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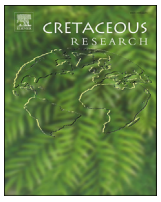

Mortoniceratinae (Ammonoidea) from the lower upper Albian of the Basque-Cantabrian basin (Western Pyrenees): New records, new taxa and their taxonomic and biostratigraphical value

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ABSTRACT

The subfamily Mortoniceratinae comprises Albian to early Cenomanian ammonoids whose phylogeny forms the basis of a biozonation for the upper Albian due to their highly evolving nature and worldwide distribution. However, both morphological plasticity of the group and the known common occurrences in many condensed successions call for accurate taxonomy and stratigraphy in order to ascertain the phylogeny and temporal/spatial relationships. Here, early late Albian Mortoniceratinae from mostly uncondensed successions, with a continuous record, are described from a hyperextended pericratonic rift basin in the Western Pyrenees. Although quite rare in the study area, we can here provide a detailed taxonomic study of 55 specimens, representing 19 species, with a single new genus and five new subspecies, all recovered over a period of 30 years from upper Albian strata in eight sedimentary areas covering nearly 1000 square kilometres and more than 4000 m of measured logs. Most of these mortoniceratines show morphologies that are in agreement with their known and accepted phyletic lineage in which tuberculation stages are key; however, we also record tri- and quadrituberculate forms that depart from the main and represent unsuccessful offshoots. A reassessment of *Mortoniceras* (*M.*) *fallax* is presented, inclusive of a more complete, emended diagnosis, and referral of the eponymous biozone to the lower upper Albian. The palaeobiogeographical distribution of species studied corresponds to the western Mediterranean area, part of the central Tethyan Realm, in the Basque-Cantabrian Basin (Western Pyrenees) which faces the northern European basins of the Boreal Realm. This strategic location is interpreted to be a nexus between worldwide basins, as the striking cosmopolitan character of most species studied suggests. The ammonoid fauna studied is proposed as support of the western Mediterranean biozonation; it is tentatively correlated interregionally as well.

1. Introduction

The subfamily Mortoniceratinae Douvillé, 1912 comprises late Albian to early Cenomanian brancoceratids (Ammonitina, Acanthoceratoidea) whose morphological changes through time have traditionally formed the basis for a biostratigraphical division of the upper Albian substage, together with other brancoceratid relatives (e.g., Owen, 1976). However, despite being cosmopolitan elements, their relative abundance (scarce in many successions) and the high morphological diversity found in separate basins have hampered accurate taxonomic relationships to be established. Actually, this group underwent several phases of lumping and splitting (e.g., South African forms; van Hoepen, 1931, 1941, 1946, 1951). During the last decades, many workers have tried to understand the phylogeny of the group better (e. g., Scholz, 1979; Renz, 1982; Kennedy et al., 1998), a prerequisite for a reliable biostratigraphy. From the early days in studies of Albian ammonoids in the European province, there have been attempts to construct a comprehensive biostratigraphy (e.g., Jacob, 1908 for France), leading to global correlation of stratigraphical units with identical or similar faunal components (e.g., Haas, 1942 for Angola). Spath (1941) divided the English Gault (Albian) into four ammonoid zones (and 12 subzones), subsequently modified (Owen, 1976). Unfortunately, most of studies mentioned above

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pertain to ammonoid occurrences in successions with condensed beds which yield well-preserved specimens, but represent an admixture of species from distinct biozones. However, the Folkestone (UK) succession (Spath, 1941) provided a comprehensive account of the ammonoid succession, with the upper Albian part being reference to occurrences of Brancoceratidae.

Basins with thick mid-Cretaceous successions provide the key for a better understanding of the evolution of this group and one of the best examples of this kind is the Basque-Cantabrian Basin (BCB, Western Pyrennes, northern Spain; Fig. 1). For this area, Wiedmann (1962) and Wiedmann and Kauffman (1978) produced a biozonation. The latter authors pointed out that, "this region can be regarded as one of the key regions for study and definition of the "Middle" Cretaceous" (Wiedmann and Kauffman, 1978, p. III.1), highlighting the great sedimentary thickness lacking condensation in most cases, excellent exposures, a variety of marine environments, and fossil assemblages from both Mediterranean (Tethyan) and northern European (Boreal) realms that assist in correlations and subsequent integrated biostratigraphy. During recent decades, work on Aptian-Albian successions in the BCB have demonstrated what Wiedmann and Kauffman (1978) noted, providing accurate accounts of new occurrences of Aptian (e.g., García-Mondéjar et al., 2009; Najarro et al., 2011) and Albian (López-Horgue et al., 1999, 2009; Millán et al., 2014) ammonoids and of their biozonation. Owen (1999) and López-Horgue et al. (1999) introduced an ammonite biozonal scheme for the upper Albian of the western Mediterranean area (Tethyan Realm) after modification of that introduced by Wiedmann and Kauffman (1978). This scheme is the first attempt at biozonal correlation since it is based on occurrences of cosmopolitan brancoceratids in both European (England-based) and Tethyan areas. Additionally, Amédro (e.g., 1981, 2002; amended by Kennedy and Latil, 2007) introduced a comprehensive biozonation for most of the upper Albian based on the phyletic succession of mortoniceratines in which the first occurrences of index taxa are used to define interval biozones. Amedro's scheme was adopted by the Lower Cretaceous Ammonite Working Group (Kilian Group) in 2010 (Reboulet et al., 2011), and recently (2022) improved by the same group (Szives et al., 2023b).

Despite the improved stratigraphy of the Aptian-Albian successions in the Western Pyrenees, most earlier works document nominal determinations of ammonite species or genera only; taxonomic descriptions are few and far between (e.g., Wiedmann and Boess, 1984).

For the present paper, we have studied for the first time the detailed taxonomy of 55 specimens of mortoniceratines from the lower upper Albian of the Western Pyrenees. This succession shows variable thicknesses from near 200 m to 1700 m due to a tectonic control during the Albian with structural shallower highs facing deeper troughs bounded by active faults. Ammonoids have been found in a variety of facies at different beds, from offshore prodelta facies to turbiditic troughs and submarine volcaniclastics, but they are usually rare. This explains why this collection took more than 30 years to amass, via bed by bed recovery, allowing detailed stratigraphical successions to be documented.

Improvement of our knowledge of this subfamily and of accurate occurrences at localities studied will result in a better understanding of the phylogeny of the group and in reinforcing the commonly adopted biozonal scheme for the western Mediterranean (López-Horgue and Owen, 2022), as part of the Tethyan subtropical province facing the northern European colder region.

2. Geological setting and stratigraphy

The Western Pyrenean area developed as part of the Pyrenean Mesozoic rift system which originated as a result of the breakup between Iberian and European plates, leading to the opening of the Bay of Biscay (e.g., Jammes et al., 2009). Accordingly, the basin here (Fig. 1) formed from the Triassic to the Albian after several phases of important crustal thinning (Barnolas and Pujalte, 2004). During the Aptian–Albian, increased faulting and stretching of the crust led to a hyperextension phase with lithospheric mantle exhumation (e.g., Tugend et al., 2015) that created high subsidence rates and volcanism as main basin-controlling factors. In the Albian–Cenomanian transition, rift structures substantially became less active giving way to a long-ranging thermal subsidence phase (e.g., López-Horgue et al., 2014). Under these circumstances the pericratonic BCB showed during the Aptian-Albian a tectonic architecture with relative highs bounded by faults, with shallow coastal to marine sedimentation, that faced deeper troughs with main deeper-water siliciclastic sediments (e.g., Agirrezabala and López-Horgue, 2017). The overall lower upper Albian succession in the BCB shows near 400 m shallow-marine carbonate successions on highs, coeval to 1000–3000 m thick siliciclastic trough deposits of deltaic, turbiditic and submarine volcanic origin (e.g., López-Horgue et al., 2009, fig. 4). One of the studied successions, the Armintza section (Fig. 1), represents sediments deposited on the northern, narrower, margin of the basin where active faults controlled rapid transitions from shallow coastal to marine environments to deep-water turbiditic troughs (e.g., Agirrezabala and López-Horgue, 2017). The Ondiz, Bolibar and Meñakoz successions (Figs. 1, 2) are examples of volcanic and sedimentary deposits from the deeper central axis of the basin where mantle exhumation conditioned the heat flow, the development of submarine volcanism and the local uplift of the mantle lithosphere. The Karrantza, Legutio, Irurtzun and Estella-Lizarra successions (Fig. 1) formed on the southern margin of the basin were fault-bounded troughs were infilled by siliciclastic sediments of a prograding deltaic system.

2.1. Northern margin of the BCB: the Armintza section

The Armintza section exposes middle to upper Albian and lower Cenomanian silty marls and lutites with intercalated, usually fine-grained and cm-thick, siliciclastic turbidites and volcaniclastics (tuffs); at the base of the section, a pillow-basalt unit rests unconformably on fan-delta deposits (García-Mondéjar and Pujalte, 1985; Robles et al., 1988). The turbidites are arranged in a fining-upward main sequence about 800 m thick which is overlain by a coarsening-upward sequence of nearly 400 m thick, both corresponding to the Black Flysch Group.

In the present paper we confined ourselves to the section between 430 and 660 m; this yielded an interesting sample of early late Albian ammonoids from its lower part (López-Horgue et al., 2009; levels A2 to A8 in Fig. 3). The base of this partial section is marked by the last occurrence of a middle Albian ammonoid (level A1; Fig. 3) and the top is the likely base of the planktonic foraminifer *Thalmanninella appenninica* Zone (*sensu* Agirrezabala et al., 2023), which is traditionally considered approximately coeval to the base of *Stoliczkaia dispar* ammonite Zone (Caron, 1985; Fernández-Mendiola and García-Mondéjar, 1997; Amédro, 2002; Gale et al., 2011). Ammonoids occur uncrushed in siderite nodules of early diagenetic origin and pyritic nuclei (internal moulds) formed at shallow depths in the sediment beneath the sea floor (Ábalos and Elorza, 2012), but more usually are crushed, occurring as sideritic or marly composite moulds. Environmental conditions correspond to a hemipelagic trough with hypoxic to anoxic deep waters (Agirrezabala et al., 2023) and incursions of turbiditic currents

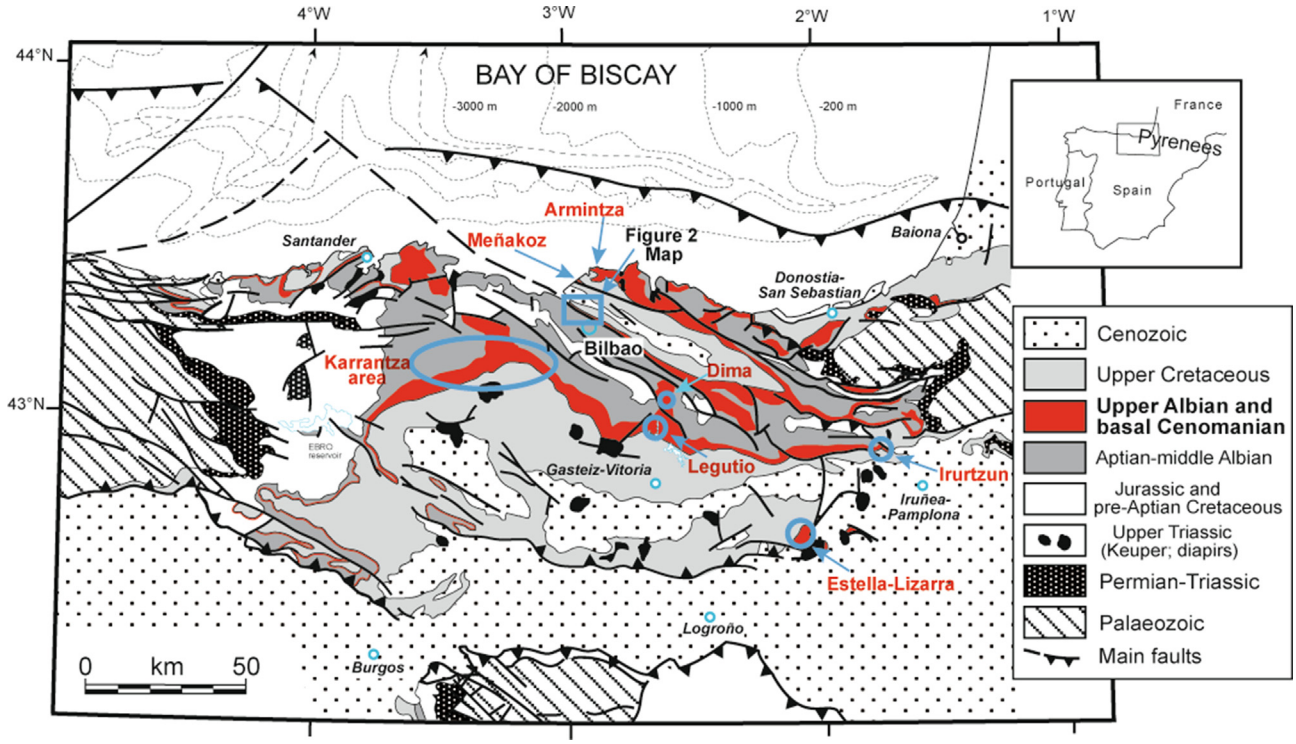


Fig. 1. Geological map of the Basque-Cantabrian basin (Western Pyrenees, northern Spain), with highlighted upper Albian to basal Cenomanian deposits and outcrops studied, and showing the location of the map in Fig. 2 to the north of Bilbao, in the central part of the basin.

that represent the input of sediment and shallow oxygenated waters — this is substantiated by common beds of turbidites plenty of trace fossils that modified the primary structures. Similarly, bioturbated volcaniclastic tuffs represent the input of nutrients by volcanic episodes. Ammonoids inhabited epipelagic to mesopelagic depths (Agirrezabala and López-Horgue, 2017), recently suggested to have been as deep as about 600 m (Agirrezabala et al., 2023).

2.2. Central part of the BCB: Ondiz, Bolibar and Meñakoz sections

The Ondiz and Bolibar sections are part of the NW-SE oriented corridor of Albian deposits to the north of Bilbao (Figs. 2, 3) along the southern flank of the Biscay Syncline. The Ondiz section is composed of lutites and scarce, cm-thick turbidite beds of the Black Flysch Group overlain by a 350-m-thick unit of trachytes followed by submarine pillow-basalts with thin intervening volcaniclastites. The trachytes form a unit that thins out (over 3 km) to the south-east where it is coeval to a gabbroic sill unit, both being overlain by deep-marine talus deposits (slumps, debrites) and turbidites (lower part of the Bolibar section); the entire Bolibar succession is not represented here because we have no update on ammonoid-bearing beds. Pillow-basalts overlying the trachytes are thickest in the Ondiz section and extend over 9 km to the south-east where this unit overlies the turbiditic succession and gradually thins to coeval lutites, turbidites and slump-debrites represented in the upper part of the Bolibar section. Trachytes may represent a lava-flow dome or an intrusive dome (Carracedo and Larrea, 1998) that created an uplifted area (Ondiz) with talus transitions to deeper siliciclastic sedimentary areas. Later, submarine extrusive volcanism took place in approximately the same area occupied by the trachytes and spread out towards deeper-marine areas. Early late Albian ammonoids occur in volcaniclastites (level O1) and calcareous lutites at Bolibar (level B1). Here, we study only ammonoids from level O1; these occur as 3D-preserved resedimented clasts of volcaniclastic breccias and tuffs, with recrystallised shells and phragmocone chambers filled with calcite and/or very fine sediment of likely volcanic origin.

The Meñakoz section is located seven km to the north of the Ondiz section (Figs. 1, 3). The lower upper Albian unit is composed of siliciclastic, cm-thick turbidites and calcareous lutites arranged in a 65-m-thick, thinning- and fining-upward succession overlain by volcaniclastic beds of the topmost lower upper Albian and basal uppermost Albian. Turbiditic deposits are derived from northerly siliciclastic inputs and may be ascribed to the Black Flysch Group. Ammonoids occur as laterally flattened recrystallised shells in lutites, as external moulds at the base of turbidites (level M1) and as 3D-preserved resedimented specimens with chloritic fills in volcaniclastic deposits (levels M2 and M3).

2.3. Southern margin of the BCB: Karrantza, Irurtzun, Legutio and Estella-Lizarra sections, plus the Dima area

The Karrantza section is located in the south-western part of the margin; it was briefly studied by López-Horgue et al. (2009). The succession is represented by nearly 600 m of deep-water limestone breccias, calcareous and siliciclastic, cm-thick turbidites and marls that are gradually succeeded by 1100 m of shallow-marine offshore and deltaic, cm-to dm-thick sandstones and lutites of the Valmaseda Formation (Fig. 3). This thick succession is indicative of the filling and shallowing of the deep-marine troughs and subsequent overfill and progradation of the coastal siliciclastics, while marine carbonate sedimentation took place in shallower uplifted blocks (López-Horgue et al., 2009, figs. 2—4). Early late Albian ammonoids (levels K1 to K11 in Fig. 3) have been found in the intervening marls

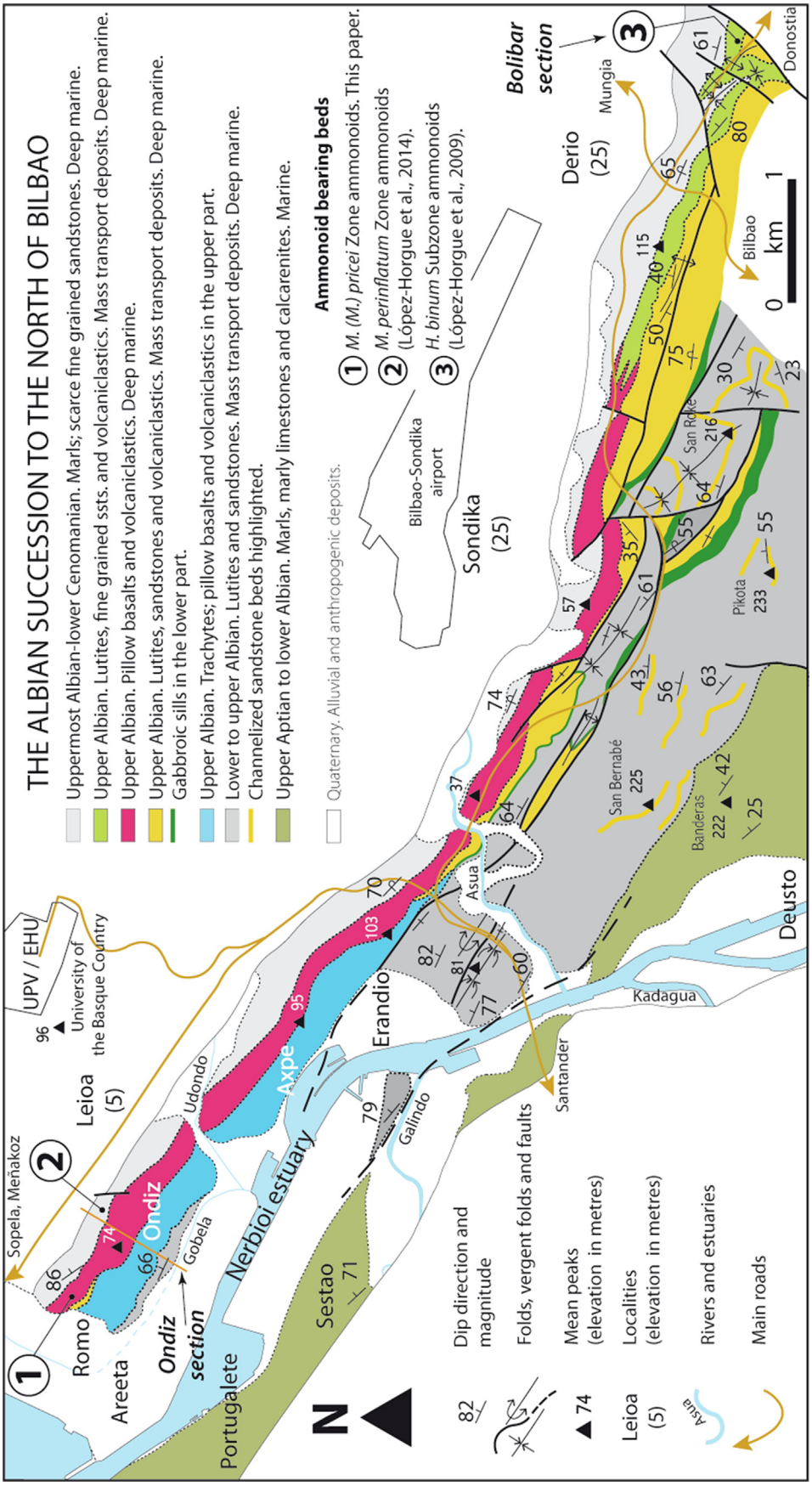


Fig. 2. Geology of the Albian succession to the north of Bilbao. The Ondiz and Bolibar sections were correlated in the field by means of cartographic tracking of stratigraphical boundaries and key beds.

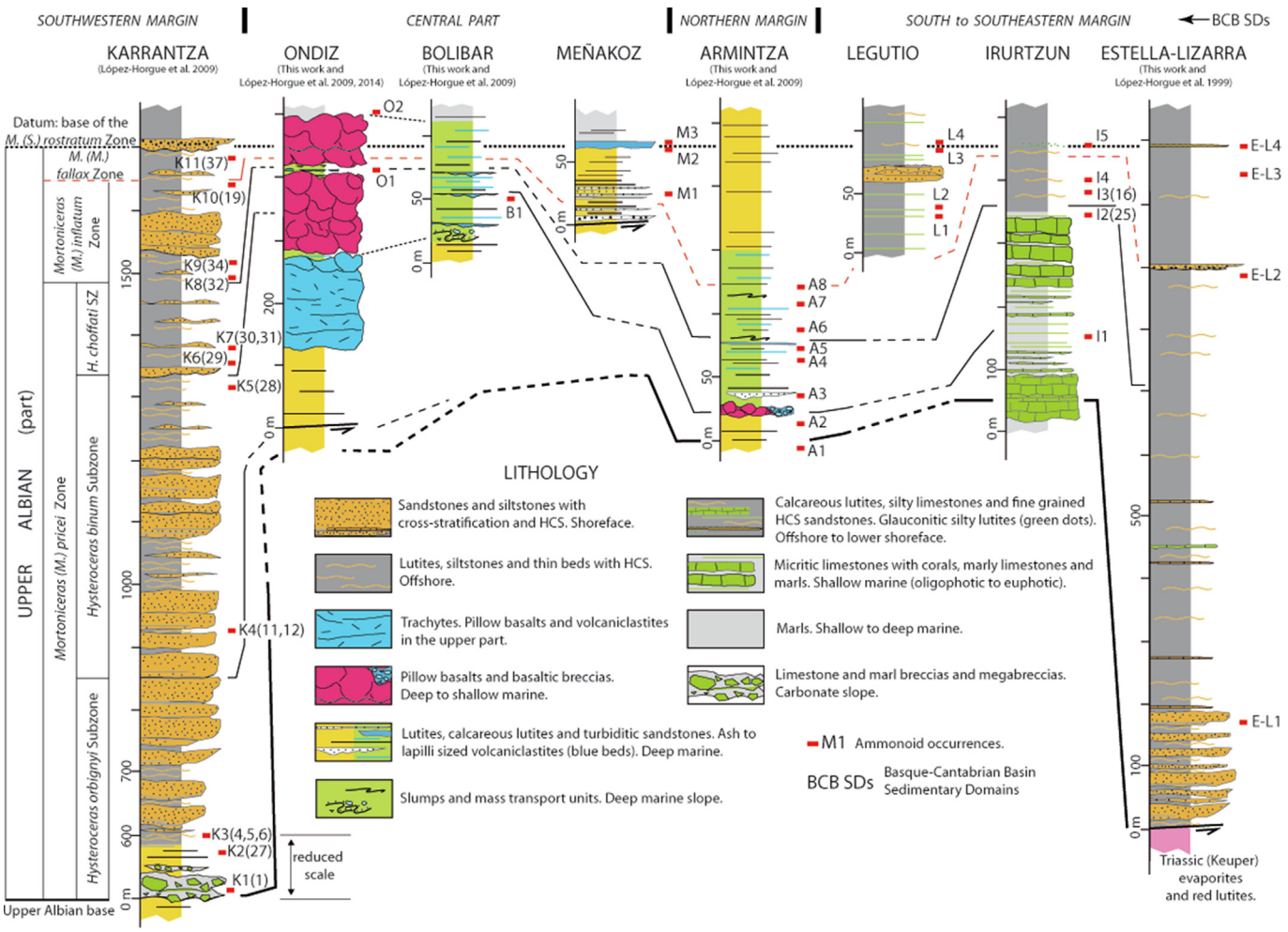


Fig. 3. Correlation of lower upper Albian sections with mortoniceratine ammonoids studied. Correlation on the basis of ammonoid zones has been possible by identification of ammonoid material recovered (see Table 1). Ammonoids representative of the first biozone of the upper Albian have not been found. Striking thickness variations are linked to differential subsidence and sedimentary rates between uplifted areas and troughs. Red squares indicate the levels with ammonoids studied. No ammonoids have been recovered from the lower part of the upper Albian succession at Bolibar and Legutio; these are not represented here. Levels in the Karrantza area and at Irurtzun show (in parentheses) their equivalent number in López-Horgue et al. (2009) and in Wiedmann (1962), respectively. The base of the *M.* (*S.*) *rostratum* Zone at Armintza is based on the occurrence of *T. appenninica* documented by Agirrezabala et al. (2023).

of the breccia beds as laterally crushed specimens with shell remains; in the shallow succession they are scarcely found as composite internal moulds in lutites and usually encountered in silty limestones early cemented by siderite atop of sandstones. These latter facies represent concentration beds of wave reworked marine fauna (corals, brachiopods, bivalves, ammonoids, bryozoans among others) after abandonment of deltaic bars (López-Horgue et al., 1998) and subsequent local deepening (transgression).

Legutio is a town in the province of Araba; in this section the base of the upper Albian is not well constrained due to Alpine faulting. Here we show the upper part of the lower upper Albian where ammonoids have been found (levels L1 to L3), as well as the uppermost Albian level (L4) (Fig. 3). The Dima area to the north is not represented in Legutio: it corresponds to underlying beds of the lower upper Albian. The localities of Dima and Legutio (Fig. 1) both have good outcrops of the siliciclastic deltaic Valmaseda Formation. The lithology is similar to that of the Karrantza section but the mud fraction is predominant. Ammonoids are preserved uncrushed or slightly deformed in early diagenetic sideritic nodules and silty limestones whereas they are laterally crushed in silty calcareous marls. In both types of preservation the shell is replaced by calcite.

The Irurtzun section comprises shallow-marine, cm-to dm-thick limestones and marls with intervening silty marls and cm-thick sandy tempestites, the latter forming the topmost siliciclastic unit of the upper Albian. These deposits originated in the shallowest part of a carbonate platform system with micritic buildups forming a margin five km to the west that faces a deeper siliciclastic trough (López-Horgue et al., 2022, their fig. 3). New levels with ammonoids are numbered I1 and I4; levels I2 and I3, as well as an intervening coeval one, were studied by Wiedmann (1962) (see Fig. 3; Table 1). Level I5 corresponds to the upper upper Albian interval.

The Estella-Lizarra section is the type section of the Zufia Formation, studied in detail by López-Horgue et al. (1999). Lower upper Albian deposits are here represented by 200 m of deltaic, cm-to dm-thick sandstones and lutites and 900 m of offshore silty marls with discrete cm-thick, storm-generated sandy beds with punctuated episodes of silty limestones with corals (at 450 m) and sandstones (at 900 m) interpreted as shallowing episodes (López-Horgue et al., 1999). The top of this succession is marked by a condensed glauconitc sandstone (at 1100 m) of the upper upper Albian interval. The overall succession represents sedimentation in a shallow-marine

Table 1
Ammonoid associations occurring in levels exposed in the study area and their corresponding biozones, with indication of 20 mortoniceratine taxa described herein. Armintza levels are also referred to the section in López-Horgue et al. (2009). Reference is made to Figure 3 for the stratigraphy of the various levels.

