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TRILOBITES AND STRATIGRAPHY OF THE MARIANIAN STAGE (CAMBRIAN SERIES 2) OF THE OSSA-MORENA ZONE, SW IBERIA

TRILOBITES E ESTRATIGRAFIA DO MARIANIANO (SÉRIE 2, CÂMBRICO) DA ZONA DE OSSA-MORENA, SW DA IBÉRIA

Tese no âmbito do Doutoramento em Geologia orientada pela Doutora Sofia Raquel Cardoso Pereira e pelo Professor Doutor Eduardo Jesús Mayoral Alfaro e apresentada ao Departamento de Ciências da Terra da Faculdade de Ciências e Tecnologia da Universidade de Coimbra

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Doutoramento em Geologia – Processos Geológicos

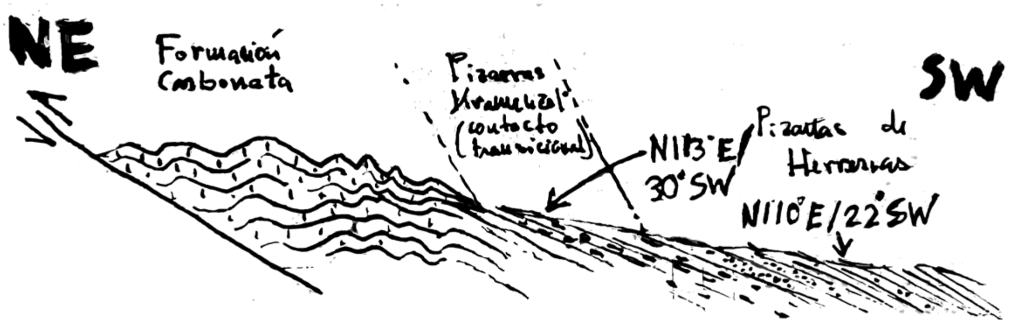
Orientadora: Sofia Raquel Cardoso Pereira
Coorientador: Eduardo Jesús Mayoral Alfaro

“We must preach up travelling (…) as the first,
second, and third requisites for a modern geologist,
in the present adolescent stage of Science.”

***Sir Charles Lyell**, letter to Roderick Murchison*
(January 12th, 1829),

“Las arcillas son como el agua: van de Saliente a Poniente. Pero la ‘cal prieta’ no sigue orientación ninguna, y se retuerce sobre sí misma.”

Anonymous shepherd *from Cañaveral de León (Huelva), who, accidentally, described the geology of his village.*



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We are taught to write within the parameters of a determinate scientific journal. However, no parameter is worth when it comes to a section like this, which tends to be personal and passionate. And now that I am facing the blank paper, I find it more difficult than I thought.

To begin with, there can be no other person than the one responsible for the fact that I am writing this thesis today. My mentor, advisor, and friend Dr. Sofia Pereira.

I had the immense pleasure (and luck) of meeting her for the first time in September 2018 during the IV Congresso Ibérico de Paleontologia in Vila Real (Trás-os-Montes, Portugal). I was completely captivated by her presentation, her way of speaking and her knowledge about trilobites. At that time, I could not have imagined that, shortly afterwards, I would have the chance to work with her side by side. In July 2020, I had the opportunity to visit the Museu Geológico de Lisboa to review the trilobite collections of the Cambrian of Vila Boim, collected by Nery Delgado in the early twentieth century, under her supervision. That would be the beginning of our collaboration up to this day.

Moreover, it is particularly noteworthy that, thanks to her tireless efforts, I received my pre-doctoral grant (with all the "misadventures" that this process entailed).

Leaving strictly academic matters aside, Sofia has been a constant support throughout all these years. She always pulled me through, even when I felt I was not good enough or my work was pointless. Her supervision, her way of working and her way of thinking have given me a critical view. I will never be grateful enough for all she has done for me.

Next, I would like to dedicate a few words to my "scientific father" in the world of Palaeontology and the co-supervisor of this work: Prof. Eduardo Mayoral.

I have known him since I started studying Geology at the University of Huelva. Since the beginning of my university studies, everyone in the faculty talked to me about an "exceptional professor of Palaeontology" and, certainly, I had the opportunity to experience it myself both in the classroom and during fieldwork. From that moment on, it was clear that I wanted him to be my supervisor for my Final Degree Project. That privilege has lasted until today, the end of my thesis, and I hope it is only the beginning of a long journey. Throughout these years, we had countless experiences (especially during fieldwork), which I remember with especial fondness and longing. I wish that we can continue to live many more experiences together. Thank you, Eduardo, for your help, support, and advice.

In the same way that Eduardo introduced me to the world of Palaeontology, there is another person to whom I owe my first contact with trilobites and the Cambrian Period: Prof. Rodolfo Gozalo.

Although he could not be one of the co-supervisors of this work for formal reasons, he has not stopped collaborating with me until today. He was my supervisor during my MSc thesis at the University of Valencia, and many of the notions I have today about trilobite systematics, biostratigraphy and palaeobiogeography of the Cambrian Period are thanks to him. His critical comments and experience in international Cambrian correlation have been fundamental in developing the different papers included in this work. Thank you for introducing me to the "trilo-community", for the fieldwork campaigns, for the trips to different conferences and, in general, for your kindness and generosity.

The fourth great personality behind this thesis, with whom I have had the good fortune to work with, is undoubtedly the greatest expert on the Cambrian rocks of the Ossa-Morena Zone (and, certainly, of Iberia), as well as a great teacher and person: Prof. Eladio Liñán.

It would be unfair not to say that Eladio laid the foundations of this thesis. During the elaboration of the MAGNA series (and in subsequent fieldwork campaigns), he collected, studied, and classified many trilobites from the Marianian of the Ossa-Morena Zone, which I have had available for study during my thesis. He also established the biostratigraphy of the rocks of this region. The truth is that I have only been able to meet Prof. Liñán on a few occasions: to do some fieldwork in Huelva, Seville and Toledo, to review the trilobite collections in his office at the University of Zaragoza, and to finish some of the papers we were carrying out. Besides personal meetings, Prof. Liñán and I have frequently communicated about my work. It has been gratifying to benefit from his more than fifty years of experience in the Cambrian Period and trilobites field. He is a reminiscence of the untold work done by the few for the benefit of the many. Spain and Portugal's geological and palaeontological communities owe him a great deal.

Throughout the preparation of this thesis and all the papers that comprise it, I have received many comments, criticisms, and corrections from various experts in the field who have acted as reviewers of those articles. I would like to dedicate this paragraph to thank them for their work: firstly, Dr. Frederick Allen Sundberg (Arizona), who has reviewed most of my published works and has contributed remarkably to each of them; Prof. Gerd Geyer (Germany) for his comments, corrections, and help with the stratigraphical details of the Cambrian of Morocco; Profs. Peter Jell (Australia) and Igor V. Korovnikov (Russia) for their criticism, and finally Prof. Per Ahlberg (Lund, Sweden), Dr. James D. Holmes (New England, Australia), Dr. Mark Webster (Chicago, USA) and Dr. Lukas Laibl (Czech Republic) for their positive feedback.

Apart from the numerous fieldwork campaigns in the southwest of the Iberian Peninsula, I have been lucky enough to review the different fossil collections collected by different palaeontologists throughout the twentieth century (e.g., Nery Delgado, Rudolf and Emma Richter, Klaus Sdzuy, Mª Dolores Gil Cid, among others). This paragraph is dedicated to all the good people who have assisted me during the visits to different museums and universities to review these collections: Miguel Ramalho, in loving memory, from the Museu Geológico de Lisboa; Ignacio Canudo Sanagustín and Esther Díaz Berenguer from the Museo de Ciencias Naturales of the University of Zaragoza; Mª de la Concepción Herrero Matesanz, Gema García Martín and Isabel Díaz Megías from the Complutense University of Madrid; Jessica D. Cundiff from the Museum of Comparative Zoology of Harvard; and, with especial affection, Mónica M. Solórzano Kraemer from the Senckenberg Natural History Museum of Frankfurt.

Aside from all the professionals I mentioned above, there are other people who, although they do not belong to the professional world of Palaeontology, have contributed hugely not only to my work, but also to my life. One of those people is my colleague and friend Ignacio Garzón.

Ignacio Garzón is from Puerto Moral (Huelva), although he has lived in Cortegana for years until today. Since he was young, his interests have been very broad, from poetry to ufology. However, his two greatest passions have always been the same: Geology and Palaeontology. For years, Ignacio has travelled the entire province of Huelva in search of rocks, minerals, and fossils, becoming one of the greatest experts (in my opinion) on the Geology of this province. It is especially noteworthy that Ignacio is truly passionate about graptolites, of which he has found memorable specimens over the years. In addition, he has rediscovered many palaeontological sites in the Sierra de Aracena, from the Cambrian (some of which are included in this thesis) to the Carboniferous, and especially those belonging to the Ordovician and Silurian, where most of his beloved graptolites are found. For all these reasons, we decided to dedicate a new trilobite species (*Chelediscus garzoni* Collantes et al., 2023) to him.

Ignacio started studying at UHU with me in 2013 at the age of 46 (when I started as an Environmental Science student, before moving to Geology in 2014). Every week, and several times a week, he drove 1h 40min from Cortegana to Huelva to attend to his classes. At times, he had to combine his classes with whatever job he had at that moment. Moreover, all this while overseeing his family. He was the one who gave me my first fossils in 2013. And years later, he was the one who took me to some of the Cambrian fossil sites I have studied over the last years. A huge part of my thesis has been thanks to his work, knowledge, and commitment.

Today, 10 years later, Ignacio is still driving 1h 40min several times a week to attend to his classes and is very close to finishing his degree in Geology. I would like this text to serve as a reward for all his efforts and to express my pride in him. In the same way, thanks to his wife (Dolores Alonso González) and son (Ignacio Garzón Alonso) for their support and for believing in our project.

On a different note, there is a especial place in the Sierra de Aracena to which I owe more than just a few words: the village of Cañaveral de León.

I met this little village by chance during one of my first fieldwork campaigns in the Sierra de Aracena. I never thought that a place like this would mean that much to me. Its people, its views, its silence, “La Laguna”, “Las callejas del agua”, etc. A charming place that I will always carry with me in my heart. However, more important than the village itself are some of its personalities who have facilitated me the course of my fieldwork campaigns throughout this territory.

The main responsible person is the mayor of Cañaveral de León, Mercedes Gordo Márquez ("Merchi"). From the very first moment, Merchi has made it possible for us to carry out our fieldwork in the surroundings of her village, giving us the village’s shelter and covering all our needs. Thanks to her, we also had the opportunity to talk about our findings to the villagers, and organize different dissemination events (e.g., Geolodía 2021) and a national congress (XX EJIP 2022). Merchi is fully involved in protecting and disseminating the palaeontological heritage of her village. For this reason, I am very grateful to her for her involvement in the development of this work.

I cannot talk about Cañaveral de León without mentioning the family that has looked after me on each of my travels: the family Carbajo Navarro from “Bar San Sebastián”. There are no words to thank Paco Carbajo and Ángeles Navarro (“Angelita”), together with their sons and daughters (Cristina, Jesús, Francisco, Lucía and Carmen) for the exceptional treatment they have given me throughout all these years. The bonfire, the hot food, the "amarguinha", the love, and the good conversation have made the long days of hammering rocks less hard. I can never repay your unconditional love. Thank you for being my family; thank you for being my home.

Much of my PhD was done in the Laboratory of Tectonics and Palaeontology of the Department of Earth Sciences of the University of Huelva, where all the samples I collected over the years were deposited. Therefore, I have a great connection with this university, especially with many of its professors who, from the beginning of my studies, have believed in me and my work. I want to cite these professors in thanks for their kindness and support: Mercedes Cantano Martín, Francisco Manuel Alonso Chaves (“Francis”), Juan Antonio Morales (“er Teniente”), Manuel Toscano Macías, Teodosio Donaire Romero, and Josep Tosquella Angrill, among others. Thank you all.

I must also mention all my great geologist and environmentalist friends from the Faculty of Experimental Sciences of the University of Huelva, who make the days at the faculty so enjoyable (or, at least, less tiresome): David Amador, Víctor Amador, Jose Ramírez (“Cuadri”), Fernando Hervás, Cristóbal Cantero, Melissa León, Daniel J. Cruzado, Chema Fuentes-López, and Elena García-Villalba, among others.

At the University of Valencia, where I lived for a year, there were two people who made my time there less difficult and who have also supported me and helped me throughout my whole thesis heretofore: the “conodontologists” Prof. Jose Ignacio (‘Nacho’) Valenzuela Ríos, and Prof. Jau-Chyn (‘Teresa’) Liao. I will fondly remember all your good advice and encouragement.

I also wanted to thank my colleagues from the Departamento de Ciências da Terra of the Universidade de Coimbra for the good environment, the midday-lunches and the “Portuguese birthdays”: Prof. Maria Helena Henriques, Dr. Gustavo Gonçalves, Dr. Pedro Correia, Dr. Patricia João, Dr. Inês Pereira, Catarina Caprichoso, Salomé Custódio, Yasir Shehzad, Senay Ozkaya, Virginia Lattao, Opeyemi Adewumi, Keynesmenio Sousa, Andreia Nunes, and Rafael Mendes, among others.

A especial paragraph is dedicated to my good friends from "La paja triste". The time during my thesis has been much more bearable thanks to all of them: Nieves Ortega, Isabel Barrientos, Celia Moreno, Claudia Mariño, Marina Teréñez, Jaime Rodríguez, Rafael Segovia, Adolfo Villar, David Caparrós, and Borja R. Duque.

For my girlfriend, Ainara Rodrigo García, the greatest of gratitude. With me, she had to bear with what no one else had put up with. She had come with me to do fieldwork for several summers -even in the middle of a heatwave- to look for trilobites. She had come with me in the pouring rain, or the hardest frost, to do mapping and stratigraphy. She had travelled thousands of miles by my side. She had to put up with my frustrations more than anyone else. “*Understanding is love’s other name*”, as Katia Kraft said. Thanks for making it happen.

Thanks to my whole family.

Finally, thanks to Alexandra Elbakyan (Sci-hub) for making Science accessible to everybody.

Abstract: The Cambrian Series 2 is a challenging chronostratigraphical division. In Europe, its sequences are hard to identify due to the scarcity of the fossil record. An exception is the Ossa-Morena Zone (OMZ), SW Iberia, which has attracted the interest of numerous researchers throughout the 19th and 20th centuries. Four regional stages were proposed for the Cambrian Series 2 based on trilobites and archaeocyaths: Ovetian, Marianian, Bilbilian and Leonian (lower part). Among these, the Marianian is problematic, having undergone several conceptual modifications since its original erection and being characterised by a low trilobite diversity and abundance. Its usefulness through the Iberian Peninsula is still a subject of debate since its correlation with the global scheme lacks accuracy. The main goals of this thesis are to study the trilobite assemblages in order to correlate the Marianian Stage across the OMZ and other Iberian Cambrian domains, and to evaluate its potential for international correlation and subdivision within the global context of the Cambrian Series 2.

The Cambrian outcrops studied can be divided into six tectonosedimentary units: Alter do Chão-Elvas Sector, Alconera Block, Viar-Benalija Block, Cumbres Block, Herrerías Block, and Arroyomolinos Block. The stratigraphical and palaeontological record of their Marianian sequences was reassessed and correlated. The classical fossil sites were located and sampled. New fossil sites were discovered, and new materials were collected, with a total of 1299 trilobite fossils. In addition, 585 specimens of the most relevant trilobite collections of the Marianian from the OMZ were reviewed, including those from the Museu Geológico de Lisboa (Portugal), the Senckenberg Museum of Frankfurt (Germany), the Complutense University of Madrid (Spain) and the collections of Prof. Eladio Liñán at the University of Zaragoza (Spain).

A total of 23 trilobite species were identified in the Marianian of the OMZ, four in open nomenclature. Among these species, six have been studied in detail, which results have been published in five indexed papers: *Atops calanus, Callavia choffati, Chelediscus garzoni, Pseudatops reticulatus, Serrodiscus bellimarginatus* and *Strenuaeva sampelayoi*. For the first time in OMZ, *Hebediscus* is figured and *Kingaspis* and *Pseudatops* have been identified, and a new species was erected (*Chelediscus garzoni*). The genus '*Sdzuyomia*' is here considered a junior synonym of *Callavia*; and the species 'S*. melendezi*', '*Ellipsostrenua alanisiana'* and '*Strenuaeva marocana'* are considered junior synonyms of *S. sampelayoi*. The genus *Callavia* is assigned to 'Judomioidea', whereas *Chelediscus* is assigned to Calodiscidae, with new diagnoses being provided for both genera. Three groups (*bellimarginatus, speciosus* and *daedalus*) were proposed to encompass the species currently included in cosmopolitan *Serrodiscus*, revealing different lineages and clarifying its stratigraphical and palaeogeographical distribution.

From a biostratigraphical point of view, new data improve and refine intra- and inter-regional correlation and new links with the Central Iberian Zone and the Iberian Chains have been found. The base of the Marianian Stage is characterised by the First Appearance Datum (FAD) of *Strenuella*, being the lower Marianian characterised by *Delgadella souzai*, *Acanthomimacca*? sp. and *Saukianda andalusiae*. The middle Marianian is defined by the FAD of *Strenuaeva sampelayoi*, and characterised by *Delgadella souzai*, *Saukianda andalusiae*, *Alanisia guillermoi*, *Perrector perrectus*, *Eops eo*, *Gigantopygus* cf. *bondoni*, *Kingaspis* cf. *velata*, *Andalusiana cornuta*, *Triangulaspis fusca*, *Callavia choffati*, *Rinconia schneideri*, *Calodiscus ibericus*, *Atops calanus*, *Hicksia elvensis*, and *Termierella sevillana*. The base and top of the upper Marianian are marked, respectively, by the FAD and Last Appearance Datum (LAD) of *Serrodiscus bellimarginatus*, being this substage characterised by *Triangulaspis fusca*, *Hebediscus* sp., *Chelediscus garzoni*, *Protaldonaia morenica*, *Atops calanus*, and *Pseudatops reticulatus*.

Globally, the new biostratigraphical data strengthen the correlation with other Cambrian Series 2 sequences worldwide. Along the western Gondwana margin, the Marianian Stage correlates with the Banian Stage from Morocco and the Charlottenhof Formation from Germany. Regarding western and eastern Avalonia, it correlates with upper *Callavia* and lower *Strenuella sabulosa* Biozones. In Baltica, it correlates, on the one hand, with upper *Holmia kjerulfi* and lower *Ellipsostrenua spinosa* Biozones in Scandinavia and, on the other hand, with the upper *Holmia*-*Schmidtiellus* and lowermost *Protolenus*-*Issafeniella* Biozones in Poland. In Siberia, it is equivalent to most of the Botoman and lowermost Toyonian Stages. In addition, new biostratigraphical links have been established with the *Elliptocephala asaphoides* Biozone from the Laurentian Taconic Allochthon.

Keywords: Cambrian, Palaeontology, Iberia, Stratigraphy, Trilobita.

Resumo: A Série 2 do Sistema Câmbrico é uma divisão cronoestratigráfica desafiante. Na Europa, as suas sequências são difíceis de identificar devido à raridade de fósseis. Uma exceção é a Zona de Ossa-Morena (ZOM), no SW da Península Ibérica, que tem atraído a atenção de muitos investigadores ao longo dos séculos XIX e XX. Foram propostos quatro andares regionais para a Série 2 do Câmbrico com base em trilobites e arqueociatos: Ovetiano, Marianiano, Bilbiliano e Leoniano (parte inferior). Entre estes, o Marianiano é bastante problemático, tendo passado por várias modificações conceptuais desde a sua proposta original e sendo caracterizado por uma baixa diversidade e raridade de trilobites. A sua utilidade a nível da Península Ibérica é ainda objeto de debate, uma vez que a correlação com o esquema global é pouco precisa. Os principais objetivos desta tese são o estudo das associações de trilobites para correlação do Andar Marianiano na ZOM, bem como avaliação do seu potencial noutros domínios ibéricos e relevância para a subdivisão internacional da Série 2 do Câmbrico.

Os afloramentos câmbricos estudados distribuem-se em seis unidades tectonosedimentares: Sector Alter do Chão-Elvas, Bloco de Alconera, Bloco de Viar-Benalija, Bloco de Cumbres, Bloco de Herrerías e Bloco de Arroyomolinos. O registo estratigráfico e paleontológico das suas sequências marianianas foi reavaliado e correlacionado. As jazidas fossilíferas clássicas foram localizadas e amostradas. Foram descobertas novas localidades fósseis e recolhidos novos materiais, num total de 1299 fósseis de trilobites. Adicionalmente, foram revistos 585 espécimes das coleções de trilobites mais relevantes do Marianiano da ZOM, incluindo as do Museu Geológico de Lisboa (Portugal), do Museu Senckenberg de Frankfurt (Alemanha), da Universidade Complutense de Madrid (Espanha) e as coleções do Prof. Eladio Liñán da Universidade de Saragoça (Espanha).

Identificaram-se no total 23 espécies de trilobites no Marianiano da ZOM, quatro em nomenclatura aberta. Entre estas espécies, seis foram estudadas em pormenor e os resultados publicados em cinco artigos indexados: *Atops calanus*, *Callavia choffati*, *Chelediscus garzoni*, *Pseudatops reticulatus*, *Serrodiscus bellimarginatus* e *Strenuaeva sampelayoi*. Pela primeira vez na ZOM, *Hebediscus* é figurado e *Kingaspis* e *Pseudatops* identificados e formalizou-se uma nova espécie (*Chelediscus garzoni*). O género '*Sdzuyomia*' foi considerado um sinónimo júnior de *Callavia* e as espécies '*S. melendezi*', '*Ellipsostrenua alanisiana*' e '*Strenuaeva marocana*' consideradas sinónimos júnior de *S. sampelayoi*. O género *Callavia* é atribuído a 'Judomioidea' e *Chelediscus* a Calodiscidae, sendo apresentadas novas diagnoses para ambos os géneros. Foram propostos três morfogrupos (*bellimarginatus*, *speciosus* e *daedalus*) para englobar as espécies atualmente incluídas no género cosmopolita *Serrodiscus*, revelando distintas linhagens e esclarecendo a sua distribuição estratigráfica e paleogeográfica.

Do ponto de vista bioestratigráfico, os novos dados melhoraram a correlação intra- e inter-regional, estabelecendo-se novas correlações com as sequências da Zona Centro-Ibérica e das Cadeias Ibéricas. A base da Andar Marianiano está marcada pelo Datum do primeiro aparecimento (FAD) de *Strenuella*, sendo o Marianiano inferior caracterizado pela coocorrência de *Delgadella souzai*, *Acanthomimacca*? sp. e *Saukianda andalusiae*. O Marianiano médio é definido pelo FAD de *Strenuaeva sampelayoi* e caracterizado por *Delgadella souzai*, *Saukianda andalusiae*, *Alanisia guillermoi*, *Perrector perrectus*, *Eops eo*, *Gigantopygus* cf. *bondoni*, *Kingaspis* cf. *velata*, *Andalusiana cornuta*, *Triangulaspis fusca*, *Callavia choffati*, *Rinconia schneideri*, *Calodiscus ibericus*, *Atops calanus*, *Hicksia elvensis* e *Termierella sevillana*. A base e o topo do Marianiano superior estão marcados, respetivamente, pelo FAD e pelo Datum de último aparecimento (LAD) de *Serrodiscus bellimarginatus*, sendo este subandar caracterizado por *Triangulaspis fusca*, *Hebediscus* sp., *Chelediscus garzoni*, *Protaldonaia morenica*, *Atops calanus* e *Pseudatops reticulatus*.

De um ponto de vista global, os novos dados bioestratigráficos reforçam a correlação com outras sequências da Série 2 do Câmbrico a nível mundial. Ao longo da margem ocidental do Gondwana, o Andar Marianiano correlaciona-se com o Andar Baniano de Marrocos e com a Formação Charlottenhof da Alemanha; na Avalónia ocidental e oriental, correlaciona-se com as biozonas *Callavia* superior e *Strenuella sabulosa* inferior. Na Báltica, correlaciona-se com as biozonas *Holmia kjerulfi* superior e *Ellipsostrenua spinosa* inferior na Escandinávia e com as biozonas *Holmia*-*Schmidtiellus* superior e *Protolenus*-*Issafeniella* inferior na Polónia. Na Sibéria, é equivalente à maior parte dos Andares Botomano e Toyoniano inferior. Por fim, foram também estabelecidas novas ligações bioestratigráficas com a biozona *Elliptocephala asaphoides* do Alóctone Tacónico da Laurentia.

Palavras-chave: Câmbrico, Paleontologia, Iberia, Estratigrafia, Trilobita.

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1. Introduction

This work is a compendium of five papers published in internationally indexed journals focused on the palaeontological and stratigraphical study of the trilobite associations of the Marianian Stage of the Iberian Ossa-Morena Zone (OMZ).

The Cambrian outcrops of the OMZ are among the most extensive in Europe. Due to this especial representation of Cambrian sequences, the regional Marianian Stage (Sdzuy, 1971) was originally described in this domain. However, from a palaeontological point of view, it is characterised by a low diversity and abundance of fossils, generally poorly preserved, which has difficulted the correlation of these rocks both regionally and internationally.

The Marianian Stage has been traditionally correlated with the upper part of the Cambrian Stage 3 and the lower part of the Cambrian Stage 4, both belonging to the so-called Cambrian Series 2 (521–509 My) (Sundberg et al., 2016; Geyer, 2019; Peng et al., 2020). Given the scarcity and poor preservation of its fossil record, together with the fact that some of the classic works (e.g., Richter & Richter, 1940, 1941; Sdzuy, 1961, 1962) describing its fossil associations have gone unnoticed, the Marianian palaeontological record has been mostly overlooked by the Cambrian international community. In recent years, significant efforts have been made to establish the division of the Cambrian Series 2, especially of the base of Stage 4 (see Peng et al., 2020). Therefore, a better understanding of the Marianian Stage of Iberia and its relationship with other Cambrian domains is timely and relevant.

By studying one of the most frequent groups with the greatest potential for correlation, the trilobites, this thesis constitutes a first approach to the palaeontological and stratigraphical characterisation of the Marianian Stage in the OMZ. The main stratigraphical sections of this territory and the studied fossil sites are presented, and the trilobite diversity and implications are assessed. Relevant taxa for systematics of the group and/or biostratigraphy and palaeobiogeography were selected and studied in detail. Trilobite biostratigraphical correlation with other Cambrian outcrops of the Iberian Peninsula is explored. For those species with a wide geographical distribution, their palaeobiogeography importance is highlighted, as well as their possible role in the international correlation of the Cambrian Series 2.

1.1. Objectives

The objectives set for this thesis are:

1) Test the correlation of the Marianian Stage throughout the OMZ and with the remaining Iberia based on trilobites.

2) Explore the potential of the Marianian Stage for international correlation and division of the Cambrian Series 2.

In order to achieve the established objectives, a set of subordinate tasks were performed:

1) Review, from a stratigraphical and regional point of view, the Cambrian outcrops of the OMZ, with especial interest in the Marianian sequences.

2) Characterise and correlate the stratigraphical sequences of the different Cambrian ‘blocks’ of the OMZ (Vila Boim, Alconera, Viar-Benalija, Arroyomolinos, Herrerías and Cumbres blocks), giving especial attention to the Marianian units.

3) Determine stratigraphical markers to correlate the Marianian sequences of the OMZ with those of other Cambrian outcrops of the Iberian Peninsula.

4) Revise the existing Marianian trilobite specimens from the OMZ in national and international collections.

5) Conduct new fieldwork campaigns to search for new fossil occurrences.

6) Carry out a systematic study of selected trilobite taxa with the greatest potential for the proposed objectives and of new occurrences potentially discovered during this work.

7) Frame, from a biostratigraphical point of view, the studied fossil associations, both regionally and internationally, to improve the previous schemes or provide new ones.

8) Determine the palaeobiogeographical affinities of the fossil associations and fit them in the existing schemes of palaeogeographical realms.

9) Disseminate the results by participating in scientific meetings and publishing the obtained data in especialised international journals.

1.2. Pioneer works on the Cambrian from southwestern Iberia

The Cambrian rocks of the Iberian Peninsula have attracted the interest of numerous naturalists and researchers throughout the nineteenth and twentieth centuries from a stratigraphical and palaeontological point of view.

The first author describing the Cambrian "primordial fauna" of the Iberian Peninsula was Prado (1855), who found the trilobite '*Ellipsocephalus pradoanus'* Verneuil & Barrande, 1855 (=*Realaspis*? *pradoanus*) in Los Cortijos de Malagón, Toledo Mountains. This pioneer author was followed promptly by others who studied several Spanish Cambrian localities, although most of these works were focused on the Cambrian outcrops from the Iberian Chains and northern Spain (e.g., Verneuil, 1862; Verneuil & Barrande, 1860; Mallada & Buitrago, 1878; Delgado, 1879; Barrois, 1882). In this sense, the Cambrian outcrops from the southwestern Iberian Peninsula, including Eastern Portugal (Alentejo), Andalusia (Cordoba, Seville, and Huelva provinces), and Extremadura (Badajoz Province) have received less attention at that time.

1.2.1. Eastern Portugal

In Portugal, the earliest reference to Cambrian rocks was made by Delgado (1870), who recognized a great part of the Alentejo region sedimentary sequences as representing the stages 'A' and 'B' of Barrande (1852). This assignment was later confirmed by Delgado & Choffat (1899) and Delgado (1904), due to the discovery of a Cambrian trilobite assemblage from Vila Boim (Elvas, eastern Portugal), later revised by Teixeira (1952).

1.2.2. Cordoba Province

On the other side of the border, in Sierra Morena (Andalusia), Macpherson (1878) was the first to report a Cambrian archaeocyath from El Pedroso, Seville, named by Roemer (1878) as '*Archaeocyathus marianus*' Roemer, 1878 (=*Frinalicyathus marianus sensu* Perejón, 1984) and being the first archaeocyath report from Europe. Shortly after, during the geological explorations of Córdoba, Mallada (1880a, b) considered the putative existence of Cambrian rocks in this province, based exclusively on lithological correlation. Subsequent works by Hernández-Pacheco (1907, 1917, 1918a, b) described archaeocyath assemblages from Sierra de Córdoba similar to that of El Pedroso, confirming its Cambrian age. These works were followed by several palaeontological studies by Carbonell (1926, 1929, 1940), who also focused on the archaeocyaths of Córdoba; Richter & Richter (1927) describing the bivalved arthropod *Isoxys carbonelli* Richter & Richter, 1927 from Las Ermitas; Hernández-Sampelayo (1933), who represented a geological section from Santa María de Trassiera; and Simon (1939), who elaborated a detailed stratigraphical section from Las Ermitas, analysing the distribution of facies and archaeocyaths.

