ON THE ORIGIN OF THE CLYMENID AMMONOIDS

by M. R. HOUSE

ABSTRACT. The stratigraphical and morphological evidence relating to the abrupt appearance of the endosiphonate clymenids in the early Famennian (Upper Devonian) is reviewed. An origin from goniatites of the *Tornoceras* stock is suggested. A series of morphologically intermediate forms is described from the earliest Upper Famennian of the Holy Cross Mountains of southern Poland. This series leads to *Tornia*, a new genus here described, which is homoeomorphic with *Platyclymenia* but with a ventral siphuncle. Attention is drawn to the fact that some clymenids show a ventral siphuncle in their early ontogeny.

THE origin of the Upper Devonian endosiphonate clymenids, or Clymeniina, has been the subject of considerable past speculation. There have been some, even recently, who would derive the group direct from the Nautiloidea. But these have usually avoided the implications of their enthusiasm. The traditional view, essentially since Branco's classic ontogenetic work of 1890, has been to consider them as derived from the goniatites, but some have preferred a monophyletic, others a polyphyletic origin. The purpose of this paper is to review the stratigraphical and morphological evidence bearing on the subject and to describe, from the earliest Upper Famennian of southern Poland, certain goniatites which seem to be transitional between the Tornoceratidae and the earliest clymenids. These may provide a solution to the problem.

From their sudden first appearance in the early Upper Famennian the clymenids diversified rapidly as is indicated by an accompanying diagram (text-fig. 1) based mainly on the work of Wedekind and Schindewolf. Evolutionary diversification is both in shell form and suture pattern. Extremes in shell form are reached by the bizarre triangular *Soliclymenia* and trilobed *Wocklumeria*. Sutural variation grades from the utter simplicity of *Platyclymenia* to the multilobed *Sphenoclymenia*, superficially homoeomorphic with *Beloceras* but of distinct ontogeny, and *Wocklumeria* and *Epiwocklumeria* with ventral sutures closely homoeomorphic with *Imitoceras*. Their diversity was short lived. The close of the Famennian saw the extinction of the group. Clymenid evolution and sutural derivation has been described at length by Schindewolf in a series of papers: he favours a monophyletic origin of the group and has produced substantial evidence to support this (Schindewolf 1937, 1949*a*, *b*, 1955).

Münster (1831, p. 182) was the first to recognize the endosiphonate clymenids which he described under the name *Planulites* (*non* Parkinson 1822), a name later corrected to *Clymenia* (Münster *in* Goldfuss 1832, p. 489). It is unfortunate that the apt name *Endosiphonites* (Ansted 1838, p. 416) proposed as an alternative during the description of Cornish material is invalid. The complex nomenclatorial history of *Clymenia* and its relatives has been reviewed by Schindewolf (1949, p. 63; 1955, p. 418 et seq.) and Turner (1962).

OPINIONS ON CLYMENID AFFINITY

Following von Buch's use of siphuncle position to separate nautiloids from the ammonoids, Münster placed *Planulites* and *Clymenia* with the former. This view was

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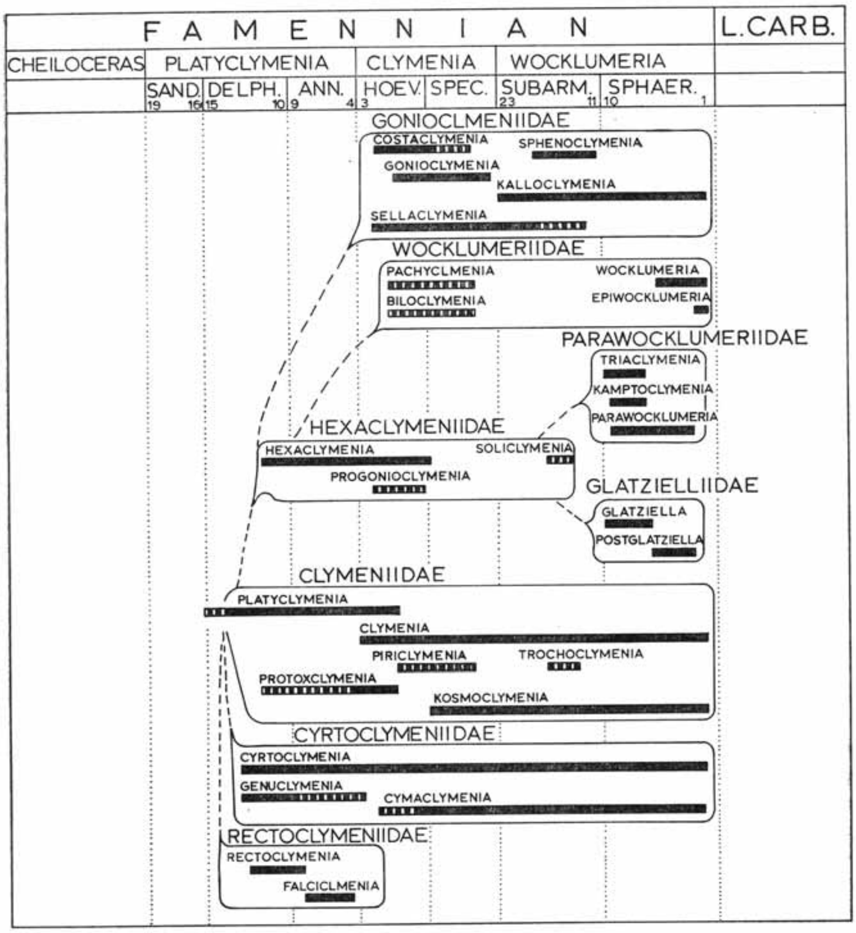


