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Isogramma Meek & Worthen, 1870 (Dictyonellida, Brachiopoda) from the Pennsylvanian of the Cantabrian Mountains (N Spain)

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ABSTRACT

Isogramma is one of the strangest and easiest to recognize brachiopod genera. Its shell is very transverse, flattened, oval, ornamented with strong concentric ridges which cover the whole exterior of both valves, apart from a smooth triangular depressed area, extending from the beak of the ventral valve forward to beyond the umbo, the colleplax. The shell is strongly punctate which gives it a spongy structure. In this paper, the morphology and shell structure of the genus are discussed, and the species from the Cantabrian Mountains assigned to the genus are revised. The species *Isogramma davidsoni*, the only one thus far described for the region, is discussed and three new species are described for the Pennsylvanian of Asturias and León: *Isogramma wagneri*, *I. casina* and *I. demuesensis*.

Keywords: *Isogramma*, Brachiopoda, Pennsylvanian, Cantabrian Mountains, Spain.

RESUMEN

Isogramma es uno de los géneros de braquiópodos más extraños y fáciles de reconocer. Su concha es muy transversa, aplanada, ovalada, con ornamentación de crestas concéntricas que cubren todo el exterior de ambas valvas excepto un área triangular lisa y deprimida que se extiende desde el gancho de la valva ventral hasta delante del umbo, el colleplax. Tiene una concha fuertemente puntuada que le confiere una estructura esponjosa. En este trabajo se discute la morfología y estructura de la concha del género y se revisan las especies de la Cordillera Cantábrica asignadas al mismo. Se discute la especie *Isogramma davidsoni*, única descrita anteriormente de la región y se describen tres nuevas especies para el Pensilvánico de Asturias y León: *Isogramma wagneri*, *I. casina* e *I. demuesensis.*

Palabras clave: *Isogramma*, Brachiopoda, Pensilvánico, Cordillera Cantábrica, España.

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1. INTRODUCTION

Isogramma Meek &Worthen, 1870 is one of the more exceptional brachiopod genera and easiest to recognize because of its very transverse, flattened shape with an ornamentation of elevated concentric ridges which cover the whole shell, apart from a smooth and exteriorly depressed triangular plate, which extends from the beak of the ventral valve to some distance in front of the umbo and also for its punctate shell with a spongy structure.

The genus is known from the Viséan to the late Permian (Lopingian). Chen & Shi (2006) recognize 56 species for the genus (including 17 uncertain species) from North America, South America (Bolivia), Europe and Asia. As can be observed in Chen & Shi (2006, fig. 6) the genus is restricted to lower and middle palaeolatitudes, which suggests its adaptation to warm tropical and subtropical waters.

Various authors have revised in detail the available data about the genus (Aigner & Heritsch, 1931; Cooper, 1952; Brand, 1970; Wardlaw *et al*., 1987; Chen & Shi, 2006). Despite this, the internal and external morphology of both valves and the microstructure of the shell are not well known. This may be due to the lack of well preserved material. According to Holmer (2000), the original structure of the shell of the Isogrammidae is unknown, and he considers that this is because they are almost always preserved as moulds or are silicified; this conservation suggests that the shell of Isogrammidae could have originally been of aragonite.

A number of the specimens studied in this paper have shell preservation which has permitted us to study in part the microstructure and characteristics of the interior of the valves, despite the factor of alteration of such spongy shell material. This makes shells very fragile and difficult to extract and clean, and also they are often covered by a crust of biological or mineral material. Another part of the material from the Cantabrian Zone is found as moulds, which has permitted us the study of the ornamentation, many details of the interior, and also the punctate shell structure.

Representatives of the genus *Isogramma* have been described or cited from materials attributed Moscovian and Kasimovian age from the Cantabrian Mountains. *Isogramma davidsoni* was originally described by Barrois (1882) and later cited by numerous authors: Delépine (1943), Winkler Prins (*in* Moore *et al*., 1971), Leyva *et al*. (1985), Luque *et al*. (1985), Wagner & Winkler Prins (1985), Villa *et al*. (1988). Breimer *in* Martínez Álvarez (1962) identified *I. concentrica*. *Isogramma* aff. *paotechowensis* (Grabau & Chao) was identified in Sánchez de Posada *et al*. (1999, 2002).There have also been various citations of indeterminate species.

Part of the material attributed in the aforementioned papers to *Isogramma davidsoni* is now included in the new species *I. wagneri*, in which are also included specimens cited previously as indeterminate at specific level. Material previously identified as *I. concentrica* and also some material identified as *I. davidsoni* is now considered to belong to a new species *I. casina*. A more detailed study of the specimens from Demués, cited previously as *I.* aff. *paotechowensis*, now demonstrates clearly sufficient differentiation to allow it to be separated and established as a new species, *I. demuesensis.*

The localities from where the specimens originated are shown in Figure 1: 1-Villamanín (León); 2- Campo de Caso (Asturias); 3- Demués (Onís, Asturias).

2. MORPHOLOGY

The most characteristic feature of the *Isogramma* shell is the presence of a smooth triangular area on the ventral umbo, without the strong concentric ornamentation of the greater part of the shell and also depressed with respect to the rest of the valve. This region, without concentric ornamentation, is caused by a perforation through the ventral valve which is developed by resorption, extends anterior to the umbo, and becomes covered by a plate, the colleplax (Holmer, 2000). This plate shows a fissure at its anterior end, which communicates with the interior of the valve, where it presents a greater length than in the exterior. In the ventral interior, it becomes an elevated platform on the valve floor. The nature and function of the plate has been much discussed and it has been given different names by different authors. These different names reflect the function that the plate is supposed to have played. Wright (1981, p. 449-450) discusses the functions attributed by previous authors and the corresponding terms, and proposes the term *colleplax* (Greek *kollesis* – that glues and *plax* – plate), because it is supposed that the shell is fixed to the substrate by means of an adherent chitinous pad which in life covers the outer surface of the colleplax and is secreted by the outer epithelium. Although most authors accept that the plate has an anterior slit-like opening which communicates with the interior of the shell (some, such as Rowell, 1965, considered that it functions as an aperture for the passage of the pedicle), others, such as Wardlaw *et al.* (1987), consider that it lacked an anterior aperture and that the communication with the interior could have been through the punctae along the margin of the plate. The term colleplax and the function attributed by Wright (1981) is followed by Holmer (2000) and is also followed in the present paper.

The platform elevated above the bottom of the ventral interior, formed by the depressed *colleplax* presents no problem for its interpretation and is considered generally as the location for insertion of muscles. It is not clear however if all muscles were fixed at this platform or if

