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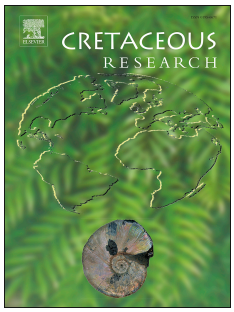


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# Size reduction and ornamental oscillation within a Barremian lineage of giant heteromorphic ammonites (Early Cretaceous, northwestern Tethyan margin)

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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, favors 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.

**Key-words.** Ancyloceratidae; Barremian; Vocontian Basin; France; Biostratigraphy; Evolution.

**Highlights.**

- The areas studied are in southeastern France and Mallorca (Spain).
- A new species (*Toxancyloceras canuti* sp. nov.) is described.
- Review of the Astier collection allows to understand misinterpretations of *T. vandenheckei*.
- Evolutionary patterns and processes of the oldest Ancyloceratidae are explained.
- 3 biostratigraphic horizons are introduced at the lower/upper Barremian boundary.

## 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 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.

New samples from the area of the Barremian stratotype of Angles (southeastern France), in levels dated at the top of the *M. moutonianum* Zone and the basal *T. vandenheckei* Zone, at the transition between the lower and upper Barremian, shed new light on the questions of the *Toxancyloceras* origin and evolution. Other data from the Mallorcan area (Balearic Islands) close gaps in the knowledge about the morphology of the studied species. Seven successive species of *Moutoniceras* and *Toxancyloceras* are identified in the present work, including a new one, and their phylogenetic relationships are considered, based on an evolutionary perspective. Biostratigraphic implications are potentially significant, given the importance of the genera *Moutoniceras* and *Toxancyloceras* in the standard Tethyan ammonite zonation (Reboulet et al., 2014). The index species *T. vandenheckei* is thus revised, taking into account the review of its holotype (Astier collection).

## 2. Geological setting and sections studied

The fossil material studied in the present work is the result of the systematic bed-by-bed sampling of several stratigraphic sections near the Barremian stratotype (southeastern France). Other ex-situ specimens of *Toxancyloceras* are from the Lloseta and Biniamar area (Mallorca, Balearic Islands, Spain). These areas both belong to the Cretaceous of the northwestern Tethyan margin (Fig. 2).

The biostratigraphic framework used for the Barremian in this work is the one proposed by the I.U.G.S Lower Cretaceous ammonite working group; the Kilian Group (Reboulet et al., 2014 – see Bert et al., 2008 for historical account). In the present work we also take into account the biostratigraphic proposals of Bert et al. (2008), Bert and Delanoy (2009), and Bert et al. (2010, 2011), which allows a high stratigraphic precision for the area studied (Fig. 3).

### 2.1. The Vocontian Basin

The Southeast France Basin (Fig. 4) is a large subsident intracratonic area, located in the southeast part of the country, between the Massif Central, which borders the West, the Alps that limit the East, the Jura in the North and the Mediterranean Sea in the South. Its Mesozoic sedimentation phase is between the Triassic (late Hercynian orogeny) and the Cretaceous (start of the Alpine orogeny), the Pyrenean-Provencal movements of the Late Cretaceous mark its demise as a basin.

Known as the Vocontian Basin (Paquier, 1900) the Southeast basin began its reduction during the Early Cretaceous. Its southern part, in the Barremian stratotype area (near Angles, Alpes de Haute-Provence, southeastern France – red star in Fig. 4), is characterised by pelagic sedimentation with an alternation of marlstones and limestones in decimetric to metric beds. This particular area is very conducive to studies thanks to the abundance and the quality of its outcrops. The continuous sedimentation and good paleontological record reveal the ammonite succession in considerable detail. The deep marine conditions of the Vocontian Basin, largely open to the Alpine Tethys, are reflected in the dominance of ammonites.

The Barremian stratotype area belongs to the protected perimeter of the Geological National Nature Reserve of Haute-Provence, managed by the Departmental Council of the Alpes de Haute-Provence. Many field sections were surveyed and studied there for almost two decades, as part of a larger work done by one of us (DB). Some of them have already been published (Bert and Delanoy, 2009; Bert et al, 2008, 2011, 2013). The sections that have provided the majority of the *Toxancyloceras* and *Moutoniceras* specimens studied here are A* and G5 (see below).

### *2.1.1. Field section A* (Fig. 5)*

*Previous work:* the Barremian historical stratotype (section A) has been designated by Busnardo in 1963 at the Symposium on the Lower Cretaceous (Busnardo, 1965b). It is located

along the road of Angles (Alpes de Haute-Provence, France) where the section A extends approximately 660 m (500 m for the Barremian itself) along two East-West oriented hills. This area has been previously studied by ammonitologists, particularly by Busnardo (1965a), Delanoy (1997) and Vermeulen (2005). The complementary section A* was described for the first time by Bert (2012).

*Description:* the trench of the road (section A) allows the entire stratigraphic succession to be seen, from bed No. 1 (upper Hauterivian) to bed No. 232 (lower Aptian), which underlies the Blue Marls Formation. The beds are almost tangential to the road, which allows them to be tracked in good conditions most of the time. Unfortunately, this exposure makes their study quite difficult. In this section, the lower part of the upper Barremian (*T. vandenheckei* and *Gerhardtia sartousiana* zones) is poorly exposed. Firstly because of access difficulties to the section that is along a cliff slope. Secondly because the growth faults disrupt the bed successions and make them impossible to study (see more explanations in Bert, 2012, p. 4). Given these difficulties in section A, a new reference section (denoted A*) was surveyed in the immediate lateral continuity of the stratotype (above the road), where there is no growth fault. For the *T. vandenheckei* Subzone, the bed numbering is the same as for stratotype A.

### *2.1.2. Field section G5 (Fig. 6)*

*Previous work:* this outcrop corresponds to the site of “Les Lumières” mentioned by Delanoy (2003, p. 3), near Angles (Alpes de Haute-Provence, southeastern France). Although it allowed the study of several complete specimens of *Toxancyloceras* of the L. Ebbo collection by the latter author, this section was never studied by means of bed-by-bed sampling. Thus, these latter *Toxancyloceras* have been assigned to the *T. vandenheckei* Zone by Delanoy (2003, p. 3, 5) without further detail. The current and more detailed work of this section

allows us to characterise the presence of the lower barremian that was never reported previously (Fig. 6, *M. moutonianum* Zone).

*Description:* the field section was surveyed in a small ravine, where the succession is clearly visible from the top of the upper Barremian (*M. moutonianum* Zone) to the *Gassendiceras alpinum* Subzone. The section borders the gigantic excavation dig that provided most of the *Toxancyloceras* collected in this section and figured by Delanoy (2003). This intensive sampling almost completely destroyed the structural surface of bed No. G5/85, making it particularly complicated to study. Thus, given the presence of this gigantic excavation, it is very likely that most of the specimens from "Les Lumières" figured by Delanoy (2003) are from bed No. G5/85. The close proximity (a few hundred meters) of the field section G5 from the Angles stratotype (section A*) allows a bed-by-bed correlation between these two sections, which are almost identical.

