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EARLY–MIDDLE JURASSIC LYTOCERATID AMMONITES WITH CONSTRICTIONS FROM MOROCCO: PALAEOBIOGEOGRAPHICAL AND EVOLUTIONARY IMPLICATIONS

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Abstract: The ammonite genus *Alocolytoceras* Hyatt, 1900 is an uncommon lytoceratid with distinctive shell ornament. A set of 58 specimens, recently collected at Amellago in the central High Atlas (Morocco), has enabled us to trace a succession of three species over eight biozones from the Toarcian to the Aalenian. Two specimens from the Lusitanian Basin are added for comparison. Following a review of the genus, based on original specimens and data from the literature, seven species are considered valid. A palaeobiogeographical synthesis of 13 regions demonstrates irregular distribution patterns over time, with a constant presence in the south-west Tethys and an instance of rapid diversification of an endemic fauna in north-west Europe. Our data challenge the conventional view that lytoceratid ammonite evolution was 'conservative'.

Key words: Ammonoidea, Toarcian, Aalenian, Morocco, biostratigraphy, systematics, palaeobiogeography.

EARLY Jurassic ammonoid cephalopods are generally assigned to three suborders, Ammonitina, Phylloceratina and Lytoceratina. The Ammonitina have come in for close study because of their biostratigraphical value for the Jurassic and Cretaceous periods. By contrast, the Phylloceratina and Lytoceratina have merely been listed occasionally in systematic papers, or even ignored. This general disregard may be attributed to their apparent evolutionary 'conservatism' (see Page 1996), inferred from their many iterative characters. However, recent analyses of lytoceratid evolutionary dynamics challenge this supposed conservatism. For instance, Dommergues (2002) recorded a rapid diversification of Sinemurian 'capricorn' lytoceratids (for more examples, see Rulleau 1998; Rakus 1999). Indeed, new data (Guex 1987; Guex *et al.* 2000) indicate that the Lytoceratina were in fact a root stock for the Ammonitina order (see below). Lytoceratid evolution may then have been every bit as dynamic as that of other ammonites, a claim that could well provide a fresh perspective for future study.

The genus *Alocolytoceras* Hyatt, 1900, a lytoceratid with constrictions, is a typical representative of the south-west Tethyan province, which ranged from the middle Toarcian to the lower Bajocian. It differs from coeval lytoceratids in shell ornament, with constrictions (a feature found in other Hettangian lytoceratids) along the shell with several megastriae (*sensu* Bucher and Guex 1990) between successive constrictions. Since the pioneering works of d'Orbigny (1842–51), Benecke (1865) and Meneghini (1867–81), this genus has been widely reported from the Toarcian and Aalenian, both in the Mediterranean (Italy, Hungary and south-east France; see Monestier 1921, 1931; Géczy 1967; Guex 1973, 1975; Dezi and Ridolfi 1975, 1978; Sciau 1993; Venturi and Ferri 2001) and in north-west Europe (southern Germany: Schlegelmilch 1976; Ohmert 1996; the British Isles: Howarth 1978). More recently, Rulleau (1995, 1997, 1998) recorded the genus from the upper Toarcian (*dispansum* Zone) of the north-west European province (Lyon area). Yet, paradoxically, only a few papers document *Alocolytoceras* from strictly Tethyan areas (*sensu* Mouterde and Elmi 1991). For example, Elmi *et al.* (1974) and Benshili (1989) recorded closely similar faunas with long-ranging taxa (middle Toarcian–early Aalenian) from the Oranese Meseta (Algeria) and the Middle Atlas (Morocco), respectively.

Newly collected material from the central High Atlas (Morocco) is described here to challenge the hypothesis that lytoceratid evolution was 'conservative'. The collection comprises 58 specimens from the Agoudim Marls

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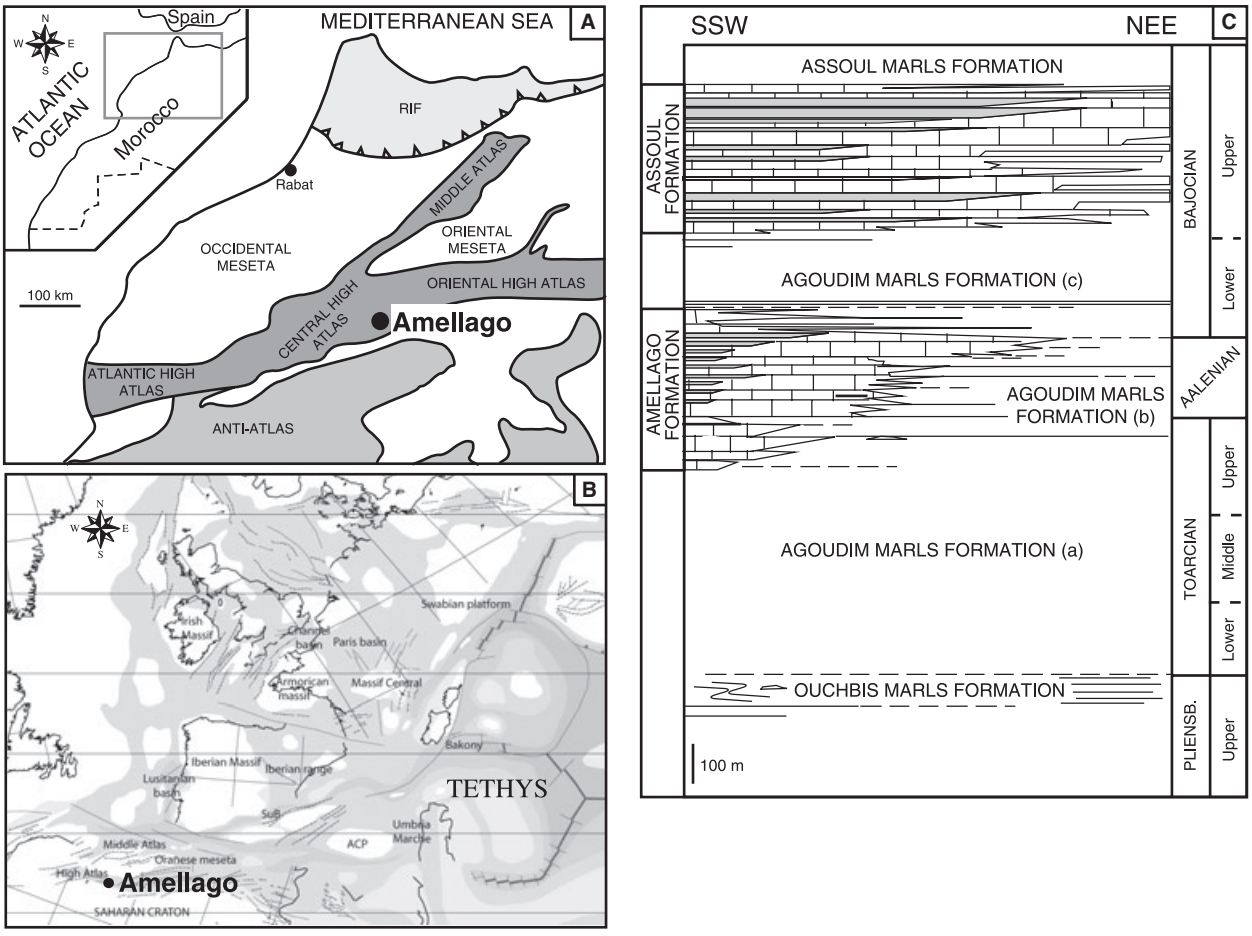
Formation (Poisson *et al.* 1998; Pierre *et al.* 2005) in the Amellago area. This faunule is of great palaeobiogeographical value, because it represents the south-westernmost occurrence of *Alocolytoceras*. Biostratigraphical and taxonomic aspects of this lot are discussed here, and a synthesis of other Tethyan areas is added in order to establish palaeobiogeographical distributions of the genus.