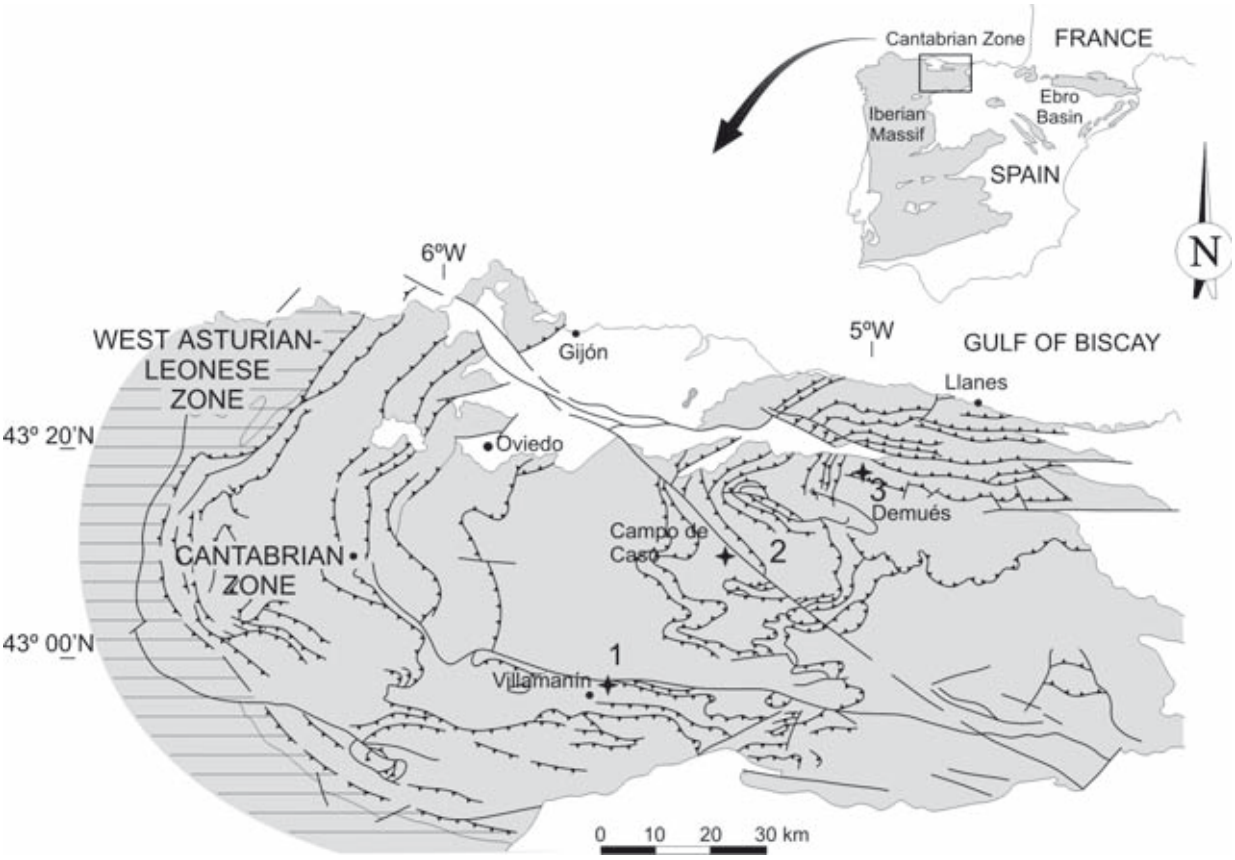


Figure 1. Geological sketch map of the Cantabrian Mountains with the fossil localities. 1: Villamanín (León); 2: Campo de Caso (Asturias); 3: Demués (Onís, Asturias).

only the adductors were inserted and the diductors, being narrow and flabelliform, were situated on the sides of the platform (Cooper, 1952). This idea was followed by Rowell (1965).

The dorsal interior has a very large cardinal process which strong myophore, extending over the hinge, fitting into the ventral valve. The shaft is well developed, bifurcates anteriorly and unites with the median septum. The median septum is very high, in sheet form and slightly warped in some specimens. The adductor muscles are fixed on both sides of the median septum, as a central and lateral pair. A pair of sub-circular posterolateral depressions, near the hinge, correspond to the lophophore platform as described by Wardlaw *et al*. (1987). However, because of the very posterior position, it seems difficult to think that the lophophore could be situated there and it seems more likely that these correspond to the gonadal prints.

The shell is practically strophic. The ventral valve has a distinct interarea, observed in some of our specimens, tapering laterally and ending at some distance from the extremities of the hinge, without occupying the whole hinge. According to Holmer (2000), the genera of the Family Isogrammidae have an open delthyrium, which has not been observed in our material. In the dorsal interior, on both sides of the cardinal process, at the cardinal extreme of the valve, a pair of lateral ridges are developed, which extend to coincide with the ventral interarea; the posterior side of these ridges is crenulated. The articulation is probably produced with the help of these lateral ridges, of which the posterior side of each fits the ventral interarea, while the outgoing cardinal process fitted into the delthyrium.

The mantle canals of Isogrammidae are poorly known. Only the dorsal valve of *Megapleuronia* is known, and has been described as pinnate (Holmer, 2000). This condition is not clearly observed in our specimens.

3. STRUCTURE OF THE SHELL

One of the unusual characteristics of *Isogramma* is the strongly punctate shell that gives it a spongy appearance. This was already noticed by Meek &Worthen (1870) in their original description of *Chonetes*? *millepunctata*: "The most remarkable character of this shell... is its extremely coarse punctate structure... they present on the inner surface... much the appearance and arrangement of the

cells of a delicate *Chaetetes*" (Meek & Worthen, 1870, p. 35). Barrois (1882, p. 328) also mentioned that the wide punctae give rise to a structure similar to that of rudists. Since this time, the wide and irregular punctae and their dense packing have been noted by all authors who have worked on the genus *Isogramma*. Most of them considered that the punctae are internal features which do not reach the exterior (Cooper, 1952; Cooper & Grant, 1974; Wright, 1981; Chen & Shi, 2006).

In the shells of our specimens of *I. casina* and *I. demuesensis,* the punctae are observed as internal; they are only observed as external when the shell is eroded (Fig. 2a). The shell appears to have two layers, a thin outer one that is not reached by the punctae, and an internal thicker, spongy one, with punctae that extend almost perpendicularly across it (Fig. 2b). The interior of the shell has an aspect as described by Wright (1981) for the external surface of *Dictyonella,* in which a reticulation is developed with large hexagonal or rhomboidal pits, separated by high, narrow ridges of shell (Fig. 2d); the pits vary in outline and size and they may contain some punctae. In the internal moulds of *I. wagneri,* the large pits and the punctae contained in them can be seen as moulds (Figs 2c, 2e). The walls of the pits may also be abraded producing a halo of micropits around the main pit (Wright, 1981, p. 454, pl. 63, fig. 7; compare with Figs 2f, 2h, herein). In some areas of the interior of valves, especially in their anterior part, the pits are not visible and only punctae are developed (Fig. 2f).

The colleplax is finely punctate with much smaller punctae than in the rest of the shell, visible on its external and internal surfaces (Fig. 2g).

4. SPECIES OF *ISOGRAMMA* FROM THE CANTABRIAN MOUNTAINS

In the Cantabrian Mountains, the genus has been frequently cited, but records are rarely accompanied by descriptions and figures. Figures have only been provided in one case, the original description of *Isogramma davidsoni* (Barrois, 1882, p. 326-329, pl. 16, figs 6a-6d); a later description of the same species was published (Delépine, 1943, p. 74-75) although without figures. Until now, this is the only species described from the Cantabrian Mountains.

In addition to the two above mentioned descriptions, *Isogramma davidsoni* is the most cited species of the genus in this region: Winkler Prins *in* Moore *et al*. (1971, p. 327, North of Villamanín, León), San Emiliano Formation, Lower Moscovian; Leyva *et al*. (1985, p. 259, Campo de Caso-Tanes, Asturias), Fito Formation, Upper Moscovian (Podolskian); Luque *et al*. (1985, p. 294, as *I.* cf. *davidsoni*, South of Sama de Langreo, Asturias), Paquete Generalas, Upper Moscovian (Podolskian); Wagner & Winkler Prins (1985, p. 399, as *I*. cf. *davidsoni*, NE León and NW Palencia), Upper Moscovian-Kasimovian; Villa *et al*. (1988, p. 339, as *I*. aff. *davidsoni*, North of Villamanín, León), San Emiliano Formation (Villamanín beds), Lower Moscovian (Vereyan).

Other species so far recorded in the region are:

Isogramma concentrica: Breimer *in* Martínez Álvarez (1962), Campo de Caso-Coballes (Asturias), Fito Formation, Upper Moscovian (Podolskian).

