

On *Callavia* (Trilobita) from the Cambrian Series 2 of Iberia with systematic status of the genus

Luis Collantes,^{1,2} Sofia Pereira,¹ Eduardo Mayoral,^{2,3} Eladio Liñán,⁴ and Rodolfo Gozalo⁵

¹Centro de Geociências, Departamento de Ciências da Terra, Universidade de Coimbra, Rua Sílvio Lima, 3030-790 Coimbra, Portugal <luis.collantes.geo@gmail.com> <ardi_eu@hotmail.com>

²Departamento de Ciencias de la Tierra, Facultad de Ciencias Experimentales, Campus de El Carmen, Universidad de Huelva, Avda. 3 de Marzo, s/n, 21071 Huelva, Spain <mayoral@uhu.es>

³CCTH—Centro de Investigación Científico Tecnológico, Universidad de Huelva, Avda. 3 de Marzo, s/n, 21071 Huelva, Spain

⁴Departamento de Ciencias de la Tierra, Facultad de Ciencias, Instituto de Ciencias Ambientales (IUCA), Universidad de Zaragoza, 50009 Zaragoza, Spain <linan@unizar.es>

⁵Departamento de Botánica y Geología, Universitat de València, Dr. Moliner 50, 46100 Burjassot, Spain <rodolfo.gozalo@uv.es>

Abstract.—Olenellid trilobites from the lower Cambrian of the Iberian Peninsula are very scarce and poorly studied, making them difficult to compare with defined species and to include in biostratigraphic and paleobiogeographic analyses. Based on newly collected specimens, we revise the species ‘*Callavia? lotzei*’ Richter and Richter, 1941 from the ‘Cumbres beds’ of Cumbres de San Bartolomé and the ‘Herrerías shale’ of Cañaverol de León, Sierra del Bujó, and Hinojales (Huelva, Spain), and ‘*Paradoxides choffati*’ Delgado, 1904 from the Vila Boim Formation of Elvas (Portugal). The new material indicates that *Callavia? lotzei* is a junior synonym of ‘*P. choffati*.’ The Iberian species are here assigned to *Callavia* Matthew, 1897, for which morphological characters are reassessed, offering a valuable opportunity to discuss characters previously misinterpreted for this genus. Traditionally assigned to the Olenelloidea Walcott, 1890, *Callavia* lacks some of the diagnostic characters of this superfamily and is here assigned to Judomioidea Repina, 1979. A new diagnosis for this genus is provided, and *Sdzuyomia* Lieberman, 2001 is considered to represent a junior synonym of *Callavia*. The genus *Callavia* is distributed across the western margin of Gondwana, from the western Mediterranean region (Iberia and Morocco) throughout all the Avalonia sectors (UK, eastern Newfoundland, and Massachusetts). Its presence in Iberia supports the faunal links between the West Gondwana domain and Avalonia during Cambrian Series 2. The Iberian records of *Callavia choffati* are assigned to the middle part of the regional Marianian Stage (uppermost Cambrian Stage 3 to the lowermost Cambrian Stage 4) and correlates with the *Callavia* Biozone of Avalonia (lower Branchian Series).

Introduction

Classification of the order Redlichiida Richter, 1932 and its main representative groups is an old controversy (e.g., Richter, 1932; Harrington, 1959; Bergström, 1973) that found a satisfying, but not consensual, solution through Palmer and Repina’s (1993) proposal. Two suborders—Olenellina Walcott, 1890 and Redlichiina Richter, 1932—are recognized, the most conspicuous character separating the two being the lack of facial sutures in the former. Apart from this character, the phylogenetic value of which is arguable (see Jell, 2003), olenellines and redlichiines are morphologically very similar, including in their developmental stages (Whittington, 1989; Briggs and Fortey, 1992). Both Olenellina and Redlichiina are widely considered paraphyletic (e.g., Geyer, 1996; Fortey, 1997; Adrain, 2011).

Olenellina is considered the most primitive group in the Trilobita, being characteristic of the late early Cambrian of Laurentia (although some olenellids are now equivalent in age to the basal paradoxidids; Sundberg et al., 2016, 2020) and a minor component of the trilobite faunas of Siberia, Baltica, Avalonia, and West Gondwana (Palmer and Repina, 1993). Curiously,

olenellines are hitherto unknown from coeval sequences of eastern Gondwana. This suborder established the base of the lower Cambrian biostratigraphic subdivisions (see Palmer and Repina, 1993, 1997) and early Cambrian biogeography (Pillola, 1991; McKerrow et al., 1992). In addition, Olenellina has provided outstanding information about evolutionary trends (e.g., Fortey et al., 1996; Smith and Lieberman, 1999; Lieberman, 2002; Paterson and Edgecombe, 2006; Paterson et al., 2019) and adaptive strategies of the basal trilobite faunas (e.g., Ortega-Hernández et al., 2013).

Classification within Olenellina has also been historically controversial (see Palmer and Repina, 1993) and it is still problematic. The revision carried out by those authors and adopted in the Treatise on Invertebrate Paleontology (Palmer and Repina, 1997) considered two superfamilies: Olenelloidea Walcott, 1890 and Fallotaspidoidea Hupé, 1953. Considerably different from previous schemes (e.g., Bergström, 1973; Ahlberg et al., 1986), this classification was soon questioned by Geyer (1996) and modified by Lieberman (1998, 1999, 2001), who divided Olenellina into three superfamilies (Olenelloidea, Judomioidea Repina, 1979, and Nevadioidea Hupé, 1953) and

removed Fallotaspidoidea based on a phylogenetic analysis. Later works (e.g., Webster, 2007; Webster and Bohach, 2014; Webster and Landing, 2016) pointed out several coding errors in these analyses and criticized the methodology (e.g., absence of ontogenetic studies). A comprehensive cladistic analysis of Olenellina is currently in preparation by M. Webster (Webster and Hageman, 2018).

Olenelline trilobites are very rare in the lower Cambrian of the Iberian Peninsula and thus are poorly studied. Presently, only three species are described: *Paradoxides choffati* Delgado, 1904 from Vila Boim (Elvas, Portugal), *Callavia? lotzei* Richter and Richter, 1941 from Cañaverale de León (Huelva, Spain), and *Andalusiana cornuta* Sdzuy, 1961 from Guadalcanal (Seville, Spain). *Paradoxides choffati* was later transferred to *Callavia* Matthew, 1897 by Richter and Richter (1941) and Teixeira (1952). In contrast, Sdzuy (1962) established several similarities between *Callavia? lotzei* and the genus *Judomia* Lermontova, 1951 and Sdzuy (2001) transferred the former to the latter. Finally, Lieberman (2001) used *Callavia? lotzei* to erect the new genus *Sdzuyomia* Lieberman, 2001.

In the present paper, *Callavia? lotzei* and *Paradoxides choffati* are revised based on previously studied and new specimens from the Cumbres de San Bartolomé, Cañaverale de León, Sierra del Bujo, and Hinojales fossil sites and the type material from Vila Boim, respectively, to clarify their taxonomy, biostratigraphy, and paleobiogeography. The new data suggest that these taxa are conspecific and support the assignment of the Iberian species to *Callavia*. As a result, *Sdzuyomia* is herein considered a junior synonym of *Callavia*. The biogeographical implications of the new systematic data are discussed in the context of early Cambrian paleogeography.

Geological setting

The studied material came from the Vila Boim locality in the Elvas Municipality, southwestern Portugal (type locality of *Paradoxides choffati*), and from four municipalities in northern Huelva province, southwestern Spain: Cumbres de San Bartolomé, Cañaverale de León (type locality of *Callavia? lotzei*), Arroyomolinos de León (Sierra de El Bujo), and Hinojales. These fossil localities are located in the Ossa-Morena Zone in the southern branch of the Iberian Massif, which comprises a lithostratigraphic sequence ranging in age from terminal Proterozoic to the Carboniferous, with a general structure of large, recumbent folds verging to the southwest (Azor, 2004). Cambrian outcrops of the Ossa-Morena Zone are divided into tectosedimentary units classically called sectors in Portugal (Oliveira et al., 1991) and ‘Cubetas’ in Spain, which correspond to ancient sedimentary basins limited and controlled by faults according to Liñán and Quesada (1990). The Portuguese locality is located in the Alter do Chão-Elvas sector and the Spanish outcrops in the Cumbres and Herrerías ‘Cubetas,’ representing the southwesternmost fossiliferous units in lower Cambrian times for Iberia (Fig. 1.1).

The Vila Boim fossil site is a classical outcrop at Monte Valbom (Fig. 1.2), first published by Delgado (1904) and located in the lower part of the Vila Boim Formation, a 600 m thick succession composed of shales, quartzites, and graywackes with some interbedded rhyolite and basalt levels (Mata, 1986) (Fig. 1.3). All specimens originate from a narrow

lenticular horizon of blue-gray shales with iron oxides, bearing two 15 cm thick fossiliferous levels separated by 1 m, located ~170 m from the base of the Vila Boim Formation. *Callavia choffati* is rare in the fossil assemblage, which is dominated by the trilobites *Hicksia elvensis* Delgado, 1904 and *Delgadella souzai* (Delgado, 1904), with fewer brachiopods, hyolithids, and bivalves (see Delgado, 1904; Teixeira, 1952). According to Liñán et al. (2004), this fossil assemblage suggests a middle Marianian age (ca. 515 Ma). The fossiliferous section is located at 38°52′2″N, 007°17′31″W.

The fossil levels from the Cumbres de San Bartolomé section belong to the ‘Alternancia de Cumbres’ (Cumbres beds), an informal lithostratigraphic unit composed of a succession of shale and sandstone of very variable thickness (350–1,100 m). The specimens studied herein were recorded from the lower levels (Fig. 1.4), together with the trilobites *Atops calanus* Richter and Richter, 1941 and *Delgadella souzai*, considered middle Marianian in age. A second level, 400 m above the former, contained a more diverse upper Marianian trilobite assemblage (Collantes et al., 2021). The base and top of the section are located at 38°03′16″N, 006°43′00″W and 38°03′14″N, 006°42′58″W, respectively.

The sections outcropping in Sierra del Bujo (Richter and Richter, 1941), Hinojales (Liñán and Mergl, 1982), and the Cañaverale de León fossil sites represent equivalent stratigraphic levels assigned to the unit ‘Pizarras de Herrerías’ (Herrerías shale), characterized by purple shales with spilitic intercalations within a sequence 200–600 m thick (Fig. 1.5). This unit ranges from the middle to upper Marianian, indicated by the presence of trilobites *Rinconia-Ellipsostrœna* in the lower levels and *Serrodiscus-Triangulaspis* in the upper levels. Sierra del Bujo section is located between 38°00′39″N, 006°27′34″W and 38°00′39″N, 006°27′38″W; Hinojales section is located between 38°00′26″N, 006°35′08″W and 38°00′24″N, 006°35′06″W; and Cañaverale de León section is located between 38°01′05″N, 006°32′23″W and 38°01′02″N, 006°32′28″W.

Materials and methods

Available material consists mainly of isolated cephalae preserved as internal or external molds, with isolated pygidia and one mostly complete, articulated exoskeleton. Specimens preserved in shales are often flattened and distorted, whereas those preserved in sandstones retain some original convexity. Specimens from Portugal were collected by the end of the nineteenth century and previously figured by Delgado (1904) and Teixeira (1952), whereas samples from Huelva, Spain, were collected in several campaigns from 1985 to the present by the authors; these have intensified since 2018.

Specimens were prepared using a pneumatic hammer, coated with ammonium chloride, and photographed using a Canon EOS 77D coupled with a Canon 100 mm f/2.8L macro lens. Terminology follows that of the revised Treatise on Invertebrate Paleontology (Palmer and Repina, 1997).

Abbreviations used in the text are: exsag. = exsagittal; L1, L2, etc. = glabellar lobes; LA = frontal lobe; LO = occipital lobe; S1, S2, etc. = glabellar furrows; sag. = sagittal; SO = occipital furrow; tr. = transversa; v = specimens have been visited in their collection and seen in person; * = type species.

