NEW LATE DEVONIAN GENERA AND SPECIES OF TORNOCERATID GONIATITES

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ABSTRACT. A brief review is given of the evolutionary relationships of generic groups in the Devonian goniatite family Tornoceratidae (Ammonoidea) as an introduction to the description of two new genera, *Falcitornoceras* and *Crassotornoceras*, from levels around the Frasnian–Famennian boundary. Species and subspecies of these genera are described from western Europe and *Crassotornoceras* is recorded also from North America. A detailed sequence of faunas with *Falcitornoceras* is described from the Montagne Noire across the Frasnian–Famennian boundary. Statistical data regarding the ontogeny of both genera are provided and a description is given of the early stages of *Falcitornoceras* which demonstrates the marked change in ornament at the end of the ammonitella stage, of the type already known in other members of the family. The following new species and subspecies are described: *C. annissi*, *F. falciculum falciculum*, *F. falciculum constrictum*, and *F. falciculum wagneri*.

EUROPEAN tornoceratids have never been the subject of thorough systematic study and new genera and species have been described in a rather random way over the last 150 years. This paper is primarily concerned with poorly known forms which appear to have some biostratigraphical usefulness around the Frasnian–Famennian boundary. The material described is wholly from western Europe, particularly from the Rhenish Schiefergebirge, Brittany, the Montagne Noire, and central Spain. As an introduction it is thought appropriate to outline something of views on the evolution of the Tornoceratidae as a whole since, apart from a popular account (House 1963*a*), there is no up-to-date review of the matter. This will serve to highlight some of the problems associated with the derivation of the new forms described. It is convenient at this stage, and pending a thorough revision, to use some generic groupings in a rather informal way, the purpose being to draw attention to species groups rather than to name them prematurely. Reference in the text is made to both ammonoid and conodont zones (text-fig. 1); correlation between the two schemes is based largely on Ziegler (1979).

EVOLUTION OF THE TORNOCERATIDAE

A generalized interpretation of the time distribution and morphological groups within the Tornoceratidae is given in text-fig. 1. The group is extremely common internationally in the Givetian and Frasnian but gradually declines in importance through the Famennian, the last record being representatives from the Wocklumeria Stufe referred by authors to *Lobotornoceras* (Pfeiffer 1954; Petter 1959; Korn 1981; Weyer 1981). A modestly wide range of shell form is represented in the family which is characterized by a distinctive sutural pattern comprising a ventral lobe, usually small and V-shaped, an adult lateral lobe which arises during early ontogeny on a highly arched lateral saddle, and a deeply V-shaped mid-dorsal lobe. Within the family certain genera have slightly more complex sutures, as outlined in the discussion below. In terms of the Russian nomenclature, the divergence from the basic VLUD pattern may be expressed as follows—$VLU_1:U_1D_1$ to $V(L_1)LUD$ to LUD to V(L)(U)D. Growth lines are almost invariably biconvex after a convex form in the ammonitella (House 1965). American tornoceratids have been monographed (House 1965); these faunas generally lack diversity in comparison with European forms, but recent finds have widened the representation known (House 1978; Kirchgasser and House 1981). Rare tornoceratids occur in South America (Leanza 1968; Hünicken *et al.* 1980). A thorough review of Russian records

[Palaeontology, Vol. 28, Part 1, 1985, pp. 159–188, pls. 16–20.]

(Bogoslovskiy 1971) unfortunately gives little emphasis to precise biostratigraphic discrimination of the faunas.

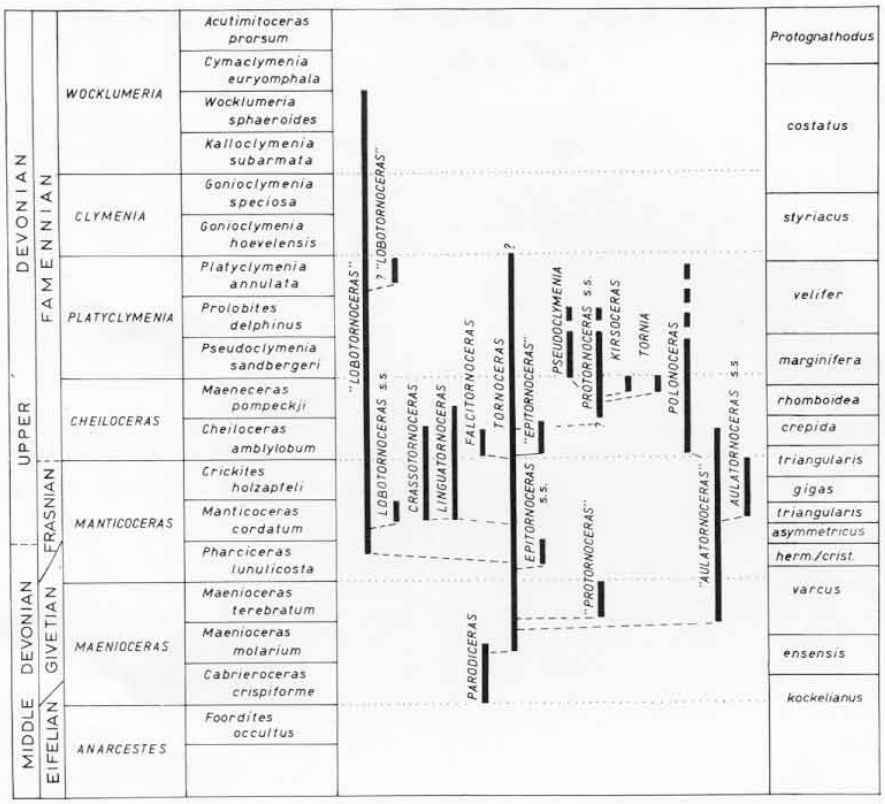
The earliest genus referred to the family is *Parodiceras*, which is thought to have arisen from Eifelian anarcestids, but no precise source has been identified. The genus *Parodiceras* seems to commence in the late Eifelian of current definition. The earliest European records appear to be from the Oderhausen Kalk in the Rhenish Schiefergebirge, probably from the conodont *kockelianus* Zone. In North America, the earliest occurrence is in the Werneroceras Bed of New York State which is placed by Klapper (1981) also in the *kokelianus* Zone, equivalent to levels in the Junkerberg Beds of the Eifel and upper Couvinian (Co2C, R/IV) of Belgium. The sutural form of *Parodiceras* shows only an incipient development of the lateral lobe which characterizes later members of the family. This fact led Petter (1959) to place the genus uniquely in a separate family, the Parodiceratidae, but this has not been generally accepted.

Tornoceras, the longest ranging member of the family, is thought to have been derived from *Parodiceras* by the acquisition of a well-developed lateral lobe; it shows biconvex growth lines but these may approach convexity in the outermost parts of the body chamber. In New York State, *Tornoceras* first appears in the Marcellus Formation, a level thought to correlate with the *ensensis* Zone (Klapper 1981). The genus is widespread in the Givetian. In the late Eifelian and Givetian, the Tornoceratidae are often accompanied by an unrelated but homoeomorphic group, including *Foordites* and *Holzapfeloceras* which Petter (1955) showed to have quite a different ontogeny, but that group becomes extinct in the early *varcus* Zone.

No detailed work to modern standards has been done on European *Tornoceras*. The commonest form referred here is *T. simplex* (von Buch, 1832, p. 42, pl. 2, fig. 7), the holograph of which is a virtually uninterpretable thumb-nail sketch which might even be a *Foordites* or *Holzapfeloceras*. The type material has not been located and until it is, or a neotype chosen, and a thorough description of it published, the name has little value. The convention has been to base the species on figures such as that of Wedekind (1917, pl. 16, fig. 12). Used in this sense, the similarity and probable synonymy between this species and *T. uniangulare* (Conrad), the type species of the genus, has generally been conceded. The precise time level of the type material of *T. uniangulare* is not clear. It comes from the Leicester Pyrite (or Marcasite) in New York State (House 1965), which represents a *remanié* bed (Huddle and Repetski 1981) derived from levels earlier than the upper *hermanni-cristatus* to lower *asymmetricus* Zone date given by conodonts (Klapper 1981), probably from an horizon immediately overlying the Leicester Pyrite. Hence the assertion that the true *T. uniangulare* is pre-Tully in age (House 1965) may be true, but it is not proven, nor likely to be. *Tornoceras* is common in the Frasnian and is very widely distributed but declines in significance in Famennian faunas. The last clear records are probably high in the Platyclymenia Stufe (Sobolev 1912; Dybczyński 1913).

A distinctive group of more stratigraphical significance is represented by *Linguatornoceras* House, 1965, in which the shell form is well-rounded rather than flattened laterally, and the lateral lobe is small, narrow, and tongue-shaped. It occurs from the mid Manticoceras Stufe to top Cheiloceras Stufe (*cordatum* to *pompeckji* Zones in ammonoid terms). Whether *Linguatornoceras* should be regarded as a separate genus, as a subgenus of *Tornoceras*, or synonymized with *Tornoceras* is a matter of varied current opinion. Its distinctiveness and stratigraphical value, however, cannot be disputed and on those grounds is kept separate here. *Tornoceras* and *Linguatornoceras* represent conservative stocks from which other genera may be derived by modification of the shell form and often additionally by changes in the sutural ontogeny. *Linguatornoceras* at present seems the most likely ancestor of *Cheiloceras* and the Cheiloceratidae by the adoption of convex growth lines, a modification already seen in the outer whorls of some Frasnian specimens.

Distinctive derivatives of *Tornoceras* are represented by *Lobotornoceras* in which a small saddle is added on the umbilical seam, and the umbilical lobe moves on to the flanks. The true *Lobotornoceras*, type species *L. ausavense* (Steininger, 1853, neotype designated by House 1978, pl. 9, figs. 8, 14), is only known with certainty from the upper *cordatum* Zone associated with a typical fauna of the Büdesheimer Schiefer at Büdesheim, West Germany. This species comprises a laterally compressed goniatite with about five prominent constrictions per whorl. Two other quite distinctive groups have



TEXT-FIG. 1. Supposed evolutionary relationships within the Tornoceratidae. The use of taxonomic names is described in the text. Note that the *amblylobum* Zone is sometimes termed the *curvispina* Zone. Correlation of ammonoid zones with conodont zones is based largely on Ziegler (1979).

been included within *Lobotornoceras*. The one marked as '*Lobotornoceras*' on text-fig. 1 has a stouter whorl form and no constrictions; the earliest record of this is from around the *lunulicosta/cordatum* Zone boundary in a fauna from Virginia (House 1978, p. 59) and it also occurs in New York State (Kirchgasser and House 1981). There is then a gap in the record, and a number of similar forms have been described from the early Famennian which include probably all of the Famennian records of *Manticoceras*, i.e. *M. superstes* Wedekind, *M. nehdense* Lange, and *M. niedzwiedzkii* (Dybczyński), as was suggested by Clausen (1968*a*) and Jux and Krath (1974). The only remaining records of *Manticoceras* from the Famennian are one specimen found loose at La Serre with the typical *Cheiloceras* fauna, and which now appears to be a case of contamination, and the record of a specimen from the *crepida* Zone of Sessacker (Ziegler 1962) which should be disregarded until convincing illustrations or descriptions of it are given to justify the determination. Later in the Famennian there are few records of *Lobotornoceras* until the last in the Wocklumeria Stufe (Weyer 1981, p. 5) which is associated with a fauna suggestive of the *paradoxa* Zone. Finally, there is the group marked as ?'*Lobotornoceras*' on text-fig. 1, in which ventrolateral furrows occur additionally. This is represented only by one record of *L.* (?) *bicaniculatum* (Petter 1959) from North Africa, and

the recognition of a similar form in Kazakhstan by Bogoslovskiy (1971). This group might equally well be developed from '*Aulatornoceras*' by sutural elaboration but intermediate forms are not recorded from the intervening *sandbergeri* and *delphinus* Zones.

Oxyconic tornoceratids have usually been referred to *Epitornoceras* although, as pointed out by House (1978, p. 60), the type species *E. mithracoides* (Frech) is trochoidal in form rather than oxyconic; the types are recorded as having come from the *lunulicosta* Zone at Eibach, West Germany. The sharply oxyconic species *E. peracutum* (Hall) from New York is from the upper part of the same zone. Both species will belong to the late Givetian if current proposals of the Devonian Subcommission are accepted. There is then a gap in the record and oxyconic forms of rather similar appearance occur in the Cheiloceras Stufe. In Poland, Dr. H. Makowski has demonstrated (to M.R.H.) that all gradations occur from typical *Tornoceras* to these oxyconic forms among faunas wholly from the Cheiloceras Stufe, indicating a contemporary derivation. The Famennian oxycones must therefore be phylogenetically distinct from and independent of the earlier group (or rather this is the simplest explanation to be accepted for the present as most probable). No new generic name is proposed for this group here but it is marked as '*Epitornoceras*' on text-fig. 1. The *Epitornoceras* recorded from the Cheiloceras Stufe of Western Australia by Petersen (1975) belongs here.

