Journal of Iberian Geology
https://doi.org/10.1007/s41513-024-00253-x

RESEARCH PAPER

Latiwitchellia (Grammoceratinae?, Ammonitina, Middle Jurassic); an eastern Pacific ammonite in the Betic Cordillera (Southern Spain)

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Received: 12 March 2024 / Accepted: 18 July 2024

Abstract
Ammonites belonging to the genus *Latiwitchellia* Imlay are described and figured for the first time outside the palaeogeographic domain of the Eastern Pacific. The Subbetic ammonites that are classified here as *Latiwitchellia evoluta* Imlay fit quite well with the North American forms (from Snowshoe Formation, Oregon) despite being slightly less evolute and having more regular ribbing. The range of stratigraphic distribution is similar, although the oldest Subbetic forms (lower part of the Discites Zone) are somewhat earlier than the North American ones (uppermost Discites Zone). The presence of the same species in the Betic Cordillera (westernmost Tethys) and in eastern Oregon (Eastern Pacific) confirms that during the early Bajocian the two palaeogeographic domains were connected via the Hispanic Corridor. *Latiwitchellia* possibly originated in the westernmost Tethys before expanding to the Eastern Pacific.

Keywords Jurassic · Bajocian · Ammonite · Betic Cordillera · Biostratigraphy · Oregon · Hispanic corridor

Resumen
Se describen y figuran por primera vez ammonites pertenecientes al género *Latiwitchellia* Imlay fuera del dominio paleogeográfico del Pacífico Oriental. Las ammonites subbéticos que se clasifican como *Latiwitchellia evoluta* Imlay encajan bastante bien con las formas norteamericanas (de la Formación Snowshoe, Oregón), aunque son un poco menos evolutos y tienen la ornamentación más regular. El rango de distribución estratigráfica es similar, aunque las formas subbéticas más antiguas (parte inferior de la Zona de Discites) son algo más antiguas que las norteamericanas (parte superior de la Zona de Discites). La presencia de la misma especie en la Cordillera Bética (extremo occidental del Tetis) y en el este de Oregón (Pacífico Oriental) confirma que durante el Bajociense temprano los dos dominios paleogeográficos estaban conectados a través del Corredor Hispánico. *Latiwitchellia* posiblemente se originó en el Tetis occidental antes de expandirse al Pacífico oriental.

Palabras clave Jurásico · Bajociense · Cordillera Bética · Bioestratigrafía · Oregón · Corredor hispánico

1 Introduction

The genus *Latiwitchellia* was established and described by Imlay (1973, p. 70) to include about 52 ammonite specimens of the Lower Bajocian from the upper part of the Weberg Member, in the Snowshoe Formation, Eastern Oregon (USA). Subsequently, only a small number of citations are known for this genus (Donovan et al., 1981, p. 143; Fernández-López, 1985, p. 68; Taylor, 1988, p. 24, 2016, p. 459; Smith & Taylor, 1992, p. 72; Westermann, 1992, p. 257; Sandoval et al., 2012; Sandoval, 2022) that refer to the North American specimens originally described by Imlay (1973), but no citations of new species are known, except an Andean form ("*L*". *atacamensis* Dietze and Hillebrandt, 2019, p. 44), which, only with certain doubts, should be included in this genus. Imlay (1980, p. 22) refers to *Latiwitchellia gracilis*, but without indicating the author of the species or any description or illustration of it.

The detailed sampling carried out since the 1970s in the Lower Bajocian of various stratigraphic sections of the Median Subbetic in the central sector of the Betic Cordillera have provided a large quantity of ammonoids, many

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Published online: 14 August 2024

of which have been taxonomically analysed, enabling fine biostratigraphic results for this stratigraphic interval (Sandoval, 1983, 1990, 2022 and references therein). Only a few of these ammonites (eight in total) have been attributed to the genus *Latiwitchellia* Imlay.

2 Geographical and geological setting

The geographical origin of the *Latiwitchellia* specimens analysed here (Fig. 1) formed part of the southern margin of the Iberian Plate, which, during the Bajocian (Middle Jurassic) was located near the eastern end of the Hispanic Corridor (Fig. 1b). This corridor was a relatively narrow sea channel that during certain time intervals (i.e. Early Bajocian–earliest Late Bajocian and Late Bathonian–Early Callovian) connected the Western Tethys with the Eastern Pacific (Sandoval, 2022 and references therein). This area was located at a palaeolatitude of about 26°N (Fig. 1c) within the southern Iberian continental margin by the Early Bajocian (~170 Ma). These sites are currently located in southern Spain (Fig. 1a), being part of the External Zones of the Betic Cordillera.