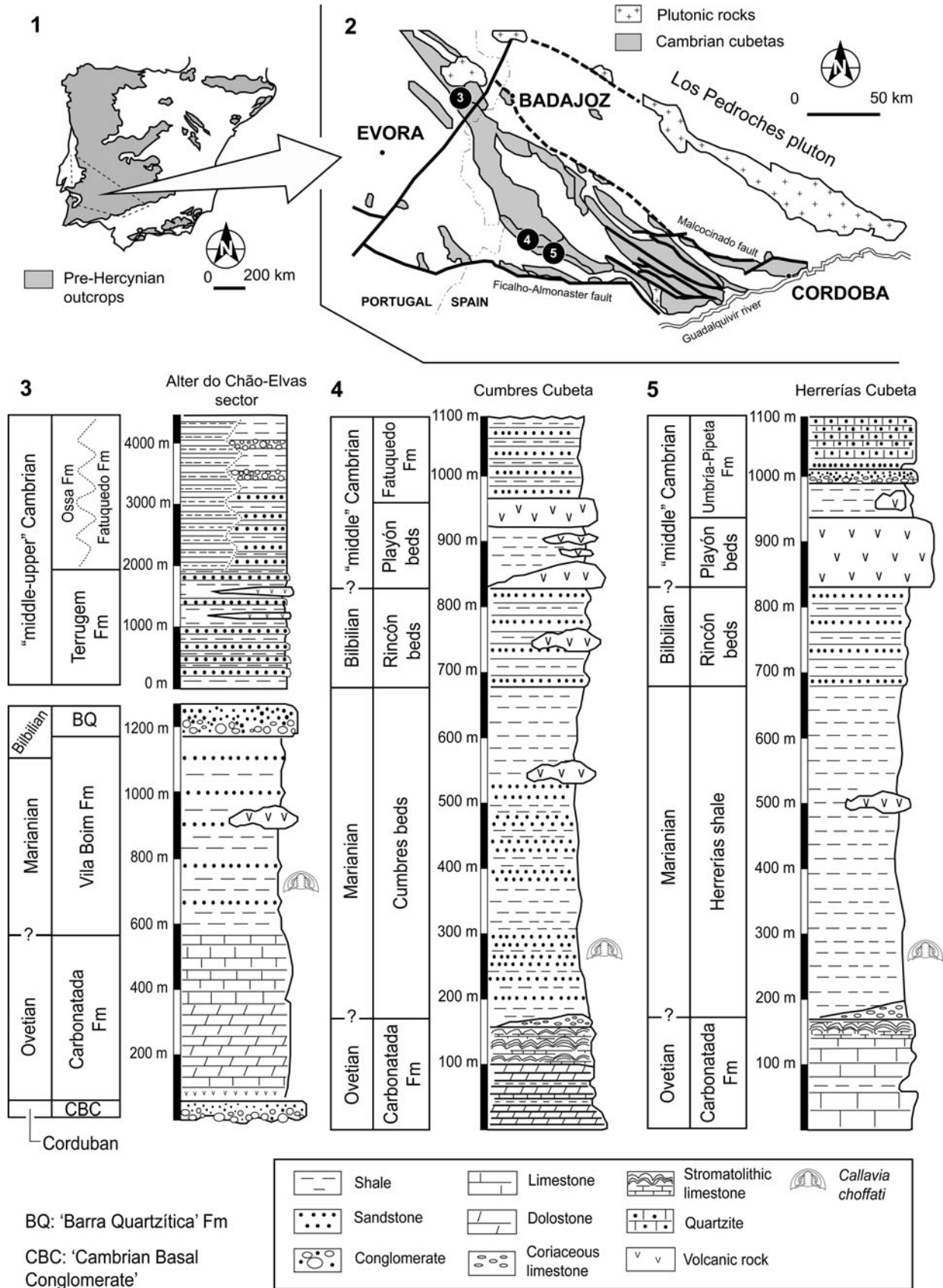


Figure 1. (1) Pre-Hercynian outcrops in the Iberian Peninsula. (2) Geological setting of fossil sites in the Cambrian sectors (fault-bounded blocks) of the Ossa-Morena Zone, indicating the position of the studied fossil sites (modified from Liñán and Quesada, 1990). (3) Stratigraphic column of the Alter do Chão–Elvas sector (modified from Liñán et al., 2004). (4) Stratigraphic column of the Cumbres ‘cubeta’ (after Collantes et al., 2020). (5) Stratigraphic column of the Herrerías ‘cubeta’ (after Collantes et al., 2020).

Table 1. List of taxa previously assigned to *Callavia* Matthew, 1897 and their currently accepted generic assignment. Notes: 1—Fletcher and Theokritoff (2008) regarded *Callavia broeggeri* (Walcott, 1890) and *Callavia crosbyi* (Walcott, 1890) as different species; 2—Lieberman (1999) considered *Paedeumias* Walcott, 1910 a junior synonym of *Olenellus* Hall, 1862. Webster (personal communication, 2021) regarded *Paedeumias breviloba* Poulsen, 1927 as an indeterminate olenelline species.

Original designation	Current designation	Reference
<i>Olenellus (Mesonacis) broeggeri</i> Walcott, 1890	<i>Callavia broeggeri</i> (Walcott, 1890)	Matthew (1897)
<i>Callavia callavei</i> (Lapworth, 1891)	<i>Callavia callavei</i> (Lapworth, 1891)	Landing et al. (2013b)
<i>Paradoxides choffati</i> Delgado, 1904	<i>Callavia choffati</i> (Delgado, 1904)	Teixeira (1952)
<i>Callavia crosbyi</i> Walcott, 1910 ¹	<i>Callavia broeggeri</i> (Walcott, 1890)	Lieberman (2001)
<i>Callavia burri</i> Walcott, 1910	<i>Nevadella burri</i> (Walcott, 1910)	Westrop and Landing (2011)
<i>Callavia cartlandi</i> Raw in Walcott, 1910	<i>Nevadella cartlandi</i> (Raw in Walcott, 1910)	Lieberman (2001)
<i>Callavia? nevadensis</i> Walcott, 1910	<i>Olenellus nevadensis</i> (Walcott, 1910)	Lieberman (1999)
<i>Callavia bicensis</i> Walcott, 1910	<i>Elliptocephala walcotti</i> (Shaler and Foerste, 1888)	Fletcher and Theokritoff (2008)
<i>Callavia perfecta</i> Walcott, 1913	<i>Nevadella perfecta</i> (Walcott, 1913)	Raw (1936)
<i>Callavia eucharis</i> Walcott, 1913	<i>Nevadella eucharis</i> (Walcott, 1913)	Raw (1936)
<i>Callavia breviloba</i> Poulsen, 1927	<i>Paedeumias breviloba</i> (Poulsen, 1927) ²	Cowie (1971)
<i>Callavia cobboldi</i> Raw, 1936	<i>Nevadella cartlandi</i> (Raw in Walcott, 1910)	Lieberman (2001)
<i>Callavia hastata</i> Raw, 1936	<i>Callavia callavei</i> (Lapworth, 1891)	Lieberman (2001)
<i>Callavia? brevioculata</i> Raw, 1936	<i>Nevadella cartlandi</i> (Raw in Walcott, 1910)	Lieberman (2001)
<i>Callavia? lotzei</i> Richter and Richter, 1941	<i>Callavia choffati</i> (Delgado, 1904)	This work

Repositories and institutional abbreviations.—Figured specimens are housed in the Department of Earth Sciences (Laboratory of Tectonics and Paleontology) of the Faculty of Experimental Sciences, University of Huelva, Spain (UHU) and in the Museu Geológico de Lisboa, Lisbon, Portugal (MG).

Systematic paleontology

Class Trilobita Walch, 1771

Order Redlichiida Richter, 1932

Suborder Olenellina Walcott, 1890

Superfamily ‘Judomioidea’ Repina, 1979 (sensu Lieberman, 2001)

Remarks.—The systematic position of *Callavia* has been controversial. Although most authors have nested it with members of Holmiidae Hupé, 1953 (e.g., Harrington, 1959; Chernysheva, 1960; Repina, 1979), Bergström (1973) included Callaviinae Poulsen in Harrington, 1959 in Daguinaspididae Hupé, 1953 and Ahlberg et al. (1986) preferred to treat it as an independent family, not related to holmiinids. Following the most consensual assignment, Palmer and Repina (1993, 1997) maintained Callaviinae within Holmiidae, thus including *Callavia* within the superfamily Olenelloidea. Nevertheless, they assigned the family Judomiidae, morphologically similar to callaviinines, to the superfamily Fallotaspidoidea, revealing an inadequacy of this proposal for these taxa. In fact, following the concept of Palmer and Repina (1993), *Callavia* cannot be included within Olenelloidea, and, consequently, in Holmiidae, because it lacks some of the diagnostic characters of the superfamily (frontal lobe [LA] enlarged and ocular lobe connected only to posterolateral part of LA, both absent in *Callavia*) and of the family (extraocular area [tr.] wider than twice the width of the interocular area, unlike in all holmiids). This was also stated by Lieberman (1998, 1999, 2001), who treated *Callavia* and a group of ‘fallotaspidooids’ (sensu Palmer and Repina, 1993) as representing an independent taxon of superfamilial rank, the Judomioidea (not Nevadioidea, as mistakenly considered by Fletcher and Theokritoff, 2008).

One of the *Callavia* morphological characters that was misinterpreted by Palmer and Repina (1993) and that were used to

justify previous assignments to Olenelloidea/Holmiidae, is the relation between the ocular lobe and the LA. This relationship was considered the principal phylogenetic trend within the Olenellina by Palmer and Repina (1993), with the earliest representatives having a glabella that is parallel-sided or tapering forward and an ocular lobe that is attached along the entire margin of the LA. *Callavia* shows this condition (see remarks on the genus). Nevertheless, it has been previously described as though the LA becomes inflated and expanded laterally and the ocular lobes connect only to its posterior part (like in Olenellidae and Holmiidae). Despite several errors in Lieberman’s (1998, 1999, 2001) phylogenetic analyses (e.g., Webster, 2007, 2009), and the very limited and unrepresentative number of species coded, we herein prefer to assign *Callavia* to the (questionably monophyletic) ‘Judomioidea’ (sensu Lieberman, 2001) instead of Olenelloidea, and we avoid family assignment within it.

Genus *Callavia* Matthew, 1897

Type species.—*Olenellus (Mesonacis) broeggeri* Walcott, 1890 from the Brigus Formation, Branchian Series (Cambrian Stage 3/4), Newfoundland, Canada.

Other species.—*Olenellus (Holmia) callavei* Lapworth, 1891 from the Comley Limestone Formation, Branchian Series (Cambrian Series 2), Shropshire, UK; *Paradoxides choffati* Delgado, 1904 from the lower part of the Vila Boim Formation, Marianian (Cambrian Series 2), Vila Boim, Portugal (see Table 1).

Emended diagnosis.—Posterior margin and posterior furrow of cephalon curved forward; base of genal spine lying slightly posterior to lateral margins of LO; genal spine broad-based; intergenal spine present, prominent to reduced; cephalic border developed as rounded ridge; anterior and lateral border furrows broad and deep; long tropidium-like structure extending across the lateral and anterior border furrows. Glabella subcylindrical, slightly tapered anteriorly; LA not contacting anterior border furrow, surrounded by a weak parafrenal band; LA not enlarged; preglabellar field very short, almost indistinct; occipital furrow (SO) not conjoined

medially; occipital spine present; four preoccipital glabellar furrows (L1–L4) shallowing anteriorly, nontransglabellar, straight to slightly obliquely backward, when followed adaxially. Ocular lobe prominent; inner margin differentiated from a broad interocular area; extraocular area slightly narrower to slightly wider (tr.) than interocular area opposite S1; posterior tip of ocular lobe opposite SO. Intergenal ridge and posterior ocular line subparallel to converging toward the intergenal spine/swelling. Sculpture of reticulated pattern on external surface and terrace ridges along the abaxial limit of the anterior border.

Remarks.—*Callavia* is one of those genera for which previous documentation and assigned species strongly exceed its currently accepted diversity (Table 1). In its most recent concepts, *Callavia* is extremely poorly diverse, ranging from monotypic (Lieberman, 2001) to including only two species (e.g., Landing et al., 2013b). Although describing *Callavia* as “the principal genus of the Olenellina from Avalonia,” Palmer and Repina (1993, p. 14) considered a greater species diversity. This could also have led these authors to diagnose *Callavia* with characters that are not present in the type species, *Callavia broeggeri*. In fact, the figured material of this species is quite limited (Grabau, 1900; Walcott, 1910; Hutchinson, 1962; Landing et al., 1980; Palmer and Repina, 1993; Lieberman, 2001; Fletcher, 2006), being mostly deformed or fragmented, including the type material (as stated by Hutchinson, 1962, p. 119).

In our opinion, several morphological characters have been misinterpreted: (1) presence or absence of the preglabellar field, (2) the tropidium-like ridge, and (3) the parafrontal band. Palmer and Repina (1993) and Lieberman (2001) considered a preglabellar field as absent, with the frontal lobe directly contacting the anterior border furrow. Nevertheless, several illustrations of type and other material of *Callavia broeggeri* (and its possible junior synonym *Callavia crosbyi* Walcott, 1910) by Walcott (1890, pl. 91, fig. 1, pl. 92, fig. 1, 1g; 1910, pl. 27, figs. 1, 4, pl. 28, fig. 4), as well as other figured specimens (e.g., Hutchinson, 1962, pl. 24, figs. 8–11; Palmer and Repina, 1993, fig. 6.8), clearly show a short but defined preglabellar field. One of the features that had contributed to this misinterpretation is the presence of a tropidium-like structure (e.g., Walcott, 1890, pl. 92, fig. 1b; 1910, pl. 28, figs. 1, 4; Hutchinson, 1962, pl. 24, figs. 7b, 8, 9; Palmer and Repina, 1993, fig. 6.8; Lieberman, 2001, fig. 2.1) that is adaxial to the true anterior border furrow. Furthermore, and as previously stated by Fletcher and Theokritoff (2008), a weak parafrontal band is present around the LA margins (e.g., Walcott, 1910, pl. 28, figs. 1, 4; Hutchinson, 1962, fig. 7a; Palmer and Repina, 1993, fig. 6.8), a character that led previous authors to consider the preglabellar field as absent in *Callavia broeggeri*. The parafrontal band is also observed in *Callavia callavei* (already stated by Lake, 1937) and *Callavia choffati* (being clear only in better preserved specimens).