Widely umbilicate tornoceratids with the simple whorl section of *Tornoceras* are referred to *Protornoceras*. The earliest is '*P.*' *foxi* House from the Givetian of Cornwall. There is then a long gap in the record; from the Cheiloceras Stufe, and slightly later, some twenty-five specific names have been proposed for tornoceratids of this type. Since the type species of *Protornoceras*, *P. polonicum* Dybczyński from the early Famennian of Kielce, Poland, is part of this latter group, it is the '*P.*' *foxi* group which must be renamed should it come to be proven that they are independently derived. There appear to be no confirmed records of *Protornoceras* higher than the *delphinus* Zone, or the *marginifera* Zone of the conodont terminology. The genus *Pernoceras* Schindewolf (1922, p. 188; 1923, p. 310) is best regarded as a synonym of *Protornoceras* but the type species of the former, *Protornoceras kochi*, shows a tabular venter and flattened sides as well as an open umbilicus and therefore approaches the group marked as '*Aulatornoceras*' on text-fig. 1.

Two genera are thought to be derived from more typical *Protornoceras* by simplification of the suture and slight changes in the shell form. In *Kirsoceras* (Bogoslovskiy 1971) the ventral lobe is lost, the lateral lobe is relatively increased in size, and the latero-umbilical lobe decreased in prominence significantly; this genus is only known from the Cheiloceras Stufe (presumably late) of the Urals. In *Tornia* House, 1970, probably from the *pompeckji* Zone of Kielce, Poland, the suture passes across the flanks from the ventral lobe with only the barest trace of a lateral or umbilical lobe. These two genera have a striking resemblance to some of the earliest clymeniids, notably in the shell form, the ventral suture, the shape of the septum, and especially the deep narrow median dorsal lobe appropriately similar to that carrying the siphuncle in the clymeniids. Schindewolf (1972) followed by Bogoslovskiy (1976) have both not accepted the view of House (1970) that this group might form the initiation point for the Clymeniida. Schindewolf preferred his own earlier hypothesis of an ancestor in *Archoceras*, arguing that the lateral lobe in the clymeniids arises from an umbilical position in early ontogeny, whereas in the tornoceratids it arises adventitiously on an arched early saddle. But this is not in dispute. The early stages of *Tornia* are not known but the point is that, judging from the early stages of other tornoceratids, with an almost non-existent adult lateral lobe *Tornia* will be very unlikely to have an adventitious lobe in the early stages at all. It is in the early stages where dorsal migration of the siphuncle occurs and where consequent modification of the sutural pattern is to be expected. Neither Schindewolf (1972) nor Bogoslovskiy (1976) addressed this problem, nor did they comment on the fact that the whole geometry of the tornoceratid septum matches that of the clymeniids, whilst the archoceratid septum (the alternative point of origin) is fundamentally unlike it. Unfortunately, so little work has been done on the early stages of all these forms that a speedy resolution of the problem seems unlikely.

Quite bizarre derivatives, presumably from *Protornoceras*, are those which develop a sigmoidally shaped lateral lobe and often an incipient lobe on the ventrolateral saddle, an overall pattern resembling that of the clymeniid *Cymaclymenia*, hence their name *Pseudoclymenia* Frech, 1897. The

type species is *Pseudoclymenia sandbergeri* after which is named the zone in which the group reaches its acme, although it occurs also in the overlying *delphinus* Zone. Many of the species of this genus have been reviewed by Bogoslovskiy (1971). Some species are almost serpenticonic in form.

Forms of tornoceratid in which ventrolateral furrows or grooves and often festoon-like constrictions and lirae occur are generally referred to *Aulatornoceras* Schindewolf, 1922. The evolution of this group is complex and virtually nothing has been done to try to sort out the various strands involved. The type species is *A. auris* (Quenstedt, 1846), the types of which have apparently been lost (there is no trace of them with Quenstedt's other material at Tübingen); they came from the Büdesheimer Schiefer and hence almost certainly from the upper *cordatum* Zone. A variety of forms, smooth to ribbed and open to closed umbilicate, have been referred to the species. In the interests of nomenclatorial clarity a neotype is here selected (Pl. 17, figs. 1–4) from the type locality. This species forms one of a group of essentially Frasnian forms which are quite heavily sculptured and which possess, to a greater or lesser extent, an open umbilicus. By contrast, there are laterally compressed, closed umbilicate forms with weakly developed ornament, but with ventrolateral furrows, which are known patchily from the late Givetian (House 1963*b*) to levels in the early Famennian; these are marked as '*Aulatornoceras*' on text-fig. 1. It has always been tempting to consider this group as making a dimorphic pair with *Tornoceras*. Ontogenetic comparison, however, gives as yet no evidence to support this view. Alternatively, an independent origin from *Tornoceras* of ventrolaterally furrowed forms on several occasions seems more probable but direct links have not been established.

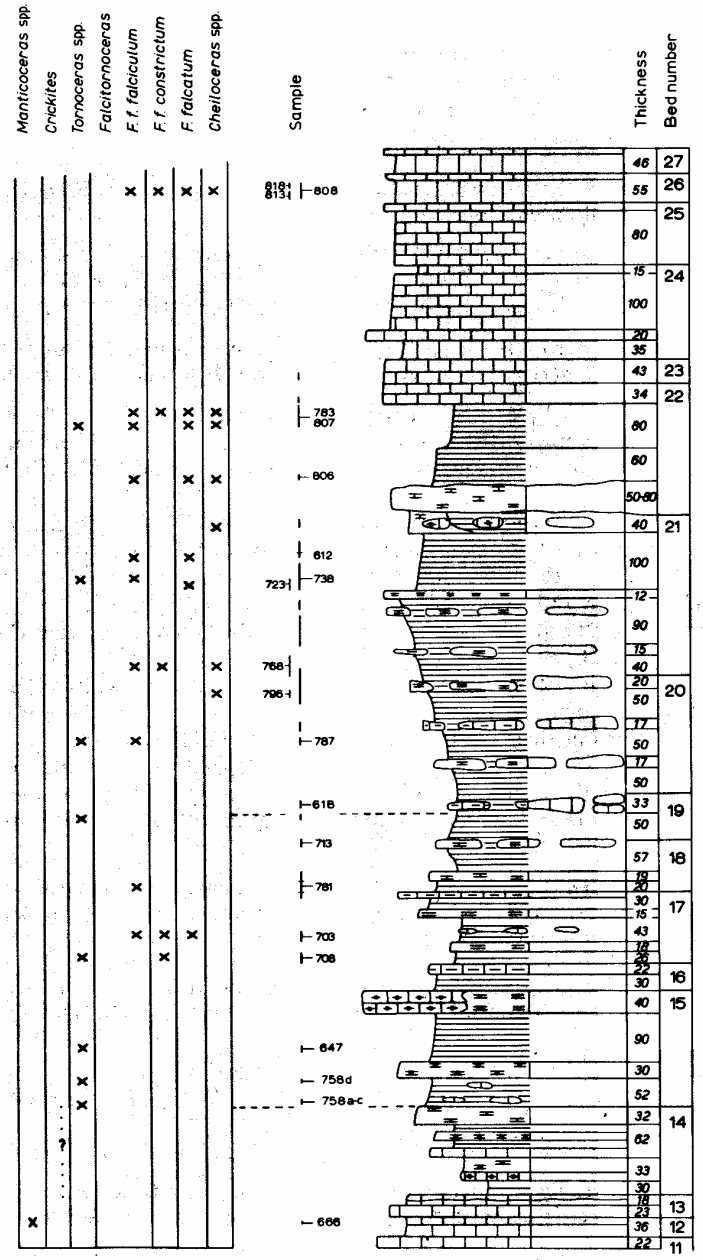
It is from the long-ranging group '*Aulatornoceras*' that *Polonoceras* (Dybczyński 1913) may have been derived by the development of slight ribbing (in some) and a discoidal form with tabular venter. Some might consider *Polonoceras* and '*Aulatornoceras*' as synonyms. If so, the former name should be used. The type species, by the designation of Miller (1938, p. 142), is *P. planum* Dybczyński, a species which was illustrated as showing a sharp angular bend in the suture from the crest of the latero-umbilical saddle to the lateral lobe; this illustration has been widely copied but the accompanying photographic illustration does not show this feature. The type came from the now defunct Sieclucki Brickpit in Kielce, and Dr. Makowski has informed one of us that the site is now the roundabout in Kielce at the junction of Al Lenina and Bohaterow Warszawy. In the absence of either evidence of the original material, or satisfactory figures on which to base the genus, a topotype is illustrated here (Pl. 17, figs. 8–10) which may serve as a better indication of the species. Forms referred to *Polonoceras* occur in the *amblylobum* Zone at La Serre, Montagne Noire, and also at Beil, Germany. It is possible that the type material was from the *pompeckji* Zone.

Finally, there are the two groups here distinguished at generic level. *Crassotornoceras* gen. nov. is named for a group of micromorphic rotund tornoceratids with periodic constrictions in the inner and often outer whorls. This genus is known from the upper *cordatum* Zone, is common in the *holzapfeli* Zone, and is known from the earliest Famennian at Nehden; it was probably derived from *Linguatornoceras*. *Falcitornoceras* gen. nov. is characterized by spectacularly close-set ribbing on the early whorls of a type not known elsewhere in the family and, indeed, unmatched in any Devonian ammonoid. These are best known only from the Cheiloceras Stufe, but they occur also before the entry of *Cheiloceras* in the section at La Serre in the Montagne Noire (text-fig. 2); whether they occur in the Frasnian will depend on how the base of the Famennian comes to be defined.

SYSTEMATIC PALAEONTOLOGY

Dimensions. All dimensions are in millimetres unless otherwise stated. Shell form parameters are abbreviated as follows: D, diameter; WW, maximum whorl width at the stated diameter; WH, projection of distance between venter and umbilical wall or shoulder, whichever is the greater, in the plane of the spiral; UW, distance between the umbilical wall, shoulder, or seam at the stated diameter and at precisely half a whorl previously, whichever is the least; Ribs, number of ribs in the whorl preceding the maximum diameter.

Repositories of specimens. BerlM, Museum für Naturkunde, East Berlin; BM(NH), British Museum (Natural History), London; IG, Institute Géologique, Université de Louvain, Belgium; LPB, Laboratoire de



TEXT-FIG. 2. Section through the uppermost Frasnian and lowermost Famennian in Trench C (text-fig. 9), around 600 m east of La Roquette, La Serre, south of Cabrières, Hérault, Montagne Noire, France, showing the levels from which goniatites have been obtained. Bed thickness in cm. Symbols follow Shell standard legend. [Note: Sample 618 should be shown as ranging throughout Beds 19 and 20.]

Paléontologie, Université de Brest, France; MRHN, Musée Royale d'Histoire Naturelle, Bruxelles, Belgium; SenckM, Senckenberg Museum, Frankfurt, West Germany; SedgM, Sedgwick Museum, Cambridge.

Suborder TORNOCERATINA Wedekind, 1917
Family TORNOCERATIDAE Arthaber, 1911
Genus CRASSOTORNOCERAS gen. nov.

Type species. Tornoceras ausavense crassum Matern, 1931.

Derivation of name. Alliterative couplet with specific appellation of type species. From Latin *crassus*, stout, referring to whorl form, and the genus *Tornoceras*.

Diagnosis. Small Tornoceratidae with subglobular inner whorls and small open umbilici with three to eight periodic constrictions per whorl following the biconvex course of the growth lines. Some specimens show weak ribs. Sutures simple tornoceratid usually with small lingulate lateral lobe.

Included species. C. crassum (Matern, 1931*a*, pl. 3, fig. 14*a*, *b*), *C. annissi* sp. nov. (herein), *C. belgicum* (Matern, 1931*b*, text-fig. 2), and *C. guestfalicum* (Frech, 1901, pl. 32*a*, fig. 8, refigured here as Pl. 16, figs. 14, 15).

Remarks. When Schindewolf (1936, p. 689) correctly recognized the oddity and extra umbilical lobe of *Goniatites ausavensis* Steininger (1853, p. 43, pl. 1, figs. 6, 6*a*, 7, 7*a*), and made it the type species of *Lobotornoceras*, this left unplaced the common and distinctive group for which the name *Crassotornoceras* is here applied.

There are several constricted forms referred to '*Aulatornoceras*' (but quite distinct from *A. auris*, the type species of that genus) which have similarities with some of the species referred here to *Crassotornoceras* but which differ in the possession of well-developed ventrolateral furrows. These include: '*A.*' *constrictum* (Steininger, 1853, p. 43, pl. 1, fig. 9, 9*a*) from the Büdesheimer Schiefer of the Eifel; '*A.*' *bickense* Wedekind (1917, p. 137), a *nomen nudem* possibly from the *holzapfeli* Zone at Bicken; and '*A.*' *loeschmanni* (Frech, 1902, pl. 5 (4), fig. 9*b*, *c*, refigured here as Pl. 16, figs. 16, 17) which shows a tabular venter but not the ventrolateral furrows which the first two share with the true *Aulatornoceras*. The time-span of this group is similar to that of *Crassotornoceras*. There is a range of possible interpretations of their relationships: either may be derived from the other; they may represent an evolving dimorphic pair; they may be quite independent. In the absence of any factual basis for knowing which of these possibilities is correct, it is hoped that the terminology used here will introduce more objectivity into the recording of these stratigraphically useful forms and posterity may solve the problem.

