GIVETIAN BRACHIOPOD FAUNAS OF THE PALENTIAN DOMAIN (N SPAIN)

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ABSTRACT

The origin, evolution, structural and stratigraphical features of the Palentian Domain (Cantabrian Mountains, N Spain) are summarily described. The boundaries of the Givetian succession (ca. 40 m thick) in that area are established from previously known conodont and ammonoid data. The base of the Givetian is situated in the upper part of the Gustalapiedra Formation, at the base of the La Pedrosa Member. The upper Givetian boundary is situated at the top of the lower calcareous interval of the Cardaño Formation. Middle Devonian brachiopods are scarce in the Palentian Domain. In fact no Givetian form has been cited in the area until now. In this paper nine brachiopod species (three new) of the Givetian interval are described and figured: *Skenidium* cf. *polonicum*, *Rhyssochonetes* aff. *douvillei*, *Prodavidsonia havliceki* n. sp., *Bifida* aff. *lepida*, *Ambothyris* cf. *infima*, "*Pyramidalia*" *palentina* n. sp., *Cingulodermis sotoana* n. sp., *Parastringocephalus* cf. *dorsalis*, and *Ense andrea*. The genera *Skenidium*, *Rhyssochonetes*, *Ambothyris*, *Cingulodermis*, *Parastringocephalus,* and *Ense* are cited in Spain for the first time. *Parastringocephalus* is moreover the first stringocephaline found in Palencia. "*Pyramidalia*" *palentina* n. sp. is an impunctate form provided with a nearly complete symphytium, a delthyrial plate and short dental plates; these features separate the genus *Pyramidalia* both from *Cyrtinaella* and *Thomasaria* with which the former genus has sometimes been synonymised. Near the base of the Cardaño Fm. a coquina with thousands of specimens of *Ense andrea* has been found. This coquina could represent the area of the famous "*Pumilio*" Event, described previously from Germany, France and North Africa. The Spanish *Ense andrea* specimens are endopunctate and a sectioned shell shows a centronelliform brachidium. The terebratulid nature of the species is certain and the features referred to above and the external morphology of the shell are closer to the Subfamily Adreninae than to the Subfamily Mutationellinae where *Ense* had previously been tentatively included.

Keywords: brachiopods, Givetian, Stratigraphy, Palentian Domain (N Spain).

RESUMEN

Se describen brevemente el origen y evolución, así como las características estructurales y estratigráficas, del Dominio Palentino (Cordillera Cantábrica, N de España). Se precisan los límites de la sucesión Givetiense (con un espesor aproximado de 40 m) en el área, basándose en datos previos de conodontos y ammonoideos; su base se sitúa en la parte alta de la Formación Gustalapiedra, al comienzo del Miembro La Pedrosa y su techo hacia la parte alta del paquete calcáreo basal de la Formación Cardaño. Los braquiópodos son escasos en el Devónico Medio del Dominio Palentino. De hecho hasta hoy nunca se habían citado formas del Givetiense. Aquí se describen y figuran, nueve taxones del intervalo Givetiense (tres nuevos): *Skenidium* cf. *polonicum*, *Rhyssochonetes* aff. *douvillei*, *Prodavidsonia havliceki* n. sp., *Bifida* aff. *lepida*, *Ambothyris* cf. *infima*, "*Pyramidalia*" *palentina* n. sp., *Cingulodermis sotoana* n. sp., *Parastringocephalus* cf. *dorsalis* y *Ense andrea*. Los géneros *Skenidium*, *Rhyssochonetes*, *Ambothyris*, *Cingulodermis*, *Parastringocephalus* y *Ense*, se citan por primera vez en España. *Parastringocephalus* es, además, el primer estringocefalino encontrado en Palencia. "*Pyramidalia*" *palentina* n. sp. tiene concha impuntuada, un symphytium casi completo, placa deltirial y placas dentales cortas en la valva ventral, características que parecen alejar el género *Pyramidalia* tanto de *Cyrtinaella* como de *Thomasaria* con los cuales fue sinonimizado. Casi en la base de la Fm. Cardaño se descubrió una lumaquela compuesta por millares de ejemplares de *Ense andrea*, que parece representar en el área el conocido Evento "*Pumilio*", descrito hasta ahora en Alemania, Francia y Norte de África; el estado del material permitió poner en evidencia la pre-

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sencia de endopuntos y de un braquidio centroneliforme, lo que asegura la naturaleza terebratúlida de la especie; dichas características y la morfología externa de la concha son más propias de la Subfamilia Adreninae, que de la Subfamilia Mutationellinae, donde tentativamente fue incluido el género *Ense*.

Palabras clave: braquiópodos, Givetiense, Estratigrafía, Dominio Palentino (Norte España).

INTRODUCTION

The Palentian Domain (Brouwer, 1964) (Fig. 1) (more or less equivalent to the Pisuerga-Carrión Province, Julivert, 1971) is considered herein as a predominantly Silurian-Lower Carboniferous allochthonous unit, that was emplaced in its present setting upon the Cantabrian Zone (Lotze, 1945), coming from the southwestern-located West-Asturian-Leonian Zone (Lotze, 1945) (references in García-Alcalde *et al.*, 1990a, b, 2002; Alonso *et al.* 2009). According to Henn & Jahnke (1984) the Palentian Domain would be the offshore southern continuation of the Asturo-Leonian platform. By the end of Namurian-Westphalian A time the so-called Palentian nappes were thrust over the Valsurvio region (Valsurvio Dome) (Fig. 1), a sub-unit of the Asturo-Leonian Domain (Lotze, 1945; Alonso *et al.*, 2009), and they underwent gravitational collapse to form rootless units in the Pisuerga-Carrión area, resting on relatively autochthonous synorogenic Carboniferous rocks. Later on, they were overprinted by strong Variscan deformation (see Rodríguez-Fernández, 1994, García-Alcalde *et al.*, 2002, and Alonso *et al.*, 2009, for a complete bibliography).

The greater part of the Palentian Devonian originated in distal shelf environments corresponding to the offshore

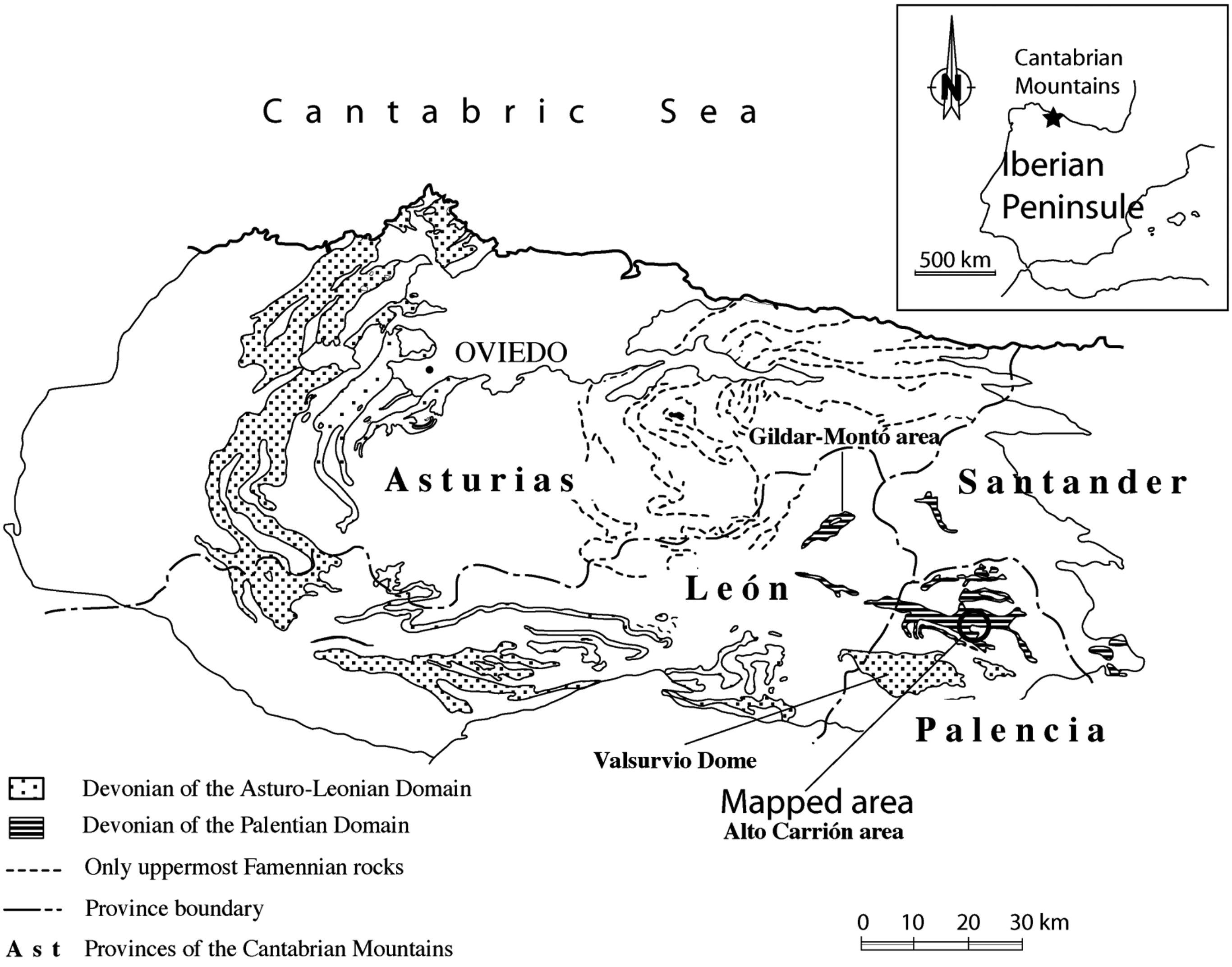


Figure 1. The Devonian in the Cantabrian Mountains. Shown are location of the areas mentioned in the text.

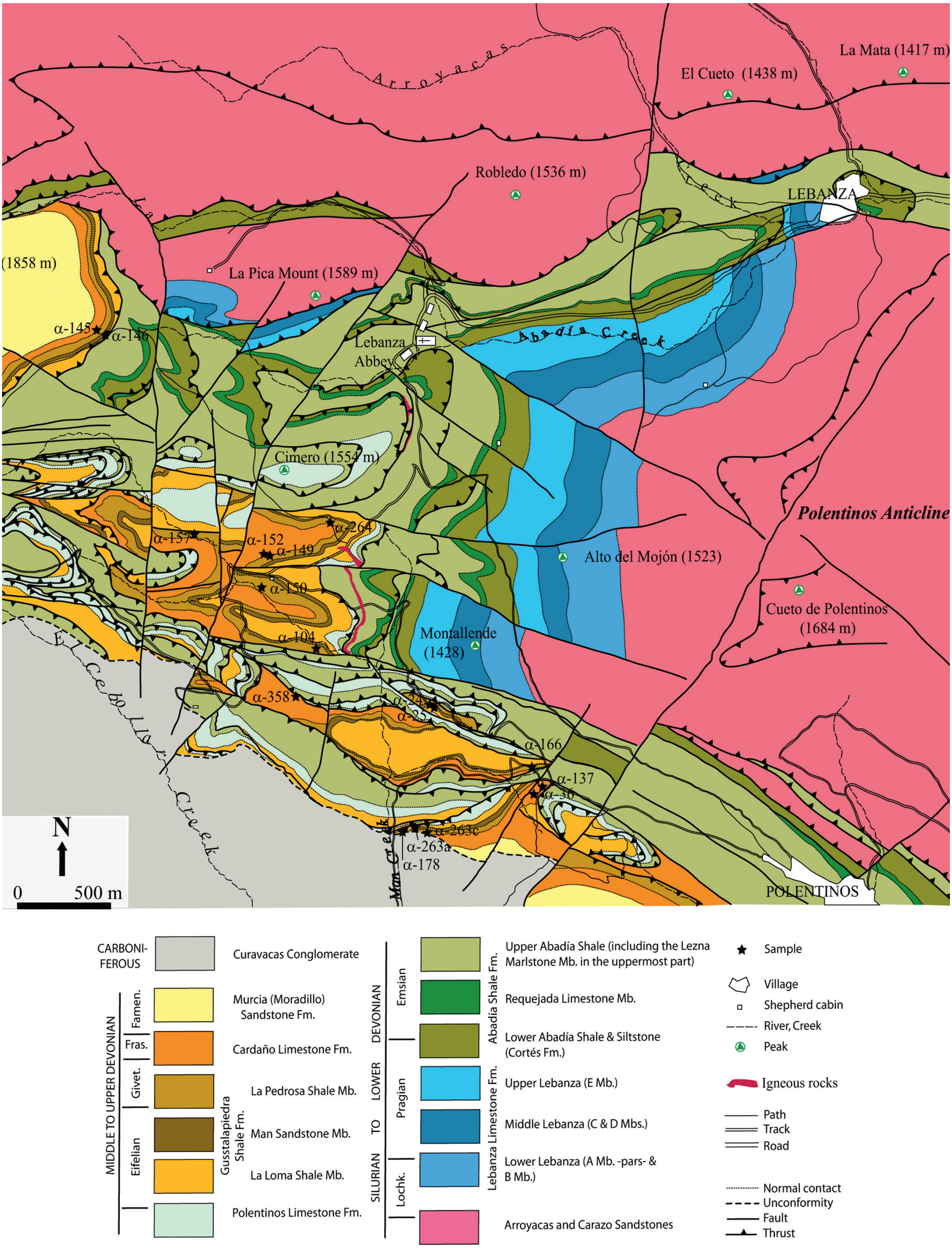


Figure 2. Simplified geological map of the Polentinos anticline-Man antiformal stack area (mapping after impublished data by the author).

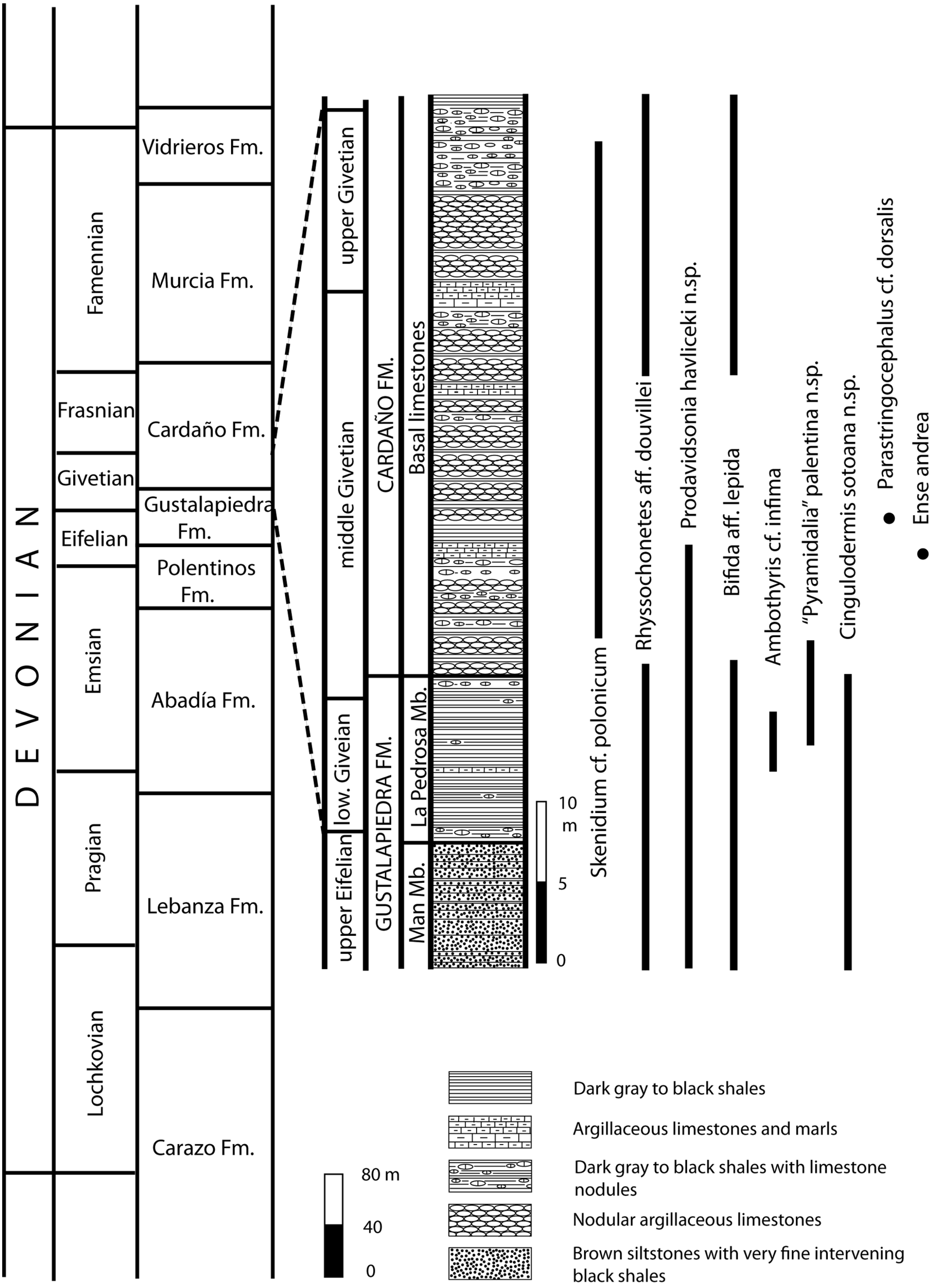


Figure 3. Stratigraphy of the Devonian of the Palentian Domain. Detail of the Givetian stratigraphy with the vertical distribution of the species studied herein.

pelagic realm. But differentiation from the more neritic Asturo-Leonian Devonian proceeded steadily from Emsian time onwards, although episodic "asturoleonian"-like neritic facies intervals occur at different levels of the post-Emsian Palentian succession (Henn & Jahnke, 1984).

