

# The trilobite *Serrodiscus* Richter & Richter from Iberia, with systematic review of the genus and its international correlation through the Cambrian Series 2

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*Serrodiscus* is considered one of the first trilobite genera showing global distribution during the Cambrian and a key component for the international correlation of this period. However, this genus encompasses many poorly documented species, ambiguous diagnoses or characters that depend on taphonomy and deformation based on one single specimen. Thus, in the present work, we carry out a systematic overview of the genus, evaluating the taphonomic and deformational variability of a large number of specimens from the same locality and horizon. In addition, and due to the difficulty of making synonymy decisions, closely related species are grouped into three different groups taking into consideration morphologic, stratigraphic and palaeobiogeographic data: *bellimarginatus* group, scattered along Avalonian and western Gondwanan margins; *speciosus* group, extending over the Laurentian domain; and *daedalus* group, being restricted to eastern Gondwana (Australia), North China and, partially, Siberia. Besides, the regional correlation through the early Cambrian of Iberia is arranged, describing specimens from both Ossa-Morena and Central Iberian zones, with a time interval restricted to the upper Marianian Stage. Regarding the biostratigraphy and palaeobiogeography of the genus, *Serrodiscus* has been reported from Laurentia, Taconic Allochthon, Greenland, Baltica, western and eastern Avalonia, western Gondwana margin, Siberia, North China and eastern Gondwana, with a temporal distribution along with the Cambrian Series 2. • Key words: Trilobita, Eodiscida, Iberia, systematics, biostratigraphy, palaeobiogeography, Cambrian Stage 4.

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For more than twenty years, the International Subcommittee on Cambrian Stratigraphy (ISCS) has been working untiringly for the global subdivision of the Cambrian System (see Peng *et al.* 2020 for review). Nonetheless, certain time slices remain problematic for division and correlation. One of the most challenging is the so-called Cambrian Series 2, including Stages 3 and 4 (see Sundberg *et al.* 2016, 2020; Zhang *et al.* 2017; Geyer 2019).

Trilobites, together with small shelly fossils, acritarchs and archaeocyaths, have played a fundamental role in the correlation and division of the Cambrian. The problem with the correlation of the Cambrian Series 2 lies in two main causes: on the one hand, the trilobites (and other fossils) present in this time interval do not show a global distribution that encompasses all palaeogeographic domains except for a few trilobite genera and species (see Álvaro *et al.* 2013, Sundberg & Webster 2021).

On the other hand, those genera and species that show a global distribution lack a precise stratigraphic known range, reducing its usefulness for stratigraphic correlation among different domains. Therefore, improving the biostratigraphic range knowledge of those worldwide distributed trilobites is a fundamental work in order to achieve the subdivision mentioned above in this timespan. Among trilobites, eodiscoids represent one of the most widespread and biostratigraphic-reliable groups, especially in the Cambrian Series 2. In line with this topic, this work constitutes a reappraisal of the genus *Serrodiscus* Richter & Richter, 1941, a wide geographically distributed eodiscoid trilobite during Cambrian Epoch 2, whose stratigraphic range is generally accurate for a significant number of occurrences.

The trilobite *Serrodiscus* was defined in 1941 by Rudolf and Emma Richter in the municipality of Cala, Huelva (southwestern Spain), occurring in the so-called “*Fauna von Cala*” (The Cala Fauna; Richter & Richter 1941). Subsequently, several species previously classified as other genera (e.g. *Microdiscus*, *Eodiscus*, among others) were assigned to *Serrodiscus*, and it has been progressively reported from several Cambrian localities (see Westrop & Landing 2011 for review), revealing a worldwide distribution. Thus, the high potential of *Serrodiscus* for international correlation of Cambrian rocks, as previously stated by Geyer & Shergold (2000) when proposed as one of the index genera for the base of the Cambrian Stage 4.

Despite its wide distribution and clear interest in international biostratigraphy, there is little study regarding the systematic status of *Serrodiscus*. Herein we review and update the occurrences of this genus and discuss the reliability of morphologic characters previously used to differentiate *Serrodiscus* species, based on a new collection from different fossil sites of the Iberian Peninsula located in the Ossa-Morena and Central Iberian zones. One of the significant difficulties is to assess the validity of all described species, many based on scarce or poorly preserved specimens or ambiguous diagnostic characters. In this sense, and in the impossibility of making well-founded decisions given the poor documentation of several occurrences, we opted for an attempt to group the species based on their morphotypes, stratigraphic range and palaeobiogeographic distribution.

On the other hand, the regional Marianian Stage of Iberia has caused some controversy in recent years (e.g. Álvaro *et al.* 2019), given the difficulty in correlating the sequences of different morpho-structural units within the Iberian Massif (e.g. Ossa-Morena and Central Iberian zones). Therefore, we demonstrate the usefulness of *Serrodiscus* to correlate different Cambrian ‘blocks’ of the Ossa-Morena Zone, and a tentative correlation to those of the Central Iberian Zone.

## Geologic context

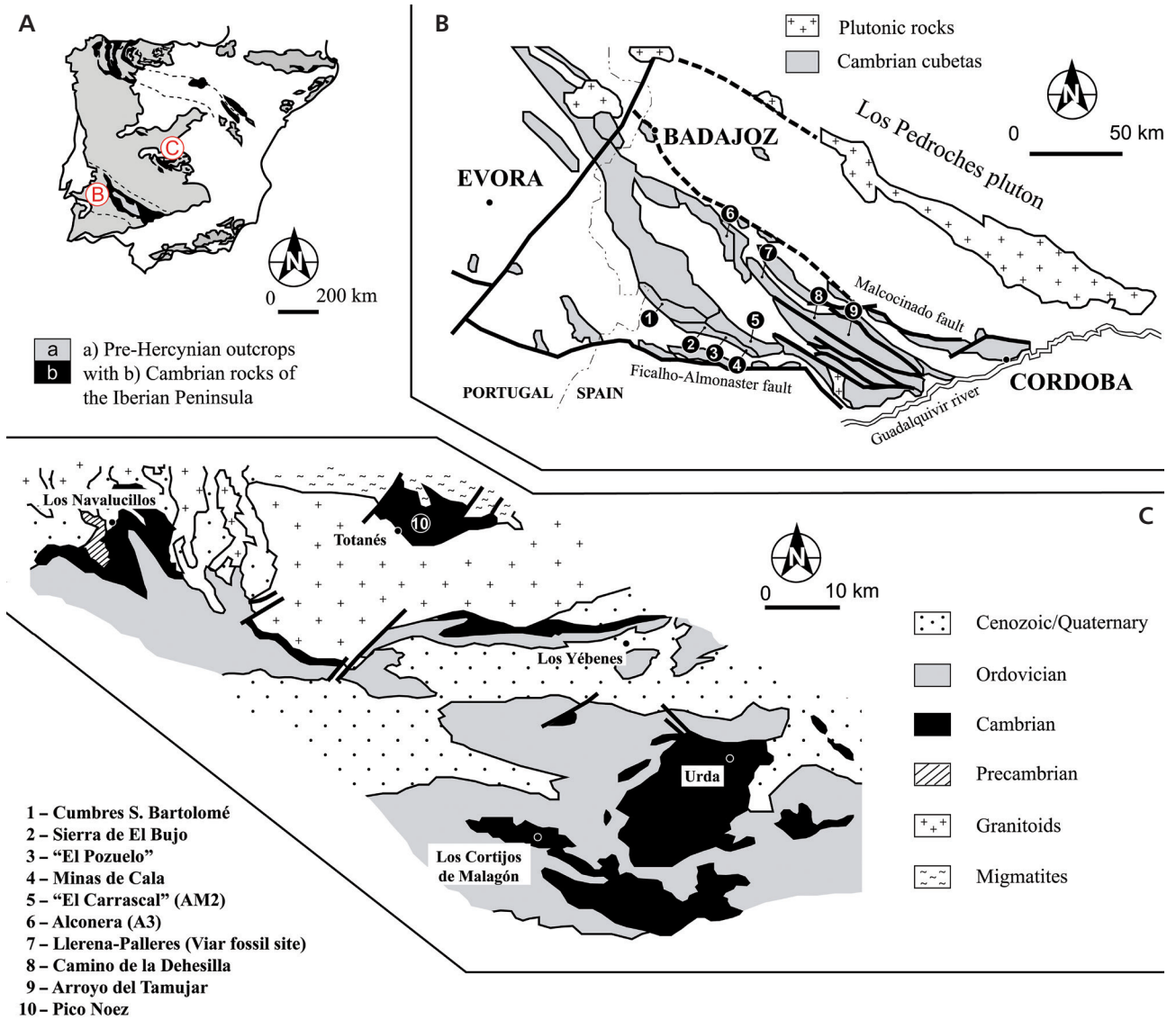
Studied areas are located within two of the most representative zones of the Iberian Massif: the Ossa-Morena Zone (OMZ) (Lotze 1945) and the Central Iberian Zone (CIZ) (Julivert *et al.* 1972; Fig. 1A):

The OMZ belongs to the southern branch of the Variscan Orogen of the Iberian Peninsula. This area comprises rocks dating from the terminal Proterozoic to the Carboniferous, with a general structure of large, recumbent folds with SW vergence, and ductile thrust-faults with the main movement towards the SW (Azor 2004). Cambrian rocks of the Ossa-Morena Zone outcrop in distinct belts or ‘blocks’ – named ‘cubetas’ in Spanish – with a notable change of facies and thickness, most likely related to downthrow and tilting along an active growth fault at the time of sediment deposition (Liñán & Quesada 1990). Specimens of *Serrodiscus* from the OMZ come from the Cumbres block (Cumbres de San Bartolomé locality), Herrerías block (Sierra del Bujo, “El Pozuelo”, and Minas de Cala localities), Arroyomolinos block (“El Carrascal” locality), Alconera block (Alconera locality, A3 section), Viar block (Llerena-Pallares locality) and Benalija block (Arroyo Tamujar and “Camino de la Dehesilla” localities) (Fig. 1B).

The CIZ is an autochthonous sector occupying the central area of the Iberian Massif. One fossil site provided *Serrodiscus* specimens in the Cambrian outcrop of Pico Noez, NE to Totanés, Toledo. This locality belongs to the “Toledo Platform” in the northern foothills of the Montes de Toledo Domain, SE of the Schist-Greywacke Complex, an extensive Proterozoic–early Cambrian succession, highly deformed, with recumbent folds and thrust-faults in its north and southern boundaries, and subvertical-axial planes folds in its central area (Martínez Catalán *et al.* 2004; Fig. 1C).

## Stratigraphic range of *Serrodiscus* and regional correlation

The regional Marianian Stage (after ‘Mariani Mountains’, Sierra Morena, Andalusia) was introduced by Sdzuy (1971). Olenelline trilobites in its lower part initially defined this regional stage; the genera *Triangulaspis* Lermontova, 1940, *Delgadella* Walcott, 1912 and *Serrodiscus* in its middle part and several trilobite genera belonging to Protolenidae, Ellipsocephalidae and Redlichiidae in its upper part. Later, Liñán (1984) subdivided the Marianian Stage into lower, middle and upper, respectively. Shortly after, Perejón (1986) established eleven archaeocyaths biozones for the Ovetian, Marianian and Bilbilian Stages. Finally, Liñán *et al.* (1993) reevaluated the lower and middle Cambrian stages in Iberia, redefining the base of the Marianian by the

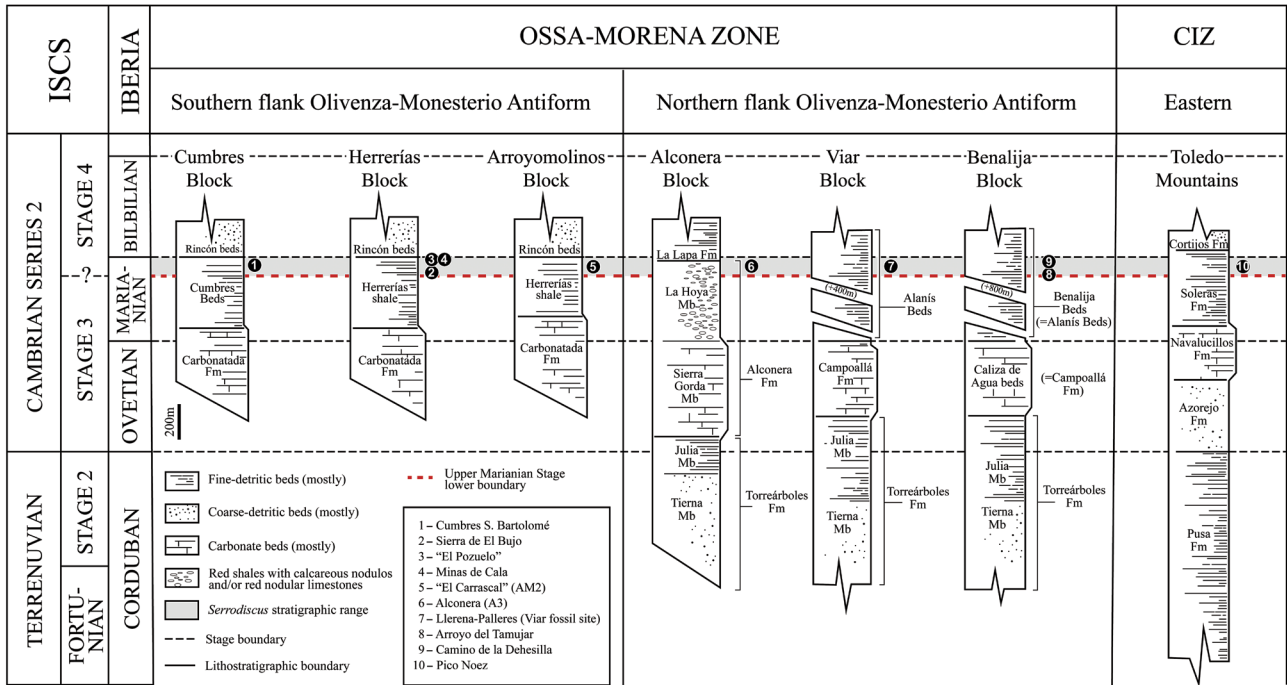


**Figure 1.** A – pre-Hercynian outcrops in the Iberian Peninsula. • B – geological setting of fossil sites in the Cambrian sectors (fault-bounded blocks) of the Ossa-Morena Zone, indicating the position of the studied fossil sites (modified from Liñán & Quesada 1990). • C – geological map of the Cambrian outcrops from the Toledo Mountains, modified from Aparicio Yagüe (1971), Roiz (1979) and Martín Escorza (1976).