TEXT-FIG. 1. Diagram showing the ranges of genera and families of the Clymeniina. The family groupings are those of Schindewolf (*in* Moore 1957). Pecked lines indicate ranges which are uncertain. The numbers for the Delphinus to Hoevelensis Zones correspond to bed numbers of Wedekind (1908) at Enkeberg: those for the Subamata to Sphaeroides Zones are those of Schindewolf (1937) at the Hönnetal railway cutting.

curiously strengthened when Edwards (1849, p. 50) erected the Family Clymenidae with *Clymenia* and the Tertiary *Aturia* only, being misled by the sutural similarities of the latter with the *Kosmoclymenia* group. Although the relations with *Aturia* were soon disentangled, clymenid affinities were usually given in early textbooks, following Münster, as with the Nautiloidea, for example by Roemer (in Bronn 1859–6, p. 495), Sedgwick and McCoy (1851–5, p. 312, 401), Woodward (1851–6, p. 87), Blake (1882, p. 36) and others. But a current of disagreement was growing, led by Quenstedt (1849, p. 68) and followed by Hyatt (1883–4), Nicholson and Lydekker (1889, p. 853), Hoernes (1886, p. 400) who gave clear placing of the group with the Ammonoidea even before Branco (1890, p. 34) published his work on the early stages of ammonoids which finally convinced other workers on cephalopods. From 1890 almost all writers have accepted the ammonoid relation as being the most probable. The list includes Foord and Crick (1897), Frech (1890, 1897–1902), Wedekind (1908), Schindewolf (1922, 1955), Miller (1938), Petter (1960), and Bogoslovski (in Ruzhencev, ed., 1962), that is all the most significant contributors on the Devonian Ammonoidea. Recent exceptions are Flower (1961, p. 574) and Donovan (1964, p. 271).

Of those who favoured an origin of the clymenids from typical ammonoids opinion has differed as to their precise source. Frech (1890, p. 399) derived them both (from *Anarcestes* and *Agoniatites*, presumably a generalization, and Schindewolf (1949, p. 206) favouring the anarcestid descent, derived them from *Archoceras* or a related form (1955, p. 422). These views typify the monophyletic standpoint.

Polyphyletic origin of the clymenids found Sobolew (1914*a*, *b*) as its chief exponent. Sobolew sought to derive all the diverse-sutured clymenids from their Devonian goniatite homoeomorphs. The dorsal migration of the siphuncle was held to take place along over ten unrelated lines of descent (see also Schindewolf [1949] since Sobolew's major work is very rare in western libraries: I am indebted to Professor Makowski for a copy). No stratigraphic evidence has been found to support most of these links, and Schindewolf, in several papers, has as a result of ontogenetic work and careful collecting produced a picture of an evolutionary radiation of clymenids from a simple sutured stock of *Hexaclymenia* type. Sobolew's suggestions therefore raise more problems than they solve.

STRATIGRAPHICAL EVIDENCE

Until recently it was supposed that clymenids were represented in the middle Frasnian by the anomalous *Acanthoclymenia* (Frech 1897, p. 177k; Schindewolf 1955), but it has since been demonstrated that *Acanthoclymenia* is a manticoceratid and quite unrelated to the clymenids (House 1961). The elimination of the anomalous Frasnian records clarifies the picture and it is now clear that clymenids enter the stratigraphical record a little above the base of the Upper Famennian and above the *Cheiloceras* Stufe of the German terminology. This has now been demonstrated in unambiguous sections in North Africa (Petter 1960), Spain (Kullmann 1960, 1963), England (House 1963), and Australia (Jenkins 1968), but especially in Germany (Wedekind 1908, Schindewolf 1922, Lange 1929). Similar relations hold in the U.S.A. (House 1962), Canada (House and Pedder 1963) and China (Chang 1958) although in these latter areas less detailed faunal successions have been described.

A brief review will now be given of the main German sequences which have been described showing the entry of the clymenids. This is intended as a nomenclatorial revision and the taxonomic assignments have been corrected as far as possible. The available type material has been re-examined but for Wedekind's material the bed numbers are rarely recorded with the specimens (most labels having been burnt) and the determinations are based also on his figures and descriptions. Since Wedekind's photographic illustrations are hardly ever given their correct size, and ventral views rarely given, some new illustrations of primary types are given here (Pl. 126).

The first detailed succession described was that on the western part of Enkeberg given by Wedekind (1908, pp. 569–71). The ammonoid sequence is as follows: youngest beds above, oldest below:

BED 10 (9 cm.): *Platyclymenia* (*Platyclymenia*) *sandbergeri* (Wedekind) (not listed from this bed on p. 621 or on the table), *Rectoclymenia roemeri* (Wedekind), *Cyrtoclymenia involuta* (Wedekind), *P.* (*Pleuroclymenia*) *cycloptera* (Wedekind), *Genuclymenia* (?) *dunkeri* (Münster), *Prolobites delphinus* (G. and F. Sandberger), *Sporadoceras angustisellatum* Wedekind, *S. munsteri* (von Buch), *S. inflexum* Wedekind, *S. discoidale* Wedekind, *Praeglyphioceras pseudosphaericum* Frech, and *Pseudoclymenia planidorsata* (Münster).

BED 11 (10 cm.): *P.* (*Pl.*) *brevicosta* (Münster), *P.* (*P.*) *steinmanni* (Wedekind), *Cyrtoclymenia angustiseptata* (Münster), *P.* (*P.*) *enkebergensis* (Wedekind), *R. subflexuosa* (Münster), *S. discoidale* Wedekind, *S. münsteri* (von Buch), *S. inflexum* Wedekind, *S. biferum* (Phillips), *Prolobites delphinus* (G. and F. Sandberger), and *Ps. planidorsata* (Münster).

