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Size reduction and ornamental oscillation within a Barremian lineage of giant heteromorphic ammonites (Early Cretaceous, northwestern Tethyan margin)

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ABSTRACT

Field sampling data in the Vocontian Basin (southeastern France) and Mallorca (Spain), at the transition between the lower and upper Barremian (upper *Moutoniceras moutonianum* Zone and lower *Toxancyloceras vandenheckei* Zone), provides new information about the early representatives of the ammonite family Ancyloceratidae. Several successive species of the genera *Moutoniceras* and *Toxancyloceras* are identified. A review of the history of the acquisition of the Astier collection by the Natural History Museum of London, which contains the holotype of the type-species *T. vandenheckei*, clarifies some misinterpretations which this species previously suffered. *T. vandenheckei* and *M. eigenheeri* are revised, and a new species is described: *T. canuti* sp. nov. With respect to an evolutionary perspective under biostratigraphic control, their phylogeny is considered (*M. eigenheeri* -> *T. canuti* sp. nov. -> *T. vandenheckei*). The hypothesis of the origin of the genus *Toxancyloceras* within the *Moutoniceras* is strengthened; this link is consistent both stratigraphically and morphologically. *Moutoniceras* appears to be the oldest known representative of the Ancyloceratidae, which is rooted in the early Barremian. The ontogenetic and evolutionary patterns of the phyletic lineage *Moutoniceras*/*Toxancyloceras* are twofold: the first concerns the ornamental changes (itself determined by three imbricated patterns) and the second involves the adult size. Both patterns determine two evolutionary phases through time: (1) the giant *Moutoniceras* and the progressive disappearance of the tubercles through heterochrony (paedomorphosis), and (2) the drastic size reduction and the reappearance of the tubercles from the "small" *Moutoniceras* to the *Toxancyloceras* (through heterochrony, with peramorphosis and a combination of pseudo-dwarfism, acceleration and graduaptation). The oscillation in disappearance and reappearance of the tubercles demonstrates a possible case of evolutionary reversibility where heterochrony helped by the progenesis impact, favours character repeatability in the evolutionary patterns. The results for the genera *Moutoniceras* and *Toxancyloceras* have significant biostratigraphic implications for the Tethyan Barremian. The status of *T. vandenheckei* as a zonal and subzonal index species (basal upper Barremian) is reinforced, and three new ammonite horizons are defined: the *Moutoniceras eigenheeri*, *Toxancyloceras canuti* and *T. vandenheckei* horizons. The stratigraphic distribution of all their index species is very restricted, indicating a well established evolutionary context.

1. Introduction

The ammonite family Ancyloceratidae Gill, 1871 (see Klein et al., 2007 for the generally accepted generic content) ranges from late Barremian to late Aptian (Early Cretaceous). In this family, the

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genus *Toxancyloceras* Delanoy, 2003 is the oldest known representative, as it is present at the base of the lower Barremian (*Toxancyloceras vandenheckei* Zone) with the species *T. vandenheckei* (Astier, 1851). Strong morphological convergences link *Toxancyloceras* to the more recent Aptian *Ancyloceras* s. str. through a variety of forms, but whose phyletic relationship is still poorly known (*Jaubertites* Sarkar, 1955, *Hoheneggericeras* Baudouin et al., 2008, etc.).

The origin of the genus *Toxancyloceras* was discussed by Delanoy (2003) and Vermeulen (2005). According to Delanoy (2003, p. 3), it originates in the genus *Emericiceras* (Emericiceratidae Vermeulen, 2004), and *T. vandenheckei* (Astier, 1851) is an intermediate species between *Emericiceras emerici* (Léveillé, 1837) and *Gassendiceras alpinum* (d'Orbigny, 1850) (Hemihoplitidae Spath, 1924). Vermeulen (2005, p. 159–160) considered *Honnoratia* Busnardo et al., 2003 (Emericiceratidae) as a direct ancestor of *Toxancyloceras*.

Bert and Bersac (2014) performed a phylogenetic analysis (Fig. 1) dealing with several taxa (*Toxancyloceras*, *Honnoratia*, *Emericiceras*, *Moutoniceras* Sarkar, 1955 and *Gassendiceras*). The results showed that:

- (1) neither *Emericiceras* nor *Honnoratia* can be interpreted as potential ancestors of *Toxancyloceras* (Bert and Bersac, 2014, fig. 3 and 4, p. 262). This position is reinforced by the stratigraphic hiatus of nearly two ammonite zones between the last Emericiceratidae and the first *Toxancyloceras*;
- (2) *Gassendiceras* (tested by the older forms *G. essaouirae* Bert and Bersac, 2014 and *G. multicostatum* [Sarkar 1955] in Bert and Bersac, 2014, fig. 3, p. 261) cannot be interpreted as a potential descendant of *Toxancyloceras*. Thus Hemihoplitidae and Ancyloceratidae are two independent families;
- (3) the early Barremian genus *Moutoniceras* is a sister taxon of *Toxancyloceras*.