Isogramma aff. *paotechowensis* (Grabau & Chao): Sánchez de Posada *et al*. (1999, p. 352; 2002, p. 594, Southeast of Demués (Onís, Asturias), Demués Formation, Kasimovian.

Indeterminate species of the genus have been recorded in various papers: Martínez Chacón & Winkler Prins (1985, p. 437, Gamonedo and Demués, Onís), Kasimovian; Wagner & Winkler Prins (1985, p. 399, as *Isogramma* sp. nov., various localities from NE León and NW Palencia), Upper Moscovian-Kasimovian; Río García (1998, p. 164, Central Asturian Coalfield), Paquete Tendeyón, Lena Group, Podolskian; Sánchez de Posada *et al*. (1999, p. 352; 2002, p. 595, Southeast of Demués), Demués Formation, Kasimovian.

Martínez Chacón (2015) has recently reviewed most of the material previously cited in the aforementioned papers, recognizing new species to which she gave the provisional names of *Isogramma* sp. nov. 1, *Isogramma* sp. nov. 2 and *Isogramma* sp. nov. 3. These species are formally described herein.

5. TAPHONOMY

As mentioned above, most of the *Isogramma* species are known from moulds, silicified shells or from fragmentary material which is difficult to reconstruct. Our material generally reflects these constraints. The specimens of *I. wagneri* are external and internal moulds of both valves, which show the fine detail of the ornamentation, some internal structures of both valves and also the characteristics of the punctate structure (Figs 2c, 2e). The specimens of *I. demuesensis* are partially silicified; a large proportion is fragmentary, some fragments may be reconstructed, but others are isolated fragments and some specimens are fragile and crumbly and some valves are covered by a mineral crust. Despite this it has been possible to observe the ornamentation, the punctation and some of the internal structures (Figs 2a-2b). The specimens of *I. casina* conserve the calcitic shell and, although this is frequently covered by encrusting organisms or a calcitic crust, they are the best preserved and they have permitted the most detailed studies (Figs 2d, 2f-2h).

6. SYSTEMATICS

The Family Isogrammidae was originally included in the Class Articulata, as an uncertain order, Suborder Dictyonellidina and Superfamily Eichwaldioidea, together with the Family Eichwaldiidae (Rowell, 1965). All representatives of the suborder have a punctate calcareous shell and a ventral umbo with a smooth triangular plate. This scheme was followed by Cooper & Grant (1974) and by most investigators who have worked on the genus *Isogramma* until the new classification of the brachiopods established by Williams *et al*. (1996).

Williams *et al*. (1996) created the new Class Chileata in the Subphylum Rhynchonelliformea. In the new class they included the Order Dictyonellida (Holmer, 2000). The systematics of Holmer (2000) is followed in this paper.

The material is housed in the Geology Department of the University of Oviedo (numbers prefixed DGO).

Subphylum RHYNCHONELLIFORMEA Williams *et al*., 1996

Class CHILEATA Williams *et al*., 1996

Order DICTYONELLIDA Cooper, 1956

Diagnosis. Ventral interarea variably developed; ventral perforation extending anterior to umbo through resorption and covered by colleplax; delthyrium open or covered by concave pseudodeltidium; dorsal valve with cardinal process, high median septum; dorsal mantle canals pinnate (Holmer, 2000, p. 196).

Superfamily EICHWALDIOIDEA Schuchert, 1893

Family **Isogrammidae** Schuchert, 1929

Diagnosis. Shells transversely suboval; ventral interarea wide, flattened; delthyrium open, triangular; cardinal process with well-developed shaft; posterolateral furrows small, located lateral to cardinal process (Holmer, 2000, p. 200).

Genus *Isogramma* Meek & Worthen, 1870

Type species *Chonetes?? millepunctata* Meek & Worthen, 1870

Diagnosis. Large, concavo- or planoconvex shell; ornament of strong concentric elevated ridges; myophore strong; shaft bifurcating around dorsal median ridge.

Discussion. The diagnosis is the same as Holmer (2000), except that we use "ridges" for the concentric ornamentation instead of "fila" used by Rowell (1965) and Holmer (2000). Filum (pl. fila) is a fine concentric ridge (Williams & Brunton, 1997), which is not the case for the concentric ornamentation of this genus. Ridge is a less precise term that can be specified using the proper adjective (strong, elevated, etc.).

Isogramma davidsoni (Barrois, 1882)

Remarks. *Isogramma davidsoni* is the only species described as new, so far, from the Cantabrian Mountains. Barrois described its shell as concavo-convex, transverse, ornamented by concentric ridges, with a straight hinge-line a little shorter than the width of the shell, and both valves with a median sulcus. The original figures of Barrois (1882, lám. 16, figs 6a-6d) are drawings and difficult to compare with the actual material. Aigner & Heritsch (1931) also included figures of *I. davidsoni*, but they only reproduce the figures of Barrois. Delépine (1943) discussed the species and attributed to it the specimens from Lieres (Siero, Asturias), but he does not provide pictures or drawings. Other authors have only provided unillustrated records of the species but no descriptions or figures. Barrois (1882) did not designate a holotype for his species; his material comes from different localities and from his description the type locality cannot be established. The best preserved specimen seems to be the ventral valve figured on his pl. 16, figs 6a-6b, coming from Villallana (written Villayana by Barrois) and it is the most suitable to compare with our specimens. Unfortunately, we have not had access to the original material of Barrois. Brand (1970, p. 76) has previously noted that: "The type specimens of *Aulacorhynchus davidsoni* have not yet been traced." Since the specimens described in this paper, previously assigned to *I. davidsoni,* appear to have significant differences with the figures of Barrois, we have established two new species for them.

Isogramma wagneri sp. nov.
(Figs 2c, 2e, 3a-3h)

1971 *Isogramma davidsoni* (Barrois); Winkler Prins *in* Moore *et al*., p. 327.

1988 *Isogramma* aff. *davidsoni*; Villa *et al*., p. 339.

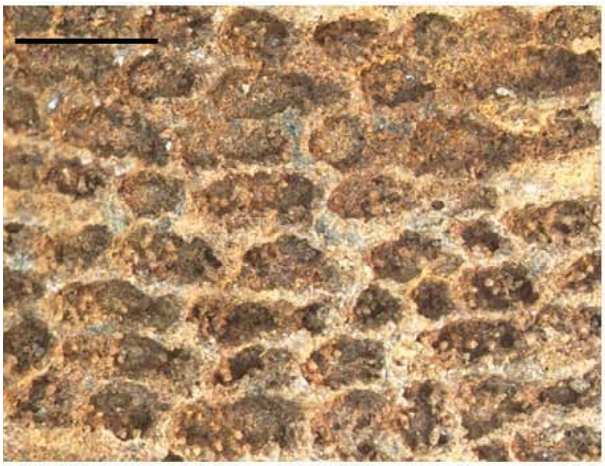
2015 *Isogramma* sp. nov.1; Martínez Chacón, p. 175.

Derivatio nominis. After Robert H. Wagner for his contribution to the knowledge of the Carboniferous System.