Offshore Palentian facies are very condensed compared to nearshore Asturo-Leonian. The entire Asturo-Leonian Devonian succession is more than twice as thick as the Palentian (ca. 2000 m for the former, ca. 800 m for the latter) (Jahnke *et al.*, 1983; García-Alcalde *et al.*, 2002). And, particular time intervals and Stages show even greater unbalanced sedimentation rates (i.e. 13:1 for the Emsian/Eifelian transition, Ellwood *et al.*, 2006; more than 8:1 for the Givetian, herein).

STRATIGRAPHY

The stratigraphy of the Palentian Devonian is extremely difficult to discern, because of strong tectonics involving numerous thrust superpositions at a vast array of scales (from centimetres to kilometres) fueled by the plastic nature of the very fine-grained mudstone and shaly rocks usual for the zone, further complicated by Alpine folding and faulting (Fig. 2). In consequence, there exist marked interpretative differences among authors that have worked in the region concerning the thicknesses and naming of stratigraphical Devonian units (i.e. compare thicknesses assigned to the Givetian by Veen, 1985; Henn, 1985; Jahnke *et al.*, 1983; García-Alcalde *et al.*, 1988; Gozalo *et al.*, 1990, and Rodríguez-Fernández, 1994). In this paper we adopt the stratigraphic bases proposed by García-Alcalde *et al.* (1988) (thickness of Givetian ca. 40 m), updated in García-Alcalde *et al.* (2002), with minor modifications and additions, for the most part related to cartographic utility (Fig. 2). The main modifications are (Fig. 3):

a) The three-fold division of the Lebanza, Abadía, and Gustalapiedra Formations,

b) The acceptance of the name La Pedrosa Member (Henn, 1985) for the upper part of the Gustalapiedra Fm. above the sandstones of the Man Member. The name La Loma Member for the Gustalapiedra Fm. succession below the Man Mb. is only provisionally accepted herein because it lacks a definite top in its type-locality (Henn, 1985, Fig. 16).

c) The inclusion in the La Loma Member of the nodular, dark gray, lime mudstones that occur just below the sandstones of the Man Mb. s.s. in the upper third of the Gustalapiedra Fm. (*vs.* García-Alcalde *et al.*, 1990a, b; Truyols-Massoni *et al.*, 1990; Gozalo *et al.*, 1990; Rodríguez-Fernández, 1994; who assigned these layers to the Man Mb. itself).

Most Devonian Palentian lithostratigraphic units have been named after localities situated at or near the mapped area (Fig. 2) (i.e. the Carazo, Lebanza, Abadía, and Polentinos Fms, and the Requejada and Man Mbs) Still, nearly all the Middle-Upper Devonian units have been defined further west, in the Cardaño de Arriba-Pico Murcia area (i.e. the Gustalapiedra, Cardaño, Murcia, and Vidrieros Fms), and further south, south of the Requejada (Vañes) Reservoir (i.e. the Loma Mb.) (see Rodríguez-Fernández, 1994).

Guide-fossils for precise correlations are scarce and their relative stratigraphic positions barely known. Conodonts have been determined mainly by Adrichem-Boogaert (1965, 1967), Mouravieff (*in* Lobato, 1977), Jahnke *et al.* (1983), and Henn (1985). These data are, however, obscure because of the strong tectonization of the zone, and they need a complete and profound updating. Ammonoids (Kullmann, 1960, 1964; Henn, 1985; Montesinos & Henn, 1986; Montesinos, 1987a, b, 1990; Montesinos *in* García-Alcalde *et al.*, 1990a, b; Montesinos & Sánz-López, 1997, 1999), and trilobites (Smeenk, 1983) are also spotty and the specimens are usually badly preserved. Dacryoconarids and homoctenids (Truyols-Massoni, 1989, 1999; Truyols-Massoni *in* García-Alcalde *et al.*, 1990a, b) and entomozoids (Gozalo & Sánchez de Posada, 1998) are abundant at some levels, but they do not provide much precise chronostratigraphic indication. The distribution of brachiopods is also sparse, and their diversity and abundance is always very low except in special cases as will be reported later.

The Eifelian/Givetian boundary in the Palentian domain could roughly be traced in the lower part of La Pedrosa Mb. (Truyols-Massoni *et al.*, 1990; García-Alcalde & Soto, 1999) (Fig. 3). Indeed, Eifelian ammonoid forms such as *Cabrieroceras crispiforme*, *C. ougartense*, *Subanarcestes macrocephalus*, *Pinacites*, and *Fidelites*, disappear either immediately below or just above the Man Mb. (Montesinos *in* Truyols-Massoni *et al.*, 1990) perhaps in the *Polygnathus ensensis* conodont Zone (Henn, 1985). On the other hand, uppermost Eifelian to Givetian forms such as *Wedekindella*, *Holzapfeloceras*, *Agoniatites costulatus*, *Parodiceras*, and *Tornoceras*, occur in the La Pedrosa Mb. itself (Montesinos *in* Truyols-Massoni *et al.*, 1990; García-Alcalde, 1999; García-Alcalde & Soto, 1999), probably in the Lower *P. varcus* conodont Zone (although clear conodont index-forms of the named zones are definitely lacking therein) (compare with MD IIA/B faunas in Becker & House, 1994). The dacryoconarid *Nowakia otomari* straddles the Man Member (Truyols-Massoni *in* Truyols-Massoni *et al.*, 1990). Among the brachiopods, an upper Eifelian brachiopod faunal assemblage, mainly characterized by the occurrence of *Paraplicanoplia infima*, *Holynetes* cf. *holynensis*, *Prodavidsonia havliceki* n. sp. and *Palentiella palentina* occurs just below the Man Mb. (García-Alcalde & Truyols-Massoni, 2000; García-Alcalde, 2009). Several brachiopod forms also straddle the Man Mb. (i.e. *Cingulodermis sotoana* n. sp., *Rhyssochonetes aff. douvillei*, *Prodavidsonia havliceki* n. sp., *Bifida* aff. *lepida*) and are associated usually with younger forms, such as "*Pyramidalia" palentina* n. sp., *Ambothyris* cf. *infima,* and *Skenid-*

ium cf. *polonicum*, in the uppermost part of the La Pedrosa Mb. in beds of probable lower to middle Givetian age. On the other hand, the litho-, bio- and magnetosusceptibility events that occur near the Man Mb. (both below and immediately above) are related to the so-called Kačak-*Otomari* Event (Truyols-Massoni *et al.*, 1990; García-Alcalde *et al.*, 2001; Ellwood, *pers*. *com*. 2009 on MSEC interpretation), an uppermost Eifelian global event recorded worldwide.

In turn, the Givetian/Frasnian boundary would be placed in an undetermined level of the Cardaño Formation, probably in the upper part of the basal limestones of the formation (Fig. 3). These basal limestones have yielded middle to upper Givetian conodonts (Middle *P. varcus* to Lowermost *P. asymmetricus* or Lower *Mesotaxis falsiovalis* Zones), such as *Ozarkodina semialternans*, *Icriodus eslaensis*, *Polygnathus ensensis*, *P. xylus*, *P. varcus*, *P. ovatinodosus*, *P. cristatus*, *Schmidthognathus hermanni*, and *S. wittekindti*, *Palmatolepis disparilis*, and *Ancyrodella binodosa* (Mouravieff, *in* Lobato, 1977; Henn, 1985). And, in the upper part of the same limestones an important multilobate pharciceratid radiation (*Pharciceras pargai*, *P. applanatum*, *P.* cf. *pargai*, *P.* sp. *A*, *Timanites* ? *taouzense,* and *Stenopharciceras* cf. *kseirense* (Henn, 1985; Montesinos & Henn, 1986) occurs. This radiation would represent the post-Taghanic Event phase in the region (García-Alcalde *et al.*, 1988) that occurs in the *Hermanni* Zone

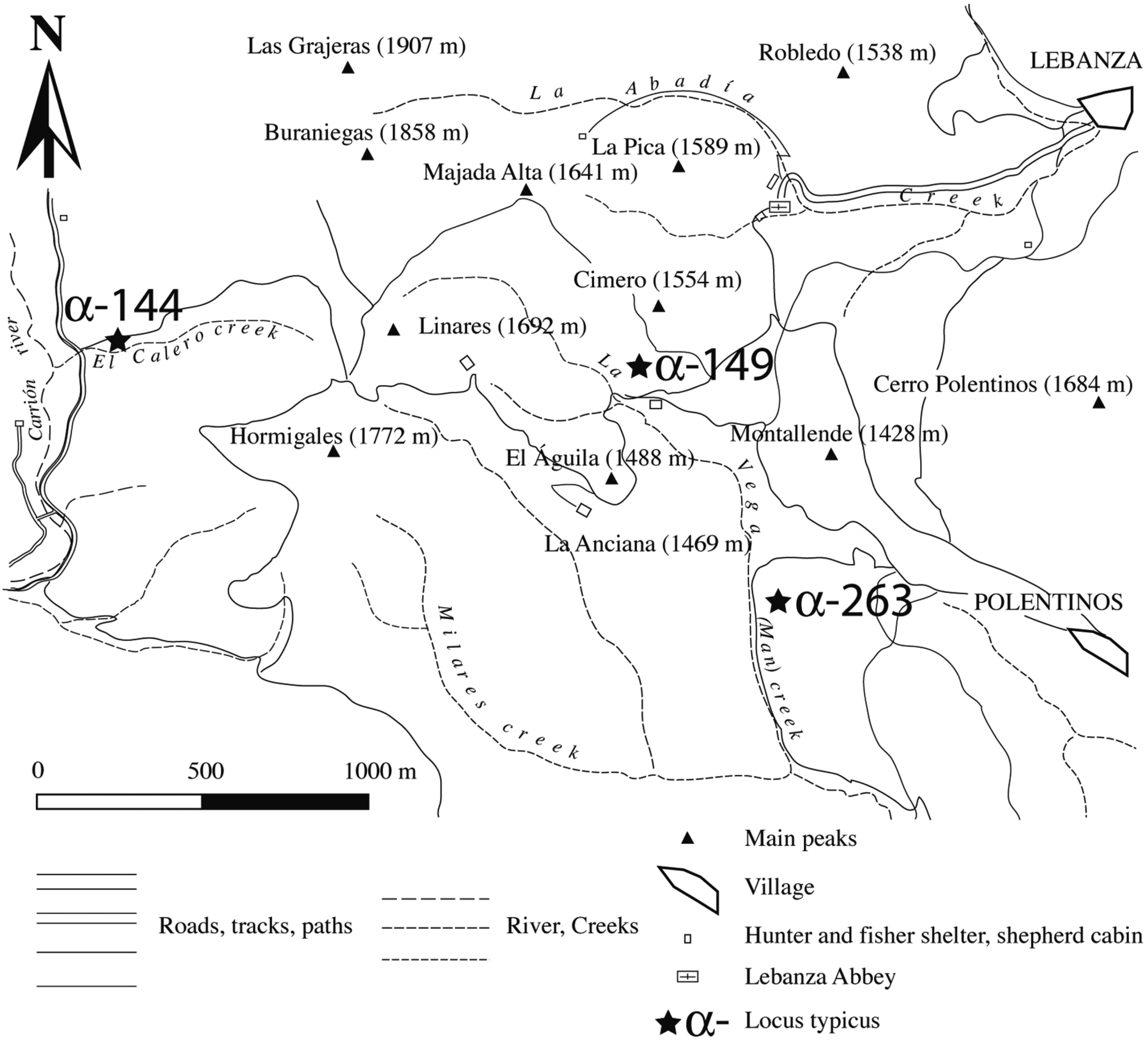


Figure 4. Geographical setting of the type localities of the new species proposed herein: *Prodavidsonia havliceki* n. sp. (α-263), "*Pyramidalia*" *palentina* n. sp. (α-144), and *Cingulodermis sotoana* n. sp. (α-149).

(compare with MD III B to C Faunas in Becker & House, 1994). In younger levels (note that in the stratigraphical columns by Henn, 1985, Fig. 41, and by Montesinos & Henn, 1986, Fig. 4, the calcareous lower member of the Cardaño Fm. would be tectonically reversed), *Petteroceras errans* occurs (probably belonging in the uppermost Givetian *Skeletognathus norrisi* conodont Zone; compare with Becker & House, 1994), and Frasnian forms, as *Mesobeloceras housei*, *Mesobeloceras* sp. and other Beloceratidae (Henn, 1985; Montesinos & Henn, 1986) have been found a little higher. The brachiopods recovered at the base of the Cardaño Fm., mainly *Ense andrea* Struve, 1992 (in a level possibly equivalent to the famous "*Pumilio"* horizons; Lottmann, 1990a, b) and *Parastringocephalus* cf. *dorsalis* d'Archiac & de Verneuil, 1842 (see below), are currently dated as middle Givetian, *Rhenanus/Varcus* to lowest *Ansatus* Zones (Bultynck & Hollard, 1980; Weddige, 1988; Lottmann, 1990a, b; Becker & House, 1994; Brice & Loones, 2002).

The middle and upper parts of the Cardaño Fm. yield Frasnian conodonts, ammonoids, and homoctenids (Adrichem-Boogaert, 1967; Mouravieff *in* Lobato, 1977; Henn, 1985; Montesinos, 1987b; Montesinos & Sánz-López, 1997; Sánz-López *et al.*, 1999; Truyols-Massoni, 1989, 1999). Finally, the Frasnian/Famennian transition is well represented in the upper part of the Cardaño Fm. (Fig. 3), at least in the Gildar-Montó area (Fig. 1), according to the occurrence of conodonts of the *Palmatolepis rhenana* to Upper *P. triangularis* Zones (Montesinos & Sánz-López, 1997, 1999; Sánz-López *et al.*, 1999).

