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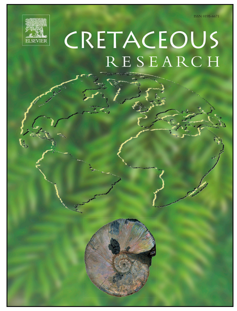


*Glaucoceras* gen. nov., a small uncoiled ammonoid from the Tethyan late Hauterivian (Early Cretaceous): evolutionary implications at the dawn of the diversification of heteromorphic lineages

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# *Glaucoceras* gen. nov., a small uncoiled ammonoid from the Tethyan late Hauterivian (Early Cretaceous): evolutionary implications at the dawn of the diversification of heteromorphic lineages

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## Abstract

The poorly-known species *Baculites Renevieri* Ooster, 1860 is revised using the type material from Switzerland and new conspecific specimens collected in deposits from

Mallorca and the Betic Cordillera (Western Mediterranean), listing all the previous mentions of the species. The uniqueness of its ornamentation pattern and shell shape compared to other coeval ammonoid faunas demands for the description of *Glaucoceras* gen. nov. to contain this species. In addition, a thorough comparison of *Glaucoceras renevieri* to other morphologically reminiscent genera or species is provided. This new set of data allows to improve the knowledge of one of the many phylogenetic lines of heteromorphic ammonites that diversified over the latest Hauterivian in the Mediterranean Province, also providing hints about the timing of those radiation events. This aspect is preliminary explored using data on other coeval heteromorphic ammonoid groups from the literature and new finds, concluding that there occurred two main radiation events of heteromorphic ammonites at the latest Hauterivian, most likely related to environmentally stressful episodes, specifically, transgressive events.

**Keywords:** Mallorca, Betic Cordillera, External Prealps, Ammonoidea, Hauterivian

## 1. Introduction

The Barremian small to medium-sized heteromorphic ammonoids have recently been vastly studied and revised by Vašíček & Wiedmann (1994), Vermeulen (2005, 2006, 2009, 2010a, 2010b), Vermeulen & Vašíček (2011) and Vermeulen *et al*. (2007, 2010a, 2012b, 2013a, 2013b, 2014a, 2014b), among others. In the latest Hauterivian (Tab. 1), the variety of forms might be as numerous as in the Barremian (*e.g*., Vašíček & Hoedemaeker, 2003; Vermeulen *et al*., 2012a, 2013a; Lukeneder, 2018), however remaining mostly unstudied. In Mallorca and in the Betic Cordillera, the deposits from the aforementioned age have delivered a great number of forms, belonging both to Protancyloceratina Vermeulen, 2005 or to Ancyloceratina Wiedmann, 1966 (the latter considered herein as a senior synonym of Turrilitina Beznosov & Mikhailova, 1983, sensu Vermeulen, 2006). The present study focuses on a particular genus, *Glaucoceras* gen. nov., described to contain the poorly known species *Baculites Renevieri* Ooster, 1860. All the aforementioned data on this species is compiled, completing its diagnosis and comparing it to similar species in order to avoid any possible confusions in their identification. Also, a probable phylogenetical position is suggested based on shell shape and ornamental affinities. This enables to clarify the taxonomy of one of the many groups of small heteromorphic ammonites that appeared at the latest Hauterivian. The better comprehension of these groups will in turn be relevant in future attempts to study the evolution of heteromorphic ammonoid shape and lineages through time, most probably linked to abiotic events, since the heteromorphic groups tended to radiate as a response to environmental stresses (further explored in '5. Discussion' herein).

## 2. Geological context and fossil localities

### 2.1. External Prealps

#### 2.1.1. Veveyse de Châtel (46°31'N 06°55'E)

This historical outcrop is located along the Veveyse de Châtel torrent, at about 2 km eastward from the small city of Châtel-St-Denis (Fribourg, Switzerland) (Fig. 1A-a). The stream crosses several geological units such as the Subalpine Molasse and the Préalpes nappes. The external Préalpes nappe has been classically attributed to the Ultrahelvetic domain (Weidmann *et al.*, 1993), a distal hemipelagic setting following the southern front of the neritic Helvetic domain. The Ultrahelvetic nappe is arranged under the form of a succession of tectonic scales (Gagnebin, 1924; Anatra, 1986; Weidmann *et al*., 1993). The primary scale, or 'Riondonnaire scale', is composed by an isoclinal stratigraphic succession spanning from the Upper Jurassic to the Lower Cretaceous (Gagnebin, 1920). The Veveyse de Châtel section was described in detail by several authors (Gagnebin, 1934, 1945; Charollais & Rigassi-Studer, 1961; Rigassi & Roveda, 1964), and studied for its palaeontological richness, especially for its ammonoid content by Ooster (1860–1863) and Sarasin & Schöndelmayer (1901–1902). A detailed stratigraphic and biostratigraphic work based on ammonites was later carried out by Busnardo *et al*. (2003) who reviewed the previous existing collections and collected new material bed-by-bed. They described an excellent profile in the group of outcrops located higher up in the torrent, consisting in an alternation of marlstones and limestones of upper Hauterivian to lowermost Barremian age, which they attributed to their informal 'Alternances supérieures de marnes et de calcaires tachetés' unit (Charollais *et al*., 1981, 1993).

## 2.2. Mallorca

Mallorca, the largest of the Balearic Islands, is included in the Betic System and its series are correlated with the Subbetic Domain (see also '2.3. Southeastern Iberian Peninsula'). As for Hauterivian strata, the dominant lithologies consist in marly limestones rhythmically intercalated with marlstones. They are assigned to the 'Maiolica' facies, which represent a long-lasting pelagic sedimentation event with particular abundance of ammonites (Colom, 1975, Vera, 2004). The Mallorcan specimens studied in this work come from four different localities (Fig. 1B), all of which have been recently described for the first time by Juárez-Ruiz & Matamales-

Andreu (2015, unpublished). In this work, only the sections of interest within each locality will be cited as follows:

**2.2.1. Biniamar (39°43'N 02°52'E)**

This outcrop, also mentioned in Bert *et al*. (2017), is located between the towns of Lloseta and (mostly) Biniamar (Fig. 1B-b), and constitutes a nearly complete series from the Berriasian to the upper Barremian. However, it is mostly covered by pastureland, thus making it difficult to observe at some points, resulting in several stages having only been recognised by *ex situ* samples. A section comprising three beds from the upper Hauterivian (Krenkeli Subzone, Balearis Zone) has been intensively sampled (Fig. 1C), delivering three partial specimens of *G. renevieri*. Previous works on Cretaceous outcrops of this area include Fallot (1910, 1922), Fallot & Termier (1923) and Wiedmann (1962a, 1962b, 1964, 1967), although it is impossible to know whether they referred to the same outcrops we studied as the region is quite rich in fossiliferous Cretaceous rocks.

**2.2.2. Can Negret (39°43'N 02°50'E)**

This quarry, located at the southwest of the town of Lloseta (Fig. 1B-c) and mentioned in Bert *et al*. (2017), possesses the most complete stratigraphic succession of the Lower Cretaceous of the island of Mallorca, currently under exploitation by the cement industry. Its stratigraphic range covers almost continuously from the Lower Jurassic to the uppermost Lower Cretaceous. However, sections cannot be measured and exhaustively sampled due to the ever-changing nature of the locality. Therefore, the samples are relatively dated upon direct association to index taxa. One fragmentary specimen of *G.* aff. *renevieri* has been found in direct association with *Balearites* *krenkeli* (Sarkar, 1955), thus indicating Krenkeli Subzone, Balearis Zone (upper Hauterivian).