The parafrontal band was also described by Walcott (1910), who erected the new species *Callavia crosbyi* based on this character, among others. We agree with Lieberman (2001) who considered *Callavia crosbyi* as a junior synonym of *Callavia broeggeri*. Fletcher and Theokritoff (2008) argued that *Callavia*

crosbyi is a valid species, differing from *Callavia broeggeri* in having a much narrower (tr.) extraocular area and a distinct pygidium and posteriormost thoracic segments. Nevertheless, the only *Callavia crosbyi* specimen preserving the thorax and the pygidium (Fletcher and Theokritoff, 2008, fig. 5.16) shows an extraocular area proportionally similar to that of *Callavia broeggeri*.

Another misinterpreted character of *Callavia broeggeri* is the morphology of S1, which Lieberman (2001) considered conjoined medially and different from the condition observed in *Callavia callavei*. Based on this difference, he erected the new monotypic genus *Callavalonia* Lieberman, 2001 for this latter species. Although the glabellar segmentation of *Callavia callavei* and *Callavia broeggeri* present some differences, namely the glabellar furrows are apparently more deeply incised and the anteriormost furrows longer (tr.) in the former, it is not possible to assure that S1 is conjoined medially in *Callavia broeggeri*. Fletcher and Theokritoff (2008) also considered this character to be unrecognizable. In the studied material of *Callavia choffati*, the collapse due to the flattening of the glabella in some specimens created an artifact, with S0 or S1 appearing conjoined medially (e.g., Fig. 2.1, 2.5). Nevertheless, in specimens preserving glabellar convexity, either in *Callavia choffati* (e.g., Fig. 3.5, 3.16) or in *Callavia broeggeri* (see Palmer and Repina, 1993, fig. 6.8), it is clear that they are not transglabellar.

Lieberman (2001) also differentiated *Callavalonia* from *Callavia* by the relative width of the thoracic pleural furrow, which he considered to extend approximately two-thirds of the width of the inner pleural region in *Callavia callavei*, being longer (tr.; approximately four-fifths) in *Callavia broeggeri*. This character seems to be dependent on the thoracic segment number as well as on preservation. On a complete specimen of *Callavia choffati* (Fig. 4.1), it is possible to verify pleural furrows extending to different widths of the inner pleura (e.g., compare the first, second, third, and sixth segments). On the other hand, complete specimens of *Callavia broeggeri* (see Palmer and Repina, 1993, fig. 6.5) show a pleural furrow extension similar to that of *Callavia callavei* (occupying only two-thirds of the inner pleura). For these reasons, we agree with Jell and Adrain (2002), Fletcher (2006), Fletcher and Theokritoff (2008), and Landing et al. (2013b), who treated *Callavalonia* as a junior synonym of *Callavia*. Nevertheless, we do not concur with Fletcher (2006) and Fletcher and Theokritoff (2008), who treated *Callavia broeggeri* and *Callavia callavei* as synonyms. Landing et al. (2013b) criticized this synonymy based on different eye-lobe positions, and we add cephalic segmentation to the list of differences between the two species.

Lieberman (2001) erected *Sdzuyomia* as a monotypic genus represented by *Callavia? lotzei* (herein revised). We consider *Callavia? lotzei* a junior synonym of *Paradoxides choffati* (see remarks on species) and assign it to the genus *Callavia*. Consequently, *Sdzuyomia* is treated as a junior synonym of *Callavia*. Lieberman (2001) carried out a phylogenetic analysis of the suborder Olenellina and erected the genus *Sdzuyomia* to incorporate solely the type species *Callavia? lotzei*, grouping it within the superfamily Judomioidea with *Callavalonia* (= *Callavia*), *Bondonella* Hupé, 1953, *Neltmeria* Hupé, 1953, *Callavia*, and *Judomia*. Based on the new specimens from the Cumbres de San Bartolomé, Cañaveral de León, Sierra del Bujo, and Hinojales



Figure 2. *Callavia choffati* (Delgado, 1904), Vila Boim Formation, middle Marianian, Vila Boim, Portugal: (1) MG 15781, lectotype; (2) MG 15782a, paralectotype; (3, 4) MG sn, paralectotype (latex): (3) dorsal view; (4) detail of terrace lines of the lateral cephalic border; (5) MG 15786, paralectotype; (6) MG 16684 (latex). Scale bars = 2 mm (4); 10 mm (1–3, 5, 6).

fossil sites, it is possible to verify that Lieberman's (2001) erection of *Sdzuyomia* was based on miscoded characters in both the Spanish species and *Callavia broeggeri*. Among other characters, he considered the intergenal spines as absent in *Sdzuyomia* (character 39) and that in *Callavia*, the LA contacts the anterior furrow (character 5), the S1 is conjoined medially (character 30), and the thoracic pleural furrows occupy almost all of the inner pleural region (character 51). In our opinion, these characters were misinterpreted by both Lieberman (2001) and Palmer and Repina (1993). We do consider *Callavia broeggeri*, *Callavia callavei*, and *Callavia choffati* to be comparable in most of the significant olenelline features (cephalic outline, border structure, position and configuration of the ocular lobes and their relationship with the glabella, presence and position of the intergenal spines, glabellar outline and lobation, and thoracic structure). As Geyer (2007) argued, the establishment of *Sdzuyomia* by Lieberman (2001) was premature, especially because to that date the known material of '*Callavia? lotzei*' was poorly preserved and very limited. Currently, and with better knowledge of this Iberian species, we reinforce its assignment to *Callavia*.

Previous generic assignment of Spanish material ('*Callavia? lotzei*' = *Callavia choffati*) to the genus *Judomia* by Sdzuy (2001) is here rejected. After comparison with figured material from Siberia (Khomentovskii and Repina, 1965; Repina et al., 1974; Korobov, 1989; Pegel, 2000; Ponomarenko, 2005; Rozanov and Varlamov, 2008) and Laurentia (Fritz, 1973; McMenamin, 1987; Gapp et al., 2011), we do not agree that

Callavia choffati mainly differs from *Judomia* in ocular structure. The ocular lobes in *Judomia* are located very close to the glabella, thus the interocular area is almost absent. Furthermore, the inner margin of the ocular lobe is undifferentiated or only weakly differentiated from the interocular area in *Judomia*, which is a very narrow (tr.), depressed area (e.g., *J. granulata* Repina in Repina et al., 1974, *J. mattajensis* Lazarenko, 1962, *J. tera* Lazarenko in Kryskov et al., 1960, and *J. rasskasovae* Korobov, 1963 as figured by Repina et al., 1974, pls. 27, 28). On the contrary, in *Callavia*, the interocular area is broad and inflated, almost the same width as the extraocular area opposite S1, and the inner margin of the ocular lobes is well differentiated from it. Other characters are the straight and deep posterior border furrow in *Judomia* (e.g., *J. tera* by Repina et al., 1974, pl. 28, fig. 1; Palmer and Repina, 1993, fig. 10.7), being faint and curved forward in *Callavia* due to a prominent intergenal ridge; and the posteriormost LA in direct contact with the ocular lobes in *Judomia* (e.g., *J. rasskasovae* as figured by Repina et al., 1974, pl. 27, fig. 9). Other putative differences based on Palmer and Repina's (1993) diagnosis of *Judomia* (e.g., the absence of intergenal spines) are not considered herein because some *Judomia* species do bear tiny intergenal spines very similar to those observed in *Callavia choffati* (e.g., *J. rasskasovae* as figured by Repina et al., 1974, pl. 27, fig. 4.5), although in a more proximal position (adaxial to the adgenal angle). Even though we do not agree with Sdzuy's (2001) assignment of '*Callavia? lotzei*' to the genus *Judomia*, we do recognize several characters in common, not only in cephalic morphology

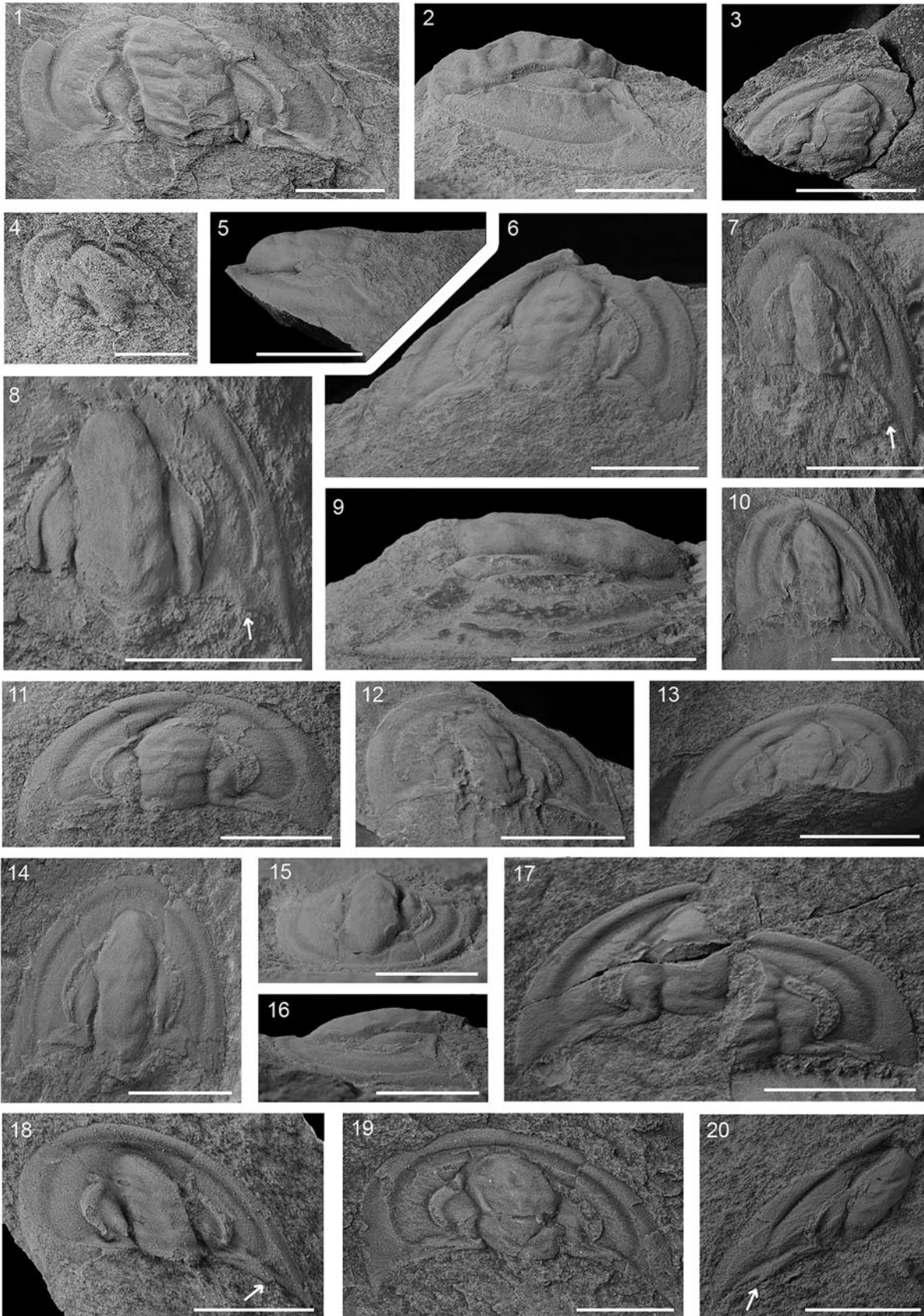


Figure 3. *Callavia hoffati* (Delgado, 1904), ‘Herrerías shale,’ middle Marianian, Cañaverl de León (1–13, 15–20) and ‘Cumbres beds,’ middle Marianian, Cumbres de San Bartolomé (14), Spain: (1, 2) UHU-CVL 01: (1) dorsal view; (2) lateral view; (3) UHU-CVL 03; (4) UHU-CVL 05; (5, 6) UHU-CVL 09: (5) lateral view; (6) dorsal view; (7) UHU-CU 1/1/1; (8, 9) UHU-CVL 12: (8) dorsal view; (9) lateral view; (10) UHU-CVL 10; (11) UHU-CVL 17 (latex); (12) UHU-CVL 20; (13) UHU-CVL 40; (14–16) UHU-CVL 32: (14) dorsal view; (15) frontal view; (16) dorsal view; (17) UHU-CVL 29; (18) UHU-CVL 42 (latex); (19) UHU-CVL 46; (20) UHU-CVL 48. Scale bars = 2 mm (4); 5 mm (6, 7, 11, 13–16, 18); 10 mm (1–3, 5, 8–10, 12, 17). Arrows in 7, 8, 18, and 20 indicate intergenal spines.