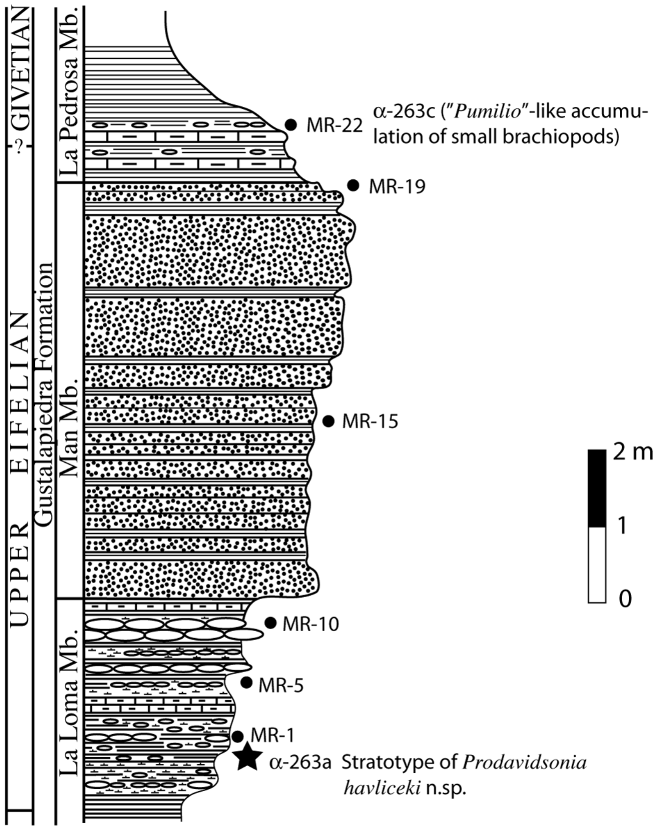


Figure 5. Stratotype (black star) of *Prodavidsonia havliceki* n. sp. Levels MR-1 and so on: paleontological and magnetosusceptibility sampling. Setting of a layer with a "*pumilio*"-like accumulation of small, undetermined brachiopods in bed MR-22 (See also García-Alcalde *et al.*, 1990a, Fig. 7). Symbols as in Fig. 3.

Brachiopods are diverse and abundant in the Devonian nearshore Palentian facies, i.e. in the upper part of the Carazo Fm. (Lochkovian), in the Lebanza Fm. (Lochkovian to Pragian) and in the Lezna Mb. of the Abadía Fm. (upper Emsian) (Binnekamp, 1965; Jahnke *et al.*, 1983; García-Alcalde *et al.*, 1988, 1990b), but their importance fades away in offshore facies. Benthic faunal decrease is specially enhanced from upper Eifelian levels upwards. In fact, no Givetian brachiopod species has been described, figured nor mentioned in the Palentian Domain until now. In this paper, nine species (three new), coming from the Gustalapiedra and Cardaño Fms (Fig. 3) are described and figured. *Parastringocephalus* cf. *dorsalis* is the sole stringocephalid found until now in the Palentian Domain, but it is unfortunately represented by a unique specimen, from a not too precisely settled level (it was picked up by students long ago) in the basal calcareous part of the Cardaño Fm. *Ense andrea* also occurs at the base of the Cardaño Fm. in a thin coquina (maximum thickness: 7 cm) composed of thousands, usually disarticulated specimens, in at least one Palentian locality (α-36) (Fig. 2). In a similar stratigraphical position, in another locality (α-152) (Fig 2) a "*pumilio*"-like coquina of small, mainly unornamented, yet unclassified brachiopods occurs. The greater part of the studied species occur in outcrops belonging in an antiformal stack, extensively exhumed by the La Vega Creek (likewise called in the region Man River, Los Caños River, Monderrío Creek, and La Riba Creek) and its tributaries (Figs 2, 4). A section, west of the mapped area (Fig. 2), near the confluence of the Carrión River and its tributary, the Calero Creek (Fig. 4), has also yielded several lower to middle Givetian brachiopods but age control by conodont or ammonoid faunas is badly needed therein.

The probable age, and the massive occurrence of *Ense andrea* in Palencia reminds one of the same species and other *Ense* forms (*E. pumilio*, *E. albertii*), formerly collectively known as "*Terebratula pumilio*", in levels representing the so-called "*Pumilio*" Event in Germany, France, Morocco, and Algeria (Lottmann, 1990a, b). In fact the "*Pumilio"* Event comprises two separate events in those regions, named the Lower and the Upper "*Pumilio"* Events, the latter subdivided in several lithological units (Lottmann, 1990a, b; papers in El Hassani (ed.), 2004; Bultynck & Gouwy, 2008; among others). According to Lottmann (1990a, b) the Lower "*Pumilio*" horizon is a single accumulation of small "*pumilio*" brachiopod shells that cannot be further subdivided. In this respect the Palentian horizons could just represent the Lower "*Pumilio*" event. As indicated above, the "*Pumilio*" horizons have been dated usually as middle Givetian, *Rhenanus/Varcus* to *Ansatus* conodont Zones. However, Ebbighausen *et al.* (2004) and Becker *et al.* (2004) reported accumulations of pumiliform brachiopods in a few Eifelian localities in Morocco, and Wendt *et al*. (2009) suggest an early to middle Givetian age (*Timorensis*/*Rhenanus* conodont Zones) for the single "*Pumilio*" horizon they found in Algeria. A similar accumulation of very minute, non-pumiliform, yet undetermined brachiopods, probably of uppermost Eifelian-lowermost Givetian age, occurs also in the upper part of the Gustalapiedra Fm. locality α-263c (Figs 2, 5). What triggered these brachiopod events, and whether the great accumulation of shells represents either true "mass mortalities" with transport and allochthonous deposition due to tsunamis, as suggested by Lottmann (1990a, b), or periodic "opportunistic blooms" related to sudden and episodic short-term increase of the trophic level (eutrophication) (Ebbighausen *et al.*, 2004) is debatable (García-Alcalde, 2000). Still, as it has been stated before, accumulation horizons (with different brachiopod forms involved, not only of "*pumilio*" type) seem more abundant than previously reported (see also Brice & Ouali Mehadji, 2009).

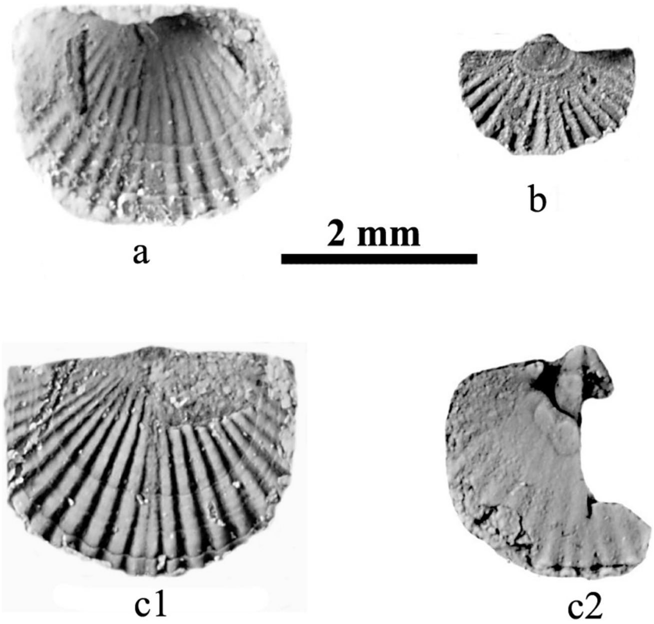


Figure 6. *Skenidium* cf. *polonicum* Gürich, 1896. **a**: external ventral mould, DPO 127850; **b**: external dorsal mould, DPO 127851, showing the protegular umbonal area, devoid of radial ornamentation; **c1-c2**: external dorsal mould, and partially broken internal dorsal mould of the same individual, DPO 127849A-B.

SYSTEMATICS

DPO: acronym of the Área de Paleontología de Oviedo; specimens housed at the collection of the Museo de Geología, Departamento de Geología de la Universidad de Oviedo, Spain. Abbreviations in the tables of measurements: L, length; w, width; t, thickness.

Order PROTORTHIDA Schuchert & Cooper, 1931
Superfamily **Skenidioidea** Kozłowski, 1929
Family **Skenidiidae** Kozłowski, 1929
Genus *Skenidium* Hall, 1860
Type-species: *Orthis insignis* Hall, 1859.

Skenidium cf. *polonicum* Gürich, 1896
Figs 3, 6.

Material: Four numbered specimens, DPO 127849-127852, and several, unnumbered very badly preserved, doubtful moulds and shell fragments. The specimens DPO 127849-127851 are limonitized moulds coming from the Frasnian shales of the Cardaño Fm., in the locality α-137 (Fig. 2). DPO 127849 is an external dorsal mould (A) and an incomplete internal dorsal mould (B) of the same individual (Fig. 6c1-c2). DPO 127850 is an external ventral mould (Fig. 6). DPO 127851 is an external dorsal mould of a juvenile specimen with a marked protegulal umbonal area, including the protegulum itself and the brephic, non plicate shell (Fig. 6). Specimen DPO 127852 is a partial dorsal valve (A) and their external mould (B), coming from mudstones of the lower part of the Cardaño Fm., locality α-144 (Figs 3, 4), probably of middle Givetian age.

Descriptive remarks: DPO 127849A is a minute, slightly convex, transverse dorsal valve (less than 3 mm length), with the greatest width along the posterior margin that is prolonged in small, acute ears (the left one well preserved in the specimen). Median, narrow and shallow dorsal sulcus. 25-26 high, narrow, subangular, single radial plications with slightly larger, rounded interspaces; on the sulcate median part of the valve there are three weaker radial elements, two of them starting near the umbo of valve, and the third amid the anterior ones, bifurcating from one of them. Growth lines numerous, crowded anteriorly; some of the growth lines, are stronger, irregularly spaced, and imbricate. The internal dorsal mould DPO 127849B, corresponding to the same individual described above, show the broad, bilobed, deep, and rounded septalium typical of skenidiids, extending ahead a quarter of the valve length; septalium supported by a long, thin, acute, very high, tapering off anteriorly, median septum, that reaches 3/4 of the valve length. On the middle part of septalium a strong, ridgelike cardinal process, expanding slightly anteriorly that seems discontinuous with the dorsal median septum, occurs. On both sides of the septalium strong, divergent brachiophores and incomplete fulcral plates occur. The bottom of the septalium is grooved by fine concentric lines indicating the gradual growth of the platform. The external radial ornamentation is weakly reflected in the shell interior on the anterior part of the valve, around the indistinct, unimpressed adductor muscle field (Fig. 6c2).

Specimen DPO 127851 is an external dorsal mould of semicircular outline corresponding to a juvenile individual, ca. 1.5

mm length, with up to 19 single, straight, strong, radial plications, with a median dichotomous rib, shorter and weaker than the others. A broad, semi-circular, nonplicate, brephic protegular area, furrowed by several concentric growth lines occurs at the umbonal portion of valve, extending ahead 1/3 of the valve length (Fig. 6b).

Specimen DPO 127850 is a damaged external ventral mould of semicircular outline, ca. 2.2 mm length, strongly convex, transverse, with obtuse hinge angles, provided by more than 21 strong, single, straight, radial plications and a weaker and shorter median dichotomous rib (Fig. 6).

Discussion: The outline, external ornamentation and internal dorsal features of the available specimens are typical of skenidiids, and particularly of the genus *Skenidium* Hall, 1860. The Palentian forms are closely similar to *S. polonicum* Gürich, 1896, from the Givetian Skały beds in Poland. The very detailed revision of the Polish species by Biernat (1959) has showed, in particular, that the long persistence of a marked protegular area is typical of the species, and it is a feature that occurs also in the Spanish material. The scarce Palentian fossils compel us to leave our form in open nomenclature.

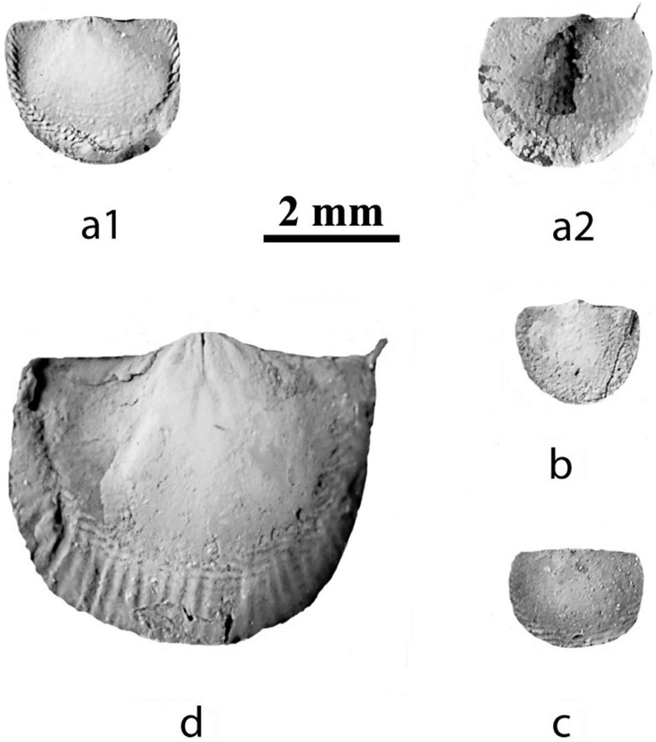


Figure 7. *Rhyssochonetes* cf. *douvillei* (Rigaux, 1892). **a1-a2**: internal and external ventral moulds of the same individual, DPO 127890A-A', the former showing the typical corrugated ornamentation, and the latter, an orthomorph, oblique, high-angled cardinal spine; **b**: internal ventral mould, DPO 127891, showing the corrugated ornamentation; **c**: internal ventral mould, DPO 127897, showing the corrugated ornamentation; **d**: internal ventral mould of a great-sized specimen, DPO 127902, showing both the radial and corrugated ornamentation, and an orthomorph, oblique, high-angled cardinal spine.

Drot (1961) described from the Givetian of Foum Medza, Dra region (Morocco) an infrequent brachiopod association composed by *Skenidium* aff. *polonicum*, *Prodavidsonia* ? sp., and *Parastringocephalus* sp. (*Stringocephalus* sp. 1, *in* Drot, op. cit., p. 60). Close or identical forms occur in Palencia in Givetian levels of the lower part of the Cardaño Formation, although they have not yet been found associated.

Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959
Suborder CHONETIDINA Muir-Wood, 1955
Superfamily **Chonetoidea** Bronn, 1862
Family **Chonetidae** Bronn, 1862
Subfamily **Dagnachonetinae** Racheboeuf, 1981
Genus *Rhyssochonetes* Johnson, 1970
Type-species: *Rhyssochonetes aurora solox* Johnson, 1970.

Rhyssochonetes aff. *douvillei* (Rigaux, 1892)

Figs 3, 7; Table 1

Material and localities: 21 specimens, DPO 127882-127885, 127887, 127889-127904, preserved as ventral, internal and external moulds (Figs 2, 4):

-127882, from locality α-157, upper part of the Gustalapiedra Fm., lower Givetian.

-127883, from locality α-146, Gustalapiedra Fm., La Loma Mb., upper Eifelian.

-127884, from locality α-24, Gustalapiedra Fm., La Loma Mb., upper Eifelian.

-127885, from locality α-149, Gustalapiedra Fm., La Pedrosa Mb., lower or middle Givetian.

-127887, 127889, from locality α-25, Gustalapiedra Fm., La Loma Mb., upper Eifelian.

-127890-127891, and 127903-127904, from locality α-166, Gustalapiedra Fm., La Pedrosa Mb., middle Givetian.

-127892 to 127902, from locality α-137, Cardaño Fm., lower Frasnian.

Descriptive remarks: Small, concavo-convex, weakly transversely elongate (average w/L: 1.29), semicircular shells. Greatest width at the hinge or near it. Ornamentation consists of 26-42 (average: 34) rounded, bifurcating and inserted costellae. Orthomorph, oblique, high-angled spines (usually only one spine is visible on the available material; Fig. 7a2, d). Periphery of ventral interior ornamented with numerous, undulating ridges, concentrically disposed and parallel to the anterior commissure but oblique to both the lateral commissures and the postero-lateral ventral margins (Fig. 7a1, b-d). Muscle field subdued, reaching less than 1/3 of length; adductor scars, narrow, longitudinally elliptical, separated by a short, narrow, sharp myophragm; diductor scars subtriangular, longitudinally ridged, with rounded anterior margins, prolonged forward the adductor scars; two inconspicuous, divergent vascular trunks start at the adductor anterior margins, bordering the internal margins of diductor (Fig.7a1, d). Dorsal interior unknown.