Studied sections and levels	Ammonoid associations	Biozones (this work)
This work and previous references		
KARRANTZA (In López-Horgue et al., 2009)		
K1 (1)	*Oxytropidoceras* (*Venezoliceras*) aff. *bituberculatum* Collignon *Idiohamites* cf. *spiniger* (J. Sowerby) *Hemiptychoceras* cf. *gaultinum* (Pictet)	K1 *M. (M.) pricei* Z./*H. varicosum* S.Z.
K2 (27)	*Oxytropidoceras* (*Venezoliceras*) aff. *venezolamun* Stieler *Hysteroceras carinatum* Spath	K2 *M. (M.) pricei* Z./*H. varicosum* S.Z.
K3 (4, 5, 6)	*Hysteroceras orbignyi* (Spath) *Kossmatella muhlenbecki* (Fallot) *Mortoniceras* (*Deiradoceras*) sp. juv.*	K3 *M. (M.) pricei* Z./*H. varicosum* S.Z.
K4 (11, 12)	*Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath* *Hysteroceras* aff. *varicosum* (J. de C. Sowerby) *Desmoceras latidorsatum* (*Michelin*) *Knemiceras compressum* Hyatt	K4 *M. (M.) pricei* Z./*H. binum* S.Z.
K5 (28)	*Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath)* *Puzosia provincialis* (Parona and Bonarelli) *Desmoceras latidorsatum* (Michelin)	K5 *M. (M.) pricei* Z./*H. binum* S.Z.
K6 (29)	*Mortoniceras* (*Mortoniceras*) sp. juv. cf. *fissicostatum* (Spath)* *Goodhallites goodhalli* (J. Sowerby)* *Hysteroceras choffati* Spath *Hemiptychoceras gaultinum* (Pictet) *Kossmatella romana* Wiedmann *Desmoceras latidorsatum* (Michelin)	K6 *M. (M.) pricei* Z./H. choffati S.Z.
K7 (30, 31)	*Goodhallites balmatianum* (Pictet)*1 *Mortoniceras* (*Deiradoceras*) cunningtoni Spath* *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath)* *Mortoniceras* (*Mortoniceras*) *neokentroides* (Wiedmann and Dieni)*2 *Prohysteroceras* sp. juv.*2 *Hysteroceras choffati* Spath *Hysteroceras bucklandi* Spath A *Kossmatella muhlenbecki* (Fallot) *Kossmatella romana* Wiedmann *Desmoceras latidorsatum* (Michelin)	K7 *M. (M.) pricei* Z./*H. choffati* S.Z.
K8 (32)	*Mortoniceras* (*Mortoniceras*) cf. *kiliani* (Lasswitz)*3 *Pseudhelicoceras spinosa* (Kossmat)	K8 *M. (M.) inflatum* Z.
K9 (34)	*Mortoniceras* (*Mortoniceras*) sp. juv. cf. *pricei* (Spath)* *Goodhallites* sp. juv.*4	K9 *M. (M.) inflatum* Z.
K10 (19)	*Hysteroceras* sp. juv.*1 *Knemiceras* sp.	K10 *M. (M.) inflatum* Z.
K11 (37)	*Goodhallites* cf. *candollianum* (Pictet)* *Mortoniceras* (*Mortoniceras*) sp. juv. cf. *fissicostatum* (Spath)*	K11 *M. (M.) fallax* Z.
ONDIZ		
O1 (this work)	*Hysteroceras binum* Spath *Hysteroceras orbignyi* (Spath) *Mortoniceras* (*Mortoniceras*) sp. juv. cf. *pricei* (Spath)* *Goodhallites* sp. juv. cf. *goodhalli**	O1 *M. (M.) pricei* Z./*H. binum* – *H. choffati* S.Z.
O2 (in López-Horgue et al., 2014)	*Mortoniceras* (*Durnovarites*) sp *Cantabrigites* sp. *Stoliczkaia* sp. *Anisoceras* sp.	O2 *M. (S.) rostratum* Z.
BOLIBAR (in López-Horgue et al., 2009)		
B1	*Labeceras plasticum* Spath	B1 *M. (M.) pricei* Z./*H. binum* S.Z.
MEÑAKOZ (this work)		
M1	*Mortoniceras* (*Mortoniceras*) *fallax* (Breistroffer)*	M1 *M. (M.) fallax* Z.
M2	*Desmoceras latidorsatum* (Michelin) *Scaphites* (*Scaphites*) *simplex* Jukes-Browne *Scaphites* (*Scaphites*) *hugardianus* (d'Orbigny) *Cantabrigites* aff. *minor* Spath *Cantabrigites* aff. *subsimplex* Spath *Idiohamites spiniger* (J. Sowerby) *Idiohamites* cf. *desorianus* (Pictet)	M2 *M. (M.) fallax* Z.
M3	*Stoliczkaia* (*Stoliczkaia*) *rhamnonotus* (Seeley) *Anisoceras* (*Anisoceras*) *saussureanum* (Pictet) *Idiohamites tuberculatus* (J. Sowerby) *Pseudhelicoceras convolutum* (Quenstedt)	M3 *M. (S.) rostratum* Z.
ARMINTZA (in López-Horgue et al., 2009)		
A1 (429.7 m)	*Oxytropidoceras* cf. *roissyanum* (d'Orbigny)	A1 *H. dentatus* Z. (Middle Albian)

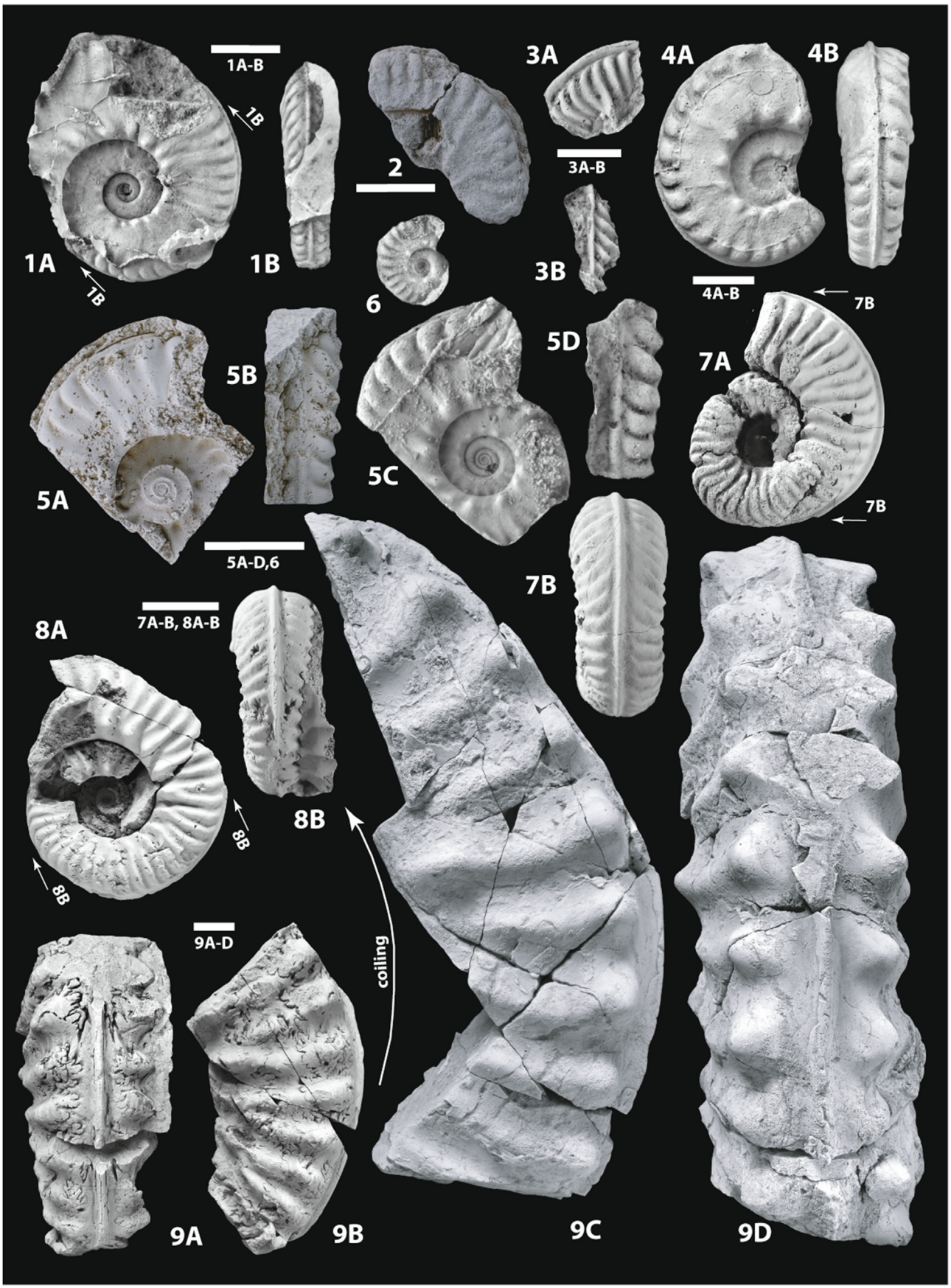
Table 1 (*continued*)

Studied sections and levels	Ammonoid associations	Biozones (this work)
A2 (454.4–458.6 m)	*Hysteroceras binum* Spath *Hysteroceras varicosum* (J. de C. Sowerby) *Kossmatella muhlenbecki* (Fallot) *Kossmatella romana* Wiedmann *Kossmatella oosteri* Breistroffer *Kossmatella schindewolfi* Wiedmann and Dieni *Puzosia* (*Anapuzosia*) *tucuyensis* (von Buch) *Jauberticeras jaubertianum* (d'Orbigny) *Desmoceras latidorsatum* (Michelin) *Parasilesites kilianiformis* (Fallot) *Hypophylloceras moreti* (Mahmoud) *Hypophylloceras subalpinum* (d'Orbigny) *Hypophylloceras seresitense* (Pervinquière)	A2 *M. (M.) pricei* Z./*H. binum* S.Z.
A3 (468.0–474.0 m)	*Mortoniceras* (*Deiradoceras*) cf. exilis (van Hoepen)*5 *Craginites* sp.*6	A3 *M. (M.) pricei* Z./*H. choffati* S.Z.
A4 (500.0–505.0)	*Mortoniceras* (*Deiradoceras*) *exilis* (van Hoepen)*5 *Mortoniceras* (*Deiradoceras*) *bispinosum* (Spath)*7 *Arestoceras* cf. *splendidum* van Hoepen*	A4 *M. (M.) pricei* Z./*H. choffati* S.Z.
A5 (517.1)	*Puzosia mayoriana* (d'Orbigny)	A5 *M. (M.) pricei* Z./*H. choffati* S.Z.
A6 (528.0–535.0)	*Mortoniceras* (*Deiradoceras*) *bispinosum* (Spath)*7 *Mortoniceras* (*Mortoniceras*) *crassinodatum* (van Hoepen)*	A6 *M. (M.) inflatum* Z.
A7 (551.0–555.0)	*Anisoceras armatum* (J. Sowerby) *Arestoceras* cf. *splendidum* van Hoepen*	A7 *M. (M.) inflatum*
A8 (562.0–565.0)	*Mortoniceras* (*Mortoniceras*) indet. gr. *rostratum*8 *Mortoniceras* (*Deiradoceras*) *bispinosum* (Spath)*	A8 *M. (M.) inflatum* – *M. (M.) fallax* Z.
LEGUTIO (former Villarreal de Álava) (this work)		
L1	*Mortoniceras* (*Mortoniceras*) *fallax* (Breistroffer)* *Desmoceras latidorsatum* (Michelin)	L1 *M. (M.) fallax* Z.
L2	*Pseudhelicoceras spinosa* (Kossmat)	L2 *M. (M.) fallax* Z.
L3	*Mortoniceras* (*Mortoniceras*) *juleni* n. sp.*	L3 *M. (M.) fallax* Z.
L4	*Mortoniceras* (*Subschloenbachia*) *rostratum* (J. Sowerby) *Stoliczkaia* sp.	L4 *M. (S.) rostratum* Z.
IRURTZUN		
I1 (this work)	*Navarreites egiarretensis* n. gen. n. sp.* *Desmoceras latidorsatum* (Michelin) *Kossmatella* sp.	I1 *D. cristatum*? to *M. (M.) pricei* Z./*H. varicosum* – *H. binum* S.Z.
Equivalent beds between I1 and I2 (in Wiedmann, 1962, loc. 15)	*Hysteroceras* sp. *M. (Mortoniceras)* cf. *geometricum* (Spath) *Kossmatella muhlenbecki* (Fallot) *H. (Stomohamites) virgulatus* (Brongniart) *H. (Plesiohamites) multicostatus* (Brown)	I1 to I2 coeval sediments: *M. (M.) pricei* Z./*H. choffati* S.Z.
I2 (in Wiedmann, 1962, loc. 25; 1979)	*Kossmatella muhlenbecki* (Fallot) *Tetragonites timotheanus* (Pictet) *Tetragonites nautiloides* (Pictet) *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath	I2 *M. (M.) pricei* Z./*H. choffati* S.Z.
I3 (in Wiedmann, 1962. loc. 16)	*Elobiceras subelobiense* Spath *Zelandites dozei schroederi* Wiedmann *Kossmatella romana* Wiedmann *Tetragonites timotheanus* (Pictet)	I3 *M. (M.) inflatum* Z.
I4 (this work)	*Elobiceras* (*Craginites*) *subelobiense* Spath*	I4 *M. (M.) inflatum* Z.
I5 (this work)	*Mortoniceras* (*Durnovarites*) sp. *Anisoceras* cf. *armatum* (J. Sowerby)	I5 *M. (S.) rostratum* Z.? – *M. (S.) perinflatum* Z.
ESTELLA-LIZARRA (in López-Horgue et al., 1999)		
E-L1	*Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath *Hypengonoceras* cf. *decaryi* Collignon	E-L-1 *M.(M.) pricei* Z./*H. binum* – *H choffati* S.Z.
E-L2	*Mortoniceras* (*Mortoniceras*) sp.*9	E-L-2 *M.(M.) inflatum* Z.
E-L3	*Mortoniceras* (*M.*) *apertum* Spath*10	E-L-3 *M. (M.) fallax* Z.
E-L4	*Stoliczkaia* (*Stoliczkaia*) *clavigera* (Neumayr) *Stoliczkaia* (*Stoliczkaia*) aff. *dispar* (d'Orbigny) *Stoliczkaia* (*Stoliczkaia*) *dorsetensis* Spath *Stoliczkaia* (*Stoliczkaia*) *notha* (Seeley) *Anisoceras* cf. *pseudoelegans* (Pictet and Campiche) *Mariella* (*Mariella*) *crassituberculata* Spath *Mortoniceras* (*Subschloenbachia*) *rostratum* (J. Sowerby)	E-L-4 *M. (S.) rostratum* Z. – *M. (S.) perinflatum* Z.
DIMA (this work)	*Mortoniceras* (*Deiradoceras*) *aldakor* n. sp.*	DIMA. *M. (M.) pricei* Zone, probably.

* MORTONICERATINAE STUDIED IN THIS WORK

EMENDED DETERMINATIONS (THIS WORK):

1-*Mortoniceras* (*Deiradoceras*)? *balmatianum* (Pictet) 2-*Mortoniceras* (*M.*) *aitzindari* n. sp. 3-*Mortoniceras* (*M.*) cf. *equidistans* (Cregin)
4-*Goodhallites* sp. juv. cf.*goodhalli* (J. Sowerby) 5-*Mortoniceras* (*Deiradoceras*) *bispinosum* (Spath) 6-*Elobiceras* (*Craginites*) *subelobiense* Spath
7-*Mortoniceras* (*Deiradoceras*) *armintzekalensis* n. sp. 8-*Mortoniceras* (*M.*) *crassinodatum* (van Hoepen) 9-*Mortoniceras* (*M.*) *tremulum* (van Hoepen)
10-*Mortoniceras* (*M.*) *fallax* (Breistroffer) A-*Hysteroceras* aff. *bucklandi* Spath


1A-B
1B
1A
1B
2
6
3A
3A-B
3B
4A
4B
4A-B
7B
5A
5B
5C
5D
5A-D,6
7A
7B
7B
7A-B, 8A-B
8A
8B
8B
8B
9A-D
coiling
9A
9B
9C
9D

area, near 50 m deep and separated from the main sandy inputs in coeval areas to the west (e.g., the Karrantza area).

3. Ammonoid biostratigraphy

Here we follow the revised upper Albian zonal scheme of the Standard Ammonite Zonation of the Western Tethyan Mediterranean Province, proposed by the Kilian Group at its last meeting at Warsaw, on August 21, 2022, recently published by Szives et al. (2023b). Minor modifications to the upper Albian ammonoid biozonation on the basis of data presented here, are discussed below.

Most of the Mortoniceratinae studied here are of cosmopolitan occurrence with examples from North and South America, Africa and other Tethyan basins, as well as in basins in the North European province.

4. Methodology, material and conventions

Stratigraphical sections were measured in the field bed by bed, at detailed scales between 1:100 and 1:500, then reduced in drawings as to create a comprehensive sketch. The Estella-Lizarra, Karrantza and Armintza sections were presented in previous works (López-Horgue et al., 1999, 2009). Special attention was given to any fossil content of the successions. Ammonoids are rare in these beds; accurate collecting during about 150 field days over the last 32 years was done in order to obtain the most reliable sample of ammonoid associations, occasionally with the help of colleagues and friends. Here we confine ourselves to mortoniceratines which comprise less than 20 per cent of the entire ammmoid sample. The collection studied comprises 55 specimens, mostly with well-preserved morphological characters; only three specimens, preserved in muddy rocks, are flattened.

In view of great distances between type series, field correlation was deemed extremely important in most of the cases, which resulted in local mapping and reliable bed equivalences. Maps of the Estella-Lizarra and Karrantza areas were presented previously (López-Horgue et al., 1999, 2009). Here, we present a detailed map of the Albian to the north of Bilbao, since this is the key for our understanding of the central part of the BCB. Maps of the Legutio, Irurtzun and Meñakoz areas will be presented in forthcoming papers. Armintza and Meñakoz are correlated by their good ammonoid occurrences.

Fossil preparation (by the senior author) included mechanical removal of matrix by small chisels and a mini drill, followed by acetic dissolution of the matrix, application of potassium hydroxide to remove marly and silty matrixes, the merging of fragments, their joining and fixing; the coating of iron oxide-preserved fossils with paraloid B-72® so as to render hardness and avoid problems with manipulation, and lastly, production of silicone casts from well-preserved external moulds. Most of the photographs were taken following ammonium chloride coating, but images of some specimens were better uncoated.

Material described and illustrated here is housed at the Museo de Ciencias Naturales de Álava in Vitoria-Gasteiz (MCNA), except for a single specimen which is in the Hontza Museoa (HONTZA) of the town of Mañaria, province of Biscay.

5. Systematic palaeontology

Here we follow the classification of Wright et al. (1996), with some discussions of the genera *Mortoniceras* and *Arestoceras*. All dimensions are shown in millimetres: diameter (D), whorl height (Wh), whorl width (Ww) and umbilical diameter (U), are taken from the best-preserved whorl section along ribs (costal) at the indicated diameter. If a specimen preserves only one side, the whorl width is only considered approximate. In some cases, we have also measured whorl dimension between ribs (intercostal: ic) at the given diameter. Other additional parameters are used for descriptions and for comparison with other specimens: whorl section ratio, Wh/Ww; whorl-height change rate, Wh at a given diameter/Wh at the indicated smaller diameter (a parameter useful in slightly deformed and incomplete specimens in order to represent whorl growth). Preservation of specimens obscures in most cases a complete visible suture line, so that it is only described in few cases. Occurrences are given separately for the Basque-Cantabrian Basin (BCB), followed by those in other basins. Biozones for the BCB occurrences follow the zonation in Szives et al. (2023b) with minor modifications. The rest of the occurrences are given as indicated in previous references, with comments added in some cases.

Order Ammonoidea von Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Acanthoceratoidea Grossouvre, 1894
Family Brancoceratidae Spath, 1934
Subfamily Mortoniceratinae H. Douvillé, 1912

Genus *Goodhallites* Spath, 1932

Goodhallites sp. juv., cf. ***goodhalli*** (Sowerby, 1820)
Fig. 4/1A, B

*1820 *Ammonites goodhalli* J. Sowerby, p. 100, pl. 255.
1849 *Ammonites goodhalli* J. Sowerby; Brown, p. 20, pl. 14, fig. 10.
1934 *Prohysteroceras* (*Goodhallites*) *goodhalli* (J. Sowerby); Spath, p. 447, pl. 50, fig. 1; pl. 56, fig. 9; text-fig. 155 (with synonymy).
1942 *Hysteroceras semileve* Haas, p. 42, pl. 5, figs. 19–21; pl. 9, fig. 3.
1971 *Prohysteroceras* (*Goodhallites*) *goodhalli* (J. Sowerby); Renz, p. 593, pl. 3, fig. 15; text-fig. 15.
2002 *Goodhallites goodhalli* (Sowerby, 1820); Henderson and Kennedy, p. 239, fig. 2A–D, 3, 4, 5A–D, 6A, B, 7A–F (with additional synonymy).
2009 *Goodhallites goodhalli* (J. Sowerby); López-Horgue et al., p. 392.
2009 *Goodhallites* sp. juv.; López-Horgue et al., p. 392.

Type. The original of Sowerby (1820), The Natural History Museum, London, no. NHMUK 43949a.
Material. Three specimens: MCNA 13424 (Fig. 4/1A, B), an uncrushed fragmentary internal mould and a fairly complete

Fig. 4. Early late Albian Mortoniceratinae from the Western Pyrenees; all housed at Museo de Ciencias Naturales de Álava (MCNA), unless indicated otherwise. For levels, see Fig. 3 and Table 1. **1A, B.** *Goodhallites* sp. juv. cf. *goodhalli* (J. Sowerby, 1820), in lateral and ventral views, respectively; silicone cast of specimen MCNA 13424, level K6, *H. choffati* Subzone. **2**. *Goodhallites* cf. *candollianum* (Pictet, *in* Pictet and Roux, 1847); specimen MCNA 13460; level K11, *M.* (*M.*) *fallax* Zone. **3A, B**. *Mortoniceras* (*Deiradoceras*) sp. juv., in lateral and ventral views, respectively; specimen MCNA 13411; level K3, *H. varicosum* Subzone. **4A, B.** *Mortoniceras* (*Deiradoceras*)? *balmatianum* (Pictet, *in* Pictet and Roux, 1847), in lateral and ventral view (cast of holotype); The Natural History Museum, London, NHMUK C35927. **5A, B.** *Mortoniceras* (*Deiradoceras*)? *balmatianum* (Pictet, *in* Pictet and Roux, 1847), lateral and ventral views, respectively; specimen MCNA 13455; **5C, D.** silicone rubber cast of the same specimen; level K7, *H. choffati* Subzone. **6.** *Mortoniceras* (*Deiradoceras*)? *balmatianum* (Pictet, *in* Pictet and Roux, 1847), specimen MCNA 13464, lateral view; level K10, *M.* (*M.*) *inflatum* Zone. **7A, B.** *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath, 1933, in lateral and ventral views, MCNA 17131. **8A, B.** *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath, 1933, in lateral and ventral views, specimen MCNA 17132. **9A–D.** *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath, 1933, specimen MCNA 13451, ventral and lateral views of inner whorls at middle growth stage, and lateral and ventral views of body chamber; 7–9 from level K7, *H. choffati* Subzone. Scale bar equals 10 mm.

counterpart external mould from which a cast has been made; MCNA 13452, cast of an external mould (crumbled after casting) of a juvenile and MCNA 17137, a juvenile preserved in calcite.

Description. Phragmocone of MCNA 13424 ending at diameter of 26.6 mm; half a whorl comprising body chamber. Umbilicus equalling 26 per cent and 33 per cent of 23 mm and 37.2 mm diameter, respectively. Flanks initially subparallel, slightly convex on body chamber. Faint ribbing, slightly radial, very subtle or absent on smooth flanks of internal whorls; appearing progressively and clearly visible on last whorl and a half, becoming distinctive and flexuous, with irregularly branching from sharp tubercles in umbilical edge. Ribs wider than interspaces. Umbilical wall high and steep. Rounded ventrolateral shoulders where ribs are widest, becoming subtly sharp and then projecting adorally towards elevated keel. Whorl growth high: Wh at 37.2 diameter/Wh at 23 diameter = 1.71.

Inner whorls of MCNA 13452 smooth; ribbing evident at around 8 mm diameter; inner flank smooth. Ribs starting at mid-flank and rapidly widening towards venter, bending adorally; narrow interspaces. Keel only preserved on outer end of shell. Umbilicus widening progressively from 28 to 33 per cent of 7.0–11.9 mm diameters, respectively. Outer whorl overlapping as much as half of flank of contiguous inner whorl. High rate of whorl growth (Wh at 11.9/Wh at 7.0 = 1.67). Compressed.

MCNA 17137 of similar size and characteristics as MCNA 13452, showing persistent keel and ventrolateral shoulders with markedly wide ribs. Flanks subparallel with faint ribs. Whorl growth 1.67.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13424 (Fig. 4/1A, B)	37.2	16.3	8.4	12.4
	23.0	9.5	6.0	6.0
MCNA 13452	11.9	4.7	–	3.9
	7.0	2.8	–	2.0
MCNA 17137	11.7	5.5	3.7	3.0
	7.0	3.5	2.2	–

Discussion. MCNA 13424 is a compressed form in which the umbilical area takes one-third of the diameter. This feature, together with the type of ribbing, persistent keel and steep umbilical wall, are all cited by Spath (1934) to characterise *Goodhallites goodhalli*, especially young specimens. Actually, his text-figure 155-d (NHMUK 23679) of a typical young *goodhalli* is directly comparable to our specimen. The lack of more persistent rectiradiate ribbing suggests no connection with other forms of *Goodhallites* (e.g., Spath, 1922, 1934; Haas, 1942). The external suture line is comparable to that of typical *Goodhallites* spp. A "*Hysteroceras*" stock with persistent keel, described by Haas (1942) from Angola, shares a similar whorl section, umbilical diameter, ribbing and an external suture line that is more complex than his *Hysteroceras*-type one, suggests reference to young *Goodhallites* (see *Hysteroceras semileve* Haas, 1942, pl. 5, figs. 19–21; pl. 9, fig. 3). MCNA 13452 and 17137 may be considered early juveniles on account of whorl growth, persistent keel, evolution degree, type of ribbing and comparison to inner whorls of the larger-sized specimen, MCNA 13424.

Occurrence. *BCB — Hysteroceras choffati* Subzone of *M. (M.) pricei* and *M. (M.) inflatum* zones: levels K6 (MCNA 13424) and K9 (MCNA 13452) of the Karrantza section (La Escrita Unit, Valmaseda Formation in Trucíos) and level O1 (MCNA 17137) of the Ondiz volcanic succession. Biscay province, Basque Country, Western Pyrenees, Spain. Elsewhere this species is known from the *M. (M.) pricei* Zone, essentially *H. binum* Subzone and lower *Mortoniceras inflatum* Zone of England, France, Venezuela and Australia.

Goodhallites cf. ***candollianum*** (Pictet, *in* Pictet and Roux, 1847) Fig. 4/2

*1847 *Ammonites candollianus* Pictet, *in* Pictet and Roux, p. 105, pl. 11, fig. 1a, b.
1934 *Prohysteroceras* (*Goodhallites*) *candollianum* (Pictet); Spath, p. 453, text-fig. 156, pl. 51, fig. 1; pl. 54, fig. 1; pl. 56, fig. 10 (with synonymy).
2009 *Goodhallites* cf. *candollianum* (Pictet); López-Horgue et al., p. 395, fig. 8M.

Type. The lectotype, designated by Spath (1922, p. 104), is the original of Pictet, *in* Pictet and Roux (1847), reillustrated by Spath (1934).

Material. Poorly preserved 90° of a whorl, most likely body chamber, of a small specimen, MCNA 13460.

Description. Keel high. Ribs coarse (1 mm wide), widely separated, rounded and crossing flank from faintly bullate umbilical tubercle to rounded ventrolateral shoulder with blunt bullate tubercle, ending approximately at right angle with respect to keel. Some ribs branching from umbilical tubercle, others intercalated; rectiradiate to prorsiradiate.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13460 (Fig. 4/2)	–	10.6	–	–

Discussion. Spath (1934, text-fig. 156) illustrated the original drawing of *Ammonites candollianus* by Pictet (*in* Pictet and Roux, 1847, pl. 11), noting that it was fairly correctly drawn. That drawing shows the ribbing to be fairly constant from the juvenile stage onwards. Despite poor preservation, our specimen, possibly a juvenile, matches the style of ribbing and tuberculation of the lectotype and is also comparable to a specimen from bed XII at Folkestone, south-east England (Spath, 1934, pl. 51, fig. 1). The tuberculation is comparable to a specimen identified as 'sp. ind. *candollianum* group' and illustrated by Spath (1934, pl. 56, fig. 10). This species is allied to *G. goodhalli*, but the present specimen differs in that the ribs are less flexuous, prorsiradiate, with secondaries not reaching the umbilical wall; moreover, it occurs 150 m above (level K 11) the last occurrence of *G. goodhalli* (level K 9) in the study area (Karrantza section; see Fig. 3). Spath (1934, p. 456) argued that stratigraphical distribution of the two species sufficed to keep them separate.

Occurrence. *BCB — Mortoniceras* (*M.*) *fallax* Zone; level K11 in the Karrantza section, La Escrita Unit, Valmaseda Formation, at Parea (Trucíos, Biscay province), Basque Country, Western Pyrenees, Spain. Elsewhere known from Bed XII (upper *Callihoplites auritus* Subzone = upper *M. inflatum* Zone of Owen, *in* López-Horgue et al., 1999) of Folkestone and equivalent in Devizes, southern England, and France; also U7 of the upper Albian Gault Group in southern England (Owen, *in* Jattiot et al., 2023, appendix A).

Genus *Mortoniceras* Meek, 1876

Discussion. As one of us pointed out in a document dated 2014 (Owen, *in* Jattiot et al., 2023, appendix A), a further taxonomic revision of the genus *Mortoniceras* was possible as some of van Hoepen's genera were applicable to English species, and some other genera and subgenera might be better considered synonyms. Of these, Owen stated that, "if the type of *Mortoniceras* (*M. vespertinum* Morton) is proved to be generically separated from the English forms, *Pervinquieria* Böhm would become valid for the *inflatum-rostratum* lineage".

Recently, Kennedy, *in* Gale et al. (2019) started to use *Pervinquieria* Böhm as a separate genus and subgenus on the basis of differences with *Mortoniceras vespertinum*, the type species of *Mortoniceras*. These differences were outlined in detail by Kennedy, *in* Gale and Kennedy (2020), by comparing the ontogenetic development of the type species of *Mortoniceras* (*Ammonites vespertinus* Morton, 1834) and *Pervinquieria* (*Ammonites inflatus* Sowerby, 1818). Jattiot et al. (2022) did not see genus-level differences in the ornament of both type species, and thus considered *Pervinquieria* a synonym of *Mortoniceras*, a point of view we concur with. The main differences listed by Kennedy, *in* Gale et al. (2019, p. 213) and by Kennedy, *in* Gale and Kennedy (2020, pp. 30–38, 40–41) may be summarised as follows: spatulate ventrolateral rib termination, presence of spiral ridges and a feeble lateral tubercle are characteristic of *Pervinquieria*; strong inner and feeble outer ventrolateral clavi in the earliest growth stage, later effacing of outer ventrolateral clavi and appearance of a lateral tubercle row and no spiral ridges are typical of *Mortoniceras*.

