

New Lower Kimmeridgian ataxioceratin ammonite from the eastern Iberian Chain, Spain: Systematic, biogeographic, and biostratigraphic relevance

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New ammonites collected bed-by-bed from the upper part of *Ataxioceras hypselocyclum* Chronozone deposits in the eastern Iberian Chain are described as *Geyericeras* gen. nov. The new genus includes micro- and macroconchiate Ataxioceratinae of small size, with moderate to loose coiling and subpolyplocoid ribs, a character crucial for its identification. Key points for the comparative identification of *Geyericeras* gen. nov. are: (i) microconchiate *Geyericeras* show morphological convergence with evolute specimens of the stratigraphically older genus *Schneidia* [m]; (ii) contemporary Ataxioceratinae genera such as *Ardescia* [m, M] and *Lithacosphinctes* [m, M] did not develop subpolyplocoid ribbing; (iii) smoothing of sculpture combined with short primary ribs are not realized in *Geyericeras* gen. nov. [M] and can be therefore used to separate the new genus from *Ataxioceras* [M]; and (iv) smaller shells, and weaker and less dense ribbing with no parabolic structures differentiate *Geyericeras* gen. nov. [m, M] from *Parataxio-ceras* [m, M], as well as the type of subpolyplocoid ribs seen among microconchiate specimens of these two genera. The new species *Geyericeras aragoniense* sp. nov. is the index and guide fossil for identification of a biohorizon occurring below the first occurrence of the genus *Crussoliceras* in the eastern Iberian Chain.

Key words: Ammonoidea, Ataxioceratinae, *Geyericeras*, Lower Kimmeridgian, Jurassic, Iberian Chain, Spain.

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Introduction

Ataxioceratids were Late Jurassic ammonites which developed significant evolutionary innovations expressed especially in their complex shell sculpture (e.g., Callomon in Donovan et al. 1981). This ammonite group thrived in inland sea environments across southern Europe, and more generally on epicontinental shelves submitted to the influence of Tethyan water masses, developing extreme phenotypes having a recurrent pattern referred to as diachronous homeomorphism. This paper presents a case study of this phenomenon in an analysis resulting in the description of a new ataxioceratid genus. The analysis was possible because of the precise stratigraphic control possible from other stratigraphically important ammonites. The proposed paleontological interpretation favors a paleobiological approach in which micro- and macroconchs of the paleo-biospecies are described under a single species name.

Institutional abbreviation.—UGR, University of Granada, Spain (Palaeontological collection of the Department of Palaeontology).

Other abbreviations.—C, number of constrictions; Dm, maximum shell diameter measured; FAD, first appearance datum; H, whorl high; M, macroconchs; m, microconchs; Ph, maximum diameter for the phragmocone; RI, ribbing index calculated as the number of peripheral ribs per ten umbilical ribs; U, size of the umbilicus; W, whorl width; UR, number of umbilical ribs per complete whorl; UR/2, number of umbilical ribs per half-a-whorl.

Geological setting

The studied lower Kimmeridgian succession is 10 to 40 m thick and consists of limestone beds, up to 50 cm thick, intercalated with marl and marly limestone layers up to 1 m thick. These rocks belong to the Loriguilla Formation (Gómez and Goy 1979). Paleoenvironmental interpretations for the eastern Iberian Chain during early Kimmeridgian times suggest a rather inland sea within the vast epicontinental shelf system developed on Iberia during the Late Jurassic (e.g., Aurell et al. 2002). The sea was apparently poorly connected to the open waters adjacent to the epicontinental environment (Moliner and

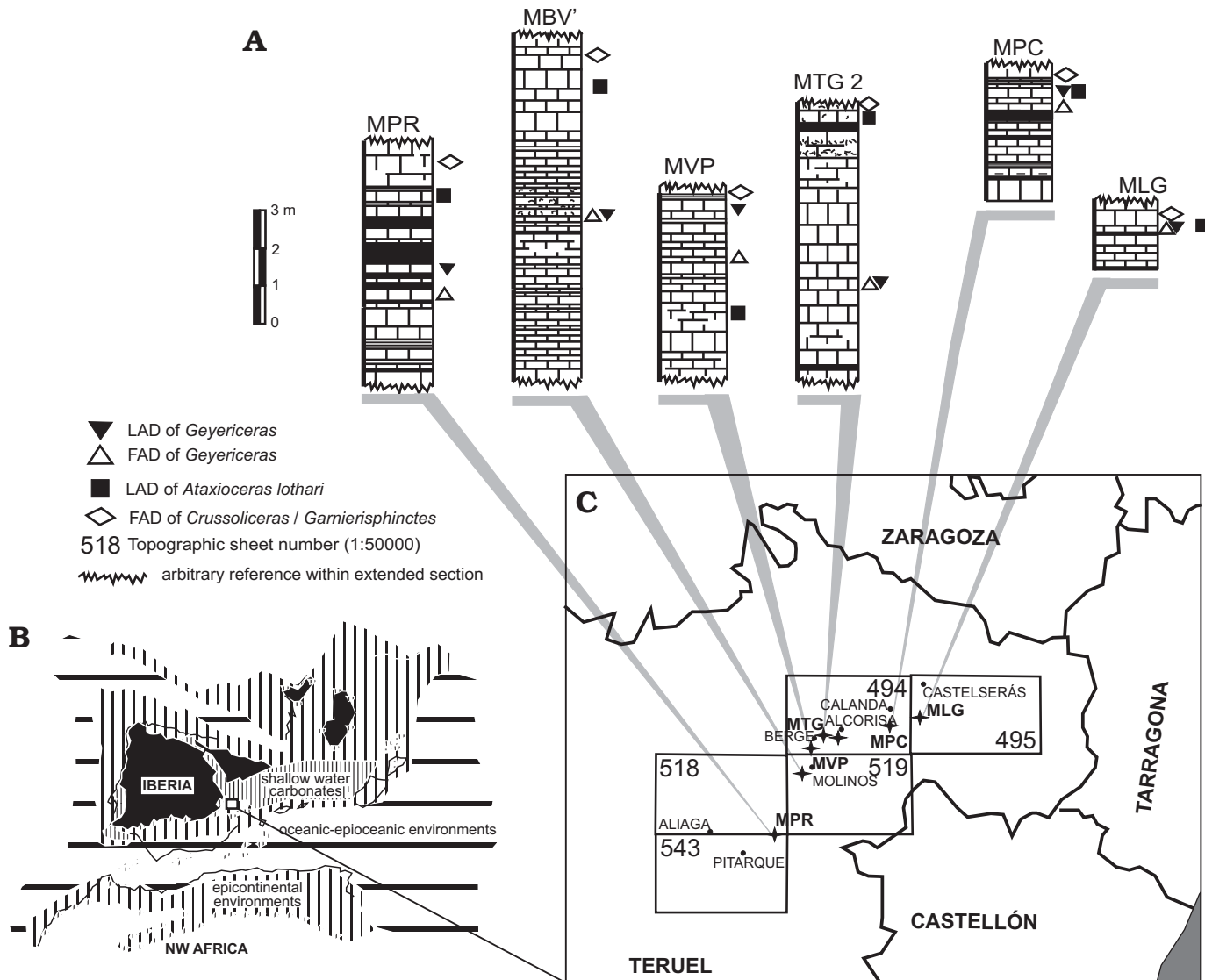


Fig. 1. Location (C), palaeogeography (B), and studied sections (A) with indication of *Geyericeras* records together with others ataxioceratins relevant for biostratigraphic correlation. Sections labeling as follows: Villarluengo [MPR], Berge-Molinos [MBV, MVP], Alcorisa-Gallipuéen [MTG], and Calanda [MLG, MPC] areas. FAD and LAD for First and Last Appearance Data, respectively.

