Crural Bases Position as a Structural Criterion for Supraspecific Diagnosis of Early Jurassic Zeilleriid Brachiopods

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Crural bases position as a structural criterion for supraspecific diagnosis of Early Jurassic zeilleriid brachiopods

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Analysis of the internal structure carried out on several representative genera of the brachiopod family Zeilleriidae from the Lower Jurassic of the Betic Ranges (SE Spain), complemented with specimens from nearby domains such as the Iberian Range and Lusitanian Basin, has enabled to propose a model for discrimination of genera based on the relative position of the crural bases with respect to the hinge plates. This particular feature has been analysed in the genera *Zeilleria*, *Bakonyithyris*, *Securina*, *Neozeilleria*, *Cincta*, *Aulacothyris*, and *Plesiothyris,* revealing three different basic patterns of crural bases arrangement: a *Zeilleria*-type, with crural bases distinctly arising from the ventral side of the hinge plates; a *Securina*-type, with crural bases originating transversally to the hinge plates and dorsally prominent; and a *Bakonyithyris*-type, intermediate between both previous patterns.

Key words: Brachiopoda, Zeilleriidae, systematics, brachidium architecture, Jurassic, Western Tethys.

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Introduction

The family Zeilleriidae Schuchert, 1929 (nom. transl. Allan 1940) is one of the most diverse groups of Mesozoic terebratulid brachiopods concerning diversity in the Mesozoic fossil record of the order Terebratulida. Internally, they have dental plates, dorsal median septum, no cardinal process, and a long-looped brachidium that is not supported by the septum at adult stages (Baker 2006; Smirnova 2008).

However, the complexity of the brachidium, together with the well-known limitations of the transverse serial section methodology, i.e., time consuming work, paucity of material, recrystallized infilling or tilted orientation (see Manceñido and Motchurova-Dekova 2010 for a revision on this issue), impose a restriction to the knowledge of certain structures of systematic relevance. For the Early and Middle Jurassic specimens, these difficulties are increased because of the scarcity of favourable facies containing fossils that enable separation of the valves, and direct study of the internal structure, more frequently possible with Cainozoic material.

As a consequence, the internal morphological characters have often been left aside when dealing with the Jurassic taxa studied in this paper, enhanced by the overall internal similarity among known members of the family (dental plates shorter or longer, presence of dorsal median septum and septalium, dorsal development of the crura and zeilleriid-type brachidium). Thus, internal morphological criteria to distinguish different genera are frequently based on features with rather low diagnostic value, such as the morphology of the delthyrial and umbonal cavities, profile of the deltidial plates, crenulations on hinge teeth and sockets, and presence of pedicle collar.

On the other hand, criteria such as the relation that exists between the cardinal features and the initial stages of the crura, a highly diagnostic criterion in other groups, has been insufficiently investigated in the zeilleriids. Crural types and their evolution have a relevant taxonomic and phylogenetic significance in post-Paleozoic Rhynchonellida (e.g., Ager et al. 1972; Manceñido and Owen 2001; Savage et al. 2002; Tomasovych 2006; Manceñido et al. 2007; Radulović et al. 2007; Manceñido and Motchurova-Dekova 2010). This feature has also been used in the systematics of terebratulides. For instance, Licharev (1936) described two cardinalia types within the same family (Notothyrididae), one with the crural bases in the ventral area of the inner hinge plates and a second type with the crural bases in the dorsal area. Tkhorzhevskiy (1993) extended this twofold distinction to all long-looped Mesozoic brachiopods. Middlemiss (1959, 1980) and Cox and Middlemiss (1978), described the hinge plates-crural bases system in great detail in their studies of Cretaceous terebratulides.

In this paper we present a study of the initial position of the crural bases in relation to the hinge plates in several zeilleriid species commonly recorded in the Lower Jurassic of Western Tethys, with the aim of showing its diagnostic value at supraspecific level.

Institutional abbreviations.—DCTMA-UA, Department of Earth and Environmental Sciences, University of Alicante, Spain; DPUCM, Department of Paleontology, Complutense University of Madrid, Spain; JdC Collection, Jiménez de Cisneros historical collection, Paleontological Museum of Murcia, Spain.

Material and methods

Several genera of the family Zeilleriidae Schuchert in Schuchert and LeVene, 1929 (nom. transl. Allan 1940), such as *Zeilleria* Bayle, 1878, *Plesiothyris* Douvillé, 1879, *Cincta* Quenstedt, 1868, *Aulacothyris* Douvillé, 1879, *Bakonyithyris* Vörös, 1983, *Securina* Vörös, 1983, and *Neozeilleria* Andrade, 2006 are among the most abundant and representative taxa in the Lower Jurassic brachiopod assemblages of the Western Tethys. Systematic discrimination of these genera has traditionally been based on external morphological features, such as the presence of a rounded outline in *Cincta*, a marked dorsal sulcus in *Aulacothyris* and *Bakonyithyris*, or an axiniform outline in *Securina*.

The recent systematic study of brachiopod assemblages from the Lower Jurassic of the Betic Ranges (Baeza-Carratalá 2008, 2013) provided an abundant collection of specimens belonging to the Zeilleriidae, in certain cases with several species of the same genus, thus allowing a thorough analysis of their internal structure. To enhance such analysis, the study of the internal structure of specimens from other nearby domains such as the Iberian Range has been added in this paper. A selected sample of the studied specimens is shown in Fig. 1. The descriptions of the crural bases of *Neozeilleria* species from the Lusitanian Basin made by Andrade (2006) were also considered in our analysis. Acetate peels of *Zeilleria quadrifida* (type species of *Zeilleria*) have been also examined due to courtesy of María José Comas-Rengifo (Complutense University of Madrid, Spain). The specimens that were serially sectioned for this work and their respective provenance data are indicated in Table 1.

Serial sections of 18 specimens were made at intervals of 0.10 mm and, when more detail was considered necessary, at 0.05 mm. Crural bases position was observed both directly on the serial sections using an optical microscope (Nikon CFI60 E600POL) and on high resolution photographs of acetate peels of these sections. The acetate peels accentuate the relative orientation of the calcite fibres that build the shell substance, allowing to distinguish between different internal structures (e.g., cf. Baker 1972; cf. Dagys 1974; Tkhorzhevskiy 1974, 1993; Smirnova 1984, 2008; Sulser et al. 2010). Though the descriptive terminology used in these papers is heterogeneous, the position of the crural bases seems always to be distinct, with clearly perpendicular orientation of the fibres in relation to the hinge plates and the outer socket ridges.