GEOLOGICAL SETTING

The ammonite faunule described was collected during 2001–2005 from the sides of Gheris Valley in the Amellago area (Text-fig. 1A), some 30 km north of Goulmima. The Amellago cliffs, regarded as a Jurassic reference transect in the area (Durlet *et al.* 2001; Pierre *et al.* 2005), extend over a length of 37 km and are between 800 and 1000 m high. From Late Triassic to mid-Jurassic times, the High Atlas formed an east–west intracontinental rift basin, up to 1000 km in length and approximately 100 km wide (Text-fig. 1B), with carbonate platforms on both sides (Warme 1988; Milhi *et al.* 2002). Hadri (1993) and Pierre *et al.* (2005) subdivided the Toarcian–Aalenian depositional history into three phases (Text-fig. 1C). The upper Pliensbachian/Toarcian transition saw the formation of a hemipelagic basin represented by the lower portion of the Agoudim Marls Formation (Text-fig. 1C); this event was linked to the onset of a second-order transgressive phase (Hardenbol *et al.* 1998) and corresponded locally to the start of post-rift sedimentation (Laville *et al.* 2004). The second phase (late Toarcian–early early Bajocian) resulted in the northward advance of an oolitic ramp system. The shallow ramp, representing the proximal portion of deposits, had as its distal equivalent the second member of the Agoudim Marls Formation [(b) in Text-fig. 1C], from which most of the ammonites of the present study were collected. During the early Bajocian, a major transgressive pulse (Sadki 1996) permanently inundated the Amellago oolitic ramp. The Agoudim Marls Formation is composed mostly of ammonite-rich, blue and grey marls, with some bivalves, brachiopods and gastropods, representing deposition in lower- to upper-

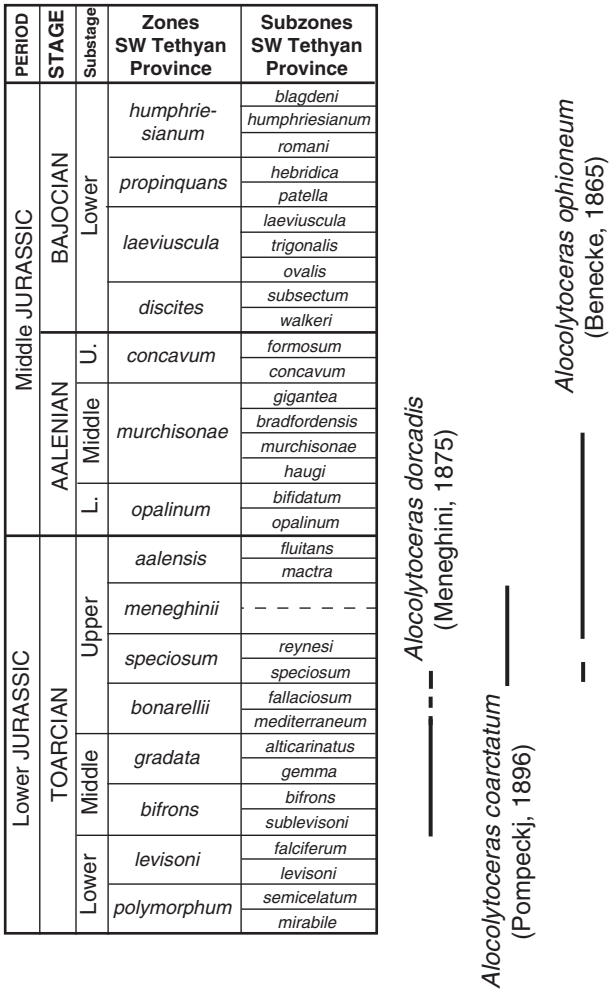


TEXT-FIG. 1. Map of the study area (A) and local stratigraphy (C). B, a mid Toarcian palaeogeographical map (modified after Thierry and Barrier 2000).

offshore settings (Hadri 1993; Poisson *et al.* 1998; Durlet *et al.* 2001). The formation usually contains thin micritic bioclastic beds that are storm deposits (Pierre *et al.* 2005). It varies in thickness from 400 to 1500 m from south to north along the Amellago transect.

BIOSTRATIGRAPHY

Ammonite zonal schemes for the Toarcian and Aalenian, as established by Elmi *et al.* (1997) and Contini *et al.* (1997), respectively, are taken here as a reference (Text-fig. 2). Zonal assignments rely on ammonites (Ammonitina, excluding the taxa under study here) and brachiopods, which document the lower Toarcian (*polymorphum* Zone) to the lower Bajocian (*humphriesianum* Zone). All mid Toarcian–mid Aalenian zones have been recognized. The first appearance datum (FAD) of the genus *Alocolytoceras* equates with the beginning of the mid Toarcian (*bifrons* Zone, *sublevisoni* Subzone). The last appearance datum (LAD) of the genus in the study area is in the mid Aalenian (*murchisonae* Zone). This long, unbroken succession provides new data for the south-west Tethyan occurrence of this genus and should, therefore, be of great use in palaeobiogeography.