Table 1. Measurements of *Rhyssochonetes* aff. *douvillei.*

DPO	L	w	L/w	Nº of costellae
127882	1.80	2.04	1.13	36
127883	2.07	2.73	1.32	-
127884	1.53	1.73	1.13	34
127885	1.53	2.33	1.52	30
127887	2.13	2.67	1.25	38
127890 (Fig.7a1-a2)	2.47	3.07	1.24	34
127891 (Fig.7b)	1.47	1.87	1.27	-
127895	2.33	3.27	1.40	-
127896	2.33	3.33	1.43	34
127897 (Fig.7c)	1.93	2.40	1.24	-
127898	3.60	4.80	1.33	36
127901	2.47	2.87	1.16	26
127902 (Fig.7d)	5.07	6.27	1.24	42
127903	1.47	2.07	1.41	-
127904	1.27	1.67	1.31	32

Discussion: The outline, the disposition of ventral spines, the number and morphology of costellae, and the corrugated ventral interior of the described forms reminds one of *Rhyssochonetes douvillei* (Rigaux, 1892) from the Givetian of the Boulonnais, France. The Spanish shells are, however, smaller, more strongly concavoconvex and their dorsal interior is unknown. Due the poor preservation this material is left for the moment in open nomenclature.

Order ATRYPIDA Rzhonsnitskaia, 1960
Suborder DAVIDSONIIDINA Copper, 1996
Superfamily **Davidsonioidea** King, 1850
Family **Davidsoniidae** King, 1850
Genus *Prodavidsonia* Havlíček, 1956
Type-species: *Prodavidsonia dalejensis* Havlíček, 1956.

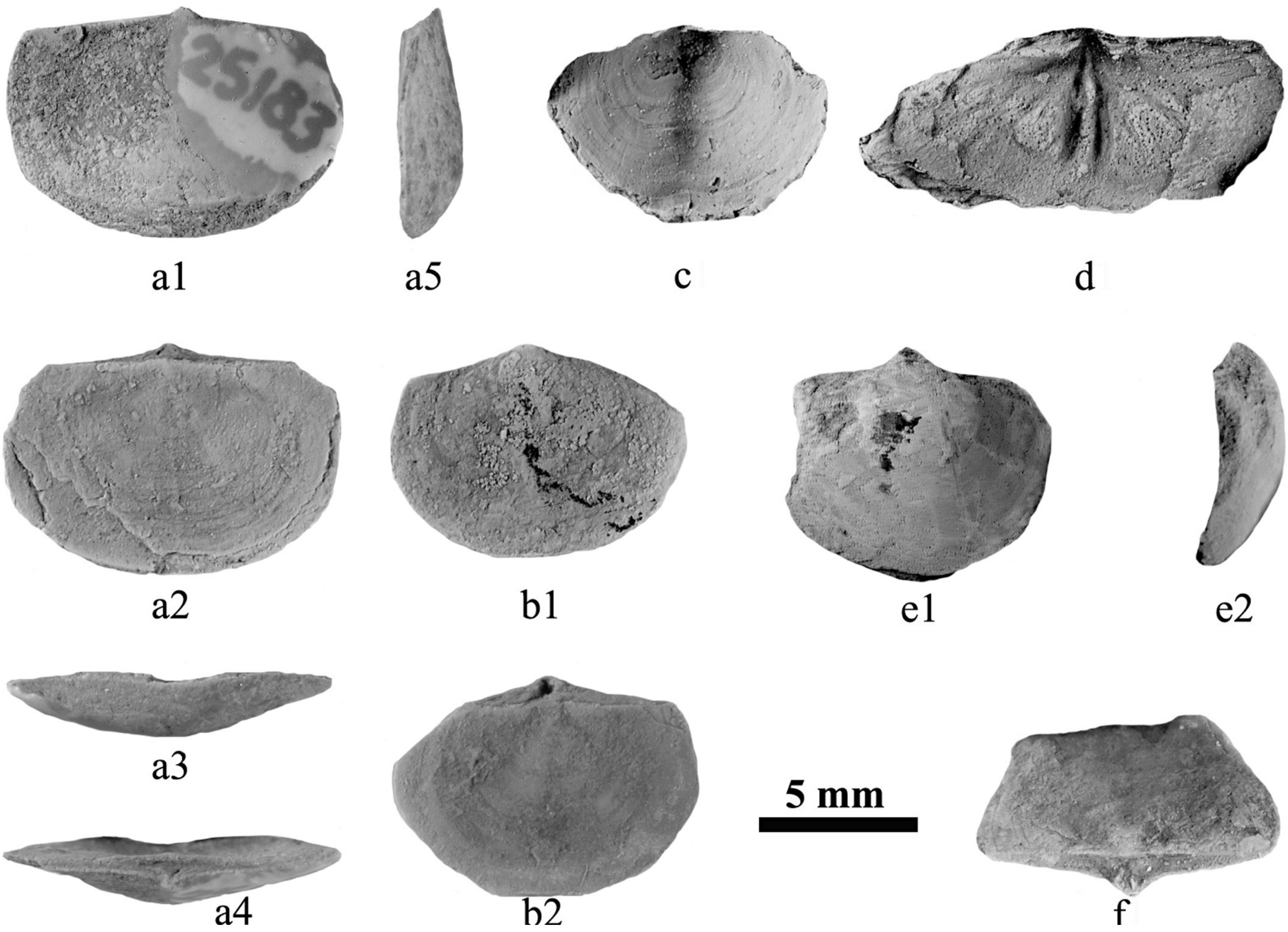


Figure 8. *Prodavidsonia havliceki* n. sp. **a1-a5**: Holotype DPO 25183, ventral, dorsal, anterior, posterior, and lateral views. **b1-b2**: partially broken specimen DPO 34098, ventral and dorsal views; **c**: external ventral mould, DPO 127846, showing the medial carina and the concentric ornamentation; **d**: Paratype DPO 25184, latex of an internal ventral mould; **e1-e2**: partially broken specimen DPO 127848, ventral and lateral views; **f**: specimen DPO 13271, postero-dorsal view showing the ventral interarea, deltidium, and foramen.

Prodavidsonia havliceki n. sp.

Figs 3, 5, 8; Table 2

v. 1990a *Prodavidsonia dalejensis* Havlíček; García-Alcalde *in* García-Alcalde *et al.*, Fig. 7, Fig. 9.18-19.
v. 1990a *Quasidavidsonia* cf. *vicina* (Havlíček); García-Alcalde *in* García-Alcalde *et al.*, Fig. 7, Fig. 9.20.
v. 1990b *Prodavidsonia* sp.; García-Alcalde *in* García-Alcalde *et al.*, Fig. 1.
v. 1999 *Prodavidsonia* cf. *dalejensis*; García-Alcalde, Fig. 2.
v. 1999 *Quasidavidsonia* cf. *vicina*; García-Alcalde, Fig. 2
v. 2009 *Prodavidsonia dalejensis* Havliček, 1956; García-Alcalde, p. 81, Fig. 2, Fig 5a-c.
v. 2009 *Quasidavidsonia* cf. *vicina*; García-Alcalde, Fig. 5c.

Derivatio nominis: In honour of the late Prof. Vladimir Havlíček, *Ustřední ústav geologicky*, Prague, Czech Republic, for his vast contribution to the study of Palaeozoic brachiopods.

Material: Holotype DPO 25183 (figured *in* García-Alcalde, 2009, Fig. 5.a1-a2, and herein, Fig. 8a1-a5) and Paratype DPO 25184 (figured *in* García-Alcalde, 2009, Fig. 5.c, and herein, Fig. 8d) from the locus and stratum typicum. Four specimens, DPO 13271, 34098, 127847-127848, near the El Calero Creek and the Carrión River confluence, Carrión River Valley, ENE of Vidrieros, Palencia, black shales with sparse mudstone nodules in the uppermost part of the La Pedrosa Mb., Gustalapiedra Formation, middle Givetian, locality α-144 (Figs 3, 4). Two specimens, DPO 127845-127846, from the upper part of La Pedrosa Mb., Gustalapiedra Fm., lower or middle Givetian, locality α-149 (Figs. 2-4). One specimen DPO 127872, from the lower part of the Cardaño Fm. (middle Givetian), locality α-145 (Figs 2, 3).

Locus and stratum typicum: Locality α-263a (Figs 2, 4). An usually dry, small tributary of the La Vega (=Man) Creek in the eastern slope of the La Vega Creek valley, ca. 800 m WSW of La Pedrosa Saddle, at the altitude of 1,180 m. Dark grey shales and marly, nodular limestones of the upper part of La Loma Mb., Gustalapiedra Fm., ca. 2 m below the sandstones of the Man Mb., just below level MR-1 (Fig. 5), upper Eifelian.

Diagnosis: Small, transverse shell; weakly developed median ventral carina and dorsal sulcus. Shell ornamented with relatively strong concentric growth lamellae and numerous intervening growth lines. Ventral brachidial cones, low.

Description: Shell liberosessile, symmetrical, small (for the genus) (average of L and w, for 7 measured specimens; 6.9 and 9.4 mm, respectively; holotype, L=7.6 mm; w=11.1 mm), semicircular to semi-elliptical, wider than long (average w/L: 1.34; Holotype: 1.5), flat (average t/L: 0.26; holotype: 0.26), weakly concavo-convex. Cardinal extremities obtuse, rounded; greatest width near hinge. Anterior commissure rectimarginate. Valves ornamented by numerous, irregularly distributed growth lamellae and intervening growth lines (Fig. 8c). Ventral valve carinate (Fig. 8a1, a4), weakly convex, margins bent in antero-dorsal direction forming a narrow commissural trail (Fig. 8a1, a5, e2); the median carina weakens anteriorly to nearly disappear at the commissure. Ventral beak sharp, slightly projecting, with more or less obtuse apical angle. Interarea low, rather flat, apsacline; deltidium broad, gently convex; pedicle foramen sub-mesothyrid, large, longitudinally elliptical, bounded basally by conjunct deltidial plates (Fig. 8f). Brachial valve weakly concave, provided by an inconspicuous median furrow that widens and weakens anteriorly to nearly disappear at the commissure; dorsal interarea linear or lacking.

Interior of ventral valve (Fig. 8d) with weakly developed, spiral grooves on very low, dorsally directed brachidial cones; strong longitudinal ridge on the bottom of a deep, median furrow, starting at the delthyrial chamber; median ridge provided by a strong button-like swelling, that stands out on the ridge, at the distal end of the adductor scars; diductor scars, weakly flabellate, posterior to the spiral cones; interior surface delicately pitted; vascular markings weakly impressed. Dorsal interior unknown.

Table 2. Measurements of *Prodavidsonia havliceki* n.sp.

Dimensions (in mm)	L	w	t
Holotype DPO 25183 (Fig. 5. a1-a2 in García-Alcalde, 2009; and herein, Fig. 8a1-a5)	7.6	11.1	2
DPO 13271 (Fig. 8f)	7	ca. 10	1.8
DPO 34098 (fig. in García-Alcalde, 2009, Fig. 5. b1-b2, and herein Fig. 8.b1-b2)	6.6	9.2	1.7
DPO 127845	6.4	7.8	1.7
DPO 127846 (Fig. 8c)	6.4	9.3	-
DPO 127848 (Fig. 8e1-e2)	7.4	9.6	-
DPO 127872	7	9	-

Discussion: The weakly concavo-convex lateral profile and the occurrence of a weak anterior trail in the best-preserved specimens allows us to include the Palentian material in *Prodavidsonia* Havlíček, 1956 and separate them from all the *Quasidavidsonia* species, *Q. vicina* (Havlíček, 1967), *Q. mediocarinata* (Havlíček, 1967), and *Q. tenuissima* (Barrande, 1879). *Prodavidsonia havliceki* n. sp. is smaller, less transverse and more weakly carinate and sulcate than *P. dalejensis*.

Copper (1996, 2002) has considered, with no discussion, *Quasidavidsonia* Havlíček, 1987 as a junior synonym of *Prodavidsonia*. The new figures given in the *Treatise on Invertebrate Palaeontology* (Copper, 2002, Fig. 2a-e) although assigned to *Prodavidsonia dalejensis* Havlíček, 1956, the type-species of *Prodavidsonia*, correspond in fact both to the named species (Fig. 2e) and to *Quasidavidsonia vicina* (Figs 2a-d), the type species of *Quasidavidsonia* (meaning *Q. vicina* would also be a junior synonym of *P. dalejensis*?). The reversed convexity and convexo-concave profile of the *Quasidavidsonia* species, easily visible in the referred figures, makes at least debatable both the generic and the supposed specific synonymy (see Havlíček, 1998).

Order ATHYRIDIDA Boucot, Johnson & Staton, 1964
Superfamily **Dayioidea** Waagen, 1883
Superfamily **Anoplothecoidea** Schuchert, 1894
Family **Anoplothecidae** Schuchert, 1894
Subfamily **Anoplothecinae** Schuchert, 1894
Genus *Bifida* Davidson, 1882

Type-species: *Terebratula lepida* d'Archiac & de Verneuil, 1842.

Bifida aff. *lepida*
(d'Archiac & de Verneuil, 1842)

Figs. 3, 9; Table 3

v. 1990a *Bifida* spp.; García-Alcalde *in* García-Alcalde *et al.*, Fig. 7.
v. 1999 *Bifida lepida*; García-Alcalde, p. 601, Tabla I.

Material: Ten specimens in variable preservation state, usually as external moulds of isolated valves, DPO 127905-127911 (Figs 2-4):

-DPO 127905 from locality α-48a, Gustalapiedra Fm., La Loma Mb., upper Eifelian.

-DPO 127906 from locality α-149, Gustalapiedra Fm., La Pedrosa Mb., lower Givetian.

-DPO 127907-127910 from locality α-263a, Gustalapiedra Fm., La Loma Mb., upper Eifelian.

-DPO 127911 from locality A.PIN-6, Cardaño Fm., middle to upper Givetian.

-DPO 127912 from locality B97-44, a complete, articulated shell, Cardaño Fm., middle to upper Givetian.

-DPO 127913-127914 from locality α-144, uppermost part of Gustalapiedra Fm., lower to middle Givetian. The DPO 127913 is a complete, articulated shell.

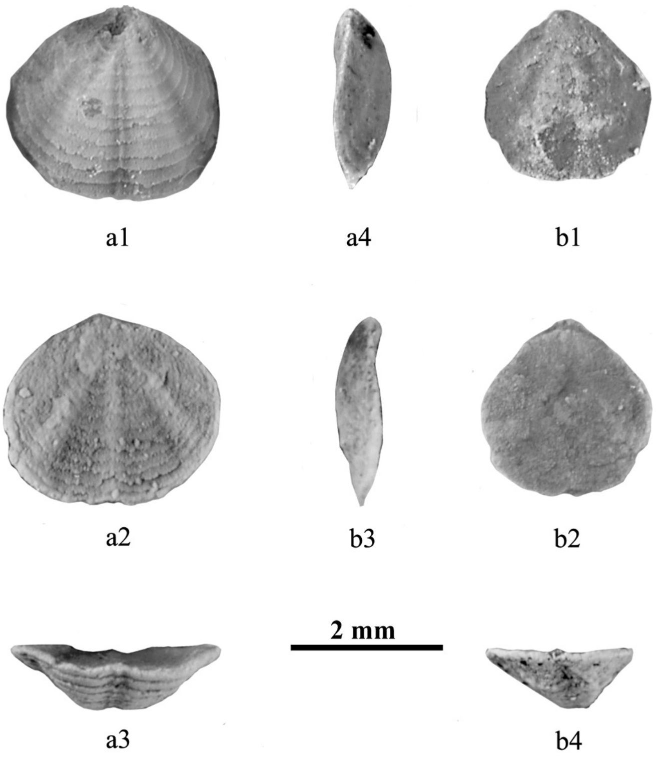


Figure 9. *Bifida* aff. *lepida* (d'Archiac & de Verneuil, 1842). **a1-a4**: ventral, dorsal, anterior, and lateral views of the specimen DPO 127912; **b1-b4**: ventral, dorsal, lateral, and anterior views of the specimen DPO 127913.

