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TESTING FOR A DECLINE IN DIVERSITY PRIOR TO EXTINCTION: LANGUEDOCIAN (LATEST MID-CAMBRIAN) DISTRIBUTION OF CINCTANS (ECHINODERMATA) IN THE IBERIAN CHAINS, NE SPAIN

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Abstract: The middle Cambrian strata of the Iberian Chains (north-eastern Spain) and the Montagne Noire (southern France) record an adaptative radiation of cinctans and trilobites, which spanned the Leonian–early Languedocian interval. A diachronous diversity peak was reached by both benthic groups when favourable palaeoenvironmental conditions (clayey vs. silty substrates) were established. The acme in diversity was followed by a gradual decline and a barren interval associated with the onset of the mid-Languedocian regression, well constrained throughout the western Mediterranean region. For trilobites, the aftermath of the regression is characterized by a late-Languedocian major faunal turnover of families, followed by a renewed Furongian–early Tremadocian radiation related to the stepwise immigration of trilobite invaders from northern and eastern Gondwana, under persistent transgressive conditions. In contrast, the cinctans reappeared only patchily in late-Languedocian monospecific coquinas and finally disappeared before the Furongian. Thus, the late Languedocian is a crucial interval in which to analyse the decline in diversity and final extinction of cinctans in the aftermath of the mid-Languedocian regression.

Key words: biodiversity, biogeography, echinoderms, trilobites, sequence framework, West Gondwana.

KNOWLEDGE of the taxonomy and affinities of Cambrian echinoderms has greatly increased in the last decade, but, at present, only some clades have been studied in detail for biostratigraphical applications. The taxonomic term 'carpoid' refers to a paraphyletic group of primitive preradial echinoderms that includes cinctans, solutes, ctenocystoids and stylophorans (Smith 2005). These early Palaeozoic echinoderms were flattened, asymmetric to more or less bilaterally symmetric, benthic vagrant low-level suspension or deposit feeders, and colonized a wide diversity of soft substrates.

Cinctans are a clade of echinoderms with a very uneven fossil record, chronologically confined to the mid Cambrian (Smith and Zamora 2009) and palaeogeographically to western Gondwana (including Avalonia) and Siberia (Schroeder 1973; Friedrich 1993, 1995; Rozhnov 2006; Zamora and Smith 2008). As with other echinoderms, cinctans were fully encased in a multi-plated calcite skeleton that provided protection and support for soft tissues (Text-fig. 1). This skeleton commonly disarticulated and became dispersed after death, and so taxonomic studies are largely dependent on taphonomic preservation under special conditions in Echinoderm-Lagerstätten (Smith 1988; Brett *et al.* 1997; Nebelsick 2004; Lefebvre 2007). The middle Cambrian offshore shale of the western Mediterranean region (e.g. Iberian Chains, Cantabrian Zone and Montagne Noire; Text-fig. 2A) is rife with disarticulated ossicles of cinctans and periodically includes complete specimens. The vertical alternation of a different kind of shell accumulations suggests slow background deposition (relatively quiet water) punctuated by rapid, storm-induced events (Álvaro and Vennin 1997).

The Iberian Chains (north-eastern Spain) and the Montagne Noire (southern France) provide the most complete record of cinctan diversity. There, the clade extends from the earliest mid Cambrian until just prior to the mid Cambrian–Furongian boundary (chemostratigraphically marked by the SPICE event; Álvaro *et al.* 2008), and shows apparent rises and falls in diversity.

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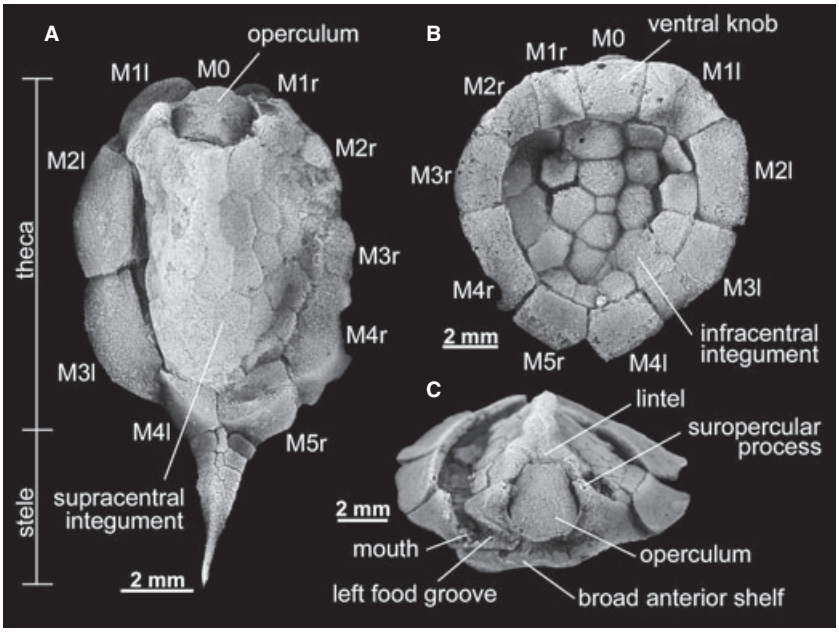
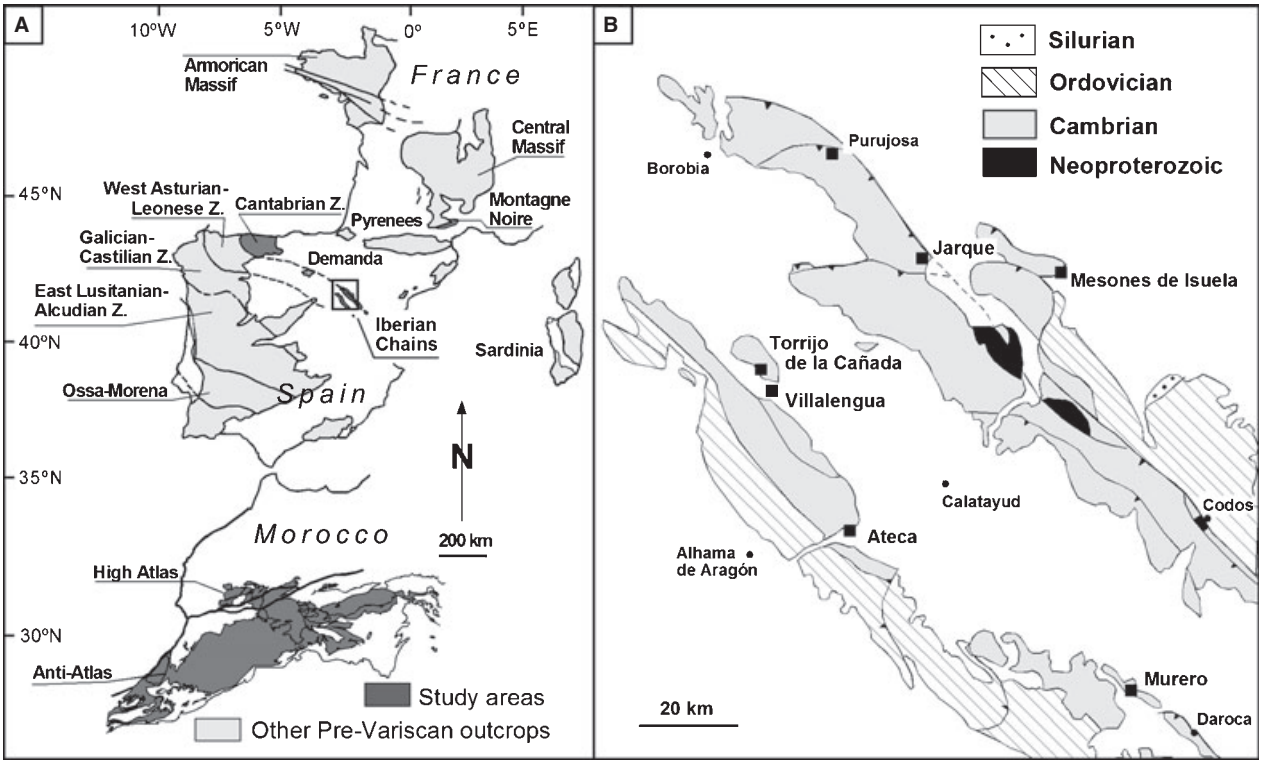


TEXT-FIG. 1. *Gyrocystis testudiformis* Friedrich (1993), a cinctan from the middle Cambrian of the Iberian Chains showing major anatomical features. A, specimen MPZ2009/150. B, specimen MPZ2009/155. C, specimen MPZ2008/4.

However, it is important to establish whether the cinctan diversification patterns are truly biological in nature or artificially inflated by sampling biases. Fine-scale stratigraphical studies that examine the Languedocian decline in cinctan diversity were undertaken to improve sampling of younger cinctans in the Iberian Chains.

In this paper, we document the specific distribution of cinctans from the Languedocian (latest mid Cambrian) of the Iberian Chains for the first time. A comparison with similar strata of the Cantabrian Zone, Morocco and the Montagne Noire is carried out. Fluctuations in cinctan diversity through the middle Cambrian are then analysed,



TEXT-FIG. 2. A, Geological sketch of the pre-Hercynian outcrops reported in the text from the western Mediterranean area, western Gondwana. B, Geological map of the Iberian Chains with indication of localities where specimens have been collected.

to test whether their final decline (1) was a consequence of sampling bias; (2) can be characterized as sharp or gradual over time; and (3) is a response to correlatable external disturbances.

GEOLOGICAL AND STRATIGRAPHICAL FRAMEWORK

In the western Mediterranean region, the middle Cambrian (or third Cambrian Series) is regionally subdivided into three stages, named Leonian, Caesaraugustan and Languedocian in the Iberian Peninsula and Montagne Noire (Liñán *et al.* 1993; Álvaro and Vizcaïno 1998); and named Agdzian, Caesaraugustan and Languedocian (last revision in Geyer and Landing 2004) in Morocco. The bases of the Leonian and Agdzian are obviously different (for a discussion, see Álvaro and Clausen 2005), but as our work is focused on Iberian and French material, we will follow the former scale.