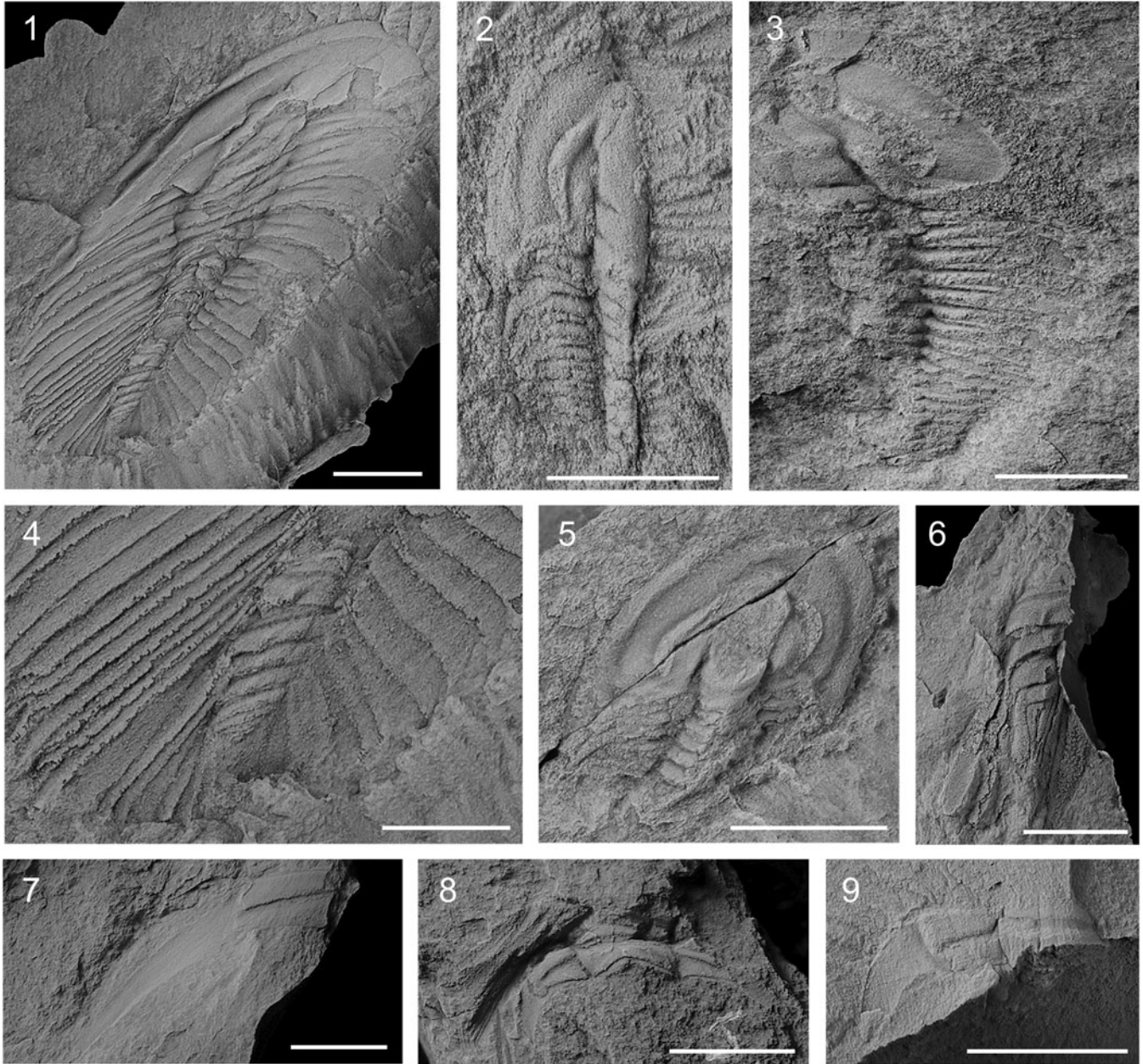


Figure 4. *Callavia choffati* (Delgado, 1904), Vila Boim Formation, middle Marianian, Vila Boim, Portugal (1, 4, 6–9) and ‘Herrerías Shale,’ middle Marianian, Cañaverl de León, Spain (2, 3, 5): (1, 4) MG 15787b, paralectotype (latex): (1) overview; (4) detail of pygidium; (2) UHU-CVL 49; (3) UHU-CVL 36; (5) UHU-CVL 37; (6) MG 15707b, paralectotype (latex); (7) MG 15764, paralectotype; (8) MG 15714, paralectotype; (9) MG 16658, paralectotype. Scale bars = 5 mm (2–5); 10 mm (1, 6–9).

but also in the thoracic structure (compare Fig. 4.1 with Palmer and Repina, 1993, fig. 10.7). A close relationship between these taxa was already suggested by Lieberman (2001) through a classification that is adopted herein (see remarks on the superfamily).

With regard to other documented occurrences of *Callavia*, and excluding those listed in Table 1, the genus was identified in the Purley Shales, Warwickshire, by Rushton (1966) and Williams et al. (2013), who described as *Callavia?* sp. a few fragments, mainly based on sculpture similar to that presented by *Callavia callavei*. Part of this material had been previously

documented by Pringle (1913), Illing (1913, 1916), and Smith and White (1963). Based on the figured material (Rushton, 1966, pl. 4, figs. 27, 28; Williams et al., 2013, fig. 4), it is not possible to identify them to generic or suprageneric levels, and additional material from those beds is necessary to confirm the presence of *Callavia* in those levels.

After several misconceptions that indicated the presence of *Callavia* in the lower Cambrian of Morocco (Neltner and Pockey, 1950; Hupé, 1959) these were later reassigned by Geyer and Palmer (1995) to other genera. Geyer and Landing (2002) reported the presence of this genus in this region, namely a

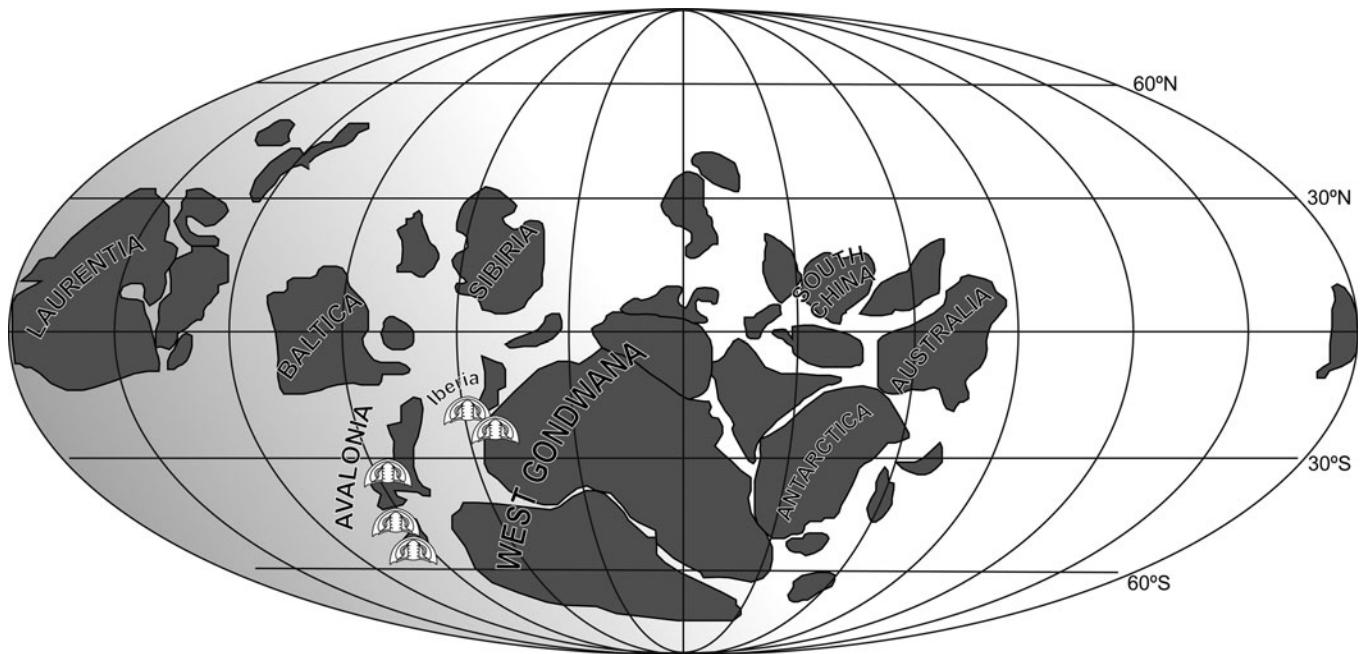


Figure 5. Distribution of *Callavia* plotted on the Cambrian paleogeographic map (modified from Scotese and McKerrow, 1990; McKerrow et al., 1992; Dalziel, 1997; and Malinky and Geyer, 2019).

single cephalic fragment in the Bani section, Moroccan Anti-Atlas (Geyer, personal communication, 2020).

Callavia choffati (Delgado, 1904)
Figures 2–4

- v *1904 *Paradoxides choffati* Delgado, p. 319, pl. 1, figs. 1–3, 16?, pl. 5, fig. 3.
- v 1904 *Paradoxides* sp. aff. *P. abenacus* Matthew, 1886 var. (?); Delgado, p. 322, pl. 1, fig. 10, pl. 5, fig. 35.
- v 1904 *Paradoxides* sp. n. aff. *P. spinosus* Boeck, 1827; Delgado, p. 323, pl. 1, fig. 12.
- v 1904 *Paradoxides costae* Delgado, p. 323, pl. 1, fig. 6.
- v 1904 *Olenellus? macphersoni* Delgado, p. 347, pl. 4, fig. 5, pl. 5, fig. 21, pl. 6, fig. 11.
- v 1904 *Olenopsis* sp.; Delgado, p. 325, pl. 1, fig. 8.
- 1941 *Callavia? lotzei* Richter and Richter, p. 34, pl. 3, figs. 36–40, pl. 4, fig. 66.
- 1941 *Callavia (?) choffati*; Richter and Richter, p. 62.
- v 1952 *Callavia choffati*; Teixeira, p. 170, pl. 1, fig. 1, pl. 2, figs. 1–3, pl. 3, figs. 1–7, pl. 4, figs. 1–6, pl. 12, figs. 1, 2.
- 1962 *Callavia? lotzei*; Sdzuy, p. 193, pl. 19, figs. 6–14, pl. 22, fig. 11.
- v 1982 *Callavia? lotzei*; Liñán and Mergl, p. 212.
- v 1982 *Callavia? sp.*; Liñán and Mergl, p. 212.
- 2001 *Judomia lotzei*; Sdzuy, p. 96, figs. 25–27.
- v 2001 *Callavia choffati*; Sdzuy, figs. 13, 14.
- 2001 *Sdzuyomia lotzei*; Lieberman, p. 113.
- v 2019 *Sdzuyomia lotzei*; Collantes et al., p. 81, fig. 2.

Type specimens.—Lectotype (selected herein), MG 15781, an internal and external mold of a cephalon (Fig. 2.1), figured by

Delgado (1904, pl. 1, fig. 3) and Teixeira (1952, pl. 1). Paralectotypes of one incomplete exoskeleton, MG 15787a with counterpart 15787b (Fig. 4.1; Delgado, 1904, pl. 1, fig. 16, pl. 5, fig. 3; Teixeira, 1952, pl. 4, figs. 1–3); MG 15782a with counterpart 15782b, five cephalons (Fig. 2.2; Delgado, 1904, pl. 1, fig. 1; Teixeira, 1952, pl. 2, figs. 1–3; MG 15785, external mold (Teixeira, 1952, pl. 4, figs. 5, 6); MG 15786, internal mold (Fig. 2.5; Delgado, 1904, pl. 1, fig. 1; Teixeira, 1952, pl. 12, figs. 1, 2); MG 16684, external mold; MG sn, external mold (Fig. 2.3; Teixeira, 1952, pl. 3, figs. 3, 4); MG 15779a with counterpart 15779b, two cephalic fragments (Delgado, 1904, pl. 4, fig. 53; Teixeira, 1952, pl. 3, figs. 5, 6; MG 15780a with counterpart 15780b (Teixeira, 1952, pl. 3, fig. 7); MG 16658, three thoracic segments (all internal molds) (Fig. 4.9; Delgado, 1904, pl. 1, fig. 12); MG 15714 (Fig. 4.8; Delgado, 1904, pl. 1, fig. 8); MG 15764 (Fig. 4.7; Delgado, 1904, pl. 1, fig. 6); MG 15707a with counterpart 15707b, one pygidium (Fig. 4.6; Delgado, 1904, pl. 1, fig. 10, pl. 5, fig. 35).

Emended diagnosis.—Intergenal spine reduced; S4 poorly defined and short (tr.); interocular area width approximately four-fifths width of the extraocular area opposite S1; intergenal ridge and posterior ocular line equally prominent, subparallel to the intergenal spine. Thorax of 18 or probably 19 segments, tapering posterior to fifth segment.

