

Dimorphism and evolution of *Albarracinites* (Ammonoidea, Lower Bajocian) from the Iberian Range (Spain)

Sixto Rafael Fernandez-Lopez*

Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Madrid, Spain

Several tens of specimens of Lower Bajocian *Albarracinites* (type species *A. albarraciniensis* Fernandez-Lopez, 1985), including microconchs and macroconchs from the Iberian Range, have been studied. This ammonite genus ranges in the Iberian Range from at least the **Ovale Zone** to the uppermost **Laeviuscula Zone** of the Lower Bajocian (Middle Jurassic). The macroconch counterpart is thought to be a group of stephanoceratids previously attributed to *Mollistephanus*, *Riccardiceras* and other new forms described in this paper. Two chronologically successive species of *Albarracinites* have been identified: *A. albarraciniensis* and *A. submediterraneus* sp. nov. The evolution of the *Albarracinites* lineage represents a hypermorphic peramorphocline starting from depressed, small and slender serpenticones of *A. westermanni*, to larger planorbicones with more cadiconic phragmocones and body chamber of subcircular cross section belonging to *A. submediterraneus* sp. nov., through *A. albarraciniensis* Fernandez-Lopez. In contrast, *Mollistephanus planulatus* (Buckman), *M. cockrodensis* Chandler & Dietze and *M. mollis* Buckman represent a peramorphocline by acceleration, producing adults of similar size but more compressed and with increasing ontogenic variation of shell ornament. *Albarracinites* and *Mollistephanus* subsequently developed two opposite peramorphoclines or gradational series of morphological changes undergoing greater development and ontogenic variation. These two genera show diverse palaeobiogeographical distributions too. *Albarracinites* is rarely recorded in the Mediterranean and Submediterranean from the Discites to the Laeviuscula Zone, whereas *Mollistephanus* is more common in north-western Europe and other biochoremas of the western Tethys from the Discites Zone to the Sauzei Zone. *Albarracinites* seems to be the earliest stephanoceratid lineage in western Tethys, branching off from the oitoid *Riccardiceras* by proterogenetic change and resulting in paedomorphosis at the Aalenian/Bajocian boundary.

Keywords: ammonites; *Albarracinites*; *Mollistephanus*; Submediterranean Province; North-Western Europe Province; Mediterranean Province; Jurassic

Introduction

Lower Bajocian stephanoceratid ammonites from Europe comprise two genera – *Mollistephanus* and *Albarracinites* – characterized by potentially dimorphic small and slender serpenticonic and planorbiconic shells, representing macroconchs and microconchs, respectively (Fernandez-Lopez 1985; Chandler & Dietze 2004). Dimorphism is a special kind of intraspecific variability, well documented in ammonoids, whereby individuals with a similar early ontogeny have polarized adult morphologies probably representing different sexes (Davis *et al.* 1996). New studies in the Lower Bajocian deposits of the Masada Toyuela area (Sierra de Albarracin, Teruel, Spain, Fig. 1) have yielded a significant number of ammonites in recent years, which have been described by Fernandez-Lopez (1985) from the type locality of *Albarracinites albarraciniensis* and several nearby sections. Collections made from Masada Toyuela (MT) comprise over 1500 ammonites that are particularly relevant to the interpretation of the

Albarracinites beds belonging to the Ovale and Laeviuscula zones. *Albarracinites* is relatively common in some levels but still represents less than 5% of specimens.

The present work is concerned with the systematic position of the genus *Albarracinites*, which has been monospecific since its erection 25 years ago. A new species of *Albarracinites* is identified among the specimens recently collected in the Iberian Range, and new biochronological and palaeobiological results about the phyletic origination of Stephanoceratidae are given.

Palaeoenvironmental and palaeobiogeographical setting

Aalenian and lowermost Bajocian deposits of the Iberian Range are commonly represented by condensed sections containing stratigraphical discontinuities in the lower part of the El Pedregal Formation (Chelva Group, Gomez & Fernandez-Lopez 2006). The *Albarracinites* beds

*Email: sixto@geo.ucm.es

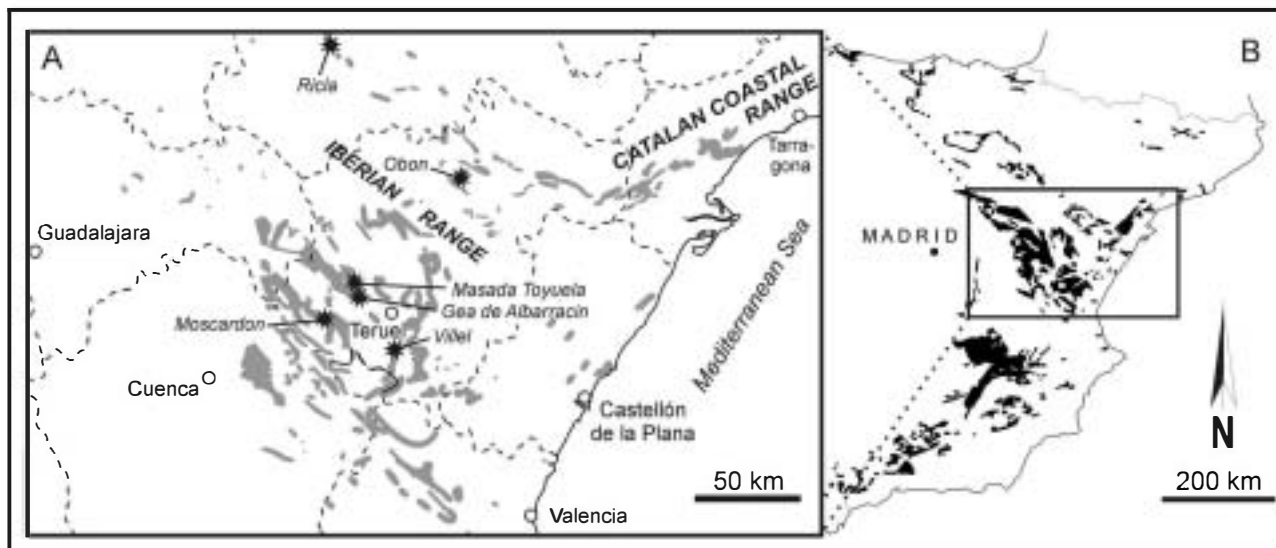


Figure 1. Locality maps. **A**, asterisks indicate the stratigraphical sections cited in text; grey areas represent outcrops of Middle Jurassic deposits in the Iberian Range and the Catalan Coastal Range (Spain); dashed lines indicate the province boundaries. **B**, black areas represent Jurassic outcrops.

correspond to condensed sections, composed of decimetric or centimetric, expanded-deposit intervals, stacked and showing an overall thinning upward, which constitute a deepening sequence developed in shallow-water, open-marine, carbonate environments of the External Castilian Platform during the *Ovale* and *Laeviuscula* biochrons (Fig. 2). Taphonomic analyses corroborate the development of an incipient-deepening phase, which represents the first episode of a deepening half-cycle of third order in the Albarracín area within the Castilian Platform (Fernandez-Lopez & Gomez 2004; Fernandez-Lopez 2011).

In a general palaeobiogeographical context, the biodispersal of individuals can lead to their settlement in new areas if suitable ecological conditions are present, and can give rise to population migration with ontogenic and/or sexual segregation. Populations remaining in a new area may give rise to offspring, leading to sustained colonization. However, the individuals or populations that live and mate in an area may be residents or migrants (Cecca 2002). To separate elements or assemblages produced by resident or migrant populations from elements or assemblages produced by nekrokinosis and post-mortem transport, it is useful to distinguish between demic and non-demic taxa. The former are identified from fossils found in the living area, and the latter from fossils found outside the living area (Fig. 3A). In turn, among demic taxa three categories have been distinguished: endemic (recorded in their living and breeding area), midemic (recorded in a living area without breeding, and present there as a result of active biodispersal), and parademic (recorded in a living area without breeding and present there as a result of occasional passive biodispersal).

In ammonite palaeobiogeography, the crucial dispersal can be by taphonomic modifications such as the sorting of shell size distribution and ontogenic stages due to processes of nekrokinosis and post-mortem transport. Macroconchs (abbreviated as M) and microconchs (abbreviated as m) of ammonites represent distinct taphonomic groups, or taphons, due to their structural and behaviour differences (Fernandez-Lopez 2006, 2007). Taphons are integrated by local taphonic populations, which can be preserved in particular environments. In order to describe and analyse ammonite fossil assemblages, three types of taphonic populations can be identified (Fig. 3B). A type-1 taphonic population comprises a monospecific group of shells, with unimodal size-frequency distributions of positive asymmetry, dominant juveniles, adults virtually absent, and dimorphism well represented. A type-2 taphonic population comprises monospecific or polyspecific shells, with unimodal or polymodal, normal distribution of size-frequencies, pre-adults or adults dominant, very scarce juveniles, and microconchs usually in low proportions. A taphonic population of type 3 comprises monospecific or polyspecific shells, with unimodal or polymodal size-frequency distributions of negative asymmetry, adults dominant, juveniles absent, and dimorphism poorly represented. As a result of taphonomic dispersal, type-1 taphonic populations are indicative of endemic taxa, whereas type-3 taphonic populations are indicative of ademic taxa. Monospecific and dimorphic taphonic populations of type 2, with pre-adults present, are characteristic of midemic taxa, whereas monomorphic taphonic populations of type 2, with adults dominant, are characteristic of parademic taxa.