Description: Shell minute (average length: 2.06 mm), subcircular to subpentagonal in outline, nearly equidimensional (average w/L: 0.98), strongly unequally biconvex, lenticular (thickness less than 1 mm), carinate. Hinge very narrow, greatest width at midlength or slightly anterior. Ventral valve strongly convex, carinate; greatest thickness at midlength or posterior; midpair of strong, rounded plications that start at the apex and widen and lose height gradually anteriorly; one or two pairs of lateral costae, weaker than the median ones. Exceptionally, a fine, narrow, low costa, occurs amidst the midpair (Fig. 9a1, a3). Dorsal valve with a large, median depression and flattened to slightly convex postero-lateral margins; five radial plications: a median, rather strong plication in the middle of the sulcus, and two pairs of bordering lateral costae; the plications start at the apex of valve and widen and lose height gradually anteriorly; the first lateral pair of costae is larger than the median one and stands out of it; the second, postero-lateral pair of costae is very weak, nearly inconspicuous. (Fig. 9a2-a3). Surface of shell provided by numerous, even, imbricate growth lamellae with spiny margins (Fig. 9.a1-a4). Internal characters unknown.

Discussion: Our form reminds us externally of *Bifida lepida* (d'Archiac & de Verneuil, 1842). The shell of the latter species is however larger, ventri-biconvex, and longer than wide. Authors have included in *B. lepida* numerous, possibly different Emsian to Frasnian forms. A revision of the type material is thus badly needed.

The Palentian forms occur in beds of the Gustalapiedra and Cardaño Fms, of upper Eifelian to middle or upper Givetian age.

Table 3. Measurements of *Bifida* aff. *lepida.*

DPO	L	w	t	w/L
127905	2.13	1.87	-	0.88
127906	2.20	1.87	-	0.85
127907	0.93	1.13	-	1.21
127908	2.33	2.47	-	1.06
127909	2.27	2.27	-	1
127911	1.07	0.93	-	0.87
127912 (Fig. 9a1-a4)	2.53	2.87	1	1.13
127913 (Fig. 9b1-b4)	2.27	2.27	0.87	1
127914	2.80	2.47	-	0.88

Order SPIRIFERIDA Waagen, 1883
Suborder SPIRIFERIDINA Waagen, 1883
Superfamily **Ambocoelioidea** George, 1931
Family **Ambocoeliidae** George, 1931
Subfamily **Rhynchospiriferinae** Paulus, 1957
Genus *Ambothyris* George, 1931

Type-species: *Spirifera infima* Whidborne, 1893.

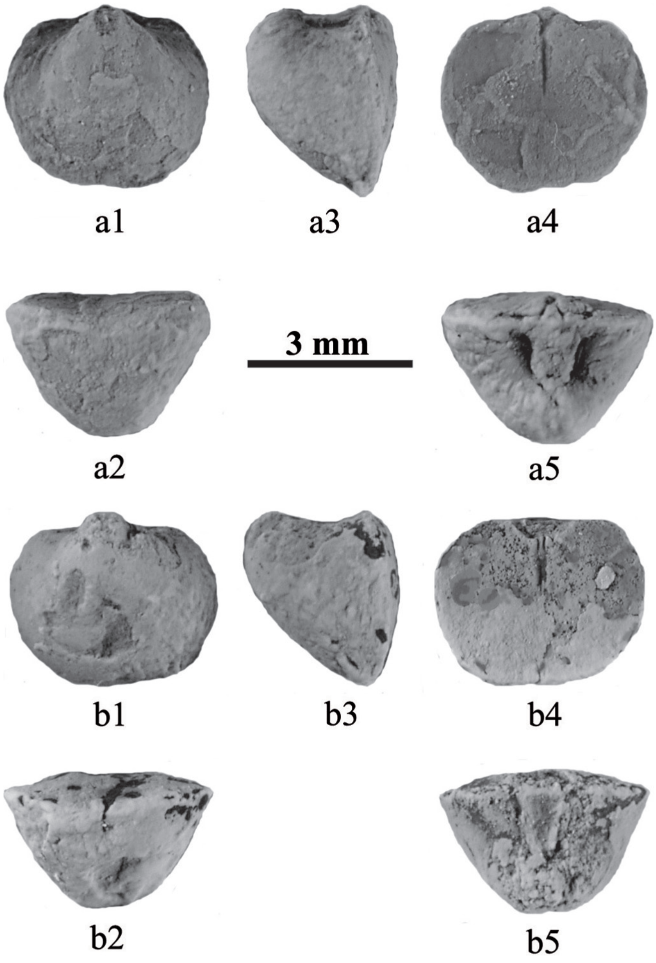


Figure 10. *Ambothyris* cf. *infima* (Whidborne, 1893). **a1-a5**: ventral, anterior, lateral, dorsal, and posterior views of the specimen DPO 127842; **b1-b5**: ventral, anterior, lateral, dorsal, and posterior views of the specimen DPO 127843.

Ambothyris cf. *infima* (Whidborne, 1893)

Figs 3, 10-11; Table 4

Material: Two articulated, strongly weathered specimens, DPO 127842 (locality α-150, Fig. 2) and DPO 127843 (locality α-104, Fig. 2), upper part of the Gustalapiedra Fm., lower Givetian.

Description: Shell minute, strongly ventri-biconvex, elliptical in outline, slightly wider than long, brachythyrid, with rounded cardinal extremities; surface smooth except for the occurrence of subdued median depressions in both valves; anterior commissure weakly sulcate (Fig. 10a2); antero-lateral margins rounded, turned up dorsally; greatest width at the first third of length; greatest height posterior to midlength. Ventral interarea high, catacline, curved, with ill-defined margins (Fig. 10a3, a5, b3); delthyrium open, broad, occupying more than 1/3 of the interarea width, with discrete, narrow deltidial plates; beak incurved, small; apical angle obtuse. Ventral valve hemipyramidal, umbo inflated, median furrow inconspicuous. Dorsal valve low, weakly and evenly convex; subdued median depression, very enlarged forward. Concentric ornamentation formed by a short number of strong growth lamellae crowded anteriorly and finer intervening lines. Shell substance fibrous, impunctate. The radial fibrous fabric of shell, visible in exfoliated parts of the studied specimens, sometimes gives the impression of a capillate microornament. Dental plates lacking, ventral muscle field, long, narrow, weakly impressed. Crural plates long, converging anteriorly (Fig. 10a4, b4; Fig. 11b); dorsal muscle field inconspicuous.

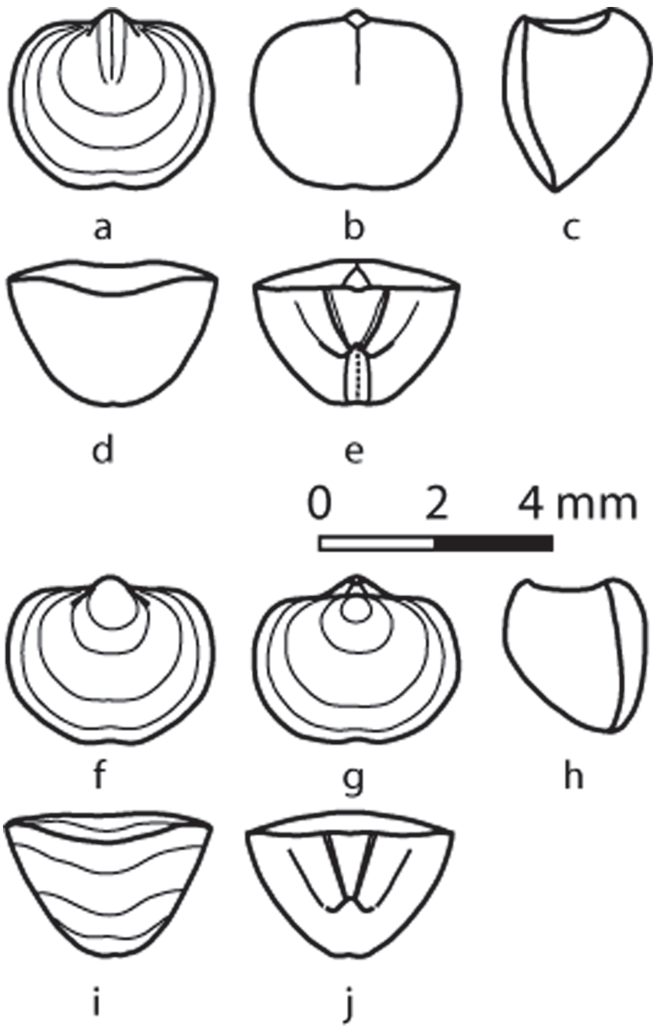


Figure 11. *Ambothyris* cf. *infima* (Whidborne, 1893). Camera lucida drawing (enlarged and slightly idealized) of the specimens figured in Fig. 10, DPO 127842, **a-e**: ventral, dorsal, lateral, anterior, and posterior views, partially showing the ventral muscle field and the crural plates uniting anteriorly; and DPO 127843, **f-j**: ventral, dorsal, lateral, anterior, and posterior views, showing both the concentric ornamentation and the high, catacline interarea.

Table 4. Measurements of *Ambothyris* cf. *infima.*

DPO	L	w	t	w/L
127842 (Fig. 10a1-a5)	3.3	3.6	2.6	1.1
127843 (Fig. 10b1-b5)	3.4	3.7	2.5	1.1

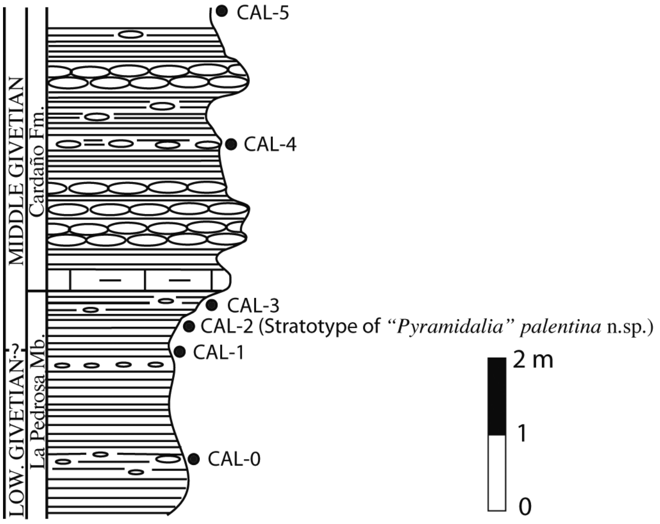


Figure 12. Stratotype of "*Pyramidalia*" *palentina* n. sp. Levels CAL-1 and so on: sampling for conodonts. Symbols as in figure 3.

Remarks: The described form reminds us very much *Ambothyris infima*, but differs slightly in outline and lateral profile.

Suborder DELTHYRIDINA Ivanova, 1972
Superfamily **Reticularioidea** Waagen, 1883
Family **Reticulariidae** Waagen, 1883
Genus *Pyramidalia* Nalivkin, 1947

Type-species: *Spirifera simplex* Phillips, 1841.

"*Pyramidalia*" *palentina* n. sp.

Figs. 3, 12-14; Table 5

v. 1990a *Pyramidalia simplex*; García-Alcalde, *in* García-Alcalde *et al.*, Fig. 7

Derivatio nominis: After the name Palencia, the Spanish province where the species has been found.

Material: Holotype DPO 127824 (Fig. 14a1-a5) and four paratypes, DPO 127825-127828 from the *locus* and *stratum typicum*. Two specimens, DPO 127829-127830 (the latter sectioned to show the pedicle interior, Fig. 13), from the locality α-104, a shepherd path between the La Abadía de Lebanza-Polentinos track and the La Abadía de Lebanza-Carrión valley track, near the El Águila water trough (Fig. 2), upper part of the Gustalapiedra Fm., lower to middle Givetian (Fig. 3). Four specimens, DPO 127820-127823 (Fig. 14a1-a5), from the locality α-149, southern Cimero Peak slope, above the La Abadía de Lebanza-Carrión valley track, NW of a shepherd's hut, at the altitude of 1,400 m (Figs 2, 4), upper part of the Gustalapiedra Fm., lower to middle Givetian (Fig. 3).

Locus and stratum typicum: Section near the El Calero Creek and the Carrión River confluence, Carrión River valley, ENE of Vidrieros, Palencia (Fig. 4). Black shales with sparse mudstone nodules of the uppermost part of the La Pedrosa Mb., Gustalapiedra Formation, α-144, level CAL-2 (Figs. 3, 12). Possibly middle Givetian.

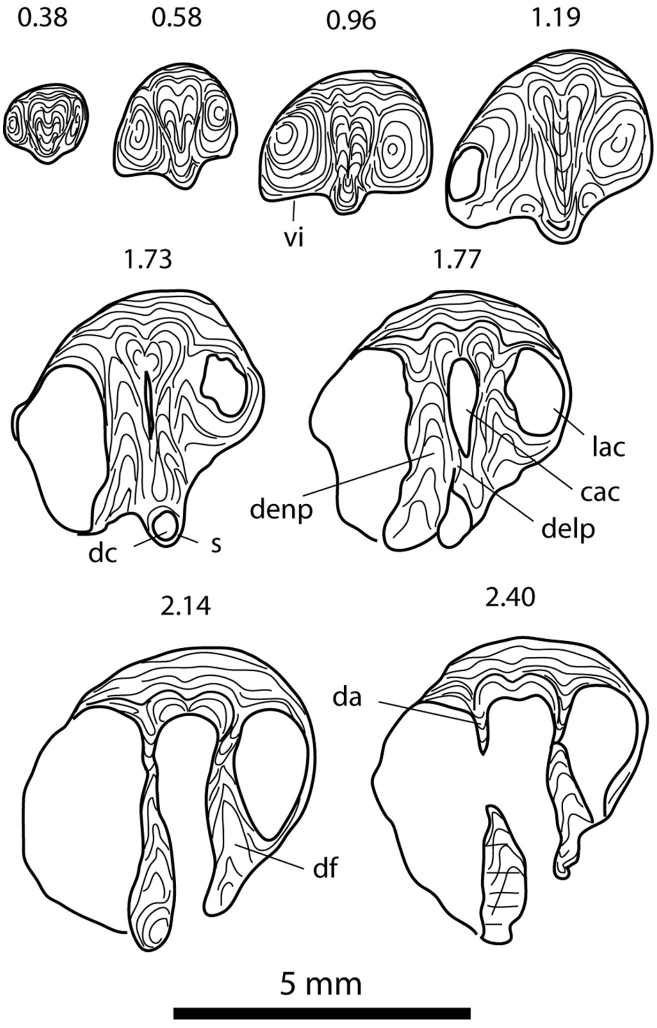


Figure 13. "*Pyramidalia*" *palentina* n. sp. Camera lucida drawing of the serial sections of the specimen DPO 127830. Distances in mm measured to the ventral apex. cac: Central apical cavity; da: dental adminiculum; dc: delthyrial cavity; df: dental flange; delp: delthyrial plate; denp: dental plate; lc: lateral apical cavity; s: symphytium; vi: ventral interarea.

Diagnosis: Shell impunctate, small, smooth, strongly ventri-biconvex, transversely ellipsoidal, brachythyrid, with very rounded cardinal extremities. Ventral sinus and dorsal fold obscure, narrow. Ventral valve hemipyramidal; interarea high, strongly apsacline to catacline, even procline, longitudinally curved; delthyrium narrow, covered by a nearly complete, strong symphytium with a minute, non-functional apical foramen and a relatively large basal arc. Dental plates short, thin, weakly divergent, with well-differentiated dental flanges and adminicula. Apical plates joining below level of interarea forming a delthyrial plate situated high into the delthyrial cavity. Cardinal process bilobed, apparently non-striated, crural plates short, sub-parallel.