Occurrence.—Vila Boim Formation (type locality), Marianian (Cambrian Series 2) of Vila Boim, Portugal; lower part of Cumbres beds, middle Marianian (Cambrian Series 2), Cumbres de San Bartolomé, Huelva, Spain; and lower part of Herrerías shale, middle Marianian (Cambrian Series 2), Sierra del Bujo (Arroyomolinos de León), Cañaveral de León and Hinojales, Huelva, Spain.

Description.—Cephalon crescent-shaped; sagittal length ~40% of maximum width at posterior margin, with higher relief of the anterior border, the ocular ridges, and the glabella. Known cephalon range 2.1–18.9 mm length and 5.2–42.4 mm width. Posterior margin of cephalon curved backward distally. Glabella hourglass-shaped to parallel-sided, with faint constriction at S1, inflated dorsally, exceeding the genal areas in lateral view; maximum glabellar elevation at half of glabellar length, sloping downward anteriorly with rounded profile. Glabella longer than wide; posterior glabellar width ~115–120% the anterior glabellar width; corresponding to 25% of maximum cephalic width; sagittal glabellar length ~75–80% sagittal cephalic length. Axial furrows deep, slightly sinuous (outlining glabellar lobes). Occipital furrow moderately deep to shallow medially, oblique backward when traced adaxially; occipital ring moderately convex dorsally, frequently preserved as two symmetrical subrectangular lobes, bearing a small axial node near posterior margin. Four glabellar furrows (excluding occipital furrow) shallowing anteriorly, nontransglabellar, nearly straight, oblique, inward and backward ~10–15° to a transverse line. S1 subparallel to SO, occupying approximately two-thirds of glabellar width; L1 subrectangular, moderately inflated dorsally; S2 slightly less oblique than S1; L2 similar to L1; S3 subparallel to S2 but shorter (tr.); L3 shorter (exsag.) and narrower (tr.) than L1 and L2; S4 poorly defined, very shallow and narrow (tr.), located immediately posterior to the parafrontal band; L4 poorly defined, typically merged with the frontal lobe (Fig. 3.17). Frontal lobe of glabella tapered to slightly pointed, surrounded by parafrontal band connecting ocular ridges. Preglabellar field short, < 10% of sagittal cephalic length. Some specimens showing shallow furrow connecting preglabellar furrow with anterior border furrow (Fig. 3.7). Lateral border inflated dorsally, widened posteriorly, reaching maximum width at base of genal spines, defining broad genal point, directed backward. Anterior and lateral border furrows broad, deep, merging into significantly shallower posterior border furrow, but deeper at genal areas. Interocular area dorsally arched, elongated (exsag.), trapezoidal in outline, with two differentiated interocular swellings. Width (tr.) of interocular area approximately four-fifths of extraocular area width at S1 level. Ocular lobe prominent, arc-shaped, located slightly closer to glabella than to lateral border; exsagittal length equivalent to 40% of sagittal cephalic length. Posterior tip of ocular lobe opposite SO; anterior tip opposite L3. Inner margin of ocular lobe well defined. Ocular lobes anteriorly connected by parafrontal band, posteriorly connected to posterior ocular line. Pronounced intergenal ridge, slightly curved to sigmoidal, extending into reduced, almost indistinct, intergenal spine (Fig. 3.8, 3.18, 3.20), giving rise to change of convexity of posterior margin (small dorsal swelling). Intergenal spine located in exsagittal line with inner edge of lateral border furrow. Genal angle greater than intergenal angle. Sculpture composed of reticulated pattern, with extraocular genal caeca, and terrace ridges along abaxial limit of anterior border (Figs. 2.4, 3.19).

Thorax composed of 18, probably 19 thoracic segments in only complete specimen (Fig. 4.1, 4.2). Wide (sag.), convex, little-pronounced axial rings, narrowing toward back. Axial ring

width (tr.) occupying 20% of total thoracic width anteriorly, 35% posteriorly. Axial ring furrows deep. Axial nodes on each thoracic segment. Lateral extension of pleural region not surpassing extension of genal spine of cephalon. Pleural region subtly widened (tr.) to third pleura, then progressively narrowing (tr.) toward posterior end. Pleurae thin (sag.), knife-shaped, slightly curving backward; curvature progressively increasing posteriorly. Pleural furrow deep, wide, extending 35% of whole pleura (tr.), slightly oblique. Curvature located at approximate midlength of pleural width, with pleural spine widened (exsag.) at that point. Last segments of thorax fused with pygidium.

Pygidium very reduced, relatively narrow. Pygidial rachis well-defined, with triangular outline, composed of three faint axial rings. Pleural regions poorly preserved, posteriorly extended.

Materials.—Type specimens plus additional material: Cumbres beds, Cumbres de San Bartolomé: UHU-CU1/1/1, 1/2/3, two cephalon.

Herrerías shale: Hinojales: UHU-LH1/1/8, 1/1/12, 1/1/26, 1/2/2, 1/2/7, 1/2/24, 1/2/25, seven cephalon; UHU-LH1/1/4, thoracic segment. Cañaveras de León: UHU-CVL36 (Fig. 4.3), 37 (Fig. 4.5), 49 (Fig. 4.2), three articulated incomplete cephalothoraxes; UHU-CVL01–13, 15–35, 38–43, 46–48, 50, 44 cephalon. Sierra del Bujo: UHU-LBU/0/1, /0/2, /0/3, /1/1, four cephalon; UHU-LBU/0/2, cephalic fragment.

Remarks.—*Callavia choffati* differs from the type species *Callavia broeggeri* and *Callavia callavei* in having shorter and narrower intergenal spines, shorter (tr.) interocular areas than in *Callavia broeggeri*, and a different glabellar lobation (fainter glabellar furrows and shorter S3 and S4) than in *Callavia callavei*.

A group of specimens described by Delgado (1904) under different species names are conspecific with '*Paradoxides*' *choffati*, as previously stated (e.g., Richter and Richter, 1941; Teixeira, 1952; see synonymy for further information). *Callavia choffati* was originally described by Delgado (1904) as a species of *Paradoxides* and quickly after his publication, Charles Schuchert (in Dana, 1905, p. 159) stated that "*Paradoxides choffati* is clearly an *Olenellus*." In fact, Delgado (1904, p. 320) expressed the same opinion in the original publication: "... ces exemplaires pourraient être exclus du genre *Paradoxides* (s. str.) et réunis plutôt à *Olenellus*, sous-genre *Holmia* ..." It was the observation of 'clear' facial sutures in Delgado's (1904) opinion, especially in the specimen herein selected as lectotype (Fig. 2.1), which justified the assignment to *Paradoxides*. Today, it is widely agreed that these cephalic 'lines' observed in many specimens of *Olenellina* are in fact fractures (Whittington, 1989, 1997), and that the suborder *Olenellina* is characterized by lacking dorsal sutures throughout its entire ontogeny. But during several decades, the regular presence in olenellines and the curious configuration of these lines (which mimic the anterior branches of a facial suture) led to much discussion about their significance (e.g., Størmer, 1942; Hupé, 1953; Bergström, 1973). As Geyer (1996) stated, they could represent favored loci for fracturing due to thinner or less calcified cuticle. In the studied material of *Callavia choffati*, these fractures are, in fact very common (Fig. 3.7, 3.10, 3.11, 3.13–3.19).

Some decades after Delgado's (1904) publication, Richter and Richter (1941) erected a new species, *Callavia? lotzei*, from the northern Huelva province (Spain). These authors suggested for the first time that '*Paradoxides? hoffati*' should be also assigned to the genus *Callavia*. Nevertheless, and although they considered it very similar to the newly erected *Callavia? lotzei*, they did not specify the morphological features that justified the erection of a new species. Furthermore, Richter and Richter (1941) considered that Portuguese and Spanish *Callavia*-bearing assemblages are coeval and share some taxa at specific levels, thus correlation would benefit from such discussion and eventual synonymy. While revising Delgado's (1904) material, Teixeira (1952) followed Richter and Richter's (1941) suggestion and maintained the Portuguese species assigned to the genus *Callavia*. A few years later, Hupé (1960) suggested that *Callavia? lotzei* and *Callavia hoffati* might be synonyms, but Sdzuy (1962) rejected this hypothesis based on deeper glabellar furrows and larger cephalons of *Callavia hoffati*. Furthermore, Sdzuy (1962) considered that both Iberian species bear significant differences when comparing with *Callavia*, namely the lack of intergenal spines and the absence of a large occipital spine (both structures are indeed present but based on the poorly preserved material that Sdzuy had at his disposal, it was not possible to verify them). For these reasons, Sdzuy (1962) suggested that *Callavia hoffati* was more closely related to *Kjerulfia Kiær*, 1917, whereas *Callavia lotzei* should be assigned to *Judomia*, with which it shares several morphological characters, although he maintained both species as *Callavia?*. This proposed assignment was later reinforced by the author (Sdzuy, 2001), who definitely transferred the Spanish species to the genus *Judomia*, stating that it was unexpected because *Judomia* is characteristic of the Siberian domain. Among the characters that Sdzuy (2001) listed in common, are the absence of intergenal spines and the pygidium configuration, which he considered to be much more similar to those of *Judomia* than *Callavia*. Nevertheless, the intergenal spines are present in *Callavia lotzei*, and Whittington (1989, p. 134) stated that the "pygidium attributed to *Callavia* by Raw (1936, pl. 21, figs. 3a–c) is composed largely of one pair of spines similar in form to those of" *Judomia tera*. In that work, Sdzuy (2001) also reinforced the independence of *Callavia hoffati* and *Callavia lotzei* through photographic retrodeformation of Portuguese figured specimens, but the results are not reliable (Sdzuy, 2001, figs. 13, 14).

The new data described in this work suggest that *Callavia hoffati* and *Callavia lotzei* are synonyms and support the assignment of the Iberian species to the genus *Callavia*. The previous poor documentation of *Callavia hoffati* from the Vila Boim Formation (Portugal), namely short descriptions and low resolution photographs (Delgado, 1904; Teixeira, 1952), together with the large size of the available specimens, certainly hinder proper comparison with '*Callavia? lotzei*' from the Herrerías shale (Spain). On the other hand, in erecting '*Callavia? lotzei*,' Richter and Richter (1941) included specimens in this species belonging to *Gigantopygus* cf. *G. bondoni* Hupé, 1953, a redlichiine, and Sdzuy (1962, pl. 19, figs. 7–11) included some additional material of meraspides. These compromised comparison with the Portuguese material. The great number of newly collected, well-preserved specimens from the

Herrerías shale allowed clarification of the morphology of '*Callavia? lotzei*' and verification that it agrees with *Callavia hoffati* in all characters. Reduced intergenal spines are present in both sets of specimens, located in similar positions (e.g., Fig. 3.1–3.17). This structure seems to be progressively reduced to a tiny spine or node on the posterior cephalic border through ontogeny, being larger and more evident in small specimens (Fig. 3). Due to the deformation and large size of the type specimens (Fig. 2), the intergenal spine is not evident, being expressed as a swelling on the posterior border, and more evident in only one specimen (Fig. 2.3). The inflated cephalic border, widening posteriorly, is one of the characters that Sdzuy (2001) considered to separate Portuguese and Spanish forms; it has the same configuration in all of the studied specimens. The apparent relatively shorter cephalic border in the Portuguese material (Fig. 2.1–2.5) could be attributable to differences in size due to ontogenetic allometry. Another important comparative character is the glabellar morphology and lobation; both sets of specimens show a constriction opposite S1 (Figs. 2.1, 3.17, 3.19), resulting in a faint hourglass-shaped glabella in specimens preserving part of the original convexity. The outline and position of the ocular lobes are indistinguishable in Portuguese and Spanish specimens, including the typical swellings of the interocular areas (e.g., Figs. 2.1, 2.2, 3.11, 3.17). Furthermore, both bear an entirely comparable, faint parafrenal band surrounding the LA (Figs. 2.1–2.3, 3.7, 3.13–3.18) and a well-marked posterior ocular line subparallel to the intergenal ridge (Figs. 2.1, 3.18, 3.19). The few articulated specimens also show the same thoracic structure (compare Sdzuy, 1962, pl. 9, fig. 6 with Fig. 4.1). For these reasons, '*Callavia? lotzei*' is herein considered a junior synonym of *Callavia hoffati*.

