. 40086 (× 3·3). *E*, growth line of C.U.P.L. 40086 (× 3·3), reversed for comparison.

Early sutures have not been seen. By 2·9 mm the lateral lobe has formed (figure 6*A*) and progressively the ventro-lateral saddle becomes more angular, and the lateral lobe deeply wide, asymmetric and rounded (figure 6*C*). The ventrad face of the latero-umbilical saddle in the adult is steep, and sharply folded over at its crest to slope gently down to the umbilical seam. The dorsal suture has not been seen throughout ontogeny, but even at 7 mm diameter the fold at the crest of the latero-umbilical saddle is reflected in a similar fold at the crest of the umbilico-dorsal saddle. The dorsal lobe widely diverges.

Remarks

This extremely distinctive species is diagnosed by the ribbing on the early whorls and by their curious backward deflexion on the mid-flanks. From a rather higher horizon in the King Ferry Shale at Portland Point is a crushed specimen (figure 25, plate 6) showing the aperture particularly well. This shows the prominence of the lower lateral salient seen in *T. amuletum* (compare with figure 50, plate 6), but since the inner whorls of this specimen have not been seen it can only be referred with doubt to that species.

Specimens and locality

All specimens are from concretions in the upper part of the Ledyard Shale a few feet below the overlying King Ferry Shale just north of Lucky Stone Lodge (to which the specific appelation applies) at Sheldrake Point, Cayuga Lake, and all were collected by Professor J. W. Wells and are in his collection at Cornell.

(*e*) ***Tornoceras (Tornoceras) uniangulare widderi*** subsp.nov., figures 26, 31, 36, plate 5; figures 7*A* to *M*, 17*B*.

Material

Seventy-three specimens from the lower Widder Shale of the Arkona–Thedford region of Ontario. All are pyritic internal moulds. Holotype selected as U.S.N.M. 137701.

Description

	dimensions				
specimen	*D* (mm)	*WW* (mm)	*WH* (mm)	*UW* (mm)	*Wh* (mm)
D. 1557	2·3	1·2	1·05	—	—
	4·3	1·6	1·4	—	—
	6·0	2·8	3·25	—	—
M.M.P. 38509	7·1	2·9	4·5	—	—
M.M.P. 38466	8·7	3·8	4·6	0·3	—
U.S.N.M. 137702	9·6	4·1	5·0	0·6	—
M.M.P. 38467	11·5	5·5	7·0	—	3·8
M.M.P. 38465	16·1	*ca.* 6·5	9·5	*ca.* 1·0	5·0
U.S.N.M. 137701 (holotype)	31	—	—	—	11·5
	21	9·3	*ca.* 11·2	—	—

The protoconch is sub-barrel shaped with a rounded outline and transversely elongate. Transverse width 0·93 (D. 1557) to 0·95 (D. 1559), in the latter case with a slight angular displacement of the axis relative to the later whorls. The whorl width decreases slightly at first away from the protoconch (D. 1557) with the whorl width crescentic at the first half-whorl. The relative whorl height has increased significantly by the end of the first whorl which has a diameter of about 1·5 mm. The umbilicus is still open. Whorl height equals whorl width at between 4 and 6 mm diameter. By these diameters the umbilicus has commenced to close, and testate specimens probably would have closed umbilici at these and higher diameters. Later features of the shell form are illustrated in figures 7, 17.

The ornament of the protoconch has not been seen. On the early whorls convex lirae have been observed up to 1·5 mm in diameter. They are subradial but pass slightly back across the flanks to form a shallow sinus on the venter. Lirae number four in 0·14 mm on the venter at this stage (*D*. 1554). A subradial constriction is seen at about 1·5 mm diameter on this specimen, and convex lirae extend for a short distance beyond the constriction. The change to the adult pattern of growth lines occurs shortly after. Evidence on the course of the growth lines at greater diameters is given in figures 7*D*, *F*. Some evidence of weak spiral lines has been seen on the moulds.

The prosuture has not been clearly seen. The first suture (figure 7*A*) shows a highly arched ventro-lateral saddle and broadly V-shaped ventral lobe. By 2·0 mm the saddle has flattened and a lobe formed upon it (figures 7*B* to *D*). The subsequent sutural ontogeny is illustrated in figures 7*E* to *H*, *K*. Noteworthy is the early steepness of the ventral face of the umbilico-lateral saddle which approaches concentricity with the umbilicus at the

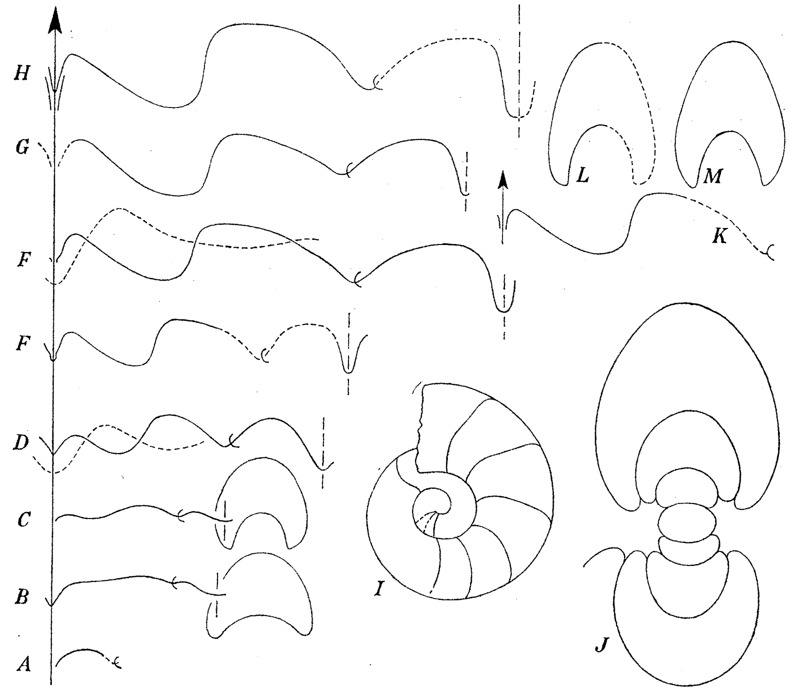

FIGURE 7. Diagrams illustrating the ontogeny of *Tornoceras* (*T.*) *uniangulare widderi* subsp.nov. from the Widder Shale of southern Ontario. *A*, the first suture; D. 1553 (×13). *B*, suture and whorl section at 2·2 mm diameter; D. 1553 (×12·3). *C*, suture and whorl section at 3·9 mm diameter; D. 1553 (×6). *D*, suture and growth line at 5·4 mm diameter; D. 1552 (×6), reversed for comparison. *E*, suture at 8·7 mm diameter; M.M.P. 38466 (×4·3). *F*, suture and growth line at 13·3 mm diameter; D. 1550 (×4). *G*, suture at 16·1 mm diameter; M.M.P. 38465 (×3·3). *H*, suture at 29·6 mm diameter; U.S.N.M. 137701 (×2·1). *I*, lateral view of early whorls showing the development of the lateral lobe; D. 1554 (×12). *J*, median section of the early whorls at 6 mm diameter based on D. 1556 (×8·4). *K*, suture at 20·6 mm diameter based on U.S.N.M. 137701 (×2). *L*, whorl section at 16·1 mm diameter based on M.M.P. 38465 (×2·1). *M*, whorl section at 8·7 mm diameter based on M.M.P. 38466 (×4·2).

largest diameters seen (U.S.N.M. 137701 at 29·6 mm diameter, figure 7*H*). Also distinctive is the narrowness of the median dorsal lobe. The septal frequency is consistently high and shows little variations as the following typical figures illustrate.

specimen	*D* (mm)	septal frequency
D. 1553	3·9	19
D. 1558	5·6	17
D. 1552	5·7	14
M.M.P. 38466	8·7	17
D. 1548	10·4	18
M.M.P. 38467	11·5	21
D. 1551	12·8	19
D. 1550	13·4	18
M.M.P. 38465	16·1	18

Remarks

Several characters may be used to distinguish tornoceratids from the Widder Shale from *T. arkonense* from the underlying Arkona Shale. The main characters are as follows.

1. Widder specimens show a more sinuous suture, with a steeper ventrad face to the latero-umbilical saddle except in some juveniles.

2. Widder specimens have a more compressed whorl section (see tables of dimensions) and the maximum whorl width tends to lie nearer the umbilicus.

3. Widder specimens between 7 and 15 mm diameter show dorsal lobe that is narrower and more pointed than *T. arkonense.*

4. Arkona specimens not infrequently show a slight displacement of the ventral lobe to the left or right (figure 4*G*). This has not been observed on Widder specimens.

5. Widder specimens commonly show indication of swellings or callus structures on the inside of the shell. (Figure 36, plate 5). This is rarely seen on Arkona specimens. In a collection of some thirty Widder Shale tornoceratids in the collection of Dr R. Flower, ten show evidence of surface callosities.

6. Almost invariably *T. arkonense* shows more widely spaced septa than does *T. uni-angulare widderi.*

In Stauffer's collection at Berkeley (U.C.B. A4797) there is a single specimen from the Widder Shale (figures 20, 21, plate 5), unfortunately unlocalized, which appears to represent a new species of *Tornoceras*: it is not described here. From about 100 ft. above the Centerfield Limestone at Ithaca is a specimen (C.U.P.L. 40114, figure 22, plate 5) which shows the steepness of the ventrad face of the umbilico-lateral saddle which is typical of specimens of *Tornoceras* from above the Centerfield.

Specimens of localities

All specimens come from the Widder Shale in the Arkona–Thedford area of south-western Ontario. They include M.M.P. 38465–38468, 38469 (three specimens) from an outcrop on the S.W. side of King's Highway 82 about one mile east of Thedford; the top of the shale here lies about 15 ft. below a cherty horizon in the Widder Shale exposed in a rock cut on Highway 82 about 500 ft. S.E. of the shale outcrop; specimens collected by Dr and Mrs G. M. Ehlers and Mr and Mrs E. P. Wright: M.M.P. 38506, 7 and 38508 (six specimens) from 15 to 16 ft. below the base of Southworth's 'Shell Stone' on the S.W. side of King's Highway one mile east of Thedford: M.M.P. 38509, 38510 from a shale cut 10 to 12 ft. in height exposed in an escarpment elevation 600 ft. above sea level on the E. side of a country road about ½ mile S.E. of the intersection of King's Highway 21 and Port Frank Road, Thedford, collected by Mr and Mrs E. P. Wright. Also specimens collected by the writer from scree above the Hungry Hollow Limestone on the N. side of the Ausable River at Hungry Hollow, 2½ miles east of Arkona, D. 1548–1545, 1546 (two specimens): from scree at the same level at Hill no. 4, D. 1557, 1558 (five specimens): from scree at the same level in Rock Glen, Arkona, D. 1559, 1560 (three specimens): U.S.N.M. 137671 collected by Dr G. A. Cooper and Mr P. E. Cooper from the Widder Shale at Hill no. 4; U.S.N.M. 137672–5 labelled 'Widder (lower hard bed), Rd to Port

Franks, about 6 mi. N.W. of Thedford Ontario', collected by Dr and Mrs G. A. Cooper. Also thirty-seven specimens in the collections of Dr R. Flower from the Widder Shale of the Thedford district.

(*f*) ***Tornoceras* (*Tornoceras*) *uniangulare aldenense*** subsp.nov., figures 48, 51 to 57, 60, 64, plate 7; figures 89 to 91, 94 to 96, plate 10; figure 8.

Tornoceras uniangulare Beecher (1890, pp. 71–75, pl. 1, figs. 1–14).
T. (*Tornoceras*) *uniangulare* (pars) Miller (1938, pp. 157–166, text-figures 34A–M).
Tornoceras uniangulare Fisher (1951, p. 370, pl. 55, fig. 17).

Material

Nine specimens described by Beecher, and twelve other specimens all from the Alden Marcasite (Fisher 1951), all are preserved in marcasite or partially in calcite. Holotype selected as M.M.P. 31497a.

Description

	dimensions					
specimen	*D* (mm)	*WW* (mm)	*WH* (mm)	*UW* (mm)	*Wh* (mm)	*S*
P.M.Y. 20839	5·1	2·7	4·2	0	—	—
M.M.P. 31497*b*	7·6	*ca.* 3·3	3·2	0·3	—	—
P.M.Y. 20836	10·4	4·8	6·0	0	3·2	17
M.M.P. 31497*a*	18·5	10·5	15·2	—	—	—
(holotype)	39·3	14·8	23·5	*ca.* 1·0	14·2	—

The protoconch is ovate, the width exceeding the diameter, with dimensions ranging from $D = 0{\cdot}89$, $W = 1{\cdot}09$ (D. 1366) to $D = 1{\cdot}0$, $W = 1{\cdot}1$ (P.M.Y. 2043/11, D. 1402). Proseptum regularly concave, reniform in outline with the siphyncle one-fifth the way across (figure 8*J*). Evidence of the protoconch apparatus (in P.M.Y. 20827) shows the siphuncle extending 0·3 mm posterior from the proseptum into a subcircular caecal area which commences 0·17 mm behind the proseptum and extends for 0·23 mm. The posterior portion of the area is sharply invaginated to fuse with the contracted tip of the siphuncle (figure 8 *L*). Few specimens show this development, although the siphuncle is seen to extend well into the protoconch, and this is interpreted as showing that the caecum was commonly not in contact with the protoconch wall. There is no evidence of a cicatrix. One protoconch which is preserved in crystalline calcite (P.M.Y. 20830), shows a dark band in the mid-line within the protoconch which extends for 0·5 mm and becomes deeper towards the proseptum. This is intepreted as a prosiphon, and it is in a position to join the posterior end of the caecum, but this cannot be seen in the specimen. Away from the protoconch the whorl width increases slowly. At 1·5 mm diameter the width is 1·0 mm, and whorl width and height are equal at about 11 mm diameter, beyond which the whorl height is the greater.

The early parts of the protoconch are covered with fine granules as described by Beecher (P.M.Y. 20829). The outer parts of the protoconch have raised growth-line lirae, weakly convex in form, and the fine granules occur between them. The lirae continue without interruption as the ornament of the first whorl, and on the first chamber the lirae are 0·05 mm apart on the mid-flanks (figure 8*K*). At exactly one whorl beyond the proseptum there is a shallow constriction; this passes convexly backwards across the flanks from a small bullate node on the umbilical shoulder (P.M.Y. 20831); orad of the constriction is a ridge which is strongly developed in some specimens (P.M.Y. 20831) and weak in others (P.M.Y. 20833). At the constriction the form of the growth-line lirae changes markedly from convex to biconvex and it is at this stage that the adult pattern is reached, but at first the lirae are rather finer and less regular than those on the first whorl. Biconvex growth lines continue to at least a diameter of 20 mm, but one well-preserved specimen at a diameter of 30 mm (M.M.P. 31497a) shows a loss of the lateral sinus.

Description of plate 5

Figures 20, 21. *Tornoceras* (*T.*) sp.nov. Lateral and ventral views of U.C.B. A4797 (Stauffer Coll.) from the Widder Shale (unlocalized) of Southern Ontario (× 3).

Figure 22. *T.* (*T.*) sp. Lateral view of C.U.P.L. 40114 (loc. 14) from the Ludlowville Formation about 100 ft. above the Centerfield Limestone at Ithaca, N.Y. (× 1·4).

Figure 23. *T.* (*T.*) sp. Lateral view of U.S.N.M. 137715 from the Silica Shale in a quarry $2\frac{1}{2}$ miles S.W. of Sylvania, Ohio (× 2·5).

Figure 24. *T.* (*T.*) aff. *mesopleuron* sp.nov. Lateral view of U.S.N.M. 137719 from the Silica Shale at the same locality (× 1·5).

Figure 25. *T.* (*T.*)? *amuletum* sp.nov. Lateral view of C.U.P.L. 40112 from the upper part of the King Ferry Shale at Portland Point, Cayuga Lake (natural size).

Figure 26. *T.* (*T.*) *uniangulare widderi* subsp.nov. Lateral view of U.S.N.M. 137701 from the Widder Shale at Hill no. 4, Arkona, Southern Ontario (× 2).

Figure 27. *T.* (*T.*) sp. Lateral view of C.U.P.L. 40013 (Wells Coll.) from the Delphi member of the Skaneateles Formation at Pratt's Falls, Onondaga Co., N.Y.

Figure 28. *T.* (*T.*) *arkonense* House sp.nov. Lateral view of M.M.P. 38470 from the lower Arkona Shale at Rock Glen, Southern Ontario (× 5·1).

Figures 29, 30. *Parodiceras discoideum* (Hall). Lateral and ventral views of the holotype, N.Y.S.M. 4055, from the Cherry Valley Limestone west of Manlius, N.Y. (× 2).

Figure 31. *Tornoceras* (*T.*) *uniangulare widderi* subsp.nov. Lateral view of M.M.P. 38515 from the Widder Shale (unlocalized) of Southern Ontario (× 2).

Figures 32, 33. *T.* (*T.*) *mesopleuron* sp.nov. Ventral and lateral views of the holotype, M.M.P. 34466, from the upper Arkona Shale at the Tileyard, Thedford, Southern Ontario (natural size).

Figure 34. *Parodiceras discoideum* (Hall). Enlarged lateral view showing the growth lines of C.U.P.L. 40123 (Jewett Coll.) from the Cherry Valley Limestone west of Manlius, N.Y. (× 5).

Figure 35. *Tornoceras* (*T.*) *arkonense* sp.nov. Lateral view showing the dorsal septal line of M.M.P. 38500 from the banks of the Ausable River $\frac{1}{3}$ mile downstream from the mouth of Hill no. 4 Creek, east of Arkona, Southern Ontario (natural size).

Figure 36. *T.* (*T.*) *uniangulare widderi* subsp.nov. Lateral view showing impression of a shell callus on M.M.P. 38467 from the Widder Shale on the south-west side of King's Highway 82, one mile E. of Thedford, southern Ontario (× 2·5).


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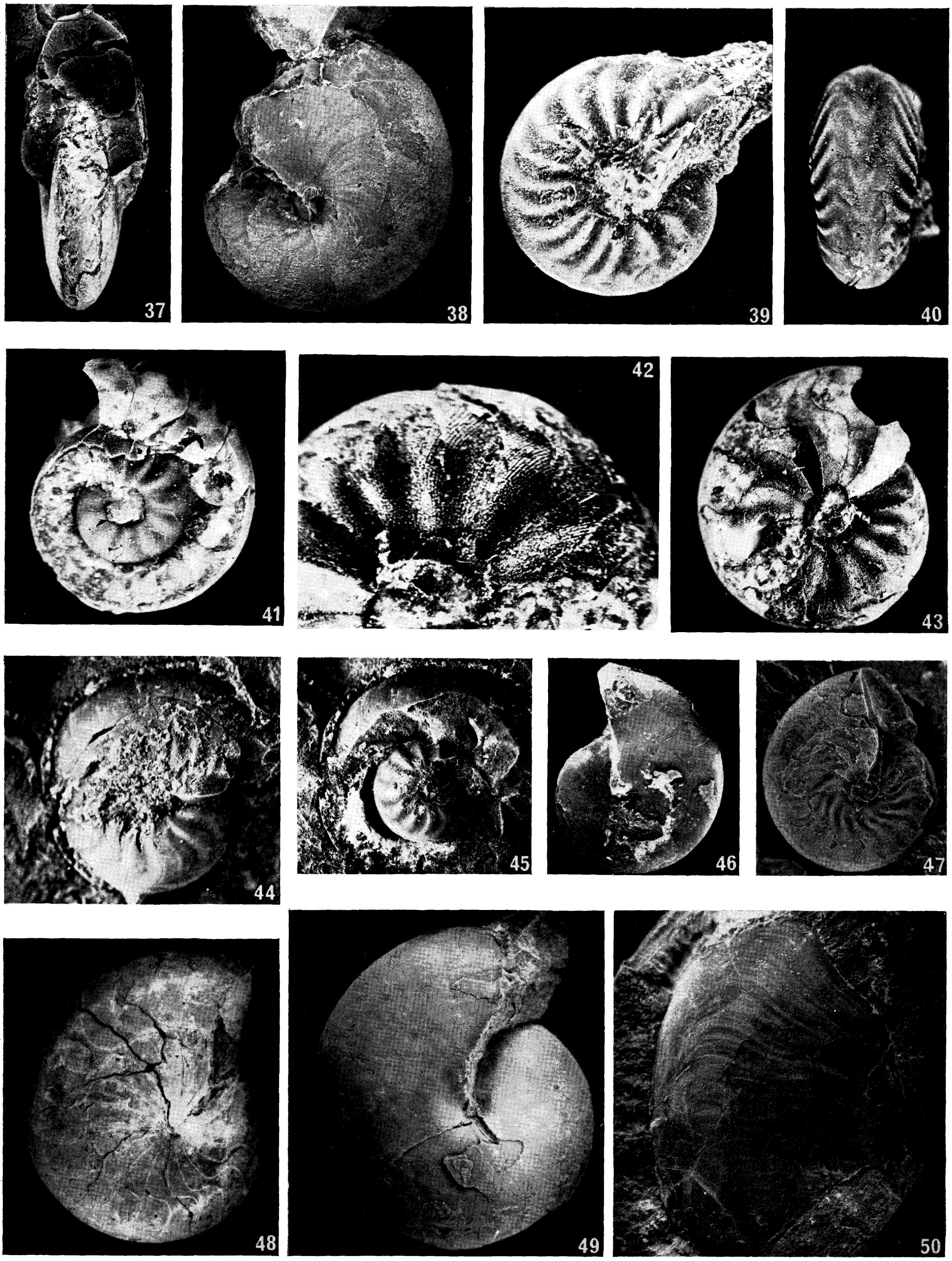
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Description of plate 6

Figures 37 to 45, 47, 49, 50. *Tornoceras* (*T.*) *amuletum* sp.nov. All specimens collected by Professor J. W. Wells from the Ledyard Shale near Lucky Stone Lodge, Cayuga Lake, N.Y. 37,38, ventral and lateral views of C.U.P.L. 40088 (natural size). 39, 40 lateral and ventral views of C.U.P.L. 40085 (× 8·5). 41 to 43, lateral views and an enlargement to show the wrinkle layer of C.U.P.L. 40091. 41, 43 (× 6·3), 42 (× 12). 44, 45, lateral views of C.U.P.L. 40084 (× 3·2). 47, lateral view of C.U.P.L. 40085 (× 2). 49, lateral view of C.U.P.L. 4007 (natural size). 50, lateral view of C.U.P.L. 40086 (natural size).