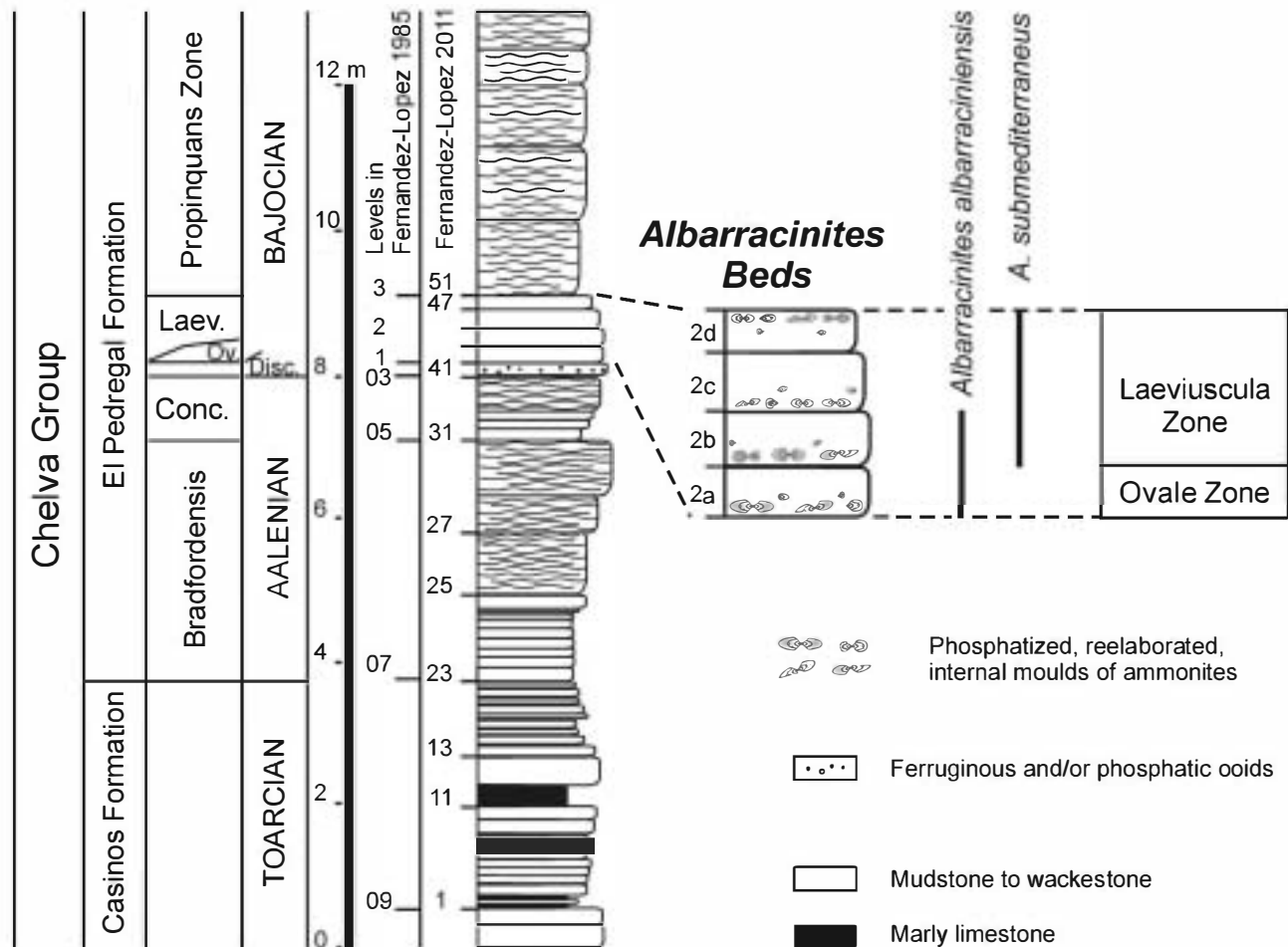


Figure 2. Stratigraphical log of the Upper Toarcian–Lower Bajocian transition in the section at Masada Toyuela (Albarracín, Teruel), and detailed stratigraphical distributions of the two species of *Albarracinites* described in the text. Bed 2a is the type horizon of *A. albarraciniensis*, whereas bed 2c is the type horizon of *A. submediterraneus*. Chronostratigraphical zonation after Fernandez-Lopez (2012).

Aalenian and Early Bajocian ammonite populations dominated by juveniles and indicative of eudemic taxa (i.e. in their breeding area, according to Callomon 1985) were absent in the Castilian Platform. Most recorded ammonite genera are represented by polyspecific groups of adult shells, generally macroconchs, produced by ademic or parademic taxa that arrived at their present location by regional nektonesis or passive biodeispersal, respectively. However, the exceptional occurrence of monospecific populations, including macroconchs and microconchs such as in *Hebertoxyites* (Fernandez-Lopez 2012, fig. 2), or even with predominance of microconchs as in *Albarracinites* (Fig. 4; Fernandez-Lopez 2011, fig. 9), lacking juveniles but dominated by pre-adults, suggests autochthonous biogenic production of shells by midemic taxa (i.e. in an area occupied by active biodeispersal, but where breeding does not occur), after immigration in the eastern Iberian platform system. Two regional bio-events controlled by changes

of relative sea level in the Castilian Platform have been identified: (1) regional appearance of immigrant ammonite taxa, such as *Hebertoxyites* and *Albarracinites*, at the Discites/Ovale transition; and (2) regional disappearance of these midemic ammonite taxa at the Laeviuscula/Sauzei transition (Fernandez-Lopez 2012).

Systematic palaeontology

Class Cephalopoda Cuvier, 1798

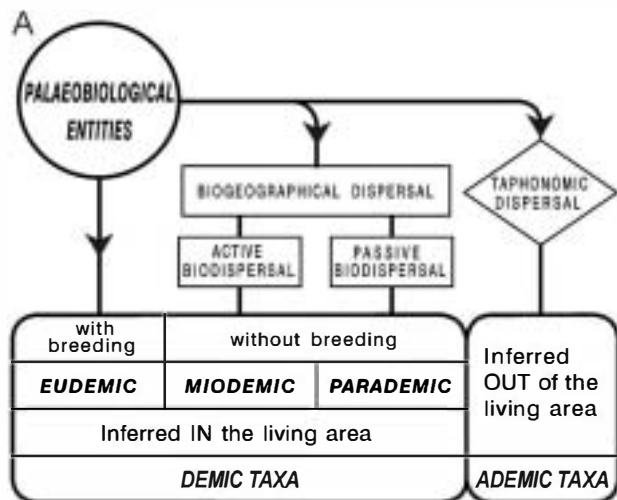
Subclass Ammonoidea von Zittel, 1884

Order Ammonitida Fischer, 1882

Superfamily Stephanoceratoidea Neumayr, 1875

Family Stephanoceratidae Neumayr, 1875

Remarks. The superfamily Stephanoceratoidea Neumayr, 1875 branched from Aalenian Erycitidae Spath, 1927 of the



B

TAPHONIC POPULATIONS:			
TYPE-1	TYPE-2		TYPE-3
positive asymmetry	normal distribution	normal distribution	negative asymmetry
dominant juveniles	present pre-adults	dominant adults	dominant adults
dimorphic	dimorphic	monomorphic	monomorphic
monospecific genera	monospecific genera	monospecific or polyspecific	polyspecific genera

Figure 3. Palaeobiogeographical and taphonomic categories mentioned in text. **A**, the palaeobiological entities (organisms, populations or species) are demic when their fossils are recorded in their living area. Conversely, they are ademic species (or taxa) when they are recorded or inferred outside of their living area. Demic species may be recorded in their breeding area (eudemic), in an area normally occupied by active biodispersal but where they do not breed (miodemic), or in a living area occasionally reached by passive biodispersal (parademic) (according to Fernandez-Lopez 1991, 1995, 2007; Fernandez-Lopez & Melendez 1996; Fernandez-Lopez & Chong Diaz 2011). **B**, taphonic populations of type 1 are indicative of sustained colonization by eudemic taxa. In contrast, taphonic population of type 3 are indicative of ademic taxa. Taphonic populations of type 2, displaying intermediate or normal size distribution, are indicative of colonization by miodemic or parademic taxa. Monospecific and monomorphic taphonic populations of type 2 with sorting of adults are characteristic of parademic taxa, whereas monospecific and dimorphic taphonic populations of type 2 with sorting of pre-adults are characteristic of miodemic taxa.

superfamily Hammatoceratoidea Schindewolf, 1964 that gave rise to Ootitidae Mascke, 1907, which includes taxa such as *Docidoceras* [M]-*Trilobiticeras* [m], *Riccardiceras* [M and m] and *Westermannites* [M]. At the Aalenian/Bajocian transition, in turn, Ootitidae were the source of Stephanoceratidae Neumayr, 1875, including *Mollistephanus* [M and m] and *Albarracinites* [M and m], according to the results and conclusions below (cf. Arkell

1952; Westermann 1956, 1964a, 1993, 1995; Arkell *et al.* 1957; Geczy 1966; Westermann & Riccardi 1979; Callomon 1981; Tintant & Mouterde 1981; Pavia 1983; Sandoval 1983; Fernandez-Lopez 1985; Page 1996, 2008; Sandoval *et al.* 2000; Dietze *et al.* 2001, 2010; Chandler & Dietze 2004; Moyné & Neige 2004; O'Dogherty *et al.* 2006; Shevyrev 2006; Howarth 2013).

The morphological terms used herein follow the Glossary of the *Treatise on Invertebrate Paleontology* (Arkell *et al.* 1957) and other terms presented by Westermann (1996, 2005). The family Stephanoceratidae is characterized by serpenticones, planorbicones and cadicones, with ribbing ventrally uninterrupted, and egressive coiling at maturity, differentiated into dimorphic groups: (1) microconchs [m] with lateral lappets and short body chambers ribbed to the end; and (2) macroconchs [M] with simple apertures and long body chambers (near to, or longer than, 360°) that are smooth or distantly ribbed. The septal suture is complex, with deeply divided lateral saddles and retracted umbilical lobes in the macroconchs, but slightly simplified in the microconchs. Lateral saddle E/L is asymmetrical and higher than L/U2.

Genus *Albarracinites* Fernandez-Lopez, 1985 [m and M]

Type species. *Albarracinites albarraciniensis* Fernandez-Lopez, 1985, Lower Bajocian, Iberian Range, Spain.

