ACANTHOCLYMENIA, THE SUPPOSED EARLIEST DEVONIAN CLYMENID, IS A *MANTICOCERAS*

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ABSTRACT. Evidence is presented to show that the supposed earliest clymenid, the Frasnian *Acanthoclymenia neapolitana* of New York State, is in fact a *Manticoceras*. A lectotype is chosen which shows the suture and indicates the position of the siphuncle. The family Acanthoclymenidae Schindewolf thus becomes a synonym of the Gephuroceratidae. Revisionary comments are made concerning the origin of the clymenids.

INTRODUCTION

THE records of clymenids from the Frasnian, or basal Upper Devonian, in North America have posed particular problems for two reasons. Firstly, these records have been taken to show that, since clymenids do not occur until the Platyclymenia Stufe of the Famennian in Europe, the American forms must belong to a different faunal province. Secondly, the elucidation of phylogeny in the Clymeniina has been rendered uncertain by the supposed occurrence of complex-sutured forms at the earliest appearance of the group. The purpose of this note is to show that the supposed Frasnian clymenids in fact belong to the genus *Manticoceras*, and are in no way anomalous: thus the problem of the origin of the Clymeniina can now be stated more clearly.

Historical survey. In 1892 John M. Clarke described as *Clymenia* (*Cyrtoclymenia*) *Neapolitana* some ammonoids from the Lower Portage Shale (Cashaqua Shale) of Shurtleff's Gully, New York State. This locality is probably the one mentioned by Luther (1894, p. 228) as in the eastern part of the town of Livonia; Foord, in the same year, reported this record in the *Geological Magazine* and stressed the anomalously low horizon.

Clarke added some further details in a subsequent description of the species (1898, p. 131), and gave several new localities for it, but these were all within the Cashaqua Shale. In 1900 Hyatt (in Eastman–Zittel, p. 548) proposed the genus *Acanthoclymenia* with *C. neapolitana* as the type and sole representative apparently without examining the original material. Later Schindewolf (1934, p. 347), after examining the types, and sectioning one, stated that he was unable to locate the siphuncle. But A. K. Miller, who gives the fullest synonomy for the species and who reprinted Clarke's description and figures, stated that he 'definitely located the siphuncle in two of the hypotypes' and that it was 'dorsal and marginal in position and is in contact with the dorsal wall of the conch or essentially so' (Miller 1938, p. 192). Miller did not quote the museum numbers of these specimens and gave no new illustrations of them.

Accepting Miller's evidence, Schindewolf (1955, p. 422) erected the family Acanthoclymenidae with *Acanthoclymenia neapolitana* as the only species. The stratigraphical anomaly of the genus as a clymenid is well illustrated in the evolutionary diagram of the Clymeniina which Schindewolf has published (1955, p. 422; 1957, p. L38).

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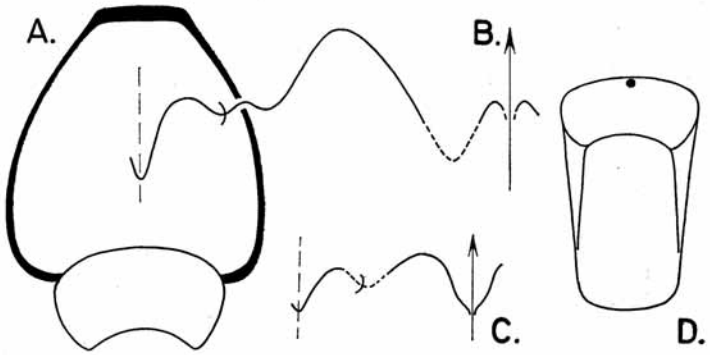
DISCUSSION

In his earliest description Clarke illustrated two specimens showing a dorsal structure which he took to be the siphuncle (1892, p. 63, figs. 3, 4). At least the second of these (Clarke's fig. 4) must be one of the hypotypes which satisfied Miller, for he reillustrated it (1938, p. 180, fig. F), and presumably would not have done so were he unconvinced of its authenticity. This specimen is NYSM. 11264, and the inner, and only complete, whorl is figured here (Pl. 75, figs. 8, 9; text-fig. 1D). The other specimen which Clarke figured as showing the siphuncle is NYSM. 3625, and this specimen is also figured here (Pl. 75, figs. 1–4; text-fig. 1A, B): since this specimen shows the dorsal structure better than any of the other types it is to be presumed that it is the other specimen mentioned by Miller. It appears to have formed the basis for Clarke's diagram of the mature suture. This last specimen, NYSM. 3625, which was initially figured by Clarke (1892, p. 63, fig. 3), is here designated the lectotype.