Horizons and range. Crassotornoceras has a restricted time range from the upper *cordatum* Zone probably only up to the *amblylobum* Zone (i.e. doIγ to doIIα). The genus is probably commonest in the *holzapfeli* Zone. The only certain record outside Europe occurs in the Angola Shale of upstate New York (Kirchgasser and House 1981, p. 49) just below records of *C. holzapfeli* in the Hanover Shale. There are only rare records in the *amblylobum* Zone, including two records by Frech (1902) from the Nehden Schiefer at Nehden and probably the record by Grüneberg (1925, p. 67, pl. 1, fig. 11, 11*a*, 11*b*) from the same level in the Herzkamp Syncline.

Crassotornoceras crassum (Matern, 1931)

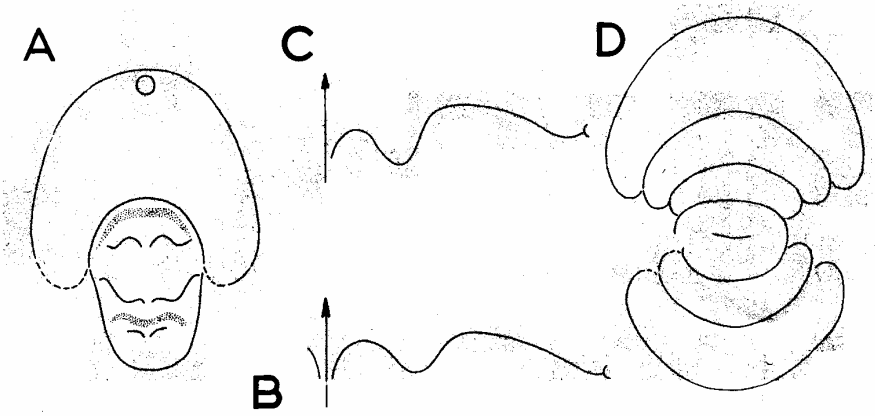
Plate 16, figs. 4, 8–11; text-figs. 3A, B, D, 4

1931 *Tornoceras ausavense crassum* Matern (1931*a*), p. 27, pl. 3, fig. 14*a*, *b*.

Holotype. SenckM XI 342*a* (*sic*, figured Matern 1931*a*, pl. 3, fig. 14*a*) from Büdesheim, Eifel, West Germany; Büdesheimer Schiefer, upper *cordatum* Zone, doIβ/γ.

Diagnosis. Species of *Crassotornoceras* with three to five constrictions which pass from the umbilicus to the venter; micromorphic.

Material. The holotype and about sixty other specimens collected by Matern, now in the Senckenberg Museum. Thirty-two specimens collected by M.R.H. from the type locality (BM(NH) C85201–85232). Belgian material is



TEXT-FIG. 3. A, B, D, *Crassotornoceras crassum* (Matern) showing whorl form, suture, and cross-section based on BM(NH) C85231 from the Büdesheimer Schiefer, Büdesheim, West Germany; A, B, ×6·9; D, ×15·3. C, *C. belgicum* (Matern), a suture based on the holotype, ×16·5.

from the Schistes de Matagne, some of it studied by Matern, and includes IG 83090 from Mariembourg and three specimens among IG 4630 from the quarry behind the church at Boussu en Fagne.

Dimensions	D	WW	WH	UW
Holotype SenckM XI 342*a*	7·2	3·3	—	—
Topotypes BM(NH) C85204	6·93	4·32	3·42	0·9
BM(NH) C85205	5·96	3·6	2·97	0·6
BM(NH) C85230	4·23	2·97	2·25	0·45
BM(NH) C85229	2·7	1·62	1·08	0·54

Description. The protoconch has not been dissected out but in BM(NH) C85231 its width is about 1·2 mm with a maximum diameter less than 0·93 mm. Early whorls show a rotund form, open umbilicus, maximum whorl width close to the umbilicus (text-fig. 3D), and depressed reniform whorl section. Whorl height increases

EXPLANATION OF PLATE 16

Figs. 1–3. *Crassotornoceras belgicum* (Matern). MRHN unnumbered, holotype, from a quarry behind the church at Boussu en Fagne, Belgium, figured by Matern (1931*b*), ×8·7.

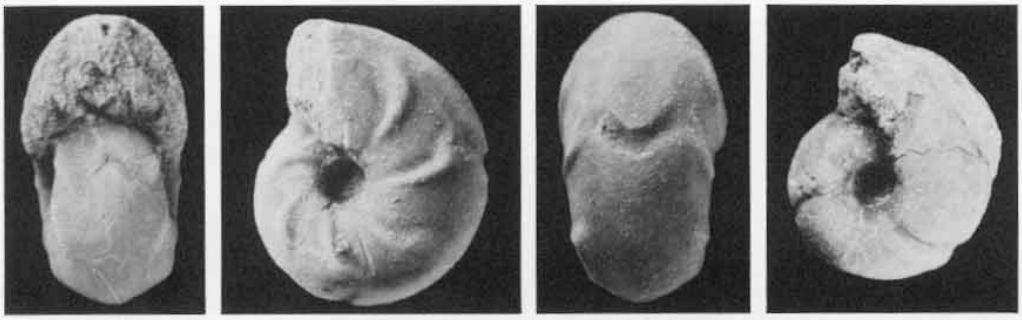
Figs. 4, 8–11. *C. crassum* (Matern). 4, MRHN unnumbered, from a quarry behind the church at Boussu en Fagne, Belgium, ×4. 8, 9, BM(NH) C85232, from the Büdesheimer Schiefer at Büdesheim, West Germany, ×5. 10, 11, BM(NH) C85201, from the Büdesheimer Schiefer at Büdesheim, West Germany, ×4.

Figs. 5–7. *Aulatornoceras* cf. *A. auris* (Quenstedt). MRHN unnumbered, from a quarry behind the church at Boussu en Fagne, Belgium, ×3·5.

Figs. 12, 13. *C. annissi* sp. nov. SedgM H1541, holotype, from the Saltern Cove Goniatite Bed, Waterside Cove, Devon, ×5.

Figs. 14, 15. *C. guestfalicum* (Frech). BerlM c475/1, holotype, from the Nehden Schiefer at Nehden, West Germany, figured by Frech (1901, pl. 32*a*, fig. 8), ×3.

Figs. 16, 17. '*A.*' *loeschmanni* (Frech). BerlM c475/2, lectotype, from the Nehden Schiefer at Nehden, West Germany, figured by Frech (1902, pl. 5 (4), fig. 9*b*, *c*), ×3.



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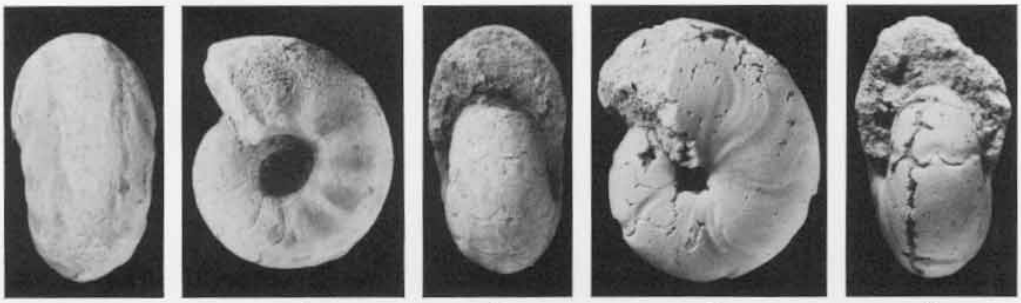

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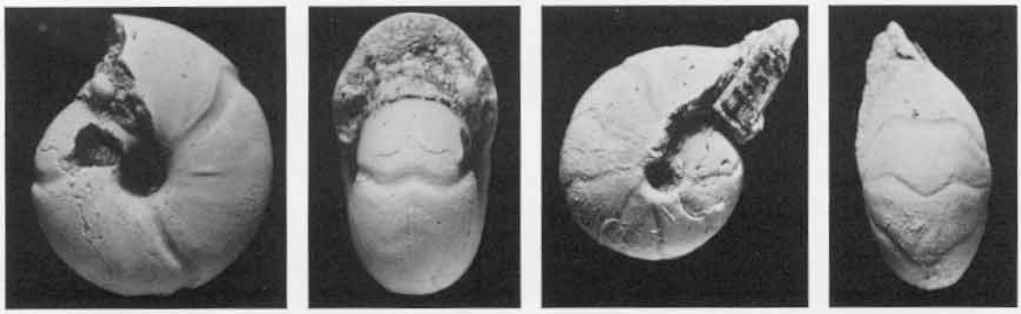

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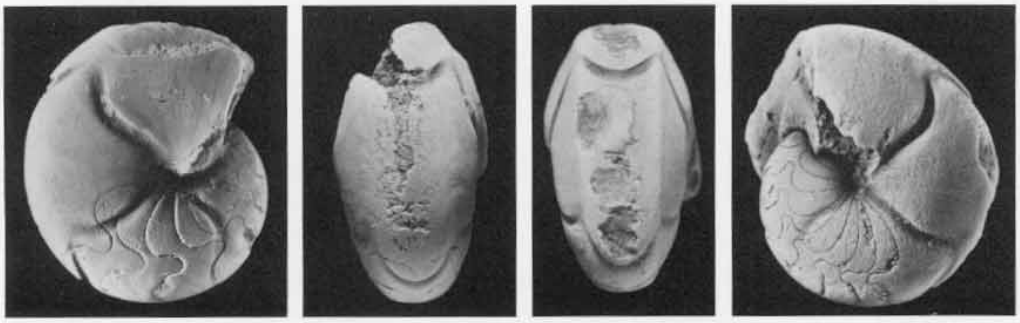
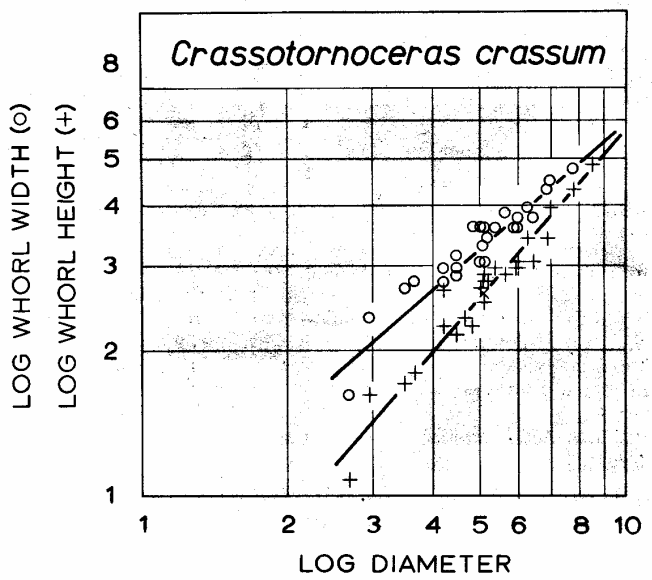


14 15 16 17

HOUSE and PRICE, *Crassotornoceras*, *Aulatornoceras*



TEXT-FIG. 4. Dimensions of *Crassotornoceras crassum* (Matern) based on twenty-four topotypes from the Büdesheimer Schiefer, Büdesheim, West Germany.

regularly in relation to width (text-fig. 3D); the statistics for the BM(NH) material are plotted in text-fig. 4. Growth lines are biconvex and the three to five constrictions per whorl follow the same course. None of the specimens exceeds 9 mm in diameter.

Remarks. This is a common form in the Büdesheim fauna, the rest of which is also micromorphic. There is no evidence of large specimens elsewhere but *Tornoceras* never shows inner whorls of this type.

Horizon and locality. The topotype material from Büdesheim was collected loose and this will certainly be true also for Matern's material. Details of this classic locality have been given by Clausen (1968*b*). In ammonoid terms the fauna is interpreted as of the upper *cordatum* Zone since *Crickites* has only been rarely recorded (Clausen 1968*b*) and is presumed to be from a rather higher level than the typical fauna. Clausen reported a determination by Ziegler of a sample from the type locality as having conodonts of the lower *gigas* Zone. Similarly the Belgian faunas, at least that from the Boussu en Fagne, are probably from levels below the entry of common *C. holzapfeli* rather higher in the Assise de Matagne. Mouravieff (1982) was unable to locate the typical deeper-water conodont guide fossils in this part of the Belgian sequence. In New York the level producing specimens of *Crassotornoceras* aff. *C. crassum* is from the Point Breeze Goniatite Bed in the early part of the Angola Shale, close to Lake Erie (Kirchgasser and House 1981): this part of the succession is referred to the *gigas* Zone by Oliver *et al.* (1969).

Crassotornoceras annissi sp. nov.

Plate 16, figs. 12, 13

1963 Gen. et sp. nov. House (1963*b*), p. 8.

Derivation of name. In honour of Dr. L. G. Anniss who made systematic goniatite collections from the type locality (Anniss 1927).