Diagnosis. Microconch (Dmax = 15–35 mm) and macroconch (Dmax = 50–170 mm) stephanoceratids of small to medium size (Figs 5–10). Macroconchs bear a simple aperture, with trumpet-like expansion of the adult peristome. Microconchs have a peristome with lateral lappets. Adult body chamber, with eccentric coiling, is typically over a half whorl in microconchs and a little over one whorl in macroconchs. The coiling is planulate, more involute on the inner whorls (U/D = 36–50%) and becomes more evolute towards the adult aperture (Fig. 5). The whorl section is oval and depressed on the inner whorls (W/H = 200–160%), rather cadiconic in appearance (W/D = 50–35%), and becomes more rounded and subcircular on the outer whorls (W/H = 140–100%). Ribbing is straight to slightly sinuous, blunt and persists throughout ontogeny. Bifurcate or trifurcate ribs show a rursiradiate tendency, particularly in the inner and intermediate whorls. Secondary ribs are uninterrupted on the venter, becoming blunter, of variable strength and spacing, in the outer whorls. Tubercles can be present at furcation points. Lateral saddle E/L is high and narrow. The lateral lobe is shorter than, or similar to, the external lobe and oblique. U2 is shorter and more oblique than L.

Remarks. According to this new diagnosis of the genus, *Albarracinites* [m and M] differs from *Mollistephanus* Buckman, 1922 [M and m] (type species *M. mollis* Buckman, 1902 [M] in 1909–1930, TA-IV, pl. 344;

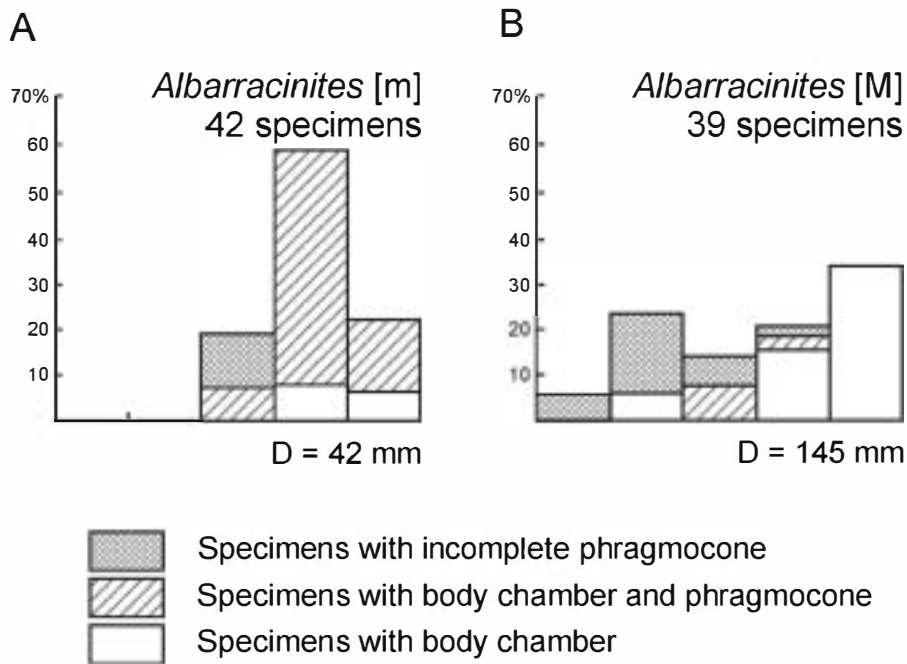


Figure 4. Size–frequency distributions of *Albarracinites* shells from the Iberian Range. **A**, microconchs; **B**, macroconchs. The histograms of taphonic populations are plotted in terms of five frequency classes, indicating the proportion of body chambers, complete shells (with body chamber and phragmocone) and incomplete phragmocones. Note the higher relative abundance of body chambers in the intermediate classes or frequency groups, as diagnostic criterion of taphonic populations of type 2.

holotype refigured by Chandler & Dietze 2004, fig. 4.1a, b, and Rulleau 2011, pl. 48, fig. 2a, b; allegedly from Coombe, probably Sandford Lane, near Sherborne, Dorset, England, Trigonalis Subzone, Laeviuscula Zone) by less serpenticonic coiling and a less compressed section on the outer whorls (Fig. 11A–F). The ribbing is blunter, with a less pronounced ventral furcation point. The secondary ribs of variable strength and spacing in the outer whorls of the *Albarracinites* microconchs are a further difference.

Other minute Early Bajocian stephanoceratids from the Mediterranean–Caucasian Subrealm, such as *Phaulostephanus* Buckman, 1927 [M and m] (type species *P. paululus* Buckman, 1927 [M] in 1909–1930, TA-VII, pl. 754; holotype from Clatcombe, near Sherborne, Dorset, Romani Subzone, Humphriesianum Zone) show more serpenticonic coiling, with secondaries more proverse and a shorter body chamber than *Albarracinites* (cf. Galacz 2012).

Skirroceras Mascke, 1907 [M] (type species ‘*Ammonites Humphriesianus macer*’ Quenstedt, 1886, p. 528, pl. 65, fig. 11; lectotype designed by Buckman, 1921, pl. 248 and refigured by Schlegelmilch 1985, pl. 23, fig. 2; from the Humphriesianum–Oolith, Swabia, Germany, Lower Bajocian) and *Stephanoceras* Waagen, 1869 [M] (type species ‘*Ammonites Humphriesianus*’ J. de C. Sowerby, 1825 in Sowerby & Sowerby, 1812–1846, pl. 500; holotype reproduced as a photograph by Fallot & Blanchet 1923, pl. 13, fig. 1; from Sherborne, Dorset, Inferior Oolite, Lower

Bajocian) display more complex suture lines, with subparallel, deep and narrow lateral lobes and strongly retracted suspensive lobes. Both genera are longidome, the body chamber surpassing 450° and reaching 750° in *Skirroceras*, whereas it varies from 360° to 450° in *Stephanoceras* (Fernandez-Lopez 1985; Westermann 2005). The microconch counterpart of *Skirroceras*, *Epaxites* Mascke, 1907 [m] (type species *Ammonites contractus anceps* Quenstedt, 1886, p. 521, pl. 64, fig. 20; holotype refigured by Westermann 1954, pl. 28, fig. 1; from Lauffen, Germany, Dogger-δ, probably Sauzei Zone) and the microconch counterpart of *Stephanoceras*, *Itinsaites* McLearn, 1927 [m] (type species *Itinsaites itinsae* McLearn, 1927, p. 73, holotype figured in pl. 1, fig. 7; refigured by Westermann 1954, pl. 26, fig. 5; from the lower Yakoun Formation, south Balch Island, Skidegate Inlet, Queen Charlotte Islands, Canada, in the *Chondroceras oblatum* Zone, probably Humphriesianum Zone, after Hall & Westermann 1980, p. 41 and Hall *et al.* 1991, p. 144) display sharper ribbing than *Albarracinites* [m]. *Normannites* Munier-Chalmas, 1892 [m] (type species *Normannites orbigny* Buckman, 1908, p. 146, 1927, pl. 734; neotype designated by Westermann 1954, p. 136; from Clatcombe, Sherborne, Dorset, Humphriesianum Zone, Lower Bajocian) also shows sharper ribbing than *Albarracinites* [m] and represents the dimorph of *Teloceras* Mascke, 1907 [M] (type species *Ammonites blagdeni* J. Sowerby, 1818 in Sowerby & Sowerby, 1812–1846, p. 231, pl. 201; holotype from Dorset,

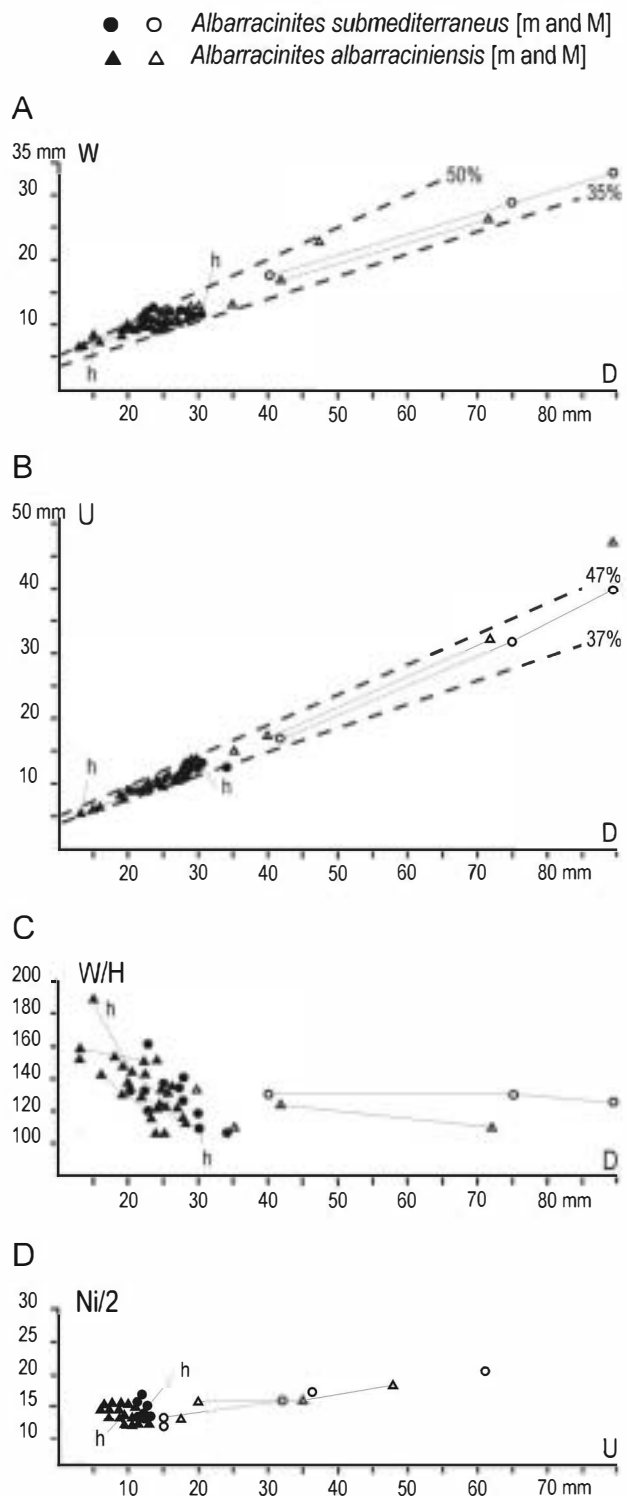


Figure 5. Plots of measurements of *Albarracinites* from the Iberian Range. **A**, whorl width (W) versus shell diameter (D); **B**, umbilical diameter (U) versus shell diameter (D); **C**, whorl width/whorl height ratio (W/H) versus shell diameter (D); **D**, internal ribs per half whorl (Ni/2) versus umbilical diameter (U). Abbreviations: m, microconch; M, macroconch; h, holotype.

uppermost Humphriesianum Zone, Lower Bajocian); both of these are coronate cadicones of greater size.