FAD of *Delgadella* and the top by the LAD of *Andalusiana* Sdzuy, 1961 and *Serrodiscus*. Later on, Liñán *et al.* (1996) modified the Marianian base and top boundaries (FAD of the *Strenuella* Matthew, 1887 for the base, and the FAD of *Realaspis* Sdzuy, 1961 and *Pseudolenus* Hupé, 1953a for the top) and they correlated it with the Botoman Stage of Siberia. Subsequent works (*e.g.* Liñán *et al.* 2002, 2004; Gozalo *et al.* 2003) have admitted the following division: the base of the lower Marianian is defined by the FAD of *Strenuella* and the archaeocyathan zones VIII and IX of Perejón (1994), the base of the middle Marianian by the FAD of *Strenuaeva* Richter & Richter, 1940 and the base of the upper Marianian by the FAD of *Serrodiscus*. In addition, the Marianian Stage has been approximately

correlated with the *Heliosphaeridium dissimulare*–*Skiagia ciliosa* acritarch Zone, according to the Baltic Zonation (*sensu* Palacios & Moczyłowska, 1998). Nonetheless, a trilobite biozonation is still missing.

Although Sdzuy (1971) reported the occurrence of *Andalusiana* and *Triangulaspis* in the lower part of the Huérmeda Fm. of the Iberian Chains, tentatively correlating this sector with the Marianian rocks of the Ossa-Morena Zone, he did not figure nor describe the specimens. For this reason, Álvaro *et al.* (2019) considered that the presence of these genera in the Iberian Chains, and thus the correlation between both domains, is not possible to verify. However, recently, Sepúlveda *et al.* (2022) figured *Andalusiana aff. cornuta* from the base of



**Figure 2.** Tentative correlation of the northern and southern Cambrian blocks from the Ossa-Morena and Central Iberian Zones, indicating the stratigraphic range of *Serrodiscus*. Stratigraphic data from San José *et al.* (1974), Zamarreño *et al.* (1976), Liñán & Perejón (1981), Gozalo *et al.* (2003), Liñán *et al.* (2004) and Collantes *et al.* (2020, 2021a, b). Abbreviations: Fm – Formation; Mb – Member.

Huérmeda Fm. in the Iberian Chains. In addition, Álvaro *et al.* (2019) considered the biostratigraphic zonation of the Marianian Stage in Iberia to be poorly defined and lacking radiometric dating, being invalid for correlation throughout the Iberian Peninsula.

The current concept of the Marianian Stage is much more improvable and does need an in-depth revision. However, it is noteworthy that the occurrence of *Serrodiscus* is synchronous throughout the different Cambrian blocks of the OMZ and the eastern CIZ, as previously noted by several works (e.g. Liñán *et al.* 2002, 2004). Therefore, its usefulness to the concept of the Marianian Stage for correlation among these domains must be explored.

In Iberia, *Serrodiscus* is typically recorded together with *Triangulaspis*. Traditionally, the concurrent range of these genera has been used throughout the Iberian Peninsula sequences as the boundaries for the upper Marianian (ca. possible global base of undefined Cambrian Stage 4; Fig 2).

## Ossa-Morena Zone

### Southern flank of the Olivenza-Monesterio Antiform

**Cumbres block.** – *Serrodiscus* specimens come from the Cumbres de San Bartolomé fossil site, located at 38° 02'

43.90° N, 61° 43' 02.11" W. They occur in siliciclastic sandstones and shales of the Cumbres beds (350–1100 m), dated as middle–late Marianian based on the trilobites *Delgadella souzai* (Delgado, 1904), *Callavia choffati* (Delgado, 1904) and *Atops calanus* Richter & Richter, 1941 restricted to the lower part (middle Marianian); and *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888) in Shaler (1888), *Pseudatops reticulatus* (Walcott, 1890), *A. calanus* Richter & Richter, 1941, *Calodiscus ibericus* Sdzuy, 1962, *Triangulaspis fusca* Sdzuy, 1962, *Hicksia?* sp. indet., *Marocella morenensis* (Yochelson & Gil Cid, 1984), brachiopods, and hyoliths in the upper part (upper Marianian, Collantes *et al.* 2020, 2021a, b).

**Herrerías block.** – *Serrodiscus* come from three localities: Sierra de El Bujó fossil site, located at 38° 00' 51.40" N, 6° 28' 57.23" W, El Pozuelo fossil site, located at 37° 58' 59.14" N, 6° 24' 18.82" W, and Minas de Cala fossil site, located at 37° 57' 10.51" N, 6° 19' 49.37" W. All correspond to purple shales with spilitic intercalations, the 'Herrerías shale' (200–500 m), with age ranging from middle to late Marianian based on the presence of *D. souzai*, *Rinconia schneideri* (Richter & Richter, 1941), *Gigantopygus cf. bondoni* Hupé, 1953a, *Hicksia hispanica* (Richter & Richter, 1941), *Protaldonaia morenica* Sdzuy, 1961, *C. choffati*, *A. calanus* and *Ellipsostrenua* sp. in the lower part (middle Marianian), and *S. bellimarginatus*, *C. ibericus*, *T. fusca*, *Pro. morenica*, *Pseu. reticulatus*, and

the mollusc *M. morenensis* and brachiopods (*Obolella* sp.) in the upper levels (upper Marianian, Collantes et al. 2020, 2021a, b).

**Arroyomolinos block.** – The specimens of *Serrodiscus* originate from “El Carrascal” fossil site, Arroyomolinos de León, located at 37° 59′ 17.88″ N, 6° 21′ 30.60″ W. The material was collected in the Herrerías shale (300–400 m), corresponding to purple, grey, and green shales, with metric intercalations of acid volcanic tuffs and spilites. The age of this unit extends from the middle to late Marianian, as indicated by the presence of *D. souzai* and *H. hispanica* in the lower levels (middle Marianian) and *S. bellimarginatus* and *Pseu. reticulatus* in the upper levels (upper Marianian).

#### **Northern flank of the Olivenza-Monesterio Antiform**

**Alconera block.** – *Serrodiscus* specimens come from A3 section, located at 38° 24′ 25.56″ N, 6° 27′ 50.20″ W. The material is from the ‘La Hoya’ Member (~ 400 m), consisting of shales with calcareous nodules, nodular calcilutites, and limestones located in the upper part of the Alconera Fm. (~ 900 m; Liñán & Perejón 1981, Liñán et al. 2004). The trilobite assemblage of this member is composed of *D. souzai*, *Strenuaeva sampelayoi* Richter & Richter, 1940, *Saukianda andalusiae* Richter & Richter, 1940, *H. hispanica*, *S. bellimarginatus*, *Realaspis strenoides* Sdzuy, 1961, and *Pro. morenica*, together with brachiopods and hyoliths. This fossil assemblage suggests an age extending from early to late Marianian.

**Viar block.** – The Viar fossil site is located at 38° 08′ 31.45″ N, 6° 05′ 51.07″ W. Within the Viar block, fossiliferous levels with *Serrodiscus* occur in the upper part of the ‘Benalija beds’ (~ 1000 m), an informal unit divided into three members, being composed of monotonous greenish shales with carbonate nodules as well as some levels of purple shales, calcareous and volcanic basic rocks (Aparategui et al. 1983). A middle to late Marianian age is indicated by the occurrence of *Termierella seviliana* Sdzuy, 1961, *Pro. morenica*, *S. bellimarginatus*, and *M. morenensis* (Collantes et al. 2020).

**Benalija block.** – Specimens of *Serrodiscus* are recognized from different sections of the Benalija block and come from the Camino de la Dehesilla fossil site, located at 38° 05′ 19.58″ N, 5° 50′ 23.41″ W, and the Arroyo Tamujar fossil site, located at 38° 02′ 43.44″ N, 5° 49′ 49.06″ W. The material occurs in greenish to greyish shales with carbonate nodules, assigned to the upper part of the “Alanís beds” (~ 1400 m). The trilobite assemblage comprises *S. bellimarginatus*, *D. souzai*, *Andalusiana*

*cornuta* Sdzuy, 1961, *T. seviliana* and *Pro. morenica*, and hyoliths, brachiopods, and cancelloriid sclerites. This fossil assemblage suggests an age that extends from the medial to late Marianian.

#### **Eastern Central-Iberian Zone**

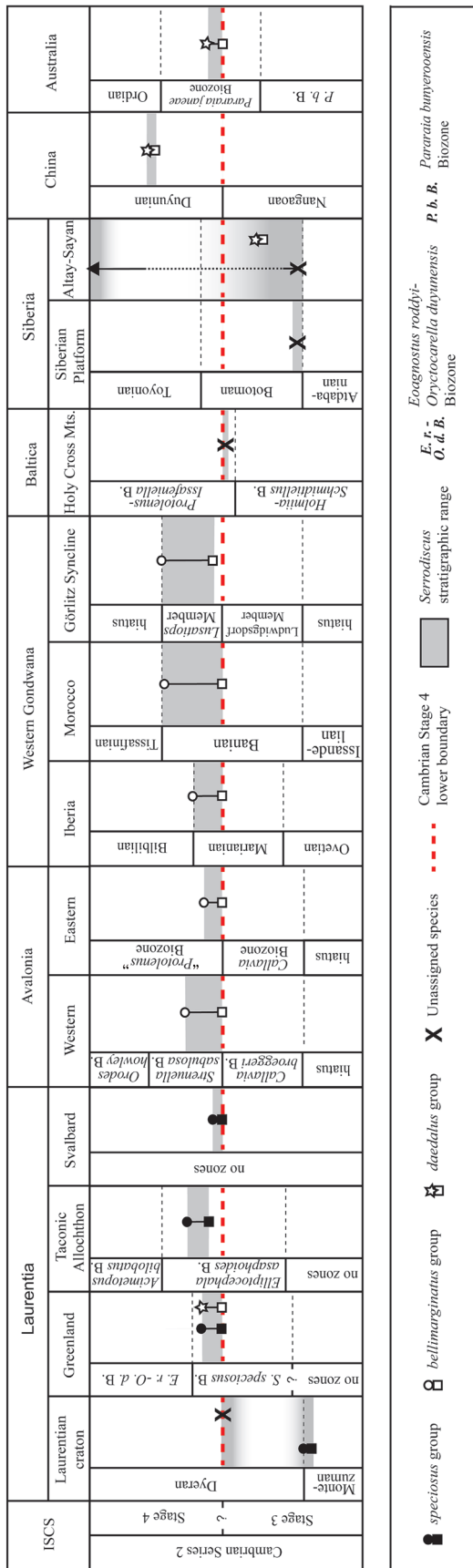
The CIZ specimens come from the Pico Noez fossil site, located at 39° 42′ 49.97″ N, 4° 12′ 19.20″ W. *Serrodiscus* occurs in the Aparicio Yagüe’s (1971) informal “Serie Verde” (green succession) (~ 1000 m), which consists mainly of shales and intercalated limestones and dolostones (Aparicio Yagüe 1971, Aparicio Yagüe & Gil Cid 1972); those materials have been considered equivalent to the Soleras Fm. by Liñán et al. (1993, 2002, 2004). It co-occurs with the trilobite *Andalusiana* (Liñán et al. 1993, Sepúlveda et al. 2021). This association suggests an upper Marianian age and allows correlation with the Spanish Ossa-Morena Zone and Iberian Chains sequences.

#### **International correlation**

The genus *Serrodiscus* shows a widespread geographic distribution and restricted chronostratigraphic range, broadly coincident with Stage 4 of the Cambrian System. Previously, Geyer & Shergold (2000) discussed possible markers to establish the lower boundary of the Cambrian Stage 4, namely the potential reliability of the base of the *Hebediscus*–*Calodiscus*–*Serrodiscus*–*Triangulaspis* band (HCST band). In addition, Geyer & Shergold (2003, p. 193) noted that “most of the [*Serrodiscus*] species have a relatively limited occurrence, but their range do show some regional overlap and associated taxa permit a subglobal recognition”. Nowadays, the ISCS has suggested the establishment of the base of Stage 4 at a level based on the FAD of a single trilobite species (Peng et al. 2020). In this line, they offered a wide range of possible species to select, including *Olenellus* s.l., *Redlichia* s.l., *Judomia*, *Bergeroniellus*, or *Oryctocarella* (Babcock et al. 2011, Peng et al. 2020), but without taking a decision. In addition, the genera mentioned above do not include any eodiscoid species, although they do include some of the trilobites with the broadest geographic distribution during the Cambrian Stage 4.

In this section, we revise the biostratigraphy of *Serrodiscus* from the Cambrian worldwide (Fig. 3). Justification of the different established groups is explained in the Discussion section of the present work.

**Laurentia.** – In the Laurentian domain, *Serrodiscus* was documented in Alaska (Palmer 1968), in the lower *Arcuolenellus arcuatus* Zone, middle Dyeran Stage (*sensu* Webster 2011), in the MacKenzie Mountains (Fritz 1973)



in the *Nevadella* Zone, upper Montezuman Stage (*sensu* Palmer 1998), and in the *Elliptocephala asaphoides* to *Acimetopus bilobatus* zones of the Taconic Allochthon (Rasetti 1967). In addition, Blaker & Peel (1997), Peel & Willman (2018) and Peel & Skovsted (2021) reported *Serrodiscus* in the upper part of the Buen Fm. (Dyerian Stage) and the Aftenstjernesø Fm. (Dyerian Stage, low to the middle part of the *Serrodiscus speciosus* Zone; Blaker & Peel 1997) of Greenland and the Slaklidalen Limestone Fm. (Major & Winsnes 1955), in Spitzbergen Island, Svalbard, Norway, in rocks with age equivalent to the lowermost Cambrian Stage 4.

**Avalonia.** – In western Avalonia (eastern Newfoundland and Massachusetts), *Serrodiscus* occurs in the *Dipharus* (= *Hebediscus*) *attleborensis* Subzone, *Callavia broeggeri* Zone to the top of the *Morocconus notabilis* Zone (Fletcher 2006, Fletcher & Theokritoff 2008, Westrop & Landing 2011). In eastern Newfoundland (United Kingdom), Rushton (1966) reported *Serrodiscus* from the Purley Shale of Warwickshire and Basset *et al.* (1976) from the lower Cambrian of Hell’s Mouth Grits, in North Wales, with an age corresponding to the lower *Strenuella sabulosa* Zone, uppermost Stage 3 to lowermost Stage 4 (*sensu* Rushton *et al.* 2011) or “*Protolenus*” Zone (*sensu* Geyer 2019).

**Baltica.** – *Serrodiscus* was only reported from the *Protolenus*–*Issafeniella* Zone, Holy Cross Mountains (Żylińska & Szczepanik 2009, Żylińska 2013b).

**Western Gondwana.** – In Spain, *Serrodiscus* occurs in the upper Marianian (tentatively correlated with the lowermost Cambrian Stage 4); in Morocco, from below the *Antatlasia guttapliviae* to upper *Sectigena* zones, corresponding to uppermost Cambrian Stage 3 to lowermost Cambrian Stage 4 (Geyer 1988, 2005; Geyer unpublished data according to Sundberg *et al.* 2016); in Germany, in the Górlitz Synclinorium, in rocks assigned to the *Lusatiops* Member, with age equivalent to uppermost Cambrian Stage 3 and lowermost Cambrian Stage 4 (Geyer & Elicki 1995).

