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Original article

Resolving polyphyly within the Endocerida: The Bisonocerida nov., a new order of early palaeozoic nautiloids☆

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ABSTRACT

Although the Early Palaeozoic cephalopod order Endocerida is generally regarded as monophyletic, alternative views have been expressed. These invoke origins from different lineages within the order Ellesmerocerida. To test these alternatives, various aspects of endocerid morphology (including conch shape, structure of the ectosiphuncle, form of the endosiphuncular deposits, nature of the apical portion of the conch, and distribution of muscle attachment scars) are reviewed and compared with those of potentially related ellesmerocerids, taking regard of their stratigraphical distribution. The taxonomic distribution of endocones and endocone-like structures, combined with the potential for endosiphuncular diaphragms to evolve into endocones, suggests that the presence of endocones cannot be used to diagnose the Endocerida. Two distinct groups of Early Ordovician cephalopods that bear endocones may be recognised. One includes the longiconic Proterocameroceratidae possessing septal necks of variable length, conical and simple endocones, unflated apical portion of the siphuncle, and probable dorsomyarian muscle attachment scars. The second group includes the Piloceratidae, Manchuroceratidae and younger Allotrioceratidae and Najaceratidae. All are characterised by complex endosiphuncular deposits of endocones with conchiolin and calcareous crests, holochoanitic to macrochoanitic septal necks, and probable oncomyarian muscle attachment scars. The earliest pilocerids possess compressed cyrtochoanitic conchs. The coeval appearance of these groups and the similarity of each group to distinct ellesmerocerid taxa suggest that the Endocerida are polyphyletic, and a new order, the Bisonocerida is proposed for this second group.

1. Introduction

The pilocerids and related forms (including bisonocerids and manchurocerids) are a group of mainly Early Ordovician cephalopods, which form a characteristic component of many low latitude assemblages, especially in North America and China. With some exceptions, the remains of these organisms are restricted to siphuncles containing massive endosiphuncular deposits, the presence of which has conventionally been taken as evidence of their taxonomic assignment to the nautiloid order Endocerida. The ancestry and early phylogeny of the Endocerida has been discussed for over 75 years, with several workers making important contributions to the debate including Kobayashi (1935), Flower (1976b), Dzik (1984) and Kröger and Landing (2008). Crucially, analysis has focused on the detailed morphology and stratigraphical occurrence of the two earliest 'endocerid' families, the Piloceratidae and Proterocameroceratidae, and their relationship with the ancestral Ellesmerocerida. Endocones or endocone-like structures are known from a number of distantly related groups of 'nautiloid' cephalopods apart from the Endocerida, such as the Dissidocerida and the Discosorida. Furthermore, siphonal structures that represent either conical endosiphuncular diaphragms (or possibly even endocones) occur in at least three different ellesmerocerid families. Consequently, cephalopods possessing endocones may have originated from more than one lineage within the Ellesmerocerida. Although the stratigraphical relationships between the earliest known pilocerids and proterocameroceratids is equivocal, study of the endosiphuncular deposits indicates that those of the Piloceratidae, Manchuroceratidae (and the younger Emmonsoceratidae, Allotrioceratidae and Najaceratidae) are more complex and distinctly different from the 'simple' endocones found in the Proterocameroceratidae and Endoceratidae. Other differences include overall conch form (cyrto-breviconic in the Piloceratidae and Manchuroceratidae; longiconic in the Proterocameroceratidae) and septal neck morphology (consistently holochoanitic to macrochoanitic throughout the pilocerids; shorter in the earlier proterocameroceratids). There may also be differences in the form of muscle attachment scars, although evidence is limited.

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In this paper, we present several lines of evidence supporting a polyphyletic origin of the Endocerida (in the original sense), and propose that the Piloceratidae and related families should be separated as a new order of Early Palaeozoic cephalopods: the Bisonocerida. This separation still retains the Endocerida (in a restricted sense) as a diverse, large and important group of Ordovician-Silurian cephalopods. The following taxonomic discussion is mainly restricted to type material of type species; a full monographic treatment of the Bisonocerida nov., including supplementary material, is in preparation by the authors, but is beyond the scope of this paper.

2. Historical views and current situation

The taxonomic scheme proposed by Flower (1976b: text-fig. 3; reproduced here with modifications as Fig. 1) summarises the uncertain knowledge of systematics of the Endocerida at that time. The ellesmerocerid *Pachendoceras* Ulrich and Foerste, 1936 was considered to give rise to the Proterocameroceratidae, and the Piloceratidae originated from an early member of the Proterocameroceratidae such as *Clitendoceras* Ulrich and Foerste, 1936. The ancestry of the Manchuroceratidae was poorly understood, with the Proterocameroceratidae and the Piloceratidae both mooted as possible ancestors. The ancestries of several later Ordovician endocerid families such as the Allotrioceratidae and Emmonsoceratidae were regarded as uncertain. Occurrences of 'simple' or 'complex' endosiphuncular deposits and the presence or absence of *Nanno*-like structures (apically 'swollen pre-septal cones') were also widely distributed amongst different families with no obvious pattern. Flower (1976b: p. 24) reported that in the oldest faunas then known in North America, representatives of the Proterocameroceratidae co-occurred with members of the Piloceratidae. This would imply that the derivation of the Piloceratidae from a proterocameroceratid ancestor was very rapid.