It is true that spiral ridges are not observed in *M. vespertinum*, but this character is not always present or effaces/disappears in adult stages of some species that may be assigned to *Pervinquieria* (e.g., examples of *Ophryoceras* in van Hoepen, 1945); however, this feature usually is constant in the genus *Elobiceras*. The spatulate rib termination is not a common character, and different degrees of ending ribs are usual (e.g., see *Mortoniceras* spp., herein). Ventrolateral rib differentiation is a trait observed in *Mortoniceras* (as here understood) from the upper portion of the lower upper Albian (this paper), with development of outer clavi in some species (e.g., *M. fallax* in juvenile stages; see Jattiot et al., 2021), being common in latest Albian species.

Accordingly, we think that the generic characters of both type species (*M. vespertinus* and *P. inflatus*) should be understood as variations inside the basic generic makeup of the genus *Mortoniceras*, the diagnosis of which may be summarised as: slightly involute to evolute, keeled forms with square to subsquare whorl sections, usually strong ribbing with strong umbilical and ventrolateral rows of tubercles, leading to trituberculate and quadrituberculate forms by acquisition of lateral and outer ventrolateral tubercles (Wright et al., 1996), being linked to the overall plasticity of members of the subfamily Mortoniceratinae.

Subgenus *Deiradoceras* van Hoepen, 1931

Mortoniceras (***Deiradoceras***) sp. juv.
Fig. 4/3A, B

2009 *Mortoniceras* (*Deiradoceras*) sp. juv.; López-Horgue et al., p. 392, fig. 6C.

Material. A single specimen, MCNA 13411 (Fig. 4/3A, B), a quarter of a whorl, internal and external moulds and a rubber cast extracted from the latter. Slightly crushed.

Description. Prominent keel (2 mm in height), separated by subtle sulcus from ribs. Ribs strong, as wide as interspaces, sigmoidal, bending adorally on ventrolateral rounded shoulder. Prominent, flare-like umbilical bulla, covering inner half of flank, in which ribs bifurcate at one-third upflank. Width between flared ribs about 13.5 mm (restored).

Dimensions (mm)	D	Wh	Ww	U
MCNA 13411 (Fig. 4/3A, B)	–	14.0	10.3 (restored)	–

Discussion. Although small, sufficient features are present to allow comparison with inner (juvenile) whorls of *M.* (*Deiradoceras*) spp. with flare-like ribs (e.g. Spath, 1931, pl. 36, fig. 10; Spath, 1932, pl. 39, fig. 5; Spath, 1933, pl. 43, fig. 5). Inner whorls of this subgenus tend to have rounded venters as in *Dipoloceras* spp., but the whorl section of MCNA 13411 differs from that in that genus.

Occurrence. Upper *Hysteroceras varicosum* Subzone of *M.* (*M.*) *pricei* Zone. Level K3 in Karrantza section, La Escrita Unit, Valmaseda Formation, in Argañeda (Karrantza), Biscay province, Basque Country, Western Pyrenees, Spain.

Mortoniceras* (*Deiradoceras*)? *balmatianum (Pictet, in Pictet and Roux, 1847)
Fig. 4/4A, B, 5A–D, 6

*1847 *Ammonites balmatianus* Pictet, *in* Pictet and Roux, p. 97, pl. 9, fig. 1a–c.
1907 *Ammonites inflatus* (Pictet); Jacob, pp. 330, 383, 385.
1933 *Mortoniceras* (*Deiradoceras*) *balmatianum* (Pictet); Spath, pp. 424, 427, text-fig. 148.
1942 *Hysteroceras carinatum* Spath; Haas, pl. 5, figs. 14, 15; pl. 6, figs 13, 14.
2009 *Goodhallites balmatianum* (Pictet); López-Horgue et al., p. 392.
2009 *Hysteroceras* sp. juv.; López-Horgue et al., p. 395.

Type. Holotype is the original of Pictet, *in* Pictet and Roux (1847), a cast of which is housed at the Natural History Museum, London (Fig. 4/4A, B).

Material. A body chamber preserved as internal mould (about one-third of outer whorl), with external mould of phragmocone (MCNA 13455; Fig. 4/5A–D) and rubber casts. Specimen MCNA 13464 (Fig. 4/6) is an external mould of a juvenile. A cast of the type specimen (NHMUK C35927) has been measured for comparison (Fig. 4/4A, B).

Description. MCNA 13455 (Fig. 4/5) with subquadrate whorl section, parallel flanks; high persistent keel. Ribbing rectiradiate with very slight tendency to become flexuous. High and steep umbilical wall, tending to be less steep in last half whorl. Distinctive tubercles arising at umbilical edge on inner whorls, becoming prominent, spine-like, in last whorl preserved. Ribs single, irregularly branching from umbilical tubercles, almost imperceptible at mid-flank. On ventrolateral shoulder ribs becoming wider and pronounced, with tendency to develop two ventrolateral tubercles on each rib ending. On venter ribs directed adorally towards keel. Ribbing conspicuous from early growth stage, at diametre of 8 mm. Ribs subtly concave between umbilical and ventrolateral tubercles at end of last whorl. MCNA 13464 (Fig. 4/6): early juvenile form comparable to MCNA 13455 at same diameter on basis of comparable umbilical width (around 35 per cent of diameter), very subtle umbilical tubercles at end of preserved whorl, ventrolateral tubercle and effaced ribs on flank.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13455 (Fig. 4/5A–D)	25.5	9.6	8.6	8.9
MCNA 13464 (Fig. 4/6)	8.5	3.0	–	3.1
NHMUK C35927 (Fig. 4/4A, B)	36.7	15.8	13.4	12.8

Discussion. The continuous keel, well-defined umbilical tubercles and tendency for the twofold division of ventrolateral tubercle are features used to separate this from *Hysteroceras*. The rate of coiling, whorl section, ribbing pattern, keel and smooth flanks are features that preclude comparison with young *Goodhallites* spp. (see MCNA

13424; Fig. 4/1), or even to young *Prohysteroceras*. The holotype of *Ammonites balmatianus* (cast NHMUK C35927; Fig. 4/4) shows most of the features of our specimen, with the conspicuous smooth flanks, persistent keel, strong and blunt ventrolateral tubercles with a tendency to divide into two, the type of ribbing and umbilical size; it differs only in possessing a more rectangular whorl section (Wh/Ww = 1.17) and its size. Spath (1933, p. 426) recorded that the inner whorls of transitional forms of *Goodhallites* (*G. goodhalli* var. *tuberculata*) only differed from those of *A. balmatianus* in being more compressed and possessing a smaller umbilicus. On the other hand, Spath (1933, pp. 424–426) referred *A. balmatianus* to his new species, *Mortoniceras* (*Deiradoceras*) *albense* and compared it directly with a small specimen of *M.* (*D.*) cf. *devonense* (Spath, 1933, pl. 41, fig. 5). He suggested that the species name *balmatianum* should not be used until new material was found which showed conspicuous strengthening of the ribs between the tubercles. In addition, he noted that *M.* (*D.*) *albense* is related to the group of *Goodhallites goodhalli* and hence, there are transitional forms between them; a similar situation is seen in other species of *Deiradoceras*. When comparing young forms of these Mortoniceratinae, it seems evident that all of them must be related taxa, but we think *A. balmatianus* may be a valid species with distinct features, being more closely related to forms of *Deiradoceras* due to its lower keel than to young *Goodhallites*. In its rate of coiling, *balmatianum* could also be considered a young *M.* (*D.*) *albense*, in which case, Pictet's name would have priority. The Mozambique species, *Prohysteroceras* (*Goodhallites*) *besakatrense* Collignon (see Förster, 1975, pl. 15, figs. 1, 6) and *P.* (*G.*) *gracillimum* (Kossmat) (see Förster, 1975, pl. 15, fig. 3) may be forms related to *balmatianum* on account of their type of ribbing and umbilical size (between 33 and 35 per cent of diameter). Finally, some individuals of *Hysteroceras carinatum* and *Hysteroceras semileve* Haas from Angola, with persistent keels, show the typical ribbing, whorl section and smooth flanks as seen in *A. balmatianus* (Haas, 1942, pl. 5, figs. 15, 19–22). However, the species *semileve* shows a degree of volution that compares better with *Goodhallites*. The suture line of *H. carinatum* from Angola (Haas, 1942, pl. 6, figs. 13, 14) is also comparable to that of *A. balmatianus* (see Spath, 1933, text-fig. 148).
Occurrence. BCB — Hysteroceras choffati Subzone of *M.* (*M.*) *pricei* Zone and *M.* (*M.*) *inflatum* Zone; levels K7 (MCNA 13455) and K10 (MCNA 13464) in the Karrantza section (La Escrita Unit, Valmaseda Formation), Biscay province, Basque Country, Western Pyrenees, Spain. Elswhere, it is known from the upper *Hysteroceras varicosum* Zone and ?lower *Mortoniceras inflatum* Zone; Switzerland, Angola.

Mortoniceras (Deiradoceras) cunningtoni (Spath, 1933)
Fig. 4/7A, B, 8A, B, 9A–D

1929 *Pervinquieria* sp. nov., Cunnington, p. 6.
1932 *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath, pl. 37, fig. 2; pl. 39, fig. 5; pl. 41, fig. 6; pl. 42, fig. 7.
*1933 *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath, p. 416, text-fig. 143, pl.43, fig. 3; pl. 48, fig. 1.
1950 *Deiradoceras* sp. aff. *cunningtoni* Spath; Collignon, p. 73, pl. 12, figs. 1, 2.
1978 *Pervinquieria* (*Deiradoceras*) *cunningtoni* (Spath); Wiedmann and Kauffman, pl. 3, fig. 4.
1979 *Pervinquieria* (*Deiradoceras*) *cunningtoni* (Spath); Wiedmann, pl. 3, fig. 4.
1997 *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath; Kennedy et al., p. 466, pl. 9, figs. 6, 7.
2009 *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath; López-Horgue et al., p. 392, fig. 9A, B.
2017 *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath; Benzaggagh et al., p. 83, figs. 10B, 11C.
2018 *Mortoniceras* (*Deiradoceras*) *cunningtoni* Spath; Ayoub-Hannaa et al., p. 304, fig. 20A–D.

Type. The holotype is the original of Spath (1932), NHMUK C31709 (The Natural History Museum, London).
Material. Specimen MCNA 13413 comprises a fully septate one-sixth of a whorl and a fragment of the venter with high keel; preserved as undeformed internal mould, one flank not. Specimen MCNA 13451 (Fig. 4/9A–D) is an incomplete internal mould with portions of body chamber and phragmocone preserved; dimensions given correspond to the best-preserved, undeformed pieces. Specimens MCNA 14388, 17131 (Fig. 4/7A, B) and 17132 (Fig. 4/8A, B) are small-sized internal moulds of phragmocone and body chamber. MCNA 17134 is a small fragment, retaining 90° of body chamber whorl.
Description. MCNA 13451 (Fig. 4/9): keel prominent, gradually becoming more elevated over venter (from 2.4 mm [fragment 4] to 5.3 mm [fragment 2]). Whorl section subquadrate, widest at umbilical tubercle. Flanks almost parallel, slightly inclined towards keel. Ribs strong, of similar width to interspaces on phragmocone; grouped in V-shaped pairs branching from umbilical tubercle; rectiradiate to slightly prorsiradiate. At around last septa ribs becoming single, long and short, with wider interspaces. Bullate umbilical tubercle prominent, laterally projected, arising from middle part of steep and high umbilical wall. Ventrolateral tubercle on inner whorls bullate, with subtle rounded projection on inner part; on body chamber, sharp with upper end almost at right angles with keel; wide, flat venter. Subtle mid-flank tubercle on phragmocone becoming bullate on body chamber. Spiral striation on phragmocone ribs not evident on body chamber. Suture line with well-developed mid-flank lateral lobe. Specimen MCNA 13413 [stratigraphically older] lacking mid-flank tubercles and outer ends of ribs adorally feebly projected.
Specimens MCNA 14388, 17131 (Fig. 4/7) and 17132 (Fig. 4/8) bearing sharp crowded ribs arising from slightly rounded umbilical wall, bullate in shape, some high, with conical tubercle high on umbilical shoulder. Then branching into two flexuous ribs, with some secondaries intercalated, arising from mid-flank. Single ribbing common from 30 mm diameter, slightly concave between umbilical and ventrolateral shoulders and with wider interspaces. Ribs widening on rounded ventrolateral shoulder and projecting feebly adorally without reaching high keel, separated by parallel sulcus. Whorl section quadrate and slightly depressed at smaller diameters (23 mm), progressing to slightly compressed with parallel flanks later (33 mm). Specimen MCNA 17134 showing compressed whorl section and concave ribbing at low diameter (possibly 20 mm).

Dimensions (mm)	D	Wh	Ww	U
MCNA 13413	–	53.5	48.0 (restored)	–
MCNA 13451 (Fig. 4/9C, D) fragment 2 (body chamber)	–	70.2	64.0	–
MCNA 13451 (Fig. 4/9A, B) fragment 4 (phragmocone)	–	40.1	36.6	–
MCNA 14388	23 (max 31.0)	9.0	10.0	8.0
MCNA 17131 (Fig. 4/7A, B)	30.5	12.0	12.8	12.0
MCNA 17132 (Fig. 4/8A, B)	33.5	12.0	11.0	13.0
MCNA 17134	20.0 (restored)	9.0	7.5	–

Discussion. These specimens show the prominent tubercles and high keel characteristic of *Deiradoceras*, plus the bifurcate ribbing seen on the inner whorls of MCNA 13451 (Fig. 4/9A, B). The subquadrate, yet high, whorl sections favour assignment to *D. cunningtoni* and sets them apart from congeners. Despite being

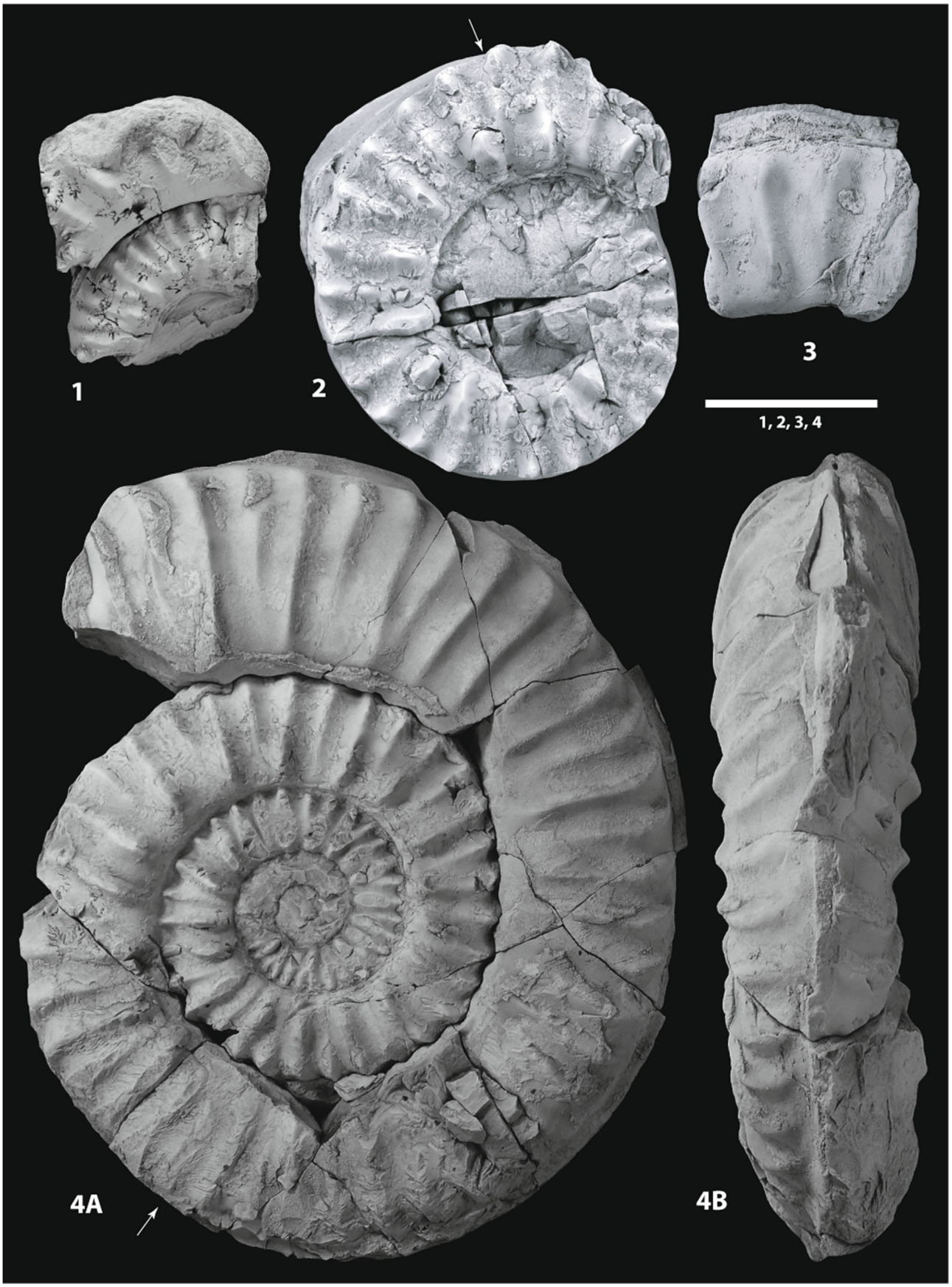


Fig. 5. *Mortoniceras* (*Deiradoceras*) *bispinosum* (Spath, 1921). **1**. MCNA 17145, lateral view; between levels A4 and A5, *H. choffati* Subzone. **2**. MCNA 13513, lateral view; level A4, *H. choffati* Subzone. **3**. MCNA 17138, lateral view of a body chamber fragment; level A4, *H. choffati* Subzone. **4A, B.** MCNA 17143, lateral and ventral views of complete specimen, lacking rostrum; level A8, *M.* (*M.*) *inflatum* Zone. Arrow indicates position of last septum. Scale bar equals 50 mm. All housed at Museo de Ciencias Naturales de Álava (MCNA).

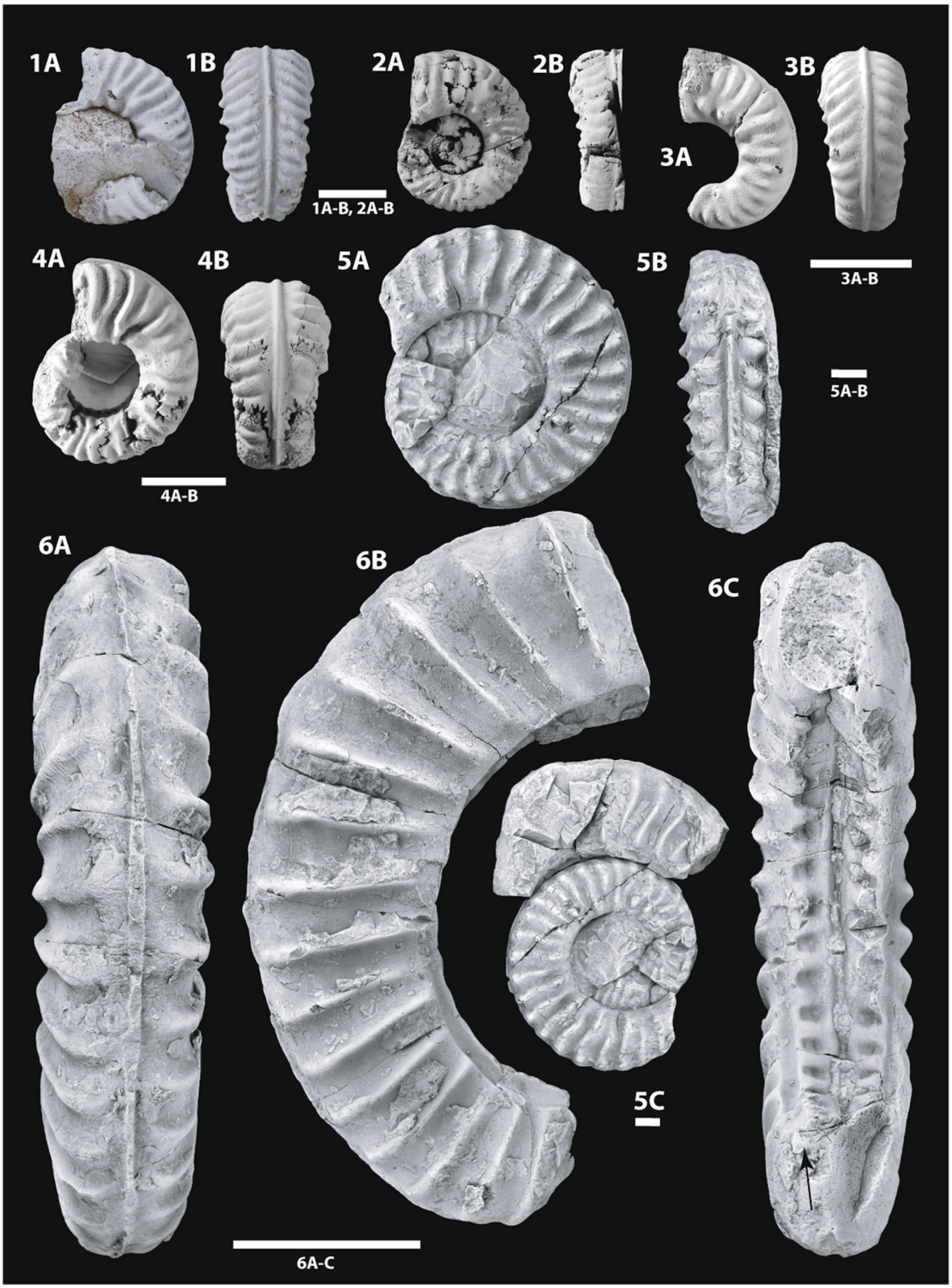


Fig. 6. Early late Albian Mortoniceratinae from the Western Pyrenees; all housed at Museo de Ciencias Naturales de Álava (MCNA). **1A, B.** *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921), MCNA 13422, lateral and ventral views; level K5, *H. binum* Subzone. **2A, B.** *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921), MCNA 14389, lateral and ventral

fragmentary, specimen MCNA 13451 is comparable to the holotype (Spath, 1933, pl. 41, fig. 6), except for the mid-flank tubercle. Spath (1933, p. 418; text-fig. 145d; pl. 43, fig. 3) reported transitional forms of *Deiradoceras* to *Mortoniceras* gr. *pricei* in which there was a tendency to develop a mid-flank tubercle on the longest ribs, but these forms differ from our specimen in being more involute and in having denser ribbing. Consequently, specimen MCNA 13451 is here suggested to be a late form of *D. cunningtoni*, possibly transitional to evolute trituberculate forms of *Mortoniceras* spp., but more material is needed to test this hypothesis. Collignon's specimens (1950, pl. 12, figs. 1, 2) from Madagascar show a ribbing pattern (maybe with a subtle mid-flank tubercle; not clear in Collignon's photographs) and suture line that are comparable to that of the phragmocone of MCNA 13451 (Fig. 4/9A, B). Another specimen of *D. cunningtoni* from the I2 level in Irurtzun (Geologisch-Paläontologisches Institut der Universität Münster, GPIM L6003), illustrated by Wiedmann and Kauffman (1978, pl. 3, fig. 4), is a slightly depressed form (Wh/Ww = 0.92), but otherwise closely comparable to MCNA 13451 (Fig. 4/9).

The small specimens MCNA 14388, 17131 (Fig. 4/7) and 17132 (Fig. 4/8) show a common ribbing pattern evolving from rounded branched ribs and a slightly depressed whorl section to single ribs, slightly concave and more separated, and slightly compressed whorl sections. This type of ribbing is closely comparable to juvenile specimens assigned to *D. cunningtoni* by Spath (1932, pl. 37, fig. 2; var. *flexuosa*, and pl. 39, fig. 5; sp. nov. – diameters of 43 and 46 mm, respectively). Specimen MCNA 17134 shows concave ribbing between tubercles that matches the ribbing of typical *D. cunningtoni* at larger diameters. The occurrence of all specimens of *D. cunningtoni* in the same bed suggest likely intraspecific variability at least in early growth stages.

Occurrence. *BCB – Hysteroceras binum* and *H. choffati* Subzones of *M.* (*M.*) *pricei* Zone, La Escrita Unit, Valmaseda Formation; level K4 in Peñaranda (Karrantza) and level K7 in Lastrillas (Trucíos), province of Biscay, Basque Country, Western Pyrenees, Spain. Albian IV of Wiedmann (1962, 1979) and Wiedmann and Kauffman (1978) (level I2 herein; *H. choffati* Subzone), Irurtzun, Navarre, Western Pyrennes, Spain. Elsewhere this species is known from the *Hysteroceras orbignyi* Subzone (bed IX at Folkestone) of *Hysteroceras varicosum* Zone to lower *Mortoniceras inflatum* Zone (bed XI at Folkestone), south-east England; probably of the same age in Madagascar; upper *Mortoniceras* (*M.*) *pricei* Zone in France (Foix, eastern Pyrenees); *Mortoniceras* (*M.*) *pricei* Zone in the Talerhza basin, Morocco; condensed upper Albian, Serbia.

Mortoniceras (Deiradoceras) bispinosum (Spath, 1921)
Fig. 5/1–3, 4A, B

*1921 *Subschloenbachia bispinosa* Spath, p. 285, pl. 24, fig. 9.
1931 *Deiradoceras bispinosum* Spath; van Hoepen, p. 54, text-fig. 12.
1941 *Deiradoceras bispinosum* Spath; van Hoepen, p. 75, pl. 12; text-figs. 33–35.
1941 *Deiradoceras exilis* van Hoepen, p. 78, pl. 14; text-figs. 40, 41.
1950 *Deiradoceras* cf. *exile* van Hoepen; Collignon, p. 74, pl. 13 (4), fig. 1; text-fig. 4.
?1950 *Deiradoceras* (*Mimoceras?*) *mokarahaense* Collignon, p. 77, pl. 13 (4), fig. 3; text-fig. 8.
1975 *Mortoniceras* (*Deiradoceras*) *bispinosum* (Spath, 1921); Förster, p. 228, pl. 12, figs. 2, 5 (with synonymy).
?2006 *Mortoniceras* (*Deiradoceras*) cf. *exile* (van Hoepen), Owen and Mutterlose, p. 720, text-fig. 3I.
2009 *Mortoniceras* (*Deiradoceras*) cf. *exilis* (van Hoepen); López-Horgue et al., p. 395 (specimen 13510).
2009 *Mortoniceras* (*Deiradoceras*) *exilis* (van Hoepen); López-Horgue et al., p. 395 (specimen 13513).

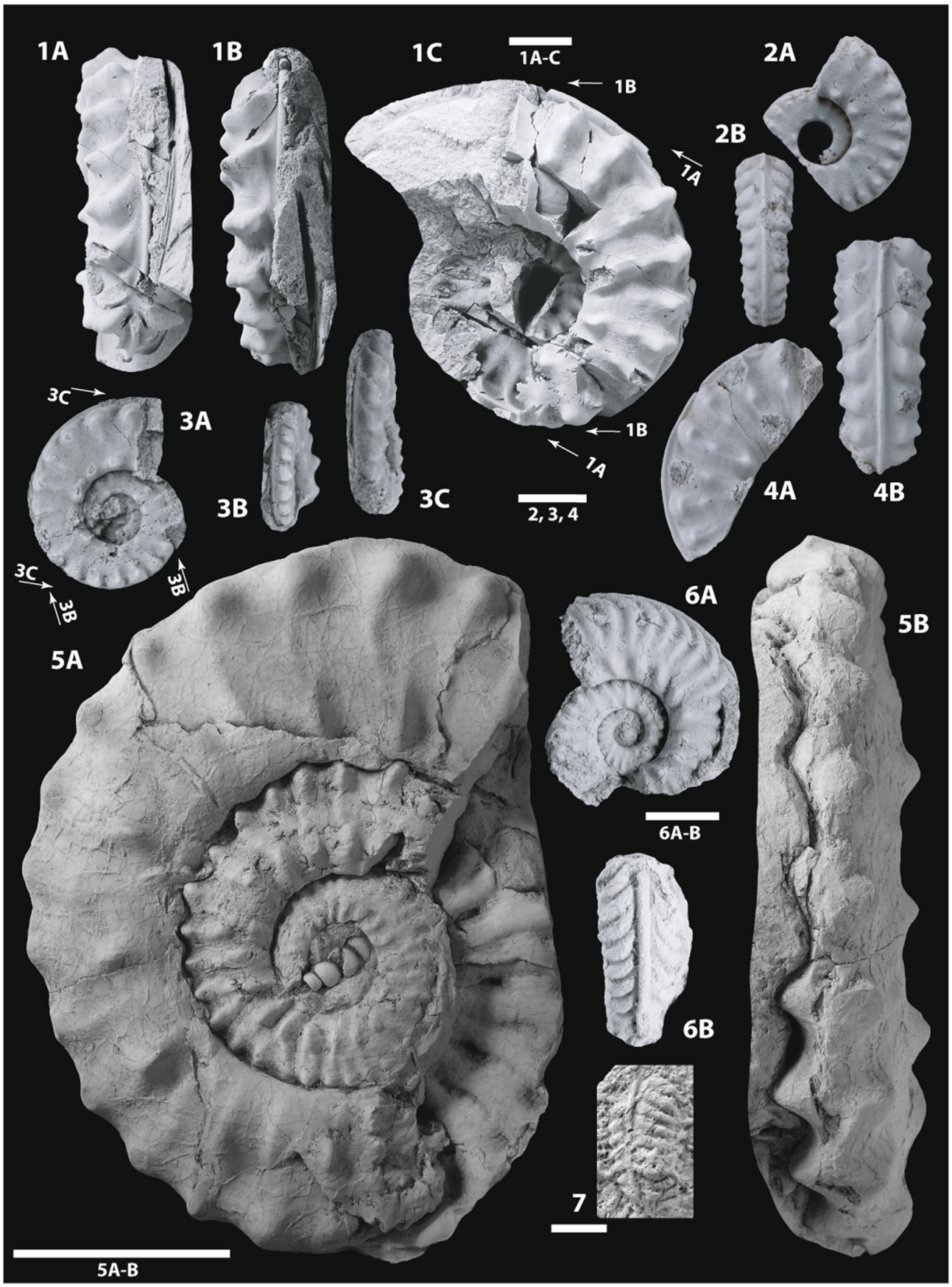
Type. The original of Spath (1921), specimen SAM PCZ 19477 in the Natural History collections of the South African Museum, Cape Town; recently reillustrated by Kennedy and Klinger (2023b, text-fig. 6).