Several authors had previously described crural bases in Early–Middle Jurassic Zeilleriidae (e.g., Delance 1974; Vörös 2009), but these descriptions were based on transverse

Table 1. List of specimens in which the internal structure has been studied in this paper. Abbreviations: DCTMA-UA, Department of Earth and Environmental Sciences, University of Alicante; DPUCM, Department of Paleontology, Complutense University of Madrid; JdC Collection, Jiménez de Cisneros historical collection (Paleontological Museum of Murcia); cb: crural bases; hp: hinge plates.

hp/cb pattern	Species	Specimen	Locality	Age	Housing institution
Zeilleria-type	*Zeilleria batilla* (Geyer, 1889)	O-VI-SE-Ba-1	Eastern Subbetic	Pliensbachian	JdC Collection
	Zeilleria mutabilis (Oppel, 1861)	I-XI-17-20	Eastern Subbetic	Pliensbachian	JdC Collection
	Zeilleria aff. *venusta* (Uhlig, 1879)	Ze-Ve-1	Eastern Subbetic	Pliensbachian	JdC Collection
	Neozeilleria anglica (Oppel, 1856)	FZ-148.1	Fuentelsaz (Iberian Range)	Early Aalenian	DPUCM
	Cincta peiroi Baeza-Carratalá, 2011	I-I-25-3(H)	Eastern Subbetic	Pliensbachian	JdC Collection
Bakonyithyris-type	*Bakonyithyris gastaldii* (Parona, 1880)	O-VI-SE-3-4	Eastern Subbetic	Pliensbachian	JdC Collection
	Aulacothyris blakei (Davidson, 1878)	Ci.2-102	Cillas (Iberian Range)	Late Toarcian	DPUCM
	Aulacothyris resupinata (Sowerby, 1816)	1-Ar.52.1	Ariño (Iberian Range)	Early Toarcian	DPUCM
	Plesiothyris verneuili (Deslongchamps, 1863)	P.Ve-Cr-1	Rama Castellana (Iberian Range)	Pliensbachian	DPUCM
	Plesiothyris sp. Baeza-Carratalá, 2008	I-VI-11-T8(a)-2	Eastern Subbetic	Pliensbachian	JdC Collection
Securina-type	*Securina partschi* (Oppel, 1861)	CCO-B-P1	Cerro de la Cruz, Eastern Subbetic	Pliensbachian	DCTMA-UA
	Securina plicata (Geyer, 1889)	M2Sp13	Sierra Los Frailes, Eastern Subbetic	Late Sinemurian–Early Pliensbachian	DCTMA-UA
	Securina securiformis (Gemmellaro, 1874)	S.SE-1	Sierra Pelada, Eastern Subbetic	Late Sinemurian–Early Pliensbachian	DCTMA-UA
	Securina oxygonia (Uhlig, 1879)	ZOx.CC8-A.1	Cerro de la Cruz, Eastern Subbetic	Pliensbachian	DCTMA-UA