3 Material and methods

As mentioned above, the specimens of the genus *Latiwitchellia* studied here come from selected stratigraphic sections of the Subbetic domain (Betic Cordillera, southern Spain). Whenever possible, these sections were numbered, measured, and sampled in detail, bed by bed. Localities and stratigraphic sections were abbreviated to a letter-number code following the customary rules of the Department of Stratigraphy and Palaeontology (University of Granada, Spain). Among the numerous stratigraphic sections sampled, the only sites where *Latiwitchellia* were collected are (Fig. 1a): Sierra de Alta Coloma area and Barranco de Agua Larga, Campillo de Arenas and Noalejo (Jaén Province); Rio Fardes, Gorafe (Granada Province).

After being prepared and cleaned in the laboratory, the ammonites were coated with magnesium oxide and then photographed.

The present work follows the standard ammonite zonation for the Mediterranean Province (Rioult et al., 1997), but raising the Ovale Subzone to zonal rank. The Propinquans Zone is equivalent to the Sauzei Zone used by German and some British researchers.

3.1 Abbreviations

3.1.1 Measurements

The most significant specimens were measured, for which the following abbreviations are used: D, diameter of the shell (mm); U, umbilical diameter of the shell (mm); H, whorl-section height of the shell (mm); W, whorl-section width of the shell (mm); h = H/D; u = U/D; w = W/D. Some of these parameters are approximate, because some of the specimens were laterally flattened (crushed) by compression.

3.1.2 Other abbreviations

PH, phragmocone; BC, body chamber; E external lobe; L, lateral lobe; U_2-U_5, umbilical lobes; HT, holotype; OD, original designation; [M], macroconchs; [m], microconchs.

3.1.3 Housing institution

The specimens studied are on deposit in the "Departamento de Estratigrafía y Paleontología", University of Granada, Spain (UGR). Only representative specimens are figured.

4 Systematic palaeontology

Order AMMONITIDA Fischer, 1882
Suborder AMMONITINA Fischer, 1882
Superfamily HILDOCERATACEOIDEA Hyatt, 1867
Family HILDOCERATIDAE Hyatt, 1867
Subfamily GRAMMOCERATINAE Buckman, 1905

4.1 Genus LATIWITCHELLIA Imlay, 1973

Type species by OD. *Witchellia* (*Latiwitchellia*) *evoluta* Imlay, 1973, p. 70, pl. 32, Figs. 1, 2, 5, 6; HT.

4.1.1 Description (emended after Imlay, 1973)

Shells evolute with slow growth of the whorl, ovate or subquadrate-compressed to moderately compressed whorl-section, flat or slightly convex flanks, venter gently rounded to almost flat with a rather high keel limited by smooth flat bands or bordered by shallow furrows. Rectiradiate to rursiradiate ribs, mainly simple, some bifurcate on the middle third of the flanks, and rarely arise freely on the flanks; ribs bend sharply forward high on the flanks, vary considerably in strength from one specimen to another, and can vary during ontogeny; small nodes can develop on the upper part of flanks at the points where ribs bend forward, these occurring mostly on the intermediate and outer whorls of