1.2.3. Seville Province

In 1937, an extensive, preliminary geological expedition throughout the Andalusian Palaeozoic was carried out by German engineers Frank Lotze and Wilhelm Henke, with the support of the engineer Wilhelm Pasch, settled in Bilbao. Prof. Lotze and Henke entrusted two talented geologists, Rudolf Richter and Wilhelm Simon, to study the northern area of Seville to find fossils that would make it possible to precise the age of the rocks. Their joint fieldwork campaign occurred from the Summer of 1937 to the Spring of 1938 (Simon, 1951). During this period, Wilhelm Simon and Rudolf Richter visited and mapped an extensive area extending from Cantillana to San Nicolás del Puerto, focusing on the Lower Palaeozoic sequences. It was on this trip that these geologists found a rather unusual trilobite assemblage between the localities of Cazalla de la Sierra and Alanís, which they described as the "*Saukianda* Fauna" (due to the abundant presence of the newly erected trilobite *Saukianda andalusiae* Richter & Richter, 1940) (Fig. 1). The results of this discovery were published by Richter & Richter (1940), who stated that this trilobite assemblage, composed of eleven different taxa, showed no relationship to any other known from the rest of Europe, Africa or the “Acadobaltic Province” (i.e., Atlantic region). It was, in turn, linked to the Cambrian faunal realms of North America, East Asia, and South Asia, placed around the Pacific region. Thus, the “*Saukianda* Fauna” was recognized as “the first Pacific trilobite fauna in the European Cambrian”. In addition, those rocks were assigned to the ‘Upper Cambrian’ based on the correlation with North American trilobites.

However, Wilson (1948) considered that the *Saukianda* Fauna “seemed more likely to be pre-*Paradoxides* in age and, quite likely, Lower Cambrian”. However, the petrographical study of these levels, later published by Simon (1950), suggested a possible "*Paradoxides*" (i.e., ‘Middle Cambrian’) age for these rocks through comparison with other ‘Middle Cambrian’ outcrops from Spain. Subsequently, Richter & Richter (1949) addressed the controversies regarding the age of the “*Saukianda* Fauna”, discussing all the evidence and comments stressed in letters from other authors, and suggested that a ‘Lower Cambrian’ age for these trilobites was plausible.

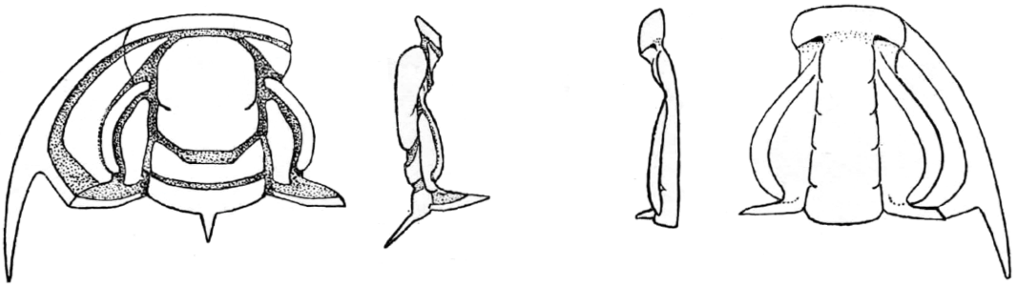
In his unpublished thesis, Fricke (1941) studied some of the Cambrian outcrops from northern Seville and southern Badajoz, establishing the Precambrian-Cambrian lithostratigraphical units currently used for these regions (e.g., ‘Malcocinado Series’, ‘Calizas de Agua’, ‘Benalija beds’).

Simon (1941) independently worked in the locality of San Nicolás del Puerto, mainly focusing on its lower Palaeozoic rocks. Years later, he published an extensive work including both the mapping and stratigraphy carried out together with Rudolf Richter between 1937 and 1938 in northern Seville, and formally defining the Cambrian lithostratigraphical units that he and Richter & Richter (1940) had previously used for this territory (e.g., ‘Tambor Series’, ‘Campoallá Series’, ‘Alanís beds’) (Simon, 1951, tab. 1).

Posterior contributions from northern Seville include those of Debrenne (1958), who identified an archaeocyathid specimen from the ‘Alanis beds’ considered to be closely related to *Beticocyathus* Simon, 1939, and Henningsmoen (1958), who reviewed the trilobite collection of the “*Saukianda* Fauna” published by Richter & Richter (1940). This author also collected new material from the type area, defending that many of the trilobite species previously reported were taphonomical variations of the same species, thus reducing the diversity from eleven to six species.

1.2.4. Huelva Province

The earliest works describing the Cambrian rocks from northern Huelva (Andalusia) date back to the nineteenth century, when Gonzalo y Tarín (1887), with the help of the Portuguese geologists Carlos Ribeiro and Nery Delgado, reported ‘uppermost’ Cambrian rocks below a unit bearing the so-called “third Silurian fauna” (*sensu* Barrande, 1852). These were reported between Santa Olalla del Cala and Cumbres de San Bartolomé localities, and no Cambrian fossils were found then. It was not until the preliminary reports by Lotze (1937, 1939) that the first trilobite assemblage was found in Arroyomolinos de León, representing the first occurrence of the group from Sierra Morena. Since this moment, new in-depth stratigraphical and palaeontological



a. *Saukianda andalusiae.* $^{1}/_{1}$.

b. *Perrector perrectus.* $^{2}/_{1}$.

c. *Resserops resserianus.* $^{2}/_{1}$.

d. *Eops eo.* $^{2}/_{1}$.

e. ***Strenuella (Strenuaeva) sampelayoi.*** $^{3}/_{1}$.

f. ***Strenuella (Strenuaeva) insecta.*** $^{5}/_{1}$.

g. *Camaraspis guillermoi.* $^{3}/_{1}$.

h. *Camaraspis onyx.* $^{3}/_{1}$.

Figure 1: Original illustrations of the "*Saukianda* Fauna", extracted from Richter & Richter (1940).

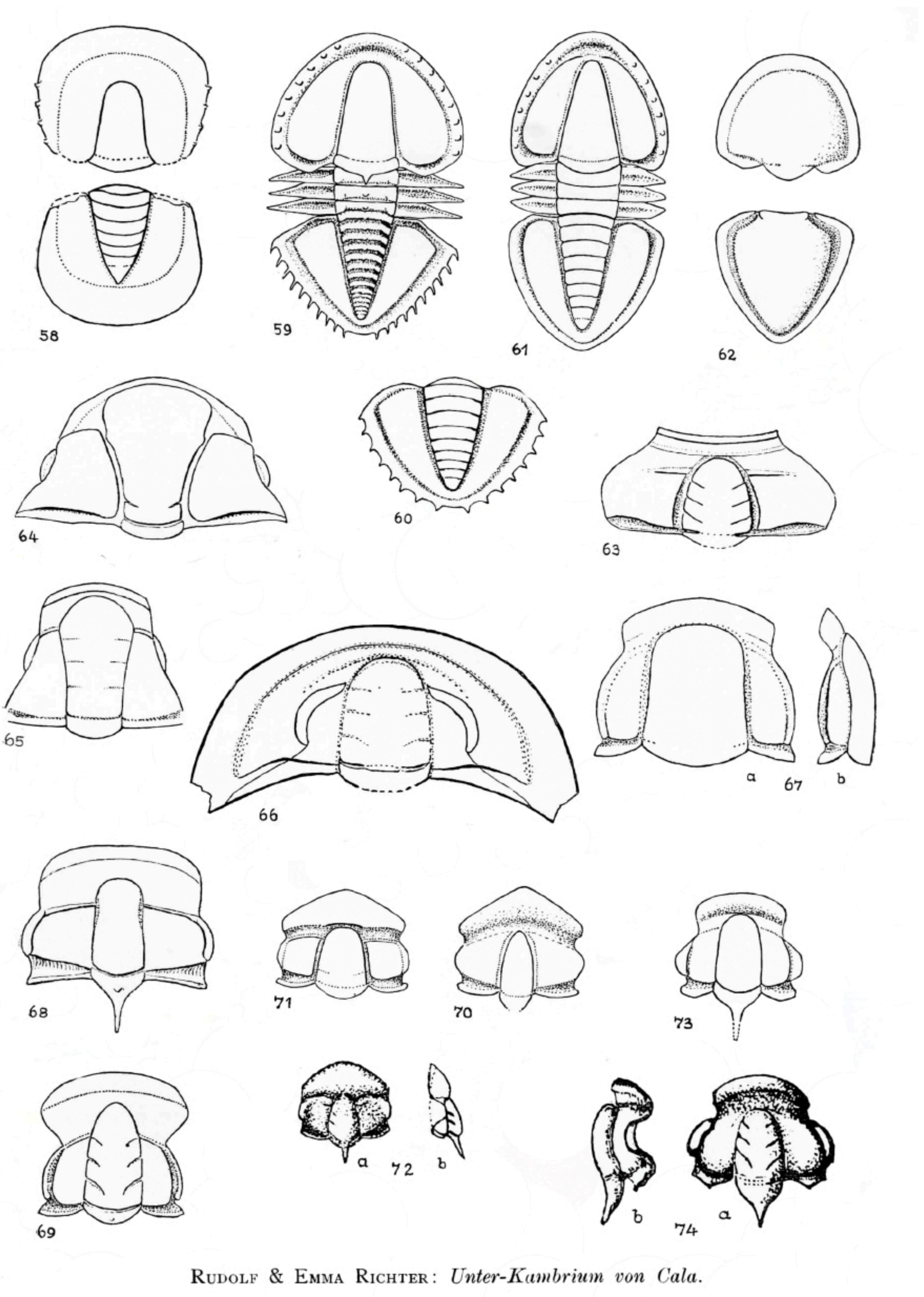


Figure 2: Original illustrations of the "Cala Fauna", extracted from Richter & Richter (1941).

works were developed, beginning with the stratigraphical synthesis carried out by Schneider (1939, 1941), who established the former lithostratigraphical units for the Precambrian-lower Palaeozoic of Huelva (i.e., ‘Los Bonales shales, ‘Arroyomolinos mottled beds’, ‘Cañuelo limestones’, ‘Herrerías marls’, ‘Rincón beds,’ and ‘Umbría-Pipeta green beds’) and followed by the taxonomical and biostratigraphical works by Richter & Richter (1941). In this work, Richter & Richter (1941) named the so-called "*Fauna von Cala*" (Cala Fauna), describing nine different taxa from 22 sites between Cañaveral de León and Arroyomolinos de León, and in the surroundings of Minas de Cala, Huelva (Fig. 2). Given the widespread record of the trilobite *Eodiscus* (*Serrodiscus*) *serratus* Richter & Richter (1941) (=*Serrodiscus bellimarginatus sensu* Collantes et al., 2022), the assemblage was assigned to a biostratigraphical horizon named "*serratus*-band", corresponding to the upper levels of the 'Herrerías marls'.

1.2.5. Badajoz Province

Regarding the Cambrian studies of the Badajoz Province, the first work was done by Gonzalo y Tarín (1879), who first mapped the area. The described fossils were assigned to the "second Silurian fauna" (mostly trilobites and brachiopods), underlying those of the "third Silurian fauna" (graptolites) (*sensu* Barrande, 1852). The published studies in this area at the end of the nineteenth and the beginning of the twentieth century are very scarce, except for brief mentions by Mallada (1897), Hernández-Pacheco (1902) and Hernández-Sampelayo (1933, 1935), in which already-known information is compiled. Subsequent mapping and palaeontological works were developed by Meléndez (1941a, b, 1943), who reported the first archaeocyaths from the Alconera limestone quarries near Zafra. Lately, Roso de Luna & Hernández-Pacheco (1954; 1955a, b, 1956) provided geological maps for different territories of Badajoz, including Zafra, Burguillos del Cerro, Villafranca de los Barros, and Bótoa, discovering new fossil localities, mostly of archaeocyaths.

1.2.6. Other contributions

The first work synthesising the Cambrian of Iberia was the one of Mallada (1987). During the first half of the twentieth century, several syntheses of the Cambrian of the Iberian Peninsula were produced, like those by Hernández-Sampelayo (1933, 1935) and Meléndez (1943, 1944). In this line, Lotze (1958) proposed a preliminary biostratigraphical scheme for the Cambrian of Spain, with 11 horizons based on different fossil associations (mainly trilobites). Shortly after, Lotze (1961) summarized all the known data on the Cambrian of Spain, adding information from his research and the one of his students. As a result, based on his knowledge of the trilobites from all over Iberia, he divided the Iberian Cambrian record into 32 different "trilobite horizons". For the 'Lower Cambrian', he defined 16 horizons and subdivided them into three levels: "Lower Cambrian A" (horizons 1–3), "Lower Cambrian B" (horizons 4-8), and "Lower Cambrian C" (horizons 8-16). It is worth noting that, at that time, Lotze (1945) also established the former six geological zones for the Iberian Massif: Cantabrian Zone, West Asturian-Leonese Zone, Galician-Castilian Zone, East Lusitanian-Alcudian Zone, Ossa-Morena Zone and South Portuguese Zone. Among these, the Ossa-Morena Zone (from now on, OMZ) comprises the Cambrian outcrops from the Sierra Morena studied in this work.

Later contributions by Prof. Lotze on the Cambrian of Iberia include the one of Debrenne & Lotze (1963), a synthesis of the Spanish archaeocyaths collections in Germany. This led to the erection of a new genus and new species from Alanís and to report several new occurrences for this region.

Regarding the trilobite record of Iberia, Sdzuy (1961) summarized their state of the art, adding his systematic considerations and describing new genera and species. Soon after, Sdzuy (1962) focused on the 'Lower Cambrian' trilobites from Sierra Morena, discussing the biostratigraphical scheme and defining several "trilobite horizons" (e.g., '*souzai-schneideri* horizon', '*cornuta-sevillana* horizon', 'cf. *speciosus-morenica* horizon' '*Saukianda* beds') together with new trilobite species.

Other contributions for Sierra Morena include those of Mingarro (1962), describing several archaeocyath and trilobite specimens from northern Seville, and the geological map of Constantina by Meléndez et al. (1967). From Córdoba, Cabanás (1964) discovered archaeocyaths in the surroundings of Alcolea; Cabanás & Meléndez (1966) published a new fossil site in the Arroyo de Pedroche; Mingarro & López de Azcona (1969) and Cabanás (1971) provided new data on the lithological successions and faunal assemblages from Cerro de Las Ermitas and Arroyo de Pedroche; Perejón (1969) made a preliminary study of the archaeocyaths from the area surrounding Córdoba; and Perejón (1971) published and described the new archaeocyath *Pachecocyathus cabanasi* Perejón, 1971 from the Las Ermitas. In Badajoz, Suhr (1964, 1969) and Bard (1964a) described the 'Middle Cambrian' stratigraphy and some trilobites from Zafra; Laus (1969) studied the Cambrian stratigraphy from Zafra and reported more trilobite taxa from this area; Meléndez & Mingarro (1962) made the geological map of

Guadalcanal; and Vegas (1971a, b) commented on several aspects of the Cambrian geology of Badajoz. From Huelva, Jean Piere Bard drew several geological sections and stratigraphical columns across the northern mountain range (Bard, 1964b, 1965). Later, in his PhD thesis, Bard reported ‘Lower Cambrian’ trilobites from Cumbres Mayores (Bard, 1969).

Up to that point, and although several biostratigraphical aspects have been addressed throughout the cited literature, most of the authors have overlooked chronostratigraphical issues of the Iberian Cambrian. From 1971 on, the first formal proposal for the subdivision of the Cambrian System of Iberia into stages was put forward by Prof. Klaus Sdzuy, marking a turning point in the chronostratigraphy of the Cambrian of Spain and Portugal.

1.3. The subdivision of the Cambrian System of Iberia

1.3.1. Previous works

Following the compilation of all the previous work developed on Cambrian sequences and fossils of the Iberian Peninsula, Sdzuy (1971a) proposed the first formal subdivision for the ‘Lower Cambrian’ of Iberia. In this scheme, Sdzuy noted that there were differences between the faunas from the lower, middle and upper part of the ‘Lower Cambrian’, establishing three subdivisions for this interval: Ovetian (lowermost ‘Lower Cambrian’), Marianian (middle ‘Lower Cambrian’) and Bilbilian (uppermost ‘Lower Cambrian’). Sdzuy (1971b) also proposed three 'provisional' divisions for the ‘Middle Cambrian’, based on trilobite biostratigraphy: ‘*Paradoxides* (*Acadoparadoxides*)‘ stage, ‘Solenopleuropsidae’ stage and ‘Solenopleuropsidae-free’ stage. This division marked a before and an after in subsequent works on the Cambrian of the Iberian Peninsula. Posterior modifications and further explanation of this division will be given in subsection 1.3.2 (“The problem of the Marianian Stage and the Cambrian Series 2”).

Many publications on the Cambrian of southwestern Spain followed Sdzuy's first formal division of the Iberian Cambrian. From Córdoba, Liñán (1972) started studying a small sector, describing some Cambrian outcrops. Lately, he established the former Cambrian formations for this region (Torreárboles Formation, Pedroche Formation, Santo Domingo Formation, and Los Villares Formation; Liñán, 1974). Among these, Liñán & Dabrio (1974) carried out a detailed lithostratigraphic study of the Pedroche Formation, followed by the PhD thesis of Liñán (1978), who studied the biostratigraphy of the Sierra de Córdoba, with a broad interest in the Cambrian rocks and, especially, the Cambrian trilobites from this territory. Posteriorly, Liñán & Sdzuy (1978) described new trilobites from the Pedroche Formation (Ovetian), while Liñán et al. (1981) focused on the fossil assemblages from the basal levels of this unit. Liñán & Schmitt (1981) documented some microfossils from the Precambrian of Córdoba and discussed the tentative placement of the Precambrian-Cambrian boundary. This was also discussed lately by Liñán & Palacios (1983), through the analysis of acritarch assemblages from different outcrops of Sierra de Córdoba. Liñán & Mergl (1982) also reported lower Cambrian brachiopods from the Arroyo Pedroche section. On the other hand, Liñán (1984a) and Liñán & Fernández-Carrasco (1984) examined the ichnofossils from the lowermost Cambrian of Córdoba. They determined that their presence below the first occurrence of trilobites in the Iberian Cambrian made it necessary to establish a new, lowermost stage: the Cordubian. In this line, Fedonkin et al. (1985) also contributed to studying the Precambrian-Cambrian ichnofossils from this area.

One of the fossil groups that have contributed most to our knowledge of the Spanish Cambrian is that of the archaeocyaths. Regarding the study of their biostratigraphy, palaeobiogeography and palaeoecology (together with the study of stromatolites and reef mounds), Prof. Antonio Perejón was key, developing an extensive collection of works on the Cambrian of Córdoba, as well as from other localities of the OMZ (Perejón, 1973, 1974, 1975a, b, c, 1976a, b, 1977, 1984, 1987, 1989, 1994, 1996; Perejón & Moreno-Eiris, 2006, 2007; Perejón et al., 2008). Other contributions on this topic include those of Moreno-Eiris (1987a, b, c, d, 1988), Moreno-Eiris et al. (1995, 2004), Menéndez (1998, 1999), Menéndez et al. (1999, 2015a, b, 2016), Zamarreño & Debrenne (1977), Wittke (1978), Schmitt (1982), Creveling et al. (2013) and Iglesias-Álvarez (2014).

Another important group for Cambrian biostratigraphy is the so-called "small shelly fossils" (SSF), which constitute an artificial taxonomical grouping of organisms belonging to different classes (e.g., arthropod segments, small molluscs, sponge spicules, etc.). A considerable number of SSF species have been described from the Pedroche Formation of Córdoba (e.g., Fernández-Remolar, 1995, 1996, 1998, 2001a, b, 2002; Gubanov et al., 2004).

Regarding the ‘Middle Cambrian’, Liñán et al. (1995a) described both trilobites and ichnofossils from Córdoba, and Gil Cid (1985a, b) studied selected trilobite groups from this territory as agnostids or paradoxidids. More recently, Liñán et al. (2005) described new Ovetian trilobites from Córdoba, including the new species *Lemdadella perejoni* Liñán, Dies, Gámez-Vintaned, Gozalo, Mayoral & Muñiz, 2005.

Moving to Seville, only a few studies have focused on the research of trilobites in recent times: Gil Cid (1972a) described the new species *Strenuaeva melendezi* Gil Cid, 1972a (=*Strenuaeva sampelayoi* Richter & Richter, 1940) from the Marianian of Alanís. Gil Cid (1975), Gil Cid & Bernal Barreiro (1989, 1991a, b), and more recently, Gil Cid et al. (2009) reviewed the "*Saukianda* Fauna" from the 'Alanís beds'. In another vein, Mayoral (2008, 2020) studied the Cerro del Hierro Natural Monument (San Nicolás del Puerto, Seville) from different points of view, including palaeontological (trilobites, archaeocyaths and bioconstructions), stratigraphical, structural and geomorphological. Along the same line, Perejón et al. (1999) studied the chronology of the different karstic processes affecting the Cambrian reef mounds of Cerro del Hierro. Regarding other fossil groups, Liñán & Mergl (1982, 2001) described several brachiopods from Arroyo Galeón and Arroyo del Tamujar sections; Ubaghs & Vizcaïno (1991) named a new eocrinoid from Alanís, *Gogia* (*Alanisicystis*) *andalusiae* Ubagh & Vizcaïno, 1991 (=*Alanisicystis andalusiae*), and Mayoral et al. (2004) reported the presence of stranded jellyfish impressions from the basal Torreárboles Formation (Cordubian) from Constantina, Seville, naming the new species *Cordubia gigantea* Mayoral et al., 2004.

Back to the Badajoz region, one of the best studied Cambrian territories is that of Zafra, and especially the village of Alconera: from this area, Vegas (1971a, b) defined some Cambrian formations, as the 'Castellar Formation' and the Playón Formation. Gil-Cid (1973) made a preliminary note on the stratigraphy and palaeontology of Zafra and Alconera, with a summary of its 'Lower' and 'Middle Cambrian' trilobites. Regarding the archaeocyaths, Perejón (1973, 1975a, c, 1976a) made notable advances in the systematics and biostratigraphy of the archaeocyathid assemblages from Alconera. Also, Dupont & Vegas (1978) and Dupont (1979) made important contributions regarding the Cambrian volcano-sedimentary rocks from southern Badajoz, with especial interest in their metallogenic implications. One of the most remarkable contributions is the one by Liñán & Perejón (1981), describing the 'Lower Cambrian' (Cordubian?–Bilbilian) sequence from the "Alconera Unit", defining the Alconera Formation (divided into Sierra Gorda and La Hoya members) and La Lapa Formation (divided into Las Vegas and Vallehondo members), as well as analysing their palaeontological content (trilobites, archaeocyaths, brachiopods, ichnofossils, and SSF) and biostratigraphical implications. In addition, Odriozola et al. (1983) made an updated geological map of the Zafra area. Besides, Liñán & Mergl (1982) studied the 'Lower' Cambrian brachiopods from Alconera and also from the “Camino de la Dehesilla” section (southern Badajoz). Palacios (1993) analysed the acritarch assemblages from the Playón Formation, a study that has been recently updated and improved by Palacios et al. (2021). In 1995, in the context of the “XIII Reunión de Geología del Oeste Peninsular” (XIII RGOP), Liñán et al. (1995b) published a synthesis of the knowledge on the ‘Lower’ and ‘Middle’ Cambrian stratigraphy and palaeontology from the Alconera Unit. Posterior contributions include those of Álvaro et al. (1998) evaluating the biostratigraphical implications of the trilobite *Ferralsia* Cobbold, 1935; Sánchez-García (2001) studying the Cambrian volcanism of the Alconera Unit (see also Sánchez-García et al., 2008, 2010, for the rifting-phase of the OZM); and, more recently, Liñán et al. (2008a) describing new Ovetian trilobites from the Sierra Gorda Member of the Alconera Formation.

Regarding the ‘Middle Cambrian’ from Zafra and Alconera, Prof. Mª Dolores Gil Cid carried out several works comprising different fossil groups, including trilobites (Gil Cid, 1980, 1982a, b, 1984, 1986), brachiopods (Gil Cid & Melou, 1986) and echinoderms (Gil Cid & Domínguez, 1995, 1998). In this line, Gozalo et al. (1994) also studied the solenopleuropsid trilobites from the Alconera Unit.

From the area of Llerena, southern Badajoz, Perejón et al. (1981) reported new specimens of ‘Lower Cambrian’ archaeocyaths from the northern sector of this locality, and Yochelson & Gil Cid (1984) described the new Cambrian mollusc *Scenella morenensis* Yochelson & Gil Cid 1984 (=*Marocella morenensis*) from the Viar river section. For the same section, Gil Cid (1988a) contributed with new data and fossils, and Liñán & Mergl (2001) described new brachiopod occurrences.

Other works regarding less-studied Cambrian outcrops from southern Badajoz are the ones by Gil Cid (1988b), studying the trilobite assemblage from Puebla del Maestre, or Gil Cid (1985c), reporting a new occurrence of the trilobite *Delgadella* from Nogales. Finally, Palacios et al. (2013) published a new geological map of Extremadura.

In Huelva, Gutiérrez-Elorza et al. (1971) described physiographical aspects from Sierra de Aracena and southern Badajoz, recognizing Cambrian outcrops in this territory, while Gil Cid (1971, 1972b, 1978) found new trilobite sites and studied the trilobite assemblages from Cumbres Mayores and Sierra del Bujo. Also, Coullaut et al. (1975, 1980) studied the metallogenic aspects of the Cumbres Mayores area and subsequently proposed a tentative stratigraphic division for the Cambrian sequences of northern Huelva. Liñán & Mergl (1982) reported brachiopods from several localities of Huelva, including Cumbres Mayores, Hinojales, Sierra del Bujo and Sª Olalla del Cala. On the other hand, Mette (1987, 1989) analysed the lower Palaeozoic acritarchs assemblages from western Sierra Morena, reporting 'Middle Cambrian' acritarchs from Ventas del Ciervo section (Cañaveral de León–Aracena). In recent years, Sdzuy (2001) evaluated the retrodeformation for different Marianian trilobites from the OMZ, concluding that some species result from taphonomical variations.

Recent palaeontological contributions to the Cambrian of southeastern Portugal include those of Gonçalves (1971), improving the lithostratigraphical knowledge from northeastern Alentejo, Mata (1986) and Mata & Munhá (1990) studying the geochemistry and metallogeny of the volcano-sedimentary rocks from the same sector; and Oliveira et al. (1991), Pereira (1999) or Araújo et al. (2013) focused on the regional geology of the Portuguese sector of the OMZ, working on its tectono-stratigraphical aspects and domains. More recently, and already within the scope of this work, Collantes et al. (2021b) reviewed the trilobite *Callavia choffati* (Delgado, 1904) from Vila Boim.

Parallel to all these contributions, there are plenty of works synthesising and reviewing the knowledge on the Cambrian from the OMZ and the Iberian Massif, beginning with Zamarrero (1983), Liñán (1984b, 1998), Liñán & Quesada (1990), Liñán et al. (1993,1997, 2002, 2004), Perejón & Moreno-Eiris (1992), and Gozalo et al. (2003). In addition, Gil Cid (1991) reviewed the Cambrian palaeontology from the OMZ and its correlation with Morocco and Central Europe, and Perejón (1994) reviewed the palaeogeographical and biostratigraphical implications of the archaeocyath record from Spain, among other contributions.

The following subsection is focused on the Marianian Stage, a problematic and historically controversial Iberian Cambrian subdivision proposed by Klaus Sdzuy. We review its different subdivisions and modifications heretofore and evaluate its chronostratigraphical and operational potential and the role it plays in the international correlation of the Cambrian Series 2.

1.3.2. The problem of the Marianian Stage and the Cambrian Series 2

The regional Marianian Stage (after the latin '*Mariani*', Sierra Morena, Andalusia), introduced by Sdzuy (1971a), was initially defined by the appearance and predominance of olenelline trilobites in its lower part, by the trilobite genera *Triangulaspis* Lermontova, 1940, *Delgadella* Walcott, 1912 and *Serrodiscus* Richter & Richter, 1941 in its middle part and by several trilobite genera belonging to Protolenidae, Ellipsocephalidae and

Redlichiidae in its upper part (see Sdzuy, 1971a). Subsequent modifications of Sdzuy's former division of the 'Lower Cambrian' have succeeded each other over the years (Tab. 1).

Later, Liñán (1984b) divided the Marianian Stage into 'lower, middle and upper', each of them characterised by a different trilobite assemblage (see Liñan, 1984b, fig. 3). Shortly after, Perejón (1984) established up to eleven archaeocyaths biozones for the Ovetian (Zones I to VII), Marianian (Zones VIII to X) and Bilbilian (Zone XI) stages (see Perejón, 1984, tab. 8).

In this line, Liñán & Quesada (1990) completed a full revision of the sequences representing the Cambrian rifting phase of the OMZ, including stratigraphy, sedimentology, tectonics, and biostratigraphy. In this work, they also proposed an updated trilobite biozonation for the Marianian Stage: the lower Marianian was characterised by the trilobites *Delgadella*, *Saukianda* Richter & Richter, 1940, *Gigantopygus* Hupé, 1953a, *Alanisia* Richter & Richter, 1940, *Perrector* Richter & Richter, 1940, and *Eops* Richter & Richter, 1940, the middle Marianian was represented by *Protaldonaia* Sdzuy, 1961 *Hicksia* Delgado, 1904, *Atops*?, *Strenuaeva* Richter & Richter, 1940, *Rinconia* Hupé, 1953a *Saukianda*, *Eops*? *Triangulaspis*, *Andalusiana* Sdzuy, 1961 *Callavia*? and *Longianda*? and finally the upper Marianian was characterised by *Serrodiscus*, *Hebediscus* Whitehouse, 1936, *Chelediscus* Rushton, 1966 *Termierella* Hupé, 1953a, *Strenuaeva* and *Triangulaspis*.

Liñán et al. (1993) revaluated the different lower and middle Cambrian stages and stratotypes in Iberia, re-defining the base of the Marianian by the First Appearance Datum (FAD) of *Delgadella* and the top by the Last Appearance Datum (LAD) of *Andalusiana* Sdzuy, 1961 and *Serrodiscus*. The stratotype for the Marianian was selected in Alconera sections 1 and 3, although no lower boundary was indicated. Later on, Liñán et al. (1996) correlated the Marianian with the Banian Stage of Morocco, the Botoman Stage of Siberia, and the Cambrian sequences of Newfoundland, Germany and Sardinia. In addition, they also modified the base and top boundaries of the former: FAD of the *Strenuella* Matthew, 1887 for the base and the FAD of *Realaspis* Sdzuy, 1961 and *Pseudolenus* Hupé, 1953a for the top.

Subsequent works (e.g., Liñán et al., 2002, 2004; Gozalo et al., 2003) followed a slightly different division for the Marianian Stage: the base of the lower Marianian is marked 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*, and the base of the upper

Marianian by the FAD of *Serrodiscus* (see Liñán et al., 2004). In addition, the Marianian Stage has been approximately correlated with the *Heliosphaeridium dissimilare–Skiagia ciliosa* acritarch Zone, according to the Baltic Zonation (*sensu* Palacios & Moczydłowska,1998). Nonetheless, a formal trilobite biozonation is still missing.

Informal biozonation schemes have been recently used in several works (e.g., "*Strenuella*", "*Andalusiana-Strenuaeva*" and "*Serrodiscus*" in Moczydłowska & Yin, 2012; Sundberg et al., 2016; or *Lusatiops ribotanus* interval in Geyer, 2019), due to its operational usefulness.

Regarding the usefulness of the Marianian Stage within Iberia, Sdzuy (1971a) mentioned the presence of the trilobites *Andalusiana* and *Triangulaspis* in the lower part of the Huérmeda Formation (Iberian Chains), suggesting a tentative correlation between the Marianian sequences of the OMZ and those of the former. Nevertheless, the specimens mentioned above from the Iberian Chains were not figured nor described. Thus, Álvaro et al. (2019) remarked that the presence of *Andalusiana* and *Triangulaspis* in the Iberian Chains is not verified, criticizing the correlation between both areas based on this assumption. In addition, they argued that the biostratigraphical zonation of the Marianian Stage in Iberia is poorly defined and lacks radiometric dating, being invalid for correlation throughout the Iberian Peninsula. Nevertheless, Sepúlveda et al. (2022) recently documented and figured *Andalusiana* aff. *cornuta* from the base of Huérmeda Formation from the Iberian Chains, as formerly indicated by Sdzuy (1971a).

