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Origin of the Tethyan Hemihoplitidae tested with cladistics (Ancyloceratina, Ammonoidea, Early Cretaceous): an immigration event?

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Abstract: The Late Barremian Hemihoplitidae (Ancyloceratina, Ammonoidea) are widely known in the northern Tethyan Margin and the Essaouira-Agadir Basin (Morocco). Their rapid evolution and diversification make them one of the key groups for that period, but their origin remains poorly known and several competing hypotheses have been published. These hypotheses are tested here with cladistic analysis in order to reject those receiving the least support and discuss those well supported. The analysis discards the Crioceratitidae, Emericiceratidae (*Emericiceras* and *Honnoratia*) and *Toxancyloceras* as stem-groups of the Hemihoplitidae (*Gassendiceras*). The *Toxancyloceras* appear instead to be a sister-taxon of the *Moutoniceras*, so we propose the latter to be classified with the Ancyloceratidae rather than with the Heteroceratidae. The best supported hypothesis assumes that the Hemihoplitidae first appeared suddenly in the Essaouira-Agadir Basin at the end of the Early Barremian from small populations of Boreal *Paracrioceras*. These latter could have migrated southward episodically before invading the northern Tethyan margin at the beginning of the Late Barremian. As a consequence, the Paracrioceratidae fam. nov. is proposed to include the Boreal groups *Fissicostaticeras* / *Paracrioceras* / *Parancyloceras*, and *Gassendiceras essaouirae* sp. nov. is proposed as a new name for the Moroccan endemic "*Barrancyloceras*" *maghrebiense sensu* COMPANY *et al.*, 2008, non IMMEL, 1978.

Key Words: Ammonites; Hemihoplitidae; Barremian; cladistics; allopatry; founder effect; palaeobiogeography.

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Résumé : *L'origine des Hemihoplitidae téthysiens testée par la cladistique (Ancyloceratina, Ammonoidea, Crétacé inférieur) : un événement migratoire ?.* Les Hemihoplitidae du Barrémien supérieur (Ancyloceratina, Ammonoidea) sont connus sur la plus grande partie de la marge Nord Téthysienne et dans le Bassin de Essaouira-Agadir (Maroc). Leur évolution et leur diversification rapide en font un des groupes clés pour cette période, mais leur origine reste peu connue et plusieurs hypothèses contradictoires ont été développées dans la littérature. Ces hypothèses sont testées ici par une analyse cladistique afin d'écartier les moins étayées d'entre elles et de discuter les meilleures. L'analyse écarte les Crioceratitidae, les Emericiceratidae (*Emericiceras* et *Honnoratia*) et les *Toxancyloceras* en tant que groupe-souche pour les (*Gassendiceras*). D'autre part, les *Toxancyloceras* apparaissent être taxon-frère des *Moutoniceras*, aussi est-il proposé de classer ces derniers parmi les Ancyloceratidae plutôt que dans les Heteroceratidae. L'hypothèse la mieux soutenue suggère que les Hemihoplitidae seraient initialement apparus soudainement à la fin du Barrémien inférieur dans le Bassin d'Essaouira-Agadir à partir de petites populations de *Paracrioceras* boréaux. Ces derniers auraient pu migrer épisodiquement vers le Sud avant d'envahir la marge Nord-Téthysienne au début du Barrémien supérieur. En conclusion, la Famille des Paracrioceratidae fam. nov. est proposée pour individualiser le groupe boréal *Fissicostaticeras* / *Paracrioceras* / *Parancyloceras*, et *Gassendiceras essaouirae* sp. nov. est proposé comme nom nouveau pour désigner les "*Barrancyloceras*" *maghrebiense sensu* COMPANY *et al.*, 2008, non IMMEL, 1978, endémiques du Maroc.

Mots-clefs : Ammonites ; Hemihoplitidae ; Barrémien ; cladistique ; allopatrie ; effet fondateur ; paléobiogéographie.

1. Introduction

The marine Late Barremian (*pro parte*) ammonite family Hemihoplitidae SPATH, 1924 (Ancyloceratina WIEDMANN, 1960), is widely known in the northern Tethyan Margin and the Essaouira-Agadir Basin (Morocco), where it

represents a separate entity from the Ancyloceratidae GILL, 1871. Their rapid evolution and diversification make it one of the key groups for that period. The Hemihoplitidae are currently under revision (D.B.) and several contributions have already been published (BERT & DELANOY,

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2000, 2009; BERT, 2012, 2013; BERT & BERSAC, 2012, 2013; BERT *et al.*, 2006, 2008, 2009, 2010, 2011, 2013). These works helped to recognise three major developments for this family. These developments are taxonomically characterized by three subfamilies (Fig. 1), from which the Gassendiceratinae BERT *et al.*, 2006, represents the stem of the whole group; the group is present from the early Late Barremian Vandenheckei Zone to the Giraudi Zone.

The Gassendiceratinae include the genera *Gassendiceras* BERT *et al.*, 2006, *Pseudoshasticrioceras* DELANOY, 1998, and *Imerites* ROUCHADZE, 1933, which have close

phylogenetic relationships. The genus *Gassendiceras* spans the Vandenheckei and Sartousiana zones. This latter genus is characterized by a particularly recognizable morphology with an uncoiled shell and main trituberculate ribs strongly marked alternately with spineless intercalary ribs (smooth). The *Pseudoshasticrioceras* are derived from the *Gassendiceras* in the Feraudianus Horizon or a little earlier. They show a tighter coiling, depletion of spineless ribs and proliferation of weakly tuberculate intermediate ribs (ribs are less differentiated from each other on the ventral margin – BERT & DELANOY, 2009).

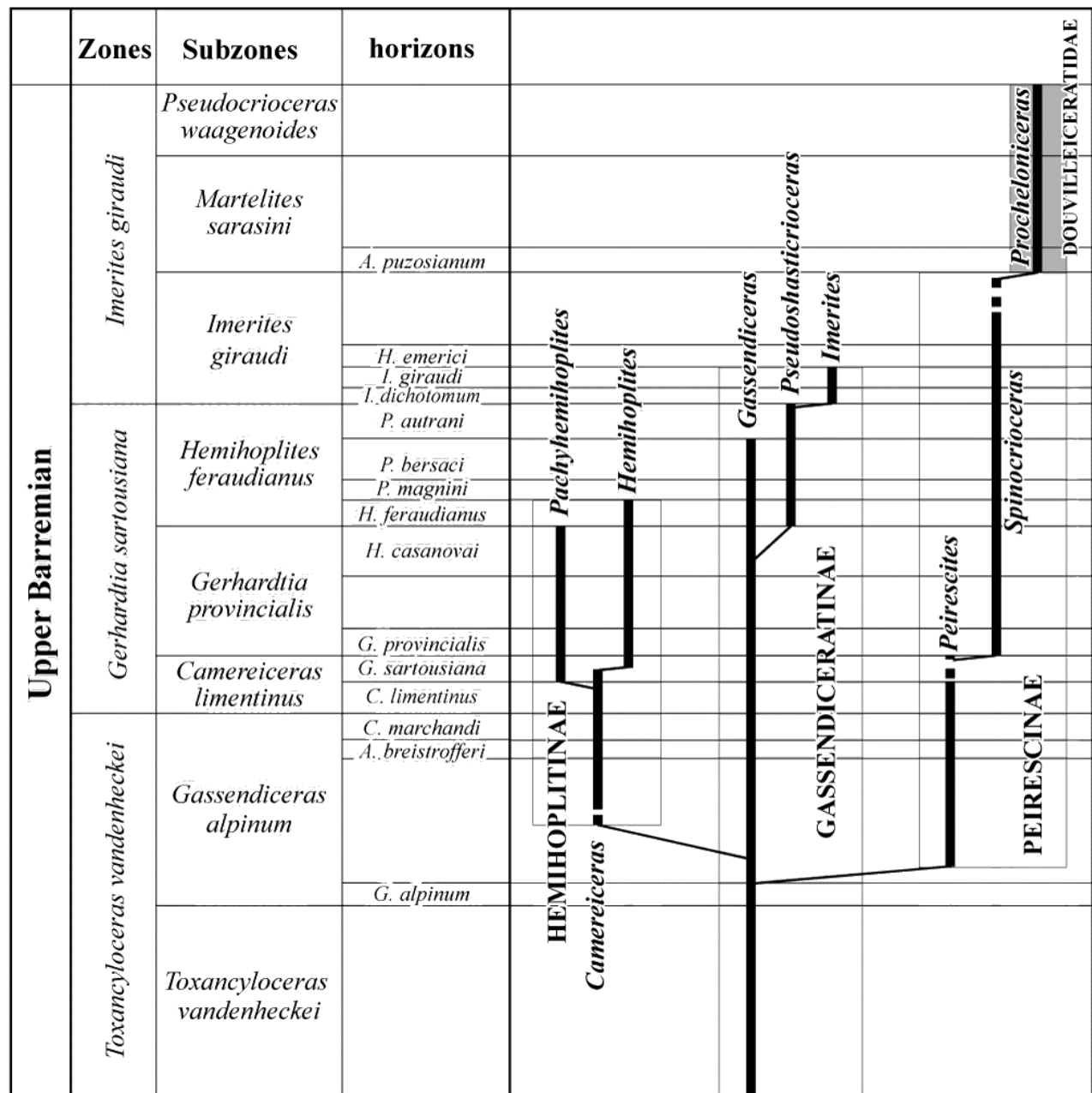


Figure 1: Relationships within the Hemihoplitidae (after BERT, 2012).