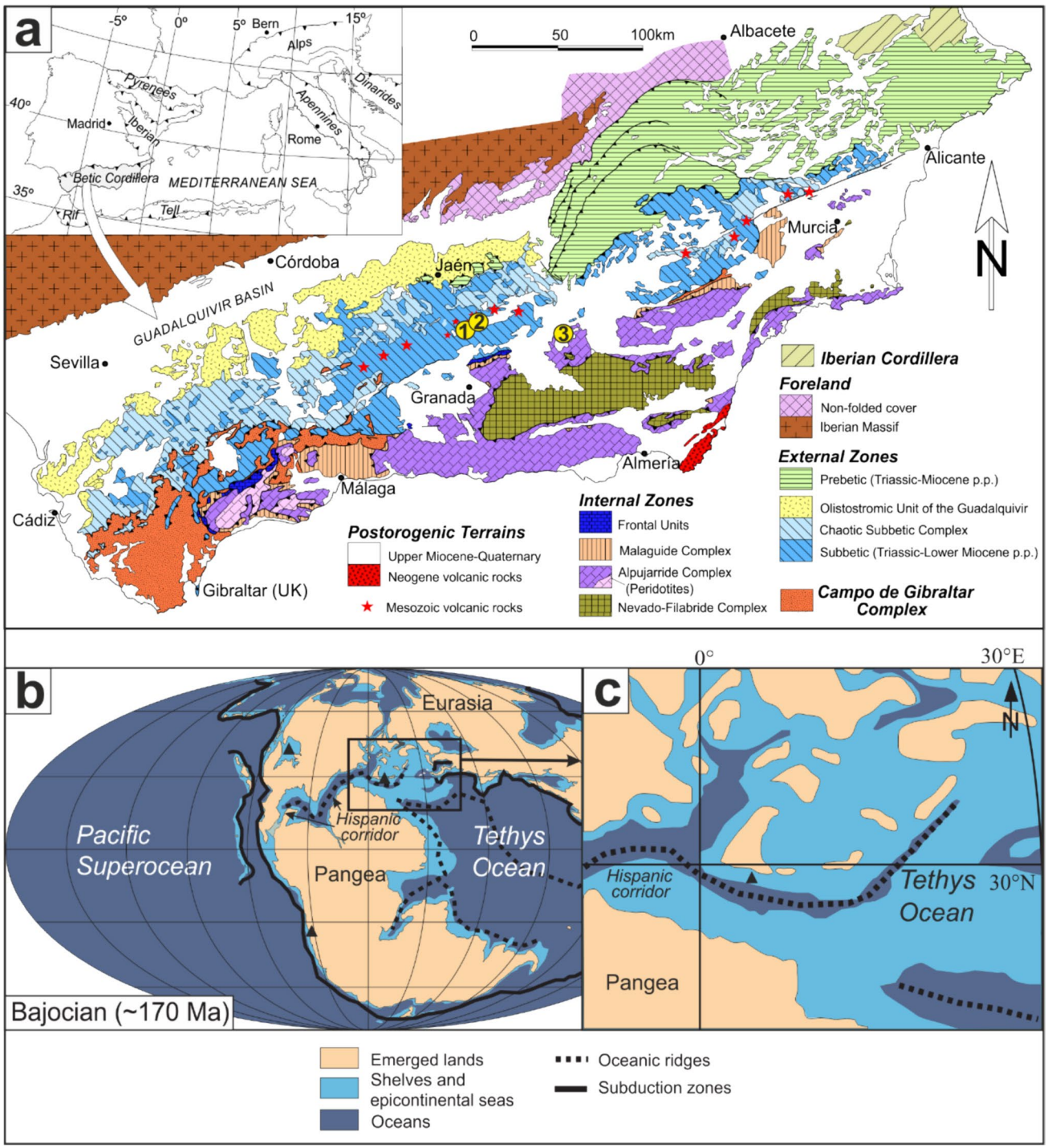

Fig. 1 **a** General sketch of the Betic Cordillera with approximate location of the areas with the sections containing *Latiwitchellia*: *1* Sierra de Alta Coloma (JAC3 and JAC11 sections); *2* Barranco de Agua Larga (JAQ1 and JAQ2 sections), Jaén Province; *3* Rio Fardes (JFB2 section), Granada Province. **b** Palaeogeographic map (Mollweide projection) showing the distribution of oceans and lands in the Early Bajocian (*c.* 170 Ma); *stars* indicate the approximate areas where *Latiwitchellia* has been recorded. **c**, Focus on the Western Tethys-Central Atlantic showing the approximate location of the Subbetic basin (*rectangle*) in relation to the trans-Pangaean seaway; the *black triangles* indicate the approximate position of the palaeodomains where *Latiwitchellia* has been recorded. Modified after Sandoval (2022).

coarsely ribbed specimens. The aperture is marked by a deep constriction that is followed by a swelling. The septal suture is very simple with little ramification: the E-L saddle is extremely broad and irregularly rounded; the lateral lobe (L) is not deep, trifid, moderate in width, about the same depth as the E (external lobe), and considerably deeper than the umbilical (U_2); the suspensive lobe rises slightly to the umbilical seam. Although forms of different sizes appear among the specimens figured by Imlay (1973, pls 31–33), the existence of dimorphism is not shown. All of these specimens are apparently macroconchs. However, some of the specimens included in *Pelekodites* by Imlay (1973, p. 74, pl. 34, Figs. 1–18) could represent the dimorphous partner [m] of *Latiwitchellia* [M].