Type locality and horizon. Railway cutting S of Villanueva de la Tercia (Villamanín, León), at 2-3 m S of km 48. Sandstone layer 2-3 m above a bed with *Diplocraterion*, Villamanín Beds, San Emiliano Formation, early Moscovian (Vereisky) (Villa *et al*., 1988), see Figure 1.

a

b



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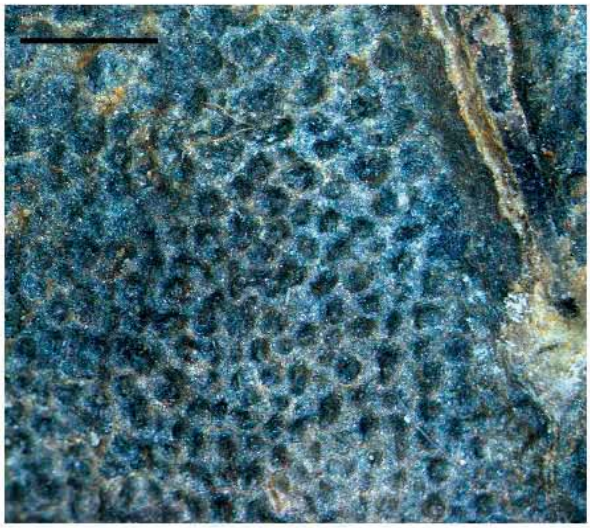

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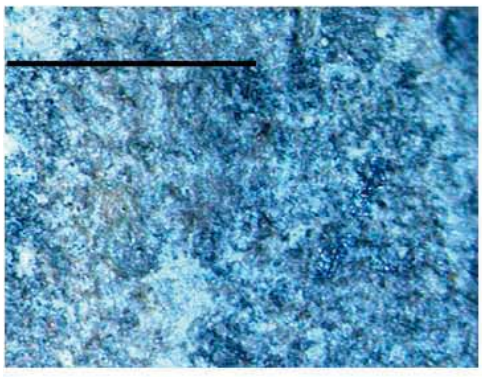

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h

Material. Holotype, DGO 3852, internal mould of an incomplete ventral valve (Figs 2c-2d, 3a) and some 15 specimens more from the type locality and horizon (DGO 3853-3859), preserved as external or internal moulds of one or the other valve, the majority ventral ones. One specimen (DGO 3860) is identified as *I.* cf. *wagneri* (Figs 3i-3k); it comes from the section along the track to the Navidiello Hill, some 4 km E of Puente de los Fierros (Lena, Central Asturian Coalfield), lutites in the upper part of Paquete Generalas, some 145 m above the limestone that forms the base of the "paquete", late Moscovian (Podolsky).

Diagnosis. Ventral valve slightly convex, dorsal valve very gently concave to flat, outline semi-elliptical, maximum width a little in front of the hinge and slightly wider than it; no sulcus or fold. Long colleplax reaching approximately half the length of the valve, and relatively wide.

Description. Shell gently concavo- to plano-convex, with outline transversely semielliptical, hinge line straight and cardinal extremities rounded; maximum width slightly anterior to the hinge; no sulcus or fold.

Ventral valve slightly convex, with umbo strongly curved and projecting beyond the hinge. Colleplax depressed, originating at beak and rather wide; it bears a median groove; at the anterior end it has a slit-like opening and continues under the outer shell (Figs 3d-3e). Ornamentation of elevated and thin concentric ridges, separated by spaces wider than the ridges, covering the valve except the colleplax; some 15 ridges are counted in 5 mm. The colleplax is finely punctate.

Dorsal valve gently concave to flat. Ornamentation same as that of the other valve.

Dimensions of a number of specimens are presented on Table 1.

Ventral interior with elevated platform corresponding to the colleplax, which is longer than in the exterior, the platform bears a deep median groove, in which the dorsal median septum fits, and one or two lateral pairs of grooves radiating from the apex and corresponding to the adductor scars. In the internal moulds the large pits and the punctae contained in them can be seen as moulds (Figs 2c, 2e).

Dorsal interior with cardinal process with a strong myophore and shaft bifurcating around the posterior part of the elevated median septum. In some specimens the septum is flexuous and not straight (Fig. 3h).

Table 1. Measurements (in mm) of *Isogramma wagneri* sp. nov. L: Length; Ld: length of dorsal valve; W: Width; Lcoll: length of colleplax; Wcoll: width of colleplax; ridg/5mm: number of ridges in 5 mm width at the anterior part of shell; * Holotype.

Specimen	L	Ld	W	Lcoll	Wcoll	ridg/5mm
*DGO 3852	27.6		~50.7	15.6	10.8	12
DGO 3853	25.3		>39.3	14.1	10.2	13
DGO 3854	16.9		36.1	11.6	7.4	14
DGO 3855	25.1		43.8			17
DGO 3856		18.8	39.2			

Discussion. The closest species, *I. texanum* Cooper, 1952 is distinguished by its more transverse shell, narrower colleplax and wider concentric ridges.

The material from the type locality was previously attributed to *I. davidsoni* (Winkler Prins *in* Moore *et al*., 1971; Villa *et al*., 1988). The new species differs from *I. davidsoni* in its smaller size, absence of median fold and sulcus, long and wide colleplax and different outline, with more gradual tapering of the width towards the anterior than observed in *I. davidsoni*.

The specimen identified as *I.* cf. *wagneri* (Figs 3i-3k) is comparable to *I. wagneri* in its outline, size, characters of the colleplax and ornamentation, but cannot be identified as such with certainty because its profile is more pronounced concavo-convex and the cardinal process and median septum are stronger.

Figure 2. a-b) *Isogramma demuesensis* sp. nov. **(a)** DGO 3872, detail of the exterior of a slightly eroded ventral valve showing punctae on the sulci between ridges, and practically absent on ridges, Demués (Onís, Asturias), sample DM-10 (Sánchez de Posada *et al*., 1999, 2002), Demués Formation, early Kasimovian. **(b)** DGO 3882, longitudinal section of a fragmentary valve, exterior up, Demués, sample DM-12, early Kasimovian. **c, e)** *Isogramma wagneri* sp. nov. Holotype, DGO 3852, two details of the ventral internal mould showing the disposition of large pits and smaller punctae inside of some of these, Villamanín (León), railway section, San Emiliano Formation, early Moscovian (Vereisky) (Villa *et al.*, 1988). **d, f-h)** *Isogramma casina* sp. nov., former road between Coballes and Campo de Caso (Asturias), (Leyva *et al*., 1985), Fito Formation, late Moscovian (Podolsky). **(d)** DGO 3866 ("tramo" 25 of Leyva *et al*., 1985), sample U-274, detail of ventral interior with part of dorsal median septum showing the large pits. **(f, h)** DGO 3864, two details of the interior with the punctae on the calcite walls of large pits and the small punctae on the anterior part of valve (f). **(g)** DGO 3862, detail of the exterior of the colleplax showing the fine punctae. Scale bars = 1 mm.

