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

To cite this version:

HAL Id: insu-01071656
https://hal-insu.archives-ouvertes.fr/insu-01071656
Submitted on 17 Oct 2014

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L’archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d’enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.
Origin of the Tethyan Hemihoplitidae tested with cladistics
(Ancyloceratina, Ammonoidea, Early Cretaceous): an immigration event?

Didier BERT 1, 2
Stéphane BERSAC 2

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 Toxancyloceras. 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 essauirai 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.


Résumé : L’origine des Hemihoplitidae téthysiens testée par la cladistique (Ancyloceratina, Ammonoidea, Crétaçé inférieur) : un événement migratoire ?.- Les Hemihoplitidae du Barrémien supérieur (Ancyloceratidae, Ammonoidea) sont connus sur la plus grande partie de la marge Nord Téthysienne et dans le Bassin d’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’é écarter 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 episodiquement 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 essaui re 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 ; allopatry ; effet fondateur ; paléobiogéographie.

1. Introduction

The marine Late Barremian (pro parte) ammonite family HemihoplitidaeSPATH, 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, 1978, IMMEL, 1978, COMPANY et al., 2008).

1 UMR CNRS 6118 Géosciences, Université de Rennes 1, campus Beaulieu, bâtiment 15, F-35042 Rennes 1 cedex (France)
paleo-db@orange.fr
2 Laboratoire du Groupe de recherche en Paléobiologie et biostratigraphie des Ammonites (G.P.A.), Bois-Mésange, quartier St Joseph, F-04170 La Mure-Argens (France)
Published online in final form (pdf) on October 14, 2014
[Editor: Michel MOULLADE; language editor: Robert W. SCOTT; technical editor: Bruno GRANIER]
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).](image-url)
The transition to *Immerites* (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 (eustacy, 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 Hoejemaeker (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 Delany (1992, p. 52), the *Gassendiceras* (= group of "E. barremense") would be derived from the *Emericiceras* Sarkar, 1954, of the *E. emerici* group (Emericeratidae *Vermeulen*, 2004) via the *Toxancyloceras* Delany, 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: *Criocratites maghrebiensi* 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 *maghrebiensi* 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 Morrocan 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 stadtaenderi (Müller, 1892) / *elegans* (von Koenen, 1902) group, be-
cause they share many features. Both genera have in particular the trituberculate main ribs (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 & Hoe德maeker, 2010; Bert et al., 2013). The intermediate ribs bear weak ventrolateral and sometimes lateral tubercles in some species of Paracruceras as they do in Gassendiceras.

The Paracruceras of the studtlaenderi / elegans group are usually known in the Boreal Denckmani Zone (which is placed in the Late Barremian and probably correlates with the Tethyan Vandenheckeii and Sartousiana zones – see Rawson, 1983, p. 494, tab. 1; Rawson, 1995, Fig. 2; Ogg & Hinno, 2012). In fact, they are present from the boundary between the Elegans and the Fissicostatum zones (see Kakabadze & Hoe德maeker, 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

---

**Figure 2:** Comparison of Hauterivian-Barremian Boreal and Tethyan 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 Essaouria-Agadir Basin (Morocco) with G. essaouriae sp. nov. The stratigraphic positions of Paracruceras studtlaenderi (Boreal Realm, see Kakabadze & Hoe德maeker, 2010, G. essaouriae sp. nov. (Essaouria-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 Essaouria-Agadir Basin, and secondly from the latter to the Tethyan Realm (see text).
first Paracriloceras of the stadlaenderi / elegans group arose in the equivalent of the Moutonianum Tethyan Zone.