4.1.2 Remarks

According to Imlay (1973, p. 70), who considered *Latiwitchellia* to be a subgenus of *Witchellia*, and consequently included it in the family Sonniniidae Buckman, 1892, this differs from W*itchellia* Buckman (1889) in having more evolute coiling, a relatively broader whorl section that does not become higher or compressed on the BC, less common ribs furcation near the base of the flanks, only slight weakening of its ribs adorally on the BC, and blunt nodes high on the flanks on some coarsely ribbed variants.

Donovan et al., (1981, p. 143) considered *Latiwitchellia* to be synonymous with *Fontannesia* and included it in the Family Sonniniidae.

Fernández-López (1985, p. 68) highlighted the significant differences between *Witchellia* and *Latiwitchellia* (coiling, whorl-section, ventral region, ribbing) and concluded that these morphological differences, in addition to their biostratigraphic distribution, bring *Latiwitchellia* closer to the forms of the genus *Fontannesia* than to *Witchellia*.

Fontannesia Buckman, 1902, p. 6 (type species, *Dumortieria grammoceroides* Haug, 1887, p. 137, pl. 5, Fig. 5; OD), is quite similar to *Latiwitchellia*, but it is more involute with greater whorl spiral expansion, has an ovate rather than subrectangular whorl-section and, the ribs, generally more uniform and persistent throughout ontogeny, are rarely bifurcate or twinned at the umbilical edge. Since the establishment of this taxon by Buckman, many authors, including Howarth (2013 in the new Treatise, p.119, who indicated that it is a Bajocian homeomorph of *Grammoceras*), have included *Fontannesia* in the family Sonniniidae. However, others, such as Westermann and Getty (1970, p., 240), Westermann & Wang (1988, p. 314), Linares and Sandoval (1988), and Sandoval et al. (2012) and Sandoval (2022), showed that *Fontannesia* should be included in the Grammoceratinae Buckman, 1905, with which it shares more common characters. The specimens described and figured by Imlay (1973, pp. 58–59; pl. 5, Figs. 1–19) as *Fontannesia* cf. *F. luculenta* (Buckman), *F.* cf. *F. carinata* (Buckman) and *F.* cf. *F. evoluta* (Buckman) show considerable resemblance to the various morphotypes of the type species of *Latiwitchellia* and should possibly be included in this genus.

Linaresites Sandoval, 2012 (in Sandoval et al., 2012, p. 115; type species, *Fontannesia montillanensis* Linares & Sandoval, 1988, p. 8, pl. 1, Figs. 12, 13 (OD)) is perhaps the genus most closely related to *Latiwitchellia*. The two genera share a markedly evolute coiling, the same type of whorl-section, keel, and similar shape as well as thickness of ribbing and very simple sutures, but *Linaresites* is much smaller and appears earlier in the stratigraphic record.

Dietze & Hillebrandt (2019, p. 40) regarded (as Imlay, 1973) *Latiwitchellia* as being closely related to the genus *Witchellia,* including this evolute member in the subfamily Witchelliinae Callomon & Chandler, 2006 in Chandler et al., (2006, p. 370). They separated *Latiwitchellia* from the evolutionary line *Vacekia- Asthenoceras–Linaresites*, as Sandoval et al., (2012, p. 117, Fig. 3) had proposed, because of the much smaller size and the thin and notably high keel of these Grammoceratinae. However, as can be seen in some of the specimens described and figured by Imlay (1973, pls 32 and 33), these also have a quite thin and high keel, while the various specimens of *Linaresites* (see Sandoval et al., 2012, Figs. 2L–O), a genus with clear phylogenetic relationships to *Asthenoceras* and *Latiwitchellia*, do not have a tall, thin keel.

Linaresites and *Latiwitchellia* (both being overlooked by Howarth, 2013 in the new version of the *Treatise*, and *Linaresites* also being overlooked by Dietze and Hillebrandt, 2019) show clear phylogenetic relationships with *Asthenoceras* Buckman, 1899, of which the former two genera are possibly close descendants (Sandoval et al., 2012, p. 117, Fig. 3; Sandoval, 2022, p. 809). According to Sandoval et al., (2012, p. 117), *Latiwitchellia,* which has the oldest records in the lowermost Bajocian (Discites Zone, Walkeri Subzone), appears to be the latest representative of the subfamily Grammoceratinae, rather than a primitive Witchelliinae. *L. evoluta* is possibly a neotenic form of *L. montillanensis*, and it may represent the last Grammoceratinae. The taxonomic status and phylogenetic relationships of *Fontannesia* with other taxa are less clear, possibly descending from some of the more strongly ribbed *Asthenoceras* (Fig. 2). New analyses on more abundant and well-preserved material will be necessary to clarify such relationships.