**2.2. Mallorca**

Mallorca is the largest of the Balearic Islands (East of Spain). Geologically, it is closely related to the Betic System in Southeast Iberian Peninsula. In Mallorca, the Cretaceous is mostly known in the West of the Sierra de Tramuntana but also in the centre of the island (called Es Pla) and in Sierra de Llevant. These Sierras originated in the Alpine orogeny (Colom, 1975). The Lower Cretaceous is formed by *ammonitico rosso* facies, but from the upper Berriasian to upper Barremian the marlstones and limestones of Maiolica facies are dominant. The lower Aptian is absent from the stratigraphical record and the upper Aptian is only present in the Southwest area. After this stratigraphical gap, the Lower Cretaceous is represented by marcasite-rich marls and marly limestones up to the upper Albian. The studied area (see below) is located in the middle part of Tramuntana (red star in Fig. 7).

As they are collected ex-situ (see below), the specimens from Mallorca were not taken into account when considering the biostratigraphic part, but they were used (1) to enlarge the understanding of the morphology of the species studied (the fossils studied are often fragmentary due to the heteromorphic state of the shells, thus there is a real need to increase the number of specimens), and (2) for palaeobiogeographical purpose.

### *2.2.1. Can Negret Quarry*

*Previous work:* the quarry was studied only recently in a work conducted by one of us (Juárez-Ruiz and Matamales-Andreu, unpublished), who described the Cretaceous ammonite biozonation of the area and part of the representative taxa.

*Description:* this active quarry, which represents the largest mining enterprise in the Balearic Islands, is located near the town of Lloseta, in the middle of Tramuntana. Can Negret is the richest Cretaceous fossil locality in Mallorca and one of the most abundant in Spain, with more than 220 recognised ammonite species. Unfortunately, the activity of the quarry and the extreme deformation of the series (common in most of the Mallorcan Cretaceous sites) make it almost impossible to carry out accurate bed-by-bed sampling. However many ammonite zones from the upper Valanginian to upper Albian are recognised by their index species and faunal association, including the *M. moutonianum* and *T. vandenheckei* zones.

### *2.2.2. Lloseta-Biniamar area*

*Previous work:* several small and dispersed Cretaceous outcrops in the area between Lloseta and Biniamar were studied or mentioned from the end of the 19th Century (Hermite, 1879; Nolan, 1895). The area near Lloseta is especially famous for having delivered the type specimen of *Kotestishvilia sauvageaui* (Hermite, 1879). Fallot (1910, 1922) and Fallot and Termier (1923) also mentioned some species near this town. Wiedmann (1962a, 1962b, 1964,

1967) described some Valanginian, Barremian and Albian ammonites from this area. Recently, Juárez-Ruiz and Matamales-Andreu (unpublished) recognised most of the ammonite zones from the upper Valanginian to the upper Barremian, and they found taxa previously unknown in Mallorca, including taxa also unreported in Spain.

*Description:* this area shows some dispersed outcrops, which are hard to study because they are usually covered by cultivated land. The stratigraphy can be studied only with faunal association in *ex situ* samples in most of the cases. However, some small sections are located from the *Kotetishvilia compressissima* to *T. vandenheckei* zones, which are especially rich in ammonites in most of their beds.

## 3. Material

The explanations about the material studied, and an overview of the Astier collection, which contains the holotype of the index species *Toxancyloceras vandenheckei*, are in the additional online material of the present work.

## 4. Systematic paleontology

The detailed systematic part (including the description of *Toxancyloceras canuti* sp. nov. and the revisions of *T. vandenheckei* and *Moutoniceras eigenheeri*) and the photographic figures of the studied material are in the additional online material of the present work.

## 5. Results: phylogenetic and evolutionary perspective under patterns and processes

The new data exposed in the present study strengthens the phyletic link Bert and Bersac (2014) proposed, based on a cladistic analysis (Fig. 1) between the genera *Moutoniceras* and *Toxancyloceras*. It appears that this link is consistent both stratigraphically and morphologically. The stratigraphic data obtained in the Vocontian Basin (southeastern

France) shows that the genus *Moutoniceras* disappeared with the tuberculate species *M. eigenheeri* at the very end of the early Barremian, stratigraphically just below the First Occurence (FO) of the genus *Toxancyloceras* (beginning in the upper Barremian). In the Barremian stratotype area of Angles the latter genus appears only one bed higher from the former (Figs. 5, 6), so a real continuity exists from a stratigraphic point of view between these two genera. On the other hand, the general morphology of the large tripartite ancyloceratic shell is very close to *Moutoniceras* and *Toxancyloceras*. Actually, in the beds around the boundary between the lower and upper Barremian of this area, there are no other large ancyloceratic ammonites aside from these two genera. Under these conditions, the following phylogenetic succession (from the oldest to the youngest) can be established: *M. eigenheeri* -> *T. canuti* sp. nov. -> *T. vandenheckei*.

Paleontological and stratigraphic data, resulting from analytical systematics, enable us to highlight ontogenetic and evolutionary patterns in this phyletic lineage. This succession is completed for the lower Barremian by older *Moutoniceras* species. More data about the development of the *Moutoniceras* species are required to make an accurate cladistic analysis, which requires further research into the *Nicklesia pulchella*, *K. compressissima* and *M. moutonianum* zones (lower Barremian). In any case, the species of the genus *Moutoniceras* need a revision under intraspecific variability and evolutionary perspectives. In summary, the evolution of *Moutoniceras* / *Toxancyloceras* goes through a decrease in adult size from the upper *M. moutonianum* Zone (Fig. 8), and also by heterochronies in the duration of the different ontogenetic stages (Fig. 9), and finally by modification of the tubercles, which oscillate between appearance and disappearance (Fig. 9):

- The adult size seems relatively stable between *M. nodosum* (lower part of *K. compressissima* Zone – H=1160 mm) and *M. moutonianum* (lower *M. moutonianum* Zone –

H=1280 mm), and also probably in *M. berti* (upper part of *K. compressissima* Zone). However, in the upper part of the *M. moutonianum* Zone the adult size of *M. marii* is reduced significantly (pseudo-dwarfism / progenetic process, in the sense of Dommergues et al., 1986). Although no sufficiently complete specimen of this latter species is known to date, the height of around 600-700 mm is assumed by data collected by one of us [DB]. The tuberculation is present on the outer whorl of the coil (bituberculate pattern) and at the top of the shaft in *M. nodosum* (peri-ventral tubercles reduced to the state of bulges on the rest of the shaft). It then regresses gradually from *M. berti* to *M. marii*. In *M. berti*, the tuberculation is represented by peri-ventral clavi individualized on the outer whorl of the coil (the only currently known part of the shell in this species) and in very discrete lateral tubercles. In *M. moutonianum*, there are only mere peri-ventral bulges at the turn of the outer coil and the shaft. Finally, the tuberculation seems to disappear completely on the coil and the shaft in *M. marii*.