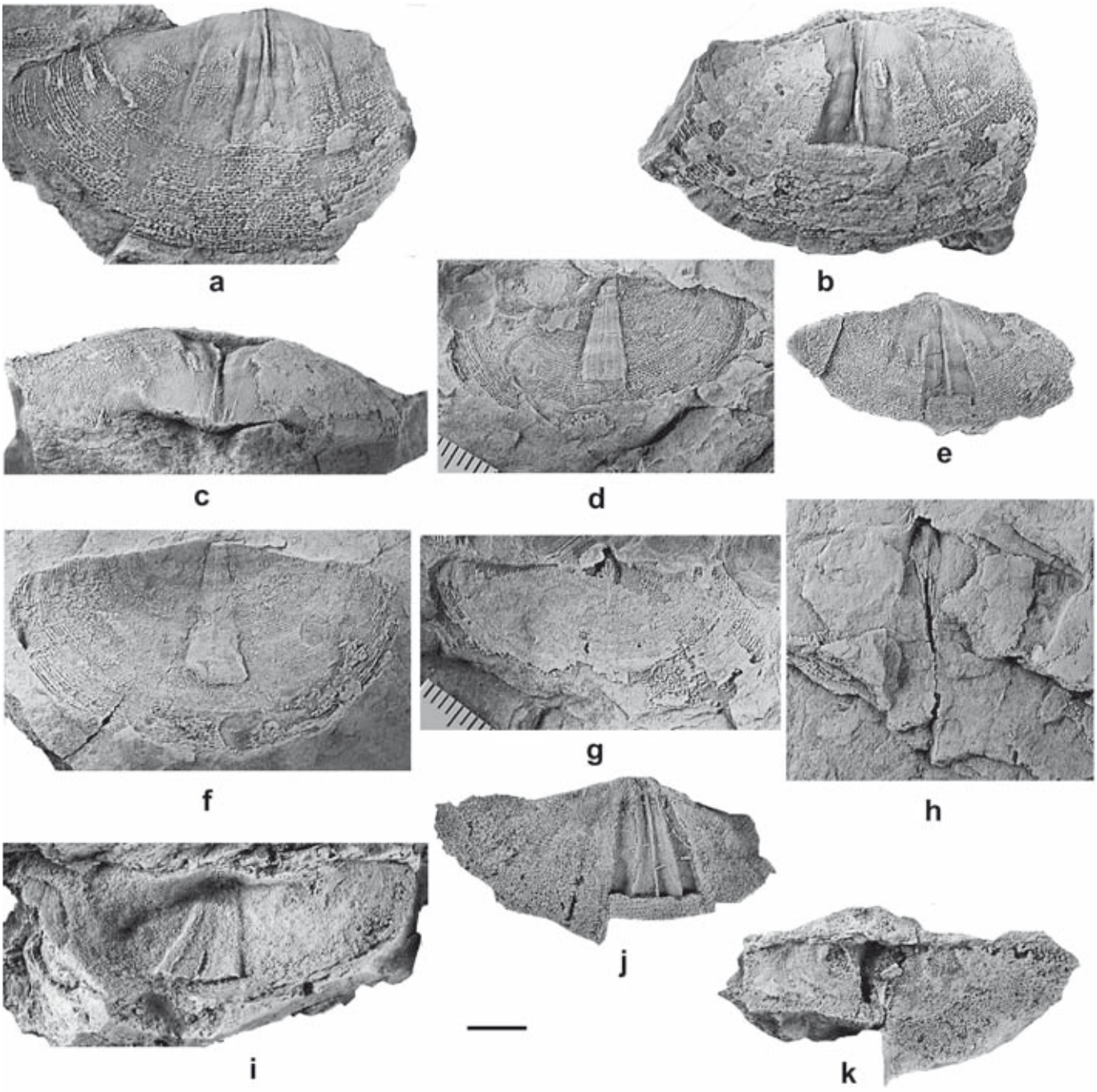

Figure 3. a-h) *Isogramma wagneri* sp. nov. Type locality, Villamanín (León), railway section, San Emiliano Formation, early Moscovian (Vereisky) (Villa *et al.*, 1988). **(a)** Holotype, DGO 3852, ventral internal mould. **(b-c)** DGO 3853, ventral internal mould in ventral and posterior views. **(d-e)** DGO 3854, ventral external and internal moulds, the last, incomplete. **(f)** DGO 3855, ventral external mould. **(g)** DGO 3856, dorsal external mould showing part of the mould of the cardinal process and median septum. **(h)** DGO 3857, incomplete dorsal internal mould showing the mould of the cardinal process, shaft and median septum. **i-k)** *Isogramma* cf. *wagneri*, DGO 3860, ventral external and internal moulds in ventral and dorsal views. Navidiello Hill, E of Puente de los Fierros, Central Asturian Coalfield, upper part of Paquete Generalas, late Moscovian (Podolsky). Scale bar = 8 mm.

Isogramma casina sp. nov.
(Figs 2d, 2f-2h, 4, 5a)

1962 *Isogramma concentrica*; Breimer *in* Martínez Álvarez, p. 90.

1962 *Isogramma* spec.; Breimer *in* Martínez Álvarez, p. 90.

1985 *Isogramma davidsoni*; Leyva *et al*., p. 259.

1985 *Isogramma* sp.; Leyva *et al*., p. 259.

2015 *Isogramma* sp. nov. 2; Martínez Chacón, p. 175.

Derivatio nominis. From Caso, Asturias; municipality of the type locality.

Type locality and horizon. Former road N-635, Oviedo-Riaño, between Coballes and Campo de Caso, Fig. 1, sample M-5 (77) in Martínez Álvarez (1962, p. 90) and COB-8 ("tramo" 19) in Leyva *et al*. (1985). Half a metre of blackish fossiliferous marls intercalated at the top of a grey limestone, Fito Formation, late Moscovian (Podolsky).

Material. Holotype, DGO 3861 (Figs 4a-4b) specimen almost complete lacking only the ventral posterior end; additionally there are another 7 specimens and several fragments from the type locality and horizon, DGO 3862-3865, 3867-3870. A further specimen, DGO 3866, has been collected from the same section, U-274 (top of the "tramo" 25) of Leyva *et al*. (1985), Fito Formation, late Moscovian (Myachkovsky).

Diagnosis. Medium-sized *Isogramma*, with thick valves, concavo-convex profile, both valves closely fitting to each other, producing a very narrow corpus cavity; subelliptic outline, maximum width approximately at the posterior third of the shell length, commissure unisulcate. Colleplax reaching approximately 1/3 of the shell length and relatively narrow. Concentric ridges strong, some 9 in 5 mm.

Description. Shell concavo-convex, outline transversely subelliptic, hinge line straight and cardinal extremities rounded; maximum width at about the posterior third of the length; commissure unisulcate. Both valves are some 3 mm thick.

Ventral valve slightly convex, with umbo bending over the hinge and projecting beyond it, so this part is often broken. Interarea clear and narrow, some 2 mm high, tapering and ending at some distance from the cardinal extremities. Median fold starting at beak, narrow and low. Colleplax originating at beak, depressed with respect to the remainder of the valve; in section it appears as an inverted V, with an elevated median ridge and external surface smooth; it continues under the outer shell. Ornamentation of strong concentric ridges, separated by spaces wider than the ridges, covering the valve except the colleplax; some 9 ridges are counted in 5 mm. The colleplax is finely punctate (Fig. 2g), finer than the rest of the valve.

Dorsal valve slightly concave, as curved as the ventral one. Median sulcus matching to the ventral median fold. Ornamentation as that of the other valve.

Dimensions of a number of specimens are presented on Table 2.

Table 2. Measurements (in mm) of *Isogramma casina* sp. nov. Th: shell thickness; rest as in Table 1.

Specimen	L	Ld	W	Th	Lcoll	Wcoll	ridg/5mm
*DGO 3861	>40.5	36.6	69.6	10.2	>15.7	8.2	9
DGO 3862	>37		65.4		12.5	8	9
DGO3863	35.8	31.3	57.6				
DGO 3864		28.8	61.8				
DGO 3866					15.7	>7.9	9
DGO 3867							8

Ventral interior with elevated platform corresponding to the colleplax; the platform bears a deep median groove corresponding to the external ridge, the groove continues to the anterior to fit the dorsal median septum; the platform is limited on both lateral sides by strong ridges. The platform probably serves as the attachment of adductor muscles; it is flanked on the valve floor by broad and elongated diductor scars. The anterior part of the valve bears a series of sulci reflecting the impressions of mantle canals.