BED 12 (9 cm.): *P.* (?*P.*) *pompecki* (Wedekind), *C. involuta* (Wedekind), *C. lotzi* (Wedekind), *P.* (*Pl.*) *cycloptera* (Wedekind) (figured here Pl. 126, figs. 8, 9; this specimen may have come from Bed 10, the precise source is not indicated), *G. frechi* (Wedekind), *G. gumbeli* (Wedekind), *G. angelina* (Wedekind) (not recorded from this bed on p. 618), *R. roemeri* (Wedekind), *G. angustiseptata* (Münster), *R. subflexuosa* (Münster), *S. angustisellatum* Wedekind, *S. munsteri pseudosphaericum* Frech, and *Prol. delphinus* (G. and F. Sandberger). *Hexaclymenia hexagona* (Wedekind) (figured here in Pl. 126, figs. 18, 19) was recorded on p. 619 as coming from this bed but was not listed on p. 570.

BED 13 (11 cm.): *C. lotzi* (Wedekind), *G. phillipsi* (Wedekind) (figured here Pl. 126, figs. 10, 11), *G. frechi* (Wedekind), *S. angustisellatum* Wedekind, *S. munsteri* (von Buch), and *Prol. delphinus* (G. and F. Sandberger).

BED 14 (12 cm.): *P.* (*P.*) *steinmanni* (Wedekind) (figured here Pl. 126, figs. 6, 7; also recorded from Bed 14 on p. 570 which could have been the source of the figured specimen), *C. involuta* (Wedekind) (recorded from this bed on p. 570 but not on p. 610), and *S. biferum* (Phillips). *G. angelina* (Wedekind) (refigured here on Pl. 126, figs. 14, 15) is recorded from this bed on p. 618 and on the table but not on p. 570. *P.* (*P.*) *sandbergeri* (Wedekind) (figured here Pl. 126, figs. 12, 13) is also recorded from this bed on p. 621 and on the table, but not on p. 570.

BED 15 (9 cm.) and BED 16 (15 cm.): no ammonoids recorded.

BED 17 (9 cm.): *Pseudoclymenia sandbergeri* (Gümbel), *Ps. sandbergeri dillensis* Drevermann, *Ps. dorsatum* (Wedekind), *Dimeroceras padbergensis* Wedekind.

In this succession *Platyclymenia s.s.* and *Cyrtoclymenia* are the first clymenids to appear above beds with abundant *Pseudoclymenia*, *Dimeroceras*, and *Sporadoceras* (Beds 22–17) with *Cheiloceras* abundant lower still (Beds 25–31). Although not relevant to the present discussion the discrepancies in Wedekind's various records and the textual inconsistencies should be noted. Also the magnifications which he gives for his illustrations are mostly incorrect. The large number of species he erected is also suspicious, and doubtless most of these will be redundant when a modern statistical analysis of the fauna is undertaken.

When the Enkeberg section was revised by Lange (1929) the collecting was not done with the same scrupulous attention to the detailed succession that characterized Wedekind's work, and the stratigraphic revision was at the crude level of zones (as on text-fig. 1) only. One cannot therefore feel other than cautious in accepting some of the changed ranges which he recognized. Thus Lange (1929, p. 16, 97) records *Platyclymenia (Varioclymenia) kayseri* as common in Zone IIIα, the Sandbergeri Zone, from Wedekind's Beds 19–16, and the entry of other clymenids above in Beds 15–10 is not recorded in detail, and in failing to do so Lange leaves himself open to the suggestion that he did not correctly interpret Wedekind's bed numbers. This matter, however, is a trivial one which will only be resolved by the next reviser of the Enkeberg section. In recording clymenids in Zone IIIα he was following Schindewolf as will be seen below.

Another detailed succession showing the entry of clymenids is the sequence at Hof described by Schindewolf (1922, p. 256; Wurm 1961, p. 118). Here the entry of clymenids is recorded as follows (again taxonomic revisions have been made).

BED 11 (0·25 m.): *S. discoidale* Wedekind, *S. munsteri* (von Buch), *R. subflexuosa* (Münster), *C. involuta* (Wedekind), *C. wedekindi* Schindewolf, *P. (P.) sandbergeri* (Wedekind), *P. (P.) prorsostriata* Schindewolf, *P. (Trigonoclymenia) crassicosta* (Wedekind), and others.

BED 10 (1·8 m.): *S. munsteri* (von Buch), *S. discoidale* (Wedekind), *R. rotunda* Schindewolf, *C. sulcata* Schindewolf, *Genu. frechi* (Wedekind), *Genu. borni* Schindewolf.

BED 9 (*c.* 1·2 m.): *R. sandbergeri* (Gümbel), *Ps. sandbergeri dillensis* (Drevermann), *S. munsteri* (von Buch), *S. contiguum* (Münster), *Praeg. pseudosphaericum* Frech *R.* (?) *kayseri* Drevermann, *C. pulcherrima* (Wedekind), *Genu. frechi* (Wedekind).

BED 8 (2·5 m.): *Ps. planidorsata* (Münster), *Cheiloceras* sp., *S. biferum* (Phillips).

Schindewolf referred Bed 8 to IIβ, the upper part of the Cheiloceras Stufe (Pompeckji Zone), Bed 9 to IIIα (Sandbergeri Zone), and Beds 10 and 11, and the overlying Bed 12 to IIIβ. Since *Prolobites delphinus* was not recorded it is to be inferred only that the latter group represent the Delphinus Zone.