Holotype. SedgM H1541 from Saltern Cove Goniatite Bed, Waterside Cove, Paignton, Devon.

Diagnosis. Species of *Crassotornoceras* without ribs but with about eight constrictions concordant with biconvex growth lines and passing from the umbilical shoulder to the venter.

Dimensions	LD	WW	WH	UW
Holotype SedgM H1541	8·0	*c.* 5·1	4·5	0·8

Description. Shell form involute, subglobular but slightly compressed, with a small open umbilicus. Whorl section shows a well-rounded venter and convex lateral slopes reaching a maximum whorl width close to the umbilicus. The umbilical shoulder is sharply rounded and the wall vertical. Growth lines pass gently back from the umbilicus to form a very shallow lateral sinus and then a shallow ventrolateral salient; their course over the venter is not seen. Ornament consists of eight prominent shallow constrictions in the last whorl which apparently accord with the course of the growth lines. On the venter the constrictions are deeper than on the flanks and form a shallow broadly rounded sinus. The suture shows a V-shaped ventral lobe, a well-rounded ventrolateral saddle, a well-rounded lateral lobe, and a large broad latero-umbilical saddle with a steeper ventrad face. The two sutures seen are well spaced.

Remarks. This form has twice the average number of constrictions seen in *C. crassum*, none of the ninety topotypes of which has so many. Further, the constrictions pass slightly backward from the umbilical shoulder rather than forward as usual in *C. crassum*.

Horizon. As has been shown earlier (House 1963*b*), the goniatites from the Saltern Cove Goniatite Bed (from which all the indications are that this museum specimen comes) find their closest analogy with the *holzapfeli* Zone (doIδ), and this is taken to be the horizon. Nevertheless, van Straaten and Tucker (1972) have shown that the Saltern Cove Goniatite Bed is part of an intraformational slump, with other derived material set in an argillite matrix, which may be as young as the Platyclymenia Stufe.

Crassotornoceras belgicum (Matern, 1931)

Plate 16, figs. 1–3; text-fig. 3c

1931 *Tornoceras belgicum* Matern (1931*b*), p. 9, text-fig. 2.

Holotype. Specimen in MRHN figured by Matern (refigured here as Pl. 16, figs. 1–3), from the Schistes de Matagne (F3b) in a quarry behind the church at Boussu en Fagne, Belgium.

Diagnosis. Small species of *Crassotornoceras* with three constrictions in the last whorl; ribs developing on the outer flanks and numbering about six in the last whorl at D = 4·5 mm.

Description. The holotype is a small internal mould (D = 4·5 mm, WW = 2.7 mm) of compressed rotund form with a small open umbilicus and well-rounded whorl section. Growth lines, mainly inferred from ornament, pass almost prorsiradiately from the umbilicus with a shallow sinus and then project forward to a ventrolateral salient and rounded sinus on the venter. Three constrictions in the last whorl follow the course of the growth lines but are only well developed on the outer flanks and venter. About six ribs are formed in the last whorl, following approximately the course of the growth lines and constrictions, and developed in the outer part of the ventral sinus and dorsad part of the ventrolateral salient. Suture as illustrated in text-fig. 3c.

Remarks. From the same locality as the holotype is another specimen (Pl. 16, figs. 5–7) with similar ribbing but developed low on the flanks; additionally it shows the development of ventrolateral furrows. This specimen is referred to *Aulatornoceras* cf. *A. auris* (Quenstedt). Otherwise no material resembling this species has been described.

Horizon. We are indebted to Sarah Gatley (Trinity College, Dublin) for information that the locality indicates the upper part of the Schistes de Matagne (F3b), corresponding to the *holzapfeli* Zone.

Crassotornoceras guestfalicum (Frech, 1901)

Plate 16, figs. 14, 15

1901 *Tornoceras guestfalicum* Frech (1897–1902), pl. 32*a*, fig. 8.
1902 *Tornoceras loeschmanni* Frech (1902), pl. 5 (4), fig. 9*a* (only).

Holotype. BerlM c475/1, figured by Frech (1901, pl. 32*a*, fig. 8) from the Nehden Schiefer at Nehden (refigured here as Pl. 16, figs. 14, 15).

Remarks. When Frech first named this species he figured only the holotype, the character of which can be seen from the illustrations given here and his description. In 1902 he considered his name a homonym of *T. westfalicum* Holzapfel (1895, p. 104) and gave the name *T. loeschmanni* to two figured specimens, one of which was the holotype of *T. guestfalicum*; the other (illustrated here on Pl. 16, figs. 16, 17) is referred to '*A.*' *loeschmanni*. Although Frech clearly intended the name to be a replacement for *T. guestfalicum*, since the spelling is different from *T. westfalicum* it is not a homonym and his action under the *Rules* is not now valid. We do not consider the species congeneric. Thus we formally designate the second specimen of Frech (1902, pl. 5 (4), fig. 9*b*, *c*) as the lectotype of *loeschmanni* which we refer to the group similar to the true *Aulatornoceras* but without the ventrolateral furrows that characterize that genus.

Genus FALCITORNOCERAS gen. nov.

Type species. Goniatites (*Tornoceras*) *subundulatus* var. *falcata* Frech, 1887.

Derivation of name. Alliterative couplet with the specific name of type species. From Latin *falcatus*, scythe-shaped, referring to the form of the ribs, and the genus *Tornoceras*.

Diagnosis. Small Tornoceratidae with characteristic chevron ornament developed early in ontogeny, consisting of falcate ribs on the flank which continue over the venter. Ribs diminish in strength towards the smooth body chamber. Narrow umbilicus; tabulate venter developed in later whorls; narrow thin ventrolateral grooves may be present. Typical tornoceratid suture-line in early whorls, with asymmetric lateral lobe; umbilical lobe moves outside the seam in mature examples.

Included species and subspecies. F. falcatum (Frech, 1887, p. 465), *F. falciculum* sp. nov. (herein), *F. falciculum falciculum* subsp. nov. (herein), *F. falciculum constrictum* subsp. nov. (herein), *F. falciculum wagneri* subsp. nov. (herein).

Remarks. Apart from reference to the type species by Frech (1887, 1897–1902), none of these forms has been recognized in accounts of Famennian goniatites from western Europe (e.g. Wedekind 1917; Schindewolf 1923; Böhm 1935) probably because they have never been adequately described or illustrated. The origin of this group, whose members appear at or near the base of the *amblylobum* Zone (= the *curvispina* Zone of earlier authors), is unknown. Ancestors are *Tornoceras* or even '*Aulatornoceras*' but lack of these in the underlying *holzapfeli* Zone makes it difficult to determine from which *Falcitornoceras* was derived.

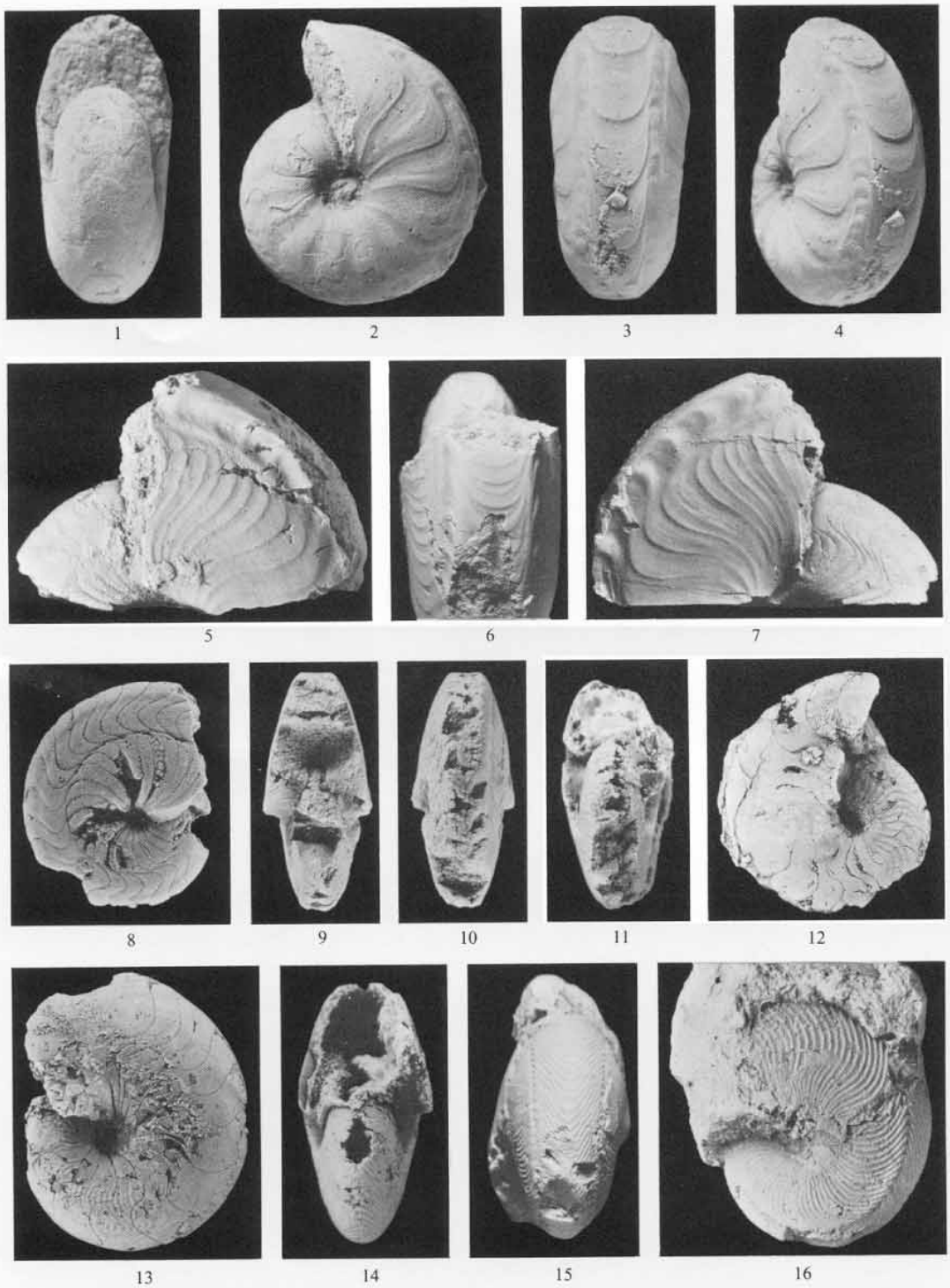
EXPLANATION OF PLATE 17

Figs. 1–7. *Aulatornoceras auris* (Quenstedt). Büdesheimer Schiefer at Büdesheim, West Germany. 1–4, SedgM H9942, neotype here designated, × 5. 5–7, SedgM H9943, topotype, × 3.

Figs. 8–10. *Polonoceras planum* Dybczyński. SedgM H9941, topotype, collected by Dr. H. Makowski from the lower Famennian at Sieclucki Brickpit, Kielce, Poland, × 2.

Figs. 11, 12. *Falcitornoceras falcatum* (Frech). BM(NH) C85169, collected by D. Korn from the Nehden Schiefer, Hohlweg, north-east of Nehden, West Germany (Mtb. 4517 Alme), × 3·5.

Figs. 13–16. *F. falciculum falciculum* subsp. nov. 13, 14, BM(NH) C85168, from the same locality and horizon as figs. 11, 12, × 3. 15, 16, LPB 4143, labelled 'base des Schistes de Porsguen, Ile Longue en Crozon, Finistère', France, × 4.



1 2 3 4

5 6 7

8 9 10 11 12

13 14 15 16

HOUSE and PRICE, *Aulatornoceras*, *Polonoceras*, *Falcitornoceras*

Two other differently ribbed tornoceratids are known. '*A.*' *bicostatum* (Hall) occurs in the *amblylobum* Zone of New York State and has a late-stage ornament indistinguishable from some specimens of *F. falciculum* but, by contrast, its inner whorls are entirely smooth (House 1965). *T. amuletum* House from the Givetian of New York State develops coarse ribbing in early ontogeny, from nodes situated near to the umbilical shoulder. These gradually develop into widely spaced concave ribs running over the flank, with a V-shaped ventral sinus, but they become rursiradiate and falcate before disappearing at a diameter of 15 mm. The ribs, however, are quite different from those of *Falcitornoceras*.

Whorl width and whorl height are both plotted against diameter on logarithmic axes in text-fig. 5 but there seems to be little discrimination between the species and subspecies described here. Regression lines have been omitted from some of the plots because they overlap considerably and their inclusion would obscure many of the data points. The ratio of whorl width to whorl height plotted against diameter is useful in distinguishing between the taxa, as also is the plot of rib frequency against diameter (text-fig. 6). A reduced major axis has been computed using the method of Imbrie (1952).

Horizon and range. Falcitornoceras is known only from the Famennian *amblylobum* Zone and members have been reported from the Montagne Noire (Frech 1887, 1902), Thuringia (Zimmermann 1893), and Rostellec, Brittany (Frech 1897). Reports of lower Famennian ammonoids from Guadalmez by Groth (1914) and of *Reticuloceras superbilingue* from the same locality by Almela *et al.* (1961) may refer to occurrences of *Falcitornoceras*. Examples are described here from the lower Famennian shales at La Serre, the Nehden Schiefer at Nehden, and Guadalmez, central Spain. *F. falcatum* and *F. falciculum* have practically identical stratigraphic ranges, from Beds 17 to 26 in Trench C at La Serre (text-figs. 2, 9).