Dorsal interior with strong cardinal process, myophore extending towards the posterior, trilobate, with triangular median lobe, slightly depressed in the middle and much bigger than the poorly defined lateral lobes. At the base of the myophore, a relatively deep pair of grooves with striated surface are developed on both sides (Figs 4e, 5a), probably serving as articulatory structures fitting the sides of the ventral delthyrium. Shaft highly thickened (Fig. 4k), it converges with the median septum without interruption. Median septum strong and high, with its highest in the posterior part, descending towards the front and ending some 5-6 mm before the front. A pair of lateral ridges are located laterally to the cardinal process and articulate with the ventral interarea; ridges are crenulated posteriorly. Adductor scars consist of a median pair, elongate and narrow, located on each side of the median septum, and another lateral pair also elongate but slightly wider (Figs 4k, 5a). In each postero-lateral region, behind the muscle field, a subcircular depression (length = 10.8 mm, width = 12.1 mm, specimen DGO 3863, Figs 4k, 5a) was observed, narrowing towards the cardinal process and septum, similar to that described and figured by Cooper & Grant (1974,

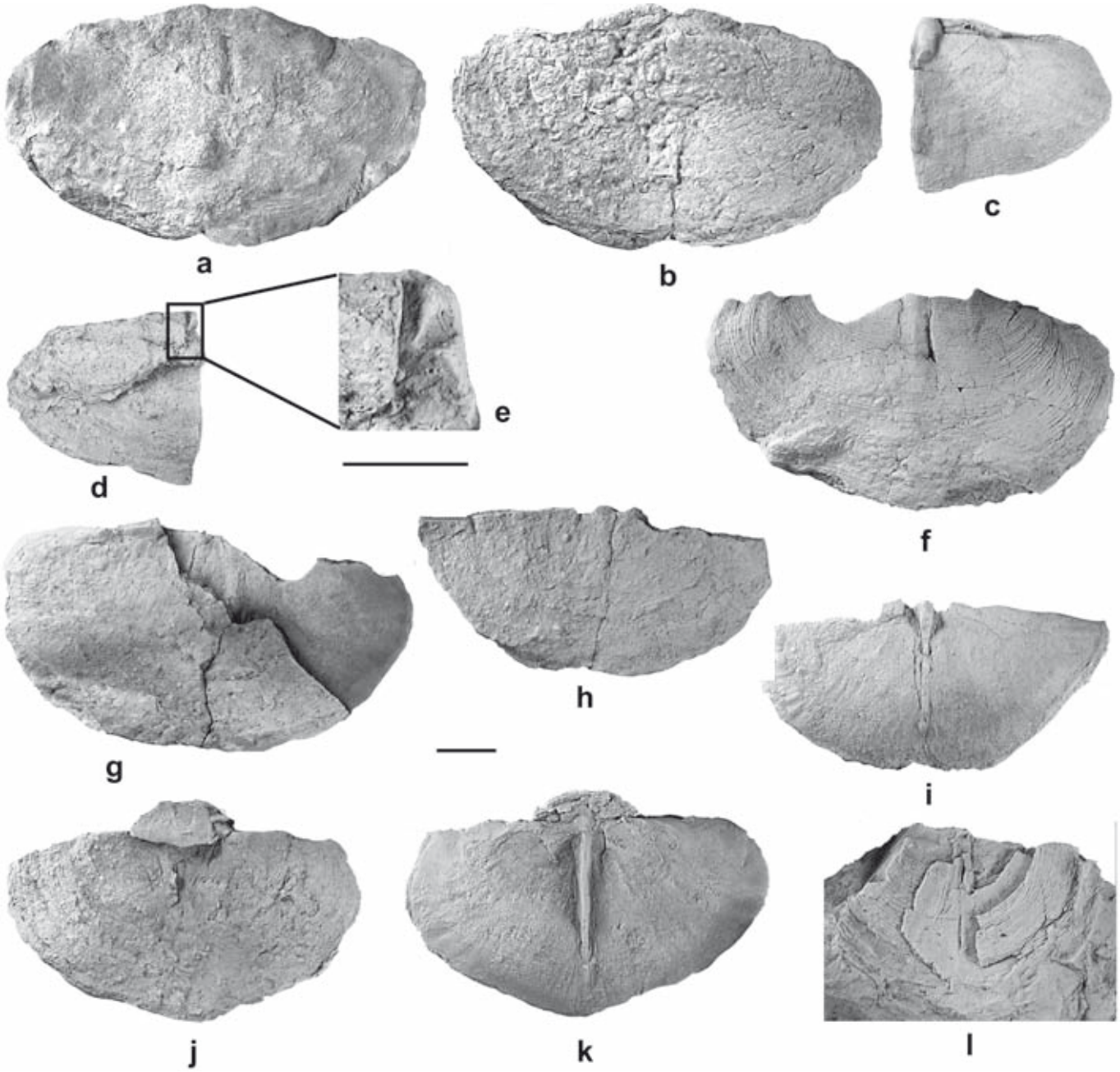

Figure 4. *Isogramma casina* sp. nov. Former road between Coballes and Campo de Caso, Fito Formation, late Moscovian (Podolsky). **a-k)** Type locality, sample COB-8, "tramo" 19 (Leyva *et al*., 1985). **(a-b)** Holotype, DGO 3861, ventral and dorsal views. **(c-e)** DGO 3865, incomplete dorsal valve in internal and external views and detail of part of the cardinal process. **(f-g)** DGO 3862, incomplete specimen in ventral and dorsal views. **(h-i)** DGO 3864, dorsal valve in external and internal views. **(j-k)** DGO 3863, dorsal valve with posterior part of ventral valve and dorsal interior. **l)** Sample U-274, "tramo" 25 (Leyva *et al*., 1985), DGO 3866, incomplete specimen showing fragments of dorsal exterior, ventral interior with rest of the dorsal median septum and ventral external mould. Smaller scale bar = 10 mm; larger scale = 5 mm refers only to Fig. 4e.

p. 253, pl. 24, fig. 1) and Wardlaw *et al*. (1987, p. 84, fig. 3A). The anterior part of the inner surface of the valve has the same sulci as the ventral valve: these are impressions of mantle canals. The inner surface is punctate, with rhomboidal or hexagonal large pits, surrounded by walls that bear small punctae; the pits may also contain some punctae (Figs 2d, 2f, 2h). The anterior margin of the valve bears only small punctae (Fig. 2f).

Discussion. The depressions just mentioned in the postero-lateral regions of the dorsal valve have been interpreted as "brachial ridges" (Cooper & Grant, 1974, p.