Kumatostephanus Buckman, 1922 [M] (type species *Kumatostephanus kumaterus* Buckman, 1922, pl. 345; holotype refigured by Rulleau 2011, pl. 48, fig. 1a, b; from South Main Road Quarry, Dundry, faunal horizon Bj11a, Sauzei Zone after Chandler *et al.* 2006) is more coarsely ribbed and has a more simple suture line, with a broad lateral lobe and a suspensor lobe not strongly retracted. *Gerzenites* Westermann, 1954 [m] (type species *Normannites (Gerzenites) rugosus* Westermann, 1954, p. 231, holotype figured in pl. 19, fig. 4; from the Oolites-Schichten, Gerzen, Germany, Sauzei Zone), the microconch counterpart of *Kumatostephanus*, shows sharper ribbing and more proverse secondaries than *Albarracinites* [m].

Some small and slender stephanoceratids from the East Pacific Subrealm, such as *Parabigotites* Imlay, 1961 [M] (type species *P. crassicosatus* Imlay, 1961, p. 473, pl. 64, figs 8, 10, holotype refigured by Imlay 1964, p. 54, pl. 29, figs 14, 15, and Rulleau 2011, pl. 70, fig. 1; from the Kialagvik Formation, Alaska Peninsula, upper Sauzei Zone) and *Freboldites* Taylor, 1988 [M] (type species *F. bifurcatus* Taylor, 1988, p. 136, holotype 'Stephanoceras (*Skirroceras*) cf. *dolichoechus*' of Imlay 1973, p. 88, pl. 45, fig. 8, refigured by Rulleau 2011, pl. 58, fig. 4; from Vigrass' locality 162, Weberg Member, Snowshoe Formation, Oregon, USA, Sauzei Zone and topotypes possibly also recorded in the Laeviuscula Zone) show more planorbic and evolute shells than *Albarracinites*, with subparallel and deeper lateral lobe.

Oolitids comprise cadicones and serpenticones with thick primary ribs, umbilical egression and flattening of the adult body chamber, as in *Docidoceras*, *Riccardiceras* and *Westermannites*. *Docidoceras* Buckman, 1919 [M] (type species *D. cylindroides* Buckman, 1919, pl. 133A; from Bradford Abbas, Sherborne, Dorset, Discites Zone) differs from *Albarracinites* [M] by having a shorter, more depressed and contracted adult body chamber, and more complex septal suture with the lateral lobe subparallel and deeper than the external lobe. *Trilobiticeras* Buckman, 1919 [m] (type species *T. trilobitoides* Buckman, 1919, pl. 140; from Bradford Abbas, Sherborne, Dorset, Discites Zone), as the microconch counterpart of *Docidoceras*, also shows more cadiconic coiling and shorter primaries than *Albarracinites* [m], with U2 in an outer position relative to the lateral tubercles.

Riccardiceras Westermann, 1995 [M and m] (type species *Coeloceras longalvum* Vacek, 1886 [M], p. 99, pl. 17, figs 1, 2, lectotype reproduced as a photograph by Westermann 1964a, p. 48, pl. 6, figs 1, 2, and Dietze *et al.* 2001, p. 9, fig. 6; from the San Vigilio Oolite Formation, Cap San Vigilio, Lake Garda, Italy, Upper Aalenian after Callomon *et al.* 1994), lacking a coronate-cadiconic juvenile stage, comprises serpenticones of larger adult size than

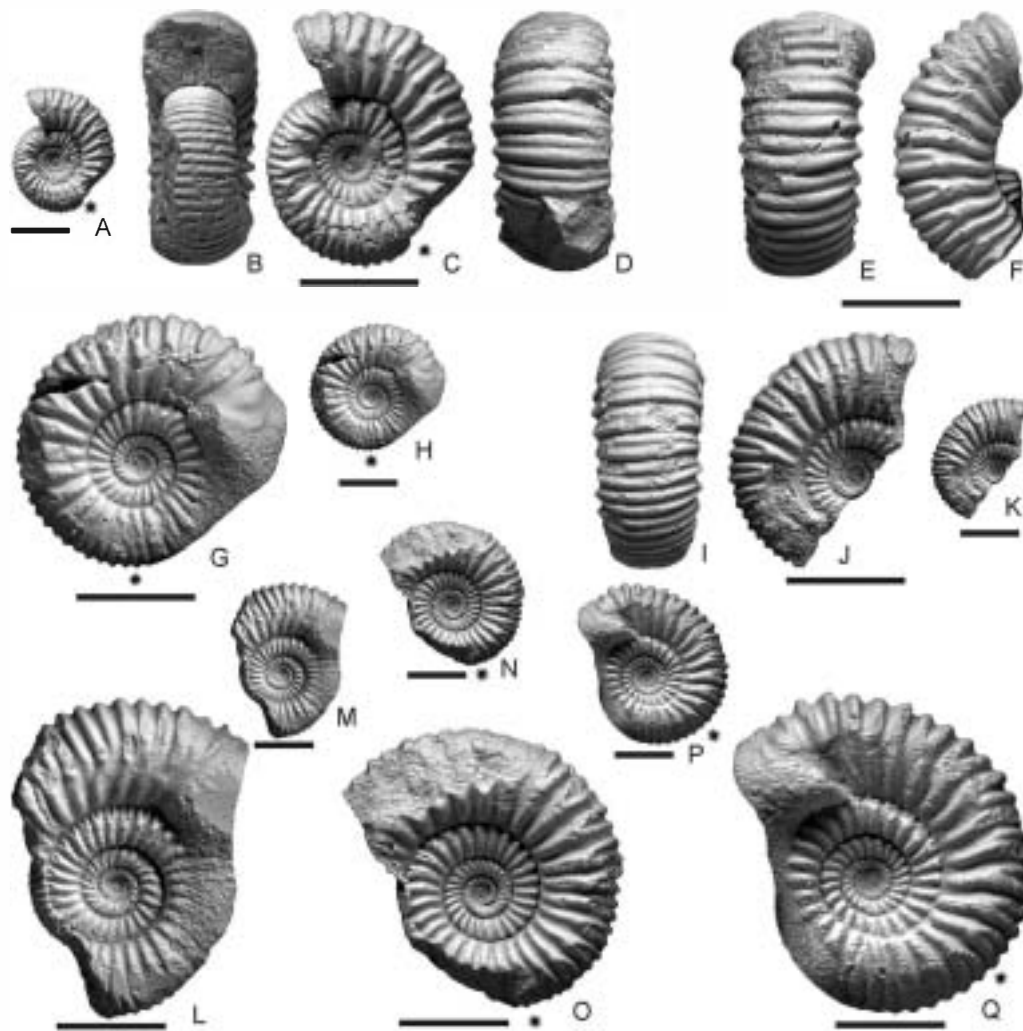


Figure 6. Microconchs of *Albarracinites albarraciniensis* from the Masada Toyuela section. Black asterisk marks the last septum of the phragmocone. The specimens were whitened with magnesium oxide prior to photography. Scale bar equals 10 mm. A–D, holotype MT2a/69, \bullet vale Zone; E,F, paratype MT2a/72, \bullet vale Zone; G,H, topotype MT2/116, lower Laeviuscula Zone; I–K, topotype MT2/120, lower Laeviuscula Zone; L,M, topotype MT2/115, lower Laeviuscula Zone; N,O, paratype MT2/68, Laeviuscula Zone; P,Q, topotype MT2/117, lower Laeviuscula Zone.

Albarracinites [M]. *Westermannites* Dietze et al., 2001 [M] (type species *Coeloceras limatum* Pompeckj, 1897 [M], pl. 31, fig. 5, holotype reproduced as a photograph by Dietze et al. 2001, p. 11, fig. 7; from Kessik-tash near Ankara, Turkey, Lower Bajocian), with a coronate-cadiconic juvenile stage, can also reach larger adult sizes than *Albarracinites* [M]. *Riccardiceras* and *Westermannites* display a subparallel lateral lobe, longer than the external lobe, instead of the oblique and short lateral lobe seen in *Albarracinites*.

Distribution. The known range of *Albarracinites* is restricted to the Lower Bajocian, with acme in the \bullet vale and Laeviuscula zones, in several areas of western Tethys. Forms of this genus have been identified from the Iberian Range (Fernandez-Lopez 1985; Fernandez-Lopez &

Aurell 1988), Basque-Cantabrian Basin (Fernandez-Lopez et al. 1988b), Lusitanian Basin (Fernandez-Lopez et al. 1989), Betic Basin (Sandoval et al. 2000, 2001, 2002) and Morocco (Sadki 1994, 1996). Among the representatives of *Albarracinites* from the Iberian Range, two species have been distinguished in the \bullet vale and Laeviuscula zones: *A. albarraciniensis* Fernandez-Lopez and *A. submediterraneus* sp. nov.

Albarracinites albarraciniensis Fernandez-Lopez, 1985
[m and M]
(Figs 6A–Q, 7D–J, 8A, 9C–G)

1985 *Albarracinites albarraciniensis* Fernandez-Lopez:
301, pl. 36, figs 1 (holotype), 2, 3 (paratypes), 33, 34.

1985 *Mollistephanus* sp. nov. 3.; Fernandez-Lopez: 251, pl.
20, figs 13, 14, 27D–F.