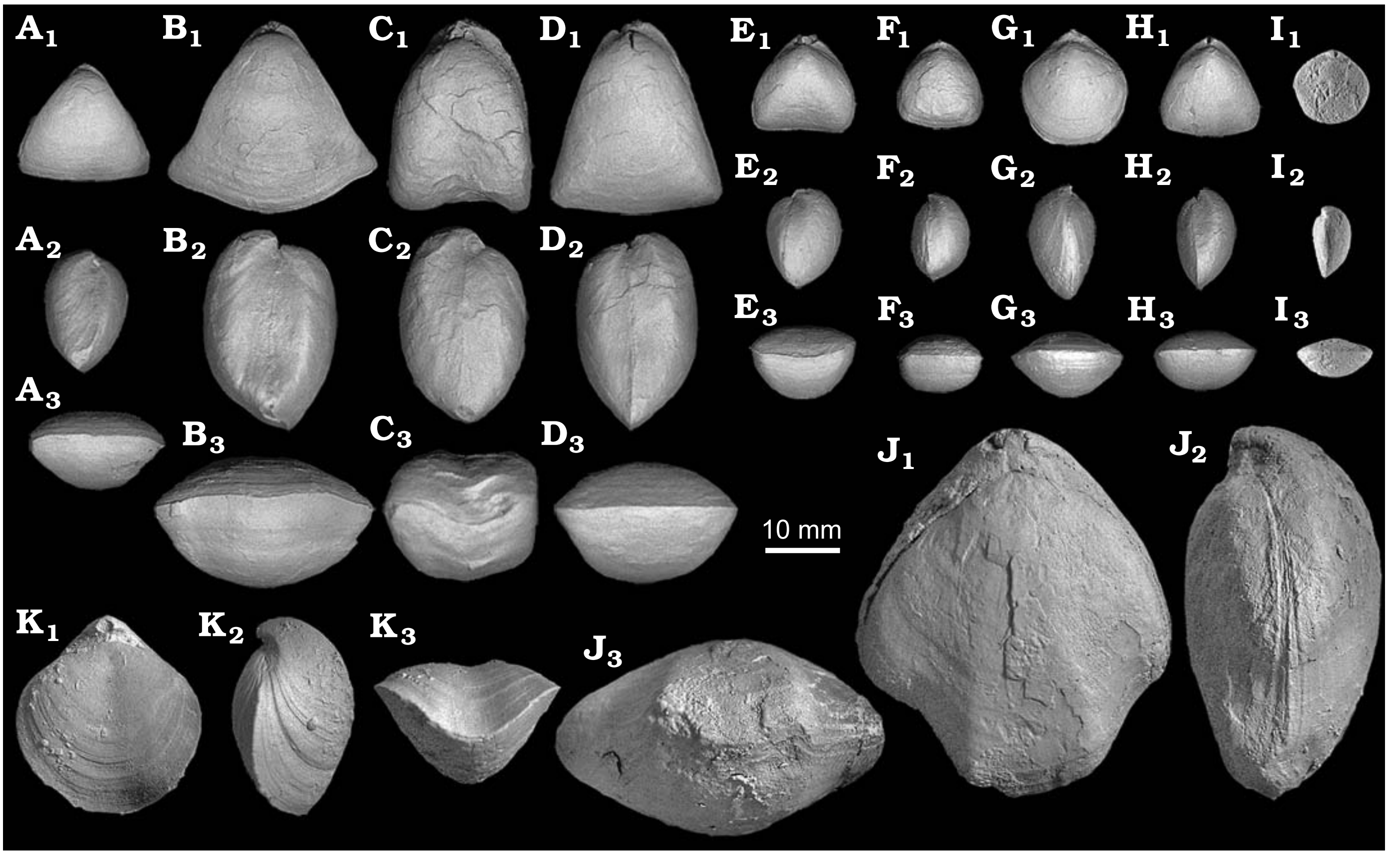


Fig. 1. Selected specimens of the zeilleriid brachiopods in dorsal (A_1–K_1), lateral (A_2–K_2), and anterior (A_3–K_3) views. **A**, **E**–**H**. Pliensbachian, Eastern Subbetic (South-East Spain). **A**. *Securina oxygonia* (Uhlig, 1879), DCTMA-UA I-XII-8-2. **E**. *Bakonyithyris gastaldii* (Parona, 1880), JdC O-VI-SE-3-2. **F**. *Zeilleria* aff. *venusta* (Uhlig, 1889), JdC O-IV-SE-4-8. **G**. *Zeilleria mutabilis* (Oppel, 1861), JdC I-XI-17-10. **H**. *Zeilleria batilla* (Geyer, 1889), JdC O-VI-SE-Ba-4. **B**–**D**. Upper Sinemurian–Lower Pliensbachian, Eastern Subbetic (South-East Spain). **B**. *Securina securiformis* (Gemmellaro, 1874), DCTMA-UA SPel-Bol-1-SSe-2. **C**. *Securina plicata* (Geyer, 1889), DCTMA-UA SF-1-M1-SP-21. **D**. *Securina partschi* (Oppel, 1861). DCTMA-UA SPel-Bol-Ca-SPa-2. **I**. *Neozeilleria anglica* (Oppel, 1856), DPUCM Fz.148.1, Lower Aalenian, Iberian Range (North-East Spain). **J**. *Plesiothyris verneuili* (Deslongchamps, 1863) DPUCM P.Ve-Cr-1, Pliensbachian, Iberian Range (North-East Spain). **K**. *Aulacothyris resupinata* (Sowerby, 1816), DPUCM 1-Ar.52, Lower Toarcian, Iberian Range (North-East Spain).

serial section outlines, the location of the crural bases estimated from the thickening of the hinge plates. Thus, Delance (1974) described in *Plesiothyris* and *Zeilleria*, hinge plates with the crural bases traces in a dorsal position and Vörös (2009) described in *Zeilleria* crural bases given off in the medial terminations of the hinge plates, generally in dorsal position, and in *Bakonyithyris* crural bases emerging from the medial thickenings of the hinge plates or given off dorsally, independent from the median septum. The microstructural observations of the crural bases presented in this paper allow describing more accurately their structural relation with the hinge plates.

Results and discussion

Crural bases position patterns

Three models of inter-relations between crural bases and hinge plates have been distinguished in this paper (Fig. 2):

Zeilleria-type.—In species belonging to *Zeilleria* Bayle, 1878, e.g., *Zeilleria quadrifida* (Lamarck, 1819), *Z. batilla* (Geyer, 1889), *Z. mutabilis* (Oppel, 1861), and *Z.* aff. *venusta* (Uhlig, 1879), the crural bases are located on the ventral side of the hinge plates and flush with them. The crura grow dorsally once they are clearly distinguishable as such (Figs. 2, 3).

Securina-type.—The species of *Securina* Vörös, 1983, i.e., *Securina partschi* (Oppel, 1861), *S. plicata* (Geyer, 1889), *S. securiformis* (Gemmellaro, 1874), and *S. oxygonia* (Uhlig, 1879), have pendent crural bases located in the inner side of the hinge plates, with its calcite fibres transverse to the hinge plates fibres, and in a dorsal position in relation to the septalial plates (Figs. 2, 4).

Bakonyithyris-type.—In *Bakonyithyris* Vörös, 1983, exemplified herein by *Bakonyithyris gastaldii* (Parona, 1880), the position is intermediate when compared to the two previous patterns, the crural bases are situated in the ventral area of the hinge plates but slightly transversal, turning dorsally while still wrapped by the hinge plates; that is, though the crural

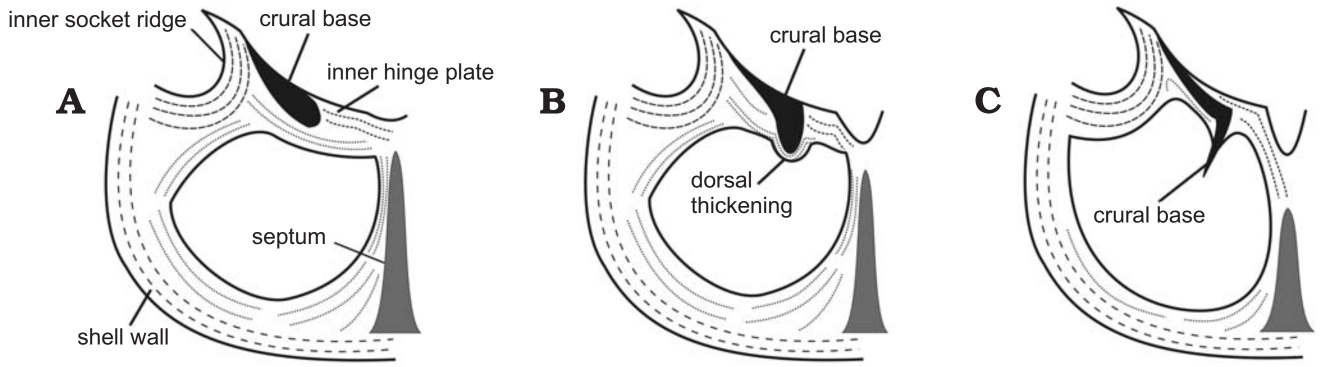


Fig. 2. Synthetic scheme of the crural bases position patterns observed in the Zeilleriidae genera analysed in this paper. **A**. *Zeilleria*-type. **B**. *Bakonyithyris*-type. **C**. *Securina*-type.

bases start from a ventral position, they immediately show a clearly dorsal development (Figs. 2, 5).