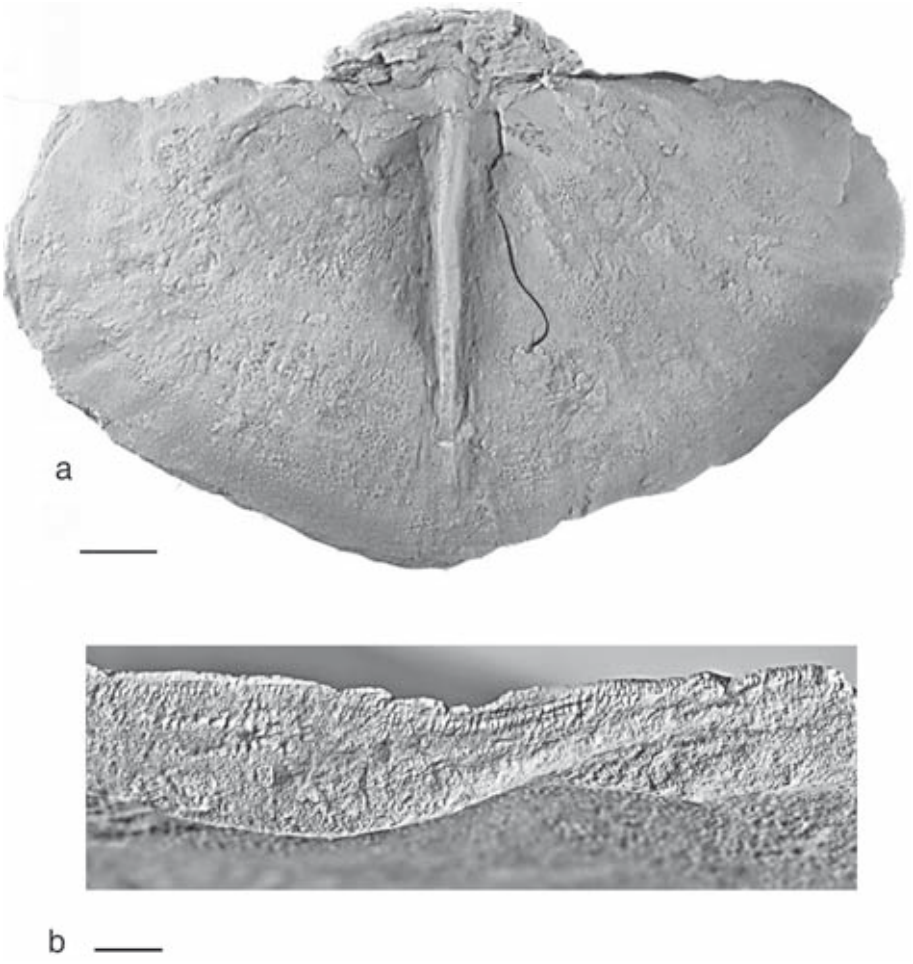

Figure 5. a) *Isogramma casina* sp. nov. DGO 3863. Same specimen as Fig. 4k, enlarged to show more clearly the dorsal internal characteristics; a line has been drawn separating the median and lateral adductor muscles of the right side of the valve. Scale bar = 5 mm. **b)** *Isogramma demuesensis* sp. nov. DGO 3878, posterior view of a fragmentary dorsal valve showing the posterior crenulations of the lateral ridge. Scale bar = 2 mm.

252) or as a lophophore platform (Wardlaw *et al*., 1987, p. 84), because they are reminiscent of the brachial ridges in productides. However, their position is more posterior than in the Productidina and their general form is also unlike that of the Productidina, as previously noted by Cooper & Grant (1974). One possibility is that they were the site of the gonadal sacs.

The striated grooves at the base of the cardinal process are interpreted here as structures for the articulation with the sides of the delthyrium.

I. concentrica Semenow (junior synonym of *I. germanica* Paeckelmann, *fide* Brand, 1970, p. 72) differs essentially from *I. casina* by its much wider and less numerous concentric ridges and more transverse shell.

I. davidsoni is similar to the new species in its dimensions, thick shell and probably also in the concentric ornament. Barrois (1882, p. 327) pointed out that both valves bear a sulcus, represented in the ventral valve exterior figured on his pl. XVI, fig. 6b; however, it is usual in this family that if one valve bears a sulcus the other bears a fold. Regardless of what type of median folding is attributed to *I. davidsoni*, the outline of both species is very different, semielliptical in *I. casina* and almost subtriangular, rapidly decreasing in width towards the front, in *I. davidsoni* (see Barrois, 1882, pl. 16, figs 6a-6b for comparison).

The very curved region of the beak with the ventral posterior part and the dorsal myophore is commonly broken, so it is rare to find specimens with its total length.

Isogramma demuesensis sp. nov.
(Figs 2a-2b, 5b, 6)

1999 *Isogramma* aff. *paotechowensis* (Grabau & Chao); Sánchez de Posada *et al*., p. 352.

1999 *Isogramma* sp.; Sánchez de Posada *et al*., p. 352.

2002 *Isogramma* aff. *paotechowensis* (Grabau & Chao); Sánchez de Posada *et al*., p. 594.

2002 *Isogramma* sp.; Sánchez de Posada *et al*., p. 595.
2010 *Isogramma* aff. *paotechowensis* (Grabau & Chao); Martínez Chacón *et al*., p. 62.
2010 *Isogramma* sp.; Martínez Chacón *et al*., p. 62.
2015 *Isogramma* sp. nov. 3; Martínez Chacón, p. 175.

***Derivatio nominis*.** From Demués, a small village of the Onís municipality in which the type locality occurs.

Type locality and horizon. Section exposed some 1400 m south of the village of Demués, Demués Formation, sample DM-10, marls and shales with abundant fossils, some 156 m above the base of the section, early Kasimovian (Sánchez de Posada *et al*., 1999, 2002).

Material. Holotype, almost complete specimen, DGO 3871 (Figs 6a-6b), a further 5 specimens (DGO 3872-3876) and 6 fragments, DGO 3877, have been collected from the type locality and horizon. Four incomplete specimens, DGO 3878-3881, and some fragments, DGO 3882, have also been collected from the same section, sample DM-12, some 20 m above sample DM-10, Demués Formation, early Kasimovian (Sánchez de Posada *et al*., 1999, 2002).

Diagnosis. Large *Isogramma*, slightly concavo-convex, with both valves thick and nearly flat; transversely semielliptical outline, with a width about 2 to 1.6 times the length; maximum width slightly anterior of the hinge. Ventral valve with a slight median fold. Colleplax relatively narrow, reaching about 1/3 to 1/4 of the length of the shell. Concentric ridges strong, some 8 in 5 mm.

Description. Shell slightly concavo-convex, with both valves thick (some 2.5 to 3.5 mm in thickness) and nearly flat, outline transversely semielliptical, hinge line straight with cardinal extremities rounded, maximum width slightly anterior of the hinge.

Ventral valve slightly convex, with umbo bending on the hinge and projecting beyond it. Interarea distinct and relatively high, 2.4 to 3.1 mm high (measured in 2 specimens), tapering laterally and ending at some distance from the extremities of the hinge. Median fold starting at some distance from the beak, broad and little high, not observed in the small specimen (DGO 3875, Fig. 6c). Colleplax, originating at beak, narrow, short, extending about 1/3 of shell length, depressed with respect to the rest of the valve. Ornamentation of strong concentric ridges, separated by spaces wider than the ridges, covering the valve except the colleplax; some 8-9 ridges are counted in 5 mm. Sometimes the ridges form concentric folds each one with a variable number (5-8) of ridges; a deeper sulcus exists between successive folds (Figs 6a, 6f, 6i). The colleplax has a fine punctation; on the rest of the valve, the punctae are visible only when the shell is eroded, especially in the spaces separating the ridges (Figs 2a-2b).

Dorsal valve slightly concave or flat. Ornamentation as that of the ventral valve but sometimes steps or lamellae corresponding to the concentric folds of the other valve, are developed (Figs 6e, 6h).

Dimensions of a number of specimens are presented on Table 3.

Table 3. Measurements (in mm) of *Isogramma demuesensis* sp. nov. Hventint: height of ventral interarea; rest as in Table 1.

Specimen	L	W	Lcoll	Wcoll	ridg/5mm	Hventint
*DGO 3871	62.3	125.5	17.6	~11.1	8 or 9	3.1
DGO 3872	52.3	82.4	20.3	9.5	9 or 10	2.4
DGO 3875	24.1	46.8			8	
DGO 3878					9	

Ventral interior with elevated platform corresponding to the colleplax.

Dorsal interior (known only from fragmentary specimens) with median septum high and thick, its anterior ending is not visible, but in the specimen DGO 3879, DM-12 (Fig. 6d) the septum continues at least as far as 16.7 mm from the front of the valve. The specimen DGO 3878, DM-12 (Figs 5b, 6g) shows a lateral ridge, crenulated on its posterior side, ending approximately at a half of the distance between the middle of the valve and the cardinal extremity; the ridge increases in height towards its end. These ridges probably served as articulatory structures fitting with the ventral interarea. In front of the lateral ridge, a depression similar to that described by *I. casina* sp. nov. is observed. The inner surface bears radial sulci corresponding to the mantle canals. Interior covered by hexagonal large pits (Figs 6d, 6g).