This review serves to emphasize that the stratigraphical evidence shows that the earliest known clymenids all have sutures showing a lateral lobe and dorsal lobe only (*Platyclymenia s.s. Rectoclymenia, Cyrtoclymenia*) with some (*Genuclymenia*) with a slightly more complex pattern. Later follow the other subgenera of *Platyclymenia* and later still, in the Clymenia Stufe, *Kosmoclymenia* and *Cymaclymenia*. *C. ornata*, an early form of the latter, is illustrated here (Pl. 126, figs. 16, 17): the figured specimen is Münster's, Schindewolf recorded this species in the lower part of Zone Vβ.

ORIGIN FROM THE TORNOCERATIDAE

It is the purpose here to suggest that a group of derivatives of the common Devonian *Tornoceras* stock which occur in the early Upper Famennian are morphologically transitional between typical tornoceratids and the earliest clymenids. The critical fauna is from the Lower Famennian of Kielce in the Holy Cross Mountains. Some of this is illustrated here (Pl. 125, 126).

The Kielce Tornoceratids

In 1913 Dybczyński published a brief account of a prolific locality for pyritized goniatites in the Holy Cross Mountains on the outskirts of the town of Kielce, from which he had collected over 5000 specimens. Sobolew (1913, 1914*a*, *b*) gave a lengthy account of this fauna with many illustrations, but described them using a complex generic nomenclature based on a root with morphologically descriptive prefixes and suffixes. Sobolew's genera, but not his species, have been declared invalid by Opinion 132 of the ICZN (Schindewolf and others 1936). The pyritic fauna is of great diversity and is almost wholly of early Famennian age. The evidence for this will briefly be discussed.

The main source of the material described by Sobolew was from shales overlying the Frasnian and perhaps earliest Famennian limestones at the Kiedelna quarry. Housing developments have now covered most of the site, but in 1962 the author was able to collect from weathered shales (but not in place) a poor fauna including *Raymondiceras* and *Sporadoceras* (with spiral ornament) confirming that a position succeeding the Cheiloceras Stufe recorded in the quarry below is proven. Fortunately Dr. H. Makowski has kindly made available a collection from Kielce thought to come wholly from the shales overlying the quarry and the Sieklucki's Brickpit there, and which forms the remnants of a pre-war collection of the Geology Department of the University of Warsaw.

Interest here centres on the remarkable suite of tornoceratids and their precise age. Rare early clymenids occur in the fauna and some were figured by Sobolew. The most readily determined tornoceratids are those similar in shell and suture form to *T. crebriseptum* from the Three Forks Shale of Montana (House 1965, p. 115). The Montana fauna contains *Platyclymenia*, *Raymondiceras*, and *Rectoclymenia* and has been referred to the Delphinus Zone. The main source at Kielce would appear to be earlier than this. (The Delphinus Zone is where the clymenids first appear, text-fig. 1). Sobolew's fauna included *Sporadoceras* and *Imitoceras*, both of which, in Germany, enter in the upper half of the Cheiloceras Stufe (Pempeckji Zone). Although there is no reason to suppose that the Kielce pyritic fauna is from a single horizon, the evidence suggests that the fauna studied here covers the range of the Pompeckji and Sandbergeri Zones. That is, the bulk of the fauna correlates with horizons immediately preceding the known entry point of the clymenids. Higher horizons, with clymenids are also known and were mentioned by Sobolew.

SYSTEMATIC PALAEONTOLOGY

The whole of the Kielce material is in need of description but the material at present available is so meagre in comparison with that formerly known and destroyed during the Second World War, that this would be unwarranted at present. Dybczyński (1913) described a number of species and the specific names given by Sobolew are still valid despite the ruling of the ICZN on his genera. The Kielce tornoceratids which are the concern here comprise some belonging to the *Tornoceras crebriseptum* Raymond group, which perhaps, should be recognized as a new subgenus. Others of the transitional series fall in *Protornoceras* and the end point in which the lateral lobe has ceased to exist except as a vestigal remnant comprise a small group for which the new generic name *Tornia* is here proposed.

Suborder GONIATITINA Hyatt 1884
Superfamily CHEILOCERATACEAE Frech 1897
Family TORNOCERATIDAE Athaber 1911
Genus TORNOCERAS Hyatt 1884

Type species. By original designation *Goniatites uniangulare* Conrad.

Tornoceras (*T.*) *crebriseptum* Raymond Group

Discussion. The tornoceratids which form the starting point of the morphological series leading to *Tornia* belong to a group represented by forms referable to *T.* (*T.*) *crebriseptum* (for a description of the type material see House 1965). The Montana type material already shows evidence, in the internal mould, that the umbilicus is open, although testate specimens may not have been. Were the latter point settled in the affirmative then they should be referred to *Protornoceras* or a new genus group. The suture, with its subdued form and flat ventro-lateral saddle is also distinctive (Pl. 125, fig. 1). Quite closely similar types occur in the Kielce fauna but these differ in showing small constrictions over the venter (Pl. 125, figs. 2–5) which, suturally are even closer to the Montana material. In view of the priority of Raymond's work over that of Dybczyński and Sobolew these may be referred to as *T.* (*T.*) aff. *crebriseptum* pending revision of the whole fauna.

Genus PROTORNOCERAS Dybczyński 1913

Type species. By original designation *Tornoceras* (*Protornoceras*) *polonicum* Dybczyński, 1913, p. 512.