4.1.3 Geographic and stratigraphic distribution

All the North American specimens (from the Weberg Member of the Snowshoe Formation) are from the Lower

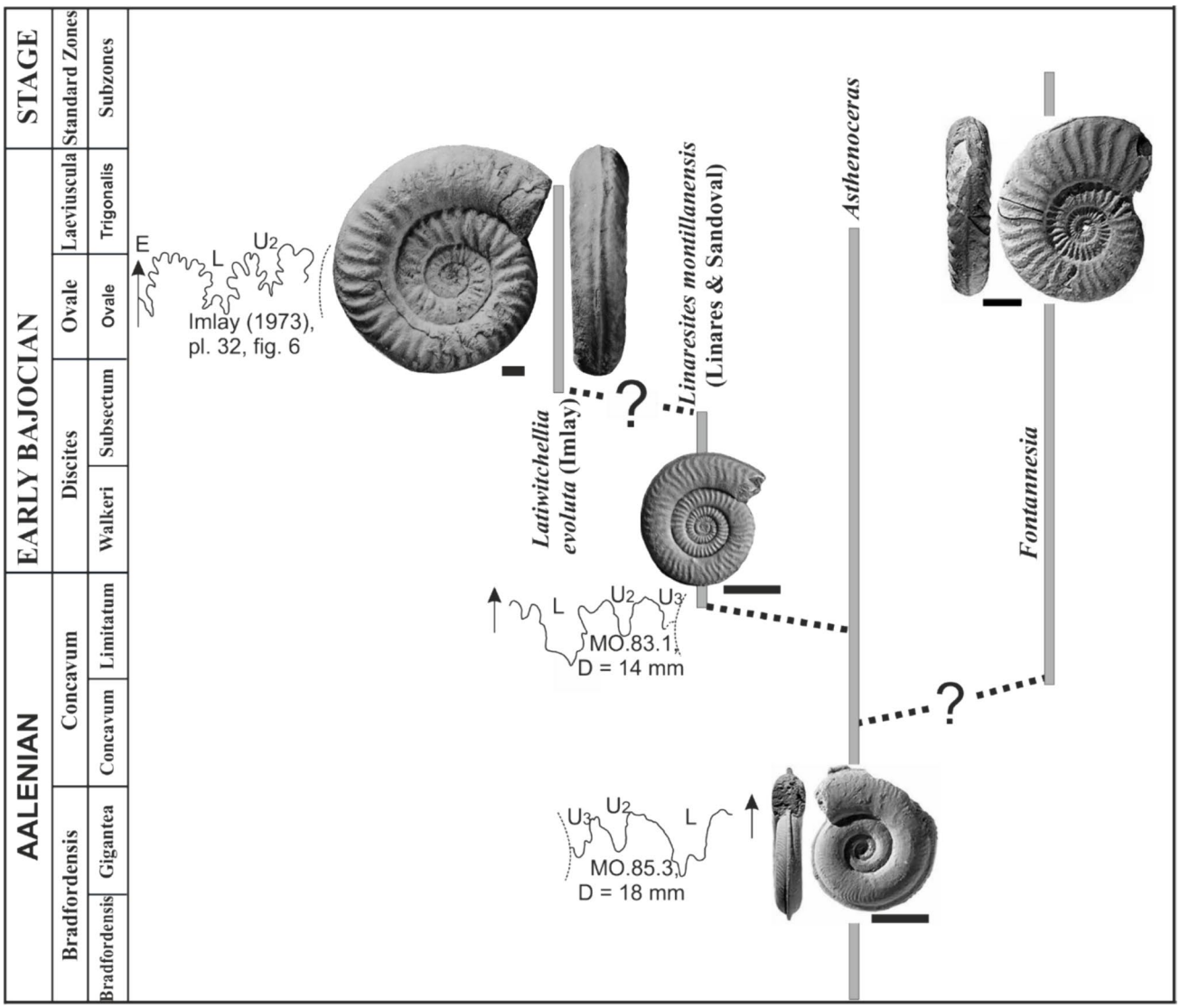

Fig. 2 Proposed phylogenetic relationships among the latest Grammoceratinae (calibrated against the Mediterranean standard zonation). The figured specimens (not the septal sutures) are the HTs of the type species of each genus. *Scale bars* 1 cm (modified after Sandoval et al., 2012)