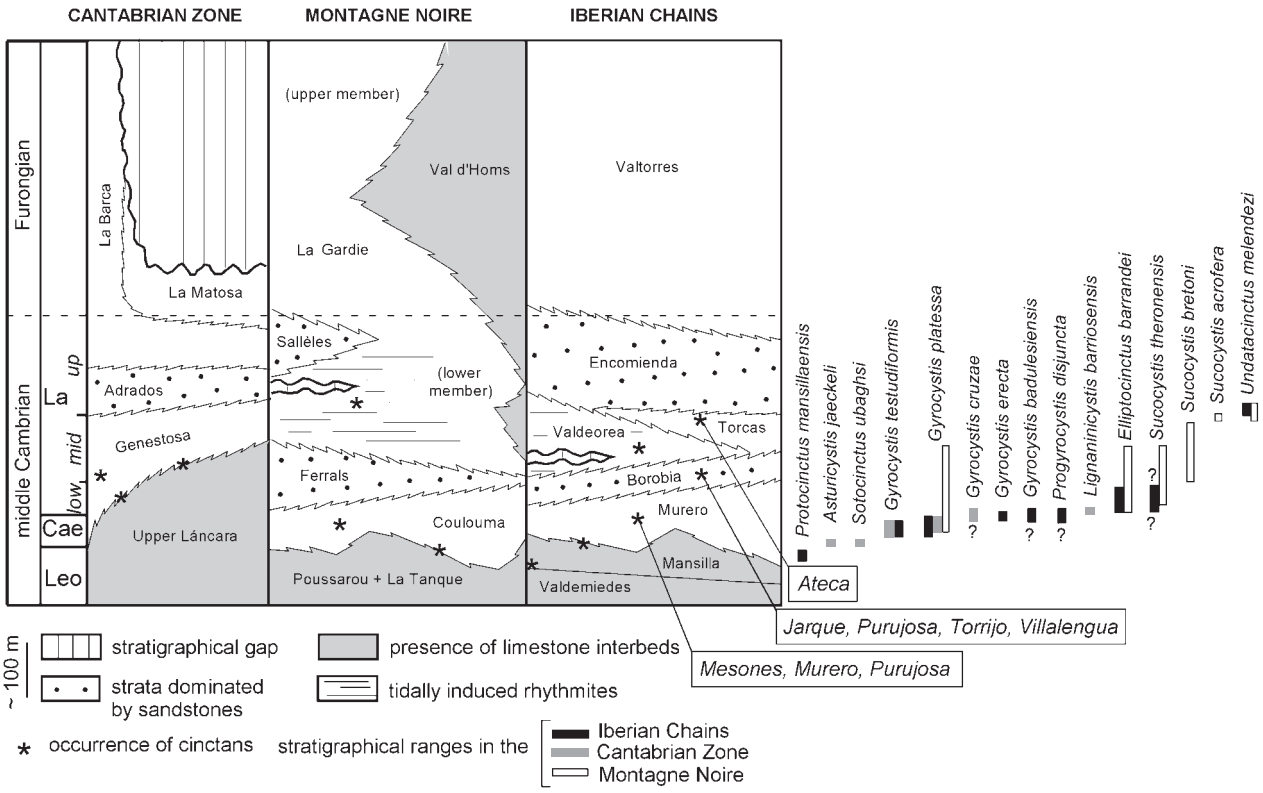
In the Iberian Peninsula (Text-fig. 2A), mid-Cambrian cinctans have been reported from two different basins i.e. the northern Cantabro-Ebroan Basin (including the Cantabrian Zone and the Iberian Chains; Prado *et al.* 1860; Mallada and Buitrago 1878; Hernández-Sampelayo 1935; Schroeder 1973; Friedrich 1993; Sdzuy 1993; Gil Cid and Domínguez 1995*b*; Zamora *et al.* 2007; Zamora and Smith 2008; Rahman and Zamora 2009) and the southern Ossa-Morena Basin (Ossa Morena Zone; Chauvel and Meléndez *in* Gutiérrez-Marco *et al.* 1984; Friedrich 1995; Gil Cid and Domínguez 1995*a*). While cinctans are relatively ubiquitous in Leonian and Caesaraugustan strata, they are poorly known from Languedocian rocks. In fact, only two papers had previously described Languedocian cinctans from the Iberian Chains; Schroeder (1973) erected the species *Undatacinctus melendezi*, and Zamora and Rahman (2008) reported the oldest occurrence of the genus *Sucocystis*, previously known from the Montagne Noire. In the Cantabrian Zone, two different species have been recently described: *Lignanicystis barriosensis* Zamora and Smith, 2008 and *Gyrocystis* sp. L (Zamora *et al.* 2007). In contrast, Languedocian cinctans are relatively abundant and diverse in the Montagne Noire (Munier-Chalmas and Bergeron *in* Bergeron 1889; Cabibel *et al.* 1959; Ubaghs 1967; Termier and Termier 1973; Friedrich 1993; Vizcaïno and Lefebvre 1999; Álvaro *et al.* 2001) and Morocco (Destombes 1964; Termier and Termier 1973; Friedrich 1993, 1995), with six and two species formally named, respectively.

In the Iberian Chains, the earliest cinctans are recorded in the lowermost part of the Leonian Mansilla Formation (Text-fig. 3). They occur as isolated ossicles embedded in variegated shale and limestone, and are taxonomically indeterminate at genus level. The presence of partly to wholly articulated skeletons in the uppermost part of the same formation has allowed the identification of *Protocinctus* Rahman and Zamora (2009). This endemic genus displays a short stratigraphical range in mixed limestone/shale substrates. Cinctans later became relatively common in shell accumulations across the Caesaraugustan–Languedocian transition (Murero and base of Borobia formations), across which seven genera and eleven species have been reported (Smith and Zamora 2009). A barren interval of cinctans, 100–300 m thick and spanning the mid–late Languedocian transition, coincides with a regional regressive event. The barren interval consists of prograding tidally influenced and shoaling depositional systems (upper part of the Borobia and the entire Valdorea formations). The sporadic re-occurrence of cinctans in the overlying transgressive Torcas Formation marks their latest record in the Iberian Chains (for a synthesis of facies associations, sedimentary patterns and sequence framework, see Álvaro *et al.* 2007).

As a result, the middle–upper Languedocian, siliciclastic-dominated strata of the Iberian Chains have yielded an impoverished and sparse record of cinctans prior to their final extinction. This suggests that these echinoderms remained as an extremely poorly diversified group in sandstone to shale substrates, which contrasts with the richer and more diversified assemblages preserved in coeval intervals of the Montagne Noire, predominantly offshore-dominated shale substrates punctuated with episodic intervals of carbonate productivity (Álvaro *et al.* 2003*a*, 2007). However, because echinoderm taxonomy is based largely upon features of articulated or partly articulated skeletons, the scarcity of articulated (and subsequently determinable) cinctans could also be related to sampling bias, and our fieldwork has tried to test this possibility. The specimens described below have been collected from seven different localities, and nine fossiliferous horizons, in the Iberian Chains (Text-fig. 2B). The strata encompassed are Languedocian in age according to the trilobite-based zonation of Álvaro and Vizcaïno (1998).

SYSTEMATIC PALAEONTOLOGY

Remarks. The cinctan skeleton consists of two parts: the main body or theca and a posterior appendage named stele (Text-fig. 1). The theca is constructed with a ring of stout large marginal plates, the so-called cinctus. It is dorsally and ventrally covered with two membranes of tessellate plates, named supra- and infracentralia, respectively. The main body orifices are situated in the anterior part of the theca, some piercing the cinctus and some the supracentral integument. One or two food grooves reach the anterior part of the cinctus that converge in the mouth, which is situated in the anterior right part of the



TEXT-FIG. 3. Stratigraphical ranges of the formally named cinctans reported in the text, found in the Cantabrian Zone (northern Spain), southern Montagne Noire (southern France) and Iberian Chains (north-eastern Spain); modified from Álvaro *et al.* (2004, 2007) and Smith and Zamora (2009).

cinctus, between the two marginal plates M1r and M2r. The stele is a posterior appendage, considered to be a prolongation of the cinctus (Jefferies 1990; Friedrich 1993; Zamora and Smith 2008).

Nomenclature and orientation largely follow Friedrich's (1993) proposal because it is the best way to recognize homologies between different cinctan species (Smith and Zamora 2009). The marginal plate that coincides with the axial plane and underlies the operculum is named M0. The rest of the plates throughout the cinctus are numbered as M1r to Mnr or M1l to Mnl, depending on their right *or* left position to M0.

Phylum ECHINODERMATA Bruguière, 1791 (ex Klein, 1734)
Class CINCTA Jaekel, 1918
Family GYROCYSTIDAE Jaekel, 1918

Genus GYROCYSTIS Jaekel, 1918

Type species. *Gyrocystis platessa* Jaekel, 1918, from the middle Cambrian Coulouma Formation, Montagne Noire, France.

Remarks. This genus is the most diversified among cinctans and consists of five different species, reported from Spain and France. Until Friedrich's (1993) monograph, only the type species was known. Friedrich (1993) erected three further species from Spanish strata. *Gyrocystis testudiformis*, from the Iberian Chains and the Cantabrian Zone, is easily differentiable because of its dome-shaped supracentral integument (Text-fig. 1). *G. badulesiensis* from the Iberian Chains shares the same general shape with *G. platessa* but differs in the presence of more developed suropercular processes and knobs under several marginal plates. *G. erecta*, an endemic species from the Iberian Chains, was known from a single specimen with a very rugose ornamented stereom. Gil Cid and Domínguez (1995*b*) erected *G. cruzae*, from the Cantabrian Zone, after revising a historic collection housed in the Geominero Museum (Madrid, Spain). However, Friedrich (1995) considered it as a junior synonym of *G. platessa*. Based on the general shape of the theca (as longer as it is wide) and the presence of a ventral knob under the marginal plate M0 in *G. cruzae*, this species is much more similar to *G. testudiformis*. However, a detailed comparison between both species is not possible because the most important feature of *G. testudiformis* (a domed supracentral integument) is not preserved in any known specimen of *G. cruzae*. As a result, further specimens are needed to determine whether *G. cruzae* is a valid species. Additional

specimens belonging to *Gyrocystis* and described in open nomenclature have been reported from the Cantabrian Zone (Zamora *et al*. 2007) and the Ossa-Morena Zone (Gil Cid and Domínguez 1995*a*).

Gyrocystis platessa Jaekel, 1918
Plate 1, figures 1–3

Material and preservation. One hundred and fifty-three complete specimens preserved as natural moulds in claystone. All of them were recovered from horizons related to obrution episodes. Repository numbers are MPZ2009/141–147 and MPZ2009/383-528.