**Siberia.** – On the Siberian Platform, *Serrodiscus* is present in rocks assigned to the lowermost Botoman (Datsenko *et al.* 1968, Astashkin *et al.* 1991), while in the Altay-Sayan Foldbelt *Serrodiscus* occur in rocks from the Botoman to Toyonian Stages from Tuva (*Menneraspis* beds’) and

**Figure 3.** Correlation chart showing the stratigraphic occurrence of *Serrodiscus*. Based on Sundberg *et al.* (2016), Zhang *et al.* (2017), and Geyer (2019).

Kuznetsk Alatau (*Kooteniella–Edelsteinaspis* Zone; see Pokrovskaya 1959, Astashkin et al. 1995, Korovnikov et al. 2013). In addition, Korobov (1980) reported *Serrodiscus* from the *Tologoja subquadrata–Margodiscus rackovskii–Sajanaspis* Zone, in Mongolia, with age equivalent to the late Atdabanian Stage (uppermost Cambrian Stage 3).

*Australia*. – In Australia, *Serrodiscus* occurs in the Arrowie and Standsbury basins in South Australia and near Mt. Wright in western New South Wales (Öpik 1975, Jell in Bengtson et al. 1990, Laurie in Brock et al. 2000), with a stratigraphic range that extends throughout the lower *Pararaia janeae* Zone (Bengtson et al. 1990, Betts et al. 2017).

*China*. – The biostratigraphic division and correlation of China's different continental blocks and terranes are unclear. Moreover, some classic series and stages are currently in disuse (e.g. North China). Thus, we refer to the stages from South China (*sensu* Geyer 2019) for clear correlation.

In China, Zhou in Zhou et al. (1982), Lin in Zhou & Zhen (2008), and later Bergström et al. (2014) reported *Serrodiscus* from the northwestern Gansu Province, in the lower Shuangyingshan Fm., Cambrian Series 2. The trilobite association reported by Bergström et al. (2014) includes *Calodiscus*, *Dinesus*, *Edelsteinaspis*, *Kootenia*, *Tannudiscus*, *Pagetides*, *Politinella*, *Ptarmiganoides?* and *Subeia*, approximately middle Duyunian Stage (lowermost Cambrian Stage 4). Table 3.1 of Lin in Zhou & Zhen (2008) shows the *Serrodiscus* distribution in the Lungwangmiaoan Stage of North China equivalent to upper Duyunian. Zhou & Zhen (2008) include this outcrop in the “middle Tianshan-Beishan Region” part of the Kazakhstan Mid Plate during the Cambrian (see Zhou & Zhen 2008, fig. 1.3)

## Palaeobiogeography

The palaeobiogeographic distribution of *Serrodiscus* is discussed in this section and summarized in Figure 4. Different groups and their palaeobiogeographic distribution are justified in the Discussion section of this work.

*Laurentia*. – While many Laurentian polymerid (and specially olenellid) trilobites were mostly endemic (Pillola 1991), several agnostid and small, planktonic trilobites have an intercontinental distribution (see Sundberg et al. 2016). For example, *Serrodiscus* is present in Northwest Territories (Fritz 1973) and Greenland (Blaker & Peel 1997), both belonging to the Laurentian craton; and also in the Taconic Allochthon, interpreted as a North American terrane which shows closely related faunas with western

peri-Gondwana margin (e.g. *Calodiscus*, *Chelediscus*, *Atops*, *Pseudatops*) in the Cambrian Series 2.

*Avalonia*. – Some palaeogeographic models place this domain attached to western Gondwana (e.g. Cocks & Torsvik 2006) or, in contrast, as a separate microcontinent (Landing 2005; Landing et al. 2013a, b, 2022). However, Álvaro et al. (2013) noted that the end of the Cambrian Series 2 is characterized by new links between Avalonia and West Gondwana, including some eodiscoids (e.g. *Serrodiscus*, *Calodiscus*, *Hebediscus*, *Chelediscus*) and other genera as *Strenuella*, *Callavia*, *Pseudatops*, or *Protolenus*. The presence of *Serrodiscus* in Iberia, together with the Moroccan and German occurrences, supports the faunal links between both domains and agrees with previous authors, who reported several other genera in common from Cambrian Series 2 onwards between Avalonia and the western Mediterranean region (e.g. Sdzuy 1972, Liñán et al. 2002; Álvaro et al. 2003, 2013; Landing et al. 2013a, b, 2022; Collantes et al. 2021a, b).

*Western Gondwana*. – Among other regions, Iberia, Morocco and Germany belong to western Gondwana's so-called Mediterranean subprovince (*sensu* Sdzuy 1972). These regions show a similar late Neoproterozoic–Cambrian Series 2 depositional record corresponding to a peri-Gondwanan context, related to the Avalonian–Cadomian active margin (Doré 1994, Pereira et al. 2006). Several authors had previously reported strong faunal links in the Cambrian of these regions (e.g. Álvaro et al. 2003, 2013; Geyer & Landing 2004). The FAD of *Serrodiscus* through the western Gondwana margin seems to be approximately coeval in Iberia and Morocco. In contrast, in the Görlitz Syncline (Geyer & Elicki 1995), its FAD seems slightly younger than the regions mentioned earlier, according to the international correlation of the German outcrops (Geyer et al. 2019). In addition, Geyer & Elicki (1995) also noted that *Lusatiops* occurs in Iberia and Görlitz region together with *Serrodiscus*.

*Baltica*. – Baltica has been traditionally subdivided into two tectonostratigraphic domains based on facies associations and trilobite faunas (Nielsen & Schovsbo 2011) – these domains include an inner-platform sector (which includes Norway and southern and central Sweden) and an outer platform sector (composed of the Holy Cross Mountains and the Digermul Peninsula). Specimens of *Serrodiscus* occur in rocks from the Holy Cross Mountains, corresponding to the outer platform sector (Żylińska & Szczepanik 2009, Żylińska 2013b). Shared trilobite genera between the western Gondwana margin and the external platform sector of Baltica during Cambrian Series 2 also include *Strenuaeva*, *Atops*, *Calodiscus*, and *Protolenus* (Cederström et al. 2009, 2011; Żylińska & Szczepanik 2009; Żylińska 2013a, b).

**Siberia.** – Siberia palaeocontinent can be divided into two major domains: Siberian Platform, which corresponds to widespread, isolated, carbonate platforms with distinct facies zonation in the Cambrian Series 2 (Astashkin *et al.* 1991, Shabanov *et al.* 2008a, b), and the Altay-Sayan Foldbelt, formed by the accretion of the Cambrosayan area, Kuznetsk Alatau, Tuva, western and northern Mongolia, and Buryatiya from the Cambrian Series 2 to Furongian (Mossakovsky *et al.* 1993, Astashkin *et al.* 1995). Trilobite assemblages that dominated the Siberian Platform during the Cambrian Series 2 were composed mainly of eodiscoids, ellipsocephalids, and fallotaspidoids (Álvarez *et al.* 2013). Some of the most remarkable trilobite genera recognized from western Gondwana and the Siberian Platform include *Serrodiscus*, *Calodiscus*, *Hebediscus*, *Delgadella*, *Triangulaspis*, *Pseudatops* and *Atops*.

From the Siberian Platform, there is only one reference of *Serrodiscus* sp. extracted from well cores near the city of Igarka (Datsenko *et al.* 1968). However, there is no figure or description of the specimens. The trilobite association is composed by *Calodiscus* sp., *Delgadella lenaica* (Toll, 1899), and *Triangulaspis lermontovae* Lazarenko, 1957. The stratigraphic position is lower Botomian (Datsenko *et al.* 1968).

In the Altay-Sayan Foldbelt, representatives of *Serrodiscus* are found in several regions, including Tuva (Tannu-Ola), Eastern Sayan, Altay and Mongolia. All these territories represented separated blocks during the early Cambrian.

**Australia.** – In Australia, eastern Gondwana, we can distinguish between shallow intracratonic basins developed across the Central Australian Craton, with a sedimentary record that extends from Neoproterozoic to early Palaeozoic (Brock *et al.* 2000) and sedimentary rocks from Neoproterozoic to Cambrian Series 2 deposited along a passive margin, corresponding to South Australia and Tasmania (Foden *et al.* 2006). Brock *et al.* (2000) summarized the biogeographic links of Australia with other domains during the Cambrian, noting a strong relationship between Australia, North, and South China during the Cambrian Series 2 (Paterson & Brock 2007). Considering the shared trilobite assemblages from western Gondwana and Australia, we found a genus-level relationship based on the genera *Serrodiscus* and *Atops* and the species *Alanisia guillermoi*. Betts *et al.* (2017) also suggest an approximate correlation between the middle–upper Marianian Stage and the *Dailyatia odyseii* Zone in South Australia.

**China.** – Trilobite occurrences reported by Zhou *in* Zhou *et al.* (1982) and later Bergström *et al.* (2014) from the Gansu Province belong to the Tarim basin (*sensu* Zhou & Zhen 2008). As previously stated, the correlation between

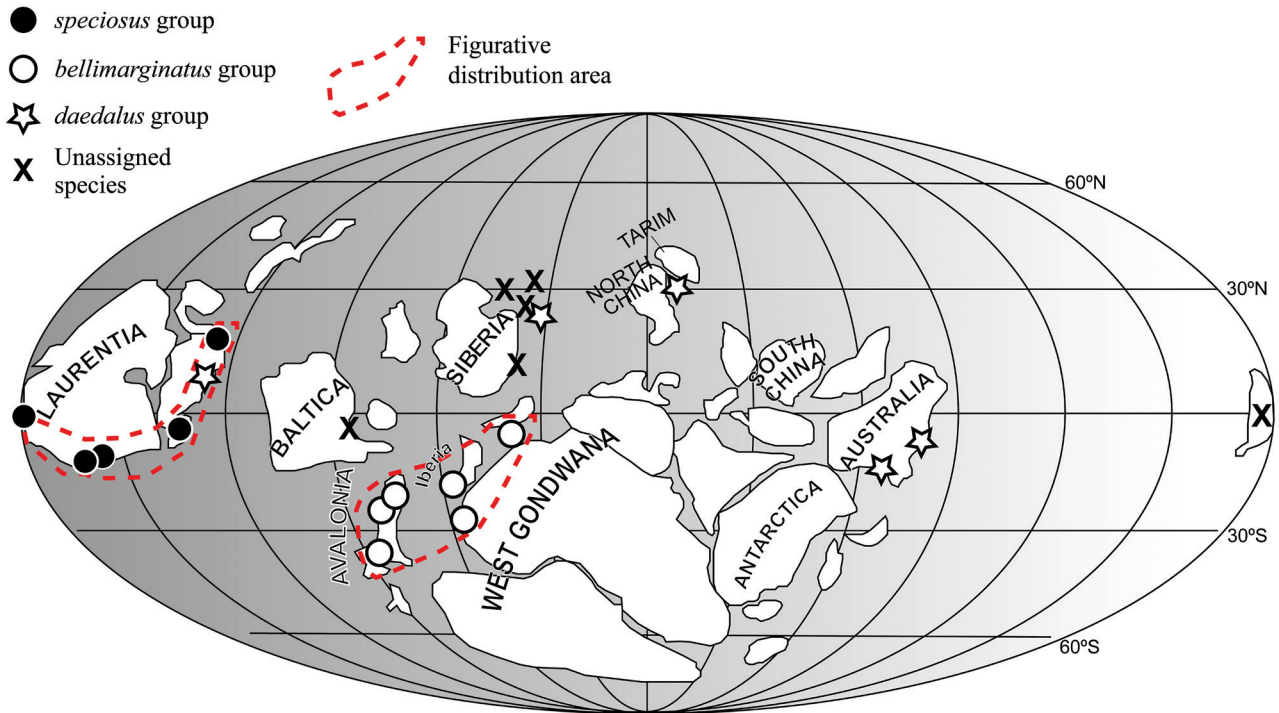
the different continental blocks, accretionary belts, and lower-scale terranes from China is not established: the palaeogeographic data from Huang *et al.* (2000) indicated that North China, South China and Tarim were located adjacent to eastern Gondwana, between the Terreneuvian and Cambrian Series 2. In contrast, Burret *et al.* (1990) indicated that North China showed faunal links with Siberia and Laurentia during Cambrian Series 2, suggesting a more distant position from Gondwana. Zhou & Zhen (2008) re-assessed the different Cambrian units from China, dividing the different continental plates and terranes based on their stratigraphic record, palaeogeographic affinities, and regional tectonics. Álvarez *et al.* (2013), as previous authors, distinguished between South China (or Yangtze block), North China (or Sino-Korean block) and Tarim, indicating that the position of the latter may have been located closer to Siberia than Gondwana during Cambrian Series 2. In support of this statement, Bergström *et al.* (2014) suggested Siberian affinities of the Tarim basin due to the trilobite assemblage reported from the Gansu Province.

To sum up, the genus *Serrodiscus* is distributed across Laurentia (Alaska, MacKenzie Mountains, Taconic Allochthon, and Greenland), western Avalonia (including Newfoundland and Massachusetts), eastern Avalonia (Warwickshire and northern Wales, United Kingdom), the western margin of Gondwana (including Iberia, Morocco, and Görlitz Syncline, Germany), eastern Gondwana (Australia), Baltica (Holy Cross Mountains and Norway), Siberia (both Siberian Platform and Altai-Sayan Foldbelt), and China (Tarim Basin).

## Taphonomic and morphologic variation remarks

*Serrodiscus* includes about thirty defined species, representing a high diversity for a few characters-bearing genus. Unfortunately, many described species are poorly documented (e.g. *S. asiaticus* Pokrovskaya, 1959, *S. communis* Pokrovskaya, 1959), based on few or even only one single specimen (e.g. *S. granulatus* Pokrovskaya, 1959, *S. pokrovskayae* Poletayeva, 1960, *S. griswoldi* Rasetti, 1967, *S. murtucus* Repina, 1979), their diagnosis are couched in jargon (more convex, more rounded, deeper, not so well defined) or based on characters that highly depend on preservation and deformation (e.g. *S. coloi* Hupé, 1953a, *S. primarius* Orłowski, 1985). Therefore, given the abundantly available material coming from the same locality and horizon in Spain, we have an opportunity to properly evaluate the role of taphonomy and deformation in the morphologic characters of *Serrodiscus* (Figs 5–7). This variability applies mainly to fossils preserved as





**Figure 4.** Distribution of *Serrodiscus* plotted on the Cambrian palaeogeographic map (modified from Scotese & McKerrow 1990, McKerrow *et al.* 1992, Dalziel 1997, and Malinky & Geyer 2019).

moulds, but some features must also be considered for mineralizations once they may represent intraspecific variability.