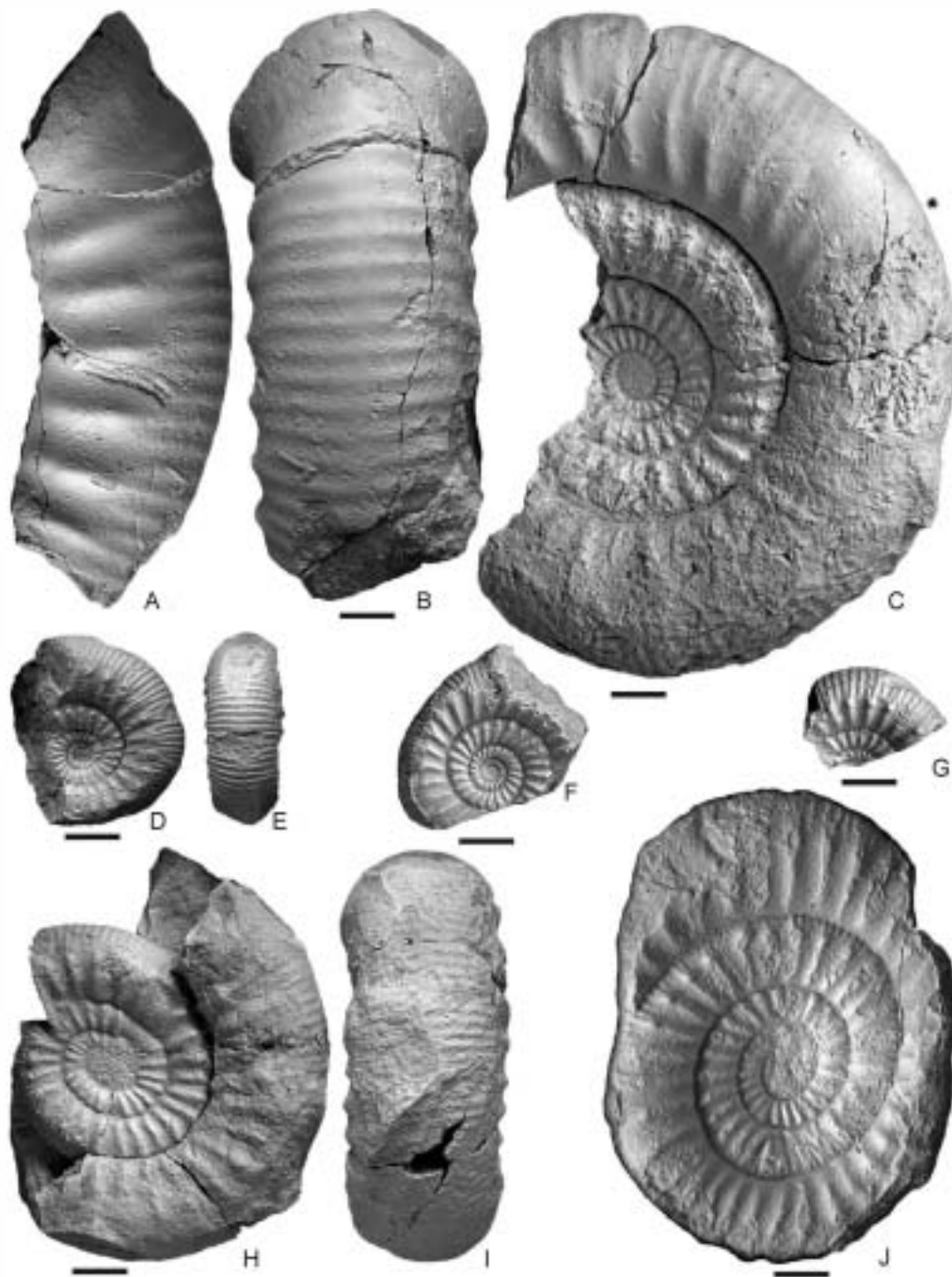


Figure 7. Macroconchs of *Albarracinites* from the Masada Toyuela section. Laeviuscula Zone. Black asterisk marks the last septum of the phragmocone. The specimens were whitened with magnesium oxide prior to photography. Scale bar equals 10 mm. A,B, *A. submediterraneus*, paratype MT2/67; C, *A. submediterraneus*, paratype MT2c/143; D,E, *A. albarraciniensis*, topotype MT2/144; F, *A. albarraciniensis*, topotype MT2/78; G, *A. albarraciniensis*, topotype MT2/80; H,I, *A. albarraciniensis*, topotype MT2/65; J, *A. albarraciniensis*, topotype MT2/77.

1988 *Albarracinites albarraciniensis* Fernandez Lopez; Gomez-Alba: 426, pl. 210, fig. 7 (holotype).

Diagnosis. Microconch (Dmax 20–30 mm) and macroconch (Dmax 150–160 mm). *Albarracinites* planorbicones of relatively small size.

Etymology. From its occurrence in the Albarracin area (Teruel, Spain).

Material. More than 28 specimens from three localities, Ovale and lowermost Laeviuscula zones: 24 specimens from Masada Toyuela (Ovale Zone: MT2a/69, 72;

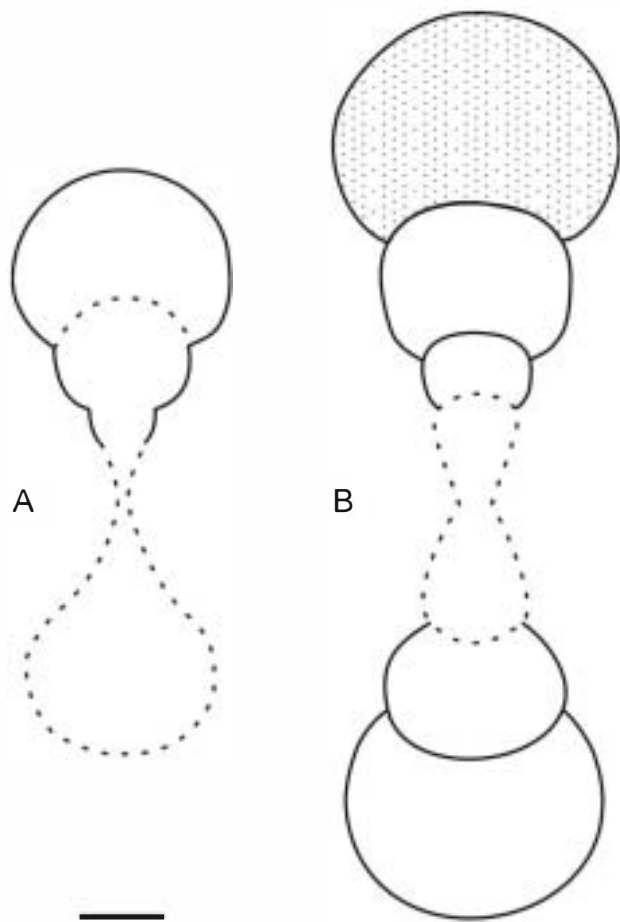


Figure 8. Whorl shape cross sections, through the phragmocone and body chamber (stippled), of *Albarracinites* from the Masada Toyuela section. Scale bar equals 10 mm. **A**, *A. albarraciniensis* [M], topotype MT2/65, Fig. 7H,I; **B**, *A. submediterraneus* [M], paratype MT2c/143, Fig. 7C.

Laeviuscula Zone: MT2/65, 68, 71, 73, 77–80, 82, 102, 104, 108, 110, 113, 115–121, 144) and four specimens from Gea de Albarracin (Ovale Zone: 2GA21/13–14; Laeviuscula Zone: 1GA39/5–6). Of these specimens from the Iberian Range, 12 microconchs and six macroconchs were measured, and 12 specimens figured.

Holotype. MT2a/69, from the Ovale Zone of Masada Toyuela, figured by Fernandez-Lopez (1985, pl. 36, fig. 1A, B; 2011, fig. 1) and Gomez-Alba (1988, pl. 210, fig. 7), is refigured here in Fig. 6A–D.

Paratypes. There are three paratypes from the Ovale Zone of Masada Toyuela (MT2a/72) and Gea de Albarracin (2GA21/13–14), and 11 paratypes from the lowermost Laeviuscula Zone of Masada Toyuela (MT2/65, 68, 71, 73, 77–80, 82) and Gea de Albarracin (1GA39/5–6). Paratype MT2a/68 figured by Fernandez-Lopez (1985, pl. 36, fig. 2A, B) is refigured here in Fig. 6N, ●. Paratype MT2/72 figured by Fernandez-Lopez (1985, pl. 36, fig. 3A,

B) is refigured here in Fig. 6E, F. Paratypes MT2/65 and MT2/80 figured by Fernandez-Lopez (1985, pl. 20, figs 13, 14) are refigured here in Fig. 7G–I.

Locus typicus. Masada Toyuela section-1, near Albarracin, Teruel, Spain.

Stratum typicum. The lowest limestone bed of the *Albarracinites* beds (2a in Fig. 2). El Pedregal Formation, Chelva Group, Lower Bajocian, Ovale Zone.

Measurements. For measurements of 15 specimens see Online Supplemental Material Table 1.

Description. Adult shells of small to medium size, from microconchs reaching 20 mm of diameter (Fig. 6H) to adult macroconchs surpassing 130 mm (Fig. 7J) and expected to surpass 150 mm (based on fragmentary material). No macroconchs are known that possess the complete body chamber. Body chamber varies from 180 to 270° in microconchs. Evolute coiling, with values of umbilical ratio ranging from 41 to 50% (Fig. 5B). Whorls vary in section from low-oval to subcircular ($W/H = 190–100\%$ in Fig. 5C), with convex flanks (Fig. 8A), decreasing the relative width in the successive ontogenetic stages ($W/D = 50–35\%$ in Fig. 5A). Ornamentation consists of straight to slightly sinuous, blunt ribs. Primary ribs are usually subradial or proverse, bifurcate or trifurcate, with additional free intercalatories that pass over the venter rectiradiately or with rursiradiate tendency. There are about 12–17 primaries per half whorl. Secondary ribs are not interrupted on the middle of the venter and became blunter, of variable strength and spacing, in the outer whorls. Small tubercles can be present at furcation points. The septal suture is relatively complex, with deeply divided, asymmetric, high and narrow lateral-saddle and retracted umbilical-lobe in the macroconchs (Fig. 9E–G), but slightly simplified in the microconchs (Fig. 9C, D). The lateral lobe is shorter than, or similar to, the external lobe and oblique. U2 shorter and more oblique than L, in inner position with respect to the lateral tubercles.