The current concept of the Marianian Stage is still problematic and needs a reappraisal. At this moment, the two major drawbacks we have are 1) the lack of complete sections with continuity of trilobite records, which permit precision of their biostratigraphical range, and 2) the absence of evolutionary lineages within trilobite genera, being most of the described genera from this area monospecific. However, it is remarkable that the occurrence of some trilobite genera is transversal and synchronous throughout the lower Cambrian sequences of the Iberian Peninsula (e.g., FAD of *Strenuaeva* for the base of the middle Marianian in OMZ and the Iberian Chains, or the FAD of *Serrodiscus* for the base of the upper Marianian in the OMZ and the Toledo Mountains, Central Iberian Zone, see Liñán et al. 2002, 2004; Collantes et al., 2022). It also should be noted that Sepúlveda et al. (2021a) recently reported, apart from *Serrodiscus*, the presence of the trilobite genera *Termierella*, *Andalusiana* and *Triangulaspis* from the upper Marianian rocks of Toledo Province. Furthermore, Gozalo et al. (2023) added to this list the genera

Table 1: Correlation chart of the chronostratigraphical units used by different authors.

FAD: First Appearance Datum
LAD: Last Appearance Datum
Arch. Zone: Archaeocyathan Zone (based on Perejón, 1986, 1994)

Lotze, 1961		Sdzuy, 1971a, 1972	Liñán, 1984b Perejón, 1986		Liñán et al., 1993		Liñán et al., 1996		Liñán et al., 2002, 2004 and this work		ISCS	
‘Lower Cambrian’	C (horizons 8 to16)	Bilbilian	Bilbilian		Bilbilian	upper	Bilbilian	upper	Bilbilian	upper FAD *Hamatolenus (H.) ibericus*	Stage 4	Cambrian Series 2
						lower LAD *Andalusiana* + *Serrodiscus*		lower FAD *Realaspis* + *Pseudolenus*		lower LAD *Serrodiscus* + FAD *Realaspis*		
	B (horizons 4 to 8)	Marianian	Marianian	upper	Marianian	upper	Marianian	upper	Marianian	upper FAD *Serrodiscus*	?	
				middle		middle		middle		middle FAD *Strenuaeva*	Stage 3	
				lower		lower FAD *Delgadella* + Arch. Zone VIII		lower FAD *Strenuella* + Arch. Zone VIII		lower FAD *Strenuella* + Arch. Zone VIII		
	A (horizons 1 to 3)	Ovetian	Ovetian	upper	Ovetian	upper	Ovetian	upper	Ovetian	upper Arch. Zone IV		
				lower		lower Arch. Zone I		lower Arch. Zone I + Bigotinidae		lower *Serrania* + Arch. Zone I	?	?
			Cordubian		Cordubian	upper	Cordubian	upper FAD *Rusophycus* + *Cruziana*	Cordubian	upper FAD *Rusophycus avalonensis*	Terre-nuvian	
						lower FAD		lower FAD		lower FAD	FAD	
						Monomorphichnus		*Monomorphichnus lineatus* + *Phycodes* (=*Trichophycus*) *pedum*		*P.* (=*Trichophycus*) *pedum* + *Monomorphichnus lineatus*	*Trichophycus pedum*	

Atops Emmons, 1844, *Pseudatops* Walcott, 1890b, *Chelediscus* Rushton, 1966 and *Acanthomicmacca* Hupé, 1953a all these genera being present either in the Ossa-Morena Zone or in Iberian Chains. Therefore, and pending further research, the correlation of the Marianian across the Iberian Peninsula seems feasible.

Taking into account this problem, one of the main purposes of this work is to improve the biostratigraphy of the Marianian sequences from the OMZ, evaluating the biostratigraphical validity of some of these trilobites as index taxa and, therefore, clarifying their correlation potential throughout the Marianian outcrops of the Iberian Peninsula.

Concerning its international correlation, the International Subcommission on Cambrian Stratigraphy (ISCS) has been working since 1961 for the global subdivision and correlation of the Cambrian System worldwide (see Peng et al., 2020 for review). Nonetheless, certain series and stages remain problematic. One of the most challenging is the so-called Cambrian Series 2, including stages 3 and 4 (see Geyer & Shergold, 2000; Shergold & Geyer, 2003; Geyer & Landing, 2004; Sundberg et al., 2016, 2020; Zhang et al. 2017; Geyer 2019).

Currently, there are two main issues regarding the correlation of the Cambrian Series 2: on the one hand, most of the trilobites (and other fossils) do not show a global distribution covering all palaeogeographical domains during this period, except for a small number of trilobite genera and species (see Álvaro et al., 2013). On the other hand, the few genera and species found globally lack a specific and well-known stratigraphic range, thus limiting their usefulness in correlating different domains.

Improving our knowledge of the biostratigraphical range of these widely distributed trilobites is crucial to achieve a sensible subdivision of this stratigraphical interval. In this regard, certain trilobites found in the Marianian deposits within the OMZ have the potential to aid in developing a robust international biostratigraphical correlation for the Cambrian Series 2.

1.4. The Marianian trilobites of the Ossa-Morena Zone: state of the art

Known since the end of the nineteenth century (Delgado, 1904), it was from the 1940s onwards that there was a significant increase in knowledge of the Marianian trilobites from the Ossa-Morena Zone (e.g., Richter & Richter, 1940, 1941; Sdzuy, 1961, 1962; Gil Cid, 1971, 1972a, 1975; Liñán & Perejón, 1981). These contributions made it possible to record trilobites of this age in different provinces of Spain and Portugal and to describe several new genera and species. They also made it possible to begin to draw up a biostratigraphical scheme for the distribution of the group in rocks of this age, with several trilobites being chosen as index taxa for the boundaries of regional chronostratigraphical divisions (e.g., Sdzuy, 1971a; Liñán & Perejón, 1981; Liñan & Quesada, 1990). More recently, there have been little new data (e.g., Álvaro et al., 1998; Sdzuy, 2001; Gil Cid et al., 2009; Mayoral et al., 2020), but most of the works that focus in some way the trilobites of the Marianian of the OMZ are reviews of the Cambrian System in this region (Gozalo et al., 2003; Liñan et al., 2002, 2004). Other studies have also explored the palaeobiogeographical information of the group at this age (e.g., Liñán, 1984b; Gil Cid, 1991; Liñán & Gámez-Vintaned, 1993; Liñán, 1998; Álvaro et al., 2013), or the palaeoecology of particular taxa (e.g., Gil Cid & Bernal Barreiro, 1989).

A total of 25 species of trilobites have been previously identified in the Marianian of the OMZ, from Elvas region of Portugal, and from Seville, Huelva and Badajoz provinces of Spain: *Alanisia guillermoi*, *Andalusiana cornuta*, *Atops*? *calanus*, *Callavia choffati*, *Calodiscus ibericus*, *Chelediscus* sp., *Delgadella souzai*, *Eops eo*, *Ferralsia saxonica*, *Gigantopygus* cf. *bondoni*, *Hebediscus* sp., *Hicksia elvensis*, *H. hispanica*, *Longianda*? sp., *Micmacca*? sp., *Perrector perrectus*, *Protaldonaia morenica*, *Rinconia schneideri*, *Saukianda andalusiae*, *Sdzuyomia lotzei*, *Serrodiscus silesius*, *Strenuaeva sampelayoi*, *Strenuella* sp., *Termierella sevillana* and *Triangulaspis fusca*. *Chelediscus* sp. and *Hebediscus* sp. had only been listed in general works, without the possibility of confirming or refuting their identification. Furthermore, *Micmacca*? sp. and *Strenuella* sp. were only recently figured (Mayoral et al., 2008, 2020), but no further study was conducted.

Although there have been periods of significant progress in this area, the comprehensive works dealing with the association of OMZ Marianian trilobites as a whole are more than 60 years old. Thus, even for the taxa studied in detail at the time, there is a need for revision in light of the current knowledge of the group. On the other hand, as this update has not been made, the opportunity to properly include the information provided by the Spanish occurrences in the biostratigraphical and palaeogeographical works of the Gondwana domain is being missed.

2. Methodology

The following sections summarize the methodologies employed throughout the present geological and palaeontological study. This methodology can be divided into three parts: fieldwork methodology, laboratory methodology and office work methodology.

2.1. Fieldwork methodology

The fieldwork methodology includes all those processes involved in the prospection, collection, and location of the samples in the study area. Within fieldwork methodology, four different phases can be distinguished: preliminary prospection, geological mapping, stratigraphy, sample collection and labelling.

Before carrying out in-depth palaeontological research in a specific territory, a preliminary survey must be carried out to evaluate the fossiliferous potential of that area. For this purpose, those areas that were prone to the presence of fossils were visited. The areas that presented the best-preserved fossils are those that show the following characteristics: 1) fine-grained rocks, 2) no erosion, 3) no surface weathering, 4) no tectonics (i.e., no faulting or folding), and 5) no metamorphism. Depending on the abundance of fossils in the surveyed area, an in-depth study was considered.

Palaeontological research involves the study of the geology of the territory. Therefore, it was necessary to carry out a detailed geological mapping of the study area before starting the sample collection. To design a mapping project, it was necessary the previous establishment of the itineraries to be followed during the fieldwork, in order to be able to survey the most complete stratigraphical series and, in addition, to select as many different sections as possible. At the same time as the geological mapping was carried out, it was necessary to establish the chronological order of the different rocks. To this end, a stratigraphical study was developed. After establishing the stratigraphical framework, sample collection was carried out.

Once the sample was collected, it was immediately labelled for posterior study in the laboratory. From a stratigraphical and biostratigraphical point of view, only the samples collected *in situ* were considered. Those samples collected outside their stratigraphical context were not considered for biostratigraphical purposes.

2.2. Laboratory methodology

Before the detailed study of the fossils collected during the field campaigns, it is necessary to prepare them correctly to appreciate all the anatomical details or, in case the fossils are poorly preserved, find the appropriate method to prepare them. The type and mode of preparation and conservation techniques of the fossil specimens are varied and extensive, dealing with fossil remains of different natures, different primary and secondary mineralogical compositions, and diverse states of preservation (Green, 2001).

The following processes were used to prepare the fossils studied in this work: cleaning, collection labelling and inventory, consolidation, replication and photography.

2.2.1. Cleaning

The purpose of cleaning is to remove the part of the rocky matrix that totally or partially covers the fossil surface, with the final objective of revealing all the preserved anatomical details of the specimen. Fossil cleaning can be carried out mainly by two types of methods, including mechanical processes and chemical processes. In the present work, and due to the type of preservation, we limit ourselves to mechanical methods.

Material preparation by mechanical methods includes various tools to remove the rocky matrix around and over the fossil. Most of these techniques are mainly applied to macrofossils. In addition to matrix removal, these techniques are occasionally used to remove the external layers of fossil materials, exposing hidden features beneath. The main objective in fossil cleaning is always to reveal the maximum amount of information while inflicting the minimum damage to the specimen.

A vast number of tools are available, powered by either electricity or compressed air. Although mechanical processes include a wide variety of different tools, in this work we mainly employed two types of tools: pneumatic tools and drill pens.

Pneumatic tools include various devices powered by compressed air, commonly supplied by an air compressor. These are used to clean the most delicate parts of the fossil, equipped with small drill bits. On the other hand, the drill is an electrically powered tool that removes a greater amount of matrix in less time.

2.2.2. Collection labelling and inventory

Each specimen was marked or labelled with a unique inventory or catalogue number, different from the fieldwork labelling. However, field numbers were preferably preserved. Care was taken to ensure that the catalogue number did not cover any anatomical character of the specimen. Specimens were labelled properly with all relevant data (taxon, locality, age, etc.).

2.2.3. Consolidation

Palaeontologists have used consolidation and stabilization techniques for over a century. For reviews on this topic, see Camp & Hanna (1937), Carreck & Adams (1969) and Greenwald (1989). Depending on the preservation of the fossil, it may require especial treatment to reduce the possibility of damage during the study and storage. One of these treatments is the consolidation. Consolidation consists of strengthening the fossil by adding a consolidating substance, which generally is a diluted adhesive. The substance can be used to 1) impregnate the whole specimen to give it internal strength (sometimes referred to in preparation as a “hardener”) or 2) coat the surface with a thin layer in order to avoid weathering. This coating helps to maintain the specimen’s surface condition and also acts as a release, making it safer to work with it without causing any damage. The dilute adhesive employed for the present work is Paraloid B72. This is an ethyl methacrylate/methyl acrylate copolymer, widely used in the conservation of cultural and natural heritage, including fossils. We used a 5% v/v solution with pure acetone [$CH_3(CO)CH_3$] as solvent. After the dissolution, we applied the necessary layers to obtain the expected result.

2.2.4. Replication

Studying the external moulds is crucial to observe the external surface morphology. Thus, replication procedures such as moulding are essential in order to study most of the anatomical characters of the fossil.

Latex casting is a rapid and easy way of replication, and resulting products can be easily transported or shared. Nevertheless, they suffer shrinkage with age, so a new latex cast must be made every so often when restudying the materials. The latex casts were made using ammonia-based single-component liquid latex for the present work. Liquid latex must be coloured to enhance contrast, preferably with a drop of Indian or Chinese ink.

To date, there is an abundant bibliography regarding latex casting. For further information about this and other replication processes, please see von Fuehrer (1938), Fischer (1939), Baird (1955), Vernom (1957), Stanley (1975), Heaton (1980), Parsley (1989), Goodwin & Chaney (1994), Davis et al. (1998), Green (2001), and Monge & Mann (2005).

2.2.5. Photography

Photographs of the specimens were taken using a Canon EOS 250D SLR camera equipped with a Canon EF 100mm f/2.8L Macro IS USM lens, all mounted on a Kaiser RS XA KA5411 copystand. Previously to the photographic process, fossils were coated with magnesium oxide (MgO) to increase contrast.

” Focus stacking” techniques were used. This consists of taking a series of photos of the same specimen focusing different planes to obtain a final image, allowing images with the necessary depth of field. Depending on the size, between three and ten photos of each of the figured specimens were taken. The photos were merged using Helicon Focus software (Helicon Soft Ltd. 2000-2021). More information about the stacking techniques is available in Mathys & Brecko (2018).

2.3. Office work methodology

The methodology can be divided into two distinct phases:

The first took place before the field and laboratory work. It consisted of a search of existing bibliography about the geological settings of the study area, as well as information about the different sites and the palaeontological content of each one. With all this information, it was possible to design the field campaigns and have a clearer idea about the stratigraphy and palaeontology of the territory. The second step of the office work involved the search for a specific bibliography for the taxonomical classification of the different fossil associations found during the field campaigns, together with the search for a specific bibliography about the biostratigraphical and palaeogeographical data.

3. Geological setting

The Ossa-Morena Zone (OMZ) represents one of the southernmost divisions of the Iberian Massif and the European Variscan Orogen. It was originally named by Lotze (1945) based on its differential tectono-stratigraphical characters among the Iberian Massif, and it has been the subject of a long debate, mainly regarding the position of its boundaries and its subdivision in domains (Parga, 1970; Julivert et al. 1974, 1980; Arthaud & Matte, 1975; Robardet, 1976; Capdevila, 1976; Herranz et al., 1977; Chacón & Pascual, 1978; Julivert, 1983; Chacón et al., 1983; Apalategui & Pérez-Lorente; 1983, Farias et al., 1987, Apalategui et al., 1990; Liñán & Quesada, 1990; Quesada, 1992; Quesada & Dallmeyer 1994; San José et al., 2004; Quesada, 2006). To the south, the OMZ is bounded by Southern Iberian Shear Zone (Crespo-Blanc & Orozco, 1988), while its northern limit remains controversial: although originally it was considered to be marked by Los Pedroches Batholith (Lotze, 1945; Julivert et al., 1972), most authors nowadays accept that this boundary is marked by the so-called Coimbra-Córdoba Shear Zone (Burg et al., 1981).

The OMZ comprises a stratigraphical record which extends from the upper Neoproterozoic to the upper Carboniferous, including sedimentary and volcanic successions, which are, in turn, intruded by different plutonic rocks. The evolution of the OMZ can be summarized in four major palaeo-tectonic phases: 1) the Cadomian orogeny, with Neoproterozoic arc-growth and accretion; 2) the Cambrian-Ordovician rifting phase; 3) the Ordovician-Devonian passive margin phase, and 4) the Late Palaeozoic convergence and continental collision (Variscan orogeny) (Quesada et al. 1990). For the full extent of the OMZ and its phases, subdivisions and boundaries, see San José et al. (2004). This section focuses on the rifting phase and the Cambrian stratigraphic record of the OMZ, describing the different tectono-stratigraphical units that compose it and to which the studied areas belong.

3.1. The Cambrian of the OMZ

The OMZ contains some of the most extensive Cambrian outcrops in southern Europe. However, this great extension has made it difficult to study them in detail in recent years. Cambrian rocks of the OMZ 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 (Fig.

3). The main characteristics of the stratigraphical record during this rifting phase are 1) considerable facies and thickness variations from one sector to another, and 2) the existence of bimodal volcanic activity, evidencing the tectonic instability in this territory during this period (Liñán & Quesada, 1990; Liñán et al., 2004).

Cambrian sequences from all different blocks of the OMZ show three major successions: 1) a lower terrigenous one, corresponding with shallow subtidal-intertidal conditions; 2) the middle carbonate unit, suggesting a subtidal environment; and 3) the upper terrigenous one, representing a foreshore environment (Liñán & Quesada, 1990). Thus, this sequence is interpreted as representing two major transgressive-regressive cycles, concurring with subaerial conditions during the Furongian (i.e., "Late Cambrian") evidenced by the absence of upper Cambrian rocks in this region, interpreted as resulting from tilting and erosion after exhumation (Quesada, 1991; Sanchez-García et al., 2003, Álvaro et al., 2007).

In the following section, we focus on the stratigraphy and palaeontological content of the different blocks in which the Cambrian of the OMZ has been divided. Only those blocks that have provided palaeontological content will be described. These blocks are Alter do Chão-Elvas Sector, Alconera Block, Viar-Benalija Block, Cumbres Block, Herrerías Block, and Arroyomolinos Block. A general view of the studied Cambrian outcrops of the OMZ is shown in Figure 4.

3.1.1. Alter do Chão-Elvas Sector

This sector (also known as Vila Boim Block, *sensu* Liñán & Quesada, 1990) (Fig. 5) belongs to the Córdoba-Elvas Domain (*sensu* Chacón et al., 1983) or the Elvas-Cumbres Mayores Domain (*sensu* Apalategui et al., 1990), according to previous authors. To the northeast, it is bounded by the Alter do Chão thrust, while it is limited by the Estremoz-Barrancos sector to the south. It comprises rocks dating from late Neoproterozoic to middle Cambrian–Furongian (Araújo et al., 2013).

The lowermost stratigraphical unit from this sector is the so-called Mosteiros Formation, constituted mostly by black shales and greywackes and dated as late Neoproterozoic based on acritarchs (Gonçalves & Palacios, 1984). This unit is considered to be equivalent to the "Série Negra" Succession (Pereira & Silva, 2001).

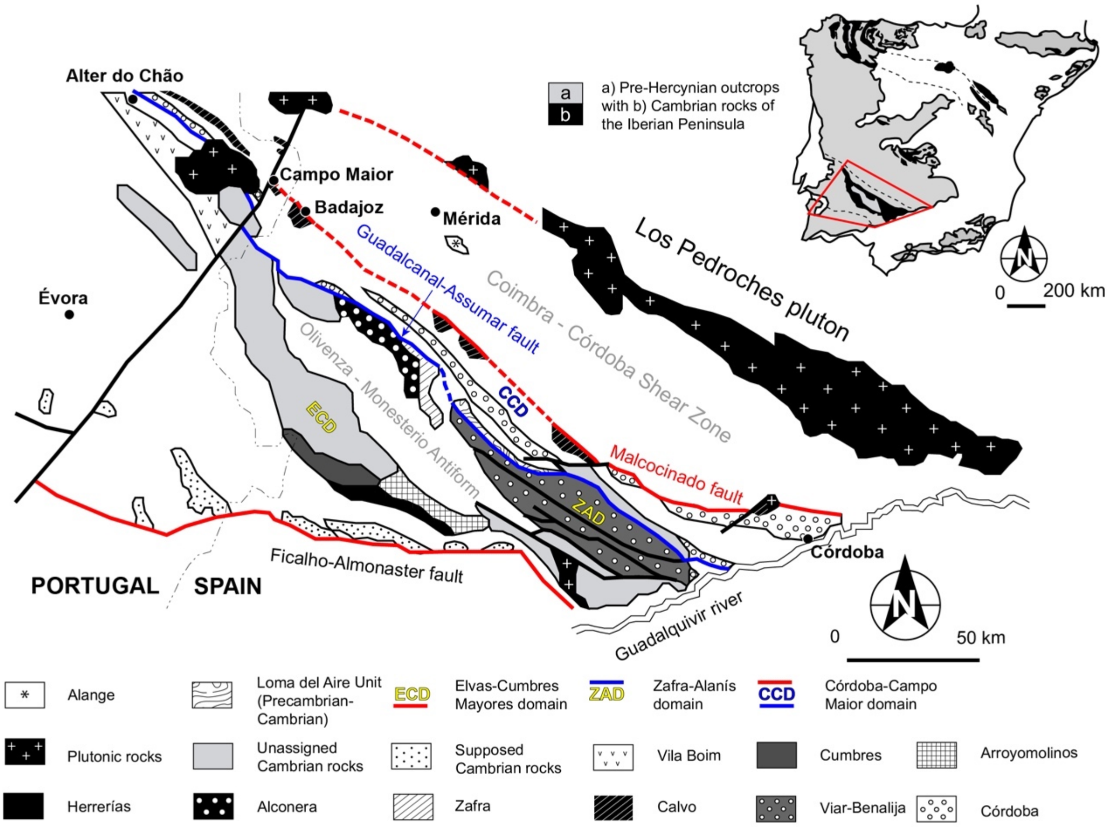


Figure 3: Cambrian blocks of the Ossa-Morena Zone, modified from Liñán & Quesada (1990).

Discordantly over the Mosteiros Formation, it is located the Conglomerado Basal do Câmbrico (Gonçalves, 1971). This unit is up to 50 meters thick and comprises conglomerates, arkoses, and intercalated volcanic levels. This unit is equivalent to the Torreárboles Formation in Spain, with an age assigned to the Cordubian (earlymost Cambrian, ca. Terrenuvian) (Pereira & Silva, 1997; Liñán et al., 2004).

Overlying the Mosteiros Formation, and discordantly, the Carbonatada Formation (Oliveira et al., 1991) takes place, a ~500 meters thick carbonate unit composed of mostly dolomites at its bottom and limestones at its top. Occasionally, laminar structures associated with stromatolites can be observed, but no fossils have been found in this unit up to this day. Regarding its age, it has been correlated with the Sierra Gorda Member of the Alconera Formation (Alconera, Badajoz), the 'Campoallá beds' of Sierra Norte de Sevilla, and some of the carbonate levels of Sierra de Aracena (Liñán & Perejón, 1981). Therefore, this unit is attributed to an age ranging from Ovetian to early most Marianian (Liñán et al., 2004).

Conformably overlying the Carbonatada Formation occurs the Vila Boim Formation (formerly, “Xistos de Vila Boim”, Gonçalves, 1978), a 600 meters thick sequence composed of shales, quartzites and graywackes with some interbedded rhyolite and basalt levels (Mata, 1986). This unit has provided a moderate number of fossils from a narrow lenticular horizon of blue-grey shales with iron oxides located ~170 m from the base. The fossil assemblage is dominated by the trilobites *Hicksia elvensis* Delgado, 1904, *Delgadella souzai* (Delgado, 1904) and, less frequently, *Callavia choffati* (Delgado, 1904), together with other fossil groups such as brachiopods, hyolithids, and bivalves (see Delgado, 1904; Teixeira, 1952). According to Liñán et al. (2004), this fossil assemblage suggests a middle Marianian age. Based on regional correlation with equivalent formations (i.e., ‘Cumbres beds’, ‘Herrerías shale’), we assign the Vila Boim Formation to the Marianian.

On top of the Vila Boim Formation is the concordant ‘Barra Quartzítica’ (Oliveira, 1984), a ~100 m unit formed by quartzites and conglomerates. Regarding its age and correlation, it has been traditionally correlated with the Castellar Formation from Alconera, previously assigned to the Bilbilian (Cambrian Stage 4). However, new biostratigraphical data from Vallehondo and Playón Formation from Alconera suggests a Leonian (i.e., Wuliuan) age for the Castellar Formation (also regarded as ‘Castellar beds’, see Palacios et al., 2021). Similarly, it may suggest a probable Leonian age for the ‘Barra Quartzitica’ unit without further criteria for precision of the age.

The ‘Barra Quartzítica’ is conformably overlain by the volcano-sedimentary Terrugem Formation (formerly “Xistos de Terrugem”, Gonçalves, 1978), consisting of shales and graywackes with intercalated bimodal volcanic rocks. The age of this unit is imprecise due to the absence of geochronological data, attributed to the middle Cambrian due to its position and correlation with the lower part of the Playón Formation (Zafra, Badajoz). The latter bears middle Cambrian trilobites, brachiopods and acritarchs (Gil Cid, 1986; Gil Cid & Melou, 1986; Palacios et al., 2021). New biostratigraphical and geochronological data by Palacios et al. (2021) suggests an early Drumian to Guzhangian age for the Playón Formation. Therefore, we tentatively assign a similar age to the Terrugem Formation.

Finally, the stratigraphical succession culminated with the Fatuquedo Formation (formerly ‘Xistos de Fatuquedo’, Delgado, 1908) consisting of a sandstone and shale alternation with a conglomeratic intercalation at the top. The minimum thickness of this unit is estimated to be 2500 meters, as the base of the formation has not been recognized.

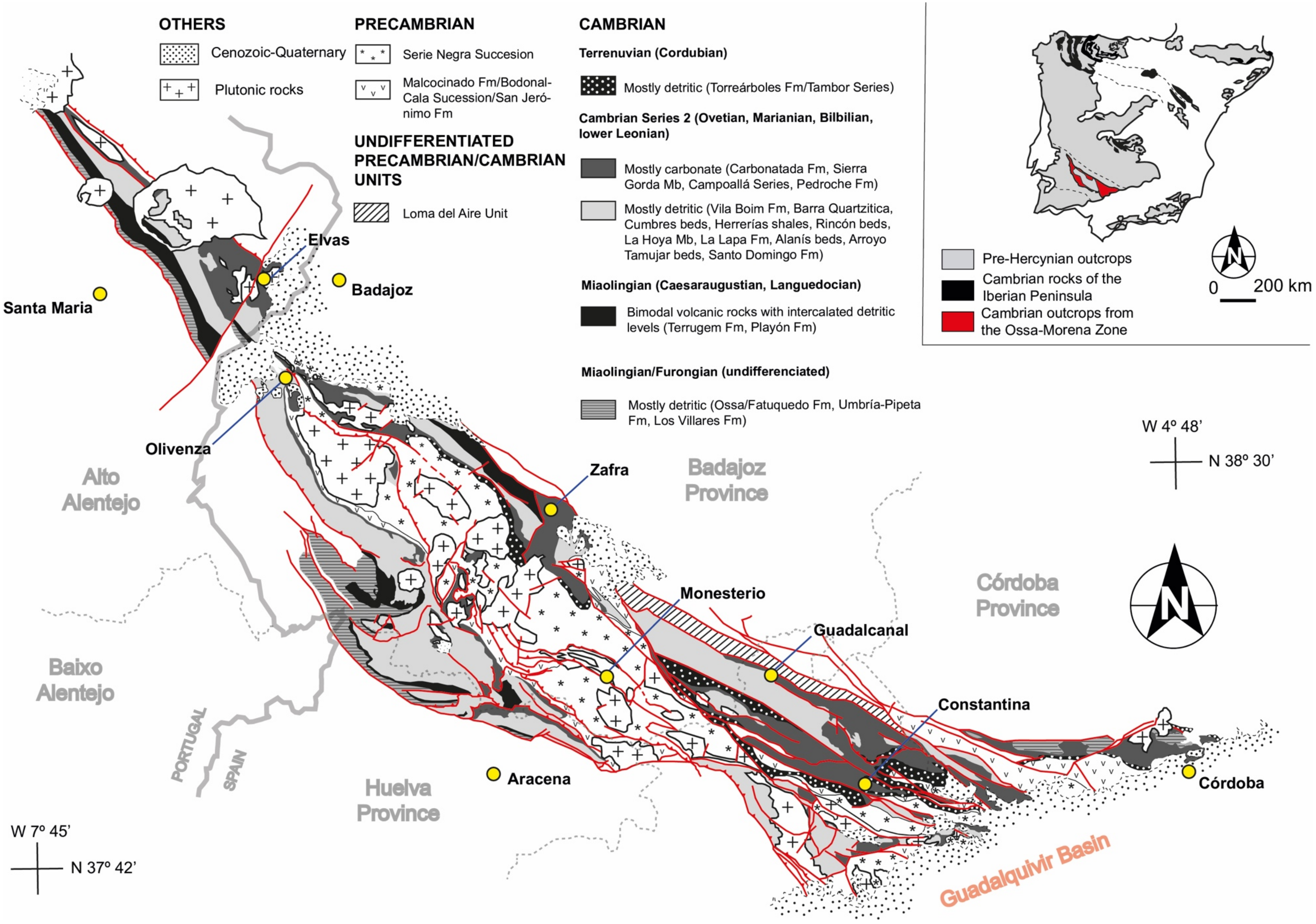


Figure 4: Chronostratigraphical and lithological sketch map of selected Cambrian outcrops of the Ossa-Morena Zone. Lithological data was based on MAGNA 1:1000000 (Rodríguez Fernández et al., 2015) with modifications.

Other authors (e.g., Liñán et al., 2004) suggested the existence of a lateral equivalent of the Fatuquedo Formation, named as Ossa Formation (Carvalhosa et al., 1987) and composed of a 3000 meters thick sequence of shales and greywackes. In respect to their age, both are considered to be a lateral equivalent of the upper part of the Playón Formation (Liñán et al., 2004) and also the Umbria-Pipeta Formation (Huelva), where Miaolingian acritarchs have been reported from the lowermost green shales of the unit (Mette, 1989).

3.1.2. Alconera Block

The Alconera Block (Liñán & Quesada, 1990) (Fig. 6) is located in the northern limb of the Olivenza-Monesterio Anticlinorium, belonging to the Córdoba-Alanís Domain (*sensu* Delgado et al., 1977) or Zafra-Monesterio Domain (Apalategui et al., 1990). In this work, it is included in the Zafra-Alanís Domain (see Fig. 3). To the north, it is bounded by the Guadalcanal-Assumar fault, while to the south it is limited by the Serie Negra Succession. This block includes rocks dating from late Neoproterozoic to middle Cambrian (Liñán & Perejón, 1981; Liñán et al., 1995b).

The first unit is the Torreárboles Formation (Liñán, 1976, 1978), consisting of conglomerates and arkosic sandstones with interbedded lutites. The thickness of this unit is up to 450 meters. Two members have been distinguished: the lower Tierna Member and the upper Julia Member (Liñán, 1984a). The lower comprises arkoses, conglomerates and shales, while the upper one consists of an alternance of sandstones and shales with abundant trace fossils (Fedonkin et al., 1983; Liñán, 1984a). The unit is assigned to the Cordubian (Liñán & Fernández-Carrasco, 1984), correlated with the 'Tambor Series' (Simon, 1951) from Seville.