Olóriz 1999; Fig. 1). Environmental conditions interpreted as low energy with turbid, nutrient-rich waters and depths in the range of 30–80 m (Moliner and Olóriz 1999; Olóriz 2000) favored ecological forcing of the local ammonite community (Olóriz et al. 1988; Moliner and Olóriz 1999; Olóriz 2000). It is hypothesized that regressive trends and ecospace contraction for the neritic ammonites peaked during the time of development of the genus *Ataxioceras* sensu stricto (the *Ataxioceras hypselocyclum* Chronozone, before a pulse of high relative sea-level (transgression) brought about the first widespread occurrence of crussoliceratid ammonites in southern Europe.

Historical background

Early Kimmeridgian ammonites in the eastern Iberian Chain (Fig. 1) have been intensively studied during the past 25 years.

This has resulted not only in greater knowledge of these cephalopods themselves but also has significantly improved understanding of the biostratigraphic position of the ammonoid-bearing deposits (e.g., Moliner 1983; Atrops and Meléndez 1984; Moliner and Olóriz 1984; Fezer and Geyer 1988; Finkel 1992; Meléndez et al. 1999; Moliner and Olóriz 1999, 2009a, b). The limestone horizons of the lower part of the Loriguilla Fm. (Gómez and Goy 1979) contain the zonal index ammonoid *Sutneria platynota*, indicating the *S. platynota* Biozone. Overlying the last occurrence of both *Sutneria platynota* and the slightly later ataxioceratid *Schneidia*, the first appearance datum (FAD) of genus *Ataxioceras* is registered. The identification of *Ataxioceras* sensu stricto is based on the occurrence ataxioceratoid sensu stricto or polyplocoid ribbing (i.e., double bifurcations) not induced by a high density of ribbing (e.g., Geyer 1961; Atrops 1982). This innovation in sculpture is recorded as a biostratigraphic event which allows

placement of the base of both the secondary standard *Ataxioceras hypselocyclum* Chronozone and its local biostratigraphic equivalent, or quasi-equivalent, the *Ataxioceras lothari* Biozone (see Moliner and Olóriz 2009b for an extended treatment). Upwards in the Lower Kimmeridgian section, the FAD of *Crussoliceras* biostratigraphically determines the lower boundary of the *Ataxioceras divisum* Chronozone in the area.

Material and methods

The material studied in this paper resulted from precise ammonite biostratigraphical investigations of six sections in the Aragonese Branch of the eastern Iberian Chain and northern Maestrazgo in northeastern Spain (Fig. 1). The extensive bed-by-bed sampling of the 1 to 4 m thick interval between FADs of *Ataxioceras* and *Crussoliceras* (lower Kimmeridgian) provided 524 ammonites, 234 of which belong to the subfamily Ataxioceratinae; among the latter, 43 specimens and fragments are described below as *Geyericer* gen. nov. [m, M].

For biostratigraphic purposes, FADs were favored for definition of biozones and intra-zone divisions. The informal term “faunal horizon” (e.g., Callomon 1984) or “biohorizon”, of common use in updated biochronostratigraphy, has been applied as the thinnest, biostratigraphically identifiable intra-biozone division; hence it differs from the term biohorizon as a stratigraphic boundary, surface, or interface considered in the International Stratigraphic Guide (e.g., Murphy and Salvador 1999).

Remarks on ataxioceratin systematics

The systematic treatment given to the studied ammonites is based on: (i) the paleontological interpretation introduced above, in which the interpretation of microconchs (with lappeted peristome) and macroconchs (with simple peristomal structures) of a given paleo-biospecies are included under a single species name, and therefore genus; (ii) the option to avoid the use of subgenus level taxa for mere morphological, sexual or evolutionary purposes; and (iii) the special relevance given to the population approach based on the combined analysis of shell morphology under precise control of biostratigraphy and paleobiogeography. Therefore, some introductory remarks are needed to support the following reinterpretation of some lower Kimmeridgian taxa belonging to the subfamily Ataxioceratinae.

Focused on the possibility of approaching paleobiospecies, we favor the application of Mayden’s (1997) morphological approach concept. Mayden’s approach is based on the identification of morphological clusters characterized by intra-group phenotypic traits showing a lesser degree of variability when compared with other groups of the same assumed age (i.e.,

intra-group phenotypic variability is lower than inter-group phenotypic variability, which results in relatively high phenotype cohesion for identified taxa) both in space and time. Hence, some degree of phenotype diversity in time and space is assumed for identified species (e.g., Miller 2001), which were considered under strict biostratigraphic control and paying attention to interpreted phylogenetic relationships. The latter served to reinforce the reinterpretation given to genus-level taxa, as well as to the redistribution of some known species among genus-level taxa. In such a context, the following comments clarify the reinterpretation made at the genus level for some lower Kimmeridgian Ataxioceratinae mentioned in this study. Comparisons with the new genus *Geyericer* are given below (see Systematic paleontology section).

Schneidia is a well-known taxon erected by Atrops (1982) for microconchs described mainly from the youngest part of the *Sutneria platynota* Chronozone. *Schneidia* Atrops, 1982 emend. [m, M] is interpreted herein to embrace discocone microconch (up to about 115 mm in diameter) and macroconch (up to about 250 mm) shells displaying involute to moderately involute outlines and with oval to subrectangular whorl sections. Dense, fine ribbing is typical on the inner whorls as well as typical subpolyplocoid ribs on the outer whorls. The absence of real ataxioceratoid, polyplocoid ribs, together with its older stratigraphic range, clearly separates *Schneidia* from *Ataxioceras* sensu stricto, which usually is more evolute. The reinterpreted taxon *Schneidia* [m, M] includes macroconchs formerly referred to as *Ataxioceras striatellum* (Schneid, 1944) (e.g., Atrops 1982 who rightly assumed no relationships with the true, younger *Ataxioceras*). As reinterpreted in the present paper, *Schneidia* represents a well-defined evolutionary cul-de-sac among early Kimmeridgian Ataxioceratinae ranging throughout the youngest part of the *Sutneria platynota* Chronozone.

*Parataxio*ceras Schindewolf, 1925 has been usually considered as a subgenus of *Ataxioceras* with variable phylogenetic meaning (e.g., Geyer 1961; Schairer 1974; Atrops 1982). *Parataxio*ceras Schindewolf, 1925 emend. [m, M] is reinterpreted herein to include microconchs (up to about 100 mm) and macroconchs (smaller than 200 mm) showing real ataxioceratoid, polyplocoid, ribs during the *Ataxioceras hypselocyclum* Chronozone. Coiling degree is moderate to low, ribbing style vigorous and parabolic structures on the phragmone are common. Rib-curves are flat to slightly decreasing in microconchs but increasing up to about 65–90 mm and then decreasing in macroconchs. Thus, *Parataxio*ceras is considered to be a genus-level taxon separated from *Ataxioceras*, which also includes micro- and macroconchs during the *Ataxioceras hypselocyclum* Chronozone corresponding to the local *Ataxioceras lothari* Biozone (Moliner and Olóriz 2009b).