Locality and age. The species has been collected from various localities and horizons ranging from the middle Caesaraugustan to the lower Languedocian. From lower Languedocian strata, the species has been found in the Murero Formation (*Manublesia thorali* Zone) of two different localities: Murero (RV1 section; Liñán and Gozalo 1986) and Purujosa (Pur3 section).

Remarks. G. platessa was first described by Jaekel (1918) with material from the Montagne Noire. His original reconstruction shows a cinctan with 12 marginal plates, a characteristic that was subsequently considered as diagnostic, and several cinctans were erroneously assigned to the genus (e.g. *G. barrandei*, now *Elliptocinctus barrandei*; see Ubaghs 1967; Schroeder 1973). Friedrich (1993) reviewed the type material from Jaekel (1918), housed in the Ernst-Moritz-Arndt-Universität Greifswald, and described and illustrated a cinctan skeleton bearing eleven marginals, an unusual characteristic for *G. platessa*.

G. platessa is a common cinctan that displays an oval-shaped theca composed of ten marginal plates (rarely eleven), a broad anterior flange on M0, small suropercular processes developed on M1, short left food groove extending to M0, and a lack of ventral knobs.

Gyrocystis erecta Friedrich, 1993
Plate 1, figures 4–9

Material and preservation. Four specimens preserved as natural moulds in grey-blue claystones. Repository numbers are MPZ2009/156–158 and MPZ2009/356.

Locality and age. The original locality where Friedrich (1993) collected the specimens was situated in the vicinity of Badules (Iberian Chains; Text-fig. 1B), but this site is at present destroyed by farm work. Additional specimens included in this work come from Purujosa (for a detailed stratigraphical setting, see Zamora *et al*. 2009). Although the stratigraphical position of Friedrich's material is not well constrained, the sampling of new specimens at the top of the Murero Formation, 2.5 m above the FAD (First Appearance Datum) of *Manublesia thorali*, allows an assignment to its homonymous biozone (early Languedocian).

Remarks. The original description of the species was based on a single specimen comprising an incomplete dorsal theca and several isolated plates. The species is easily distinguishable by its distinct dorsal theca, feebly ornamented with ridges, large suropercular processes with a spatula-like shape, and lack of ventral knobs. Other characteristics shared with the rest of *Gyrocystis* species are the oval shape of the theca and the presence of ten marginal plates, a short left food groove extending to the outer part of M0, and a lintel composed of three large suropercular plates.

Family SUCOCYSTIDAE Friedrich, 1993

Genus SUCOCYSTIS Cabibel, Termier and Termier, 1959

Type species. Sucocystis theronensis Cabibel, Termier and Termier, 1959, from the middle Cambrian Coulouma Formation, Montagne Noire, France.

Sucocystis theronensis Cabibel, Termier and Termier, 1959
Plate 2, figures 1–5, 9, 10

Material and preservation. Fourteen specimens preserved as natural moulds in siltstones. Repository numbers are MPZ2009/136–140 and MPZ2009/348–355.

Locality and age. All specimens come from a single horizon at the lowermost part of the Borobia Formation in Torrijo de la Cañada (Text-fig. 2B), dated as early Languedocian, although the associated trilobites do not presently permit assignment to a specific biozone.

Remarks. The species is easily distinguished by the presence of a large spine in the central plate of the lintel. Other features are a circular (slightly asymmetric) theca, a variable number of marginal plates (ranging from 10 to 13), the absence of a right marginal groove, a left marginal groove extending to marginal plate M1l, and the presence of small suropercular processes on plates M1, an oval-shaped ventral knob under plate M0, and two large swellings under plates M2, M3 and M4?

Sucocystis sp. M
Plate 2, figure 6

Material and preservation. A single specimen representing a dorsal theca and preserved as natural mould in a green slab of claystone. Repository number is MPZ2007/2479.

Locality and age. Mesones de Isuela (for stratigraphical details see Zamora and Rahman 2008), *Manublesia thorali* Zone, early Languedocian.

Remarks. This specimen was considered by Zamora and Rahman (2008) as the oldest representative of the genus in the Iberian Chains. Some features differentiating *Sucocystis* sp. M from other species of the genus include (1) the general shape of the theca, which is wider proximally and tapering towards the appendage in *Sucocystis* sp. M and is nearly circular in other species; (2) the length and number of food grooves: *Sucocystis* sp. M has two food grooves as *S. acrofera*, whereas *S. theronensis* and *S. bretoni* bear a single left food groove. An important autapomorphic characteristic of *Sucocystis* sp. M is that the left food groove is longer than in any other species, extending to the marginal plate M2l. The absence of more specimens prevents the erection of a new species for the moment.

Genus ELLIPTOCINCTUS Termier and Termier, 1973

Type species. Trochocystites barrandei Munier-Chalmas and Bergeron *in* Bergeron, 1889, from the middle Cambrian Coulouma Formation, Montagne Noire, France.

Elliptocinctus barrandei (Munier-Chalmas and Bergeron *in* Bergeron, 1889)
Plate 2, figures 7–8; Plate 3, figures 1–2

Material and preservation. Twenty-one complete specimens preserved in blue and yellowish siltstones. Repository numbers are MPZ2009/131–135 and MPZ2009/529–544.

Locality and age. Torrijo de la Cañada, Purujosa and Villalengua (Text-fig. 2B), Borobia Formation, *Solenopleuropsis* Assemblage Zone, early Languedocian.

Remarks. Elliptocinctus barrandei was originally assigned to the genus *Trochocystites* (Munier-Chalmas and Bergeron *in* Bergeron, 1889). Based on the number of marginals and the presence of a prominent knob under plate M0, Ubaghs (1967) erroneously assigned this species to *Gyrocystis*. The genus *Elliptocinctus* was erected by Termier and Termier (1973), who selected as diagnostic features the presence of 12 marginal plates and prominent ventral knobs under some marginal plates. Friedrich (1993) emended Termier and Termier's diagnosis and made a complete description of the taxon including a discussion about its intraspecific variation. Friedrich (1993) also included the genus within the new family Sucocystidae and indicated that *Elliptocinctus barrandei* displays a variable number of marginal plates, ranging from 10? to 13, although the most common number is 12. The ventral swellings are distributed as follows: one prominent ventral knob under marginal plate M0 and one large knob on each side of the theca forming a part of a continuous ridge with contiguous plates. The presence of a short right marginal groove extending to M2r and a medium-sized left one extending to M1l are other distinct features. The presence of large suropercular processes is another feature convergent with some species of *Gyrocystis* (Smith and Zamora 2009).

Sdzuy (1993) discussed the existence of the family Sucocystidae, proposed by Friedrich (1993), and assigned *Elliptocinctus* to the gyrocystids with retention of plesiomorphic characters, such as the large marginal grooves, which probably represent a plesiomorphic characteristic of the cinctans. Smith and Zamora (2009) validated the family Sucocystidae by using a cladistic analysis and grouped *Elliptocinctus* with *Lignanicystis* in a monophyletic clade derived within the sucocystids.

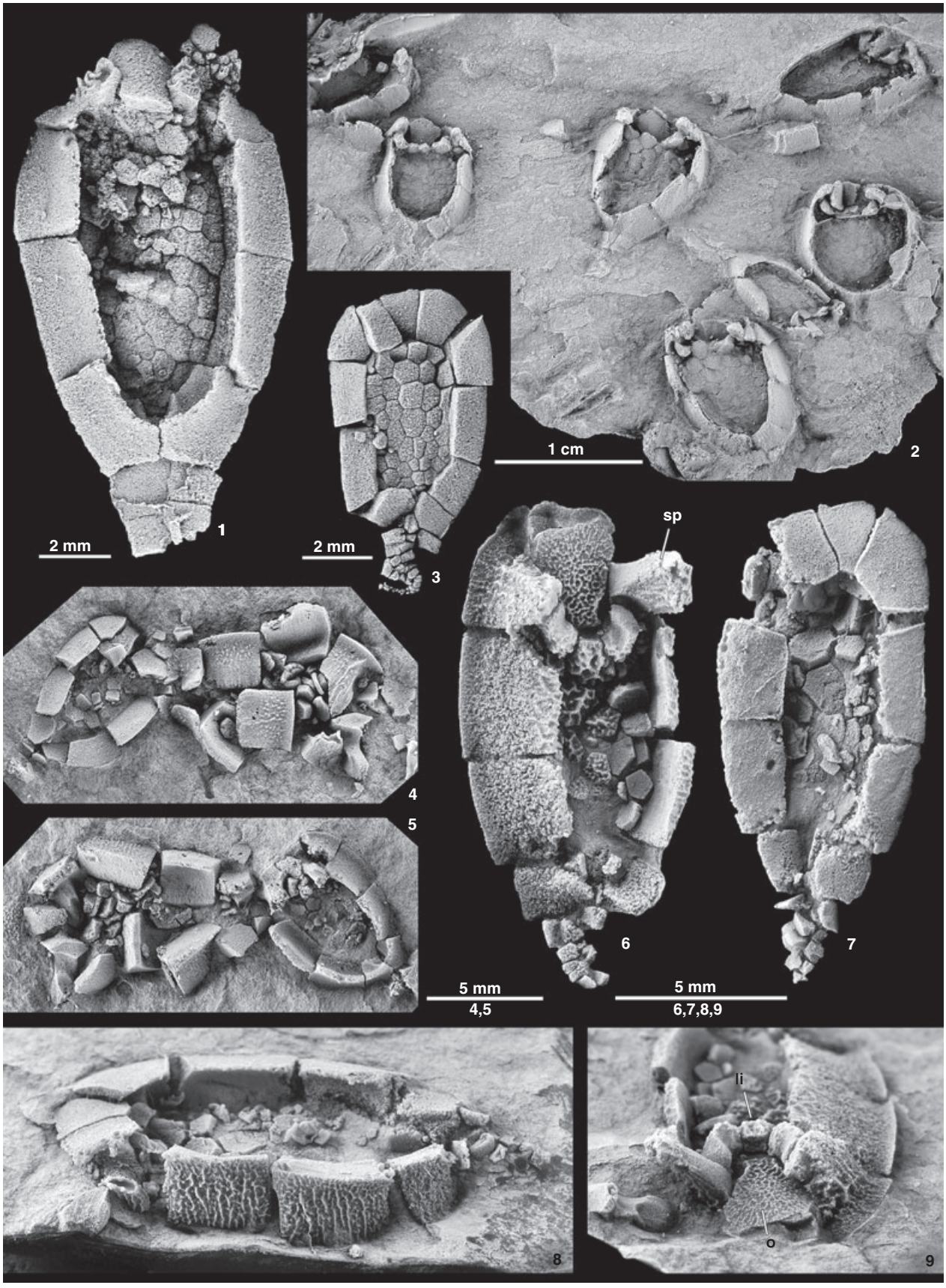
The Spanish material described in this paper can be assigned to *E. barrandei* because of the similar distribution of ventral knobs, the presence of 12 marginal plates and large suropercular processes present on M1 marginal plates, and the size and number of marginal grooves.