Overlying the Torreárboles Formation, conformably, it takes place the Alconera Formation. Within this unit, two members were recognized: the lower Sierra Gorda Member and the upper La Hoya Member (Liñán & Perjeón, 1981).

The Sierra Gorda Member consists mainly of carbonates with thin detrital levels, dated as earlymost Ovetian to earlymost Marianian. This member has been subdivided into three. The lower part (approx. 40 meters thick) is formed by laminated algal limestones, with interbedded sandstone and shale levels, the latter bearing the trilobites *Serrania palaciosi* Liñán et al. 2008a and *Serrania*? *gordaensis* Liñán et al. 2008a,

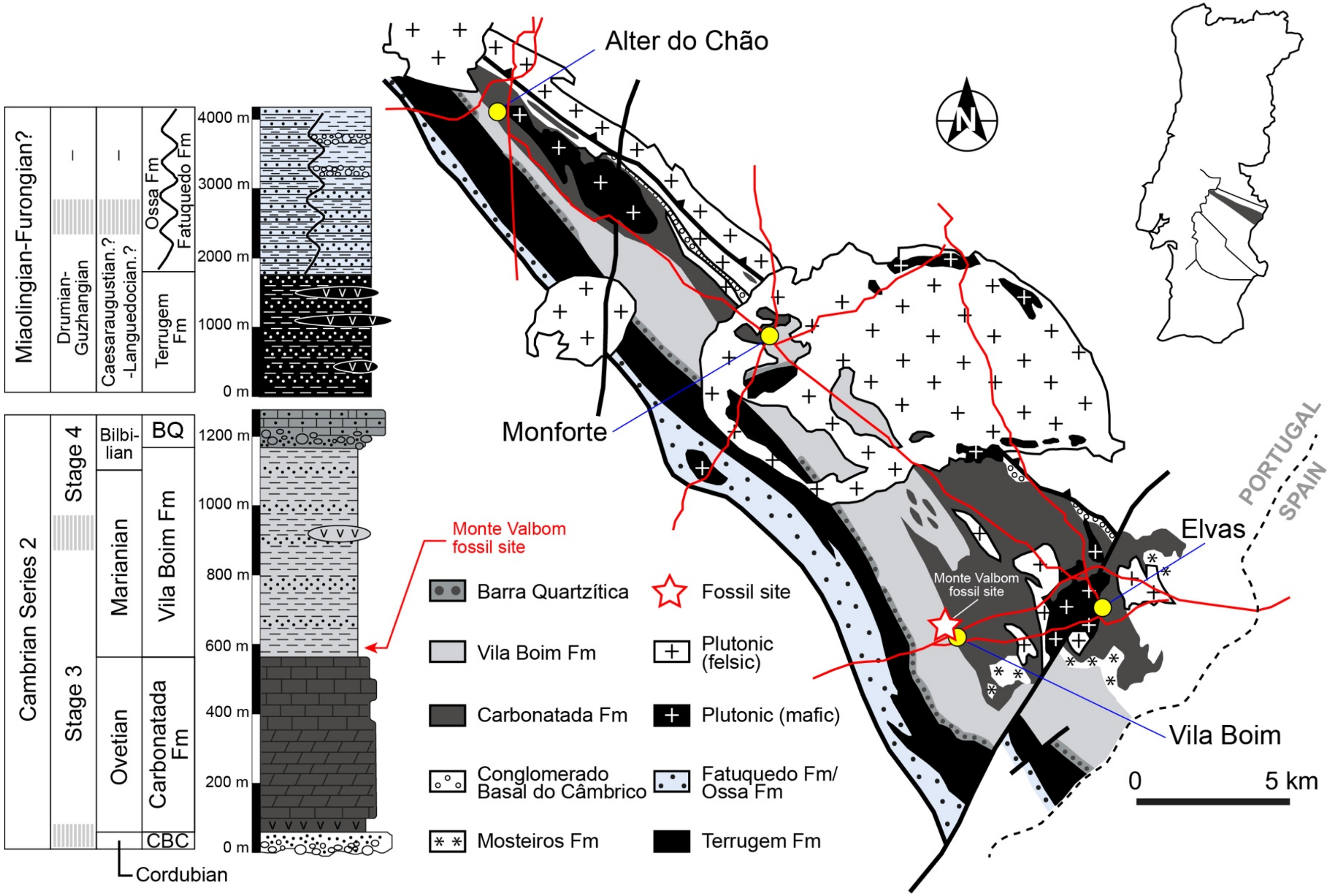


Figure 5: Geological map and synthetic stratigraphical column of the Cambrian sequence of the Alter do Chão-Elvas Sector, indicating the fossil site.

correlated with Zones I-II of Perejón (1986) and, therefore, assigned to the lowermost Ovetian (Liñán et al. 2005, 2008a). Stromatolites and stromatolitic breccias form the top of this lower part. The middle part (approx. 330 meters thick) includes massive algal limestones with interbedded fine-grained sandstones and yellowish shales. The upper part (approx. 130 m) is formed by laminated limestone at the base and massive pinkish limestones at the top. The laminated limestones are characterised by a thick level (5 meters) with chert nodules and abundant organic matter. The massive limestones at the top contain archaeocyaths classified as *Nochoroicyathus* sp., *Taylorcyathus* sp. and *Erismacoscinus* sp., among others, belonging to Zone VIII of Perejón (1986), which correlates with the upper part of this member with the lowermost Marianian.

Concordantly over the Sierra Gorda Member it was established the La Hoya Member (Liñán & Perjeón, 1981), an approximately 400 meters thick detrital succession with an important carbonate component. According to the lithological differences, it has been divided into three parts. The lower part (approx. 30 m) begins with one meter of grey nodular limestones, followed by a 2 meters thick alternance of tabular, bioclastic limestones and greyish marls, the latter with high content of organic matter and containing undetermined hyoliths and brachiopods. It is followed by white limestones with archaeocyath sections, becoming more abundant to the top, and followed by pinkish to purplish coriaceous limestones (*kramenzel*). This lower part culminated with a succession of marly limestone levels and marls with trilobites (*Strenuella* Matthew, 1887), brachiopods and hyoliths, which, together with the archaeocyath assemblages, indicate an early Marianian age (see Liñán & Perejón, 1981). The middle part (approx. 125 meters) comprises *kramenzel* limestones and marls alternating with lutites and fine-grained sandstones. The limestone and marl levels are light-coloured to purplish, with purplish to yellowish lutites and greyish sandstones. The terrigenous levels are abundantly fossiliferous, bearing a trilobite assemblage composed of *Strenuaeva sampelayoi* Richter & Richter, 1940, *Saukianda andalusiae* Richter & Richter, 1940, *Delgadella souzai* Delgado, 1904 and *Kingaspis* (*Kingaspoides*) cf. *velata* Sdzuy, 1961, together with brachiopods and hyoliths, indicating a middle Marianian age. The upper part (250 meters) is characterised by the replacement of *kramenzel* facies by lutites with carbonate nodules alternating with levels of purplish to greenish lutites. These levels bear abundant trilobites, including *Serrodiscus bellimarginatus*, *Triangulaspis fusca* Sdzuy, 1962, *Hicksia elvensis* Delgado, 1904, *Termierella sevillana* Sdzuy, 1961, *Strenuaeva sampelayoi* and *Delgadella souzai*, together with brachiopods, dated as late Marianian.

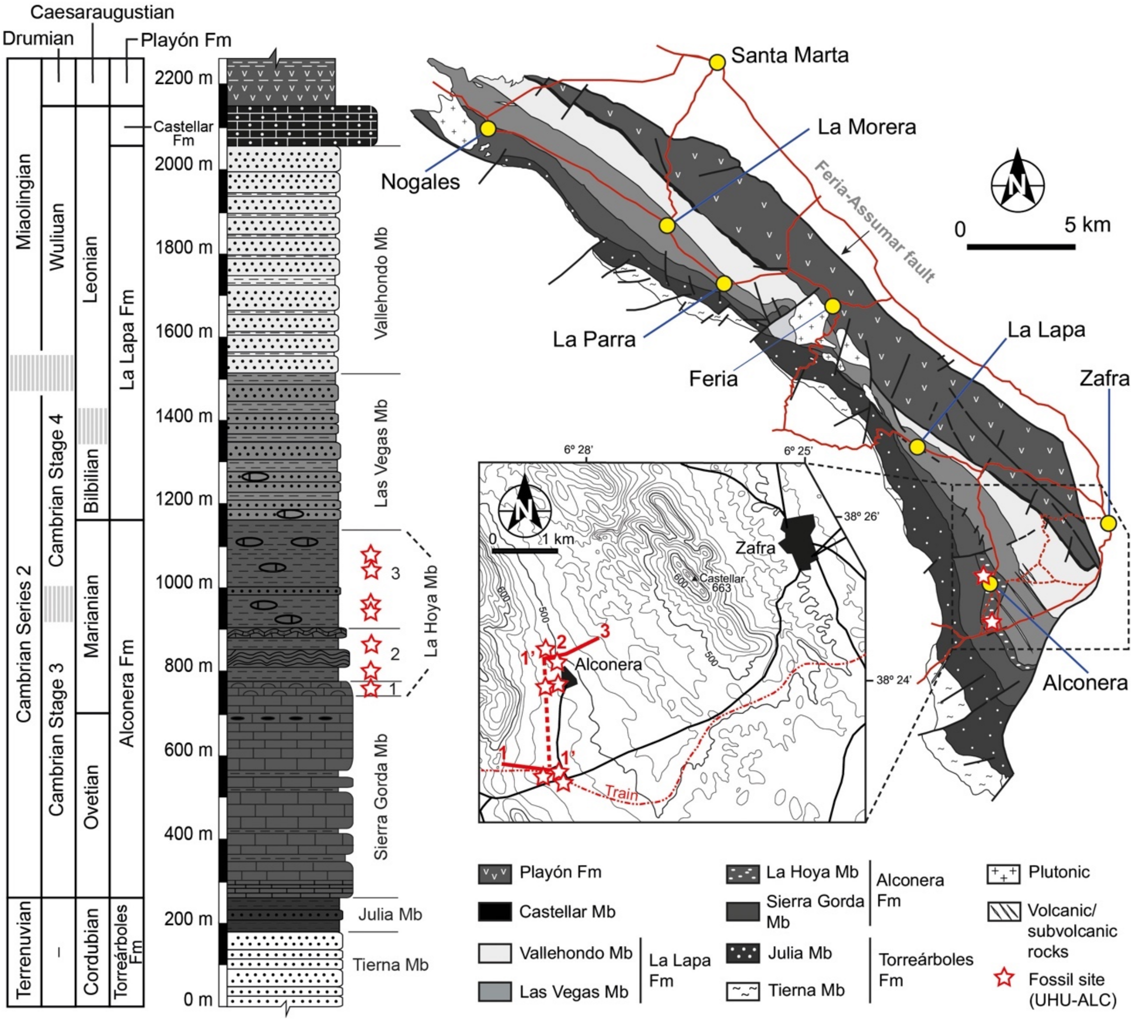


Figure 6: Geological map and synthetic stratigraphical column of the Cambrian sequence of the Alconera Block, indicating the fossil sites.

Conformably overlying the Alconera Formation, there is the La Lapa Formation, a predominantly detrital unit of yellow-greenish colour with isolated carbonate levels at the base. The formation is divided into the lower Las Vegas Member and the upper Vallehondo Member. Las Vegas Member (350 meters) is formed by an alternation of fine-grained, yellow-to-green sandstones and lutites. At the base, it shows smaller grain size and carbonate levels. Towards the top, these carbonate levels disappear, appearing with some undetermined ichnofossils. The Vallehondo Member (approx. 750 meters) consists of an alternation of fine-grained sandstones with medium-grained sandstones, frequently micaceous, with interbedded lutite levels. To the top, the sandstone levels increase in grain size considerably. Traditionally, both members of the La Lapa Formation were assigned to the Bilbilian (Liñán & Perejón, 1981; Liñán et al., 1995b, 2004). However, Palacios et al. (2021) noted the presence of paradoxidid trilobites and acritarch assemblages characteristic of the Miaolingian Series in the “upper member” of the Vallehondo Formation (=Vallehondo Member, see discussion below); thus a Bilbilian to Leonian age is attributed to the La Lapa Formation.

It should be noted that neither this stratigraphical division nor the chronostratigraphy is consensual among the authors: Palacios et al. (2021) redefine the Vallehondo Formation and divided it into a “lower member” (equivalent to the upper part of La Hoya Member of the Alconera Formation and Las Vegas Member of La Lapa Formation) and an “upper member” (equivalent to the Vallehondo Member of La Lapa Formation and the lowermost Playón Formation), bearing Miaolingian trilobites and acritarch, as previously stated. Although in the present work, we agree with the new age assignment of the Vallehondo Member (“upper member” of the Vallehondo Formation *sensu* Palacios et al., 2021), we do not agree with the stratigraphical division proposed by these authors. Therefore, we follow the original proposal by Liñán & Perejón (1981) and maintain La Hoya Member (lowermost to uppermost Marianain) of the Alconera Formation, as well as La Lapa Formation (lowermost Bilbilian to uppermost Leonian) with its respective members, reconsidering the age of the latter.

Back to the series, and conformably overlying the La Lapa Formation, takes place the Castellar Formation (40 meters), formed by massive quartzites arranged in banks of metric scale, giving rise to the Sierra del Castellar mountain range. These quartzites are generally massive, showing some laminations sporadically. Occasionally, microconglomerate levels can be distinguished. This formation was initially assigned to the uppermost Bilbilian and correlated with other regressive units throughout the OMZ (e.g., ‘Barra Quartzítica’ in Eastern Portugal and Castellar Formation in Córdoba). According to the new dating by Palacios et al. (2021), this formation is re-assigned to the upper Leonian. In addition, Palacios et al. (2021) considered that this formation does not have lateral continuity; thus, they refer to it as “Castellar beds”.

The uppermost part of the stratigraphical series of the Alconera Block is conformably overlain by the Playón Formation, a volcano-sedimentary unit composed of shales and fine-grained sandstones with interbedded acidic and basic igneous rocks. The lower part of the Playón Formation yielded several Miaolingian acritarch assemblages (lower Caesaraugustian to the uppermost Languedocian; see Palacios et al., 2021). In addition, the detrital levels from the lower part of the unit have provided brachiopods (see Gil Cid & Melou, 1986) and trilobites (see Gozalo et al., 1994). The total thickness of this formation has been estimated at 1300 meters (Sánchez-García, 2001).

3.1.3. Viar-Benalija Block

The Viar-Benalija Block (Fig. 7) is located on the northern limb of the Olivenza-Monesterio Antiform and is included in the Zafra-Alanís Domain (see Fig. 3). To the north, it is bounded by the Guadalcanal-Assumar fault, which separates this block from the Loma del Aire Unit to the northwest and undefined Cambrian blocks to the northeast, while to the south it is limited by the Serie Negra Succession to the southwest and other undefined Cambrian outcrops to the south and southeast. This block includes a stratigraphical record which ranges from late Neoproterozoic to Miaolingian.

The lowermost unit of this block, which outcrops in the Eastern part of it, is represented by a monotonous succession of grey-black shales and greywackes with volcano-sedimentary intercalations, which are correlated at a regional level with the Tentudía Succession (uppermost levels of the Serie Negra succession) and dated as late Neoproterozoic (Apalategui et al., 1989). The thickness of the outcropping rocks of this formation was not measured in this block.

Over these black shales and greywackes, there is the Malcocinado Formation, consisting of a volcano-sedimentary sequence with calc-alkaline andesitic affinity. These volcano-sedimentary sequences range in age from the terminal Neoproterozoic to the base of the Cambrian (Sarrionandia et al., 2020). The formation's total thickness is unknown, but the minimal estimated thickness is approximately 300 meters.

The Serie Negra succession and the Malcocinado Formation are not represented in the stratigraphical column (Fig. 7).

Above the Malcocinado Formation occurs the Torreárboles Formation (Liñán, 1974). In this formation, a lower and an upper member (Mb I and Mb II, respectively) are distinguished, the former made up of massive arkoses and the latter formed by an alternation of shales and sandstones, from centimetric to metric levels. The arkoses of the lower member generally present a massive texture and light colours, showing grain-classification and cross-laminated sedimentary structures. This member is approximately 200 meters thick. Conformably overlying the previous one, there is the upper member, made up of an alternation of shales with greywackes and arkoses, with grain size decreasing towards the top and the arkoses disappearing in the upper part of the member. Within these levels, sedimentary structures such as parallel and cross laminations, grain-classification and abundant bioturbation are observed. At the top of this upper member, there are also some levels of interstratified basic volcanic rocks, which have not been studied in detail. This upper member is approximately 650 meters thick. The age of these materials is Cordubian (Apalategui et al., 1989).

Conformably overlying the Torreárboles Formation, there is a carbonate-detrital formation known as 'Calizas de Agua' (*sensu* Fricke, 1941), or the ‘Campoallá beds’ (Simon, 1951), depending on the sector. No sections have been found in which the complete formation can be observed. However, it is characterised by an increase in carbonates with respect to the detrital towards the top of the series.

The ‘Campoallá beds’ lower levels are made up of an alternation of lutites and sandstones, with punctual levels of interbedded limestone. On the other hand, the limestones have a greyish colour and a characteristic banding, presumably marked by changes in the proportion of carbonates. In addition, some basic volcanic rocks have been found interstratified in the lutitic levels. This part of the formation is approximately 500 meters thick. The upper levels are characterised by a greater abundance of carbonates, with frequent levels of limestone with chert nodules. In these materials, basic volcanic levels have also been found. The last differentiated section within this formation is a 350 meters thick level of massive limestones, with stromatolitic and archaeocyaths levels and evidence of palaeokarst at its top. The archaeocyath assemblages from the upper part include taxa with a long stratigraphical range that extends from the archaeocyaths zones I to IX of Perejón (1986); thus, these archaeocyath assemblages indicate an age ranging from the early Ovetian to the early Marianian (Perejón, 1986, 1994; Perejón & Moreno-Eiris, 2006; Mayoral et al., 2020).

Overlying the limestones, there is a mostly detrital formation consisting of yellow-green shales, with some carbonate component in the intermediate levels, and with lenticular levels of sandstones and basic volcanic rocks in its basal part. This formation has been named 'Benalija beds' (*sensu* Fricke, 1941) or, more commonly, ‘Alanís beds' (*sensu* Simon, 1951). However, we consider the former as a sandstone-like lateral facies change of the latter, mostly present at the upper part of the formation. Although both the bottom and the top of the formation have been recognised, it should be noted that the complete formation has not been mapped accurately, mainly due to the abundant presence of faults, which, presumably, may have generated sequence duplications. From bottom to top, the following sections have been recognized.

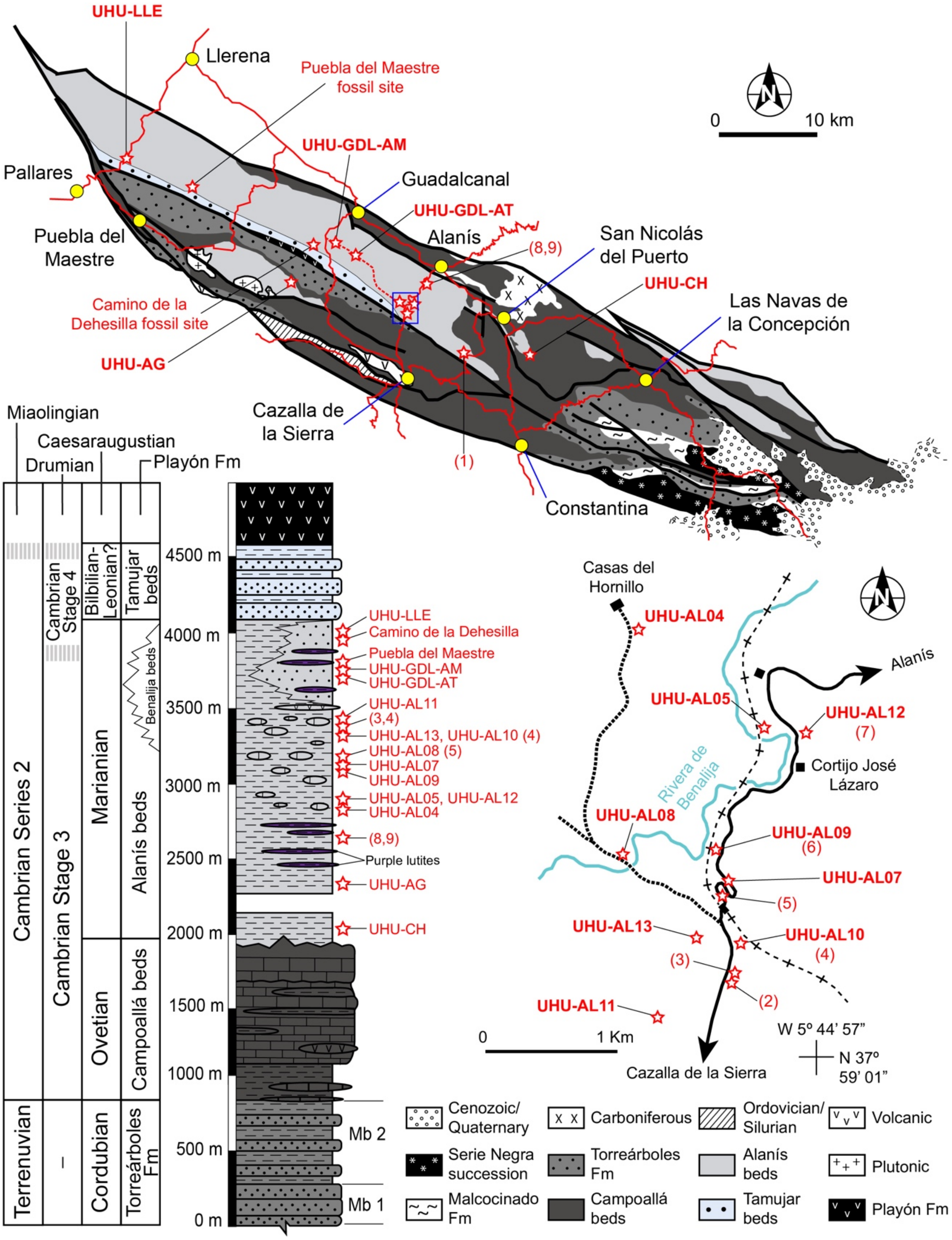


Figure 7: Geological map and synthetic stratigraphical column of the Cambrian sequence of the Viar-Benalija Block, indicating the fossil sites. The numbers in brackets indicate the original designation of the points according to Richter & Richter (1940).

Immediately above the 'Campoallá beds' and over the erosional unconformity generated by the karstification, some levels of yellow to green lutites are burying the karst, occasionally with carbonate nodules and parallel lamination. This lower section is top-limited by faults, so its relationship with the upper section cannot be observed. This formation's section is approximately 200 meters thick and shows a fossil assemblage composed of the trilobites *Strenuella* n. sp., *Acanthomicmacca*? sp., *Delgadella souzai* and, less commonly, *Saukianda andalusiae,* as well as brachiopods, hyoliths, and sponges, assigned to the lower Marianian (Mayoral et al., 2020).

The following materials consist of green shales showing a certain carbonate component, intercalated with punctual carbonate levels, and occasional thick basic volcanic levels. Towards the top, greenish shales appear interspersed with lenticular levels of purplish shales and carbonate-rich levels towards the top. These levels show a rich trilobite assemblage composed of *Saukianda andalusiae* Richter & Richter, 1940, *Strenuaeva sampelayoi* Richter & Richter, 1940, *Alanisia guillermoi* (Richter & Richter, 1940), *Perrector perrectus* Richter & Richter, 1940, *Eops eo* Richter & Richter, 1940, *Gigantopygus* cf. *bondoni*, and *Delgadella souzai* (Delgado, 1904), together with brachiopods, hyoliths, sponges, and eocrinoids (Ubagh & Vizcaïno, 1991). Upwards, these levels of green shales with a carbonate component progressively change to sandstones, with coarser-grained levels, all yellowish to light green. In the present work, we consider these levels to be those described initially by Fricke (1941) as 'Benalija beds', which we consider representing a lateral facies change of the upper part of the 'Alanís beds'. This lateral change of facies justifies different fossil associations, including the trilobites *Andalusiana cornuta* Sdzuy 1961, *Triangulaspis fusca* Sdzuy, 1962, and *Termierella sevillana* Sdzuy, 1961, together with abundant hyoliths, brachiopods and bradorids (Sdzuy, 1962, Gozalo & Hinz-Schallreuter, 2002), assigned to the middle Marianian.

The uppermost part of the series varies from green shales and greenish to yellowish fine-grained sandstones, depending on the sector, with frequent intercalations of purple shales. The top of the formation has yielded a fossil assemblage composed of the trilobites *Serrodiscus bellimarginatus*, *Protaldonaia morenica* Sdzuy, 1961, *Triangulaspis fusca* and *Chelediscus garzoni* Collantes, Pereira, Mayoral & Gozalo, 2023, as well as brachiopods and helcionellid molluscs (Sdzuy, 1961, 1962; Liñán & Mergl, 1982; Yochelson & Gil Cid, 1984; Gil Cid, 1986; Collantes et al., 2020, 2022) which indicate upper Marianian. As previously stated, the total thickness of the 'Alanís beds’ has not been precisely calculated. However, it is estimated to be more than 1450 meters, assuming that duplication along the series may exist.

Through transitional contact, there is another detrital formation called ‘Arroyo Tamujar beds'. This formation comprises dark-coloured shales and fine- to medium-grained sandstones, generally very micaceous, with frequent quartz and plagioclase clasts. The lower part of the formation is characterised by discontinuous levels of quartzites, reaching a maximum thickness of 25 meters. Along the whole formation, grain-classification and cross-lamination structures can be frequently observed. Regarding its age, being above the 'Alanís beds' (with Marianian trilobites) and below the basic volcanic rocks correlated with the Playón Formation (Miaolingian), a Bilbilian age is proposed for this formation, being stratigraphically correlatable with the Las Vegas Member of La Lapa Formation from Alconera, or the ‘Rincón beds’ from northern Huelva Province.

At the top of the series, there is an approximately 400 meters thick level of basic volcanic rocks, with an intermediate level of brown greywackes. The former has a porphyritic texture with plagioclase phenocrystals and a colour ranging from grey to greenish. Given their nature and stratigraphical position, these rocks have been correlated with the Playón Formation from the Alconera Block, Miaolingian in age.

3.1.4. Cumbres Block

The Cumbres Block (Liñán & Quesada, 1990) (Fig. 8) is located in the southern limb of the Olivenza-Monesterio Anticlinorium, in the Elvas-Cumbres Mayores Domain (*sensu* Apalategui et al., 1990) (see Fig. 3). To the north, this block is bounded by a thrust over Cambrian rocks, while to the east it is limited by the Herrerías Block. To the south, it borders with the Barrancos-Hinojales Unit. This block presents a stratigraphical record ranging from Cambrian Stage 3 to the Miaolingian or, probably, the Furongian.

This unit’s base is formed by the Carbonatada Formation, consisting of beige to greyish dolomites and white limestones to the top. The bottom of the formation is faulted and is unknown; the outcropping sequence is between 100-300 meters thick, depending on the section. No fossils have been reported for this formation; thus, it has been assigned to the Ovetian-lowermost Marianian based on regional correlation.

Above the Carbonatada Formation, a transitional contact occurs with the overlying unit, consisting of *kramenzel* facies (shales with carbonate nodules) that develop for about 10 meters thick. This transitional contact gives rise to the 'Cumbres beds', an alternation of purple shales and greywackes that extends between 350-1100 meters thick, depending on the sector. Shale and greywacke levels range from approx. 10 to 50 centimetres each, except for the later levels of the sequence, which are predominantly shale. It is also characterised by the abundance and diversity of bedform structures, predominantly in the greywacke levels. This formation has provided abundant fossils, including two assemblages: the first assemblage (from the lower part of the formation) is composed of *Delgadella souzai* (Delgado, 1904), *Callavia choffati* (Delgado, 1904), *Atops calanus* Richter & Richter, 1941, *Triangulaspis fusca*, *Hicksia elvensis* and *Rinconia schneideri*, as well as the brachiopod *Obolella* sp., corresponding with the lowermost middle Marianian. The second fossil assemblage is composed of *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), *Pseudatops reticulatus* (Walcott, 1890b), *A. calanus*, *Triangulaspis fusca*, *Chelediscus garzoni* Collantes, Pereira, Mayoral & Gozalo, 2023, the helcionelloid *Marocella morenensis* (Yochelson & Gil Cid, 1984), brachiopods, and hyoliths, representing the upper Marianian (Collantes et al., 2020, 2021a, b, 2022, 2023).

Over the 'Cumbres beds', there is a concordant contact with the 'Rincón beds', conformed by laminated lutites (approx. 100 meters) with abundant undetermined bioturbations, followed by sandstones and several metric quartzitic beds. The total thickness of this formation is estimated to be 350 meters. According to its stratigraphical position, it is assigned to the Bilbilian and, hesitantly, lower Leonian? (i.e., uppermost Cambrian Stage 4), as overlies the LO of *Serrodiscus* (top of the Marianian Stage) and underlies the pillow-lavas of the Playón Formation (Miaolingian).

Apparently concordant over the previous formation, a ca. 150 meters unit of basic volcanic rocks appears, recognized as the Playón Formation. These levels are composed mostly of basaltic pillow-lavas, with occasional isolated detrital levels, although no fossils have been found in the latter. The base of this formation is characterised by the presence of a polygenic, heterometric, matrix-supported conglomerate composed of rounded cobbles (centimetric to decimetric). The top of the formation is constituted by a volcanic breccia, probably representing the end of the volcanic sequence. As age, Caesaraugustian-Guzhangian was proposed for these rocks based on regional correlation.