Lithacosphinctes was erected by Olóriz (1978) for lower Kimmeridgian macroconchs. Later interpretations considered *Lithacosphinctes* as a subgenus-level macroconch with a more restricted range within the lower Kimmeridgian (Atrops 1982), or as a genus-level taxon including micro- and macroconchs with a longer biostratigraphic range overlapping the

uppermost Oxfordian and a lower part of the upper Kimmeridgian (Hantzpergue 1989). *Lithacosphinctes* Olóriz, 1978 emend. [m, M] is reinterpreted herein to include macro- and microconchs belonging to the group of *Lithacosphinctes evolutus* (Quenstedt, 1888) (reinterpreted as *L. siemiradzki* by Zeiss in Kiessling and Zeiss 1992) and its younger descendants. Shells are evolute. Microconchiate specimens are up to about 135 mm, and macroconchs larger than 300 mm. Rib-curves are slightly decreasing to subhorizontal from 50–80 mm, and parabolic structures occur on the phragmocone and the rear part of the body-chamber in microconchs. Polygyrate ribs are the most complex rib division in microconchs, and smoothing, even vanishing of secondary ribs occurs in the comparatively stouter macroconchs which developed variable reinforcement of primary ribs. *Lithacosphinctes* did not develop ataxioceratid sensu stricto (polyplocoid) ribbing, which is well known in other ataxioceratins (e.g., *Parataxio-ceras*). Thus, in morphological terms, *Lithacosphinctes* appears to represent the most conservative lineage among early Kimmeridgian Ataxioceratinae. Under strict biostratigraphic control, this phyletic line includes species showing persistent phenotype traits such as evolute shells, comparatively spaced and vigorous ribbing and parabolic structures in the phragmocone. In such an interpretation, *Lithacosphinctes* shows a trend to smaller, younger species which have been previously included in other genera—e.g., well-known microconchs such as *Orthosphinctes* (*Ardescia*) *proinconditus* (Wegele in Atrops, 1982), *Orthosphinctes* (*Ardescia*) *schaireri* (Atrops, 1982), *Ataxio-ceras* (*Parataxio-ceras*) *inconditum* (Fontannes in Geyer, 1961) or *Orthosphinctes* (*Ardescia*) *inconditus* (Fontannes in Atrops, 1982), and *Orthosphinctes* (*Ardescia*) *perayensis* (Atrops, 1982).

Ardescia was erected by Atrops (1982) as a subgenus of *Orthosphinctes* to include a variable group of lower Kimmeridgian microconchs lacking ataxioceratoid or subpolyplocoid ribs and showing an accentuated trend to smaller shells in younger species. Hantzpergue (1989) reinterpreted *Ardescia* as a genus-level taxon including the species groups of *Ataxioceras desmoides* Wegele, 1929 (microconchs) and *Perisphinctes pseudoachilles* Wegele, 1929 (macroconchs) and related forms. According to our interpretation of *Ardescia* Atrops, 1982, emend. [m, M], this genus ranges from the uppermost Oxfordian to the lower Kimmeridgian just below the base of the *Crussoliceras divisum* Biozone (the potential occurrence in the earliest part of the *Crussoliceras divisum* Chronozone has not been demonstrated). Showing a comparatively high phenotype plasticity, the reinterpreted taxon *Ardescia* allows the identification of endemic species in the studied area. Microconch shells are up to about 165 mm in size, while macroconchs may be slightly larger than 300 mm. In comparison with *Lithacosphinctes*, *Ardescia* shows a rather tighter coiling, less massive whorl section, more delicate ribs on the inner whorls, and rare parabolic structures. Rib curves decrease from the inner whorls (at least between 20 and 40 mm, as observed in east-Iberian specimens), but can change to sub-horizontal ribbing-curves in larger specimens which show subtle reinforcement of the periumbilical ribs. The ribbing in-

dex in *Ardescia* is higher than in *Lithacosphinctes*, especially in microconchiate specimens. In accordance with the above, morphologically conservative and evolute species formerly included in *Ardescia* (e.g., *Ammonites inconditus* Fontannes, 1879 and *Ataxioceras proinconditus* Wegele, 1929 groups) are reinterpreted as belonging to *Lithacosphinctes*.

Systematic paleontology

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Perisphinctoidea Steinman in

Steinmann and Doderlein, 1890

Family Ataxioceratinae Buckman, 1921

Subfamily Ataxioceratinae Buckman, 1921

(sensu Spath 1930; emend. Zeiss 1968)

Genus *Geyericeras* gen. nov. [m, M]

Etymology: The new taxon *Geyericeras* is dedicated to the late Professor Otto Franz Geyer (1924–2002), ammonitologist and stratigrapher of Upper Jurassic deposits in Iberia and South America.

Type species: *Geyericeras aragoniense* sp. nov.

Diagnosis.—Micro- and macroconchiate ataxioceratids of small size showing moderate to loose coiling. Whorl section subrectangular, narrower in microconchs than in macroconchs. Ribbing dense and delicate on the inner whorls. On the phragmocone ribs are mainly bifurcate, some polygyrate and less frequently subpolyplocoid, which also occur on the inner whorls in macroconchs. Intercalary ribs scarce. On the body-chamber ribs are stronger, rib inter-space slightly wider and subpolyplocoid ribs exist. Ribbing index commonly lower than 4. Rib-curve decreasing from shell size less than 50 mm. No parabolic structures are present. Constrictions common. Lappeted peristome in microconchs.

Remarks.—*Geyericeras* gen. nov. microconchs [m] are smaller than 60 mm while macroconchs [M] have a shell size up to 152 mm. The main phenotype traits defining *Geyericeras* [m, M] are the relatively tight coiling on the inner whorls, the fine and delicate ribbing in microconchs and immature macroconchs, the occurrence of subpolyplocoid ribs, and the stratigraphic range within the upper part of the *Ataxioceras lothari* Biozone identified in the eastern Iberian Chain.

At present, *Geyericeras* gen. nov. includes a single species, *Geyericeras aragoniense* sp. nov. [m, M]. The occurrence of subpolyplocoid ribs in microconchiate specimens is interpreted as forced by high-dense ribbing, and is unconnected to dense ribbing in the outer whorls of macroconchiate specimens. In macroconchs, subpolyplocoid structures result from the complete-to-defective connection of secondary ribs with the adjacent, aboral primary rib. Thus, the occurrence of subpolyplocoid ribs in microconchs resembles the dense-ribbing effect which is well known in *Schneidia* [m, M]. In contrast, in macroconchs the origin of subpolyplocoid ribs is similar to that known in some new endemic taxon from the *Sutneria platynota* Biozone, which clearly differs in ribbing style (under study by LM).

Geyericeras gen. nov. [m] is interpreted as a result of in-situ morphological evolution of Ataxioceratinae on epicontinental shelves of the present-day eastern Iberian Chain, and therefore represents phenotype dynamics related to endemism (see Olóriz et al. 1988; Moliner and Olóriz 1999; Olóriz 2000 for paleoenvironmental considerations). Microconchs show morphological convergence with evolute phenotypes belonging to the stratigraphically older *Schneidia* Atrops, 1982 [m], which developed during the *Schneidia guilherandense* Subchronozone of the *Sutneria platynota* Chronozone. By analogy with *Schneidia* Atrops, 1982 [m, M], *Geyericeras* gen. nov. [m, M] originated from the last-known cladogenetic event in the phylogenetic branch of *Ardescia* Atrops, 1982 [m, M], most probably through: (i) increased discocone structuring of shells and its effects on ribbing before maturity; and (ii) late ontogenetic innovation comprising the development of subpolyplocoid structures manifested with variable timing in the ontogeny of macroconchiate specimens (heterochrony?). Thus, the new genus *Geyericeras* [m, M] is interpreted as having originated within the branch of the older endemic *Ardescia* during the latest *Ataxioceras hippolytense* Chronozone or, alternatively, later within the *Ataxioceras lothari* Chronozone. *Geyericeras* gen. nov. [m, M] represents one of the cul-de-sac phenotype specializations which are common in Lower Kimmeridgian Ataxioceratinae—i.e., the acquisition of double furcations or real subpolyplocoid ribbing.

The resulting extreme phenotypes left no descendants, most probably because they reached a maximum for ribbing specialization in Ataxioceratinae through the combination of shell type and sculpture. Earlier in the Kimmeridgian, this ammonite group experienced analogous evolutionary changes in phenotype expression, resulting in the origination of other genera such as *Schneidia* [m, M] and new endemic forms during the *Sutneria platynota* Chronozone.

Geyericeras gen. nov. [M] differs from its microconchs through both the significantly larger adult size and wider, coarser but comparatively weakened primary ribs. However, difficulties arise in differentiating incomplete or immature specimens of similar shell size. Whatever the case, macroconchs of *Geyericeras* have more robust shells and show less frequent constrictions.

Geyericeras gen. nov. [m] is clearly separated from *Ardescia* Atrops, 1982 [m] on the basis of a finer and tighter ribbing, as well as by the more or less regular development of subpolyplocoid ribs.