Paleobiogeographical and biostratigraphical remarks

The confirmed presence of the genus *Callavia* in the Iberian Peninsula, represented by the species *Callavia hoffati*, together with its reported occurrence in Morocco (Geyer and Landing, 2002), are important with regard to the early Cambrian faunal links between the western Gondwana Domain and Avalonia. The genus *Callavia* (in its current concept), originally described from the Brigus Formation, Newfoundland, Canada (Walcott, 1890; Matthew, 1897), was later identified in the Comley Limestone Formation, Shropshire, UK (Lapworth, 1891), and soon thereafter became an index taxon for the Avalonian realm up to this day. Based on associated trilobites from the Brigus Formation in eastern Newfoundland and the Comley section of England (*Triangulaspis* Lermontova, 1940, *Delgadella* Walcott, 1912, *Serrodiscus bellimarginatus* [Shaler and Foerste, 1888]), it was possible to approximately correlate the so-called *Callavia* Biozone (Avalonian regional Branchian Series, lower Cambrian, Series 2) with other paleogeographical regions (the Banian/Marianian regional Stages of Morocco/Iberia, the '*Nevadella*' Biozone of Laurentia, the *Pagetiellus anabarus-Judomia* Biozones of Siberia, or the *Schmidtellus mickwitzii-Holmia inusitata-Holmia kjerulfi* Biozones of Baltica; see Sdzuy, 1971, 1972; Palmer and Repina, 1993, fig. 12; Fletcher, 2006; Żylińska, 2013; Sundberg et al., 2016). The type species *Callavia broeggeri* is a representative of the 'west Avalonia

sector' (= American sector), which includes the eastern North American seaboard from Newfoundland as far south as Cape Cod, Massachusetts (Cocks and Torsvik, 2006), and is present throughout this area (e.g., Grabau, 1900; Walcott, 1910; Fletcher, 2003, 2006). On the other hand, the 'eastern sector of Avalonia' (= European sector) is represented by the presence of *Callavia callavei* and several findings of *Callavia* sp. indet., a species occurring in Branchian sequences in England (Thomas et al., 1984; Rushton, 1999; Rushton et al., 2011; Williams et al., 2013).

During the early Cambrian, and probably until the end of this period (Cocks and Torsvik, 2006; Pouclet et al., 2007), Avalonia was aggregated to the margin of West Gondwana, possibly belonging to the same biochorema as Iberia, which was a peri-Gondwanan terrane located east of Avalonia at the same western margin (Courjault-Radé et al., 1992; fig. 5). According to Álvaro et al. (2013, p. 285), the end of Cambrian Series 2 is characterized by "new links between Avalonia and West Gondwana, including some eodiscoids and species of *Protolenus*, *Strenuella* and possibly *Callavia*." Our data confirm the presence of *Callavia* in Iberia, which, together with the Moroccan occurrence of the genus (Geyer and Landing, 2002), supports the faunal links between both regions and is in agreement with the ideas of previous authors, who reported several other genera in common from Cambrian Series 2 onward between Avalonia and the western Mediterranean region (e.g., Szalay, 1972; Liñán et al., 2002; Álvaro et al., 2003; Landing et al., 2013a, b, Collantes et al., 2021). Therefore, the genus *Callavia* is distributed across the western margin of Gondwana, the western Mediterranean region (Iberia and Morocco), and throughout all of the Avalonian sectors (UK, Newfoundland, and Massachusetts).

With regard to the age of the studied assemblages and their correlation with other regions, the lower part of the Vila Boim Formation (Portugal) has been assigned to the middle part of the regional Marianian Stage (see Liñán et al., 2004). In Spain, the newly collected material and the previous documented specimens of '*Callavia? lotzei*' (= *Callavia choffati*) by Richter and Richter (1941) and Szalay (1962, 2001), all come from the northern Huelva province, in rocks assigned to the Cumbres beds and the Herrerías shale, with an age corresponding to the middle Marianian (Ruiz López et al., 1979), coeval with Portuguese levels. The middle part of the Marianian regional Stage can be correlated with the uppermost Cambrian Stage 3 to the lowermost Cambrian Stage 4 (Zhang et al., 2017; Collantes et al., 2020, 2021). In the Avalonian sectors, *Callavia broeggeri* is known from the Brigus Formation and coeval levels (Purley Shales), assigned to the lower Branchian Series (top of Cambrian Stage 3 to the base of Cambrian Stage 4; Landing, 1996; Fletcher, 2003, 2006), whereas *Callavia callavei* and several findings of *Callavia* sp. indet. occur in the Comley Limestone Formation (England; Thomas et al., 1984; Rushton, 1999; Williams et al., 2013). All of these levels correspond to the *Callavia* Zone and *Strenuella sabulosa* Biozone, equivalent to uppermost Cambrian Stage 3 to lowermost Cambrian Stage 4 (Rushton et al., 2011; Williams et al., 2013).

Specimens of *Callavia?* sp. indet. collected by Illing (1913), as well as those described and figured by Rushton (1966), were obtained from calcareous nodules at the base of the Purley Shales at Camp Hill Grange Quarry (northwestern

Nuneaton), at Woodlands Quarry (Hartshill) and from Worthington Farm, UK. Later, Brasier (1984) also obtained fragments of *Callavia?* sp. indet. in Nuneaton.

All of these *Callavia*-bearing localities and beds are equivalent to uppermost Cambrian Stage 3 to lowermost Cambrian Stage 4, reinforcing partial correlation between the Marianian/Banian regional Stages and the lower Branchian Series (e.g., Geyer, 2019) and suggesting that the Avalonian *Callavia* Zone can also have some usefulness in West Gondwana.

Conclusions

A systematic reassessment of '*Paradoxides? choffati*' from Portugal and '*Callavia? lotzei*' from Spain has placed '*Callavia? lotzei*' as a junior synonym of '*P. choffati*' and led to the assignment of the Iberian taxon to *Callavia*. In turn, *Sdzuyomia* is considered to represent a junior synonym of *Callavia*, and the systematic position of this classic genus among Olenellina is better framed within the superfamily 'Judomioidea.'

Based on the revised diagnosis of *Callavia*, the genus is distributed across the western margin of Gondwana, the western Mediterranean region (Iberia and Morocco; 'West Gondwana'), and throughout all of the Avalonian sectors (UK, eastern Newfoundland, and Massachusetts), supporting faunal links between West Gondwana and Avalonia during Cambrian Series 2. The Iberian records of *Callavia choffati* are assigned to the middle part of the regional Marianian Stage (uppermost Cambrian Stage 3 to lowermost Cambrian Stage 4) and correlate with the *Callavia* Zone of Avalonia (lower Branchian Series), suggesting some usefulness of this biostratigraphical zone also in West Gondwana and strengthening correlation of the Marianian and Banian regional Stages with the lower Branchian Series.

Acknowledgments

We are grateful to M. Webster (Chicago), F.A. Sundberg (Arizona), and J.O.R. Ebbestad (Uppsala, Sweden) for their detailed reviews and constructive suggestions; and N. Hughes (California) for his efforts in editing the article. We thank the Council of Environment and Territorial Planning from the Junta de Andalucía and the Directorate of Sierra de Aracena y Picos de Aroche Natural Park for providing permission to work into the park; M. Gordo for her contribution with the facilities during the fieldwork campaigns in northern Huelva province; I. Garzón for his fieldwork assistance in Cañaverale de León; M. Ramalho (Museu Geológico de Lisboa), in loving memory, for granting access to fossil collections under his care; J. Colmenar (Centro de Geociências de Coimbra) and the remaining 'Delgaditos Team' for assisting in fieldwork in Vila Boim. The present work has been carried out with Junta de Andalucía to the RNM 276 Research Group and the Centro Científico-Tecnológico de Huelva to the Department of Applied Geosciences, together with the GIUV2017-395 research group of the University of Valencia. This study was supported by Portuguese funds by Fundação para a Ciência e a Tecnologia, I.P. (Portugal) in the frame of UID/Multi00073/2019, UIDB/00073/2020 and UIDP/00073/2020 projects of the I & D unit Geosciences Center (CGEO). This work is a contribution to the project IGCP 652.