EXPLANATION OF PLATE 1

Figs 1–3. *Gyrocystis platessa* Jaekel 1918. 1, theca in dorsal view, MPZ2009/528. 2, cluster with several specimens, MPZ2009/141–147. 3, ventral view of a complete specimen with 11 marginal plates (M5r–M5l), MPZ2009/526.

Figs. 4–7 *Gyrocystis erecta* Friedrich 1993. 4–5, two nearly complete specimens, MPZ2009/157–158. 6–9, complete specimen in different views. 6, dorsal view showing a complete theca. Note that marginal and supracentral plates are hardly ornamented. 7, ventral view. 8, lateral right view. 9, frontal view showing the operculum and a lintel composed with three large suropercular plates, MPZ2009/156. Photographs of latex casts whitened with NH_4Cl. Abbreviations: cs: central spine of lintel, dp: dorsal protuberance, li: lintel, m: mouth, o: operculum, p: porta, sop: supraoral plate, sp: suropercular process.

Scale bars represent 2 mm in 1, 3; 5 mm in 4–5 and 10 mm in 2.



ZAMORA and ÁLVARO, *Gyrocystis*

Genus LIGNANICYSTIS Zamora and Smith, 2008

Type species. Lignanicystis barriosensis Zamora and Smith, 2008, from the middle Cambrian Genestosa Member, Oville Formation, Cantabrian Zone, northern Spain.

Remarks. The genus was first included within the trochocystitids because of the presence of a line of sutural pores in the dorsal membrane, as in *Trochocystites* (Zamora and Smith 2008). Although these authors noted that *Lignanicystis* shares many features with *Sucocystis* and *Elliptocinctus*, a recent cladistic revision of all cinctans (Smith and Zamora 2009) has revealed that *Liganinicystis* can be better considered as a derived sucocystid, linked in a clade with *Elliptocinctus*.

Lignanicystis sp.
Plate 3, figures 3–4

Material and preservation. A single specimen (MPZ2009/382) preserving the dorsal part of the theca as natural mould in a greenish claystone.

Locality and age. The specimen was found in an unpublished section in Jarque de Moncayo village (Text-fig. 2B). The beds represent the base of the Borobia Formation and are early Languedocian in age (*Solenopleuropsis* Assemblage Zone).

Remarks. Although many details, such as the ventral integument, stele and right marginal groove, are not preserved, this specimen is clearly identified as *Lignanicystis* because of the presence of the following features: (1) an asymmetric theca with a right embayment; (2) a cinctus composed of 12 marginal plates (M6r–M5l); (3) the length of the left food groove, which extends to the marginal plate M1l; and (4) a lintel composed of four suropercular plates, which are ornamented.

Genus UNDATACINCTUS Smith and Zamora, 2009

Type species. Gyrocystis? *melendezi* Schroeder, 1973, from the uppermost middle Cambrian Torcas Formation of the Iberian Chains, Spain.

Undatacinctus melendezi (Schroeder, 1973)
Plate 3, figures 5–10

Material and preservation. Thirty fully articulated specimens preserved as natural moulds in brownish siltstones. Repository numbers are MPZ2009/126–130 and MPZ2009/357–381.

Locality and age. Same as the type species.

Remarks. Undatacinctus melendezi was first described as a tentative species of *Gyrocystis* (Schroeder 1973) from the middle Cambrian of the Iberian Chains. In the same year, Termier and Termier (1973) described *Trochocinctus pardailhanicu*s (at present, a junior synonym of *S. melendezi*) from the middle Cambrian of the Montagne Noire. Friedrich (1993) considered that both taxa are conspecific and that Schroeder's nomenclature must be retained because of the priority in publication (February vs. December). Friedrich (1993) also included the species within the new genus *Sucocystis*. Smith and Zamora (2009), based on a cladistic analysis, have separated *Sucocystis* (*sensu* Friedrich 1993) into two different genera: *Sucocystis*, which includes *S. theronensis*, *S. acrofera*, and *S. bretoni* and *Undataciсntus*, with *U. melendezi*, *U. quadricornuta*, and *U. undata*.

U. melendezi has a circular theca with two marginal grooves, the left one extending to M1l and the right one to M2r. The ventral knobs are distributed as follows: a single knob occurs under marginal plate M0 and extends to M1, and a large knob on each side of the theca forms a part of a continuous ridge with contiguous plates. The ventral knobs do not occupy more than half of the total

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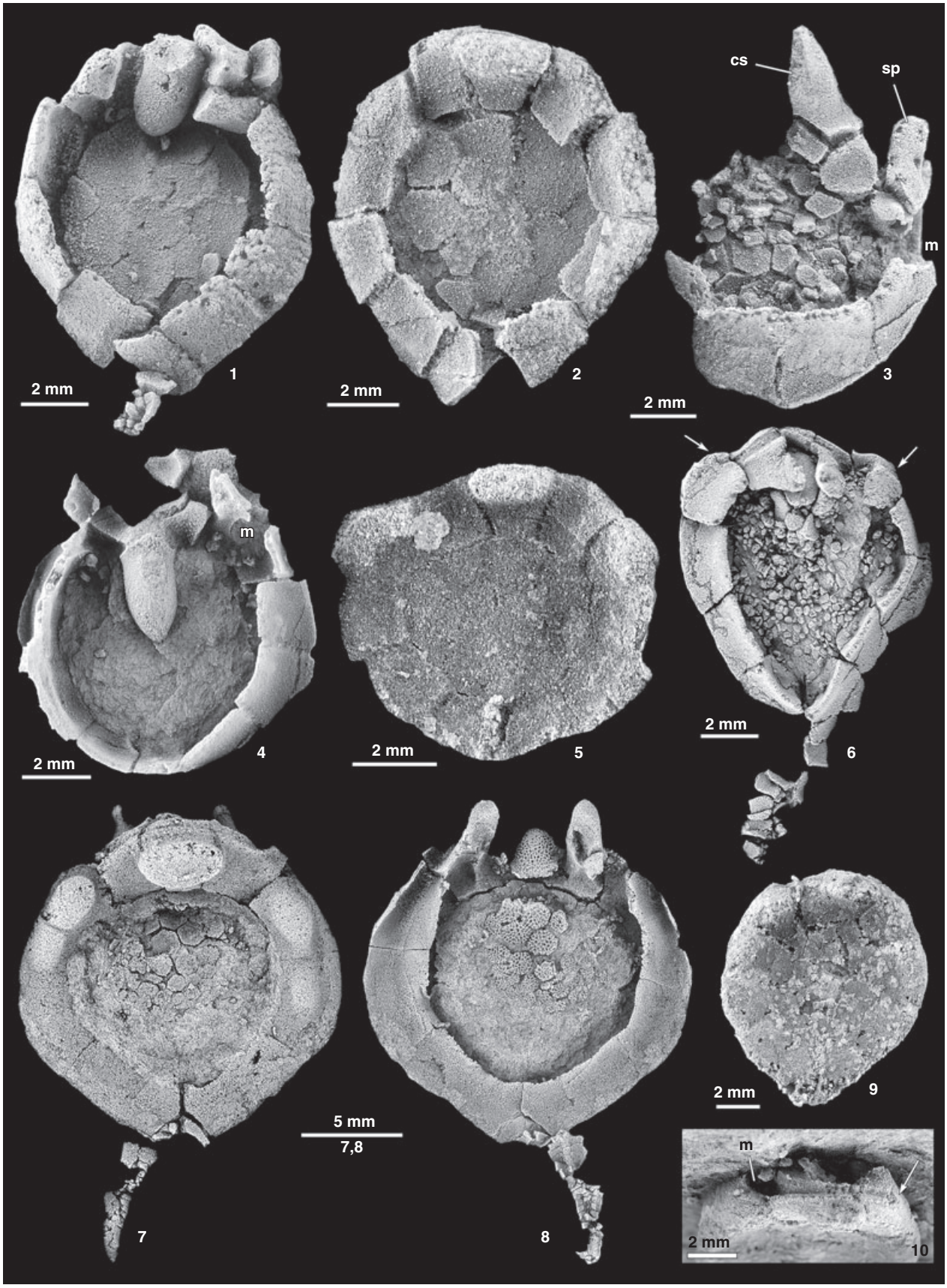
EXPLANATION OF PLATE 2

Figs 1–5, 9–10. *Sucocystis theronensis* Cabibel, Termier and Termier, 1959. 1, 2 theca in dorsal and ventral view, MPZ2009/137. 3, lateral view of an specimen showing the lintel with a diagnostic central spine, MPZ2009/138. 4, complete theca in dorsal view, MPZ2009/139. 5, specimen in ventral view with a prominent anterior knob, MPZ2009/136. 9, 10, specimen in ventral and frontal views, MPZ2009/140.

Fig. 6. *Sucocystis* sp. L, MPZ2007/2479; dorsal view.

Fig. 7, 8 *Elliptocinctus barrandei* (Munier-Chalmas and Bergeron *in* Bergeron, 1889). Complete specimen in ventral and dorsal views, MPZ2009/133. 7, the theca is composed of 12 marginal plates (M6r–M5l); note the typical distribution of ventral knobs. 8, note the two large suropercular processes. Photographs of latex casts whitened with NH_4Cl. Arrows indicate the final portion of food grooves. Abbreviations as in Plate 1.

Scale bars represent 2 mm in figures 1–5, 7; 5 mm in figure 6.



ZAMORA and ÁLVARO, *Sucocystis*, *Elliptocinctus*

ventral surface of each plate and are relegated to the margins. Another important feature emphasized by Smith and Zamora (2009) is the presence of protuberances, slightly developed on some marginal plates. The lack of suropercular processes in the Spanish specimens, by comparison with the French ones, as well as the absence of the right food groove in the French specimens (see Friedrich 1993, pl. 10, figs 6–7), warrant a future revision.