Geyericeras gen. nov. [m] is typically more evolute than *Schneidia* Atrops, 1982 [m] at their respective largest shell sizes. These two taxa are recorded from the eastern Iberian Chain, the former within the uppermost *Ataxioceras lothari* Biozone and the latter in deposits from the upper part of the *Sutneria platynota* Biozone, as observed elsewhere (e.g., Atrops 1982; Marques 1983; Olóriz and Rodríguez-Tovar 1993; Bachnou and Atrops 1996; Gradl and Schairer 1997; Villaseñor et al. 2000). *Schneidia* [M] shows short, reinforced, periumbilical ribs that are unknown in *Geyericeras* [M].

Lithacosphinctes Olóriz, 1978 [m, M] is more evolute than *Geyericeras* gen. nov. [m, M] and developed larger and stouter shells with less dense and coarser ribbing. Moreover, *Lithacosphinctes* [m, M] developed parabolas and has no polyplocoid or subpolyplocoid ribbing. Finally, the majority of the stratigraphical range of *Lithacosphinctes* [m, M] predates the appearance of *Geyericeras* gen. nov. [m, M] in the eastern Iberian Chain.

Ataxioceras Fontannes, 1879 [m] shows less dense ribbing than *Geyericeras* gen. nov. [m], and true polyplocoid ribs are typical in large microconchs of *Ataxioceras*. *Ataxioceras* [M] exhibits rib curves similar to those of *Geyericeras* [M], although its ribbing is very different, with a typical trend toward reducing reinforced primary ribs to the periumbilical zone in late ontogeny. In addition, *Ataxioceras* [M] shows a narrow-oval whorl section with a narrow venter and slightly convex flanks, whereas the whorl section in *Geyericeras* [M] is subrectangular with flattened flanks and a wide, slightly arched venter.

Parataxioceas Schindewolf, 1925 [m, M] developed larger and more evolute shells than *Geyericeras* gen. nov. [m, M], and has ribs which are stronger, less dense, and show parabolic structures. In addition, subpolyplocoid ribbing in *Parataxioceas* [m] is not related to dense ribbing as it is in *Geyericeras* [m].

No ammonites similar to *Geyericeras* gen. nov. [m, M] have been described from equivalent horizons in epicontinental shelves from southern Europe. Therefore, *Geyericeras* is interpreted as endemic, restricted to the eastern Iberian Chain.

Stratigraphic and geographic range.—Uppermost part of the *Ataxioceras lothari* Biozone (youngest part of the *Ataxioceras hypselocyclum* Chronozone) in the eastern Iberian Chain.

Geyericeras aragoniense sp. nov. [M, m]

Figs. 2–5, 7, 8.

Etymology: Refers to Aragón, the Spanish region which includes the province of Teruel, where the research was undertaken.

Type material: Holotype: UGR MLG.23.20; Fig. 7A; microconch recovered from bed number 23 in the Reservoir of Calanda section UGR MLG (Teruel Province, Spain). Paratypes [m]: UGR MPC.28.15, UGR MPC.28.72, UGR MPC.28.73, UGR MPC.29.8, UGR MLG.23.20, UGR MLG.23.23, UGR MBV'.21.1, UGR MPR.36.1. Paratypes [M]: UGR MBV'.21.2, UGR MPC.29.1, UGR MPR.36.10, UGR MPR.36.20, UGR MPR.36.21, UGR MPR.36.22, UGR MPR.36.24.

Type locality: Reservoir of Calanda, Calanda (province of Teruel, Spain).

Type horizon: Lower Kimmeridgian, *Ataxioceras lothari* Biozone, *A. lothari* Subzone, *Geyericeras aragoniense* biohorizon.

Included species: Only the type species.

Diagnosis.—Microconch: maximum adult diameter about 60 mm, moderate-to-low coiling degree ($U/Dm = 33\text{--}42\%$), and subrectangular whorl-section. Constrictions common, indistinct, limited by an adoral, incipiently reinforced edge. Ribs fine, mainly bifurcate in low angle; some polygyrates, intercalatory and less commonly subpolyplocoid ribs close

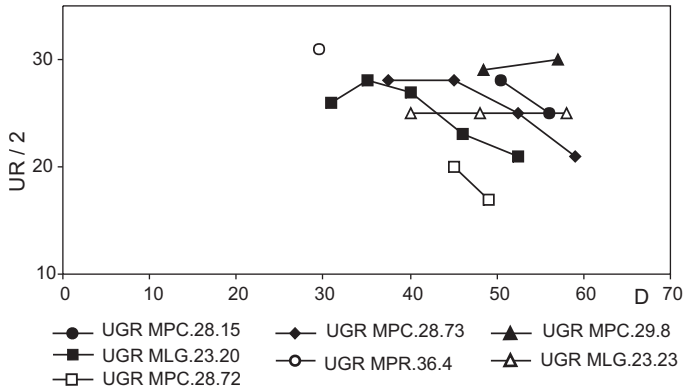


Fig. 2. Rib curve per half-a-whorl of *Geyericeras aragoniense* sp. nov. [m].

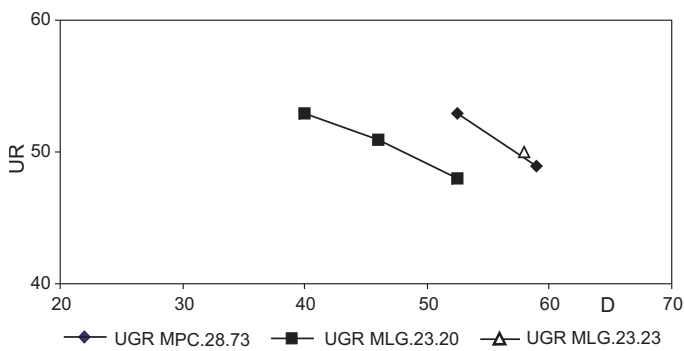


Fig. 3. Rib curve per complete whorl of *Geyericeras aragoniense* sp. nov. [m].

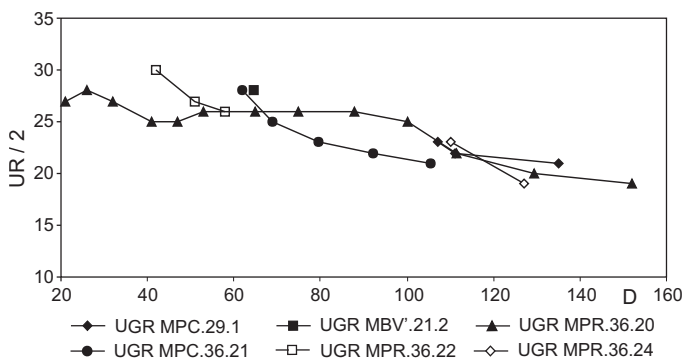


Fig. 4. Rib curve per half-a-whorl in *Geyericeras aragoniense* sp. nov. [M].

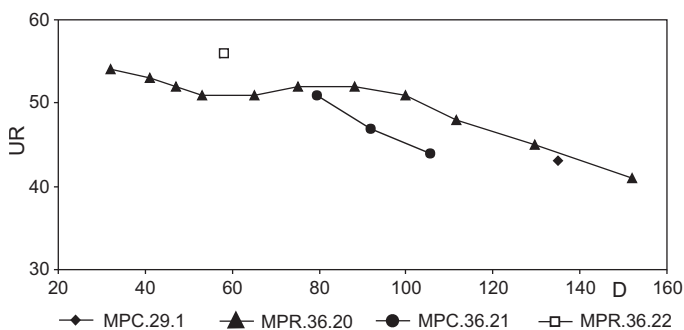


Fig. 5. Rib curve per complete whorl in *Geyericeras aragoniense* sp. nov. [M].

to the peristome. Body-chamber about three quarters to a complete whorl long. Generally, the rib curve per half-a-whorl decreases for shell sizes less than 50 mm, but cases in which it slightly increases are known. Peristomal structures unknown, but adoral convexity of ribs occurs close to the end of the body-chamber.