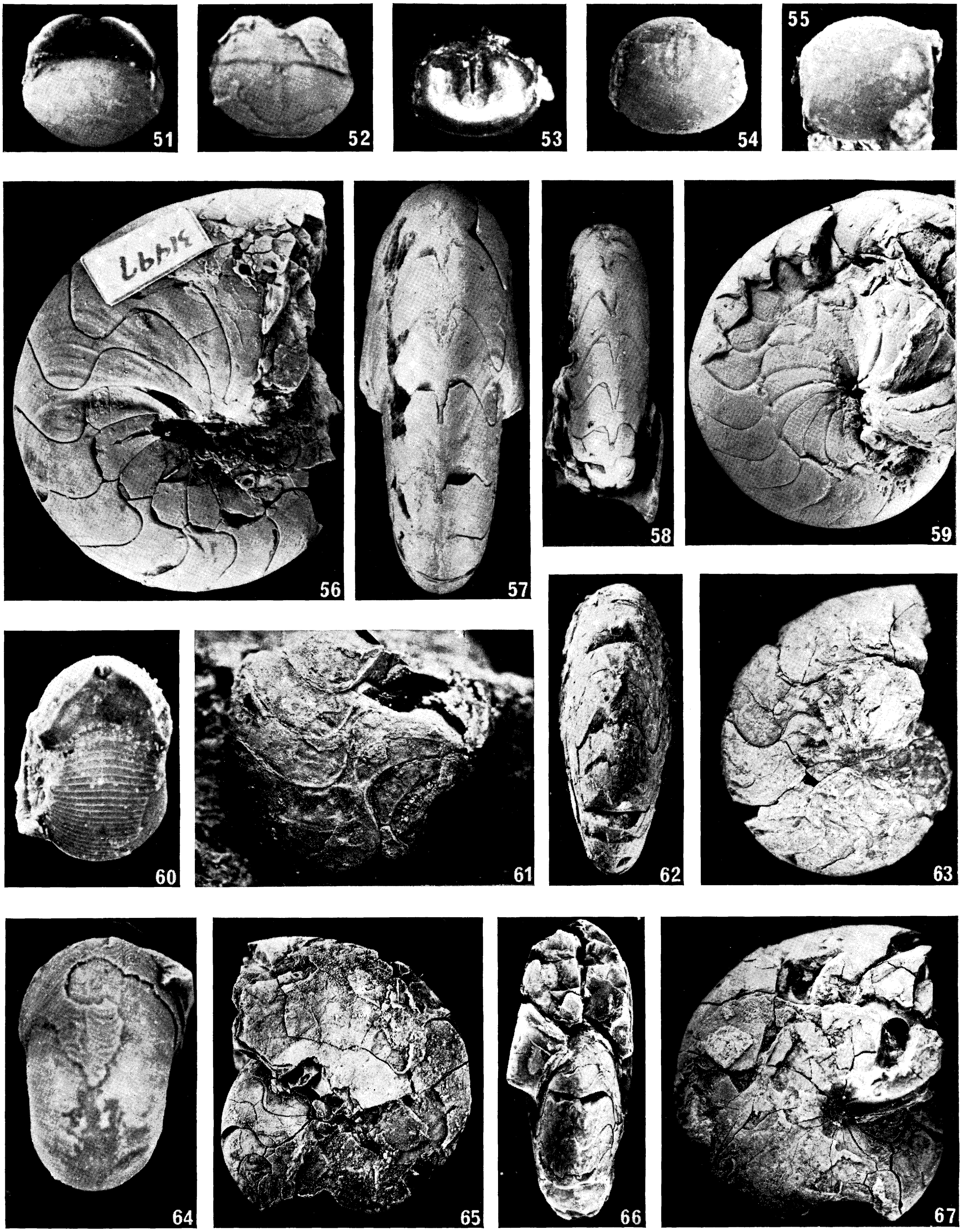
Figure 46. *Parodiceras discoideum.* Lateral view of N.Y.S.M. 4056 from the Cherry Valley Limestone, probably at Manlius, N.Y. (× 1·5).

Figure 48. *Tornoceras* (*T.*) *uniangulare aldenense* subsp.nov. lateral view of D. 1562 from the Alden Marcasite of Spring Creek, Alden, N.Y. (× 3).

Description of plate 7

Figures 51 to 57, 60, 64. *Tornoceras* (*T.*) *uniangulare aldenense* subsp.nov. All specimens thought to be from the Alden Marcasite at Spring Creek, Alden, N.Y. 51, 52, protoconch and first chamber of P.M.Y. 20831 (× 30). 53, 54, protoconch, showing impression of caecal apparatus of P.M.Y. 20831 (both × 30). 55, protoconch of P.M.Y. 20930 (× 30). 56, 57, lateral and ventral views of M.M.P. 31497a (× 2). 60, the first whorl, showing ornament of P.M.Y. 20832 (× 30). 64, a second whorl, showing biconvex ornament of P.M.Y. 20833 (× 30).

Figures 58, 59, 61 to 63, 65 to 67. *T.* (*T.*) *uniangulare uniangulare*. All specimens from the Leicester Pyrite near Leicester, Livingstone Co., N.Y. 58, 59, ventral and lateral views, D. 1426 (× 2·61), lateral view, C.U.P.L. 40115b (X3). 62, 63, ventral and lateral views C.U.P.L. 40115 (× 2·2). 65 to 67, lateral and ventral views of a cotype, A.M.N.H. 5476 (× 2·5).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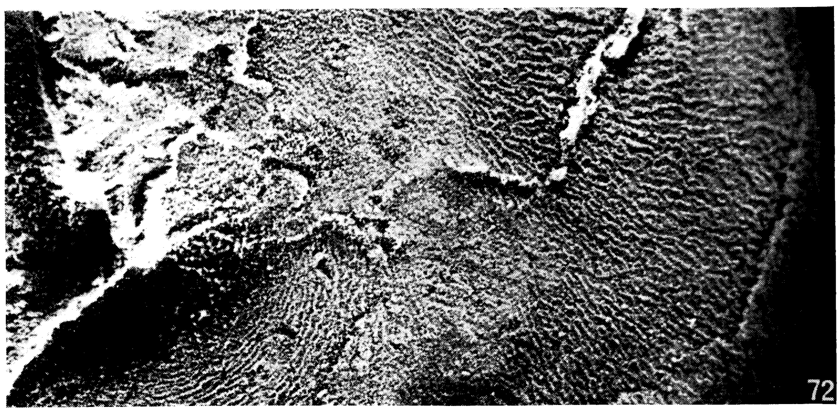
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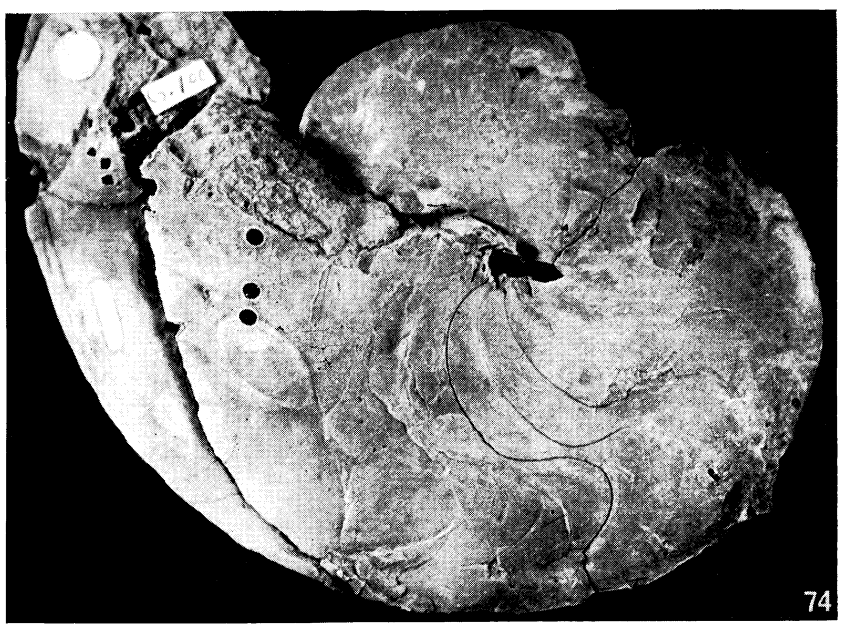
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Description of plate 8

Figures 68, 69, 71. *Tornoceras* (*T.*) *arcuatum* sp.nov. Lateral and ventral views and an enlargement showing the wrinkle layer of D. 1436 from the Squaw Bay Limestone at Partridge Point, Alpena, Michigan. 68, 69, × 3; 71, × 7.

Figure 70. *T.* (*T.*) *arcuatum* sp.nov. Lateral view of D. 1440 from the same locality and horizon (× 3).

Figure 72. *T.* (*T.*) *uniangulare obesum*. An enlargement showing the wrinkle layer of N.Y.S.M. 11263 from the Cashaqua Shale, probably from Shurtleff's Gully, Livingstone Co., N.Y. (× 30).

Figure 73. *Epitornoceras peracutum*. Lateral view of the holotype, N.Y.S.M. 4091, probably from the Ithaca Beds at Ithaca, N.Y. (× 1·1).

Figure 74. *E.* aff. *peracutum*. Lateral view of C.U.P.L. 39652, probably from the Ithaca Beds at Ithaca, N.Y. (natural size).

Description of plate 9

Figures 75 to 77. *Tornoceras* (*T.*) *uniangulare obesum*. Ventral and lateral views and an oblique view of the umbilicus of D. 1365 from the Cashaqua Shale in Shurtleff's Gully, Livingston Co., N.Y. 75, 76, × 1, 77, × 2.

Figures 78, 79. *T.* (*T.*) *uniangulare obesum*. Lateral and ventral views of N.Y.S.M. 11263 labelled as from the Naples Group near Naples, N.Y. (both × 3).

Figures 80, 81. *T.* (*T.*) sp.nov. Lateral views showing ventral chevrons of N.Y.S.M. 11633 from the West Brook member of the Tully Limestone near Borodino, N.Y. (both × 1).

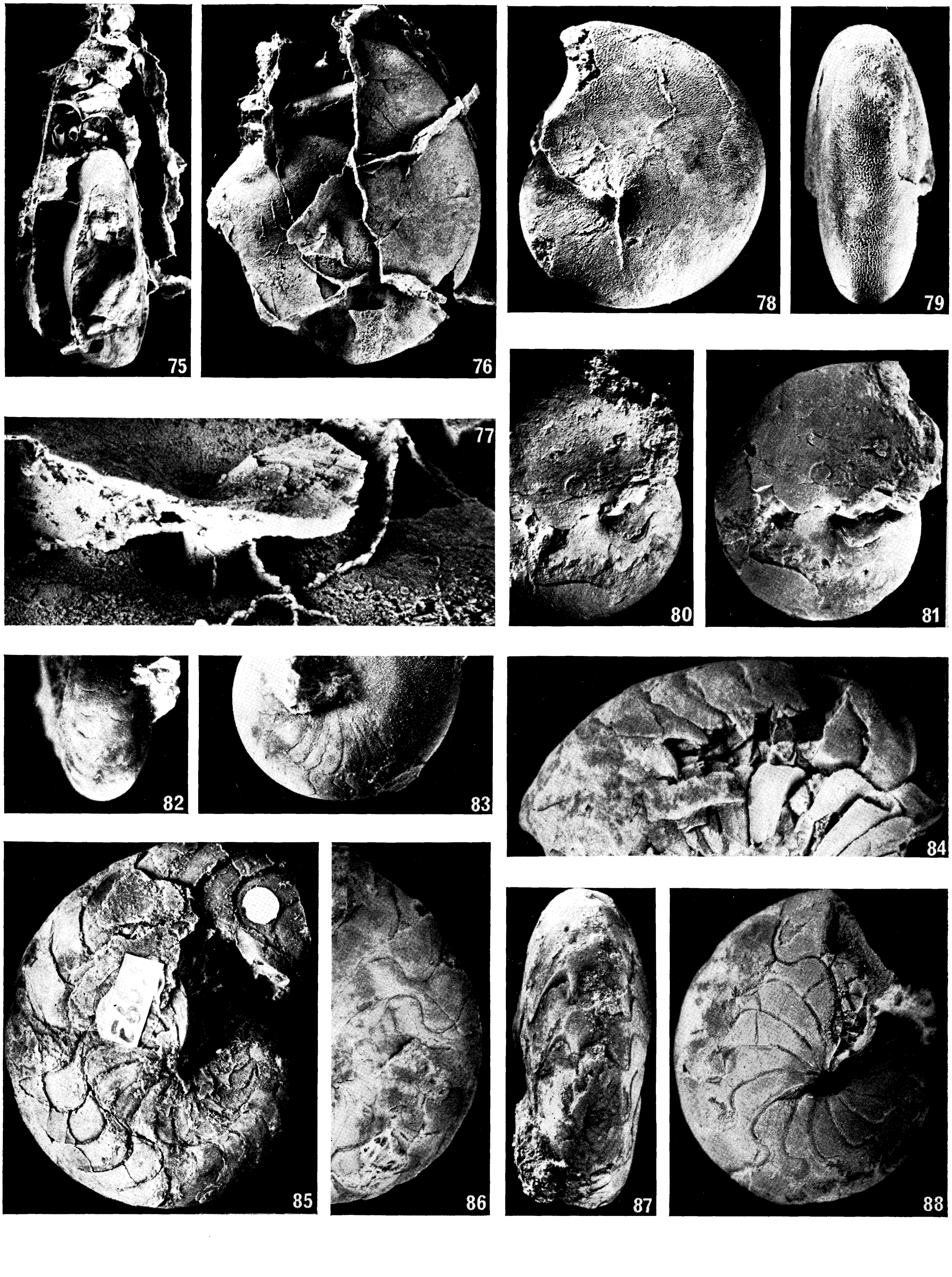
Figures 82, 83. *T.* (*Linguatornoceras*) aff. *linguum*. Ventral and lateral views of N.Y.S.M. 11248 from the Gardeau Shales in Gibson's Glen, 2 miles S.W. of Warsaw, Wyoming Co., N.Y. Collected by D. D. Luther in 1897 (× 5).

Figure 84. *T.* (*T.*) *concentricum* sp.nov. Lateral view of N.Y.S.M. 11243 from the lower Gowanda Shale at Corell's Point on Lake Erie shore (× 5).

Figure 85. *T.* (*T.*) *uniangulare* subsp., from the 'Naples formation' at Mount Morris, Livingstone Co., N.Y. N.Y.S.M. 4093 (× 1·5).

Figure 86. *T.* (*T.*) *concentricum*. Lateral view of U.S.N.M. 137667 from the lower Gowanda Shale at Corell's Point on Lake Erie Shore (× 2).

Figures 87, 88. *T.* (*T.*) *concentricum*. Ventral and lateral view of D. 1401, showing a displacement of the siphuncle. From the same locality and horizon (× 3).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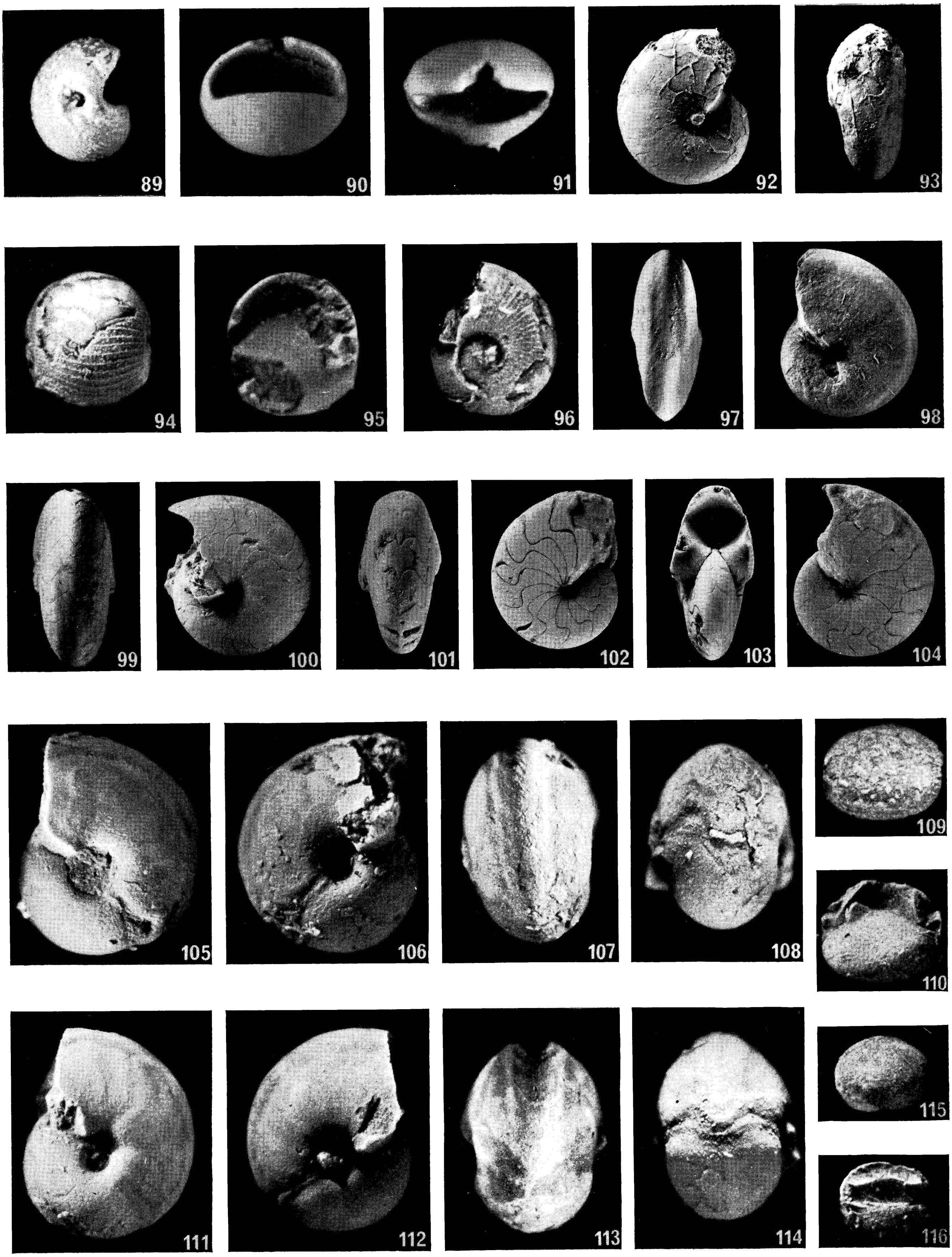
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Description of plate 10

Figures 89 to 91. *Tornoceras* (*T.*) *uniangulare aldenense* subsp.nov. Views of the protoconch of D. 1366 from the Alden Marcasite at Spring Creek, Alden, N.Y. (× 25).

Figures 92, 93. *T.* (*T.*) aff. *uniangulare*. Lateral and ventral views of D. 1425 from the upper Windom Shale at Grove's Creek Quarry, Seneca Co., N.Y. (× 4·5).

Figures 94 to 96. *T.* (*T.*) *uniangulare aldenense* subsp.nov. Views of the first whorl of D. 1402 from the Alden Maracasite at Spring Creek, Alden, N.Y. (× 23).

Figures 97 to 100. *T.* (*T.*) aff. *uniangulare*. Ventral and lateral views of D. 1442 and D. 1441, respectively from the upper Windom Shale at Grove's Creek Quarry, Seneca Co., N.Y. (both × 4).

Figures 101, 102. *T.* (*T.*) *concentricum* sp. nov. Lateral and ventral views of N.Y.S.M. 6679E from the lower Gowanda Shale at Corell's Point on the shore of Lake Erie (× 2).

Figures 103, 104. *T.* (*T.*) *concentricum* sp.nov. Ventral and lateral views on N.Y.S.M. 6679D from the same locality and horizon (× 1·5).

Figures 105 to 110. *T.* (*T.*) *concentricum*. sp.nov. Showing the nepionic constriction and the deveopment of ventro-lateral furrows after the constriction and the protoconch. All based on D. 1401, from the same locality and horizon. 105 to 108, × 20; 109, 110, × 25.

Figures 111 to 114. *Aulatornoceras bicostatum*, showing the nepionic constriction and the development of ventro-lateral furrows after the constriction of D. 1364 from the same locality and horizon (all × 20).

Figures 115, 116. *A. bicostatum*. The protoconch and part of the first chamber of D. 1360 from the same locality and horizon (both × 25).

Description of plate 11

Figure 117. *Tornoceras* (*T.*) *crebriseptum*. Lateral view of the holotype, C.M.P. 464, from the Three Forks Shale at Three Forks, Montana (× 2).

Figures 118, 119. *T.* (*T.*) *crebiseptum*. Lateral and ventral views of the holotype of *T. douglassi*, C.M.P. 476, from the same locality and formation (× 2).

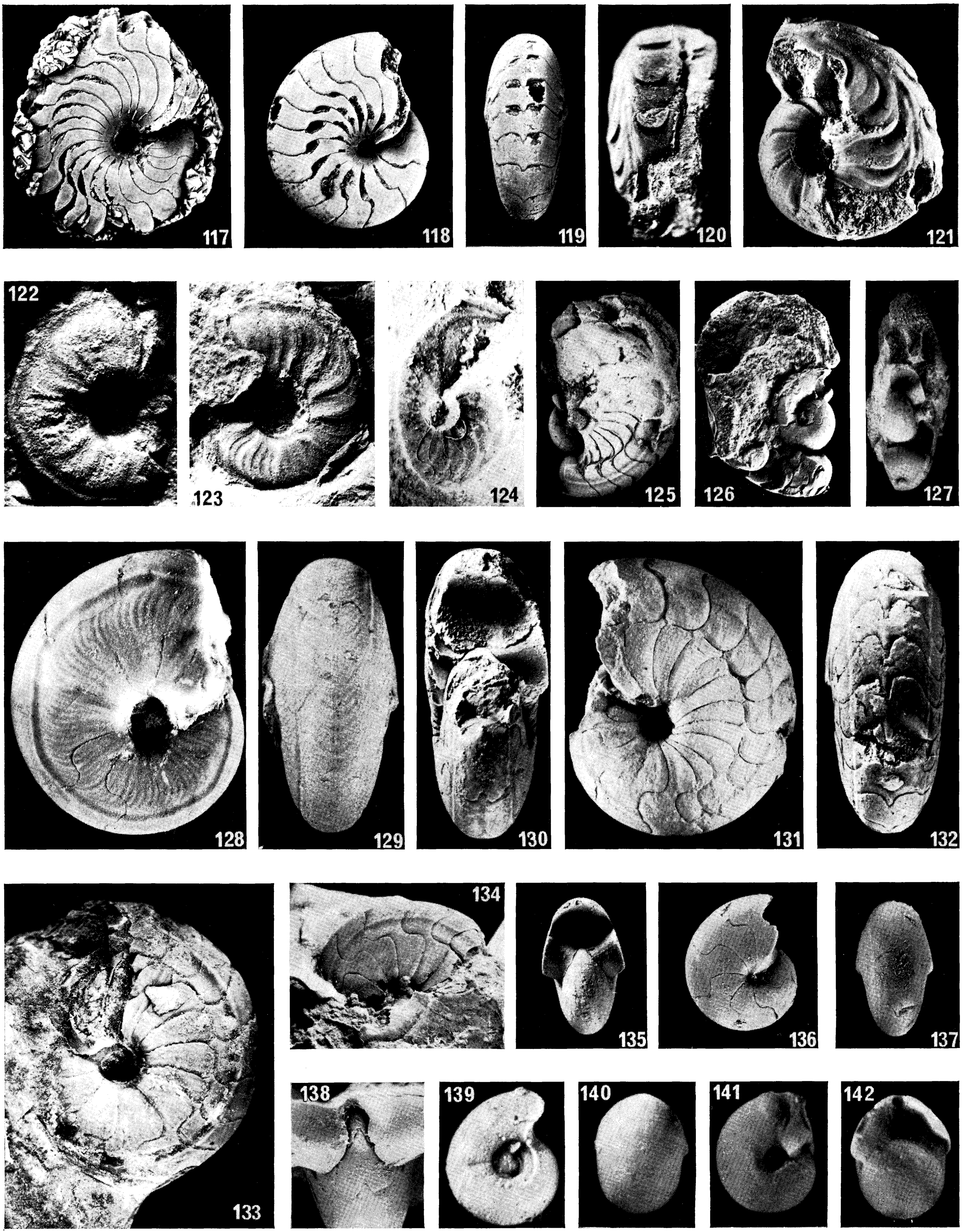
Figures, 120, 121. *Aulatornoceras rhysum*. Ventral and lateral views of B.M.N.S. E 22464, probably from the Hanover Shale (× 4).