TEXT-FIG. 2. Stratigraphical ranges of species of *Alocolytoceras* in the Amellago area. Toarcian, Aalenian and lower Bajocian zones and subzones for the south-west Tethyan region are after Elmi *et al.* (1997), Contini *et al.* (1997) and Rioult *et al.* (1997), respectively.

SYSTEMATIC PALAEONTOLOGY

All material is housed at the Centre des Sciences de la Terre, Université de Bourgogne (abbreviation: UBGD), Dijon, France. Specimens were coated with ammonium chloride prior to photography. All dimensions are given in millimetres.

Abbreviations. D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Estimates (for deformed material) are in brackets.

Class CEPHALOPODA Cuvier, 1797
Subclass AMMONOIDEA von Zittel, 1884
Order PSILOCERATIDA Houša, 1965 (emend. Guex, 1987)

Remarks. For Jurassic ammonoids, traditionally three taxonomic entities have been used: Phylloceratina, Lytoceratina and Ammonitina, of the rank of order or suborder. More recently, some authors (e.g. Guex 1987; Taylor 1998; Guex *et al.* 2000; Dommergues 2002; Dommergues *et al.* 2005) have criticized this division and proposed an alternative arrangement. The main reason for doing so was the discovery of primitive members of 'traditional' Ammonitina, which might well be the ancestors of the 'Lytoceratina' lineage, and thus the 'Ammonitina' could be viewed as paraphyletic. This hypothesis implies the use of a taxonomic framework that combines 'Ammonitina' and 'Lytoceratina' in the order Psiloceratida, as proposed by Houša (1965) and emended by Guex (1987). This view is adopted here.

Superfamily LYTOCERATOIDEA Neumayr, 1875
Family LYTOCERATIDAE Neumayr, 1875
Subfamily ALOCOLYTOCERATINAE Spath, 1927

Genus ALOCOLYTOCERAS Hyatt, 1900

Type species. Ammonites germaini d'Orbigny, 1842, p. 320, pl. 101, figs 1–2, 4–5, by subsequent designation of Hyatt (1900, p. 572).

Remarks. *Alocolytoceras* could be confused with the similarly constricted, yet smooth (i.e. non-striated) genus *Audaxlytoceras* Fucini, 1923 (range: upper Sinemurian–lower Toarcian). Morphologically, the early Toarcian *Audaxlytoceras spirorbis* (Meneghini, 1875) is close to *Alocolytoceras dorcadis* of mid–late Toarcian age; *Audaxlytoceras* might have given rise to *Alocolytoceras*. Some authors consider *Audaxlytoceras* to be confined to the Mediterranean province, but the general view is that both genera belong to a single lineage (Venturi and Ferri 2001; Becaud *et al.* 2005). We adopt this view here and use *Alocolytoceras*, which takes precedence over *Audaxlytoceras*.

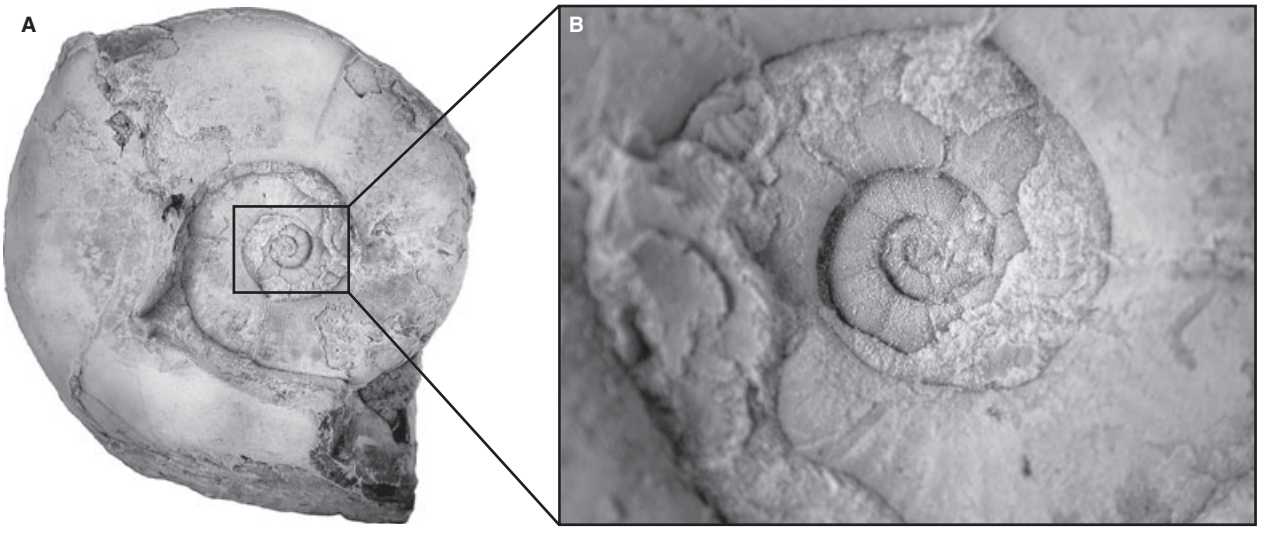
Alocolytoceras dorcadis (Meneghini, 1875)
Plate 1, figures 1–3; Text-figure 3

* 1875 *Ammonites* (*Lytoceras*) *Dorcadis* Meneghini, p. 107 (*partim*), pl. 21, fig. 1.
1899 *Lytoceras dorcadis* (Meneghini); Bonarelli, p. 216.
1900 *Lytoceras dorcadis* (Meneghini); Bellini, p. 128, fig. 1.
1906 *Lytoceras dorcadis* (Meneghini); Parisch and Viale, pl. 7, figs 3–4.
1931 *Lytoceras Dorcadis* (Meneghini); Monestier, p. 10, pl. 7, figs 1, 3–4, 6–7; pl. 9, fig. 10.
1967 *Alocolytoceras dorcadis* (Meneghini); Géczy, p. 79, pl. 22, fig. 1; pl. 64, fig. 32.
1968 *Alocolytoceras dorcadis* (Meneghini); Pinna, p. 13, pl. 1, figs 7, 10, 15; pl. 2, fig. 8.
1969 *Alocolytoceras dorcadis* (Meneghini); Pinna, p. 19, pl. 6, fig. 5.
1972 *Alocolytoceras dorcadis* (Meneghini); Guex, pl. 7, fig. 7.
1974 *Alocolytoceras dorcadis* (Meneghini); Elmi *et al.*, pp. 45, 50.
1975 *Alocolytoceras dorcadis* (Meneghini); Dezi and Ridolfi, p. 12, pls 12–13, figs 10–12a.
1989 *Alocolytoceras dorcadis* (Meneghini); Benshili, p. 85.
1993 *Lytoceras dorcadis* (Meneghini); Sciau, p. 36, pl. 18, fig. 2.
2001 *Audaxlytoceras dorcadis* (Meneghini); Venturi and Ferri, p. 92, fig. A.