Material. MCNA 13510 is a poorly preserved inner mould from a basal turbidite, while MCNA 13513 (Fig. 5/2) is an undeformed, wholly septate, inner sideritic mould of a whorl with calcite-replaced shell partially preserved. Keel only partially preserved. MCNA 17143 (Fig. 5/4A, B) is a near-complete specimen in comparable preservation, only slightly crushed on last quarter whorl of the phragmocone, while MCNA 17139 is a crushed body chamber fragment comprising one-eighth of a whorl, and MCNA 17138 (Fig. 5/3) is a 25° whorl fragment of a body chamber, well preserved in siderite. MCNA 17146 is a 90° whorl fragment of a crushed phragmocone, while MCNA 17145 (Fig. 5/1) is a 90° whorl fragment of a well-preserved sideritic phragmocone and contiguous partial whorl showing the last septum.

Description. MCNA 13513 (Fig. 5/2): evolute, umbilicus equalling 46 per cent of diameter. Whorl section subtrapezoidal, widest at umbilical tubercles. High keel rising 2–3 mm over venter. Coarse, wide ribs, equally spaced, mainly rectiradiate but subtly rursiradiate in first half, and prorsiradiate in second half also occurring. On first half of whorl, ribs forked, bifurcating from very high, prominent and flared umbilical bullae; in last half of whorl mainly intercalated long and short single ribs, but some still forked. Ribs slightly wider towards venter. Sharp ventrolateral tubercles gently projected adorally towards keel, without reaching it. All ribs with deep concavity between tubercles. Very subtle mid-lateral swelling observed on some ribs, at end of whorl. Umbilical wall initially high and almost vertical, becoming rounded towards end of whorl. Shallow groove on umbilical wall of last one-eighth of whorl. Wh/Ww ratio 0.8 (slightly depressed).

MCNA 17143 (Fig. 5/4): serpenticone with wider umbilicus comprising 52, 50 and 48 per cent at diameters of 120, 160 and 250 mm, respectively. Up to diameter of 70 mm, sharp ribs branching into two from high and sharp umbilical bullate tubercle, crossing flank towards high ventrolateral tubercle; only some single ribs intercalated. Up to diameter of 95 mm branched ribs replaced by single ribbing. Primaries showing increasing strength of umbilical and ventrolateral tubercles, with former becoming flared. Secondaries arising from mid-flank, bearing only ventrolateral tubercle. Very shallow swelling at mid-flank observed on some ribs at diameter of 100–135 mm. All ribs showing a concave shape between tubercles, as wide as interspaces and slightly bent adorally on ventrolateral shoulder, not reaching high keel; but this general strength decreasing gradually up to diameter of 150 mm at end of phragmocone and

views; level K7, *H. choffati* Subzone. **3A, B.** *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921), MCNA 17130, lateral and ventral views; level K7, *H. choffati* Subzone. **4A**, **B**, *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921), MCNA 17136, lateral and ventral views; level K7, *H. choffati* Subzone. **5A–C.** *Mortoniceras* (*Deiradoceras*) *armintzekalensis* nov. sp., MCNA 13520 (**holotype**), lateral, ventral views of fully septate specimen, and partial body chamber in corresponding position; level A4, *H. choffati* Subzone. **6A–C.** *Mortoniceras* (Deiradoceras) *armintzekalensis* nov. sp., MCNA 13516, ventral, lateral and dorsal views of final part of body chamber; level A6, *M.* (*M.*) *inflatum* Zone [arrow indicates ridge in adapical part of body chamber preserved as a trough on internal mould]. Scale bar equals 10 mm, except for 6 where it is 50 mm.


1A
1B
1C
1A-C
1B
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3C
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3B
3C
1B
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4A
4B
3C
3B
3B
5A
6A
5B
6A-B
6B
7
5A-B

adapical part of body chamber. Accordingly, rib density changing from 31 ribs per whorl (95 mm diameter), to 34 at 150 mm diameter and 43 at 250 mm diameter. Body chamber ribs single, with primaries bearing low umbilical tubercle and conspicuous strengthening at ventrolateral shoulder where ribs strongly bend adorally, not reaching very high keel (5–6 mm). Whorl section changing from subquadrate trapezoidal (Wh 38/Ww 47 = 0.8) at 110 mm diameter to compressed with convergent flanks on body chamber (Wh 67/Ww 58 = 1.15) at diameter of 250 mm. Spiral ridges conspicuous only in some ventrolateral tubercles of last half whorl of phragmocone.

Specimen MCNA 17139 showing ribbing pattern similar to body chamber of MCNA 17143; MCNA 17138 (Fig. 5/3) showing ornament corresponding to adoral part of phragmocone and adapical part of body chamber. MCNA 17145 (Fig. 5/1) and 17146 match branched ribbing pattern of inner whorls of species well.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13510	80.0	–	–	–
MCNA 13513 (Fig. 5/2)	133.0	49.5 (rest.)	60.0 (rest.)	61.0
MCNA 17143 (Fig. 5/4A, B)	250.0	67.0	58.0	120.0
MCNA 17139	–	51	–	–
MCNA 17138 (Fig. 5/3)	–	54	–	–
MCNA 17146	–	31	–	–
MCNA 17145 (Fig. 5/1)	–	29	28	–

Discussion. Spath (1921, p. 285) first described *Subschloenbachia bispinosa* on the basis of a weathered fragmentary specimen from South Africa. Although his description is very general, he did record simple ribbing "near the end of the shell" and "peculiar whorl section with depressed outer tubercle" as typical of this species. In a recent revision of South African *Deiradoceras*, Kennedy and Klinger (2023b) considered *D. bispinosum* and *D. exilis* to be synonyms of *D. prerostratum* (*Pervinquieria* (*Deiradoceras*) *prerostrata* of authors). However, we here suggest that forms related to *D. prerostratum* bear an overall denser and more rursiradiate ribbing with less strong tubercules, and a less wide umbilicus, different from that of *D. bispinosum* and *D. exilis*. Kennedy and Klinger (2023b, text-figs. 6 and 14, respectively) reillustrated the holotypes of *Subschloenbachia bispinosa* and *Deiradoceras exilis*; both have a closely similar, wide umbilicus (48 and 47.9 per cent of diameter, respectively), with ribs as wide as interspaces, prominent umbilical bullate tubercles and ventrolateral slightly bullate tubercles not reaching the keel. Moreover, the holotype of *D. exilis* (diameter 160 mm) shows a highly comparable ribbing to that of *Deiradoceras bispinosum* figured by van Hoepen (1941, pl. 12) at the same diameter, with also a closely similar evolute coiling where the umbilicus comprises 50 per cent of its maximum diameter. MCNA 13513 (Fig. 5/2) and MCNA 17143 (Fig. 5/4) also share the wide umbilicus (46 and 50 per cent, respectively), strong tubercles and a similar rib number per whorl (30–34) at a diameter of 130–160 mm, with the South African specimens of *D. bispinosum* and *D. exilis*. MCNA 17143 bears 43 ribs on the last whorl (near three-quarters of it being body chamber), showing a gradual change from quadrate to compressed whorl section, a characteristic that sets it apart from the body chamber of van Hoepen's (1941) specimen (pl. 12). However, the gradual change to a single ribbing pattern on the body chamber and the highly comparable inner whorls (with similar whorl section and tubercles) suggest they may be variants of the same species. The lack of a rostrum in our specimens precludes interpretation as micro- or macroconch.

The whorl section and whorl height/whorl width ratio at similar diameters near 160 mm (0.80) in both Basque specimens is close to that of the South African holotypes of *D. exilis* (0.83; van Hoepen, 1941, text-fig. 40) and *D. bispinosum* (0.89; van Hoepen, 1941, text-fig. 34). Overall, they are less depressed than those of the holotype of *D. prerostratum* (see Kennedy and Klinger, 2023b). The presence of a very subtle mid-flank tubercle is an exclusive feature of the Basque specimens that suggest these may be late forms of the species.

Specimens of *D. bispinosum* from Mozambique as illustrated by Förster (1975, pl. 12, figs. 2, 5) share the forked ribbing of the inner whorls, changing adorally to single ones, the same degree of evolution and a wide umbilicus (49 per cent), strong tubercles and a similar quadrate whorl section (Förster, 1975, fig. 73) with the Basque specimens.

Deiradoceras amsburyi Young, 1957 (see also Kennedy, *in* Gale and Kennedy, 2020) is an allied species with a weaker ornament; the body chamber with ribs adorally projected and feebly convergent flanks is similar to features seen in MCNA 17143 (Fig. 5/4).

MCNA 13510 is assigned tentatively to the present species on the basis of its forked ribs at a diameter of 50–60 mm.

Occurrence. *BCB – Hysteroceras choffati* Subzone of *M.* (*M.*) *pricei* Zone to *M.* (*M.*) *fallax* Zone, Deva Formation; Armintza (province of Biscay), Basque Country, northern Spain. Records from the Armintza section are as follows: MCNA 13510 at A3 (at 474 m), 13513 at A4 (at 505 m), 17138 and 17139 at A5 (at 515–517 m), 17145 and 17146 between levels A4 and A5 (coeval Basorda section to the east), and 17143 at A8 (at 565 m); m referring to the section in López-Horgue et al. (2009). Elsewhere this species is known from the upper Albian, Mzinene River area, Zululand, South Africa (van Hoepen, 1941; Albian V, locality 51 in Kennedy and Klinger, 1975), upper Albian, Mokaraha, Madagascar; *D. cristatum-H. varicosum* (*sensu* Förster, 1975) zones, Rio Zepundune, South Mozambique; a likely *H. binum* to *H. choffati* Subzones in offshore Suriname.

Mortoniceras* (*Deiradoceras*) *prerostratum (Spath, 1921)
Fig. 6/1A, B, 2A, B, 3A, B, 4A, B

*1921 *Subschloenbachia prerostrata* Spath, p. 284, pl. 24, fig. 10.
1933 *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921); Spath, p. 419, text-fig. 144d.
1933 *Mortoniceras* (*Deiradoceras*) sp.; Spath, p. 422, pl. 36, fig. 10; pl. 43, fig. 5.

Fig. 7. Early late Albian Mortoniceratinae from the Western Pyrenees (Museo de Ciencias Naturales de Álava (MCNA), unless indicated otherwise). **1A–C.** *Mortoniceras* (*Mortoniceras*) *aitzindari* nov. sp., MCNA 17129 (**holotype**), ventral and lateral views of complete adult; level K7, *H. choffati* Subzone. **2A, B.** *Mortoniceras* (*Mortoniceras*) *aitzindari* nov. sp., MCNA 13449 (**paratype**), lateral and ventral views of fully septate juvenile; level K7, *H. choffati* Subzone. **3A–C.** *Mortoniceras* (*Mortoniceras*) *aitzindari* nov. sp., MCNA 14391 (**paratype**), lateral and ventral views of a juvenile with body chamber; level K7, *H. choffati* Subzone. **4A, B.** *Mortoniceras* (*Mortoniceras*) *aitzindari* nov. sp., MCNA 13450 (**paratype**), lateral and ventral views of adult body chamber; level K7, *H. choffati* Subzone. **5A, B.** *Mortoniceras* (*Deiradoceras*) *aldakor* nov. sp., lateral and ventral views of **holotype** HONTZA 20134; lower upper Albian, Dima, near Urkiola, Biscay. **6A, B.** *Mortoniceras* (*M.*) sp. juv. cf. *pricei* (Spath, 1922), MCNA 17147, lateral and ventral views, fully septate; level O1, *H. binum* to *H. choffati* Subzones. **7.** *Mortoniceras* (*M.*) sp. juv. cf. *pricei* (Spath, 1922), MCNA 13453, plaster cast with ventral to lateral view; level K9, *Mortoniceras* (*M.*) *inflatum* Zone. Scale bar equals 10 mm (1–4, 6) and 50 mm (5).

1941 *Deiradoceras prerostratum* Spath sp.; van Hoepen, p. 73, text-figs. 29–32; pl. 11.
1941 *Deiradoceras linguatum* van Hoepen, p. 79, text-figs. 42, 43.
1963 *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921), Collignon, p. 170, pl. 311, fig. 1317.
1971 *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921); Renz, p. 602, pl. 8, fig. 1a.
1971 *Mortoniceras* (*Deiradoceras*) cf. *exile* (van Hoepen); Renz, p. 602, pl. 11, fig. 1; text-figs. 6e, 7l.
1975 *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921); Förster, p. 230, pl. 13, fig. 2a.
1982 *Mortoniceras* (*Deiradoceras*) cf. *exile* (van Hoepen); Renz, p. 54, pl. 12, fig. 5.
1999 *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath, 1921); Kennedy et al., p. 1109, text-figs. 10, 11.
2009 *Mortoniceras* (*Deiradoceras*) *prerostratum* (Spath); López-Horgue et al., p. 392, fig. 7P, P1.
2023b *Pervinquieria* (*Deiradoceras*) *prerostrata* (Spath, 1921); Kennedy and Klinger, p. 3, text-figs. 1–5, 9.

Type. The original of Spath (1921), specimen SAM PCZ 4970 (Natural History collections of the South African Museum, Cape Town), reillustrated by Kennedy and Klinger (2023b, text-fig. 1).
Material. MCNA 13422, 14389, 14390, 17130, 17135 and 17136 (Fig. 6/1–4), all inner moulds of undeformed small-sized specimens, corresponding to phragmocones, most of them with up to half a whorl of body chamber.
Description. Keel low, slightly above ventrolateral ending of ribs. Depressed, with Wh/Ww = 0.73. Evolute, with umbilicus equalling between 36 and 40 per cent of diameter. Dense ribbing, between 14 and 21 ribs per half whorl. Deep umbilicus with initially steep walls in smallest specimens (15–23 mm diameter) changing to rounded walls later at greater diameter (28 mm). Ribs arising from umbilical wall with different strengths between specimens, but with overall bullate shape, reaching umbilical shoulder, where sharp conical tubercle perched; from this tubercle branching into two ribs through short parallel flanks, with adapical rib rursiradiate and adoral one rectiradiate. Afterwards reaching ventrolateral shoulder, presenting subtle tubercle, and widening on rounded ventral area at right angles to keel or slightly adorally oriented; conspicuous sulcus parallel to keel. Occasional single ribs arising from mid-flank. In some specimens, ribs effacing on mid-flank. Umbilical tubercles increasing in strength at end of preserved specimen, rendering shape of flare.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13422 (Fig. 6/1A, B)	28.6	10.8	14.8	11.2
MCNA 14389 (Fig. 6/2A, B)	27.5	10.0	14.0	10.0
MCNA 14390	24.5 (restored)	10.0	12.0	10.0
MCNA 17130 (Fig. 6/3A, B)	15.0	6.0	8.0	5.5
MCNA 17135	17.0	6.0	8.0	6.0
MCNA 17136 (Fig. 6/4A, B)	24.0	9.0	13.0	9.5

Discussion. Well-preserved inner whorls of specimens of *M.* (*D.*) *prerostratum* were first illustrated by van Hoepen (1941), following the cursory description of the type by Spath (1921), who presented merely a drawing of two consecutive inner and outer whorl sections. Spath (1933, p. 419, text-fig. 144d) referred to this species again, this time on the basis of a formally undescribed specimen collected by himself in Zululand and now housed at the Natural History Museum (NHMUK C52980); this individual has recently been described by Kennedy and Klinger (2023b, p. 12, text-fig. 9). It shows a well-preserved third of each of two consecutive inner and outer whorls; the inner whorl has dense ribbing, adapically inclined umbilical flares and a quite depressed whorl section (Wh 25.1/Ww 31.3 ratio = 0.8) that compares well with the present specimens. The holotype whorl section also shows a depressed inner whorl with a low keel (Spath, 1921, pl. 24, fig. 10). Juvenile specimens of *M.* (*Deiradoceras*) sp. figured by Spath (1933) share the similarly flared ribbing and a depressed whorl section. The individual illustrated by van Hoepen (1941, text-figs. 29–32) shows inner whorls with denser ribbing and typical flares, a depressed whorl section (Wh/Ww = 0.83) and an umbilicus that equals 35.5 per cent of the diameter. *Deiradoceras linguatum* van Hoepen, 1941 (text-figs. 42, 43), with an identical whorl section to our specimens, is likely a juvenile specimen of *D. prerostratum*. Renz (1971) illustrated a good example of the inner whorls of this species with a similar depressed section and flared ribbing; inner whorls of *D. mokarahaense* and *D.* cf. *exile* of Renz (1971) are similar, but not flared and not quite as dense as in *D. prerostratum*, respectively. Specimen XXVII 91 of Förster (1975, pl. 13, fig. 2a) shares a quite similar shape at a similar diameter (25–35 mm) with the Basque specimens, with dense and flared ribbing.
The holotype of *D. prerostratum* (South African Museum, no. 4970) was illustrated by Kennedy et al. (1999, fig. 10/1–4) and again by Kennedy and Klinger (2023b, text-fig. 1); the inner whorl corresponds to a greater diameter than the present specimens, but the denser, slightly flared ribbing is still apparent. The holotype bears strong spiral striations on the ribs of the inner whorl, a feature less conspicuous in NHMUK C52980, due to preservation, and not observed in the Basque specimens, because the latter are internal moulds of juveniles.
Occurrence. *BCB – Hysteroceras binum* and *H. choffati* Subzones of *M.* (*M.*) *pricei* Zone, La Escrita Unit, Valmaseda Formation (levels 28 and 30 in López-Horgue et al., 2009); Balmaseda, Biscay province, Basque Country (Western Pyrenees), Spain. Elsewhere this species is known from the lower upper Albian of Zululand (South Africa) and Madagascar; *H. binum* and *H. choffati* Subzones, southern England; *H. binum* Subzone, Venezuela; lower upper Albian, South Mozambique; *H. varicosum* Zone (*H. binum* to *H. choffati* Subzones in this work), Texas.

Mortoniceras* (*Deiradoceras*) *armintzekalensis nov. sp.
Fig. 6/5A–C, 6A–C

2009 *Mortoniceras* (*Deiradoceras*) *bispinosum* (Spath); López-Horgue et al., p. 395.

Types. The holotype (MCNA 13520; Fig. 6/5A–C) and paratype (MCNA 13516; Fig. 6/6A–C) are from the upper Albian at Armintza on the Biscay coast, Basque Country, Western Pyrenees, Spain, from levels A4 (MCNA 13520; m 505.0, *H. choffati* Subzone of *M.* (*M.*) *pricei* Zone) and A6 (MCNA 13516; m 528.5, *M.* (*M.*) *inflatum* Zone); metre reference as in López-Horgue et al. (2009).
Derivatio nominis. In reference to the Bay of Armintzekale, at Armintza (Biscay, Basque Country, northern Spain).
Diagnosis. *Deiradoceras* with single ribbing composed of flexuous primaries and secondaries on phragmocone, changing to slightly flexuous and less sculptured at beginning of body chamber and subsquently to stronger and rectiradiate and flared to end of conch.
Description. MCNA 13520 (Fig. 6/5): phragmocone, with adapical part of body chamber (75° whorl), showing quadrate whorl section at diameter of 88 mm, with umbilicus comprising 43 per cent. Whorl section of body chamber feebly compressed, higher than wide, with umbilicus increasing to 55 per cent at 135 mm diameter, changing from evolute to serpenticone. Whorl section widest at umbilical tubercles. Keel high in both specimens, about 4 mm above venter in MCNA 13516 (Fig. 6/6). MCNA 13520 bearing 33 ribs at 88 mm diameter. From a diameter of *c.* 45 mm,

ribbing being single, composed of almost regularly arranged primaries and intercalated secondaries slightly wider than interspaces. Primaries arising from high and steep umbilical wall, gradually becoming rounded, bearing high and slightly flared umbilical bullae, then crossing flank to ventrolateral shoulder, showing a sharp conical inner ventrolateral tubercle, subsequently widening and slightly bending adorally towards keel on flattish venter. Ribs feebly flexuous, rectiradiate on lower flank to rursiradiate at mid-flank and then prorsiradiate on upper flank. Secondaries arising on lower flank, of same strong ventrolateral development as primaries. All ribs slightly concave between umbilical and ventrolateral tubercles, and secondaries from mid-flank to ventrolateral tubercle, but presence of shallow swelling at mid-flank from diameter of *c.*70 mm onwards (both on phragmocone and beginning of body chamber) making them appear flat between tubercles. Subtle spiral ridges conspicuous only on some ventrolateral tubercles on phragmocone. On body chamber, all ribs primaries, less flexuous and less sculptured than on phragmocone.

MCNA 13516: 120° fragment of body chamber with only rectiradiate to slightly rursiradiate single primaries, progressively strengthening adorally, being elevated and distant (interspaces wider than ribs), arising from umbilical edge with feeble bullate umbilical tubercle towards ventrolateral tubercle, firstly bullate and then flared, ending from very subtle adoral bend to right angles with respect to keel towards aperture. Flanks slightly convergent towards venter. Spiral groove, 8 mm wide, along umbilical slope visible on first half and disappearing at 90° before end of shell (Fig. 6/6B, C); same feature also conspicuous on body chamber part in MCNA 13520.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13520 (holotype)	135.0 (restored)	42.5	39.1	71.0
(Fig. 6/5A–C)	88	31.0	32.0	38.0
MCNA 13516 (paratype)	–	56.7	50.0	–
(Fig. 6/6A–C)				

Discussion. Subquadrate whorl section, widest at umbilical bullae, strongly bituberculate, with concave ribs between tubercles are the main features of *Mortoniceras* (*Deiradoceras*) spp. The presence of a mid-flank tubercle suggest late forms of the subgenus. MCNA 13516 (Fig. 6/6) represents the natural extension of the body chamber of MCNA 13520 (Fig. 6/5C): an imprint of ventrolateral tubercles of the contiguous inner whorl on the dorsal part of MCNA 13516 (Fig. 6/6C) reproduces exactly the same ornament seen on the venter of MCNA 13520 (Fig. 6/5B) at a corresponding diameter (80–100 mm); the size of the spiral groove observed in the adapical part of MCNA 13516 (Fig. 6/6C) is equivalent to the same feature observed on the umbilical wall of the body chamber of MCNA 13520 (Fig. 6/5C); finally, the ribbing pattern clearly reproduces the transition on the body chamber from slightly flexuous in MCNA 13520 to rectiradiate, stronger ribs in MCNA 13516. Accordingly, a maximum diameter of 200 mm with an umbilicus of 95 mm (47.5 per cent) may be reconstructed.

The body chamber resembles some species of the subgenus *Mortoniceras*, such as *M. arietiforme* and *M. geometricum*, but those lack pronounced tubercles. Our specimens are close to *Deiradoceras bispinosum* as described by van Hoepen (1941, pl. 12; text-figs. 33–35) from the upper Albian of South Africa, sharing a very evolute shell, similar whorl section, concave ribbing and similar ornament change from the phragmocone to the body chamber. However, the Basque specimens differ from South African *D. bispinosum* and other Basque specimens described above in the following respects: only single ribbing from very early stages (45 mm diameter) onwards, being flexuous up to the beginning of the body chamber and then mainly rectiradiate, with an overall lower concavity and common mid-flank swelling. These characteristics make this new species stand apart from congeners. Specimen 1967 XXVII 88 of *M.* (*D.*) *bispinosum* from Mozambique, as described and illustrated by Förster (1975, pl. 12, fig. 5), shares with the new species described here a slightly flexuous, inner whorl ribbing and a slightly flared ventrolateral tubercle on the body chamber, but the umbilicus is less wide and has a weaker umbilical tubercle. The umbilical tubercle in *M.* (*D.*) *armintzekalensis* nov. sp. remains constant in its position, whereas congeners (e.g., *D. prerostratum*) have it higher on the flank and show typically forked rursiradiate ribs. *Mortoniceras (D.) besairiei* (Collignon, 1950, pl. 12 (3), figs. 3, 4) from Madagascar is a depressed and less evolute form with also forked ribs. An umbilical groove (ridge-shaped thickening on the inner body chamber) seems to be another diagnostic feature of some species of *Deiradoceras*, being a character that is not shared with other subgenera of *Mortoniceras*. Spath reported these grooves in *D, prerostratum* from South Africa and *D. cunningtoni* from France (Spath, 1921, p. 284; 1931, p. 419). Collignon (1950) cited it for *D. fibulatum*, a form that is very close to *D. prerostratum*. The function of this feature remains to be determined; so far, it has been noted in only few specimens. We suggest that this structure might be related to muscle insertions of the soft body.

Occurrence. As for types.

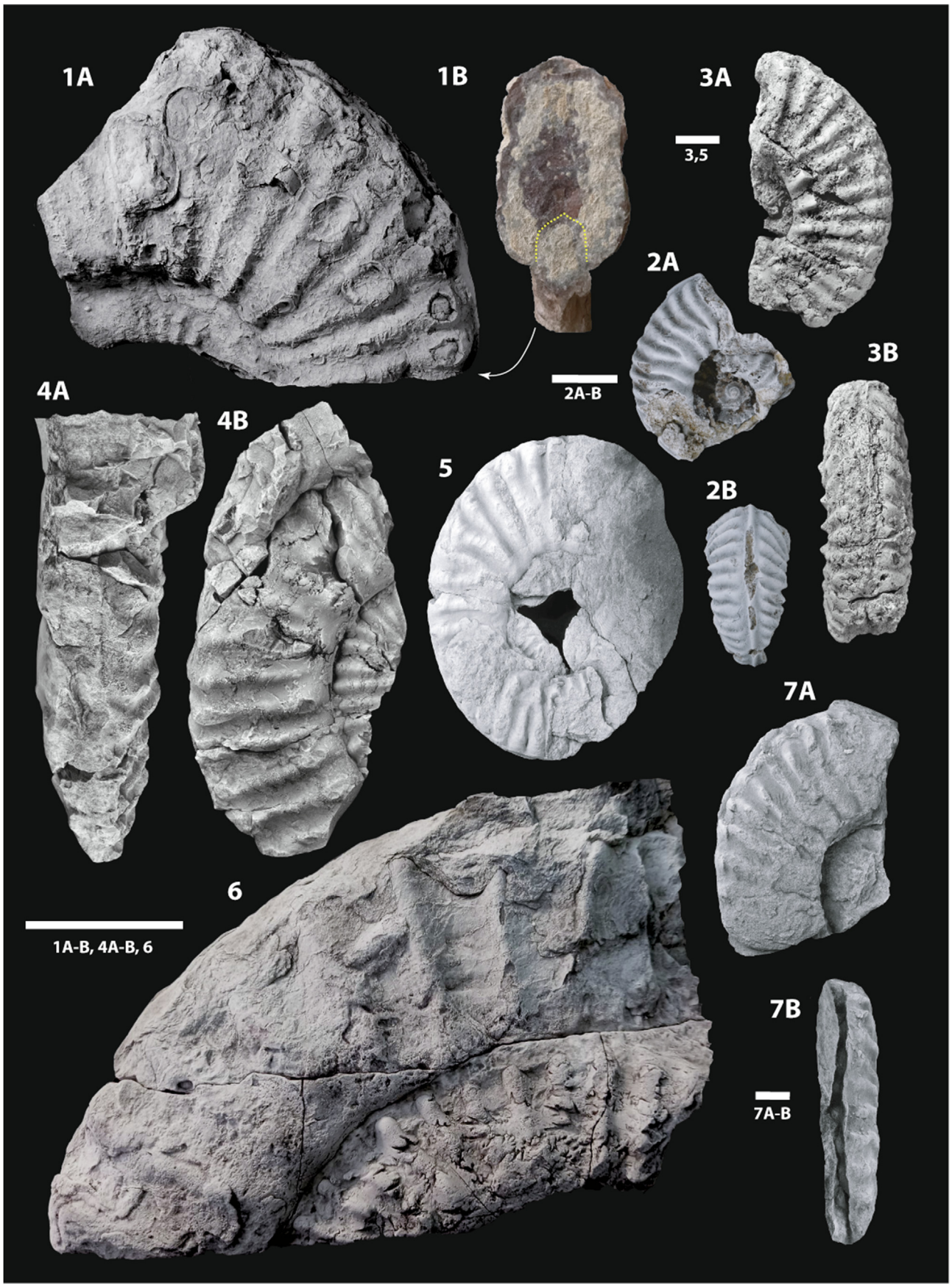
Mortoniceras (Deiradoceras) aldakor nov. sp.
Fig. 7/5A, B

Type. The holotype is specimen Hontza 20134 (Fig. 7/5A, B), preserved as a laterally crushed internal mould, with two counterpart fragments of the inner phragmocone and body chamber, from the lower upper Albian at Dima (province of Biscay), north of Legutio (province of Araba), Basque Country, Western Pyrenees, Spain.

Derivatio nominis. In Basque language, 'aldakor' means changing, in reference to the marked change of ribbing from the phragmocone to the body chamber; mainly strong tuberculation is seen on the latter.

Diagnosis. Evolute *Deiradoceras* showing a median growth stage (up to diameter of 65 mm) with ribs of similar width to interspaces, branching from high umbilical bullae up to sharp bullate ventrolateral tubercles. Only single ribbing with wider interspaces and effacing at mid-flank on body chamber. From diameter of 55 mm, primaries becoming markedly concave between high umbilical bullae and strong, high, bullate to conical ventrolateral tubercles; intercalated secondaries arising from low on flank with only ventrolateral tubercles.