Regarding the cephalon, several characters show variability among studied specimens.

(1) The anterior border is continuous and regular with the lateral one in most of the specimens, but a few presents a medial widening (sag.) (compare Fig. 6B and 6P). Thus, slight changes in this structure seem to depend highly on deformation, not being significant to distinguish at a specific level. However, some *Serrodiscus* species show a significant and constant widening of this structure (e.g. *S. daedalus*, *S. gravestocki*), which can be considered reliable.

(2) The continuous and regular border furrow is widened frontally in some specimens (compare Fig. 6M and 6P), which seems to be related to compression, once there are intermediate morphologies.

(3) A few, but still significant, specimens do not show a preglabellar area, presenting the anterior border furrow merged with the preglabellar furrow. This character may vary depending on deformation, but some well-preserved cephalons suggest intraspecific variability (Figs 5S; 6P, S).

(4) The paired nodes in the cephalic border represent coaptative structures (Westrop & Landing 2011) and must be a fixed number for each species. Nevertheless, the number and even the presence of nodes in the cephalic

border is highly dependent on preservation (see Fig. 6O, right and left border), being one of the most variable characters among the studied specimens. Therefore, species differentiation based on this number and the putative absence of these nodes should be cautious.

(5) Frontal glabellar lobe morphology highly depends on deformation, being variably convex and its anterior outline more rounded to tapering forwards (e.g. Fig. 6H, I).

(6) The pre-occipital tubercle is preserved in solely two specimens (Fig. 6P, S), being rarely preserved. This structure is expected to be a cross-cutting structure in *Serrodiscus*.

(7) The occipital lobe and the occipital furrow are easily deformed (e.g. Fig. 6M) and obliterated (e.g. Fig. 6R). Moreover, smaller specimens bear unfurrowed glabellae with no traces of SO or LO (Fig. 5A–T).

(8) Glabellar furrows vary ontogenetically, absent in smaller specimens and therefore progressively differentiated according to the ontogenetic stage. Furthermore, these structures are highly dependent on preservation (e.g. Fig. 6A, Q).

Similarly, the pygidium also presents a significant variability concerning particular characters.

(9) The pygidial axis does not reach the posterior border in most specimens, bearing a short (sag.) post-axial region. Nevertheless, in a significant number of specimens, a post-axial area is absent (e.g. Fig. 7K–N),

which may be related to deformation that collapses this structure posteriorly. This character has been used previously to erect new species (e.g. *S. coloi*), but it does not seem to be reliable.

(10) The axial rings differentiation strongly varies, from very well-defined rings (e.g. Fig. 7J) to the merest hint of segmentation (Fig. 7A), depending on preservation.

(11) The number, size and even the presence/absence of nodes on the axial rings are highly dependent on preservation. A few specimens show these nodes up to the posteriormost segment (e.g. Fig. 7N, P), which would probably be valid for all individuals. Still, these structures are easily obliterated in internal moulds, leading one to interpret that only the anterior rings would bear them or that the rings would be smooth (e.g. Fig. 7A). Moreover, the type of fossil-diagenesis product should also influence, since depending on a more or less hollow structure of these nodes, their evidence in moulds or mineralizations for the same species can be very distinct.

(12) The pygidial marginal spines vary from ventrally (e.g. Fig. 7D, E) to laterally (e.g. 7F–H) directed, being easily deformed and obliterated.

## Systematic palaeontology

Class Trilobita Walch, 1771

Order Eodiscida Kobayashi, 1939

*Remarks.* – It has been widely accepted that eodiscoids evolved from polymeric trilobites by paedomorphosis (Stubblefield 1936), an idea that has persisted by some authors heretofore (Jell 1975, 1997; Shergold 1991; Cederström *et al.* 2009). Kobayashi (1939, 1943) proposed one of the first phylogenetic classifications, dividing Eodiscida into families and subfamilies. Regarding a hypothetical relationship to the order Agnostida Salter, 1864, some authors (e.g. Størmer 1942) suggested that the differences between the initial growth stages of agnostoids and eodiscoids were enough to classify them into different orders; however, Rushton (1966) postulated that both agnostoids and eodiscoids belonged to the order Agnostida.

Another view was held by Jell (1975), who suggested that eodiscoids emerged from the polymerid trilobites of the early Cambrian by heterochrony, recognizing three major lineages within the superfamily while agnostoids were polyphyletic descendants of several eodiscoid genera. In this line, Shergold (1991) proposed that the most suitable taxonomic position for the eodiscoids was within the order Ptychoparida. The cladistic analysis carried out by Babcock (1994) suggested that eodiscoids seemed to be polyphyletic, evolving from polymerid trilobites by heterochrony, reinforcing the view of Jell (1975). In

addition, Babcock (1994) concluded that agnostoids and eodiscoids did not originate from a common ancestor.

Subsequent works as the ones of Fortey (1990) and Cotton & Fortey (2005) argued that agnostoids were derived from eodiscoids, while others like Walossek & Müller (1990), Bergström (1992), Stein *et al.* (2005) or Cederström *et al.* (2009) argued that agnostoids and eodiscoids were phylogenetically separated, being the agnostoids more closely related to crustaceans than to trilobites. Finally, Jell (2003) presented a phylogenetic analysis suggesting that the eodiscoid trilobites were descendants of Bigotiniidae Hupé, 1953a, and also that the ptychoparioids probably emerged from the ellipsocephaloids.

In the present work, we follow the classification proposed by Adrain (2011), who indicates that agnostoids are not regarded as an ingroup of Trilobita. Instead, Eodiscida is considered a monophyletic group.

Family Weymouthiidae Kobayashi, 1943

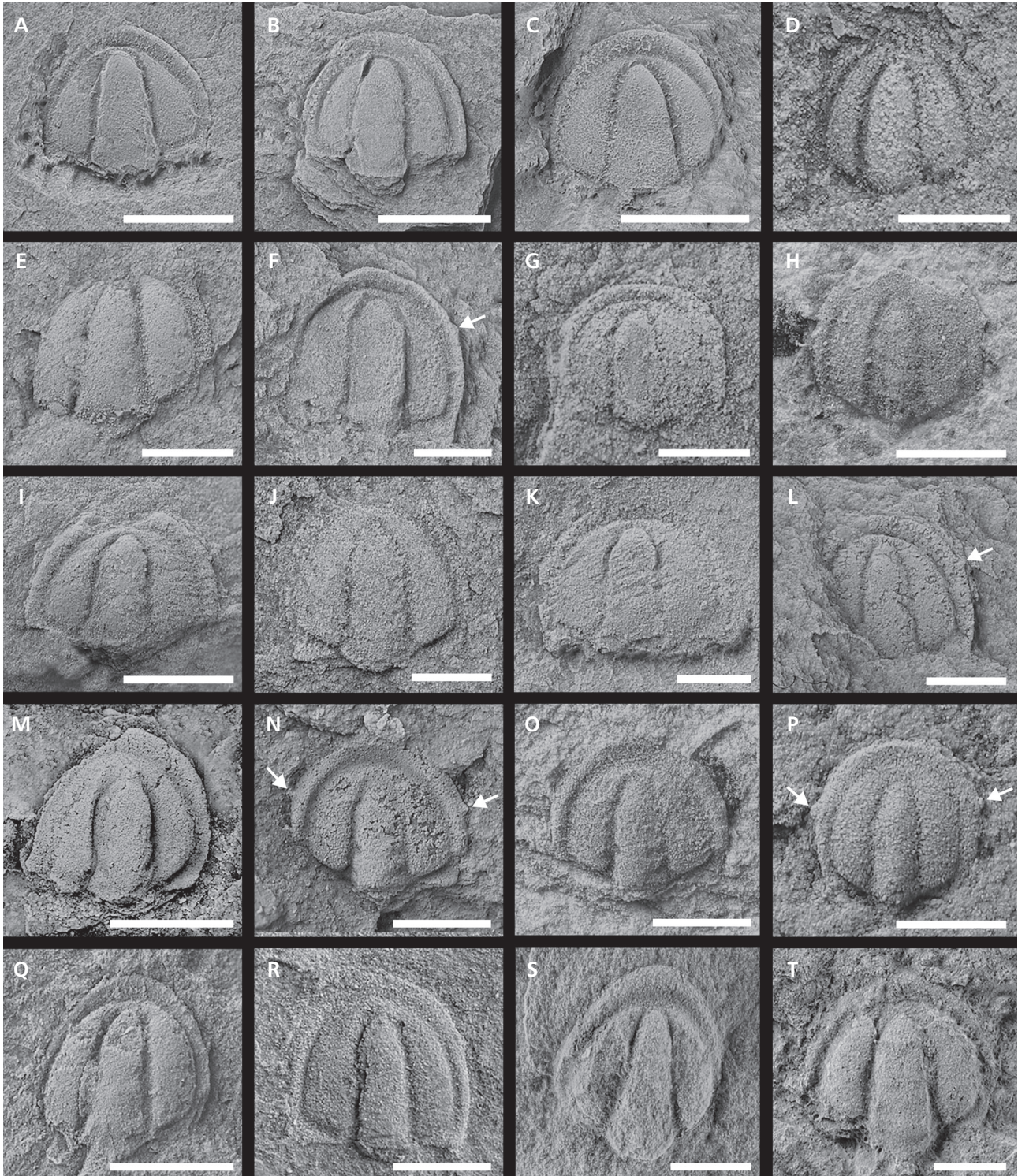
### Genus *Serrodiscus* Richter & Richter, 1941

[= *Paradiscus* Kobayashi, 1943]

*Type species.* – *Eodiscus* (*Serrodiscus*) *serratus* Richter & Richter, 1941, a junior subjective synonym of *Microdiscus bellimarginatus* Shaler & Foerste, 1888 in Shaler (1888).

*Diagnosis.* – See Jell, 1997 (p. 398).

*Remarks.* – In his revision of the North American eodiscoids, Rasetti (1952) identified *Weymouthia nobilis* (Ford, 1873) in Massachusetts (see Rasetti 1952, p. 447, pl. 52, fig. 18). However, Basset *et al.* (1976) considered *Weymouthia nobilis* a *nomen dubium*, as the syntypes from the lower Cambrian of New York are currently lost (see Ford in Walcott 1886, p. 151) and, in addition, no topotypes have been designated after. Thus, Basset *et al.* (1976) suggested restricting *Weymouthia nobilis* to Ford's lost specimens, while British specimens are classified as the new species *Runcinodiscus index* Rushton, 1976 in Basset *et al.* (1976). Subsequently, Fletcher & Theokritoff (2008) re-assign the North American specimens of *Weymouthia* to *Serrodiscus* Richter & Richter, 1941 and considered *Runcinodiscus* a junior synonym of the latter, erecting the new species *Serrodiscus weymouthoides* Fletcher & Theokritoff, 2008. This species was described based on two complete specimens, plus one cephalon and one pygidium (see Fletcher & Theokritoff 2008, figs 4.18–4.21). According to Fletcher & Theokritoff (2008), this species is characterized by softened surface axial features (e.g. glabella, axial furrows, pygidial rachis and absent axial pygidial furrows) and the presence of eight pairs of tubercles on the cephalic border, being described as a “smooth



**Figure 5.** *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888) in Shaler (1888), Cumbres beds, upper Marianian, Cumbres de San Bartolomé, Huelva (A–R); Alanís beds, upper Marianian, Camino de la Dehesilla, Seville (S); La Hoya Mb., upper Marianian, Alconera Fm., Alconera Badajoz (T). A – UHU–CSB121. B – UHU–CSB126. C – UHU–CSB152. D – UHU–CSB153. E – UHU–CSB155 (latex). F – UHU–CSB156. G – UHU–CSB157. H – UHU–CSB160. I – UHU–CSB164. J – UHU–CSB165. K – UHU–CSB167. L – UHU–CSB218 (latex). M – UHU–CSB249 (latex). N – UHU–CSB250. O – UHU–CSB253. P – UHU–CSB255 (latex). Q – UHU–CSB259. R – UHU–CSB265. S – MPZ2021/324. T – MPZ2021/329. Scale bars: 5 mm (A), 3 mm (B–C, R, T), 2 mm (I, M, Q, S), 1 mm (D–H, J–L, N–P). Arrows in F, L, N and P indicate lateral tubercles.

*Serrodiscus*?. However, Westrop & Landing (2011) treat *Runcinodiscus* as a subgenus of *Serrodiscus*; they wrote *Serrodiscus (Runcinodiscus)* (p. 219) or *Serrodiscus (Runcinodiscus) index* (p. 234); they considered *Serrodiscus weymouthoides* as a close relative of the later species and, probably this species would be classified as *Runcinodiscus*. Thus, for the moment, we prefer to keep *Runcinodiscus* at a generic level. Nevertheless, based on the figured specimens, we consider this species to be very different to others belonging to *Serrodiscus*. Therefore, and due to the lack of the diagnostic characters of the genus, here we exclude *S. weymouthoides* and *S. (Runcinodiscus) index* from *Serrodiscus*.

Rasetti (1966) described *Calodiscus occipitalis* from North Chatham, New York, being later reassigned to *Serrodiscus* by Fletcher (1972), who described new specimens from Cape St. Mary's Peninsula (Newfoundland; see also Fletcher, 2006), considering it to be conspecific with Rasetti's material. Nevertheless, these forms are quite distinctive, bearing a robust occipital spine and lacking the cephalic lateral border nodes; thus, its assignment to *Serrodiscus* is doubtful.