**2.2.3. Manacor (39°32'N 03°14'E)**

This outcrop is located at the south-east of the town of Manacor (Fig. 1B-d), near the road Ma-4015. *In situ* stratigraphic sections from the Binelli Subzone to the Picteti Subzone (upper Hauterivian) have been recorded, although they are unfortunately mostly covered by pastureland and therefore most of the samples were recovered from *ex situ* rocks. A fragment of *G. renevieri* was found in the Krenkeli Subzone, in association with *Balearites* '*majoricensis*' (Nolan, 1894), while the only probable subadult part has been found related to the index species of the aforementioned subzone.

**2.2.4. Son Macià (39°30'N 03°13'E)**

The fields at the north and west of the village of Son Macià (Fig. 1B-e), used as pastureland, contain several sections exposing upper Hauterivian rocks from the Ligatus Zone to the Mortilleti Subzone (Ohmi Zone). In an *ex situ* rock, however in association with a fragment of *Pseudothurmannia pseudomalbosi* Sarasin & Schöndelmayer, 1901 (exclusive from the *P. mortilleti* Subzone, as concluded by Company *et al*., 2003), one partial specimen of *G. renevieri* has been recovered.

**2.3. Southeastern Iberian Peninsula**

**2.3.1. Arroyo Gilico (38°09'N 01°40'W)**

The Arroyo Gilico section (Murcia, SE Spain) (Fig. 1D-f) is part of the External Subbetic, in the Betic External Zones, within the Betic Cordillera. The Betic System constitutes a strip of variable width, broadly arranged following a SW–NE orientation. Its sediments are variably represented depending on the zone, combining episodes with high sedimentation rates, as well as condensed sequences and even stratigraphic hiatuses, mainly caused by the tectonic activity (Vera, 2004). In the zone referred in the present work, the Cretaceous is mostly represented by pelagic sequences (see Vera, 2004; Company *et al*., 2005). A detailed biostratigraphic approach on the Arroyo Gilico section has been recently carried out (Aguado *et al*., 2008, 2014), although some fossils of this locality have been studied in other works (*e.g.*, Company *et al*., 2003, 2005, 2010; Vermeulen *et al*., 2010b; Matamales-Andreu, 2017a, 2017b; Matamales-Andreu & Company, 2018). The outcrop has been extensively bed-by-bed sampled over the years by different researchers. This section covers from the Balearis Zone (upper Hauterivian) to the Vandenheckei Zone (upper Barremian) (Aguado *et al.*, 2008). For detailed stratigraphic description see Aguado *et al*. (2014).

## 3. Material and methods

For this work, a total of 13 fragmentary specimens have been studied. The type specimen of *Baculites renevieri* Ooster is housed in the Naturhistorisches Museum Bern (NMBE) (Bern, Switzerland). The specimens from Mallorca are deposited in the Museu Balear de Ciències Naturals (MBCN) (Sóller, Balearic Islands, Spain). The ones from the Arroyo Gilico section are part of the Company-Sandoval-Tavera collection, housed in the Universidad de Granada (X.V1 refers to the Arroyo Gilico section) (Granada, Andalucía, Spain). All the specimens have been measured using a manual calliper or by digital means on the scaled pictures. The measurements have been taken as follows: [1]

The minimum and maximum shell width in both preserved ends of the shell, [2] The maximum preserved length of the shell, [3] The growth rate calculated as ((maximum shell width) – (minimum shell width)) : (shell length), [4] The number of constrictions in the preserved fragment of the shell, [5] The number of constrictions per centimetre, calculated as (number of constrictions) : (maximum length). The terminology for the regions of heteromorphic tripartite shells has been taken from Vašíček (1972), that is, *proversum* for the first shaft, *flexus* for the bend and *retroversum* for the second shaft. The biostratigraphic framework follows Matamales-Andreu & Company (2018), which is slightly modified from the standard zonation presented by Reboulet *et al*. (2018).

## 4. Systematic palaeontology

**Order:** Ammonitida Agassiz, 1847

**Suborder:** Protancyloceratina Vermeulen, 2005

**Superfamily:** Bochianitoidea Spath, 1922

**Family** Bochianitidae Spath, 1922

**Genus** *Glaucoceras* gen. nov.

**Type species:** *Baculites Renevieri* Ooster, 1860 (p. 91, pl. 60, fig. 4).

**Derivation of name:** Because of the morphological similarity of the constantly constricted shell of the ammonite to the segmented and straight loments of the extant *Coronilla valentina* subsp. *glauca*, a bush of the subfamily Papilionoideae, widespread over the calcareous soils of the Mediterranean floristic region.

**Diagnosis:** Medium size, probably up to about 10 cm. Heteromorphic shell shape, most probably baculiconic, although a hamuliconic or ptychoconic shape cannot be definitely ruled out. Subcircular section; flanks, dorsum and venter convex. Width growth rate descending over ontogeny. Ornamentation pattern consisting in more or less sharp, slightly prosriradiate constrictions that may result in very wide, rounded ribs. They cross the venter without alteration, and become less marked on the dorsum.

**Specific content:** *Glaucoceras renevieri* (Ooster, 1860).

**Stratigraphic and geographic distribution:** Latest Hauterivian, from the *B. binelli* Subzone (*B. balearis* Zone) to the *P. mortilleti* Subzone (*P. ohmi* Zone). Reported from Switzerland (Ooster, 1860), southern Iberian Peninsula and the Balearic Islands (the present work) (Tab. 1).

**Remarks:** *Glaucoceras* is similar to some genera of Protancyloceratina, especially in their initial stages. *Glaucoceras* is reminiscent of *Bochianites* Lory, 1898, but they can be differentiated because the latter may either bear attenuated prosriradiate ribs or simply lack any kind of ornamentation, in contrast of the annular constrictions of *Glaucoceras*. Some species of *Bochianites* can also develop constrictions, but are accompanied by ribs, and are never as deep and conspicuous as the ones in *Glaucoceras* (see Mandov, 1971). Finally, the genus *Bochianites* is thought to disappear in the earliest Hauterivian (*e.g.*, Company, 1987; Reboulet, 1996), whereas *Glaucoceras* has only been found in the latest Hauterivian. *Baculina* d'Orbigny, 1850 *sensu* Vašíček (1999) is similar to *Glaucoceras* in its baculiconic shape and ornamentation based on sporadic, well-marked, straight and prosriradiate constrictions. The main difference is that the constrictions of *Baculina rouyana* d'Orbigny, 1850 *sensu* Vašíček (1999) are more spaced, and it bears wide, inconspicuous intercalated ribs. In the diagnosis of the holotype of that species, however, neither d'Orbigny (1850) nor Cottreau (1934) ever mentioned the presence of constrictions, so Vašíček (1999)'s specimen could belong to a different species altogether. Nevertheless, the stratigraphic range of both specimens appears to be restricted to the Valanginian (Cottreau, 1934; Vašíček, 1999), contrarily to *Glaucoceras*, which appears exclusively in the latest Hauterivian. *Glaucoceras* is similar to *Hamulinites* Paquier, 1900, with which it shares part of its stratigraphic range, especially in the ornamentation of the initial ontogenetic stages of the latter. However, they may be differentiated on the basis of stronger, denser, thinner and sharper costulation of *Hamulinites*. Also, *Glaucoceras* appears to be larger in size. The juvenile stage of *Euptychoceras* Breistroffer, 1952 possesses similar dimensions and morphology than *Glaucoceras*, but they may be differentiated because the former does not possess any kind of ornamentation on the juvenile region, only developing it further in the ontogeny, consisting in very faint, wide, weakly tuberculated ribs.