Bajocian (Tuberculatum Zone, Ochocoense Subzone, and lower part of the Burkei Zone), more or less equivalent to the upper part of the Discites Zone, the Ovale Zone, and the basal part of the Laeviuscula Zone of the Mediterranean standard zones (see Taylor, 2016, pp. 459–460, Figs. 7 and 8). *"L." atacamensis* Dietze & Hillebrandt comes from Lower Bajocian (Giebeli Zone, Multiformis Subzone, equivalent to the lower part of the Sauzei Zone; see Dietze & Hillebrandt, 2019, p. 26, text-Fig. 2) of Portezuelo, El Padre Section, Manflas area, Copiapó Province, Atacama, Northern Chile. In the Subbetic, *Latiwitchellia* has been recorded in the Lower Bajocian (Discites and Ovale zones) from the Barranco de Agua Larga and Sierra de Alta Colomaa, Campillo de Arenas, and Noalejo (Jaén Province) and the Rio Fardes area, Gorafe (Granada Province).

4.1.4 *Latiwitchellia evoluta* Imlay, 1973

Fig. 3a–e

1973? *Fontannesia* cf. *F. evoluta* (Buckman). - Imlay, p. 59, pl. 4, Figs 1–3.

1973 *Witchellia* (*Latiwitchellia*) *evoluta* Imlay n. sp. - Imlay, p. 70, pls 31-33 (HT in pl. 32, Figs. 1–3, 5, 6).

1991 *Fontannesia* cf. *grammoceroides* (Haug). - Hernández-Molina et al., p. 95, Fig. 15, 2.

4.1.4.1 Material JAC3.5.1, JAC3.14.2, JAC3.(14–20)0.1, JAC11.(3–7)0.1, JAQ1.(-32)0.2, JAQ1.(-16)0.2, JAQ2.20.23 and JFB2.4.1

4.1.4.2 Measurements

Specimen	D	U	u	H	h	W	w	R	Remarks	Biostratigraphy
JAQ1.-32. 2	47.0	22.0	0.47	14.0	0.30	9.00	0.20	25	[M], adult	Discites Zone
	43.0	20.0	0.47	12.7	0.30	8.7	0.20			
JAQ2.20.23	51.0	22.0	0.43	14.5	0.28				[M], adult. Complete?	Discites Zone
	40.0	15.3	0.38	12.5	0.31					
JAC3.(14–20)0.1	60.0	25.0	0.42	20.0	0.33				[M], adult, complete?	Ovale Zone
	43.0	17.5	0.41	15.2	0.35					
JAC11.3.7	46.0	19.5	0.42	15.5	0.34	10.0	0.22	18	[M]	Ovale Zone
	36.5	14.0	0.38	13.3	0.36					
JFB2.4.1	49.0	22.5	0.46	15.0	0.31	13.5	0.26	17	[M]	Ovale? Zone
	37.0	17.0	0.46	12.0	0.32					

4.1.4.3 Description Medium-sized shells, evolute (O/D varying from 0.49 to 0.42), although somewhat less than for the specimens described by Imlay (1973, pp. 70–71), with slow whorl-spiral expansion. In specimens not laterally crushed, the whorl-section varies from subquadratic in internal whorls to suboval compressed in the BH; the oblique to rounded umbilical wall merges with the rounded umbilical edge; the flanks vary from almost flat to gently convex and converge to the venter, which is gently rounded to almost flat and bears a more or less high keel bordered by furrows sometimes replaced by flat bands in the BH of most evolutes and strongly ornamented specimens or even in earlier stages in less evolute and less strongly ribbed specimens. None of the Subbetic specimens seems to preserve the adult aperture, which in the North American forms inclines gently forward on the flanks and projects strongly forward on the venter. The ribbing, quite irregular, can vary considerably throughout ontogeny and from one specimen to another; ribs are mainly simple, some bifurcate on the lower third of the flanks and rarely a few arise freely near the middle flanks. Inner and intermediate whorls bear ribs that are dense, well marked, and nearly rectiradiate on the lower parts of the flanks; these become higher and generally rursiradiate on the middle parts, becoming still higher and projected forward high on the flanks and near the venter. On outer whorls, on the PH end, and on the BH the ribs become progressively more spaced, weaken or even vanish in the lower part of the flanks, while remaining very wide and strong in the upper part of the flank and in the venter region, where they project forward. Some specimens develop nodes or thickenings high on the flanks at the points where the flank ribs bend forward, this occurring mostly on the intermediate and outer whorls of coarsely ribbed forms (see JFB2.4.1 and JAQ1.-32.2). The less evolute specimens, stratigraphically higher up, may not have bifurcate or free intercalate ribs. The septal suture, partially observable in specimens JAQ1-32.2 and JAC11(3–7)0.1, is very simple with the E-L saddle and L-U_2 broad and barely ramified; L is somewhat shallow, trifid, narrow, barely ramified, and somewhat deeper than the U_2.