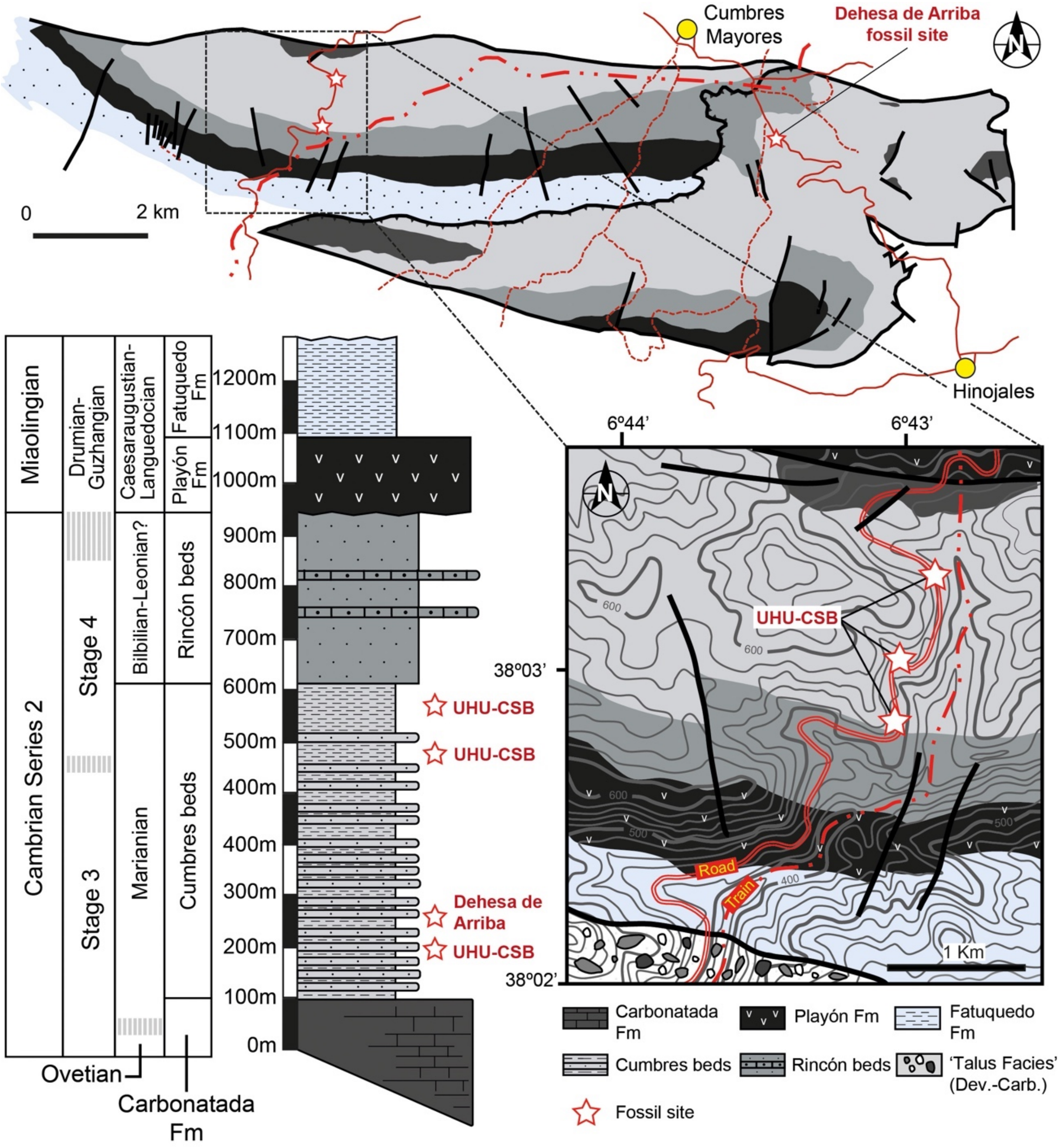


Figure 8: Geological map and synthetic stratigraphical column of the Cambrian sequence of the Cumbres Block, indicating the fossil sites.

The Cambrian series is culminated by a 150-350 meters succession of monotonous green shales, with punctual intercalated sandstone levels, correlated with the Fatuquedo Formation from Portugal (Apalategui et al., 1979). No fossils have been found in the unit, only abundant bioturbation in some levels. Given its stratigraphical position above the Playón Formation, it is attributed to the Miaoligian or even the Furongian, without further criteria to help precision the assignment. These rocks could also be correlated with the lower member (Mb 1) of the Umbría-Pipeta Formation, Miaolingian in age.

3.1.5. Herrerías Block

The Herrerías Block (Liñán & Quesada, 1990) (Fig. 9) is located in the southern limb of the Olivenza-Monesterio Anticlinorium, belonging to the Elvas-Cumbres Mayores Domain (*sensu* Apalategui et al., 1990). This block is bounded to the northwest by a thrust over volcanic rocks (Playón Formation), to the northeast is thrusting over the Arroyomolinos Block, and is limited by the Barrancos-Hinojales Unit to the south. It includes one of the most complete stratigraphical sequences of the entire OMZ, with rocks dating from the Cambrian Series 2 (Ovetian) to the Middle Devonian (lower Emsian).

The lowest part of this unit is made up of thick levels of dolomites and limestones, with punctual detrital levels (mainly shales) intercalated. The dolomites are beige, while the limestones on the top are white to cream. Although the bottom of the formation is not known (as it is thrusting over the northern units), the outcropping succession is approximately 200 meters thick. These rocks were named 'Cañuelo limestones' (Schneider, 1941), although they have been considered equivalent to those of the Carbonatada Formation of Portugal (Eguiluz et al., 1980). No fossils have been found in this unit. However, palaeontological reports from the MAGNA of Monesterio (nº 897) (Eguiluz et al., 1980) reported the presence of archaeocyaths moulds (*Coscinocyathus* sp. and *Aldanocyathus* sp.) from the *kramenzel* facies at the top of this formation. Thus, based on regional correlation, its age has been established as Ovetian to earlymost Marianian.

The contact between the Carbonatada Formation and the overlying unit is marked by a transitional levels of lutites with carbonate nodules (*Kramenzel*). These materials reach up to 25 meters thick.

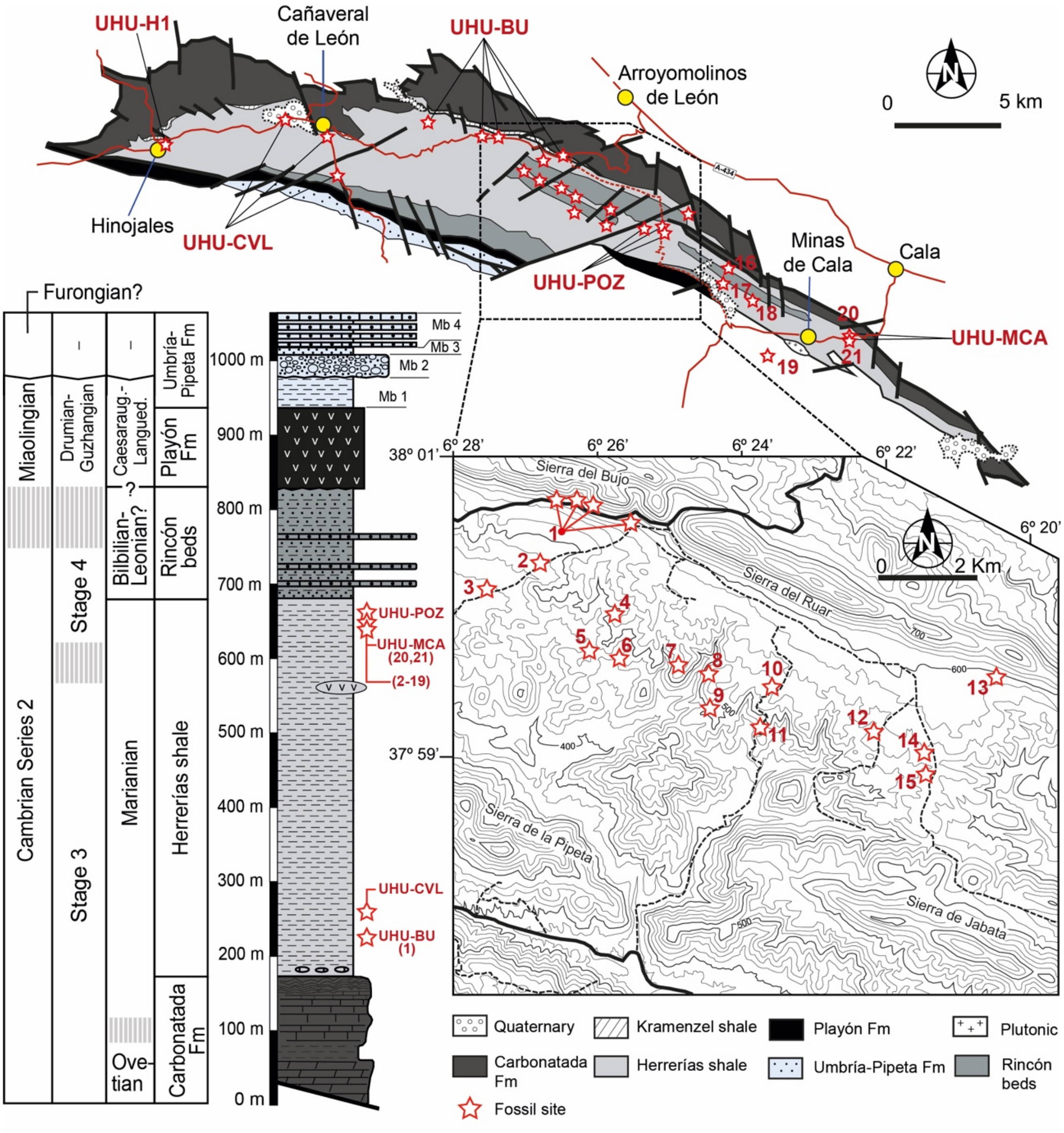


Figure 9: Geological map and synthetic stratigraphical column of the Cambrian sequence of the Herrerías Block, indicating the fossil sites. The numbers 1 to 21 indicate the points studied by Richter & Richter (1941).

The overlying formation is named ‘Herrerías shales’, a monotonous (approx. 500 m) succession of purple lutites with punctual sandstone levels. Occasionally, levels (up to 3 meters thick) of interstratified basic volcanic rocks appear. The lower levels of this formation are characterised by the presence of the trilobites *Delgadella souzai*, *Rinconia schneideri* (Richter & Richter, 1941*), Gigantopygus* cf. *bondoni*, *Hicksia elvensis* Delgado, 1904, *Protaldonaia morenica* Sdzuy, 1961, *Callavia choffati* (Delgado, 1904), *Atops calanus* Richter & Richter, 1941, *Calodiscus ibericus* Sdzuy, 1962, *Strenuaeva* *sampelayoi* Richter & Richter, 1940, and *Triangulaspis fusca* Sdzuy, 1962, assigned to the middle Marianian (Collantes et al., 2021a, b). The upper part of the formation has yielded the trilobites *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), *T. fusca*, *Pseudatops reticulatus* (Walcott, 1890b), *P. morenica*, and *Chelediscus garzoni* Collantes, Pereira, Mayoral & Gozalo, 2023, as well as brachiopods (*Obolella* sp.), undetermined hyoliths and the helcionelloid *Marocella morenensis* (Yochelson & Gil Cid, 1984), all of them corresponding to the upper Marianian (Collantes et al., 2020, 2021a, 2022, 2023).

Following the 'Herrerías shale', conformably, it takes place the 'Rincón beds' (Schneider, 1939), formed mainly by fine-grained sandstones, intercalated with thin lutitic levels, as well as punctual quartzitic beds of metric scale. This formation has not yielded body fossils, only undetermined ichnofossils. The average thickness of this formation ranges between 150-200 metres, although some sections have reached 350 meters. Given their stratigraphical position above the LO of *Serrodiscus bellimarginatus* and below the volcanic levels of the Playón (Caesaraugustian-Guzhangian at the Alconera Block), these rocks have been tentatively assigned to the Bilbilian and, hesitantly, to the lower Leonian (Cambrian Series 2, Stage 4).

Overlying the 'Rincón beds' through mechanical contact occur the volcanic rocks of the Playón Formation, which are constituted mainly by basaltic pillow-lavas and no detritial levels, in contrast with the bimodal volcanism of the Alconera Block, also with fossil-bearing lutitic intercalations. As previously noted, these rocks are dated as Caesaraugustian-Guzhangian in this section based on regional correlation with the Alconera Block.

The top of the Cambrian series is constituted by the Umbría-Pipeta Formation (Schneider, 1939), which, in turn, comprises four members. The lowermost member (Mb 1) is formed by yellowish to greenish lutites, about 40 meters thick, providing Miaolingian acritarchs (Mette, 1987, 1989). The following member (Mb 2) is constituted by conglomerates formed by polygenic, mostly rounded cobbles (centimetric to decimetric), going from matrix-supported to clast-supported and vice versa, and showing greywacke-like matrix. Regarding its relationship with the underlying member, there are different opinions: on the one hand, Apalategui et al. (1990) noted a 10-20 meters transitional contact between the lutites and the conglomerates, apparently being in stratigraphical continuity; however, Robardet & Gutiérrez-Marco (2004) reported the presence of an erosional unconformity at the base of the conglomerates, marking a sedimentary breakup, with which we agree. The overlying member (Mb 3) is formed by 10 meters of feldspathic sandstone, presumably concordant over the conglomerates. Finally, the top member (Mb 4) is a 50 meters quartzite succession deposited concordantly over the underlying sandstones, with occasional shale and tufite levels and showing parallel to cross-bedding from bottom to top, as well as ripples and lenticular beds.

Regarding the age of Mb 2 to Mb 4, conglomerates of Mb 2 were initially assigned to the Ordovician by Schneider (1939), who assumed they represented the beginning of the Sardic phase, while quartzites of Mb 4 were correlated initially with the Armorican Quartzite by the same author. After the assignment of the Mb 1 to the 'Middle Cambrian' (i.e., Miaolingian) based on the acritarch assemblages (Mette, 1987, 1989), Robardet & Gutiérrez-Marco (2004) assigned the Mb 2, 3 and 4 to the 'Middle Cambrian'. However, López-Guijarro et al. (2007, 2008) carried out the U–Pb zircon dating of several K-bentonites interbedded in quartzites of Mb 4, which provided a ca. 489 Ma, indicating a late Furongian age for these levels. Despite the isotopic dating of the Mb 4 denoted a clear late Furongian age, these rocks have been treated as "early Tremadocian" (López-Guijarro et al., 2008) and considered as the basal Ordovician unconformity by several authors (e.g., Quesada, 2006; López-Guijarro et al. 2008; Álvaro et al. 2014, 2018). In contrast, Gutiérrez-Marco et al. (2019) proposed a late Furongian age for the quartzites (Mb 4); thus, we follow the same assignment and regard the Mb 2, 3 and 4 as Furongian? pending new dating of the uppermost member of this formation.

3.1.6. Arroyomolinos Block

The Arroyomolinos Block (Liñán & Quesada, 1990) (Fig. 10) represents the easternmost unit of the Elvas-Cumbres Mayores Domain (*sensu* Apalategui et al., 1990), in the southern limb of the Olivenza-Monesterio Anticlinorium. It is bounded to the north by the Serie Negra succession from the axial zone of the Olivenza-Monesterio Anticlinorium. To the south, it is bounded by the Herrerías Block. This block shows a stratigraphical record dating from the latest Neoproterozoic to the Miaolingian.

The base of this unit is made up of rocks of the Tentudía Succession, the upper part of the Serie Negra Succession, a monotonous sequence of metagreywackes with intercalated black shales and quartzites, amphibolites, and marble intercalations, among other lithologies. All these materials show a low degree of metamorphism and are dated as late Proterozoic (Eguiluz & Quesada, 1980; Eguiluz & Ramón-Lluch, 1983; Eguiluz et al., 1980).

In this area, the Tentudía succession is unconformably overlain by the Bodonal-Cala succession (originally “Bodonal-Cala porphyroids”, Hernández-Enrile, 1971), and considered equivalent to the Malcocinado Formation (Sánchez-Carretero et al., 1990). It is a volcano-sedimentary complex including acid volcanic rocks (dacites, rhyolites, among others) and intermediates (andesitic tuffs), showing a calc-alkaline geochemical signature (Sánchez-Carretero et al., 1989, 1990) and very low-grade metamorphism. Regarding its age, samples obtained for the igneous lithologies of this succession were dated 514 ± 9 Ma (Ordóñez, 1998). However, this isotopic age disagrees with its stratigraphical position and the Ediacaran-earliest Cambrian assignment of the Malcocinado Formation (Sarrionandia et al., 2020).

Tentudía and Bodonal-Cala successions were omitted from the stratigraphical column in the present work (Fig. 10).

Overlying the Bodonal-Cala succession (presumably, in normal contact), it takes place the Carbonatada Formation. These rocks were originally named ‘Cañuelo limestones’ (Schneider, 1941) and consist of a 250 metres (max.) succession of dolomites and limestones, with punctual detrital intercalations. The lower dolomites are beige, while limestones are white to greyish. This formation has not yielded any fossils, so its age is assigned to the Ovetian-uppermost Marianian by regional correlation.

At some points in the Arroyomolinos Block (on a non-mapping scale), there is a transitional contact between the Carbonatada Formation and the overlying unit conformed by *kramenzel* facies, consisting of lutites with carbonate nodules. These rocks have a variable thickness between 5 and 25 meters. In other sectors, the overlying formation is placed conformably over the limestones.

The next unit is composed of several lithologies: at the top of the carbonate rocks, there is a grey shale succession of variable thickness (50-100 metres), which gives rise to lateral facies change into another unit formed by massive sandstones, with punctual volcano-sedimentary deposits. Following these sandstones, a monotonous (300-400 metres) succession of purple to greenish shales with parallel lamination bearing intercalated bimodal volcanic rocks takes place. Schneider (1941) referred to this whole detrital group as ‘Capas abigarradas de Arroyomolinos’ (‘Arroyomolinos mottled beds’) and stratigraphically placed it below the ‘Cañuelo limestone’. However, in the present work, we consider the different levels of this unit as lateral facies changes equivalent to the ‘Herrerías shale’, as represented in Fig. 10.

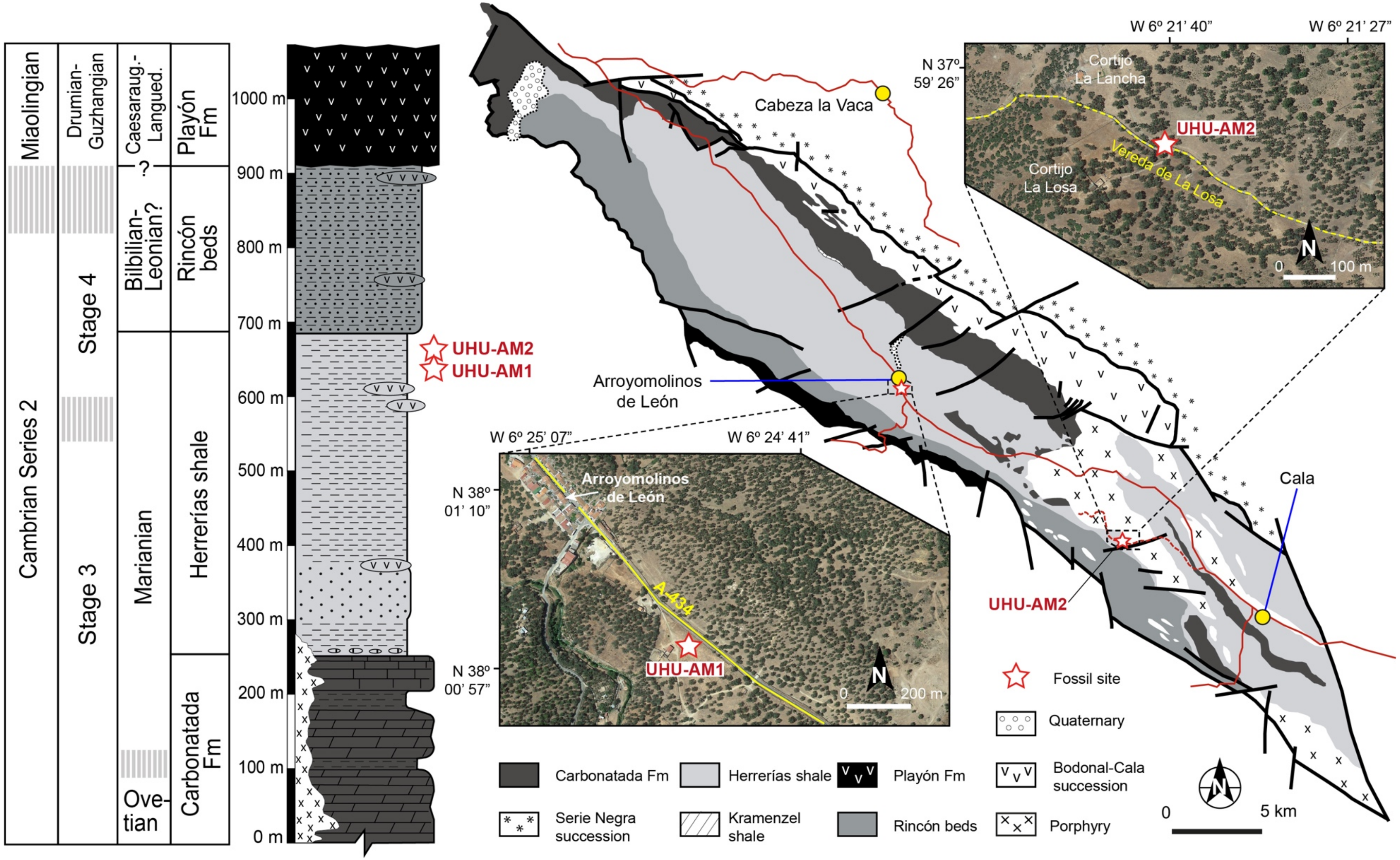


Figure 10: Geological map and synthetic stratigraphical column of the Cambrian sequence of the Arroyomolinod Block, indicating the fossil sites.

Based on correlation with the other blocks of the Elvas-Cumbres Mayores Domain, this formation is assigned to the lower to upper Marianian. Trilobites in this block are very scarce, with only a few specimens found in the formation's uppermost part. This assemblage is composed of *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), *Triangulaspis fusca* Sdzuy, 1962 and *Pseudatops reticulatus* (Walcott, 1890b), which suggest a late Marianian age for these levels.

On top of the 'Herrerías shale', there is another concordant formation assigned to the 'Rincón beds', composed of white to yellowish shales and sandstones with quartzitic levels, also differentiated by a more evident lamination and intense bioturbation at some levels, and followed by another detrital unit considerably coarser in grain and including isolated, reduced volcanic levels. The total thickness of this formation is between 200-250 metres, depending on the section. Being above *Serrodiscus* occurrence in the 'Herrerías shale', as well as below the volcanic rocks of the Playón Formation (Miaolingian), this unit is assigned to the Bilbilian or, with doubts, to the lower Leonian, without further criteria to determine the age.

The top of the Arroyomolinos Block is represented by the Playón Formation, a volcanic succession overlying the detrital materials previously described and constituting the most modern unit of the Arroyomolinos Block. This formation consists of submarine lava flows, in which some pillow-lava structures can be distinguished occasionally, as well as levels of volcanic tuff. As previously stated for the other blocks, these rocks have an age assignment to the Caesaraugustian-Guzhangian (Miaolingian) based on regional correlation.

4. Material

This work included a review of the existing collections and several field campaigns to collect specimens that were incorporated into pre-existing collections and/or constituted new collections.

4.1. Collected material

Fieldwork started in 2017 as part of the author's Bachelor's degree work and was conducted along different fossiliferous Cambrian sections of the OMZ. The studied sections and localities are: Vila Boim-Terrugem section (Elvas, Portugal), Alconera A1-A3 sections (Badajoz, Spain), Viar river section (also Llerena-Pallares section, Badajoz), Puebla del Maestre fossil site, Arroyo Galeón fossil site, Camino de la Dehesilla fossil site (Badajoz), Guadalcanal (Arroyo del Molino and Arroyo del Tamujar sections, Seville, Spain), Cazalla de la Sierra-Alanís (Seville), Cerro del Hierro (Seville), Minas de Cala (Huelva, Spain), Arroyomolinos de León (AM1, AM2, El Pozuelo and Sierra del Bujo sections, Huelva), Cañaveral de León (Huelva), Hinojales (Huelva), Cumbres Mayores (Dehesa de Arriba section, Huelva), and Cumbres de San Bartolomé section (Huelva).

A total number of 1299 trilobites were collected. All specimens are housed in the Laboratorio de Tectónica y Paleontología from the Departamento de Ciencias de la Tierra, University of Huelva (UHU).

4.1.1. Vila Boim-Terrugem section (Fig. 5)

This fossil site was originally studied by Nery Delgado (1904) together with other fossil sites nearby, and later revised by Carlos Teixeira (1952). Currently, the type collection is housed in the palaeontological collections of the Museu Geológico de Lisboa (see “Other collections” below in this section for more specific information), and it was collected by the end of the nineteenth century by the Geological Survey of Portugal. Lately, in the 1930’s, a new collection of material was conducted by Romão de Sousa, which is housed at the Museu de História Natural e da Ciência da Universidade de Lisboa.

Subsequent fieldwork campaigns have been carried out in this section, including the ones of Prof. Eladio Liñán's and Prof. Sofia Pereira's teams, relocating the fossiliferous levels studied by Delgado and collecting new material.

The author carried out new field campaigns from 2021 to 2023 between the localities of Vila Boim and Terrugem. Only fragmentary material was found, and it was not incorporated into any collection.

4.1.2. Alconera sections (A1-A3) (Fig. 6)

These sections were formally described by Liñán & Perejón (1981) and constitute the composite type-section of the Marianian Stage from the OMZ (see Liñán et al., 1993). Several new samplings from A1 and A3 sections were carried out by the author from 2020 to 2023, collecting additional specimens of species previously reported in the area and representatives of genera and species recognized for the first time in this locality.

A total number of 159 specimens were collected from La Hoya Member. These are housed with the code UHU-ALC.

4.1.3. Viar river section (Llerena–Pallares, Badajoz) (Fig. 7)

Lotze (1958) and Sdzuy (1961, 1962) made the first comments regarding this section. Posterior works in this section include those of Gil Cid (1988a), Yochelson & Gil Cid (1984) and Collantes et al. (2020, 2022), as well as the MAGNA of Puebla del Maestre (nº 898) (Apalategui et al., 1989). The author sampled this area in 2021, collecting new specimens of species previously reported there. A total of 27 specimens were found in the uppermost 'Benalija beds', housed with the code UHU-LLE.

4.1.4. Puebla del Maestre fossil site (Fig. 7)

This fossil site was first studied in detail by Gil Cid (1988b), who reported a low-diversity trilobite fauna from this point. Subsequently, this locality was also represented in the MAGNA of Puebla del Maestre (nº 898) (Apalategui et al., 1989). The few specimens found during this work are highly fragmented, so no material from this fossil site has been inventoried.

4.1.5. Arroyo Galeón fossil site (Fig. 7)

The first reference to this fossil site is given in the palaeontological preliminary report by Prof. Eladio Liñán and Prof. Antonio Perejón for the MAGNA of Puebla del Maestre (nº 898) in 1981, describing a rich trilobite fauna from the eastern bank of the Galeón stream. So far, only four specimens were found, housed with the code UHU-AG.

4.1.6. Camino de la Dehesilla fossil site (Badajoz) (Fig. 7)

The first reference to this fossil site is Liñán & Mergl (1982), noting the presence of trilobites and brachiopods. It corresponds to the uppermost ‘Benalija beds’. The author sampled it, but no new significant material was found, apart from several fragments.

4.1.7. Arroyo del Molino-Arroyo Tamujar sections (Guadalacanal, Seville) (Fig. 7)

Both sections are included together as they represent equivalent levels and fossil assemblages. These sections were mentioned by Lotze (1958) and later by Sdzuy (1961, 1962), Apalategui et al. (1985), and more recently by Gozalo & Hinz-Schallreuter (2002).

Both sections have been mapped within the framework of the present work. While the Arroyo del Tamujar section has not been prolific, the Arroyo del Molino section has provided abundant fossils. 62 trilobites have been found in this section, from levels assigned to the middle ‘Benalija beds’, housed with the code UHU-GDL-AM and UHU-GDL-AT.

4.1.8. Cazalla de la Sierra-Alanís section (Seville) (Fig. 7)

This section was originally described by Richter & Richter (1940), and it is where the “*Saukianda* Fauna” was defined. This section originally reported nine fossiliferous levels along the road between Cazalla de la Sierra and Alanís. This number has risen to fifteen in recent years, including fossiliferous sites found in parallel sections.

Among these sites, two have been especially prolific and where most trilobites were collected: AL05 and AL08.

391 specimens were found from the middle 'Alanís beds' rocks, housed with the code UHU-AL05 and UHU-AL08.

4.1.9. Cerro del Hierro sections (Seville) (Fig. 7)

Trilobites from this locality are fairly abundant and well preserved, although the references reporting their occurrence are scarce (Mayoral et al., 2008, 2020). In total, 183 specimens were collected from the lowermost 'Alanís beds', housed with the code UHU-CH.

4.1.10. Dehesa de Arriba section (Cumbres Mayores, Huelva) (Fig. 8)

The only reference to this fossil site is the one of Liñán & Mergl (1982). However, it has provided many trilobites (Prof. Liñán collection housed at the Museo de Ciencias Naturales, Universidad de Zaragoza). Nowadays, this section is destroyed.

Only fragmentary material has been found, but it was not incorporated into any collection.

4.1.11. Cumbres de San Bartolomé section (Huelva) (Fig. 8)

The first report of this fossil site is the one of the MAGNA from the Higuera la Real (nº 896) (Apalategui et al., 1979). Most recent references are the ones of Collantes et al. (2020, 2021a, b, 2022, 2023) as an output of the present work.

Up to date, 260 trilobites from the uppermost 'Cumbres beds' have been found in this fossil site. These are housed with the code UHU-CSB.

4.1.12. Minas de Cala (Huelva) (Fig. 9)

This is one of the fossil sites originally described by Richter & Richter (1941) where the so-called "*Fauna von Cala*" was reported, being also represented in the MAGNA of Santa Olalla del Cala (nº 918) (Apalategui et al., 1986).

Only 13 classifiable specimens from rocks assigned to the uppermost 'Herrerías shales' have been found in this fossil site. These are housed with the code UHU-MCA.

4.1.13. El Pozuelo fossil site (Arroyomolinos de León, Huelva) (Fig. 9)

This fossil site was only represented in the MAGNA of Santa Olalla del Cala (Apalategui et al., 1986).

114 specimens were collected from levels assigned to the ‘Herrerías shales’, housed with the code UHU-POZ.

4.1.14. Sierra del Bujo section (Arroyomolinos de León, Huelva) (Fig. 9)

Several fossiliferous levels along this section extend along the road between Cañaveral de León and Arroyomolinos de León localities. Some of these were previously reported by Lotze (1937, 1939) and later by Richter & Richter (1941) when defining the “Cala Fauna”.

During recent fieldwork campaigns, 20 classifiable specimens were collected from rocks assigned to the lower ‘Herrerías shales’. These are housed with the code UHU-BU.

4.1.15. Cañaveral de León fossil site (Huelva) (Fig. 9)

This fossil site was found by Ignacio Garzón González to the west of the Cañaveral de León locality. Although fossils are scarce, this site has provided an interesting trilobite assemblage, partially published by Collantes et al. (2021b).

A total of 50 specimens were collected from the lower part of the ‘Herrerías shales’. These fossils are housed with the code UHU-CVL.

4.1.16. Hinojales fossil site (Huelva) (Fig. 9)

The only reference to this fossil site is the one by Liñán & Mergl (1982), reporting the presence of trilobites and brachiopods. A total of 13 specimens were collected from the ‘Herrerías shales’, housed with the code UHU-H1.

4.1.17. AM1-AM2 fossil sites (Arroyomolinos de León, Huelva) (Fig. 10)

The few fossils collected in this area were found during the construction works carried out in the village of Arroyomolinos de León and in the vicinity of the "La Losa" county, near the same village. The latter is represented in the MAGNA of Santa Olalla del Cala (Apalategui et al., 1986).

Only three trilobite specimens have recently been found from rocks assigned to the ‘Herrerías shales’. These are housed with the codes UHU-AM1 and UHU-AM2.

4.2. Other collections

The study of Marianian trilobites from the OMZ included the review of existing collections from several institutions. Not only collections that include Iberian material were reviewed, but also foreign collections that allowed the comparison with the Spanish and Portuguese material to clarify several taxonomical problems. Specimens from five pre-existing collections were studied: Senckenberg Research Institute, Frankfurt (Germany), Museu Geologico de Lisboa (Portugal), Museo de Ciencias Naturales, University of Zaragoza (Spain), Departamento de Paleontología of the Complutense University of Madrid, and Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts, USA).