BIOSTRATIGRAPHICAL AND BIOGEOGRAPHICAL IMPLICATIONS

Cinctans are widely distributed in western Gondwana (Morocco, Spain, and France). They usually occur as disarticulated debris locally punctuated by well-preserved specimens. Their study is therefore related to Echinoderm-Lagerstätte conditions, commonly produced as a result of obrution deposits.

Languedocian cinctans are known only from one locality within the Cantabrian Zone (Los Barrios de Luna). There, the Genestosa Shales (Oville Formation) have yielded the species *Gyrocystis platessa* from the *Manublesia thorali* Zone (early Languedocian; Álvaro and Vizcaïno 1998, Vizcaïno *et al.* 2008) and *Gyrocystis* sp. L and *Lignanicystis barriosensis* from the *Solenopleuropsis* Assemblage Zone (early Languedocian; updated from Zamora *et al.* 2007; Zamora and Smith 2008).

In the Montagne Noire, the Languedocian cinctans, more abundant and diverse, are biostratigraphically distributed (Friedrich 1993; Álvaro *et al.* 1999; Vizcaïno *et al.* 2008) as follows: *Gyrocystis platessa* and *Elliptocinctus barrandei* from the *Manublesia thorali* to *Jincella convexa* zones of the Coulouma Formation; *Sucocystis theronensis* from the *Solenopleuropsis* to *Jincella convexa* zones; *Sucocystis* aff. *theronensis* and *Sucocystis bretoni* from the *Jincella convexa* Zone; *Sucocystis acrofera* from the *Bailiella souchoni* Zone; *Undatacinctus melendezi* from the *B. souchoni* to *Eccaparadoxides macrocercus* zones of the La Gardie and Val d'Homs formations; and a single specimen of *U.* aff. *quadricornuta* (that needs revision) from the *B. souchoni* Zone.

Only three named species are known from the Languedocian of Morocco: *Undatacinctus undata* and *U. quadricornuta* from the *Bailella* cf. *levyi* Zone of the Bailiella Formation (Friedrich 1993; Geyer *et al.* 1995), and *Sucocystis*? *maroccana*, the latter being biostratigraphically unconstrained. One unnamed species (gen. nov. sp. M) was reported from the same zone by Friedrich (1995).

Finally, seven different species have been recognized in the Languedocian of the Iberian Chains (see Systematic palaeontology): (1) *Gyrocystis platessa*, *Gyrocystis erecta* and *Sucocystis* sp. from the Murero Formation, and *Lignanicystis* sp. from the Borobia Formation, all of them belonging to the *Manublesia thorali* Zone (*Sucocystis theronensis* was reported from the early Languedocian); (2) *Elliptocinctus barrandei* from the *Solenopleuropsis* Assemblage Zone of the Borobia Formation; and (3) *Undatacinctus melendezi* from the *Eccaparadoxides macrocercus* Zone (late Languedocian) of the Torcas Formation.

The restricted stratigraphical ranges of cinctans can aid biostratigraphical and biogeographical correlations throughout the uppermost middle Cambrian of western Gondwana. Owing to the scarcity of the fossil record that characterizes the Languedocian strata of neighbouring basins, the cinctans can be used as a key group for regional correlation in the absence of biostratigraphically significant trilobites (Text-fig. 3).

DIVERSITY PATTERNS OF MIDDLE CAMBRIAN CINCTANS

A total of 22 cinctan species are known from the middle Cambrian of West Gondwana. They occur in four marine platforms, the relics of which occur in the Cantabrian Zone and its south-eastern prolongation, the Iberian Chains (Spain), the Montagne Noire (France), and the Atlas Mountains (Morocco).

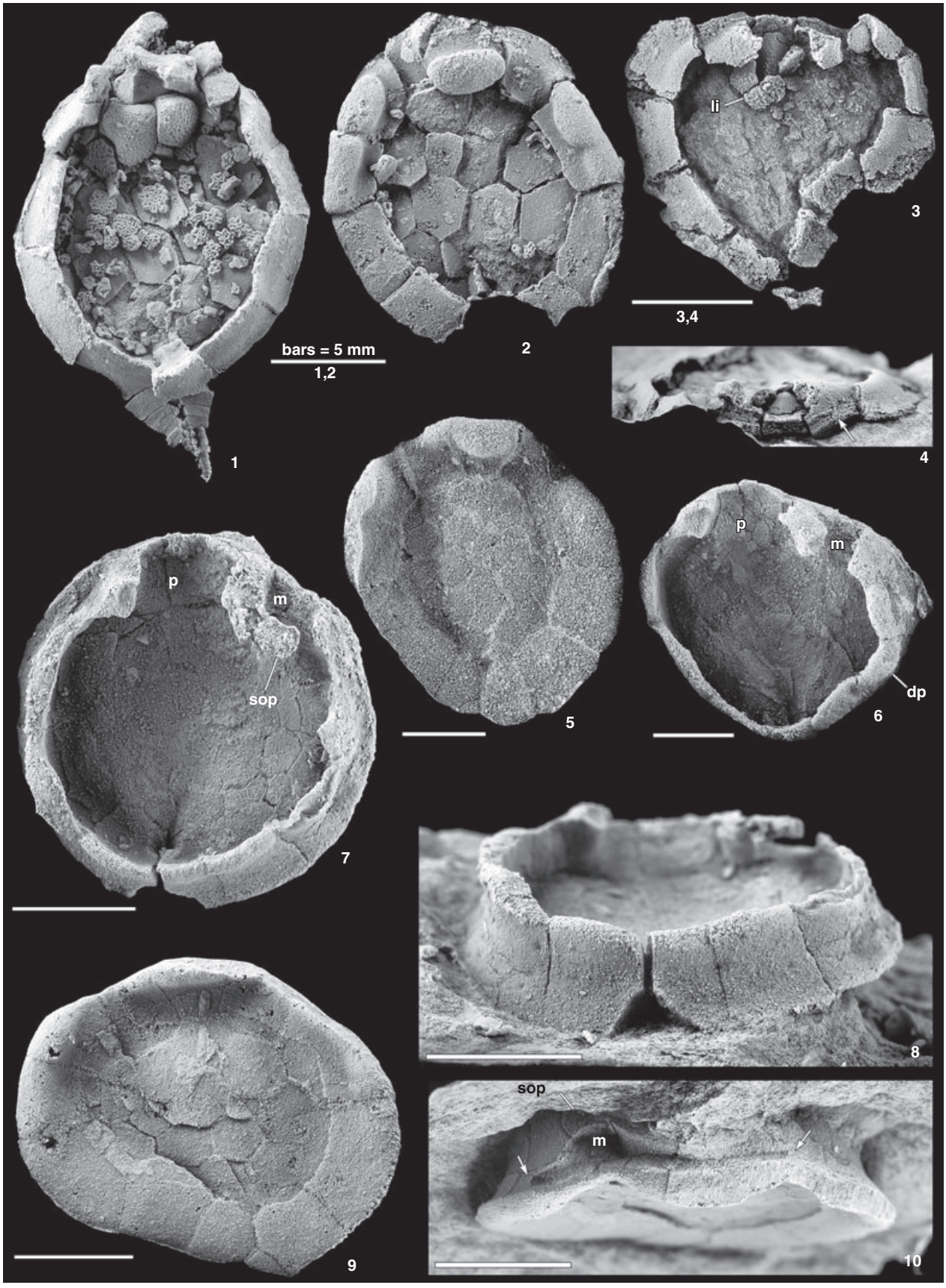
EXPLANATION OF PLATE 3

Figs 1–2, *Elliptocinctus barrandei* (Munier-Chalmas and Bergeron *in* Bergeron, 1889). MPZ2009/131. 1, dorsal view of a theca with 12 marginal plates (M6r–M5r). 2, ventral view showing the disposition of knobs.

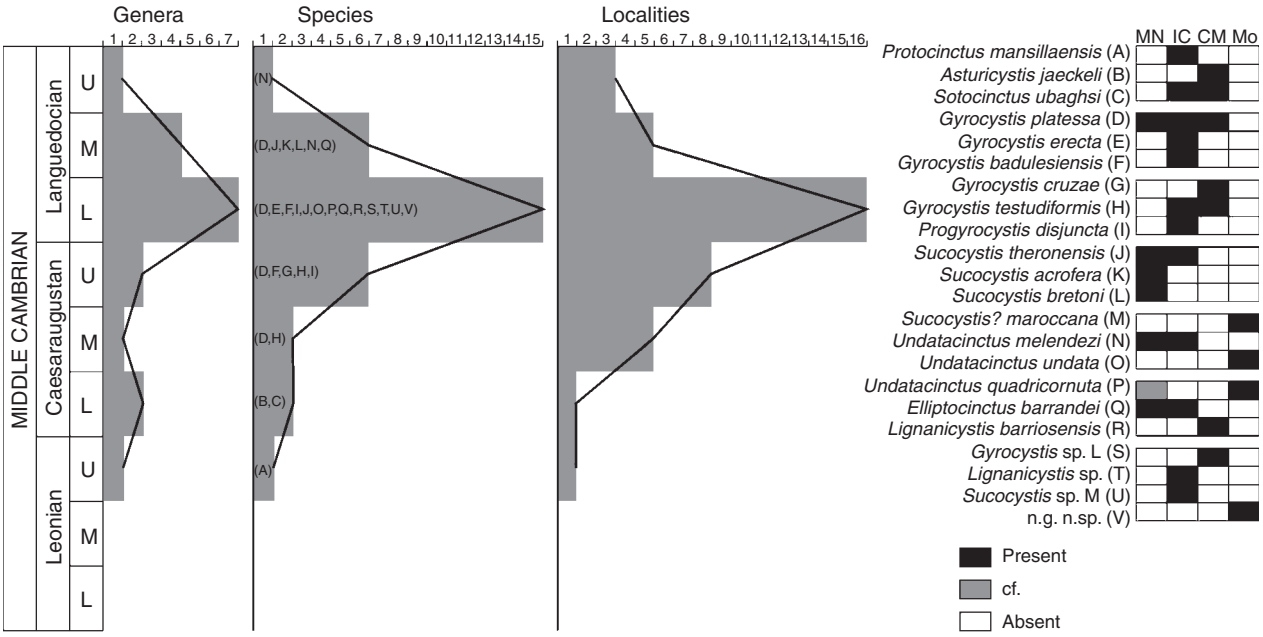
Figs 3–4, *Lignanicystis* sp. MPZ2009/382. 3, dorsal view of a weakly asymmetric theca with twelve marginal plates (M6r–M5l). 4, frontal view; arrow indicates the final portion of left food groove.