All the remaining genera included in this study can be assigned to one of these three types as follows:

Genus *Neozeilleria* Andrade, 2006.—According to the diagnosis of this Toarcian–Aalenian genus (Andrade 2006), it can be deduced that this taxon is very closely related to *Zeilleria* Bayle, 1878. This proximity is supported by the very similar pattern observed in crural bases position. Andrade (2006) indicates that the position of the crural bases ranges from central positions close to the dorsal median septum to more lateral, practically on the inner socket ridges. Examination of the microphotographs of *Neozeilleria duartei*, *N. nuskae*, *N. anglica*, and *N. sharpei* (Andrade 2006: 76, 80, 84, 88) shows without doubt the ventral position of the crural bases. Serial sections performed on *Neozeilleria anglica* (Oppel, 1856) specimens from the Lower Aalenian of the Iberian Range (Fig. 3E), corroborate the presence of *Zeilleria*-type crural bases in this genus.

Genus *Cincta* Quenstedt, 1868.—The systematic relation between the genera *Cincta* and *Zeilleria* is controversial and has been widely discussed (e.g., Buckman 1907; Delance 1974), different species having been variously included in either genus by several authors. Delance (1974) grouped both taxa as subgenera within the genus *Zeilleria* whereas more recently Baker (2006) and Smirnova (2008) have considered both as independent genera within the Zeilleriidae.

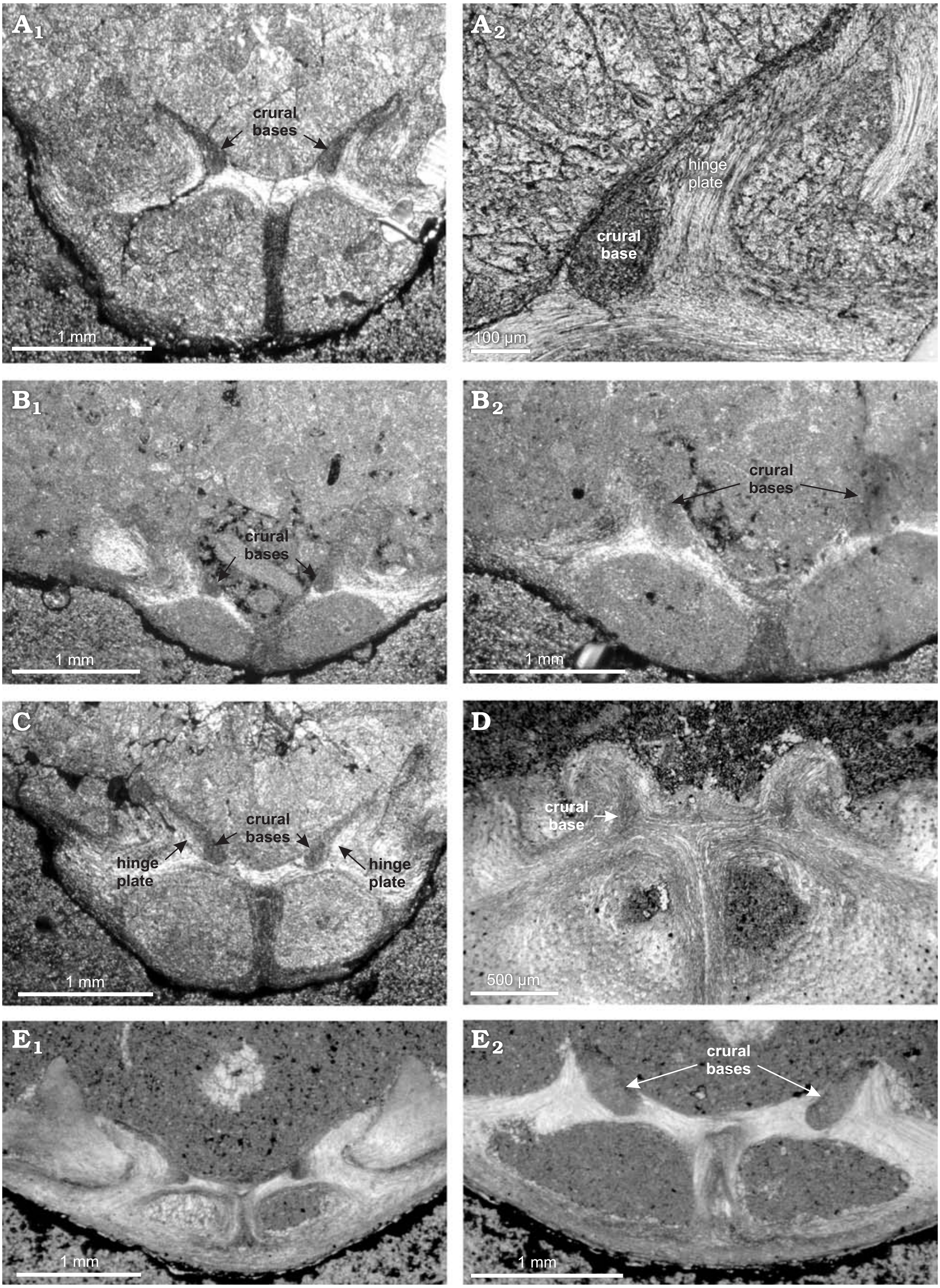
In the Lower Jurassic of the Betic Ranges, the genus *Cincta* is represented by the species *Cincta peiroi* Baeza-Carratalá, 2011. In the specimens of this species their internal structure displays curved hinge plates dorsally convex and converging. The crural bases are of rectangular section and originate on the ventral side of the hinge plates; the crura develop dorsally once individualized (Baeza-Carratalá 2011: fig. S6). This arrangement agrees with the *Zeilleria*-type of crural bases. Unfortunately, no peels of these serial sections were done, and the sparitic infilling in the remaining specimens of *C. peiroi* prevents performing a detailed study of their microstructure.