There are also some important similarities of *Glaucoceras* and the juvenile stages of a several genera of Anahamulinidae Breistroffer, 1952, sharing the baculiconic initial shell shape (which later becomes hamuliconic in the Anahamulinidae), even though their ornamentation pattern is always different. In this sense, *Amorina* Vermeulen, 2005 and *Auritina* Egoian, 1989 differ from *Glaucoceras* in their thinner and denser ornamentation based on prosriradiate ribs that may or may not be accompanied by sporadic constrictions (see Supplementary Material 1), as well as because of the larger size of the adult specimens of the former genera. *Anahamulina* Hyatt, 1900, *Vasicekina*

Vermeulen, 2005, *Lazarina* Vermeulen, 2009 and *Mascarellina* Vermeulen, 2009 are more similar in size, but their ornamentation still consists in thin, sharp and prosriradiate ribs, in contrast with the constrictions of *Glaucoceras*. This same problem occurs with genera such as *Ptychohamulina* Vermeulen, 2005, *Leptohamulina* Vermeulen, 2006, *Guiomarina* Vermeulen *et al*., 2007, *Bulotina* Vermeulen, 2009, *Davouxina* Vermeulen, 2009, *Badina* Vermeulen & Vašíček, 2011 and *Defayella* Vermeulen, 2013b that, apart from the thinner and sharper costulation on the *proversum*, possess a smaller adult size. Similarly, *Djamaina* Vermeulen *et al*., 2010a, *Baqueina* Vermeulen *et al*., 2010a, *Pacaudina* Vermeulen *et al*., 2010a and *Curiolina* Vermeulen, 2010a are smaller than *Glaucoceras* in their adult size, but this group does possess thicker ribs, that in some cases might remind of the interspaces between constrictions of *Glaucoceras*. They may be differentiated because the ribs are more prosriradiate and always sharper in the former genera group, never forming true constrictions. *Duyeina* Vermeulen, 2005 is perhaps the most similar genus, both in terms of shell size and ornamentation. It possesses a pattern based on straight, simple and very thick, slightly prosriradiate ribs, which could be confused with the interspaces between constrictions of *Glaucoceras*. However, the interspaces between ribs in *Duyeina* are clearly not as sharp as the constrictions of *Glaucoceras*. What is more, their stratigraphic range is quite distant: latest Hauterivian for *Glaucoceras* opposed to late Barremian for *Duyeina* spp. (Vermeulen, 2005), making homeomorphy the most plausible explanation for their morphological coincidence. Finally, their phylogenetic relationships seem to be rather unlinked as well, since *Duyeina* probably evolved from some Barremian Anahamulinidae such as *Pacaudina* Vermeulen *et al*., 2010a (Vermeulen *et al*., 2012b). *Glaucoceras*, on the other hand, is herein thought to be related to the late Hauterivian *Euptychoceras* (see ‘Remarks’ below). In fact, the first occurrences of all of the mentioned genera in this paragraph are younger than the last occurrence of *Glaucoceras* (Barremian vs. Hauterivian) except for *Amorina* and *Anahamulina*, which are coeval.

*Glaucoceras* also shares a similar morphology to many Baculitidae Gill, 1871, although this group is much younger. It differs from *Baculites* Lamarck, 1799 because the latter does not bear any kind of ornamentation on juvenile stages (*Glaucoceras* already possesses the constrictions) and *Lechites* Nowak, 1908, because it only possesses faint constrictions or very weak costulation on its juvenile stage. The similarity is greater in the case of *Sciponoceras* Hyatt, 1894, since this genus is characterised by an ornamentation pattern consisting in deep and sharp constrictions. However, bearing in mind that this genus is stratigraphically very distant (Hauterivian vs. Albian–Cenomanian), and that it is a direct descendant of *Lechites* (see Monks, 1999), any relationship with *Glaucoceras* besides homeomorphy seems unlikely.

*Glaucoceras* gen. nov. is herein provisionally referred to the family Bochianitidae Spath, 1922. Nevertheless, and due to lack of well-preserved suture information, only shell morphology and stratigraphic position can be taken into account to support the hypotheses presented in this work. Any relationship with Anahamulinidae Breistroffer, 1952 (in the suborder Ancyloceratina Wiedmann, 1966, superfamily Hamulinoidea Gill, 1871, family Anahamulinidae Breistroffer, 1952) has been dismissed because the latter possess a hamuliconic shell shape, with slightly curved initial stages, and a juvenile ornamentation pattern consisting in very thin, dense, prosriradiate ribs. Moreover, the first Anahamulinidae appeared in the *B. binelli* Subzone, at the same time that *Glaucoceras*. Whereas the former preserved the ornamentation pattern of their supposed ancestors (Megacrioceratidae Vermeulen, 2006), *Glaucoceras* shows a deeply modified ornamentation based on constrictions without any trace of ribs. Similar reasons make it possible to exclude *Glaucoceras* from the Leptoceratoididae Thieuloy, 1966 (in the suborder Protancyloceratina Vermeulen, 2005): the shell shape of the latter may range from hamuliconic, to toxoconic, to more or less crioconic, albeit never baculiconic. Moreover, the ornamentation pattern of the Leptoceratoididae consists in thin, dense, prosriradiate ribs, which may bifurcate or bear tubercles. Bochianitidae is the only phylogenetic group that fully agrees with the morphological characters of *Glaucoceras*. Although the only coeval representative of this family is *Euptychoceras*, which possesses no sensible ornamentation on the *proversum* and has a ptychoconic shell shape, *Glaucoceras* is reminiscent of several older Bochianitidae, which are in turn the supposed ancestors of *Euptychoceras*. Therefore, *Glaucoceras* may be considered as a late Hauterivian offshoot of *Euptychoceras*, or, however less likely, it may represent a surviving member of the *Bochianites* lineage beyond the basal Hauterivian.

*Glaucoceras renevieri* (Ooster, 1860)

(Fig. 2A–K)

*v. pars* *1860 *Baculites Renevieri* Ooster 1860; Ooster, p. 91, pl. 60, fig. 4, *non* fig. 5 (=*Amorina pictetiformis*).

1902 *Bochianites Renevieri*, Ooster; Sarasin & Schöndelmayer, p. 180.

1952 *Bochianites* (?) *Renevieri* Oost. 1860 sp.; Breistroffer, p. 51.

*non* ? 1979 *Bochianites* cf. *renevieri* (Ooster, 1860); Klinger & Kennedy, p. 17, fig. 3, E (=*Bochianites* sp.).