4.2.1. Collections from the Senckenberg Research Institute, Frankfurt (Germany)

The Senckenberg Research Institute, Frankfurt, houses the type-material of most of the Marianian trilobites described from southwestern Iberia, specifically Huelva, Seville and Badajoz provinces, which are included in the ‘Palaeozoology I’ collection. These specimens were collected by Rudolf and Emma Richter between 1937 and 1938 and later by Prof. Klaus Sdzuy before 1961. The collection from Huelva comprises 90 specimens, the Seville collection 114 specimens, and the Badajoz collection 13 specimens. The inventoried material from these collections comprises 217 specimens, arranged in 23 drawers. All specimens from this institution are referred with the code SMF X.

4.2.2. Collections from the Museu Geológico de Lisboa (Portugal)

These fossils were found between the end of the nineteenth century and the beginning of the twentieth century during the former works of the Geological Survey of Portugal, coming from five different sites close to Elvas: Monte Valbom, Chafariz d'El-Rei, Monte da Cavaleira, Fonte do Baldio and Vila Fernando. The palaeontological results were published by Delgado (1904) and subsequently revised by Teixeira (1952). The latter also included the fossils collected in 1930 by Romão de Sousa and Manuel de Matos, housed at the Museu Nacional de História Natural e da Ciência of the Lisbon University, and a few samples collected by Joaquim Pintassilgo in 1941, housed at Geology Museum of the Superior Technical Institute, Lisbon.

The collection is located in the cabinet nº 69 and includes 184 fossils, of which 149 correspond to trilobite specimens. In addition, there are 86 specimens with no inventory number. All specimens from this institution are referred with the code MG.

4.2.3. Collections from the Museo de Ciencias Naturales, University of Zaragoza (Spain)

This collection was gathered by Prof. Eladio Liñán and his team during the palaeontological prospection and research parallel to the elaboration of the MAGNA series of the OMZ. The collection includes specimens from Alconera A1 and A3 sections, Viar river section, Arroyo del Tamujar section, Arroyo Galeón section, Cazalla de la Sierra-Alanís section, Cerro del Hierro sections, Sierra del Bujo section, Hinojales fossil site, Cumbres Mayores (Dehesa de Arriba fossil site), and Cumbres de San Bartolomé section. The vast majority of this collection is not formally inventoried yet. For the present work, 125 trilobites have been formally inventoried. All specimens from this institution are referred with the codes MPZ 2021 and MPZ 2022.

4.2.4. Collections from the Departamento de Paleontología of the Complutense University of Madrid.

These specimens were collected by Prof. Mª Dolores Gil Cid and her collaborators. It is not formally inventoried and contains a considerable amount of material. It is scattered in different numbered boxes, which, in turn, have different cases with a code (DPM). Each of these codes corresponds to one or more published works. The boxes that have been reviewed are 116 (DPM-A145), 700 (DPM-A185, DPM-A200), 727 (DPM-A202), 817 (DPM-A231, DPM-A232, DPM-A233), 818 (DPM-A232), 819 (DPM-A232), 820 (DPM-A232), 821 (DPM-A232), 823 (DPM-A181, DPM-A233), 824 (DPM-A234, DPM-A235), 827 (DPM-A49), 828 (DPM-A49), 830 (DPM-A49), 831 (DPM-A49).

The collection includes specimens from Alconera A1 and A3 sections, the Viar River section, Cazalla de la Sierra-Alanís section and Cumbres Mayores. 59 specimens were selected. All specimens from this institution are referred with the code DPM.

4.2.5. Collections from the Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts, USA)

Only two specimens were requested from this institution: MCZ IP 105035 and MCZ IP 114068, corresponding to cephala of *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), for comparison with the Spanish material.

5. Published results

This thesis is a compendium of five scientific papers published in internationally indexed journals. These have also been presented and discussed at national and international conferences.

In this chapter, the different output papers are presented, each as a subsection.

5.1. Atopidae (Trilobita) in the upper Marianian (Cambrian Series 2, Stage 4) of Iberia (Collantes et al., 2021a in Journal of Paleontology, 95)

5.1.1. Abstract.

New atopid trilobites are described from the lower Cambrian 'Cumbres beds' and 'Herrerías shale' of northern Huelva Province (Andalusia, Spain) and are dated as middle–late Marianian (Cambrian Series 2, Stage 4). New specimens of *Atops calanus* Richter & Richter, 1941 are described and the Laurentian species *Pseudatops reticulatus* (Walcott, 1890b) is recognized for the first time in the Mediterranean subprovince. The associated trilobite assemblage studied herein suggests an age close to the base of Cambrian Stage 4.

5.1.2. Introduction

Atopidae Hupé, 1954 is a little investigated trilobite family based on *Atops* Emmons, 1844. Family membership has had a long and contentious history (Howell & Stubblefield, 1950) and constituent genera were regularly included in the Conocoryphidae based on their secondary blindness; this assignment continued beyond Hupe's (1954) erection of the family (Harrington et al., 1959; Korobov, 1973; Jell et al., 1992). In Spain, this genus was doubtfully recognized by Richter & Richter (1941) as *Atops*? *calanus* Richter & Richter, 1941 in the "Cala Fauna" from Huelva, and that occurrence has been cited by Lotze (1958, 1961) and Sdzuy (1961, 1962). Herein, we describe several cranidia and fragments that enable positive assignment to *Atops*. *Pseudatops* Lake, 1940 is described for the first time in the Iberian Peninsula, with recognition of the Taconic North American species *Pseudatops reticulatus* (Walcott, 1890b). Its presence allows biostratigraphical and palaeobiogeographical correlations with other Avalonian and Taconic localities.

5.1.3. Geological setting

The trilobites were collected in northern Huelva Province, southwestern Spain (Fig. 11), in the Sierra de Aracena y Picos de Aroche Natural Park. Cambrian rocks of the Ossa-Morena Zone are placed in distintict 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). The stratigraphy of the different Cambrian blocks in northern Huelva has been little studied. Only early Cambrian formations have been established (Collantes et al., 2020) although not formally defined.

In the Cumbres Block (Cumbres Cubeta), the siliciclastic sandstones and shales of the 'Cumbres beds' (350–1100 meters) are dated as middle–late Marianian, based on the trilobites *Delgadella* Walcott, 1912, *Hicksia* Delgado, 1904, *Rinconia* Hupé, 1953a, and *Triangulaspis* Lermontova, 1940 in the lower part and *Serrodiscus* Richter & Richter, 1941 and *Triangulaspis* in the upper part (Liñán & Mergl, 1982; Liñán et al., 2002).

The Cumbres fossil site (CU1) is located in the upper 'Cumbres beds' (Collantes et al., 2020). The 24-meters section at CU1 is between 38°02′45.74″N, 006°43′07.40″W and 38° 02′43.90″N, 006°43′07.80″W. Atopid trilobites occur seventeen, nineteen, and twenty meters from the base in association with *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), *Triangulaspis fusca* Sdzuy, 1962, *Marocella morenensis* (Yochelson & Gil Cid, 1984), brachiopods, and hyoliths.

In the Herrerías Block (Herrerías Cubeta), the 'Herrerías shale' (200–500 meters) (Schneider in Richter & Richter, 1941) consists of purple shales with spilitic intercalations and has an age ranging from middle to late Marianian, based on *Delgadella*, *Calodiscus*, *Rinconia*, *Atops*, *Gigantopygus* Hupé, 1953a, *Hicksia*, *Protaldonaia* Sdzuy, 1961, *Callavia* Matthew, 1897, and *Strenuaeva* Richter & Richter, 1940 in the lower part, and *Serrodiscus* and *Triangulaspis* in the upper part (Richter & Richter, 1941; Sdzuy, 1962; Ruiz López et al., 1979; Liñán & Mergl, 1982). The El Pozuelo fossil site (POZ1) is in the upper 'Herrerías shale' with *S. bellimarginatus*, *Protaldonaia morenica* Sdzuy, 1961, *Marocella morenensis*, and brachiopods. Base and top of the 48-meters section at the collecting site are at 37°58′59.17″N, 006°24′18.92″W and 37°58′56.90″N, 006°24′19.93″W, respectively, with atopid trilobites seven and nine meters from the base (Collantes et al., 2020).

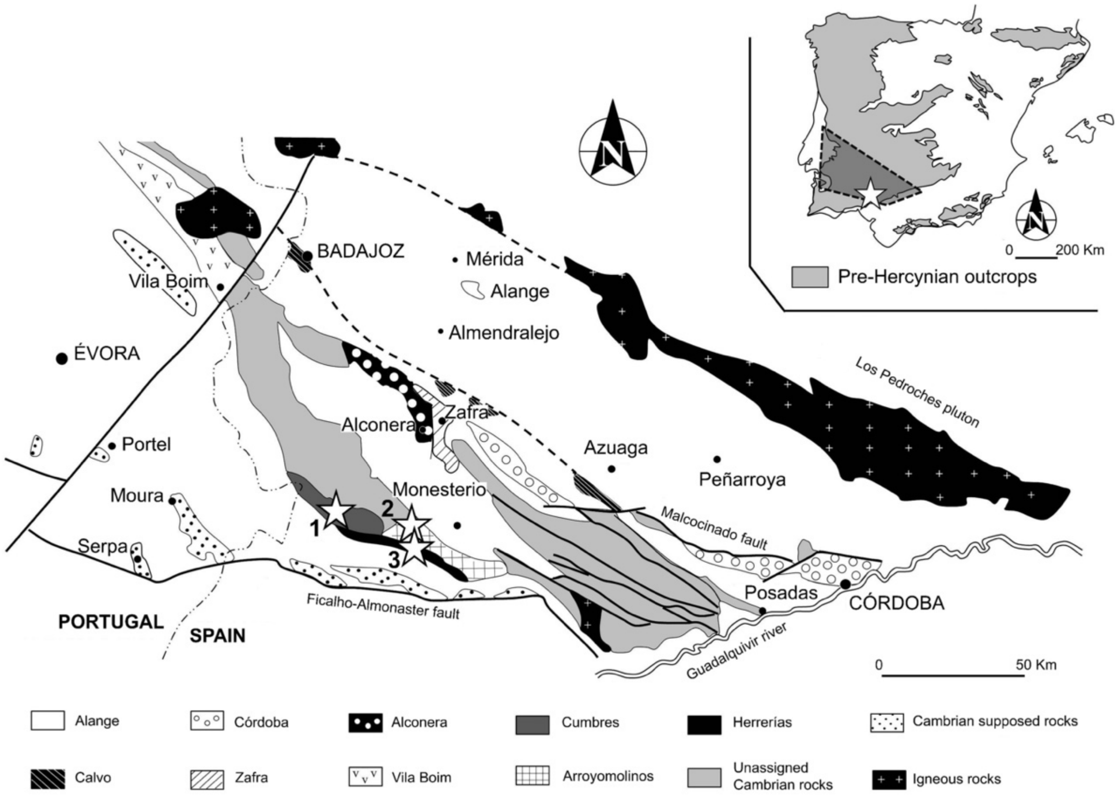


Figure 11: Geological setting of fossil sites in the Cambrian Cubetas (fault-bounded blocks) of the Ossa-Morena Zone, with white stars indicating the positions of the studied fossil sites in each Cubeta. 1 = Cumbres de San Bartolomé site (CU1); 2 = Arroyomolinos de León site (AM1-2); 3 = El Pozuelo site (POZ1). Modified from Liñán & Quesada (1990).

In the Arroyomolinos Block (Arroyomolinos Cubeta), the 'Herrerías shale' (300–400 meters) includes purple, gray, and green shales, with metric intercalations of acid volcanic tuffs and spilites. Base and top of the 65-meters section at the AM1 collecting site are at 38°00′49.58″N, 006°44′47.27″W and 38°00′57.50″N, 006°24′50.14″W, respectively. *Pseudatops reticulatus* occurs with *Serrodiscus bellimarginatus* 46 meters from the base. The AM2 section (37°59′15.90″N, 006°21′17.95″W) is no longer accessible.

5.1.4. Materials and methods

The available material consists of isolated cranidia preserved as internal and external moulds in purple shales with limonitic mineralization. Most of the studied specimens are deformed and/or fragmented.

Repositories and institutional abbreviations: Figured specimens are housed in the Department of Earth Sciences (Laboratory of Tectonics and Palaeontology) of the Faculty of Experimental Sciences, University of Huelva (UHU). Other cited repositories are: SMF=Senckenberg Museum, Frankfurt, Germany; USNM=Smithsonian Institution, National Museum of Natural History, Washington, DC.

5.1.5. Systematic palaeontology

Class Trilobita Walch, 1771

Order uncertain

Family Atopidae Hupé, 1954

Included genera: *Atops* Emmons, 1844 (=*Ivshiniellus* Korobov, 1966), *Pseudatops* Lake, 1940, and *Atopina* Korobov, 1966.

Diagnosis: See Cotton (2001, p. 185, 186).

Remarks: Cotton (2001) carried out a systematic review and a phylogenetic proposal of several blind ptychoparid trilobites, which had been previously included in Conocoryphidae, concluding that it was a polyphyletic group. Within that review, he amended the diagnosis of Atopidae, which he included within the superfamily Ellipsocephaloidea. Given the classification problems, Adrain (2011) proposed not to assign it to any order until a complete revision of the trilobite basal groups was carried out. Jell et al. (1992) included *Ivshiniellus nikolai* Korobov, 1966, *I. patulus* Korobov, 1966, and *I. briandailyi* Jenkins & Hasenohr, 1989 in *Atops*. Cotton (2001) pointed out that in *I. briandailyi*, the tapering of the glabella represented in their reconstruction (Jenkins & Hasenohr, 1989, fig. 4) is not matched by that of the specimens, and the species closely resembles the other Australian species, *Atops rupertensis* Jell, Jago, and Gehling, 1992. We accept that *Ivshiniellus* is a junior subjective synonym of *Atops* as proposed by Jell et al. (1992) and Cotton (2001).

Jell et al. (1992) suggested that *Atopina* could be a junior synonym of *Pseudatops*, arguing that Atopina was erected based on distorted material, in which diagnostic differences compared to *Pseudatops* are due to tectonic distortion. The holotype of the type species *Atopina antiqua* Korobov, 1966 (figured by Korobov, 1973, pl. 12, fig. 5) shows several characters that resemble *Pseudatops*. However, the phylogenetic analysis carried out by Cotton (2001, figs. 2, 3) shows that *Atopina* is closer to *Atops* than to *Pseudatops*. Therefore, we prefer to keep *Atopina* as a separate genus, pending better-preserved specimens.

Several conocoryphids from the Sekwi Formation, Mackenzie Mountains, Canada (Fritz, 1973) have been moved to *Atops* (Jell et al., 1992; Cotton, 2001) based on their blindness, the form of the genal ridges, position of the suture, and glabellar taper. Monospecific *Avalonia* Walcott, 1890a was moved from Atopidae (Jell & Adrain, 2002) to the order Corynexochida based on the subquadrangular (Walcott, 1890a, p. 647) to anteriorly expanding (Walcott, 1890a, pl. 95, fig. 3) glabellar shape.

Genus ***Atops*** Emmons, 1844

Type species: *Atops trilineatus* Emmons, 1844.

Other species: *Atops calanus* Richter & Richter, 1941, *Atops nikolai* (Korobov, 1966), *Atops patulus* (Korobov, 1966), *Atops granulatus* Orlowski, 1985a, *Atops briandailyi* (Jenkins & Hasenhor, 1989), *Atops rupertensis* Jell, Jago, & Gehling, 1992, *Atops korobovi* Romanenko in Repina et al., 1999, *Atops* sp. indet. of Cotton (2001), and Conocoryphidae gen. indet. sp. indet. of Fritz (1973).

Diagnosis: See Jell et al. (1992, p. 192, 195).

Remarks: The most notable differences between *Atops* and *Pseudatops*, according to Lake (1940) and Jell et al. (1992), are: 1) in *Atops*, the glabella extends to the anterior furrow, whereas in *Pseudatops*, it invades the anterior border; 2) in *Atops*, the anterior border furrow is deep, and the anterior border is slightly turned upward, whereas in *Pseudatops*, the anterior furrow is shallow, and the anterior border is flat or even downturned; 3) in *Atops*, the facial suture extends from the anterior to lateral margin across the anterior furrow, whereas in *Pseudatops*, the suture only cuts a small portion of the lateral border and the genal spine; and 4) *Atops* has granular ornament, but *Pseudatops* has reticulate ornament.

Atops calanus Richter & Richter, 1941

Figure 12

1941 *Atops*? *calanus* n. sp. – Richter & Richter, p. 55, pl. 3, fig. 41, pl. 4, fig. 63.

1958 Atops? *calanus* – Lotze, p. 743.

1961 *Atops*? *calanus* – Lotze, p. 164.

1961 *Atops*? *calanus* – Sdzuy, p. 230.

1962 *Atops*? *calanus* – Sdzuy, p. 212, pl. 23, figs. 14, ?15, 16.

2018 *Atops* cf. *calanus* – Collantes et al., p. 567, fig. 4.7.

Holotype: SMF X 1227.

Emended diagnosis: *Atops* with long, conical, tapered glabella, subtle ridge between anterior border furrow and preglabellar furrow. Glabella extends to marginal border furrow, giving rise to a preglabellar area laterally. Anterior border upturned, slightly convex anteriorly. Prominent ocular ridge running laterally from frontal lobe. Suture cutting the gena close to the lateral furrow.

Occurrence: The new specimens come from the upper part of 'Cumbres beds' and 'Herrerías shale', upper Marianian (Cambrian Stage 4). Richter & Richter (1941) cited *Atops*? *calanus* in their horizon cbM2/cbM3, which corresponds with the lowermost middle Marianian.

Description: Cranidium subtrapezoidal, of pronounced relief, wider than long, 12.9–22.3 mm long, 19.4–41.8 mm wide. Opistoparian facial suture close to the lateral margin, cutting the gena near the lateral furrow. Straight or slightly curved anterior margin. Anterior border short (sag.), homogeneous, sloping upward from the anterior border furrow, turning upward. Anterior furrow pronounced, deep. Pregrablellar field short, laterally extended, subtrapezoidal. Preglabellar furrow slightly pronounced. Glabella conical, with rounded frontal lobe, gradually widened towards the back, with length equivalent to 4/5 of the cephalon, with three pairs of deep, narrow, non-transglabellar furrows (S1–S3), slightly curving toward the posterior, all equal in length. Axial furrows narrow, deep, with a slightly convergent tendency toward the anterior area. Occipital furrow (S0) deep. Occipital lobe subtrapezoidal, planoconvex. Preocular field reduced, triangular. Preocular furrow deep, thin. Ocular ridge pronounced, connected between the frontal lobe of the glabella and the lateral furrow, presenting a slight curvature with convexity toward the front. Subtrapezoidal palpebral area wide, with slightly convex relief. Posterior furrow wide, deep, slightly curved. Posterior border thin (sag.), slightly curved. Subtriangular genal area, exsagital extension. Ornamentation composed of coarse granules with massive structure, more pronounced in the preocular and palpebral area and softer in the glabella. For reconstruction of the cephalon, see Figure 13.

Materials: Seven partially preserved cranidia (UHU-CU1001-20, CU1010–CU1013-20, POZ020-20, AM1002-20; moved to UHU-CSB, UHU-POZ and UHU-AM1, respectively). Additional fragments assigned to *Atops calanus* are deposited in the same collection.

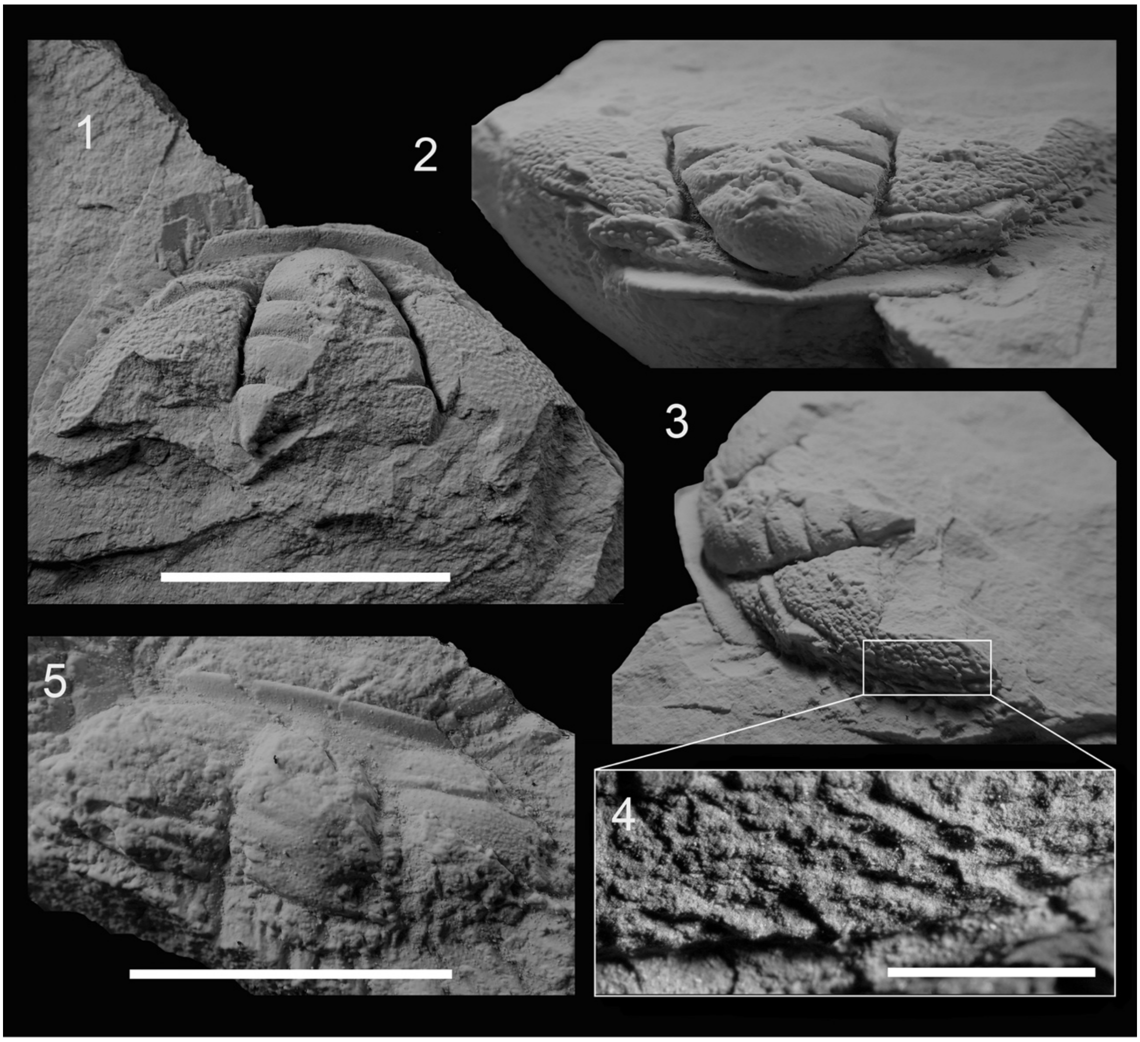


Figure 12: *Atops calanus* Richter & Richter, 1941, 'Cumbres beds', upper Marianian, Cumbres de San Bartolomé, Huelva. **1**–**4**) UHU-CU1001-20; **1**) dorsal view; **2**) frontal view; **3**) anterolateral view; **4**) detail of the granular ornamentation. **5**) UHU-CU1002-20, dorsal view. Scale bars = 20 mm (**1**–**3**); 5 mm (**4**).

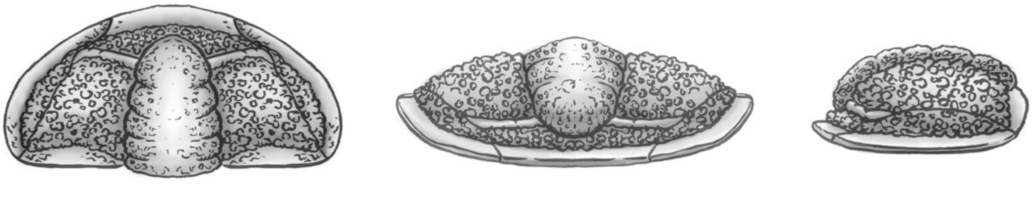


Figure 13: Reconstruction of the cephalon of *Atops calanus* Richter & Richer, 1941, in (left to right) dorsal, frontal, and lateral views. Illustration by Gabriel Feria Marquínez.

Remarks: The description above is based solely on the material collected for this study. Richter & Richter (1941) differentiated *Atops*? *calanus* from *Atops trilineatus* according to the distance between the anterior border furrow and the frontal lobe of the glabella, with a longer glabella reaching the anterior border in *Atops trilineatus* and a shorter, tapered glabella in *Atops*? *calanus*, with a subtle ridge between anterior border furrow and preglabellar furrows. In Huelva specimens, these differences could be due to deformation and are not necessarily taxonomical characters (Figs. 12.1–12.3, note that the frontal lobe of the glabella invades the preglabellar field and reaches the anterior border due to deformation). *Atops rupertensis* and *Atops briandailyi* from Australia are differentiated by the proportions of the cephalon, prominent parafrontal band, and a wide anterior border becoming narrower at the sides. Moreover, the glabella is considerably narrower and shorter with four pairs of thin, lateral, non-transglabellar furrows pointing backward and giving rise to less-pronounced glabellar lobes, and shallower, less-pronounced axial furrows. The palpebral area of both *Atops rupertensis* and *Atops briandailyi* is more extensive in proportion to the cephalon than in *Atops calanus*. In *Atops rupertensis*, the posterior furrow is shallower and broader than in *Atops calanus*, becoming thicker at the sides. The posterior border is thin and uniform in both *Atops calanus* and *Atops rupertensis*.

Orlowski (1985a) established *Atops granulatus* from the lower Cambrian of the Holy Cross Mountains, Poland, and argued that *Atops*? *calanus* does not belong in *Atops*. The most distinctive characters of *Atops granulatus* are the parallel-sided glabella, the lack of a preglabellar field, and the configuration of the glabellar furrows (S1 not parallel to S2 and S3). In contrast, *Atops calanus* has a tapered glabella and parallel glabellar furrows. In *Atops granulatus*, the facial suture extends across the lateral border, but in *Atops calanus*, the facial suture extends across the cheek to the ocular ridge, then to the genal area.

Atops korobovi from Russia is similar to *Atops calanus* but is distinguished by its more tapered frontal glabella lobe. *Ivshinellus nikolai* and *I. patulus*, now both assigned to *Atops* (Jell et al., 1992), are based on distorted material (Korobov, 1973), but in comparison with *Atops calanus*, they show a subelliptical outline of the cephalon and a wider anterior border (especially in *Atops nikolai*). Furthermore, these Russian species have more narrowly triangular glabellae. Both Russian species also have subtler granular ornament. Rushton (1966) described *Atops*? sp. indet. from the Purley Shales, England. The partial cranidium (Rushton, 1966, pl. 5, fig. 19) resembles *Atops trilineatus* especially in glabellar shape and suture configuration.

Conocoryphidae gen. indet. sp. indet. of Fritz (1973) has a conical glabella, narrower than in *Atops calanus*, a shorter plegabellar field, and coarse granular ornament all over the fixigenae and glabella.

Cotton's (2001, pl. 1, figs. 2–4) *Atops* sp. indet. from Saltwater Pond, Canada Bay, Newfoundland, has a higher glabella in comparison with the cephalon, a preglabellar field sagittally extended, and a wider anterior border. Despite these differences, it resembles *Atops calanus* in the outline of the cephalon, geometry of the glabella, and distribution of the granular ornamentation.

Genus ***Pseudatops*** Lake, 1940

Type species: *Conocoryphe reticulata* Walcott, 1890b, by original designation (Lake, 1940, p. 291).

Other species: *Pseudatops viola* Woodward, 1888, and *Pseudatops perantiquus* Korobov, 1973.

Emended diagnosis: Atopidae with flat or slightly downward-turned anterior border; the absence of a preglabellar area due to the invasion of the frontal lobe of the glabella; the glabella reaching the anterior border; a facial suture that cuts only the genal spine and part of the lateral border; and bright, reticulated ornamentation.

Remarks: Lake (1940) established *Pseudatops* based on the differences that he found between *Atops trilineatus* and *Atops reticulatus* var. *comleyensis* Cobbold, 1936, designating the latter species as type of the new genus.

Pseudatops reticulatus (Walcott, 1890b)

Figure 14

1890b *Conocoryphe reticulata* – Walcott, p. 649, pl. 95, fig. 6, 6a.

1936 *Atops reticulatus* var. *comleyensis* – Cobbold, p. 231, pl. 15, fig. 1a–e.

1940 *Pseudatops reticulatus* – Lake, p. 291, pl. 2, figs. 1–3.

2001 *Pseudatops reticulatus* – Cotton, pl. 2, figs. 1–3.

2006 *Pseudatops reticulatus* – Fletcher, pl. 27, fig. 21.

2018 *Pseudatops* n. sp. – Collantes et al., p. 567, fig. 4.8.

Holotype: USNM 18431.

Emended diagnosis: *Pseudatops* with trapezoidal cranidium, surrounded externally by a nearly flat border; elongated, subrectangular glabella and facial suture confined to the lateral border.

Occurrence: *Pseudatops reticulatus* occurs in the *Elliptocephala asaphoides* Biozone in the Taconic Allochthon; in the *Hebediscus attleborensis* Subzone of the *Callavia broeggeri* Biozone in Avalonia; and in the upper Marianian of Iberia (herein).

Description: Cranidium trapezoidal, wider than long, ranging 8.5–26.8 mm in length, 19.5–51 mm in width. Marginal facial suture only cutting the lateral border of the cephalon and not affecting the lateral furrow. Anterior margin slightly curved. Anterior border narrow (sag.), homogeneous, planoconvex, slightly turned downward. Anterior furrow shallow, sagittally invaginated toward the front due to the intrusion of the glabella, with a fairly broad and well-defined subtriangular shaped area originating on each side of the frontal lobe of the glabella. Glabella elongated, extending all along the cranidium, subrectangular, with rounded frontal lobe and deep axial furrows. Three pairs of non-transglabellar furrows with slight curvature pointing toward the posterior area. Occipital furrow deep, curving toward the front (convexity toward the posterior area). Occipital lobe narrow, trapezoidal, slightly curved with convexity toward the posterior area and subtle occipital tubercle. Preocular field slim, convex. Ocular ridge slightly pronounced, inserting toward the frontal lobe of the glabella and reaching the lateral furrow. Palpebral area flat, wide, trapezoid, with slight slope toward the posterior area. Posterior furrow well marked, wide. Posterior border narrow, flat, thickened near the genal area due to an incurved posterior border. Lateral border narrow, homogeneous. Genal angle ~90°, with a minimal genal spine. Surface of the cephalon subtly reticulated. For reconstruction, see Figure 15.

Materials: A total of 13 cranidial fragments were available (UHU-CU1002–CU1009-20, CU1014–CU1016-20, POZ021-20, AM2001-20; moved to UHU-CSB, UHU-POZ and UHU-AM1, respectively). Additional fragments are deposited in the same collection.

Remarks: The description above is based solely on the material collected for this study.

The differences between North American *Pseudatops reticulatus* (New York and Newfoundland) and Spanish specimens are minimal: the cephalon, especially the frontal lobe of the glabella, presents a more significant relief in the North American specimens. This could be taphonomical because the American specimens are preserved in limestone and the Spanish ones in shales.