No figures of peels from serial sections of *Cincta* specimens are available in the literature, but Tkhorzhevskiy (1993: fig. 15A, B) makes detailed descriptions of the cardinalia of *Zeilleria subcensoriensis* from the Upper Jurassic of Crimea and in *Cincta numismalis* from the Lower Jurassic of Stara Planina, including figures which show in both species a "mediotest" (a microstructural term that includes crural bases) that resembles the *Zeilleria*-type pattern described in this paper.

Genus *Aulacothyris* Douvillé, 1879.—This genus has a distinct external morphology with a carinate outline and a dorsal sulcus, as exemplified by the type-species *Aulacothyris resupinata* (Sowerby, 1816). This genus has an extended stratigraphic distribution that ranges from the Middle Triassic to the Upper Jurassic, and probably is in need of a systematic revision. It has been traditionally included in the Zeilleriidae (cf. Muir-Wood et al. 1965; Delance 1974; Baker 2006), but Smirnova (2008), based on the studies of Babanova 1964) and Antoshchenko (1970), situated this genus within the superfamily Dallinoidea (family Dallinidae), because of dallinoid-type stages of brachidium development observed in this taxon. However, this stage of development is also present in *Zeilleria* (Baker, 1972) and the criteria given in the "Treatise" (MacKinnon and Lee, 2006: 2242) to recognize the Dallinidae differ from those considered by Smirnova (2008).

Concerning the crural bases, in diagnosis of the genus by Muir-Wood et al. (1965), they are described as ventrally

Fig. 3. Microphotographs of acetate peels of selected specimens belonging to *Zeilleria* Bayle, 1878 and *Neozeilleria* Andrade, 2006 showing the *Zeilleria*-type crural bases. **A**–**C**. Pliensbachian, Eastern Subbetic (South-East Spain). **A**. *Zeilleria batilla* (Geyer, 1889), JdC O-VI-SE-Ba-1, section at 1.20 mm from the apex (A_1), detailed view of the crural bases position (A_2). **B**. *Zeilleria mutabilis* (Oppel, 1861), JdC I-XI-17-20, sections at 2.40 mm (B_1) and 2.70 mm (B_2) from the apex showing the development of the crural bases emerging ventrally from the hinge plates. **C**. *Zeilleria* aff. *venusta* (Uhlig, 1879), JdC Ze-Ve-1, section at 2.10 mm from the apex showing the hinge plates with the crural bases emerging ventrally. **D**. *Zeilleria quadrifida* (Lamarck, 1819), DPUCM 2CU.20, kindly provided by Olivia Chico and María José Comas-Rengifo, Late Pliensbachian, Iberian Range (North-East Spain), section at 2.30 mm from the apex. **E**. *Neozeilleria anglica* (Oppel, 1856), DPUCM FZ-148, Lower Aalenian, Iberian Range (North-East Spain), sections at 1.75 mm (E_1) and 2.10 mm (E_2) from the apex. →


A1
crural
bases
1 mm
A2
hinge
plate
crural
base
100 μm
B1
crural
bases
1 mm
B2
crural
bases
1 mm
C
crural
bases
hinge
plate
hinge
plate
1 mm
D
crural
base
500 μm
E1
1 mm
E2
crural
bases
1 mm

directed, agreeing with the *Zeilleria*-type pattern. However, Tkhorzhevskiy (1993: figs. 9, 13B) described specimens of *Aulacothyris* sp. from the Pliensbachian of the Carpathians and "*Aulacothyris" pala* from the Upper Jurassic of Armenia with a "mediotest" including crural bases in a more dorsal position. The serial sections made in specimens of the Iberian Range of the type-species *Aulacothyris resupinata* (Sowerby, 1816) from the Lower Toarcian and in *A. blakei* (Davidson, 1878) from the Upper Toarcian, confirms Tkhorzhevskiy's (1993) observations, showing a pattern that seems to correspond to the *Bakonyithyris*-type (Fig. 5B). Thus, the crural bases are seen in a ventral position and slightly transverse to the hinge plates, and dorsal to the septalial plates. This early dorsal development produces a slight but conspicuous dorsal thickening of the hinge plates (Figs. 2, 5).

Genus *Plesiothyris* Douvillé, 1879.—The genus *Plesiothyris* is represented in the Subbetic Basin by the type-species *Plesiothyris verneuili* (Deslongchamps, 1863) and *Plesiothyris* sp. Baeza-Carratalá, 2008, a taxon morphologically very close to the type-species. The material of the former species is scarce and inadequately preserved, preventing the study of its internal structure. In the latter species crural bases originate on the ventral side of the hinge plates and develop dorsally in the posterior part of the brachidium (Baeza-Carratalá 2008: fig. 113).

Delance (1974: 292, fig. 14.1) figured serial sections of two specimens of *P. verneuili*, which are practically identical to those from *Plesiothyris* sp. Baeza-Carratalá, 2008. However, he described the crural bases arising dorsally from the hinge plates "les plaques cardinales portent dorsalement les ébauches des bases crurales" (Delance 1974: 289). As previously stated, this observation is based on hinge plate's outline and not on its microstructure. Serial sections performed for this paper on a specimen of *P. verneuili* from the Pliensbachian of the Iberian Range show *Bakonyithyris*-type crural bases, ventral to the hinge plates but transversally developed, that gives place to a dorsal thickening (Fig. 5C).

Implications for the specific composition of *Securina*

After applying the diagnostic criteria of crural bases position to the Eastern Subbetic Zeillerid species, several species have been confirmed or reassigned to the genus *Securina*:

Securina plicata (Geyer, 1889).—Previously this taxon had been included in several genera, such as *Waldheimia* by Geyer (1889), *Zeilleria* by Jiménez de Cisneros (1923a, b) or *Propygope* by Tent-Manclús (2003). The generic position of *Waldheimia hierlatzica* Oppel var. *plicata* Geyer, 1889 within *Securina* Vörös, 1983, was first suggested by Baeza-Carratalá and Tent-Manclús (2004). Later, Baeza-Carratalá (2008), Vörös (2009), and Siblík (2010) agreed with this generic assignment which has been finally established as *Securina plicata* by Baeza-Carratalá (2011). According to our results the assignment to the genus *Securina* is strengthened since the crural bases are pendent and clearly start from the dorsal part of the hinge plates, giving rise to an extensive loop that reaches almost to the anterior margin of the shell (cf. Baeza-Carratalá 2011 and Fig. 4A herein).