Discussion. The current use applies this generic name to all open umbilicate tornoceratids without the ventro-lateral grooves and other characters which distinguish *Aulatornoceras*. Middle Devonian examples, such as *P. foxi* House (1963 p. 19, pl. 2*a*, *d–g*, text-fig. 8*a–g*) seem clearly to be unrelated directly to those of the Lower Famennian and should, at some stage, receive another generic name. The Polish material forms the type for the genus and some representatives are figured here (Pl. 125, figs. 6–22). Many specific names belong here which we owe to Dybczyński, Sobolew, and Wedekind. The group is a variable one and many of these names will be lost in synonomy when they come to be revised.

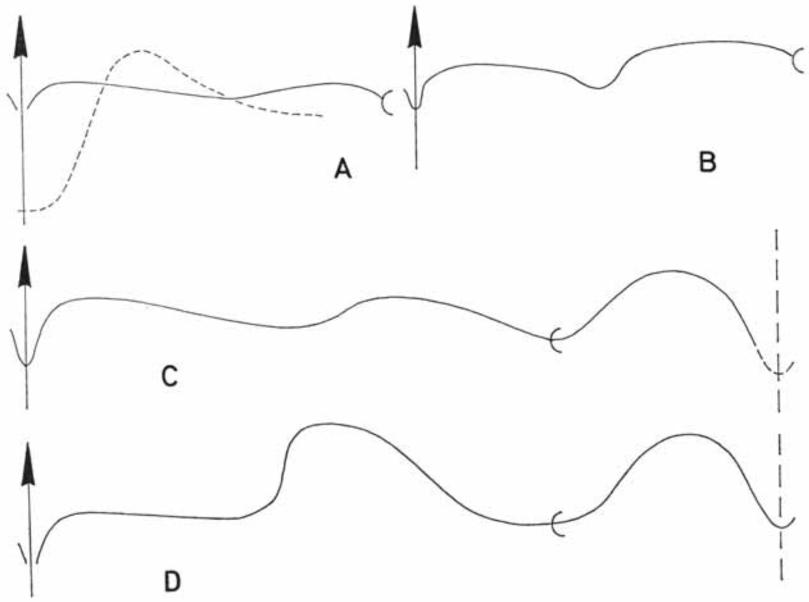
The importance in the present context is that as well as showing a progressive opening of the umbilicus the group also shows sutural characters linking it with the crebriseptum

EXPLANATION OF PLATE 125

Figs. 1–5. *Tornoceras* (*Tornoceras*) spp. 1, *T.* (T.) *crebriseptum* Raymond, holotype from the Three Forks Shale of Montana in the Carnegie Museum, Pittsburgh No. 464; ×2. 2–5, *T.* (*T.*) aff. *crebriseptum* (Raymond) from Kielce; 2, ×2·5; 3–5, ×2.

Figs. 6–22. *Protornoceras* spp. 6–8, *P.* cf. *planidorsatum* (Wedekind) from Kielce; ×2. 9–19, *P. simplificatum* (Sobolew) from Kielce; 9, 10, ×2·5, 11–13, ×2, 14–19, ×3. 20–22, *P.* cf. *zuberi* Dybczyński from Kielce; ×2·5.

group of *Tornoceras s.s.* Further, in the Polish material all morphological gradations can be seen from sutures typical of *Tornoceras s.s.* to those in which the elements become progressively subdued (text-figs. 2B, C; Pl. 125, figs. 6–20; Pl. 126, figs. 1, 2).



TEXT-FIG. 2. Early Famennian tornoceratids from the Sieklucki Brickpit Kielce, Poland; all ×20. A, *Tornia mirabile* (Dybczyński), suture at 13 mm. diameter. B, *Protornoceras* cf. *zuberi* Dybczyński, suture at 11·9 mm. diameter (also figured on Pl. 125, figs. 21, 22). C, *Protornoceras simplificatum* (Sobolew), suture at 15 mm. diameter (also figured on Pl. 125, figs. 17–18). D, *Tornoceras* (*T.*) aff. *crebriseptum* Raymond, suture at 11·8 mm. diameter (also figured on Pl. 125, fig. 2).

Genus TORNIA gen. nov.

Type species. Here designated *Tornia mirabile* Dybczyński 1913, p. 514, pl. 1, fig. 4, pl. 2, fig. 4.

Diagnosis. Open umbilicate tornoceratids with ventral siphuncle, biconvex growth-lines and mature suture forming a broad shallow lateral lobe, a narrow ventral lobe and a deep linguiform dorsal lobe.

Remarks. Morphologically this form is identical with some platyclymenids apart from the ventral position of the siphuncle. Relic traces of the typical tornoceratid adventitious lobe can be seen in the broad lateral lobe, but this cannot be crossed by a radial line drawn from the umbilicus and in this respect differs from the presumed *Protornoceras* antecedents (e.g. Pl. 125, figs. 21, 22 Pl. 126, figs. 1, 2;), and there is no arched latero-umbilical saddle as is also characteristic of tornoceratids. The genus closely approaches homoeomorphy with the Middle Devonian genus *Agoniatites*.

Tornia mirabile (Dybczyński)

Plate 126, figs. 3–5, text-fig. 2A

Neotype. The holotype having been lost one specimen belonging here will be described and is designated the neotype: this is an internal haematite mould showing some 90° of body chamber. A tendency to orad sutural approximation and evidence of shell thickenings in the body chamber suggest maturity. This specimen is in Professor H. Makowski's collection at the Polski Akademia Nauk, Warsaw.