Specimens from the Montagne Noire. Most of the material used in this study was collected at La Serre, Cabrières, Hérault, either *in situ* in trenched sections or loose on the surface. The trenches (text-fig. 9) were dug under a research programme of Dr. R. Feist (University of Montpellier) and funded by the French CNRS. Trench C is situated 600 m east of the farmhouse La Roquette (68265e, 14006n) and exposes a sequence (text-fig. 2) of dolomitized Frasnian microsparites, uppermost Frasnian interbedded shales, cherts, and bituminous limestones (below Bed 13), lower Famennian shales and mudstones (Beds 14–22), middle and upper Famennian microsparites and nodular argillaceous limestones, and lower Tournaisian shales, mudstones, and oolites. Sample numbers (prefixed by LS), lithologies, and faunal ranges of the groups of interest here are shown on text-fig. 2. The highest manticoceratid collected *in situ* came from Bed 12; Bed 15 yielded only *Tornoceras* sp. and *Protornoceras* sp. The *Crickites* record shown came from levels corresponding to Beds 14 and 15, but in trench D according to information provided by Dr. Feist. *Falcitornoceras* was found as low as the base of Bed 17 in Trench C but the lowest *Cheiloceras*, currently used as the indicator for the base of the Nehden and Cheiloceras Stufe, occurred 5·5 m higher in Bed 20. Preliminary conodont dating provided by Dr. G. Klapper indicates that Bed 16 is already within the Famennian upper *triangularis* Zone.

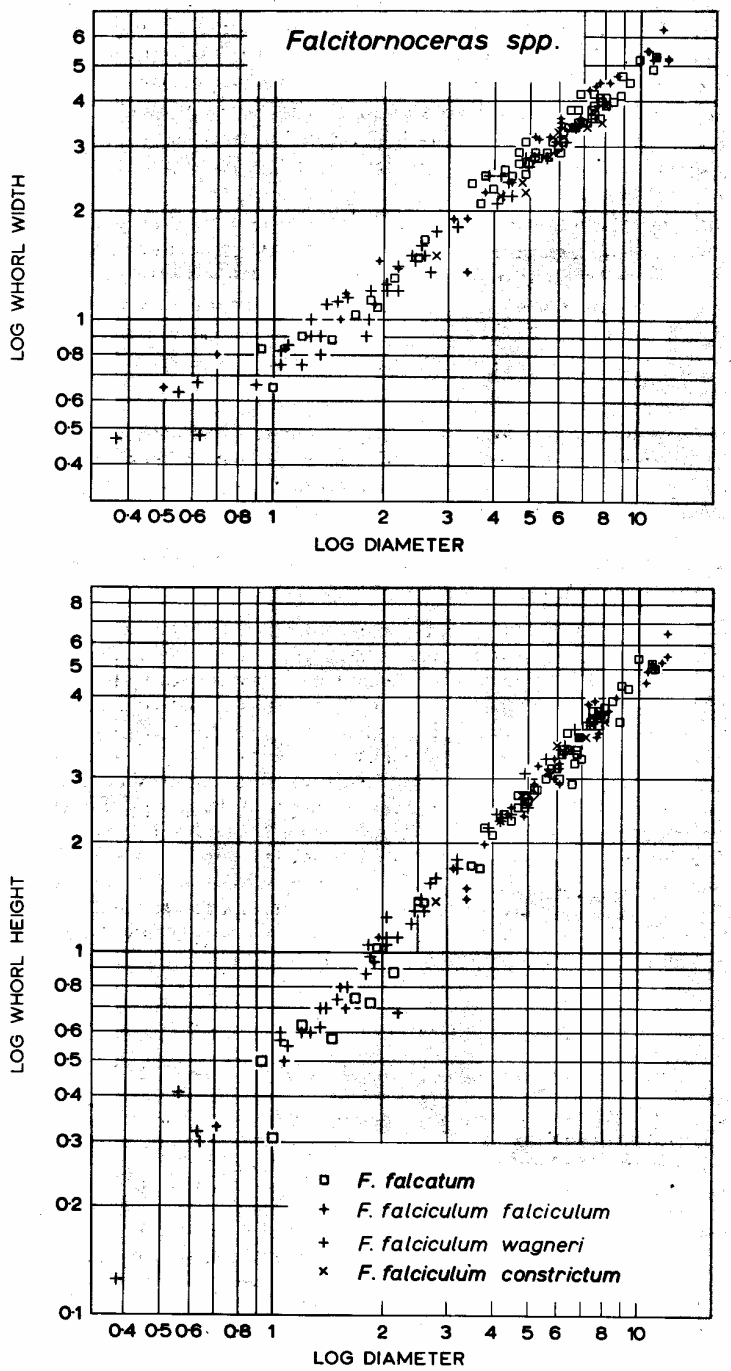
Falcitornoceras falcatum (Frech, 1887)

Plate 17, figs. 11, 12; Plate 18, figs. 5, 6; Plate 19, figs. 1–5, 9, 10, 13, 14; Plate 20, figs. 6, 7; text-figs. 7J–M

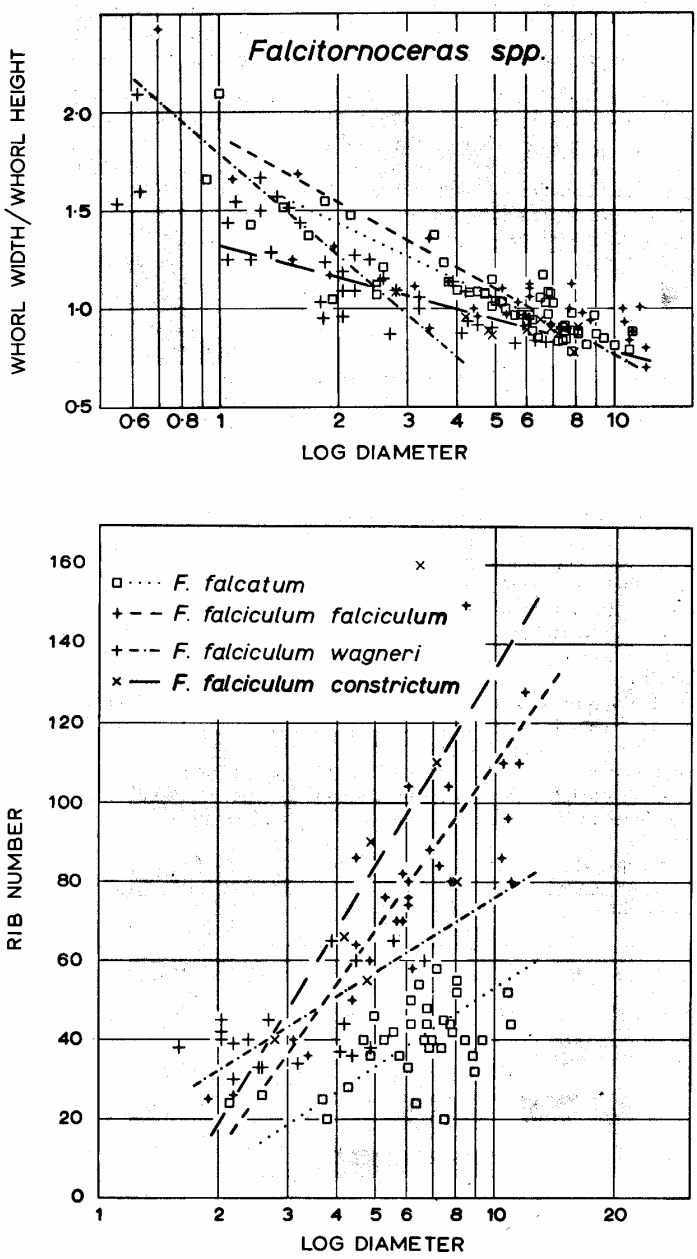
*1887 *Goniatites* (*Tornoceras*) *subundulatum* var. nov. *falcatum* Frech, p. 465.
1897 *Tornoceras falcatum* Frech; Frech (1897–1902), p. 177.
non 1897 *Tornoceras falcatum* Frech; Foord and Crick, p. 115, fig. 52.
1902 *Tornoceras subundulatum* var. *falcatum* Frech; Frech (1902), p. 50.

Neotype. BM(NH) C85039 (Pl. 19, figs. 1–3) from 600 m east of La Roquette, La Serre, Cabrières (68265e, 14006n), Hérault, France; Bed 17 (sample LS703), Trench C, *amblylobum* Zone, Famennian.

Material. Available for study besides the neotype were eleven paratypes (BM(NH) C85040–85050) and fifteen topotypes collected *in situ* (BM(NH) C85051–85065). A further eighteen specimens (BM(NH) C85068–85085), not included in the type series, were found loose at the surface within the area of the trenches (text-fig. 9); there is a single specimen from the nearby slopes of Val d'Izarne (BM(NH) C85067). BM(NH) C85169 was collected from the Hohlweg, north-east of the village of Nehden (West Germany, Mtb. 4517, Alme, r 34758, h 57000). All examples are preserved as haematitic internal moulds.



EXT-FIG. 5. Dimensions of *Falcitornoceras* spp. based on 102 specimens. For further details see text. Regression lines omitted for clarity.



TEXT-FIG. 6. Graphs of the ratio whorl width/whorl height, and rib number, plotted against diameter for *Falcitornoceras* spp; reduced major axis regression lines are included.

Diagnosis. Falcitornoceras with prominent chevron-shaped ribs numbering twenty to sixty per whorl (mean 38, at mean diameter 6·4 mm; text-fig. 6), and diminishing in strength towards the body chamber. Ventrolateral grooves sometimes present but only on the body chamber.

Description. The neotype (Pl. 19, figs. 1–3), a relatively large specimen, attains a maximum diameter of 10 mm and shows well the ribbing (the characteristic feature of the species). The prorsiradiate ribs, about forty-two per whorl, are falcate with a very weak salient on the umbilical shoulder where the ribs commence. The ventrolateral shoulder is prominent and angular; the ventral sinus is deep and U-shaped. Over the flanks the rib cross-sectional profile approaches semicircular, with rib spacing being approximately half of rib width. Over the venter the ribs thicken, assuming a lunate shape with an asymmetrical cross-sectional profile, the orad face being the steeper. The body chamber extends for over 75% of a whorl, the first third of which has increasingly weaker and approximated ribs. The last rib occurs at a diameter of 6·5 mm; thereafter the body chamber is smooth but with a further third showing weak ventrolateral furrows occupying the same site as the ventrolateral salient of the ribbing.

Other specimens allow details of the ontogeny and specific variation to be determined. The protoconch and first half whorl are smooth (BM(NH) C85049). At early diameters, where the whorl section is depressed (D = 1 mm; WW/WH = 2·6 in BM(NH) C85049), ornament develops consisting of forwardly pointing chevron-shaped ribs on the outer flanks and a U-shaped ventral sinus. The whorl section, rounded and depressed on the inner whorls, becomes compressed at a diameter of 5·5 mm and above where the flanks are subparallel and the venter tabulate (text-fig. 7J).