- *M. eigenheeri* (top of the *M. moutonianum* Zone, in the new *M. eigenheeri* Horizon in this work): the adult size of *M. eigenheeri* continues its reduction compared to *M. marii* (H around 500-600 mm) with a large spiral part of about 200 mm in diameter. The tubercles, which were missing in *M. marii*, reappear on the early whorls of the coil (bituberculation with the fibula pattern) and the shaft (peri-ventral tubercles). The acquisition of the lateral tubercles on the shaft is very discreet, but this is new for the genus *Moutoniceras* on this part of the shell (lateral tubercles are known in *M. nodosum* but only on the outer coil). It is here that the trituberculation known in the immediately more recent *Toxancyloceras* begins to occur. This trituberculation appears however in a very fleeting manner at the very top of the shaft (the peri-dorsal bulges are very discreet). There are four ontogenetic stages in *M. eigenheeri*: (1) the inner part of the coil with differentiated ribs; (2) the outer part of the coil

with all identical ribs; (3) the shaft with ribs differentiated again; and (4) the hook with a more irregular ornamentation.

- *T. canuti* sp. nov. (lower part of the *T. vandenheckei* Zone and Subzone, in the new *T. canuti* Horizon, in this work): the adult size is a little further reduced (360<H<550 mm), as the spiral part reduces (110-140 mm). This implies an increase of the shell curvature and an increase in the whorl height growth. The main ribs of the coil and the shaft become systematically trituberculate; however the tubercles never become strongly expressed. The four ontogenetic stages are still present, although there are some changes from *M. eigenheeri*: (1) the inner part of the coil has strong differentiated ribs and regular alternation between main and intercalary ribs. The new pattern with looped ribs is likely an evolution of the pattern with fibula ribs known in *M. eigenheeri*: the lower tubercle closes the fibula and forms the loop; (2) the alternation of main / intercalary ribs of the outer part of the coil becomes much less regular. As in *M. eigenheeri*, the intercalary ribs maintain their strengthened appearance on the venter and on the peri-ventral margin, where they are sometimes even slightly tuberculate; (3) the shaft has differentiated ribs, but the number of intercalary ribs increases; and (4) the hook is almost identical.

- *T. vandenheckei* (lower part of the *T. vandenheckei* Zone and Subzone, in the new *T. vandenheckei* Horizon, in this work): the adult size is reduced and seems to be stabilised (H around 425 mm), as well as the spiral uncoiled part (95-160 mm). In terms of ornamentation, the intermediate bituberculate ribs, which were ornamental remains of *Moutoniceras*, disappear. At the same time the tubercles become stronger on the main ribs, while the peri-ventral strengthening of the intercalary ribs becomes anecdotal. There are no more than three ontogenetic successive stages during growth since the stage with differentiated ribs invaded the entire coil.

To summarize, two imbricated evolutionary trends are highlighted in the *Moutoniceras* / *Toxancyloceras* lineage. The first major trend concerns the ornamental changes, itself determined by three imbricated patterns (Fig. 9):

- (1) An ornamental oscillation of the appearance (*M. nodosum*), regression (*M. berti*, more in *M. moutonianum*), disappearance (*M. marii*), then reappearance (*M. eigenheeri*) and finally increasing amplification (*T. canuti* sp. nov., more in *T. vandenheckei*) of the tuberculate pattern over time. This oscillation is adjusted by: (1) the retardation of the ornamentation (the progressive disappearance of the tuberculation by the extension of the non-tuberculate young stage during ontogenesis – stage 1 in Fig. 9), which is a paedomorphosic process; and (2) by the acceleration of the ornamentation (invasion of the tuberculate pattern increasingly early through ontogenesis), which is a peramorphic process.

- (2) A differentiation of the ornamentation in main and intercalary ribs, increasingly clear in *M. eigenheeri* and the subsequent species. The tuberculation becomes more present and powerful on the main ribs over time, to become a true trituberculate pattern in *Toxancyloceras* (by the acquisition of the lower tubercles and the generalisation of the median tubercles on the main ribs).

- (3) A mitigation and disappearance of the marginal strengthening of the intermediate ribs. This evolutionary trend (as for the previous pattern) likely corresponds to graduaptation. This term was introduced by Chaline (1999) to designate the adaptations of a characteristic that take place gradually under the pressure of natural selection. These iterative and reversible changes (as this is the case here for the *Moutoniceras* / *Toxancyloceras* lineage) are understood under the model of the punctuated equilibrium/disequilibrium (Chaline, 1984, 1987) in the sense of a continuous and flexible adaptation to environmental changes, possibly causing minimal genome changes.

The second major evolutionary trend of this group regards the reduction in adult size throughout the transition from *Moutoniceras* to *Toxancyloceras* (Fig. 8), which seems to be expressed by a decrease in the duration of the different stages in a rather balanced way. This could be interpreted in terms of heterochronies (accelerated progenesis = pseudo-dwarfism in the sense of Dommergues et al., 1986). It is important to note that, as this is usually the case for numerous heteromorph ammonites species (see Bert, 2014), the adult size is subject to variation from one specimen to another (see the systematic part in the online additional material), thus, the evolutionary trend recognised here concerns only the maximal possible reached size.

## 6. Discussion

*Moutoniceras marii* and *M. eigenheeri* are both at the limit of the two phases recognised in the evolution of the lineage formed by the *Moutoniceras* and the *Toxancyloceras* species. Obviously, the *Toxancyloceras* morphology is already predefined in *Moutoniceras* where there already exists a tendency to form tubercles. In addition, the peri-ventral bulges on smooth ribs, which persist in earlier *Toxancyloceras*, are an inherited trait of the *Moutoniceras*.

Thus, from a merely taxonomic point of view, the choice could have been made to separate the small *Moutoniceras* species (*M. marii* and *M. eigenheeri*) from their giant ancestors. This proposition would have been coherent in evolutionary terms, since the use of evolutionary progenesis events are usually used to separate taxa at the genus-group level (Dommergues et al., 1986). There were two taxonomic options: either (1) we group *M. marii* and *M. eigenheeri* to the *Toxancyloceras* to match the generic cut-off with the drastic reduction in the size of *M. marii*; (2) either we group *M. marii* and *M. eigenheeri* into a separate genus (the genus

*Ewaldiceras* proposed by Vermeulen in 2003 for the latter species) separate from *Moutoniceras* and *Toxancyloceras*.