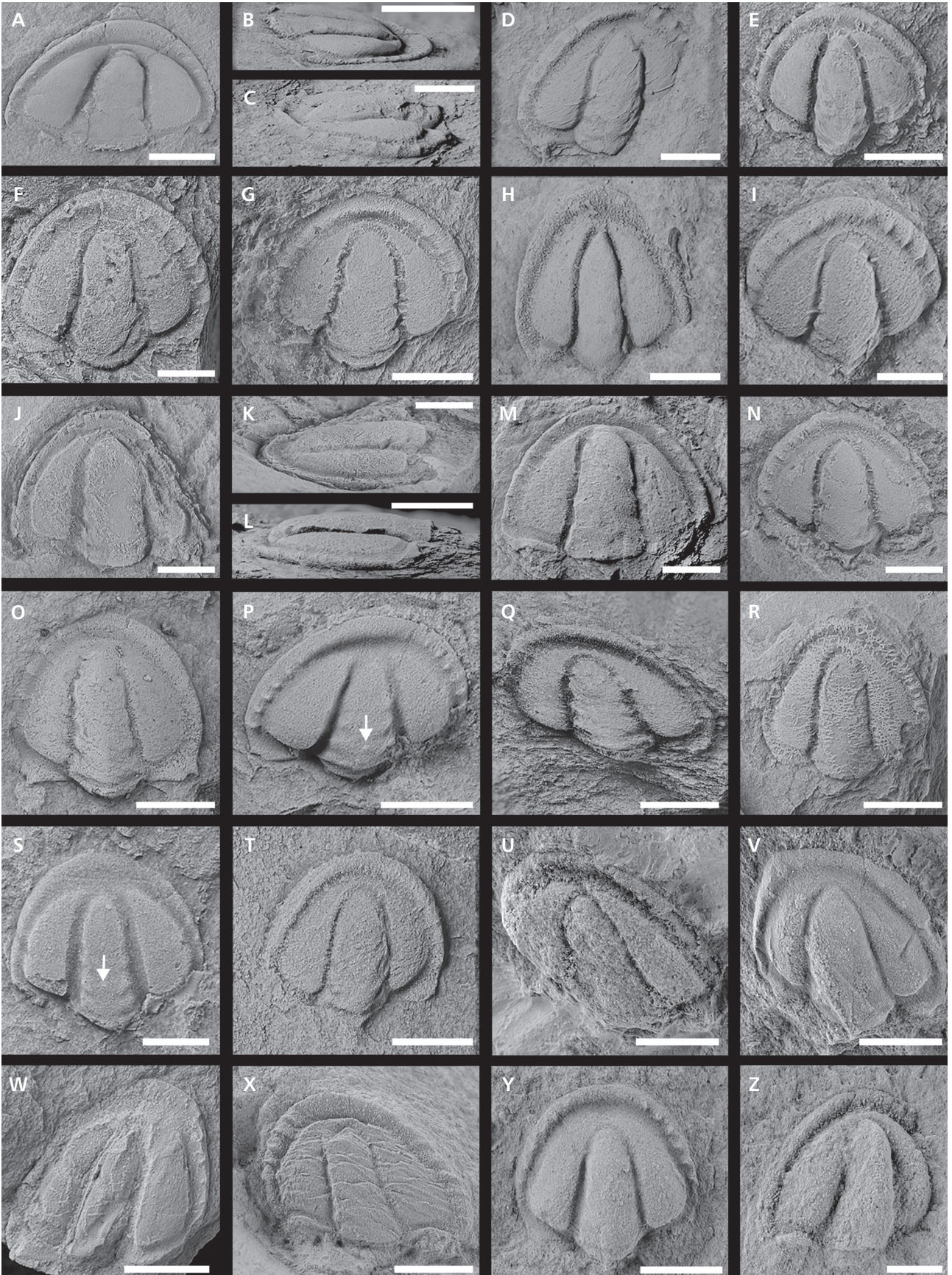
*Species included.* – *Serrodiscus speciosus* (Ford, 1873); *S. sibiricus* Pokrovskaya, 1959; *S. pokrovskayae* Poletayeva, 1960; *S. agnostoides* Poletayeva, 1960; *S. ctenoa* Rushton, 1966; *S. mackenziensis* Fritz, 1973; *S. fossuliferus* Repina, 1964 in Repina et al. (1964); *S. daedalus* Öpik, 1975; *S. murtucus* Repina, 1979; *S. coniformis* Korobov, 1980; *S. areolus* Zhou, 1982 in Zhou et al. (1982); *S. primarius* Orłowski, 1985; *S. gravestocki* Jell, 1990 in Bengtson et al. (1990).

***Serrodiscus bellimarginatus* (Shaler & Foerste, 1888) in Shaler (1888)**

Figures 5–9

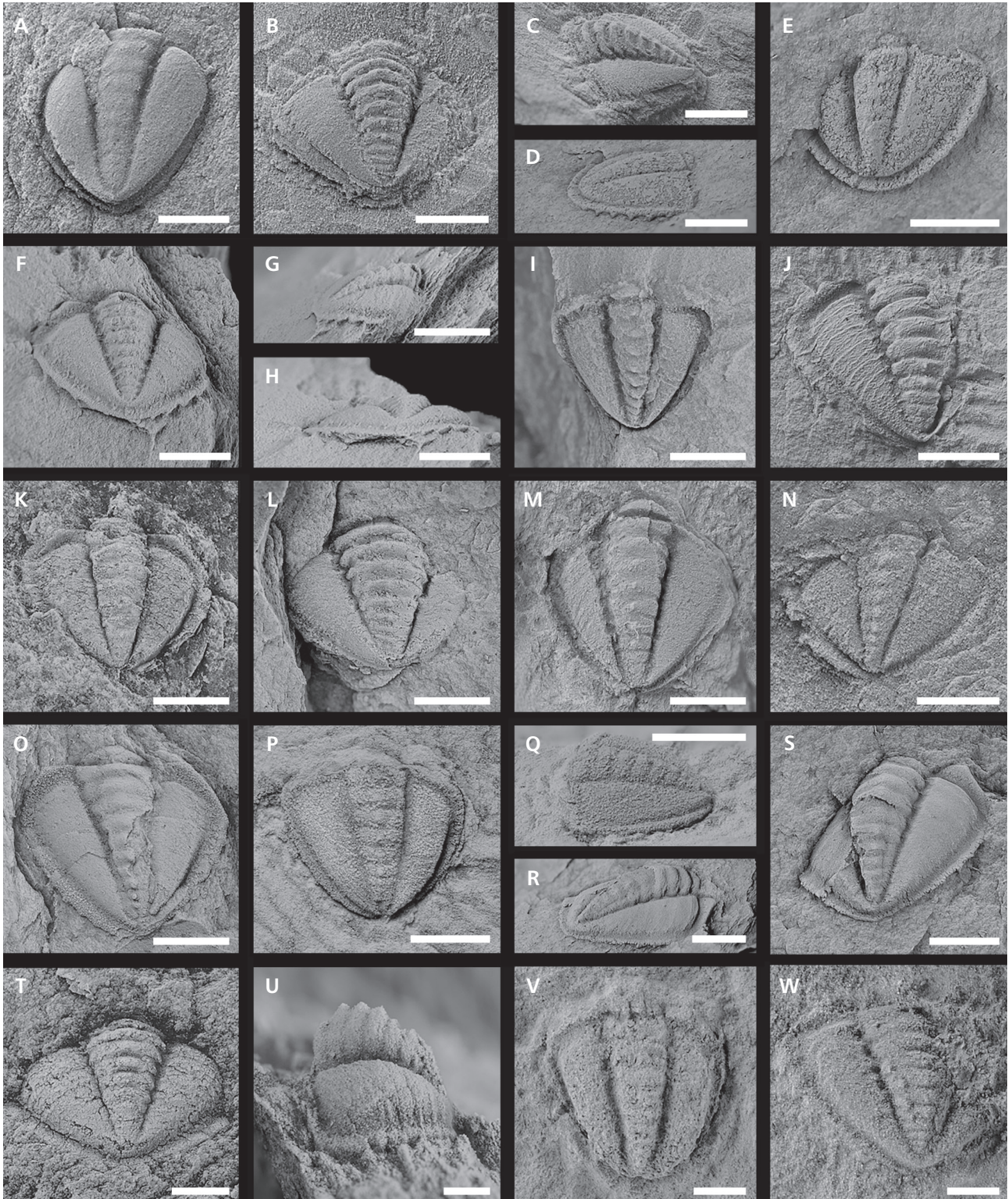
- 1888 *Microdiscus bellimarginatus*; Shaler & Foerste in Shaler, p. 35, pl. 2, figs 19, 19a.
- 1890 *Microdiscus bellimarginatus* Shaler & Foerste. – Vodges, p. 125.
- 1891 *Microdiscus bellimarginatus* Shaler & Foerste. – Walcott, p. 630, pl. 81, figs 2, 2a, b.
- 1896 *Microdiscus bellimarginatus* Shaler & Foerste. – Matthew, p. 29.
- 1899 *Microdiscus bellimarginatus* mut. *insularis*. – Matthew, p. 75.
- 1905 *Microdiscus bellimarginatus* Shaler & Foerste. – Gorham, pl. 2, figs 19, 19a.
- 1907 *Microdiscus speciosus* Ford. – Lake, p. 33, pl. 3 fig. 7.
- 1913 *Eodiscus bellimarginatus* (Shaler & Foerste). – Raymond, p. 103, fig. 7.
- 1923 *Eodiscus bellimarginatus* (Shaler & Foerste). – Clark, p. 476.
- 1924 *Eodiscus* cf. *speciosus* (Ford). – Richter & Richter, pp. 732, 733, fig. 14.
- 1931 *Eodiscus bellimarginatus* (Shaler & Foerste). – Cobbold, p. 460, pl. 38, figs 12–14.
- 1932 *Eodiscus speciosus* (Ford). – Schwarzbach, pp. 452–454.
- 1933 *Eodiscus* cf. *speciosus* (Ford). – Richter, p. 851, fig. 13.
- 1933 *Eodiscus speciosus* (Ford). – Schwarzbach, pp. 586, 591.
- 1934 *Eodiscus speciosus* (Ford). – Schwarzbach, pp. 15, 16, 18, 19, 30, 32, 33, pl. 2, fig. 17.
- 1934 *Eodiscus* sp. – Schwarzbach, p. 18.
- 1936 *Eodiscus speciosus* (Ford). – Schwarzbach, p. 34.
- 1939 *Eodiscus speciosus* (Ford). – Schwarzbach, pp. 770, 771, pl. 51, fig. 12.
- 1941 *Eodiscus (Eodiscus) llarenai* n. sp. – Richter & Richter, p. 23, pl. 2, figs 25, 26; pl. 4, fig. 58.
- 1941 *Eodiscus (Serrodiscus) serratus* n. sp. – Richter & Richter, p. 24, pl. 1, figs 1–10; pl. 2, figs 22–24; pl. 4, fig. 59.
- 1941 *Eodiscus (Serrodiscus) silesius* n. sp. – Richter & Richter, p. 26, pl. 1, figs 11–14; pl. 4, fig. 60.
- 1941 *Eodiscus (Serrodiscus)* cf. *speciosus* (Ford). – Richter & Richter, p. 27, pl. 1, figs 17–21; pl. 4, fig. 61.
- 1941 *Eodiscus (Serrodiscus)* cf. *speciosus* (Ford). – Richter & Richter, p. 29, pl. 1, figs 15, 16.
- 1944 *Eodiscus bellimarginatus* (Shaler & Foerste). – Kobayashi, p. 52, pl. 1, fig. 5b.
- 1950 *Eodiscus (Serrodiscus) bellimarginatus* (Shaler & Foerste). – Shaw, p. 582, pl. 79, figs 19–23.
- 1952 *Serrodiscus bellimarginatus* (Shaler & Foerste). – Rasetti, p. 445, pl. 52, figs 12–17.

**Figure 6.** *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888) in Shaler (1888), Cumbres beds, upper Marianian, Cumbres de San Bartolomé, Huelva (A–T, W); Alanís beds, Viar fossil site, upper Marianian, Llerena-Palares road, Badajoz (U); La Hoya Mb., upper Marianian, Alconera Fm., Alconera, Badajoz (V); Herrerías shale, upper Marianian, Arroyomolinos de León (X) and Sierra de El Bujo (Y), Huelva; Soleras Fm., upper Marianian, Pico Noez, Totanés, Toledo (Z). A – UHU–CSB103, dorsal view. B – UHU–CSB103, lateral view. C – UHU–CSB119, lateral view. D – UHU–CSB119, dorsal view. E – UHU–CSB120. F – UHU–CSB124. G – UHU–CSB125. H – UHU–CSB129 (latex). I – UHU–CSB137. J – UHU–CSB104, dorsal view. K – UHU–CSB104, lateral view. L – UHU–CSB112, lateral view. M – UHU–CSB112, dorsal view. N – UHU–CSB138. O – UHU–CSB162 (latex). P – UHU–CSB180. Q – UHU–CSB161. R – UHU–CSB111. S – UHU–CSB116. T – UHU–CSB134. U – MPZ2021/334. V – MPZ2021/328. W – UHU–CSB109. X – MPZ2021/314. Y – MPZ/2021/321. Z – MPZ2021/338. Scale bars: 5 mm (A–B), 3 mm (C–D, F–H, J–N, P, R, V–Y), 2 mm (I, O, Q, S–U, Z). Arrows in P and S indicate preoccipital glabella tubercles.