The transition to *Imerites* (base of the Giraudi Zone) is accomplished by a major restructuring of the shell (appearance of the helical early stage), which also determines the morphological appearance of dimorphism (BERT *et al.*, 2009). Taxonomy, intraspecific variability and ontogenetic development of the genus *Gassendiceras* have been revised recently based on abundant material from south-eastern France (BERT *et al.*, 2013; BERT, 2013), and its phylogenetic reconstruction was carried out using cladistic analysis (BERT & BERSAC, 2013). The results were compared to palaeoenvironmental external data (eustasy, palaeoclimate proxies) and show that *Gassendiceras* has an anagenetic evolution of palinogenesis type associated with a constant selection under environmental control (transgressive sequence).

The origin of the Hemihoplitidae remains poorly known despite this revision, and several competing hypotheses have been published. The purpose of the present paper is to test these hypotheses with cladistics and to resolve the origin of the whole Hemihoplitidae clade, of which the *Gassendiceras* are the oldest representatives

2. Hypotheses on the Hemihoplitidae origin

2.1. The literature hypotheses

Authors proposed previously four hypotheses about the origin of the Hemihoplitidae:

1- Crioceratitidae GILL, 1871, as stem-group: for WIEDMANN (1962, p. 112 and Fig. 35), "*Hemihoplitidae* [are] derived from *Pseudothurmannia* and perhaps from other Crioceratitidae genera with similar suture". Despite the large stratigraphic gap between the last Crioceratitidae (Late Hauterivian) and the first Hemihoplitidae (early Late Barremian), WIEDMANN (followed by IMMEL, 1979, and more recently by KLINGER & KENNEDY, 1992, and MIKHAILOVA & BARABOSHKIN, 2009) classified the forms of the "*barremense*" KILIAN, 1895 / *alpinum* d'ORBIGNY, 1850 group (here *Gassendiceras*) into the genus *Crioceratites* LÉVEILLÉ, 1837. The former species are supposed to be derived from the latter by the increasingly tight coiling of the shell. A neighbouring position was supported recently by KAKABADZE and HOEDEMAEKER (2004, p. 82), who considered the Hemihoplitidae invalid in favour of the Ancyloceratidae.

2- *Emericiceras emerici* (LÉVEILLÉ, 1837) and *Toxancyloceras vandenheckei* (ASTIER, 1851) as stem-group: according to DELANOY (1992, p. 52), the *Gassendiceras* (= group of "*E. barremense*") would be derived from the *Emericiceras* SARKAR, 1954, of the *E. emerici* group (Emericiceratidae VERMEULEN, 2004) via the *Toxancyloceras* DELANOY, 2003, of the *T. vandenheckei* group (Ancyloceratidae) of which

they were supposed to be the descendants. This evolution would be carried out through a process of shell recoiling. Such an origination would be supported by very strong ornamental convergences between the juvenile whorls of both the *Gassendiceras* and *Toxancyloceras*, which are also present partially in *Emericiceras* (alternation of trituberculate main ribs and smooth interribs). For IMMEL (1978, Fig. 11, p. 70) *E. emerici* could be directly at the origin of the *Gassendiceras* (= "*E. barremense*").

3- *Honnoratia thiollierei* (ASTIER, 1851) as stem-group: for VERMEULEN (2000, p. 130), the Hemihoplitidae originated in the Emericiceratidae, but from *Honnoratia thiollierei* instead of the *Emericiceras emerici* group. This assumption is based probably on the uncoiling and the ornamental similarities between *Honnoratia* BUSNARDO *et al.*, 2003, and *Gassendiceras* with the trituberculate main ribs alternating with smooth interribs.

4- "*Barrancyloceras*" *maghrebiense* (*sensu* COMPANY *et al.*, 2008, *non* IMMEL, 1978) as stem-group: *Crioceratites maghrebiense* IMMEL, 1978, was classified into the genus *Barrancyloceras* VERMEULEN, 2000 [of which the type species *B. barremense* (KILIAN, 1895) is a *nomen dubium* – see BERT *et al.*, 2010] by KLEIN *et al.* (2007) and COMPANY *et al.* (2008). Following VERMEULEN (note 198, p. 225 in KLEIN *et al.*, 2007), we consider however that the type specimen of the Moroccan taxon *maghrebiense* s.s. (*sensu* IMMEL, *non* COMPANY *et al.*) is rather an Early Barremian *Emericiceras* unrelated to the Hemihoplitidae. According to COMPANY *et al.* (2008, p. 19) "*Barrancyloceras*" *maghrebiense* (*non* IMMEL, 1978 – here renamed into *Gassendiceras essaouirae* sp. nov., see point 6) could be an ancestral endemic Moroccan representative of the Hemihoplitidae (Agadir-Essaouira Basin). It characterizes a horizon at the top of the Moutonianum Zone (end of the Early Barremian).

Note about the name of *T. vandenheckei*. As previously explained by BERT *et al.* (2013), the original spelling (ASTIER, 1851) of this species is Vanden-Heckii. According to the I.C.Z.N article 32.5.2.3, this name has to be corrected into *vandenheckii*. But this species was dedicated to the Abbot VANDEN-HECKE (ASTIER, 1851, p. 452), so the name of the species should be *vandenheckei*. The terminal *-ii* is incorrect and corresponds probably to an inadvertent error (*lapsus calami*). The name therefore has to be corrected to *vandenheckei* wherever it appears (I.C.Z.N article 32.5.1).

2.2. A new hypothesis

Following SPATH (1924, p. 82-83) it is possible to point out the very strong morphological affinities between Tethyan taxa currently classified in the genus *Gassendiceras* and the Boreal *Paracrioceras* of the *stadtlaenderi* (MÜLLER, 1892) / *elegans* (von KOENEN, 1902) group, be-