The shell form (see Pl. 126, figs. 4, 5) is open umbilcate but the earliest whorls are not seen. Experience with this preservation having shown that the inner whorls are rarely shown by sectioning, this has not been risked on the neotype, but moderately evolute early whorls are indicated. The whorl form shows a well-rounded venter, somewhat flat sides and a steep and rounded umbilical shoulder.

Dimensions (*in mm.*)

	D	WW	WH	UW
Holotype (data from Dybczyński)	17	6	*c.* 8	4
Specimen from Sieclucki's brickpit	16·7 (max.)	—	—	—
(Neotype)	14·4	4·1	5·9	4·3

Growth-lines, as discernible on an internal mould are biconvex, forming a slight salient on the umbilical shoulder, a broad slightly prorsiradiate sinus on the flanks and a short, stubby ventro-lateral salient or short lappet passing to a U-shaped ventral sinus. On the body chamber diffuse shell thickenings appear to have followed the same course.

The sutures vary a little among themselves. A small V-shaped ventral lobe passes to a very broad and weak lateral saddle of slightly varying very shallow depth. Traces of the position of the lateral lobe of the supposed ancestral *Protornoceras* can be discerned as a very slight ventral facing slope on the lower flanks. The dorsal suture has not been seen, but in the nearest *Protornoceras* in which a clear lateral lobe can be seen (Pl. 126, fig. 2), it shows that a typical *tornoceratid* deep lobe was present.

Remarks. This sole neotype specimen from the Sieklucki Brickpit is the end member of the sequence described under *Protornoceras*. The suture is homoeomorphic in its elements

EXPLANATION OF PLATE 126

Figs. 1, 2. *Protornoceras* aff. *zuberi* Dybczyński from Kielce; ×3.

Figs. 3–5. *Tornia mirabile* (Dybczyński) from Kielce; ×2.

Figs. 6–9. *Platyclymenia* (*P.*) Spp. 6, 7, *P.* (*P.*) *steinmanni* (Wedekind), holotype (figured Wedekind 1908, pl. 43, figs. 12, 12a) from Bed 14 at Enkeberg. ×1. Univ. Göttingen Coll. 8, 9, *P.* (?*P.*) *cycloptera* (Wedekind), holotype (figured Wedekind 1908, pl. 43, fig. 11) from Bed 11 or 12 at Enkeberg; ×2, Univ. Göttingen Coll.

Figs. 10, 11. *Genuclymenia phillipsi* (Wedekind), holotype (figured Wedekind 1908, pl. 39, fig. 26, pl. 43, fig. 6) from Bed 13 at Enkeberg; ×2, Univ. Göttingen Coll.

Figs. 12, 13. *Platyclymenia* (*P.*) *sandbergeri* (Wedekind), lectotype here designated (figured Wedekind 1908, pl. 44, figs. 9, 9a; 1914, pl. 2, fig. 7 as *P. wysogorskii* Frech) from Beds 14 to 12 at Enkeberg; ×2, Univ. Göttingen Coll.

Figs. 14, 15. *Genuclymenia angelina* (Wedekind), holotype (figured Wedekind 1908, pl. 44, fig. 6) from either Bed 13 or 14 at Enkeberg; ×1, Univ. Göttingen Coll.

Figs. 16, 17. *Cymaclymenia*(?) *ornata* (Münster); Münster's holotype in the Bayerische Staatssammlung für Paläeontologie und Historische Geologie, Munich; ×2.

Figs. 18, 19. *Hexaclymenia hexagona* (Wedekind), holotype (figured Wedekind 1908, pl. 43, figs. 7, 7a) from Bed 12 at Enkeberg; ×1·78, Univ. Göttingen Coll.

with *Agoniatites*, but the lateral lobe is much shallower. No Frasnian agoniatitids being known, and the *Protornoceras* link being demonstrable, a phylogenetic derivation from *Agoniatites* is not possible. Only the specimen figured by Sobolew as *Gomi-re-protomeroceras* (*Tornoceras*) *alobatum* Sobolew (1913, pl. 9, figs. 5, 6, ?non text-fig. 105) seems also to belong in *Tornia*; but this form is significantly more evolute than the holotype and substantially more so than the neotype specimen here described. However, the involvement of new species within Sobolew's generic formulae is so complex a matter that it is unfortunate that they were not also invalidated by the ICZN. The destruction of his collection in the Second World War renders the use of his names even more difficult and those of Dybczyński are preferred in this case although his collection is also untraced.

The comparison with the varied early clymenids (Pl. 126, figs. 6–19) in shell form and in the course of the growth-lines, and where present, ribbing is sufficiently close to raise no great problems in their derivation from *Tornia*. No other Devonian goniatite shows so close a sutural resemblance to these early clymenids as does *Tornia*. A ventral suture has been demonstrated in the early stages of some clymenids (see references given later) and this suggests that the permanent adoption of the endosiphonate condition falls wholly within the Clymeniina.

SUMMARY AND CONCLUSIONS

The demonstration that the Frasnian *Acanthoclymenia* is not a clymenid concentrates attention on the Lower Famennian sequences where clymenids appear. The Polish fauna of *Protornoceras* and *Tornia* at this level gives a morphological series leading to the earliest known clymenid genera. The reasons for favouring an origin of the clymenids from goniatites rather than nautiloids is summarized below:

1. *The form of the protoconch.* As Branco (1890, p. 35, pl. 7, figs. a–e), Schindewolf (1923, p. 24 et seq.) and others have observed the egg-shaped, often laterally elongate protoconch of the clymenids finds its closest analogy with those of the goniatites. What early stages of Devonian nautiloids homoeomorphic with coiled ammonoids are known, for example centroceratids (Flower 1952), are different. Similarly the form of the prosuture (Branco 1880, pl. 8, fig. 1*b*; Schindewolf 1923, text-fig. 2) is very similar to that of goniatites particularly the *Tornoceras* group (see House 1965).