- 1953a *Paradiscus (Serrodiscus) coloi* nov. sp. – Hupé, pp. 110, 111, fig. 13.2.
- 1953a *Paradiscus (Serrodiscus)* cf. *speciosus* (Ford). – Hupé, p. 110.
- 1953a *Paradiscus (Serrodiscus)* cf. *speciosus* (Richter & Richter). – Hupé, p. 111, fig. 13.1.
- 1953b *Paradiscus (Serrodiscus)* cf. *speciosus* Richter & Richter. – Hupé, p. 43.
- non 1955 *Serrodiscus bellimarginatus* (Shaler and Foerste, 1888). – Major & Winsnes, p. 1314, pl. 1, figs 6–9.
- 1958 *Eodiscus* cf. *speciosus* (Ford). – Lotze, pp. 743, 744.
- 1960 *Serrodiscus silesius* Richter & Richter. – Sdzuy, p. 105.
- 1960 *Serrodiscus* cf. *speciosus* (Ford). – Sdzuy, p. 105.
- 1961 *Eodiscus (Serrodiscus)* cf. *speciosus* (Ford). – Lotze, pp. 164, 169, 171.
- 1961 *Serrodiscus* cf. *speciosus* (Ford). – Sdzuy, pp. 229, 237, 238, pl. 1, figs 6–8.
- 1961 *Serrodiscus* cf. *speciosus* (Ford). – Sdzuy, pl. 1, figs 1–5, 9.
- 1961 *Eodiscus (Serrodiscus)* cf. *speciosus* (Ford). – Schwarzbach, p. 64.
- 1961 *Eodiscus (Serrodiscus) silesius* Richter & Richter. – Schwarzbach, p. 64.
- 1962 *Serrodiscus speciosus silesius* Richter & Richter, 1941. – Sdzuy, pp. 187, 188, pl. 18, fig. 6.
- 1962 *Serrodiscus bellimarginatus* (Shaler & Foerste). – Hutchinson, p. 58, pl. 1, figs 1, 2.
- 1966 *Serrodiscus* cf. *speciosus* (Ford). – Rushton, p. 12, pl. 1, fig. 1.
- 1966 *Serrodiscus bellimarginatus* (Shaler & Foerste). – Rushton, p. 13, pl. 1, figs 2–5.
- 1966 *Ladadiscus llarenai* (R. & E. Richter). – Rushton, pp. 24–26, pl. 3, figs 16–20, fig. 9a.
- 1972 *Serrodiscus bellimarginatus* (Shaler & Foerste). – Fletcher, p. 35, pl. 7, figs 11–18; pl. 8, figs 1–14; pl. 9, fig. 1.
- 1972 *Serrodiscus* sp. – Aparigio Yagüe & Gil Cid, pp. 107, 108, pl. 1, figs 1, 3–5.
- 1972 *Serrodiscus* aff. *speciosus* Ford. – Aparigio Yagüe & Gil Cid, pl. 1, fig. 2.
- 1981 *Serrodiscus speciosus* (Ford). – Gil Cid, p. 31, pl. 1, figs 4–6; pl. 2, fig. 1, 2, 6–9.
- 1981 *Serrodiscus speciosus silesius* Richter & Richter. – Gil Cid, p. 31.
- 1981 *Serrodiscus* sp. – Gil Cid, pl. 1, fig. 12.
- 1981 *Serrodiscus* (Ford). – Gil Cid, pl. 2, figs 3, 4.
- 1981 *Eodiscido*. – Gil Cid, pl. 2, fig. 5.
- 1981 *Serrodiscus* cf. *speciosus* (Ford, 1873). – Liñán & Perejón, p. 139.
- 1982 *Serrodiscus* sp. – Liñán & Mergl, p. 212.
- 1984 *Serrodiscus* cf. *speciosus*. – Yochelson & Gil Cid, p. 22.
- 1986 *Eodiscus (Serrodiscus) serratus*. – Gil Cid, pl. 1, figs 1–12.
- 1987 *Serrodiscus* cf. *speciosus* (Ford). – Prescher, p. 61.
- 1988 *Serrodiscus speciosus* Ford, 1873. – Gil Cid, p. 582, figs 4, 5, 8.
- 1988 *Serrodiscus speciosus* (Ford). – Gómez-Alba, p. 526, pl. 260, fig. 3.
- 1988 *Serrodiscus coloi* Hupé 1953. – Geyer, p. 116, figs 55–58.
- 1990a *Eodiscus speciosus*. – Christian, p. 10.
- 1990b *Eodiscus speciosus*. – Christian, p. 3.
- 1992 *Serrodiscus (Eodiscus) silesius* Richter & Richter, 1941. – Elicki & Schneider, pl. 15, fig. 5.
- 1992 *Eodiscus (Serrodiscus) speciosus* Ford. – Scheibe, pp. 299–302, fig. 4.
- 1992 *Eodiscus (Serrodiscus) speciosus silesius* Richter & Richter. – Scheibe, pp. 300–302.
- 1993 *Serrodiscus speciosus silesius* Richter & Richter. – Liñán *et al.*, p. 824.
- 1993 *Ladadiscus llarenai* (Richter & Richter). – Liñán *et al.*, p. 824.
- 1995 *Serrodiscus silesius* Richter & Richter, 1940. – Geyer & Elicki, pp. 93–97, figs 3.1–3.9, 5.1, 5.3.
- 1998 *Serrodiscus speciosus silesius* Sdzuy, 1962. – Álvaro *et al.*, 502.
- 2000 *Serrodiscus silesius* Richter & Richter, 1940. – Elicki, pl. 1, fig. 18.
- 2003 *Serrodiscus silesius* Richter & Richter, 1940. – Elicki, fig. 16.
- 2005 *Serrodiscus silesius* Richter & Richter, 1940. – Geyer, fig. 6.4.
- 2006 *Serrodiscus bellimarginatus* (Shaler & Foerste). – Fletcher, pl. 27, figs 15–17.
- 2008 *Serrodiscus bellimarginatus* (Shaler & Foerste). – Fletcher & Theokritoff, pp. 315, 316, figs 4.26–4.30.
- 2010 *Serrodiscus silesius* Richter & Richter, 1940. – Elicki & Geyer *in* Heuse *et al.*, p. 107, figs 2.1, 2.5.
- 2011 *Serrodiscus speciosus* Ford, 1873. – Gil Cid *et al.*, p. 48, pl. 3.
- 2011 *Serrodiscus bellimarginatus* Shaler & Foerste, 1888. – Bullock *et al.*, pl. 2, fig. 3.
- 2011 *Serrodiscus* (s.l.) “*bellimarginatus*” (Shaler & Foerste, 1888). – Westrop & Landing, pp. 222–234, figs 4–12.

*Material.* – Studied specimens are housed in the palaeontologic collections of the Department of Earth Sciences (Laboratory of Tectonics and Paleontology) of the Faculty of Experimental Sciences, University of Huelva, Spain (UHU), the Museo de Ciencias Naturales of the University of Zaragoza, Spain (MPZ), the Senckenberg Museum, Frankfurt, Germany (SMF) and the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ). Cumbres de San Bartolomé, Huelva: UHU–CSB100–101, UHU–CSB190, three complete specimens; UHU–CSB102–168, UHU–CSB170–187H, UHU–CS201A, UHU–CSB218A, UHU–CSB226B, UHU–CSB233B, UHU–CSB245B, UHU–CSB247A–253,



**Figure 7.** *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888) in Shaler (1888), Cumbres beds, upper Marianian, Cumbres de San Bartolomé, Huelva (A–U); Soleras Fm., upper Marianian, Pico Noez, Totánés, Toledo (W); La Hoya Mb., upper Marianian, Alconera Fm., Alconera, Badajoz (X). A – UHU–CSB229. B – UHU–CSB230, dorsal view. C – UHU–CSB230, lateral view. D – UHU–CSB215B (latex), lateral view. E – UHU–CSB215B (latex), dorsal view. F – UHU–CSB232, dorsal view. G – UHU–CSB232, lateral view. H – UHU–CSB232, post-lateral view. I – UHU–CSB236. J – UHU–CSB245. K – UHU–CSB200 (latex). L – UHU–CSB184 (latex). M – UHU–CSB187B. N – UHU–CSB204. O – UHU–CSB238. P – UHU–CSB244, dorsal view. Q – UHU–CSB244, lateral view. R – UHU–CSB212B (latex), lateral view. S – UHU–CSB212B (latex), dorsal view. T – UHU–CSB310 (latex). U – UHU–CSB213, lateral view. V – MPZ2021/339. W – MPZ2021/331. Scale bars: 2 mm (A, E–H, N–O, V), 3 mm (B–C, I–M, P–S), 1 mm (D, T, U, W).

UHU-CSB255B–273, MPZ2021/326, 128 cephalae; UHU-CSB182–189, UHU-CSB191–248A, MPZ2021/325, MPZ2021/327, 81 pygidia. Sierra de El Bujo, Huelva: MPZ2021/320–321, MPZ2021/323, three cephalae, MPZ2021/322, one pygidium. El Pozuelo, Huelva: UHU-POZ100–101, two complete specimens, UHU-POZ102, UHU-POZ105, UHU-POZ108–109, UHU-POZ112, UHU-POZ114–115, UHU-POZ117A–119, eleven cephalae, UHU-POZ103, UHU-POZ11, two pygidia. Minas de Cala, Huelva: UHU-MCA30, SMF X 1234a–2, SMF X 1234e–1, SMF X 1234h–1, SMF X 1234h–2, SMF X 1234h–4, SMF X 1234i–1, SMF X 1234l–1, SMF X 1234l–2, SMF X 1239–1, SMF X 1239–4, SMF X 1239–5, twelve cephalae, UHU-MCA31, SMF X 1234c–1, SMF X 1234d–1, SMF X 1234d–2, SMF X 1234h–3, SMF X 1234i–2, SMF X 1237a–1, SMF X 1237a–2, SMF X 1239–3, SMF X 1239–6, SMF X 1239–7, SMF X 1239–8, twelve pygidia. Arroyomolinos de León (AM1), Huelva: MPZ2021/313–315, three cephalae, MPZ2021/316–319, four pygidia. Alconera (A3 section), Badajoz: MPZ2021/328–330, three cephalae, MPZ2021/331, one pygidium, MPZ2021/332, one complete specimen. Viar fossil site, Llerena-Pallares road, Badajoz: MPZ2021/334, MPZ2021/336, two cephalae, MPZ2021/335, one pygidium. “Camino de la Dehesilla”, Guadalcanal, Seville: MPZ2021/324. Arroyo del Tamujar, Guadalcanal, Seville: MPZ2021/340, one pygidium. Pico Noez, Totanés. Toledo: MPZ2021/337, one complete specimen, MPZ2021/338, one cephalon, MPZ2021/349, one pygidium. North Attleborough, Massachusetts: MCZ-IP-105035, MCZ-IP-114068, two cephalae, MCZ-IP-105034, one pygidium.

*Diagnosis (modified from Westrop & Landing 2011).* – *Serrodiscus* with subcylindrical to subconical glabella, three (rarely four) pairs of shallow glabellar furrows, non-transglabellar, directed backwards, shallowing frontally from S1 to S3. Occipital spine present. Pygidium has well-defined axial pygidial rings and evident axial nodes.

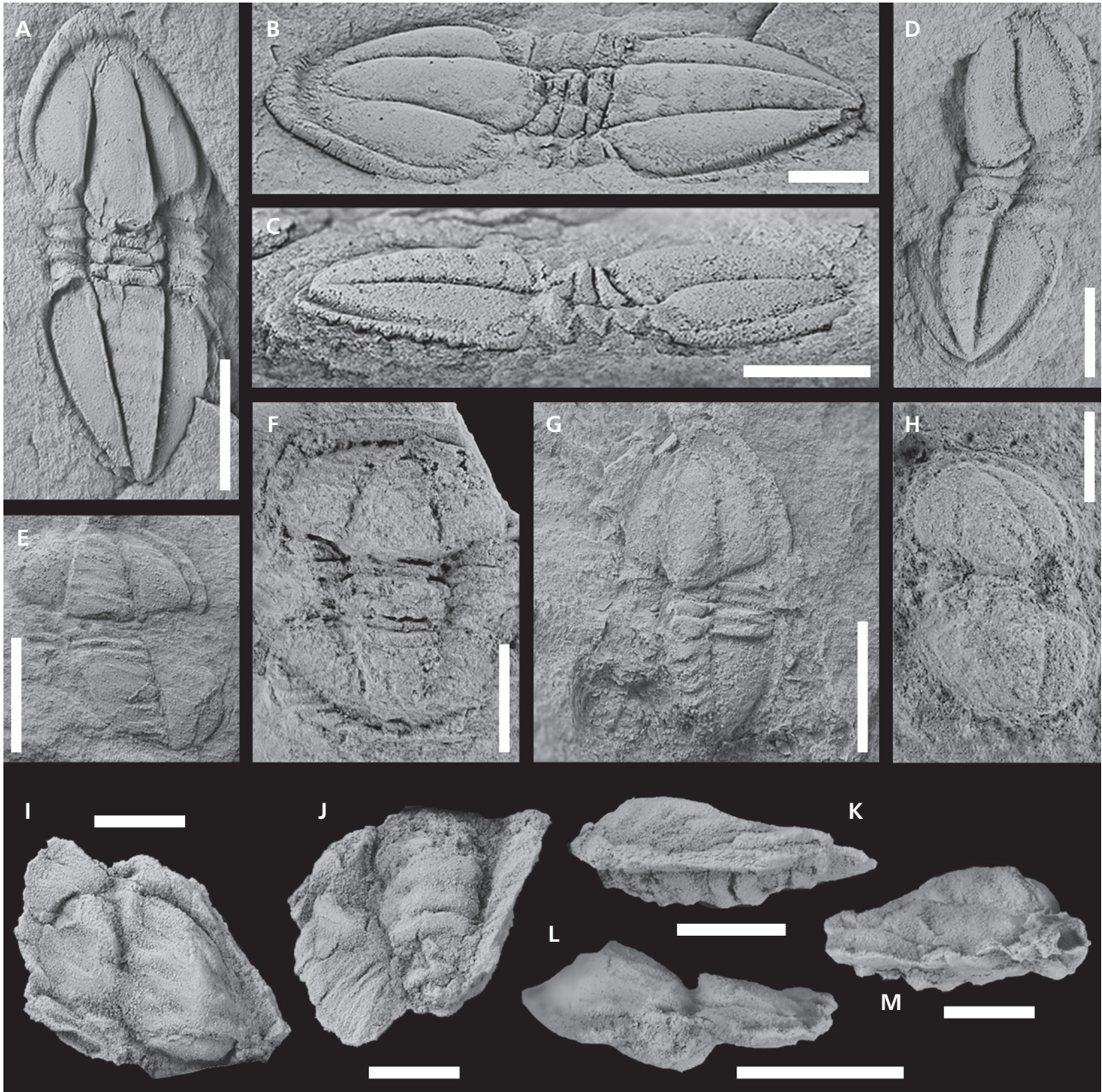
*Description.* – Semi-elliptic cephalon, semi-circular in smaller specimens (compare Figs 5 and 6), moderately convex in frontal and lateral views. Known cephalon range 1.7–14.4 mm in length and 1.3–16.2 mm in width. Anterior and lateral border continuous, about 10–15% cephalic sagittal length (including LO), convex, occasionally widened (sag.) frontally. Six to eight pairs of equally spaced nodes on the lateral border on the larger specimens (e.g. Fig 6P), being weak or absent in the smaller ones (e.g. Fig 5B). Smallest specimens bearing a pair of laterally projected tubercles (Fig. 5F, L, N, P) located opposite the frontal glabellar lobe. Border furrow is wide and moderately deep, occasionally widened at the front anterior furrow. The preglabellar area is narrow, shorter (sag.) than the

anterior border, but absent in some specimens where the preglabellar furrow merges with the border furrow (e.g. Fig. 5S; 6H, S, U; 9F) less than depressed. Preglabellar furrow, when present, is shallow to moderately deep. Glabella is subcylindrical to subconical in outline, convex (tr.), sloping forward, showing higher relief than the genae, tapered forward and widened posteriorly. Axial furrows are deep, moderately wide (tr.), more incised than the preglabellar furrow, being more parallel-sided in smaller specimens and convergent forwards in the bigger ones (Figs 5F, 6I). Glabella has about 80% cephalic sagittal length, including LO, and about 40% cephalic width (at the posterior border). There are three (rarely four) pairs of shallow glabellar furrows, non-transglabellar, directed backwards, shallowing frontally from S1 to S3, poorly defined to absent in smaller specimens (Figs 5R, 6Q). Glabellar lobes are poorly inflated, being L1 the longer (exsag.) and more pronounced. LA rounded to slightly tapered frontally, without individual convexity. Two specimens show a faint preoccipital glabellar tubercle opposite L2 (Fig. 6P, S). SO subtle, shallowing abaxially. LO convex, rectangular to trapezoidal, about 5% cephalic length (sag.), bearing a short occipital spine medially. Genae is domed, smooth and homogeneous. Posterior border continuous with lateral border, widening adaxially to posterior cephalic corner. Genal spines are small, rarely preserved, abaxially and posteriorly directed, located immediately anterior to the posterior cephalic corner (Fig. 6O, P).