? 2001 *Bochianites* cf. *renevieri* (OOSTER); Avram, p. 66, pl. 1, fig. 3 (=*Bochianites*? sp.).

2007 *Bochianites*? *renevieri* (Ooster, 1860); Klein *et al*., p. 7.

2017 Bochianitinae indet.; Tajika *et al*., p. 37, fig. 9, AH.

**Type specimens:** Syntypes depicted by Ooster, 1860, pl. 60, fig. 4, 5. We hereby establish the specimen NMBE 5007731, illustrated by Ooster (1860: pl. 60, fig. 4) as the lectotype, because it undoubtedly possesses the main diagnostic characters of this species (herein depicted in Fig. 2A).

**Studied material:** Eleven fragmentary specimens; one from an undetermined Hauterivian? bed of the Veveyse de Châtel (lectotype, NMBE 5007731), one from the Binelli Subzone of Arroyo Gilico (X.V1(–16)9), three from the Krenkeli Subzone of Biniamar (MBCN 23392, MBCN 23394, MBCN 23395), two from the Krenkeli Subzone of Manacor (MBCN 23390, MBCN 23391), one from the Krenkeli Subzone of Arroyo Gilico (X.V1(–10)21), two from the Angulicostatus Subzone of Arroyo Gilico (X.V1(–1)17, X.V1(–2)57) and one from the Mortilleti Subzone of Son Macià (MBCN 23389).

**Stratigraphic and geographic distribution:** Latest Hauterivian, from the *B. binelli* Subzone (*B. balearis* Zone) to the *P. mortilleti* Subzone (*P. ohmi* Zone). Reported from Switzerland (Ooster, 1860) and Spain (the present work).

**Emended diagnosis:** Medium size, which may reach about 10 cm. Heteromorphic shell shape, most probably baculiconic, although a hamuliconic or ptychoconic shape cannot be entirely ruled out. Subcircular section; flanks, dorsum and venter convex. Very simple ornamentation consisting in deep and sharp, slightly prosriradiate, straight constrictions, with progressively larger interspaces. They cross the venter without alteration and are very slightly weakened on the dorsum. Suture line unknown.

**Ontogenetic and intraspecific variation:** Within the pool of Swiss, Mallorcan and Murcian specimens, certain characters, such as the separation of the constrictions, have been deemed slightly variable in a same ontogenetic stage (*e.g.*, compare Fig. 2A with Fig. 2C). Likewise, separation of constrictions tends to increase along the ontogeny (*e.g.*, Fig. 2A), although some other specimens in later growth stages seem to refute this hypothesis (Fig. 2J). Ontogenetic variation of whorl width growth has also been observed, the diameter increase being faster in the juvenile stage.

**Remarks:** Ooster (1860) based the description of this species on two different specimens (Ooster, 1860: pl. 60, fig. 4, 5). A thorough review of his collection has revealed that unfortunately, the larger specimen (Ooster, 1860: pl. 60, fig. 5) is nowadays lost. Nevertheless, and as discussed below, this specimen is reckoned to belong to a different, more common species.

Ooster (1860) implied that '*Baculites*' *renevieri* had been collected in Valanginian strata from Switzerland, together with *Bochianites neocomiensis* (d'Orbigny, 1842). Were this information correct, Ooster's species would possess a much earlier stratigraphic range than our specimens. However, a close examination of the drawings of the two syntypes in Ooster's original work, where they were never explicitly referred to be part of a same individual, reveals that they may belong to two different species. The largest part

(Ooster, 1960: pl. 60, fig. 5) appears to be a fragment of some Anahamulinidae, which was also pointed out by Breistroffer (1952), who ventured an early Barremian age for Ooster's material. Specifically, the aforementioned form is particularly close to *Amorina pictetiformis* (Busnardo in Busnardo *et al*., 2003) (=*Anahamulina jourdani* sensu Company *et al*., 2005), typical from the latest Hauterivian (Busnardo *et al*., 2003). Conversely, the smaller fragment (Ooster, 1960: pl. 60, fig. 4) is clearly conspecific with the Spanish material shown in the present work. If the two specimens illustrated by Ooster were from the same age, as he implied, and the largest one were indeed part of an *A. pictetiformis*, the stratigraphic range of *G. renevieri* would be updated to the latest Hauterivian, coinciding with our specimens.

Klinger & Kennedy (1979) recorded *Bochianites* cf. *renevieri* from the Valanginian of South Africa with a small fragment bearing a particularly marked constriction (Klinger & Kennedy, 1979: fig. 3, E). Considering the fragmentary nature of their material, and following the arguments above, we think that the depicted specimen could belong to some other species of Valanginian *Bochianites*, since the constriction follows a slightly flexuous shape, whereas the specimens of *G. renevieri* studied herein bear straight constrictions.

Vašíček & Faupl (1999) illustrated a particular specimen (Vašíček & Faupl, 1999: pl. 6, fig. 1) from the upper Hauterivian ('Angulicostata-Zone' ≈ Ohmi Zone as used herein) of Austria, which is clearly hamuliconic and possesses an ornamentation pattern on the phragmocone that very much resembles both our material and Ooster's smaller syntype. They doubtfully determined it as ?*Anahamulina* sp. Due to ornamental and stratigraphic coincidence, it could be regarded to belong to the same species as the material studied in the present work. However, at the end of the *proversum* some thin ribs can be recognised. Therefore, the specimen may indeed correspond to some Anahamulinidae, the particular phragmocone 'ornamentation' being probably caused by the dissolution of the material surrounding the chambers (Z. Vašíček, pers. comm., 2019).

Avram (2001) identified a small fragment (Avram, 2001: pl. 1, fig. 3) from the early Hauterivian of Romania as *Bochianites* cf. *renevieri*. The poor preservation of that specimen makes it difficult to emit any decisive conclusions on its specific determination.

Tajika *et al*. (2017) figured a fragment from Switzerland, collected *ex situ* (K. Tschanz, pers. comm., 2018), with an ornamentation pattern consisting in relatively sharp constrictions and large interspaces, identified as Bochianitinae indet. (Tajika *et al*., 2017: fig. 9-AH). Because most of the phosphatic ammonites were collected in a phosphatic conglomerate of lower Barremian (Pulchella–Compressissima Zones) age, such time interval was considered for the Swiss specimen. That specimen is herein thought to correspond to *G. renevieri*, as both size and ornamentation are consistent. It illustrates the high ornamental variability in terms of separation of the constrictions (cf. Fig. 2J herein, which shows a specimen with very narrow interspaces at a similar diameter). The only concern is that Tajika *et al*.'s specimen is notably younger than all the Spanish well-dated material. Two possible hypotheses are put forward to explain this case: [1] Should the specimen indeed belong to the Barremian beds, it would indicate the survival of the species beyond the *P. mortilleti* Subzone, which is the youngest age in which Spanish *G. renevieri* have been collected. [2] Tajika *et al*.'s specimen could in fact belong to another, basal phosphatic and glauconitic bed present at the locality (Mortilleti Subzone). The aforementioned authors considered it to belong to the lower Barremian because the matrix was seemingly equivalent to the one of those beds. However, re-examination of the matrix of Tajika *et al*.'s specimen, characterised by a brownish colour and a high quantity of glauconite grains, reveals a strong contrast with the black colour of the phosphatic Barremian specimens. This, added to recent findings of phosphatic specimens of *Pseudothurmannia* cf. *pseudomalbosi* from the nearby Tierwis section (PK.05.A.02.07, Coll. P. Kürsteiner) could indicate that the Tajika *et al*.'s specimen originally belonged to an upper Hauterivian phosphatic bed instead, just like the rest of well-dated specimens studied in the present paper. In any case, the present work does not consider Tajika *et al*.'s specimen to frame the stratigraphic range of the species, in hopes that future collections will confirm or deny the presence of *G. renevieri* in the early Barremian.