This latter result, as well as its strong stratigraphic and morphological consistency, led these authors to consider *Moutoniceras* as an authentic representative of the Ancyloceratidae, rather than as a representative of the Heteroceratidae as it was admitted by a majority of experts until recently (Klein et al., 2007; see Bert and Bersac, 2014, p 264, for a historical account). Thus, to date, *Moutoniceras* is the oldest known Ancyloceratidae. A possible origin of the *Moutoniceras* within the Hauterivian *Pseudomoutoniceras* Autran et al., 1986 was proposed by Vermeulen (2006), but this hypothesis was challenged more recently by the same author (Vermeulen et al., 2010, p. 95) because of the very large stratigraphic gap that exists between these two genera. The review of the literature data (op. cit.) shows that there is a real gap in knowledge regarding the oldest Ancyloceratidae, and especially in their evolutionary modalities, in terms of patterns and processes.

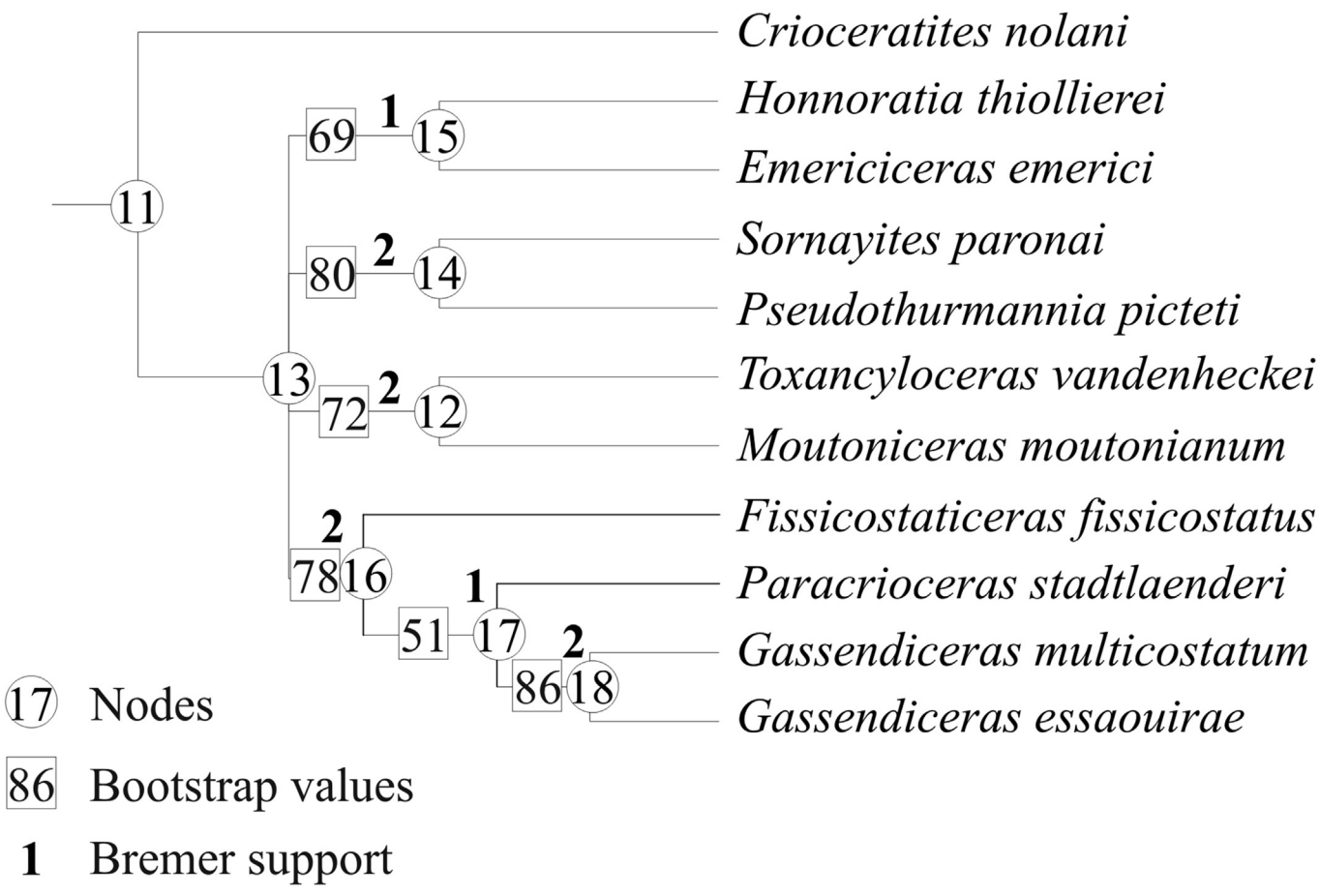

Fig. 1. Strict consensus tree computed with statistics (Bootstrap values and BREMER support) (Consistency Index CI = 0.643; Retention Index RI = 0.712; Adjusted homoplasy Aj = 3.45) by Bert and Bersac, 2014, to test some hypothesis about the origin of the Hemihoplitidae. *Toxancyloceras vandenheckei* and *Moutoniceras moutonianum* appear to be sister-taxa, without any link with the Hemihoplitidae (the clade *Fissicostaticeras*/*Gassendiceras*). The table of characters is given in Bert and Bersac (2014, appendix).