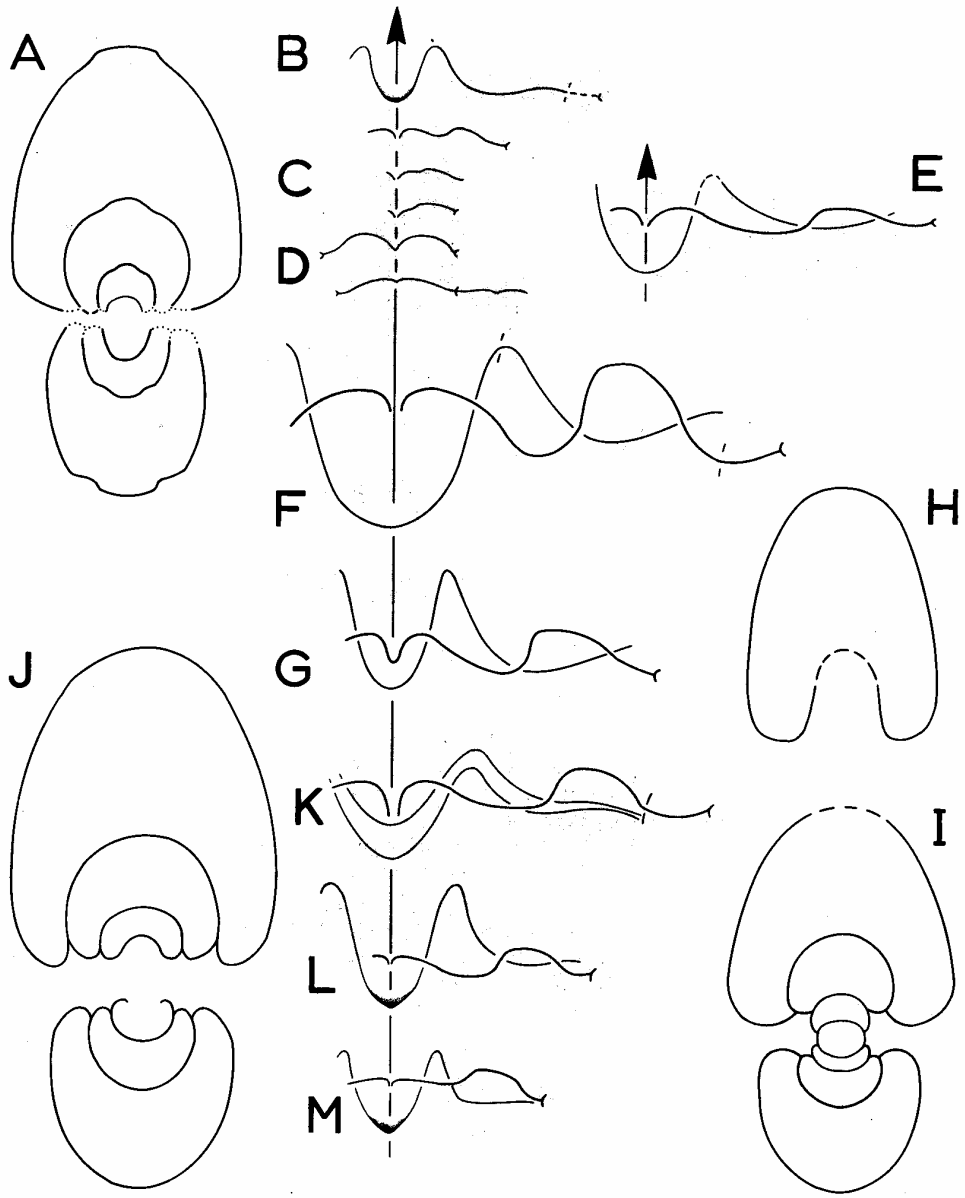
The ornament varies from specimen to specimen. Generally, the rib course becomes less angular and prorsiradiate in larger specimens (text-fig. 7K–M), and the ventral sinus more shallow. The gradual disappearance of the ribbing, to result in a smooth body chamber, is interpreted as a mature character and is associated with some septal approximation. The actual diameter where ribbing ceases was measured on twenty-one specimens (text-fig. 8); the mean diameter is 5·5 mm, in an apparently normal distribution, with a range from 2·7 mm (BM(NH) C85050) to > 9·4 mm (BM(NH) C85044; Pl. 19, figs. 13, 14) although these specimens were not from one population. In some smaller specimens (D = *c.* 2·5 mm) ribs are lost first from the flank, but persist on the venter which develops shallow ventrolateral grooves and a subcarinate shell form (BM(NH) C85048, C85050). Larger specimens lose their ribbing gradually, as on the neotype; when the ribs have disappeared there is one-third of a whorl with shallow ventrolateral grooves before these disappear too. One specimen (BM(NH) C85042; Pl. 19, figs. 4, 5) has three U-shaped constrictions on the venter of the body chamber. Large examples (e.g. BM(NH) C85043) have a funnel-shaped umbilicus. Growth curves for various parameters of species of *Falcitornoceras* are plotted in text-figs. 5, 6.

The partial sutural ontogeny is shown in text-figs. 7K–M. In large examples the umbilical lobe moves outside the seam. The course of the siphuncle can clearly be seen as it passes through the internal mould of the ribs. Usually septa are restricted to the ribbed part of the shell; no more than three are found beyond the point where the ornament is lost.

A single specimen (BM(NH) C85169; Pl. 17, figs. 11, 12), preserved as a haematitic internal mould and collected loose from the Nehden Schiefer at Nehden, is assigned to *F. falcatum*. This lacks ventrolateral grooves and shows a half-whorl of widely spaced falcate ribs.

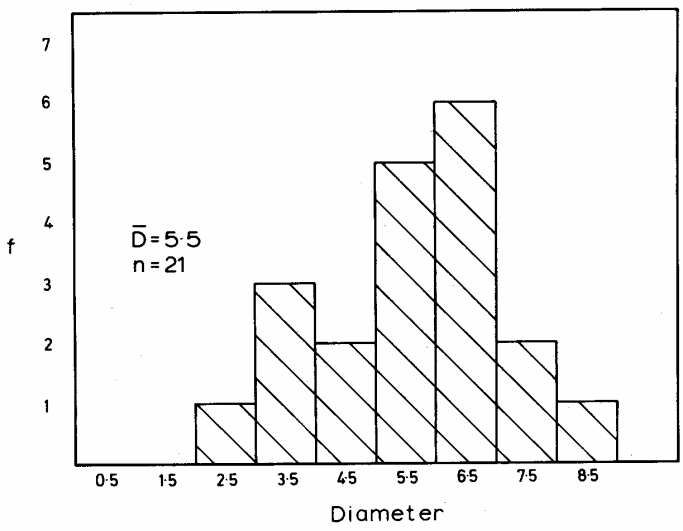
Dimensions	D	WW	WH	Ribs
Neotype BM(NH) C85039	7·3	3·9	4·4	44
BM(NH) C85044	9·4	4·5	5·3	40
BM(NH) C85042	7·55	3·68	4·35	20
	4·9	2·53	2·5	—
	3·5	2·38	1·73	—
	2·5	1·48	1·38	—
	1·85	1·13	0·73	—
	1·45	0·88	0·58	—

Remarks. No illustrations of the species *falcatum* Frech have ever been published, and the justification of it as this tornoceratid is based solely on Frech's initial description (1887, p. 465): 'Die var. [of *Gon.* (*Torn.*) *subundulatum* sp. nov.] *falcatum* zeichnet sich besonders im Ausseren durch das Vorhandsein sehr deutlicher, tief eingeschnittener Sichelrippen auf den Seiten aus, die jedoch auf der



TEXT-FIG. 7. Sutures, growth lines, and cross-sections of *Falcitornoceras* spp., all from BM(NH) specimens. A–D, *F. falciculum wagneri* subsp. nov. A, C85177, whorl cross-section, × 11; B, C85172, holotype, rib course at WW = 2·4 mm, × 10; C, C85178, early sutures (reversed for comparison) between D = 1·8 mm, WW = 1·25 mm and WW = 0·75 mm and WH = 0·5 mm, × 11; D, C85174, prosuture at D = 0·55 mm, WW = 0·63 mm, WH = 0·27 mm and first septum at WW = 0·8 mm, WH = 0·4 mm, × 15; specimens collected from Km 299·1 on the Madrid–Badajoz railway, 1 km south of Guadalmez, central Spain. E, *F. falciculum constrictum* subsp. nov. C85138, growth-line and a constriction (reversed) at D = 2·55 mm, WW = 1·5 mm, WH = 1·4 mm, × 20. F–I, *F. falciculum*

[*continued opposite*



TEXT-FIG. 8. Diameter at which the ribbed ornament is lost on *Falcitornoceras falcatum* from the lower Famennian at La Serre, south of Cabrières, Montagne Noire, France.

Wohnkammer meist vollig fehlen. Hier finden sich nun auf dem Rücken in regelmassigen Abstanden flache Einsenkungen. Ausserdem ist der Nabel sehr eng und die aussere Form mehr gerundet. Die Lobenlinie bleibt stets der das *Goniatites circumflexum* ähnlich. Beide Formen kommen in dem mittleren Oberdevon von La Serre nicht selten vor.' This description makes no mention of the ventro-lateral grooves present on *F. falciculum*, the other ribbed species present at La Serre, and is clearly appropriate for the specimens described here. No evidence of the original material has been traced. A neotype is designated to clarify its diagnosis and to provide the first illustration of the species.

Zimmermann (1893) and Frech (1897) reported this species from Thuringia, associated with *Cheiloceras curvispina* which Frech (1897) used as the index fossil of the Cheiloceras Stufe. Frech's description seems to have been adequate for Foord and Crick (1897) to believe they had recognized the species amongst material in the British Museum (Natural History) from Hérault (BM(NH) C4791). The specimen they illustrated (fig. 52), however, has strong ventral constrictions, lacks coarse ribbing, and is referred to *F. f. constrictum*. The record of the species from Thuringia can be widened by reference to museum specimens in the Geologisch-Paläontologisches Institute, Marburg, collected by Denckmann and labelled 'Schmidts Grund bei Wallenfels', a locality in nearby Oberfranken.

F. falcatum has coarser less dense ribbing than other species of *Falcitornoceras*. At La Serre examples were found with rib frequencies of twenty-four to fifty-four per whorl at diameters of 5–10 mm. This compares with figures of sixty-four to one hundred and fifty for *F. f. falciculum*

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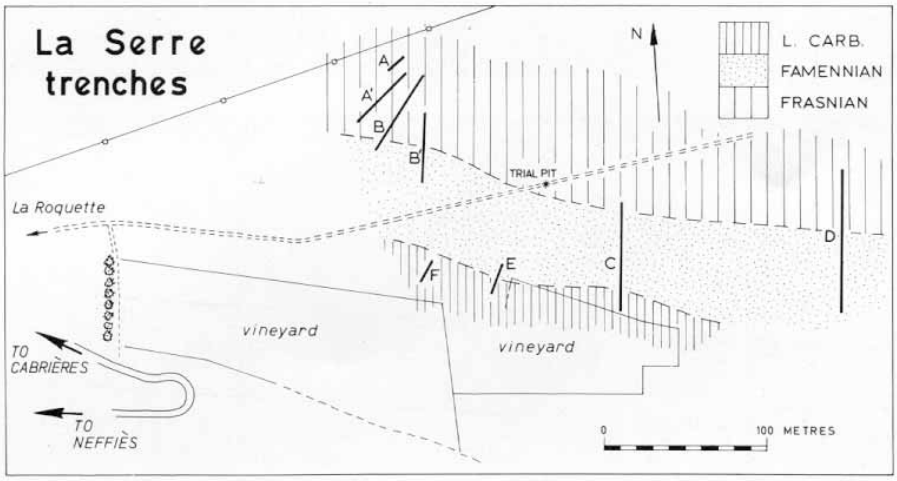
falciculum subsp. nov. F, C85090, growth-line and suture at D = 9·8 mm, WW = 5·8 mm, WH = 5·5 mm, × 10; G, C85086, holotype, growth-line and suture at WW = 2·7 mm, WH = 2·6 mm (reversed), × 11; H, C85093, whorl cross-section at WW = 5·3 mm, WH = 7·5 mm, × 5; I, C85092, whorl cross-section at D = 5·3 mm, WW = 3·2 mm, WH = 3·3 mm, × 10. J–M, *F. falcatum* (Frech). J, C85042, whorl cross-section at D = 7·5 mm, WW = 3·7 mm, WH = 4·4 mm, × 10; K, C85044, suture and rib at WW = 3·9 mm, WH = 4·2 mm, × 9; L, C85043, suture and growth-line at WW = 2·0 mm, WH = 1·8 mm, × 10; M, C85046, suture and growth-line at WW = 2·0 mm, WH = 2·6 mm, × 10.

with which it occurs. That this distinction in rib density is not determined by an arbitrary limit is clear from text-fig. 6 on which the species plot in distinct and divergent fields. *F. falcatum* also lacks the ventrolateral grooves which appear at the nepionic constriction in *F. falciculum* (Pl. 20, figs. 3–5).



TEXT-FIG. 9. Map showing the position of trenches dug at La Serre, south of Cabrières, Hérault, Montagne Noire, France, excavated during the research programme of Dr. R. Feist (University of Montpelier) and based on a survey by J.D.P. The section shown in text-fig. 2 is at Trench C.

Horizon and range. At La Serre *F. falcatum* was collected between Beds 17 (sample LS 703; refer to text-fig. 2 for location of sample numbers) and 26 (sample LS 808), and it appears in the record some 5·5 m below the first *Cheiloceras* in Bed 20 (sample LS 796).

Falcitornoceras falciculum sp. nov.

Derivation of name. From Latin *falcicula*, diminutive of Latin *falx*, sickle, alluding to the thin sickle-shaped ribs present on this species.

Holotype. See nominate subspecies.

EXPLANATION OF PLATE 18

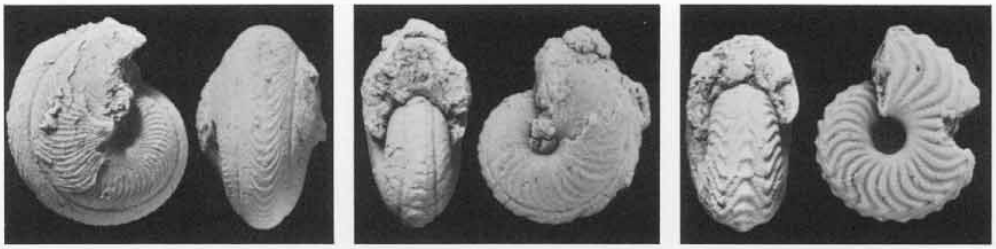
Figs. 1–17. *Falcitornoceras* gen. nov. All except 15–17 preserved as haematitic moulds. 1–10, 13, 14, from lower Famennian shales, around 600 m east of La Roquette, La Serre, Cabrières, Hérault, France.