Among the specimens illustrated in this work, almost all the juvenile shafts, similar to Ooster's type, have been found in close association with *Balearites binelli* (Astier, 1851), *Balearites krenkeli* (Sarkar, 1955) and *Balearites angulicostatus* (d'Orbigny, 1842), undoubtedly marking their respective subzones, although in different deposits. The only supposed subadult fragment (Fig. 2J) has also been collected in the Krenkeli Subzone, in association with its index species. Finally, one fragmentary specimen has been found in association with *Pseudothurmannia pseudomalbosi* Sarasin & Schöndelmayer, 1901, thus marking the M.ortilleti Subzone.

*Glaucoceras* aff. *renevieri* (Ooster, 1860)

(Fig. 2L–M)

**Studied material:** Two fragmentary specimens; one from the *B. krenkeli* Subzone from Can Negret (MBCN 23393) and one from the *B. angulicostatus* Subzone of Arroyo Gilico (X.V1(–1)56).

**Stratigraphic and geographic distribution:** Late Hauterivian, hitherto only found in the *B. krenkeli* and *B. angulicostatus* Subzones (*B. balearis* Zone). So far, only known from Spain (the present work).

**Diagnosis:** Small–?medium size. Heteromorphic shell shape, most probably baculiconic, although a hamuliconic or ptychoconic shape cannot be entirely ruled out. Subcircular section; flanks, dorsum and venter convex. Very simple ornamentation consisting in shallow and sharp, neatly radial, straight constrictions, with progressively larger interspaces. They apparently cross both the venter and the dorsum, weakening slightly on the latter. Suture line unknown.

**Ontogenetic and intraspecific variation:** Even with a small number of specimens, some characters can be regarded as variable, such as the separation of the constrictions, which seems to decrease along ontogeny and between specimens, and the depth and sharpness of constrictions, which also seems to be quite variable (see Tab. 2).

**Remarks:** *G.* aff. *renevieri* differs from the typical form of *G. renevieri* because the latter bears clearly prosriradiate constrictions, which are also more spaced from each other. Although it could be interpreted as a different species, the authors of the present paper consider that such a conclusion would be highly presumptuous with a pool of just two fragmentary specimens to compare.

## 5. Discussion

The origination of heteromorphic ammonite lineages, especially those of small size, has long been linked to stressful events, such as changes in sea level, trophic or oxygenation conditions. Some examples from the literature include: Ernst *et al*. (1983) showed that the late Turonian *Hyphantoceras* Hyatt, 1900 event corresponds to a transgressive interval. Hoedemaeker (1995) claimed that some genera of small heteromorphic ammonites (*Hamulinites* Paquier, 1900, *Karsteniceras* Royo y Gómez, 1945, *Protancyloceras* Spath, 1924, *Leptoceras* Uhlig, 1883) were opportunistic and flourished right after extinction events. Company *et al*. (1995) also recognised this pattern in the genera *Hamulinites* Paquier, 1900, *Tzankoviceras* Manolov, 1962, *Protancyloceras* Spath, 1924 and *Leptoceras* Uhlig, 1883. Cecca (1997) proposed that the cause of the diversification of Protancyloceratina in the Tithonian could be related to an increase of primary productivity, and that the diversification of 'basal ancyloceratid'-like morphologies near the Valanginian–Hauterivian boundary coincided with an anoxic event, with an increase of food resources in the shallowest parts of the water column (also studied by Reboulet, 2008 in the particular case of *Himantoceras* Thieuloy, 1965). Lukeneder (2003, 2005) described mass occurrences of *Karsteniceras* Royo y Gómez, 1945 in the Barremian, linked to dysoxic waters. Reboulet *et al*. (2003) demonstrated that the higher abundance of Valanginian *Bochianites* Lory, 1898 occurred during anoxic events, pointing to their opportunistic mode of life. Reboulet *et al*. (2005) studied the latest Albian Breistroffer interval (OAE1d), and concluded that heteromorphic ammonites diversified themselves and became more abundant during this transgressive, anoxic event. Yet, Guex (2001, 2006) discussed a seemingly opposite case: the origination of some heteromorphic ammonite lineages in response to major regressive events related to a reinitialisation of evolutionary clocks and evolutionary processes such as proteromorphosis. Additionally, Bert & Bersac (2013) reported that, although the late Barremian *Gassendiceras* Bert *et al*., 2006 species acquired heteromorphic coilings during a transgressive episode, their most uncoiled morphotypes appeared during an arid interval, which can be related to a diminished fertilisation of the ocean waters. Therefore, whereas most of the heteromorphic ammonite lineages seem to have originated during transgressive events with nutrient-rich waters, there are particular cases of other lineages becoming heteromorphic during regressive episodes or intervals of low nutrient runoff to the oceans.

For the uppermost Hauterivian, Company *et al*. (2005) located the sequence boundaries of Hardenbol *et al*. (1998) in a high-resolution biostratigraphic framework. Specifically, they placed transgressive maximums at the upper part of the Binelli Subzone and at the Ohmi–Mortilleti Subzones boundary, and regressive maximums at the upper part of the Krenkeli Subzone (SBHa6) and at the upper part of the Picteti Subzone (SBHa7).

The origination of the genus *Glaucoceras* seems to be linked to a particular diversification event of heteromorphic ammonites, located at the late *B. binelli*–early *B. krenkeli* Subzones (Fig. 3A–B), which coincides with the origination of the genera *Monodites* Bert, 2009, *Paracostidiscus* Busnardo (in Busnardo *et al*., 2003), *Garroniceras* Vermeulen *et al*. 2012a, *Amorina* Vermeulen, 2005 and *Hamulinites* Paquier, 1900 (see Supplementary Material 2 for specific references on the species). This event probably corresponds to the transgressive maximum of the late *B. binelli* Subzone pinpointed by Company *et al*. (2005), and therefore this case seems consistent with the bulk of examples in the literature: heteromorphic ammonite lineages that appear or radiate during transgressive intervals (they have often been argued to be opportunistic in nature, see above for references).

This event can be compared to the more extensively studied Faraoni Ocean Anoxic Event (Company *et al*., 2005; Föllmi, 2012; Aguado *et al*., 2014) that occurred at the *P. ohmi–P.mortilleti* Subzones boundary, and corresponds to the next and more important maximum flooding surface. By then, several small to medium-sized heteromorphic genera such as *Leptoceratoides* Royo y Gómez, 1945, *Sabaudiella* Busnardo (in Busnardo *et al*., 2003), Bastelia Vermeulen *et al*., 2012a and *Anahamulina* Hyatt, 1900 made their first appearance (Fig. 3A–B), along with the turnover of many other ammonoid taxa (Company *et al*., 2005; Supplementary Material 2 for references on heteromorphic species). That transgressive maximum was accompanied by more humid conditions, which increased the nutrient runoff from the continent (Aguado *et al*., 2014). This phenomenon increased the eutrophication of the ocean waters, leading to the decrease of dissolved oxygen levels, which affected the marine ecosystems.