Remarks. *Albarracinites albarraciniensis* reaches larger adult size, despite the lesser density of ribbing and shorter primaries than *Mollistephanus planulatus* (Buckman, 1921 [M], pl. 264, figs 1, 2; holotype refigured by Chandler & Dietze 2004, fig. 2.3a, b) from the Bradford Abbas Fossil Bed, presumably Discites Zone of Sherborne (Dorset, England). The holotype of *M. planulatus* is the only specimen published of the species according to Chandler & Dietze (2004), and was interpreted as a *Riccardiceras* macroconch by Westermann (1995) despite its small diameter (72 mm).

Mollistephanus mollis Buckman (1922 [M], pl. 344, holotype refigured by Chandler & Dietze 2004, fig. 4.1a, b and by Rulleau 2011, pl. 48, fig. 2a, b) presumably from the Sanford Lane Fossil Bed near Sherborne (Dorset,

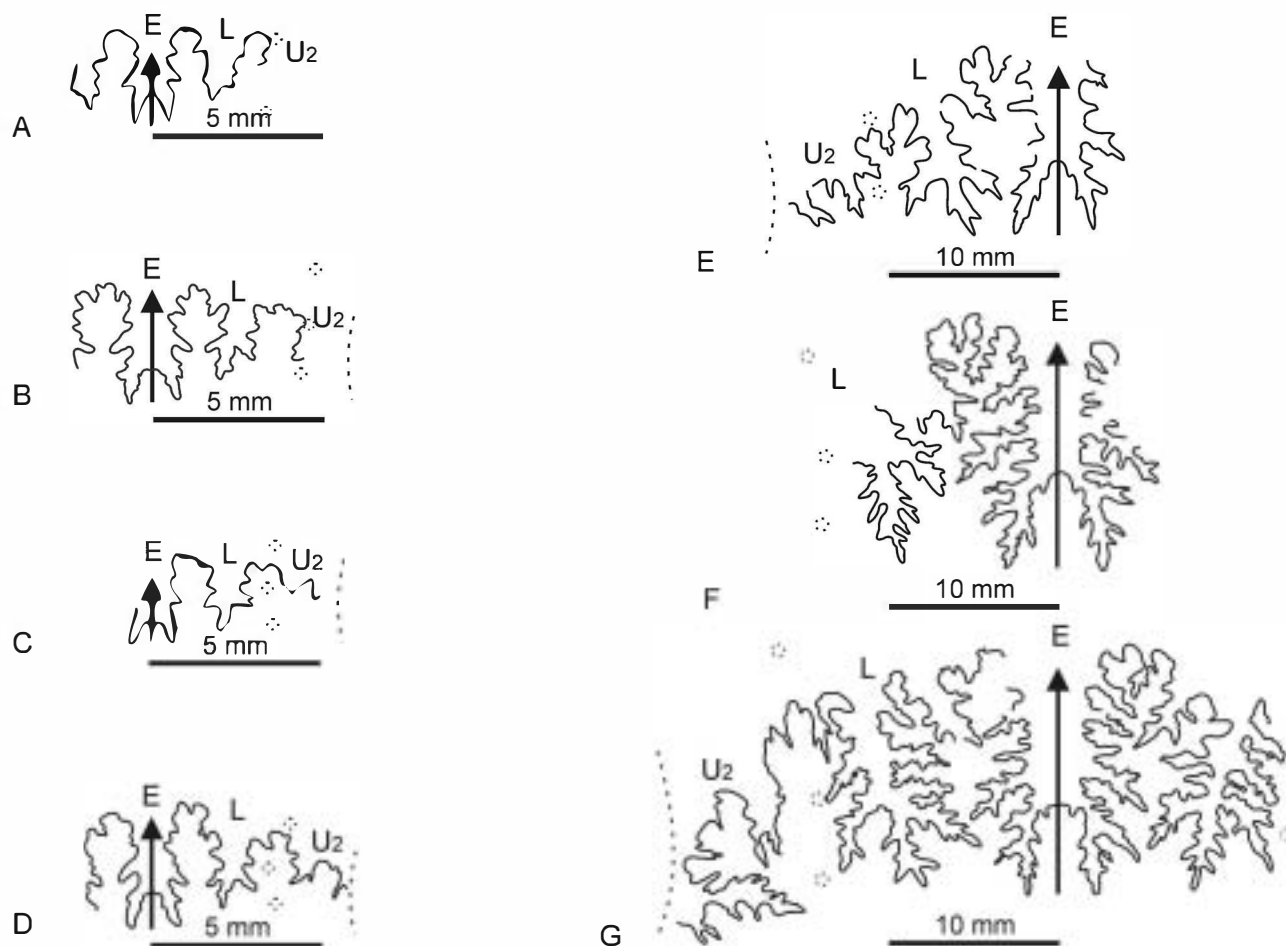


Figure 9. Suture lines of *Albarracinities* [m and M] from the Masada Toyuela section. ●vale and Laeviuscula zones. **A**, *A. submediterraneus* [m], paratype MT2c/101, Fig. 10G–J; **B**, *A. submediterraneus* [m], paratype MT2c/103, Fig. 10D–F; **C**, *A. albarraciniensis* [m], holotype MT2a/69, Fig. 6A–D; **D**, *A. albarraciniensis* [m], topotype MT2/102; **E**, *A. albarraciniensis* [M], topotype MT2/80, Fig. 7G; **F**, *A. albarraciniensis* [M], topotype MT2/65, Fig. 7H,I; **G**, *A. albarraciniensis* [M], topotype MT2/144, Fig. 7D,E. Abbreviations: E, external lobe; L, lateral lobe; U2, second umbilical lobe.

England) Trigonalis Subzone, *Mollistephanus hispanien-sis* Fernandez-Lopez (1985, p. 248, pl. 20, figs 7–9; holotype from the ●valis Biohorizon, Laeviuscula Biozone, currently ●vale Zone, of La ●lmeda section (Cuenca, Spain) and *Mollistephanus cockroodensis* Chandler & Dietze (2004 [M], p. 223, fig. 3.1a, b, 3.2a, b, holotype from the ●vale Zone and paratype from the upper Discites Zone of Cockrood Farm near Beaminster, Dorset, England) differ from *A. albarraciniensis* by smaller adult size, more serpenticonic coiling and more compressed section on the outer whorls. These morphological differences also apply to the microconchs of such taxonomic groups. The very small, serpenticonic microconchs, figured as *Albarracinities albarraciniensis* Fernandez-Lopez, 1985 [m] by Chandler & Dietze (2004, figs 4.4a–c, 4.5a–c, 5.4a–c) and refigured by Rulleau (2011, pl. 48, fig. 3a, b), showing secondary ribs of more homogeneous strength and spacing in the outer whorls, are interpreted here as micro-

conchs of *Mollistephanus mollis* Buckman (cf. Fig. 11 A–F).

Dietze *et al.* (2010, fig. 3a–c) determined *Mollistephanus* aff. *kondai* Galacz a specimen from Lauterstein-Nenningen (Christental, eastern Swabian Alb, SW Germany, Wedel-sandstein Formation, Sandmergel bed, Lower Bajocian, Laeviuscula Zone, Trigonalis Subzone, stephani Horizon) as close to *Albarracinities albarraciniensis* [M] in coiling and ornamentation, but smaller in size and without a visible suture line.

Riccardiceras westermanni Sandoval *et al.*, 2000 [M] (p. 38, pl. 4, figs 4–7; holotype from the Discites Zone of Barranco de Agua Larga, Jaen), considered as a member of *Mollistephanus* by Chandler & Dietze (2004, p. 223), displays more serpenticonic coiling, denser ribbing and shorter primaries than *A. albarraciniensis*. The maximum diameter of the syntypes is approximately 60 mm and this earliest Bajocian species shows smaller adult size than

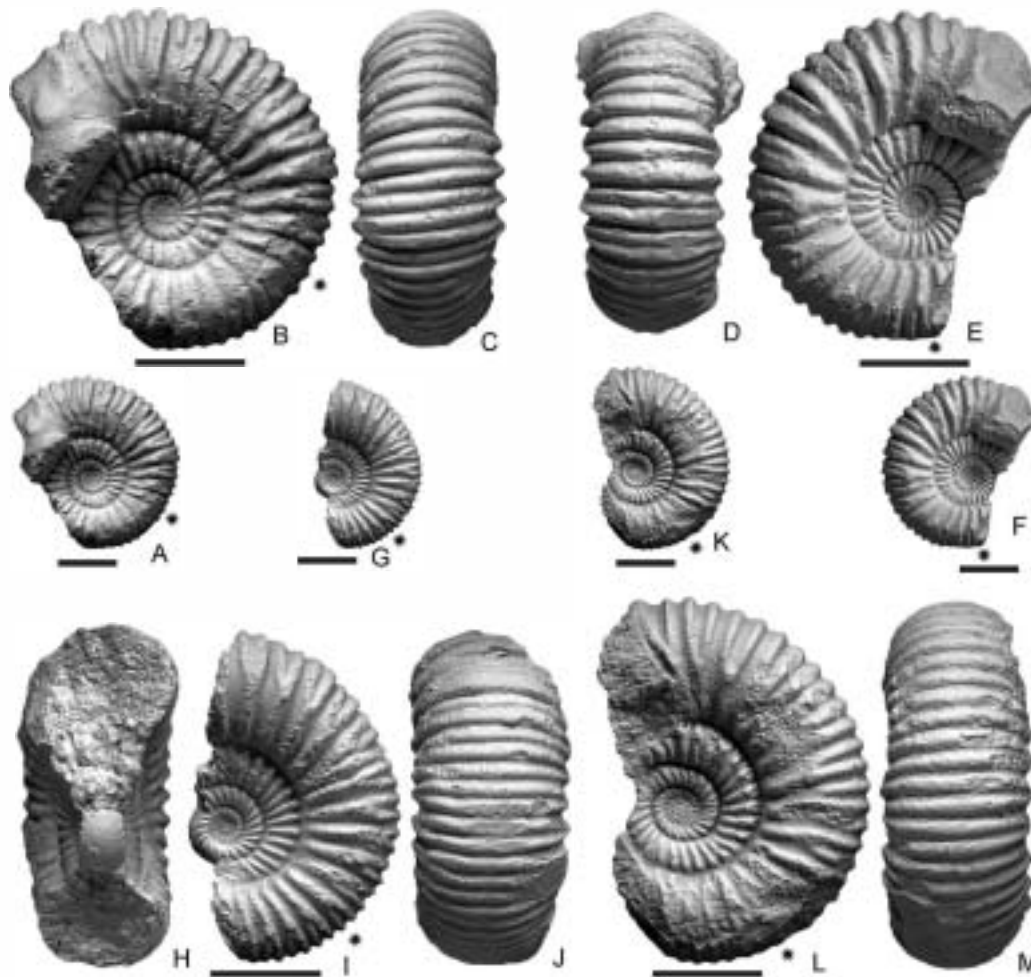


Figure 10. Microconchs of *Albarracinites submediterraneus* sp. nov. from the Masada Toyuela section, upper Laeviuscula Zone. Black asterisk marks the last septum of the phragmocone. The specimens were whitened with magnesium oxide prior to photography. Scale bar equals 10 mm. A–C, holotype MT2c/114; D–F, paratype MT2c/103; G–J, paratype MT2c/101; K–M, paratype MT2/74.

other known species of *Riccardiceras*, *Mollistephanus* or *Albarracinites*. However, none of the syntypes preserve septal suture.