Description: Shell smooth, small (Lmax 8.2 mm), ventri-biconvex, strongly inflated (average: t up to 80% of L for 4 measured specimens; t/L of the holotype: 0.84), transversely ellipsoidal (average L 79% of w for 4 measured specimens; w/L of the holotype: 1.25), with very rounded cardinal extremities and hinge shorter than maximum width (hinge width ca. 70% of the maximum width); maximum width at midlength; maximum height at the umbonal region. Shell substance impunctate. Test radially grooved internally giving the impression of a microcostulate ornament in exfoliated shells.

Ventral interarea, very high, curved, strongly apsacline to catacline, even slightly procline, transversally striated, twice wider than high, with ill-defined, rounded interarea margins (Fig. 14a4, a5, c2, c5); delthyrium rather narrow, ca. 1/4 of the hinge width, covered by a nearly complete, strongly convex symphytium; symphytium with a relatively large basal arc provided by an apical, minute, probably non-functional (because of secondary infilling) foramen (Fig. 14a4, b, c5); umbo large with a short, pointed, erect to incurved beak, apical angle up to 120º (average: 105º, for 7 measured specimens; holotype: 110º). Dorsal interarea almost flat, very low, orthocline to anacline; wide, open notothyrium, with narrow, marginal chilidial plates; umbo faint with a small rounded beak.

Ventral sinus and dorsal fold subdued, narrow (width of sinus and fold less than 1/3 of the shell width), rounded, weakly marked anteriorly; anterior commissure faintly uniplicate, rounded (Fig. 14a3, c4); antero-lateral commissures rounded, curving slightly dorsally. Ventral valve strongly convex; greatest thickness at the umbonal region. Dorsal valve weakly and evenly convex; greatest thickness at midlength. Growth lamellae few, usually much eroded. Micro-ornamentation obscure due to shell exfoliation; some preserved parts of the test show files of concentrically disposed, minute granules. Shell substance impunctate.

Dental plates thin, rather short, weakly divergent with well differentiated massive dental flanges and thin adminicula; conjunct apical plates joining to form a massive delthyrial plate situated high into the delthyrial cavity, plunged posteriorly into secondary shell (Fig. 13); a longitudinal, low, wide, median

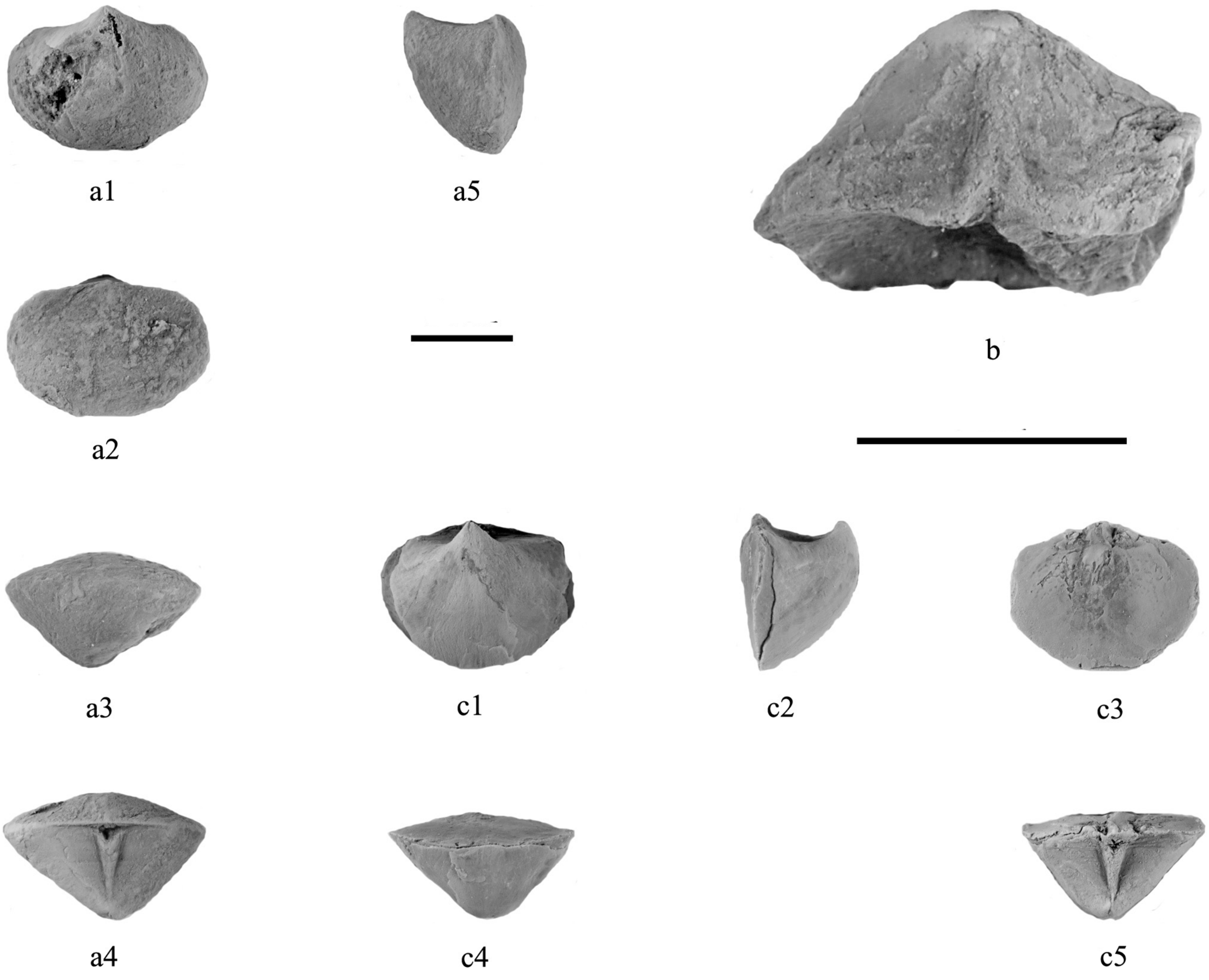


Figure 14. "*Pyramidalia*" *palentina* n. sp. **a1-a5**: Holotype DPO 127824, ventral, dorsal, anterior, posterior, and lateral views; **b**: posterior oblique view of a partially broken ventral valve DPO 127823 showing the secondarily infilled apical foramen; **c1-c5**: ventral, lateral, dorsal, anterior, and posterior views of a slightly crushed specimen DPO 127829. Scale bars: 5 mm.

Table 5. Measurements of “*Pyramidalia*” *palentina* n.sp.

DPO	L	w	t	w/L	t/L	Apical angle
Holotype 127824 (Fig. 14a1-a5)	8	10	6.7	1.25	0.84	110º
Paratype 127827	-	6.7	-	-	-	115º
Paratype 127828	-	-	9.5	-	-	110º
127820	4.5	6.3	3.4	1.40	0.75	119º
127821	8	8.9	-	1.11	-	97º
127823	5.1	7	4.5	1.47	0.88	-
127829 (Fig. 14c1-c5)	8.2	9.9	5.6	1.20	0.68	95º

ridge starts at the apex but it is also plunging into secondary shell along the delthyrial chamber (Fig. 13). Crural plates very short, sub-parallel, visible both on partial internal moulds and by transparency. Strong, bilobed, smooth cardinal process infilling the nothothyrial opening. Muscle fields not visible usually on available material. On an internal dorsal mould (DPO 127829) a rectangular, longer than wide, quadripartite, with a rather strong relief, transversally ridged dorsal muscle field is barely visible (Fig. 14c3).

Discussion: Our species reminds us of several small, smooth, hemipyramidal forms assigned to *Spirifera simplex* Phillips, 1841 in different generic combinations (i.e. associated with *Reticularia*, *Eoreticularia*, *Cyrtia*, *Plectospirifer*, *Thomasaria*, *Cyrtinaella*, or *Pyramidalia*) (see synonymies and discussions in Vandercammen, 1957; Drot, 1964; Balinski, 1979; Oleneva, 2006). *Pyramidalia* has been considered even as a junior synonym either of *Cyrtinaella* (i.e. Pitrat, 1965, *in Treatise on Invertebrate Paleontology*, p. 678), *Squamulariina* (i.e. Johnson, 2006, *in Treatise on Invertebrate Paleontology*, p. 1882), or *Thomasaria* (i.e. Balinski, 1979). But, in fact, neither an endopunctate structure nor a median ventral septum have been observed by authors describing “*simplex*” forms (i.e. Vandercammen, 1957; Drot, 1964; Balinski, 1979; among others), and the same applies to the species discussed herein. Consequently, it must be rejected that these forms belong in the Superfamily Cyrtinoidea. On the other hand, *Thomasaria* lacks both the strongly convex symphytium and the small crural plates of *Pyramidalia*, their cardinal angles are acute or at right angles, not rounded as in *Pyramidalia*, and the dental plates are longer than in the latter genus. In consequence, *Pyramidalia* would be a valid taxon, but waiting for the necessary revision of Phillips’s types we prefer for the moment to use the name with reservation. The supra-generic affiliation of *Pyramidalia* is obscure. It must belong to the Family Reticulariidae Waagen, 1883 but no genera of the accepted Subfamilies of the taxon shows the strong pseudodeltidium-like symphytium, typical of *Pyramidalia* forms.

“*Pyramidalia*” *palentina* n. sp. is smaller than “*P.*” *simplex* Phillips, lacks radial plications on the shell flanks, and the ventral sinus and dorsal fold are weaker. It also differs from *Thomasaria* cf. *altumbona* Mottequin, 2008 *non* Stainbrook, 1945, from the Frasnian of the Neuville Formation, Namur-Dinant Basin (Belgium), in the greater development of the ventral interarea and symphytium, weaker ventral sinus, dorsal fold and ventral tongue, and occurrence of crural plates.

Suborder SPIRIFERIDINA Waagen, 1883
Superfamily **Martinioidea** Waagen, 1883
Family **Tenellodermidae** Carter, Johnson & Gourvennec (*in* Carter *et al.*, 1994)

Genus *Cingulodermis* Havlíček, 1971

Type-species: *Cingulodermis cinctus* Havlíček, 1971.

Remarks: The genus *Cingulodermis* was introduced by Havlíček (1971) for brachythyrid, smooth, weakly differentiated shells, devoid of radial capillae, surficial pits or minute spines, but with strong concentric lamellae, short dental plates, non-striate cardinal process, and crural plates separated, touching the bottom of valve in proximity to the hinge. Micro-ornament features allowed the author of the genus to separate it from *Eomartiniopsis* where most of *Cingulodermis* species were initially assigned. *Cingulodermis* resembles *Eoreticularia* Nalivkin *in* Frederiks, 1924 in external outline and smooth shell surface. The latter genus, however differs from *Cingulodermis* in the granulate micro-ornamentation and in the crural plates not resting on the valve floor, sometimes united to a short median dorsal ridge.

Cingulodermis sotoana n. sp.

Figs 3, 15-17; Table 6

v. 1999 *Eoreticularia fraterna* (Barrande, 1879); García-Alcalde, Fig. 7

Derivatio nominis: Named after Francisco M. Soto Fernández, colleague in the Palaeontology section of the Faculty of Geology of Oviedo, but above all my close friend.

Material: Thirteen specimens, comprising either complete shells or external and internal moulds in variable preservation state.

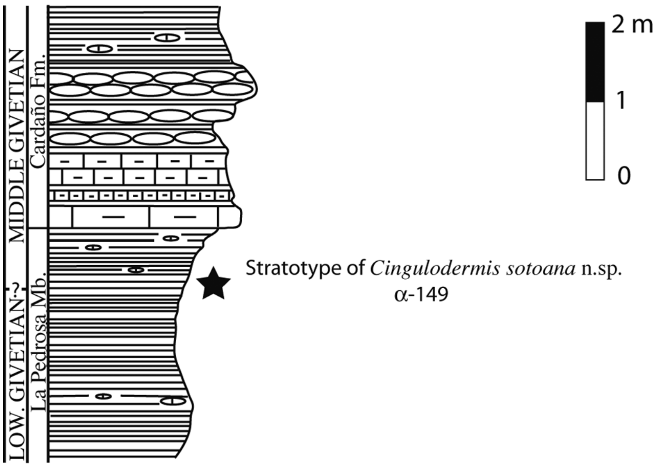


Figure 15. Stratotype of *Cingulodermis sotoana* n. sp. (black star). Symbols as in figure 3.

Holotype DPO 127834 (Fig. 17a1-a5) and Paratype DPO 127833 (Fig. 17f1-f4), both from the locus and stratum typicum. The other specimens come from the localities and stratigraphical settings below (Figs 2-4):
Gustalapiedra Fm., La Loma Mb., upper Eifelian:
Locality α-264; DPO 34112, 127840.
Locality α-263c: DPO 127835-127837.
Locality α-178: DPO 127838.
Locality α-150: DPO 127831-127832.
Gustalapiedra Fm., La Pedrosa Mb, uppermost Eifelian to middle Givetian:
Locality α-144; DPO 127841.

Locus and stratum typicum: Southern slope of the Cimero Peak, near the track La Abadía de Lebanza-Carrión Valley, NW of a shepherd's hut, at the altitude of 1,400 m, locality α-149 (Figs. 2, 4). Black shales of the uppermost part of the Gustalapiedra Fm., top of La Pedrosa Member (Fig. 15), lower to middle Givetian.

Diagnosis: Shell of small size for the genus, moderately transverse, strongly ventri-biconvex, with rounded cardinal extremities and incurved beaks overhanging the cardinal area. Fold and sulcus well defined anteriorly resulting in uniplicate commissure. Ventral interarea, high, relatively flattened, apsacline to catacline, bounded laterally by very weak edges; delthyrium open. Surface of valves non costate. Growth lamellae few, strong, irregularly spaced with fine, numerous, intervening growth lines. Micro-ornamentation devoid of radial capillae, surficial pits or spines. Dental plates, strong, of more or less curved bases, moderately divergent; ventral muscle field well impressed into the shell, partially extending beyond the distal ends of dental plates. Dorsal muscle field slightly impressed. Cardinal process small, non-striate; crural plates short, sub-parallel.

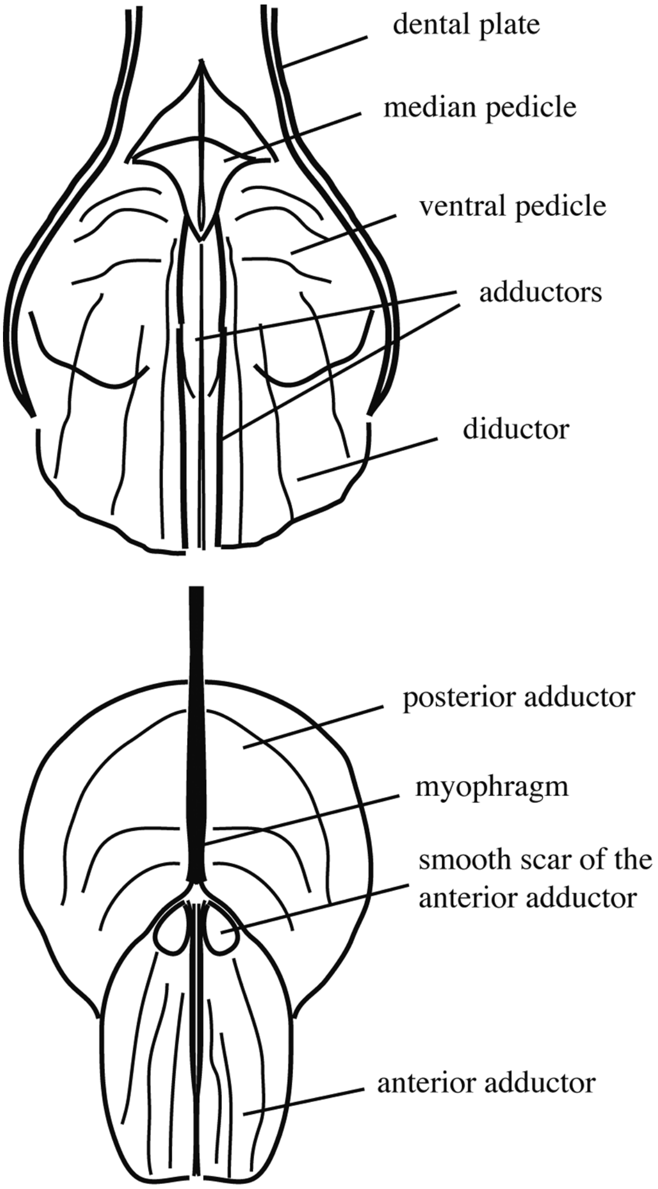


Figure 16. *Cingulodermis sotoana* n. sp. Camera lucida, slightly idealized, very enlarged drawings of the ventral (above) and dorsal (below) muscle fields, based mainly on internal moulds DPO 34112, 127831, and 127835.