Figures 122, 123. *A. clarkei*. Lateral views of N.Y.S.M. 5652 and 5654 respectively (both syntypes), possibly from the upper Gowanda Shale at Forestville, Chautauqua Co., N.Y. (122, × 1; 123, × 1·5).

Figure 124. *A. rhysum*. Lateral view of the lectotype, N.Y.S.M. 4092, from the Hanover Shale at Java, Wyoming Co., N.Y. (× 5).

Figures 125 to 137, 139 to 142. *A. bicostatum*. All from the lower Gowanda Shale at Corell's Point on Lake Erie shore. 125 to 127, lateral and ventral views of D. 1357 (× 3). 128, 129, lateral and ventral views of N.Y.S.M. 5659 (× 3). 130 to 132, ventral and lateral views of D. 1363 (× 3). 133, lateral view of A.M.N.H. 5888/1:1 (× 2). 134, lateral view of N.Y.S.M. 11238 (× 1·5). 135 to 137, an early whorl of D. 1359 (× 5). 139, lateral view showing the nepionic constriction of D. 1360 (× 25). 140 to 142, ventral and lateral views of the first whorl and nepionic constriction of D. 1359 (× 15·7).

Figure 138. *Tornoceras* (*T.*) *concentricum* sp.nov. Close-up to show the mid-dorsal lobe of N.S.Y.M. 6679, from the same locality and horizon (× 4).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The sutural ontogeny is illustrated in figure 8. The development of the lateral lobe is rather slow, but by 10 mm diameter a marked steep umbilical face to the lateral lobe is formed and a near angular relation between it and the crest of the latero-umbilical saddle.

Remarks

The earlier comments on the protoconch apparatus were largely based on specimens in Beecher's collection. It should be noted that the siphuncle lies particularly close to the

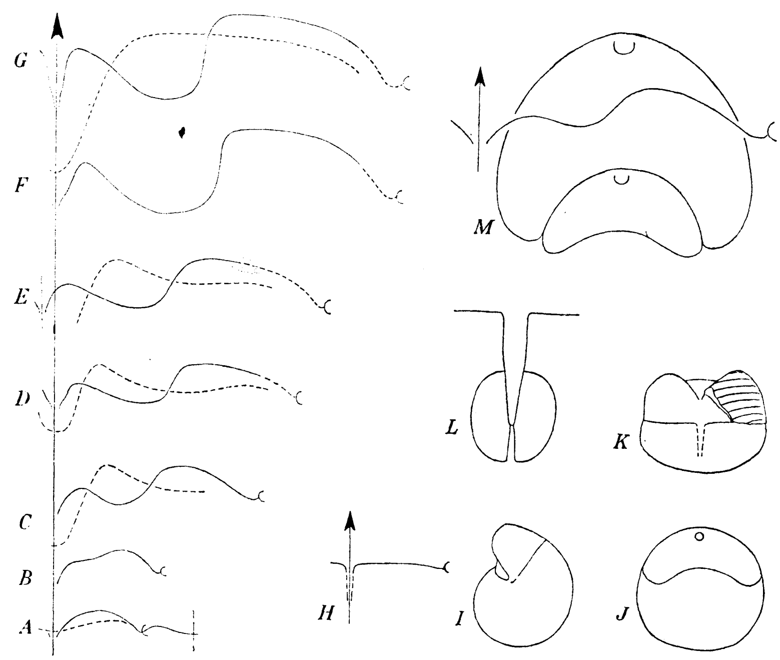

FIGURE 8. Diagrams illustrating the ontogeny of *Tornoceras* (*T.*) *uniangulare aldenense* subsp.nov. from the Alden Marcasite of the Ledyard Shale in Spring Creek, Alden, N.Y. *A*, the first suture and growth line at 1·0 mm diameter; P.M.Y. 20831 (33·3). *B*, suture at 1·5 mm diameter at the end of the first whorl; P.M.Y. 20381 (× 33·3), *C*, suture and growth line at 4·5 mm diameter; P.M.Y. 20839 (× 9·2). *D*, suture and growth line at 5·8 mm diameter; M.M.P. 314976 (× 6·7). *E*, suture, growth line and site of callus (stippled) at 7 mm diameter; P.M.Y. 20837 (× 9). *F*, suture at 10·5 mm diameter; P.M.Y. 20836 (× 6·7). *G*, suture and growth line at 31 mm diameter; M.M.P. 31497*a* (× 2·1). *H* to *J*, *K*, prosuture and protoconch; P.M.Y. 20831 (× 17). *L*, ventral lobe of the prosuture and caecal area; P.M.Y. 20827 (× 50). *M*, suture and whorl section at *ca.* 3·3 mm diameter; P.M.Y. 20829 (× 20).

ventral wall at the proseptum and in this respect is noticeably different from Arkona Shale specimens. Unfortunately most of the specimens are very small and hence the variation of sutural form throughout ontogeny has not been studied in great detail.

Specimens, horizon and locality

The source of Beecher's material is uncertain. The locality was given as Wende Station, Erie County. Dr D. W. Fisher has informed the writer that the 'station' was on the New York Central Railroad. The remaining specimens all come from Spring Creek, near Alden, at the locality described by Fisher (1951). Since this locality is only 4 miles S.E. of Wende Station, and the preservation of Beecher's material and that collected recently is quite identical, it seems highly likely that both are from the same locality. Material studied includes P.M.Y. 20826–20834, M.M.P. 31497*a*, *b* (Reimann Coll.) and D. 1366, D. 1402–1416 collected by the author.

(*g*) **Tornoceras (Tornoceras) uniangulare uniangulare** (Conrad), plate C, figures 58, 59, 61 to 63, 65 to 67, plate 7; figures 9*A* to *H*, 17*E*.

Goniatites uniangularis Conrad (1842, p. 268, pl. 16, fig. 4).
G. astarte Clarke (1885, p. 29, pl. 2, figs. 9, 10).
Tornoceras uniangulare mut. *astarte* Loomis (1903, pp. 916, 919, pl. 5, figs. 1, 2).
T. (*Tornoceras*) *uniangulare* (pars) Miller (1938, p. 157, pl. 31, figs. 8, 9; pl. 32, fig. 9; pl. 38, figs. 5, 6; pl. 35, figs. 5, 6).

Material

Twenty specimens including Conrad's original material. All indifferently preserved in marcasite.

Description

	dimensions				
specimens	*D* (mm)	*W* (mm)	*WH* (mm)	*Wh* (mm)	*UW* (mm)
N.Y.S.M. 5661	1·1	*ca.* 0·9	—	—	—
N.Y.S.M. 5662	3·9	2·3	—	—	—
D. 1351	4·8	2·6	2·9	—	—
D. 1345	7·2	3·8	*ca.* 4·0	—	—
C.U.P.L. 40115	10·1	4·7	6·4	3·5	0
A.M.N.H. 5476 (holotype)	*ca.* 19	*ca.* 8·5	11·0	6·2	*ca.* 0
A.M.N.H. 5476 (ii)	*ca.* 20·5	*ca.* 9·5	—	—	*ca.* 0

Protoconch about 0·78 mm diameter, 1·0 mm in width (N.Y.S.M. 5661). First whorl expanding evenly in width from the protoconch (figure 9*F*, *G*): the nepionic constriction has not been seen. Subsequent shell-form ontogeny illustrated in figure 17*E*.

The prosuture is rectiradiate with a slight lateral saddle: on the venter the passage of the siphuncle back into the protoconch is marked by a deep ventral lobe, 0·3 mm in length (N.Y.S.M. 5661). By 3 mm diameter the adult lateral lobe has formed but the precise position of its adventitious development has not been seen. By the fifth septum evidence of flattening of the lateral saddle has been seen (N.Y.S.M. 5661), but another specimen shows much slower development of the lateral lobe (C.U.P.L. 40120). The subsequent sutural proportions are shown in figure 9*A* to *E*. The great width of the lateral lobe, its broad, shallow base (figures 61, 63, plate 7) and the gentle slope dorsad from the crest of the latero-umbilical saddle without a sudden change of slope are particularly distinctive.

Evidence of the nature of the growth lines is scanty. At 3·9 mm diameter (N.Y.S.M. 5662) there is a deep ventral lobe, markedly V-shaped, and a projecting ventro-lateral salient. The lateral sinus is low on the flanks, and there appears to be only the slightest trace of the sub-umbilical salient which is the rule in other species of the genus. Unfortunately the course of the growth lines in the other whorls has not been seen.

Remarks

Conrad (1842, p. 268) records that the holotype was 'Found by Mr James Hall in Livingstone country, New York. Upper Silurian Slate.' Hall (1879, p. 446) states that the original specimen is from the Moscow Shales near Moscow (now Leicester). Hall's specimens are still extant, but are of disintegrating, oxidizing marcasite, showing no ornament (figured here, figures 65 to 67, plate 7). The Leicester Pyrite crops out at the top of the Windom (Moscow) Shale in several gullies just north of Leicester and there can be no doubt that this horizon is the source of the type material.

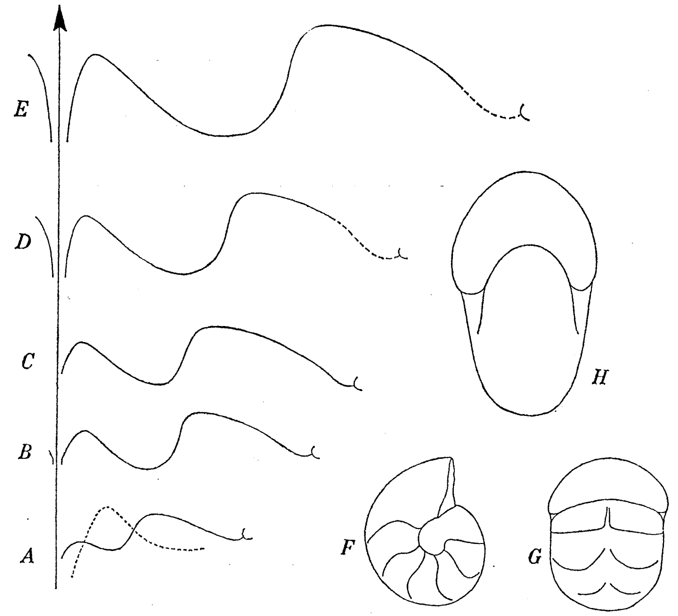

FIGURE 9. Diagrams illustrating the ontogeny of *Tornoceras* (*T.*) *uniangulare uniangulare* (Conrad) from the Leicester Pyrite. *A*, *H*, the suture, growth lines and shell form at 3·9 mm diameter; N.Y.S.M. 5662 figured by Loomis (1903, pl. 5, fig. 2) from Canandaigua Lake N.Y. (both (× 8·1). *B*, suture at 8·2 mm diameter; C.U.P.L. 40115 (i) from a gully north of Leicester, N.Y. (× 6·7). *C*, suture at 12 mm diameter based on A.M.N.H. 5476 (i) from near Leicester (× 4·7). *D*, suture at 20 mm diameter based on A.M.N.H. 5476 (ii), the holotype, from near Leicester (× 3·3). *E*, suture at a whorl height of 15·2 mm based on C.U.P.L. 40115 (iv) from a gully north of Leicester (× 3·3). *F*, *G*, the first whorl based on N.Y.S.M. 5661 figured by Loomis (1903, pl. 5, fig. 1) from Canandaigua Lake (× 15).

The best inner whorls examined are those described by Loomis (1903) from the 'Tully Pyrite' (= Leicester Pyrite) on Canandaigua Lake.

T. uniangulare aldenense usually shows a more sudden change in the slope of the suture from the lateral saddle to the umbilical seam and early whorls show a more pronounced ventro-lateral salient. Sutural differences with later forms are more obvious, but *T. uniangulare uniangulare* shows a sutural type which is typical of the main stock of the Tornoceratidae.

Specimens, horizon and locality

All material studied is from the type horizon, the Leicester Pyrite. Specimens include A.M.N.H. 5476, the holotype, and another specimen, both from near Leicester, Livingston Co., N.Y. N.Y.S.M. 5661, 5662, the types of Loomis, from Canandaigua Lake, Ontario Co., N.Y. C.U.P.L. 40115 (four specimens) from just north of Leicester: C.U.P.L. 40120 from ¼ mile south of Black Point on the W. shore of Canandaigua Lake, all collected by Professor J. W. Wells, D. 1344–1348, D. 1354–1356 from Taunton Gully, and D. 1349–1352 from Spezzano's (= Peterson's) Gully, both just north of Leicester and collected by the author.

(*h*) **Tornoceras (Tornoceras)** aff. **uniangulare** (Conrad), figures 92, 93, 97 to 100, plate 10.

Material

Thirteen small pyritized specimens, only one exceeding 8 mm in diameter.

Description

	dimensions				
specimen	*D* (mm)	*WW* (mm)	*WH* (mm)	*Wh* (mm)	*UW* (mm)
D. 1425	7·1	3·1	3·8	2·2	*ca.* 0·3
D. 1442	5·8	2·8	3·1	—	*ca.* 0·4

Early stages have not been studied. Form at about 5 mm diameter distinguished by the presence of ventro-lateral furrows close to a narrow and arched ventral band. At slightly greater diameters these furrows are gradually lost. Growth lines form a broad sinus over the flanks with a weak salient on the umbilical slope: the apex of the ventro-lateral salient just dorsad from the ventro-lateral furrow. Over the venter the growth lines form distinctive raised chevrons (figure 97, plate 10). The sutures show gentle slopes on the dorsal side of the lateral lobe and the septa seem generally to be closely set. One specimen shows twenty septa per whorl at 7 mm diameter.

Remarks

These distinctive nuclei are difficult to assign with specimens from either the Leicester Pyrite or the Tully Limestone. The ventral growth-line chevrons, however, recall those seen at much greater diameters in a new species from the Tully Limestone which Professor Flower has in manuscript (figures 80, 81, plate 9).

Specimens, horizon and locality

Three specimens, D. 1425, D. 1441, 2, collected by the writer, and nine specimens, C.U.P.L. 42402, collected by Professor Wells, all from the dark upper few feet of the Windom Shale in Grove's Creek Quarry, Seneca Co., N.Y. A larger specimen (U.S.N.M. 137721) from the Windom Shale in a quarry 1 mile S.E. of Lebanon Center, Hamilton, N.Y., reaches 30 mm in diameter and may also belong here.

(*i*) **Tornoceras (Tornoceras) arcuatum** sp.nov., figures 68 to 71, plate 8; figures 10, 17*D*.

Tornoceras (*Tornoceras*) *uniangulare* (pars) Miller (1938, p. 165, pl. 33, figs. 3, 4; pl. 34, figs. 1–4).

T. (*Tornoceras*) *uniangulare* Stumm (1951, p. 35).

Material

Forty specimens from the Squaw Bay Limestone of Michigan. The details of the early stages are mainly based on the specimens in the writer's collection. The holotype is selected as U.S.N.M. 96543*a* (figure 10*F*).

Description

specimen	dimensions *D* (mm)	*WW* (mm)	*WH* (mm)	*Wh* (mm)	*UW* (mm)
U.S.N.M. 96543*a*	39·6	13·7	23·4	12·4	*ca.* 1·0
D. 1436	23·5	10·8	15·0	9·0	—
U.S.N.M. 96550	13·2	5·2	—	—	—
D. 1430	6·7	3·0	3·9	—	—

Protoconch is ovate, transversely elongate, diameter 0·71 mm (U.S.N.M. 96550), width *ca.* 1·3 mm (D. 1440). The proseptum strongly concave (figure 10*J*), not separated into two distinct areas. Whorl width decreases from the protoconch at first so that by two-thirds of the first volution $WH = 0{\cdot}61$ and the whorl section is crescentic with rounded umbilical shoulders (figure 10*H*). The whorl height increases considerably in later whorls so that by about 4 mm diameter, at the end of the third whorl, $WH = WW$. Details of the subsequent shell proportions are illustrated graphically (figure 17*D*). The umbilicus is closed at all stages except for the first few volutions.

The orad portion of the protoconch is ornamented with regular raised lirae which number eight in 0·5 mm on the venter and of the first chamber. The lirae are convex and slightly rursiradiate; between them the test is ornamented with very fine granules arranged parallel to the lirae. This ornament continues to at least two-thirds of the first volution.

The nepionic constriction and the position of the change of ornament has not been observed, but by 3 mm diameter the adult type of biconvex growth lines have been seen. These appear on the test surface as slightly raised lirae which pass slightly back from the umbilicus to form a very shallow sinus and then sweep forward to a rounded ventro-lateral salient and back to a V-shaped, subangular ventral sinus. On internal moulds scarcely any trace of the growth lines can be discerned.

The prosuture, seen in one instance (D. 1440), forms a shallow ventral lobe and very flat lateral saddles. The dorsal course has not been seen. The first suture forms a deep and broad V-shaped ventral lobe and highly arched ventro-lateral saddles. By the tenth suture, at the end of the first whorl, the ventro-lateral has flattened and an incipient lobe is formed.

Figures 10*A* to *F* illustrate the subsequent development of the suture. By 10 mm diameter the lateral lobe has become tongue-shaped and has only a slight asymmetry: this form continues until the adult. The arching of the latero-umbilical saddle which develops above about 17 mm diameter is very characteristic, with a rather flat top and very steep ventrad face. The dorsad slope is at first moderate but in the adult it is very steep and resembles the ventrad slope, or is a little steeper. Thus the saddle becomes almost symmetrical, but at maturity the tops slope gently ventrad instead of the opposite as in earlier whorls.

At diameters above 20 mm there are between 21 and 28 septa per whorl and, as far as can be discerned, the same order of frequency occurs in the earlier whorls.

Remarks

The suture pattern of this species is distinct from that of all American species. One figured specimen from the upper Givetian of North Africa (Petter 1959, pl. 14, fig. 8) shows a suture which approaches this form, but differs in that the lateral lobe is markedly asymmetrical and not lingulate.

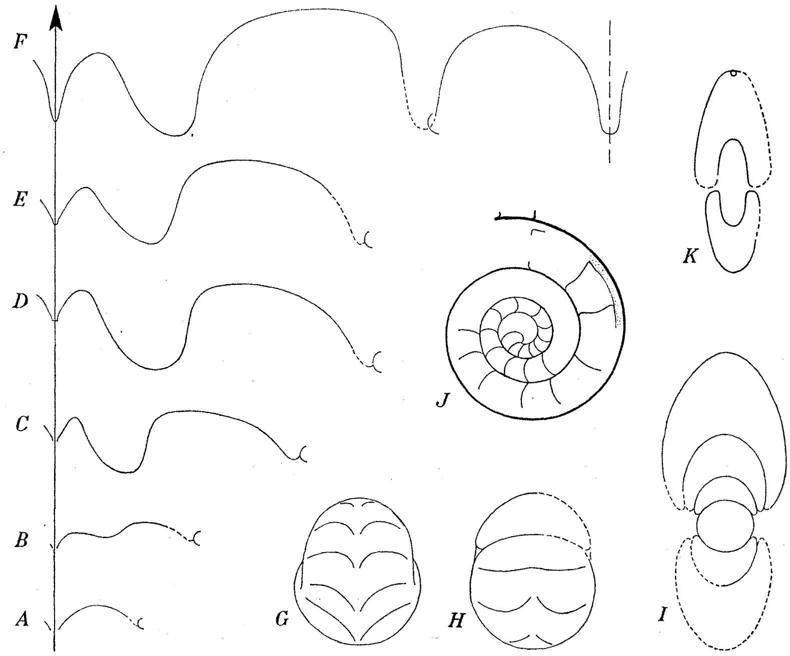

FIGURE 10. Diagrams illustrating the ontogeny of *Tornoceras* (*T.*) *arcuatum* sp.nov. from the Squaw Bay Limestone of Partridge Point, Michigan. *A*, the fourth suture at 1·14 mm diameter based on D. 1440 (× 12·4). *B*, suture at 2·4 mm diameter based on D. 1440 (× 11). *C*, suture at 12 mm diameter based on D. 1429 (× 4·2). *D*, suture at 20 mm diameter based on D. 1430 (× 3·3). *E*, suture at 27 mm diameter based on M.M.P. 47509 (× 2), reversed for comparison. *F*, suture at 38·7 mm diameter based on U.S.N.M. 96543a (× 2), reversed for comparison. *G*, *H*, the first whorl, based on D. 1440 (× 12·3). *I*, median section of the early whorls at 7·06 mm diameter based on D. 1545 (× 5·7). *J*, section in the plane of coiling based on U.S.N.M. 96550 at 3·7 mm diameter (× 7·6). *K*, median section based on D. 1439 (× 0·67).

One poorly preserved specimen from the Tully Limestone of New York is similar to this species in suture pattern (U.S.N.M. 96551*a*, figure 13*D*) but the ventral lobe may be deeper. Apart from this specimen the species is not known except from the type locality. It should be pointed out that this species is very distinct from the *Tornoceras* in the Genundewa Limestone of New York with which Cooper (1942) has correlated the Squaw Bay Limestone. The presence of *Koenenites* in the Squaw Bay Limestone shows that it is older than the Genundewa and, in terms of the goniatite zonation, both the Squaw Bay Limestone and the Tully Limestone correlate with the *lunulicosta* Zone (House 1962).

Specimens, horizon and locality

All specimens are from the Squaw Bay Limestone which crops out on the south side of Partridge Point, Alpena, Michigan. Specimens include U.S.N.M. 96543*a*, *b*, 26550

(22 specimens), M.M.P. 47509, 15975 (6 specimens) and 12 specimens in the author's collection (D. 1429–1440).

(*j*) ***Tornoceras* (*Tornoceras*) *uniangulare compressum*** Clarke, figures 11*A* to *E*, 18*A*.