cause they share many features. Both genera

have in particular the trituberculate main ribs

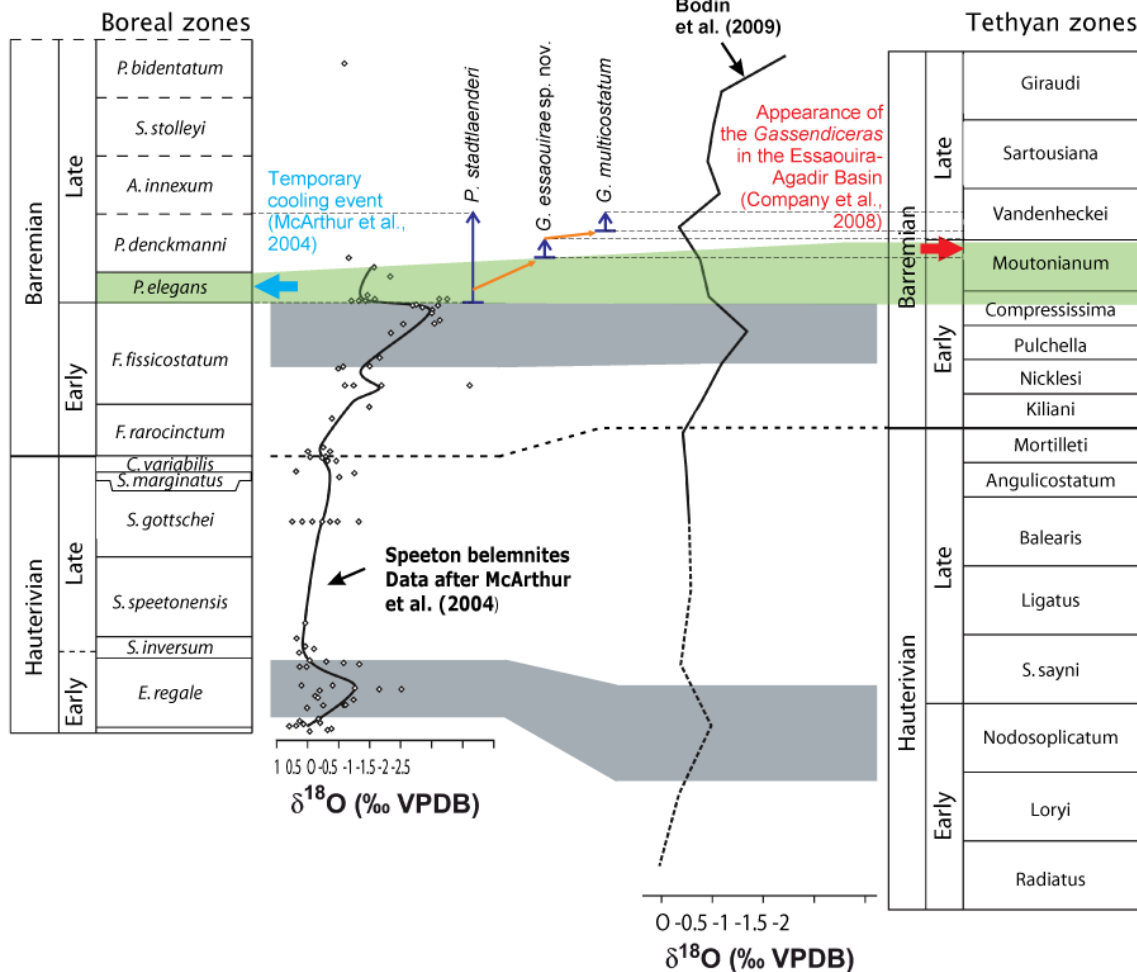


Figure 2: Comparison of Hauterivian-Barremian Boreal and Thethyan zonations after the data of BODIN *et al.*, 2009, and MCARTHUR *et al.*, 2004 (redrawn from Fig. 6 in BODIN *et al.*, 2009, modified), with long-term trends in belemnite oxygen isotope records from the Vocontian Trough (Tethyan Realm, France) and the Speeton area (Boreal Realm, England). The two major negative shifts (*i.e.*, warmer temperatures) of the Early Hauterivian and Early Barremian are highlighted by grey shading bands. The datum of both stratigraphic scales is the base of the Boreal Elegans Zone, and the green area highlights its correspondence with the Tethyan stratigraphic scale (BERT *et al.*, 2008). The blue arrow is the abrupt and temporary temperature decrease at about the time of onset of volcanism on the Ontong Java Plateau described by MCARTHUR *et al.* (2004); the red arrow marks the onset of *Gassendiceras* in the Essaouira-Agadir Basin (Morocco) with *G. essaouirae* sp. nov. The stratigraphic positions of *Paracrioceras stadtlaenderi* (Boreal Realm, see KAKABADZE & HOEDEMAEKER, 2010), *G. essaouirae* sp. nov. (Essaouira-Agadir Basin, see COMPANY *et al.*, 2008) and *G. multicostatum* (Tethyan Realm, see BERT *et al.*, 2013) are also shown; the orange arrows propose the migratory hypotheses, first from the Boreal Realm to the Essaouira-Agadir Basin, and secondly from the latter to the Tethyan Realm (see text).

(ventrolateral, lateral and umbilical tubercles) separated by one to two, rarely three or more, markedly thinner intermediate ribs between every two main ribs (= the Barremense stage). The ventrolateral spines are stronger than the lateral and umbilical tubercles. Looped ribs between the lateral and umbilical tubercles may also occur in both genera (KAKABADZE & HOEDEMAEKER, 2010; BERT *et al.*, 2013). The intermediate ribs bear weak ventrolateral and sometimes lateral tubercles in some species of *Paracrioceras* as they do in *Gassendiceras*.

The *Paracrioceras* of the *stadtlaenderi* / *elegans* group are usually known in the Boreal Denckmani Zone (which is placed in the Late Barremian and probably correlates with the

Tethyan Vandenheckei and Sartousiana zones – see RAWSON, 1983, p. 494, tab. 1; RAWSON, 1995, Fig. 2; OGG & HINNOV, 2012). In fact, they are present from the boundary between the Elegans and the Fissicostatum zones (see KAKABADZE & HOEDEMAEKER, 2010, p. 37 and 40). The limit between these latter zones is usually considered to correspond roughly to the Early - Late Barremian boundary (MUTTERLOSE & BÖCKEL, 1998; MUTTERLOSE & BORNEMANN, 2000). However, according to a more recent study, the early Elegans Boreal Zone instead corresponds to the transition between the Compressissima / Moutonianum Tethyan zones in the Early Barremian (BODIN *et al.*, 2009, p. 1260, Fig. 6 – here Fig. 2). Thus, it is reasonable to expect that the

first *Paracrioceras* of the *stadtlaenderi* / *elegans* group arose in the equivalent of the Moutonian Tethyan Zone.

Therefore, the genera *Paracrioceras* and *Gassendiceras* have a stratigraphic distribution that is highly consistent with ancestor-descendant relationship.

3. Methods

Cladistic analysis is nowadays one of the most popular methods used to infer phylogenetic relationships. Cladistics is however still little used in ammonite studies despite that it is now regarded as an available tool for their evolutionary studies (NEIGE *et al.*, 2007). The stratigraphic data for ammonites are indeed deemed of such high quality that many authors consider these sufficient for the reconstruction of phylogenetic patterns using stratophenetic methods alone (GUÉX, 2006; see ROUGET *et al.*, 2004, and MONNET, 2005, for contradictory discussions). However, in the case of the Hemihoplitidae the stratophenetic analysis failed to find their origin for which there are five competing hypotheses (see point 2). Therefore, these hypotheses were tested with cladistics (parsimony analysis) in order to take into account solely the relations of similarity among the taxa, and so to reject the hypotheses receiving the least support and to discuss the best supported.

3.1. Taxa and characters analysed

We built a taxon-character matrix (Appendix) with 11 taxa selected from the previous hypotheses. *Gassendiceras multicostatum* (SARKAR, 1955) is currently the oldest known *Gassendiceras* species from the north Tethyan Margin, so we chose it to represent the Hemihoplitidae. The genus *Pseudothurmannia* SPATH, 1923 (Crioceratitidae), to which was added the related genus *Sornayites* WIEDMANN, 1962, with robust ornamentation, represents the first hypothesis about the Hemihoplitidae origin: the one of WIEDMANN. The second hypothesis, the DELANOY's, is represented by the genera *Emericiceras* and *Toxancyloceras*. The genus *Honnoratia* was added to test the third hypothesis of VERMEULEN. *Gassendiceras essaouirae* sp. nov. corresponds to "*Barrancyloceras*" *maghrebiense* in sense of COMPANY *et al.* (non IMMEL – see point 6). Both the Boreal taxa *Paracrioceras stadtlaenderi* (MÜLLER, 1892) and *Fissicostaticeras* KAKABADZE & HOEDEMAEKER, 2010, represent the last hypothesis (this work). The genus *Moutoniceras* SARKAR, 1955, was added because it is one of the rare Tethyan heteromorphic ammonites with suture line of ancyloceratid type at the end of the Early Barremian, and therefore it could not be neglected.

Nineteen discrete characters were selected (see Appendix) after having excluded the uninformative characters (autapomorphies and

symplesiomorphies). We have taken into account the morpho-dimensional parameters of the shell (characters 0-4 and 17-18): the adult size from small to very large, the general shape of the shell with the coiling modalities (evolute normally coiled, cryptoconic, or tripartite), the growth in height whorl, and the width of the whorl section. The ontogenesis concerns characters 5-6 and 16 with the presence / absence of certain ontogenetic stages recognised classically within the oldest Hemihoplitidae (*Gassendiceras*): the Heberti, Barremense and Simplified ornamentation stages. The Heberti stage has simple thin ribs slightly differentiated and regularly trituberculate with a sub-octagonal whorl section. The Barremense stage has strongly trituberculate main ribs, intermediary ribs, and smooth thin interribs alternately. The Simplified ornamentation stage has mostly simple ribs with reduced tubercles (see BERT *et al.*, 2013, for an extensive description of these stages). Special attention was finally given to the ornamental structures (characters 7-15): the shape and position of the spines, tubercles and ribs. When the state of a character is unknown it has been coded by [?]. The characters subject to variation (*i.e.*, the multistate/polymorphic characters) for a given taxon were coded as such in square brackets with their different states.

3.2. Outgroup taxon

Polarization is necessary in cladistics to distinguish derived (apomorphic) from primitive (plesiomorphic) state of a character, so to resolve polarization of the cladogram an outgroup comparison was performed. Only one outgroup taxon has been selected for the analysis because testing the monophyly of all the taxa selected here is not the purpose of the present work. We only want to test the hypotheses of the origin of one single group (the Hemihoplitidae) and not to resolve phylogeny of the whole tested taxa. The outgroup taxon we chose is the "primitive" Ancyloceratina *Crioceratites nolani* (KILIAN, 1919), which is a large sized cryptoconic species. This taxon has also the advantage to be undoubtedly older than all the other taxa tested because it appeared in the Early Hauterivian.

3.3. Discussion about the relevancy of the matrix

3.3.1. Discretization of continuous characters

Some of the selected characters (characters 0, 2, 3 and 4, see Appendix) are objectively continuous but could not be encoded as such (see GOLOBOFF *et al.*, 2008; BERT & BERSAC, 2013) because of the lack of revision of the majority of the studied groups, which limits the numbers of reliable measurements to extract

the phylogenetic information. In the current state of knowledge, we considered that estimation is less reliable than a discretized value, so we performed discretization using the classical method: the difference between the maximum and minimum observed or estimated values was divided by the number of states for the characters 0, 2 and 3. For the character 4 (coiling hiatus), this range was divided by 2, because the "first" character-state corresponds to a value of 0.