Description. The only specimen, Hontza 20134 (Fig. 7/5), is quite complete, preserving a phragmocone of 82 mm in diameter and an almost entire body chamber, reaching a maximum diameter of 173 mm. From early growth stages onwards, it presents a very conservative wide and slightly deep umbilicus (*c.* 46 per cent of diameter), with a steep umbilical wall. The ornament is not much affected by compaction; half a whorl before the end of the phragmocone (80 mm diameter), a well-preserved quadrate whorl section with a height of 26 mm and a width of 27.5 mm (between umbilical tubercles) is seen. The phragmocone has about 14 rectiradiate, slightly flexuous, ribs in the first half whorl preserved (diameter 44 mm), and 30 in the successive whorl (diameter 80 mm). In this latter growth stage the ribs are sharp, as wide as the


1A
1B
3A
3,5
2A
3B
2A-B
4A
4B
5
2B
7A
6
1A-B, 4A-B, 6
7B
7A-B

interspaces, arising from the umbilical wall and strengthen into a high umbilical bullae where they branch into two near the base of the upper flank, crossing the mid-flank and bearing a high bullate ventrolateral tubercle. Ribs are markedly concave between the tubercles. In the last whorl of the phragmocone (both inner mould and external mould preserved) single ribs are intercalated, the last one being shorter and developed only on the upper flank. The body chamber presents a calculated whorl height of between 41 and 54 mm, representing a growth increment of 30 per cent. Here the ribbing is single, with 12 primaries and four intercalated secondaries, both effacing at mid-flank, except for the adoral part. In the first quarter of the whorl of the body chamber ribs are rectiradiate, then bending adapically at mid-flank to join the ventrolateral tubercle adorally. Both umbilical bullate and ventrolateral conical tubercles are high and strong, but comparatively less pronounced than on the phragmocone, yet preserving the rib concavity between them. The ventral zone appears slightly fastigiate at the end of the body chamber. Spiral ridges on the ribs are only conspicuous on the external mould. The suture line has long and wide lateral lobe.

Type. The holotype is specimen Hontza 20134 in the collections of the Hontza Natural Museum at Mañaria (Biscay, Basque Country), from the lower upper Albian Valmaseda Formation of deltaic origin outcropping in the municipality of Dima, near the Urkiola sanctuary (Biscay, Basque Country, Western Pyrenees).

Dimensions (mm)	D	Wh	Ww	U
Hontza 20134	173	54	–	79
(Fig. 7/5A, B)	79	27.5	26	37

Discussion. Effacing and distant ribbing on the body chamber in *M.* (*D.*) *aldakor* nov. sp. is comparable to the main rib pattern in *M.* (*D.*) *bipunctatum*, but the latter is substantially less evolute and shows an umbilicus that measures 35 per cent of the diameter; moreover, the inner whorls of the new species show an uneffaced denser ribbing that is not comparable to that of *D. bipunctatum* at the same diameter (80 mm) (holotype and other Texas specimens in Kennedy et al., 1999, fig. 12). *Mortoniceras* (*D.*) *devonense* is less evolute (umbilicus 41 per cent in the holotype; Spath, 1931, pl. 47, fig. 5), with a similarly spaced ribbing throughout ontogeny, with bifurcated ribs also in the last stages. Sharp ribs in *M.* (*D.*) *cunningtoni* are mainly rectiradiate, slightly concave, with a similar strength and spacing throughout ontogeny; the holotype is more evolute than *D. aldakor* nov. sp. (50 per cent of the diameter), but the mean dimension of the umbilicus in this species (*c.* 45 per cent) is comparable. The marked change from a phragmocone with a dense ribbing with similarly wide interspaces, to effacing and more widely separated ribs on the body chamber, but with a slightly lower tubercle strength are characteristic of the new species.

Occurrence. As for type.

Subgenus *Mortoniceras* Meek, 1876 (= *Pervinquieria* Böhm, 1910)

Mortoniceras (M.) sp. juv. cf. *pricei* (Spath, 1922)

Fig. 7/6A, B, 7

*1922 *Subschloenbachia pricei* Spath, p. 101.
1931 *Pervinquieria pricei* (Spath); Spath, pl. 36, figs. 11, 12.
1932 *Mortoniceras* (*Pervinquieria*) *pricei* (Spath); Spath, p. 391, text-figs. 131 (holotype), 132; pl. 37, fig. 3 (with synonymy).
1971 *Mortoniceras* (*Mortoniceras*) *pricei* (Spath); Renz, p. 595, text-figs. 5f, g and 7I; pl. 4, fig. 2a, b; pl. 8, fig. 2a, b; pl. 9, fig. 2a, b.
1999 *Mortoniceras* (*Mortoniceras*) *pricei* (Spath); Kennedy et al., text-figs. 8, 9, 10-6 (with additional synonymy).
2007 *Mortoniceras* (*Mortoniceras*) *pricei* (Spath, 1922); Mosavinia et al., p. 91, fig. 5C–E.

Type. The original of Spath (1932), NHMUK C12488, is the holotype.

Material. Plaster cast MCNA 13453 (Fig. 7/7), obtained from a friable limonitic external mould that was lost in the process, plus a near-complete specimen (MCNA 17147; Fig. 7/6A, B) and a small fragment of about one-fifth of a whorl (MCNA 17148), both preserved three dimensionally.

Description. MCNA 13453: distinctive keel. Flank vertical, at almost right angles with respect to quite broad venter. Ribs wider than interspaces, branching from sharp umbilical tubercles, widening on ventrolateral shoulder with adorally bending terminations without reaching keel. MCNA 17147 and 17148 sharing similar features.

MCNA 17147 showing ribs branching from sharp umbilical tubercle up to diameter of 20 mm, thereafter mainly with intercalated short and long ribbing. Ribs rectiradiate, crossing flat flank between umbilical tubercle and inner ventrolateral raised tubercle, then bending adorally on broad venter and terminating in slight ventral sulcus on both sides of sharp keel.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13453 (Fig. 7/7)	–	10.0	9.5	–
MCNA 17147 (Fig. 7/6A, B)	34	12	13.5	14
MCNA 17148	–	9	9	–

Discussion. A subquadrate whorl section, lack of a mid-flank tubercle and a lower keel than *M.* (*Deiradoceras*) spp. are features typical of early late Albian bituberculate *Mortoniceras* (*M.*) spp. that are related to *M.* (*M.*) *pricei*. There are different transitions between *M. pricei* and *Deiradoceras*, and also between the former and forms of the *M. inflatum* group. Young specimens of *Deiradoceras* may be distinguished by the flared ribbing and higher keel. Specimens of *M. pricei* studied here are not comparable to *M. (Deiradoceras)* spp. treated here as they lack a concave rib profile, have less prominent tubercles, no sharp ventrolateral tubercle expanding towards the venter and bear a lower keel.

The *M. inflatum* group and juveniles of the *M. pricei* group are at times impossible to differentiate with confidence. However, features of the material presented here allow them be compared to the inner whorls of typical specimens of *M. pricei* from Perte du Rhône (France) and Folkestone (England) in

Fig. 8. Early late Albian Mortoniceratinae from the Western Pyrenees All housed in the Museo de Ciencias Naturales de Álava (MCNA). **1A, B.** *Mortoniceras* (*M.*) *tremulum* (van Hoepen, 1946), lateral view of MCNA 17151. **B.** whorl section (uncoated) of part indicated by arrow, level E-L2, *M.* (*M.*) *inflatum* Zone. **2A, B.** *Mortoniceras* (*M.*) sp. juv. cf. *fissicostatum* (Spath, 1932), MCNA 13426, lateral and ventral views, level K6, *H. choffati* Subzone. **3A, B.** *Mortoniceras* (*M.*) cf. *equidistans* (Cragin, 1893), lateral and ventral view of fully septate specimen MCNA 13456; level K8, *M.* (*M.*) *inflatum* Zone. **4A, B.** *Mortoniceras* (*M.*) *crassinodatum* (van Hoepen, 1946), MCNA 13517, ventral and lateral views of fragmentary end of phragmocone and early portion of body chamber; level A6, *M.* (*M.*) *inflatum* Zone. **5.** *Mortoniceras* (*M.*) *crassinodatum* (van Hoepen, 1946), MCNA 17142, lateral view of fully septate specimen; level A6, *M.* (*M.*) *inflatum* Zone. **6**. *Mortoniceras* (*M.*) *crassinodatum* (van Hoepen, 1946), MCNA 17140, lateral view of partial phragmocone and contiguous body chamber; level A6, *M.* (*M.*) *inflatum* Zone. **7A, B.** *Mortoniceras* (*M.*) *crassinodatum* (van Hoepen, 1946), MCNA 13525, lateral and ventral views of fully septate specimen; level A8, *M.* (*M.*) *inflatum* to *M.* (*M.*) *fallax* Zones. Scale bars equal 50 mm (1, 4 and 6) and 10 mm (all others).

NHMUK collections and figured by Spath (1932, text-fig. 132, and 1931, pl. 36, fig. 12, respectively). However, specimen MCNA 17147 has a wider umbilicus (41 per cent) than Spath's specimens (34.7 and 37.2 per cent) suggesting a transition towards more evolute forms of *Mortoniceras* (*M.*) spp. that are frequent in upper beds.

Occurrence. *BCB — H. binum-H. choffati* Subzones of *M.* (*M.*) *pricei* Zone at level O1 (MCNA 17147 and 17148) of the volcanic succession at Ondiz (Biscay) and the lower part of the *Mortoniceras* (*M.*) *inflatum* Zone, at level K-9 (MCNA 13453) at La Escrita Unit, Valmaseda Formation, Trucíos, Biscay province, Basque Country, Western Pyrenees, Spain. Elsewhere the species is known from the *Hysteroceras varicosum* Zone (*sensu* Owen, 1999) and *Mortoniceras* (*M.*) *inflatum* Zone in England, France and South Africa, the *Hysteroceras binum* Subzone in Venezuela; presumably the *Hysteroceras varicosum* and *Mortoniceras* (*M.*) *inflatum* Zones, but originating from condensed interval of early *Stoliczkaia dispar* Zone age (equivalent to *M.* (*S.*) *rostratum* Zone age) in Poland (Marcinowski and Wiedmann, 1990), the *Hysteroceras varicosum* Zone (interval with *Actinoceramus sulcatus*) of Texas and the boundary interval of the *Hysteroceras varicosum* to *Callihoplites auritus* Subzones in Iran.

Mortoniceras (Mortoniceras) sp. juv. cf. ***fissicostatum*** (Spath, 1932)
Fig. 8/2A, B

*1932 *Mortoniceras* (*Pervinquieria*) *fissicostatum* Spath, p. 396, text-fig. 133; pl. 38, fig. 6; pl. 45, fig. 1.
1971 *Mortoniceras* (*M.*) cf. *fissicostatum* Spath, Kelly, p. 446.
2020 *Pervinquieria* (*Pervinquieria*) *fissicostatum* Spath, 1932; Gale and Kennedy, p. 48, fig. 31; pl. 15, figs. 5, 6 (with synonymy).

Type. The original of Spath (1932), NHMUK C77675, is the holotype.
Material. Two specimens, both inner moulds, slightly crushed: MCNA 13426 (Fig. 8/2A, B) is a body chamber, approximately one-third of a whorl, with attached outer moulds of inner whorls. MCNA 13461 is a small body chamber fragment of about one-eighth of a whorl.
Description. Despite poor preservation, inflated whorl section recognisable, with approximate Wh/Ww ratio of 0.83, widest at umbilical tubercle. Dense ribbing, with 13 quite sharp, slightly flexuous ribs, as wide as interspaces, in largest specimen MCNA 13426; arising from steep and high umbilical wall near umbilical seam, some branching in pairs from prominent sharp tubercle on umbilical edge, with some intercalated single ribs also arising from umbilical wall. Ribs slightly widening on likely rounded ventrolateral shoulder, ending at right angles with respect to high distinctive keel or with faint adoral bending. MCNA 13461 with similar ribbing, but apparently more compressed.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13426 (Fig. 8/2A, B)	27.7 (restored)	11.2 (rest.)	13.5 (rest.)	11.1 (rest.)
MCNA 13461	–	6.6	–	–

Discussion. These specimens may be considered typical juvenile whorls of *Mortoniceras* (*M.*) sp., with distinctive ribs branching from the umbilical tubercle. No other tubercles are developed, but as Young (1957, p. 3) considered, juvenile costation in this subgenus (his "pervinquieriine type", exemplified by *kiliani*) may not have had a very early bituberculate stage. Spath (1932, p. 396) indicated that *M.* (*M.*) *fissicostatum* did have a *kiliani*-type ribbing with less marked outer tubercle giving a rounded ventrolateral shoulder in juveniles. Actually, a specimen of this species, an uncrushed mostly body chamber from Devizes, England (NHMUK C75382) shares the following features with specimen MCNA 13426: Wh/Ww 0.89 ratio (Wh = 14.8/Ww = 16.5), sharp and dense ribbing (13 ribs in one third of a whorl, only bifurcated at indicated Wh) and lack of distinctive mid-flank and ventrolateral tubercles at Wh indicated above; it differs only in the adorally bend in rib termination.
Occurrence. *BCB — Hysteroceras choffati* Subzone of the *M.* (*M.*) *pricei* Zone and *Mortoniceras* (*M.*) *fallax* Zone, levels K6 and K11 of the La Escrita Unit (Karrantza section), Valmaseda Formation, Balmaseda, Biscay province, Basque Country, Western Pyrenees, Spain. It is also known from the *Mortoniceras* (*M.*) *inflatum* Zone (U6 and U7 of Owen, *in* Jattiot et al., 2023) of England. France and Iran and the *Pervinquieria* (*P.*) *equidistans* Zone of Texas.

Mortoniceras (M.) aitzindari nov. sp.
Fig. 7/1A–C, 2A, B, 3A–C, 4A, B

2009 *Prohysteroceras* sp. juv.; López-Horgue et al., p. 392, fig. 7, N–N1.
2009 *Mortoniceras* (*Mortoniceras*) *neokentroides* Wiedmann and Dieni; López-Horgue et al., p. 392, fig. 7, O–O1.

Type. The holotype is MCNA 17129 (Fig. 7/1A–C), a complete specimen with only the phragmocone preserved as external mould, the remainder as internal mould and counterpart. Paratypes are MCNA 13449 (Fig. 7/2A, B), an internal and external mould of a fully septate juvenile, MCNA 13450 (Fig. 7/4A, B), an internal mould of one-third whorl of the body chamber, and MCNA 14391 (Fig. 7/3A–C), an internal mould of a complete juvenile. All of these are undeformed and preserved as limonitic internal moulds, and all originate from level K7 (i.e., locality 30 in López-Horgue et al., 2009) in the Karrantza section, La Escrita Unit, Valmaseda Formation, *Hysteroceras choffati* Subzone of *M.* (*M.*) *pricei* Zone; in Trucíos, Biscay province, Basque Country, Western Pyrenees, Spain.
Derivatio nominis. From the Basque word 'aitzindari' meaning forerunner.
Diagnosis. Small, evolute, parallel-flanked, quadrate-whorled *Mortoniceras*. Umbilical wall steep and high. Widely separated, rectiradiate, alternatingly long and short ribs, with occasional bifurcating ones, effaced on inner whorls and strengthening throughout ontogeny. Sharp conical umbilical and ventrolateral, nodose, blunt tubercles from early whorls onwards; mid-flank tubercles appearing near final part of phragmocone together with division of ventrolateral tubercle into inner and outer, slightly clavate, ones. Remarkable quadrituberculate body chamber. Ventral keel high and sharp, slightly above last ventrolateral tubercles.
Description. Specimen MCNA 13449 (Fig. 7/2): phragmocone representing early growth stages. Umbilicus comprising *c.* 36 per cent of diameter. Single rectiradiate ribs, long and short from innermost whorls onwards; on last 90° of whorl two pairs of branching ribs intercalated and total of 10 ribs. Ribs conspicuous but effaced at mid-flank. Ribs arising from steep umbilical wall and showing tubercle on umbilical shoulder, initially subtle and higher from diameter of 12 mm. Ribs widest on ventrolateral area, first bearing inner ventrolateral tubercle and then both inner and outer sharp tubercles; mid-flank tubercle becoming apparent at diametre of 24 mm.
MCNA 13450 (Fig. 7/4): one-third of body chamber whorl, probably adult, representing growth stage subsequent to MCNA 13449, at restored diameter of *c.* 40 mm; bearing 7 fine rectiradiate ribs, widely separated, all with sharp, conical umbilical tubercle. All ribs bearing mid-flank conical tubercles, gradually increasing in strength, as well as sharper conical inner ventrolateral and

claviform umbilical ones. Between mid-flank and inner ventrolateral tubercles, ribs slightly concave. Both MCNA 13449 and 13450 showing subquadrate whorl sections (Wh/Ww between 1.08 and 1.16).

MCNA 14391 (Fig. 7/3): not completely mature, as indicated by equally spaced simple suture lines. Outer half of whorl corresponding to body chamber. Flanks parallel and umbilicus equalling 39 per cent of diameter. Main characters as in MCNA 13449, but ribs almost totally effaced between umbilical and ventrolateral tubercles and less densely ribbed, with 19 ribs on last whorl. Conical umbilical ribs conspicuous from diameter of 11 mm onwards, strengthening adorally. Ribs widest in ventrolateral area with slightly rhomboidal sharp termination, where initially inner ventrolateral tubercle distinguished. From diameter of 23 mm, also outer ventrolateral, adorally oriented, tubercle. MCNA 14391 possessing quadrate whorl section throughout, slightly wider than high (Wh/Ww between 0.922 and 0.938 in last half whorl), with whorl height growth index of 1.5 on last half whorl. On body chamber of MCNA 14391, development of mid-flank tubercle just apparent on last rib preserved.

MCNA 17129 (Fig. 7/1): complete adult specimen with deep umbilicus, equalling 39 to 35 percent at 36 and 59 mm diameter, respectively; similarly evolute to other specimens. Umbilical wall steep; bullate ribs arising, with sharp conical tubercle on shoulder. Ribs single, rectiradiate, long and short, with two intercalated branching pairs observable only at 20 mm diameter and with wider interspaces; delicately differentiated on flanks up to diameter of 36 mm (at adapical end of phragmocone), strengthening adorally, entire ribs becoming elevated. Conspicuous conical mid-flank tubercle developing, also showing increasing strength adorally. All ribs widest in ventrolateral area, with conical inner ventrolateral tubercle developing from innermost whorls onwards and outer one from diameter of 30 mm; latter also conical, leading to adorally oriented upper end of rib, with conspicuous sulcus separating them from keel slightly higher than ventrolateral tubercles.

All showing evolute coiling, indicated by succeeding whorl reaching inner ventrolateral tubercle only, and sharp keel slightly elevated over ventrolateral tubercles. Suture lines showing well-developed lateral lobe, as long as external lobe, with umbilical main lobe at umbilical edge, half as long as others.

Dimensions (mm)	D	Wh	Ww	U
MCNA 17129 (holotype)	59	23	25	20.5
(Fig. 7/1A–C)	36	15	17.5	14
MCNA 13449 (paratype)	24.4	9.4	8.1	8.8
(Fig. 7/2A, B)				
MCNA 13450 (paratype)	40 (restored)	13.6	12.5	16 (restored)
(Fig. 7/4A, B)				
MCNA 14391 (paratype)	28.8	10.7	11.4	11.4
(Fig. 7/3A–C)	18.5	7.0	–	7.5

Discussion. Previously, López-Horgue et al. (2009) tentatively assigned two of these specimens to other species. Actually, MCNA 13449 does show a rib pattern and whorl section that are comparable to those of juveniles of *Prohysteroceras*, but careful observations of the outer whorl of the internal mould has demonstrated the clear division of the ventrolateral tubercle and the initiation of the mid-flank tubercle, key features in assigning them to the new form and distinguishing them from that genus. MCNA 13450 was earlier identified as *M.* (*D.*) *neokentroides* Wiedmann and Dieni (1968), (probably also of late *H. varicosum* Zone age, *sensu* Owen, 1976, i.e., late *M.* (*M.*) *pricei* Zone, as understood here), on account of the strength of the umbilical and ventrolateral tubercles and the rectiradiate ribbing. However, *M. neokentroides* is more evolute, not quadrituberculate, with a depressed whorl section (Wh/Ww = 0.75), more robust ribs and ventrolateral tubercles and a suture line with narrower lateral lobe and umbilical lobe divided into three elements (see Wiedmann and Dieni, 1968, fig. 95; compare with Fig. 7 here). The Basque material described here is distinct. *Mortoniceras* (*M.*) *aitzindari* nov. sp. shares some features with *M.* (*D.*)? *balmatianum* (see above), such as the smoothness of the mid-flank, the development of a feebly trituberculate stage with subdivision of the ventrolateral tubercle and a closely similar suture line (holotype: Spath, 1933, text-fig. 148). However, *M.* (*D.*)? *balmatianum* is trituberculate in its latest stage, compressed and less evolute (umbilicus *c.* 34 per cent of diameter; new species between 36 and 40 per cent). Although not a species of *Deiradoceras*, we consider *Mortoniceras* (*M.*) *aitzindari* nov. sp. to be allied to the *balmatianum* group with increasing tuberculation at an earlier stage. In the *H. choffati* Subzone (late *M.* (*M.*) *pricei* Zone), some species of *Deiradoceras* show the development of a subtle mid-flank tubercle (e.g., *M.* (*D.*) *cunningtoni*, described herein from the same stratigraphical level), but the development of inner and clavate outer ventrolateral tubercles is a feature not described so far for Mortoniceratinae of this age. This character and the mid-flank tubercle could suffice in considering *M. aitzindari* nov. sp. a forerunner of later forms of Mortoniceratinae. This feature in the new species is homoeomorphic of the substantially younger *Mortoniceras* (*Durnovarites*) *subquadratum*, but with less pronounced tubercles (uppermost Albian; holotype: Spath, 1932, pl. 37, fig. 6), and can be compared also with the holotype of *Mortoniceras* (*Cantabrigites*) *minor,* but with less dense ribbing (*M. fallax* and *rostratum* Zones) and particularly, with the "var." *robusta* as illustrated by Spath (1932, pl. 41, figs. 1 and 2, respectively). A similar rectiradiate ribbing is shared with *Mortoniceras* (*Pervinquieria*) *quadrinodosum* Spath, 1932 (pl. 42, fig. 8), which occurs in stratigraphically younger beds of the Potterne Rock in England (lower *M. inflatum* Zone of Owen, *in* Jattiot et al., 2023 = *M. inflatum* Zone as understood here); however, this species has a very wide umbilicus (48 per cent of diameter), a lower whorl height increment (1.27), common branched ribs and orthogonal rib termination to the keel, without claviform outer ventrolateral tubercles. Until new forms of Mortoniceratinae related to the new species are discovered in younger levels of expanded sections, we cannot prove it to be the true ancestor of later forms of this group. *Mortoniceras* (*M.*) *aitzindari* nov. sp. is considered to be an offshoot derived from *Mortoniceras* (*Deiradoceras*)? *balmatianum*, and a potential forerunner of later forms. We refer it to the subgenus *Mortoniceras* on account of the tuberculation.

Occurrence. As for types.

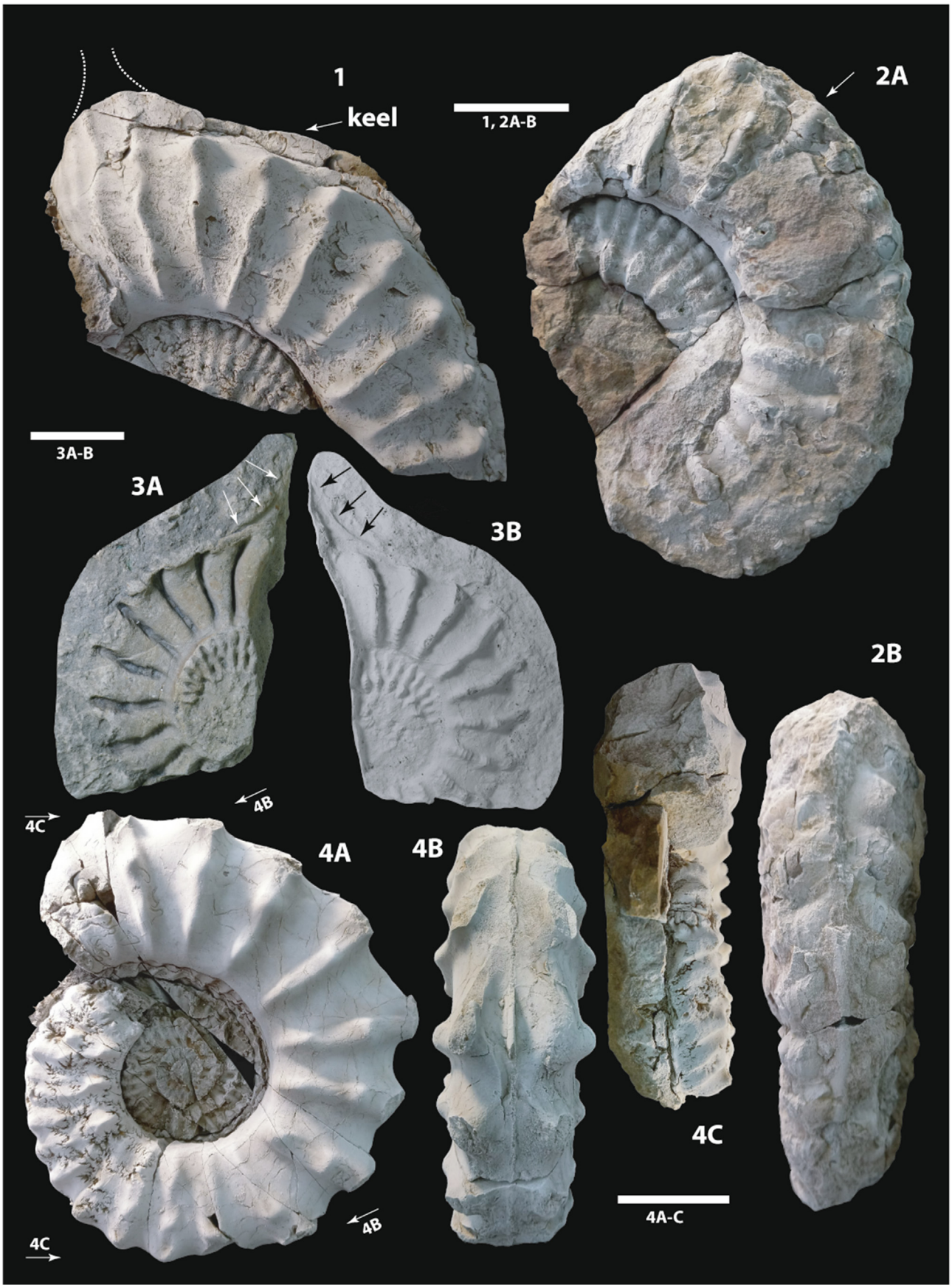
Mortoniceras (M.) tremulum (van Hoepen, 1946)
Fig. 8/1A, B

*1946 *Aidoceras tremulum* van Hoepen, p. 251, figs. 255–261.
1999 *Mortoniceras* (*Mortoniceras*) sp.; López-Horgue et al., p. 382, fig. 10a, b.

Type. The original of van Hoepen (1946, p. 253, fig. 261), specimen D. 2361.

Material. Specimen MCNA 17151 (Fig. 8/1A, B), a fragment corresponding to 90° of two contiguous whorls, corresponding to the phragmocone and preserving the original size quite well.

Description. Involute, with compressed whorl section and flanks subparallel except for ventral area, converging towards keel (roofed shape). In the adapical part of the specimen whorl height increasing from 29 to 69 mm, with outer whorl covering nearly 45 per cent of inner whorl height, and in the adoral part, change from 40 to 76 mm, and overlap less than 40 per cent; these features indicating


1
keel
1, 2A-B
2A
3A-B
3A
3B
2B
4B
4C
4A
4B
4C
4A-C
4B
4C

clearly involute form with high whorl increment of 2.4 (69/29 mm) decreasing to 1.9 (76/40 mm). Likely maximum diameter of *c.* 200 mm, with umbilicus of 80 mm (40 per cent of diameter). Single ribbing conspicuous in both inner and outer whorls, with only one clear branching rib on inner whorl. Dominant primaries arising form rounded umbilical wall and showing conspicuous umbilical bullae, somehow crested, on lower quarter of rib; rectiradiate to slightly prorsiradiate with narrower interspaces. Short swelling at mid-flank. Ribs widening substantially on upper flank; in outermost ones, from 5 mm on umbilical shoulder to 12 mm on ventrolateral shoulder, showing slightly conical inner ventrolateral tubercle and ending before keel at right angles with slight outer ventrolateral swelling. Ribs slightly concave between mid-flank swelling and ventrolateral tubercle. Conspicuous umbilical swelling only on similarly separated inner ribs.

Dimensions (mm)	D	Wh	Ww	U
MCNA 17151	200 (est.)	76	52	80 (est.)
(Fig. 8/1A, B)	170 (est.)	69	46	65 (est.)

Discussion. The degree of involution, the rapid growth in whorl height and the compressed whorl section make this specimen comparable to forms of a high-whorled stock among Mortoniceratinae, as exemplified by the genera *Goodhallites* and *Arestoceras*; however, these are less ornamented and commonly more involute. Closely comparable is *Mortoniceras* (*M.*) *pricei* with a similar umbilicus, degree of involution and slender ribbing, but this is also less ornamented, without a mid-flank tubercle and a slightly swollen outer node (Spath, 1932). Among the South African forms recorded by van Hoepen (1946), the genera *Aidoceras* and *Rusoceras* have a comparable degree of involution, whorl height increment and compressed whorl section to our specimen. Of these, *Aidoceras tremulum* (see van Hoepen, 1946, pp. 251, 254; figs. 255–256, 259) is well comparable to MCNA 17151 on the basis of its involuteness, greatest whorl thickness at umbilcal area/mid-flank, roof-shaped ventral area, broadened ribs on the ventrolateral shoulder, swelling at mid-flank and ribs slightly concave between mid-flank swelling and ventrolateral tubercle. Actually, the whorl section at a 160 mm diameter in van Hoepen's figure 259 (Wh 69/Ww 50 = 1, 38) is closely comparable to the whorl section of MCNA 17151 at an estimated 170 mm diameter (69 mm/46 mm = 1,5), with conspicuous mid-flank swellings and a roofed ventral area. *Aidoceras jubatum* (see van Hoepen, 1946, p. 248, figs. 253–254) differs only in the presence of a mid-flank swelling at the greatest diameter. *Aidoceras tremebundum* (see van Hoepen, 1946, p. 254, figs. 262, 263) is a less compressed form with finer ribbing, while *A. tremens* (see van Hoepen, 1946, p. 258, figs. 264–268) is more compressed on the outermost whorl. Overall, species of *Rusoceras* are less compressed and have subquadrate whorl sections; of these, *R. densecostatum* bears a ribbing and whorl section that are comparable to *Aidoceras* spp. Actually, Renz (1982) illustrated a Venezuelan specimen with a ribbing comparable to that of *R. densecostatum*, and argued that it might be considered a variety of *M.* (*M.*) *pricei*, but the former shows a clear mid-flank swelling and ventrolateral tubercle that are lacking in the latter. Based on this, we suggest that forms of the genera *Rusoceras* and *Aidoceras* may form a coherent stock derived from *M.* (*M.*) *pricei* by the acquisition of a mid-flank swelling and better-developed ventrolateral tubercle, that in the case of *A. tremulum* shows the first evidence of ventrolateral division in the Mortoniceratinae by a short-lived conspicuous outer swelling. On the basis of these features, *M.* (*M.*) *tremulum* is considered a form that is related to the *M.* (*M.*) *inflatum* group.