TEXT-FIG. 1. *Manticoceras neapolitanum* (Clarke). A, B, Whorl section and suture based on the lectotype, NYSM. 3625, from the Frasnian Cashaqua Shale in Shurtleff's Gully, New York State. C, D, Suture and outline based on NYSM. 11264 from the same horizon and locality. All $\times 12\frac{1}{2}$.

Evidence that the siphuncle is ventral in position. Clarke's first account shows that he did not see the siphuncle, for he wrote: 'The siphonal funnel is long, conspicuously developed, and open along its inner surface. It does not appear to have extended across the air chamber . . . and I have seen no evidence of a true siphonal tube connecting these funnels' (Clarke 1892, p. 59). It is clear from this that Clarke saw a deep adapical flexure in the dorsal part of the septum and presumed this to be a siphonal funnel and hence supposed this to show that the siphuncle was dorsal. In 1898, without presenting further evidence, the presumption was categorically stated.

The lectotype is illustrated here with enlarged photographs which show the dorsal region (Pl. 75, figs. 2–4). This is a specimen which Clarke figured as showing a dorsal siphuncle and is probably a specimen for which Miller made the same assertion. The specimen has been developed slightly. The adapical flexure in the mid-dorsal part of the septum is clearly seen (marked 'dl' upon the plate). Both figs. 2 and 3 show this septal fold passing steeply down to the preceding whorl. Despite the presence of a small adhering fragment, it will be seen that the fold almost reaches the wall of the preceding whorl

before it is truncated by the break which bounds the specimen. But both figs. 2 and 4 show the low crescent formed by the truncated extremity of the septal fold and the wall of the preceding whorl. A small transverse slit alone marks a connexion with the subsequent chamber. Clearly there is no tubular siphuncle, and none could pass through the small slit. The siphuncle therefore cannot be dorsal in position and the adapical flexure of the septum represents a deep mid-dorsal lobe. The siphuncle must be ventral in position and pass through the mid-ventral lobe (marked 'vl' on Pl. 75, fig. 1).

The smaller specimen which Clarke figured as illustrating a dorsal siphuncle is refigured here (Pl. 75, figs. 8, 9) and, although the specimen is indifferently preserved, a ventral view shows a mid-ventral lobe continued adapically into an elongate structure, which can only represent a siphuncle, ventral in position. In the earliest stages Clarke himself noted that the siphuncle was ventral in position.

Evidence that the suture is of Manticoceras *type.* In the adult suture of *Acanthoclymenia* as drawn by Clarke (1898, p. 133, text-fig. 105) and Schindewolf (1957, p. L39, text-fig. 4c) no saddle is shown in the wide ventral lobe. If one were added the suture would be typical of *Manticoceras*. At first Clarke stated that no saddle was present on the mid-ventral line (1892, p. 59), but he later changed his opinion and wrote that 'the ventral lobe also appears to be minutely divided at its apex forming a ventral saddle'. Clarke did not show this saddle on his suture diagram. The lectotype has been developed slightly in the ventral region and Clarke's later opinion has been confirmed. The saddle lies between a mid-ventral and ventro-lateral lobe (marked 'vl' and 'vll' on Pl. 75, fig. 1). Miller's statement (1938, p. 192) that he was unable to verify the existence of this saddle may therefore be dismissed.

The adult suture now presented shows all the sutural elements typical of *Manticoceras* (text-fig. 1B). Further, the earlier stages (text-fig. 1C) show a suture of *Archoceras* type, so that it can be demonstrated that the ontogeny is also typical of *Manticoceras*.

All the remaining specimens in the New York State Museum have been examined but none show evidence bearing on the position of the siphuncle or contradictory evidence on the form of the suture. In order to dispel any thought that the lectotype is atypical, the better preserved of the syntypes which do not show the suture or siphuncle are also illustrated here (Pl. 75, figs. 5–7, 10, 11). It will be seen that the proportions of coiling, the whorl form, and the details of the ornament are similar to those of the lectotype.