Dicidoceras lupheri Imlay, 1973 [M] (p. 78, pl. 38, figs 14, 15, 17; holotype from the middle of the range of *Sonninia* (*Euhoplaceras*), Weberg Member, Snowshoe Formation, of eastern Oregon, USA), considered as possibly a congeneric form of *Mollistephanus mollis* by Sandoval *et al.* (2000), is characterized by short primaries with radially elongate tubercles at the base of the flanks, a feature present in *Dicidoceras* and *Riccardiceras*, but not developed in *Albarracinites* or *Mollistephanus*.

Distribution. *A. albarraciniensis* occurs in the Ovale and lower Laeviuscula zones of the Castilian Platform. It is probably also recorded in the Lusitanian Basin (Fernandez-Lopez *et al.* 1989).

Albarracinites submediterraneus sp. nov. [m and M]
(7A–C, 8B, 9A, B, 10A–M)

Diagnosis. Microconch ($D_{max} = 25\text{--}35$ mm) and macroconch ($D_{max} \sim 170$ mm). *Albarracinites* planorbicones, rather cadicones, of medium size.

Etymology. After the Submediterranean Province, the biochorema inhabited by this species and that has yielded the syntypes of the taxon.

Material. More than 13 specimens from two localities, Laeviuscula Zone: 12 specimens from Masada Toyuela (MT2/70, 74, 101, 103, 105–107, 109, 111, 112, 114, 143) and 1 specimen from Villel (VE1t/2). Of these specimens from the Iberian Range, 12 microconchs and 1 macroconch were measured and 5 specimens figured.

Holotype. Specimen MT2c/114, from the Laeviuscula Zone of Masada Toyuela (Fig. 10A–C).

Paratypes. There are 12 paratypes from the Laeviuscula Zone. Two paratypes from Masada Toyuela (MT2d/107, 109) correspond to the uppermost Laeviuscula Zone. The

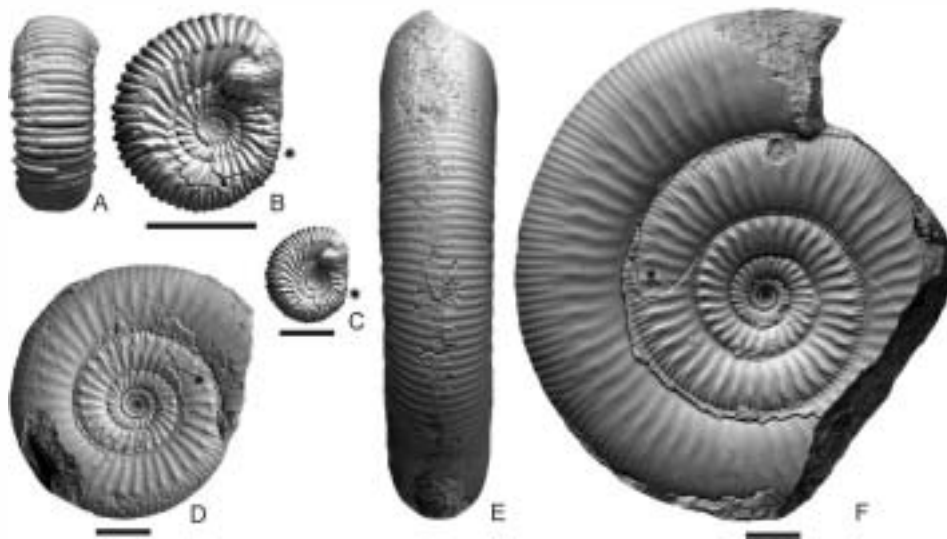


Figure 11. *Mollistephanus mollis* Buckman [m and M] from Sherborne, Dorset (England), Inferior **●**olite, Lower Bajocian, Trigonalis Subzone, Laeviuscula Zone. Black asterisk marks the last septum of the phragmocone. The specimens were whitened with magnesium oxide prior to photography. Scale bar equals 10 mm. A–C, microconch 09Rh3b/1, Blue Bed, Faunal horizon Bj-8a, Redhole Lane (W Field) after Huxtable (1999, 2003); D, macroconch 09SL6c/2, Blue Bed, Faunal horizon Bj-8a after Chandler *et al.* (2006), Sandford Lane Fossil Bed; E, F, macroconch 09SL6c/1, bed 6c (lower part), Blue Bed, Faunal horizon Bj-8a after Chandler *et al.* (2006), Sandford Lane Fossil Bed.

paratype from Villet (VE1t/2) is the microconch of largest adult-size, reaching 35 mm in diameter.

Locus typicus. Masada Toyuela section-1, near Albarracin, Teruel, Spain.

Stratum typicum. The penultimate limestone bed of the *Albarracinites* beds (2c in Fig. 2). El Pedregal Formation, Chelva Group, Lower Bajocian, Laeviuscula Zone (upper part).

Measurements. For measurements of eight specimens see **●**online Supplemental Material Table 2.

Description. Adult shells small to medium in size, from microconchs surpassing 30 mm diameter (Fig. 10F) to adult macroconchs reaching 170 mm (Fig. 7A–C). No macroconchs are known possessing the complete body chamber, but the umbilical suture surpasses 360° in the allotype (Fig. 7C) which displays egression indicative of adult development. Body chamber varies from 170 to 225° in the microconchs (Fig. 10A–M). Evolute coiling, with values of umbilical ratio ranging from 35 to 52% (Fig. 5B). Whorls vary in section from low-oval to subcircular (W/H = 190–100% in Fig. 5C), with convex flanks (Fig. 8B), decreasing the relative width in successive stages of the ontogenetic development (W/D = 50–35% in Fig. 5A). **●**Ornamentation consists of relatively coarse, straight to slightly sinuous, rounded and blunt ribs. Primary ribs are usually subradial or proverse, bifurcate or trifurcate, with additional free intercalatories that pass over the

venter rectiradiately or with rursiradiate tendency. There are about 13–21 primaries per half whorl. Secondary ribs are not interrupted on the middle of the venter and became blunter, of variable strength and spacing, in the outer whorls. Small tubercles can be present at furcation points. The septal suture is relatively complex, with deeply divided, asymmetrical, high and narrow lateral saddle and retracted umbilical lobe in the macroconchs (Fig. 7C), but slightly simplified in the microconchs (Fig. 9A, B). The lateral lobe is shorter than, or similar to, the external lobe and oblique. U2 is shorter and more oblique than L, and has an inner position in respect to, or coincident with, the lateral tubercles.

Remarks. *Albarracinites albarraciniensis*, the type species of the genus, is the most similar Bajocian representative. However, *A. submediterraneus* sp. nov. has a larger adult size, stouter whorls and more involute coiling. This new species also differs from *Mollistephanus planulatus* (Buckman) and *Riccardiceras westermanni* (Sandoval *et al.*, 2000) in its larger size, less serpenticonic coiling and rarer ribbing.

Distribution. *Albarracinites submediterraneus* has been identified in the Laeviuscula Zone from different localities of the Albarracin area and the Villet section (Central External Castilian Platform). It seems to be an endemic or characteristic species of the Submediterranean Province, very scarce and miodemidic in the open marine, carbonate environments of the Castilian Platform, eastern Iberian platform

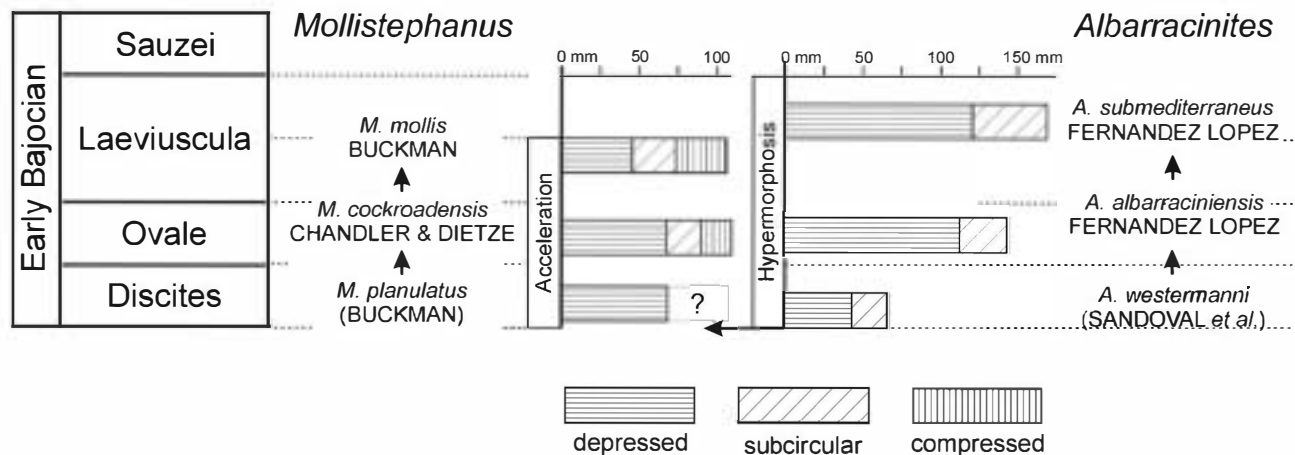


Figure 12. Schematic diagram of heterochrony by peramorphosis in early Bajocian *Mollistephanus* and *Albarracinites*. The successive states of ontogenetic development are represented by bands of diverse shading versus size of shell. Evolutionary change by acceleration in *Mollistephanus*, from *M. planulatus* to *M. mollis*, produced more compressed adult shells of similar size. In contrast, evolutionary change by hypermorphosis in *Albarracinites*, from *A. westermanni* to *A. submediterraneus*, produced larger adult shells of similar shape.

system, and phyletically derived from *A. albarraciniensis* in the earliest Laeviuscula Zone.