## 6. Conclusions

Detailed sampling of different outcrops both from Mallorca and the Betic Cordillera allowed the recovery of fragments of 13 ammonoid fossil shells attributed to the newly created genus *Glaucoceras* gen. nov. The bed-by-bed collecting process (in the case of Arroyo Gilico) or the direct association with the respective index fossils (in the Mallorcan deposits) allowed to provide precise biostratigraphic range for each sample. Two morphotypes can be distinguished within this new genus, which appears to be quite rare, since only two specimens had been illustrated by previous authors. *Glaucoceras renevieri*, a new combination for Ooster (1860)'s species *Baculites Renevieri*, seems widespread from the *B. binelli* Subzone to the *P. mortilleti* Subzone. Contrarily, *Glaucoceras* aff. *renevieri* appears to span from the *B. krenkeli* Subzone to the *B. angulicostatus* Subzone. This data improves the knowledge of the heteromorphic ammonoid fauna during the late Hauterivian, which is a period of great diversification of these groups. Specifically, the bulk of heteromorphic genera were originated in two specific events, coinciding with the consecutive transgressive maximums in the late *B. binelli*–early *B. krenkeli* Subzones and in the *P. ohmi*–*P. mortilleti* Subzones boundary (Faraoni Ocean Anoxic Level). This allows to put forward the hypothesis that latest Hauterivian heteromorphic ammonoids became more diverse during eustatic maximums, when ocean waters flooded the continental shelves, resulting in the increase of nutrient runoff to the sea, favouring the development of epipelagic forms. However, further research will be required to ascertain the specific traits that made several independent lineages of heteromorphic ammonites ecologically more successful in nutrient-rich waters, to determine if there exist differences in evolutionary patterns between small- and large-sized heteromorphic ammonoids, and to prove whether both size classes were opportunistic or not (hitherto, only small-sized heteromorphs were regarded as such).

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**Table 1:** Stratigraphic framework used herein (from Matamales-Andreu & Company, 2018) and distribution of the studied species in each of the considered localities. Veveyse de Châtel not included because the stratigraphic position of the only specimen is uncertain. Dark blue (×): *Gl. renevieri*; Orange (+): *Gl.* aff. *renevieri*.



| Age | | | Locality | | | | |
|---|---|---|---|---|---|---|---|
| Stage | Zone | Subzone | Arroyo Gilico | Can Negret | Biniamar | Son Macià | Manacor |
| Late Hauterivian *pro parte* | *Pseudothurmannia ohmi* | *P. picteti* | | | | | |
| | | *P. mortilleti* | | | | × | |
| | | *P. ohmi* | | | | | |
| | *Balearites balearis* | *B. angulicostatus* | × + | | | | |
| | | *B. krenkeli* | × | + | × | | × |
| | | *B. binelli* | × | | | | |
| | | *B. balearis* | | | | | |

**Table 2:** Biometric measurements of all the studied specimens. Width and length taken in cm.

| Specimen | Species | Minimum–maximum width | Maximum length | Growth rate | Number of constrictions | Constrictions per cm |
|---|---|---|---|---|---|---|
| NMBE 5007731 | *Gl. renevieri* | 0.24–0.58 | 4.73 | 0.072 | 14 | 3 |
| MBCN 23389 | *Gl. renevieri* | 0.31–0.34 | 1.80 | 0.017 | 11 | 6 |
| MBCN 23392 | *Gl. renevieri* | 0.18–0.38 | 2.04 | 0.098 | 18 | 8 |
| MBCN 23390 | *Gl. renevieri* | 0.51–1.00 | 5.97 | 0.082 | 24 | 4 |
| MBCN 23391 | *Gl. renevieri* | 0.35–0.56 | 2.41 | 0.087 | 9 | 3 |
| MBCN 23395 | *Gl. renevieri* | 0.27–0.32 | 1.22 | 0.041 | 10 | 8 |
| MBCN 23394 | *Gl. renevieri* | 0.33–0.34 | 1.18 | 0.008 | 7 | 5 |
| X.V1 (–16) 9 | *Gl. renevieri* | 0.15–0.30 | 1.75 | 0.086 | 24 | 13 |
| X.V1 (–10) 21 | *Gl. renevieri* | 0.20–0.24 | 1.04 | 0.038 | 17 | 16 |
| X.V1 (–2) 57 | *Gl. renevieri* | 0.25–0.30 | 0.99 | 0.051 | 7 | 7 |
| X.V1 (–1) 17 | *Gl. renevieri* | 0.29–0.32 | 1.33 | 0.024 | 16 | 12 |
| MBCN 23393 | *Gl.* aff. *renevieri* | 0.42–0.52 | 1.15 | 0.087 | 9 | 7 |
| X.V1 (–1) 56 | *Gl.* aff. *renevieri* | 0.29–0.50 | 1.53 | 0.137 | 19 | 12 |

**Figure 1.** Location of the studied sites. **A:** Geological map of SW Switzerland with the location of Veveyse de Châtel (**a**). **B:** Geological map of Mallorca with the four location of Biniamar (**b**), Can Negret (**c**), Manacor (**d**) and Son Macià (**e**). **C:** Studied section in the locality of Biniamar. **D:** Geological map of the Betic Cordillera with the location of Arroyo Gilico (**f**).

**Figure 2. A–K:** *Glaucoceras renevieri* (Ooster, 1860). **A:** Specimen NMBE 5007731, Holotype, upper Hauterivian, Veveyse de Châtel. **B:** Sample MBCN 23391 in association with *B.* "*majoricensis*", Krenkeli Subzone, Manacor. **C:** Sample MBCN 23392 in association with *Phyllopachyceras winkleri*, Krenkeli Subzone, Biniamar. **D:** Sample MBCN 23394 in association with *B.* "*majoricensis*", Krenkeli Subzone, Biniamar. **E:** Specimen MBCN 23395, Krenkeli Subzone, Biniamar. **F:** Specimen X.V1 (–1) 17, Angulicostatus Subzone, Arroyo Gilico. **G:** Specimen X.V1 (–16) 9, Binelli Subzone, Arroyo Gilico. **H:** Specimen X.V1 (–10) 21, Krenkeli Subzone, Arroyo Gilico. **I:** Sample MBCN 23389 in association with *P. pseudomalbosi*, Mortilleti Subzone, Son Macià. **J:** Specimen MBCN 23390, Krenkeli Subzone, Manacor. **K:** Specimen X.V1 (–2) 57, Angulicostatus Subzone, Arroyo