Figs 5–10. *Undatacinctus melendezi* (Schroeder, 1973). 5, ventral view showing the disposition of knobs, MPZ2009/128. 6, dorsal view, arrow indicates the position of dorsal protuberances on marginal plates, MPZ2009/130. 7–8, specimen in dorsal and posterior view, MPZ2009/126. 9–10, specimen in ventral and frontal view, MPZ2009/127. Photographs of latex casts whitened with NH_4Cl. Arrows indicate the termination of food grooves. Abbreviations as in Plate 1.

Scale bars represent 5 mm in all figures.



ZAMORA and ÁLVARO, *Elliptocinctus, Lignanicystis, Undatacinctus*



TEXT-FIG. 4. Taxonomic diversity of cinctan species and genera throughout the middle Cambrian, represented by three successive stages and nine substages spanning this interval; updated from Friedrich (1993), Álvaro *et al.* (2001), Smith and Zamora (2009) and this work. Number of localities in West Gondwana yielding cinctans per time interval is also plotted. Abbreviations: MN, Montagne Noire; IC, Iberian Chains; CM, Cantabrian Mountains; Mo, Morocco; U, upper; M, middle; L, lower.

A histogram of diversity has been constructed based on the presence or absence of genera and species in different substages (Text-fig. 4). The biostratigraphical timescale used divides the middle Cambrian into three stages (Leonian, Caesaraugustan, and Languedocian), which are subsequently subdivided into three further substages.

We have revised the type material of all of the species and re-sampled many of their type localities to evaluate their biostratigraphical position accurately. Only one taxon (*Sucocystis*? *maroccana*) has not been considered because its biostratigraphical placement is not well constrained (Friedrich 1993). The stratigraphical ranges of two taxa (*Progyrocystis disjuncta* and *Gyrocystis badulesiensis*) are not known in detail; they were reported from the ancient '*Solenopleuropsis* Stage', which now includes the upper Caesaraugustan–lower Languedocian interval. For this reason, we have plotted these species in both substages (Text-fig. 4). There are several taxa (18 per cent) reported in open nomenclature, which have also been included in the diagram. They are sufficiently morphologically distinct that they certainly represent new species. Their presence or absence only affects the absolute value of an early Languedocian diversity peak.

Cambrian rocks from western Gondwana (in our case study, Spain and France) show the most complete fossil record of cinctans worldwide. The oldest cinctan record comes from the middle Leonian of the Iberian Chains. It is represented by ossicle debris and the absence of complete specimens is probably because of taphonomic bias. The same taphonomic condition, marked by the onset of the griotte facies (purple to reddish, limestone/shale couplets deposited on the top of tectonically induced palaeohighs), is diachronous and spans more time in the Montagne Noire than in the Iberian Chains (Álvaro and Vennin 1997; Álvaro and Vizcaïno 1998). The oldest described species is *Protocinctus mansillaensis* Rahman and Zamora, 2009, from the Mansilla Formation (upper Leonian) of the Iberian Chains. Cinctans then increased in diversity until the late Caesaraugustan–early Languedocian boundary interval. During the mid Caesaraugustan–early Languedocian interval, the genus *Gyrocystis* flourished, and its remains are conspicuous throughout the Murero Formation. In the earliest Languedocian, cinctans peak in diversity with the appearance of new genera, such as *Elliptocinctus*, *Lignanicystis*, *Sucocystis*, and *Undatacinctus*. Peak diversity was reached slightly later in the Montagne Noire, where it is reached across the early/mid-Languedocian boundary interval (Álvaro *et al.* 2001).

An important regression is documented in the middle Languedocian of western Gondwana, and is represented by the Ferrals Formation in the Montagne Noire and the Borobia and Valdeorea formations in the Iberian Chains. As a result, an interval barren of cinctans is documented in both regions. Again, the time span involved in both regressive stratigraphical packages is slightly diachronous and is represented by thicker units in the 'proximal'

Iberian Chains (100–300 m) than in the 'distal' Montagne Noire (50–150 m; Álvaro *et al.* 2007). After this regressive barren interval (named 'regression-induced extinction' in the trilobite literature; Álvaro *et al.* 1999), only two cinctan species survived in the Montagne Noire: *Sucocystis acrofera* and *Undatacinctus melendezi*. During the late Languedocian, the transgressive conditions of the overlying Torcas (Iberian Chains) and La Gardie/Val d'Homs (Montagne Noire) formations allowed re-colonization of inner-platform substrates, with the single record of *U. melendezi* in both areas. Because the mid Languedocian regression shows a strong influence on cinctan diversity patterns, a comparison with benthic trilobite response to this regression was undertaken (stratigraphical ranges of trilobite species in the Iberian Chains and Montagne Noire were updated in Liñán *et al.* 1996; Álvaro and Vizcaïno 1998; Álvaro *et al.* 2001).

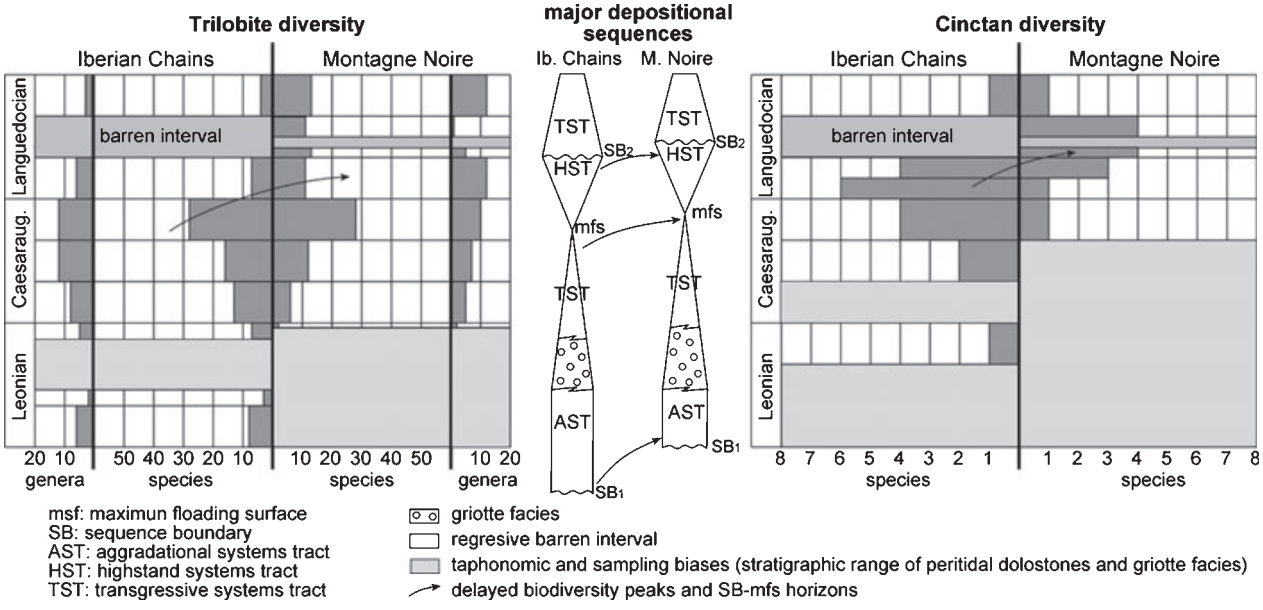
CINCTAN VS. TRILOBITE RESPONSES TO ENVIRONMENTAL PERTURBATIONS

Depositional changes that accompanied the mid Cambrian aggradational, transgressive and regressive sedimentary cycles recorded in the Iberian Chains and Montagne Noire exerted a strong influence on shallow marine benthic communities. This influence can be evaluated by comparing the superposed, facies-controlled patterns of benthic trilobites and cinctans.

The data set from both marine platforms consists of more than 80 species of trilobites and 15 of cinctans, from mixed (carbonate-siliciclastic) and siliciclastic depositional systems (Text-fig. 5). Total species diversity was determined for each chronostratigraphical interval and does not document population (specimen) diversity, but only taxonomic richness (Friedrich 1993, 1995; Álvaro *et al.* 1999, 2001, 2003*b*, 2007; Álvaro and Vennin 2001; Smith and Zamora 2009).

The Leonian–Caesaraugustan radiation

Trilobites underwent a distinct Leonian–Caesaraugustan radiation, during which most families appeared without ancestors in the regional fossil record, in a major migratory radiation (Álvaro *et al.* 1999). The synsedimentary breakdown of this passive margin led to deposition of high-energy mixed strata on the top of dispersed palaeohighs (the so-called griotte facies). The diachroneity of this tectonic setting and the observation that only disarticulated and fragmented have created episodic gaps in the Leonian fossil record. This is represented in Text-figure 5 as a taphonomic bias that underlies the late Leonian-Caesaraugustan immigration and radiation of trilobites. This radiation is not facies-controlled because trilobites appeared in a widespread variety of facies and environments during the Leonian. Diversity increased and species proliferated during the Caesaraugustan, a time span characterized by relative environmental stability.



TEXT-FIG. 5. Comparative sketch of the mid Cambrian diversity patterns exhibited by trilobites and cinctans and sequence framework between the Iberian Chains and southern Montagne Noire; note the parallel delayed distribution of biodiversity peaks and sequence discontinuities; modified from Álvaro *et al.* (1999, 2007), Álvaro and Clausen (2005), Wotte *et al.* (2007), Smith and Zamora (2009), and this work.

The earliest mid Cambrian faunal diversification can be regarded as the adaptative radiation of an immigrant trilobite community that progressively invaded the western Gondwana margin from deeper-water environments. The Leonian immigration is characterized by the stepwise appearance of relatively cosmopolitan trilobites, such as the acrocephalitids, agraulids, corynexochids, conocoryphids, paradoxidids, solenopleurids and agnostids (condylopygids, phalacromids and spinagnostids). The western Mediterranean region apparently operated as a centre of evolutionary radiation (or a site of speciation), from which the species were able to spread outwards into adjacent platforms, in some cases by sympatric speciation. There were no physical barriers preventing trilobite dispersal, which was favoured by uniform seafloor conditions (open-platform, clayey offshore substrates) and low-temperature gradients (Álvaro and Vizcaïno 2003).

Cinctans mimicked the immigration-radiation patterns exhibited by trilobites, although their abundance and variety did not reach comparable values, and their biogeographical distribution, outside the western Mediterranean region, is exclusively represented by spotty occurrences in Avalonia and Siberia.