Macroconch: maximum adult size about 160 mm, evolute to very evolute (37–52%) with subrectangular whorl section. Constrictions common, narrow and shallow. Scarce subpolyplocoid ribs on the phragmocone and more frequent on the body-chamber. Rib curves per complete whorl and per half-a-whorl decrease in shells smaller than 40 mm. The body-chamber is about a whorl long; peristome simple.

Description.—The holotype UGR MLG.23.20 [m] (Figs. 2, 3, 7A) is 52.5 mm in size and shows a coiling degree of 41%. This specimen preserves slightly more than three-quarters of the spire pertaining to the body-chamber, which begins at ca. 34 mm. The whorl section is slightly subrectangular with flattened flanks. Seven narrow and oblique constrictions can be seen on the outer whorl. Ribs are crowded and bifurcate, and some polygyrate and subpolyplocoid ribs are present in the mature shell. The ribbing index slightly varies, generally around 2.5, and the rib curve per half-a-whorl decreases from 35 mm onwards (Fig. 2).

Among microconch paratypes (measurements in Table 1), UGR MLG.23.23 (Figs. 2, 3) is morphologically very similar to the holotype but slightly greater in size—58 mm in diameter. Three-quarters of the outer whorl belong to the body-chamber, which starts at 34.5 mm of the shell diameter. Six constrictions are observed on the outer whorl. Ribbing is similar to the holotype and slightly prorsiradiate, showing a single, incomplete subpolyplocoid rib towards the end of the preserved shell. The rib curve per half-a-whorl is horizontal from at least 40 mm in shell size (Fig. 2).

UGR MPC.28.15 (Figs. 2, 7C) is 56 mm in size and slightly more involute (U/Dm ratio 38%). The outer three-quarters of the outer whorl belong to the body-chamber, showing at least five more-or-less distinct constrictions and fine, dense, rather rigid and prorsiradiate ribs that bifurcate through low angles close to the shell periphery. Close to the end of the preserved inner mould there are some intercalatory and subpolyplocoid ribs.

UGR MPC.29.8 (Figs. 2, 7B) is 57 mm in size and shows a wide, slightly arched venter. The body-chamber starts at 34 mm and occupies slightly more than three-quarters of the outer whorl, showing at least four rather indistinct constrictions, which are shallow, narrow and oblique to the fine, prorsiradiate and dense ribbing. Furcations through small angles are close to shell periphery, and there are indistinct rib divisions allowing for individualization of a single rib from its adjacent intercalatory rib in rare cases. The ribbing index is low—2.6. Towards the end of the ontogeny, the rib curve per half-a-whorl increases gradually (Fig. 2).

UGR MPC.28.73 (Figs. 2, 3, 7D) reaches 59 mm in size and is very similar to the holotype. Constrictions occur from the inner whorls onwards, and at last five oblique and rather

Table 1. Measurements of *Geyericeras aragoniense* sp. nov. [m]; (*) for approximate values.

	Dm	Ph	U	H	U/Dm	H/Dm	U/H	UR	UR/2	RI	C
UGR MPC.28.15.	56	–	21	20	0.38	0.36	1.05	–	25	–	5*
	50.5	–	19	–	0.38	–	–	–	28	–	–
UGR MPC.28.73	59	32	24	22	0.41	0.37	1.09	49	21	4	5*
	52.5	–	20	20	0.38	0.38	1.00	53	25	–	–
	45	–	17	14	0.38	0.31	1.21	–	28	2.6	–
	37.5	–	12.5	13	0.33	0.35	0.96	–	28	–	–
UGR MPC.29.8	57	34	21.5	20	0.38	0.35	1.08	–	30	–	4*
	48.5	–	17	18.5	0.35	0.38	0.92	–	29	2.2	–
	43	–	14.5	15.5	0.34	0.36	0.94	–	–	2.6	–
UGR MPC.28.72	49	–	20	17.5	0.41	0.36	1.14	–	17	–	7
	45	–	19	14.5	0.42	0.32	1.31	–	20	2.5	–
UGR MLG.23.20	52.5	34	21.5	18	0.41	0.34	1.19	48	21	2.5	7
Holotype	46	–	19	15.5	0.41	0.34	1.23	51	23	2.4	4
	40	–	–	–	–	–	–	53	27	–	–
	35	–	–	–	–	–	–	–	28	–	–
	31	–	–	–	–	–	–	–	26	–	–
UGR MPR.36.4	29.5	–	10	13	–	0.44	0.77	57	31	1.8	4
UGR MLG.23.23	58	34.5	21	21	0.36	0.36	1	50	25	2.9	6
	48	–	18	17.5	0.38	0.36	1.03	–	25	2.8	4
	40	–	–	16	–	0.4	–	–	25	2.4	1
	33	–	–	12.5	–	0.38	–	–	–	–	–

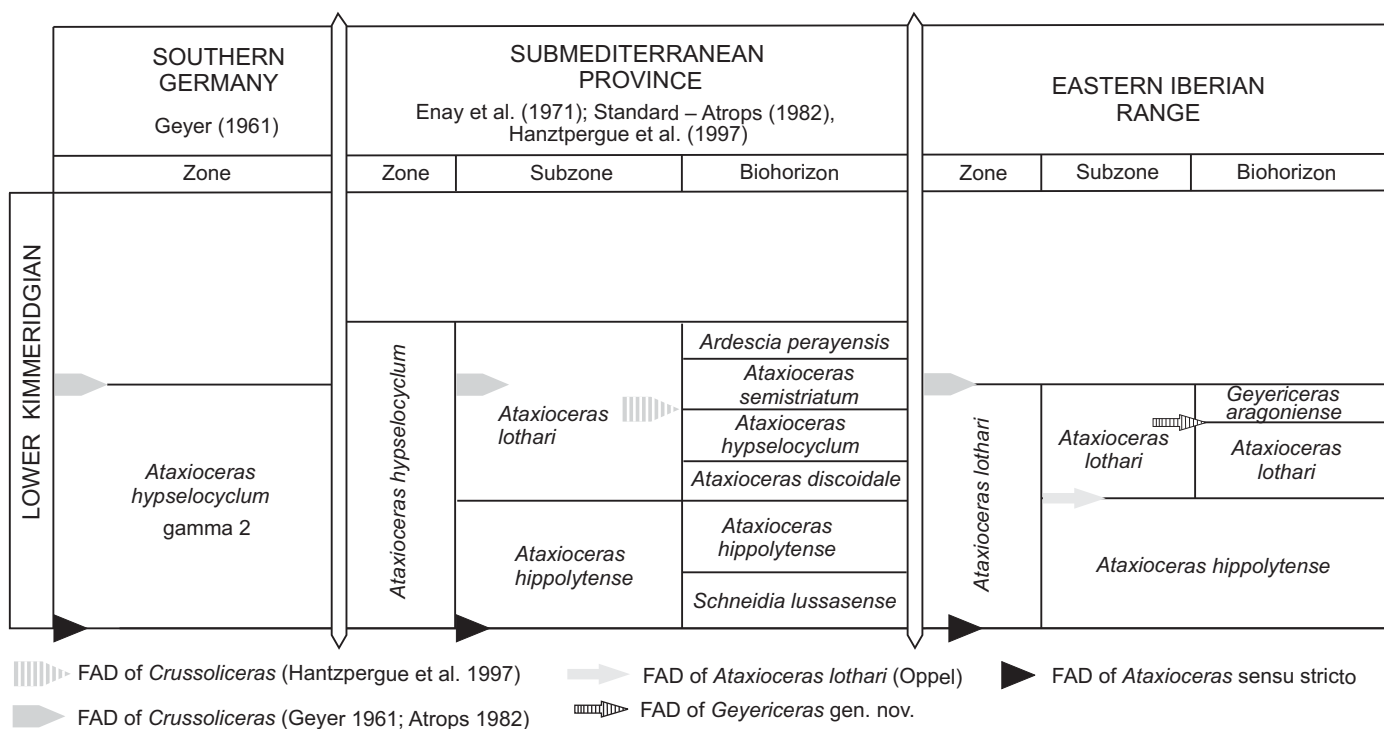


Fig. 6. Stratigraphic position of the *Geyericeras aragoniense* biohorizon recognized in the eastern Iberian Chain and biostratigraphic correlation of the regional *Ataxioceras lothari* Zone with the Secondary Standard *Ataxioceras hypselocyclus* Zone used in epicontinental sections from southern Europe.

indistinct constrictions can be observed in the outer whorl, as identified in UGR MPC.28.15. The body-chamber extends across ca. 320°. Rib crowding diminishes toward the end of the shell, some polygyrate ribs exist, and the rib index increases abruptly from 2.6 to 4.0. The rib curve per half-whorl decreases from 45 mm in shell size onwards (Fig. 2).