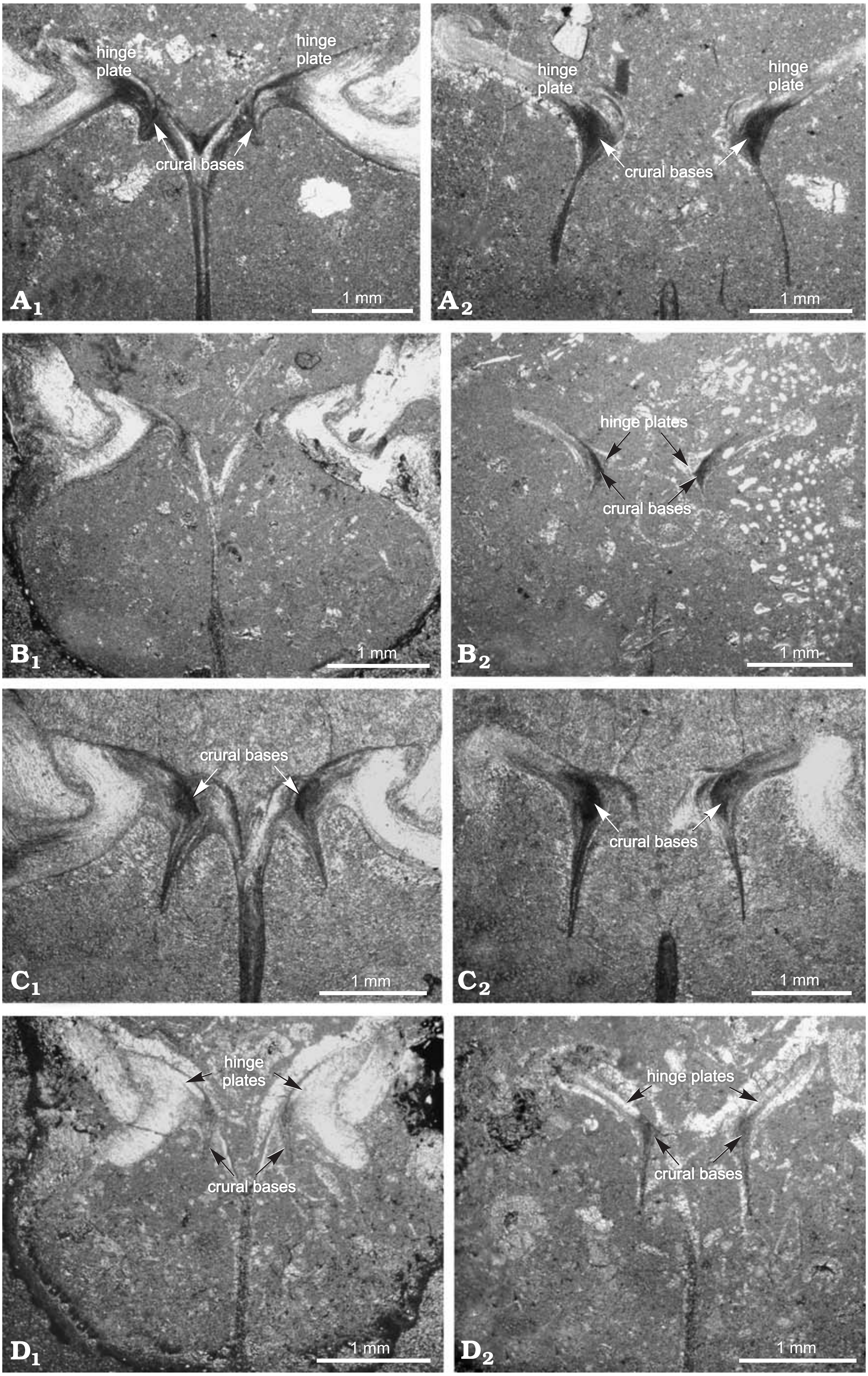
Securina oxygonia (Uhlig, 1879).—Due to its axiniform outline, *Securina oxygonia* is very similar to other representatives of the genus *Securina* Vörös, 1983, but according to the criteria established by Vörös himself for this genus (1983: 24), it differs in its lateral commissure, which is arched and adjacent to the beak ridges of the dorsal valve. This feature should exclude this species from *Securina*, as the original diagnosis of this genus implies a straight lateral commissure located in the middle of the planareas. On the other hand, the serial sections of *S. oxygonia* specimens (Baeza-Carratalá 2008: fig. 110) show an internal structure that is indistinguishable from other species of *Securina* (*S. plicata, S. partschi, S. securiformis*), in the architecture of both its ventral and dorsal valves. The arching observed in the lateral commissure is a morphological feature more suitable for discrimination at specific level. Thus, it enables to separate *S. oxygonia* from other representatives of the genus *Securina*, in the same way as the presence of a dorsal sulcus is used for *S. plicata* or the differences in the morphology of the anterior margin allows to distinguish *S. partschi* from *S. securiformis*, depending on whether it is straight or arched frontally in dorsal view. In fact, the straightness and location of lateral commissure were not included in the revised generic diagnosis for *Securina* in the *Treatise* (Baker 2006: 2174).

Furthermore, according to the results obtained in our analysis, the crural bases in *S. oxygonia* beginning from a dorsal position on the hinge plates are clearly distinct from the *Zeilleria* arrangement in which they start from a ventral position.