Type. The holotype, by original designation, is from Cesi (central Apennines, Italy); it was reillustrated by Pinna (1969, pl. 6, fig. 5); the repository is the Pisa Paleontological Museum.

Material. Seventeen internal moulds (UBGD 276063–276065, 276072, 276077–276078 and 276127–276137), mostly phragmocones, three with shell partially preserved, eight deformed or fragmentary.

Description. Relatively large, evolute shell with high expansion rate. Earliest growth stages show subrounded-oval whorl section, becoming subquadrate-oval at ultimate ontogenetic stage. Whorl section slightly compressed (Wb/Wh ratio *c.* 0.9), flanks rounded. Umbilicus quite large, representing 29–40 per cent of shell diameter, particularly deep from fourth whorl onwards; umbilical wall is steep, umbilical shoulder well rounded. Ornament of rectiradiate ribs on early whorls, becoming convex from third whorl onwards. Numerous shallow constrictions present; at least 17 on first three whorls (Text-fig. 3), separated by numerous thin, barely visible striae (13 between two constrictions on third whorl; specimen UBGD 276063). Distance between two successive constrictions increasing with shell growth.



TEXT-FIG. 3. *Alocolytoceras dorcadis* (Meneghini, 1875), UBGD 276072, *bifrons* Zone, *sublevisoni* Subzone; Amellago, Agoudim Marls Formation (a). A, lateral view; × 1. B, detail of the umbilicus; × 5.2.

Dimensions	D	Wb	Wh	Wb/Wh	U	U/D
UBGD 276064	29.7	9.5	10.4	0.91	8.8	0.29
UBGD 276077	17.8	5.9	6.3	0.93	6.3	0.35
UBGD 276078	10.8	4.0	4.3	0.93	4.3	0.40
UBGD 276063	28.1	12.0	13.5	0.89	8.4	0.30
UBGD 276072	62.7	23.4	25.9	0.90	21.8	0.35
UBGD 276065	27.4	9.2	10.4	0.88	8.1	0.29

Remarks. Alocolytoceras dorcadis differs from congeners in having a subquadrate-oval whorl section and less pronounced ornament.

Occurrence. Middle and basal upper Toarcian (*bifrons–bonarellii* zones) of the south-west Tethys, with records from the central High Atlas (present study; Text-fig. 2), the Middle Atlas (Benshili 1989) and the Oranese Meseta, Algeria (Elmi *et al.* 1974). Also known from the mid Toarcian (*bifrons* Zone) of transitional areas, with records from Causses, southern France (Monestier 1931; Sciau 1993), Bakony, Hungary (Géczy 1967), Umbria Marche (Dezi and Ridolfi 1975) and the Apennines (Venturi and Ferri 2001), Italy.

Alocolytoceras ophioneum (Benecke, 1865)
Plate 1, figures 4–12

* 1865 *Ammonites ophioneus* Benecke, p. 172, pl. 6, fig. 5.
1881 *Ammonites* (*Lytoceras*) *Dorcadis* var. *catriensis* Meneghini, p. 108, pl. 20, fig. 4a–b.
1886 *Lytoceras Beneckei* Gemmellaro, p. 5, fig. 15.
1886 *Lytoceras ophioneum* (Benecke); Vaček, p. 62, pl. 3, figs 1–4.
1939 *Lytoceras catriense* (Meneghini); Ramaccioni, p. 162, pl. 11(2), fig. 5.
1967 *Alocolytoceras ophioneum* (Benecke); Géczy, p. 81, pl. 24, figs 1–2; pl. 64, figs 34–35.
1967 *Alocolytoceras ophioneum toarcense* (Benecke); Géczy, p. 80, pl. 23, figs 1, 6; pl. 64, fig. 33.
1969 *Alocolytoceras catriensis* (Meneghini); Pinna, p. 19, pl. 5, fig. 7.
1974 *Alocolytoceras ophioneum* (Benecke); Elmi *et al.*, pp. 46, 50.
1978 *Alocolytoceras* cf. *ophioneum* (Benecke); Dezi and Ridolfi, p. 66, figs 103–104.
1982 *Audaxlytoceras catriense* (Meneghini); Venturi, p. 39, fig. 35b.
1989 *Alocolytoceras ophioneum* (Benecke); Benshili, pl. 19, fig. 6.
2001 *Audaxlytoceras catriense* (Meneghini); Venturi and Ferri, p. 92, fig. F.
2001 *Alocolytoceras ophioneum* (Benecke); Sandoval *et al.*, p. 390.
2002 *Alocolytoceras ophioneum* (Benecke); Cresta, *in* Pavia and Cresta, p. 100, fig. 54.

Type. The holotype is from Cap San Vigilio (Italy). The present whereabouts of the type material is unknown.

Material. Thirty-one internal moulds (UBGD 276066–276070, 276079–276080, 276138–276161), five with shell wholly or partially preserved, 21 deformed or fragmentary.

Description. Large, evolute, with high expansion rate; whorl section highly compressed (Wb/Wh between 0.52 and 0.83), oval, with subparallel, slightly convex flanks. Umbilicus large and shallow in early whorls, deepening and increasing in width in subsequent whorls (from 40 to 28 per cent of shell diameter); umbilical wall low, umbilical shoulder well rounded. Ornament of straight ribs on early whorls, becoming prorsiradiate and sinuous from third whorl onwards. Eight constrictions on second and third whorl, separated by numerous thin striae, 15–20 between two successive constrictions on third whorl.