The small-sized macroconchs show decreasing coiling degree throughout ontogeny (37–52%, see Table 2). The whorl section is subrectangular with flattened flanks, rounded periumbilical edge, abrupt umbilical wall, and wide, slightly convex venter. The body-chamber occupies an entire whorl. The peristome is simple. Constrictions are rather nar-

Table 2. Measurements of *Geyericeras aragoniense* sp. nov. [M]; (*) for approximate values.

	Dm	Ph	U	H	U/Dm	H/Dm	U/H	UR	UR/2	RI	C
UGR MPC.29.1	135.0	104	66.0	37.5	0.49	0.28	1.76	43	21	–	1
	111.0	–	53.0	32.0	0.48	0.29	1.66	–	22	–	–
	107.0	–	45.5	31.0	0.43	0.29	1.47	–	23	–	–
	86.5	–	37.5	28.5	0.43	0.33	1.32	–	–	–	–
UGR MBV*.21.2	64.5	64.5	24.0	25.0	0.37	0.39	0.96	–	28	2.7	3
UGR MPR.36.20.	152.0	91	77.5	43.5	0.51	0.29	1.78	41	19	–	5
	129.5	–	63	36.5	0.49	0.28	1.73	45	20	–	3*
	111.5	–	54.0	31	0.48	0.28	1.74	48	22	4	–
	100.0	–	–	28	–	0.28	–	51	25	–	–
	88.0	–	–	–	–	–	–	52	26	–	–
	75.0	–	–	–	–	–	–	52	26	–	–
	65.0	–	–	–	–	–	–	51	26	–	–
	53.0	–	–	–	–	–	–	51	26	–	–
	47.0	–	–	–	–	–	–	52	25	–	–
	41.0	–	–	–	–	–	–	53	25	–	–
	32.0	–	–	–	–	–	–	54	27	–	–
	26.0	–	–	–	–	–	–	–	28	–	–
	21.0	–	10.0	–	0.48	–	–	–	27	–	–
UGR MPR.36.21.	105.5	68.0	48.5	30	0.46	0.28	1.62	44	21	4.5	4
	92.0	–	41.0	28.5	0.45	0.31	1.44	47	22	3.8	4
	79.5	–	–	25	–	0.31	–	51	23	3.8	3*
	69.0	–	–	23	–	0.33	–	–	25	–	–
	62.0	–	–	–	–	–	–	–	28	–	–
UGR MPR.36.22	125	110	65	44	0.52	0.35	1.48	–	–	–	–
	58.0	–	22.0	–	0.38	–	–	56	26	–	–
	51.0	–	–	–	–	–	–	–	27	–	–
	42.0	–	–	–	–	–	–	–	30	–	–
UGR MPR.36.24.	127.0	87.0	60.0	35	0.47	0.28	1.71	–	19	–	4*
	110.0	–	48.5	33	0.44	0.30	1.47	–	23	–	2*
	98.0	–	–	32	–	0.33	–	–	–	3.4	–
	83.0	–	–	28.5	–	0.34	–	–	–	–	–

row, shallow, indistinct, oblique to ribbing, and adorally limited by a reinforced edge which is slightly stronger than the primary ribs. No parabolic structures were observed. Ribbing is dense, coarse and subtly prorsiradiate on the inner whorls. Whorl overlap prevents the analysis of secondary ribs on the inner whorls. On the outer whorls, ribs bifurcate through small angles and irregular polygyrate ribs show furcation points high on the flanks. Relative widening of the primary ribs is evident from the end of the phragmocone onwards. Secondary ribs are subtle and the rib index is relatively low, fluctuating around 3. Body-chamber sculpture consists of common subpolyplocoid ribs showing the lower primary/secondary rib connection on the inner half of the flank. Examples of quasi-subpolyplocoid ribs can be observed in both the phragmocone and the body-chamber, as resulting from defective connections between primary and secondary ribs. Relative sculpture smoothing and weakening of connection points among primary and secondary ribs increase along with shell size. Rib curves per complete whorl and per half-a-whorl decrease from shell size even less than 30 mm, and cases of rib curves showing variable (“undulated”) trajectory are known (Figs. 4, 5).

Among macroconch paratypes (measurements in Table 2), UGR MPR.36.20 (Figs. 4, 5, 8) has a shell 152 mm in size and

48% to 51 % in U/Dm ratio, common subpolyplocoid ribs and five indistinct constrictions on the outer whorl. Rib interspaces increase toward the end of ontogeny, and weakening of the sculpture occurs across the flank, affecting the clear definition of ribs connections. The occurrence of a simple, rigid and slightly reinforced rib close to the end of the preserved inner mould suggests that the peristome is simple and subtly oblique to the prorsiradiate ribbing. The ribbing index is 4.0 at 100 mm in shell size. Rib curves per complete and half-a-whorl decrease and show a slightly variable course (“undulated”) from 32 mm in shell size (Figs. 4, 5). The body-chamber extends across almost the entire outer whorl.

UGR MPR.36.21 (Figs. 4, 5) reaches 105 mm in shell size and shows a U/Dm ratio of 45–46% toward the end of the shell. Constrictions are common (four on the body-chamber), very narrow, shallow, oblique to ribbing and limited by an adoral edge of relief similar to that shown by primary ribs. Primary ribs are subtly prorsiradiate, crowded and relatively coarse, increasing in both wideness and inter-rib spacing throughout the ontogeny. From the adoral quarter of the phragmocone onwards, ribs are low-angle bifurcates showing some intercalatories, or they are irregular polygyrate ribs without intercalatories. Rib subdivisions are located close to the external quarter of the flank and peripheral or secondary