Tornoceras uniangulare var. *compressum* Clarke (1897 (nomen nudem), p. 54).
T. uniangulare var. *compressum* Clarke (1898 (nomen nudem), p. 54).
T. uniangulare var. *compressum* Clarke (1899, p. 116, pl. 8, fig. 18).
T. uniangulare var. *compressum* (pars) Clarke (1904, pp. 359, 361, 371).
T. (*Tornoceras*) *uniangulare* (pars) Miller (1938, p. 158, pl. 32, fig. 8).

This subspecies was erected for specimens from the Styliola Limestone (Genundewa) of New York. Later (1904) Clarke extended the variety to include the specimens described by Beecher (1890) which are here referred to the subspecies *aldenense*. Clarke's holotype (N.Y.S.M. 4098) has been flattened by crushing and the body chamber occupies the last visible whorl and no sutures can be seen. Interpretation is hence difficult. Apart from the holotype, the description which follows is based on 47 specimens in Professor J. W. Wells's collection and 35 specimens collected by the author, all from the Genundewa Limestone. The preservation of all is poor.

Description

specimens	dimensions *D* (mm)	*WW* (mm)	*WH* (mm)	*UW* (mm)
C.U.P.L. 101 ix	3·0	1·8	1·6	0
D. 1453	5·0	*ca.* 3·6	—	0
N.Y.S.M. 4098 (holotype)	16·0	*ca.* 5·5	9·4	0
D. 1456	22·8	11·8	14·2	0
D. 1447	36	15·5	20	0

The material is not suitable for the study of the early stages. The development of the shell is illustrated graphically and diagrammatically in figures 11*D*, *E*, 18*A*. The adult shells show some variation in the degree of inflation, and the form of the venter, but many specimens show a tendency to form a flattened venter in the adult. Most specimens show a higher relative whorl width than is usual in the genus.

The suture has not been seen in detail in the early whorls, but the adult suture possesses a V-shaped ventral lobe with a broad asymmetric lateral lobe (18*A*, *B*).

Growth lines on the holotype are markedly biconvex, with a deep ventral simus, a projecting ventro-lateral salient, a lateral sinus and a rounded latero-umbilical saddle. In the outer whorls of the Bethany Center specimens, however, the ventro-lateral salient is very subdued and passes into growth lines which are almost rectilinear across the flanks (D. 1445, 1447, 1450) although passing back towards the umbilicus. Several specimens show evidence of major shell damage sometimes suggestive of a fracture right across one side of the whorl (D. 1445).

Remarks

Distinction of this subspecies is not very satisfactory for the poor preservation of the inner whorls makes analysis impossible. The principal distinguishing features are the consistently high whorl width proportion, the tendency to form a tabular venter at high diameters, and the marked reduction in the prominence of the ventro-lateral salient above 20 mm diameter. It should be noted that in this last feature particularly, the Bethany Center specimens differ from the holotype, the only specimen examined from Canandaigua Lake.

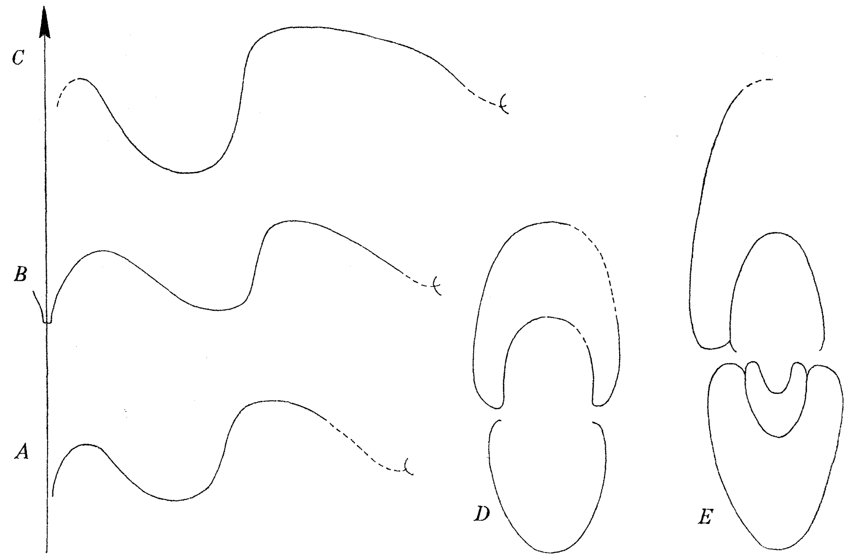

FIGURE 11. Diagrams illustrating the suture and shell form of *Tornoceras* (*T.*) *uniangulare compressum* Clarke, from the Genundewa Limestone at Bethany Center, Genesee Co., N.Y. *A*, the suture at about 20 mm diameter based on D. 1445 (× 5). *B*, the suture at about 17·5 mm diameter based on D. 1443 (× 5). *C*, the suture at a whorl height of 15·3 mm based on D. 1444 (× 5), *D*, cross-section based on C.U.P.L. 40121 (× 1·7). *E*, cross-section based on C.U.P.L. 40122 (× 1·7).

Locality and horizon

The holotype, N.Y.S.M. 4098, is from the Genundewa Limestone on Canandaigua Lake. The remaining 82 specimens all come from a road-cutting on U.S. Route 20, just S.E. of Bethany Center, Genesee County, N.Y. (this is 45 miles W. of Canandaigua Lake); they are all from the Genundewa Limestone.

(*k*) ***Tornoceras* (*Tornoceras*) *uniangulare obesum*** Clarke, figure 72, plate 8; figures 75 to 79, plate 9; figure 12, 18*B*.

Tornoceras uniangulare var. *obesum* (nomen nudum) Clarke (1897, p. 54).

T. uniangulare var. *obesum* Clarke (1899, p. 116, pl. 8, fig. 17).

T. (*Tornoceras*) *uniangulare* (pars) Miller (1938, p. 157, pl. 32, fig. 7).

Material

The holotype N.Y.S.M. 4099) and 200 specimens also barytized and probably topotypes. All are in Clarke's collection. Three other specimens from the Cashaqua Shale, or its equivalents.

Description

specimen	*D* (mm)	*WW* (mm)	*WH* (mm)	*Wh* (mm)	*UW* (mm)
	dimensions				
N.Y.S.M. E346. i	4·9	3·0	2·8	1·3	0·3
N.Y.S.M. E346. ii	7·8	4·7	4·8	2·3	0
N.Y.S.M. 4099 (holotype)	12·1	7·3	—	—	0
N.Y.S.M. 11263	17·8	7·7	11·1	5·5	0
N.Y.S.M. 4093	45·0	16·5	26·0	—	0

Protoconch 0·98 mm in diameter, 0·99 mm wide (N.Y.S.M. 11244). Relations at the nepionic constriction not seen. Subsequent shell development illustrated by a graph (figure 18*B*) and by drawings (figures 12*D* to *H*). At the large diameters (N.Y.S.M. 4097) the whorl section is distinctly rotund and inflated.

Details of the ornament not seen and the sutural ontogeny has not been worked out in detail, but at all stages the lateral lobe is distinctly asymmetrical (figures 12*A* to *C*) as in all the *T. uniangulare* group. Wrinkle layer is visible on several specimens (N.Y.S.M. 4096, 4099).

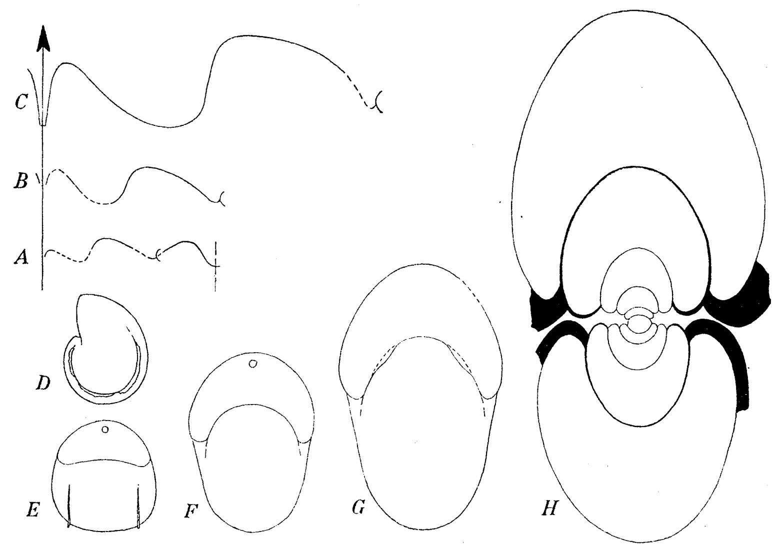

FIGURE 12. Diagram illustrating the ontogeny of *Tornoceras* (*T.*) *uniangulare obesum* from the Cashaqua Shale near Honeoye Lake and the Naples Formation. *A*, *F*, the suture and shell form at 1·76 mm diameter based on N.Y.S.M. 11246 (× 13·3). *B*, *G*, the suture and shell form at 2·7 mm diameter based on N.Y.S.M. 11247 (× 13·3). *C*, the suture at 31 mm diameter based on N.Y.S.M. 4093 (× 1·1). *D*, *E*, the protoconch (possibly not of this species), based on N.Y.S.M. 11245 from the Naples Formation at Mount Morriss, N.Y. (× 11). *H*, median section based on N.Y.S.M. 4097 at 11·4 mm diameter from the Naples Formation at Naples, N.Y. (× 6·1). All sutures reversed for comparison.

Remarks

Adequate comparison of this barytized material with the pyritic internal moulds from other horizons is difficult. The type specimen of *T. uniangulare* var. *obesum* is fully septate and barytized. The close relation of all these specimens is not in doubt, and the statistical figures support this (figure 18*B*, table 2). The changes in the *WW*/*WH* ratio are particularly distinctive after 3 mm diameter. Such a regular and sharp fall has not been seen in any other species of *Tornoceras* yet examined. The sutures do not appear fundamentally different from those of *T. uniangulare*.

Specimens, localities and horizon

The holotype N.Y.S.M. 4099, also N.Y.S.M. 11262, 11263, E346 (about 200 specimens), all barytized and from the Cashaqua Shale probably in Honeoye Lake area. Shurtleff's Gully (Shurger's Glen) is also a source of barytic specimens (including D. 1365): at this locality the septaria yielding these specimens are in the upper 6 ft. of the Cashaqua Shale. In Shurtleff's Gully, 2·75 miles S.E. of Livonia, Livingston Co., N.Y., the barytized septarian horizon is at an elevation of between 1190 and 1210 ft., according to information supplied by Professor Wells. Specimens from the 'Naples Group' include N.Y.S.M. 11245 from Mount Morriss, and N.Y.S.M. 4097 from Naples, Ontario Co., N.Y.

(*l*) ***Tornoceras* (*Linguatornoceras*)** aff. ***linguum*** (G. & F. Sandberger), figures 82, 83, plate 9; figure 13*E*.

Material

One specimen preserved in dark grey mudstone associated with a common rotund *Manticoceras*.

Description

	dimension			
specimen	*D* (mm)	*WW* (mm)	*WH* (mm)	*UW* (mm)
N.Y.S.M. 11248	max. 19·4	—	—	—
	16·6	8·5	9·0	0

Shell form

Ovate and well rounded with closed umbilicus. No trace of surface ornament. The last half whorl is body chamber, there are thirteen septa in the last half whorl of the phragmocone. The suture (figure 13*E*) shows a small ventral V-shaped lobe, a flatly arched ventro-lateral saddle, a lingulate lateral lobe and a very asymmetric latero-umbilical lobe with a steep ventrad face and very gentle dorsad slope to the umbilical seam.

Remarks

This specimen is remarkably close in shell form and suture pattern to the common *Tornoceras* of the Eifel Budesheimer Schiefer or from the *holzapfeli* Zone at Saltern Cove, Devon (figure 13*G*). Although the German forms are usually referred to *T. simplex* they do not belong to that species which is probably a *Foordites*. The earliest valid name appears to be *Goniatites retrorsus* var. *lingua* of the Sandberger brothers (1852, p. 109, pl. 10, figs. 20, 21), which shows a similar suture pattern but is rather more compressed than usual, and certainly more compressed than the New York specimen.

Locality and horizon

The specimen N.Y.S.M. 11248 is labelled as having come from the Portage at 'Gibson's Glen, a small ravine 2 miles S.W. of Warsaw', Wyoming Co., N.Y., and was collected by

D. D. Luther in 1897. It is possible that it came from the horizon of 'beautifully preserved fossils, mostly small specimens of *Manticoceras*...', noted at the mouth of Gibson's Glen by Clarke & Luther (1908, p. 59), that is within the Gardeau Shale member of the West Falls formation.

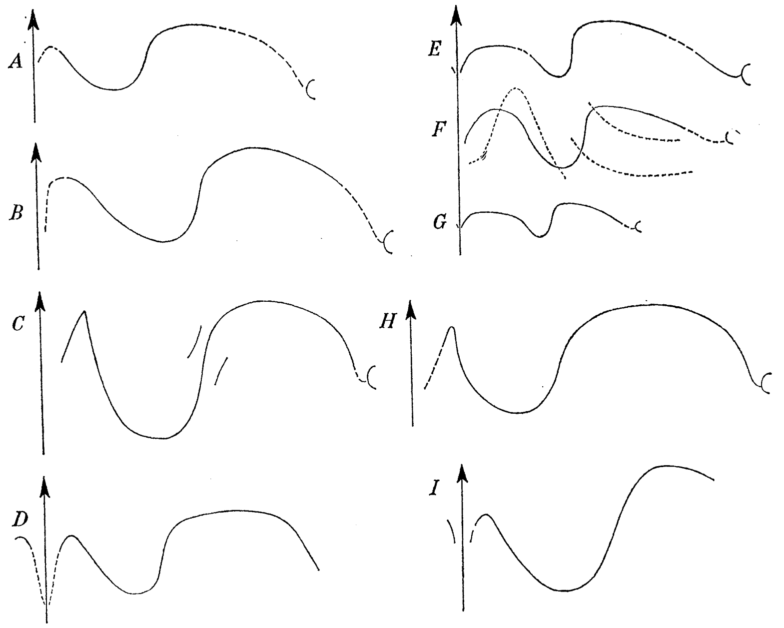

FIGURE 13. Diagrams illustrating the sutures of *Linguatornoceras*, *Tornoceras* and *Epitornoceras* spp. from New York State, Michigan and Europe. *A*, *Tornoceras* (*T*).) sp. Suture at 42 mm diameter based on M.M.P. 47507 from the Antrim Shale at Huron Portland Cement Company Quarry, Paxton, Alpena Co., Michigan (× 1). *B*, *Tornoceras* (*T.*) sp. Suture at a whorl height of 31·5 mm based on M.M.P. 47508 from the same horizon and locality (× 1). *C*, *Epitornoceras peracutum* (Hall). Suture at whorl height of 41 mm based on the holotype, N.Y.S.M. 4091, probably from the Ithaca Formation, Ithaca, N.Y. (× 1). *D*, *Tornoceras* (*T.*) cf. *arcuatum* sp.nov. Suture at an estimated diameter of 41 mm, based on U.S.N.M. 96551 (*a*) from the Platyceras Bed of the Tully Limestone, ½ mile N.W. of Georgetown, N.Y. (× 1·3). *E*, *Tornoceras* (*L.*) aff. *linguum* (G. & F. Sandberger). Suture at 13 mm diameter based on N.Y.S.M. 11248 from the Gardeau Flags, Gibson's Glen, Warsaw, Wyoming Co., N.Y. (× 4). *F*, *Aulatornoceras rhysum* (Clarke). Suture of the lectotype at 5 mm diameter from the Hanover Shale at Java, Wyoming, Co., N.Y. N.Y.S.M. 4092 (× 12). *G*, *Tornoceras* (*L.*) aff. *linguum* (G. & F. Sandberger). Suture based on a specimen from the Frasnian of Saltern Cove, Devon, S.M. H1526 (× 4·2), reversed for comparison. *H*, *Epitornoceras* aff. *peracutum* (Hall). Suture at about 80 mm diameter, based on C.U.P.L. 39652, figured by Harris in 1899 from the Ithaca Formation, Ithaca, N.Y. (× 1). *I*, *Tornoceras* (*T.*) sp. Suture at an estimated whorl height of 29 mm, based on U.S.N.M. 96551 (*b*) from the Platyceras Bed of the Tully Limestone, ½ mile N.W. of Georgetown, N.Y. (× 1·5).

(*m*) ***Tornoceras* (*Tornoceras*) *concentricum*** sp.nov.; figures 84, 86 to 88, plate 9; figures 101 to 110, plate 10; figure 138, plate 11; figure 14.

Tornoceras sp.nov. House (1962, p. 262).

Material

Ten specimens preserved as internal moulds in iron pyrites. Holotype selected as N.Y.S.M. 6679D.

Description

specimens	dimensions *D* (mm)	*WH* (mm)	*WH* (mm)	*UW* (mm)	*Wh* (mm)
N.Y.S.M. 6679D (holotype)	20·5	9·4	12·7	*ca.* 1·0	7·5
D. 1401	18·0	7·9	10·5	*ca.* 0	—
N.Y.S.M. 6679E	13·3	6·7	8·0	0	—
U.S.N.M. 137668	12·3	5·0	—	0	—
D. 1401	1·5	1·01	0·7	0·23	—

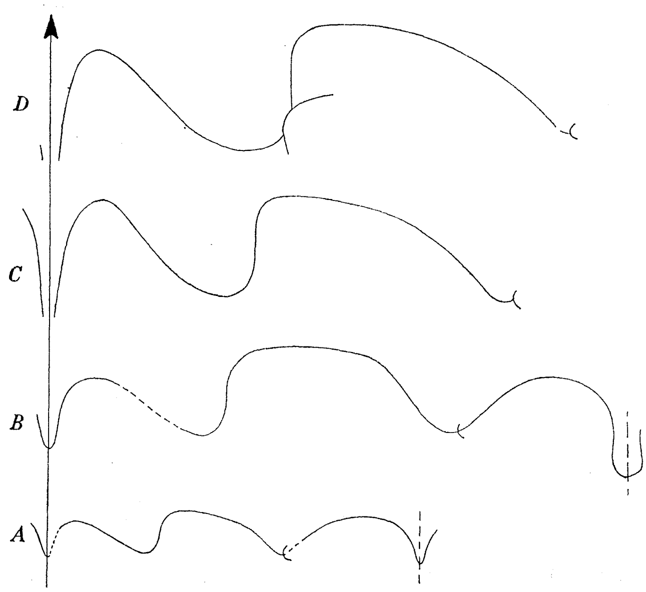

FIGURE 14. Diagrams illustrating the sutural development of *Tornoceras concentricum* sp.nov. from the Gowanda Shale at Corell's Point, Lake Erie shore. *A*, suture at 11·8 mm diameter based on U.S.N.M. 137668 (×4). *B*, suture at 12·9 mm diameter based on N.Y.S.M. 6679E (×4). *C*, suture at 20 mm diameter, a composite diagram from adjacent septa, based on N.Y.S.M. 6679D (×3·3). *D*, suture at 28 mm diameter based on U.S.N.M. 137667, reversed for comparison (×3·3). *E*, suture at 48 mm diameter based on N.Y.S.M. 11243, reversed for comparison (×3·15).

Protoconch 0·75 mm wide, *ca.* 0·55 mm in diameter (D. 1401, figures 109, 110, plate 10). Whorl section of the first whorl is well rounded with no evidence of ventro-lateral furrows. The nepionic constriction has been seen at 1·4 mm diameter (D. 1401) and shows a deep ventral sinus and is radial on the flanks (figures 105, 106, plate 10). The constriction is double both on the flanks and ventro-laterally. Immediately following the nepionic constriction ventro-lateral furrows appear, and these continue up to diameters of between 4 and 6 mm, after which they are lost (U.S.N.M. 137668, D. 1401 etc.). Stages above 10 mm diameter are characterized by flat flanks which converge towards a well-rounded venter. The largest specimen seen reaches 48 mm diameter and is still phragmacone (N.Y.S.M. 11243, figure 84, plate 9).

The prosuture has not been clearly seen. Early sutures show the typical highly arched, rounded saddle, but specimens examined show a deeper dorsal lobe, in the first whorl, than in other species of the genus. The adventitious adult type lateral lobe has developed by 1·8 mm diameter. By 8 mm diameter the steepness of the dorsal face of the lateral lobe is already apparent and is maintained and emphasized in the outer whorls (figure 14).

The growth lines of the nepionic whorl have not been clearly seen, but traces suggest they are more or less rectiradiate. After the nepionic constriction growth lines are concave on the flanks, form a projecting salient along the ventro-lateral furrows, and form a deep, linguiform sinus on the venter (figure 107, plate 10). This typical pattern apparently continues to the adult, but growth lines have not been observed above 15 mm diameter.

Remarks

The specific name draws attention to the extremely steep dorsal face of the lateral lobe which lies concentric to the umbilicus: this is diagnostic of the species. Only one protoconch has been examined, but this is markedly smaller than any other species of *Tornoceras* here studied. Similarly the development of ventro-lateral furrows in the early whorls is also distinctive and they are even more prominently developed than those in *Tornoceras* aff. *uniangulare* from the Windom Shale.

Pyritic moulds of the early whorls often do not show the suture, possibly owing in part to shell pyritization. The similarity of the early whorls of this species to those of *Aulatornoceras bicostatum* is obvious from the illustrations (figures 111 to 116, plate 10). This tempts the speculation that *A. bicostatum* and *T. concentricum* are dimorphic forms of one species, but there is little additional evidence to support such a view.

Specimens, horizon and locality

Specimens are known only from the lower Gowanda Shale at Corell's Point on the shore of Lake Erie, 2·85 miles W. of Brocton, Chautauqua Co., New York. Specimens include: U.S.N.M. 137667, 137668 collected by Mr W. Moran, N.Y.S.M. 11243 collected by J. M. Clarke and D. D. Luther in 1898, N.Y.S.M. 6679E collected by Dr L. V. Rickard, and D. 1358, 1401, 1428. The horizon is to be correlated with the lower *Cheiloceras* Stufe of Europe (House 1962).

(*n*) ***Tornoceras* (*Tornoceras*) *crebriseptum*** Raymond, figures 117 to 119, plate 11; figures 15, 18*C*.

Tornoceras crebriseptum (pars) Raymond (1909, p. 153, pl. 8, figs. 5 to 7, text-fig. 4).
T. douglassi Raymond (1909, p. 155, pl. 8, figs. 9–14, text-fig. 6).
T. (*Tornoceras*) *crebriseptum* Miller (1938, p. 149, pl. 38, figs. 7–16, text-fig. 32).

Miller (1938) has given a full synonymy of this species and followed Schindewolf (1934, p. 333) in considering that *T. douglassi* and *T. crebriseptum* are conspecific. The adult characters of the species have been described both by Raymond and Miller. The following account adds details concerning the ontogeny of the species.