Dimensions	D	Wb	Wh	Wb/Wh	U	U/D
UBGD 276079	66.9	16.1	30.8	0.52	18.4	0.28
UBGD 276080	42.8	13.1	17.6	0.74	14.8	0.34
UBGD 276069	17.0	6.3	8.9	0.71	6.9	0.40
UBGD 276068	34.8	10.9	13.2	0.83	13.0	0.37
UBGD 276067	23.0	7.0	9.3	0.75	8.8	0.38
UBGD 276070	35.1	9.9	15.8	0.62	11.2	0.32

Remarks. Alocolytoceras ophioneum is characterized by an oval, compressed whorl section and shows a very particular pattern of ornament with numerous striae.

Occurrence. Basal upper Toarcian (upper *bonarellii* Zone or *speciosum* Zone)–mid Aalenian (*murchisonae* Zone, *murchisonae* Subzone) in the south-west Tethys, with records from the central High Atlas (present study; Text-fig. 2), the mid upper Toarcian (*meneghinii* Zone)–Aalenian in the Oranese Meseta, Algeria (Elmi *et al.* 1974), the uppermost Toarcian (*aalensis* Zone)–mid Aalenian (*murchisonae* Zone) in the Iberian Cordilleras (Sandoval *et al.* 2001) and upper Toarcian–lower Aalenian of the Middle Atlas (Benshili 1989), Italy (Meneghini 1881; Dezi and Ridolfi 1978; Venturi and Ferri 2001; Cresta in Pavia and Cresta 2002) and Hungary (Géczy 1967).

Alocolytoceras coarctatum (Pompeckj, 1896)
Text-figure 4

1885 *Ammonites interruptus striatus* Quenstedt, p. 387, pl. 48, figs 6, 8.
* 1896 *Lytoceras coarctatum* Pompeckj, p. 147.
1902 *Lytoceras coarctatum* (Pompeckj); Janensch, p. 46, pl. 2, fig. 4.
1921 *Lytoceras rude* Monestier, p. 13, pl. 2, fig. 17; pl. 3, figs 7–8.
1921 *Lytoceras angustum* Monestier, p. 15, pl. 1, figs 8–11, 17–19; pl. 6, fig. 14.

1973 *Lytoceras* (*Alocolytoceras*) *rude* (Monestier); Guex, p. 4, pl. 2, fig. 6.
1973 *Lytoceras* (*Alocolytoceras*) *angustum* (Monestier); Guex, p. 4, pl. 2, fig. 7.
1975 *Alocolytoceras rude* (Monestier); Guex, p. 119, pl. 9, figs 3–5.
1975 *Alocolytoceras angustum* (Monestier); Guex, p. 119, pl. 6, fig. 22; pl. 9, fig. 1.
1976 *Alocolytoceras coarctatum* (Pompeckj); Schlegelmilch, p. 30, pl. 4, fig. 3.
1978 *Alocolytoceras angustum* (Monestier); Dezi and Ridolfi, p. 67, figs 105–106.
1983 *Alocolytoceras coarctatum* (Pompeckj); Knitter and Ohmert, pl. 1, fig. 4.
1989 *Alocolytoceras angustum* (Monestier); Benshili, p. 107.
1995 *Alocolytoceras coarctatum* (Pompeckj); Rulleau, pl. 1, fig. 5.
1998 *Alocolytoceras coarctatum* (Pompeckj); Rulleau, p. 63, pl. 23, figs 5–6; pl. 24, fig. 4.
2002 *Alocolytoceras* gr. *germaini* (d'Orbigny); Fauré, p. 696, pl. 2, fig. 3a–b.

Type. The holotype is the original of *Ammonites interruptus striatus* Quenstedt, 1885 (Institut und Museum für Geologie und Paläontologie der Universität Tübingen), Ce 5/48/6; it was reillustrated by Schlegelmilch (1976, pl. 4, fig. 3).

Comments on synonymy. Lytoceras angustum Monestier, 1921 and *L. rude* Monestier, 1921 are both characterized by a more regular ornament, but are otherwise closely similar to *Alocolytoceras coarctatum.* The difference in number of striae between these taxa is probably linked to intraspecific variability (Rulleau 1998).

Material. Seven internal moulds (UBGD 276073–276075, 276081, 276163–276165), of which three retain well-preserved shell and four are deformed or fragmentary. Two more specimens are used here for comparison and come from the Lusitanian Basin (São Gião, UBGD 276076, 276162).

Description. Medium-sized, evolute with medium expansion rate. Whorl section constant and well rounded (Wb/Wh ratio *c.* 1). Umbilicus wide, *c.* 40 per cent of shell diameter, deep from third whorl onwards, with straight umbilical wall. Deep constrictions with high, sharp edges separated by 4–8 deep, well-marked megastriae; fewer constrictions in later whorls. Ribs straight on early whorls, becoming slightly prorsiradiate and undulating on later whorls.

Dimensions	D	Wb	Wh	Wb/Wh	U	U/D
UBGD 276074	43.6	17.2	16.0	1.07	19.1	0.44
UBGD 276073	36.6	14.7	15.1	1.12	14.7	0.40
UBGD 276081	44.1	15.6	16.4	0.95	14.0	0.32

Remarks. This species is characterized not only by a near-perfectly rounded whorl section but also by its strong ornament; changes in shell shape are comparable to those in *Al. ophioneum*, but it has a lower expansion rate than either *Al. ophioneum* or *Al. dorcadis*.

Occurrence. Relatively widely distributed, with records from the upper Toarcian (*speciosum–meneghinii* zones) in the central High Atlas (present study; Text-fig. 2). Other records include the *dispansum* (= *speciosum*) Zone only in the Pyrenees, Causses and Lyon area, France (Monestier 1931; Sciau 1993; Rulleau 1998; Fauré 2002) and the upper Toarcian of southern Germany (Schlegelmilch 1976) and Italy. In the Lusitanian Basin (new data; see Text-fig. 4E) and in the Middle Atlas (Morocco; see Benshili 1989), it is restricted to the *aalensis* Zone.

Alocolytoceras sp.
Plate 1, figure 13

Material. A single large, deformed internal mould (UBGD 276071).

Description. Very large, evolute specimen, *c.* 93 mm in diameter, with high expansion rate; two constrictions visible. Deformation precludes specific assignment.

Dimensions	D	Wb	Wh	Wb/Wh	U	U/D
UBGD 276071	92.9	(17.0)	(31.3)	(0.43)	31.3	0.33

Occurrence. Central High Atlas, Toarcian, Aalenian or Lower Bajocian (Agoudim Marls Formation); collected loose.