Unfortunately, neither of these solutions is really satisfactory. In the former, morphological coherence would be lost since *M. eigenheeri* and *M. marii* have an ornamentation strongly rooted in the *Moutoniceras* morphology (this is especially the case for *M. marii*). They do not have the apomorphies known in the more recent *Toxancyloceras*, and especially the trituberculate pattern, which is a diagnostic criterion for defining the genus (discriminative character). The second solution has the disadvantage of pulverizing the group by introducing a third artificial taxon to create the link which doesn't make much sense in terms of palaeobiology and clearly poses a problem in overestimating biodiversity. These risks have been evaluated and criticised by several authors from other ammonites groups (see a review in Bert, 2014).

Ideally, it is better to foster generic cuts to major changes in the evolutionary rhythms. So the choice was made in the present work to maintain *M. marii* and *M. eigenheeri* in the genus *Moutoniceras*, with the interest of maintaining a certain nomenclatural stability, and also to reserve this taxonomic hyphenation of the genus-group level for another major morphological aspect in the evolution of the group: the appearance of the trituberculate pattern. All this shows that even if taxa of the genus-group level are essential to separate formally phylogenetic lineages, they are also very conventional. Thus, they should not be used to measure biodiversity without some care to ensure they were introduced on a solid phylogenetic basis, taking into account the variability of species and evolutionary data (Bert, 2014).

When interpreting (see above, chapter 5) the two major evolutionary patterns of the *Moutoniceras* / *Toxancyloceras* lineage in terms of heterochronies, it is understood that two

399 evolutionary processes are underlying these patterns in the history of this group. The first is
400 paedomorphic and concerns the large sized *Moutoniceras*, in which it causes the progressive
401 reduction in tuberculation by retardation of the ontogeny with the disappearance of
402 ornamental stages (Fig. 9). However, during this process the morphology and the adult size
403 remain remarkably stable (Fig. 8). The second process is peramorphic and, determines the
404 second phase of the evolutionary history of the group (small *Moutoniceras* species and
405 transition to the genus *Toxancyloceras* – Fig. 9): an increasingly early appearance of the
406 ontogenetic stages (acceleration). Between these two phases, the start of the size reduction is
407 effective from *M. marii* and is quite sudden, usually corresponding to a progenesis
408 (interpreted here as pseudo-dwarfism in the sense of Dommergues et al., 1986). This change
409 in size also corresponds to the minimum expression of the tubercles, which reappear later
410 (oscillation) and are strengthened to give the *Toxancyloceras* morphology. It is tempting to
411 interpret this progenetic phenomenon as a result of environmental stress, e.g. due to
412 environmental changes. At the same time, the maximum regressive (named SbB3 in Arnaud,
413 2005) occurs, which corresponds to the top-early Barremian peak of $\delta^{18}O$ (Baudin et al.,
414 2009), corresponding with a “drastic” decrease in temperature.
415
416 It is very interesting to consider the ornamental oscillation, with the gradual disappearance
417 and then reappearance of the tuberculate pattern along the evolutionary trend of the group.
418 Ornamental oscillation implies that some evolutionary patterns are ultimately not completely
419 irreversible and that they are certainly subject to external variations (Guex, 2016). This is the
420 very idea of the graduaptation (see above chapter 5), which designates the adaptations of a
421 characteristic that take place gradually under the pressure of natural selection. If these
422 conditions are reversed, some evolutionary trends seem able to reverse also, even to oscillate,
423 but not without resulting in some internal upheavals requiring morphological adaptations.

424 And that's what seems to happen here with the progenetic event of *M. marii*, which causes the
425 reduction in size and the heterochrony inversion (peramorphosis *versus* paedomorphosis
426 previously).
427 Evidence appears to suggest that this oscillation occurs as a possible case of evolutionary
428 reversibility, which at first glance seems to contradict the Dollo law on the irreversibility of
429 evolution (Dollo, 1893; Gould, 1970). Although genetic (Marshall et al., 1994) and molecular
430 experimentations (Bridgham et al., 2009) seem to show the veracity of this law, exceptions
431 have already been reported in literature, often based on heterochrony (eg. Collin and Cipriani,
432 2003; Diogo and Woods, 2012; Kerney et al 2011; Whiting et al., 2003; see review in Wiens,
433 2011), to the extent that its relevance could be questioned (Colin and Miglietta, 2008). In any
434 case, and as Gould stated (1970), Dollo Law strictly concerns the impossibility for the
435 organisms (or a sufficiently complex biological structure) to return to their ancestral state
436 using the same complete but reversed path (to a question of probabilities based on
437 complexity). However, Dollo Law doesn't objectively exclude the possibility of certain
438 characteristics returning to an ancestral state, regardless of the function they occupied before.
439 Without being a real violation of Dollo Law in the strict sense (Gould, 1970), the example of
440 *Moutoniceras* / *Toxancyloceras* shows that there may be a form of repeatability in the
441 evolutionary patterns in ammonites. It is here favored by heterochrony (due to the progenesis
442 impact), as it was demonstrated with the re-evolution of coiling in some gastropods of the
443 family Calyptraeidae (Collin and Cipriani, 2003). Besides the developmental process
444 highlighted by heterochrony, it is also tempting to think that some of these iterative
445 phenomena may cause minimal modifications of the genome and may occur through
446 epigenetic processes, whose influence seems to be confirmed as might suggest some recent
447 studies (Goudarzi et al., 2016).

**Remarks about the dimorphism in the *Moutoniceras* / *Toxancyloceras* lineage:** in the literature data, the dimorphism has never been demonstrated for the genera *Moutoniceras* and *Toxancyloceras* (Delanoy et al., 1995). The specimens studied in the present work do not document it either, even if size variation is observed between some specimens. There is no evidence that this size variation could be due to dimorphism, especially because the extreme variants seem to be linked by intermediates. This size variation very likely corresponds to the instraspecific "normal" variation, as it is known for other genera of heteromorph ammonites (see for example Delanoy, 1997 for the genus *Heteroceras* d'Orbigny, 1849). Of course, this non-documentation does not mean that the dimorphism is absent from these genera, but that further research is needed to highlight it.