Therefore, the genera Paracriloceras 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 (Gues, 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 multicoostatum (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 Surrayities Wiedmann, 1962, with robust ornamentation, represents the first hypothesis about the Hemihoplitidae origin: the one of Wiedmann. The second hypothesis, the Delandy’s, is represented by the genera Emericiceras and Toxancyloceras. The genus Hono- raritia was added to test the third hypothesis of the Hemihoplitidae origin: the one of Wiedmann. The second hypothesis, the Delandy’s, is represented by the genera Emericiceras and Toxancyloceras. The genus Honnoratia was added to test the third hypothesis of Vermeulen. Gassendiceras essouriae sp. nov. corresponds to “Barrancyloceras” maghrebiense in sense of Company et al. (non Immel – see point 6). Both the Boreal taxa Paracriloceras stadlaenderi (Müller, 1992) and Fissicostraticeris K-kabazze & Hoedemaeker, 2010, represent the last hypothesis (this work). The genus Moutoniceras Sarkar, 1955, was added because it is one of the rare Tethyan heteromorph 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, crioconic, 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/polyomorph 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 nolali (Kilian, 1919), which is a large sized crioconic 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-EMMONDS 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 Pseudothumarannia picteti SARKAR, 1955, Sornayites paronai SARKAR, 1955, Emericiceras emeric (LÉVEILLÉ, 1837), Toxancylloceras vandenheckeri ASTIER, 1851, Honoratia honoratiana (d’ORBIGNY, 1842), Fissicostaticeras fissicostatum RDEMER, 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 (GOLDBOFF 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 (KLUÈGE & 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 Toxancylloceras vandenheckei and Moutoniceras moutonianum, Sornayites paronai and Pseudothurmannia picteti, Emericiceras emericis and Honnoratia thiollerei 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.](image-url)
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 thiollieri); the one consisting of the Crioceratitidae (Pseudothurmannia picteti and Sornayites paronai; the pair Moutoniceras and Toxancyloceras; and the clad consisting of Paracruci ceras / Fissicostaticeras and Gassendic eras. This latter clad 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 fissicostatum, Paracruci ceras stadtaenderi and the two species of Gassendiceras. This latter clade is the most robust of the tree (Fig. 4).

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 Wied mann hypothesis): the adult size, the evolute coiling and the shape of the dorsum are the synapomorphic characters supporting the clad of Pseudothurmannia / Sornayites (node 14 – Fig. 5). The other characters are all homoplasic. 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 thiollieri as stem-group (the Vermeulen hypothesis): Honnoratia thiollieri 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 homoplasic (see Fig. 5). There are five convergent characters (homoplasies) between the Honnoratia and the clad 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 Delany hypothesis): the link Delany 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 thiollieri (both Early Barremian Emericiceratidae) as seen above, and they have relationship neither the Hemihoplitidae nor the Toxancyloceras (Ancylotoritidae). Moreover, this latter genus appears to be sister taxon of Moutoniceras. The synapomorphic character of the clad 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 link, and in Gassendiceras the uncouling 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- **Gassendiceras essaouirae** sp. nov. (= "Barrancycloceras" maghrebiense sensu COMPANY et al., 2008, non IMMEI, 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 **Gassendiceras** close to **G. multicostatum**. Their uniqueness merits a new species name (see below the taxonomic implications), thus **G. essaouirae** sp. nov. would now represent the oldest known **Gassendiceras**. **G. essaouirae** sp. nov. is sister taxon of **G. multicostatum** 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 intercalary ribs. The presence of the ontogenetic Heberti stage might be a synapomorphy of this clade as well as a synapomorphy of the Paracrioceras-Gassendiceras clade, due to the unknown state of the character 5 (Fig. 5). The origin of the Tethyan **Gassendiceras** within the Moroccan species is also stratigraphically consistent because **G. essaouirae** sp. nov. is from the latest Early Barremian and **G. multicostatum** (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 **Gassendiceras** clade. This close relationship between **Paracrioceras** and **Gassendiceras**, 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 **Fississtaticiceras** – 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 IMMEI 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 DELANOV & FERAUD, 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 DELANOV & FERAUD, 1995).
Palaeoclimatically, at least three positive δ¹⁸O 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 δ¹⁸O 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 Paracriloceras 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 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 Paracriloceras 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., Aurnan et al., 1986, p. 1060; Delanoy et al., 1991; Company et al., 2008) proposed a classification in the Ancyloceratidae, while others (e.g., Kakabadze & Theiloy, 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 Feraudianus 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).
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.
v 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., 1981, and DERCOURT et al., 2000) with extension of the Tethyan Gassendiceras and the Boreal Paracrioceratidae fam. nov.
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 whors 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 whors 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 BERR and BERSAC (2013) for the genus Gassendiceras itself, the rise of a new group (here Fissicostaticeras) 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 *Hoe demaeker* (2010) but probably closer to the *Crioceratitidae* sensu lato. The *Paracrioceratidae* fam. nov. seem to be at the origin of the Tethyan *Hemihoplilritidae* (*Gassendicerasitidae*) by allopatry and founder effect.

**Remarks.** It should be noted that *Kakabadze* and *Hoe demaeker* (2010) used the genus *Acriceras* *Hyatt*, 1900, in a different way than French authors. Some specimens they figured [e.g., *Acriceras* 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 *Ropo lo* and *Gonnet* (1995), and for some *Hemihoplilritidae* (*Delanoy et al.*, 1995; *Bert et al.*, 2009; *Bert*, 2012, 2013).