3.3.2. Treatment of polymorphic characters

The matrix contains eight characters (42%) with a polymorphic state (see Appendix). They represent 8.3% of the total phylogenetic information and 8.2% of the total data (the four unknown states represent 1.8% of the total data). Multistate characters coded as such are problematic because they introduce "extra" homoplasy in providing soft reversals (according to KORNET & TURNER, 1999, p. 366, "[a soft reversal takes place when an unfixed evolutionary novelty disappears from a polymorphic lineage](#)", see KORNET & TURNER, 1999, for explanations) and thus, they should be avoided as much as possible. Therefore, the polymorphic characters were treated here according to the method proposed by KORNET and TURNER (1999), which gives the most congruent results. When possible, the polymorphic characters were coded according to their ancestral state (Inferring Ancestral State, or IAS method). In case of impossibility to discriminate the ancestral state from the derived state, the polymorphic characters were coded as such ("[ambiguous coding](#)" of KORNET & TURNER, 1999, p. 370). In fact, most of the polymorphism (94.7%) is because we used seven taxa of generic rank (= 63.6% of the taxa – Appendix): coding the characters of supraspecific taxa consists of adding the different character states of their species, which increases the probability of polymorphic characters (KRON & JUDD, 1990; NIXON & DAVIS, 1991; PRENDINI, 2001). The accuracy of the numerous methods available to treat polymorphic characters of supraspecific taxa in cladistics has long been debated (see PRENDINI, 2001, and SIMMONS & GLEISER, 2002, for a discussion). From one method to another, the supraspecific taxa could be replaced in the matrix by one species or specimen (*exemplar method*), or the polymorphic characters could be coded separately according to one state only (the ancestral state or the most frequent state). The separate coding of polymorphic characters (*e.g.*, IAS / ancestral / compartmentalization, democratic methods, see KORNET & TURNER, 1999; PRENDINI, 2001, for a short description) can bias the results of the cladistic analysis because it presents the risk in providing a chimeric taxon (see PRENDINI, 2001). Such a chimeric taxon, with all its polymorphic characters "forced" to their ancestral state (*i.e.*, a hypothetical ancestor), is

problematic if it belongs to the ingroup of the study (BRYANT, 1997). In the present paper, we chose to treat the supraspecific taxa according to the exemplar method as described by PRENDINI (2001 – one or more of its representative species replaced each generic taxon of the matrix). Selecting a representative species usually consists in choosing the most common or the supposed earliest / ancestral species (BININDA-EMONDS *et al.*, 1998; PRENDINI, 2001). However, in the present study this method is problematic because the relative abundance and the evolutionary patterns of the treated taxa are not precisely known (non-revised taxa most of the time, cf. *supra*), and because their monophyly has never been tested. In other words, the risk here is to select an inappropriate species, which does not belong to the genus it is supposed to represent. For this study, only one species per genus was selected to not overload the cladogram: the type species in order to ensure that it belongs for sure to its genus. So the seven taxa at the generic level of the matrix were replaced (see point 3.1) by *Pseudothurmannia picteti* SARKAR, 1955, *Sornayites paronai* (SARKAR, 1955), *Emericeras emerici* (LÉVEILLÉ, 1837), *Toxancyloceras vandenheckei* (ASTIER, 1851), *Honnoratia honnoratiana* (d'ORBIGNY, 1842), *Fissicostaticeras fissicostatum* (ROEMER, 1841), and *Moutoniceras moutonianum* (d'ORBIGNY, 1850) respectively. After replacing each generic taxon by its type species, then applying as far as possible the IAS method for polymorphisms (or ambiguous method if not possible), only two characters (10.5%) remain polymorphic for seven taxa: characters 3 and 12 (Appendix). As a result of using this method, the proportion of polymorphisms *versus* the total phylogenetic information in the matrix decreases from 8.3% to 3.9%. We chose not to follow the recommendation of PRENDINI (2001) to represent supraspecific (here genera) taxa by several species (including the type species) in order to take into account their phenotypic diversity and eventually to test their monophyly. In the present study, as pointed above, the "non-type" species may not belong to their genus for sure. Therefore, including such species in the cladistic analysis would potentially add useless information, because the goal of the present paper is not to test the monophyly of the generic selected taxa.

3.4. Analysis method

The analysis was performed with the TNT software (*Tree analysing using New Technology*), version 1.1 for Windows (GOLOBOFF *et al.*, 2008) using the "[branch-and-bound](#)" method *via* the *Implicit Enumeration* option (collapsing rule used is maximum length = 0) that allows finding for sure the most parsimonious trees. The characters were considered unordered and unweighted in order to avoid the inference of pre-analytical assumptions. The Consistency Index (KLUGE & FARRIS, 1969), the

Retention Index (FARRIS, 1989) and the Adjusted Homoplasy (GOLOBOFF *et al.*, 2008) quantified homoplasy. In case of multiple most parsimonious trees, a strict consensus cladogram was computed in order to analyse consistency between the trees. Then the eventual ambiguous apomorphies were performed by ACCTRAN optimization (accelerated transformation – FARRIS 1970; SWOFFORD & MADDISON, 1987, 1992), which favours reversals over convergences.

A resampling technique using bootstrap method (*standard bootstrap* of TNT with 1000 replications, using implicit enumeration, collapsing groups below 1%, result given in absolute frequency, see GOLOBOFF *et al.*, 2008) and a decay analysis (BREMER, 1994, *Absolute BREMER Support* in TNT, support calculation with Tree Bisection and Reconnection from existing trees, retained suboptimal trees by 20 steps and null relative fit difference, see GOLOBOFF *et al.*, 2008) were performed with TNT in order to assess the confidence of the nodes and to test the robustness of the tree topology. The bootstrap indicates the stability of the most parsimonious clades under random weighting of characters. So the more this value is high means the more times a given branch occurs in the consensus bootstrap trees, and the more robust this clade is assumed to be. The BREMER support indicates the robustness of a clade by calculating the number of extra steps needed to collapse this clade.

4. Results

4.1. The most parsimonious trees

The analysis results in 5 most parsimonious trees (Fig. 3) of 40 steps each, which reveal the presence of homoplasies (Consistency Index = 0.675; Retention Index = 0.75; Adjusted Homoplasy = 2.95 to 3.05). These five trees have some important topologic similarities since some taxa are systematically paired as sister taxa. This is the case for *Toxancyloceras vandenheckei* and *Moutoniceras moutonianum*, *Sornayites paronai* and *Pseudothurmannia picteti*, *Emericiceras emerici* and *Honnoratia thiollierei* and the two species of *Gassendiceras*. The other most important similarity between the trees is the clade with *Paracrioceras*, *Fissicostaticeras* and the two species of *Gassendiceras*, which is systematically present in the same structure.

4.2. The strict consensus tree

The structure of the strict consensus tree is given in Figure 4. Most of the nodes receive bootstrap value around or greater than 70% and a significant BREMER support value (from 1 to 2 – Fig. 4), which values are overall coherent between each other. The node with bootstrap value lesser than this threshold (node 17) is not

uninteresting but it has to be considered more carefully. Nevertheless, a BREMER value of 1 can be used to assess and reinforce the interest of this node.

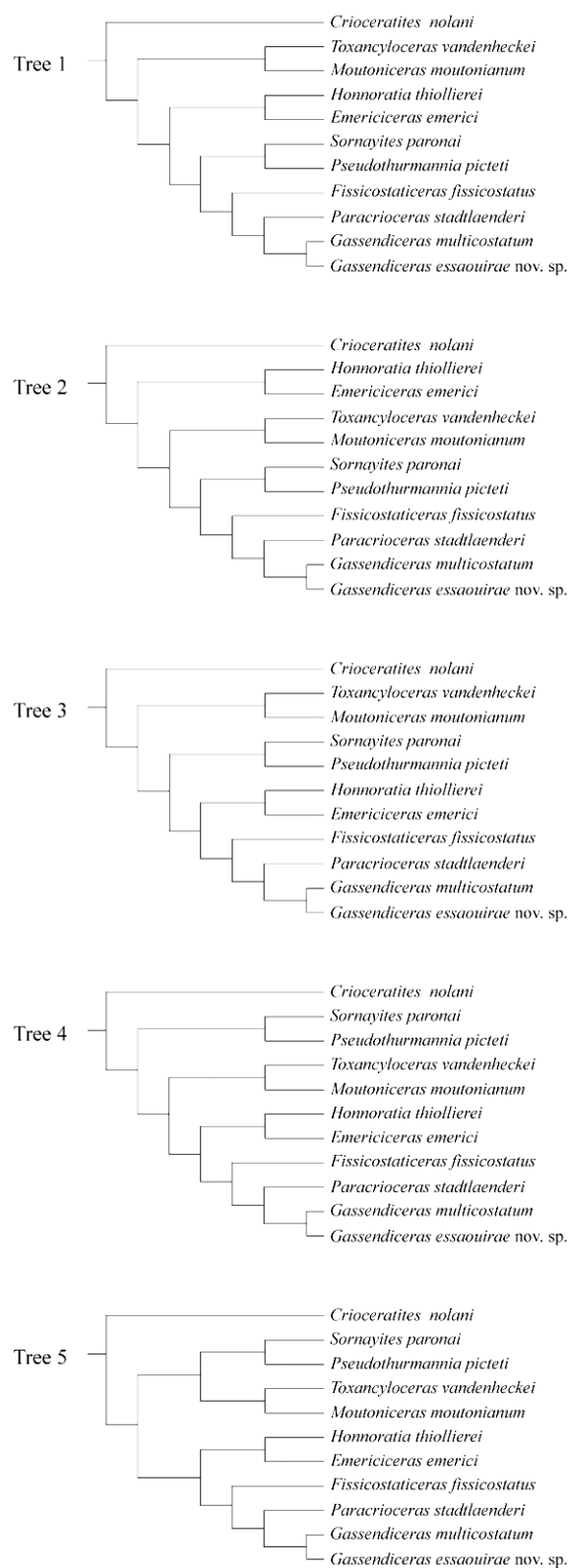


Fig. 3: The five most parsimonious trees obtained at first run with TNT.