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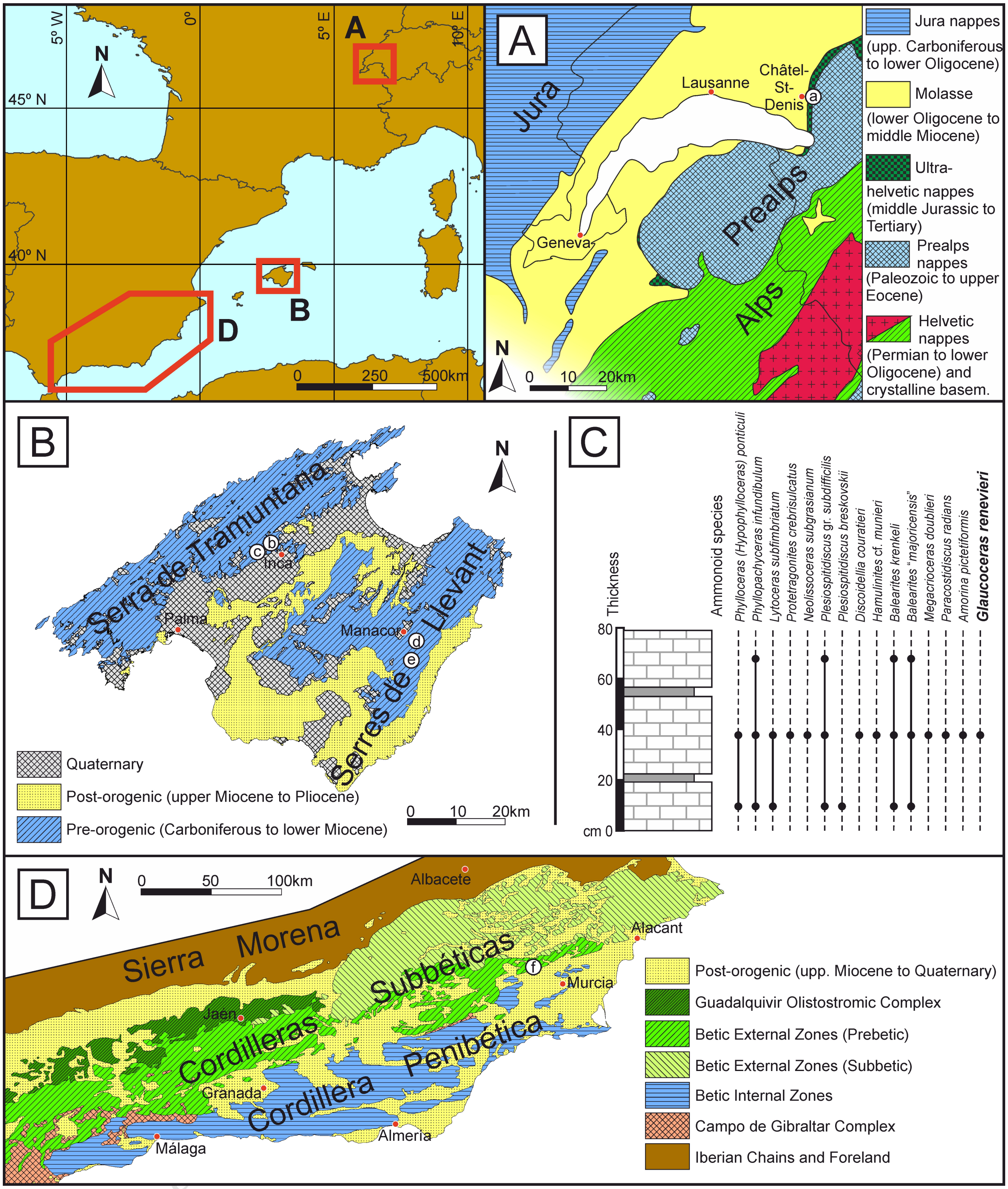
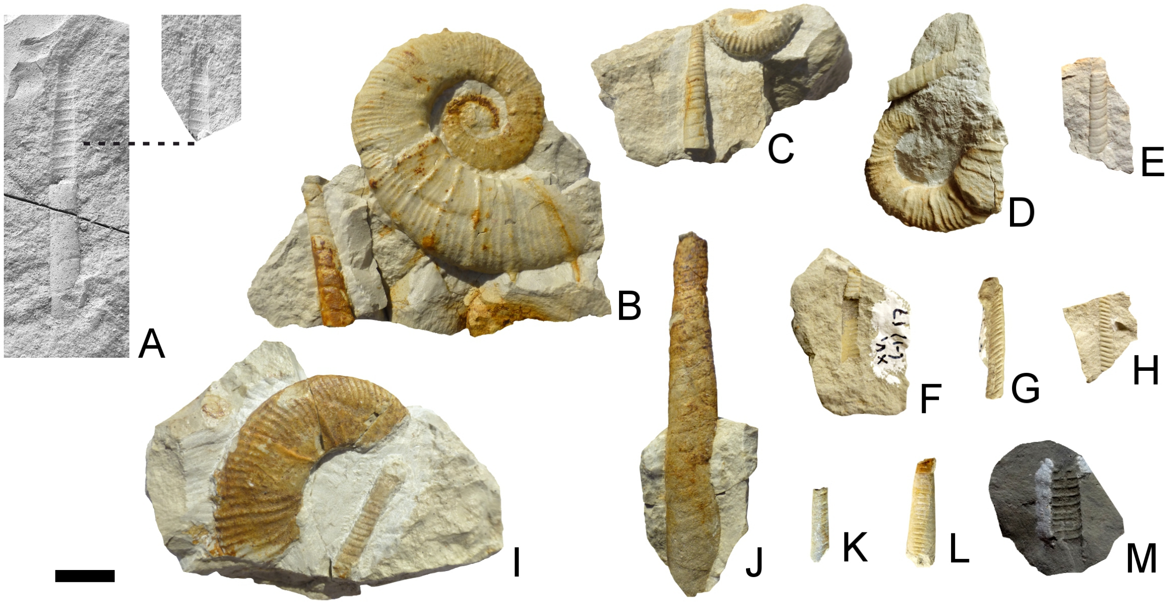
Gilico. **L–M:** *Glaucoceras* aff. *renevieri*. **L:** Specimen X.V1 (–1) 56, Angulicostatus Subzone, Arroyo Gilico. **M:** Specimen MBCN 23393, Krenkeli Subzone, Can Negret. Scale bar: 10 mm.

**Figure 3. A:** Stratigraphic distribution of heteromorphic ammonoid genera for the latest Hauterivian (*B. balearis* and *P. ohmi* Zones). Data on sources of information on stratigraphic ranges can be consulted in Supplementary Material 2. Biozonation framework as in Tab. 1 herein. Sea level information taken from Company *et al*. (2005). Dashed lines indicate possible phyletic relationships. Question marks represent unknown parts of the ammonites. The star marks the possible diversification event of heteromorphic ammonites at the *B. binelli*–*B. krenkeli* Subzones boundary. **B:** Stacked area chart showing the changes of diversity of heteromorph ammonoids over the latest Hauterivian, using the data presented in the Supplementary Material 2. Arrows indicate the two diversification events.