Occurrence. *BCB — Mortoniceras* (*M.*) *inflatum* Zone. Level E-L-2 in the Estella-Lizarra section, Zufia Formation in Zubielki, Navarre, western Pyrenees, Spain. Elsewhere this species is known from the Umsinene Beds at Ridge West of Beacon 624, Zululand, South Africa. On the basis of the *Mortoniceras* type occurring at the latter locality and its relative stratigraphical position (van Hoepen, 1926; Kennedy and Klinger, 1975; Klinger, 1976; Kennedy and Klinger, 2023a, p. 2, text-fig. 1; Kennedy and Klinger, 2023b, table 1) we suggest it corresponds to the *Mortoniceras* (*M.*) *inflatum* Zone as here understood.

Mortoniceras* (*M.*)** cf. ***equidistans (Cragin, 1893)
Fig. 8/3A, B

*1893 *Schloenbachia leonensis* Conrad var. *equidistans* Cragin, p. 241.
1904 *Schloenbachia kiliani* Lasswitz, p. 25, text-fig. 6, pl. 8, fig. 1.
1932 *Mortoniceras* (*Pervinquieria*) *kiliani* (Lasswitz); Spath, p. 408, text-fig. 140, pl. 38, fig. 2; pl. 47, fig. 1 (with synonymy).
1940 *Pervinquieria fallax* var. *kilianiformis* Breistroffer, p. 140.
1971 *Mortoniceras* (*M.*) *kiliani* Spath ?non Lasswitz; Kelly, p. 446.
2020 *Pervinquieria* (*Pervinquieria*) *equidistans* (Cragin, 1893); Kennedy, *in* Gale and Kennedy, pp. 42–48, figs. 26, 30A; pl. 14, figs. 1–3 (with additional synonymy).

Type. According to Kennedy (*in* Gale and Kennedy, 2020, pp. 42, 43, fig. 26), the presumed holotype of *Schloenbachia leonensis* Conrad var. *equidistans* is a specimen in the Cragin Collection, which presumably came from the Duck Creek Formation of Texas; it is housed in the Colorado College, Colorado Springs, Colorado. The holotype of *Schloenbachia kiliani* bears the repository number IZUWra/7 in the collections of the Henryk Teisseyere Geological Museum of the University of Wrocław, Poland, and has recently been illustrated by Gale and Kennedy (2020, pl. 14, figs. 1–3); it is from Austin (Travis County, Texas).

Material. A single specimen, MCNA 13456 (Fig. 8/3A, B); a limonitic inner mould of one-third of septate whorl, slightly crushed.

Description. Keel poorly preserved. Flanks subparallel. Moderately evolute. Whorl section (measured in undeformed innermost part) higher than wide, subquadrate, widest at umbilical tubercle. Umbilical wall steep, but rounded between ribs. Dense ribbing (15 counted) of slightly prorsiradiate sharp ribs, wider than interspaces. Most of ribs beginning at umbilical wall and bifurcating from sharp and slightly bullate umbilical tubercle not extending towards mid-flank. Also irregularly intercalated short ribs beginning near umbilical edge. At mid-flank, all ribs with initially subtle but subsequently conspicuous tubercle. Ribs widening at apparently slightly rounded

Fig. 9. Early late Albian Mortoniceratinae from the Western Pyrenees. All housed in the Museo de Ciencias Naturales de Álava (MCNA). **1.** *Mortoniceras* (*M.*) *fallax* (Breistroffer, 1940), MCNA 17154, lateral view of partial phragmocone and contiguous final part of body chamber with preserved base of rostrum; level L1. **2A, B.** *Mortoniceras* (*M.*) *fallax* (Breistroffer, 1940), MCNA 17152, lateral and ventral views of partial phragmocone with beginning of body chamber (arrows indicating position of last septum); level E-L3. **3A, B.** *Mortoniceras* (*M.*) *fallax* (Breistroffer, 1940), MCNA 17153, outer mould preserved at base of turbidite (level M1) and silicone rubber cast of same; arrows indicating outline of preserved rostrum. **4A–C.** *Mortoniceras* (*M.*) *juleni* nov. sp., MCNA 17155 (**holotype**), lateral, ventral and ventral-apertural views; level L3. All specimens are from the *M.* (*M.*) *fallax* Zone. Scale bar equals 50 mm.

ventrolateral shoulder, ending with adorally projected bullate blunt tubercles bearing feeble spiral striations.

Measurements (mm)	D (restored)	Wh	Ww	U
MCNA 13456 (Fig. 8/3A, B)	78	25.0 (without keel)	23.8	–

Discussion. Non-trapezoidal whorl section, blunt ventrolateral tubercles and moderate degree of evolution make this Basque specimen stand apart from forms of *Mortoniceras* (*M.*) gr. *inflatum*. It is close to *M.* (*M.*) gr. *pricei* in degree of evolution and compression and type of ribbing, but differs in the presence of a differentiated mid-flank tubercle. Spath (1932, p. 392) suggested that there were continuous transitional forms between *pricei* and *kiliani*, and grouped them in the var. *intermedia* of the former. As an example of a transitional form, he recorded (p. 392) a Zululand *pricei* (NHMUK C52979) with an elevated keel and the lateral aspect of *kiliani*. Actually, this Zululand example shares a similar ribbing pattern (with 17 ribs on equivalent part) and whorl section at the same degree of evolution (Wh 24.5, without keel, Ww 21.0) with MCNA 13456. However, the mid-flank tubercle is slightly more marked in the latter. A specimen from Devizes, southern England (NHMUK C75389) referred to *Mortoniceras* (*M.*) *kiliani* is also very similar to both discussed specimens (e.g., same ribbing), but the keel is substantially lower than that of the Zululand example and the whorl section is slightly depressed (Wh 22.4, with keel, Ww 23.7). Another *M. pricei* var. *intermedia*, with broader ribs and resembling the specimen figured by Spath (1932, pl. 38, fig. 5), was recorded from Madagascar by Collignon (1963, p. 176, pl. 314, fig. 1325). *Pervinquieria undulato-costata* (van Hoepen, 1942, p. 95, text-figs. 61–63; Wh 44.0, Ww 46.0) and *Mimeloceras macronodosum* (van Hoepen, 1946, p. 207, text-figs. 186–188; Wh 23.7, Ww 24.0; now *Pervinquieria* (*Deiradoceras*) *binodosa*, see Kennedy and Klinger, 2023c, text.-fig. 11) are South African bituberculate forms related to *M. pricei*, but maybe transitional to *Mortoniceras* (*M.*) gr. *inflatum* on account of a more elevated keel and a slight degree of depression. *Pervinquieria fluctuato-costata* (van Hoepen, 1942, p. 96, text-figs. 64–66; Wh 37.0, Ww 35.0), with the same dense ribbing pattern as the previous species, is a trituberculate form with square whorl section and lower keel that could be referred to *M. equidistans*.

In a recent revision of *M. equidistans*, Kennedy (*in* Gale and Kennedy, 2020, fig. 26) illustrated the presumed holotype of the species (Cragin, 1893), as well as the holotype of *M. kiliani* of Lasswitz (1904) (pl. 14, figs. 1–3). The specimen studied here is closely comparable to both holotypes in both ribbing type and density, and tuberculation at the same diameter. *Mortoniceras* (*M.*) *fallax* (see below) is an allied form but has coarser ribbing and a well-marked lateral tubercle; in our material, *M. fallax* occurs at levels above this sole occurrence of *M. equidistans*.

Occurrence. BCB – *Mortoniceras* (*M.*) *inflatum* Zone, La Escrita Unit, Valmaseda Formation; level K8 (Karrantza area, Biscay province), Basque Country (northern Spain). Elsewhere this species is known from the *M.* (*M.*) *inflatum* Zone in England; upper Albian of Texas, New Mexico and Chihuahua (Mexico), and possibly Zululand, South Africa.

Mortoniceras* (*M.*) *crassinodatum (van Hoepen, 1946)
Fig. 8/4A, B, 5, 6, 7A, B

*1946 *Ophryoceras crassinodatum* van Hoepen, p. 219, figs. 207, 208.
2009 *Mortoniceras* (*M.*) *crassinodatum* (van Hoepen); López-Horgue et al., p. 395, fig. 5.
?2009 *Mortoniceras* (*M.*) sp. indet. cf. gr. *rostratum* (Sowerby, 1817); López-Horgue et al., p. 395, fig. 5.

Type. The original of van Hoepen (1946, p. 220, fig. 208) is specimen D. 2599.

Material. Four specimens corresponding to different growth stages, and another poorly preserved one that is assigned here with a query. MCNA 13517 (Fig. 8/4A, B) and MCNA 17140 (Fig. 8/6) are sideritic inner moulds, slightly crushed, with remnants of calcite-replaced shell, both corresponding to one quarter of contiguous whorls. MCNA 17142 (Fig. 8/5), 17144 and 13525 (Fig. 8/7A, B) are preserved as crushed marly internal moulds.

Description. Diameter estimates take into account whorl height increment of contiguous whorls preserved. MCNA 17142 (Fig. 8/5) and MCNA 17144 correspond to evolute specimens of medium to larger sizes (D = 74 and 105) and umbilici about 40 per cent of diameter. Strong, rectiradiate ribs (18 on last half whorl) arising from umbilical wall and branching from bullate sharp umbilical tubercle (about 8 ribs per quarter whorl); on ventrolateral shoulder, sharp inner ventrolateral tubercle giving way to broad rib termination at right angles to conspicuous keel. From approximate diameter of 70 mm, ribs mostly single with well-marked umbilical and inner ventrolateral tubercles and slight mid-flank swelling. Ribs bearing conspicuous spiral ridges in small specimen.

MCNA 13517 (Fig. 8/4; estimated 145 mm diameter): representing phragmocone of adult stage; innermost whorl preserved showing ribbing type of smaller specimen, with keel elevated over almost tabulate venter. Flanks subparallel. Whorl section high (Wh/Ww ratio = 1.15), widest at umbilical tubercles. Ribs as wide as interspaces (11 ribs on one-quarter of outer whorl), rectiradiate, slightly prorsiradiate but ending with very subtle adapical bend on venter, apparently reaching keel; short and long ribs alternating in both septate whorls, short ones beginning at end of inner third of flank. Long ribs arising from rounded umbilical edge bearing bullate but fairly prominent umbilical tubercle. Umbilical wall steeper on body chamber. All ribs bearing distinctive but not prominent mid-flank tubercle and prominent inner ventrolateral rounded tubercles. Ribs slightly concave in upper half below ventrolateral tubercle. Whorl-overlap covering half of ventrolateral tubercle of preceding whorl. Suture with very conspicuous lateral bifid and umbilical trifid lobes. Very evolute form, with umbilicus near 46 per cent of diameter. Subtle spiral ridges on both whorls.

MCNA 17144: fragment of adult, large-sized specimen; diameter estimated at 275.5 mm, with umbilicus comprising 47 per cent. Innermost whorl part of phragmocone with ribbing type as in MCNA 13517, at similar diameter. Outermost whorl final part of body chamber, with rectiradiate strong ribs and wider interspaces; only ventrolateral, slightly conical tubercle persisting and concavity in upper half of ribs disappearing.

MCNA 13525 (Fig. 8/7): ribbing pattern as in adult stages at diameters of 70–200 mm, differing only in presence of slight outer ventrolateral tubercle. Keel looking elevated on venter.

Dimensions (mm)	D	Wh	Ww	U
MCNA 17142 (Fig. 8/5)	74	26	–	29.0
MCNA 17144	105 (est.)	–	–	42
MCNA 13517 (Fig. 8/4A, B)	145 (est.)	47.0	40.8 (restored)	67 (est.)
MCNA 17140 (Fig. 8/6)	275 (est.)	83.0	60.0 (restored)	130 (est.)
? MCNA 13525 (Fig. 8/7A, B)	–	36.6	–	–

Discussion. Very evolute trituberculate form of *Mortoniceras* with distinctive early bifurcated ribs, short-long ribbing from mid-

growth stage onwards and compressed whorl section, in nothing comparable to forms of the *M. inflatum* group, which are typically inflated, less evolute and with less marked mid-flank tubercles. The moderately dense ribbing with slightly concave ribs between mid-flank and ventrolateral tubercles, prominent ventrolateral rounded tubercles, high whorl section and tabulate venter with elevated keel are main features shared with *Ophryoceras* spp. of van Hoepen (1942, 1946), matching the type species, *jugosum*, well. Actually, these South African species clearly constitute a separate group of evolute *Mortoniceras* also characterised by long umbilical tubercles, a quite constant umbilicus of about 43 per cent of diameter and bifurcations of ribs beginning in the second third of the flank (up at the umbilical tubercle) that are common in early stages and subordinated to a single ribbing pattern in later ones. In the suture line, the Basque specimens show the same type of lobes as those of the type species, *O. jugosum* (see van Hoepen, 1946, fig. 204) (Fig. 8 here). However, it matches *Ophryoceras crassinodatum* best, sharing an almost identical 1.18 Wh/Ww ratio, similar rib-density, mid-flank slightly bullate tubercles and a congruently wide umbilicus (42 per cent). The South African form differs only in having a less pronounced umbilical tubercle and slightly prorsiradiate ribs in the outermost whorl. *Ophryoceras jugosum* can be differentiated from the Basque material also in a feeble mid-flank tubercle and denser ribbing. *Ophryoceras undosum* have less pronounced ribbing and ornament.

MCNA 13525 (Fig. 8/7) occurs in a bed above the other Basque material assigned to the present species; the presence of an outer ventrolateral tubercle at a medium growth stage would suggest transition to a *M. fallax*-like form, but due to the preservation it is only tentatively assigned here to *M. crassinodatum*.

Occurrence. *BCB — Mortoniceras* (*M.*) *inflatum* Zone and likely *M.* (*M.*) *fallax* Zone, Deva Formation; Biscay province, Basque Country, Western Pyrenees, Spain. Basque material assigned to *M. crassinodatum* occurs at level A6 in the Armintza section, whereas MCNA 13525 is known from level A8 level in the same section. Elsewhere this species is known from the Umsinene Beds at Beacon 624, Zululand, South Africa; likely *Mortoniceras* (*M.*) *inflatum* Zone equivalents in South Africa (see distribution for *M.* (*M.*) *tremulum* above).

Mortoniceras* (*M.*) *fallax (Breistroffer, 1940)

Fig. 9/1, 2A, B, 3A, B

Type. The holotype is the original (SMC B56) of Spath, 1932 (pl. 40, fig. 1) from the remanié phosphatic late Albian fauna at the base of the lower Cenomanian Cambridge Greensand in Cambridgeshire (England), originally identified as *Mortoniceras* (*Pervinquieria*) *rostratum*.

Remarks. Breistroffer created this species for phragmocones identified by Spath as *M.* (*P.*) *rostratum* (i.e., holotype and NHMUK C35199) and *M.* (*P.*) *kiliani* (NHMUK 43965 and NHMUK C35201). Owen (2012) suggested that the holotype simply was a more coarsely tuberculate *M. rostratum*, whereas Kennedy (*in* Gale and Kennedy, 2020) identified NHMUK C35201 as *Pervinquieria* (*P.*) cf. *equidistans*, a fact that clearly indicates affinities within these mortoniceratines. Additionally, Breistroffer (1940) indicated affinities with *Pervinquieria pachys*, *P. nana* and *P. minor*, but these species may be differentiated clearly (see e.g., Kennedy et al., 2008; Jattiot et al., 2021).

Despite the fact that this species has traditionally been placed as occurring between beds with *M.* (*M.*) *inflatum* and those with *M.* (*S.*) *rostratum*, most of the known occurrences are from condensed beds in Europe, including that of the holotype, a fact meaning that admixtures with earlier and later allied forms are likely. Besides, specimens usually are phragmocones or fragments, with only three records presenting body chambers (fragmentary in Latil, 1994 and partial in Kennedy et al., 2008; a complete specimen illustrated in Vincent et al., 2020). A comprehensive account of the few occurrences of this species known to date may render an idea of its scarce and incomplete record.

Wiedmann and Kauffman (1978) illustrated a fragmentary phragmocone from Legutio (Villarreal de Álava), from expanded upper Albian successions of the Basque-Cantabrian Basin (Western Pyrenees), while Scholz (1979) supplied the first description after Breistroffer on the basis of juvenile to intermediate phragmocones from a condensed interval in the Bakony Mountains (Hungary).

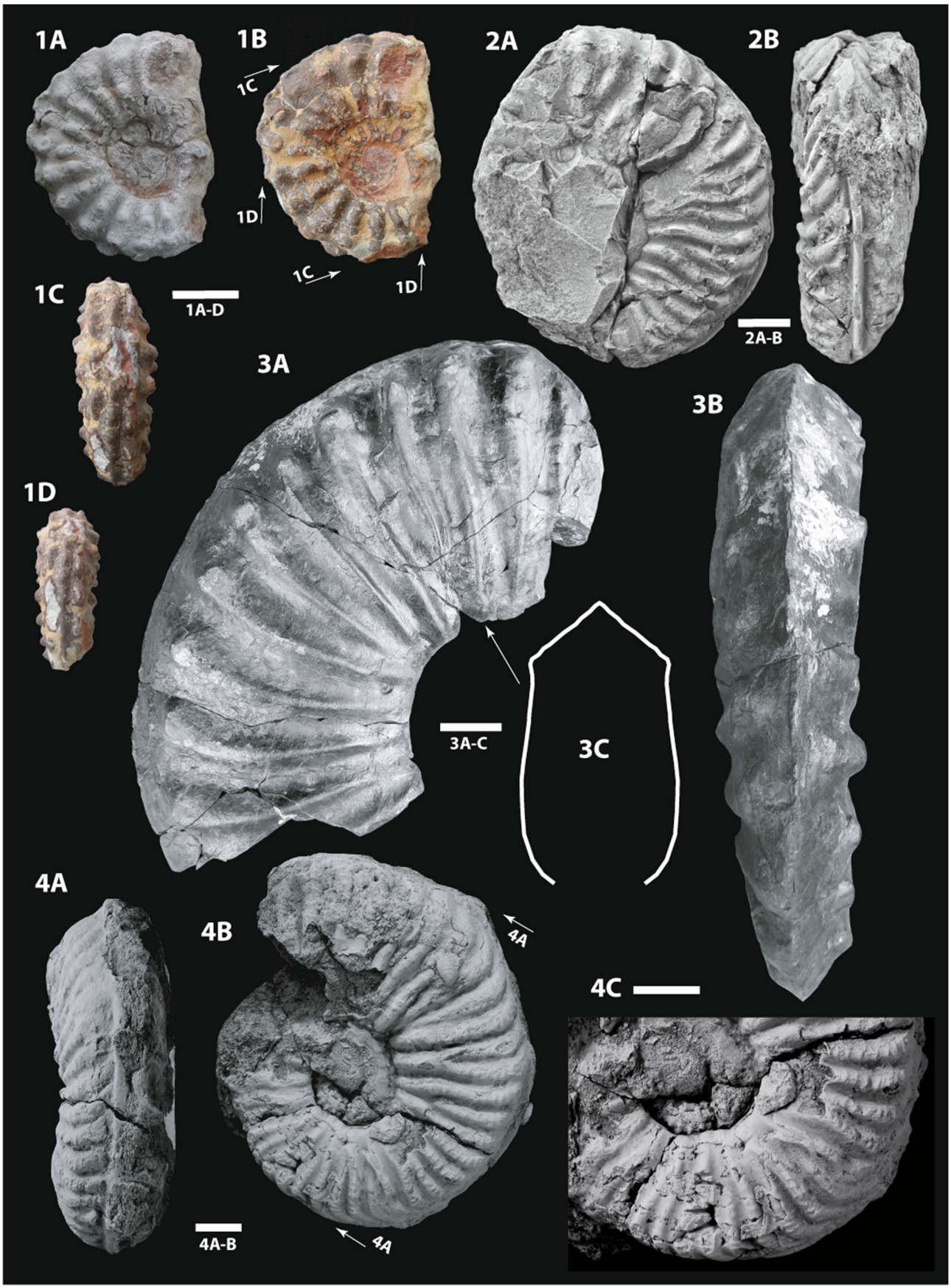
Latil (1994) recorded two phragmocones (diameters of 120 and 140 mm) and a fragmentary body chamber from a condensed interval at Mas Pradon (Gard, France), indicating that large size and appearance of a trituberculate stage prior to the onset of the body chamber help in identifying the species. Kennedy and Latil (2007) followed Latil's (1994) point of view in separating it from *M.* (*S.*) *rostratum*. Kennedy et al. (2008) recorded two specimens from a 40-m-thick succession (Bracquegnies Formation, Mons Basin, southern Belgium), intercalated between Barremian and Turonian rocks; these coarse-ribbed forms are a phragmocone (160 mm diameter) and a near-complete specimen (200 mm diameter) with inner whorls different to those of the holotype at the same diameter. These latter authors also illustrated two specimens previously referred to by Amédro (2002), but indicated these to have been lost.

Gale et al. (2011) referred to the occurrence of *M.* (*M.*) *fallax* in the expanded section of Col de Palluel (Hautes Alpes, France) above the last occurrence (LO) of *M.* (*M.*) *inflatum* and below the first occurrence (FO) of *M.* (*S.*) *rostratum*, but only figured a likely phragmocone (50 mm diameter) with dense ribbing.

Benzaggagh et al. (2017) figured a fragment showing only 6 ribs from above beds with *M.* (*M.*) *inflatum* and below an occurrence of *M.* (*M.*) *pachys*. Vincent et al. (2020) noted a complete specimen (270 mm diameter) from a condensed interval below levels with *M.* (*S.*) *rostratum*, being the only known specimen with a complete body chamber and rostrum preserved. Jattiot et al. (2021) revised the phosphatised latest Albian fauna occurring in the 0.7-m-thick condensed level at Salazac (Gard, France) under a quantitative morphological and biometric analysis; they referred to 12 specimens of *M.* (*M.*) *fallax*, likely phragmocones, from juvenile to intermediate ontogenetic stages. Other dubious occurrences are not included here (e.g., Renz, 1968).

As shown above, *M.* (*M.*) *fallax* is a species based mainly on occurrences from condensed beds and from partial remains from expanded sections, but not sufficient for an in-depth discussion. Most of the records of *M.* (*M.*) *fallax* correspond to phragmocones and very few, mostly partial, body chambers. Moreover, its stratigraphical position has been established on records from condensed sections in England (Cambridgeshire), southern Belgium (Strépy-Thieu) and France (Salazac) (Kennedy and Latil, 2007). Given the material on record, *M.* (*M.*) *fallax* appears to be a valid species, but its resemblance to juvenile and intermediate stages of *M.* (*S.*) *rostratum* makes the identification of phragmocones from condensed intervals difficult and dubious, especially in consideration of the duration of condensation processes and the more than likely mixture of elements from different biozones (e.g., levels of the *M.* (*M.*) *fallax* biozone with basal *M.* (*S.*) *rostratum* biozone).

Here we report three new specimens from the expanded upper Albian succession in the BCB (Western Pyrenees), at intervals above *M.* (*M.*) *inflatum* Zone sedimentary rocks and below intervals with *M.* (*S.*) *rostratum* and ammonoid associations typical of its eponymous zone. Apart from their stratigraphical occurrence, these specimens show sufficient characteristics needed to complete an ontogeny-based description of the species.


1A
1B
1C
1D
1C
1D
1A-D
2A
2B
2A-B
1C
1D
3A
3B
3A-C
3C
4A
4B
4A
4A
4A-B
4C

1932 *Mortoniceras* (*Pervinquieria*) *rostratum* (J. Sowerby); Spath, p. 400 (pars), pl 40, fig. 1.
1932 *Mortoniceras* (*Pervinquieria*) *kiliani* (Lasswitz); Spath, p. 408, pl. 38, fig. 1.
*1940 *Pervinquieria fallax* Breistroffer, p. 137.
1978 *Pervinquieria* (*Pervinquieria*) *fallax* (Breistroffer); Wiedmann and Kauffman, pl. 3, fig. 1.
1979 *Pervinquieria* (*Pervinquieria*) *fallax* (Breistroffer); Wiedmann, pl. 3, fig. 1.
1979 *Pervinquieria* (*Pervinquieria*) *fallax* Breistroffer, 1940; Scholz, p. 109, pl. 29, figs. 3–5, 7, 8, 10.
1994 *Mortoniceras fallax* (Breistroffer, 1940); Latil, pl. 3, figs. 1–3; pl. 4.
1999 *Mortoniceras* (*Mortoniceras*) *apertum* Spath; López-Horgue et al., fig. 11c, d.
2002 *Mortoniceras* (*Mortoniceras*) *fallax*; Amédro, pl. 1, fig. 1; pl. 2, figs. 2, 3; pl. 7.
2002 *Mortoniceras* (*Mortoniceras*) aff. *fallax*; Amédro, pl. 8.
2002 *Mortoniceras* (*Mortoniceras*) *pachys*; Amédro, pl. 9, fig. 1.
2008 *Mortoniceras* (*Mortoniceras*) *fallax* (Breistroffer, 1940); Kennedy et al., p. 42, pl. 6, figs. 1–3; pl. 7, figs. 1, 2; pl. 10, figs. 9–11, 16.
2011 *Mortoniceras* (*Mortoniceras*) *fallax* Breistroffer, 1940; Gale et al., p. 76, fig. 25E.
2017 *Mortoniceras* (*Mortoniceras*) *fallax* (Breistroffer, 1940); Benzaggagh et al., p. 87, fig. 12 H-1, 2.
2020 *Mortoniceras fallax* (Breistroffer, 1940); Vincent et al., p. 5, fig. 2B.
2021 *Mortoniceras* (*Mortoniceras*) *fallax* (Breistroffer, 1940); Jattiot et al., p. 33, fig. 18A–N, Q–W.

Material. MCNA 17153 (Fig. 9/3A, B), an external mould comprising a partial phragmocone and body chamber, preserved at the base of a turbidite in the Meñakoz section (level M1); a silicone rubber cast has been obtained from this. MCNA 17154 (Fig. 9/1) is a partial phragmocone and body chamber preserved as an internal mould, slightly crushed laterally, from a muddy ramp succession at Legutio (level L1). MCNA 17152 (Fig. 9/2A, B) preserves a partial phragmocone and the beginning of the body chamber, occurring as an internal mould with calcitic conch from an expanded muddy ramp succession at Estella-Lizarra (level E-L3). Another specimen, MCNA 17156, from the same level (E-L-3) shows similar ribbing and tuberculation but because of poor preservation this is only tentatively assigned here.