The consensus tree shows four major clades well separated within the ingroup from a clearly unresolved node (node 13 – Fig. 4), which contains no synapomorphy in our study. This result is quite logical due to the spread choice of the taxa belonging to different families. The four clades are as follow: the one consisting of the Emericiceratidae (*Emericiceras emerici* and *Honnoratia thiollierei*); the one consisting of the Crioceratitidae (*Pseudothurmannia picteti* and *Sornayites paronai*); the pair *Moutoniceras* and *Toxancyloceras*; and the clade consisting of *Paracrioceras* / *Fissicostaticeras* and *Gassendiceras*. This latter clade has a pectined structure (each node gives birth to a single taxon and a clade), with the respective apparition going upward although the cladogram of *Fissicostaticeras fissicostatus*, *Paracrioceras stadlaenderi* and the two species of *Gassendiceras*. This latter clade is the most robust of the tree (Fig. 4).

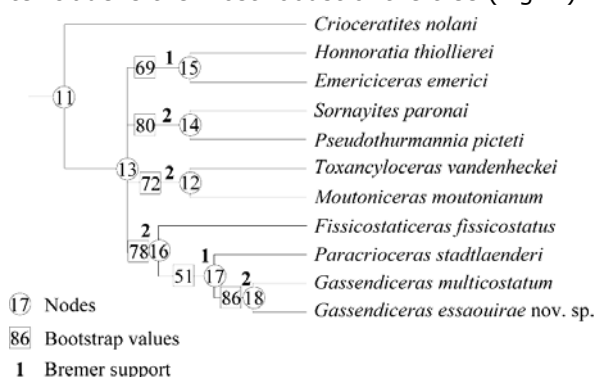


Fig. 4: Strict consensus tree computed with statistics (Bootstrap values and BREMER support) (Consistency Index CI = 0.643; Retention Index RI = 0.712; Adjusted homoplasy Aj = 3.45).

5. Discussion

It is possible to discuss the hypotheses exposed above (point 2) in light of the cladogram obtained.

1- Crioceratitidae as stem-group (the WIEDMANN hypothesis): the adult size, the evolute coiling and the shape of the dorsum are the synapomorphic characters supporting the clade of *Pseudothurmannia* / *Sornayites* (node 14 – Fig. 5). The other characters are all homoplastic. It appears in fact that the hypothesis of the Crioceratitidae as stem of the Hemihoplitidae is the result of a typological conception of both the Late Hauterivian Crioceratitidae and the Barremian Hemihoplitidae based on morphological convergences (homoplasies) without any phyletic link between these groups. The hypothesis of such a link is anyway hampered by the very large stratigraphic gap between the last *Pseudothurmannia* (latest Hauterivian) and the first Hemihoplitidae (Late Barremian).

2- *Honnoratia thiollierei* as stem-group (the VERMEULEN hypothesis): *Honnoratia thiollierei* appears to be a sister taxon of *Emericiceras emerici* and they are both grouped into the Emericiceratidae. The coiling of the shell (node

15) and the presence of fibulate ribs are the synapomorphic characters supporting this clade. The very large adult size is homoplastic (see Fig. 5). There are five convergent characters (homoplasies) between the *Honnoratia* and the clade of the two species of *Gassendiceras* (characters 4, 9, 11, 14, 17 – see Appendix). Therefore, the hypothesis of an origin of the Hemihoplitidae within the *Honnoratia* is problematic in terms of morphology (shape of the shell and ornamentation). It is also problematic considering the stratigraphic gap of nearly two ammonite zones (Compressissima and Moutonianum zones) between the last *Honnoratia* (Early Barremian) and first *Gassendiceras* (early Late Barremian or extremely late Early Barremian according to COMPANY *et al.*, 2008).

3- *Emericiceras emerici* and *Toxancyloceras vandenheckei* as stem-group (the DELANOY hypothesis): the link DELANOY had evoked between the *Emericiceras* and *Toxancyloceras* is not recognised from the cladistic analysis, as the "group" forming these two genera is clearly polyphyletic and thus unacceptable. *Emericiceras emerici* is the sister taxon of *Honnoratia thiollierei* (both Early Barremian Emericiceratidae) as seen above, and they have relationship with neither the Hemihoplitidae nor the *Toxancyloceras* (Ancyloceratidae). Moreover, this latter genus appears to be sister taxon of *Moutoniceras*. The synapomorphic character of the clade supported by *Toxancyloceras* and *Moutoniceras* is the strict ancyloceratic coiling (Fig. 5). The coil of some robust *Toxancyloceras* of the *T. vandenheckei* group may resemble some *Gassendiceras* to a strictly ornamental point of view, especially when they have many inermous (smooth without any tubercles) interribs. *Toxancyloceras* and *Gassendiceras* share common characters: their adult size is similar (character 0); the ribs can be reduced on the venter (character 8), are wedge shaped (character 13), and they often bear robust tubercles (character 15). The flanks are rounded in the same way (character 17). These similarities are however convergences (homoplasies) with no phyletic link, and in *Toxancyloceras* the uncoiling is more pronounced with a higher spiral gap (characters 1 and 4), growth in height whorls is lower (character 2), and the smooth interribs are still more numerous (character 10). The shaft of *Toxancyloceras* is also more slender, straight and longer in proportion than in the few tripartite species belonging to the genus *Gassendiceras* (see BERT *et al.*, 2013). The hook is longer, rounded and less tuberculate near the ventral marginal area in *Toxancyloceras*. The possibility of an origin of the *Gassendiceras* within the *Moutoniceras* is utterly inconceivable because of their strongly divergent morphology, and such a hypothesis would not be supported by the present cladistic analysis anyway.

4- *Gassendicerias essaouirae* sp. nov. (= "*Barrancyloceras*" *maghrebiense sensu* COMPANY *et al.*, 2008, *non* IMMEL, 1978) as stem-group (the COMPANY *et al.* hypothesis): examination of casts of the Moroccan specimens figured by COMPANY *et al.* (2008, Pl. 8, figs. L, M) allows the consideration of their classification into the genus *Gassendicerias* close to *G. multicostratum*. Their uniqueness merits a new species name (see below the taxonomic implications), thus *G. essaouirae* sp. nov. would now represent the oldest known *Gassendicerias*. *G. essaouirae* sp. nov. is sister taxon of *G. multicostratum* on the cladogram as the most robust clade (bootstrap of 86% consolidated with the significant BREMER support value of 2 – Fig. 4), and this is strongly in favour of the COMPANY *et al.* hypothesis. The synapomorphy that supports this clade is the scarcity of the intercalatory ribs. The presence of the ontogenetic Heberti stage might be a synapomorphy of this clade as well as a synapomorphy of the *Paracrioceras*-*Gassendicerias* clade, due to the unknown state of the character 5 (Fig. 5). The origin of the Tethyan *Gassendicerias* within the Moroccan species is also stratigraphically consistent because *G. essaouirae* sp. nov. is from the latest Early Barremian and *G. multicostratum* (the oldest-known Tethyan Hemihoplitidae) is from the early Late Barremian (see Fig. 2).

5- *Paracrioceras* as stem-group (hypothesis of the present work): in the cladogram, *Paracrioceras* is the sister taxon of the *Gassendicerias* clade. This close relationship between *Paracrioceras* and *Gassendicerias*, and both the correspondence between their appearance on the cladogram (starting from the root) and their stratigraphical distribution (see above point 2.2 and Fig. 2) are consistent with this hypothesis (see BERT & BERSAC, 2013, for a discussion about cladogram and phylogenetic tree). They are supported by some synapomorphies (as for the *Fissicostaticeras* – node 16 – Fig. 5), especially concerning the ontogeny (the presence of the Barremense and the Simplified ornamentation stages, characters 6 and 16). Therefore, the link between these taxa is consolidated, and the origin of the Hemihoplitidae is compatible with the migration event hypothesis developed above (point 2.2).

The cladistic analysis clearly dismisses the first three hypotheses. The two remaining hypotheses are in contrast consolidated. There is no incompatibility between them and they should be regarded as complementary. It is indeed quite possible that the Hemihoplitidae appeared in the Essaouira-Agadir Basin at the end of the Early Barremian (COMPANY *et al.*, 2008), before invading the northern Tethyan margin at the beginning of the Late Barremian. They could be derived from small populations of Boreal *Paracrioceras*, which might have migrated southward episodically.

Palaeogeographically, the Essaouira-Agadir Basin is of intermediate position on the only possible migration route (Fig. 6), while any other communication path between the Boreal and Tethyan realms was closed again in the Barremian (Neocomian Polish Furrow), or not yet opened (Russian Platform, Pyrenean Furrow, Paris Basin, Polish Through – DERCOURT *et al.*, 2000). This Basin has a distinctly Mediterranean character (COMPANY *et al.*, 2008), and the sudden onset of the Hemihoplitidae at the end of the Early Barremian in Morocco is thus strongly consistent with the migratory hypothesis of this group towards the Tethys. The beginning of the transgressive system tract (HARDENBOL *et al.*, 1998) at the end of the Early Barremian / beginning of the Late Barremian *s.l.* also provides an additional argument with the greater ease of communication induced.