Suggestions for the supra-generic systematic arrangement of zeilleriids

All the genera studied in this paper are currently included in the subfamily Zeilleriinae Schuchert, 1929 (the first proper use of this taxon is that of Schuchert in Schuchert and LeVene 1929: 24, as subfamily Zeilleriinae. Therefore, Schuchert

Fig. 4. Microphotographs of acetate peels of selected specimens belonging to *Securina* Vörös, 1983, showing the relationship between hinge plates and pendent crural bases. **A**, **C**. Uppermost Sinemurian–Lower Pliensbachian, Eastern Subbetic (South-East Spain). **A**. *Securina plicata* (Geyer, 1889), DCTMA-UA M2-SP.13, sections at 4.70 mm (A_1) and 6.00 mm (A_2) from the apex showing crural bases located on the inner extreme of the hinge plates and dorsal to the septalial plates. **C**. *Securina securiformis* (Gemmellaro, 1874), DCTMA-UA S.SE-1, sections at 4.40 mm (C_1) and 4.80 mm (C_2) from the apex. **B**, **D**. Pliensbachian, Eastern Subbetic (South-East Spain). **B**. *Securina partschi* (Oppel, 1861), DCTMA-UA CCO-B-P1, sections at 2.50 mm (B_1) and 3.10 mm (B_2) from the apex. **D**. *Securina oxygonia* (Uhlig, 1879), DCTMA-UA ZOx.CC8-A.1, sections at 3.00 mm (D_1) and 3.30 mm (D_2) from the apex showing the hinge plates with the crural bases emerging dorsally. →


hinge plate
hinge plate
crural bases
A1
1 mm
hinge plate
hinge plate
crural bases
A2
1 mm
B1
1 mm
hinge plates
crural bases
B2
1 mm
crural bases
C1
1 mm
crural bases
C2
1 mm
hinge plates
crural bases
D1
1 mm
hinge plates
crural bases
D2
1 mm

should be correctly regarded as author of this family group name, as argued by Manceñido 1993: 93).

After the revision published in the "Treatise" (Baker 2006; Lee et al. 2007), this subfamily is the most numerous of the superfamily Zeillerioidea, including thirty three genera distributed from the Lower Triassic to the Lower Cretaceous. Among other diagnostic criteria used to define the subfamily, that revision states crural bases given off dorsally (Baker 2006: 2164).

The distinction of three patterns of crural bases arrangement proposed in this paper seem useful to establish new suprageneric divisions within the Zeilleriidae based on this criterion, in a similar way as in other brachiopod groups such as the rhynchonellides. In this way, a new subfamily Securininae could be erected for the genus *Securina* (possibly including other taxa with similar crural bases structure) that have true crural bases given off dorsally. *Bakonyithyris*, *Aulacothyris*, *Plesiothyris* and other genera with similar pattern of crural bases could be grouped in the subfamily Aulacothyrinae Babanova, 1964 (introduced as "tribu Aulacothyrini trib. nov." by Babanova 1964: 66); whereas Zeilleriinae could be restricted to *Zeilleria* and close genera with ventrally oriented crural bases. The scheme proposed in this paper, however, is based only on some Early and Middle Jurassic representatives of the group, and needs to be corroborated or extended by studying the micro-structure of the cardinalia in as many genera as possible from the family, and other closely related family-group taxa before to make a formal proposition of new subfamilies.

According to our results an emendation of the diagnosis of the family Zeilleriidae is required. Notice that in this family (as understood up to now) crural bases are herein shown to originate ventrally from the hinge plates, rather than only dorsally or medially, as stated in the "Treatise" (Baker 2006: 2164, 2183).

Systematic palaeontology.

Order Terebratulida Waagen, 1883

Suborder Terebratellidina Muir-Wood, 1955

Superfamily Zeillerioidea Allan, 1940

Family Zeilleriidae Allan, 1940

Subfamily Zeilleriinae Allan, 1940

Emended diagnosis.—Large exceptionally, outline commonly subpentagonal or variant, valves usually biconvex, less commonly ventribiconvex or globose, anterior commissure typically rectimarginate, umbo with persistent beak ridges, deltidial plates exceptionally disjunct or forming symphytium, pedicle foramen oval typically mesothyrid, commonly telate; dental plates unenveloped, or enveloped exceptionally, relatively strong and long; cardinal process absent, or exceptionally represented by callus lobe, crural bases given off ventrally, septalium occasionally U- or W-shaped and deep, median septum triangular, rarely acutely triangular, or long, transverse band of loop occasionally broad, with posterior projections.

Stratigraphic and geographic range.— Induan (Lower Triassic)–Kimmeridgian (Upper Jurassic), ?Berriasian–?Hauterivian (Lower Cretaceous). This subfamily virtually shows a cosmopolitan distribution.

Subfamily Aulacothyrinae Babanova, 1964.

Emended diagnosis.—Small to large, commonly pentagonal or subpentagonal outline, valves usually lobate, bilobate, or quadrilobate, planoconvex to ventribiconvex; anterior commissure typically unisulcate, rarely sulciplicate or antiplicate, umbo with persistent beak ridges, pedicle foramen oval and typically mesothyrid, crural bases initially situated in the ventral part of the hinge plates but with dorsal development.

Stratigraphic and geographic range.—Middle Triassic–Upper Jurassic (Oxfordian). This subfamily is widely recorded in the Western Tethys, mainly from the Apeninnes, Crimea, Hungary, southern Alps, England, Yugoslavia, France, Spain, and Sicily.