Figs. 1, 2, 9–14, 17. *F. falciculum falciculum* subsp. nov. 1, 2, BM(NH) C85091, ×5. 9, 10, BM(NH) C85089, from Trench C (sample LS 808), ×8. 11, 12, BM(NH) C85066, mature individual which has lost its ribs on the body chamber, Val d'Isarne (628), Cabrières, Hérault, France, ×8. 13, 14, BM(NH) C85086, holotype, from Trench C (sample LS 738), ×5. 17, LPB 5542*b*, external mould labelled 'Formation des Marettes La Rabine en La Chapelle Chaussée, Ille et Vilaine', France, ×4.

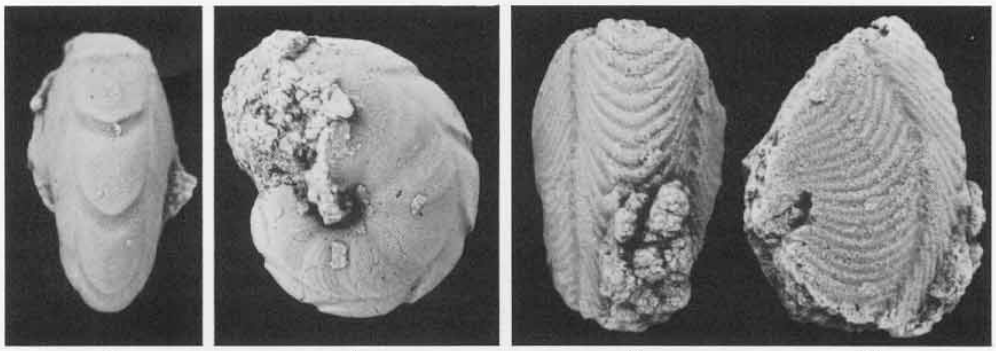
Figs. 3, 4, 7, 8. *F. falciculum constrictum* subsp. nov. 3, 4, BM(NH) C85138, showing U-shaped constrictions over the venter, from Trench C (sample LS 818), ×8. 7, 8, BM(NH) C85139, ×6.

Figs. 5, 6, *F. falcatum* (Frech). BM(NH) C85041, from Trench C (sample LS 818), ×8.

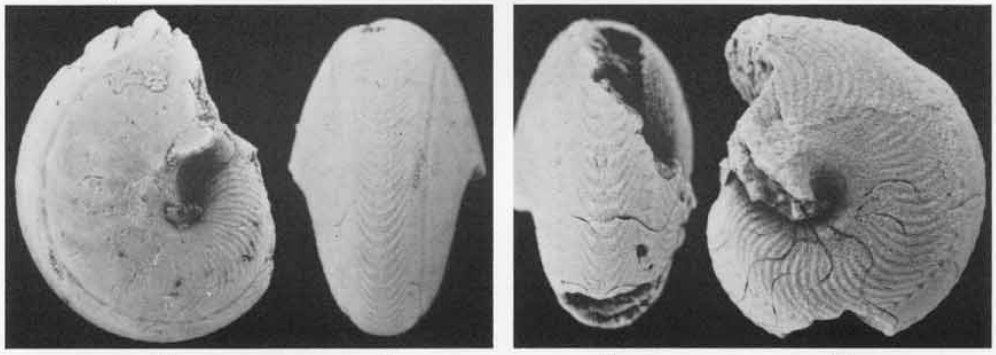
Figs. 15, 16. *F. falciculum* sp. nov. Nodule band in the Nehden Schiefer, Nehden, West Germany (Mtb. 4517 Alme). 15, BM(NH) C85171, ×8. 16, BM(NH) C85170, ×8.



1 2 3 4 5 6



7 8 9 10



11 12 13 14

15 16 17

HOUSE and PRICE, *Falcitornoceras*

Diagnosis. Falcitornoceras with chevron-shaped ribs numbering twenty-five to one hundred and fifty per whorl and diminishing in strength towards the body chamber. Ventrolateral grooves may be present at the nepionic constriction but may be lost in mature specimens.

Remarks. Three subspecies, *constrictum*, *falciculum*, and *wagneri*, are erected here, the last two distinguished solely by their ribbing frequencies, and the first by its numerous lateral constrictions. Two specimens of *F. falciculum* (BM(NH) C85170, C85171; Pl. 18, figs. 15, 16) from a calcareous nodule in the Nehden Schiefer at Nehden, cannot easily be assigned to any of these subspecies. They are preserved complete with shell and have a ribbing frequency (sixty ribs per whorl) intermediate between *falciculum* and *wagneri*. The ribs have a rounded cross-sectional shape and the ventrolateral grooves are only weakly developed. No constrictions are visible, although generally these can be seen only on internal moulds.

Horizon and range. As for the genus. Conodonts extracted from the matrix of the specimens from Nehden were kindly identified by Professor W. Ziegler (Senckenberg Museum, Frankfurt) and indicate the upper *crepida* to lower *rhomboidea* Zones, Famennian.

Falcitornoceras falciculum falciculum subsp. nov.

Plate 17, figs. 13–16; Plate 18, figs. 1, 2, 9–14, 17; Plate 19, figs. 16, 17; Plate 20, figs. 8–10, 12, 13; text-figs. 7F–I.

1935 *Tornoceras sandbergeri* Foord and Crick; Böhm, p. 55, fig. 9.

Holotype. BM(NH) C85086 (Pl. 18, figs. 13, 14; text-fig. 7G) from La Serre; sample LS 738, Bed 21, Trench C, *amblylobum* Zone, Famennian.

Material. Nine specimens (BM(NH) C85088–85096) collected from the type locality are selected as paratypes, together with one (BM(NH) C85087) from the nearby slopes of Val d'Isarne. Eleven specimens are designated topotypes (BM(NH) C85097–85107). A further twenty-five specimens (BM(NH) C85108–85132), not included in the type series, were collected from scree at La Serre; one (BM(NH) C85135) at Col du Puech de la Suque, St. Nazaire de Ladarez, Hérault; one (BM(NH) C85134) from La Tourrière, Cabrières, Hérault; and two (BM(NH) C85167, C85168) from the Nehden Schiefer at Nehden. Six specimens from Brittany (LPB 5542, 5543*a*, *b*, 5544*a–c*) were labelled 'Formation des Marettes, La Rabine en La Chapelle Chausée' (Ille et Vilaine, see Babin and Paris 1973); and two (LPB 4136, 4143) were labelled 'base du Schistes du Porsguen, Ile Longue en Crozon', Finistère.

Diagnosis. F. falciculum with fine concave or falcate ribs, twenty-five to one hundred and fifty per whorl (mean 78 at mean diameter 6 mm; text-fig. 6). Compressed whorl form with tabulate or arched venter bounded by two thin ventrolateral grooves developed early in ontogeny.

EXPLANATION OF PLATE 19

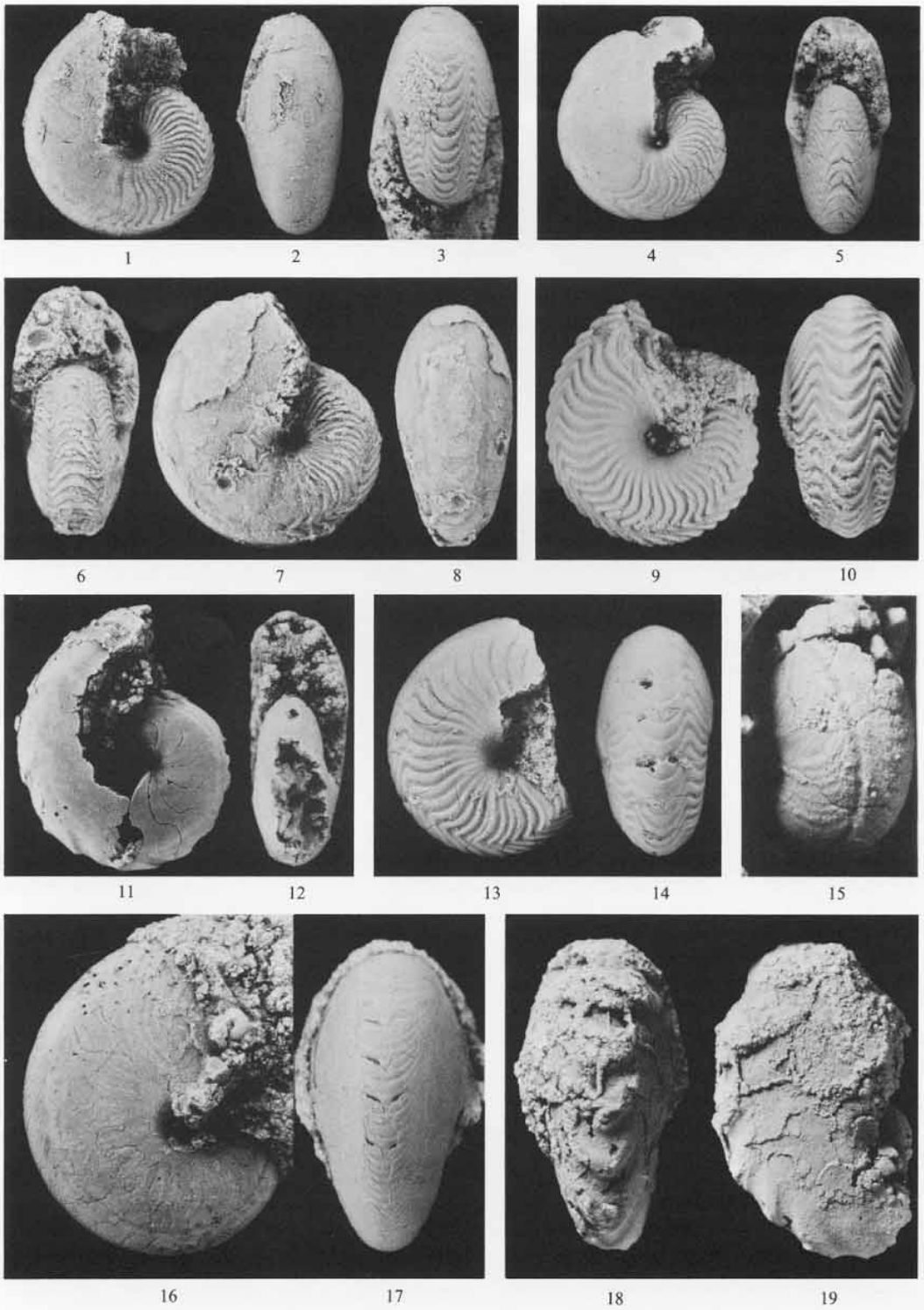
Figs. 1–17. *Falcitornoceras* gen. nov. All except 6–8 and 16, 17 preserved as haematitic internal moulds and are from lower Famennian shales, around 600 m east of La Roquette, La Serre, Cabrières, Hérault, France.

Figs. 1–5, 9, 10, 13, 14. *F. falcatum* (Frech). 1–3, BM(NH) C85039, neotype, side view and two ventral views half a whorl apart, from Trench C (sample LS 703), ×4 (1, 2) and ×5 (3). 4, 5, BM(NH) C85042, with ventral constrictions on the body chamber, ×4·5. 9, 10, BM(NH) C85045, ×6. 13, 14, BM(NH) C85044, ×4.

Figs. 6–8. *F. falciculum wagneri* subsp. nov. BM(NH) C85172, holotype from Km 299·1 on the Madrid–Badajoz railway, 1 km south of Guadalmez, central Spain, ×6.

Figs. 11, 12, 15, 18, 19. *F. falciculum constrictum* subsp. nov. 11, 12, BM(NH) C85136, holotype from Trench C (sample LS 783), ×4. 15, 18, 19, BM(NH) C85137, ribbed inner whorls and views of smooth, constricted venter and flanks of body chamber, from Trench C (sample LS 703), ×10 (15) and ×4 (18, 19).

Figs. 16, 17. *F. falciculum falciculum* subsp. nov. BM(NH) C85167, from the Nehden Schiefer at the Hohlweg, north-east of Nehden, West Germany (Mtb. 4517 Alme), ×5.



1 2 3 4 5

6 7 8 9 10

11 12 13 14 15

16 17 18 19

HOUSE and PRICE, *Falcitornoceras*

Dimensions	D	WW	WH	Ribs
Holotype BM(NH) C85086	6·9	3·6	3·9	88
	5·2	3·2	2·9	—
Paratypes BM(NH) C85092	5·33	3·15	3·25	76
	3·8	2·25	1·98	—
	1·95	1·45	1·10	—
	1·58	1·18	0·7	—
	1·08	0·83	0·7	—
	0·7	0·8	0·33	—
	0·5	0·65	—	—
BM(NH) C85093	12·0	5·25	7·5	128

Description. The holotype (Pl. 18, figs. 13, 14; text-fig. 7G), although the best preserved of the specimens found *in situ*, illustrates the features of the subspecies rather poorly. It has eighty-eight falcate ribs in the whorl prior to a diameter of 6·9 mm. The flatly rounded venter is bounded by two shallow grooves. The suture is shown in text-fig. 7G.