## 7. Biostratigraphic implications

Some biostratigraphic implications can be drawn from the understanding of the relationship between the genera *Toxancyloceras* and *Moutoniceras* at the turn of the early and late Barremian in the northwestern Tethyan margin. On the one hand, the revision of the classic species *T. vandenheckei* reinforces its status as index for the *T. vandenheckei* zone and subzone (lower upper Barremian). On the other hand, the review of *M. eigenheeri* and the discovery of *T. canuti* sp. nov., which was confused in the past with *T. vandenheckei* for various reasons (see above, chapter 4), allow us to propose three new biostratigraphic horizons for the Vocontian Basin (Fig. 3): the *M. eigenheeri* Horizon at the top of the lower Barremian (*M. moutonianum* Zone), and the *T. canuti* and *T. vandenheckei* horizons at the lower upper Barremian (*T. vandenheckei* Zone and Subzone). The stratigraphic distribution of all the index species proposed in the present work (Fig. 3) is very restricted and now precisely known. The importance of their being part of an evolutionary context is now well established

(this work, Figs. 8 and 9). The relative frequency of these species, in respect to the other contemporary ammonite faunas, makes them serious and legitimate candidates to the status of index species. Finally, the presence of representatives of the *Moutoniceras* and *Toxancyloceras* genera over a large geographical area, coupled with the discovery of *T. canuti* sp. nov. from Spain (Mallorca) to Tyrol (= *T. vandenheckei*, fig. 8a-b in Lukeneder, 2012) and Hungary (Fözy and Janssen, 2009, fig. 5b, 5f-g), suggests a high potential of correlation for these horizons on the whole northwestern Tethyan margin.

***Moutoniceras eigenheeri* Horizon (new)**

*Index species*: *Moutoniceras eigenheeri* (Vermeulen, 2003), which is revised in the present work. This species is currently known in the Vocontian Basin only, but as it is the mother-species of *T. canuti* sp. nov., it could potentially extend to the same area.

*Reference section*: the section G5 of the Angles area (southeastern France, Vocontian Basin) is chosen as the reference section of the *M. eigenheeri* Horizon. The index species is present in the beds 78, 80 and 82, which are equivalent to the stratotype beds 141, 143-1a and 143-1c respectively (sections A, A' and A*, see Figs 5 and 6 and Bert, 2012).

*Status*: this horizon is defined by the First Occurrence (FO) of its index-species. In fact, the latter is present in the uppermost thick bed of the lower Barremian in the stratotype area, and the horizon corresponds to the total distribution of the index species. In 2009, Reboulet et al. restored the division of the *M. moutonianum* Zone into two horizons: a *Coronites darsi* Horizon at the base, and a *Heinzia caicedi* Horizon at the top. The latter horizon encompasses the upper half of the *M. moutonianum* Zone; however, *Heinzia caicedi* (Karsten, 1856) is virtually absent from the basin, where the horizon is rendered of difficult use. The latter species is almost exclusively present in the platform borders where the levels are often quite condensed. Compared to the reference zonal scheme (Reboulet et al., 2014), the *M. eigenheeri*

Horizon is more recent than the *H. caicedi* Horizon, as the disappearance of *M. eigenheeri* coincides with the end of the lower Barremian. It immediately precedes the appearance of *T. canuti* sp. nov., which serves as index species of the overlying horizon: the first one of the upper Barremian.

*Faunal assemblage*: the ammonites are relatively scarce at the top of the lower Barremian. In spite of that, *M. eigenheeri* is relatively abundant (often in fragments) with respect to other ammonite faunas of the *M. eigenheeri* Horizon, where it is the most significant and easy-to-use ammonite for non-specialists. The index species is associated with numerous Barremitidae; the holcodiscids are well represented with *Holcodiscus uhligi* (Karakasch, 1907) and *Parasaynoceras* sp.; *Kotetishvilia sauvageaui* (Hermite, 1890) and *Silesites vulpes* (Matheron, 1880) are also present.

***Toxancyloceras canuti* Horizon (new)**

*Index species*: *Toxancyloceras canuti* sp. nov., which is introduced and described in an evolutionary context in the present work. It is known currently in southeastern France, in South Tyrol, in Hungary and in Spain (Mallorca), where the new horizon could be used.

*Reference section*: the field section A* is chosen as reference for the *T. canuti* Horizon. The index species is present in beds No. 144 and 145. It may be present in the small beds No. 143-2 and 143-3 (where the change in lithology known at the lower/upper Barremian boundary occurs), but so far these beds have delivered no fossils. The *T. canuti* Horizon corresponds to the beds No. 84 and 85 of the neighbouring section G5 (see Figs 5 and 6).

*Status:* this horizon is defined by the FO of its index species immediately above the last thick beds of the lower Barremian in the stratotype area (Angles, southeastern France), and the horizon corresponds to the total distribution of the index species. The choice to place the *T. canuti* Horizon into the upper Barremian instead of the lower Barremian does not modify the

lower limit of the *T. vandenheckei* Zone. The first reason is that *T. canuti* sp. nov. has often been confused with *T. vandenheckei* (see synonymy, chapter 4), and therefore the *T. vandenheckei* Zone was already starting *de facto* with the appearance of *T. canuti* sp. nov. The second reason is that the ammonite fauna of the *T. canuti* Horizon is closer to that of the upper of *Heinzia sayni* Hyatt, 1903, which was used as index of the first zone of the upper Barremian in the past (Vermeulen, 1997). The acceptance of the *T. canuti* Horizon as the lowest horizon of the upper Barremian at the basis of the *T. vandenheckei* Zone requires only very slight modification of its definition. It no longer starts with its index species, but with the emergence of the *Toxancyloceras* genus (in the evolutionary context *Moutoniceras* -> *Toxancyloceras*), which ultimately facilitates its recognition by non-ammonite specialists.

*Faunal assemblage*: the *T. canuti* Horizon undoubtedly marks the appearance of the *Toxancyloceras*. *T. canuti* sp. nov., which is relatively abundant, appears simultaneously with rare specimens of *Heinzia sayni*. Note the extreme scarcity of the Holcodisciidae (scarce *Holcodiscus uhligi* and *Parasaynoceras* sp.), and the total disappearance of the *Moutoniceras*. Present in this horizon are also: *Macroscaphites rakusi* (Uhlig, 1883) ([m&M]), *Kotetishvilia sauvageaui*, *Silesites vulpes* and numerous Barremitidae.

***Toxancyloceras vandenheckei* Horizon (new)**

*Index species*: *Toxancyloceras vandenheckei* (Astier, 1851), which is revised in the present work. This species is currently known in southeastern France, Spain (incl. Mallorca), Slovakia, Italy, and maybe in South Tyrol and Japan.

*Reference section*: the field section A* is chosen as the reference for the *T. vandenheckei* Horizon. The index species appears there from bed No. 146. This level corresponds to bed No. 86 of the neighbouring section G5 (see Figs 5 and 6).

*Status:* this horizon is defined by the FO of its index species, and the horizon corresponds to the total distribution of its index species as understood in the present work. *T. vandenheckei*, now revised, is strengthened as index species for the *T. vandenheckei* Zone and Subzone. On the other hand, while it is now recognised that *T. vandenheckei* does not appear at the base of its zone, it is not necessary to rename it the "*T. canuti* Zone". Indeed, the lower limit of an interval zone, of which the use has been recommended by the IUGS Lower Cretaceous Ammonite Working Group (Reboulet et al., 2011, p. 790), is defined by a horizon (Thierry, 1997). In this case, it is not mandatory that a horizon starts with its index taxon (unlike a distribution zone, for example).