Description

specimens	D (mm)	WW (mm)	WH (mm)	UW (mm)	S
U.S.G.S. G. Beck Coll.	34·2	13·3	16·2	5·5	*ca.* 22
D. 1462	22·1	9·3	11·6	—	—
C.M.P. 464 (Lectotype)	21·5	*ca.* 11·0	—	2·1	*ca.* 23
C.M.P. 476 (Raymond 1909, pl. 8, figs. 13, 14)	17·2	7·9	9·3	1·2	*ca.* 15
D. 1463	11·8	5·6	6·8	—	—
M.C.Z. 5220	9·2	4·3	4·9	0·7	12
C.M.P. 463 (Raymond 1909, pl. 8, figs. 5–6)	8·3	4·3	*ca.* 4·3	*ca.* 1·0	*ca.* 20
M.C.Z. 5221	5·2	3·2	—	0·7	—

(D, WW, WH, UW, S: dimensions)

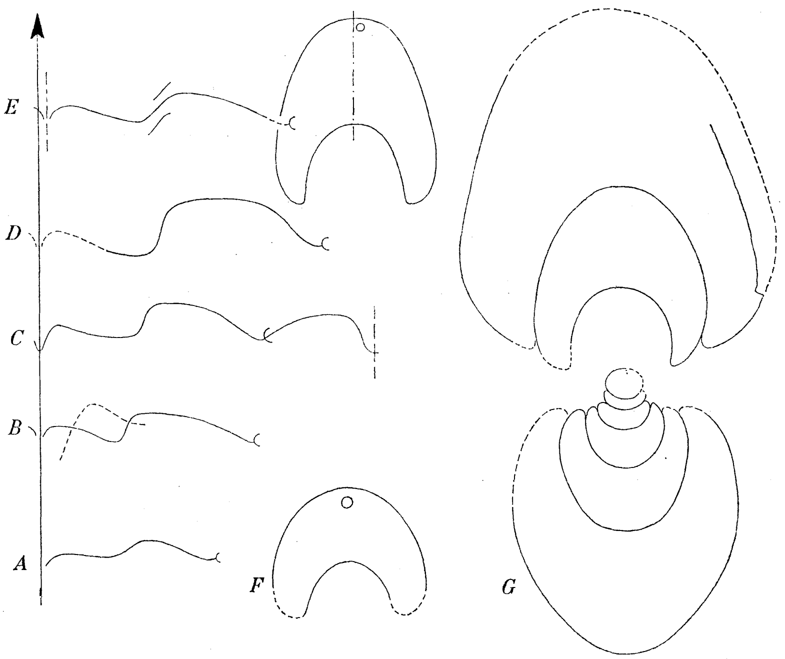

Figure 15. Diagrams illustrating the ontogeny of *Tornoceras* (*T.*) *crebriseptum* Raymond from the Three Forks Shale of Montana. *A*, suture at 2·5 mm diameter based on M.C.Z. 5228 (× 10). *B*, suture and growth line at 5·2 mm diameter based on M.C.Z. 5221 (× 6·7). *C*, suture at 17 mm diameter based on the holotype of *T. douglassi* (= *T. crebriseptatum*), C.M.P. 476 (× 2·7). *D*, suture at 20 mm diameter based on the holotype of *T. crebriseptatum*, C.M.P. 464 (× 2·7). *E*, suture and whorl section at 19·4 mm diameter based on M.C.Z. 5225 (× 2·3). *F*, whorl section at 2·5 mm diameter based on M.C.Z. 5228 (× 15). *G*, median section based on D. 1461 (× 6·2).

The protoconch has not been seen, but it is about 1 mm wide. Early whorls are markedly evolute (figure 15*G*), with a very depressed whorl section. A rotund form is reached, with *WW* = *WH*, at about 5 mm diameter; whorl section (figure 15*G*) at higher diameters with a broad, well-rounded venter, and flanks sloping convexly out to a maximum width about four-fifths of the way across. Umbilicus in mould open throughout ontogeny and progressively widening, maximum of 5·5 mm seen on a phragmocone of 34·2 mm diameter (U.S.G.S. G. Beck Coll.) which also shows orad approximation of septa, suggesting maturity. The relative changes in shell proportion are illustrated in figure 18*C*.

Very little trace of surface ornament is shown on the moulds. At 5·2 mm diameter a very deep, narrowly V-shaped ventral sinus is formed with a projecting rounded ventro-lateral salient and wide shallow lateral sinus (M.C.Z. 5221) and a similar pattern continues at least to 13·5 mm diameter (M.C.Z. 5226). There are traces on the mould of a faint spiral ridge along the venter (Miller 1938, p. 149).

The prosuture and early sutures have not been seen. By 2·5 mm diameter (M.C.Z. 5228) a shallow lateral lobe has formed, and by 5·2 mm diameter (M.C.Z. 5221) the typical asymmetric genuflexion of the adult lateral lobe is formed (figure 15*B*). At higher diameters in some specimens the latero-umbilical saddle becomes flat-topped and rather symmetrical, but in one specimen (M.C.Z. 5225, figure 15*E*), which may be pathological since the siphuncle is displaced, the whole suture at 19·4 mm diameter is remarkably flat. Septal frequency is usually high, commonly with over twenty camerae per whorl.

Remarks

Raymond separated two species in this fauna mainly on septal frequency, and his original specimens show that *T. crebriseptum*, as he conceived it, showed 20 or more septa per whorl above 8 mm diameter, whilst there are only 15 per whorl by 17 mm in *T. douglassi*. This distinction has not been substantiated, and insufficient specimens show the dorsal suture which he claimed to be 'broadly V-shaped' in *T. crebriseptum* and 'somewhat tongue-shaped' in *T. douglassi*, observations which were apparently based on a comparison of C.M.P. 463 at 8·3 mm diameter and C.M.P. 476 at 17·2 mm diameter. Schindewolf (1934) pointed out that one of Raymond's types (1909, pl. 8, fig. 8, C.M.P. 465) is a *Raymondiceras* and not *Tornoceras* and that another specimen, in which Raymond thought the 'suture line is exactly reversed', is a normal *Tornoceras* and merely incorrectly orientated.

The open umbilicus which progressively develops in this species might be considered grounds for including it in *Protornoceras*, but since all the specimens are internal moulds, it may well be that testate specimens would still have a closed umbilicus. Detailed discussion of this point must await more precise description of the Polish forms of approximately the same age recorded by Dybczynski (1913) and Sobolew (1913).

Specimens, horizon and locality

All specimens are from the Three Forks Shale of Montana and are from the Three Forks region. Specimens examined include: Raymond's types, C.M.P. 463, 464 (not 465 which is a *Raymondiceras*), 476, 517, 518, 526; twenty-two specimens (D. 1461–1483) collected by the author from the W. side of the main valley N. of Three Forks; eight specimens in a collection by W. Haynes in the M.C.Z. including M.C.Z. 5220–5227; a group of specimens in the collections of the U.S.G.S. collected by G. Beck and T. Dutro. It has not been possible to assemble sufficient specimens from the two divisions of the Three Forks Shale in which Raymond noted that this species occurs to test whether there are differences between them.

(3) Genus ***Epitornoceras*** Frech, 1902

The type-species by the original designation of Frech (1902, p. 51) is *Goniatites mithracoides* Frech (1887, p. 30). Both Miller (1938, p. 140) and Schindewolf (1933, p. 103) have regarded *Epitornoceras* as a synonym of *Tornoceras*. Separation at generic level is adopted here for three reasons. First, the pointed ventro-lateral saddle and deep, symmetrical lateral lobe which diagnose the genus make these forms easily recognized and distinguished. Secondly, there is evidence that the adolescent and adult stages were oxyconic, and hence very different from typical *Tornoceras*. Thirdly, the genus appears to be restricted to the lower Frasnian, that is the *lunulicosta* Zone and the lower part of the *cordatum* Zone, and hence is of stratigraphical significance.

(*o*) ***Epitornoceras peracutum*** (Hall), figure 73, plate 8; figure 13*C*.

Goniatites peracutus Hall (1879, pl. 69, fig. 8, pl. 74, fig. 13).
Tornoceras peracutum Clarke (1898, p. 118, fig. 96).
T. (*Tornoceras*) *peracutum* Miller (1938, p. 155, pl. 31, figs. 1, 2).

The holotype of this species (N.Y.S.M. 4091) was described by Miller (1938) and he was aware of no other specimens. Professor Wells has additional material in his collections, but the specimens are crushed and it is still not possible to give a full description of the species.

Description

	dimensions		
specimens	*D* (mm)	*WH* (mm)	*UW* (mm)
N.Y.S.M. 4091 (holotype)	—	41	0
C.U.P.L. 40105	240	—	0
C.U.P.L. 42401 (111 *g*)	*ca.* 174	—	0
C.U.P.L. 39652 (T. aff. *peracutum*, figured Harris 1899)	*ca.* 90	*ca.* 55	0

Shell form apparently oxyconic. All specimens part crushed, outer whorls only seen. Form involute with closed umbilicus (N.Y.S.M. 4091, C.U.P.L. 39652).

Ornament seen at 160 mm diameter with growth lines backwardly retracted across the flanks, without a ventro-lateral salient, forming a deep ventral sinus.

Suture with a broad V-shaped ventral lobe, an acutely pointed ventro-lateral saddle, a deep, well-rounded, almost symmetrical lateral lobe. Latero-umbilical saddle broad and almost symmetrical.

Remarks

Sufficient specimens are now available to affirm that the acuteness of the ventro-lateral saddle is not due to crushing. Further, evidence of oxyconic adult form is forthcoming. The large and deep lateral lobe serves to distinguish this species from all other American species. The depth of this lobe may vary somewhat with age, being shallower at the largest diameters. This is suggested by the specimen figured by Harris (1899, pl. 6, fig. 35, refigured herein, figure 13*H*), but until this can be demonstrated it is probably advisable to mark the distinction in this respect. C.U.P.L. 40105 is the largest tornoceratid known from the American Devonian, with a maximum diameter of *ca.* 240 mm. C.U.P.L. 42401 is of interest in showing, at the aperture, a backward deflexion of the growth lines across the flanks which become slightly more radial on the outer flanks, but they are deflected back, as usual into the deep ventral sinus. The available material is too poor to ascertain whether there are consistent differences between specimens from the Geneseo formation and those from the overlying Ithaca formation. There is no doubt, however, that the genus is represented in both divisions.

Specimens, horizon and localities

From the Geneseo formation C.U.P.L. 42401, from 40 ft. below the top of the formation in Lodi Glen, Seneca Co., N.Y., and C.U.P.L. 40105 (conforming to the species) from the top of the formation in Hubbard's Quarry, Seneca Co. From the Ithaca Formation, the holotype, N.Y.S.M. 4091, from Ithaca, N.Y., and C.U.P.L. 39652 from the same locality and horizon (showing affinity with this species).

(4) Genus **Aulatornoceras** Schindewolf, 1922

The type-species by original designation of Schindewolf is *Goniatites auris* Quenstedt. The group of species now generally referred to the genus is probably polyphyletic. Typical specimens of *A. auris*, like *A. rhysum*, show a rather tongue-shaped lateral lobe and are open umbilicate in the adult. In *A. bicostatum* and the European Givetian and Frasnian species best referred at present to *A. sandbergeri* (Foord & Crick 1897, p. 112, for *Goniatites retrosus* var. *undulatus* G. & F. Sandberger 1851 non *G. undulatus* Brown 1841) tend to have a more closed umbilicus and asymmetric lateral lobe. A revision of the genus is clearly desirable. Also necessary is an investigation of *Polonoceras* Dybczynski, which may be a senior synonym of *Aulatornoceras*.

(*p*) ***Aulatornoceras rhysum*** (Clarke), figures 120, 121, 124, plate 11; figure 13*F*.

Tornoceras rhysum Clarke (1899, p. 121, text-fig. 100, pl. viii, fig. 14).

T. (*Tornoceras*) *rhysum* Miller (1938, p. 156, pl. xxx, text-fig. 33).

Remarks

The lectotype is here designated as N.Y.S.M. 4092, that is, the only specimen which Clarke considered susceptible of illustration. It was described in detail by Miller (1938) and it is only necessary here to justify the revised generic assignment. Two additional specimens have been examined: another specimen of *A. rhysum* on the same block as the lectotype, and a fine specimen collected by I. G. Reimann, probably from the Hanover Shale (B.M.N.S. E 22464; figures 120, 121, plate 11). The holotype is an incomplete external mould which shows only poorly the development of a flattened venter, on which are developed festoon-like corrugations corresponding with the growth-line sinus. Ventro-laterally are paired grooves in which lie the projecting salients. The species therefore belongs to *Aulatornoceras*.

This species shows similarities to *A. auris*, from the Büdesheimer Schiefer. But from the few New York specimens available it would appear that in *A. rhysum* the festoons are stronger. There are several undescribed Frasnian forms of Devon and Belgium which resemble *A. rhysum* more closely.

Specimens, horizon and locality

The lectotype, N.Y.S.M. 4092, is labelled 'Hanover Shale, Java, Wyoming Co.' and *Manticoceras cataphractum* occurs in the same block with another example of *A. rhysum*. B.M.N.S. E 33464 is from Hampton Brook, above Hampton, N.Y.

(*q*) **Aulatornoceras bicostatum** (Hall), figures 111 to 116, plate 10; figures 125 to 137, 139 to 142, plate 11; figure 16.

Goniatites bicostatus Hall (1843, p. 246, text-fig. 107 (8)).

Tornoceras (*Aulatornoceras*) *bicostatum* (pars) Miller (1938, p. 167; pl. 14, fig. 5; pl. 32, figs. 1–4.)

Aulatornoceras bicostatum House (1962, p. 262).

It has been remarked elsewhere (House 1962) that the source of Hall's type for this species was almost certainly Corell's Point on the shore of Lake Erie where it has recently been found in a fauna with *Cheiloceras* (*C.*) *amblylobum* (G. & F. Sandberger) in the lower part of the Gowanda Shale. Both Clarke (1898, pp. 118 *et seq.*) and Miller in their descriptions of this species included material from various localities and horizons. The account below is based on the original types and topotypes alone, a total of twenty-two specimens.

Description

	specimens				
specimens	*D* (mm)	*WW* (mm)	*WH* (mm)	*Wh* (mm)	*UW* (mm)
D. 1359	1·12	0·93	0·62	0·4	—
D. 1360	1·3	0·85	0·6	0·43	0·34
D. 1359	5·0	2·8	3·1	—	—
D. 1364	6·2	3·2	3·2	—	—
A.M.N.H. 5888/1:2	7·3	—	3·1	—	1·8
N.Y.S.M. 6679A	13·7	6·7	7·4	—	*ca.* 1·7
D. 1363	15·3	7·5	8·5	—	1·9
U.S.N.M. 137667	*ca.* 18·0	—	*ca.* 8·8	—	*ca.* 2·6
N.Y.S.M. 6629C	18·2	8·7	8·5	—	1·9
N.Y.S.M. 6679B	21·1	8·8	10·5	—	2·9
A.M.N.H. 5888/1	22·5	—	*ca.* 11·3	—	—
A.M.N.H. 5888/1:1	*ca.* 25·0	10·5	12·3	—	2·8

The protoconch is small, 0·5 mm in diameter and 0·58 mm wide (D. 1360, figures 115, 116, plate 10). The first whorl gradually becomes involute and is about 25% of the diameter at the nepionic constriction which, in the specimens examined, is weak and occurs at about a diameter of 1·3 mm (D. 1359, D. 1360). Until this point the whorl section is broadly rounded, but after the constriction the ventro-lateral furrows appear and are well marked at all later stages of ontogeny. Until about 6·2 mm diameter, whorl width exceeds whorl height, but thereafter the reverse holds true. In the adult (figures 125, 131, 133, 134, plate 11; figure 16*D*) the ventro-lateral furrows are slightly laterally placed and have a sharp ridge within them. The spiral course of the furrow is often irregular (figure 128, plate 11).

Ornament on the nepionic whorl shows weak, slightly convex raised lines across the flanks and venter, and these are subrectiradiate. After the nepionic constriction a biconvex pattern is immediately established and this continues to the adult. The change is sudden and the ventro-lateral furrows appear immediately after the constriction, which is itself biconvex, agreeing with the post-nepionic growth lines, and often, but not invariably, double (figure 112, plate 10).

Full details of the sutural ontogeny have not been elucidated, and the prosuture has not been seen. But the adventitious lateral lobe develops during the course of the first whorl in the cases seen. The distinctive factors of the suture and observed ontogeny are given in figure 16.

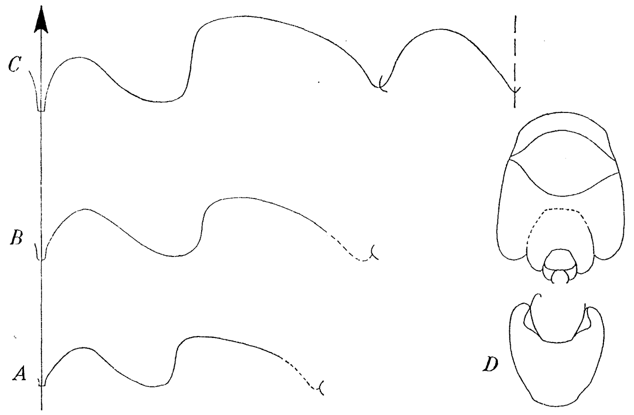

FIGURE 16. Diagrams illustrating the sutural development and shell form of *Aulatornoceras bicostatum* (Hall) from the Gowanda Shale at Corell's Point on the shore of Lake Erie. *A*, suture at 4·5 mm diameter based on D. 1364 (×5). *B*, suture at 12·5 mm diameter based on D. 1363 (×5). *C*, suture at about 20 mm diameter based on U.S.N.M. 137662 (×3·3). *D*, median section at 18·7 mm diameter based on N.Y.S.M. 6679 (×2).

Remarks

Although it has frequently been alleged, there is little similarity between *A. bicostatum* and *A. auris*, and there is a significant age-difference between the two species. *A. clarkei* differs in having a rather more evolute umbilicus, and in the development of strong ribs on the flanks.

Specimens, horizon and locality

The original types of Hall, and all the material here described, come from the lower Gowanda Shale at Corell's Point on the shore of Lake Erie, 2·85 miles west of Brocton, Chautauqua Co., New York. Material includes Hall's types, A.M.N.H. 5888/1 (Hall 1843, p. 245, fig. 8; 1879, pl. 72, fig. 9), 5888/1:1 (Hall 1879, pl. 72, fig. 8; pl. 74, fig. 1), 5888/1:2 (Hall 1879, pl. 72, fig. 10). Also U.S.N.M. 137667, N.Y.S.M. 6679 A, B, C (L. V. Rickard Coll.), 11238 (J. M. Clarke and D. D. Luther Coll. 1898), several specimens in the C.U.P.L. and D. 1357–64, D. 1422–24 collected by the author.

(*r*) ***Aulatornoceras clarkei*** (Miller), figures 122, 123, plate 11.

Gephyroceras cf. *G. domanicense* Clarke (1904, pp. 345, 380).
Manticoceras clarkei Miller (1938, p. 80, pl. 14, figs. 15–17).
Aulatornoceras clarkei House (1962, p. 262).

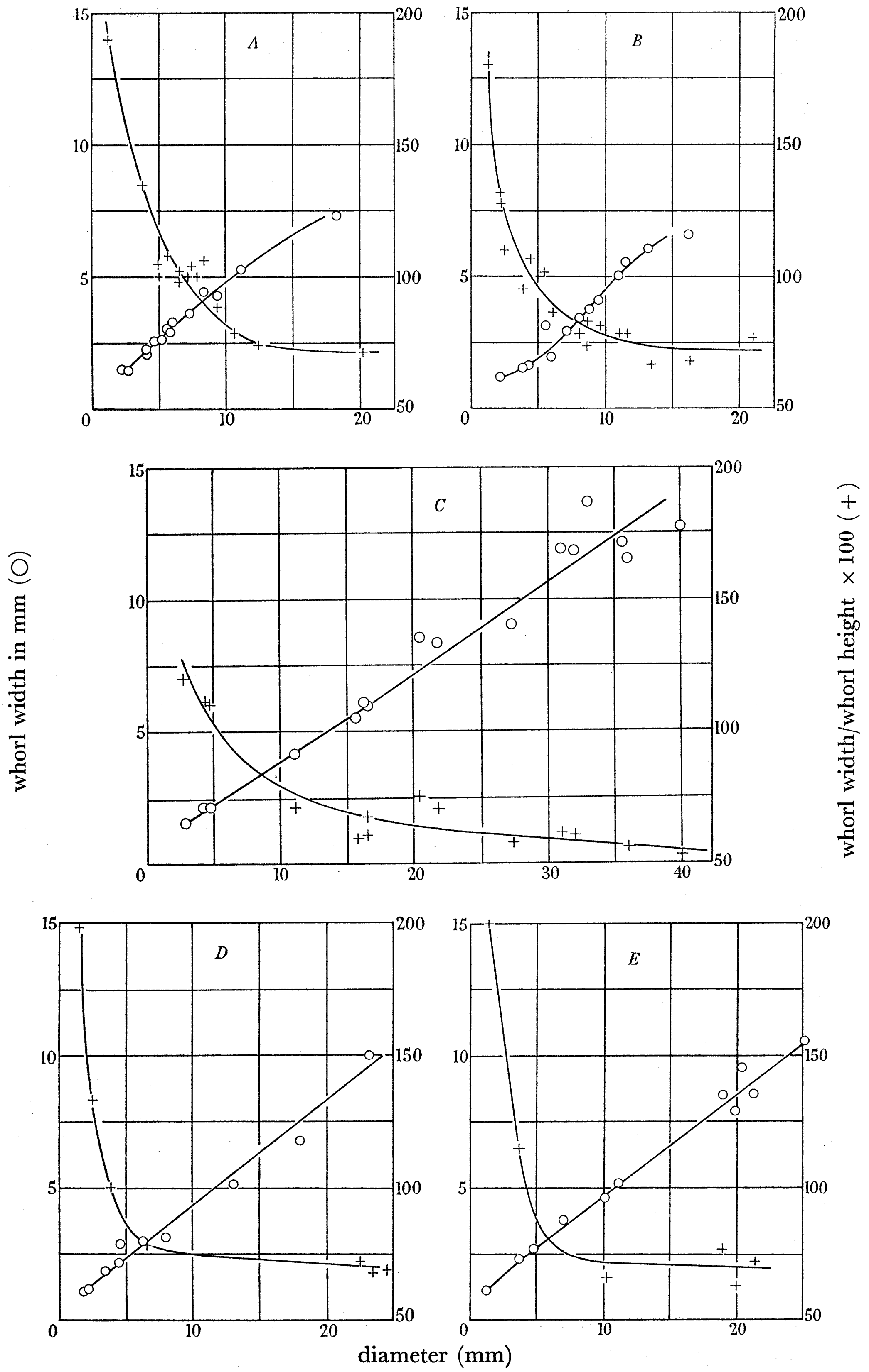

FIGURE 17. Graphs illustrating the shell ontogeny of: *A*, *Tornoceras* (*T.*) *arkonense* from the Arkona Shale; *B*, *T.* (*T.*) *uniangulare widderi* from the Widder Shale; *C*, *T.* (*T.*) *amuletum* from the Ledyard Shale; *D*, *T.* (*T.*) *arcuatum* from the Squaw Bay Limestone; *E*, *T.* (*T.*) *uniangulare uniangulare* from the Leicester Pyrite.