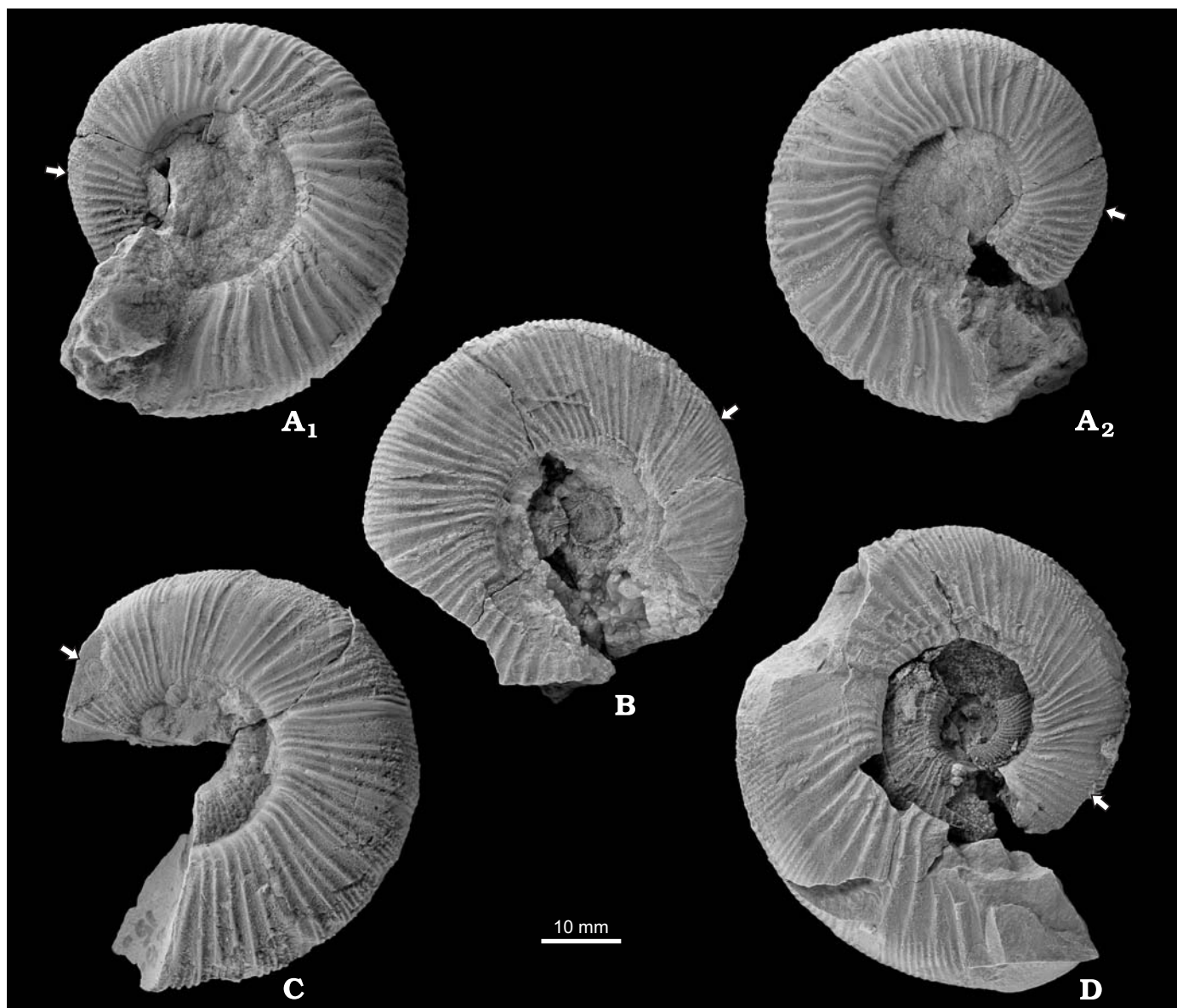


Fig. 7. Ataxioceratin ammonite *Geyericeras aragoniense* sp. nov. [m] from the Lower Kimmeridgian *Ataxioceras lothari* Biozone, *A. lothari* Subzone, *G. aragoniense* biohorizon in the eastern Iberian Chain, Spain. **A.** Holotype UGR MLG.23.20; Reservoir of Calanda section in the Calanda area, in left (**A₁**) and right (**A₂**) side views. **B.** Paratype UGR MPC.29.8; Morrón section at the Calanda area, in right side view. **C.** Paratype UGR MPC.28.15; Morrón section at the Calanda area, in left side view. **D.** Paratype UGR MPC.28.73; Morrón section at the Calanda area, in right side view. Arrows indicate the beginning of the body chamber. Scale for shell size reference.

ribs are weaker than primary ones. Subpolyplocoid ribs occur on the camerate shell and are common on the body-chamber, which starts at 68 mm and extends slightly more than 225°. The ribbing index increases up to 4. Rib curves per complete and half-a-whorl decrease from 79 mm and 62 mm in shell size, respectively—which are the smallest shell sizes for which measurements were available (Figs. 4, 5).

UGR MPR.36.22 shows inner whorls very similar to those of UGR MPR.36.20 but sculptured with a more dense ribbing, which no doubt relates to the occurrence of some subpolyplocoid ribs (UR = 56 at 58 mm in shell diameter). The unfavourable preservation of the outer whorl impedes precise description other than identification of a single, indis-

tinct constriction and slightly prorsiradiate and rigid ribs with very external and low-angle furcations.

UGR MPR.36.24 (Fig. 4) is 127 mm in size and preserves the end of the phragmocone and three-fourths of the body-chamber, which starts at 87 mm. The shell coiling fluctuates between 44% and 47% in the outer whorls. Towards the end of the phragmocone and the beginning of the body-chamber ribs are slightly prosiradiate, rigid and coarse, showing low-angle bifurcations placed very high on the flanks. One or two intercalatory ribs occur in inter-ribs spaces, which determine a ribbing index of 3.4. Four subpolyplocoid ribs have their second connection points on the inner one-third of the flank. On the outer half-a-whorl ribs are more distant, weaker, with indis-

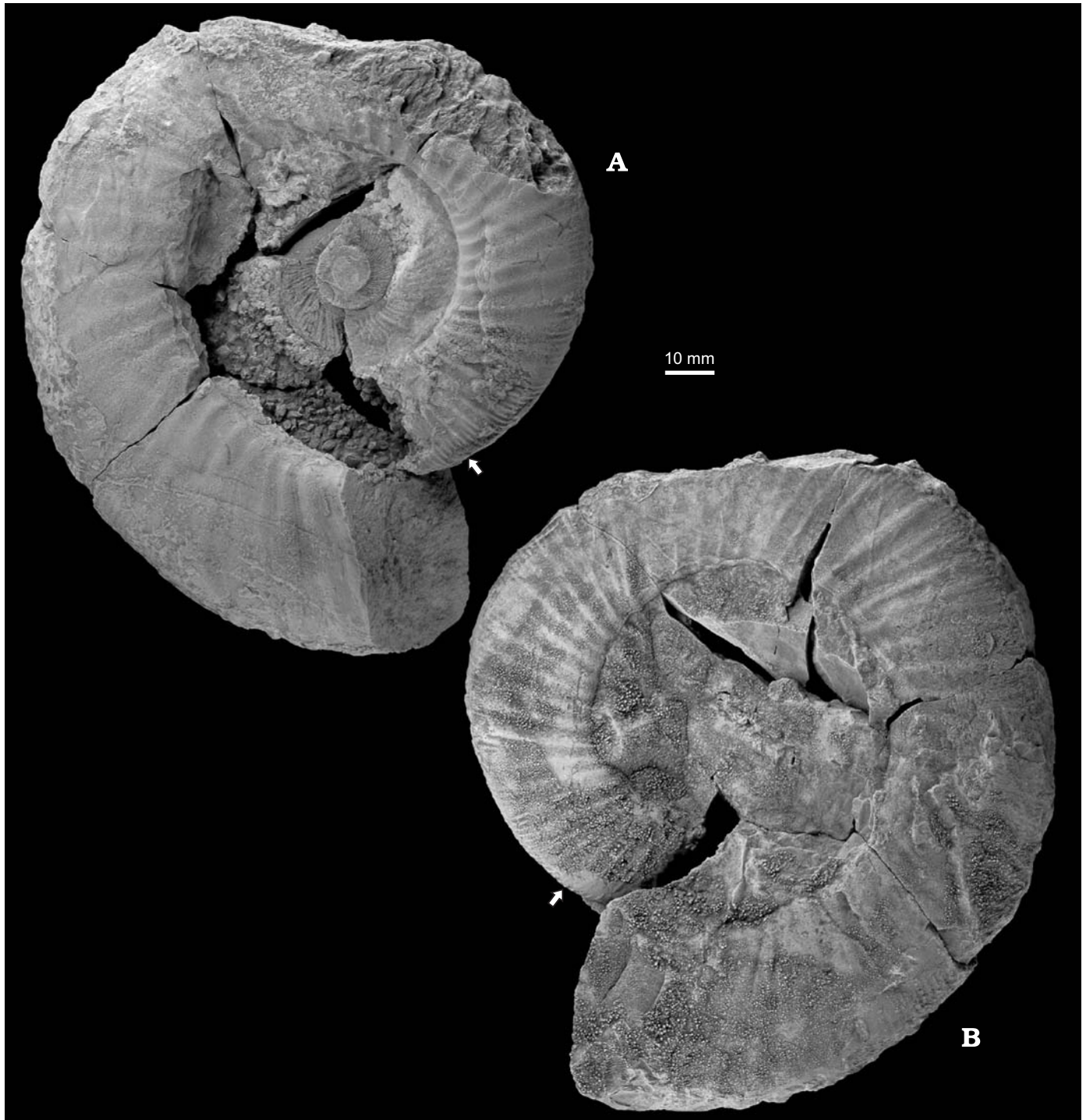


Fig. 8. Ataxioceratin ammonite *Geyericeras aragoniense* sp. nov. [M] from the Lower Kimmeridgian *Ataxioceras lothari* Biozone, *A. lothari* Subzone, *G. aragoniense* biohorizon in the eastern Iberian Chain. Paratype UGR MPR.36.20; Guadalupe River section at the Villarluengo area, in right (A) and left (B) side views. Arrows indicate the beginning of the body chamber. Scale for shell size reference.

tinct connection points between primaries and secondaries. Four narrow, shallow and indistinct constrictions showing an adoral, reinforced ridge are observed on the body-chamber.