Discussion and conclusions

Early Bajocian stephanoceratids of the genera *Mollistephanus* and *Albarracinites*, characterized by small planorbicones and respectively typified by macroconchs and microconchs, have a close phyletic relationship (Fernandez-Lopez 1985; Chandler & Dietze 2004). However, ontogenetic development and variation of shell ornament in the forms from the Masada Toyuela area corroborate that these two taxonomic groups do not represent intraspecific dimorphs. A chronocline or gradational series of morphological changes, from depressed, small and slender planorbicones to greater planorbicones with more cadiconic phragmocones and body chambers of subcircular cross section, can be recognized within the genus *Albarracinites* in the Lower Bajocian of the Iberian Range. Two chronologically successive species of *Albarracinites* from the Ovale to the Laeviuscula zones have been identified: the type species *A. albarraciniensis* [m and M] and *A. submediterraneus* sp. nov. [m and M]. The macroconch counterpart of this genus is a group of stephanoceratids previously attributed to *Mollistephanus*, *Riccardiceras* and other new forms described in the present paper.

Albarracinites and *Mollistephanus* developed two opposite peramorphoclines or gradational series of morphological changes undergoing greater development and ontogenetic variation by hypermorphosis (sexual maturation delay) and acceleration (morphological development acceleration), respectively, during the Discites, Ovale and Laeviuscula zones (Fig. 12; cf. Gould 1977, 2002; Dommergues

et al. 1986, 1989; Dommergues 1990; Davis et al. 1996; McNamara 2001; Guex et al. 2003; Guex 2006). The evolution of known species of *Albarracinites* represents a hypermorphic peramorphocline from *A. albarraciniensis* Fernandez-Lopez to *A. submediterraneus* sp. nov., producing larger adults of similar shape and ontogenetic variation of shell ornament. In contrast, *Mollistephanus planulatus* (Buckman), *M. cockroadenensis* Chandler & Dietze and *M. mollis* Buckman represent a peramorphocline by acceleration, producing adults of similar size but more compressed and with increasing ontogenetic variation of shell ornament. *Albarracinites* and *Mollistephanus* also show different patterns of palaeobiogeographical distribution, in accordance with their respective life-history strategies. *Albarracinites* is mainly recorded in Mediterranean and Submediterranean areas (Iberian Range, Lusitanian and Betic basins), whereas *Mollistephanus* is relatively common in NW European (Parsons 1974, 1979; Fernandez-Lopez & Mouterde 1994; Rioult et al. 1997; Dietze et al. 2001; Chandler & Dietze 2004; Chandler et al. 2006; Dietze & Chandler 2008), Submediterranean (Fernandez-Lopez 1985; Fernandez-Lopez et al. 1988a, 1989, 1996; De Baets et al. 2008; Dietze et al. 2001, 2010; Rulleau 2011) and Mediterranean (Sandoval 1983; Galacz 1986, 1988; Sadki 1994, 1996; Sandoval et al. 2000, 2001; Cresta et al. 2002; O'Dogherty et al. 2006; Marek 2007) provinces of the western Tethys through the Discites, Ovale, Laeviuscula and Sauzei zones. The development of endemic species of the Submediterranean Province within the *Albarracinites* lineage, associated with the immigration and colonization of the eastern Iberian platform system, occurred at least during the Laeviuscula Zone (prior to the regional disappearance of such endemic ammonite taxa at the Laeviuscula/Sauzei transition).

Adult, primitive *Albarracinites* resemble juvenile, derived *Riccardiceras*. In this evolutionary setting, *Riccardiceras westermanni* Sandoval *et al.*, 2001 seems to be the earliest species of the genus *Albarracinites*. During the Aalenian/Bajocian transition, the otoitid *Riccardiceras* evolved into the stephanoceratid *Albarracinites* by proterogenesis (i.e. the appearance in the early stages of an organism's life of features characteristic of adult forms of its evolutionary descendants), decreasing the size of the adults and changing the monaxial ('planulate') into the biaxial ('bullate') septum (cf. Westermann 1956, 1958, 1964b, 1967, 1995; Fernandez-Lopez 1985; Dietze *et al.* 2001; Chandler & Dietze 2004). In turn, *Mollistephanus* probably derived from an early species of *Albarracinites* at the Aalenian/Bajocian transition. Later, both new lineages underwent lasting palaeogenetic changes with diverse peramorphic results by opposite mechanisms (hypermorphosis versus acceleration). Therefore, *Albarracinites* seems to be the earliest stephanoceratid lineage in western Tethys, branching off from the otoitid *Riccardiceras* at the Aalenian/Bajocian transition by proterogenetic change and resulting paedomorphosis.

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Supplemental material

Supplemental material is available online <http://dx.doi.org/10.1080/14772019.2013.818071>

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Appendix

Abbreviations and measurements of the specimens of *Albarracinites* from the Iberian Range. Stratigraphic information is indicated by locality number, section letter and stratigraphic level: sections MT (Masada Toyuela), 1GA and 2GA (sections 1 and 2 of Gea de Albarracin) and VE (Vilhel); stratigraphic levels; /n = number of specimen. [M] and [m] indicate macroconch and microconch. Measurements are given in mm and include maximum shell diameter at which the following measurements were made (D), whorl-height (H), whorl-height/diameter ratio (H/D), whorl-width (W), whorl-width/diameter ratio (W/D), umbilical diameter (U), umbilicus/diameter ratio (U/D), whorl-width/whorl-height ratio (W/H) and external ribs per half whorl (Ne/2).

Table 1. Measurements for the specimens of *Albarracinites albarraciniensis* Fernandez-Lopez, 1985 [m & M].

Specimens	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	f
MT2/65	Figs. 7H-I	[M]	72.0	23.3	32.4%	26.0	36.1%	33.0	45.8%	1.12	17	59	3.5
MT2/144	Figs. 7D-E	[M]	35.0	11.8	33.7%	12.8	36.6%	15.3	43.7%	1.08	12	—	—
2GA21/14		[m]	27.0	8.9	33.0%	10.4	38.5%	12.8	47.4%	1.17	13	25	1.9
MT2/115	Figs. 6L-M	[m]	27.0	8.7	32.2%	10.7	39.6%	11.7	43.3%	1.23	—	—	—
			19.0	6.1	32.1%	9.1	47.9%	8.0	42.1%	1.49	15	—	—
MT2/117	Figs. 6P-Q	[m]	27.0	7.6	28.1%	10.2	37.8%	11.3	41.9%	1.34	12	—	—
MT2/108		[m]	26.0	7.8	30.0%	10.3	39.6%	10.9	41.9%	1.32	13	—	—
MT2/110		[m]	25.0	9.1	36.4%	10.3	41.2%	10.1	40.4%	1.13	—	—	—
MT2/121		[m]	24.0	8.3	34.6%	9.3	38.8%	9.7	40.4%	1.12	13	26	2.0
MT2/102		[m]	24.0	7.8	32.5%	9.5	39.6%	10.9	45.4%	1.22	—	—	—
MT2/118		[m]	24.0	7.5	31.3%	9.4	39.2%	10.7	44.6%	1.25	—	—	—
MT2/68	Figs. 6N-O paratype	[m]	24.0	7.2	30.0%	10.9	45.4%	10.1	42.1%	1.51	15	30	2.0
MT2/116	Figs. 6G-H	[m]	22.0	7.5	34.1%	9.1	41.4%	9.8	44.5%	1.21	12	24	2.0
MT2/120	Figs. 6I-K	[m]	23.0	8.0	34.8%	9.5	41.3%	10.9	47.4%	1.19	—	—	—
MT2/71		[m]	22.0	6.1	27.7%	9.2	41.8%	9.5	43.2%	1.51	16	30	1.9
MT2/69	Figs. 6A-D holotype	[m]	21.0	6.4	30.5%	9.3	44.3%	9.0	42.9%	1.45	13	24	1.8

Table 2. Measurements for the specimens of *Albarracinites submediterraneus* sp. nov. [m & M].

Specimens	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	f
MT2/143	Fig. 7C paratype	[M]	120.0	30.5	25.4%	37.0	30.8%	61.4	51.2%	1.21	21	—	—
			75.0	22.0	29.3%	29.0	38.7%	32.0	42.7%	1.32	16	—	—
VE1t/2		[m]	34.0	12.0	35.3%	13.1	38.5%	12.1	35.6%	1.09	13	—	—
MT2/114	Figs. 10A-C holotype	[m]	30.0	10.4	34.7%	11.5	38.3%	12.7	42.3%	1.11	15	27	1.8
			23.0	8.7	37.8%	10.4	45.2%	9.4	40.9%	1.20	—	—	—
MT2/74	Figs. 10K-M paratype	[m]	30.0	9.3	31.0%	11.1	37.0%	13.1	43.7%	1.19	13	26	2.0
			22.0	8.2	37.3%	10.9	49.5%	—	—	1.33	—	—	—
MT2/101	Figs. 10G-J paratype	[m]	28.0	9.4	33.6%	12.1	43.2%	12.1	43.2%	1.29	17	34	2.0
MT2/105		[m]	28.0	8.4	30.0%	11.8	42.1%	11.3	40.4%	1.40	15	—	—
MT2/103	Figs. 10D-F paratype	[m]	27.0	9.1	33.7%	10.7	39.6%	11.4	42.2%	1.18	13	24	1.8
			20.0	7.1	35.5%	9.8	49.0%	9.5	47.5%	1.38	—	—	—
MT2/70		[m]	27.0	8.5	31.5%	11.6	43.0%	11.9	44.1%	1.36	13	26	2.0