4.1.4.4 Remarks To date, apart from *Latiwitchellia evoluta* (Imlay), only one other ammonite species (*"L." atacamensis* Dietze & Hillebrandt, 2019, p. 44, pl. 11, Figs. 2, 4, HT by monotype) has been originally assigned to the genus *Latiwitchellia*. This Andean species is more involute and has the faintest ribbing on inner whorls and very regular ribbing in the BC; except for the ventral grooves, these features bring it closer to *Fontannesia* or even to *Dorsetensia*, than to *Latiwitchellia*.

The Subbetic specimens here analysed and classified as *L. evoluta* match quite well with several of the specimens figured by Imlay (1973, pls 31–33), mainly with the variants that are less coarsely ribbed or intermediate, although North American forms have a slightly wider umbilicus and a slightly stronger and irregular ribbing. The specimen classified by Imlay (1973, p. 59, pl. 4, Figs. 1–3) as *Fontannesia* cf. *F. evoluta* (Buckman) is similar to some of the morphotypes of *L. evoluta* and could fall within the variability range of this species. Some *Fontannesia* species bear quite resemblance to *L. evoluta* (see Fig. 3f), but, are more involute, have an ovate whorl-section and a more sigmoidal, more persistent and regular ribbing throughout ontogeny. The more involute Subbetic specimens (JAQ2.20.23, JAC3.(14–20)0.1, JAC11.3.7) show similarities with some specimens of *Asthenoceras intermedium* (Imlay, 1973, p. 57, pl. 4, Figs. 7–15), but this species, which precedes *L. evoluta* in the stratigraphic record, is more involute and has finer ribs, many of which are divided in the lower third of the flank. Likewise, the same specimens share some similarities with the specimens from Tibet described and figured as *Fontannesia kiliani* (Kruzinga) by Westermann & Wang (1988, p. 316, pl. 20, Figs. 1–4, 6–7), which are