*Faunal assemblage*: *T. vandenheckei* is common in the horizon of which the ammonite fauna is very similar to the *T. canuti* Horizon. *Heinzia sayni* specimens however, become more frequent, while Holcodisciidae become scarcer. As in the previous horizon, *Macroscaphites rakusi* ([m&M]), *Kotetishvilia sauvageaui*, *Silesites vulpes* and numerous Barremitidae are present.

## 8. Conclusions

The new data from several stratigraphic sections near the Barremian stratotype (the Angles area in southeastern France) and from the Lloseta and Biniamar area (Mallorca, Balearic Islands, Spain), allow us to demonstrate that the upper Barremian ammonite genus *Toxancyloceras* originates in the lower Barremian *Moutoniceras*. The genus *Moutoniceras* disappeared with the tuberculate species *M. eigenheeri* at the very top of the lower Barremian, just below the FO of *T. canuti* sp. nov., which is the oldest species of the genus *Toxancyloceras* at the base of the upper Barremian. Thus, *Moutoniceras* is now the oldest currently known representative of the ammonite family Ancyloceratidae, and this genus

cannot be considered as a Heteroceratidae. Of course, this classification does not exclude the hypothesis that the Heteroceratidae themselves probably derive from the Ancyloceratidae.

This new data sheds new light on the comprehension of the *Moutoniceras* and *Toxancyloceras*. Especially, the revision of the species *M. eigenheeri* and *T. vandenhecki,* and a new species (*T. canuti* sp. nov.) is described. *T. vandenheckei* is considered in the historical context of the acquisition of the Astier collection by the Natural History Museum of London, and its holotype is figured here for the first time other than by a drawing. The examination of this latter specimen, which is not totally identical with the original drawing of 1851, partly explains some misinterpretations of the species. Seven successive species of *Moutoniceras* and *Toxancyloceras* are considered and their phylogeny is established as follow: *M. nodosum -> M. berti -> M. moutonianum -> M. marii -> M. eigenheeri -> T. canuti* sp. nov. *-> T. vandenheckei*. However, more data about the development of the *Moutoniceras* species is required to make an accurate cladistic analysis, which requires further research into the *Nicklesia pulchella*, *K. compressissima* and *M. moutonianum* zones (lower Barremian). In any case, the species of the genus *Moutoniceras* need revision with consideration into the perspectives of intraspecific variability and evolutionary.

Biostratigraphically, the status of *T. vandenheckei* as zonal and subzonal index at the base of the 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, forming part of a well established evolutionary context.

There are two phases in the evolutionary history of the *Moutoniceras* / *Toxancyloceras* lineage, underlined by two processes. The first is paedomorphosis and it concerns the large

*Moutoniceras* species with the progressive disappearance of the tubercle pattern over time through a retardation of the ontogeny and the disappearance of ornamental stages (Figs. 8, 9). The second process is peramorphosis with the acceleration of the ornamentation in the small *Moutoniceras* species and the *Toxancyloceras* (Figs. 8, 9). Between these two phases occurs a progenesis with the quite sudden reduction in adult size effective from *M. marii*. This size reduction is interpreted here as pseudo-dwarfism (in the sense of Dommergues et al., 1986) where the duration of the different ontogenic stages decreases. This change in size also corresponds to the pattern of minimum expression of the tubercles, which reappear later (oscillation). This progenesis is concomitant with some environmental changes (maximum regressive of the late Barremian, and "drastic" decrease in temperatures) and it would be tempting to correlate the two phenomenon.

The oscillation of the tuberculate pattern is adjusted by: (1) a process of paedomorphosis (retardation of the ornamentation with extension of the non-tuberculate young stage during growth that implies the progressive disappearance of the tuberculation); and (2) by a peramorphic process (acceleration of the tuberculate pattern, which appears increasingly early through ontogenesis). Finally, two other ornamental patterns are related to graduaptation processes. The first is the differentiation in main and intercalary ribs, with the increase of the tuberculation to a true trituberculate pattern (in *Toxancyloceras*). The second is the mitigation and disappearance of the marginal strengthening of the intermediate ribs.

The ornamental oscillation of the tuberculate pattern could act a possible case of evolutionary reversibility. Actually, the Dollo law is not violated as this latter does not objectively exclude the possibility for certain characteristics to return to an ancestral state, regardless of the function they occupied before. Here, the example of *Moutoniceras* / *Toxancyloceras* shows that there exist a form of repeatability in the ammonites evolution favoured by the heterochronies.

621

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**CAPTION OF THE FIGURES:**

**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).

**Fig. 2.** Palaeogeographic map of the Western Tethyan Realm at the Barremian, modified after Bert and Bersac, 2014 (reconstructed from Barron et al., 1981, and Dercourt et al., 2000), with the position of the Vocontian Basin (southeastern France), and the Balearic Islands (Spain).

**Fig. 3.** Barremian biostratigraphy of the stratotype area (southeastern France), according to Reboulet et al. (2014) completed by the data of Bert et al. (2008, 2009, 2010, 2011). The three new horizons are in red (*Moutoniceras eigenheeri*, *Toxancyloceras canuti* and *T. vandenheckei*). Note that the *Hemihoplites astarte* Horizon replaces the *H. casanovai* Horizon of Bert et al., 2008, because of the objective synonymy of *H. casanovai* Delanoy, 1992 with *H. astarte* (Fallot and Termier, 1923) (new unpublished data – forcoming work).

**Fig. 4.** Palaeogeographic map of the Vocontian Basin (southeastern France – modified after Arnaud, 2005). The red star points out the Barremian stratotype area near Angles.

**Fig. 5.** Outcrop section A* near Angles (stratotype of the Barremian stage, southeastern France). ME: *Moutoniceras eigenheeri* Horizon; TC: *Toxancyloceras canuti* Horizon; TV: *T. vandenheckei* Horizon; GA: *Gassendiceras alpinum* Horizon.

**Fig. 6.** Outcrop section G5 in the Angles area (southeastern France). ME: *Moutoniceras eigenheeri* Horizon; TC: *Toxancyloceras canuti* Horizon; TV: *T. vandenheckei* Horizon; GA: *Gassendiceras alpinum* Horizon.

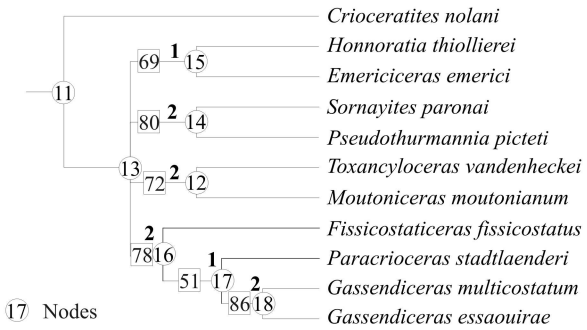
**Fig. 7.** Simplified geological map of Mallorca (Balearic Islands, Spain). The red star points out the outcrops studied in the Sierra Tramuntana.