2. *The lack of an umbilical perforation.* This is the rule in the clymenids and of the goniatites from which it is here argued they are derived. It does not appear to be a character of the groups of nautiloids from which Donovan (1964, p. 271) would derive the clymenids. There is no doubt, however, that information on the early stages of some relevant Devonian nautiloid genera is lacking.

3. *Transitional position of the siphuncle.* As Branco (1880, pl. VII, fig. 3*b*) and Schindewolf (1955, p. 420) have described, some early clymenids show a ventral siphuncle in the early stages. Later the siphuncle migrates to a dorsal position. Sandberger (1853, pl. 6, fig. 1) has illustrated sagittal sections of *Clymenia compressa* showing that in early whorls, but not the earliest, the siphuncle is often well away from the dorsum.

To these factors the present paper adds a description of forms which show evidence of:

4. *Transitional shell form.* The sequence of tornoceratids described here from the

Lower Famennian of Southern Poland shows a progressive opening of the umbilicus and lateral forward projection of the adult aperture which approaches that of the earliest known clymenids.

5. *Transitional Suture Forms*. The same sequence shows a simplification of the *Tornoceras* suture to one showing a deep dorsal lobe, and a shallow lateral lobe: both features of the earliest known clymenid genera. The trend culminates in the new genus, *Tornia*.

6. *Stratigraphic intermediates*. The horizon of the new intermediate forms appears to lie just below the level at which clymenids appear.

It seems to the author that it is the summation of this evidence which makes an origin of the clymenids from goniatites, and a specific origin from the *Tornoceras* stock, probable.

Some comments may be made on another contendor as ancestor, *Archoceras* (Schindewolf 1955) which is a late Frasnian and earliest Famennian genus. For several reasons it does not seem very suitable. There is a clear gap in the record of *Archoceras* before the appearance of clymenids. The sutural pattern of the genus, although simple (House 1962, p. 367, text-fig. 7), is not such as to enable ready derivation of the clymenid suture. The large lateral saddle is directly the reverse of the shallow lateral lobe of the earliest clymenids. Also the deep ventral lobe, combined with a deep dorsal lobe, makes the septum highly arched orad, and hence any migration of the siphuncle across this is difficult to envisage. The suitability of *Tornia* and its relatives is particularly shown here since the septal mid-line actually slopes dorsad along the line of the siphuncle migration. When *Acanthoclymenia* was thought to be a Frasnian clymenid, *Archoceras* did seem to offer attractions, but these have now been lost.

What the functional advantages of a dorsal siphuncle were it is difficult to assess, but the rapid evolution after the inception of the character suggests that the survival value was considerable. The wholesale extinction of the clymenids at the close of the Devonian need not be related to any change in this factor necessarily since goniatite groups are also affected by the extinctions. But during the late Famennian the diversification of the clymenids seems matched by an over-all decline of goniatite stocks. Migration of the siphuncle occurs in other ammonoid groups also (*contra* Donovan 1964, p. 271), for example in the Permian *Pseudoholorites* and *Neoaganides* (Miller and Furnish 1957, p. 1044), but at no other time in ammonoid history does the fully dorsal siphuncle position appear to have been adopted again.

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M. R. HOUSE
Department of Geology
The University
Kingston upon Hull
Yorkshire