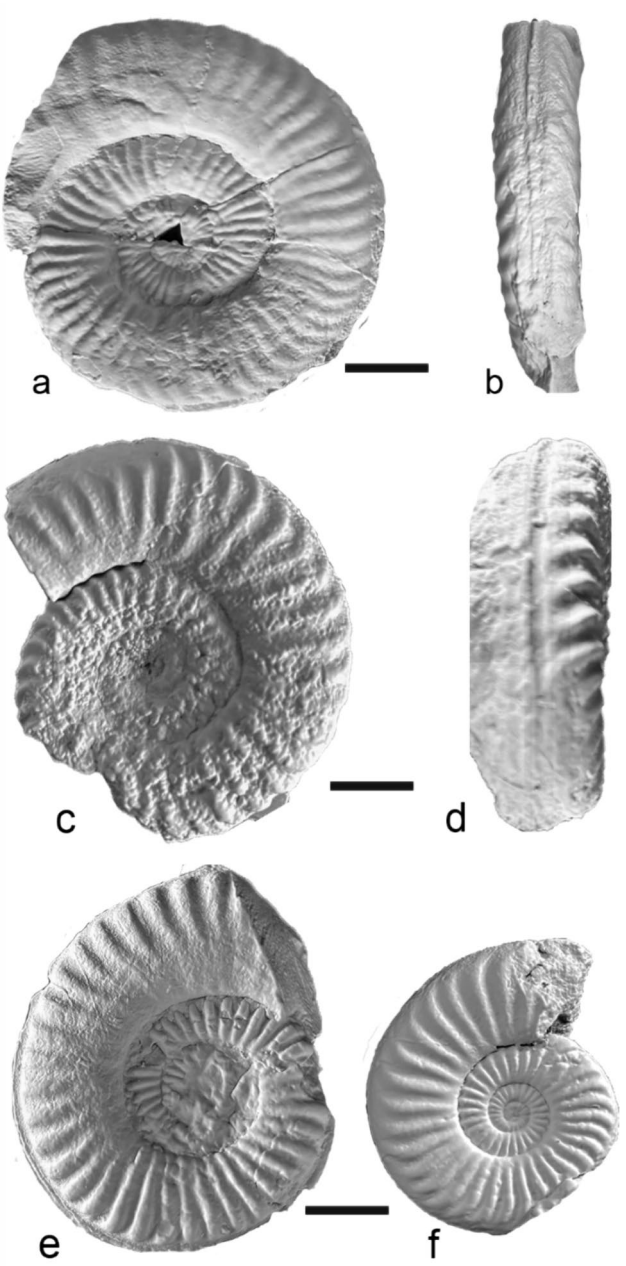

Fig. 3. *Latiwitchellia evoluta* Imlay, 1973 [M]: **a**, **b** JAQ1.-32. 2, lateral and ventral views, Discites Zone, Subsectum Subzone, Barranco de Agua Larga (JAQ1 section); **c**, **d** JFB2.4.1, lateral and ventral views, Ovale Zone?, Río Fardes (JFB2 section), specimen figured in Hernández-Molina et al., 1991, Fig. 15.2; **e** JAC3.(14–20)0.1, lateral view, Ovale Zone, Sierra de Alta Coloma (JAC3 section). **f** *Fontannesia* sp., JRi2.1.1, Discites Zone, Walkeri Subzone, Sierra de Ricote (JRi2 section), Murcia province. *Scale bars* 1 cm

also more involute and have more irregular ribs, many of which are furcate. *Linaresites montillanensis* (Linares & Sandoval, 1988) shares morphological similarities with *L. evoluta,* mainly in the evolute coiling, whorl-section, type of ribs, and very simple suture; however, these forms, later in time, are substantially larger. *L. evoluta*, possibly a neotenic form of *L. montillanensis*, may represent the last Grammoceratinae.

4.1.4.5 Distribution The Subbetic specimens are from Lower Bajocian, Discites Zone of the Barranco Agua Larga (sections JAQ1 and JAQ2), Noalejo (Jaén Province) and from Ovale Zone of sections of Barranco de la Jarropa (JAC3), La Torquilla (JAC11) in Sierra de Alta Coloma area, Campillo de Arenas, and Noalejo (Jaén Province), and Rio Fardes (JFB2), Gorafe (Granada Province).

5 Conclusions

(1) The analysis of the abundant Lower Bajocian ammonites collected in several stratigraphic sections from Subbetic domain (Betic Cordillera, southern Spain) has revealed the presence of a few specimens belonging to *Latiwitchellia*, an ammonite genus that to date has been found only in the Eastern Pacific Domain (North American Western Cordillera, Oregon, USA) and Chile.

(2) The Subbetic *Latiwitchellia* specimens show clear similarities with the North American forms and have been considered as variants (morphotypes) of a same species, *L. evoluta* Imlay.

(3) The analysis of the taxonomic relationships among *Latiwitchellia* and other Middle Jurassic ammonite genera such as *Asthenoceras*, *Linaresites*, and *Fontannesia* reveals a close phylogenetic relationship between these four genera (Fig. 2), which have typical characters of the Grammoceratinae, especially ornamentation and suture. This definitively excludes *Latiwitchellia* from Witchelliinae (Sonniniidae), leading it to be included in Grammoceratinae (Hildoceratidae). The relationship among *Asthenoceras*, *Linaresites*, and *Latiwitchellia* seems clear, whereas the possible relationship with *Fontannesia* remains more doubtful, although it seems feasible (based on morphology as well as biostratigraphy) that both *Linaresites* and *Fontannesia* descended directly from *Asthenoceras* in the late Aalenian.

(4) The biostratigraphic range of *Latiwitchellia* is quite similar in the Subbetic and North American Western Cordillera, although the oldest Subbetic forms (from lowermost Discites Zone) are somewhat earlier in time than the North American forms (uppermost Discites Zone). This implies that although *Latiwitchellia* is more abundant in the eastern Pacific domain, it could have originated in the western end of the Tethys.

(5) The Hispanic Corridor connecting Westernmost Tethys and Eastern Pacific was the oceanic channel that, at least temporarily, allowed the migration of *Latiwitch-*

ellia and other ammonite taxa between the two palaeogeographic domains.

Acknowledgements This study forms part of the results of the EMMI Research Group (RNM 0178 Junta de Andalucía, Spain). I am also grateful to my colleague G. Jiménez for photographic assistance and to Mr. D. Nesbitt for reviewing the English text. I am very grateful to two anonymous reviews whose constructive comments led to improvements in the final version of this paper.

Funding This research was supported by EMMI Research Group (RNM 0178 Junta de Andalucía, Spain).

Declarations

Conflict of interest The author declares that there is no conflict of interest.

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