References

- Adrain, J.M., 2011, Class Trilobita Walch, 1771, in Zhang, Z.-Q., ed., Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness: *Zootaxa*, v. 3148, p. 104–109, <https://doi.org/10.11646/zootaxa.3148.1.15>.
- Ahlberg, P., Bergström, J., and Johansson, J., 1986, Lower Cambrian olenellid trilobites from the Baltic faunal province: *Geologiska Föreningens i Stockholm Förhandlingar*, v. 108, p. 39–56, <https://doi.org/10.1080/11035898609453745>.
- Álvarez, J.J., Elicki, O., Geyer, O., Rushton, A.W.A., and Shergold, J.H., 2003, Palaeogeographical controls on the Cambrian trilobite immigration and evolutionary patterns reported in the western Gondwana margin: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 195, p. 5–35, [https://doi.org/10.1016/S0031-0182\(03\)00300-6](https://doi.org/10.1016/S0031-0182(03)00300-6).
- Álvarez, J.J., Ahlberg, P., Babcock, L.E., Bordonaro, O.L., Choi, D.C., Cooper, R.A., Ergaliev, G.K.H., Gapp, I.W., Ghobadi Pour, M., Hughes, N.C., Jago, J.B., Korovnikov, L., Laurie, J.R., Lieberman, B.S., Paterson, J.R., Pegel, T.V., Popov, L.E., Rushton, A.W.A., Sukhov, S.S., Tortello, M.F., Zhou, Z., and Zylinska, A., 2013, Global Cambrian trilobite palaeobiogeography assessed using parsimony analysis of endemism, in Harper, D.A.T., and Servais, T., eds., *Early Palaeozoic Biogeography and Palaeogeography: Memoirs of the Geological Society of London*, v. 38, p. 273–296, <http://dx.doi.org/10.1144/M38.19>.
- Azor, A., 2004, Zona de Ossa-Morena, in Vera Torres, J.A., ed., *Geología de España: Madrid, Sociedad Geológica de España e Instituto Geológico y Minero de España*, p. 65–198.
- Bergström, J., 1973, Classification of olenellid trilobites and some Balto-Scandinavian species: *Norsk Geologisk Tidsskrift*, v. 53, p. 283–314.
- Boeck, C.O.B., 1827, Notitser til Laeren om Trilobiterne: *Magazin for Naturvidenskaberne Christiania*, v. 8, no. 1, p. 11–44.
- Brasier, M.D., 1984, Microfossils and small shelly fossils from the lower Cambrian *Hyolithes* Limestone at Nuneaton, English Midlands: *Geological Magazine*, v. 121, p. 229–253, <https://doi.org/10.1017/S0016756800028296>.
- Briggs, D.E.G., and Fortey, R.A., 1992, The early Cambrian radiation of arthropods, in Lipps, J.H., and Signor, P.W., eds., *Origin and Early Evolution of the Metazoa*: New York, Plenum Press, p. 335–373.
- Chernysheva, N.E., 1960, [Arthropoda: Trilobitomorpha and Crustacea], in Chernysheva, N.E., ed., [Fundamentals of Ethology]: Moscow, Akademiya Nauk SSSR, Ministerstvo Geologii i Okhrany Nedr SSSR, p. 17–54. [in Russian]
- Cocks, L.R.M., and Torsvik, T.H., 2006, European geography in a global context from the Vendian to the end of the Palaeozoic: *Memoirs of the Geological Society of London*, v. 32, p. 83–95, <https://doi.org/10.1144/GSL.MEM.2006.032.01.05>.
- Collantes, L., Gozalo, R., Mayoral, E., Garzón, I., Chirivella, J.B., and Liñán, E., 2019, Trilobites olenelinos en el Cámbrico inferior (Marianense) de la provincia de Huelva, in *Libro de Resúmenes, Jornadas de la Sociedad Española de Paleontología*, 35th, Baza, Spain, 2–5 October: Málaga, Spain, Universidad de Málaga, p. 79–82.
- Collantes, L., Mayoral, E., Chirivella, J.B., and Gozalo, R., 2020, New data on *Marocella* (Mollusca, Helcionelloida) from the Cambrian (Series 2–Miaoilingian) of the Iberian Peninsula: *GFF*, v. 142, p. 190–205, <https://doi.org/10.1080/11035897.2020.1762722>.
- Collantes, L., Mayoral, E., Liñán, E., and Gozalo, R., 2021, Atopidae (Trilobita) in the upper Marianian (Cambrian Series 2, Stage 4) of Iberia: *Journal of Paleontology*, v. 95, 123–132, <https://doi.org/10.1017/jpa.2020.71>.
- Courjault-Radé, P., Debrenne, F., and Gandin, A., 1992, Paleogeographic and geodynamic evolution of the Gondwana continental margins during the Cambrian: *Terra Nova*, v. 4, p. 657–667, <https://doi.org/10.1111/j.1365-3121.1992.tb00615.x>.
- Cowie, J. W., 1971, Lower Cambrian faunal provinces, in Middelmiss, F.A., Rawson, P.F., and G. Newall, eds., *Faunal provinces in space and time: Geological Journal Special Issue*, v. 4, p. 31–46.
- Dalziel, I.W.D., 1997, Neoproterozoic–Paleozoic geography and tectonics: Review, hypothesis, environmental speculation: *Bulletin of the Geological Society of America*, v. 109, p. 16–42, [https://doi.org/10.1130/0016-7606\(1997\)109<0016:ONPGAT>2.3.CO;2](https://doi.org/10.1130/0016-7606(1997)109<0016:ONPGAT>2.3.CO;2).
- Dana, E.S., ed., 1905, *Scientific intelligence*, 2, *Geology*, 5, Faune cambrienne du Haut-Alemtejo (Portugal), par J.F. Nery Delgado: *American Journal of Science*, v. 20, no. 116, p. 159–160.
- Delgado, J.F.N., 1904, La faune cambrienne du Haut-Alemtejo (Portugal): *Comunicações da Commissão dos Trabalhos do Serviço Geológico de Portugal*, v. 5, p. 307–374.
- Fletcher, T.P., 2003, *Ovatortycocara granulata*: The key to a global Cambrian Stage Boundary and the correlation of the olenellid, redlichiiid and paradoxiid realms: *Special Papers in Paleontology*, v. 70, p. 73–102.
- Fletcher, T.P., 2006, Bedrock geology of the Cape St. Mary's Peninsula, southwest Avalon Peninsula, Newfoundland (includes parts of NTS maps sheets 1M/1, 1N/4, 1L/6 and 1K/13), Newfoundland: Government of Newfoundland and Labrador, Geological Survey, Department of Natural Resources, v. 6, no. 2, p. 1–117.
- Fletcher, T.P., and Theokritoff, G., 2008, The early Cambrian of eastern Massachusetts: *Northeastern Geology and Environmental Science*, v. 30, p. 304–329.
- Fortey, R.A., 1997, Classification, in Kaesler, R.L., ed., *Treatise on Invertebrate Paleontology, Part O (Revised), Arthropoda 1, Trilobita*: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. O289–O302.
- Fortey, R.A., Briggs, D.E.G., and Wills, M.A., 1996, The Cambrian evolutionary ‘explosion’: Decoupling cladogenesis from morphological disparity: *Biological Journal of the Linnean Society*, v. 57, p. 13–33, <https://doi.org/10.1006/bjil.1995.0002>.
- Fritz, W.H., 1973, Medial lower Cambrian trilobites from the Mackenzie Mountains, north-western Canada: *Geological Survey of Canada*, v. 73, no. 24, p. 1–43.
- Gapp, I.W., Lieberman, B.S., Pope, M.C., and Dilliard, K.A., 2011, New olenelline trilobites from the Northwest Territories, Canada, and the phylogenetic placement of *Judomia absita* Fritz, 1973: *Zootaxa*, v. 2918, p. 15–28, <https://doi.org/10.11646/zootaxa.2918.1.2>.
- Geyer, G., 1996, The Moroccan fallotaspid trilobites revisited: *Beringeria*, v. 18, p. 89–199.
- Geyer, G., 2007, The early Cambrian trilobite *Gigantopygus*: Its morphology, taxonomy, ecology, with remarks on the facial suture of *Gigantopygus angustalatus*: *Beringeria*, v. 37, p. 41–60.
- Geyer, G., 2019, A comprehensive Cambrian correlation chart: Episodes, v. 42, p. 1–12, <https://doi.org/10.18814/epiugs/2019/019026>.
- Geyer, G., and Landing, E., 2002, The Bani Stage and its significance for Cambrian intercontinental correlation, in Álvarez, J.J., and Clausen, S., eds., *Programme and Abstracts, Conference of the Cambrian Stage Sub-division Working Group*, 8th, International Subcommittee on Cambrian Stratigraphy, Caunes-Minervois, Languedoc, France, 12–14 September: Lille, France, International Subcommittee on Cambrian Stratigraphy, p. 12–14.
- Geyer, G., and Palmer, A.R., 1995, Neltneriidae and Holmidae (Trilobita) from Morocco and the problem of early Cambrian intercontinental correlation: *Journal of Paleontology*, v. 69, p. 459–474, <https://doi.org/10.1017/S0022336000034867>.
- Grabau, A.W., 1900, Paleontology of the Cambrian terranes of the Boston Basin: *Occasional Papers of the Boston Society of Natural History*, v. 4, no. 3, p. 601–694.
- Hall, J., 1862, Supplementary note to the thirteenth report of the Regents of the State Cabinet: *Annual Report of the New York Cabinet for Natural History*, 15th, Albany, State of New York, p. 113–119.
- Harrington, H.J., 1959, Suborder Redlichina, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press)*, p. O190–O194.
- Hupé, P., 1953, Contribution à l'étude du Cambrien inférieur et du Précambrien III de l'Anti-Atlas marocain: *Notes et Mémoires du Service Géologique du Maroc*, v. 103, p. 1–402.
- Hupé, P., 1959, Nouvelle contribution à l'étude du Cambrien marocain [Ph.D. Thesis]: Paris, Université de Paris, 447 p.
- Hupé, P., 1960, Sur le Cambrien inférieur du Maroc, in Asklund, B., and Poulsen, C., eds., *Late Pre-Cambrian and Cambrian Stratigraphy, International Geological Congress, 21st, Norden: Copenhagen, Det Berlingske Bogtrykkeri*, p. 75–85.
- Hutchinson, R.D., 1962, Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland: *Bulletin of the Geological Survey of Canada*, v. 88, 156 p.
- Illing, V.C., 1913, Recent discoveries in the Stockingford Shales near Nuneaton: *Geological Magazine*, v. 10, p. 452–453, <https://doi.org/10.1017/S0016756800127487>.
- Illing, V.C., 1916, The paradoxidian fauna of a part of the Stockingford Shales: *Quarterly Journal of the Geological Society of London*, v. 71, p. 386–448.
- Jell, P.A., 2003, Phylogeny of early Cambrian trilobites: *Special Papers in Paleontology*, v. 70, p. 54–57.
- Jell, P.A., and Adrain, J.M., 2002, Available generic names for trilobites: *Memoirs of the Queensland Museum, Brisbane*, v. 48, p. 331–553.
- Khomentovskii, V.V., and Repina, L. N., 1965, [Lower Cambrian of the Stratotype Section of Siberia]: *Nauka, Moscow*, 196 p. [in Russian]
- Kiær, J., 1917, The lower Cambrian *Holmia* fauna at Tømten in Norway: *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo, I, Matematisk-Naturvidenskapelig Klasse*, v. 1916, no. 10, p. 1–140.
- Korobov, M.N., 1963, [New Lower Cambrian trilobites from Kharaulakhsk Mountains]: *Paleontologicheskii Zhurnal*, v. 4, p. 64–75. [in Russian]
- Korobov, M.N., 1989, [Lower Cambrian biostratigraphy and polymeroid trilobites of Mongolia]: *Transactions of the Soviet-Mongolian Geological Expedition*, v. 46, 202 p. [in Russian]

- Kryskov, L.N., Lazarenko, N.P., Ogienko, L.V., and Tchernysheva, N.E., 1960, New early Palaeozoic trilobites of eastern Siberia and Kazakhstan, in Markovsky, B.P., ed., *New species of prehistoric plants and invertebrates of the USSR*, v. 1, no. 2: Moscow, VSEGEI, p. 211–255. [in Russian]
- Lake, P., 1937, A monograph of the British Cambrian trilobites: Palaeontographical Society Monograph, v. 10, p. 225–248.
- Landing, E., 1996, Avalon: Insular continent by the latest Precambrian, in Nance, R.D., and Thompson, M.D., eds., *Avalonian and Related Peri-Gondwanan Terranes of the Circum-North Atlantic*: Geological Society of America Special Paper, v. 304, p. 29–63, <https://doi.org/10.1130/0-8137-2304-3.29>.
- Landing, E., Nowlan, G.S., and Fletcher, T.P., 1980, A microfauna associated with early Cambrian trilobites of the *Callavia* Zone, northern Antigonish Highlands, Nova Scotia: Canadian Journal of Earth Sciences, v. 17, p. 400–418, <https://doi.org/10.1139/e80-038>.
- Landing, E., Geyer, G., Brasier, M.D., and Bowring, S.A., 2013a, Cambrian evolutionary radiation: Context, correlation, and chronostratigraphy—Overcoming deficiencies of the first appearance datum (FAD) concept: Earth-Sciences Reviews, v. 123, p. 133–172, <https://doi.org/10.1016/j.earscirev.2013.03.008>.
- Landing, E., Westrop, S.R., and Bowring, S.A., 2013b, Reconstructing the Avalonia palaeocontinent in the Cambrian: A 519 Ma caliche in South Wales and transcontinental middle Terreneuvian sandstones: Geological Magazine, v. 150, p. 1022–1046, <https://doi.org/10.1017/S0016756813000228>.
- Lapworth, C., 1891, On *Olenellus callavei* and its geological relationships: Geological Magazine, v. 8, p. 530–536.
- Lazarenko, N.P., 1962, [New lower Cambrian trilobites of the Soviet Arctic]: Collected Works on Paleontology and Biostratigraphy, Leningrad, v. 29, p. 29–78. [in Russian]
- Lermontova, E.V., 1940, Klass trilobity, in Vologdin, A.G., ed., Atlas Rukovodyashchikh Form Iskopaemykh Faun SSSR, 1, Kembriy: Moscow, State Editorial Office for Geological Literature, p. 112–162. [in Russian]
- Lermontova, E.V., 1951, [Lower Cambrian Trilobites and Brachiopods from Eastern Siberia]: All Moscow, Union Sciences-Research Geological Institute (VSEGEI), Ministry of Geology, 218 p. [in Russian]
- Lieberman, B.S., 1998, Cladistic analysis of the early Cambrian olenelloid trilobites: Journal of Paleontology, v. 72, p. 59–78, <https://doi.org/10.1017/S0022336000024021>.
- Lieberman, B.S., 1999, Systematic revision of the Olenelloidea (Trilobita, Cambrian): Bulletin of the Peabody Museum of Natural History, v. 45, p. 1–150.
- Lieberman, B.S., 2001, Phylogenetic analysis of the Olenellina (Trilobita, Cambrian): Journal of Paleontology, v. 75, p. 96–115, <https://doi.org/10.1017/S0022336000031930>.
- Lieberman, B.S., 2002, Phylogenetic analysis of some basal early Cambrian trilobites, the biogeographic origins of the Eutrilobita, and the timing of the Cambrian Radiation: Journal of Paleontology, v. 76, p. 692–708, <https://doi.org/10.1017/S0022336000041950>.
- Liñán, E., and Mergl, M., 1982, Lower Cambrian brachiopods of Sierra Morena, SW Spain: Boletín de la Real Sociedad Española de Historia Natural (Geología), v. 80, p. 207–220.
- Liñán, E., and Quesada, C., 1990, Ossa-Morena Zone, Stratigraphy, Rift phase (Cambrian), in Dallmeyer, R.D., and Martínez García, E., eds., *Premesozoic Geology of Iberia*: Berlin, Springer-Verlag, p. 259–266.
- Liñán, E., Gozalo, R., Palacios, T., Gámez Vinaned, J.A., Ugidos, J.M., and Mayoral, E., 2002, Cambrian, in Gibbons, W., and Moreno, T., eds., *The Geology of Spain*: London, Geological Society, p. 17–29, <https://doi.org/10.1144/GOSPP.3>.
- Liñán, E., Perejón, A., Gozalo, R., Moreno-Eiris, E., and Oliveira, J.T., 2004, The Cambrian system in Iberia: Cuadernos del Museo Geominero, Instituto Geológico y Minero de España, v. 3, 63 p.
- Malinky, J.M., and Geyer, G., 2019, Cambrian Hyolitha of Siberian, Baltican and Avalonian aspect in east Laurentian North America: Taxonomy and palaeobiogeography: Alcheringa, v. 43, p. 171–203, <https://doi.org/10.1080/03115518.2019.1567813>.
- Mata, J., 1986, Estudo Geoquímico de Metavulcanitos Câmbricos e Lamprófitos Tardihercínicos do Nordeste Alentejano: Evidência para a Abertura e Fecho do Prototethys: Lisbon, Dissertação e Capacidade Científica, 205 p.
- Matthew, G.F., 1886, Illustrations of the fauna of the St. John's Group continued, No. 3, Description of new genera and species (including the description of a new species of *Solenopleura* by J.F. Whiteaves): Transactions of the Royal Society of Canada, Section 4 [for 1885]: 29–89, pls. 5–7.
- Matthew, G.F., 1897, What is the *Olenellus* fauna?: The American Geologist, v. 19, p. 396–407.
- McKerrow, W.S., Scotese, C.R., and Brasier, M.D., 1992, Early Cambrian continental reconstructions: Journal of the Geological Society, v. 149, p. 599–606, <https://doi.org/10.1144/gsjgs.149.4.0599>.
- McMenamin, M.A.S., 1987, Lower Cambrian trilobite zonation, and correlation of the Puerto Blanco Formation, Sonora, Mexico: Journal of Paleontology, v. 61, p. 738–749, <https://doi.org/10.1017/S0022336000029097>.
- Neltner, L., and Poctey, N., 1950, Quelques faunes géorgiennes du Maroc: Notes et Mémoires du Service Géologique du Maroc, v. 2, no. 74, p. 53–83.
- Oliveira, J.T., Oliveira, V., and Piçarra, J.M., 1991, Traços gerais da evolução tectono-estratigráfica da Zona de Ossa-Morena, em Portugal: Cuadernos do Laboratorio Xeolóxico de Laxe, v. 16, p. 221–250.
- Ortega-Hernández, J., Esteve, J., and Butterfield, N.J., 2013, Humble origins for a successful strategy: Complete enrollment in early Cambrian olenelloid trilobites: Biology Letters, v. 9, p. 1–5, <https://doi.org/10.1098/rsbl.2013.0679>.
- Palmer, A.R., and Repina, L.N., 1993, Through a glass darkly: Taxonomy, phylogeny and biostratigraphy of the Olenellina: University of Kansas Paleontological Contributions, n. ser., v. 3, 35 p.
- Palmer, A.R., and Repina, L.N., 1997, Introduction to suborder Olenellina, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology*, Part O, Arthropoda 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. O405–O429.
- Paterson, J.R., and Edgecombe, G.D., 2006, The early Cambrian trilobite family Emuellidae Pocock, 1970: Systematic position and revision of Australian species: Journal of Paleontology, v. 80, p. 496–513, [https://doi.org/10.1666/0022-3360\(2006\)80\[496:TTECTFE\]2.0.CO;2](https://doi.org/10.1666/0022-3360(2006)80[496:TTECTFE]2.0.CO;2).
- Paterson, J.R., Edgecombe, G.D., and Lee, M.S.Y., 2019, Trilobite evolutionary rates constrain the duration of the Cambrian explosion: Proceedings of the National Academy of Science, v. 116, p. 4394–4399, <https://doi.org/10.1073/pnas.1819366116>.
- Pegel, T.V., 2000, Evolution of trilobite biofacies in Cambrian basins of the Siberian Platform: Journal of Paleontology, v. 74, p. 1000–1019, <https://doi.org/10.1017/S0022336000017571>.
- Pillola, G.L., 1991, Trilobites du Cambrien inférieur du SW de la Sardaigne, Italie: Palaeontographia Italica, v. 78, p. 1–173.
- Ponomarenko, A.G., 2005, [Unique Sinsk localities of early Cambrian organisms (Siberian Platform)]: Transactions of the Palaeontological Institute, Moscow, Nauka, v. 284, 143 p. [in Russian]
- Poucllet, A., Aarab, A., Fekkuk, A., and Benharref, M., 2007, Geodynamic evolution of the north-western paleo-Gondwanan margin in the Moroccan Atlas at the Precambrian-Cambrian boundary: Geological Society of America Special Paper, v. 423, p. 27–60, <https://doi.org/10.1130/SPE423>.
- Poulsen, C., 1927, The Cambrian, Ozarkian, and Canadian faunas of northwest Greenland: Meddelelser om Gronland, v. 70, p. 233–343.
- Pringle, J., 1913, Summary of Progress of the Geological Survey of Great Britain and the Museum of Practical Geology for 1912: London, 71 p.
- Raw, F., 1936, Mesonacidae of Comley in Shropshire, with a discussion of classification within the family: Quarterly Journal of the Geological Society of London, v. 92, p. 236–293, <https://doi.org/10.1144/GSL.JGS.1936.092.01-04.13>.
- Repina, L.N., 1979, [Dependence of morphologic features on habitat conditions in trilobites and evaluation of their significance for the systematics of the superfamily Olenelloidea]: Trudy Instituta Geologii i Geofiziki, v. 431, p. 11–30. [in Russian]
- Repina, L.N., Lazarenko, N.P., Meshkova, N.P., Korshunov, V.I., Nikiforov, N.I., and Aksarina, N.A., 1974, [Lower Cambrian biostratigraphy and fauna of Kharaulakh (Tuora-Sis Ridge)]: Transactions of the Institute of Geology and Geophysics, Nauka, Moscow, v. 235, 299 p. [in Russian]
- Richter, R., 1932, Crustacea (Paläontologie), in Dittler, R., Joos, G., Korschelt, E., Linek, G., Oltmanns, F. and Schaum, K., eds., *Handwörterbuch der Naturwissenschaften* (second edition): Jena, Germany, Gustav Fisher, p. 840–864.
- Richter, R., and Richter, E., 1941, Die Faune des Unter-Kambrians von Cala in Andalusien: Abhandlungen der Senckenbergische Naturforschenden Gesellschaft, v. 455, p. 1–90.
- Rozanov, A.Y., and Varlamov, A.I., 2008, The Cambrian system of the Siberian platform, Part 1, The Aldan-Lena Region: International Field Conference of the Cambrian Stage Subdivision Working Group (Siberian Platform, western Yakutia), 13th, Yakutia, Russia, 20 July–1 August: Novosibirsk, Paleontological Institute, Russian Academy of Science, 300 p.
- Ruiz López, J.L., Fernández Carrasco, J., Collaut Saenz de Sicilia, J.L., and Apalategui, O., 1979, Memoria de la hoja no. 896 (Higuera la Real), Mapa Geológico de España E, 1:50.000 (MAGNA): Madrid, Instituto Geológico y Minero de España, ser. 2, edition 1, 47 p.
- Rushton, A.W.A., 1966, The Cambrian trilobites from the Purley Shales of Warwickshire: Palaeontographical Society Monographs, v. 120, p. 1–55.
- Rushton, A.W.A., 1999, Cambrian rocks of England, in Rushton, A.W.A., Owen, R.M., and Prigmore, J.K., eds., *British Cambrian to Ordovician Stratigraphy*: Geological Conservation Reviews Series, The Joint Nature Conservation Committee, v. 18, p. 69–87.