Thorax is about 15% total sagittal length of the exoskeleton, composed of three equivalent thoracic segments. Rachis occupies about 40% of the total thoracic width, higher than the pleurae. Axial rings are narrow (sag.) and convex. Pleural furrow is subtriangular (narrowed abaxially), shallow, extending almost to the triangular pleural tips.

Subtriangular pygidium, moderately convex in frontal and lateral view. Known pygidium range 1.3–13.2 mm in length and 1.5–11.5 mm in width. The pygidial axis is conical, prominent, and convex (tr.), higher than the adjacent pleurae; length is about 90–95% total pygidial length, width about 30–35% anterior pygidial width. Small post-axial area occasionally absent. Nine well-differentiated pygidial axial rings plus one terminal piece. Axial rings bearing medial nodes, present on all the segments except the terminal piece, and getting smaller towards the back. Pygidial axial furrow is broad and deep. Pleurae are moderately convex, smooth and homogeneous. Border furrow is wide, deep and continuous. Anterior pleural border sloping posteriorly, narrowing abaxially, thus showing a subtriangular outline and articulating half-ring widened (sag.) medially, slightly arched anteriorly. The lateral border is continuous with the anterior one, convex and homogeneous posteriorly, bearing at least seven marginal spines, sometimes ventrally directed (Figs 7C–E; 9A, B).





**Figure 8.** *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888) in Shaler (1888), Cumbres beds, upper Marianian, Cumbres de San Bartolomé, Huelva (A–D, G, I–M); Herrerías shale, upper Marianian, El Pozuelo, Arroyomolinos de León, Huelva (E); Soleras Fm., upper Marianian, Pico Noez, Totanés, Toledo (F); La Hoya Mb., upper Marianian, Alconera Fm., Alconera, Badajoz (H). A – UHU–CSB100 (latex), dorsal view. B – UHU–CSB100 (latex), lateral view. C – UHU–CSB101 (latex), lateral view. D – UHU–CSB101 (latex), dorsal view. E – UHU–POZ100. F – MPZ2021/337. G – CSB190. H – MPZ2021/332. I – UHU–CSBsn, dorsal view. J – UHU–CSBsn, ventral view. K – UHU–CSBsn, lateral view (left), L – UHU–CSBsn, post-lateral view. M – UHU–CSBsn, lateral view (right). Scale bars: 5 mm (A, E), 2 mm (B–D, F–K, M), 3 mm (L).

**Remarks.** – The erection of *Serrodiscus serratus* by Richter & Richter (1941) was based on very poorly preserved material (Fig. 9A–H) and justified by characters such as the cephalic and pygidial outlines, which are undifferentiable from other species of the genus. When erecting this species from Huelva (Spain), Richter & Richter (1941) also erected *S. silesius* from Görlitz Synclinorium (Germany) and

documented *S. cf. speciosus* from both regions. However, the differences were doubtful (*e.g.* cephalic and pygidial outlines), having been discussed by Rasetti (1952) and Sdzuy (1962). Later, Geyer & Elicki (1995) considered the differences between *S. silesius* and *S. serratus* to be minimal, differentiating both species based on the number of lateral nodes on the cephalon and the frontal lobe of the

glabella reaching the anterior furrow in *S. serratus* (being here demonstrated to be unreliable; see taphonomical remarks).

For several decades, the knowledge of the type species of the genus, *S. serratus*, was very limited, especially in the details that could support an identity distinct from that of other well-documented species, such as *S. bellimarginatus* or *S. speciosus*. More recently, Westrop & Landing (2011), based on the very little available data of the Spanish and German material, considered that *S. s.l. serratus* shares with *S. s.l. "bellimarginatus"* can be differentiated by the conspicuous spinose nodes on a relatively narrower pygidial axis in the latter. Similarly, the total absence of nodes on the pygidial axial rings of *S. s.l. silesius* was pointed out by these authors to differentiate this other Richter & Richter (1941) species. As demonstrated above, based on a representative number of specimens coming from the same locality, the number, size and even the presence/absence of nodes on the axial rings are highly dependent on preservation. A few specimens show conspicuous nodes up to the posteriormost segment, which would probably be valid for all individuals. This character is entirely comparable to *S. bellimarginatus* pygidial rachis (compare Fig. 7N, O herein and Westrop & Landing 2011, figs 6, 7), and we must take into consideration the type of fossil-diagenesis product (moulds for *S. serratus* vs. mineralizations for *S. bellimarginatus*) that will result in different appearance of such exoskeleton structures. Similarly, there are no differences in the width of the pygidial rachis in the type-material of both species or in additional documented specimens (e.g. compare Fig. 7, Fig. 9K, L herein and Westrop & Landing 2011, fig. 7). Therefore, we consider Richter & Richter's (1941) material to be conspecific and a junior synonym of *S. bellimarginatus*, with which it shares all the stable and significant characters for the genus, namely the presence of an occipital spine, the glabellar structure, the range number of nodes on the cephalic border, the number and well-defined structure of the axial pygidial rings and the presence of evident axial nodes.

*Serrodiscus silesius*, another poorly documented and justified species, is here regarded as conspecific with *S. serratus* type-material, and therefore also a junior synonym of *S. bellimarginatus*. Geyer & Elicki (1995) had already considered the differences between *S. silesius* and *S. serratus* to be minimal, and those putative characters (the number of pygidial axial nodes and the glabellar frontal lobe configuration) were here demonstrated to be unreliable (see taphonomical remarks). Several works had previously reported specimens of *S. speciosus* from different localities of western Gondwana, including Iberia (e.g. Richter & Richter, 1941, pl. 1, figs 15, 16; see also Sdzuy 1961, 1962; Gil Cid 1981, 1986; Gil Cid *et al.* 2011) and Germany (e.g. Richter & Richter 1924, fig. 14

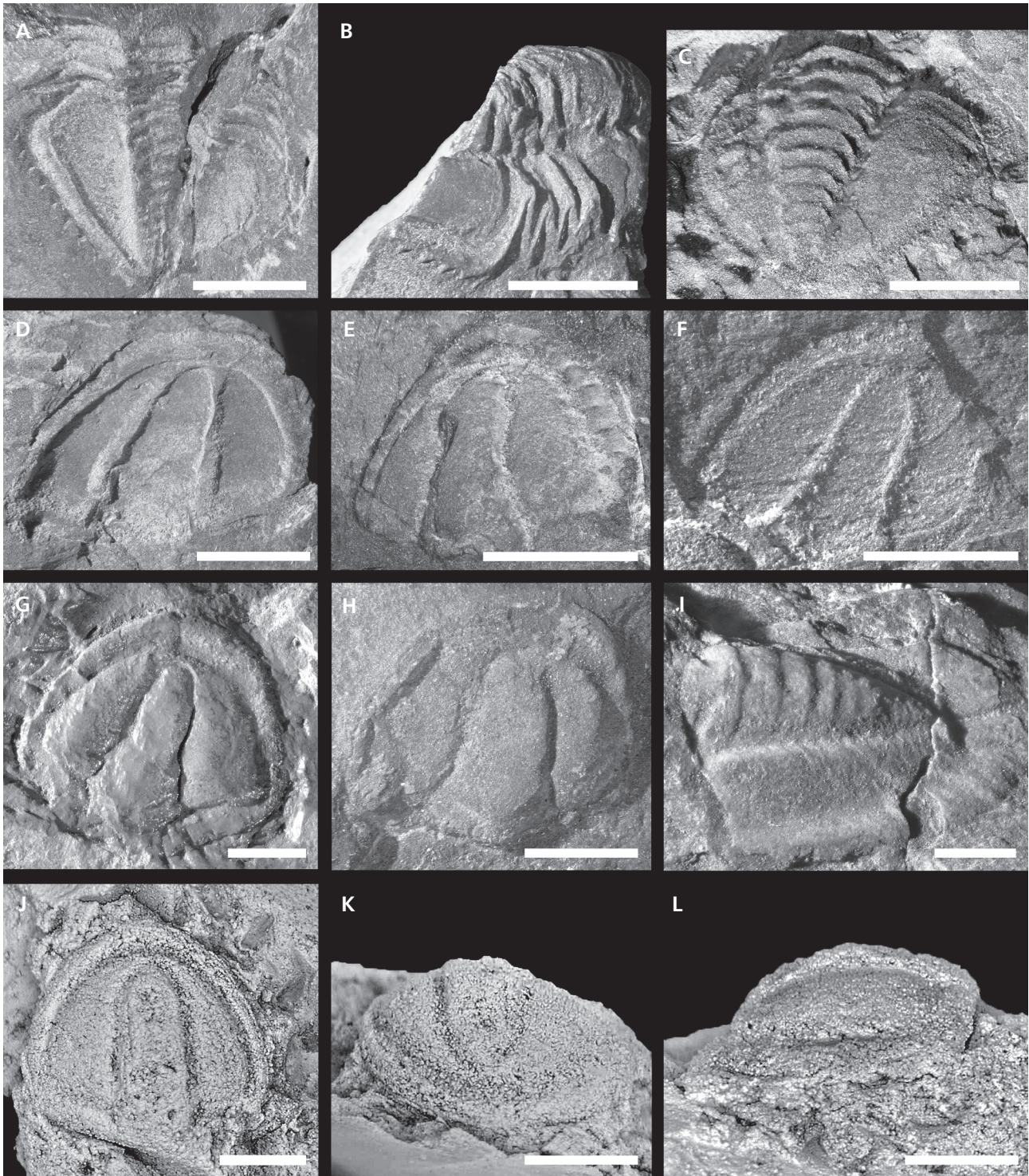
and 1941, pl. 1, figs 17–21; see also Schwarzbach 1932, 1934). Nonetheless, they bear occipital spine and pygidial axial nodes, both absent in *S. speciosus*, and they are entirely comparable to the remaining *Serrodiscus* occurrences from this domain. This way, we consider there is only one single species of *Serrodiscus* represented in the Western Gondwana region, which is here recognized as *S. bellimarginatus*.

Richter & Richter (1941) also described *Eodiscus (Eodiscus) llarenai* Richter & Richter, 1941, based on a fragmented cephalon and pygidium. After some different generic assignment proposals (e.g. Rushton 1966, p. 24; Soloviev 1964, p. 36), Öpik (1975) and Blaker & Peel (1997) transferred it to *Serrodiscus*. Herein we consider these specimens conspecific with the remaining Spanish material, merely deformed, generating artefactual characters used to diagnose that species. Another species we believe to be conspecific with the Spanish specimens, and thus also a junior synonym of *S. bellimarginatus*, is *S. coloi* Hupé, 1953a from the coeval Issafen Fm. of Morocco. Some specimens were figured and discussed by Geyer (1988, figs 55–58) and Geyer & Elicki (1995), who maintained *S. coloi* as valid, but the characters used to support this differentiation (e.g. shorter glabella, wider occipital ring, wider pre-glabellar area) were here demonstrated to be unreliable (see taphonomical remarks) and entirely comparable in Spanish and Moroccan types. Therefore, based on the previous considerations, *S. serratus*, *S. silesius*, *S. llarenai* and *S. coloi* are regarded as junior synonyms of *S. bellimarginatus*. There are no morphological differences that support the individualization of these species, so to keep them would be to maintain a geographic and lithostratigraphic systematics and not, as it should be, a morphological one.

Major & Winsnes (1955) reported *S. bellimarginatus* from Spitsbergen island (Norway). However, figured specimens (Major & Winsnes 1955, pl. 1, figs 6–9) do not show an occipital spine and bear very faint axial furrows on the pygidium, being, in our opinion, better classified as *S. speciosus*.

## Discussion

*Serrodiscus* encompasses a great diversity at the species level. Nonetheless, a part of the defined species is poorly documented. Those (and others) may be diagnosed based on characters highly dependent on taphonomy and deformation that seem to represent minor morphologic changes within an isolated *Serrodiscus* community. Even though direct analysis of existing material, it would be complicated to make synonymy decisions for several proposed species, as these are based on poorly preserved and very limited number of species. For this reason, and



**Figure 9.** A–H – type material of ‘*Serrodiscus serratus*’ Richter & Richter, 1941 [= *S. bellimarginatus* (Shaler & Foerste, 1888) in Shaler (1888)], Herrerías beds, upper Marianian, Minas de Cala, Huelva; A – SMF X 1234a-1, dorsal view; B – SMF X 1234a-3, dorsal view; C – SMF X 1234c-1, dorsal view; D – SMF X 1234h-1, dorsal view; E – SMF X 1234a-2, dorsal view; F – SMF X 1234h-2, dorsal view; G – SMF X 1234l-2, dorsal view; H – SMF X 1234e-1, dorsal view. • I – type material of ‘*Eodiscus llarenai*’ Richter & Richter, 1941 (= *S. bellimarginatus*), Herrerías beds, upper Marianian, Minas de Cala, Huelva, SMF X 1237a-1, lateral view. • J–L – type material of *S. bellimarginatus* (Shaler & Foerste, 1888) in Shaler (1888), Hoppin limestone, lower Cambrian, North Attleborough, Massachusetts, MCZ 105035. Scale bars: 5 mm (A–E, G–H), 2 mm (F–I), 1 mm (J–L). Credits: Robin Kunz, Senckenberg Museum (A–I) and Mark D. Renczkowski, Museum of Comparative Zoology (J–L).

in addition to comments regarding the validity of some taxa, the existing species will be tentatively grouped in different groups that seem to be more closely related, taking into account morphologic, stratigraphic and palaeobiogeographic data. Previously, Westrop & Landing (2011) conducted a phylogenetic analysis of *Serrodiscus* and related genera. The results are broadly consistent with our proposed groups, being the few differences justified by our inclusion of non-morphological data (namely stratigraphic and palaeobiogeographic provenance).

**Bellimarginatus group (Fig. 10A–E).** – This group includes *S. bellimarginatus* (with *S. serratus*, *S. silesius*, *S. llarenai* and *S. coloi* as junior synonyms) and *S. ctenoa*. The *bellimarginatus* group encompasses occurrences that come from a palaeogeographic area comprising western Gondwana (Germany, Spain, Morocco), eastern Avalonia (United Kingdom) and western Avalonia (Newfoundland).

Two of the most representative species of *Serrodiscus* are *S. speciosus* and *S. bellimarginatus* (see Westrop & Landing 2011). Among the differences pointed out by Westrop & Landing (2011), we consider the presence of an occipital spine, the relief of the axial rings furrows and the presence of (much more developed) axial nodes in the latter as reliable characters to differentiate both species.