Remarks

No material other than the type-specimens has been examined and these were described both by Clarke and by Miller. None of the types shows the suture and in the absence of this generic assignment might be considered uncertain, but the ventro-lateral furrows and the ribbing on the flanks suggest that they should be referred to *Aulatornoceras*. They are quite close to the type-specimens of *A. bicostatum*, but differ in having a wider umbilicus and strongly marked periodic ribbing on the flanks.

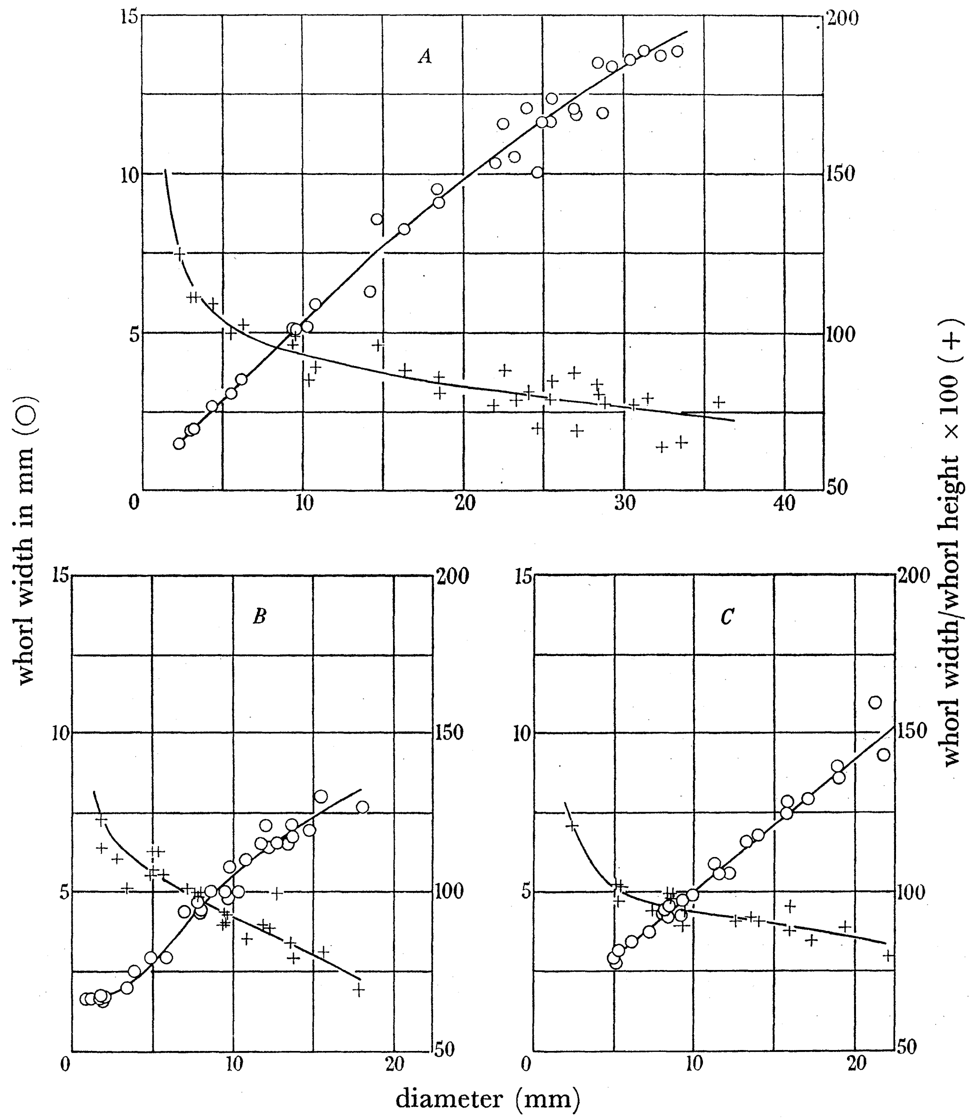

FIGURE 18. Graphs illustrating the shell ontogeny of: *A*, *T.* (*T.*) *uniangulare compressum* from the Genundewa Limestone; *B*, *T.* (*T.*) *uniangulare obesum* from the Cashaqua Shale; *C*, *T.* (*T.*) *crebriseptum* from the Three Forks Shale. Conventions as for figure 17.

Specimens, horizon and locality

The specimens (N.Y.S.M. 5652–5654) are all from Forestville, Chautauqua Co., N.Y., probably from either the upper Gowanda Shale, the Laona Siltstone or the Westfield Shale.

The specimen has a museum label of recent date which gives the horizon as the Gowanda Shale, but it has not been confirmed that this is the correct horizon.

VI. Evidence of the evolution of *Tornoceras*

From the analyses of successive representatives of the Tornoceratidae in North America certain general features of the evolution of the *Tornoceras* stock emerge which will now be summarized. Full comparisons with forms from other continents and a general synthesis must await a fuller description of those forms.

(*a*) *The origin of the Tornoceratidae*

Attention has been drawn to the similarity between *Parodiceras* and early members of *Tornoceras*, which succeed it in time. *Parodiceras* also occurs in Europe and North Africa and is widespread especially near the Eifelian/Givetian boundary: apparently everywhere it precedes *Tornoceras* in time. In *Parodiceras* the suture shows a weak ventro-lateral saddle and a lateral suture which is convexly retracted, showing no well-developed ventro-lateral lobe. The earliest *Tornoceras* studied in detail, *T. arkonense*, shows a transition between *Parodiceras* and *Tornoceras* in this respect. Separation of *Parodiceras* into a separate family, as has been proposed by Petter, is unwarranted and it seems reasonable to infer that *Parodiceras* is ancestral to the later tornoceratids. The precise origin of *Parodiceras* is obscure, but it was most probably derived from involute Eifelian anarcestids.

(*b*) *Evolution in the genus* Tornoceras

The successive faunas of *Tornoceras* which have been examined give little evidence of distinctive trends consistently maintained from one population to another. Rather it appears that each fauna may be defined in morphological terms, but that there is no clear successive pattern. Some general trend can be observed, however, in the changes in form and absolute size of the protoconch and in the general form of the suture. Changes in these features will now be discussed.

(1) *Protoconch*

Changes in the overall dimensions of the protoconch are summarized in an accompanying table (table 1). Attention is drawn to the fact that few specimens were available which showed all dimensions and it has not been possible to analyse variation in the protoconch form and size for this reason.

Table 1. Data on protoconch dimensions for *Tornoceras*

	diameter (mm)	width (mm)
T. (*T.*) *crebriseptum*	—	*ca.* 1·0
T. (*T.*) *concentricum*	*ca.* 0·55	0·75
T. (*T.*) *arcuatum*	0·73	1·3
T. (*T.*) *uniangulare uniangulare*	*ca.* 0·78	1·0
T. (*T.*) *uniangulare aldenense*	0·98–1·0	1·0–1·1
T. (*T.*) *uniangulare widderi*	—	0·93–0·95
T. (*T.*) *arkonense*	0·8	0·82–0·85

Clarke stated that the protoconchs of American Middle Devonian specimens of *Tornoceras* were smaller than those from the Upper Devonian. The present evidence suggests that through the Middle Devonian and Lower Frasnian there is a steady increase in the protoconch width, but that the diameter shows no regular change. The protoconch of the earliest form *T. arkonense* (figure 3*J* to *L*) has a sub-barrel-shaped form and at higher horizons the protoconch appears to become more ovate and rotund. Also the proseptum of *T. arkonense* shows a sharp fold within it (figure 3*L*) and this is seen also in *T. uniangulare aldenense* (figure 89, plate 10), but at higher levels the proseptum appears to be more evenly concave.

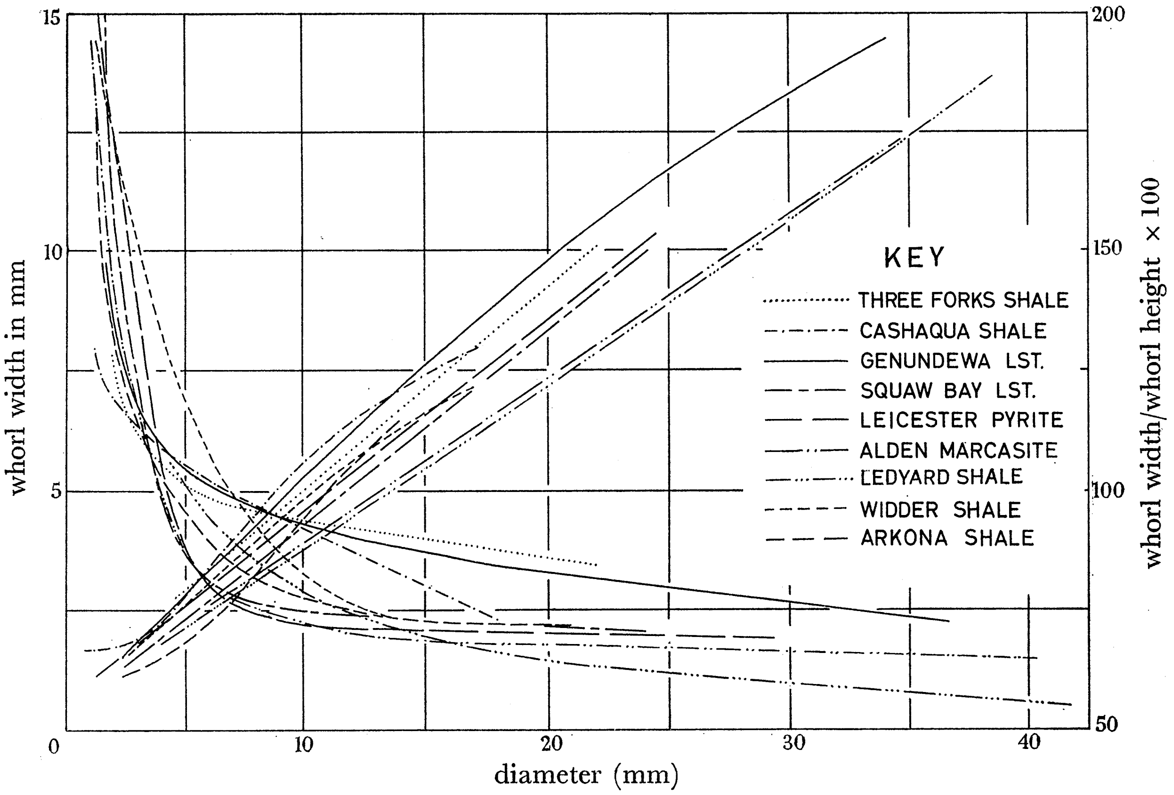

FIGURE 19. Diagram collating regressions drawn by observation on figure 17*A* to *E* and figure 18*A* to *C*, for *Tornoceras* from the horizons indicated.

(2) *Shell form*

The analyses of shell development which have been made are of particular interest in showing no regular pattern of evolutionary change between successive populations. The variation and mode at particular horizons are usually distinct, but independent from those at other levels. This can most reasonably be interpreted as evidence that successional differences are due to phenotypic variation among the successive populations varying independently according to environmental conditions during ontogeny. Graphical relations based on regressions qualitatively are collated in figure 19. The relation between whorl width and diameter has been analysed statistically for the successive populations on the assumption of an isometric regression of the form $y = ax+b$ (where x = diameter and y = whorl width) and the quantitative results are given in table 3. It should be observed that in some cases the relation clearly is not isometric for, example in *T. uniangulare widderi* (figure 15), although it approaches regularity in all cases as the correlation coefficients (r) show. Tests of significance based on the assumption of a regular regression using the statistic z have been made between the populations, each with each, and the results are given in table 3. Values above 1·95 are to be regarded as significant. When these are taken in conjunction with the changes in the whorl width/whorl height ratio against diameter (figures 17, 18, 19) it is apparent that some assemblages can be separated from others on shell development alone. This confirms that the populations may well be biocoenoses.

Table 2. Statistics for assemblages of certain species and subspecies of *Tornoceras* described in the text

	N	$\bar{x}$	$\bar{y}$	s_x	s_y	r	a	b
T. (*T.*) *arkonense*	14	6·81	3·33	4·02	1·49	0·990	0·376	+0·778
T. (*T.*) *u. widderi*	13	8·86	3·90	4·98	2·17	0·990	0·440	+0·00
T. (*T.*) *u. aldenense*	12	8·45	4·04	10·49	4·12	0·979	0·401	+0·645
T. (*T.*) *amuletum*	16	21·77	7·79	11·80	3·93	0·976	0·341	+0·546
T. (*T.*) *uniangulare uniangulare*	11	13·11	5·88	7·94	3·08	0·992	0·391	+0·757
T. (*T.*) *arcuatum*	11	11·42	4·74	11·10	3·92	0·986	0·354	+0·656
T. (*T.*) *u. compressum*	32	19·64	9·21	10·13	4·19	0·988	0·419	+0·983
T. (*T.*) *u. obesum*	31	8·44	4·59	4·49	2·11	0·981	0·480	+0·540
T. (*T.*) *crebriseptum*	24	12·92	6·18	6·69	2·66	0·983	0·404	+0·961

Table 3. The discriminating statistic z for comparisons between assemblages of certain species and subspecies of *Tornoceras*. Figures greater than 1·95 represent probability levels less than 5 %

	T. (*T.*) *u. widderi*	*T.* (*T.*) *u. aldenense*	*T.* (*T.*) *amuletum*	*T.* (*T.*) *uniangulare uniangulare*	*T.* (*T.*) *arcuatum*	*T.* (*T.*) *u. compressum*	*T.* (*T.*) *u. obesum*	*T.* (*T.*) *crebriseptum*
T. (*T.*) *arkonense*	**2·88**	0·95	1·52	0·54	0·91	1·84	**4·77**	1·38
T. (*T.*) *u. widderi*	—	1·30	**4·02**	1·64	**3·43**	1·00	1·67	1·54
T. (*T.*) *u. aldenense*	—	—	**2·05**	0·31	1·58	0·66	**2·70**	0·09
T. (*T.*) *amuletum*	—	—	—	1·68	0·54	**3·73**	**5·73**	**2·72**
T. (*T.*) *uniangulare uniangulare*	—	—	—	—	1·21	1·04	**3·02**	0·46
T. (*T.*) *arcuatum*	—	—	—	—	—	**3·04**	0·51	**2·10**
T. (*T.*) *u. compressum*	—	—	—	—	—	—	**3·00**	**2·57**
T. (*T.*) *u. obesum*	—	—	—	—	—	—	—	**3·35**

(3) *The form and ontogeny of the suture line*

Through the Middle Devonian horizons there appears to be a general trend towards increasing the steepness of the ventrad face of the latero-umbilical saddle. But this is not constant in degree, for example, *T. uniangulare aldenense* shows a sharper flexure from the ventrad face to the saddle crest than is found in the later *T. uniangulare uniangulare*. Little pattern can be seen in the successional ontogenies except that *T. arkonense* shows a significantly slower development of the lateral lobe than subsequent species.

The basic Middle Devonian stock with markedly asymmetric lateral lobes and a steep-faced latero-umbilical saddle certainly continues through the Frasnian to *T. concentricum* of the lower Famennian, but examples in the American Frasnian are sparse and mostly insufficient for critical analyses. In Europe, however, this type occurs commonly in the

Frasnian. It is to be supposed that from this basic stock other groups, regarded here as subgenera, arose. *T. arcuatum*, of the lowest Frasnian of Michigan, with its broad, nearly symmetrical lateral lobe appears to be a likely ancestor for *Epitornoceras* which occurs near the *lunulicosta/cordatum* Zone boundary, but this genus is distinguished by a sharply acute ventro-lateral saddle, and by an oxyconic form. Also from the basic stock must have arisen *Linguatornoceras*, a distinctive Frasnian and lowest Famennian group with a small linguiform lateral lobe and flat-topped ventro-lateral saddle. *T.* (*L.*) *haugi* is recorded from the lowest Fammenian and seems to be the youngest member of the group.

The Three Forks Shale *T. crebriseptum*, probably of *delphinus* Zone age (House 1962, p. 262), is of interest in showing a reversion to a subdued suture form. Further, adult specimens occasionally show an opening of the umbilicus. These two factors combine to suggest that *T. crebriseptum* is transitional between typical *Tornoceras* and species of *Protornoceras*. Indeed, the type-species of *Protornoceras* is *P. polonicum* from Kielce in the Holy Cross Mountains and Dybczynski recorded with the type-species '*Rectoclymenia*' and '*Anarcestes nuciformis*'. The former genus has recently been identified in the Three Forks Shale fauna (House 1962) and the latter is suggestive of *Raymondiceras*, in which case the faunal similarity is strengthened. The upper Givetian *Protornoceras foxi* (House 1963) is probably independently derived from *Tornoceras* s.s.

(4) *Growth lines and ornament*

Attention has already been drawn to the fundamental difference between the growth-line pattern of the nepionic whorl and that of later stages. Analyses of growth-line development in the successive populations has been handicapped by the fact that pyritic material, which has formed a substantial basis for the study of sutural and shell morphology, in general does not preserve shell ornament except to the limited extent by which this may be shown on internal moulds. The sub-linear, slightly rectiradiate pattern on the flanks which characterizes *Parodiceras* is not unusual in the older stages of *Tornoceras* s.s., although the early stages invariably show a markedly biconvex growth line. Simplification of the aperture is also a feature of adult *Epitornoceras*. Insufficient material was available to show whether the distinctive pattern, with no lateral sinus, seen in *T. uniangulare aldenense* (figure 5*G*), is shown by other upper Hamilton forms, particularly by the genotype.

(5) *Wrinkle layer*

Specimens of *Tornoceras* from several horizons show evidence of the wrinkle layer, especially those from the Squaw Bay Limestone (figure 71, plate 8), the Ledyard Shale (figure 42, plate 6), and the barytized specimens from the Cashaqua Shale (figure 72, plate 8). It has not been observed on pyritized specimens. The evidence shows that it forms a distinct, thin layer laid down in the body chamber, extending close to the aperture —and deposited dorsally, on top of the preceding whorl. The pattern is distinctive and forms backwardly directed spirals across the lower flanks which become sub-radial on the outer flanks (figure 78, plate 9). No significant differences has been noted between the various species and subspecies. Interest lies in the few other genera which show this unusual pattern. *Parodiceras* shows a similar pattern, confirming that it is closely related to *Tornoceras*. So also does *Cheiloceras* (House & Pedder 1963, p. 530) and this, together with the similar type of sutural ontogeny, leads to the suggestion that the Cheiloceratidae was derived from the Tornoceratidae merely by the adoption of convex growth lines. Evidence has been presented herein to show that in the *Tornoceras* stock at several levels there was a tendency to lose the usual marked biconvexity of the growth lines, and hence the permanent adoption of such a character is not unlikely.

List of abbreviations used in the text

Measurements

BC	maximum length of body chamber in degrees
D	diameter measured across the umbilicus (mm)
UW	umbilical width
S	number of septa in the previous complete whorl
WH	whorl height at the stated diameter (mm)
Wh	distance (mm) between the ventral crest of one whorl and that of the succeeding whorl at the stated diameter
WW	Whorl width at the stated diameter (mm)

Repository of collections

A.M.N.H.	American Museum of Natural History, New York.
B.M.N.S.	Buffalo Museum of Natural Sciences, Buffalo, N.Y.
C.M.P.	Carnegie Museum, Pittsburgh, Pennsylvania.
C.U.P.L.	Cornell University Paleontological Laboratory, Ithaca, N.Y.
D.	Author's collection, now deposited in the N.Y.S.M.
M.C.Z.	Museum of Comparative Zoology, Cambridge, Massachusetts.
M.M.P.	Michigan University Museum of Paleontology, Ann Arbor, Michigan.
N.Y.S.M.	New York State Museum, Albany, N.Y.
O.C.	Oberlin College Dept. of Geology and Geography, Oberlin, Ohio.
P.M.Y.	Peabody Museum, Yale University, New Haven, Connecticut.
S.M.	Sedgwick Museum, Cambridge.
U.C.B.	Geology Department, University of California, Berkeley, California.
U.S.G.S.	United States Geological Survey, Washington, D.C.
U.S.N.M.	United States National Museum, Washington, D.C.