Other specimens allow the subspecies to be described in more detail. The protoconch has not been observed. Early whorls up to 2 mm diameter have strong concave ribs over the flank, twenty-six per whorl, and a tabular venter bounded by clearly visible grooves (BM(NH) C85094, at D = 2·2 mm; Pl. 20, figs. 8–10). Later the ribs become more densely spaced, thirty-six per whorl at D = 3·4 mm (BM(NH) C85088, Pl. 20, figs. 12, 13).

The whorl section (text-fig. 7H, I), with globose inner whorls, develops rounded flanks but becomes compressed by a diameter of 6·5 mm (text-fig. 7I). Ventrolateral grooves are still present on the largest specimen (BM(NH) C85093) at a whorl height of 7·5 mm. The dense ribbing persists throughout the phragmocone and on to the body chamber; BM(NH) C85096 has a body chamber one whorl in length, all of which is ribbed; BM(NH) C85090, 11·6 mm in diameter and wholly septate, has ribs which diminish in strength during the last quarter whorl. But BM(NH) C85095 loses its ribs by a diameter of 5·8 mm, having a body chamber three-quarters of a whorl in length, the first third of which is densely ribbed and smooth thereafter but with ventrolateral grooves and weak plications. The same modification in ornament is seen on BM(NH) C85066 (Pl. 18, figs. 11, 12) which loses all its ribs by a diameter of 4 mm. At the mean diameter for this sample (5·9 mm), the mean number of ribs per whorl is 80. The sutural ontogeny is similar to *F. falcatum*, but on BM(NH) C85090 (D = 11·6 mm) (text-fig. 7F) the umbilical lobe lies outside the seam and the lateral saddle is high, rounded, and asymmetric.

Two relatively large (D = 11 mm) specimens, preserved as haematitic internal moulds and collected from the Nehden Schiefer at Nehden (Mtb. 4517 Alme), show only the first few degrees of body chamber (BM(NH) C85167, Pl. 19, figs. 16. 17; BM(NH) C85168, Pl. 17, figs. 13, 14). On BM(NH) C85167 ribs are present throughout the whole of the last whorl seen but become coarser and more widely spaced towards the body chamber. Ribs are still visible over the venter at a stage when they are much reduced in strength over the flanks. Coincident with the decrease in rib strength and frequency is the disappearance of marked ventrolateral grooves. BM(NH) C85168 has fine ribbing but lacks ventrolateral grooves.

Horizon and range. At La Serre this subspecies occurs between Beds 17 (sample LS 703) and 26 (sample LS 808) in Trench C, in and below the *amblylobum* Zone, Famennian.

Falcitornoceras falciculum constrictum subsp. nov.

Plate 18, figs. 3, 4, 7, 8; Plate 19, figs. 11, 12, 15, 18, 19; text-fig. 7E

1897 *Tornoceras falcatum* Frech; Foord and Crick, p. 115, fig. 52.

Derivation of name. From Latin *constrictum*, narrow, referring to the constrictions of the ventral area.

Holotype. BM(NH) C85136 (Pl. 19, figs. 11, 12) from La Serre (see under *F. falcatum*); sample LS 783, Bed 22, Trench C, *amblylobum* Zone, Famennian.

Material. Five specimens (BM(NH) C85137–85141) are designated as paratypes, and a further seventeen (BM(NH) C85142–85158) as topotypes.

Diagnosis. Like *F. f. falciculum* but with a different late-stage shell form consisting of narrower whorl width and a venter with V-shaped constrictions numbering at least six per whorl, and in some examples extending across the flank to form weak plications.

Dimensions	D	WW	WH	Ribs
Holotype BM(NH) C85136	6·0	3·3	3·7	—
Paratypes BM(NH) C85138	2·8	1·5	1·38	40
BM(NH) C85139	6·9	3·5	3·9	—

Description. The holotype is a relatively large specimen (D = 10 mm) and shows rather well the late stage ornament which distinguishes this subspecies. The earliest part of the last whorl has finely ribbed flanks bounded by thin ventrolateral grooves. Only one ventral constriction is visible, on the ribbed portion; otherwise the venter is damaged. The ribbing strength diminishes over the last half whorl so that by the position of the last septum (at D = 6 mm) there are no ribs and the ventrolateral grooves are much reduced in depth. The last half whorl is body chamber, with six ventral constrictions which run into the ventrolateral groove.

Other specimens allow details of the ontogeny and variation to be determined. Early whorls were not seen. The shell form is like *F. f. falciculum*, except in large specimens where the whorl width is less, but no specimens were well enough preserved to be sectioned. The smallest specimen seen (BM(NH) C85138; Pl. 18, figs. 3, 4) has forty concave ribs, ventrolateral grooves, and six weak ventral constrictions. The last three septa are approximated (at D = 2·5 mm) suggesting that, although small, this specimen may be mature. The body chamber is preserved through 90°. Two slightly larger specimens, BM(NH) C85141 (D = 4·2 mm) and C85139 (Pl. 18, figs. 7, 8), have a similar ornament but the constrictions are deeper, more extensive, and associated with shallow plications on the flanks near to the umbilicus. This modification of the ornament is even more pronounced on BM(NH) C85140 (D = 4·8 mm). The holotype has a smooth body chamber; the smallest specimen on which a smooth body chamber is developed is BM(NH) C85139, where the ribbing disappears at a diameter of 5 mm, leaving smooth plicate flanks with strong ventral constriction. At similar diameters on BM(NH) C85142 there is no plication, only ventral constrictions and ventrolateral grooves. The largest specimen seen, BM(NH) C85137 (D < 13 mm; Pl. 19, figs. 15, 18, 19), has closely spaced constrictions numbering five in one-quarter whorl, and smooth compressed flanks which run into the high arched venter. The suture line (text-fig. 7E) does not differ from *F. f. falciculum*.

Remarks. These specimens differ only slightly from *F. f. falciculum* which was collected from the same stratigraphic levels. Examples less than 5 mm in diameter are difficult to distinguish but, when larger than this, that subspecies has a shell and more especially a body chamber which retains fine ribbing and ventrolateral grooves (although it may become smooth), whereas *F. f. constrictum* develops constrictions and a smooth plicate body chamber. No specimens were found with only few constrictions which might be considered as being intermediate between these two subspecies. This suggests that they are distinct and separate, although they could represent sexual dimorphs. Hitherto sexual dimorphism in the Tornoceratidae has been postulated only on the basis of bimodal size distribution (Makowski 1962).

Horizon and range. This subspecies is only known from the Famennian *amblylobum* Zone at La Serre, Hérault, in Trench C between Beds 17 (sample LS 703) and 26 (sample LS 818).

Falcitornoceras falciculum wagneri subsp. nov.

Plate 19, figs. 6–8; Plate 20, figs. 1–5, 11, 14–18; text-fig. 7A–D

?1961 *Reticuloceras superbilingue* Bisat; Almela *et al.*, p. 211, fot. 7, 8, 11, 12.

Derivation of name. Named for Drs. R. H. Wagner and C. H. Th. Wagner Gentis who collected the material described here.

Holotype. BM(NH) C85172 (Pl. 19, figs. 6–8; text-fig. 7B) from Km 299·1 on the Madrid–Badajoz railway, 1 km south of Guadalmez, central Spain (see Almela *et al.* 1961); Lower Famennian Shales.

Material. The holotype, six paratypes (BM(NH) C85173–85178), and twenty-two topotypes (BM(NH) C85179–85200) preserved complete or as internal moulds in yellow weathering calcareous mudstone.

Diagnosis. F. falciculum with twenty-five to sixty-five (mean 43, at diameter 3·1 mm) falcate ribs per whorl, with prominent ventrolateral grooves developed at the nepionic constriction and persisting until the mid-stage of the otherwise unornamented body chamber.

Dimensions	D	WW	WH	Ribs
Holotype BM(NH) C85172	6·7	3·5	4·1	60
	5·0	2·65	2·5	—
Paratypes BM(NH) C85175	2·55	1·6	1·4	33
	2·45	1·45	1·3	—
	1·83	1·0	1·05	—
BM(NH) C85174	0·55	0·63	0·41	—
	1·05	0·75	0·6	—
Topotype BM(NH) C85195	0·37	0·47	0·13	—

Description. The holotype (BM(NH) C85172, Pl. 19, figs. 6–8) shows only the features of the mature shell; the ontogeny is described from other specimens. The spindle-shaped protoconch (BM(NH) C85195) quickly increases in whorl height resulting in a globose shell form at early diameters (BM(NH) C85174, Pl. 20, figs. 1, 2, 11). The nepionic constriction was observed on six specimens (BM(NH) C85176, Pl. 20, figs. 3–5; C85186, C85193, C85194, C85196, C85197), at diameters 0·9–1·05 mm. The constriction is visible more clearly on the internal mould and is prorsiradiate and concave over the flank, with a shallow ventral sinus. The ornament consists of concave ribs with a U-shaped ventral sinus and clear ventrolateral grooves, and appears at the nepionic constriction as demonstrated for *Tornoceras* by House (1965). The shell form (text-fig. 7A) is globose in early whorls, with a maximum whorl width midway across the flanks, a tabulate venter, and ventrolateral grooves; compressed flanks develop at a diameter of 3 mm and the point of maximum whorl width migrates to the umbilical shoulder. A funnel-shaped umbilicus is formed. Growth curves for various parameters are shown in text-figs. 5, 6.

The ribbing maintains its concave prorsiradiate course over the flanks (Pl. 20, fig. 4) up to the point where an umbilical shoulder is formed (D = *c.* 3 mm); here a weak umbilical salient is developed (text-fig. 7B), giving the ribs a true falcate shape. The ribs have an angular asymmetrical profile when viewed in cross-section, with the steeper face orad, rather like those on *F. falcatum*. The last three ribs on some specimens (e.g. BM(NH) C85172, Pl. 19, figs. 6–8) are widely spaced and subdued, after which the body chamber is smooth with only weak ventrolateral grooves persisting for about a third of a whorl before they too disappear. The smooth body

EXPLANATION OF PLATE 20

Figs. 1–5, 11, 14–18. *Falcitornoceras falciculum wagneri* subsp. nov. 1, 2, BM(NH) C85174, internal mould of protoconch, ×30. 3–5, BM(NH) C85176, showing the nepionic constriction and appearance of the ventrolateral furrows and ribs at that point, ×25. 11, BM(NH) C85174, prosuture and first suture, ×55. 14, BM(NH) C85173, ×10. 15–17, BM(NH) C85175, ×15. 18, BM(NH) C85173, ×20. All specimens collected by Dr. R. H. Wagner and C. H. Th. Wagner-Gentis from Km 299·1 on the Madrid–Badajoz railway, 1 km south of Guadalmez, central Spain.

Figs. 6, 7. *F. falcatum* (Frech). BM(NH) C85040, haematitic internal mould collected from lower Famennian shales, about 600 m east of La Roquette, La Serre, Cabrières, Hérault, France, ×15.

Figs. 8–10, 12, 13. *F. falciculum falciculum* subsp. nov. lower Famennian shales, about 600 m east of La Roquette, La Serre, Cabrières, Hérault, France. 8–10, BM(NH) C85094, ×18. 12, 13, BM(NH) C85088, from Trench C (sample LS 703), ×10.

All scanning electron micrographs.

HOUSE and PRICE, *Falcitornoceras*

chamber extends for half a whorl. One specimen (BM(NH) C85183) has no ventrolateral grooves at a diameter of 1·8 mm, much denser (sixty-five per whorl) and finer ribs, and a more globose shell form.

The suture is known only from juvenile examples (text-fig. 7C, D); the prosuture and first suture are visible in Pl. 20, fig. 11.

Remarks. The material from which these specimens were extracted contained many juvenile goniatites, most of which were just early whorls and so could not be identified. *F. f. wagneri* is distinguished from *F. f. falciculum* by its lower rib density (mean 43 per whorl, compared with 80). *F. falcatum* has a similar number of ribs (mean 39 per whorl) but lacks the ventrolateral grooves formed at the nepionic constriction.

Horizon and range. Other species of *Tornoceras* and *Lobotornoceras* were found together with *F. f. wagneri* but there were no *Cheiloceras*, suggesting that this occurrence was low in the *amblylobum* Zone, Famennian. Preparation of conodont samples produced no stratigraphically useful forms.

Acknowledgements. We are indebted to a number of individuals for granting access to material in their charge or arranging the loan of specimens, including Professor C. Babin (Brest), Professor H. K. Erben (Bonn), Dr. H. Jaeger (East Berlin), Mr. D. Korn (Sundern), Mr. D. Phillips (London), Dr. R. B. Rickards (Cambridge), and Dr. W. Struve (Frankfurt). We appreciate especially the co-operation with Dr. R. Feist (Montpelier) in his trenching programme in the Montagne Noire, and the advice of Professor G. Klapper (Iowa City) on matters relating to conodont dating of samples from the trenches. We are both indebted to the University of Hull for facilities and to the Natural Environment Research Council for support of the research programme of which this work forms a part.

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Typescript received 7 March 1984
Revised typescript received 15 May 1984