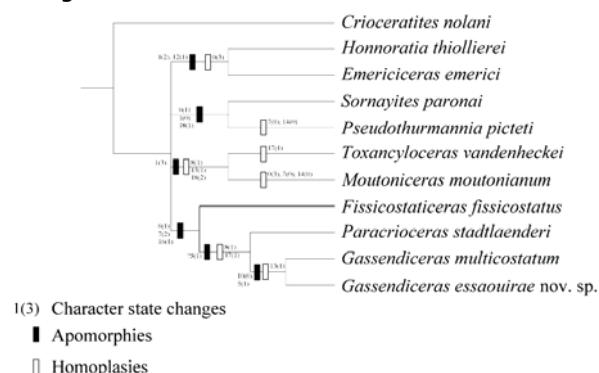


Fig. 5: Strict consensus tree with character state changes labelled (see Appendix for the list of characters).

On the other hand, a communication between the Boreal Realm and the Atlantic for the "Mittelbarrême" was argued by IMMEL and MUTTERLOSE (1978, p. 265). These latter authors also suggested multiple Boreal influences during the Moroccan Cretaceous [based on ROCH's work (1930) who reported several Barremian Boreal ammonite taxa in the Agadir area], although COMPANY *et al.* (2008) did not confirm it for the Barremian.

Note that an East communication path (from the Boreal Ocean North of the Scandinavian Shield and through all the Russian Platform) has been proposed to explain the presence of *Paracrioceras denckmani* in the early Late Barremian of Crimea (KAKABADZE, 1981, Pl. 2, fig. 1, reconsidered as *P. cf. elegans* in KAKABADZE, 1983, p. 506; see also DELANOY & FÉRAUD, 1995, Fig. 4 and p. 211). However this determination is challenged here because KAKABADZE's specimen instead belongs to *Hemihoplites feraudianus* (robust morphology), which is unknown in the Boreal Realm. So, this theory is not supported by data until the dissemination of *Spinocrioceras polyspinosum* KEMPER, 1973, in the Late Barremian (spread out from the late Sartousiana Zone in western Tethys, to the early Giraudi Zone in Crimea, and to the early Bidentatum Zone in the Boreal area – see DELANOY & FÉRAUD, 1995).

Palaeoclimatically, at least three positive $\delta^{18}\text{O}$ excursions are between the end of the Early Barremian and the earliest Late Barremian of the Angles section (the Barremian stratotype in the Tethyan Realm) in a "greenhouse" context (WISSLER *et al.*, 2002; BODIN *et al.*, 2005). Such peaks are usually regarded as significant to a temporary climatic destabilization (cooling). But here most probably, according to the authors (MCARTHUR *et al.*, 2004, p. 265-266), these peaks of high frequency oscillations are probably due to local diagenetic overprint. But in their paper MCARTHUR *et al.* (2004, p. 269, based on $\delta^{18}\text{O}$ and Mg proxy) demonstrated that through the Barremian in the Boreal Realm (Eastern England), temperature increased to a peak of 20°C in the Elegans Zone then, in the same zone, precipitately and temporarily decreased to around 14°C at about the time of onset of volcanism on the Ontong-Java Plateau, before returned to around 16°C. As recently stated by BODIN *et al.* (2009, p. 1260, Fig. 6 – see Fig. 2 and above point 2.2), the early Elegans Boreal Zone corresponds to the transition of the Compressissima / Moutonianum Tethyan zones in the Early Barremian, and thus the Late Moutonianum Zone (where the *Gassendiceras* appear in the Essaouira-Agadir Basin) could be contemporary with this temporary cooling.

Therefore, it might be tempting to hypothesize that migration of small populations of Boreal *Paracrioceras* could occasionally be established under favourable conditions during their expansion into the lower latitudes (REBOULET *et al.*, 1992; REBOULET & ATROPS, 1995; REBOULET, 2007). Such small populations were able to establish themselves locally in the Essaouira-Agadir Basin (Atlantic Realm). The exploitation of new ecological niches (for example those left vacant by the disappearance of the Emericeratidae a long time before in the Pulchella Zone, and maybe used later by the *Moutoniceras*) would then have allowed local adaptation leading to the evolution towards the *Gassendiceras* morphology (allopatry and speciation by founder effect in sense of MAYR, 1974). Then, the newly emerging Hemihoplitidae invaded and diversified through the northern Tethyan margin from this intermediate geographic position at the beginning of the Late Barremian (Fig. 6).

Note also that in the Boreal Realm, during the Denkmanni Zone (Late Barremian), the *Paracrioceras* continue to evolve in northern Europe towards forms close morphologically to the southern *Gassendiceras* [*e.g.*, *P. tuba* (von KOENEN, 1902)], although they lived in different environments. This might suggest the existence of a common gene pool rather than a simple transient morphological convergence.

6. Taxonomic implications

6.1. Classification of the genus *Moutoniceras*

When introduced, the genus *Moutoniceras* was classified in the Heteroceratidae SPATH, 1922 (SARKAR, 1955, p. 24). More recently this attribution was challenged by some authors. Some (*e.g.*, AUTRAN *et al.*, 1986, p. 1060; DELANOY *et al.*, 1991; COMPANY *et al.*, 2008) proposed a classification in the Ancyloceratidae, while others (*e.g.*, KAKABADZE & THIEULOY, 1991) proposed a classification in the Crioceratitinae. WRIGHT *et al.* (1996, p. 216) more or less accepted *Moutoniceras* with doubt in the Ancyloceratidae, but they also suggested that it could be a Crioceratitinae. Finally, VERMEULEN (1997) proposed to reinstate the genus in the Heteroceratidae because of strong morphological convergences. In fact until 2007 and the work of KLEIN *et al.* (2007) there was no robust consensus about the classification of the genus *Moutoniceras*. In the latter work, no less than nine co-authors, specialists of the Barremian (including DELANOY, KAKABADZE and VERMEULEN, but excepting COMPANY according to the footnote No. 130, p. 174), finally considered the genus to be a Heteroceratidae. Nevertheless, the present cladistic analysis shows *Moutoniceras* as a sister taxon of *Toxancyloceras* (strict Ancyloceratidae). A link between both genera is consistent, first stratigraphically and secondly morphologically: in the Vocontian Basin (South-East of France) the genus *Moutoniceras* disappeared with the tuberculate *M. eigenheeri* (VERMEULEN, 2003) at the very end of the Early Barremian, just below the First Apparition Dating (FAD) of the genus *Toxancyloceras* (beginning of the Late Barremian). It seems highly probable that the genus *Toxancyloceras* originated from *Moutoniceras*, mainly by the acquisition of the lower tubercles, and the generalisation of the median tubercles, on main ribs. The direct link between *Toxancyloceras* and *Moutoniceras* involves ranking the genus *Moutoniceras* among the Ancyloceratidae rather than in the Heteroceratidae. The Heteroceratidae are not beyond the scope of the present work, and thus they have not been added in the cladistic analysis, however we can note that the apparition of the primitive Heteroceratidae was much more discreet and belated. Exceptionally rare fragments of possible Heteroceratidae were reported from the lower part of the Sartousiana Zone (VERMEULEN, 1995), but the first true representatives of the genus *Heteroceras* d'ORBIGNY, 1850, are only known with certainty at the end of the Feraudian Subzone (Autrani Horizon – see DELANOY, 1994; BERT *et al.*, 2008) with *Heteroceras coulleti* DELANOY, 1994. This stratigraphic position makes a gap of more than one and half ammonite zones between the last *Moutoniceras* and the first known *Heteroceras* s.s. (*i.e.*, with a known helical part).