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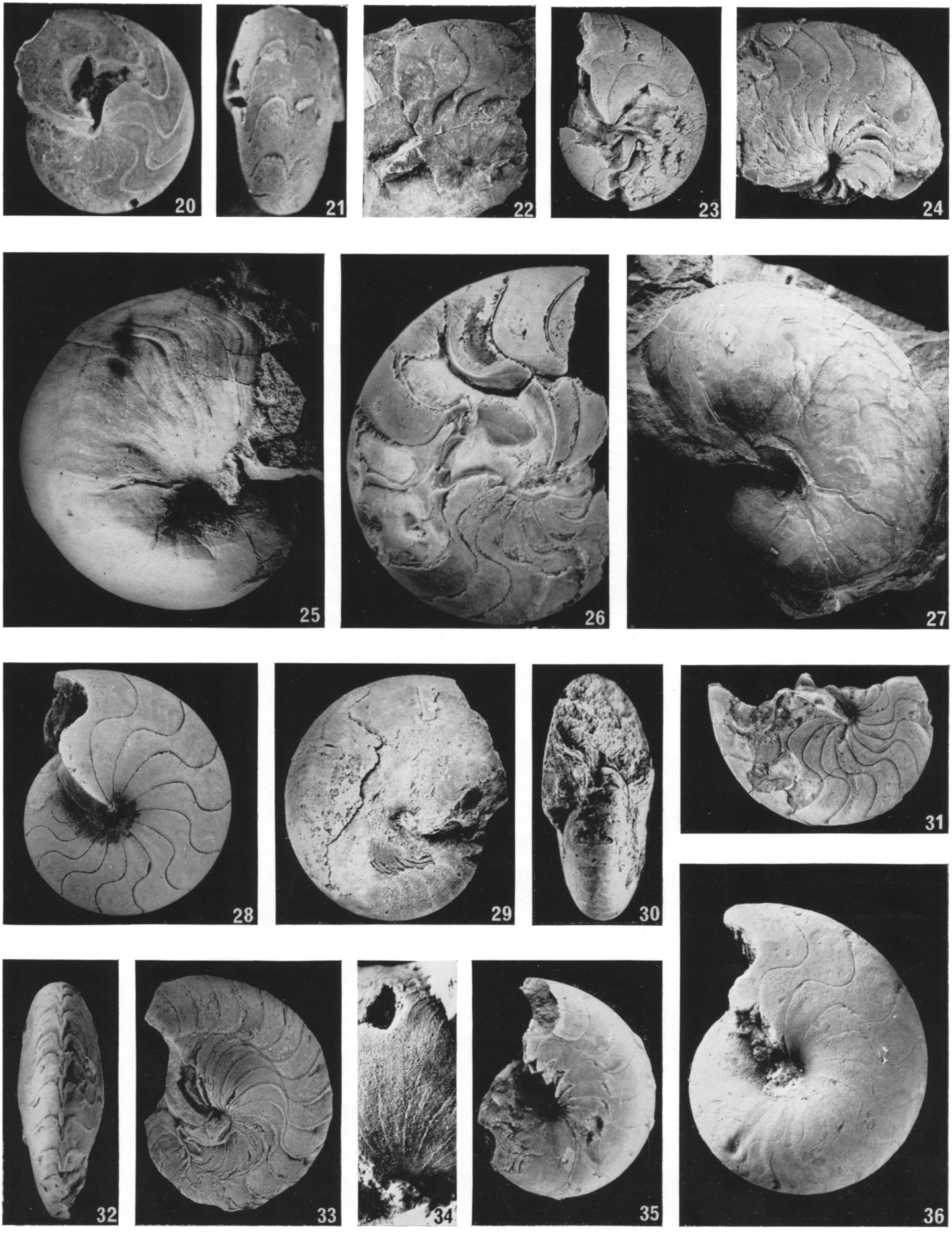
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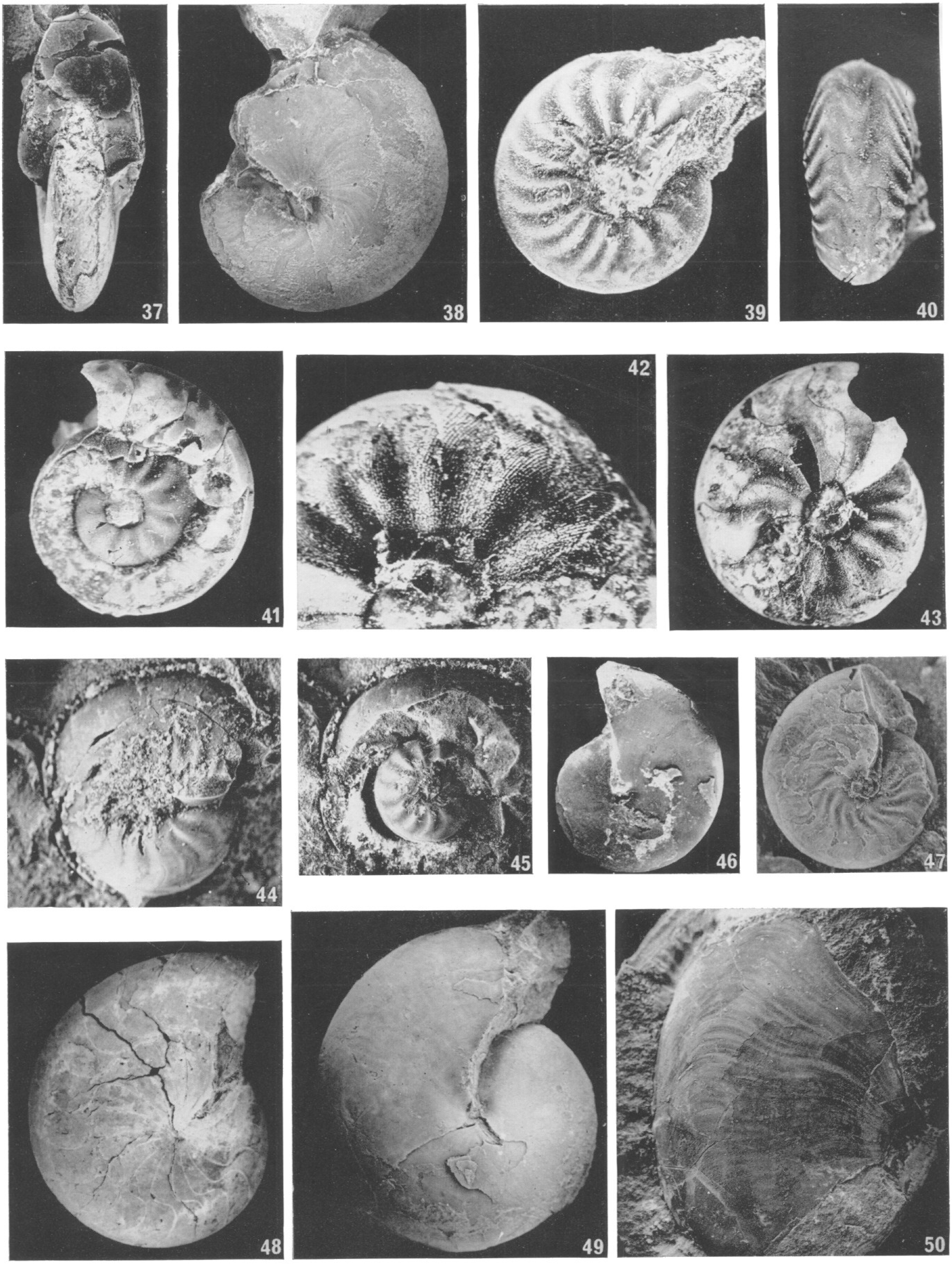
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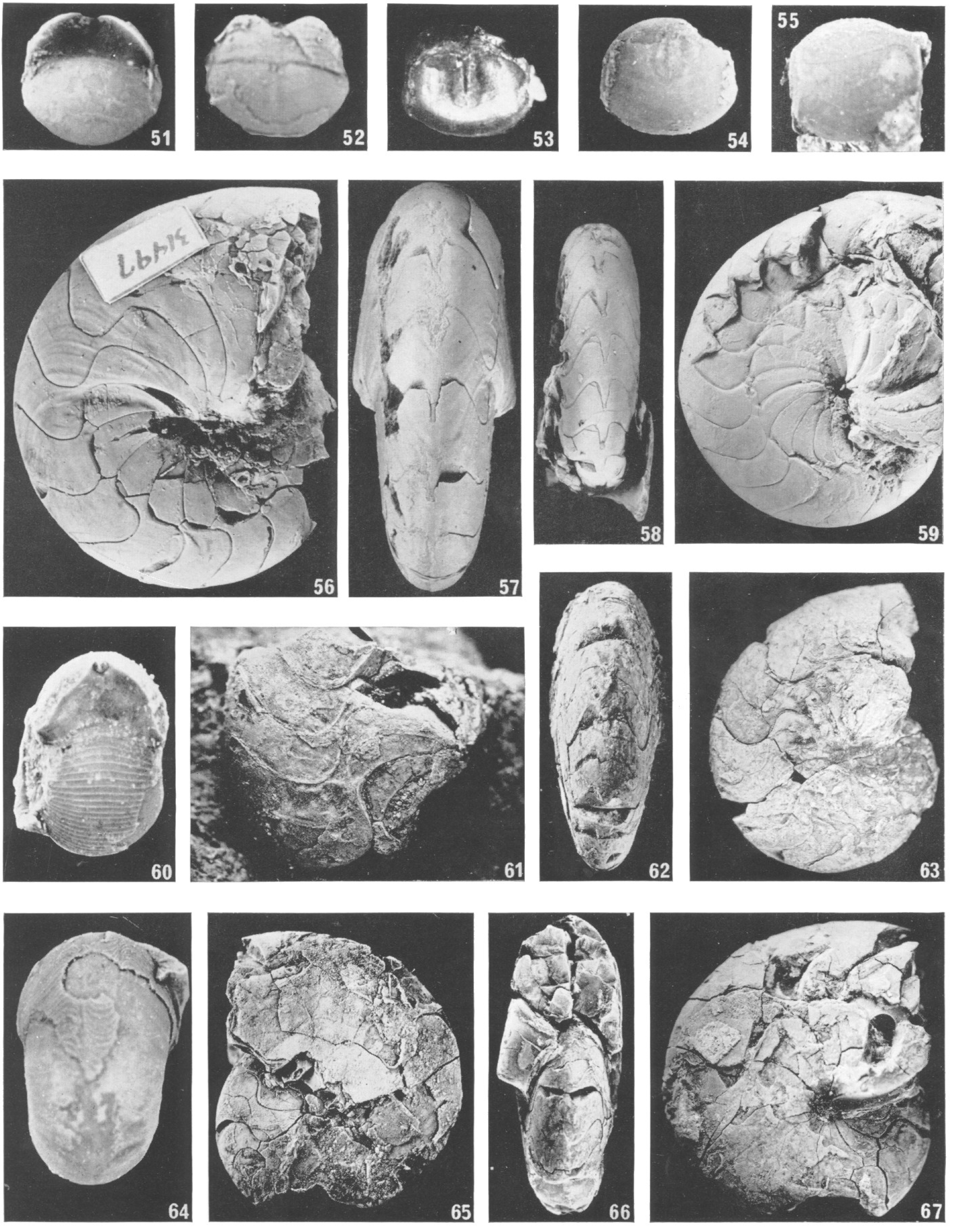
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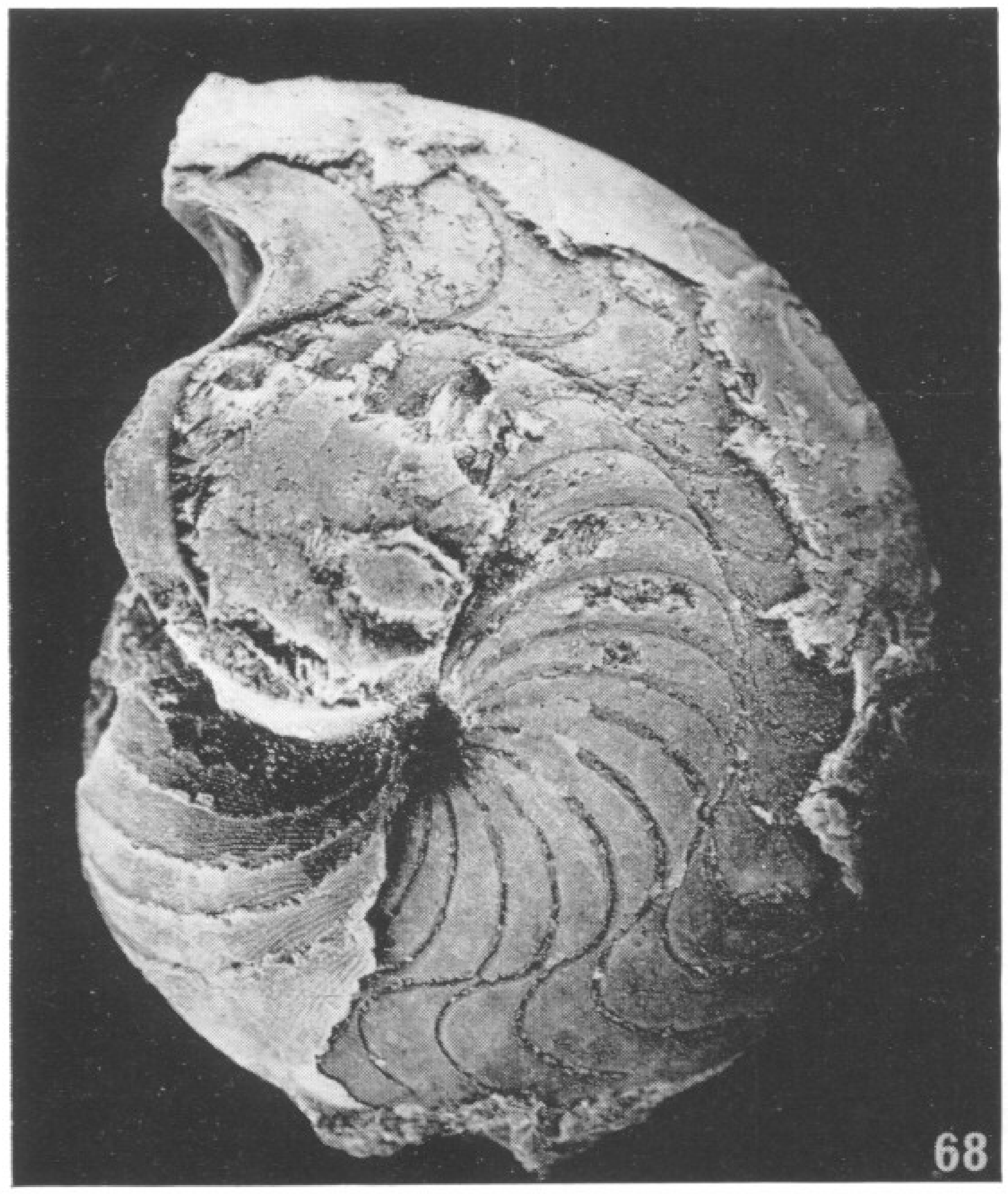
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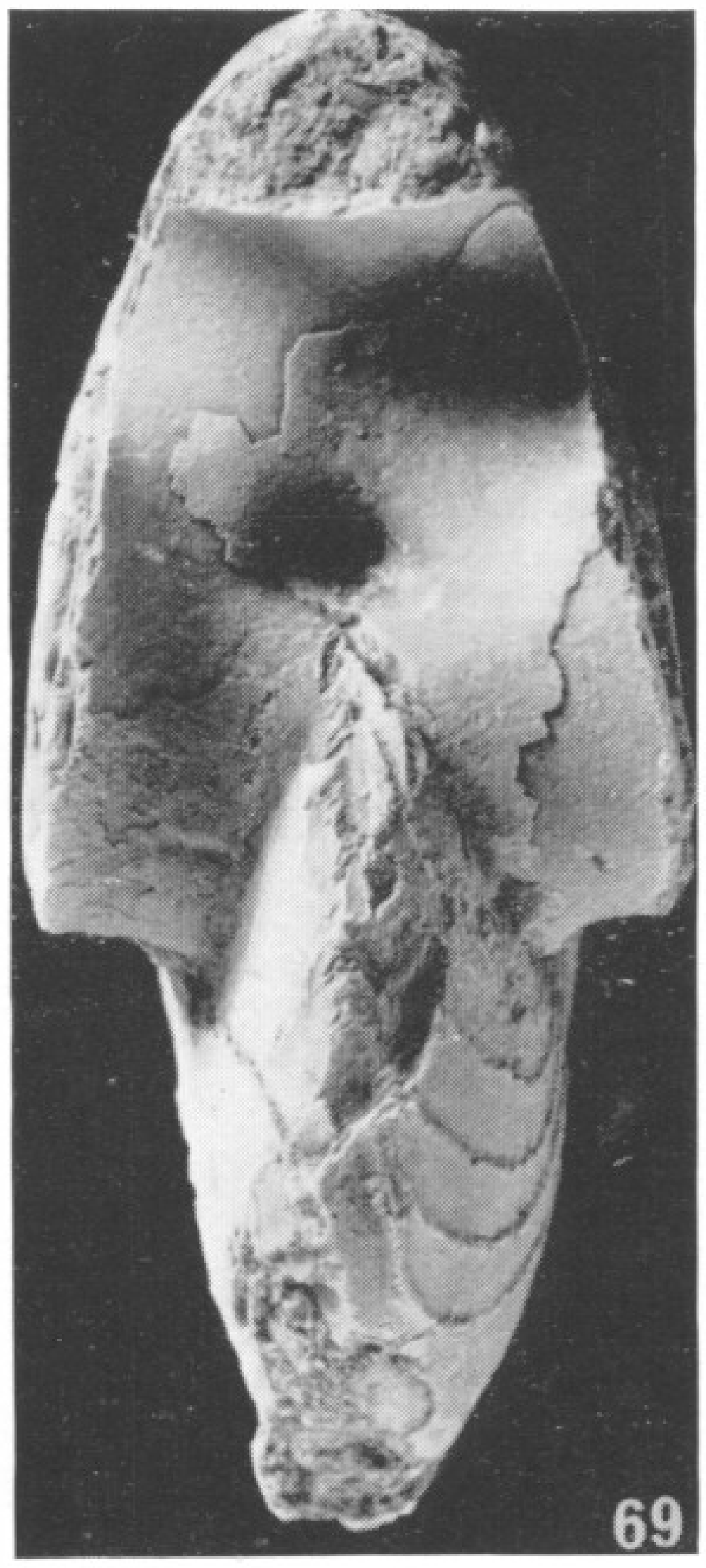
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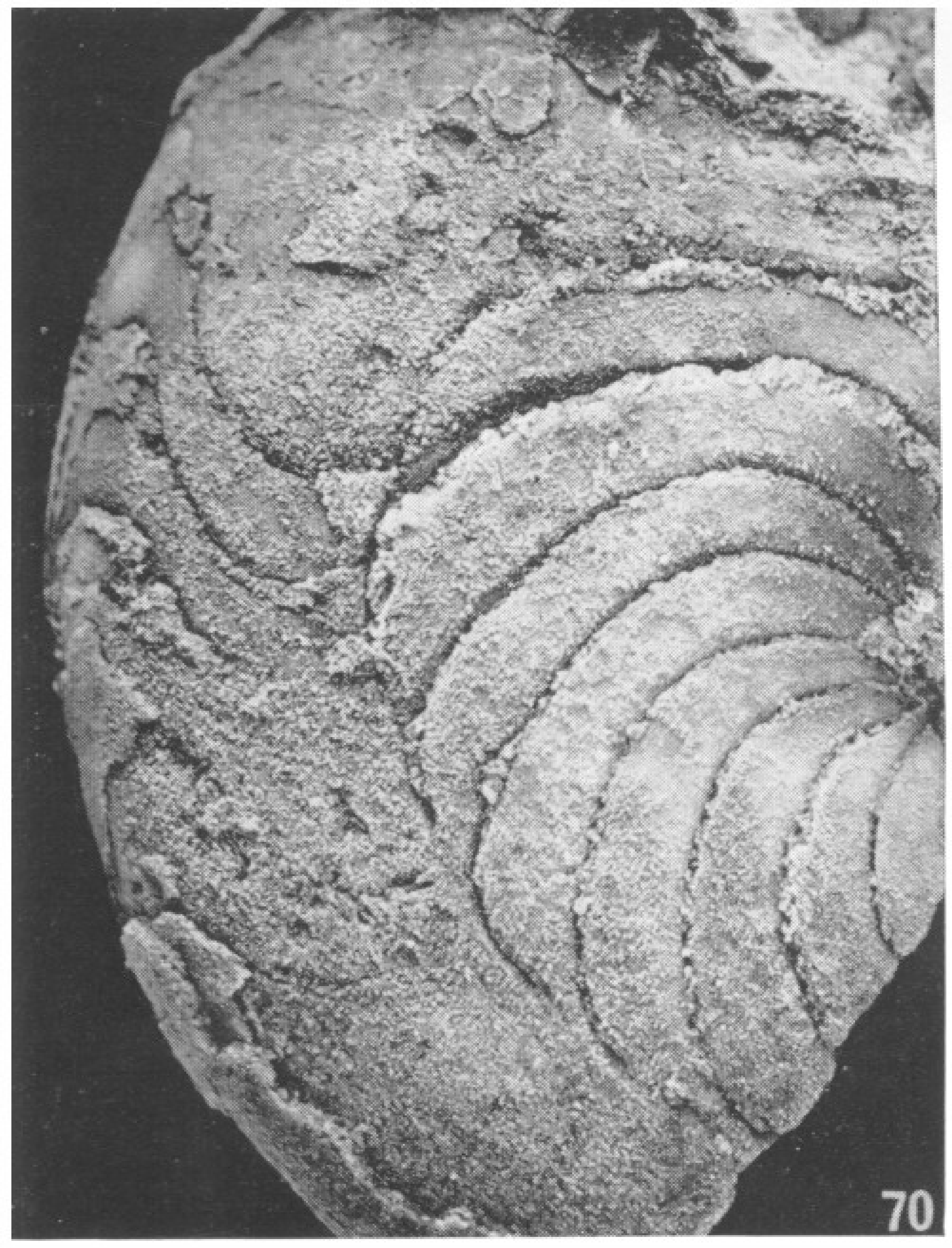
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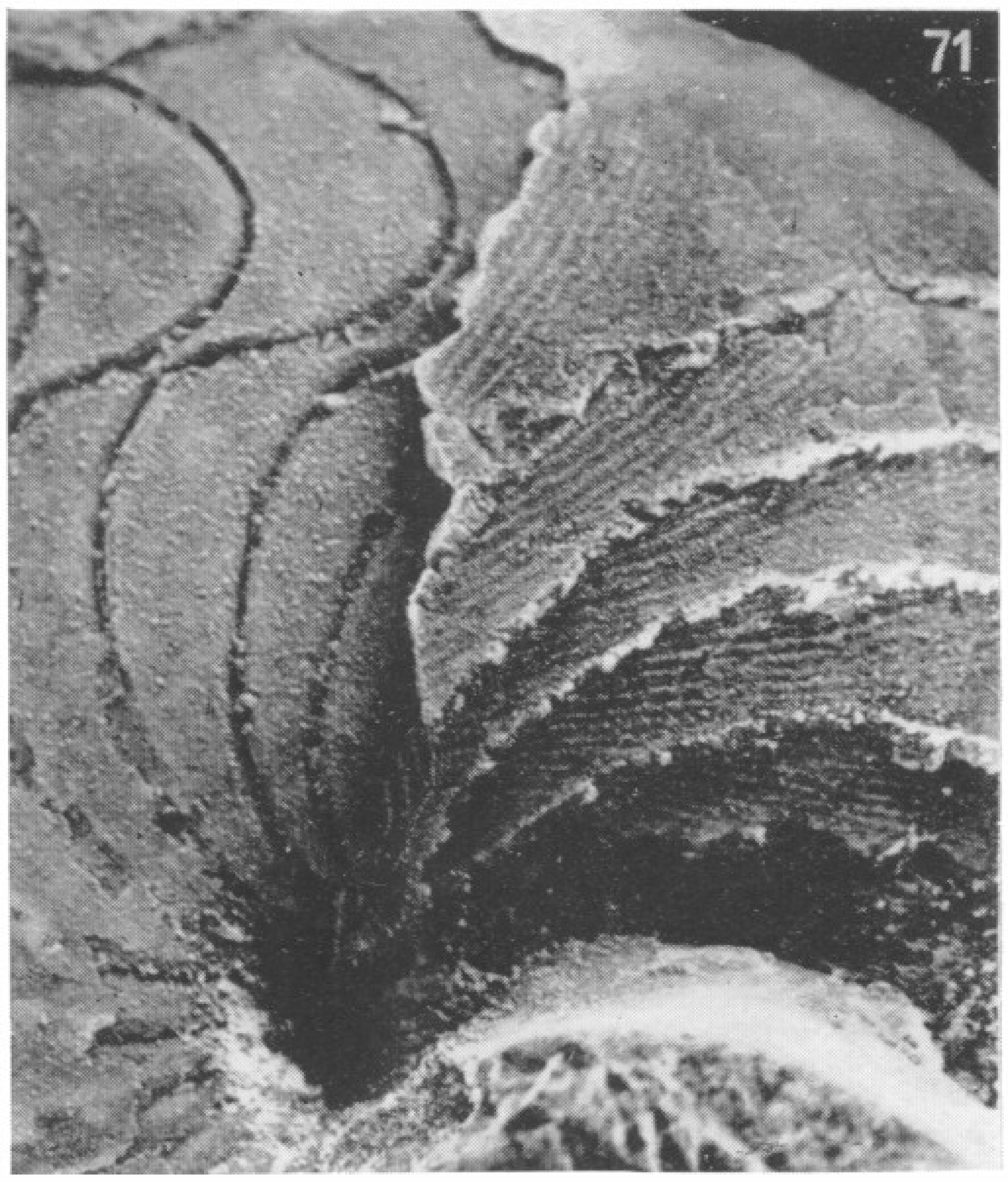
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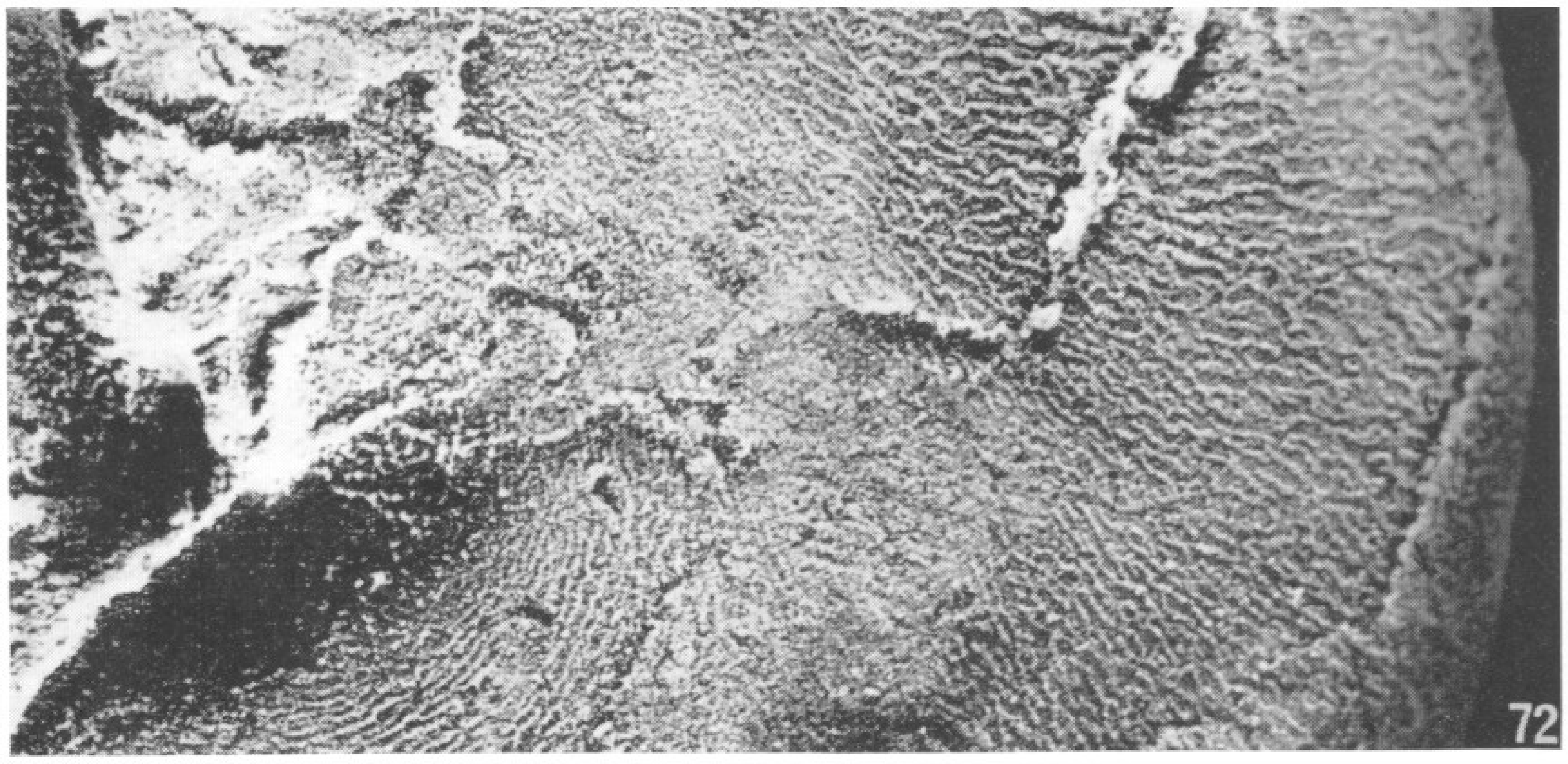
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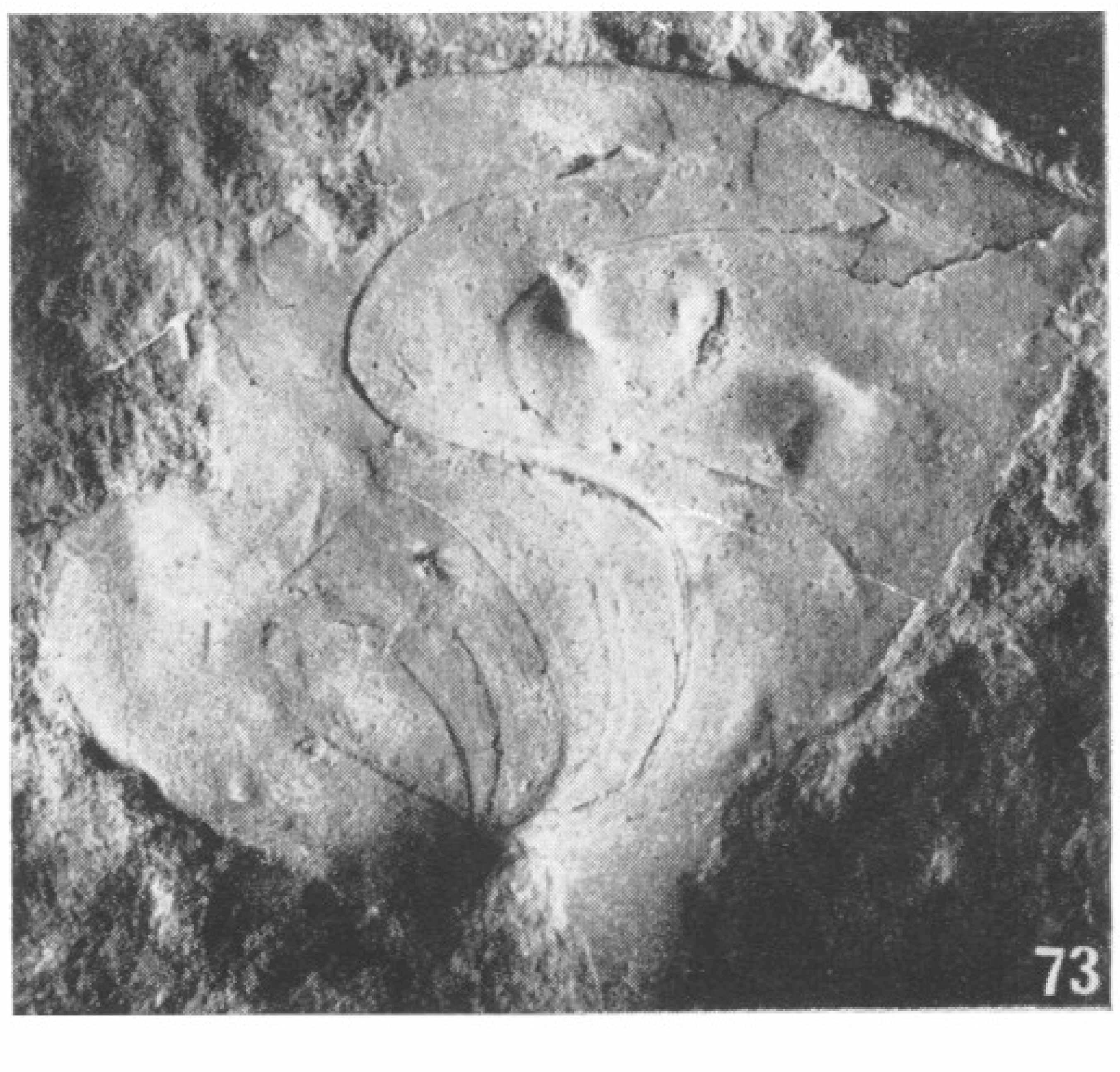
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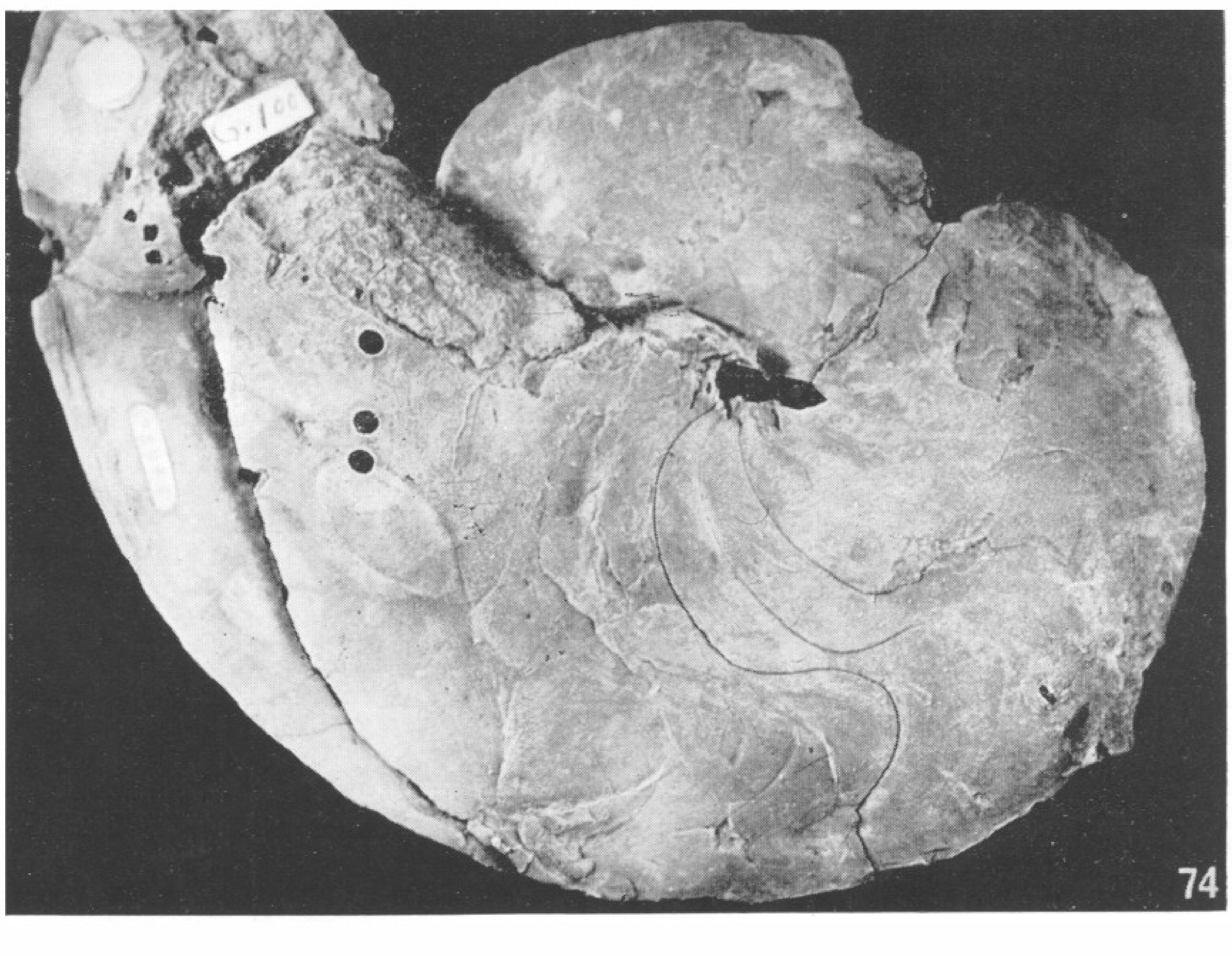