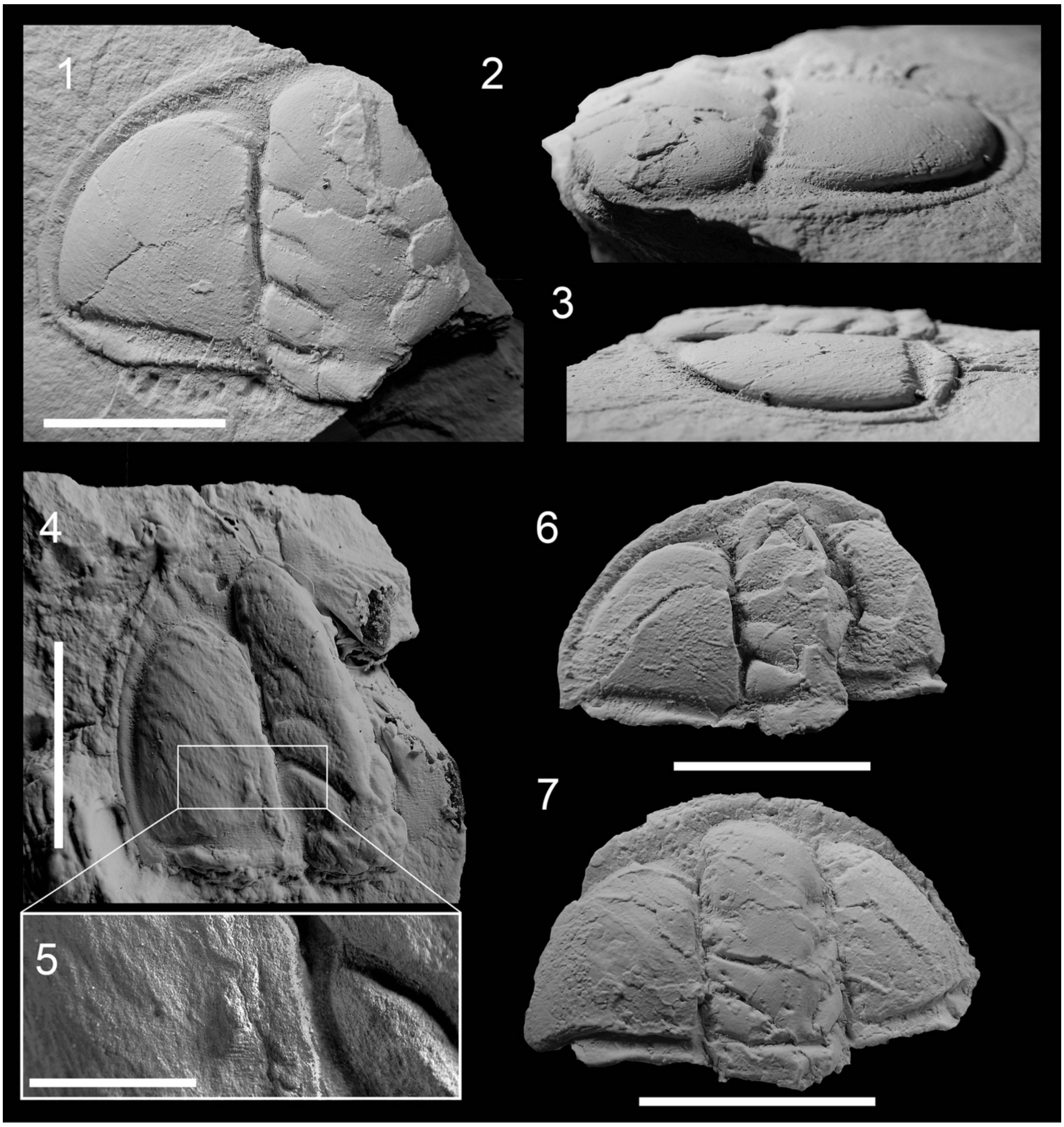


Figure 14: *Pseudatops reticulatus* (Walcott, 1890b), Cumbres de San Bartolomé, 'Cumbres beds', upper Marianian (**1**–**3**, **6**–**7**), Arroyomolinos de León, 'Herrerías shale', middle-upper Marianian (**4**–**5**). **1**–**3**) UHU-CU003-20, **1**) dorsal view; **2**) frontal view; **3**) lateral view; **4**–**5**) UHU-AM2001-20; **4**) dorsal view; **5**) detail of the reticular ornamentation; **6**) UHU-CU1004-20, dorsal view; **7**) UHU-CU1005-20, dorsal view. Scale bars = 20 mm (**1**–**4**, **6**–**7**); 5 mm (**5**).

Figure 15: Reconstruction of the cephalon of *Pseudatops reticulatus* (Walcott, 1890b), in (left to right) dorsal, frontal, and lateral views. Illustration by Gabriel Feria Marquínez.

Pseudatops viola has a cephalon with a semiovate outline, in contrast with the trapezoidal to semicircular cephalon of *Pseudatops reticulatus*. In *Pseudatops viola*, the facial suture crosses the lateral border furrow and a narrow sliver of the cheek, whereas in *Pseudatops reticulatus*, it is confined to the lateral border. The more marginal facial suture also occurs in numerous conocoryphids (see Sdzuy, 1961; Liñán & Gozalo, 1986). Korobov (1973) erected *Pseudatops perantiquus* from the Ishim River, comparing it with *Pseudatops viola* and *Pseudatops reticulatus*. *Pseudatops perantiquus* differs from *Pseudatops viola* by a wider anterior border, wider anterior and posterior border furrows, and a subtriangular fixigena (Korobov, 1973). *Pseudatops perantiquus* has a wider cranidium, posterior border furrows running directly into the occipital furrow, a wider anterior border, and wider anterior and posterior furrows than *Pseudatops reticulatus*. Korobov (1973) noted that the Russian specimens have a wider, more uniform border in comparison with that of *Pseudatops reticulatus*. The smaller, conical glabella pointing forward and the three pairs of deep, wide lateral furrows are especially remarkable. The frontal lobe of the glabella reaches the anterior furrow without invading the anterior border, but it has the characteristic reticulated ornament of *Pseudatops*.

5.1.6. Discussion

The Atopidae have a worldwide distribution. The stratigraphical distributions of *Atops* and *Pseudatops* are summarized in Figure 16.

Atops trilineatus occurs in the Taconic Allochthon, in the 'Lower Faunule' of the *E. asaphoides* Zone (Lochman, 1956; Rasetti, 1967). In Baltica, *Atops granulatus* occurs in the Holy Cross Mountains (Poland), in the middle *Holmia*-*Schmidtiellus* Biozone (Orlowski, 1985; Żylińska, 2013b). *Atops calanus* occurs in the middle to upper Marianian (Cambrian Stage 4) with *Serrodiscus* and *Triangulaspis* (Richter & Richter, 1941; Sdzuy, 1962; Collantes et al., 2018). In Australia, *Atops rupertensis* and *A. briandailyi* occur in the *Pararaia janeae* Biozone (Jell et al., 1992; Jago et al., 2006). *Atops korobovi* occurs in the Sanashtykgol Horizon of the Botomian stage in the Altai-Sayan Fold Belt (Repina et al., 1999). *Atops nikolai* and *Atops patulus* from Tuva Republic are from the upper Aldan Stage or, possibly, lowermost Lenan Stage (Korobov, 1973, table 1). Because the Lenan is now assigned to the Toyonian Stage (Astashkin et al., 1991), this species is likely upper Botomian. *Atops*? sp. indet. of Rushton (1966) from the Purley Shales (locality 2A) occurs with *Serrodiscus ctenoa* Rushton, 1966 of the

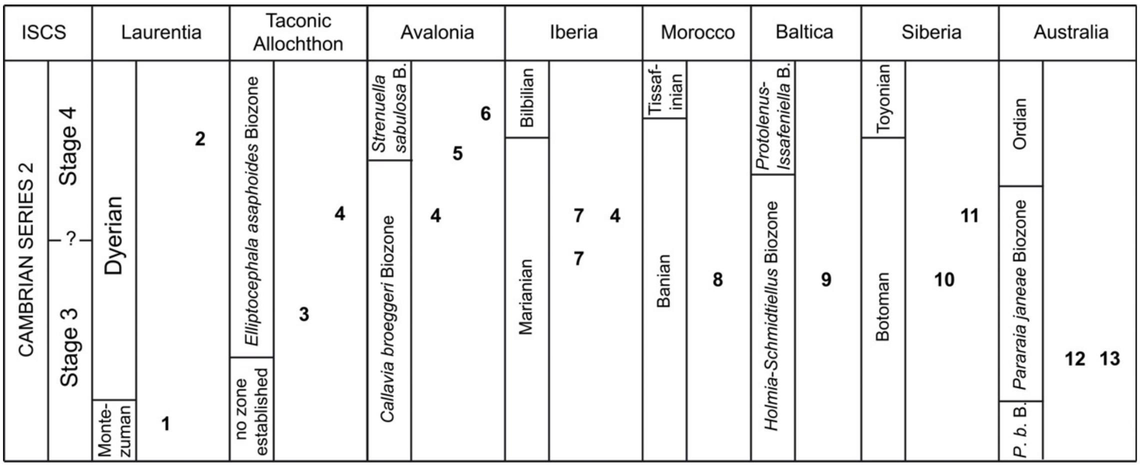


Figure 16: Correlation chart showing the stratigraphical occurrence of Atopidae. 1 = Conocoryphidae gen. indet. sp. indet. of Fritz (1973); 2 = *Atops* sp. indet. of Cotton (2001); 3 = *Atops trilineatus* Emmons, 1844; 4 = *Pseudatops reticulatus* (Walcott, 1890b); 5 = *Pseudatops viola* (Woodward, 1888); 6 = *Atops*? sp. indet. of Rushton (1966); 7 = *Atops calanus* Richter & Richter, 1941; 8 = *Pseudatops* sp. indet. of Geyer in Sundberg et al. (2016); 9 = *Atops granulatus* Orlowski, 1985a; 10 = *Atops nikolai* (Korobov, 1966), *Atops patulus* (Korobov, 1966), *Atopina antiqua* Korobov, 1966, and *Pseudatops perantiquus* Korobov, 1973; 11 = *Atops korobovi* Romanenko in Repina et al., 1999; 12 = *Atops briandailyi* (Jenkins & Hasenohr, 1989); 13 = *Atops rupertensis* Jell, Jago, & Gehling, 1992; B. = Biozone; *P. b.* B. = *Pararaia bunyerooensis* Biozone. Based on Sundberg et al. (2016); Zhang et al. (2017); and Geyer (2019).

Cephalopyge Biozone in the upper Cambrian Stage 4 (Rushton et al., 2011; Williams et al., 2013). Conocoryphidae gen. indet. sp. indet. of Fritz (1973) in the Mackenzie Mountains, northwestern Canada, assigned here to *Atops*, occurs in the lower Sekwi Formation, dated as *Nevadella* Biozone (upper Cambrian Stage 3 to lower Stage 4). Although Cotton (2001) did not offer information about the stratigraphical position of his *Atops* sp. indet., Murray studied the Salt Water Pond Series in 1864 (Murray & Howley, 1881; Schuchert & Dunbar, 1934) and the first three levels are included in the Forteau Formation (Betz, 1939, table 2), the horizon of which is assigned to the *Bonnia*-*Olenellus* Biozone, Dyeran Stage (Skovsted & Peel, 2007; Stouge et al., 2017).

Pseudatops reticulatus is present in the ‘Upper Faunule’ of the *E. asaphoides* Zone in the Taconic Allochthon (Lochman, 1956; Basset et al., 1976); in the *H. attleborensis* Subzone of the *C. broeggeri* Zone of Avalonia (Fletcher, 2006); in horizon Ac3 of the Comley Limestones (Cobbold, 1921, 1936) of the *Callavia* Biozone (Thomas et al., 1984; Rushton et al., 2011) and Iberia, with *Atops calanus*, in the middle and upper Marianian. In North Wales and Shropshire, *Pseudatops viola* appears in the *Strenuella sabulosa* Biozone (Howell & Stubblefield, 1950; Basset et al., 1976). In Morocco, *Pseudatops* is present in the *Antatlasia guttapluviae* Biozone (unpublished data, G. Geyer, according to Sundberg et al., 2016). *Pseudatops perantiquus* occurs in the Tuva Republic, in the *Callavia*-*Olenellus*-*Holmia* Biozone (Korobov, 1973, table 11).

Atopina is restricted to the Aldan Stage in Siberia (Korobov, 1973).

The Atopidae is known from Laurentia (northwestern Canada), the Taconic Allochthon (New York), western Newfoundland, western and eastern areas of Avalonia (eastern Newfoundland and the United Kingdom, respectively), Baltica (Poland), Siberia (Tuva Republic), the western margin of Gondwana (Iberia and Morocco), and Gondwana (Australia). Figure 17 shows that the distribution of Atopidae is mainly in the Southern Hemisphere, close to the equator.

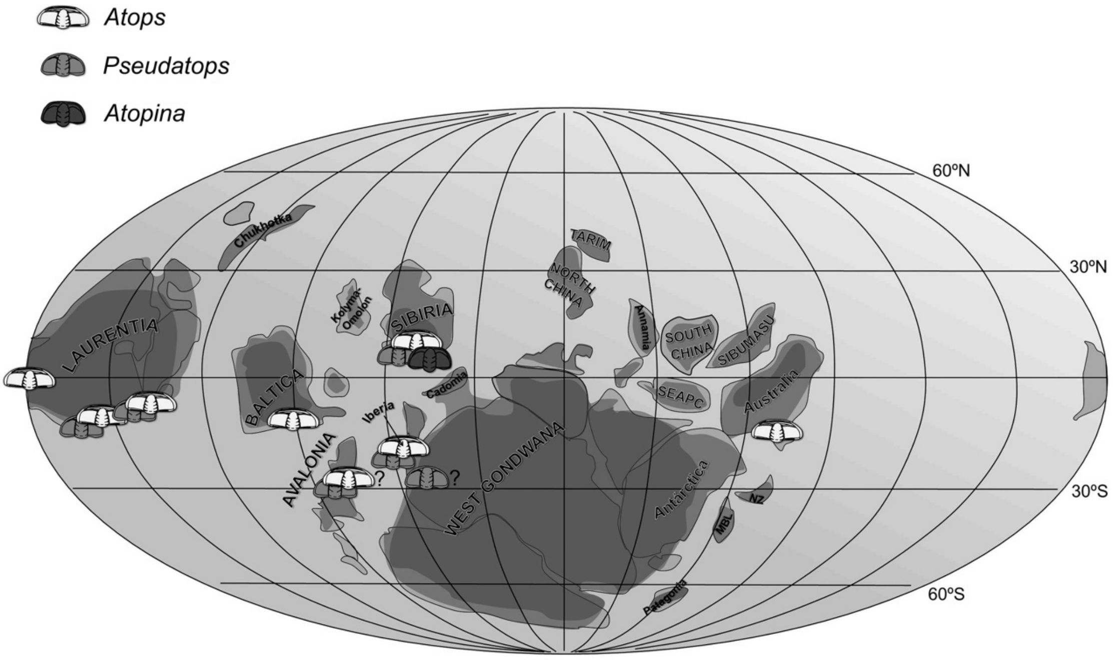


Figure 17: Distribution of the Atopidae, plotted on the Cambrian palaeogeographical map. Based on Dalziel (1997), Scotese & McKerrow (1990), McKerrow et al. (1992), and Malinky & Geyer (2019).

5.1.7. Conclusions

Trilobites of the family Atopidae have been found for the first time in the lower Cambrian rocks of northern Huelva Province (Andalusia, Spain). These rocks are named as ‘Cumbres beds’, with a trilobite assemblage that indicates a middle–late Marianian (Cambrian Series 2, Stage 4) age. These atopid trilobites have been described as *Atops calanus* Richter & Richter, 1941 and *Pseudatops reticulatus* (Walcott, 1890b), the latter being recognized for the first time in southern Europe and, therefore, in the Mediterranean subprovince.

While *Atops* has been previously recorded from the Taconic Allochthon (Laurantia), Holly Cross Mountains (Baltica), the Altai-Sayan Fold Belt (Siberia) and Australia, *Pseudatops* has been reported from Taconic Allochthon, western and eastern Avalonia (Newfoundland and United Kingdom, respectively), Morocco (western Gondwana), and Tuva Republic (Siberia). The new Iberian reports strengthen the faunal links of this territory with the domains mentioned above along the Cambrian Series 2.

5.2. On *Callavia* (Trilobita) from the Cambrian Series 2 of Iberia with systematic status of the genus (Collantes et al., 2021b in Journal of Paleontology, 95)

5.2.1. 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 biostratigraphical and palaeobiogeographical analyses. Based on newly collected specimens, we revise the species '*Callavia*? *lotzei*' Richter & Richter, 1941 from the 'Cumbres beds' of Cumbres de San Bartolomé and the 'Herrerías shale' of Cañaveral de León, Sierra del Bujo, 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, 1890b, *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 Epoch 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).

5.2.2. 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 & Repina's (1993) proposal. Two suborders—Olenellina Walcott, 1890b 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 & 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 & Repina, 1993). Curiously, olenellines are hitherto unknown from coeval sequences of eastern Gondwana. This suborder established the base of the lower Cambrian biostratigraphical subdivisions (see Palmer & 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 & Lieberman, 1999; Lieberman, 2002; Paterson & 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 & Repina, 1993) and it is still problematic. The revision carried out by those authors and adopted in the Treatise on Invertebrate Palaeontology (Palmer & Repina, 1997) considered two superfamilies: Olenelloidea Walcott, 1890b and Fallotaspidoidea Hupé, 1953a. 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, 1953a) and removed Fallotaspidoidea based on a phylogenetic analysis. Later works (e.g., Webster, 2007; Webster & Bohach, 2014; Webster & 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 & 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 known: *Paradoxides choffati* Delgado, 1904 from Vila Boim (Elvas, Portugal), *Callavia*? *lotzei* Richter & Richter, 1941 from Cañaveral de León (Huelva, Spain), and *Andalusiana cornuta* Sdzuy, 1961 from Guadalcanal (Seville, Spain). *Paradoxides choffati* was later reassigned to *Callavia* Matthew, 1897 by Richter & Richter (1941) and Teixeira (1952). In contrast, Sdzuy (1962) recognized 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 material and new specimens from the Cumbres de San Bartolomé, Cañaveral de León, Sierra del Bujo, and Hinojales fossil sites and the type material from Vila Boim, respectively, to clarify their taxonomy, biostratigraphy, and palaeobiogeography. 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 palaeogeography.

5.2.3. 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, Cañaveral de León (type locality of *Callavia*? *lotzei*), Arroyomolinos de León (Sierra de El Bujo), and Hinojales. These fossil localities are in the Ossa-Morena Zone, in the southern branch of the Iberian Massif, which comprises a lithostratigraphical 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 tectonosedimentary 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 & Quesada (1990). The Portuguese locality is in the Alter do Chão-Elvas Sector and the Spanish outcrops in the Cumbres and Herrerías 'Cubetas,' representing the southwesternmost fossiliferous units in early Cambrian times for Iberia (Fig. 18.1–18.2).

The Vila Boim fossil site is a classical outcrop at Monte Valbom (Fig. 18.2), first published by Delgado (1904) and located in the lower part of the Vila Boim Formation, a 600-meters thick succession composed of shales, quartzites, and graywackes with some interbedded rhyolite and basalt levels (Mata, 1986) (Fig. 18.3). All specimens originate from a narrow lenticular horizon of blue-gray shales with iron oxides, bearing two 15-centimeters thick fossiliferous levels separated by one meter, located ~170 meters 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 fossiliferous levels from the Cumbres de San Bartolomé section belong to the 'Cumbres beds', an informal lithostratigraphical unit composed of a succession of shale and sandstone of very variable thickness (350−1,100 m). The specimens studied herein were collected from the lower levels (Fig. 18.4), together with the trilobites *Atops calanus* Richter & Richter, 1941 and *Delgadella souzai*, considered middle Marianian in age. A second level, 400 meters above the former, contained a more diverse upper Marianian trilobite assemblage (Collantes et al., 2021a). 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 & Richter, 1941), Hinojales (Liñán & Mergl, 1982), and the Cañaveral de León fossil sites represent equivalent stratigraphical levels assigned to the unit 'Herrerías shale', characterised by purple shales with spilitic intercalations within a sequence 200–600 meters thick (Fig. 18.5). This unit ranges from the middle to upper Marianian, indicated by the presence of trilobites *Rinconia*-*Strenuaeva* 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 Cañaveral de León section is located between 38° 01′05″N, 006°32′23″W and 38°01′02″N, 006°32′28″W.

5.2.4. Materials and methods

Available material consists mainly of isolated cephala preserved as internal or external moulds, 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.

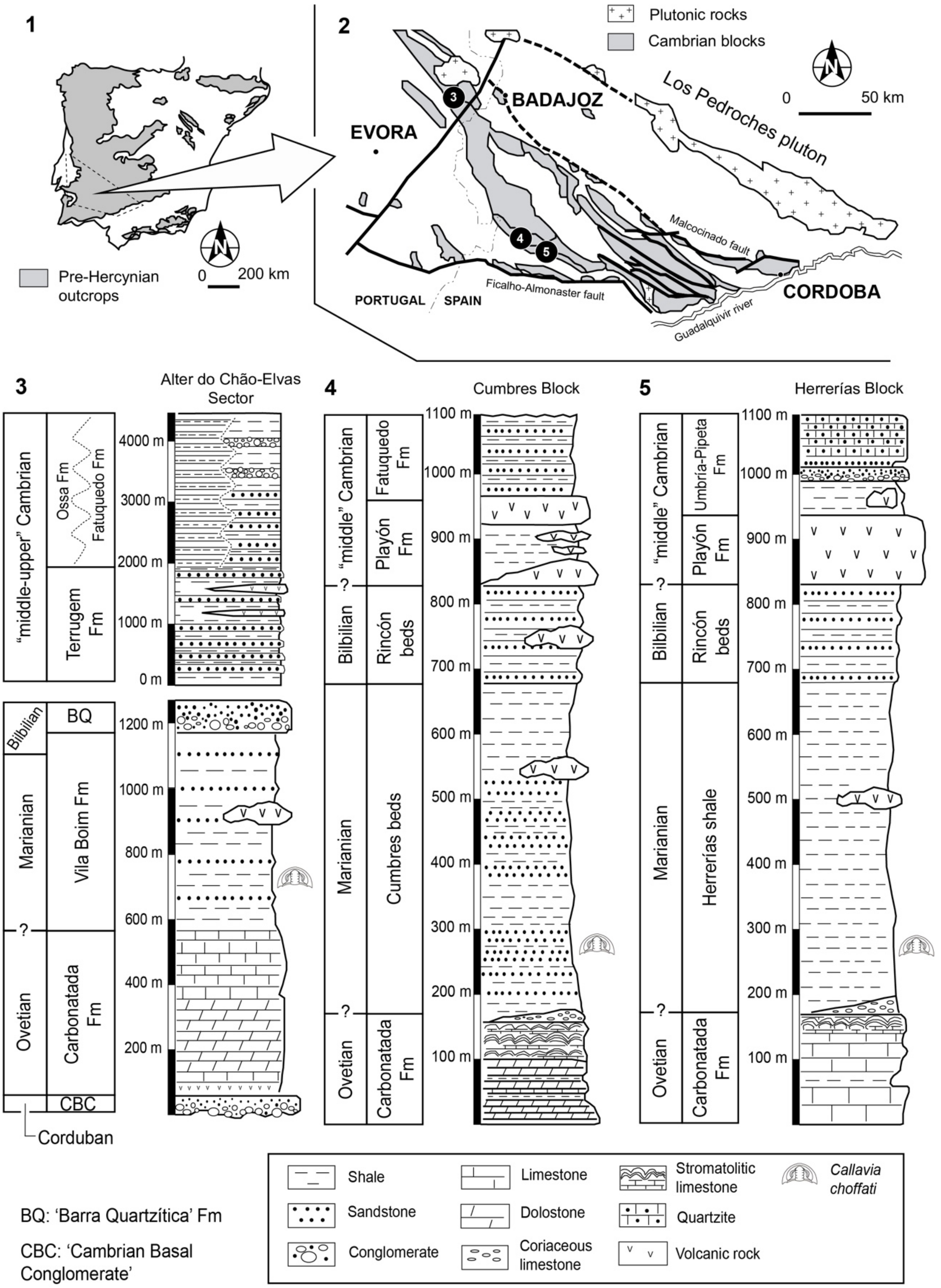


Figure 18: **1**) Pre-Hercynian outcrops in the Iberian Peninsula **2**) Geological setting of fossil sites in the Cambrian sectors (fault-bounded blocks) of the Ossa-Morena Zone, indicating the position of the studied fossil sites (based on Liñán & Quesada, 1990). **3**) Stratigraphical column of the Alter do Chão-Elvas Sector (based on Liñán et al., 2004). **4**) Stratigraphical column of the Cumbres block. **5**) Stratigraphical column of the Herrerías Block.

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 Palaeontology (Palmer & Repina, 1997).

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

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

5.2.5. Systematic palaeontology

Class Trilobita Walch, 1771

Order Redlichiida Richter, 1932

Suborder Olenellina Walcott, 1890b

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, 1953a (e.g., Harrington, 1959; Chernysheva, 1960; Repina, 1979), Bergström (1973) included Callaviinae Poulsen in Harrington, 1959 in Daguinaspididae Hupé, 1953a and Ahlberg et al. (1986) preferred to treat it as an independent family, not related to holmiinids. Following the most consensual assignment, Palmer & 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 & 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 'fallotaspidoids' (*sensu* Palmer & Repina, 1993) as representing an independent taxon of superfamiliar rank, the Judomioidea (not Nevadioidea, as mistakenly considered by Fletcher & Theokritoff, 2008).

One of the *Callavia* morphological characters that was misinterpreted by Palmer & 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 & 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, 1890b from the Brigus Formation, Branchian Series (Cambrian Stage 3/4), Newfoundland, Canada.

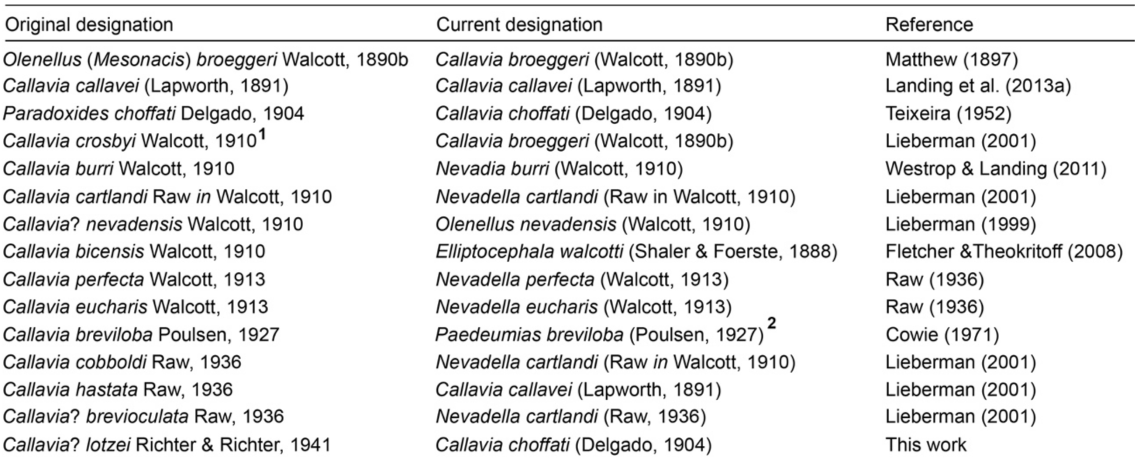
Other species: *Olenellus* (*Holmia*) *callavei* Lapworth, 1891 from the Comley Limestone Formation, Branchian Series (Cambrian Series 2), Shropshire, UK; *Paradoxides choffati* Delgado, 1904 from the lower part of the Vila Boim Formation, Marianian (Cambrian Series 2), Vila Boim, Portugal (see Table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

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 parafrontal 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, non-transglabellar, 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 2). 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 & 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 & 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 & 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 (1890b, 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 & 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, 1890b, pl. 92, fig. 1b; 1910, pl. 28, figs. 1, 4; Hutchinson, 1962, pl. 24, figs. 7b, 8, 9; Palmer & 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 & 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 & 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).

Table 2: List of taxa previously assigned to *Callavia* Matthew, 1897 and their currently accepted generic assignment. Notes: 1—Fletcher & Theorokritoff (2008) regarded *Callavia broeggeri* (Walcott, 1890b) and *Callavia crosbyi* (Walcott, 1890b) 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
Olenellus (*Mesonacis*) *broeggeri* Walcott, 1890b	*Callavia broeggeri* (Walcott, 1890b)	Matthew (1897)
Callavia callavei (Lapworth, 1891)	*Callavia callavei* (Lapworth, 1891)	Landing et al. (2013a)
Paradoxides choffati Delgado, 1904	*Callavia choffati* (Delgado, 1904)	Teixeira (1952)
Callavia crosbyi Walcott, 1910[1]	*Callavia broeggeri* (Walcott, 1890b)	Lieberman (2001)
Callavia burri Walcott, 1910	*Nevadia burri* (Walcott, 1910)	Westrop & Landing (2011)
Callavia cartlandi Raw *in* Walcott, 1910	*Nevadella cartlandi* (Raw in Walcott, 1910)	Lieberman (2001)
Callavia? *nevadensis* Walcott, 1910	*Olenellus nevadensis* (Walcott, 1910)	Lieberman (1999)
Callavia bicensis Walcott, 1910	*Elliptocephala walcotti* (Shaler & Foerste, 1888)	Fletcher &Theokritoff (2008)
Callavia perfecta Walcott, 1913	*Nevadella perfecta* (Walcott, 1913)	Raw (1936)
Callavia eucharis Walcott, 1913	*Nevadella eucharis* (Walcott, 1913)	Raw (1936)
Callavia breviloba Poulsen, 1927	*Paedeumias breviloba* (Poulsen, 1927)[2]	Cowie (1971)
Callavia cobboldi Raw, 1936	*Nevadella cartlandi* (Raw *in* Walcott, 1910)	Lieberman (2001)
Callavia hastata Raw, 1936	*Callavia callavei* (Lapworth, 1891)	Lieberman (2001)
Callavia? *brevioculata* Raw, 1936	*Nevadella cartlandi* (Raw, 1936)	Lieberman (2001)
Callavia? *lotzei* Richter & Richter, 1941	*Callavia choffati* (Delgado, 1904)	This work

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 & 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 & 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 & 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. 19.1, 19.5). Nevertheless, in specimens preserving glabellar convexity, either in *Callavia choffati* (e.g., Fig. 20.5, 20.16) or in *Callavia broeggeri* (see Palmer & 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. 21.1), 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 & 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 & Adrain (2002), Fletcher (2006), Fletcher & 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 & 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 amonotypic 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, 1953a, *Neltneria* Hupé, 1953a, *Callavia*, and *Judomia*. Based on the new specimens from the Cumbres de San Bartolomé, Cañaveral de León, Sierra del Bujo, and Hinojales 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 & 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 & Repina, 1965; Repina et al., 1974; Korobov, 1989; Pegel, 2000; Ponomarenko, 2005; Rozanov & 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 & 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 & 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 but also in the thoracic structure (compare Fig. 21.1 with Palmer & 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 2, 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 & 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 & Poctey, 1950; Hupé, 1959) these were later reassigned by Geyer & Palmer (1995) to other genera. Geyer & Landing (2002) reported the presence of this genus in this region, namely a single cephalic fragment in the Bani section, Moroccan Anti-Atlas (Geyer, personal communication, 2020).