- Rushton, A.W.A., Brück, P.M., Molyneux, S.G., Williams, M., and Woodcock, N.H., 2011, A Revised Correlation of the Cambrian Rocks in the British Isles: London, Geological Society, Special Report, v. 25, 62 p.
- Scotese, C.R., and McKerrow, W.S., 1990, Revised world maps and introduction, in McKerrow, W.S., and Scotese, C.S., eds., Palaeozoic Palaeogeography and Biogeography: The Geological Society of London Memoir, v. 12, p. 1–21.
- Sdzuy, K., 1961, Das Kambrium Spaniens, 2, Trilobiten: Akademie der Wissenschaften und der Literatur, Abhandlungen der Mathematisch-naturwissenschaftlichen Klasse, v. 1961, nos. 7/8, p. 217–408.
- Sdzuy, K., 1962, Trilobiten aus dem Unter-Kambrium der Sierra Morena (S. Spanien): Senckenbergiana Lethaea, v. 43, p. 181–229.
- Sdzuy, K., 1971, Acerca de la correlación del Cámbrico Inferior en la Península Ibérica: Congreso Hispano-Luso Americano de Geología Económica, 1st, Sección 1, Geología, Volume 2, Madrid, 19–23 September and Lisbon, 23–34 September: Madrid, Instituto Geológico y Minero de España, p. 753–768.
- Sdzuy, K., 1972, Das Kambrium der acadobaltischen Faunenprovinz: Zentralblatt für Geologie und Paläontologie, v. 1972, nos. 1/2, p. 1–91.
- Sdzuy, K., 2001, La reformación de fósiles deformados demostrado en trilobites del piso Marianiense (Cámbrico inferior) del Sur de la Península Ibérica: Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica, v. 96, p. 85–100.
- Shaler, N.S., and Foerste, A.F., 1888, Preliminary description of North Attleborough fossils: Bulletin of the Museum of Comparative Zoology, Harvard University, ser. 2, v. 16, p. 27–41.
- Smith, J.D.D., and White, D.E., 1963, Cambrian trilobites from the Purley Shales of Warwickshire: Palaeontology, v. 6, p. 397–407.
- Smith, L.H., and Lieberman, B.S., 1999, Disparity and constraint in olenelloid trilobites and the Cambrian radiation: Paleobiology, v. 25, p. 459–470.
- Størmer, L., 1942, Studies on Trilobite morphology, 2, The larval development, the segmentation and the sutures, and their bearing on trilobite classification: Norsk Geologisk Tidsskrift, v. 21, p. 49–164.
- Sundberg, F.A., Geyer, G., Kruse, P.D., McCollum, L.B., Pegel, T.V., Zylinska, A., and Zhuravlev, A., 2016, International correlation of the Cambrian Series 2–3, Stages 4–5 boundary interval: Australasian Palaeontological Memoirs, v. 49, p. 83–124.
- Sundberg, F.A., Karlstrom, K., Geyer, G., Foster, J.R., Hagadorn, J.W., Mohr, M.T., Schmitz, M.D., Dehler, C.M., and Crossey, L.J., 2020, Asynchronous trilobite extinctions at the early to middle Cambrian transition: Geology, v. 48, p. 441–445, <https://doi.org/10.1130/G46913.1>.
- Teixeira, C., 1952, La faune cambrienne de Vila Boim au Portugal: Boletim da Sociedade Geológica de Portugal, v. 10, p. 169–188.
- Thomas, A.T., Owens, R.M., and Rushton, A.W.A., 1984, Trilobites in British stratigraphy: Geological Society of London, Special Report, v. 16, 76 p.
- Walch, J.E.I., 1771, Die Naturgeschichte der Versteinerungen zur Erläuterung der Knorr'schen Sammlung von Merkwürdigkeiten der Natur: Nürnberg, Felßbecker, 235 p.
- Walcott, C.D., 1890, Descriptive notes of new genera and species from the lower Cambrian or *Olenellus* Zone of North America: Proceedings of the U.S. National Museum, v. 12, p. 33–46.
- Walcott, C.D., 1910, *Olenellus* and other genera of the Mesonacidae: Smithsonian Miscellaneous Collections, v. 53, no. 6, p. 231–422.
- Walcott, C.D., 1912, Cambrian Brachiopoda: U.S. Geological Survey, Monograph 51, Part 1, 872 p.
- Walcott, C.D., 1913, Cambrian geology and paleontology: Smithsonian Miscellaneous Collections, v. 57, no. 11, p. 310–326.
- Webster, M., 2007, Ontogeny and evolution of the early Cambrian trilobite genus *Nephrolenellus* (Olenelloidea): Journal of Paleontology, v. 81, p. 1168–1193, <https://doi.org/10.1666/06-092.1>.
- Webster, M., 2009, Ontogeny, systematics, and evolution of the effaced early Cambrian trilobites *Peachella* Walcott, 1910 and *Eopeachella* new genus (Olenelloidea): Journal of Paleontology, v. 83, p. 197–218, <https://doi.org/10.1666/08-106.1>.
- Webster, M., and Bohach, L.L., 2014, Systematic revision of the trilobite genera *Laudonia* and *Lochmanolenellus* (Olenelloidea) from the lower Dyeran (Cambrian Series 2) of western North America: Zootaxa, v. 3824, p. 1–66, <https://doi.org/10.11646/zootaxa.3824.1.1>.
- Webster, M., and Hageman, S.J., 2018, *Buenellus chilhoweensis* n. sp. from the Murray Shale (lower Cambrian Chilhowee Group) of Tennessee, the oldest known trilobite from the Iapetan margin of Laurentia: Journal of Paleontology, v. 92, p. 442–458, <https://doi.org/10.1017/jpa.2017.155>.
- Webster, M., and Landing, E., 2016, Geological context, biostratigraphy and systematic revision of late early Cambrian olenelloid trilobites from the Parker and Monkton formations, north-western Vermont, USA: Australasian Palaeontological Memoirs, v. 49, p. 193–240.
- Westrop, S.R., and Landing, E., 2011, Lower Cambrian (Branchian) eodiscoid trilobites from the lower Brigus Formation, Avalon Peninsula, Newfoundland, Canada: Memoirs of the Association of Australasian Palaeontologists, v. 42, p. 209–262.
- Whittington, H.B., 1989, Olenelloid trilobites: Type species, functional morphology and higher classification: Philosophical Transactions of the Royal Society of London, B, Biological Sciences, v. 324, p. 111–147, <https://doi.org/10.1098/rstb.1989.0041>.
- Whittington, H.B., 1997, The trilobite body, in Kaessler, R.L., ed., Treatise on Invertebrate Paleontology, Part O (Revised), Arthropoda 1, Trilobita: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. O87–O135.
- Williams, M., Ruston, A.W.A., Cook, A.F., Zalasiewicz, J., Martin, A.P., Condon, D.J., and Winrow, P., 2013, Dating the Cambrian Purley Shale Formation, Midland Microcraton, England: Geological Magazine, v. 150, p. 937–944, <https://doi.org/10.1017/S0016756813000010>.
- Zhang, X., Ahlberg, P., Babcock, L.E., Choi, D.K., Geyer, G., Gozalo, R., Hollingsworth, J.S., Li, G., Naimark, E.B., Pegel, T., Steiner, M., Wotte, T., and Zhang, Z., 2017, Challenges in defining the base of Cambrian Series 2 and Stage 3: Earth-Science Reviews, v. 172, p. 124–139, <https://doi.org/10.1016/j.earscirev.2017.07.017>.
- Żylińska, A., 2013, The oldest Cambrian trilobites from the Holy Cross Mountains, Poland: Taxonomic, stratigraphic and biogeographic reappraisal: Acta Geologica Polonica, v. 63, p. 57–87, <https://doi.org/10.2478/agnp-2013-0002>.

Accepted: 23 May 2021