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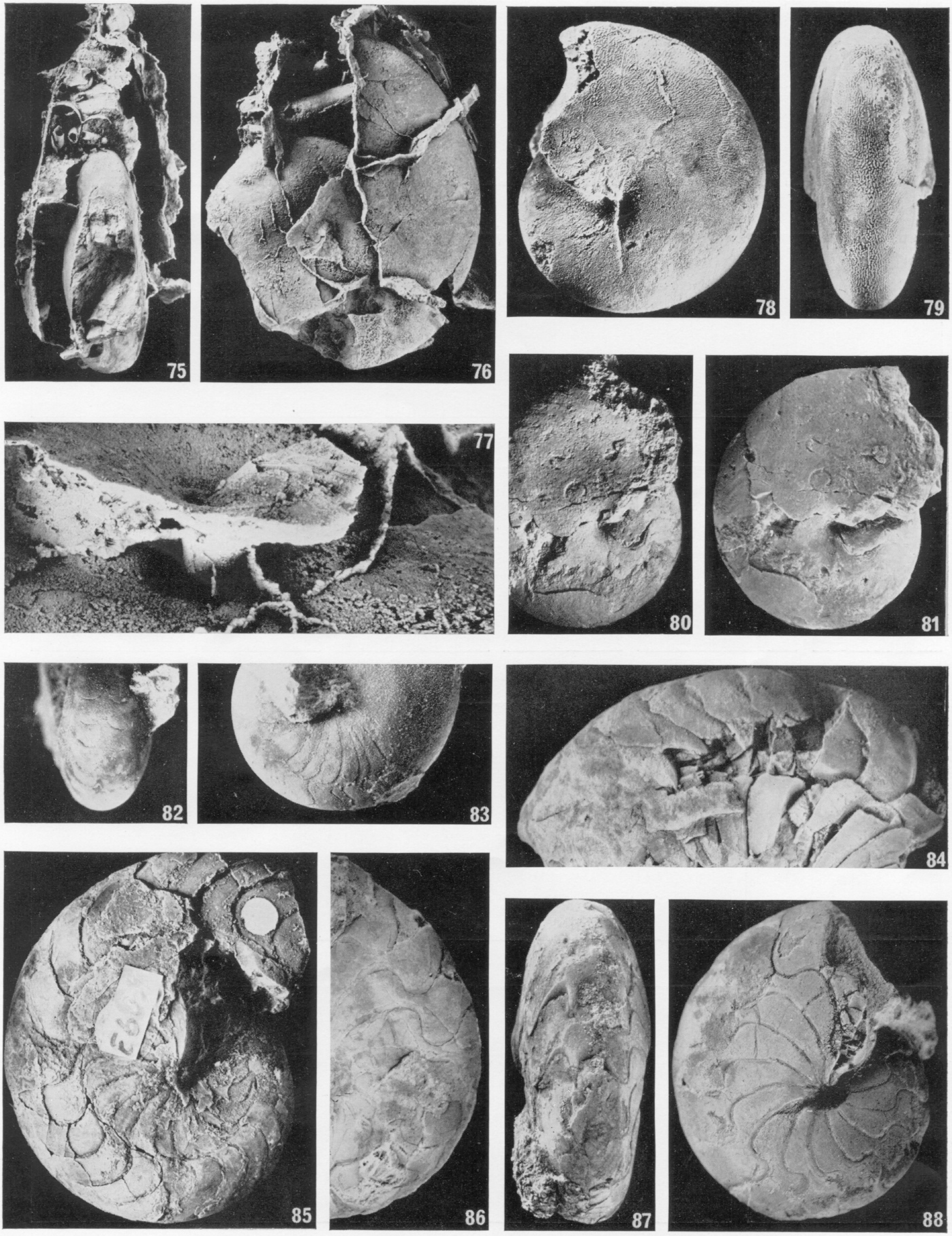
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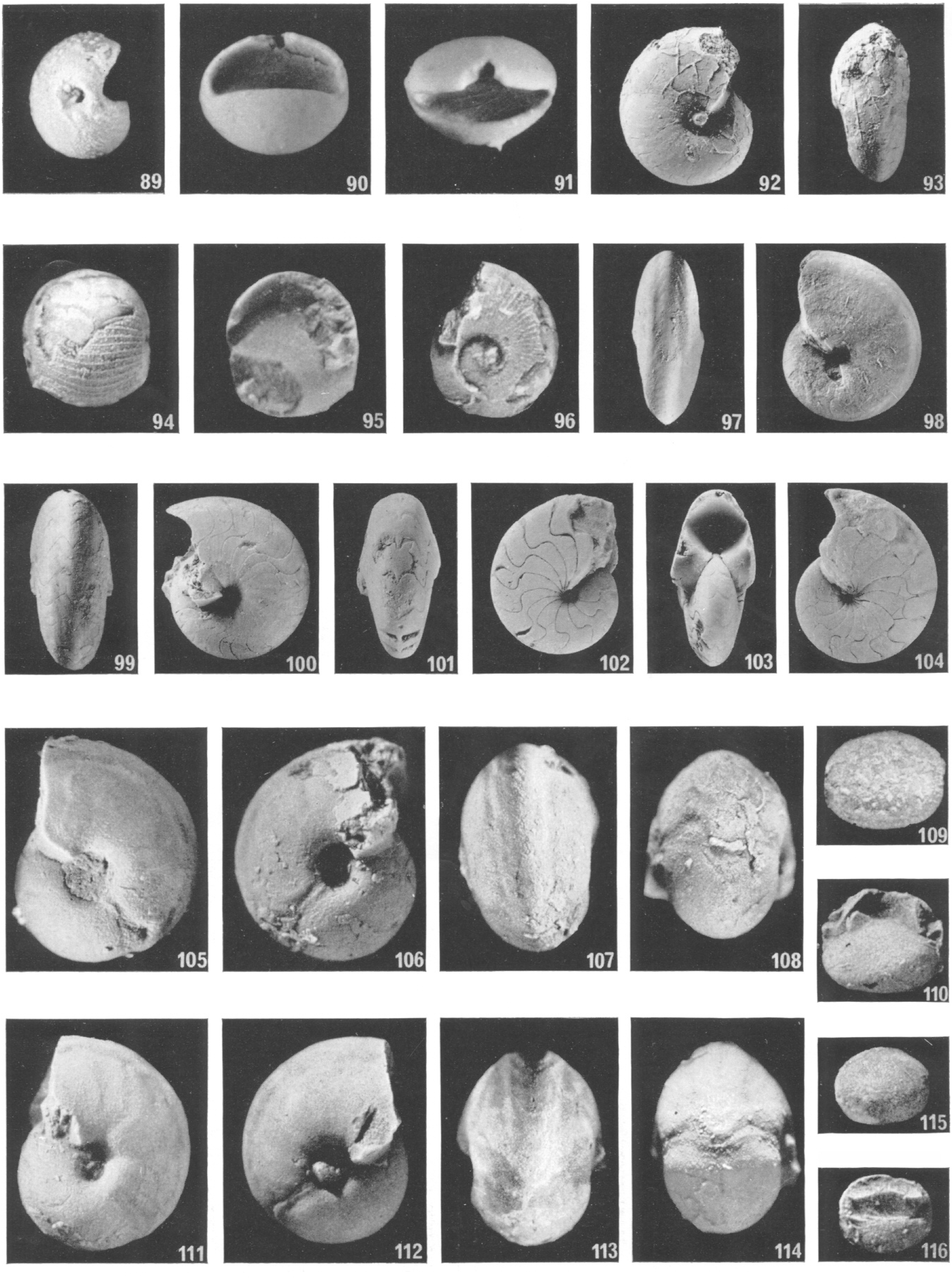
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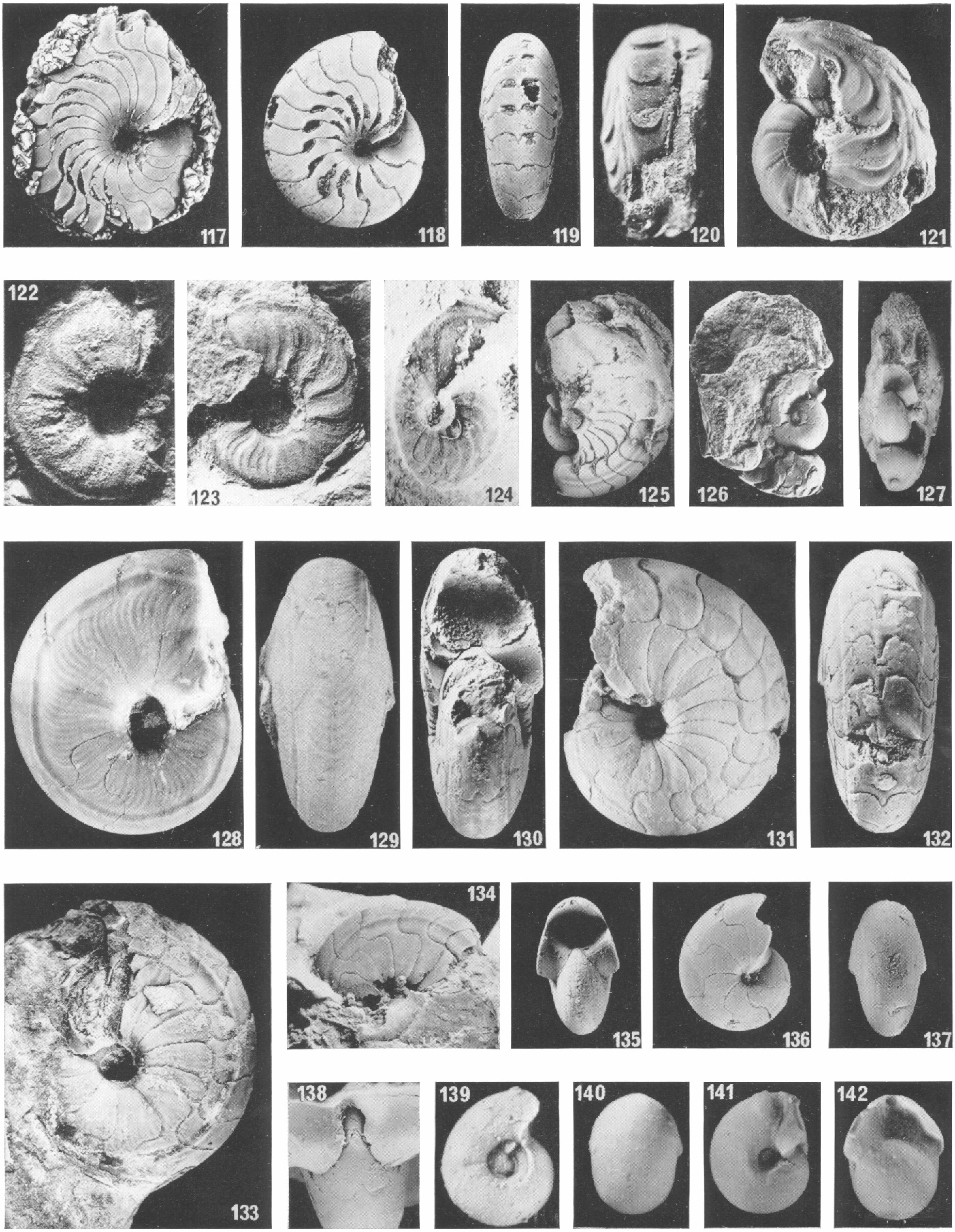
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