Within the *bellimarginatus* group, but accepted as a different species, we also include *S. ctenoa* Rushton, 1966 from the Purley Shale of Warwickshire County (United Kingdom). However, this contrasts with the cladogram presented by Westrop & Landing (2011, fig. 3), in which *S. ctenoa* falls out of the clade that contains *S. speciosus* and *S. bellimarginatus*. This species comes from a horizon (2A in Rushton, 1966) stratigraphically above *S. bellimarginatus* (horizon 1B, op. cit). The main difference of *S. ctenoa* is the glabellar outline, being wider (tr.) frontally, almost clavate-shaped. A similar morphologic difference is present in *S. subclavatus* from the Shodack Fm., North Chatham (Columbia County, Georgia), which co-occurs with standard “tapered forwards” glabella forms (e.g. *S. spinulosus*). Thus, we regard this morphologic character as of minor importance within the genus, potentially developing in isolated communities, like other minor changes, as the presence/absence of occipital spines or more-or-less developed pygidial axial nodes/rings. As for the remaining characters that placed *S. ctenoa* distant from *S. bellimarginatus* and *S. speciosus* in Westrop & Landing (2011, fig. 3), the absence of a pre-glabellar area in the former is not definite. In type-material figured by Rushton (1966, pl. 1), a very short pre-glabellar area is present in some specimens, not very different from the one observed in *S. bellimarginatus* specimens (e.g. compare Rushton, 1966, pl. 1, figs 2a, 7c). Besides, as demonstrated for the set of Spanish specimens studied herein, several specimens do not show a preglabellar area and many other

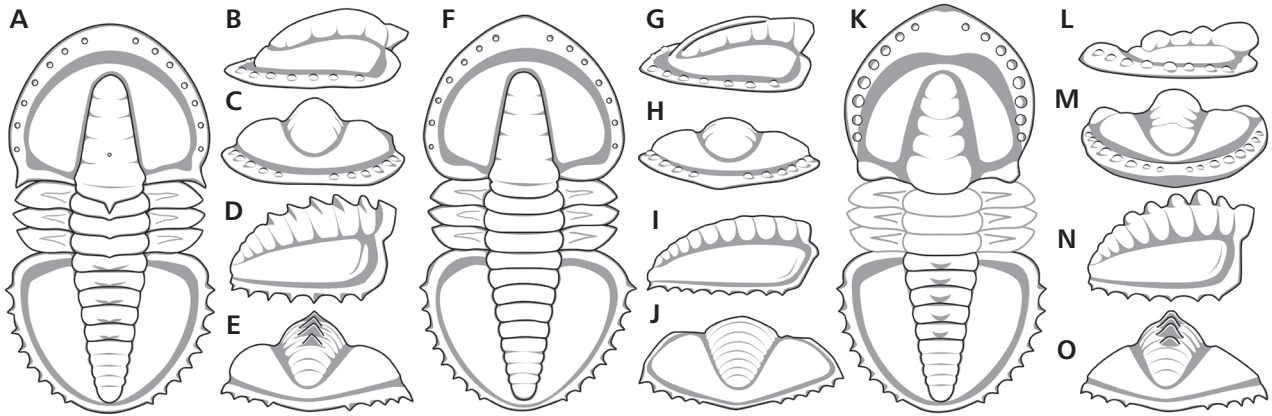
do, this structure preservation depends on taphonomy and/or intraspecific variability. Thus, this character alone does not seem to be significant within the genus. Apart from the glabellar outline, which has a specific value within the genus and was discussed above, there are no significant differences (with a supra-genus value) between *S. ctenoa* and *S. bellimarginatus* and *S. speciosus*.

**Speciosus group (Fig. 10F–J).** – This group includes *S. speciosus*, *S. mackenziensis*, *S. spinulosus*, *S. latus*, *S. subclavatus* and *S. griswoldi*, with a distribution restricted to the Laurentian domain (including the Laurentia craton, Greenland, Taconic Allochthon and Svalbard).

As previously discussed, *S. speciosus* do present significant differences compared to *S. bellimarginatus*, observed in well-preserved material (Westrop & Landing 2011), although both species are morphologically similar and, possibly, hard to differentiate if preserved as moulds. They probably belong to the same lineage within the genus. It is expected that several forms may present minimal variations, like those mentioned for the *bellimarginatus* group. Thus, a group of species with subtle morphologic differences but sharing stratigraphic and palaeogeographic provenance are herein grouped in *speciosus* group. This includes *S. mackenziensis* erected by Fritz (1973, pl. 1, fig. a, pl. 3, figs 1–17) from the Sekwi Fm., Mackenzie Mountains, which also lacks an occipital spine as *S. speciosus* but bears better developed axial nodes on the pygidium. The phylogenetic analysis presented by Westrop & Landing (2011, fig. 3) rendered *S. mackenziensis* closely related to both *S. speciosus* and *S. bellimarginatus*. Given *S. mackenziensis* palaeogeographic settings, it is herein grouped in *speciosus* group.

Additionally, four *Serrodiscus* species defined by Rasetti (1966, 1967), *S. spinulosus*, *S. latus*, *S. subclavatus* and *S. griswoldi*, herein grouped in the *speciosus* group. Rasetti’s species came all from the same locality and showed subtle morphologic variations, which may be due to taphonomic processes or deformation. Anyway, if they represent different species, they are likely to be closely related. The most distinctive of the four is *S. subclavatus*, which presents a clavate, almost eight-shaped glabella. Nevertheless, a similar morphologic variation was observed in stratigraphically successive species (*S. bellimarginatus* and *S. ctenoa*) from the Purley Shale of the Warwickshire County (Rushton 1966), supporting that it represents a simple modification within the genus. Finally, Blaker & Peel (1997) regarded ‘*S. levis*’ as conspecific with *S. speciosus* due to their similarity with the specimens from Nyeboe Land (Greenland), which statement is followed here.

**Daedalus group (Fig. 10K–O).** – This group includes *S. daedalus* Öpik, 1975, *S. fossuliferus* Repina, 1964 in



**Figure 10.** Schematic illustrations of the representative dorsal characters of the *Serrodiscus* groups. • A–E – *bellimarginatus* group; A – dorsal view; B – lateral view of the cephalon; C – frontal view of the cephalon; D – lateral view of the pygidium; E – posterior view of the pygidium. • F–J – *speciosus* group; F – dorsal view; G – lateral view of the cephalon; H – frontal view of the cephalon; I – lateral view of the pygidium; J – posterior view of the pygidium. • K–O – *daedalus* group; K – dorsal view; L – lateral view of the cephalon; M – frontal view of the cephalon; N – lateral view of the pygidium; O – posterior view of the pygidium. Credits: Bernat Vázquez.

Repina *et al.* (1964), *S. gravestocki* Jell, 1990 in Bengtson *et al.* (1990), and *S. areolus* Zhou, 1982 in Zhou *et al.* (1982). Representatives of the *daedalus* group are present in Australia, China, Siberia and Greenland.

The species *S. daedalus* was defined in the Cymbric Vale Fm. (New South Wales, Australia) and later reported by Blaker & Peel (1997) from the Aftenstjernesø Fm. (northern Nyeboe Land, northwestern Greenland). It differs from other *Serrodiscus* species in having a considerably wider (sag.) anterior border, an anterior furrow widened (sag.) medially, and a narrow (tr.), subconical glabella with pronounced glabellar segmentation. Öpik (1975) compared *S. daedalus* with *S. fossuliferus* from Altai Sayan Region, Siberia, distinguishing the Siberian species due to a narrower (sag.) cephalic border. Subsequently, Blaker & Peel (1997) presented a set of characters that differentiate *S. fossuliferus* and *S. daedalus*, with which we agree. On the other hand, *S. gravestocki* from the Oraparina Shale of South Australia is remarkably similar to *S. daedalus*. In this work, the grouping of these species is supported by Westrop & Landing's (2011, fig. 3) cladogram, representing *S. daedalus* and *S. gravestocki* as a separate monophyletic group. In addition, the strict consensus tree presented by Cotton & Fortey (2005) also supports this view, including *S. daedalus* and *S. gravestocki* in the same clade. Bengtson *et al.* (1990) considered the lack of marginal pygidial spines in *S. daedalus* the most remarkable difference. However, the figured pygidium of *S. daedalus* by Blaker & Peel (1997, fig. 25.8) from the Aftenstjernesø Fm. (North Greenland) shows fine marginal spines, and we cannot exclude the possibility of *S. daedalus* and *S. gravestocki* being conspecific.

Finally, *S. areolus* from northwestern Gansu Province, North China is here also nested with the *S. daedalus*, *S. gravestocki*, and *S. fossuliferus*, with which it

shares wide (sag. and tr.) anterior and lateral borders, a broad preglabellar area and strongly marked glabellar lobation. *S. areolus* is easily distinguished from other *Serrodiscus* species by its wider (sag.) preglabellar field, a large occipital and pygidial axial rings bearing prominent median spines or spine-like tubercles (see Bergström *et al.* 2014, fig. 3a–k).

*Unassigned species.* – Some poorly documented *Serrodiscus* species are impossible to relate to a particular group.

Four species included in this group were erected by Pokrovskaya (1959) from the lower Cambrian of the Tuva Republic, Siberia: *S. sibiricus* Pokrovskaya, 1959; *S.?* *granulatus* Pokrovskaya, 1959; *S. communis* Pokrovskaya, 1959 and *S. asiaticus* Pokrovskaya, 1959. Among these species, *S. sibiricus* (see Pokrovskaya, 1959, pl. 11, figs 2–4, 9, 21) was erected based on three complete specimens, one cephalothorax and a pygidium with the thorax partially preserved; *S. granulatus* was erected with a single pygidium (Pokrovskaya, 1959, pl. 11, fig. 18), while *S. communis* and *S. asiaticus* were not even figured in the original work; thus a trustworthy comparison with both species cannot be handled. Later on, Poletayeva (1960, pl. 1, figs 1–10) described two additional species of *Serrodiscus* also from the Tuva Republic: *S. pokrovskayae* Poletayeva, 1960 and *S. agnostoides* Poletayeva, 1960, the former represented by three poorly preserved cephalon and six pygidia (see also Repina & Romanenko 1978, pl. 1, figs 1–4) and the later based on solely two cephalon (see also Repina & Romanenko 1978, pl. 1, figs 4, 5). Another species, *S. murtucus* Repina, 1979, was described from Murtuk, eastern Sayan (Siberia) and was defined based on three specimens, only one being figured (Repina in Zhuravleva & Meshkova 1979, pl. 1, figs 1, 2). Finally, *S. conformis* Korobov, 1980 from

Prikhubsugulye (northern Mongolia) was defined based on four well-preserved cephalons (Korobov, 1980, pl. 9, figs 12–14), although its diagnosis lacks unambiguous characters (Korobov, 1980, p. 98).

The species *Serrodiscus primarius* Orłowski, 1985 from Kamieniec, Poland, is based on a single complete specimen initially assigned to *S. speciosus* by Samsonowicz (1962, fig. 6). Orłowski stated, “it differs from *S. speciosus* by a longer and parallel-sized glabella, nodes in the border in front of the glabella, and by smooth axial part of pygidium” (see Orłowski 1985, p. 249, pl. 3, fig. 1; Żylińska & Szczepanik 2009, pl. 1, fig. 9). Nevertheless, we do not think it is possible to differentiate it from other well-known *Serrodiscus* species (e.g. *S. speciosus*).

The established groups of *Serrodiscus* species, based primarily on morphology, present distinct palaeobiogeographic distributions (Fig. 4). The *speciosus* group is mainly restricted to the Laurentian domain. On the other hand, the *bellimarginatus* group is distributed between the eastern-western Avalonian sectors and the western peri-Gondwanan domains. Several works (e.g. Cocks & Torsvik 2006, Pouclet *et al.* 2007) argued that Avalonia was aggregated to the margin of West Gondwana, belonging to the same biochorema as Iberia, a peri-Gondwanan terrane located to the east of Avalonia (see Courjault-Radé *et al.* 1992). Previously, Álvaro *et al.* (2013) noted that the end of Cambrian Series 2 is characterized by new faunal links between Avalonia and West Gondwana, including *Serrodiscus* and other eodiscoid trilobites. The distribution of the *bellimarginatus*-group supports the strong faunal link between these regions.

From a biostratigraphic point of view, it is remarkable that the FAD of most species belonging to both *speciosus* and *bellimarginatus* groups approximately coincides with a tentative Cambrian Stage 4 lower boundary, with the exceptions of MacKenzie Mountains (Laurentia) (Fig. 3). Thus, it must be noted that the FAD of the species of *Serrodiscus* belonging to the *speciosus* and *bellimarginatus* groups may be reconsidered as a reliable candidate for the definition of this boundary, as previously suggested by other authors (e.g. Geyer & Shergold 2000, 2003).

The *daedalus* group has a broader distribution: although it characterizes present Australia (*S. daedalus* and *S. gravestocki*) and China (*S. areolus*), it also occurs in Siberia (*S. fossuliferus*) and Laurentia (*S. daedalus*). This group shows a certain disparity: regarding its biostratigraphic record occurrences from the Altai-Sayan region, it shows an earlier record than other *Serrodiscus* species. In China, they appear considerably later than the beginning of the Cambrian Stage 4 (Fig. 3). However, members of the *daedalus* group from Greenland and Australia depict a closer position to a tentative Cambrian Stage 4 lower boundary.

## Conclusions

*Serrodiscus* has been reported from several localities of the Ossa-Morena Zone, being present in distinct Cambrian ‘blocks’ (Cumbres, Herrerías, Arroyomolinos, Alconera, Viar, Benalija), and also in the Central Iberian Zone, at Pico Noez fossil site. Given the stratigraphic range of *Serrodiscus* from all the studied localities, the first occurrence of this trilobite is considered a reliable marker for the base of the upper Marianian in Iberia.

The Iberian occurrences of *Serrodiscus* have been re-assigned to *S. bellimarginatus*, being *S. serratus*, *S. silesius*, *S. llarenai* and *S. coloi* treated as junior synonyms of the former. The diagnosis of this species has been emended. In addition, and due to the morphologic variability of studied specimens from at the same locality and horizon, a taphonomic and deformational analysis has been carried out. Given the present problems regarding synonymies between different species, some of which are poorly known, *Serrodiscus* species are encompassed here into three groups considering morphologic, stratigraphic and palaeobiogeographic data. The three groups established are: *bellimarginatus* group, occupying Avalonian sector (Newfoundland, Massachusetts, United Kingdom) and western Gondwanan margin (Germany, Iberia, Morocco); *speciosus* group, occupying the Laurentian domain (including the Taconic Allochthon and Greenland); *daedalus* group, being restricted to Australia, North China and, partially, Siberia and Greenland.

*Serrodiscus* is widely distributed worldwide, being a potential candidate for the international correlation of the rocks belonging to the Cambrian Series 2, particularly the base of the Cambrian Stage 4. Along with this biostratigraphic range through the Cambrian Series 2, the palaeobiogeographic distribution of the genus extends over the Cambrian rocks of Laurentia, Taconic Allochthon, Greenland, Baltica, Siberia, western and eastern Avalonia, western Gondwana margin, Tarim basin, North China and Australia.

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