EXPLANATION OF PLATE 1

Figs 1–3. *Alocolytoceras dorcadis* (Meneghini, 1875). 1, UBGD 276063, *bifrons* Zone, *sublevisoni* Subzone. 2–3, UBGD 276064, incomplete phragmocone, *bifrons* Zone.

Figs 4–12. *Alocolytoceras ophioneum* (Benecke, 1865). 4, UBGD 276138, *speciosum* Zone. 5–6, UBGD 276066, incomplete phragmocone, *murchisonae* Zone. 7–8, UBGD 276067, incomplete phragmocone, *speciosum* Zone. 9, UBGD 276068, incomplete phragmocone, *speciosum* Zone. 10, UBGD 276069, incomplete phragmocone, *speciosum* Zone. 11–12, UBGD 276070, *speciosum* Zone.

Fig. 13. *Alocolytoceras* sp., UBGD 276071, Toarcian, Aalenian or Lower Bajocian.

All specimens from the Amellago area, central High Atlas, Morocco. 1–3, Agoudim Marls Formation (a); 4–12, Agoudim Marls Formation (b).

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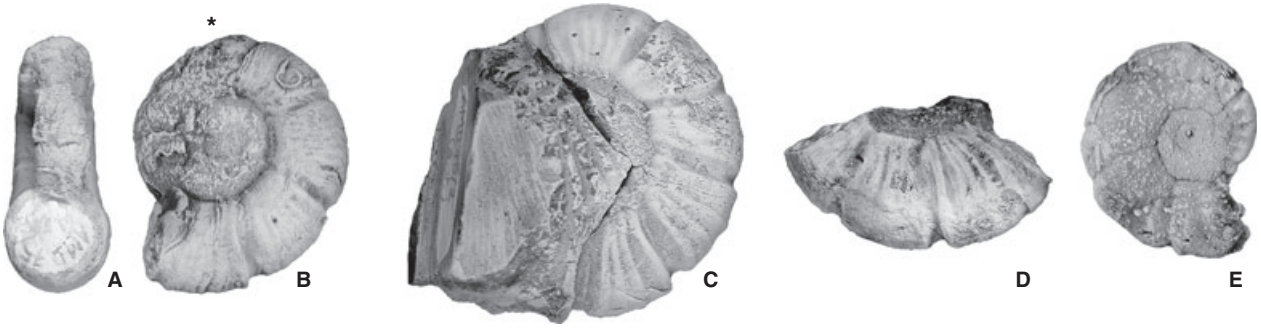


TEXT-FIG. 4. *Alocolytoceras coarctatum* (Pompeckj, 1896). A–B, UBGD 276073, asterisk marks the beginning of the body chamber; *meneghinii* Zone; Amellago, Agoudim Marls Formation (b). C, UBGD 276074, *meneghinii* Zone; Amellago, Agoudim Marls Formation (b). D, UBGD 276075, *meneghinii* Zone; Amellago, Agoudim Marls Formation (b). E, UBGD276076, incomplete phragmocone, *aalensis* Zone, *aalensis* Subzone; Portugal, São Gião. All × 1.

PALAEOBIOGEOGRAPHY

The faunal succession at Amellago, as defined here, complements the biostratigraphical and palaeobiogeographical distribution of lytoceratids with constrictions. Our analysis of distribution relies primarily on Rulleau (1998) for north-west Europe and Venturi and Ferri (2001) for the Apennines. About 19 nominal species belonging to *Alocolytoceras* have been recorded in the literature from the stratigraphical interval studied in this paper. After reviewing these we consider only seven to be valid, namely *Alocolytoceras dorcadis*, *Al. coarctatum*, *Al. ophioneum*, *Al. germaini*, *Al. rugiferum* (Pompeckj, 1896), *Al. alsaticum* (Janensch, 1902) and *Al. trautscholdi* (Oppel, 1862). These occur in the following regions: the High Atlas (present study), the Middle Atlas (Benshili 1989), the Oranese Meseta (Elmi *et al.* 1974), the Lusitanian Basin (present study), the Iberian Cordilleras (Sandoval *et al.* 2001), Umbria Marche and the Apennines (Meneghini 1867–81; Pinna 1969; Dezi and Ridolfi 1975, 1978; Venturi and Ferri 2001), Bakony (Géczy 1967), the Causses, Pyrenees and Lyon area (Monestier 1921, 1931; Guex 1972, 1973, 1975; Sciau, 1993; Rulleau 1995, 1998; Fauré 2002), southern Germany (Schlegelmilch 1976; Ohmert 1996) and Northamptonshire, England (see Howarth 1978, p. 240, noted only in a list). A comparison of ranges in these areas shows five distinct palaeobiogeographical patterns during the mid Toarcian–mid Aalenian interval (Text-fig. 5). As tectonic processes act over long periods of time, we consider the palaeogeography established by Thierry and Barrier (2000) for the *bifrons* Zone to be valid for the whole of this interval. These patterns are as follows:

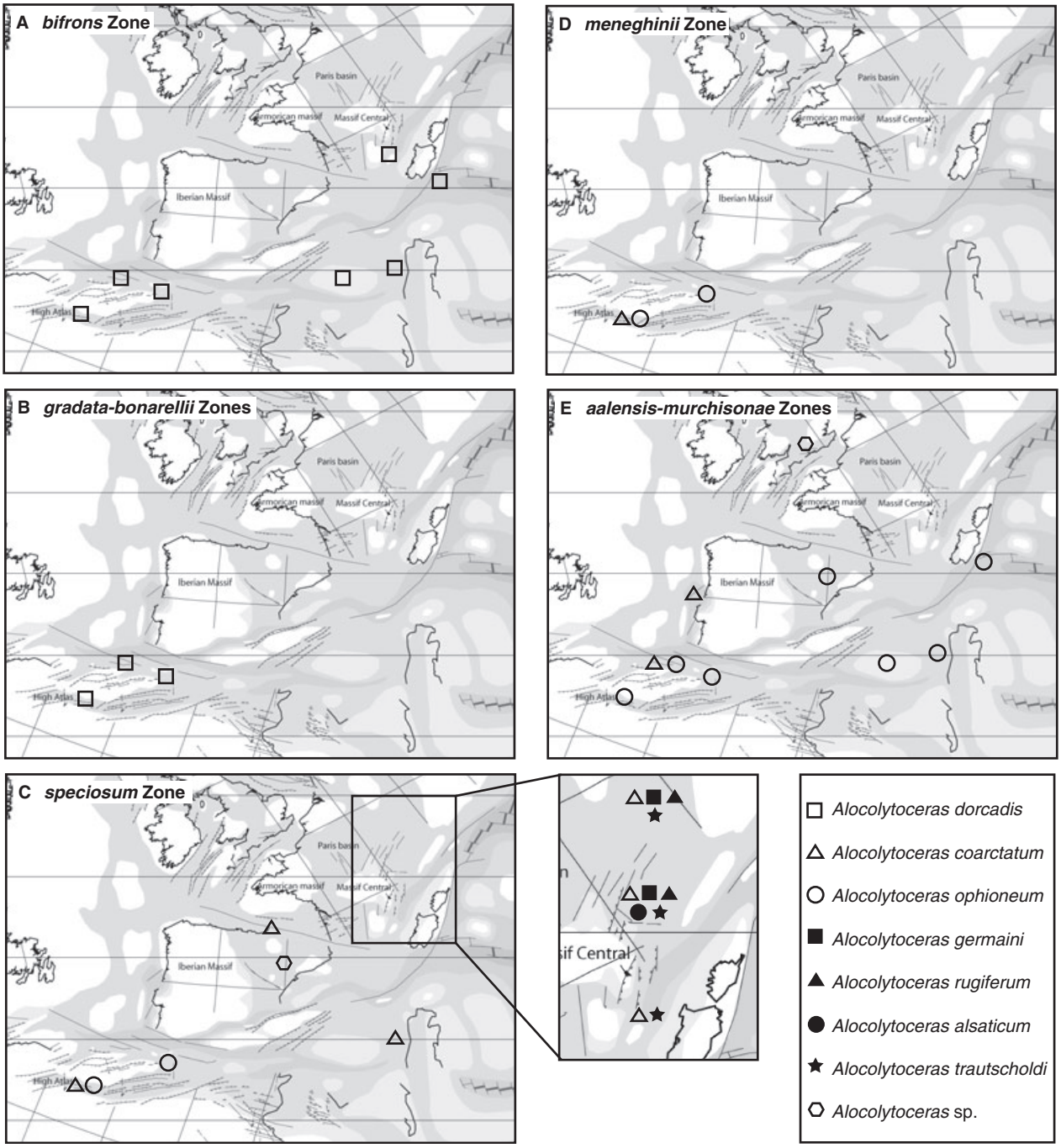
1. *bifrons* Zone (Text-fig. 5A): *Alocolytoceras*, represented solely by *Al. dorcadis*, is widely distributed, being found not only in the High Atlas, Middle Atlas and Oranese Meseta but also in Bakony, Umbria Marche, the Apennines and the Causses.

2. *gradata–bonarellii* zones (Text-fig. 5B): during the mid/upper Toarcian transition, *Al. dorcadis* was restricted to the High Atlas, Middle Atlas and Oranese Meseta. No other occurrences of this or any other species of the genus are known.

3. *speciosum* Zone (Text-fig. 5C): this unit is marked by a spectacular increase in diversity, with six species known. In the south-west Tethys, the near-synchronous origination (uppermost *thouarsense* Zone; see Rulleau 1998) of *Al. coarctatum* (central High Atlas and Middle Atlas) and *Al. ophioneum* (central High Atlas and Oranese Meseta) should be noted. These two species appear to co-occur only in the High Atlas. Whereas *Al. ophioneum* is limited to the south-west Tethys, *Al. coarctatum* is relatively widely distributed (Pyrenees, Causses, Lyon area and southern Germany). The presence of the genus in the Iberian Cordilleras (*Al.* sp.; see Sandoval *et al.*, 2001) should also be noted. In north-west Europe, there are four endemic species, viz. *Al. germaini*, *Al. rugiferum*, *Al. alsaticum* and *Al. trautscholdi* (see Text-fig. 5C), all confined to the *dispansum* Zone (= equivalent of *speciosum* Zone). These differ morphologically from Tethyan taxa in being larger and with an unusual semicircular whorl section (*Al. germaini*); in addition, ornament effaces during growth, the shell becoming smooth in later whorls.

4. *meneghinii* Zone (Text-fig. 5D): similar to the *gradata–bonarellii* zones, the genus is restricted to the south-west Tethys from where two species have been recorded, *Al. coarctatum* (central High Atlas) and *Al. ophioneum* (central High Atlas, Oranese Meseta).

5. *aalensis–murchisonae* zones (Text-fig. 5E): this interval comprises the Toarcian/Aalenian boundary, and shows a predominance of *Al. ophioneum* with a wide distribution including the south-west Tethys, Iberian Cordilleras, Umbria Marche and Apennines and Bakony as well as records from the *aalensis* Zone in the Middle Atlas and Lusitanian



TEXT-FIG. 5. Palaeobiogeographical patterns for eight species of *Alocolytoceras* during five distinct intervals between the mid Toarcian and mid Aalenian. Map modified after Thierry and Barrier (2000).

Basin (at São Gião; Text-fig. 4E). The genus has also been reported from the British Isles (Northamptonshire).

DISCUSSION

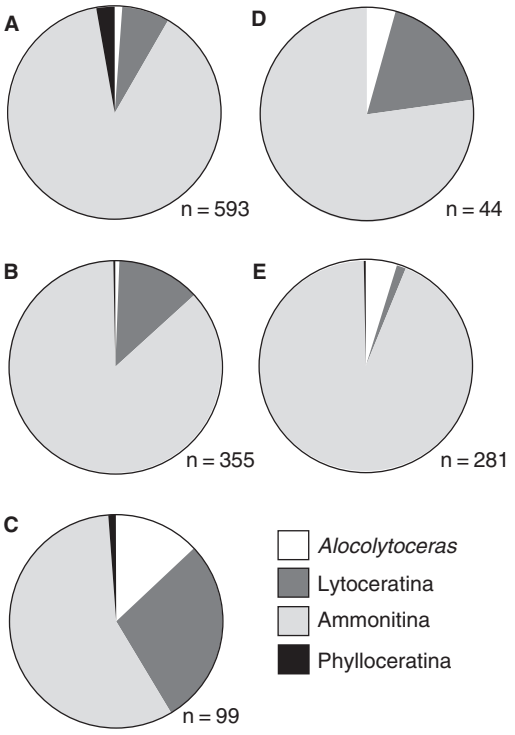
Our *Alocolytoceras* faunule from Amellago comprises two typically south-west Tethyan taxa, *Al. dorcadis* and *Al. ophioneum*, as well as one ubiquitous species, *Al. coarctatum*. The Amellago outcrop has permitted sampling of a continuous succession, thus confirming and complementing previous studies. A detailed analysis of Toarcian ammonoid faunas is that of Mouterde and Elmi (1991), who defined two regions for the Toarcian Stage, exhibiting faunal segregation: the western European region, extending from England south to the Caucasus, and the