**7. Conclusions**

The marine Late Barremian ammonite family *Hemihoplilritidae* (*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 *Toxancylcoceras* as stem-group) and our analysis shows that they were in fact the result of typological conceptions. *Gassendicerasessaouirae* sp. nov. appears now to be the best candidate as an ancestral endemic Moroccan representative of the group that invaded the *Moutonian Zone* (end of the Early Barremian). Cladistics also supports an origin of the *Hemihoplilritidae* (incl. *G.essaouirae* sp. nov.) from the Boreal *Paracrioceratidae* fam. nov. (migration hypothesis). *Paracrioceras* of the *stadtlaenderi* 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 *Hemihoplilritidae* 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 (*Hemihoplilritidae*), which invaded and diversified through the northern Tethyan margin. Therefore, the origin of the *Hemihoplilritidae* 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* fam. nov. could be found to explain the origin of the *Hemihoplilritidae*? Meanwhile, it remains the best candidate.

**Acknowledgements**

The authors warmly thanks Miguel Company and Gérard Delanoy for sending us the casts of *G. essaouirae* sp. nov. Special thanks are due to Steve Friedrich who kindly improved our original English text. We also acknowledge the three reviewers, Miguel Company, Jérémie Bar din and an anonymous reviewer, for their constructive remarks, which helped us to improve the manuscript.

**Bibliographic references**


BERT D. & DELANOY G. (2009).- Pseudosasticrioceras versaci nov. sp. (Ammonoidea, Gassendiceratinae), and new ammonite biohorizon for the Upper Barremian of southeastern France.- Carnets de Géologie [Notebooks on Geology], Brest, Article 2009/02 (CG2009_A02), 22 p.


BERT D., DELANOY G. & BERSAC S. (2008).- Propositions pour un nouveau découpage biozonal ammonitique, et nouveaux bio-horizons pour le Barrémien supérieur.- Carnets de Géologie [Notebooks on Geology], Brest, Article 2008/03 (CG2008_A03), 18 p.

BERT D., DELANOY G. & BERSAC S. (2011).- The Dichotomy Horizon: proposal for a new biochronologic unit of the Giraudi Zone of the Upper Barremian of southeastern France, and considerations regarding the genus Immites ROUCHADZÉ (Ammonoidea, Gassendiceratinae).- Carnets de Géologie [Notebooks on Geology], Brest, Article 2011/01 (CG2011_A01), 12 p.


BERT D., BUSNARDO R., DELANOY G. & BERSAC S. (2010).- Problems in the identity of "Crioce- ras" barremense KLIAN, 1895 (Ancyloceratida, Late Barremian), and their proposed resolution.- Carnets de Géologie [Notebooks on Geology], Brest, Article 2010/01 (CG2010_A01), 17 p.


groups as natural units of biological classification. - *Taxon*, Chambéry, n° 59, n° 6, p. 1641-1653.


WIEDMANN J. (1962).- Underkreide-Ammoniten von Mallorca. 1. Lieferung: Lytoceratina, Aptychi.- Abhandlungen der Akademie der Wissenschaften und der Literatur, Mayence, (Mathematisch-naturwissenschaftliche Klas-


Appendix

List of characters

00. Adult size: (0) little; (1) median; (2) large; (3) very large.
01. Coiling shape: (0) evolute normally coiled; (1) crioconic 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 interrubs: (0) absent; (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):

<table>
<thead>
<tr>
<th>Taxa / Characters</th>
<th>00</th>
<th>01</th>
<th>02</th>
<th>03</th>
<th>04</th>
<th>05</th>
<th>06</th>
<th>07</th>
<th>08</th>
<th>09</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crioceratites nolani</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>[01]</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Emericiceras</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>[01]</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>[01]</td>
<td>0</td>
</tr>
<tr>
<td>Fissicostaticeras</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>[01]</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>G. multistatum</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Honnoratia</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>[01]</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Moutoniceras</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>[01]</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>[01]</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>[01]</td>
<td>0</td>
</tr>
<tr>
<td>Paracioceratas stadtaenderi</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>[01]</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Pseudothurmannia</td>
<td>[01]</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sornayites</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>[01]</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>[01]</td>
<td>1</td>
</tr>
<tr>
<td>Toxancyloceras</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>[01]</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Taxa / Characters</th>
<th>00</th>
<th>01</th>
<th>02</th>
<th>03</th>
<th>04</th>
<th>05</th>
<th>06</th>
<th>07</th>
<th>08</th>
<th>09</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crioceratites nolani</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>[01]</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Emericiceras emerici</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>[01]</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fissicostaticeras fissicostatum</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>[01]</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Gassendiereras essauireiae nov. sp.</td>
<td>[?]</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>[?]</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>G. multistatum</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Honnoratia thilleri</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>[01]</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Moutoniceras moutonianum</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>[01]</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>[01]</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Paracioceratas stadtaenderi</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>[01]</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

272