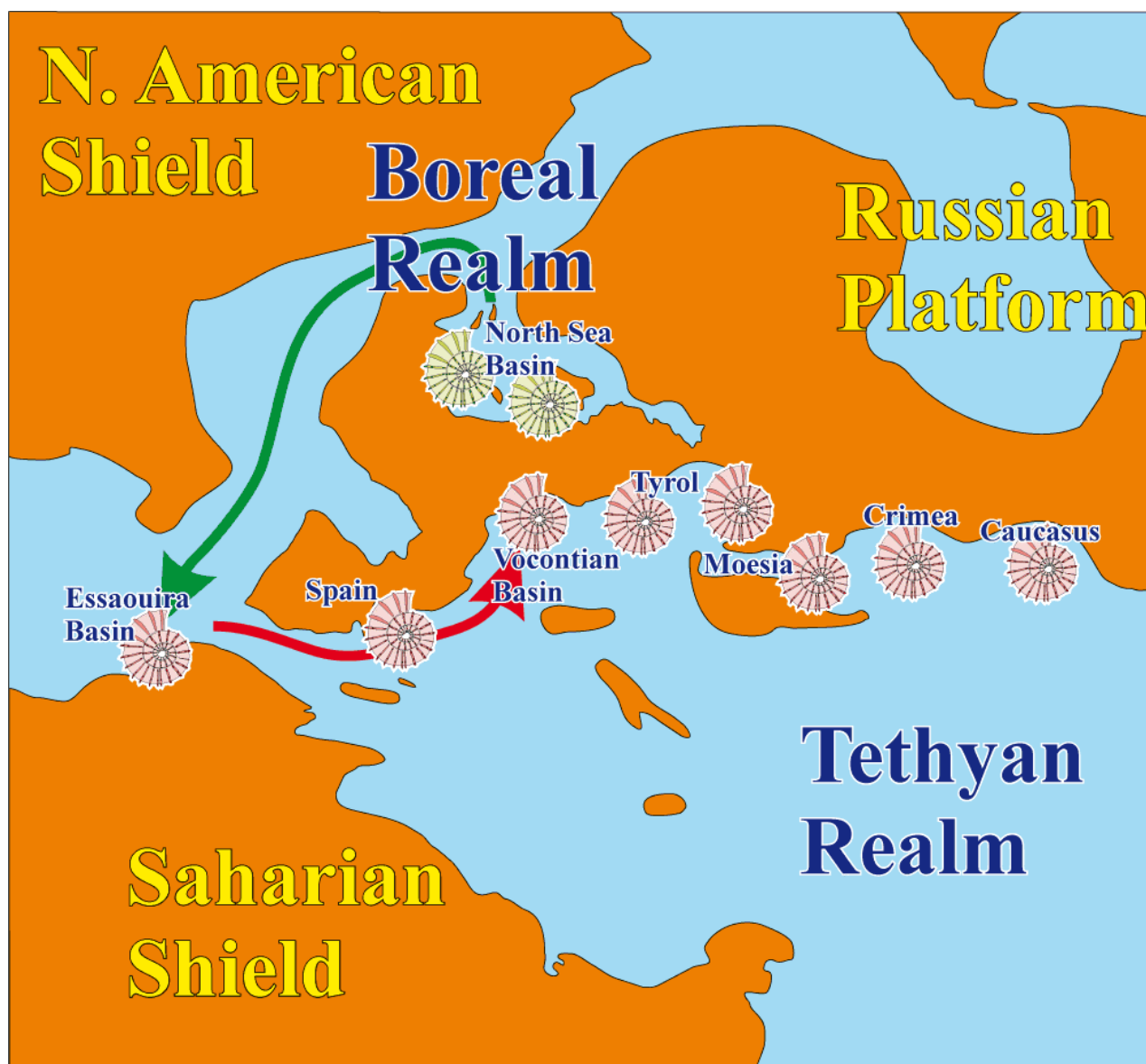


Fig. 6: Palaeogeographic map of the Barremian (reconstructed from BARRON *et al.*, 1981, and DERCOURT *et al.*, 2000) with extension of the Tethyan *Gassendiceras* and the Boreal Paracrioceratidae fam. nov.

6.2. The Moroccan *Gassendiceras*

According to the present analysis, it is necessary to recognise under a new name the "*Barrancyloceras*" *maghrebiense* sensu COMPANY *et al.*, 2008, non IMMEL, 1978, which ranks near the Tethyan *Gassendiceras*. We propose the name *Gassendiceras essaouirae* sp. nov.

Family Hemihoplitidae SPATH, 1924

Subfamily Gassendiceratinae BERT *et al.*, 2006

Genus *Gassendiceras* BERT *et al.*, 2006

***Gassendiceras essaouirae* sp. nov.**

Synonymy

- non 1978. *Crioceratites* (C.) *maghrebiensis* nov. sp.: IMMEL, p. 59, tab. 10b, Pl. 8, fig. 1.
- ✓ 2008. "*Barrancyloceras*" *maghrebiense* (IMMEL, 1978): COMPANY *et al.*, Fig. 8L-M.

Derivation of the name. Because of its origin (from Essaouira).

Holotype. The specimen No. X.OG.R.23 from Tafadna (Morocco), housed in the palaeontological collections of the University of Granada (Spain). Specimen figured by COMPANY *et al.* (2008, Fig. 8M).

Paratype. The specimen No. X.MS.R.9 from Imsouane (Morocco), housed in the palaeontological collections of the University of Granada. Specimen figured by COMPANY *et al.* (2008, Fig. 8L).

Type locality. The Tafadna section (coordinates 31°05'46"N 9°48'22"W), 16 km NW of Tamanar; outcrop on the right bank of the Oued Igouzouln, some 2 km before it joins the Atlantic Ocean on Tafadna beach, Essaouira Basin, Morocco (COMPANY *et al.*, 2008).

Bed type. The bed of the specimen chosen here as holotype was not indicated by COMPANY

et al. (2008), but the species is present in beds 57-58 of the Imsouane section where the para-type specimen comes from (COMPANY *et al.*, 2008, Fig. 3).

Geographic distribution. *Gassendiceras essaouirae* sp. nov. is actually only known in the Essaouira-Agadir Basin (Morocco), Atlantic Realm.

Stratigraphic distribution. Uppermost Lower Barremian strata dated from the end of the Moutonianum Zone. Following COMPANY *et al.* (2008) this species characterizes the Moroccan "Maghrebiense Horizon", here renamed as the Essaouirae Horizon.

Diagnosis. Only the inner whorls are known up to $D = 80$ mm (the first whorls are unknown). Massive shell with tight crioconic coiling; whorl section very broad and rounded of sub-octagonal shape at ornamentation. Only one ornamental stage, very close to the Heberti stage, is known: ribs slightly differentiated, trituberculate, radial or slightly retroverted, and sometimes wedge shaped. Tubercles small, conical and well defined. They are located at the lower and upper thirds of the flanks, and at the peri-ventral border.

Note. The authors of the present work could observe the presence of the Barremense and Simplified ornamental stages (and of the Heberti stage in the innermost whorls of the shell) on complete and unrestored Moroccan specimens of *G. essaouirae* sp. nov. and thus coded the matrix of the cladistic analysis accordingly (see Appendix). It is to note that these specimens cannot be figured for ethical reasons because they were extracted for commercial use and because their trace has been lost since (pictures of one of them can be sent on demand).

Differential diagnosis. The adult developments of *Gassendiceras essaouirae* sp. nov. are not known on the basis of the type material (COMPANY *et al.*, 2008), but this species is unique and different from all the other *Gassendiceras* described. Even if the innermost whorls are unknown, the Heberti stage looks to have a significantly longer duration, at least until $D = 80$ mm. This falls perfectly within the evolutionary trends of the Tethyan *Gassendiceras* defined by BERT and BERSAC (2013). The shell has also a stronger general appearance with larger ribs but smaller tubercles.

"*C. (C.) maghrebiensis* IMMEL, 1978, differs from *G. essaouirae* sp. nov. by the presence of many smooth interribs between the main ribs. The former bears only small tubercles, which are better defined in the latter. In addition, IMMEL's species shows the ribs projected forward on the uppermost part of the flanks, while in *G. essaouirae* sp. nov. the ribs are radial (stronger and more spaced), even on the ventral area.

Stratigraphically and geographically *G. essaouirae* sp. nov. is very unique because it is yet

known only in Morocco, and only at the extreme end of the Early Barremian (see COMPANY *et al.*, 2008).

6.3. The case of Fissicostaticeras / Paracrioceras

If we consider only the Boreal Realm, the genera *Fissicostaticeras* and *Paracrioceras* (and also *Parancyloceras* SPATH, 1924, not added in the present cladistic analysis – see KAKABADZE & HOEDEMAEKER, 2010) are a monophyletic clade, which requires them to be placed into a separate family. However, the present cladistic analysis resulted in the recognition of a possible phyletic link between the Boreal *Fissicostaticeras* / *Paracrioceras* and the Atlantic / Tethyan *Gassendiceras* (Figs. 4 - 5), which makes *de facto* the former a paraphyletic clade. As explained by BERT and BERSAC (2013) for the genus *Gassendiceras* itself, the rise of a new group (here *Gassendiceras*) would not affect the older group (here the phylum *Fissicostaticeras* / *Paracrioceras*). This reflects the reality of coexistence (even in different geographic areas) of different lineages (HÖRANDL, 2007), because of evolutionary processes where descendants exist without concomitant extinction of the parental group. Such processes rendering the parental group paraphyletic (any group of descendants automatically cancels out the monophyly of the ancestral group; see HÖRANDL, 2006). As HÖRANDL and STUESSY (2010) recognised, cladogenesis is the main source of paraphyly and paraphyly is a normal stage in the evolutionary process whereby a new species arises.

Considering that paraphyletic groups are acceptable as taxa in evolutionary classifications, the proposition of allopatric origin of the Tethyan Hemihoplitidae from the Boreal *Paracrioceras* via the Essaouira-Agadir Basin requires separating taxonomically the Boreal lineage *Fissicostaticeras* / *Paracrioceras* / *Parancyloceras* from the Emericiceratidae in which they are currently classified (cf. KLEIN *et al.*, 2007). Therefore, we propose to introduce a new family: the Paracrioceratidae fam. nov.

Superfamily Ancyloceratoidea GILL, 1871

Family Paracrioceratidae fam. nov.

Type genus. *Paracrioceras* SPATH, 1924.