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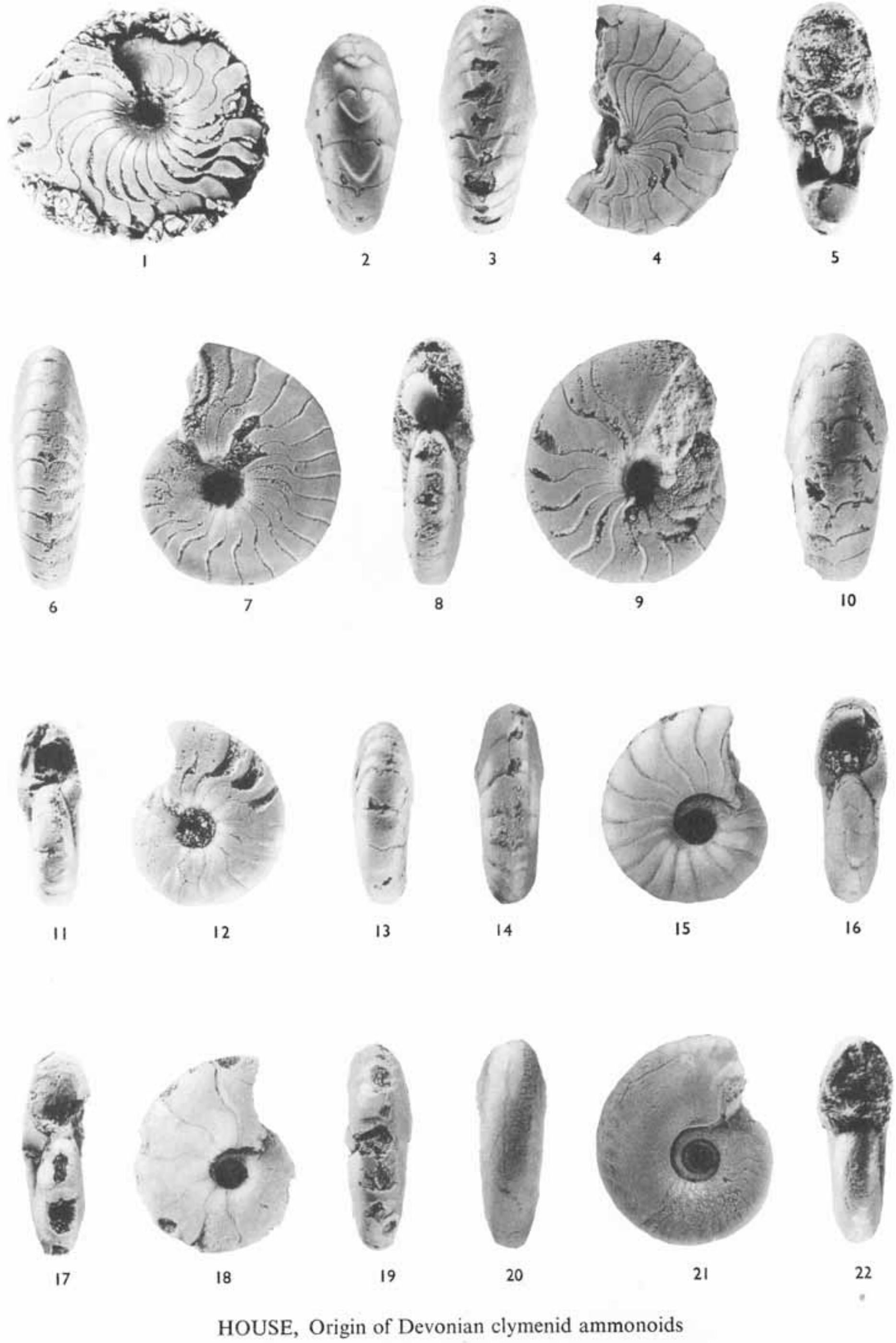
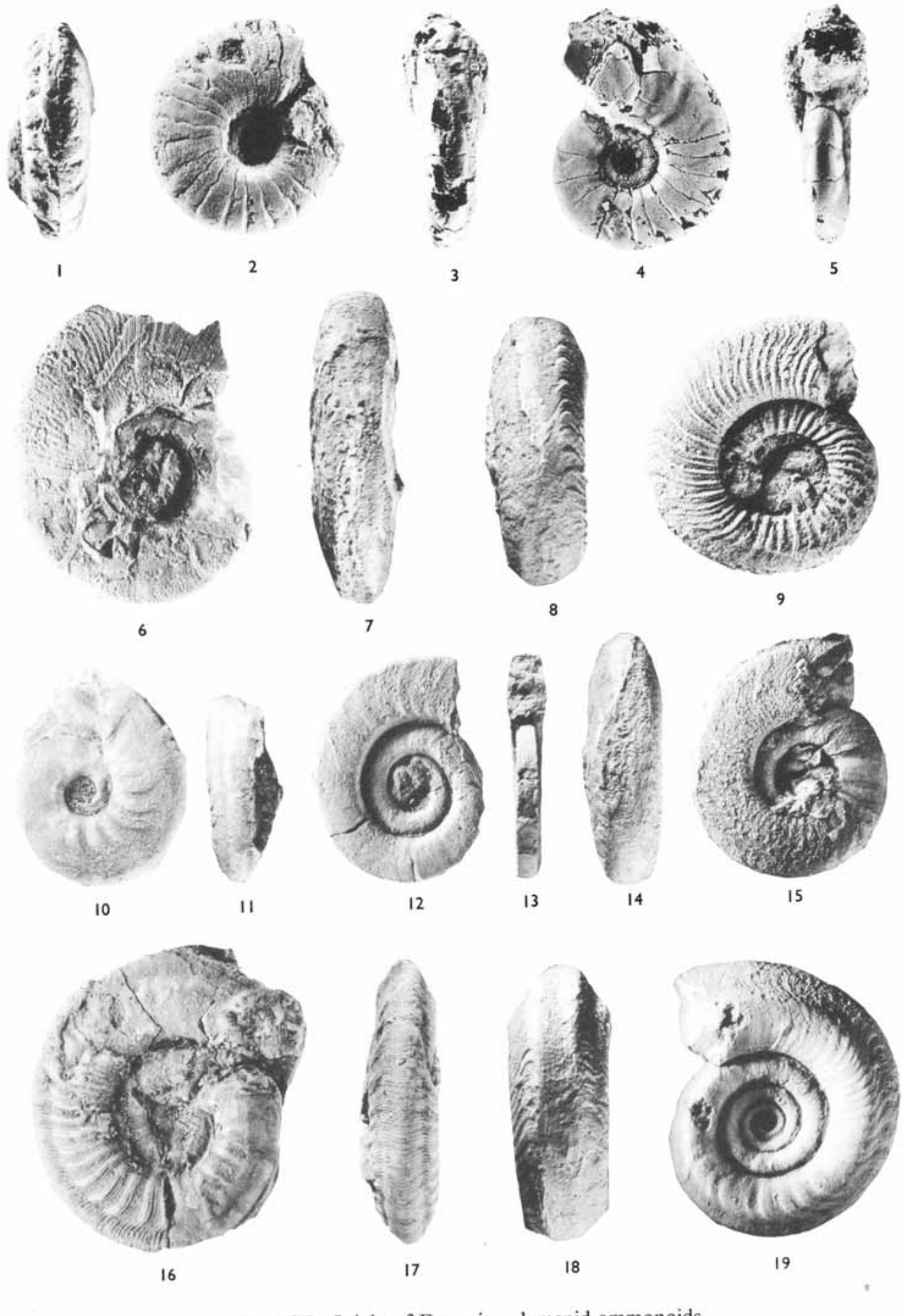


HOUSE, Origin of Devonian clymenid ammonoids



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