Dimensions (mm)	D	Wh	Ww	U
MCNA 17153 (Fig. 9/3A, B)	170	48.0 (without keel)	–	70
MCNA 17154 (Fig. 9/1)	260	85.0 (without keel)	–	115
MCNA 17152 (Fig. 9/2A, B)	250	48.0 (without keel)	–	110
?MCNA 17156	230	–	–	95

Description. Adults, showing evolute coiling with wide umbilicus between 41 and 44 per cent of diameter; umbilical wall high with broadly rounded shoulders; whorl section higher than wide. Ribs straight, rectiradiate to slightly prorsiradiate. MCNA 17153 (Fig. 9/3), of estimated diameter of 170 mm (without rostrum), 70 mm umbilicus. Six strong and high umbilical bullae on preserved one quarter of inner whorl corresponding to phragmocone; giving rise to straight primaries with three intercalated secondaries starting at mid-flank with sharp bullate to conical tubercle; inner ventrolateral tubercles partially visible. Only primary ribs on body chamber, widely separated (twice width of rib), straight in lower half and prorsiradiate in upper, bearing umbilical bullae, conical mid-flank and high ventrolateral tubercles, all weakening adorally, with last three ribs shaping elevated crests. High keel only observable near aperture, rising to form rostrum at right angle to venter. Spiral ridges visible on most ribs, being especially conspicuous on umbilical bullae.
Specimen MCNA 17154 (Fig. 9/1): partial phragmocone (one quarter of innermost whorl) and body chamber (one third of last whorl), with estimated diameter of 260 mm, 115 mm corresponding to umbilicus. Umbilical bullae on phragmocone giving rise to single or bifurcated ribs, slightly prorsiradiate, with some single intercalated ribs starting at mid-flank, all bearing conspicuous elongated tubercle; ventrolateral ribs wide, with inner outward projection and outer spatulate termination towards keel. Total 14 ribs conspicuous on phragmocone, some with conspicuous spiral ridges. Body chamber ribs slightly prorsiradiate, strong, with wide interspaces (about 1.5 times width of ribs), with only two secondaries from mid-flank, and bearing umbilical and mid-flank bullate and ventrolateral conical tubercles; ribs not reaching high sharp keel on wide ventral area. Rib and tubercle strength decreasing only on last two ribs, where keel rises from venter at likely right angles forming the base of rostrum. At aperture, two effaced shorter ribs.
Specimen MCNA 17152 (Fig. 9/2): partial phragmocone with beginning of body chamber corresponding to estimated minimum diameter of 250 mm and umbilicus of 110 mm. Innermost whorl observable (one quarter), part of phragmocone and bearing 11 rectiradiate ribs. Six primaries arising from umbilical bullae and intercalated 5 secondaries from lateral tubercle, all bearing lateral elongated to conical and wider inner ventrolateral tubercles. Outermost whorl representing outer phragmocone with last four ribs corresponding to body chamber. Rib interspace wider than on phragmocone (approximately rib width). Rectiradiate to slightly prorsiradiate primaries arising from umbilical bullae, some branching into two ribs near end of phragmocone. Secondaries arising from slightly elevated position from mid-flank. Lateral tubercles elongated and high, weakening on body chamber. All ribs bearing elongated inner ventrolateral tubercles, showing wide prorsiradiate termination towards sharp keel; ventrolateral tubercles higher on body chamber. Spiral ridges conspicuous on all ribs.
Discussion. Breistroffer (1940) introduced the names *Pervinquieria kiliani* var. *alstonensis* and *Pervinquieria fallax* var. *kilianiformis* for the originals *M.* (*P.*) *kiliani* (Lasswitz) of Spath (1932, pl. 38, figs. 1 and 2, respectively). Kennedy (*in* Gale and Kennedy, 2020) accepted the synonymy of *kiliani* and *equidistans* proposed by Cobban (1985, 1987) and listed Breistroffer's *P. kiliani* var. *alstonensis* as *P.* (*P.*) *fallax* and *P. fallax* var. *kilianiformis* as *P.* (*P.*) cf. *equidistans*. These two forms are allied evolute trituberculate forms of *Mortoniceras* with a well-developed lateral tubercle reaching the body chamber and the lack of a conspicuous outer ventrolateral tubercle. However, *M.* (*M.*) *equidistans* differs from *M.* (*M.*) *fallax* in that the lateral tubercle appears later in the ontogeny, being less marked; umbilical bullae are less strong; there is a tendency of the ventrolateral tubercle to be claviform; there is denser ribbing at a similar growth stage

Fig. 10. Early late Albian Mortoniceratinae from the Western Pyrenees (Museo de Ciencias Naturales de Álava MCNA). **1A–D.** *Navarreites egiarretensis* nov. gen., nov. sp., MCNA 17149, coated and uncoated lateral views of **holotype**, and two ventral views, respectively; level I1, likely *M.* (*M.*) *pricei* Zone, *H. varicosum* to *H. binum* Subzones. **2A, B.** *Arestoceras* cf. *splendidum* van Hoepen, 1951, MCNA 13512, lateral and ventral views of fully septate specimen; level A4, *H. choffati* Subzone. **3A–C.** *Arestoceras* cf. *splendidum* van Hoepen, 1951, MCNA 17141, lateral and ventral views (without coating) of final part of body chamber of very large specimen, and whorl section reconstruction at rib indicated; level A7, *M.* (*M.*) *inflatum* Zone. **4A–C.** *Elobiceras* (*Craginites*) *subelobiense* Spath, 1922, MCNA 17150, ventral, lateral and detail of phragmocone/body chamber transition, respectively; level I4, *M.* (*M.*) *inflatum* Zone. Scale bar equals 10 mm, except for 3 where it equals 50 mm.

represented by the holotype of *M.* (*M.*) *fallax*; ribs usually are prorsiradiate and flexuous in some specimens.

Another allied form is *Mortoniceras M.* (*M.*) *pachys*; we follow the differences proposed by Kennedy et al. (2008), considering *M.* (*M.*) *pachys* to be a form with crowded, markedly flexuous, ribbing and a pronounced spiral lateral depression and broad venter. Also allied is *M.* (*M.*) *stoliczkai*, similar to *M.* (*M.*) *fallax*, but with a denser ribbing in the early stages and overall a less marked tuberculation, especially on the body chamber where the ventrolateral conical tubercle is the only one bearing similarity to *M.* (*M.*) *fallax* (see cast of the holotype in Latil, 1994, pl. 15, fig. 1; Kennedy, *in* Gale et al., 2019, pl. 15).

Mortoniceras (*S.*) *rostratum* is a closely allied form. Actually, the holotype of *M.* (*M.*) *fallax* is the original *M.* (*P.*) *rostratum* of Spath (1932, pl. 40, fig. 1), a phragmocone of an intermediate growth stage. Jattiot et al. (2021) showed early juveniles of *M. fallax* from Salazac with a four-tubercle stage (up to approximately 35 mm in diameter; see their fig. 18A–I, L–N), followed by the next stage (juvenile to intermediate) (up to approximately 60 mm in diameter; see their fig. 18J, K, Q, R, S) in which the ribs are only trituberculate, bearing one inner ventrolateral tubercle and a broader termination. Scholz (1979) also illustrated juvenile and intermediate growth stages of *M. fallax* from the Bakony Mountains, Hungary (his pl. 29, figs. 3–5, 7, 8, 10). These ontogenetic stages are comparable to that of *M.* (*P.*) *rostratum* (sensu Spath, 1932) for early juveniles (see Spath, 1932, pl. 39, fig. 4a, b; pl. 40, fig. 7) and for juveniles/intermediates (Spath, 1932, pl. 38, fig. 4; pl. 40, fig. 1, holotype of *M* (*M.*). *fallax*) from Cambridgeshire and Folkestone. Specimens figured in Spath (1932), Scholz (1979) and Jattiot et al. (2021) all come from condensed sections. Similarly, also comparable are an early juvenile and juveniles/intermediates of *M.* (*S.*) *rostratum* from north-east Texas (Kennedy et al., 1998: figs. 15D, E and 15A–C, respectively) and from Tamil Nadu (India) (Kennedy, *in* Gale et al., 2019, pl. 14, figs. 1, 2); the latter are closely comparable to the holotype of *M.* (*M.*) *fallax*. Jattiot et al. (2022) showed early juveniles of *M.* (*S.*) *rostratum* from Clansayes (their pl. 13, figs. 1–9), comparable to specimens of *M.* (*M.*) *fallax* of the same growth stage from Salazac (Jattiot et al., 2021). These resemblances and the occurrence of both *M.* (*M.*) *fallax* and *M.* (*S.*) *rostratum* in the same bed A(c) at Rockshaw led Owen (2012) to consider that the holotype of *M.* (*M.*) *fallax* was merely a slightly more coarsely tuberculate individual of *M.* (*S.*) *rostratum*. Taking into account the similarities at juvenile/intermediate growth stages it is clear that early stages may be difficult to identify properly when later growth stages and body chambers are lacking; actually, Latil (1994) suggested that *M.* (*M.*) *fallax* and *M.* (*S.*) *rostratum* could only be distinguished by their adult stages.

Only very few examples corresponding to the adult stage are known. Latil (1994) illustrated two large phragmocones (his pl. 3, fig. 3; pl. 4; 130 and 145 mm diameter, respectively) showing the change in ribbing occurring at the end of the phragmocone towards the body chamber, where ribs become separated, the ventrolateral tubercle becomes high and conical, and the lateral and umbilical tubercles maintain their strength. *Mortoniceras* (*S.*) *rostratum* shows at the end of the phragmocone a division of the ventrolateral tubercle into coarse inner and claviform outer tubercles, a feature that extends to the beginning of the body chamber where both join to form a high claviform tubercle that effaces adorally, together with the umbilical and lateral tubercles, the aperture showing a backwardly coiled rostrum (e.g., exemplified by specimens of *M.* (*S.*) *rostratum* illustrated by Kennedy and Latil, 2007; see also Jattiot et al., 2022); this type of ornament is a striking difference to *M.* (*M.*) *fallax*. The change in ribbing in the latter is observable also in a phragmocone (160 mm diameter) and a near-complete specimen (200 mm diameter) figured by Kennedy et al. (2008, pls 6, 7); however, these specimens show more widely spaced ribbing on the early whorls and the lateral tubercle is less strong. A similar example to these latter is shown in Vincent et al. (2020, fig. 2 B; 270 mm diameter), with more widely spaced ribbing, but strong tubercles and a rostrum growing out radially. Specimens from the Basque-Cantabrian Basin studied here match the common ribbing pattern shown by the holotype at juvenile-intermediate growth stages and by the adult example in Latil (1994, pl. 3, fig. 3); MCNA 17153 shows a rostrum that is closely comparable to that of the specimen in Vincent et al. (2020), being also comparable that of the *M.* (*M.*) *inflatum* body chamber described from the northern margin of the BCB (Agirrezabala et al., 1992). These specimens clarify the ontogenetic evolution of ribbing from late phragmocones onwards and present clues for our understanding of the body chamber and aperture.

Emended diagnosis. Early juvenile (up to 35 mm diameter) with umbilical and ventrolateral tubercles; ventrolateral one dividing into two and lateral tubercle appearing at end of growth stage. Juvenile-intermediate growth stages (up to 60 mm) showing transition from quadrituberculate to trituberculate stage by merging two ventrolaterals (observable prior to onset of body chamber in adult specimens). Trituberculate stage maintained up to adult stage; all tubercles gaining strength and maintained up to end of body chamber. Umbilical bullae high and extending up to near mid-flank. Lateral tubercle bullate to conical, situated near base of upper flank. Ventrolateral tubercle high and conical on body chamber. Rostrum rectiradiate, extending in length as much as whorl height at near-right angles to venter.

Occurrence. BCB — Mortoniceras (*M.*) *fallax* Zone in the expanded sections of Meñakoz, Legutio and Estella-Lizarra (Basque-Cantabrian Basin, Western Pyrenees, Spain). Elsewhere this species is known from Col de Palluel (France) and Jebel Nesrani (Morocco), condensed beds in Cambridgeshire (England), Bakony Mountains (Hungary), Salazac and Mas Pradon (France), Strépy-Thieu (southern Belgium) and Les Faïsses (France).

Mortoniceras* (*M.*) *juleni nov. sp.
Fig. 9/4A–C

Type. The holotype, by monotypy, is MCNA 17155 (Fig. 9/4A–C), comprising an entire internal mould and near-complete external counterpart. The last whorl retains its original dimensions, the remainder being crushed; however, the external mould show the ornament well. It stems from level L3 in the Legutio section, *Mortoniceras* (*M.*) *fallax* Zone, Valmaseda Formation in Legutio, Araba province, Basque Country, Western Pyrenees, Spain.

Derivatio nominis. Dedicated to Julen García Sancho, a student of geology who found the specimen while working on his final project on stratigraphy supervised by the senior author.

Diagnosis. Evolute *Mortoniceras* with mostly single ribs, umbilical bullate and elongated ventrolateral high tubercles from very early growth stage; lateral conical tubercle conspicuous from early growth stage. All tubercles gradually becoming stronger and maintained up to penultimate rib. Ribs strong, wide and deep umbilicus, with subquadrate depressed whorl section.

Description. Evolute, whorls overlapping preceding ones only at ventrolateral shoulder. Umbilicus wide, 45 per cent and 41 per cent in diameters of 131 mm and 195 mm, respectively; deep with steep umbilical wall. Ribs arising from umbilical wall at least from 40-mm diameter, but moving progressively with growth up to umbilical shoulder onset. Ribbing denser on inner whorls, with 35 ribs per whorl, as wide as interspaces, at diameter of 90 mm; on last whorl (diameter of 195 mm) 23 ribs, separated by progressively wider interspaces, up to 20 mm wide between 12 mm wide ribs on body chamber. At diameter of 25 mm, high conical umbilical tubercles developing, bullate in shape at diameter of 40 mm up to end of

shell. Ribs rectiradiate to slightly prorsiradiate, becoming only rectiradiate from 75 mm diameter. From early stages, ribs bifurcating from umbilical tubercle, with increasing number of intercalated singles, becoming only single from 115 mm diameter. Conical (and slightly bullate in some ribs) mid-flank tubercle conspicuous from 50 mm diameter, on body chamber moving up to base of upper flank. Ribs on ventrolateral area wide and blunt, gently bent adorally, developed at least from diameter of 70 mm. At end of phragmocone, ventrolateral area developing inner conical tubercle, gradually elevating up to second rib of body chamber; ventrolateral ribs rising gradually to shape a claviform, asymmetrical and adorally projected very high tubercle (up to 7–8 mm), almost reaching lower (4–5 mm) keel obliquely. Overall, flanks parallel to slightly convergent towards venter on body chamber; intercostal areas convex. Whorl section subquadrate and slightly compressed, widest at umbilical tubercle, but widest at lateral tubercle on body chamber. Growth rate on last whorl 1.16 (Wh at 195 mm diameter/Wh at 131 mm). In adapical 90° section of body chamber, a very shallow and 9-mm-wide trough at umbilical wall. Body chamber with delicate growth lines and spiral ridges conspicuous on intercostal areas and umbilical tubercles, respectively. Suture line with long ventral bifid and lateral trifid saddles, separated by wide bilobate lobe extending from near keel to mid-flank; lateral lobe as wide as lateral saddle and bifid saddle on umbilical shoulder. Last three suture lines gradually less widely separated (measured between apex of lateral saddles), from 26 to 23 and then to 22 mm.

Dimensions (mm)	D	Wh	Ww	U
MCNA 17155	195	63	66	81
(holotype)	195	61 (ic)	58 (ic)	81
(Fig. 9/4A–C)	179	65	72	71
	131	54	60.5	59

Discussion. Based on the sharp trituberculation and ribbing, MCNA 17155 may be considered an ally of trituberculate species of *Mortoniceras* with a marked lateral tubercle. Among the South African stock of such forms, *Ophryoceras spinosum* van Hoepen, 1946 (his fig. 211) is similarly evolute and bears a prominent lateral tubercle, but differs in its slightly compressed whorl section, a denser ribbing and less prominent umbilical tubercle. Among the Texas stock (Gale and Kennedy, 2020), *Mortoniceras vespertinum*, *Pervinquieria* (*P.*) *equidistans*, *P.* (*P.*) *smedlae* and *P.* (*P.*) *asper* all show a good development of the lateral tubercle but they are compressed forms with common prorsiradiate ribs and overall less-developed ornament towards adult stages. *Mortoniceras* (*M.*) *fallax*, as here understood, bears a persistent lateral tubercle in the latest adult stages, but is a compressed form that shows an outer ventrolateral tubercle at the middle stage of growth on the phragmocone. Specimens of the Indian *Mortoniceras* (*M.*) *stoliczkai,* both the holotype (Stoliczka, 1865 [*in* 1863–1866], pl. 27, and pl. 29, fig. 2; a cast in Latil, 1994) and that figured in Gale et al. (2019, pl. 15) share with *M.* (*M.*) *juleni* nov. sp. a similar evolute morphology with the umbilicus comprising 40 to 42 per cent of the diameter, a persistent lateral tubercle and subquadrate depressed whorl section. However, the new species differs from *M.* (*M.*) *stoliczkai* in a less dense ribbing (23 ribs on the last whorl; the holotype of *M.* (*M.*) *stoliczkai* has 42 ribs), a lack of prorsiradiate ribs from a 75-mm diameter onwards; the lateral tubercle is mainly conical, developed at mid-flank and only moves slightly up on the flank during ontogeny; the presence of a strong claviform adorally projected ventrolateral tubercle on the body chamber; and a low whorl height growth rate of 1.16 (compared to approximately 1.40 in *M.* (*M.*) *stoliczkai*). *Pervinquieria* (*P.*) *stoliczkai* specimens from Hungary figured in Scholz (1979, pls 23, 24) are similarly coarsely ribbed forms but with less pronounced tubercles and a loss of the lateral tubercle on the body chamber, close to other *M.* (*M.*) *stoliczkai* from Alicante (Spain) figured in Cremades and Linares (1982). Marcinowski and Naidin (1976) figured a specimen of *M.* (*M.*) *stoliczkai* from Crimea (Ukraine) with no lateral, attenuated umbilical and no adorally projected ventrolateral tubercles on the body chamber.

All occurrences of *M.* (*M.*) *stoliczkai* noted above are associated with *M.* (*S.*) *rostratum*, both in condensed (Hungary, Crimea) and expanded successions (India, Spain). The new species erected here occurs 5 m below the FO of *M.* (*S.*) *rostratum* in the study area, so it may be considered a precursor of the *M.* (*M.*) *stoliczkai* morphotype.

Occurrence. As for type.

Genus *Navarreites* nov.

Type species: *Navarreites egiarretensis* nov. sp., herein.

Diagnosis. Small, slightly involute *Mortoniceras*-like trituberculate form. Ribs coarse, with coarser and high umbilical bullate, mid-flank conical and ventrolateral strongly claviform and differentiated long tubercles. Flat venter with a crenulate keel as high as ventrolateral tubercles.

Discussion. Navarreites nov. gen. is here interpreted as a dwarf offshoot of *Mortoniceras* on the basis of its ribbing and tuberculation, the persistent keel and coiling that resembles some trituberculate species of the latter genus. Ventrolateral clavi are characteristic of some adult stages of a number of strongly ornamented Mortoniceratinae such as *Mortoniceras vespertinum*, *Pervinquieria* (*P.*) *equidistans* and *P.* (*P.*) *smedlae* from north-east Texas (Gale and Kennedy, 2020, figs. 18, 27, 28, 33) and *Mortoniceras* (*Subschloenbachia*) *rostratum* from Europe (e.g., Scholz, 1979, pl. 27, fig. 2; Jattiot et al., 2022, pl. 6). Ventrolateral clavi are also seen in, for example, *Elobiceras* (*Craginites*) and *Paracraginites* (see also Gale and Kennedy, 2020), but these do not bear such strong mid-flank tuberculation. Juvenile forms of *M.* (*S.*) *rostratum* (e.g., Jattiot et al., 2022, pl. 13, figs. 1–9) and *M.* (*M.*) *fallax* (Jattiot et al., 2021, fig. 18L–N), together with both *Cantabrigites minor* and *C. spinosum* (e.g., Kennedy, 2004, fig. 12; Kennedy, 2020, pl. 10; Jattiot et al., 2021, figs. 15AD–AL, 16), all show sculptured ribbing and outer ventrolateral clavi more or less developed parallel to the keel; however, they differ from *Navarreites* nov. gen. in bearing a commonly adorally projected rib termination, less pronounced outer ventrolateral clavi and an inner ventrolateral, mostly conical, tubercle. Some *Durnovarites* spp. have comparable but more elevated ventrolateral clavi, but at that stage are quadrituberculate forms (e.g., *D. subquadratum*; see Spath, 1933, pl. 47, fig. 4; pl. 48, fig. 2). Among small forms of Brancoceratidae, *Neokentroceras* and some *Hysteroceras* bear strong single ribs and tubercles at adult stages, but they are bituberculate forms without clavi.

Derivatio nominis. The genus name refers to the ancient Navarre kingdom; the specific epithet means 'from Egiarreta', the Navarran town near Irurtzun from where the specimen originates.

Navarreites egiarretensis sp. nov.

Fig. 10/1A–D

2022 *Mortoniceras* sp.; López-Horgue et al., pp. 147–150, figs. 4, 5:8.

Type. The holotype, by monotypy, is the unique specimen from level I1 (*M.* (*M.*) *pricei* Zone, *H. varicosum* to *H. binum* Subzones) near the town of Egiarreta (Irurtzun section, Navarre, Western Pyrenees, Spain). It is a internal mould preserved in pyrite, filled by and within a silty matrix cemented by siderite; slightly sheared along the coiling plane.

Dimensions (mm)	D	Wh	Ww	U
MCNA 17149	38.0	13.5 (restored)	–	13.5
(holotype)	30.5	11.0	13.0	10.5
(Fig. 10/1A–D)	25	10.0	10.0	9.0

Description. Small; outermost half whorl preserved corresponding to body chamber at diameter of 38 mm, with umbilicus of 13.5 mm (35 per cent of diameter). Involute coiling, with outer whorl overlapping about 35 per cent of the preceding. At diameter of 25 mm, umbilicus equalling 36 per cent of diameter. Umbilicus shallow, with rounded umbilical wall. Despite preservation of innermost whorls at diameter of 25 mm, ribs seen to be strong, some bifurcating from umbilical shoulder. On best-preserved part at diameter of 30 mm, whorl section subquadrate, slightly depressed, widest at umbilical tubercle. On last whorl preserved, single ribs arising from umbilical shoulder and covering almost lower one third of flank, showing bullate shape and high conical umbilical tubercle in upper part. Ribs as wide as interspaces but widening remarkably from umbilical tubercle towards venter, especially on last ribs where more than twice initial width (from 2 to 4.5 mm), together with loss of strength on upper flank. All ribs showing mid-flank conical tubercles arising low on upper flank, tending to be slightly clavate adorally. Ribs terminating on ventrolateral shoulder with elevated ventrolateral clavi as long as rib width. Clavi separated from crenulate parallel keel of similar height. Ribs concave between tubercles.

Discussion. See also under the genus (above). The ventrolateral clavi, the single ribbing and the crenulate keel make this specimen resemble Late Cretaceous Texanitinae, but *Navarreites* nov. gen. co-occurs with *Kossmatella* sp. and *Desmoceras latidorsatum* above levels with the late Albian benthic foraminifer *Mesorbitolina aperta* and below beds (I2 to I5) with ammonites from the *H. choffati* Subzone up to the uppermost Albian. Accordingly, we consider the new genus to be a homoeomorph of the Texanitinae.

The change in character of the ribbing and tubercles from the innermost whorls onwards and especially on the body chamber is indicative of an adult form, so it may be considered a dwarf offshoot of *Mortoniceras*, as explained above.

In the Western Pyrenean area, the first specimens with a conspicuous mid-flank tubercle occur in the *H. choffati* Subzone (present paper), corresponding to *M.* (*D.*) *cunningtoni* and *M.* (*M.*) *aitzindari* nov. sp. (level K7), but none of these bear the striking ventrolateral clavi of *Navarreites* nov. gen. Actually, the new genus has concave ribs between tubercles as in *Deiradoceras*, but the presence of ventrolateral clavi seems to be a trait that appears at the end of the early late Albian to culminate in the latest Albian with the end of the majority of the group. However, the relationship of *Navarreites* gen. nov. with forms from the *M.* (*M.*) *inflatum* to *M.* (*S.*) *perinflatum* Zones is not clear. The most proximal Mortoniceratinae are Texan forms discussed above (e.g., *M.* (*M.*) *equidistans*, *M.* (*M.*) *vespertinum*) of likely similar age (the presence of *M.* (*M.*) *equidistans* in Texas suggests equivalence to the *M.* (*M.*) *inflatum* Zone in western Europe; Gale and Kennedy, 2020, p. 9), but the lack of more data prevents further discussion.

Occurrence. As for type.

Genus *Arestoceras* van Hoepen, 1942

Remarks. In a recent revision of several type species of mortoniceratine genera proposed by van Hoepen between 1942 and 1951 and by other authors, Cooper (2018) resurrected the subfamily Arestoceratinae van Hoepen, 1942 for a group of strongly compressed, generally bituberculate, late Albian brancoceratids currently understood as part of the Mortoniceratinae.

Arestoceras-like coiled Mortoniceratinae, generally compressed, high-whorled, from involute to evolute forms and bituberculate (*Goodhallites* Spath, 1932; *Cainoceras* van Hoepen, 1942; *Letheceras* van Hoepen, 1942; *Lethargoceras* van Hoepen, 1942; *Aidoceras* van Hoepen, 1946; *Pagoceras* van Hoepen, 1951; *Poikiloceras* van Hoepen, 1951 and *Conlinites* Kennedy, 2004) may form a natural group separated from the Mortoniceratinae, but all of them need detailed revision and evaluation of intraspecific variability (e.g., many similar genera defined by van Hoepen could be assigned to the same species), but this is outside the scope of the present paper.

Arestoceras cf. splendidum van Hoepen, 1951
Fig. 10/2A, B, 3A–C

*1951 *Arestoceras splendidum* van Hoepen, p. 337, text-figs. 428–430.
2009 *Arestoceras* cf. *splendidum* van Hoepen; López-Horgue et al., p. 395.

Type. The holotype, by monotypy, is the original of van Hoepen (1951, p. 337, figs. 428–430), specimen D. 2762.

Material. MCNA 13512 (Fig. 10/2A, B) is a fully septate half whorl, undeformed, with partially preserved shell replaced by calcite, the keel being preserved in the first part. The suture line is not clear. MCNA 17141 (Fig. 10/3A–C) is a partial body chamber of a very large specimen preserved as a sideritic internal mould with slight lateral compression.

Description. MCNA 13512: flanks parallel, slightly inclined towards keel. Whorl section compressed, higher than wide, with high keel rising above rounded venter and ribs. Dense ribbing, 19 in all, quite sharp and as wide as interspaces. Ribs flexuous, arising from gently rounded umbilical wall, initially branching in pairs, and then long and short; latter arising from upper part of lower flank. Umbilical bullate tubercles not reaching mid-flank. Ribs bearing slightly bullate and markedly adorally projected ventrolateral tubercle, some of them with faint inner ventrolateral swelling.

MCNA 17141: laterally compressed, affecting basically lower flank; dimensions being rough estimations, but based on likely whorl increment (Wh at 580 mm diameter/Wh at 440 mm diameter = 1.13). Rounded whorl section, with rounded umbilical wall, convergent flanks and fastigiate obtuse venter. Single ribs arising from near umbilical shoulder on adapical part and at umbilical shoulder on adoral part. Interspaces slightly wider than ribs; increasing sharpness and width gradually up on flank, being initially rectiradiate and adorally projected from mid-flank up to venter. On ventrolateral shoulder, wider than interspaces and showing bullate ventrolateral tubercle with inner ventrolateral claviform swellings. Ribs effacing rapidly on venter, not reaching the fastigiate edge.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13512	67.4 (keel restored)	29.6 (rest.)	22.0 (rest.)	23.7
(Fig. 10/2A, B)				
MCNA 17141	580.0 (est.)	250.0	120.0	170.0
(Fig. 10/3A–C)	440.0 (est.)	220.0	95.0	130.0

Discussion. MCNA 13512 (Fig. 10/2) is a compressed form (Wh/Ww ratio = 1.34) with a distinctive keel and flexuous ribbing that can be referred to a *Goodhallites*-type mortoniceratine. The inner whorls of this specimen are not preserved, but the distinctive and conservative ribbing, together with a high whorl section with near-parallel flanks and rounded venter in the septate stage, suggest a relative in the South African bituberculate *Arestoceras* sp. Actually, the whorl section of our specimen is close to that of the type species

of *Arestoceras* at a similar diameter (*A. collinum* van Hoepen, 1942, text-figs. 106–109). *Arestoceras splendidum* (see van Hoepen, 1951, p. 337, text-figs. 428–430) is the closest form, sharing with the Basque specimen a flexuous dense ribbing (22 ribs per half whorl at nearly the same diameter) and whorl section (Wh/Ww ratio = 1.41) differing in a less projected adoral end of the ribs. *Arestoceras rugosum* (van Hoepen, 1942, p. 121, text-figs. 111, 112) is possibly a related form, with a less flexuous ribbing and slightly angular shoulders with slightly wider tubercles, and a similar degree of compression.

MCNA 17141 (Fig. 10/3) is interpreted as the final part of the body chamber of a very large *Arestoceras*. Comparison of umbilical width (34 per cent of diameter) with that of the small specimen (28 per cent) shows a typical growth to less involute whorls and low umbilical width comparable to that of *Arestoceras* spp. (e.g., van Hoepen, 1951, p. 338). Whorl section changes during growth in the type species *A. collinum* van Hoepen, 1942 (his fig. 108) from subquadrate and compressed to rounded and higher with a fastigiate venter; these are compatible with the whorl section change observed in the smaller specimen, MCNA 13512, to the very large MCNA 17141. The latter may be considered a giant form among the Mortoniceratinae. Large, but smaller, forms of *Arestoceras* (diameters 300–330 mm), with more coarsely ribbed inner whorls and more fastigiate, less ornamented, body chamber have been recorded from the uppermost Albian of Sumbe, Angola (*Arestoceras goliath* Haas, 1942; see Meister et al., 2011, pls 5, 7).

Occurrence. BCB – Hysteroceras choffati Subzone of *M.* (*M.*) *pricei* Zone and *M.* (*M.*) *inflatum* Zone, Deva Formation, levels A4 and A7 in the Armintza section, Biscay province, Basque Country, Western Pyrenees, Spain. Elsewhere *A. splendidum* and *A. rugosum* have been recorded from the lower upper Albian Mzinene Beds of Zululand, South Africa (van Hoepen, 1951; dating following Kennedy and Klinger, 1975).

Genus *Elobiceras* Spath, 1921
Subgenus *Craginites* Young, 1957

Elobiceras (Craginites) subelobiense Spath, 1922
Fig. 10/4A–C

1905 *Schloenbachia elobiensis* Choffat, p. 67 (37), pl. 4, fig. 5.
1922 *Elobiceras subelobiense* Spath, p. 132.
1962 *Elobiceras subelobiense* Spath; Wiedmann, p. 221.
2009 *Craginites* sp.; López-Horgue et al., p. 395.
2020 *Elobiceras* (*Craginites*) *subelobiense* Spath, 1922; Gale and Kennedy, pl. 6, figs. 1–4; pl. 7, figs. 1–4.

Type. The holotype is the original of *Schloenbachia elobiensis* of Choffat (1905) from the upper Albian of Lobito, Benguela province, Angola, later changed (*nomen novum*) to *Elobiceras subelobiense* by Spath (1922, p. 132) and illustrated in Gale and Kennedy (2020, pl. 6, fig. 2).

Material. Specimen MCNA 13509 is an inner mould of nearly half a whorl, laterally crushed and weathered, but diagnostic features preserved. Suture not visible. MCNA 17150 (Fig. 10/4A–C) is a medium-sized phosphatic specimen with part of the shell preserved.

Description. MCNA 13509: high keel and flexuous ribs, irregularly short and long. Short ribs beginning at end of first third of flank or at mid-flank. Apparent branching in two pairs of ribs. Robust ribs, wider than interspaces, possibly bullate on umbilical edge and on ventrolateral ends; adorally projected on venter. Distinctive spiral ridges on ribs, especially on ventrolateral shoulder.