943

944 **Fig. 8.** Size and reconstructed morphology of the successive species of the lineage
945 *Moutoniceras* / *Toxancyloceras*. The ammonites are at the scale. From left to right (the oldest
946 to the youngest) are: **a**, *Moutoniceras nodosum*; **b**, *M. berti*; **c**, *M. moutonianum*; **d**, *M. marii*;
947 **e**, *M. eigenheeri*; **f**, *Toxancyloceras canuti* sp. nov. and **g**, *T. vandenheckei*. The numbers
948 correspond to the ontogenetic stages explained in Figure 9. Original drawings by José Juárez-
949 Ruiz.

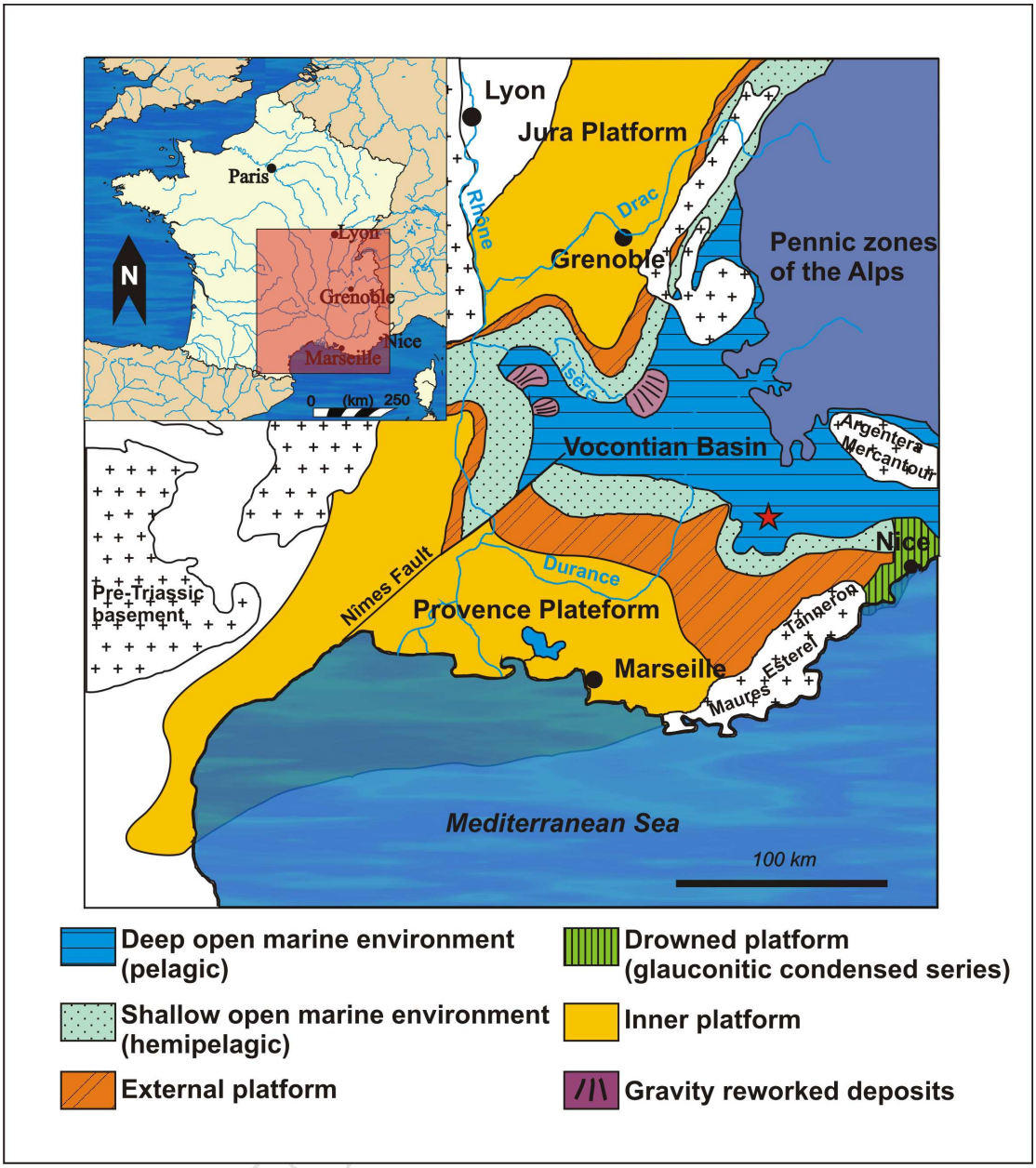
950

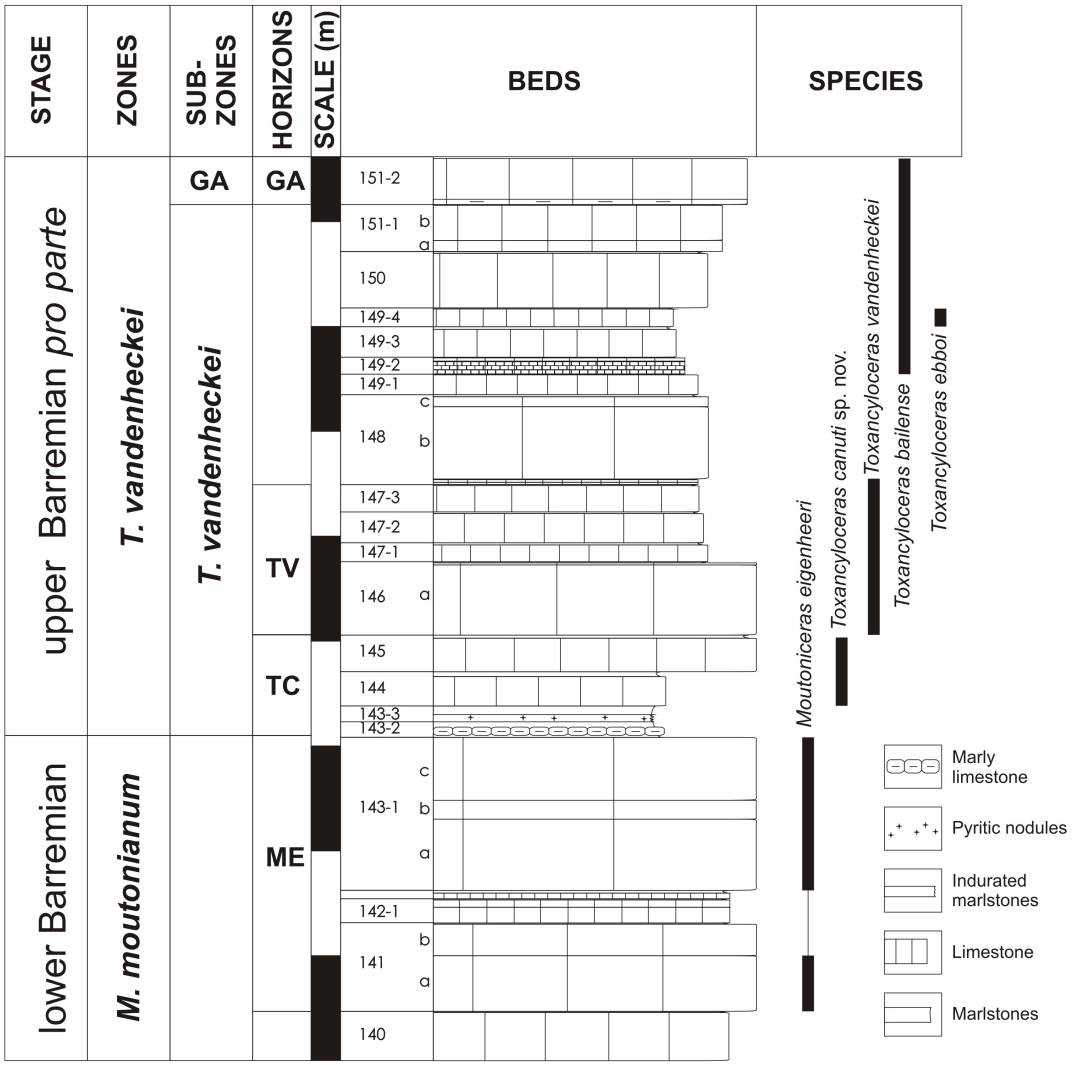
951 **Fig. 9.** Ontogeny and heterochronies within the *Moutoniceras* / *Toxancyloceras* lineage. The
952 ornamental stages are: **1**, Tubercle less ribs, which are ventrally reinforced; **2**, Fibulate /
953 looped rib pattern (tuberculate); **3**, Coil with differentiated ribs (regular alternation of
954 trituberculate / smooth ribs); **4**, Bituberculate pattern (coil); **5**, Tubercle-less ribs; **6**,
955 Bituberculate pattern (shaft); **7**, Irregular trituberculate pattern (shaft); **8**, Bend and hook (this
956 stage is considered here as an 'adult variation' without any evolutionary implications – see
957 Delsol, 1977). See text, chapter 5, for explanations.




N. American
Shield
Boreal
Realm
Russian
Platform
Vocontian
Basin
Balearic
Islands
Tethyan
Realm
Saharian
Shield
N

| Standard Tethyan ammonite zonation of Reboulet et al. (2014) with the biostratigraphic proposals of Bert et al. (2008, 2009, 2010, 2011) | | | | | Distribution of the *Moutoniceras* / *Toxancyloceras* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Stages** | | **Zones** | **Subzones** | **Horizons** | ***M. nodosum*** | ***M. berti*** | ***M. moutonianum*** | ***M. marii*** | ***M. eigenheeri*** | ***T. canuti* sp. nov.** | ***T. vandenheckei*** |
| **BARREMIAN** | upper | *Imerites giraudi* | *Pseudocrioceras wagenioides* | | | | | | | | |
| | | | *Martelites sarasini* | | | | | | | | |
| | | | | *Leptoceratoides puzosianum* | | | | | | | |
| | | | *I. giraudi* | *Heteroceras emerici* | | | | | | | |
| | | | | *I. giraudi* | | | | | | | |
| | | | | *I. dichotomus* | | | | | | | |
| | | *Gerhardtia sartousiana* | *Hemihoplites feraudianus* | *Pseudoshasticrioceras autrani* | | | | | | | |