Previously, Kobayashi (1935: pp. 748–750) indicated that the Piloceratidae originated separately from the Ellesmerocerida on the grounds of the compressed cross-section of the conch, although he considered them derived from ellesmerocerids with a long-iconic conch. The Endocerida were treated as a monophyletic group by Dzik (1984), but he considered the possibility (Dzik, 1984: p. 26) that the Piloceratidae might have originated from "*Clarkoceras*-like" ellesmerocerids on the basis of their overall conch form and the shape of the endosiphocone. Although not ruling out a polyphyletic origin, Kröger and Landing (2008) considered that the two groups were coeval in origin and that there was sufficient gradation in their broad morphologies to regard them as a monophyletic group.

Thus, there is considerable uncertainty as to the composition and systematics of the Endocerida, the relationship between proterocameroceratids and piloceratids, as well as their potential ancestry. Here, we consider a polyphyletic origin for the Endocerida. Our evidence falls into five categories, each of which is discussed further below:

- General morphology of the phragmocone and siphuncle wall;
- Origins of endoconic-type deposits and diaphragms;
- Morphology of endosiphuncular deposits;
- Muscle attachment scars;
- Stratigraphic distribution.

3. General morphology of the phragmocone and siphuncle wall

In describing the general morphology of early pilocerids and endocerids, we refer to several of the families that Teichert (1964)

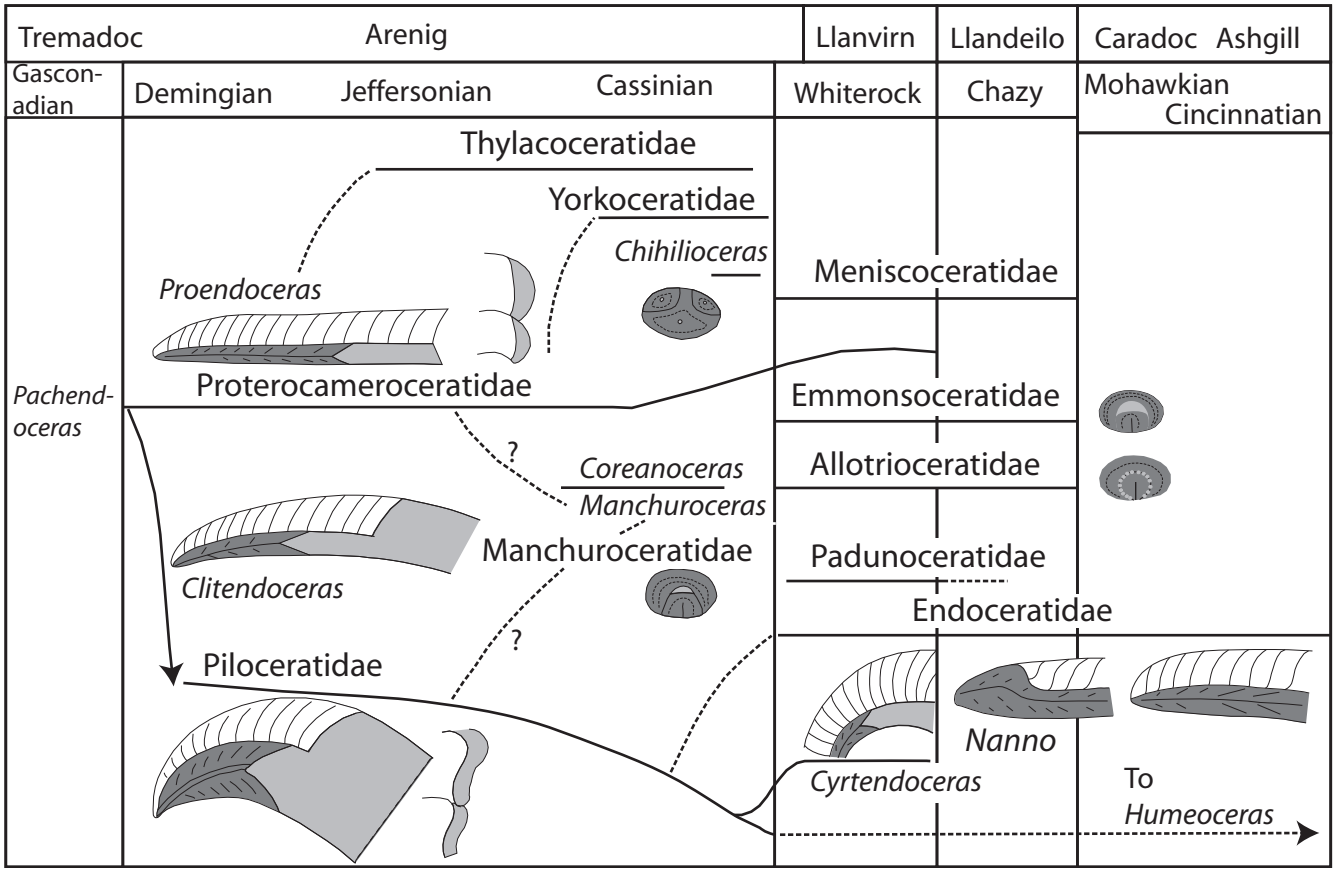

Fig. 1. Summary of endocerid systematics as formerly interpreted by Flower (1976b: text-fig. 3).