5° W
0°
5° E
10° E
45° N
40° N
N
A
B
D
0
250
500km
A
Jura
Lausanne
Châtel-St-Denis
a
Geneva
Prealps
Alps
N
0
10
20km
Jura nappes (upp. Carboniferous to lower Oligocene)
Molasse (lower Oligocene to middle Miocene)
Ultra-helvetic nappes (middle Jurassic to Tertiary)
Prealps nappes (Paleozoic to upper Eocene)
Helvetic nappes (Permian to lower Oligocene) and crystalline basem.
B
N
Serra de Tramuntana
Inca
b
c
Palma
Manacor
d
e
Serres de Llevant
Quaternary
Post-orogenic (upper Miocene to Pliocene)
Pre-orogenic (Carboniferous to lower Miocene)
0
10
20km
C
Thickness
80
60
40
20
cm 0
Ammonoid species
Phylloceras (Hypophylloceras) ponticuli
Phyllopachyceras infundibulum
Lytoceras subfimbriatum
Protetragonites crebrisulcatus
Neolissoceras subgrasianum
Plesiospitidiscus gr. subdifficilis
Plesiospitidiscus breskovskii
Discoidellia couratieri
Hamulinites cf. munieri
Balearites krenkeli
Balearites "majoricensis"
Megacrioceras doublieri
Paracostidiscus radians
Amorina pictetiformis
Glaucoceras renevieri
D
N
0
50
100km
Albacete
Sierra Morena
Alacant
Subbéticas
f
Murcia
Jaén
Cordilleras
Penibética
Granada
Cordillera
Almeria
Málaga
Post-orogenic (upp. Miocene to Quaternary)
Guadalquivir Olistostromic Complex
Betic External Zones (Prebetic)
Betic External Zones (Subbetic)
Betic Internal Zones
Campo de Gibraltar Complex
Iberian Chains and Foreland


A
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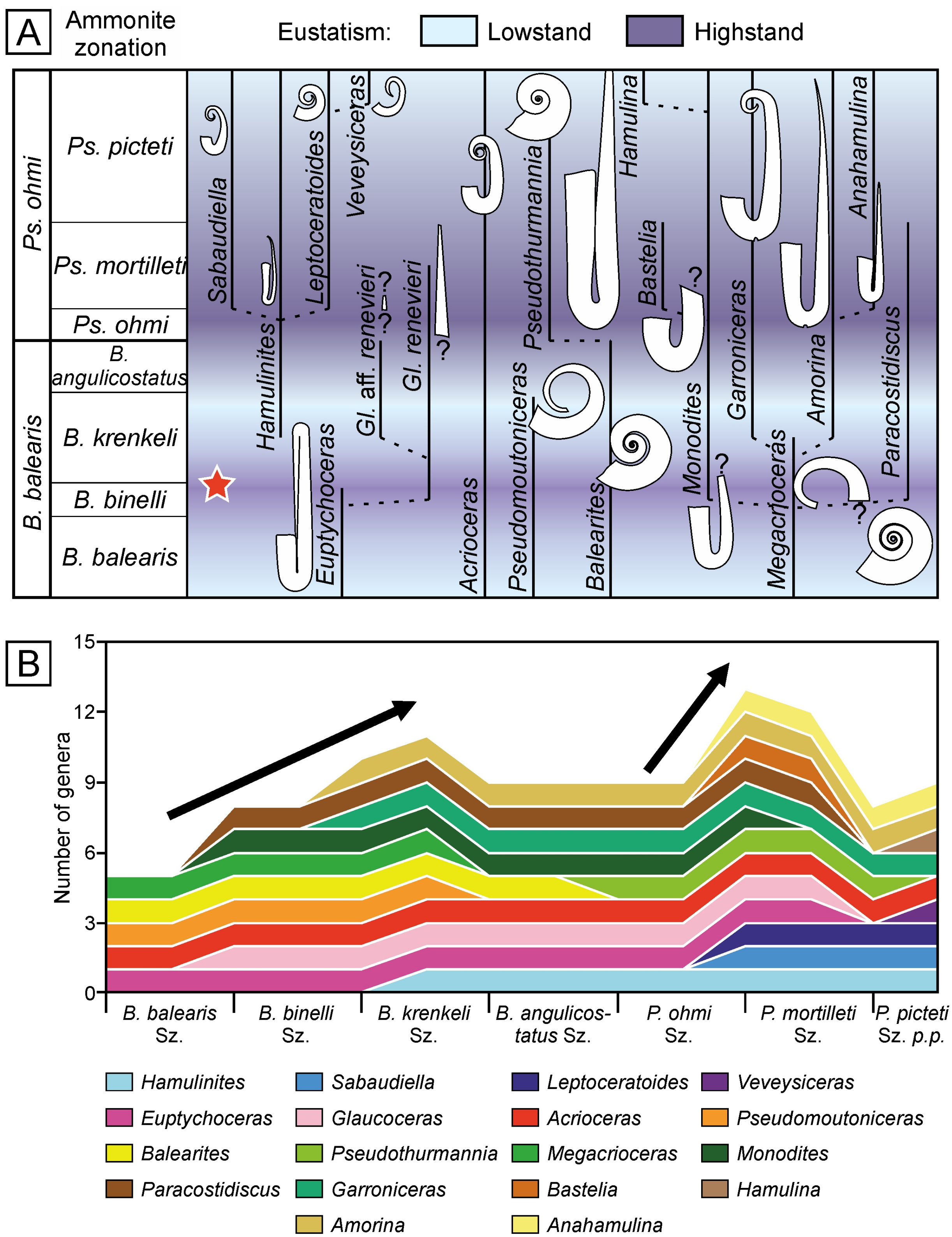

A
Ammonite zonation
Eustatism:
Lowstand
Highstand
Ps. ohmi
Ps. picteti
Ps. mortilleti
Ps. ohmi
B. balearis
B. angulicostatus
B. krenkeli
B. binelli
B. balearis
Sabaudiella
Hamulinites
Leptoceratoides
Euptychoceras
Veveysiceras
Gl. aff. renevieri
Gl. renevieri
Acrioceras
Pseudothurmannia
Pseudomoutoniceras
Hamulina
Bastelia
Balearites
Monodites
Garroniceras
Megacrioceras
Amorina
Anahamulina
Paracostidiscus
B
Number of genera
15
12
9
6
3
0
B. balearis Sz.
B. binelli Sz.
B. krenkeli Sz.
B. angulicos-tatus Sz.
P. ohmi Sz.
P. mortilleti Sz.
P. picteti Sz. p.p.
Hamulinites
Sabaudiella
Leptoceratoides
Veveysiceras
Euptychoceras
Glaucoceras
Acrioceras
Pseudomoutoniceras
Balearites
Pseudothurmannia
Megacrioceras
Monodites
Paracostidiscus
Garroniceras
Bastelia
Hamulina
Amorina
Anahamulina

- The genus *Glaucoceras* gen. nov. is described to include the poorly-known species *Baculites Renevieri* Ooster, 1860. *Glaucoceras renevieri* is revised and compared with other similar taxa.

- The stratigraphic range of *Glaucoceras renevieri* is updated, revealing that it appears between the *Balearites binelli* Subzone (*Balearites balearis* Zone) and the *Pseudothurmannia mortilleti* Subzone (*Pseudothurmannia ohmi* Zone) of the latest Hauterivian (Early Cretaceous).

- The palaeoenvironmental event that is thought to have led to the origination of this genus is further explored, concluding that it corresponded to a transgressive maximum that occurred at the *Balearites binelli*–*Balearites krenkeli* Subzones (*Balearites balearis* Zone).

- Two successive transgressive events in the latest Hauterivian are interpreted as the triggers of the diversification of many other heteromorphic ammonoid lineages.