Generic content. This family includes the Boreal genera *Paracrioceras*, *Fissicostaticeras* and *Parancyloceras* in order to recognise their phylogenetic relationships. A Boreal phyletic lineage *Fissicostaticeras* -> *Paracrioceras* -> *Parancyloceras* may be considered taking into account the similarity between these genera, as well as stratigraphic and paleogeographic arguments (KAKABADZE & HOEDEMAEKER, 2010).

Phyletic position. The Paracrioceratidae fam. nov. appear from crioconic forms classified

in the genus *Emericeras* [*sic*] by KAKABADZE and HOEDEMAEKER (2010) but probably closer to the Crioceratitidae *sensu lato*. The Paracrioceratidae fam. nov. seem to be at the origin of the Tethyan Hemihoplitidae (Gassendiceratinae) by allopatry and founder effect.

Remarks. It should be noted that KAKABADZE and HOEDEMAEKER (2010) used the genus *Acrioceras* HYATT, 1900, in a different way than French authors. Some specimens they figured [*e.g.*, "*Acrioceras*" of the *nodulosum* (von KOENEN, 1902) group] could possibly correspond to microconchs of the contemporary Paracrioceratidae fam. nov. (same ornamental evolution over time). This hypothesis was suggested by RAWSON (1975, p. 282) about the small tripartite genus *Hoplocrioceras* SPATH, 1924, which could correspond possibly to the microconch of *Fissicostaticeras* (= *Paracrioceras* for RAWSON). These small tripartite forms would then have to be included in the Paracrioceratidae fam. nov. if this dimorphism was demonstrated. Such a dimorphism had been comparatively successfully advanced for the Crioceratitidae by DELANOY *et al.* (1995), and ROPOLLO and GONNET (1995), and for some Hemihoplitidae (DELANOY *et al.*, 1995; BERT *et al.*, 2009; BERT, 2012, 2013).

7. Conclusions

The marine Late Barremian ammonite family Hemihoplitidae (Ancyloceratoidea) is diversified in most of the northern Tethyan Margin and the Essaouira-Agadir Basin (Morocco). However, their origin remained hardly known because several competing hypotheses have been developed in literature until recently. Most of the literature hypotheses were rejected by cladistics (Crioceratitidae, Emericiceratidae and *Toxancyloceras* as stem-group) and our analysis shows that they were in fact the result of typological conceptions. *Gassendiceras essaouirae* sp. nov. appears now to be the best candidate as an ancestral endemic Moroccan representative of the Hemihoplitidae at the end of the Moutonian Zone (end of the Early Barremian). Cladistics also supports an origination of the Hemihoplitidae (incl. *G. essaouirae* sp. nov.) from the Boreal Paracrioceratidae fam. nov. (migration hypothesis). *Paracrioceras* of the *stadlaenderi* group have indeed very strong morphological affinities with the Tethyan *Gassendiceras*. Stratigraphically, the former is known beginning at the boundary of the Fissicostatus / Elegans Boreal zones (late Early Barremian). Because it is recognised that the Elegans Zone corresponds roughly to the Moutonian Tethyan Zone, this distribution is strongly concordant for relationships of ancestor-descendant type between both these two groups.

According to our hypothesis, the Hemihoplitidae first appeared suddenly in the Essaouira-Agadir Basin at the end of the Early Barremian, before invading the northern Tethyan margin at

the beginning of the Late Barremian. They may have been derived from small populations of Boreal *Paracrioceras*, which could have migrated southward episodically. Such a migration of the *Paracrioceras* would have been enabled by the establishment of favourable climatic conditions during their expansion towards the lower latitudes (an abrupt and temporary temperature drop in the middle part of the Elegans Zone). This is supported paleogeographically because the Essaouira-Agadir Basin is of intermediate position on the only possible migration route, the Atlantic one (Fig. 6), in times of transgressive shorelines that probably induced a greater ease of communication. The exploitation of new ecological niches (for example those left vacant by the disappearance of the Emericiceratidae) would then have allowed local adaptation leading to the evolution towards the *Gassendiceras* morphology (Hemihoplitidae), which invaded and diversified through the northern Tethyan margin. Therefore, the origin of the Hemihoplitidae looks to be a case of allopatry and speciation by founder effect.

Migration from the Boreal Ocean towards the Essaouira-Agadir Basin is supported morphologically by cladistics and by other arguments, but of course, it remains a hypothesis that needs to be tested more thoroughly, especially because there is no evidence currently of other faunistic Boreal influence in Morocco during the early Late Barremian. Maybe in the future a better competitor than the Paracrioceratidae nov. fam. could be found to explain the origin of the Hemihoplitidae? Meanwhile, it remains the best candidate.

Acknowledgements

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Appendix

List of characters

00. Adult size: (0) little; (1) median; (2) large; (3) very large.
01. Coiling shape: (0) evolute normally coiled; (1) cryptoconic uncoiled; (2) tripartite tight; (3) tripartite strict.
02. Height whorl growth: (0) low; (1) moderate; (2) high.
03. Whorl section shape: (0) thick; (1) compressed.
04. Coiling hiatus: (0) almost joined whorls; (1) weak; (2) large.
05. Heberti stage: (0) absent; (1) present.
06. Barremense stage: (0) absent; (1) present.
07. Spines: (0) absent; (1) long and thin; (2) short and massive.
08. Shape of the main ribs on the venter: (0) not or mainly not altered; (1) attenuated.
09. Looped ribs: (0) absent; (1) present.
10. Smooth interribs: (0) rare; (1) frequent.
11. Bifurcated or polyfurcated ribs: (0) absent or scarce; (1) present.
12. Fibulate ribs: (0) absent; (1) present.
13. Wedge-shaped ribs: (0) absent; (1) present.
14. Position of lateral tubercles: (0) absent; (1) upper third; (2) upper quarter.
15. Shape of the tubercles: (0) slender; (1) robust.
16. Simplified ornamentation stage: (0) absent; (1) present.
17. Shape of the flanks: (0) flattened; (1) rounded.
18. Shape of the dorsum: (0) flattened; (1) concave; (2) convex.

Taxon-character matrix with generic taxa (generic taxa in white, polymorphic states in red):

Taxa / Characters	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18
<i>Crioceratites nolani</i>	2	1	0	[01]	2	0	0	1	0	0	1	0	0	0	1	0	0	0	0
<i>Emericeras</i>	3	2	0	[01]	1	0	0	1	0	1	1	1	1	0	1	0	0	[01]	0
<i>Fissicostaticeras</i>	2	1	1	[?]	1	0	[01]	2	0	1	1	1	[01]	0	2	[01]	1	0	0
<i>Gassendiceras essaouirae</i> nov. sp.	[?]	1	1	0	1	1	1	2	1	[?]	0	0	0	1	1	1	1	1	0
<i>G. multicostratum</i>	2	1	1	0	1	1	1	2	1	1	0	0	0	1	1	1	1	1	0
<i>Honnoratia</i>	3	2	0	[01]	1	0	0	1	0	1	1	0	1	0	1	0	0	1	2
<i>Moutoniceras</i>	3	3	0	[01]	2	0	0	0	1	0	[01]	0	[01]	1	0	[01]	0	0	2
<i>Paracrioceras stadtlaenderi</i>	2	1	1	0	1	[?]	1	2	0	1	1	1	0	0	2	1	1	1	0
<i>Pseudothurmannia</i>	[01]	0	2	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
<i>Sornayites</i>	1	0	1	[01]	0	0	0	2	0	0	1	1	0	0	1	1	0	[01]	1
<i>Toxancyloceras</i>	2	3	0	1	2	0	0	1	[01]	0	1	0	[01]	1	1	1	0	1	2

Modified taxon-character matrix with generic taxa replaced by species:

Taxa / Characters	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18
<i>Crioceratites nolani</i>	2	1	0	[01]	2	0	0	1	0	0	1	0	0	0	1	0	0	0	0
<i>Emericeras emerici</i>	3	2	0	[01]	1	0	0	1	0	1	1	1	1	0	1	0	0	0	0
<i>Fissicostaticeras fissicostatum</i>	2	1	1	[?]	1	0	1	2	0	1	1	1	[01]	0	2	1	1	0	0
<i>Gassendiceras essaouirae</i> nov. sp.	[?]	1	1	0	1	1	1	2	1	[?]	0	0	0	1	1	1	1	1	0
<i>G. multicostratum</i>	2	1	1	0	1	1	1	2	1	1	0	0	0	1	1	1	1	1	0
<i>Honnoratia thiollerei</i>	3	2	0	[01]	1	0	0	1	0	1	1	0	1	0	1	0	0	1	2
<i>Moutoniceras moutonianum</i>	3	3	0	[01]	2	0	0	0	1	0	1	0	[01]	1	0	1	0	0	2
<i>Paracrioceras stadtlaenderi</i>	2	1	1	0	1	[?]	1	2	1	1	1	0	0	0	2	1	1	1	0
<i>Pseudothurmannia picteti</i>	1	0	2	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
<i>Sornayites paronai</i>	1	0	1	[01]	0	0	0	1	0	0	1	1	0	0	1	1	0	0	1
<i>Toxancyloceras vandenheckei</i>	2	3	0	1	2	0	0	1	1	0	1	0	[01]	1	1	1	0	1	2