| | | | | *P. magnini* | | | | | | | |
| | | | | *P. bersaci* | | | | | | | |
| | | | | *H. feraudianus* | | | | | | | |
| | | | *G. provincialis* | *H. astarte* | | | | | | | |
| | | | | *G. provincialis climax* | | | | | | | |
| | | | | *G. provincialis* | | | | | | | |
| | | | *Camereiceras limentinus* | *G. sartousiana* | | | | | | | |
| | | | | *C. limentinus* | | | | | | | |
| | | *Toxancyloceras vandenheckei* | *Gassendiceras alpinum* | *C. marchandi* | | | | | | | |
| | | | | *C. breistrofferi* | | | | | | | |
| | | | | | | | | | | | |
| | | | | *G. alpinum* | | | | | | | |
| | | | *T. vandenheckei* | | | | | | | | |
| | | | | *T. vandenheckei* | | | | | | | |
| | | | | *T. canuti* | | | | | | | |
| | lower | *Moutoniceras moutonianum* | | *M. eigenheeri* | | | | | | | |
| | | | | *Heinzia caicedi* | | | | | | | |
| | | | | *Coronites darsi* | | | | | | | |
| | | *Kotetishvilia compressissima* | | *Subtorcapella defayae* | | | | | | | |
| | | | | *H. communis* | | | | | | | |
| | | | | *Nicklesia didayana* | | | | | | | |
| | | | | *Holcodiscus fallax* | | | | | | | |
| | | *Nicklesia pulchella* | | | | | | | | | |
| | | *Kotetishvilia nicklesi* | | | | | | | | | |
| | | *Taveraidiscus hugii auctorum* | *Psilotissotia colombiana* | | | | | | | | |
| | | | *T. hugii auctorum* | | | | | | | | |


Paris
Lyon
Grenoble
Nice
Marseille
0 (km) 250
N
Lyon
Jura Platform
Rhône
Drac
Grenoble
Pennic zones of the Alps
Isère
Vocontian Basin
Argentera Mercantour
Nice
Durance
Nimes Fault
Pre-Triassic basement
Provence Plateform
Tanneron
Esterel
Maures
Marseille
Mediterranean Sea
100 km
Deep open marine environment (pelagic)
Shallow open marine environment (hemipelagic)
External platform
Drowned platform (glauconitic condensed series)
Inner platform
Gravity reworked deposits


STAGE
ZONES
SUB-ZONES
HORIZONS
SCALE (m)
BEDS
SPECIES
upper Barremian pro parte
lower Barremian
T. vandenheckei
M. moutonianum
GA
T. vandenheckei
GA
TV
TC
ME
151-2
151-1 b
a
150
149-4
149-3
149-2
149-1
148 c
b
147-3
147-2
147-1
146 a
145
144
143-3
143-2
143-1 c
b
a
142-1
141 b
a
140
Moutoniceras eigenheeri
Toxancyloceras canuti sp. nov.
Toxancyloceras vandenheckei
Toxancyloceras bailense
Toxancyloceras ebboi
Marly limestone
Pyritic nodules
Indurated marlstones
Limestone
Marlstones