Tethyan region, including the High and Middle Atlas, Algeria, Portugal, Hungary, the Apennines and the southern Alps. It should be noted that Mouterde and Elmi (1991) used the French term 'domaine' (translated as 'area' in the abstract of that paper) to designate these two main palaeobiogeographical entities. In the present paper, we prefer the term 'region' as recommended for informal naming of palaeobiogeographical entities (Westermann 2000*a*). We wish to avoid use of formal ranking (as developed by e.g. Westermann 2000*b*) in the absence of any detailed palaeobiogeographical pattern analyses for the Toarcian–Aalenian interval. The western European 'domaine' *sensu* Mouterde and Elmi (1991) comprises, depending on which authors are consulted, part of the Boreal Subrealm during the Toarcian and of the Boreal Realm during the Aalenian (following Westermann 2000*a*) or, alternatively, part of the Euro-boreal Realm following Dommergues (1987). The Tethyan 'domaine' *sensu* Mouterde and Elmi (1991) is part of the Tethyan Realm (following Westermann 2000*a*) or the equivalent of the Mediterranean Province following Dommergues (1987). According to Mouterde and Elmi (1991), regions that show mixed or intermediate faunas (i.e. the Iberian ranges and south-east France) define a transitional 'domaine'.

The palaeobiogeography of *Alocolytoceras*, alternately widely distributed and restricted during the Middle Toarcian–Middle Aalenian, fits this framework well. The genus is a typical Tethyan element that is consistently present in north-west Africa (Middle and High Atlas, Oranese Meseta) and shows episodic distribution patterns in other areas. Thus, during certain favourable intervals, the group extended over the entire Tethyan region (Umbria Marche, the Apennines and Bakony) and even occupied transitional regions. The genus is well known from western Europe only in *dispansum* Zone times, when it also occurred in both Tethyan and transitional regions. It may also occur, albeit rarely, in the uppermost Toarcian and/or lowermost Aalenian, as suggested by a single specimen reported by Howarth (1978) from the Northampton Sand Formation.

The large number of specimens collected enables us to construct a faunal spectrum for the Amellago area, extending from the mid Toarcian (*bifrons* Zone) to the Aalenian (*murchisonae* Zone). We have distinguished four main groups and counted the number of specimens in each of them: *Alocolytoceras*, other Lytoceratina, Ammonitina and Phylloceratina (Text-fig. 6).

Alocolytoceras is almost absent from the *bifrons* and *bonarellii* zones (Text-fig. 6A–B), reaches its maximum relative abundance in the *speciosum* Zone (*c.* 13 per cent; Text-fig. 6C) and then remains at relatively low values (<5 per cent) up to the *murchisonae* Zone (Text-fig. 6D–E).



TEXT-FIG. 6. Relative abundance (in per cent) of ammonoid groups in the Amellago area. A, *bifrons* Zone. B, *gradata–bonarellii* zones. C, *speciosum* Zone. D, *meneghinii* Zone. E, *aalensis–murchisonae* zones.

With this pattern documented, we can speculate on the processes underlying it. The link between relative sea level and ammonite migrations is now well understood (see Neige *et al.* 1997; Sandoval *et al.* 2002), particularly in the Tethyan region (Howarth 1973; Dommergues *et al.* 1987). The sequence-stratigraphic reference chart (Hardenbol *et al.* 1998) provides a tool for a better understanding of palaeobiogeographical distributions. Because of the fact that Early and Middle Jurassic lytoceratids are poorly described, our example of *Alocolytoceras* is of particular interest. The expansion during *bifrons* Zone times is easily linked to the relatively major maximum flooding surface (MFS) of the third-order cycle Toa 3 (Hardenbol *et al.* 1998). The distribution of species of *Alocolytoceras* is closely similar from the *aalensis* (upper Toarcian) to *murchisonae* (Aalenian) zones. The base of the *aalensis* Zone corresponds to the MFS of cycle Toa 6, which led to a general homogenization of ammonite faunas during the late Toarcian and early Aalenian, including *Alocolytoceras*. Interestingly, these two intervals also document a wide geographical expansion of some Ammonitina, e.g. *Hildoceras* (*bifrons* Zone) and *Leioceras* (*opalinum* Zone; see Sadki, 1996).

Alocolytoceras incursions in north-west Europe were very rare and seem to have been confined to the Lyon area (France), southern Germany and possibly the British

Isles. Surprisingly, the largest expansion of the genus occurs at *speciosum* Zone times, correlating with a biodiversity 'radiation'. This resulted in the origination of six species, four of which are endemic to the north-west European region. This also corresponds to the period during which the maximum proportion of *Alocolytoceras* and other 'Lytoceratina' account for more than 40 per cent of specimens found (Text-fig. 6). This interval matches a local transgressive cycle, recorded on the Iberian platform (Gomez and Goy 2005), and thus seems to have been a highly favourable period for *Alocolytoceras* and other 'lytoceratids'. Paradoxically, no particular migrations are known from the south-west Tethys for Ammonitina during this period (Sadki 1996). This also signifies that lytoceratids, at least those studied here, may have lived in the shallow waters characteristic of the north-west European region, as suggested previously by Hewitt (1996) and Westermann (1996), who proposed a habitat depth for lytoceratids between 60 and 400 m, in contrast to the general view that lytoceratids invariably inhabited deep waters.

This rapid diversification, probably linked to adaptation to the north-west European shallow continental shelf, conflicts with the traditional view of conservative lytoceratids (Page 1996). At least some taxa display evolutionary rates that are comparable to those of well-known contemporaneous Ammonitina (e.g. Hildoceratinae, Graphoceratinae and Dumortieriinae). Our data open up new paths in the study of lytoceratid evolutionary dynamics, provided that a precise biostratigraphical framework has been established first.

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