The abrupt appearance of cinctans in Spain is probably related to Leonian environmental and facies changes. In the Iberian Chains, cinctans are absent in the Valdemiedes Formation (which includes the lower/middle Cambrian boundary) but the first levels of the overlying Mansilla Formation are rife with their disarticulated ossicles (Text-fig. 5).

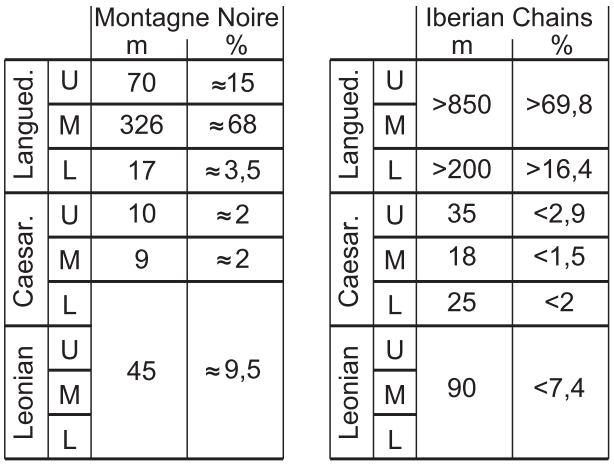
The late Caesaraugustan–early Languedocian diversity peaks

This interval, which coincides with diachronous peaks in trilobite and cinctan diversity, is represented in both areas by homogeneous shale punctuated by tempestites deposited in an offshore setting (Murero and Coulouma formations; Text-fig. 3). Palaeogeographical changes suggest that the higher-diversity assemblages were associated with more open-aspect facies brought in by a major transgression. Despite the absence of authigenic minerals representative of flooding conditions (such as glauconite and phosphate), maximum flooding can be broadly correlated with a distinct peak in trilobite families, genera and species, and a relative decrease in the record of tempestites (Álvaro and Vennin 1997). Peak trilobite was reached during the late Caesaraugustian in the Iberian Chains and the late Caesaraugustan–early Languedocian boundary interval in the Montagne Noire, a subtle diachronism based on the more distal palaeogeographical features recorded in the French platform (Álvaro *et al.* 1999). In contrast, the cinctan diversity peak is recorded in the *Manublesia thorali* Zone (early Languedocian) of the Iberian Chains and in the *Solenopleuropsis* Assemblage – *Jincella convexa* zones (early–mid Languedocian) of the southern Montagne Noire (Text-fig. 5). This diachronic relationship can be also related to the delayed onset of the following mid-Languedocian regression, the preliminary effects of which were first recorded in the Iberian Chains. As a result, early Languedocian accumulations of disarticulated cinctan ossicles embedded in siltstone strata increased dramatically, while debris of disarticulated and broken trilobite sclerites became impoverished.

Unfortunately, the regional middle Cambrian chronostratigraphical chart of the study area has not yet been constrained geochronologically, so we cannot estimate a precise time span for the reported Leonian–Caesaraugustan radiation and the acme of trilobites and cinctans, however, by comparison with the duration of the entire middle Cambrian, the following Languedocian interval was significantly longer than the rest of the system (Vizcaïno *et al.* 2008).

The mid Languedocian decline and barren interval

The middle–upper Languedocian interval is at least five times thicker than the Leonian–Caesaraugustan strata (Text-fig. 6). Its impoverished fossil record points to a long-term decline followed by a barren interval. A major reduction in the number of trilobite genera and species occurred during the mid Languedocian, at a time of widespread coarse-grained terrigenous input associated with a well-documented regression. This is characterized in both platforms by progradation of a siliciclastic rimmed platform with three major depositional systems, in ascending order (or from distal to proximal environ-



TEXT-FIG. 6. Comparative sketch of sedimentary thickness vs. substages in exposures representing distal palaeogeographical areas; updated from Álvaro and Vennin (1997), Álvaro and Vizcaïno (1998), Álvaro *et al.* (2001), Liñán *et al.* 2008 and this work.

ments): (1) offshore clayey substrates (Coulouma and Murero formations); (2) shoal and coastal complexes sequentially arranged in shoaling parasequences (Borobia and Ferrals formations); and (3) tidally induced, back-shoal rhythmites (mixed tidal flats; Valdeorea and proximal outcrops of the lower member of the La Gardie Formation; Álvaro *et al.* 2003*a*, 2007).

The late Languedocian survival: a different response of cinctans and trilobites

The subsequent late Languedocian trilobite diversification is well documented in the Montagne Noire, where it is characterized by an abrupt increase in genera and families (Álvaro *et al.* 2001, 2003*b*). The appearance of new trilobite assemblages represents a stepwise immigration event related to transgressive pulses: off-platform trilobite taxa migrated towards the inner platform, leading to a strict facies control of the establishment of suitable clayey and silty, offshore substrates. However, trilobite diversity did not reach the peak of the previous Caesaraugustan radiation. Dispersal took place to some extent, but the presence of some provincialism suggests that species exchange was selective and that oceanic areas may have served as partial barriers to migration (Álvaro *et al.* 2003*b*, 2007).

The drastic decline in trilobite and cinctan diversity is related to the regional disappearance of their habitats. This decline was catastrophic for some previously successful trilobites, such as the biostratigraphically significant Solenopleuropsinae, which disappeared in both areas over this interval, as well as for the cinctan genera *Gyrocystis*, *Sucocystis*, *Lignanicystis* and *Elliptocinctus*. The biocrisis is not a major extinction event at familial level for trilobites, but it represents a significant generic turnover. It coincides with a rapid prograding and shoaling that produced widespread areas of coarse-grained sandstones and, therefore, seems to reflect geographically extensive environmental changes.

Late Languedocian trilobites are recognized in the Torcas and La Gardie/Val d'Homs formations and are characterized by a stepwise immigration of new trilobite families. The latter was related to transgression, coincided with the retrogradation of the upper-Borobia and Sallèles shoal complexes (Text-fig. 3), and had a different faunal signature in the two areas: (1) in the Montagne Noire, by the immigration of agnostids (*Megagnostus* and *Pseudoperonopsis*), paradoxidids (*Eccaparadoxides*), conocoryphids (*Bailiaspis*, *Bailiella*, *Conocoryphe*, *Holocephalina*, and *Occatharia*), solenopleurids (*Jincella*), agraulids (*Skreiaspis*), proasaphiscids (*Chelidonocephalus*, *Derikaspis*), dorypygids (*Dorypyge*), and anomocarids (*Abharella*); and (2) in the Iberian Chains, by an impoverished assemblage of conocoryphids and paradoxidids (Schmitz 1971; Josopait 1972; Courtessole *et al.* 1988; Shergold and Sdzuy 1991; Álvaro *et al.* 1999, 2001, 2003*b*, 2007). The conocoryphid-paradoxidid-solenopleurid (CPS) assemblage, typical of Leonian–early Languedocian benthic communities throughout the Acado-Baltic Province *sensu* Sdzuy (1972), persisted during the late Languedocian. However, this palaeobiogeographical pattern changed with the input of more cosmopolitan invaders that first co-occurred with species of the CPS assemblage and subsequently replaced it (Álvaro and Vizcaïno 2001, 2003).

This influence reflects an immigration of faunas from northern and eastern Gondwana that continued during the Furongian and early Tremadocian (Feist and Courtessole 1984; Shergold *et al.* 2000; Vizcaïno and Álvaro 2003; Álvaro *et al.* 2007). The Furongian–early Tremadocian sedimentation maintained the broad transgressive-dominated depositional systems of the late Languedocian, with common offshore deposits and both clayey and carbonate substrates (upper part of the La Gardie/Val d'Homs formations in the Montagne Noire, and Valtorres Formation in the Iberian Chains; Álvaro and Vennin 1996; Álvaro *et al.* 2003*b*, 2007). In the southern Montagne Noire, the Furongian–early Tremadocian transgression recorded the stepwise immigration of Furongian (1) agnostids, anomocarids, aphelaspidids, catillicephalids, ceratopygids, damesellids, eulomids, idahoiids, linchakephalids, lisariids, pagodiids and (2) middle Tremadocian conodonts and a new trilobite assemblage composed of 10 families, 13 genera, and 15 species that include asaphids, calymenids, nileids, olenids, ptychopariids and remopleurids (Küppers and Pohler 1992; Vizcaïno and Álvaro 2003; Álvaro *et al.* 2007). In the Iberian Chains, the same transgression was represented by an impoverished immigration of aphelaspidids (*Elegasntiapis*, '*Olenus*'), idahoiids (*Valtorresia*), and probable onchonotinids (*Punctuaspis*?) (Shergold and Sdzuy 1991).

The biogeographical distribution of latest mid-Cambrian and Furongian trilobites supports brachiopod data, indicating strong faunal affinities between western Gondwana (Mediterranean region), eastern Gondwana (North China/Korea, South China, Australia, and Antarctica), and Kazakhstania during the late Languedocian, which became significantly stronger during the Furongian (González-Gómez 2005; Álvaro *et al.* 2007). This major shift in palaeobiogeographical connections, which contrasts with the Leonian–early Languedocian dominant distribution throughout the Acado-Baltic province (Álvaro *et al.* 1999), may suggest a significant change in oceanic circulation patterns throughout Gondwana, a process already suggested by Brock *et al.* (2000) and Álvaro *et al.* (2003*b*).

Discussion

Sufficient high-resolution (centimetre- to decimetre-scale) facies and chemo-, bio- and sequence stratigraphical data

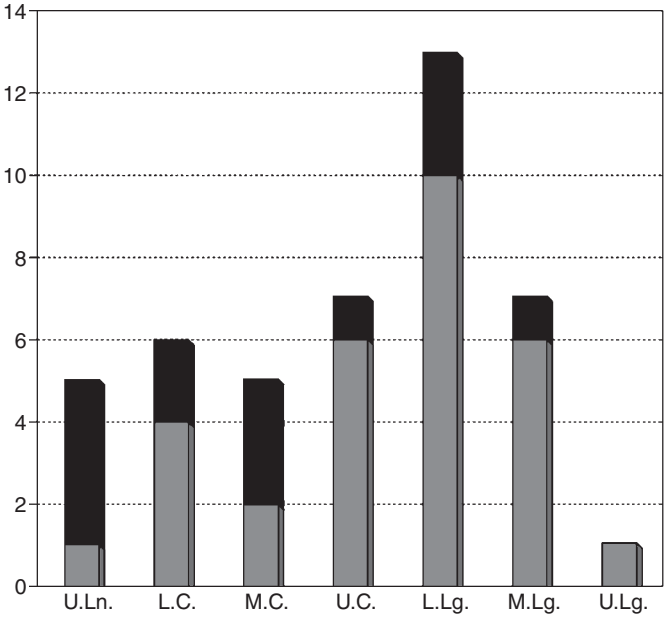
exist in the Iberian Chains and the Montagne Noire to establish the general pattern of trilobite recovery and cinctan extinction following the mid-Languedocian regression.