Discussion. The new species is similar to *I. paotechowensis* (to which it has been previously compared, see the synonymy list) by its transverse and plated shell and large size. Nevertheless, the Cantabrian species is bigger and even more transverse and has a median fold that is not present in *I. paotechowensis*. The American Pennsylvanian *I. renfrarum* Cooper, 1952, also has a large and transverse shell, which features offer comparison to *I. demuesensis*, but the American species has a larger size, much more transverse shell and has no ventral median fold.

The ornamentation of the dorsal valve, characterized by lamellae or steps, each with a group of concentric ridges, is similar to that of *I. diabloense* Cooper & Grant, 1974, from the Permian of West Texas (Cooper & Grant, 1974, pl. 25, fig. 15; pl. 26, fig. 11). However, the Permian species has a small size and much finer concentric ridges.

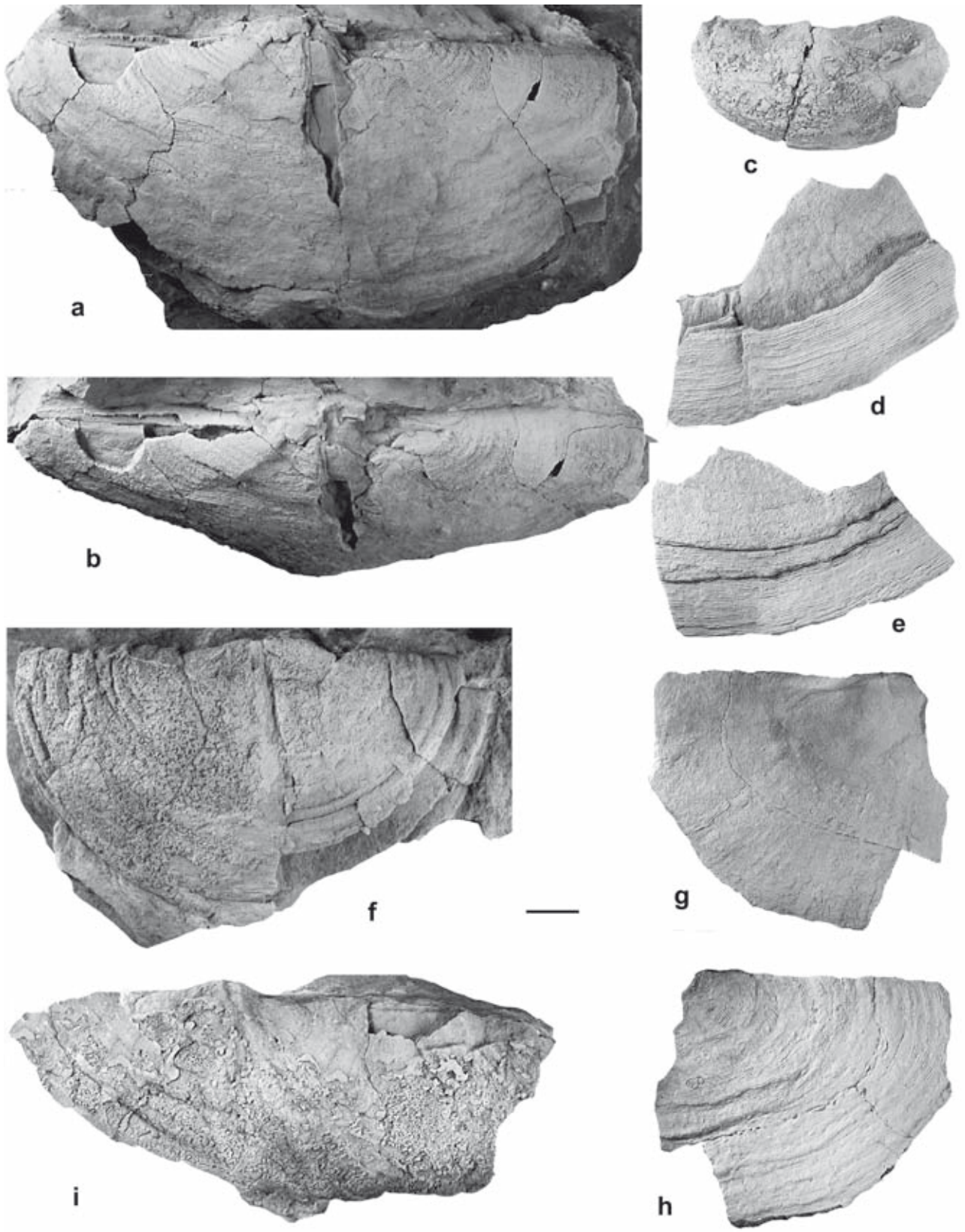

Figure 6. *Isogramma demuesensis* sp. nov. Section exposed some 1400 m S of the village of Demués (Onís, Asturias), Demués Formation, early Kasimovian (Sánchez de Posada et al., 1999, 2002). **a-c**, **f**, **i)** Sample DM-10. **(a-b)** Holotype, DGO 3871, ventral and posterior views. **(c)** DGO 3875, decorticated young specimen, ventral view. **(f)** DGO 3872, ventral view. **(i)** DGO 3874, ventral view of a deformed specimen. **d-e**, **g-h)** Sample DM-12. **(d-e)** DGO 3879, fragmentary specimen with the two valves, in ventral view showing part of dorsal interior, and dorsal view showing the ornamentation with concentric ridges and lamellae. **(g-h)** DGO 3878, fragmentary dorsal valve in internal and external views. Scale bar = 10 mm.

Isogramma spp.

Remarks. In this section we include two specimens and two fragments that it has not been possible to determine more precisely. One specimen, DGO 3883, comes from the Fito Formation, late Moscovian, Coballes (Caso, Asturias). The remaining material comes from the Paquete Generalas, late Moscovian (Podolsky), from various sections and localities of the Central Asturian Coalfield; the specimen DGO 3884 from La Inverniza section, some 10 km E of Mieres; fragment DGO 3885 from Navidiello Hill, 4 km E of Puente de los Fierros; fragment DGO 3886, from El Cellón Peak, Pajares.

7. CONCLUDING REMARKS

Isogramma is an exceptional brachiopod genus, which is not well known despite the fact that various authors have published detailed revisions. This may be due to the poor preservation of the material of this genus. The preservation of our material has permitted us to study in part the microstructure and characteristics of the interior of both valves, such as the external and internal characteristics of the colleplax, the very large cardinal process with strong myophore, the dorsal muscle scars and the so-called lophore platforms, the latter here considered more likely to be gonadal prints, and the lateral ridges with crenulations on the posterior side, developed on both sides of the cardinal process. The articulation is probably produced by the help of these lateral ridges, of which the posterior side fits the ventral interarea, while the cardinal process fits into the delthyrium, the sides of which articulate with the striated grooves at the base of the cardinal process.

The shell appears to have two layers, a thin outer layer, not penetrated by the punctae, and an internal, thicker, spongy one, crossed almost perpendicularly by punctae. The interior of the shell has an aspect similar to the external surface of *Dictyonella* described by Wright (1981), with large hexagonal or rhomboidal pits, separated by narrow walls of shell; the pits may contain some punctae and the walls around the pits are also crossed by small punctae. In some areas of the interior of the valves, especially in their anterior parts, only punctae are developed.

In the Cantabrian Mountains, representatives of *Isogramma* have been described or cited from rocks of Moscovian and Kasimovian age. *Isogramma davidsoni*, the only one species described until now for the region, has been discussed. Three new species are described for the Pennsylvanian of Asturias and León: 1) *Isogramma wagneri* sp. nov., in which is included part of the specimens attributed previously to *I. davidsoni* and other material ascribed to indeterminate species of the genus; 2) *I. casina* sp. nov., in which is included the material previously cited as *I. concentrica* and also some specimens listed as *I. davidsoni*; and finally 3) *I. demuesensis* sp. nov., listed previously as *I.* aff. *paotechowensis*.

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