Description: Shell small (Lmax: 10 mm), ventri-biconvex, inflated (average: t up to 74% of L for 7 measured specimens; t/l of the holotype: 0.76), sub-pentagonal outline, wider than long (average: L 82% of w for 8 measured specimens; w/L of the holotype: 1.11), with rounded cardinal extremities and hinge narrower than maximum width (hinge width ca. 67% of maximum width); greatest width a little behind midlength; greatest height at the first third of length.

Pedicle valve elliptical to subpentagonal outline, strongly convex, very high; greatest height in the posterior third; strong, incurved beak overhanging the cardinal area; apical angle up to 100º; ventral interarea high, relatively flattened, apsacline to catacline, 3-4 times wider than high (Fig. 17a4-a5, b2, b4, c3, c5, d1, f4); delthyrium wide, up to a third of the interarea width, bounded by two thin delthyrial plates not fused into a deltidium. Brachial valve elliptical to subpentagonal outline, gently and evenly convex, 60% as high as the ventral valve, with greatest height at midlength; dorsal interarea almost flat, low, anacline, with a large, open nothothyrium provided by thin, marginal chilidial plates; dorsal beak curved, overhanging the cardinal area.

Shell surface smooth with rounded, subdued, relatively wide ventral sinus and dorsal fold, both starting ahead of the umbon-

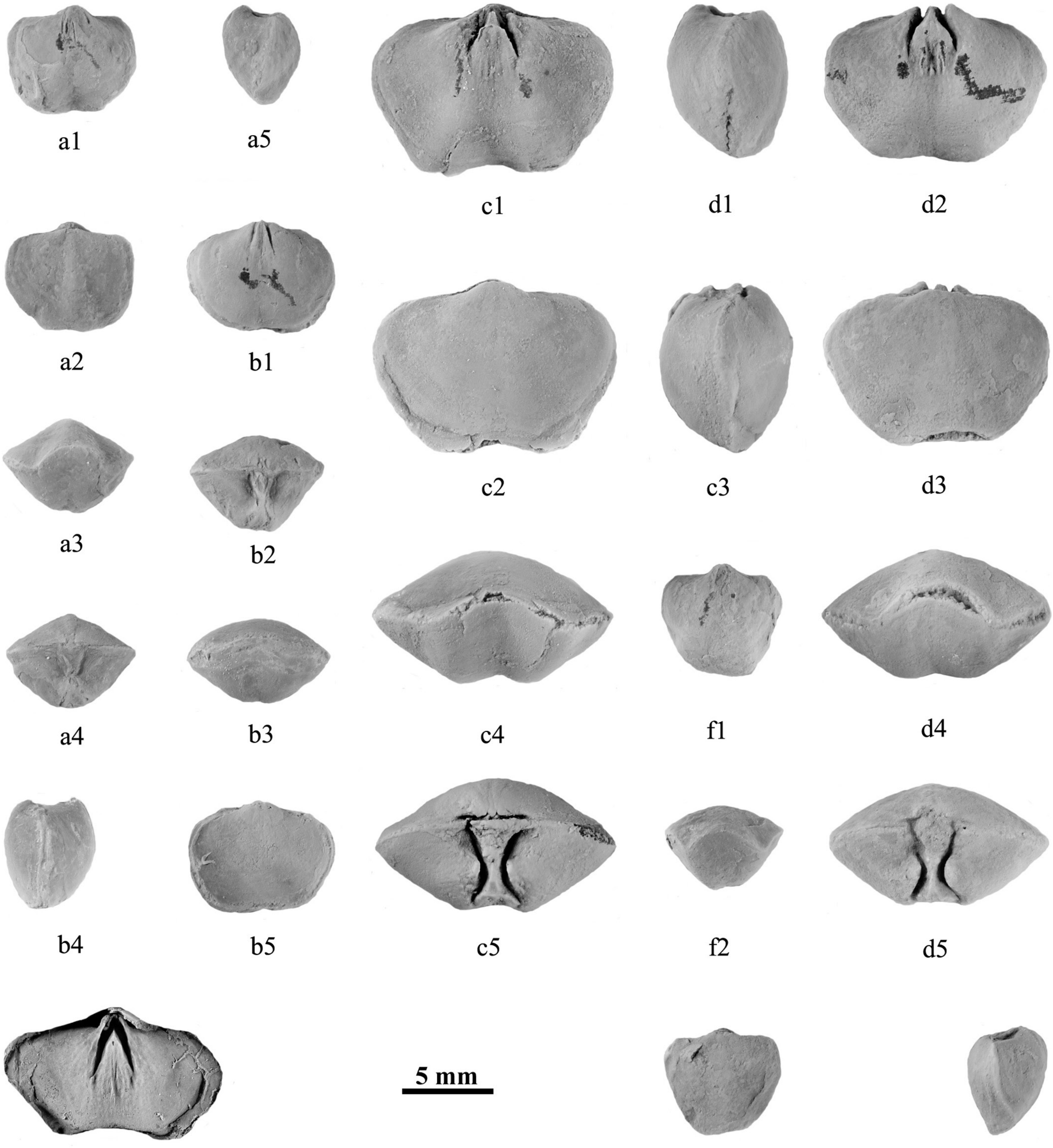


Figure 17. *Cingulodermis sotoana* n. sp. **a1**-**a5**: Holotype DPO 127834, ventral, dorsal, anterior, posterior, and lateral views; **b1**-**b5**: ventral, posterior, anterior, dorsal, and lateral views of a complete internal mould, DPO 34112, showing in **b2** the parallel, separate crural plates; **c1**-**c5**: ventral, dorsal, lateral, anterior, and posterior views of a pyritized, complete internal mould DPO 127831; **d1**-**d5**: lateral, ventral, dorsal, anterior, and posterior views of a nearly complete, pyritized, internal mould DPO 127835; **e**: pyritized internal ventral mould, DPO 127844; **f1**-**f4**: Paratype DPO 127833, ventral, anterior, dorsal, and lateral views.

al region (width of sinus and fold greater than 1/3 of the shell width); anterior commissure uniplicate; antero-lateral commissures turned up to the dorsal valve. Growth lamellae strong, few, irregularly spaced, with numerous intervening, finer growth lines. Radial capillae, surficial pits or spines lacking.

Dental plates, strong; dental flanges convergent, connected by apical callus (Fig. 17e); ventral adminicula divergent, distally curving more or less one to another, partially bounding the muscle field. Ventral muscle field clearly impressed into the shell; adductor scars, oval, flat, long, narrow, raised, bounded both by flabellate, sub-triangular diductors prolonged well ahead of the distal ends of the dental plates, and by large oval ventral pedicle scars (Fig. 16). The apical callus form, behind the adductor field, a triangular, slightly elevated platform supporting the median pedicle adjustors (Figs 16, 17b1, c1, d2, e). Cardinal process small, simple, not striate. Short, sub-parallel incisions corresponding to the crural plates, visible on well-preserved internal moulds in the immediate proximity of hinge (Fig. 17b2, c5); dorsal muscle field slightly impressed, short, divided by a thin myophragm, constituted by an anterior, subtrapezoidal adductor pair scar and a posterior, reniform adductor pair scar (Fig. 16).

Table 6. Measurements of *Cingulodermis sotoana.*

DPO	L	w	t	w/L	t/L
Holotype 127834 (Fig. 17a1-a5)	6.6	7.3	5	1.11	0.76
Paratype 127833 (Fig. 17f1-f4)	6.7	7	4.9	1.04	0.73
34112 (Fig. 17b1-b5)	6.6	8.6	5	1.30	0.76
127831 (Fig. 17c1-c5)	9.5	13.7	7.6	1.44	0.80
127832	5.9	6.6	4.5	1.12	0.76
127835 (Fig. 17d1-d5)	9.4	12.6	7	1.34	0.74
127840	4	4.8	2.6	1.20	0.65
127845	10	12.5	-	1.25	-

Discussion: *Cingulodermis sotoana* n. sp. co-occurs sometimes with "*P.*" *palentina* n. sp. in the uppermost part of the Gustalapiedra Fm., but it is larger than the latter, with well differentiated fold and sinus, and lacks both the strong, convex symphytium and the very high, curved ventral interarea of the latter species.

Eoreticularia fraterna (Barrande, 1879) is larger than *C. sotoana* n. sp., less inflated, with well- differentiated sinus and fold, low interarea bounded by obtuse edges, and micro-ornamentation granulate. Internally, the crural plates do not touch the bottom of the shell and sometimes they are united to a thin median ridge.

C. sotoana n. sp. reminds us of *C. columbina* (Havlíček, 1959) of the Suchomasty and Acanthopyge Limestones (Eifelian) in Bohemia, Czech Republic. The former species is, however, smaller, less transverse, with hinge line narrower, cardinal extremities more rounded, and growth lamellae stronger. The specimens of *C. sotoana* n. sp. show slight differences regarding the proportions and general morphology similar to those that allowed Havlíček (1959) to subdivide *C. columbina* in two subspecies, *C. columbina columbina*, and *C. columbina asellata*. Thus, the Eifelian forms of *C. sotoana* n. sp. that occur in the La Loma Mb. of the Gustalapiedra Fm. below the sandstones of the Man Mb. (of upper Eifelian age) are larger and more transverse than those occurring in the La Pedrosa Mb, in the upper part of the Gustalapiedra Fm. (of lower to middle Givetian age). In addition, the younger forms have a well developed ventral sinus and dorsal fold. To date, the available samples of *C. sotoana* n. sp. are too small to allow a further taxonomic splitting of the Palentian taxon.

Order TERЕBRATULIDA Waagen, 1883
Suborder TEREBRATULIDINA Waagen, 1883
Superfamily **Stringocephaloidea** King, 1850
Family **Stringocephalidae** King, 1850
Genus *Parastringocephalus* Struve, 1965

Type-species: *Strygocephalus dorsalis* d'Archiac & de Verneuil, 1842.

Parastringocephalus cf. *dorsalis* (D'Archiac & de Verneuil, 1842)

Figs 3, 18

Material: One single, bivalved, slightly crushed, surficially exfoliated specimen, DPO 126538, from the locality α-358, ca. 190 m East of the Águila Peak (1,488 m), high in the western slope of the Man Creek valley, south of La Abadía de Lebanza (Fig. 2); limestones of the lower part of the Cardaño Fm. (middle Givetian) (Fig. 3).

Descriptive notes: Shell of medium size (L=54 mm; w=72.5 mm; t=38 mm), ventribiconvex, wider than long (w/L=1.36), of spiriferoid, subpentagonal outline with rounded cardinal extremities (Figs. 18a1-a2). Hinge narrower than maximum width. Greatest width slightly anterior to midlength, maximum thickness at midlength. Pedicle valve with a strongly marked, relatively narrow sulcus (ca. 30% of the shell width at the anterior margin), with a flattened bottom, bounded by rounded ridges, extending from umbo to anterior (Fig. 18a1, a3). Beak erect, asymmetrical (Fig. 18a2, a4); apical angle, obtuse; beak ridges, strong. Ventral interarea high, concave, orthocline, transversally striated, strongly bounded; delthyrium broad; traces of an apical deltidium pierced by a small circular foramen. Dorsal interarea inconspicuous; dorsal beak strongly curved, hidden into the delthyrial cavity. The brachial valve bears a very low, indistinct, medially depressed fold, bounded by weak furrows (Fig. 18a2-a3). Anterior commissure, parasulcate. The shell surface of the available specimen has experienced intense abrasion, but some relatively well-preserved shell portions show a finely striate radial micro-ornamentation crossed by closely spaced, slightly undulating growth lines. Shell substance, densely endopunctate. The wearing off of the test reveals the occurrence of strong, internal median septa in both valves.

Remarks: The type-species of *Parastringocephalus*, *P. dorsalis* (d'Archiac & de Verneuil, 1842) is very close to the Palentian form in proportions, outline and medial differentiation of shell. That species has usually been cited as

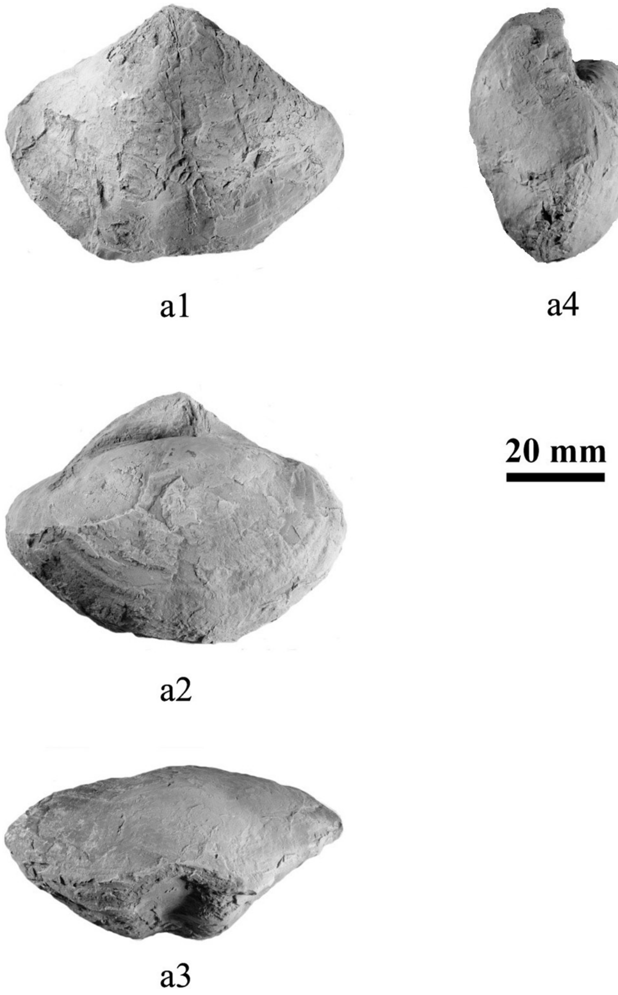


Figure 18. *Parastringocephalus* cf. *dorsalis* (d'Archiac & de Verneuil, 1842). **a1-a4**: ventral, dorsal, anterior, and lateral views.

middle Givetian (current sense, i.e. below the *Hermanni* conodont Zone) beds in Germany (Torley, 1934; Struve, 1982a,b, 1992), France (Brice & Loones, 2002), South China (Yang *et al.*, 1977) and tentatively in the Dra Valley, SW Morocco (Ebbighausen *et al.*, 2007).

Family **Meganterididae** Schuchert & LeVene, 1929
Subfamily **Adreninae** Boucot (*in* Boucot & Wilson, 1994)

Genus *Ense* Struve, 1992

Type-species: *Ense andrea* Struve, 1992.

Remarks: The species of the genus, formerly collectively known as "*Terebratula*" *pumilio*, have been extensively mentioned but seldom described. This situation is probably due to the surprising find of two consecutive synchronic (or nearly so) (see above) coquinas with great accumulations of "*pumilio*" forms (the so-called Lower, and Upper "*Pumilio*" horizons) in Germany, France, Morocco, and Algeria (Lottmann, 1990a, b; Struve, 1992), and the appealing hypothesis by Lottmann (1990a, b) that they represent mass mortality events triggered by big tidal waves, as tsunamis.