THE ORIGIN OF THE CLYMENIDS

The uncertainties concerning the ancestry of the clymenids are legion. Nor does the elimination of *Acanthoclymenia* solve the problem, but it emphasizes the sudden entry of the group in the Platyclymenia Stufe of the Famennian. The earliest genera, *Platy-*

EXPLANATION OF PLATE 75

Figs. 1–11. *Manticoceras neapolitanum* (Clarke). All specimens are from the Cashaqua Shale and from Shurtleff's Gully, Livingstone County, N.Y., except perhaps fig. 11 which may have come from a different locality. 1–4, The lectotype, NYSM. 3625. Views illustrating the dorsal structure. 'vl' = ventral lobe, 'vll' = ventro-lateral lobe, 'll' = lateral lobe, 'ul' = umbilical lobe, 'dl' = dorsal lobe. Magnifications: 1, ×10. 2, ×8·4. 3, ×6·2. 4, ×6·1. 5–7, Syntype, NYSM. 3632. All ×5·6. 8, 9, Syntype, NYSM. 11264. Both ×7. 10, Syntype, NYSM. 3629. ×4. 11, Specimen figured by Clarke, NYSM. 3631. ×4.

clymenia, *Rectoclymenia*, *Cyrtoclymenia*, and *Hexaclymenia*, all have very simple sutures: in the case of the first three the suture consists merely of a wide lateral lobe and a mid-dorsal lobe; in the case of *Hexaclymenia* there is a broad ventral lobe, a sub-umbilical lobe, and a mid-dorsal lobe (Schindewolf 1923, p. 62, 1957, pp. L37 et seq.). Forms with more complex sutures appear at higher stratigraphical levels and it is reasonable to infer that they evolved from the early, simple-sutured stocks.

Several hypotheses have been proposed to explain the origin of the clymenids, and in conclusion these may be briefly reviewed.

1. *Monophyletic origin from goniatites.* Schindewolf (1949) has argued strongly for *Archoceras*, or a related anarcestid, as the single ancestor of the clymenids. This would involve a quite sudden migration of the siphuncle to a dorsal position. *Archoceras*, a genus omitted in the systematic section of the recent *Treatise on invertebrate Paleontology*, Part L, was erected by Schindewolf (1937, p. 243; also discussed by Gallwitz in 1938). It ranges from the middle Frasnian to the lower Cheiloceras Stufe of the Famennian. It has a simple suture consisting of a deep ventral lobe, a lateral lobe, and a mid-dorsal lobe (essentially that of the early stages of *Manticoceras neapolitanum* here figured, text-fig. 1C).

2. *Polyphyletic origin from goniatites.* Sobolew contended that many clymenid genera evolved independently from goniatite genera with somewhat similar shell form and suture pattern (Sobolew 1914, see also Schindewolf 1949, p. 198). There are serious objections to this hypothesis. It would be highly curious for unrelated stocks to evolve a dorsal siphuncle independently. Further, there can be little doubt Sobolew linked homoeomorphs. Nevertheless the evidence Sobolew presented of a slight dorsal migration of the siphuncle in some goniatites deserves further attention.

3. *Origin from nautiloids.* Most early authorities up to Branco (1880) included the clymenids among the nautiloids. But Branco's demonstration that clymenids possess the typical sub-globular ammonoid protoconch convinced most subsequent authors that their affinities lie with the Ammonoidea. However, the very early stages of those Devonian centroceratids and other nautiloids somewhat homoeomorphic with the early clymenids are virtually unknown. So this possibility cannot be completely eliminated.

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REFERENCES

BRANCO, W. 1880. Beiträge zur Entwicklungsgeschichte der Fossilen Cephalopoden. 2, Goniatiten, Clymenien, Nautiliden, Belemniten und Spiruliden. *Palaeontographica*, **27**, 12–81.

CLARKE, J. M. 1892. The discovery of *Clymenia* in the fauna of the Intumescens zone (Naples Beds) of western New York, and its geological significance. *Amer. J. Sci.* (3), **43**, 57–63.

—— 1898. The Naples fauna (fauna with *Manticoceras intumescens*) in western New York. *N.Y.S. Geol. Ann. Rept.* **16**, 29–161.

EASTMAN, C. R. and ZITTEL, K. A. VON. 1900. *Text-book of palaeontology*, **1**. London.

FOORD, A. H. 1892. Note on the discovery of *Clymenia* in North America. *Geol. Mag.* **29**, 173, 4.

GALLWITZ, H. 1938. Archoceraten aus dem unteren Oberdevon Deutschlands. *Zbl. Miner. Geol. Paläont.*, B, 367–83.

LUTHER, D. D. 1894. Report on the geology of the Livonia Salt Shaft. *N.Y. State Mus., Rep.* **47,** 217–352.

MILLER, A. K. 1938. The Devonian Ammonoids of America. *Geol. Soc. Amer., Spec. Pap.* **14,** 262 pp.

SCHINDEWOLF, O. H. 1923. Entwurf einer natürlichen Systematik der Clymenoidea. *Zbl. Miner. Geol. Paläont.* 23–50, 59–64.

—— 1934. Über eine oberdevonische Ammoneen-Fauna aus den Rocky Mountains. *Neues Jb. Min. Geol. Paläont.* **72,** 331–50.