The late Languedocian to early Tremadocian transgression coincided with a stepwise and episodic immigration of trilobites, which characterizes a distinct radiation pattern that finally exceeded the diversity peak of the Leonian–Caesaraugustan radiation. This recovery in the aftermath of the mid-Languedocian regression contrasts with the final disappearance of cinctans. The regression had an important effect on the Mediterranean cinctans, which did not cross the Languedocian–Furongian boundary. Comparing trilobite and cinctan diversity patterns, two main differences stand out: (1) the delayed diversity peak exhibited by the cinctans, by comparison with the trilobites, reflects their differing onshore-offshore (or siltstone-claystone) optimal palaeoecological conditions; and (2) the endemic characteristic of the cinctans, whose biogeographical distribution was limited to western Gondwana (including Avalonia) and Siberia.

The late-Languedocian recovery coincides with the reestablishment of deeper water conditions and diverse marine associations, which were less affected by the mid-Languedocian regression than their shallow-water counterparts (Harries *et al.* 1996). Re-colonization of inner-platform settings by trilobites during this transgression occurred from an oceanic stock, but was absent (or extremely reduced) in the case of cinctans. Cinctans were possibly not able to migrate down the bathyal slope as sea level fell. As noted by Armstrong (1996), among others, some shallow-water taxa, such as the cinctans, may have run out of habitat space because of combined effects of regression and cooling. Cinctans became extinct from the region by the Furongian when widespread offshore deposits returned to the Gondwanan margin, bringing the return of echinoderm-bearing Lagerstätten (Ubaghs 1999). Finally, although the late Languedocian re-colonization of inner-platform settings shares some features with the biomere concept (Palmer 1984), the latter was sharp and often unrelated to any noticeable lithofacies change.

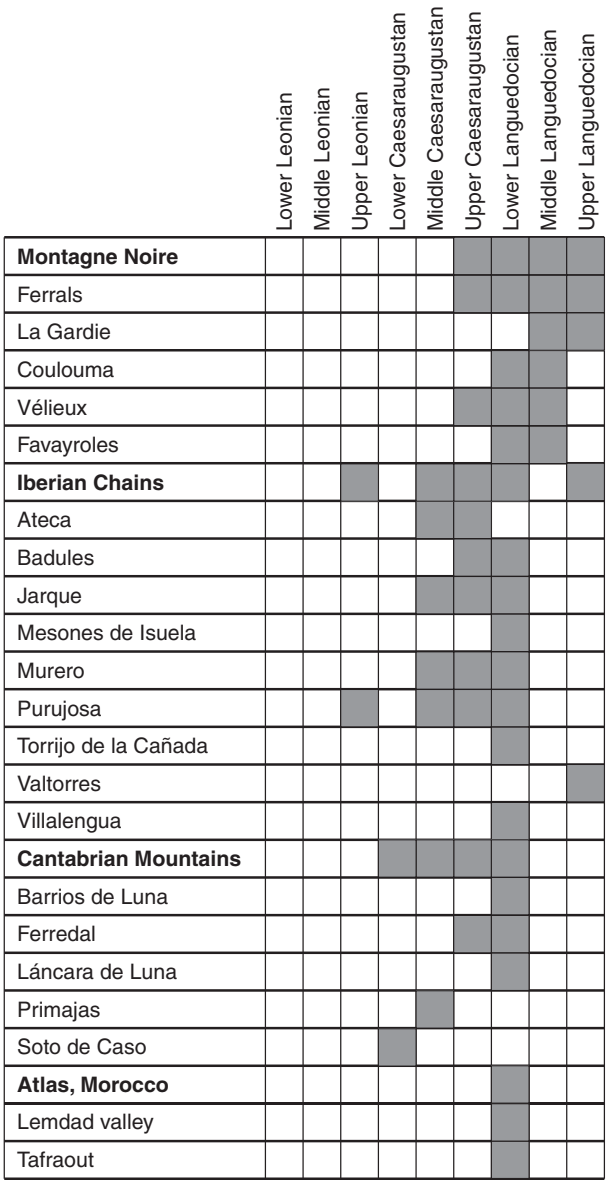
GHOST LINEAGES AND DISTRIBUTION OF SUITABLE PRESERVATIONAL FACIES

Identification and stratigraphical calibration of ghost lineages, defined as entire branches of evolutionary trees lacking fossil record (Norell 1992; Smith 1994), are key tools for estimating the completeness of the fossil record. A recent cladogram proposed for cinctans (Smith and Zamora 2009) suggests that two derived clades of cinctans (gyrocystids and sucocystids) represent important ghost lineages that are more common in earlier intervals (Text-fig. 7). It also suggests that if anything, peak diversity is slightly underestimated. Therefore, the fact that cinctan diversity rises and falls are offset in the Iberian Chains and the Montagne Noire, and that these



		Observed	Inferred to be present from phylogeny
Languedocian	Upper	1	0
	Middle	6	1
	Lower	10	3
Caesaraugustan	Upper	6	1
	Middle	2	3
	Lower	4	2
Leon.	Upper	1	4

TEXT-FIG. 7. Proportion of missing (ghost lineages) to observed taxa in each interval. Note that the earlier intervals have more ghost lineages. After modified the phylogeny from Smith and Zamora (2009) and adding in *Lignanicystis* sp. as sister taxon to *L. barroisensis*.



TEXT-FIG. 8. The number of fossiliferous localities yielding determinable cinctans vs. middle Cambrian substages in the Iberian Chains and Cantabrian Mountains (Spain), the Montagne Noire (France) and Atlas Mountains (Morocco).

follow sedimentary cycles, could be a reflection of how suitable preservational facies are distributed through time and space just as much as any possible evolutionary signal. In fact, Leonian – middle Caesaraugustan strata are rife with disarticulated cinctan ossicles and many species have not been yet described. As a result, the origin and first evolutionary steps of cinctans are controlled by taphonomic and sampling biases in the western Mediterranean region.

Two further analyses have been undertaken to investigate whether the diversity curve of cinctans depends on the availability of fossiliferous localities and the relative amount of fossiliferous strata (thickness) per time. Plotting the number of fossiliferous localities that have yielded determinable cinctas vs. substages (Text-figs 4, 8) illustrates a shift at the lower Languedocian, coinciding with the major peak of cinctan diversity. There is a positive correlation between rock outcrop area (a parameter that implies collecting potential) containing determinable cinctans and the estimated genus-level diversity. This relationship precludes a direct comparison with the Palaeozoic biodiversity/rock record ratio recorded in western Europe (Smith and McGowan 2007) that suggests that higher taxonomic diversities correlate with more crowed and populous, cinctan communities.

Another comparison that complements the diversity curve must be done with the thickness of strata available per time, an estimate dramatically constrained by the lack of radiometric ages in the study area. We cannot subdivide the middle Cambrian in equal and comparable, chronostratigraphical units; in fact, other correlation criteria (such as cyclo- and chemostratigraphy) suggest that the time encompassing the Languedocian is probably longer than the Leonian and Caesaraugustan together (Álvaro *et al.* 2000, 2008; Vizcaïno *et al.* 2008). Text-figure 6 shows the maximum thickness measured per middle-Cambrian substage of the Iberian Chains and Montagne Noire. The lower Languedocian, which records the peak in cinctan diversity, exhibits two different trends as a result of distinct changes in the accommodation rate of both platforms: a distinct increase in sedimentation rate took place in the Iberian Chains, which was recorded later (during the mid Langedocian) in the Montagne Noire. During the late Languedocian, the return to previous (lesser) sedimentation rates (related to a renewed transgression and re-establishment of offshore conditions) is associated with the re-appearance of cinctan record, its demise and final disappearance. Therefore, the end Languedocian decline in cinctan diversity cannot be driven by rock availability but by a true ecological response.

CONCLUSIONS

Cinctan echinoderms from the Languedocian (mid Cambrian) of the Iberian Chains are reported and include *Elliptocinctus barrandei*, *Gyrocystis platessa*, *G. erecta*, *Lignanicystis* sp., *Sucocystis theronensis*, *Sucocystis* sp. M, and *Undatacinctus melendezi*. All species are well-constrained biostratigraphically and many of them are reported for the first time in Spain.

Information on mid Cambrian cinctan diversity is based primarily on forms described from the western Mediterranean region (West Gondwana), mainly the Iberian Chains (north-eastern Spain) and the Montagne

Noire (southern France). Both areas were sites of temperate water, and mixed to siliciclastic sedimentation. Identification of the oldest cinctans, early–mid Leonian in age, is constrained by severe skeletal disarticulation and misidentification, and requires further investigation before they can be accepted.

The most remarkable diversification event for the trilobites occurred during the early–mid Caesaraugustan, which contrasts with the delayed early-Languedocian peak recorded by the cinctans. The latter radiated significantly in a relatively short interval of time and in a reduced palaeogeographical domain (the western Mediterranean region), from which they migrated into Avalonia and Siberia. Towards the early–middle Languedocian transition, both benthic taxa recorded a gradual decline that was followed by a dramatic fall in diversity, including their virtual disappearance related to the mid-Languedocian regression. In the late Languedocian aftermath, the cinctans re-occurred in spotted monospecific shell accumulations, dominated by trilobites. This echinoderm clade disappeared before the beginning of the Furongian.

The fluctuations in trilobite diversity coincided with the onset of mid-Cambrian transgressions (diversity rise) and regressions (barren intervals). This relationship contrasts with that exhibited by the cinctans because the aftermath of the mid Languedocian regression was not related to cinctan recovery, but to uneven immigration and final extinction. The subsequent early Languedocian peak in diversity is partly constrained by two biases: a taphonomic bias (led by environmental conditions) that affected the record of the origin and first radiation steps of cinctans, and sampling of the appropriate facies. The positive correlation between rock outcrop area containing determinable cinctans and the estimated genus-level diversity can be related to denser colonization patterns of offshore, clayey substrates across the Caesaraugustan–Languedocian transition.

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