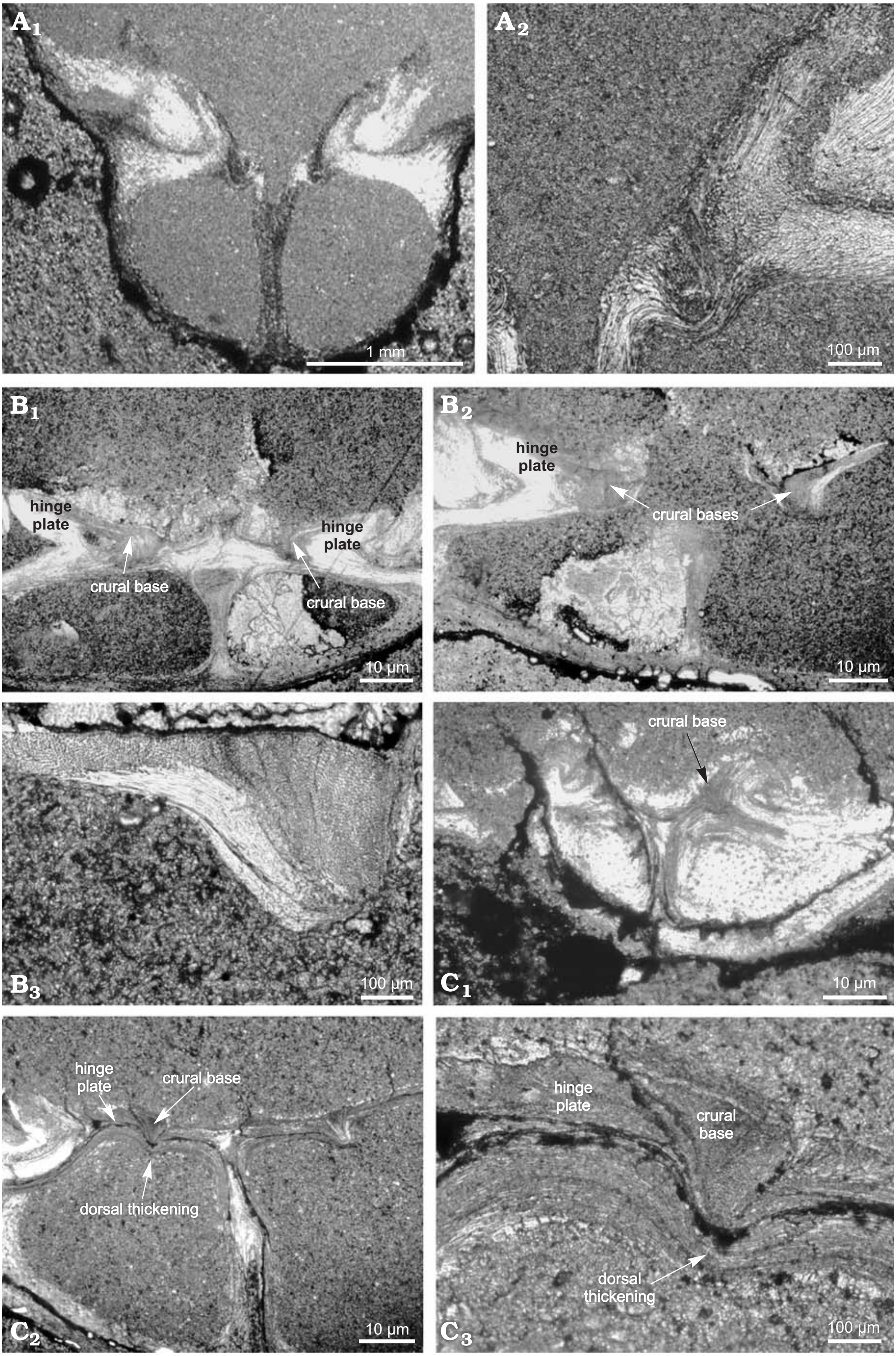
Subfamily Securininae nov.

Type genus: *Securina* Vörös, 1983.

Diagnosis.—Medium to large-sized shells with triangular outline, biconvex valves, anterior commissure commonly rectimarginate and rarely sulcate, ventral (and frequently dorsal) umbones with extended and sharp beak ridges, demarcating well-developed concave planareas, small pedicle foramen mesothyrid; dental plates relatively long; cardinal process absent; thin and long dorsal median septum connected to a V-shaped septalium, crural bases pendent on the dorsal side of hinge plates; the transversal band of the loop is usually rounded in cross-section.

Stratigraphic and geographic range.—Betic Ranges, Saharan Atlas, Sicily, Apennines, southern Alps, northern calcareous Alps, Hungary, western Carpathians. Sinemurian–Late Pliensbachian (earliest Toarcian?).

Fig. 5. Microphotographs of acetate peels showing hinge plates and crural bases relationship in selected specimens belonging to *Bakonyithyris* Vörös, 1983, *Aulacothyris* Douvillé, 1879, and *Plesiothyris* Douvillé, 1879. **A**. *Bakonyithyris gastaldii* (Parona, 1880), JdC O-VI-SE-3-4, Pliensbachian, Eastern Subbetic (South-East Spain), section at 1.60 mm from the apex (A_1), detailed view of the crural bases position (A_2). **B**. *Aulacothyris resupinata* (Sowerby, 1816), DPUCM 1-Ar.52.1, Lower Toarcian, Iberian Range (North-East Spain), sections at 2.40 mm (B_1) and 2.70 mm (B_2, B_3) from the apex. **C**. *Plesiothyris verneuili* (Deslongchamps, 1863), DPUCM P.Ve-Cr-1, Pliensbachian, Iberian Range (North-East Spain), sections at 3.80 mm (C_1) and 5.10 mm (C_2, C_3) from the apex. Note, that although the crural bases give place to a conspicuous dorsal thickening, they emerge from a position ventral to the hinge plates (see the detailed views A_2, B_3, C_3). →


A1
1 mm
A2
100 µm
B1
hinge plate
crural base
hinge plate
crural base
10 µm
B2
hinge plate
crural bases
10 µm
B3
100 µm
crural base
C1
10 µm
hinge plate
crural base
dorsal thickening
C2
10 µm
hinge plate
crural base
dorsal thickening
C3
100 µm

Conclusions

The microstructural features related with the crural bases position can help in the systematic arrangement of the zeilleriid terebratulides, in the same way as in other groups of brachiopods. Three different patterns have been observed in some representatives of the family Zeilleriidae from the Lower–Middle Jurassic of Western Tethys, leading to the emendation of the diagnosis of the subfamily Zeilleriinae and to the proposal of new systematic criteria based on the inter-relations between hinge plates and crural bases. Using these criteria a new subfamily Securininae is proposed to include genera characterized by crural bases that are given off dorsally; the subfamily Aulacothyrinae is rehabilitated for those genera with crural bases in an intermediate position, whereas Zeilleriinae (sensu stricto) would remain to accommodate the type genus, *Zeilleria*, and its close relatives that display ventrally originated crural bases. Further studies in other members of this large group will be needed to establish the general validity of this approach.

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