—— 1937. Zwei neue, bemerkenswerte Goniatiten-Gattungen des rheinischen Oberdevons. *Jb. Preuss. Geol. Landes*, **58,** 242–55.

—— 1949. Zur Phylogenie der Clymenien (Cephalop., Ammon.). *Neues Jb. Min. Geol. Paläont.*, B, 197–209.

—— 1955. Zur Taxionomie und Nomenklatur der Clymenien. Ein Epilog. Ibid. 417–29.

—— 1957. Clymeniina *in* R. C. Moore (Ed.). *Treatise on Invertebrate Paleontology. Part L. Mollusca* 4, L37–47. Geol. Soc. Amer. & Univ. Kansas Press.

SOBOLEW, D. 1914. Über Clymenien und Goniatiten. *Palaeont. Zeit.* **1,** 348–78.

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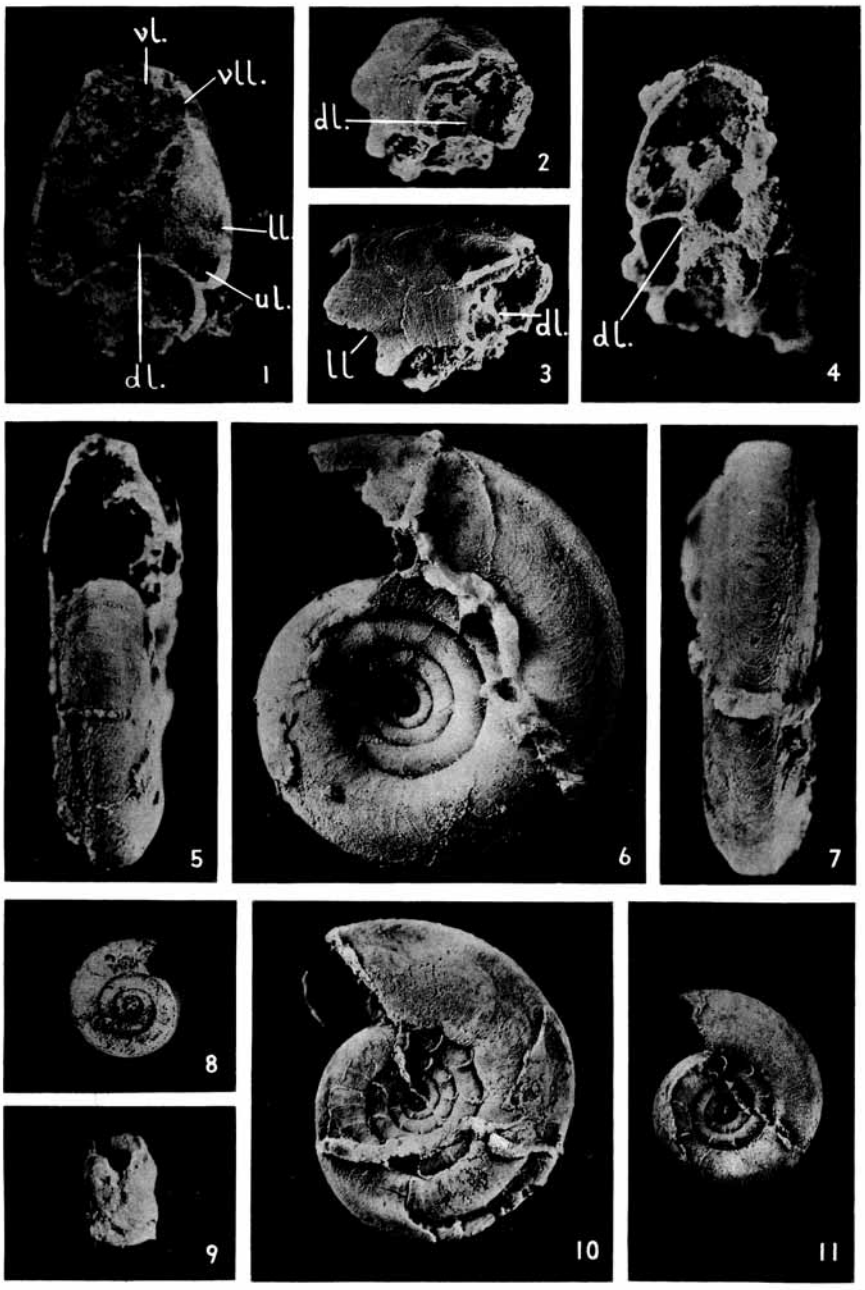

HOUSE, *Manticoceras neapolitanum* (Clarke)