In fact the "*Pumilio*" horizons have been cited in dozens of scientific articles while the systematic nature of the concerned taxa has usually been avoided. Schmidt (1960) proposed that the German "*pumilio*" forms were young stringocephalids of unknown generic affinities. Lottmann (1990a, b) supplied interesting historical information on the original "*pumilio*" forms describing in broad terms the morphology and ontogeny of the Moroccan "*pumilio*" material, that Struve (1992) considered later as belonging to his new species *Ense albertii*. Lottmann (*op.cit.*) brought the Moroccan material near the terebratulids based on the possible occurrence of a centronelliform loop in a single specimen (*op. cit.*, p. 43, pl. 1, fig. 12), but at the same time spread doubt by asserting the impunctate nature of his material (preservation problem?). Struve (1992) dealt with the systematic study of the species-group, unfortunately in too concise terms, although he formally proposed the new genus *Ense*, integrated by the type-species, *E. andrea* n. sp. and by *E. albertii* n. sp. and *E. pumilio* (F.A. Roemer, 1855), the latter considered as a doubtful species because of the lack of new data after its first, old-fashioned description. This author admitted the terebratulid nature of the "*pumilio*" species-group based on the occurrence of a centronelliform loop in a specimen of *Ense albertii* (Struve, 1990: 370). Moreover, considering the external form of shell, close to *Paranaia* Clarke, 1913, Struve (*op.cit.*) included *Ense* in the Subfamily Mutationellinae Cloud, 1942. According to the observations of the preceding authors and the occurrence in the Palentian collection of *Ense* of both endopunctae and a centronelliform dorsal loop (see below), the terebratulid nature of the taxon is irrefutable. However, the paucicostate ornamental pattern of *Ense* is closer to the taxa of the Subfamily Adreninae Boucot (*in* Boucot & Wilson, 1994), with which the discussed genus is grouped herein, than that of Mutationellinae. Adreninae should have a dorsal sulcus and a ventral fold as contrasted with the mutationellids. In particular *Cydimia* Chatterton, 1973, provided with dental plates and a septalium supported on a median septum, is very close to *Ense*. The former genus differs from *Ense* mainly in the rostrate deltidium and weaker dorsal median costa.

Ense andrea Struve*,* 1992

Figs 2, 19-21

- 1992 *Ense andrea* n. sp.; Struve, p. 613.

Material: 16 very well preserved specimens, DPO 127853-127862, 127876-127881 another 11 generally incomplete, damaged specimens, DPO 127863-127870, 127873-127875, and a coquina fragment, with hundreds or possibly thousands of specimens, DPO 127871. This material comes from marly limestones of the base of the Cardaño Fm. (middle Givetian) (Fig. 3), ca.

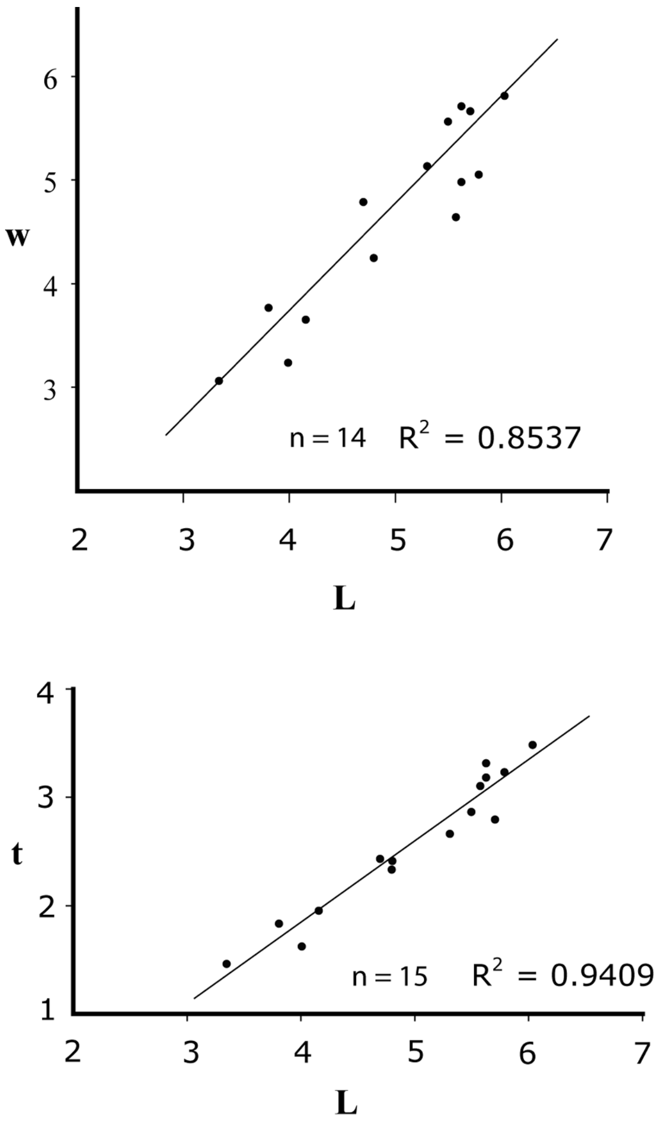


Figure 19. *Ense andrea* Struve, 1992. Length/width (L/w) and Length/thickness (L/t) dispersion diagrams.

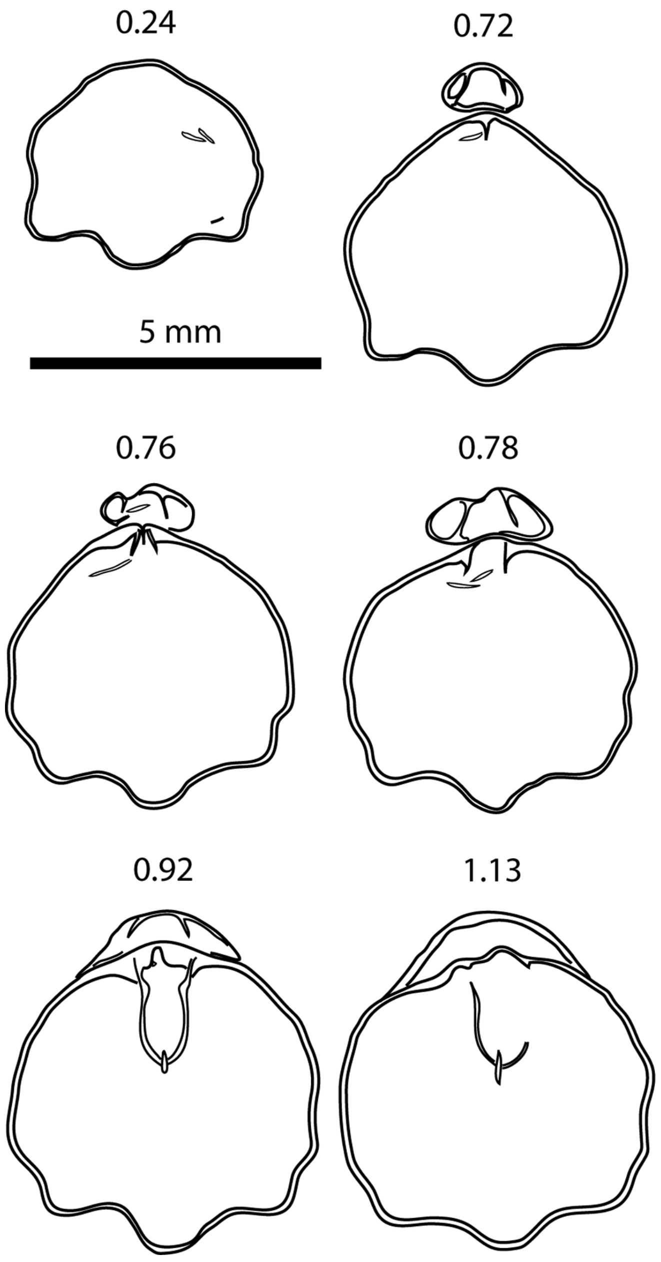
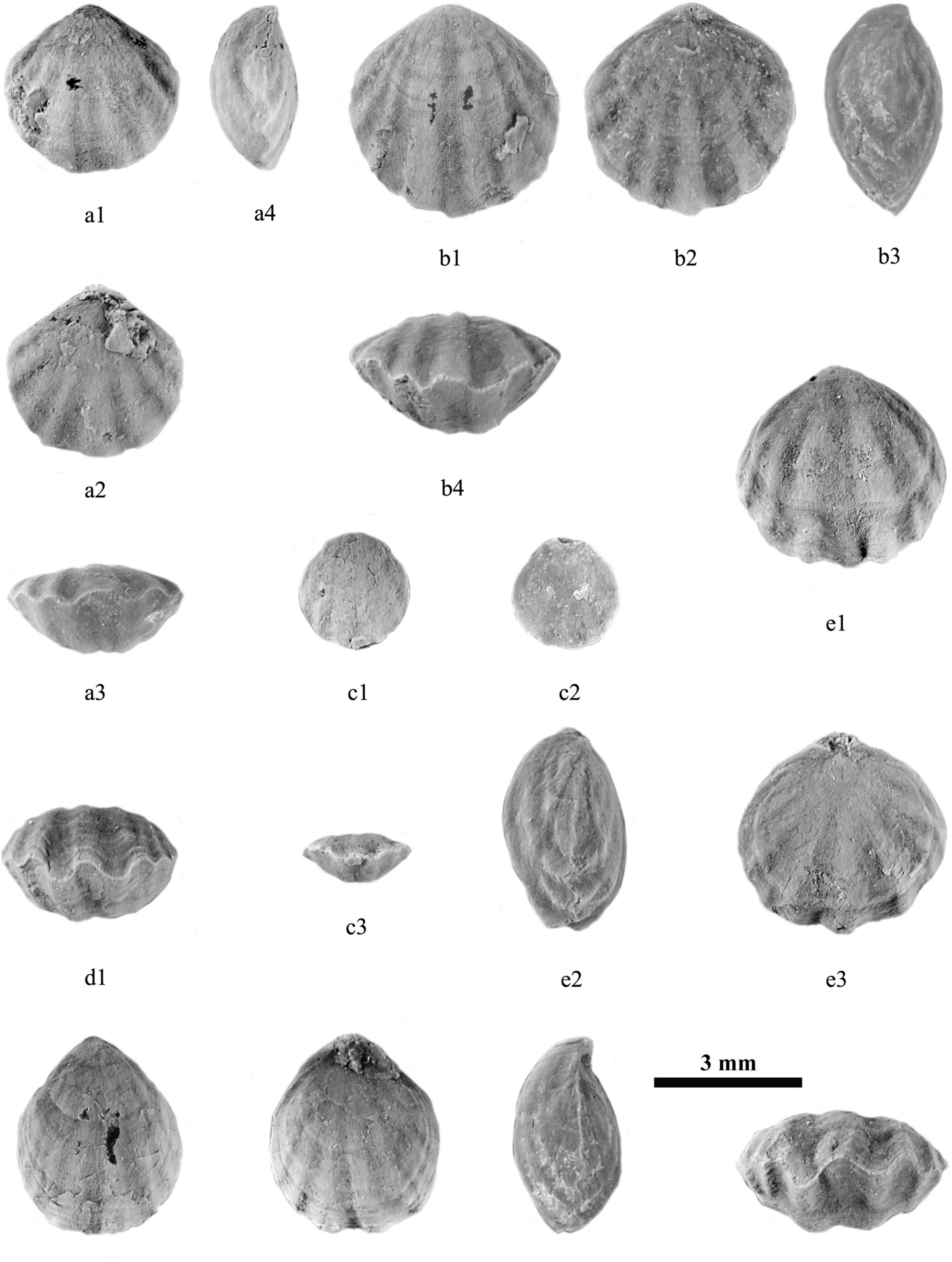


Figure 20. *Ense andrea* Struve, 1992. Camera lucida drawing of the serial sections of specimen DPO 127855. Distances in mm measured from the tangent to dorsal valve parallel to the commissure plane, ventralwards.

130 m SW of La Pedrosa saddle (W Polentinos village, Cervera de Pisuerga, Province of Palencia), locality α-36 (Fig. 2).

Description: Shell small (up to 6 mm length), thin (average t/L=0.51 for 15 measured specimens), either longer than wide, as long as wide, or wider than long (on 15 well preserved specimens, 9 are transverse and 5 longer than wide; average w/L=0.95) (Fig. 19), brachythyrid, with rounded cardinal extremities, subcircular to sub-pentagonal outline, ventri-biconvex, rostrate. Greatest width at midlength. Pedicle valve strongly convex in both transversal and longitudinal view; greatest height at midlength. Suberect (in younger individuals) to incurved beak standing out from the hinge margin; rounded beak ridges; obtuse apical angle. Low, slightly curved, apsacline to orthocline interarea; hypothyrid, circular foramen bounded by basally conjunct deltidial plates. Brachial valve weakly and evenly convex in young individuals; in adults the shell is flattened to weakly convex to ca. 2/3 of length, then it curves strongly to the commissure; greatest height in the anterior portion; dorsal beak hidden below deltidium.

In young individuals (less than 2 mm length) the shell is smooth (brephic stage). But from ca. 3 mm length and furthermore on, a paucicostate ornamentation composed by up to 8-9 strong, rounded, simple to bifurcating costae develops. In adult specimens, the umbones (representing the brephic stage of the shell growth) are smooth, ornate with only very faint growth lines. Costae extend from the first third of length to anterior; they are very weak near the umbonal region but become rapidly stronger afterwards, clearly crenulating the anterior margin.


a1
a4
b1
b2
b3
a2
b4
e1
a3
c1
c2
d1
c3
e2
e3
3 mm
d2
d3
d4
e4

Pedicle valve with 2 median costae and up to 3-4 pairs of lateral costae; median costae stronger than the lateral, situated at a higher level, and with a wide, deep, concave to slightly convex interspace; lateral interspaces, concave, slightly wider than costae; one or two of the posterior pairs of costae, obsolescent; in a single specimen (DPO 127880) the bottom of the median ventral sulcus becomes strongly convex, turning in fact into a low, median costa, starting ahead and in a slightly lower level than its neighbours. Brachial valve with a median, strong costa situated in the bottom of a faint median sinus, and up to 4-5 lateral pairs of costae, the posterior obsolescent; median costa stronger than laterals, separated from them by wider and deeper radial furrows. Commissure crenulated, faintly unisulcate.

Growth lamellae, strong, irregularly spaced, crowded at the anterior; finer and numerous growth lines in between. Shell substance densely and minutely endopunctate.

Dental plates small, thin, diverging both ventro-dorsal- and anteriorly. Hinge plates forming a septalium supported by a low, thin, short median septum. Loop centronelliform, provided with a vertical median plate, extending to near midlength (Fig. 20).

Discussion: The original division of *Ense* into species is based, according to Struve (1992), on the percent of costate to smooth shells in the Lower and Upper "*Pumilio*" coquinas. The type-species, *E. andrea* Struve, 1992, would differ from *E. albertii* Struve, 1992 in the occurrence of more than 90 percent of adult specimens being weak to moderately costate, and only ca. 10 percent with strongly costate shells, developing even a clear ventral sinus and a dorsal fold. In turn, in *E. albertii* ca. 90% of adult specimens would be smooth and only a 10% weakly to moderately costate, with weak although noticeable ventral sinus and dorsal fold. The Palentian sample is composed mainly of more or less costate adult shells, and only the younger specimens are smooth. Slight differences between the Spanish and the German/Moroccan forms would be the more variable outline of the former and the occurrence of a linear cardinal process in the latter (according to Struve 1992, p. 612) that has not been evidenced yet on the Palentian material.

ADDITIONAL REMARK

This work will be orally presented in the XXVI Jornadas de la Sociedad Española de Paleontología, in Lisboa, July 2010. A short Spanish résumé would be included in the meeting Abstracts.

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Figure 21. *Ense andrea* Struve, 1992. **a1-a4**: specimen DPO 127858, ventral, dorsal, anterior, and lateral views; **b1-b4**: specimen DPO 127877, ventral, dorsal, lateral, and anterior views; **c1-c3**: ventral, dorsal, and anterior views of a partially broken, young specimen DPO 127862; **d1-d4**: specimen DPO 127853, anterior, ventral, dorsal, and lateral views; **e1-e4**: specimen DPO 127854, ventral, lateral, dorsal, and anterior views.

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