MCNA 17150 (Fig. 10/4): fairly adult with original dimensions of phragmocone, body chamber slightly crushed; maximum preserved diameter 87 mm corresponding almost entire last whorl. Inner whorls poorly visible but outer one seemingly covering these slightly, resulting in evolute coiling. Umbilicus only 24.5 mm wide (28 per cent of diameter). Whorl height increasing substantially from 25 to 37.2 mm (48 per cent) in last half whorl. Umbilical wall high and rounded, ribs arising and increasing in strength on umbilical shoulder forming sharp, high, slightly bullate umbilical tubercle. From umbilical tubercle ribs branching into two, extending radially towards ventrolateral shoulder, there bending adorally and widening, forming blunt end and reaching sharp high keel by means of subtle ventral sulcus. On phragmocone, flanks appearing parallel and venter wide (15 mm at end of phragmocone, whorl width 18 mm), but on body chamber flanks tending to converge towards elevated ventral area. Ribs crowded, wider than interspaces, 22 ribs on last half whorl. All ribs ornamented by spiral ridges, all along development, a rib pattern being norm on last whorl with only occasional intercalated single ribs arising from upper part of lower flank.

Dimensions (mm)	D	Wh	Ww	U
MCNA 13509	35.5	16.6	–	11.6
MCNA 17150 (Fig. 10/4A–C)	87.5	37.2	34 (restored)	24.5

Discussion. MCNA 17150 matches almost exactly the ribbing pattern seen in the holotype of *E. subelobiense* (see Gale and Kennedy, 2020, pl. 6, fig. 2), with a similar diameter (90 mm), umbilicus (29 per cent of diameter) and growth increment. Texas specimens figured by Gale and Kennedy (2020) are of larger sizes, showing a single ribbing pattern on the outermost half whorl but more crowded, branched ribbing in the inner whorls comparable to that of the holotype and the present specimens. *Elobiceras* (*C.*) *neuparthi* has more crowded ribbing on the inner whorls, while *E.* (*C.*) *serratescens* is more coarsely ribbed, with a wider umbilicus, and bears well-developed ventrolateral tubercles; this latter feature is also seen in *E.* (*C.*) *sparcicostatum*. Based on a comparison with larger-sized Texas specimens, MCNA 17150, with a preserved phragmocone and body chamber, may be interpreted as a microconch.

Apparent branching can be an artifact of preservation in MCNA 13509, but this Basque specimen shows real branching ribs at the end of the whorl. The remaining ribs appear long and short. This feature, together with the fact that the ribs are wider than the interspaces, are possibly somewhat bullate on umbilical and ventrolateral shoulders and bear the spiral ornament, conforms to the diagnosis of the genus *Craginites* (Young, 1957, p. 14). MCNA 13509 seems to have a narrow umbilicus like that of MCNA 17150, a fact that makes us include it in the same species, albeit with some reservations.

Occurrence. BCB – H. choffati Subzone of *M.* (*M.*) *pricei* Zone, level A3 (m 468 in López-Horgue et al., 2009) in the Armintza section, Deva Formation. Biscay province, Basque Country, Western Pyrenees, Spain, and *M.* (*M.*) *inflatum* Zone, levels I3 and I4 in the Irurtzun section, Izurdiaga, Navarre, Western Pyrenees, Spain. Elsewhere this species is known from the Lower Duck Creek Formation, *Eopachydiscus marcianus* Zone, Texas. According to Gale and Kennedy (2020), the presence of *M.* (*M.*) *equidistans* in the upper part of this zone suggests this part might be equivalent to the lower part of the *M.* (*M.*) *inflatum* Zone of western Europe. The holotype of the species is from the upper Albian of Angola.

6. Discussion

6.1. The mortoniceratine lineage

Above, several aspects of morphological features of the Mortoniceratinae that can be used to discern differences at the generic,

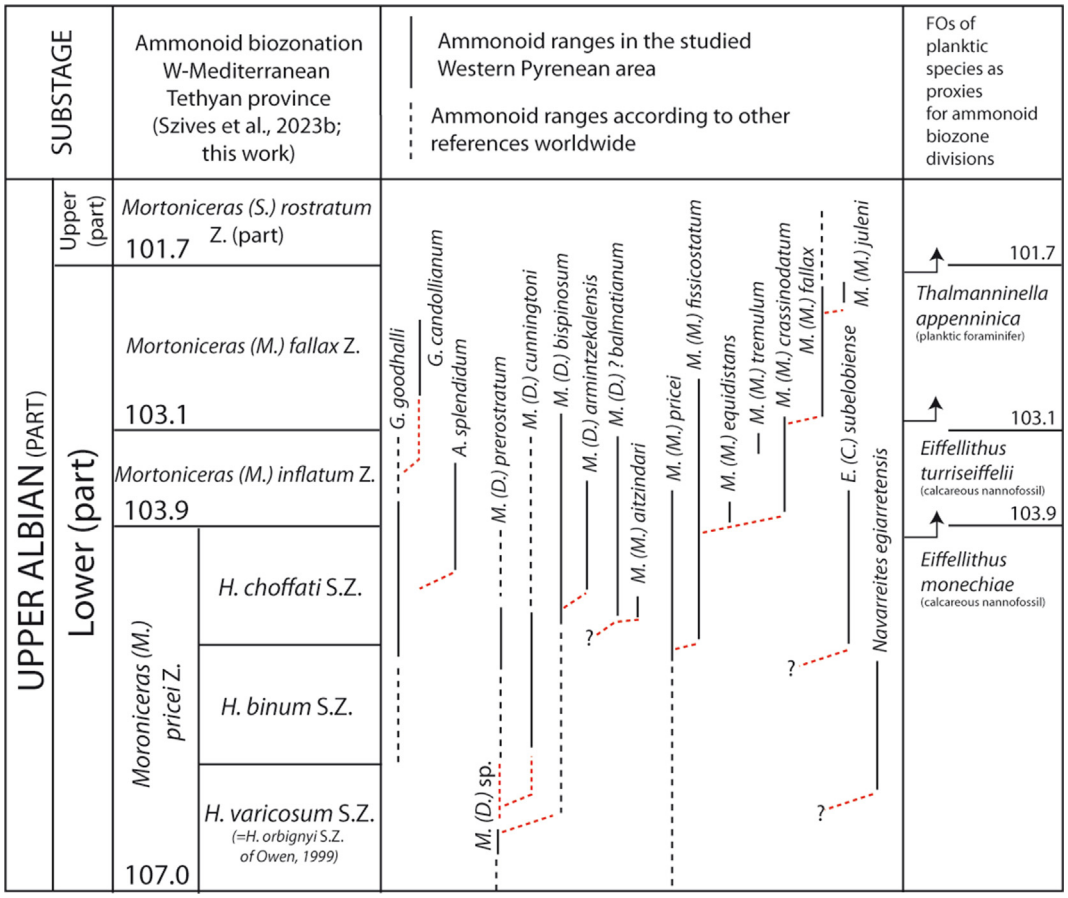


Fig. 11. Stratigraphical ranges of mortoniceratines from the Basque-Cantabrian Basin, using the present phyletic biozonation for the western Mediterranean region; maximum ranges from published data are used for comparison. The phyletic relationships are only tentative. Numbers at the base of the ammonoid zones indicate the age according to Gale et al. (2020); data on planktic foraminifera (*T. appenninica*) and calcareous nannofossils (*E. turriseiffelii* and *E. monechiae*) are from Gale et al. (2011). See text for further explanation.

subgeneric and species level have been outlined. Apart from a unique representation of a lowermost *Mortoniceras* (*M.*) *pricei* Zone element (*H. varicosum* Subzone, level K3; see Fig. 3), the common abundance in overlying biozones yields a good picture of the evolution of the group (Fig. 11). Bituberculate *Mortoniceras* (*Deiradoceras*) spp. are relatively abundant in the *H. binum* Subzone, giving rise to *Deiradoceras* with a subtle lateral tubercle in the overlying *H. choffati* Subzone. Of these, *Deiradoceras bispinosum*, originally described from South Africa, ranges up to the lower part of the *M.* (*M.*) *inflatum* Zone.

Mortoniceras (*M.*) *pricei* occurs rarely from the *H. binum* Subzone to the *M.* (*M.*) *inflatum* Zone, with only juvenile examples, thus preventing further discussion on likely relationships to other Pyrenean mortoniceratines.

Navarreites egiarretensis gen. nov., sp. nov., occurring in the *H. varicosum*–*H. binum* Subzones interval, and *Mortoniceras* (*M.*) *aitzindari* nov. sp., occurring higher in the *H. choffati* Subzone, cannot be referred to the phyletic lineage of the Mortoniceratinae in view of their respective early trituberculate and early quadrituberculate morphology and overall high morphological disparity from coexisting relatives. *Navarreites egiarretensis* gen. nov., sp. nov. shows an adult tubercle morphology that is only slightly comparable to Texan mortoniceratines as discussed above. *Mortoniceras* (*M.*) *aitzindari* sp. nov. may be a precursor of early quadrituberculate forms, but there are not enough specimens to ascertain this. Both may be better considered offshoots, with dubious success.

Mortoniceras (*M.*) cf. *equidistans*, *M.* (*M.*) *crassinodatum* and *M.* (*M.*) *tremulum* are representatives of the trituberculate stage with a shallow lateral tubercle typical of the *M.* (*M.*) *inflatum* Zone.

Regarding *M.* (*M.*) *fallax*, specimens studied here clearly document the existence of a transition to quadrituberculate forms that culminated in the overlying *M.* (*Subschloenbachia*) *rostratum* Zone. We have not found preserved rostra in earlier mortoniceratines but those observed in specimens of *M.* (*M.*) *fallax* illustrate a morphology that is intermediate between spirally to slightly upraised rostra of *M.* (*M.*) *inflatum* Zone species to backwardly recurved ones of the overlying *M.* (*S.*) *rostratum* Zone.

In the study area there are representatives of other, different stocks of the Mortoniceratinae. Members of the genera *Goodhallites* and *Arestoceras* form a stock of more involute and compressed bituberculate mortoniceratines. *Elobiceras* (*Craginites*) *subelobiense* is the only species studied here that represents a stock of involute mortoniceratines with ribs crowded by spiral ridges and with subtler tubercles.

6.2. Ammonite zonation of the upper Albian

On the basis of mortoniceratines described here and ammonoid assemblages referred to in Table 1, the phyletic zonation for the upper Albian of the western Tethyan Mediterranean Province adopted by the Kilian Group (Szives et al., 2023b) may be applied to the Pyrenean successions (Fig. 11). Moreover, the fact that the successions studied here are expanded and show a good

representation of the Mortoniceratinae in ascending order both supports the validity of the zonation and serves to clarify it.

6.2.1. The Mortoniceras (Mortoniceras) pricei *Zone*

In the study area, the index species is very rare, but the more common presence of contemporaneous species of *Hysteroceras* of the *orbignyi-binum-choffati* lineage is key to recognising this zone by differentiation of its three nominal *Hysteroceras*-based subzones, proposed by López-Horgue et al. (1999) and Owen (1999) (see discussion in Szives et al., 2023a; acceptance in Szives et al., 2023b). The subzone of *Hysteroceras orbignyi* of Owen (1999) is equivalent to the *H. varicosum* Subzone, as here understood, and explained in Szives et al. (2023b).

As an example of the validity of this subzonal division, some species of *Deiradoceras* initially recorded from South Africa, and occurring in the *M.* (*M.*) *pricei* Zone of the study area document a well-defined biostratigraphical distribution.

6.2.2. The Mortoniceras *(*M.*)* inflatum *and* M. *(*M.*)* fallax *zones*

The *M.* (*M.*) *inflatum* Zone has traditionally been accepted in the phyletic zonation as the zone intercalated between the *M.* (*M.*) *pricei* and *M.* (M.) *fallax* zones (e.g., Reboulet et al., 2018). Additionally, the *M.* (*M.*) *fallax* Zone has been considered the first division of the classic *Stoliczkaia dispar* Zone of previous authors (e.g., Kennedy et al., 2008; Gale et al., 2011, p. 68; Jattiot et al., 2021, p. 2) based on the relative position of the index species on the basis of records from Cambridgeshire (England), Strépy-Thieu (southern Belgium) and Salazac (France) (Kennedy and Latil, 2007), all of them from condensed successions.

The *M.* (*M.*) *inflatum* Zone *sensu stricto* (López-Horgue et al., 1999; Owen, 1999) has been proposed as an equivalent of the *Callihoplites auritus* Subzone of the former *M.* (*M.*) *inflatum* Zone as applied to the European Faunal Province (Owen, 1976; following Spath, 1941). Subsequently, Wiedmann and Owen (2001) and Owen (2007) proposed a division of the former *C. auritus* Subzone (European Province) into a lower and upper part on the basis of ammonoid associations distinguished in the Hannover area (northern Germany). According to Owen (2012), this lower part yields mortoniceratines with general development of a lateral tubercle as shown by typical forms of *M.* (*M.*) *inflatum*, whereas the upper part has *Cantabrigites minor*. Owen (2012) considered *M.* (*M.*) *fallax* to be synonymous with *M.* (*S.*) *rostratum*, and suggested that *M.* (*M.*) *fallax* morphotypes occurred in the latter zone. During the latest meeting of the Kilian Group (Szives et al., 2023b), the division of the *M.* (*M.*) *inflatum* Zone was accepted for the Western Tethyan zonation, with the lower and upper parts named *Hysteroceras bucklandi* Subzone and *Cantabrigites* spp. Subzone, respectively, both indexes showing cosmopolitan distribution.

In the present paper, *M.* (*M.*) *fallax* occurs in beds below the FO of *M.* (*S.*) *rostratum* at Meñakoz (level M1), Legutio (L1) and Estella-Lizarra (E-L-3) (with *Cantabrigites* aff. *minor* at level M2 above; see Fig. 3 and Table 1) and above *M.* (*M.*) *inflatum* Zone forms at Estella-Lizarra. At Karrantza, *M.* (*M.*) *fallax* has not been found, but the ammonoid assemblages from levels K8 to K10 indicate that the *M.* (*M.*) *inflatum* Zone was succeeded by the K11 association of the *M.* (*M.*) *fallax* Zone. The division observed here makes plausible the presence of two biozones between the *M.* (*M.*) *pricei* and *M.* (*S.*) *rostratum* Zones: the lower one with *inflatum* morphotypes (e.g., *M.* (*M.*) *tremulum*, *M.* (*M.*) cf. *equidistans*) and the upper one with *M.* (*M.*) *fallax* and *Cantabrigites* aff. *minor*. Accordingly, these lower and upper divisions should be assigned to the *M.* (*M.*) *inflatum* and *M.* (*M.*) *fallax* Zones of the phyletic zonation, respectively, as understood here. Thus, the newly proposed *Hysteroceras bucklandi* Subzone and *Cantabrigites* spp. Subzone of the *M.* (*M.*) *inflatum* Zone (Szives et al., 2023b) should be replaced by the *M.* (*M.*) *inflatum* and *M.* (*M.*) *fallax* Zones, respectively. Thanks to the record from the expanded successions in the study area, this makes it easier to understand the succeeding morphological changes across this interval, otherwise obscured by mixed faunas in condensed beds (see discussion in Szives et al., 2023b, p. 11). It also shows that the *M.* (*M.*) *fallax* Zone is below the traditionally adopted scheme with equivalence to the basal *S. dispar* Zone. Thus, *M.* (*M.*) *inflatum* Zone is defined as the interval zone between the FAD of the index species and the FAD of *M.* (*M.*) *fallax*, and characterised by *inflatum* morphotypes and *Hysteroceras bucklandi*. The *M.* (*M.*) *fallax* Zone extends up from the FAD of the index species to the FAD of *M.* (*S.*) *rostratum*, and is characterised by the occurrence of the index species and the first *Cantabrigites* spp.

In a recent quantitative biochronological analysis (Unitary Association Method) based on 175 species of late Albian age, Jattiot et al. (2023) proposed two Unitary Association Zones (UAZ), namely UAZ-2 and 3, into which *M.* (*M.*) *pricei* Zone would be divided. However, the *Hysteroceras*-based subzones (Szives et al., 2023b) show a better resolution. Jattiot et al. (2023) also showed a division of the former *M.* (*M.*) *inflatum* Zone into UAZ-5 and 6, below a zone of *Stoliczkaia* (*S.*) spp., somehow equivalent to the *inflatum* and *fallax* Zones as understood here. They also indicated discrepancies with the *C. auritus* Subzone (their UAZ-4) of Gallois and Owen (2020), i.e., what would be the lower part of the *M.* (*M.*) *inflatum sensu stricto*, in which they see the co-occurrence of *M.* (*M.*) *pricei* and *M.* (*M.*) *inflatum*. In the present study we record the co-occurrence of *M.* (*M.*) cf. *pricei* and *M.* (*M.*) cf. *equidistans* (a member of the *inflatum* group) in the lower part of the *M.* (*M.*) *inflatum* Zone (level K8), a fact that would need additional data, but does not invalidate the phyletic zonation for the expanded successions studied here. Other discrepancies (Jattiot et al., 2023) are linked to the coexistence of *M.* (*M.*) *fallax* and *M.* (*S.*) *rostratum* based on data from condensed sections and Owen's (2012) interpretation of the former species, arguing that the FO of *fallax* is not enough to identify its eponymous zone, and then propose both the co-occurrence of *M.* (*M.*) *fallax* with *Hysteroceras binum*, and the *M.* (*S.*) *rostratum* Zone ammonoid associations as key for zonal identification. Our data from expanded successions show that the FOs of both *fallax* and *rostratum* zonal index species are valid for zonal distinction and for considering the *M.* (*M.*) *fallax* Zone as the last biozone of the lower upper Albian, which does not invalidate the likely record of *M. fallax* in the succeeding *M.* (*S.*) *rostratum* Zone. An interesting point in the recognition of UAZs by Jattiot et al. (2023) is

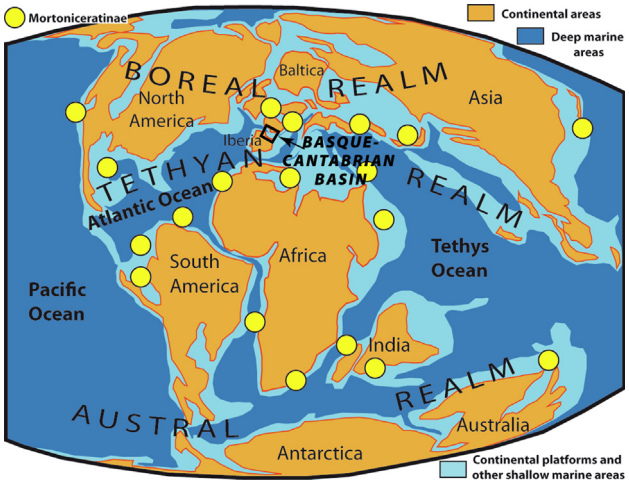


Fig. 12. Ammonoid palaeobiogeographical map for the upper Albian with indication of the mortoniceratine records worldwide and the location of the Basque-Cantabrian Basin. Map modified from R. Blakey (http://cpgeosystems.com) and Scotese (2013).

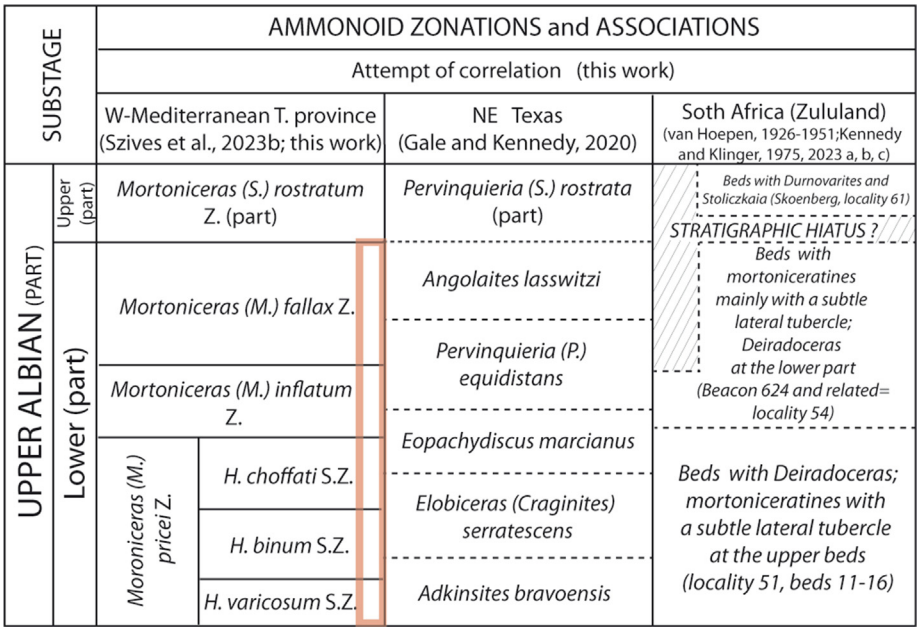


Fig. 13. Attempt at correlation of ammonoid biozones and ammonoid associations for part of the upper Albian between the Tethyan Western Mediterrenean province, north-east Texas and South Africa. The biozonation adopted here, with precisions for the *M.* (*M.*) *inflatum* and *M.* (*M.*) *fallax* biozones, is that of the latest meeting of the IUGS Lower Cretaceous Ammonite Working Group, the 'Kilian Group' (Szives et al., 2023b). Explanation in the text. The red rectangle highlights the biozones for ammonoid taxa studied for the present paper.

the contemporary ammonoid associations of the index species, which is of special interest when working with the commonly rare mortoniceratines.

Finally, another key point in interpreting the *M.* (*M.*) *fallax* Zone as the last zone of the lower upper Albian, and thus not included into the base of the traditional *S. dispar* Zone, comes from calcareous nannoplankton occurrences. In the Col de Palluel section, Gale et al. (2011, p. 125) noted the FO of *Eiffellithus monechiae* at −257.7 m, and the FO of *E. turriseiffelii* at −234.5 m, near the FO of the ammonoids *M.* (*M.*) *inflatum* at −253.1 m and *M.* (*M.*) *fallax* at −240.9 m, respectively. The record of these index nannofossils (e. g., Bown, 2001) has generally been placed within the *H. varicosum* to *C. auritus* Subzones of the European Province (*sensu* Owen, 1976, 1999). Accordingly, based on the proximity in the stratigraphical occurrences of both nannofossils and ammonoids, the FOs of these nannofossils may be used as proxies for those of *M.* (*M.*) *inflatum* and *M.* (*M.*) *fallax*, respectively. This fact makes the *M.* (*M.*) *inflatum* and *M.* (*M.*) *fallax* Zones of the Western Tethyan Mediterranean Province approximately equivalent to the traditional *C. auritus* Subzone (Owen, 1976), i.e., the lower and upper divisions of the *M.* (*M.*) *inflatum* Zone of Owen (*M.* (*M.*) *inflatum* Zone *sensu stricto* in López-Horgue et al., 1999; early and late parts of *Callihoplites auritus* Subzone in Wiedmann and Owen, 2001 and in Owen, 2012); actually, Gale et al. (2011, p. 111) suggested in their figure 49 an approximate equivalence of the *C. auritus* Subzone and both the *M.* (*M.*) *inflatum* and *M.* (*M.*) *fallax* Zones.

Additionally, Gale et al. (2011, pp. 108 and 125) recorded the FO of the planktic foraminifer *Thalmanninela appenninica* at −196.6 m, just 15.7 m above the LO of *M.* (*M.*) *fallax* (at −212.3 m) and 10.6 m below the FO of *M.* (*S.*) *rostratum* (at −186.0 m). This occurrence supports the FO of this planktic foraminifer as a proxy for the base of the *M.* (*S.*) *rostratum* Zone (Fig. 11). Recently, Vincent et al. (2020) recorded *M.* (*M.*) *fallax* at 5 m above the occurrence of *E. turriseiffelii* and some centimetres below the occurrence of their *M.* (*S.*) *rostratum*, consistent with the above data.

6.3. Correlation with other basins

The early late Albian ammonoid assemblages of which the mortoniceratines studied herein are part (Table 1) are typical of shallow-marine platforms of the Tethyan Province (López-Horgue et al., 2009), which extended from South America to Africa and India, with typical Tethyan elements such as the genera *Desmoceras*, *Puzosia*, *Kossmatella*, *Tetragonites* and *Zelandites*, co-occurring with cosmopolitan *Mortoniceras*, *Hysteroceras* and *Hamites* of wide distribution, also in European basins during the late Albian (e.g., Owen and Mutterlose, 2006). During this time the Western Pyrenean area (BCB) was located in the northern Tethyan Province, midway between South America and India, and facing the northern European basins (Fig. 12). The presence here of ammonoid elements typical of other Tethyan basins is indicative of the widespread Tethyan connection and may serve as key for correlation proposals between basins. In the study area, the *H. varicosum* Subzone contains the South American *Venezoliceras* (e.g., Renz, 1982; Luque et al., 2024); the *H. binum* Subzone yields *Mortoniceras* (*Deiradoceras*) *prerostratum* with a widespread distribution from Venezuela and Texas to England and South Africa (e.g., Renz, 1982; Kennedy et al., 1999). In the *H. choffati* Subzone, the occurrence of the South African *Mortoniceras* (*Deiradoceras*) *bispinosum* (e.g., van Hoepen, 1941) suggests a connection to the study area, also hinted at in the *M.* (*M.*) *inflatum* Zone with the South African *M.* (*M.*) *crassinodatum*. A connection to Texas and Mexico is suggested by the occurrence of *M.* (*M.*) cf. *equidistans* and *Elobiceras* (*Craginites*) *subelobiense* (e.g., Gale and Kennedy, 2020), and the latter also to Angola, all occurring in the *M.* (*M.*) *inflatum* Zone.

In the BCB, the basinal connection was favoured by the opening of the Bay of Biscay and related tectonic events that in some cases show a temporal equivalence to the record of ammonoids typical of other basins during the late Albian (Agirrezabala and López-Horgue, 2017). An increase in water depth in the basin from the *H. binum* Subzone into the *M.* (*M.*) *inflatum* Zone is suggested on the basis of

changes in morphotype associations, with an upward increase of nektonic and vertical migrants (Burgos and López-Horgue, 2019).

On the basis of the occurrences outlined above, we propose here an attempt at biozonal correlation (Fig. 13), in order to illustrate basin connections during the early late Albian and to provide the basis for future studies of the subject. For this purpose, we follow the occurrences of key elements and the correlation proposal shown in Gale and Kennedy (2020) between north-east Texas and western Europe, and the late Albian ammonoid associations and distributions in Zululand (South Africa), as discussed by Kennedy and Klinger (1975, 2023a, 2023b, 2023c). Accordingly, in north-east Texas:

1. the *Adkinsites bravoensis* Zone contains *Hysteroceras varicosum* and *Deiradoceras* spp., which are also common faunal elements in the *H. varicosum* and *H. binum* subzones of the Western Tethys;
2. the occurrence in Texas of the inoceramid *Actinoceramus sulcatus* atop the Kiamichi Formation (i.e., the top of *A. bravoensis* Zone) is correlatable with the transition to the *H. binum* Zone in Europe (e.g., Gale and Owen, 2010, figs. 1–5);
3. the *Elobiceras* (*Craginites*) *serratescens* Zone in Texas contains *Hysteroceras* cf. *varicosum* and *H.* cf. *binum*; the latter is the marker of its eponymous subzone in the Tethys (e.g., Owen and Mutterlose, 2006);
4. *Elobiceras* (*Craginites*) *subelobiense* occurs in the Lower Duck Creek Formation, *Eopachydiscus marcianus* Zone;
5. According to Gale and Kennedy (2020), the presence of *M.* (*M.*) *equidistans* in the upper part of the *Eopachydicus marcianus* Zone suggests it may be equivalent to the lower part of the *M.* (*M.*) *inflatum* Zone in western Europe.

For Zululand, this would mean:

1. Kennedy and Klinger (2023a, p. 2, text-fig. 1) and Kennedy and Klinger (2023b, table 1) listed *Mortoniceras* spp. occurring in the classic van Hoepen's Mzinene River area and surroundings, with their relative stratigraphical positions. We suggest that *M.* (*D.*) *bispinosum* (i.e., *prerostratum sensu* Kennedy after *Subschloenbachia bispinosa* Spath, 1921) may stem from levels underlying the beds with mainly *M.* (*M.*) *inflatum* Zone elements, since in the Basque-Cantabrian Basin this species occurs mostly in the *H. choffati* Subzone;
2. given the original occurrences of *Mortoniceras* (*M.*) *crassinodatum* and *M.* (*M.*) *tremulum* (van Hoepen, 1946) and compared to Basque-Cantabrian occurrences, these forms may occur at levels with *M.* (*M.*) *inflatum* Zone elements.

7. Conclusions

We have recorded and formally described an interesting fauna (55 specimens) of the cosmopolitan subfamily Mortoniceratinae from lower upper Albian non-condensed sections of the Basque-Cantabrian Basin (BCB) in the western Pyrenees. This allows the following conclusions to be drawn:

1. These ammonoids occur in different beds across eight studied successions that show a maximum thickness of 1700 m of lower upper Albian, mainly siliciclastic, shallow-marine to deeper-marine environments;
2. A detailed taxonomic study allows the identification of 19 species, of which 5 are described as new, in addition to one new genus. This is the first taxonomic account of this subfamily from a region for which there are few ammonoid taxonomic works and biostratigraphical studies;
3. *Mortoniceras* (*M.*) *fallax* is reassessed in consideration of BCB occurrences, its diagnosis emended and the eponymous zone is included into the lower upper Albian;
4. The mortoniceratine succession studied is consistent with the adopted phyletic zonation for the Western Mediterranean region, and provides clues for better definitions of the *M.* (*M.*) *inflatum* and *M.* (*M.*) *fallax* Zones;
5. Occurrences of mortoniceratines in the BCB are the basis for an attempted biozonal correlation with other Tethyan basins.

CRediT authorship contribution statement

Mikel A. López-Horgue: Writing – review & editing, Writing – original draft, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Hugh G. Owen:** Supervision, Data curation.

Declaration of competing interest

The authors declare that there is neither potential competing interest on personal relationships nor on the financial support.

Data availability

Main data come from the collections in the cited museums, all of them of public availability; anyway, any data may be requested to the corresponding author.

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