UGR MPR.36.10 is an incomplete specimen (73 mm) showing the end of the phragmocone at 70 mm. The U/Dm ratio increases throughout the ontogeny from 37% to 47%. Ribs are dense, fine and slightly prorsiradiate (UR = 45; UR/2 = 27

at 45 mm), showing indistinct connection points between primary and secondary ribs. The occurrence of two or three subpolyplocoid ribs is related to dense ribbing. In the last preserved whorl ribs bifurcate very high on the flanks, there is one intercalatory rib per inter-rib space, and two subpolyplocoid ribs are evidence of the occurrence of the innermost connection points close to the periumbilical edge. The ribbing index

is 3.4 at the end of the preserved shell. Constrictions exist on the inner whorls. Two of these constrictions, narrow and shallow, can be identified on the outer whorl preserved.

UGR MPC.29.1 (Figs. 4, 5) shows both fewer constrictions and a similar but weaker sculpture. UGR MBV'.21.2 (Fig. 4) corresponds to a camerate shell at 64.5 mm, and shows oblique, indistinct constrictions, three of which are observed on the outer whorl that belongs to the phragmocone. Ribbing is dense, prorsiradiate and bifurcates between the external one-third and one-fourth of the flank. Intercalary ribs occur occasionally, and subpolyplocoid ribs are scarce.

Complementary material, interpreted as *Geyericeras* cf. *aragoniense* sp. nov. [M, m], consists of septate internal moulds and more or less complete body-chambers showing coiling degree and sculpture equivalent to those described above (microconchs: UGR MTG2.33.1, UGR MVP.59.2, UGR MPC.28.16, UGR MPC.28.61, UGR MPC.28.78, UGR MPC.29.9, UGR MPC.29.11, UGR MPC.29.24, UGR MPC.29.26, UGR MPC.29.27, UGR MLG.23.2, UGR MLG.23.10, UGR MLG.23.13, UGR MLG.23.14, UGR MLG.23.19, UGR MPR.35.1, UGR MPR.36.4, UGR MPR.36.13, UGR MPR.36.14, UGR MPR.36.15; and macroconchs: UGR MVP.57.7, UGR MPC.28.70, UGR MPC.28.74, UGR MPC.29.13, UGR MLG.23.5, UGR MPR.35.4, UGR MPR.36.9, UGR MPR.36.12).

Stratigraphic and geographic range, associated ammonites and correlation potential.—The stratigraphic range of *Geyericeras aragoniense* sp. nov. [m, M] is restricted to the upper part of the *Ataxioceras lothari* Subzone, *A. lothari* Biozone, in lower Kimmeridgian deposits from the eastern Iberian Range, where it serves to identify and denominate the *G. aragoniense* biohorizon, below the FAD of *Crussoliceras* (Fig. 6).

The ammonite assemblage to which *Geyericeras aragoniense* sp. nov. [m, M] belongs consists of endemic *Ardescia* [m, M] (under study), *Lithacosphinctes inconditus* (Fontannes, 1879) [m, M], *Lithacosphinctes* sp. nov. gr. *L. perayensis* (Atrops, 1982) [m], *Lithacosphinctes* sp., *Parataxiceras* gr. *evolutum* Atrops, 1982 [m, M], *Ataxioceras lothari* (Oppel, 1863) morphotypes *A. lothari lothari* Oppel, 1863 [m, M] and *A. lothari semistriatum* Schneid, 1944 [m], *Ataxioceras* sp. [m, M] and other Ataxioceratinae [m, M]. Among other ammonites are *Aspidoceras* gr. *linaresi* Checa, 1985, *Aspidoceras* sp. gr. *binodum* (Oppel, 1863), *Aspidoceras sesquinosum* (Fontannes, 1876 in Dumortier and Fontannes 1876), *Aspidoceras sesquinosum* (Fontannes, 1876 in Dumortier and Fontannes 1876), *Pseudowaagenia micropla* (Oppel, 1863), *Physodoceras wolfi* (Neumayr, 1873), and other indeterminate aspidoceratins; rare *Nebroditis* sp., *Glochiceras* s. l., *Metahaploceras* gr. *subnereus* (Wegele, 1929), *Metahaploceras* sp., and *Streblites* sp. have also been identified.

The *Geyericeras aragoniense* biohorizon encompasses the stratigraphic interval between the FAD of *Geyericeras aragoniense* sp. nov. [m, M] and the FADs of *Crussoliceras* Enay, 1959 [m, M] and *Garnierisphinctes* Enay, 1959 [m, M]. Since ataxioceratid ammonites do not show major differences in the underlying *Ataxioceras lothari* biohorizon identified

within the *A. lothari* Biozone (Fig. 6), and the lower boundary is defined by the FAD of an endemic taxon, the index species *Geyericeras aragoniense* sp. nov. [m, M], the precise correlation potential of the *G. aragoniense* biohorizon is somewhat restricted to the assumption of “isochrony” for its upper boundary, which is defined by the FAD of the widespread taxon *Crussoliceras*. Future improvement of the correlation potential of the *G. aragoniense* biohorizon is envisaged on the basis of accompanying ammonite taxa other than Ataxioceratinae (research in progress by the authors).

Conclusions

Intensive sampling of ammonites from *Ataxioceras lothari* Chronozone deposits (the local equivalent of the secondary standard *Ataxioceras hypselocyclum* Chronozone as reinterpreted by Moliner and Olóriz 2009b) below the FAD of *Crussoliceras* provides new insights into the evolution of ataxioceratid ammonites and shows their usefulness for accurate biostratigraphy in the eastern Iberian Chain.

The new genus *Geyericeras* is proposed, including micro- and macroconch ataxioceratins of small size, which developed subpolyplocoid ribs. The *Geyericeras* microconch provides a new example of morphological convergence with evolute specimens of other, stratigraphically older ataxioceratins, such as *Schneidia* [m]. The macroconchs of *Geyericeras* gen. nov. clearly differ from macroconchs of *Schneidia* in the development of their sculptural elements.

Contemporary Ataxioceratinae can be distinguished from *Geyericeras* gen. nov. on the basis of: (i) lacking subpolyplocoid ribbing (e.g., *Ardescia* [m, M] and *Lithacosphinctes* [m, M]); (ii) smoothing of ephebic sculpture together with development of short primary ribs (e.g., *Ataxioceras* [M]); and (iii) the combination of greater shell size with stronger, comparatively distant ribs, and real polyplocoid and parabolic structures (e.g., *Parataxiceras* [m, M]).

The new genus *Geyericeras* is proposed for Lower Kimmeridgian ammonites collected from the upper part of the *Ataxioceras lothari* Biozone in the eastern Iberian Chain. The single identified species *Geyericeras aragoniense* sp. nov. is used as the index and guide fossil for identifying the *G. aragoniense* biohorizon below the FAD of *Crussoliceras* in the eastern Iberian Chain.

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