Callavia choffati (Delgado, 1904)

Figures 19–21

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 & Richter, p. 34, pl. 3, figs. 36–40, pl. 4, fig. 66.

1941 *Callavia* (?) *choffati* – Richter & 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 & Mergl, p. 212.

v 1982 *Callavia*? sp. – Liñán & 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 mould of a cephalon (Fig. 19.1), figured by Delgado (1904, pl. 1, fig. 3) and Teixeira (1952, pl. 1). Paralectotypes of one incomplete exoskeleton, MG 15787a with counterpart 15787b (Fig. 21.1; Delgado, 1904, pl. 1, fig. 16, pl. 5, fig. 3; Teixeira, 1952, pl. 4, figs. 1–3); MG 15782a with counterpart 15782b, five cephala (Fig. 19.2; Delgado, 1904, pl. 1., fig. 1; Teixeira, 1952, pl. 2, figs. 1–3; MG 15785, external mould (Teixeira, 1952, pl. 4, figs. 5, 6); MG 15786, internal mould (Fig. 19.5; Delgado, 1904, pl. 1, fig. 1; Teixeira, 1952, pl. 12, figs. 1, 2); MG 16684, external mould; MG sn, external mould (Fig. 19.3; 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 moulds) (Fig. 21.9; Delgado, 1904, pl. 1, fig. 12); MG 15714 (Fig. 21.8; Delgado, 1904, pl. 1, fig. 8); MG 15764 (Fig. 21.7; Delgado, 1904, pl. 1, fig. 6); MG 15707a with counterpart 15707b, one pygidium (Fig. 21.6; Delgado, 1904, pl. 1, fig. 10, pl. 5, fig. 35).

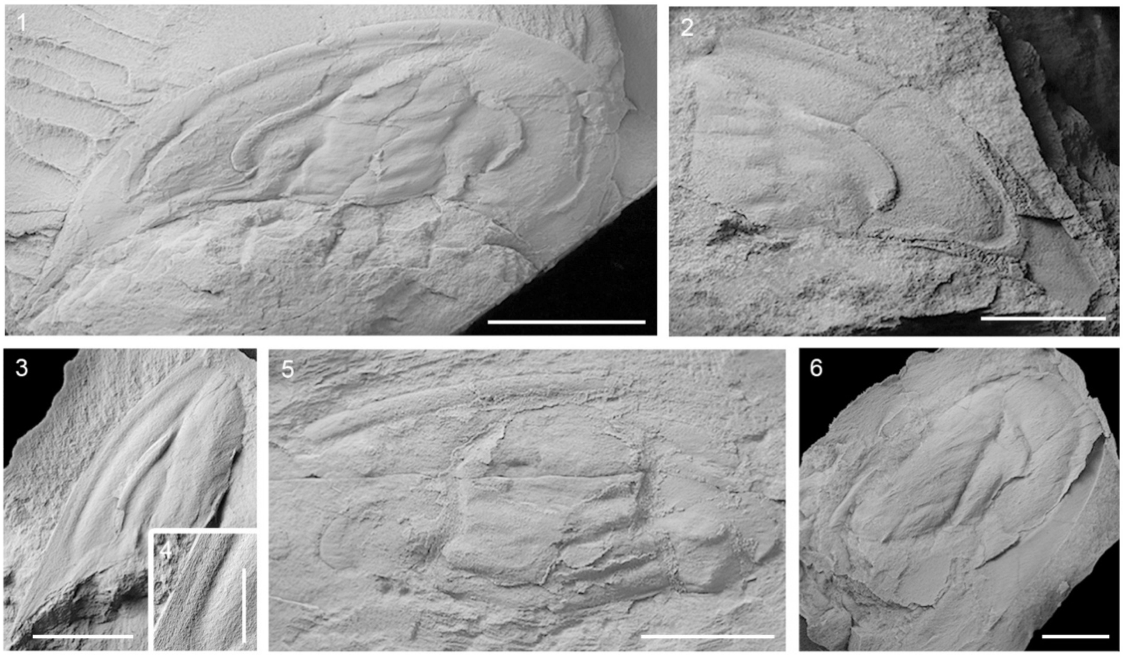


Figure 19: *Callavia choffati* (Delgado, 1904), Vila Boim Formation, middle Marianian, Vila Boim, Portugal. **1**) MG 15781, lectotype; **2**) MG 15782a, paralectotype; **3**–**4**) MG sn, paralectotype (latex). **3**) dorsal view; **4**) detail of terrace lines of the lateral cephalic border. **5**) MG 15786, paralectotype. **6**) MG 16684 (latex). Scale bars = 2 mm (**4**); 10 mm (**1**–**3**, **5**, **6**).

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 cephala 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, non-transglabellar, 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. 20.17). 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. 20.7). 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

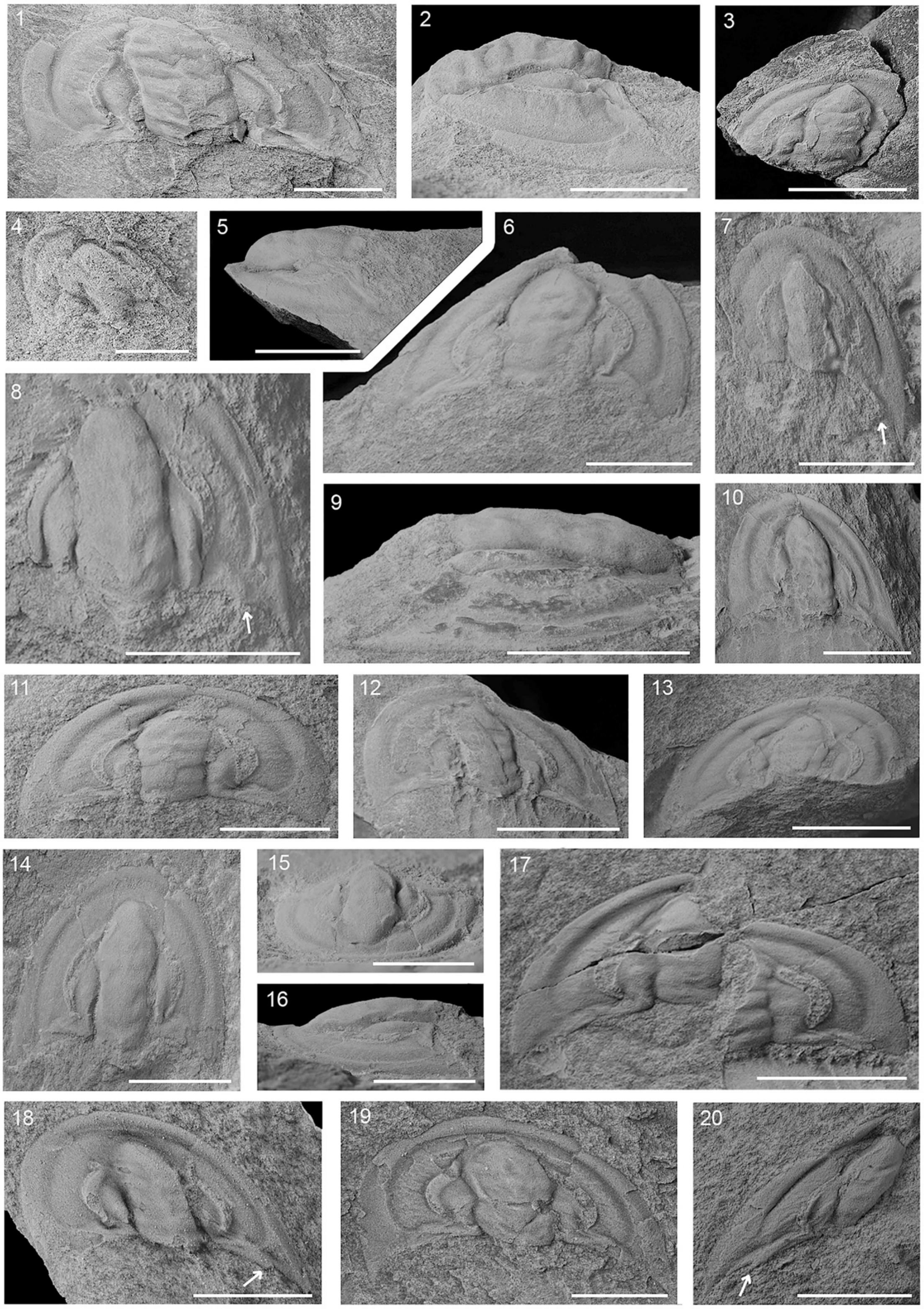


Figure 20: *Callavia choffati* (Delgado, 1904), 'Herrerías shale', middle Marianian, Cañaveral de León (**1−13**, **15−20**) and 'Cumbres beds,' middle Marianian, Cumbres de San Bartolomé (**14**), Spain. **1**–**2**) UHU-CVL 01; **1**) dorsal view; **2**) lateral view. **3**) UHU-CVL 03; **4**) UHU-CVL 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.

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. 20.8, 20.18, 20.20), 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. 19.4, 20.19).

Thorax composed of 18, probably 19 thoracic segments in only complete specimen (Fig. 21.1, 21.2). 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 (UHU-CSB), two cephala. ‘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 cephala; UHU-LH1/1/4, thoracic segment (UHU-H1). Cañaveral de León: UHU-CVL36 (Fig. 21.3), 37 (Fig. 21.5), 49 (Fig. 21.2), three articulated incomplete cephalothoraxes; UHU-CVL01−13, 15−35, 38−43, 46−48, 50, 44 cephala. Sierra del Bujo: UHU-LBU/0/1, /0/2, /0/3, /1/1, four cephala; UHU-LBU/0/2, cephalic fragment (UHU-BU).

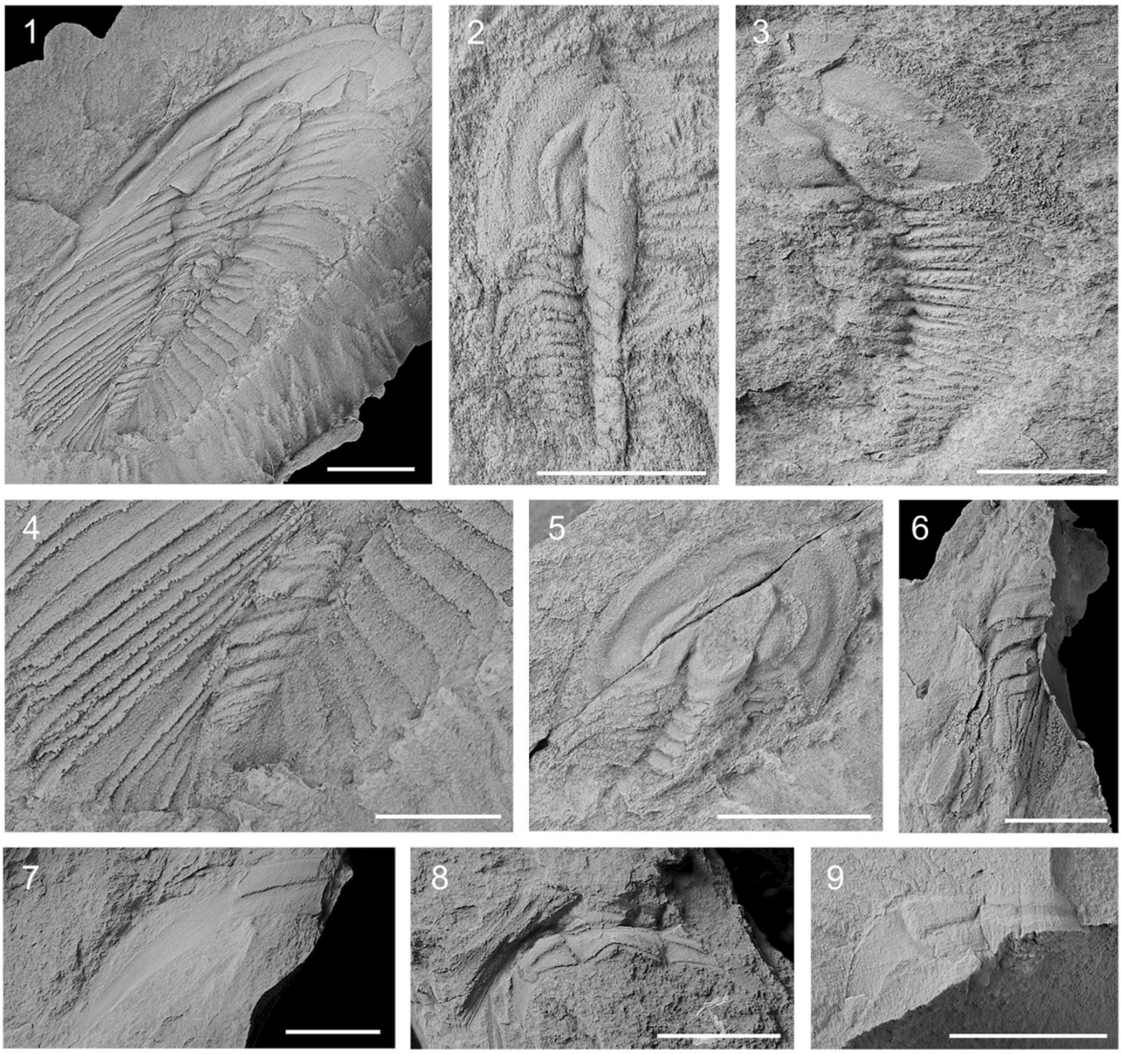


Figure 21: *Callavia choffati* (Delgado, 1904), Vila Boim Formation, middle Marianian, Vila Boim, Portugal (**1**, **4**, **6**–**9**) and 'Herrerías Shale,' middle Marianian, Cañaveral de León, Spain (**2**, **3**, **5**). **1**, **4**) MG 15787b, paralectotype (latex); **1**) overview; **4**) detail 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**).

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 & 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 characterised 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, 1953a; 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. 20.7, 20.10, 20.11, 20.13–20.19).

Some decades after Delgado’s (1904) publication, Richter & Richter (1941) erected a new species, *Callavia*? *lotzei*, from the northern Huelva Province (Spain). These authors suggested for the first time that ‘*Paradoxides*’ *choffati* 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 & 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 & 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 choffati* might be synonyms, but Sdzuy (1962) rejected this hypothesis based on deeper glabellar furrows and larger cephala of *Callavia choffati*. 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 choffati* 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 choffati* 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 choffati* and *Callavia lotzei* are synonyms and support the assignment of the Iberian species to the genus *Callavia*. The previous poor documentation of *Callavia choffati* 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 & Richter (1941) included specimens in this species belonging to *Gigantopygus* cf. *G. bondoni* Hupé, 1953a, a redlichiine, and Sdzuy (1962, pl. 19, figs. 7–11) included some additional material of meraspides. These compromised comparisons 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 choffati* in all characters. Reduced intergenal spines are present in both sets of specimens, located in similar positions (e.g., Fig. 20.1–20.17). 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. 20). Due to the deformation and large size of the type specimens (Fig. 19), the intergenal spine is not evident, being expressed as a swelling on the posterior border, and more evident in only one specimen (Fig. 19.3). 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. 19.1–19.5) 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. 19.1, 20.17, 20.19), 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. 19.1, 19.2, 20.11, 20.17). Furthermore, both bear an entirely comparable, faint parafrontal band surrounding the LA (Figs. 19.1–19.3, 20.7, 20.13–20.18) and a well-marked posterior ocular line subparallel to the intergenal ridge (Figs. 19.1, 20.18, 20.19). 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 choffati*.

5.2.6. Palaeobiogeographical and biostratigraphical remarks

The confirmed presence of the genus *Callavia* in the Iberian Peninsula, represented by the species *Callavia choffati*, together with its reported occurrence in Morocco (Geyer & 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, 1890b; 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 & Foerste, 1888), it was possible to approximately correlate the so-called *Callavia* Biozone (Avalonian regional Branchian Series, lower Cambrian, Series 2) with other palaeogeographical regions (the Banian/Marianian regional Stages of Morocco/Iberia, the '*Nevadella*' Biozone of Laurentia, the *Pagetiellus anabarus*-*Judomia* Biozones of Siberia, or the *Schmidtiellus mickwitzi*-*Holmia inusitata*-*Holmia kjerulfi* Biozones of Baltica; see Sdzuy, 1971a, 1972; Palmer & Repina, 1993, fig. 12; Fletcher, 2006; Żylińska, 2013b; 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 & 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 & 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 characterised 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 & 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., Sdzuy, 1972; Liñán et al., 2002; Álvaro et al., 2003; Landing et al., 2013a, b, Collantes et al., 2021a). 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) (Fig. 22).

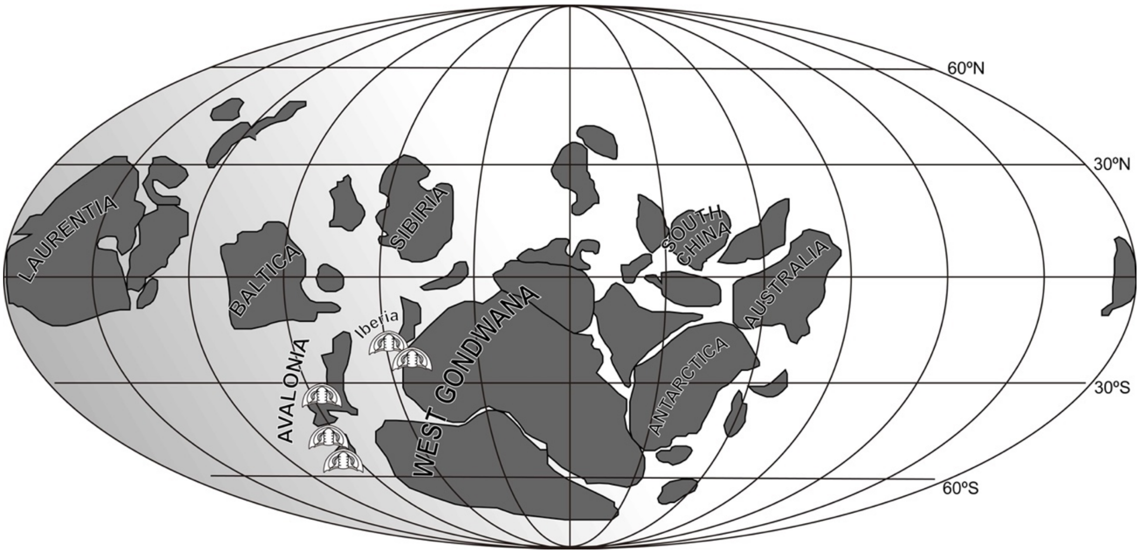


Figure 22: Distribution of *Callavia* plotted on the Cambrian palaeogeographical map. Modified from Scotese & McKerrow (1990); McKerrow et al. (1992); Dalziel (1997); and Malinky & Geyer (2019).

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 & Richter (1941) and Sdzuy (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, 2021a). 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.

5.2.7. 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.

5.3. The trilobite *Serrodiscus* Richter & Richter from Iberia, with systematic review of the genus and its international correlation through the Cambrian Series 2 (Collantes et al., 2022 in Bulletin of Geosciences, 97)

5.3.1. Abstract

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 system. 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 taphonomical 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 morphological, stratigraphical and palaeobiogeographical 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 stratigraphical 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 stratigraphical distribution throughout the Cambrian Series 2.

5.3.2. Introduction

For more than twenty years, the International Subcommission 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 stratigraphical 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 palaeogeographical 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 stratigraphical known range, reducing its usefulness for stratigraphical correlation among different domains. Therefore, improving the biostratigraphical 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 the most widespread and biostratigraphical-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 stratigraphical 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" (Cala Fauna; Richter & Richter, 1941). Subsequently, several species previously assigned to 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 morphological 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, stratigraphical range and palaeobiogeographical 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 with those of the Central Iberian Zone.

5.3.3. Geological setting

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. 23.1):

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. 23.2).

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–lower 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. 23.3).

5.3.4. Stratigraphical range of *Serrodiscus* and regional correlation

The regional Marianian Stage (after 'Mariani Mountains', Sierra Morena, Andalusia) was introduced by Sdzuy (1971a). 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 (1984b) 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 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 dissimilare*–*Skiagia ciliosa* acritarch Zone, according to the Baltic Zonation (*sensu* Palacios & Moczydłowska, 1998). Nonetheless, a trilobite biozonation is still missing.

Although Sdzuy (1971a) reported the occurrence of *Andalusiana* and *Triangulaspis* in the lower part of the Huérmeda Formation 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 Huérmeda Formation, in the Iberian Chains. In addition, Álvaro et al. (2019) considered the biostratigraphical zonation of the Marianian Stage in Iberia to be poorly defined and lacking radiometric dating, being invalid for correlation throughout the Iberian Peninsula.

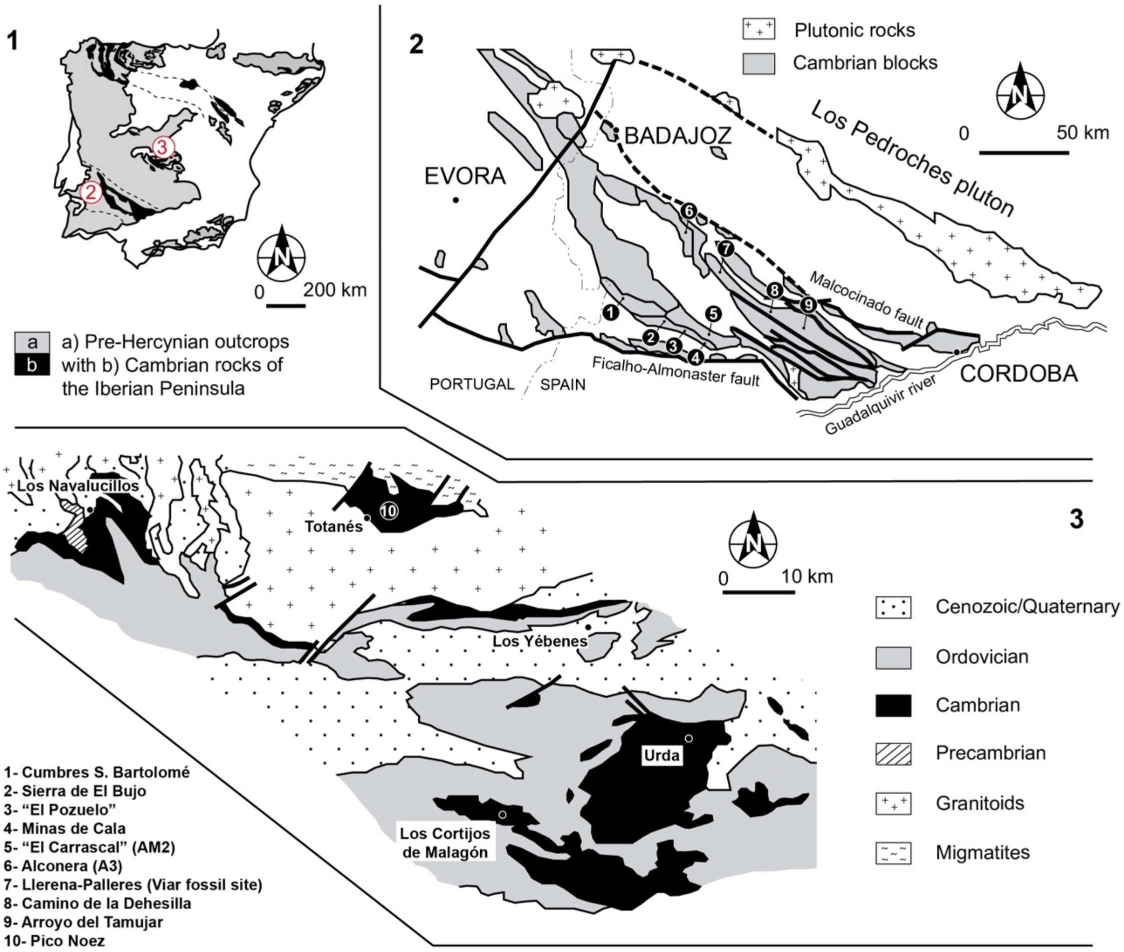


Figure 23: **1**) Pre-Hercynian outcrops in the Iberian Peninsula. **2**) Geological setting of fossil sites in the Cambrian sectors (fault-bounded blocks) of the Ossa-Morena Zone, indicating the position of the studied fossil sites (modified from Liñán & Quesada 1990). **3**) Geological map of the Cambrian outcrops from the Toledo Mountains, modified from Aparicio Yagüe (1971), Roiz (1979) and Martín Escorza (1976).

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. 24).

5.3.4.1. 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 meters), 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, 1890b), *A. calanus* Richter & Richter, 1941, *Triangulaspis fusca* Sdzuy, 1962, *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 Bujo 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 meters), 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 elvensis* Delgado, 1904, *Protaldonaia morenica* Sdzuy, 1961, *C. choffati*, *A. calanus*, *Calodiscus ibericus* Sdzuy, 1962 and *Strenuaeva sampelayoi* Richter & Richter, 1940 in the lower part (middle Marianian), and *S. bellimarginatus*, , *T.* fusca, *P. morenica*, *P.* 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 meters), 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* in the lower levels (middle Marianian) and *S. bellimarginatus*, *T. fusca* and *P. reticulatus* in the upper levels (upper Marianian).

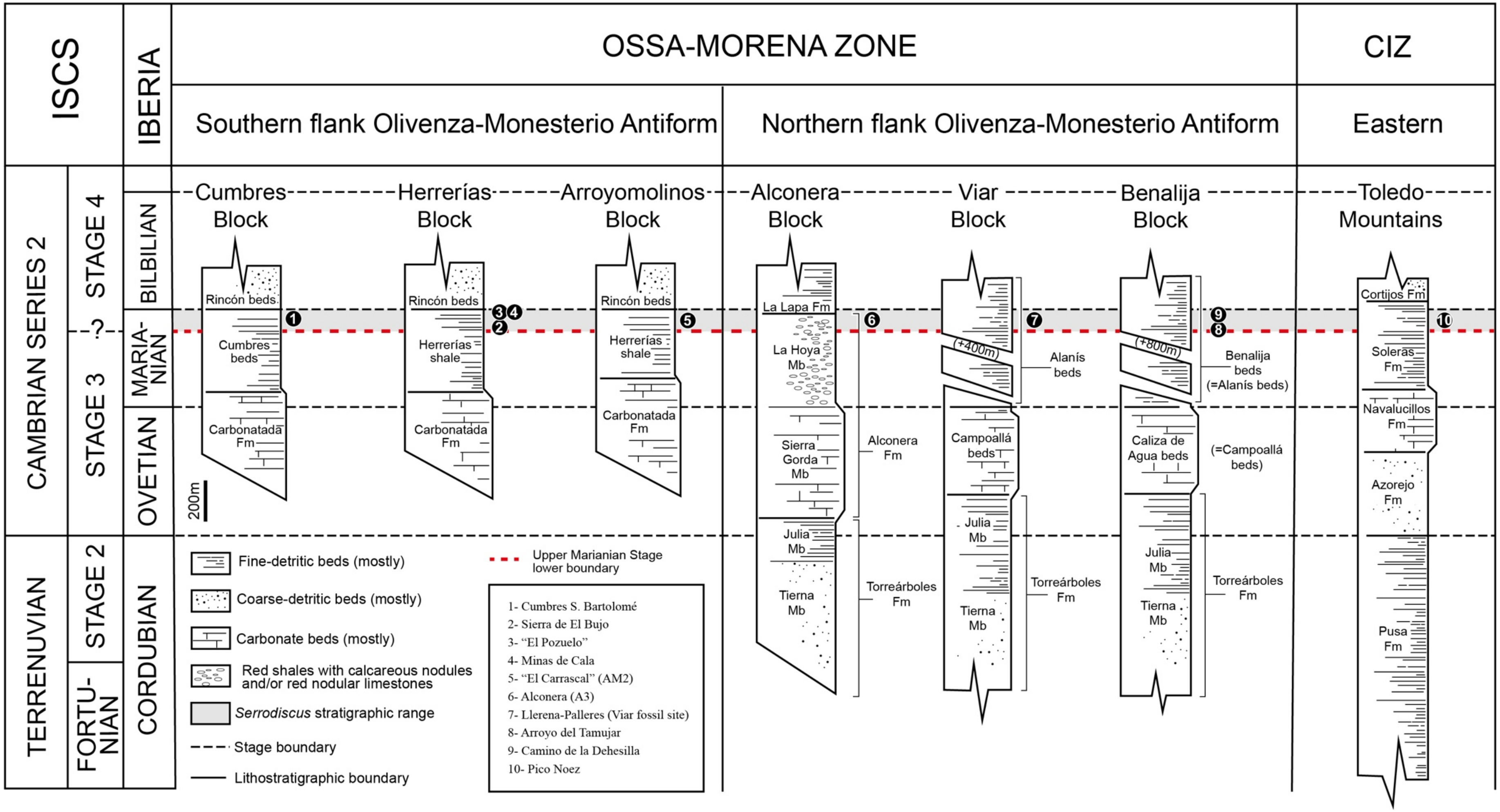


Figure 24: Tentative correlation of the northern and southern Cambrian blocks from the Ossa-Morena and Central Iberian Zones, indicating the stratigraphical range of *Serrodiscus*. Stratigraphical data from San José et al. (1974), Zamarreño et al. (1976), Liñán & Perejón (1981), Gozalo et al. (2003), Liñán et al. (2004) and Collantes et al. (2020, 2021a, b). Abbreviations: Fm = Formation; Mb = Member.

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 meters), consisting of shales with calcareous nodules, nodular calcilutites, and limestones located in the upper part of the Alconera Formation (~900 meters; 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. elvensis*, *S. bellimarginatus*, and *P. 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 meters), 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 (Apalategui et al., 1983). A middle to late Marianian age is indicated by the occurrence of *Termierella sevillana* Sdzuy, 1961, *P. 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' or 'Benalija beds' (~1400 meters). The trilobite assemblage comprises *S. bellimarginatus*, *D. souzai*, *Andalusiana cornuta* Sdzuy, 1961, *T. sevillana* and *P. morenica*, and hyoliths, brachiopods, and chancelloriid sclerites. This fossil assemblage suggests an age that extends from the medial to late Marianian.

6.3.4.2. 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 meters), 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 Formation by Liñán et al. (1993, 2002, 2004). It cooccurs with the trilobite *Andalusiana* (Liñán et al., 1993, Sepúlveda et al., 2021a). This association suggests an late Marianian age and allows correlation with the Spanish Ossa-Morena Zone and Iberian Chains sequences.

5.3.5. International correlation

The genus *Serrodiscus* shows a widespread geographical distribution and restricted chronostratigraphical 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, Shergold & Geyer (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 genera 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 genera, although they do include some of the trilobites with the broadest geographical distribution during the Cambrian Stage 4.

In this section, we revise the biostratigraphy of *Serrodiscus* from the Cambrian worldwide (Fig. 25). Justification of the different established groups is explained in the Discussion section.

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 Formation (Dyerian Stage) and the Aftenstjernesø Formation (Dyerian Stage, low to the middle part of the *Serrodiscus* speciosus Zone; Blaker & Peel 1997) of Greenland and the Slaklidalen Limestone Formation (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 Avalonia (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 guttapluviae* 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 Görlitz 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 Altai-Sayan Foldbelt *Serrodiscus* occur in rocks from the Botoman to Toyonian Stages from Tuva ('*Menneraspis* beds') and 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 stratigraphical range that extends throughout the lower *Pararaia janeae* Zone (Bengtson et al., 1990; Betts et al., 2017).

China: The biostratigraphical division and correlation of China's different continental blocks and terranes is 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.

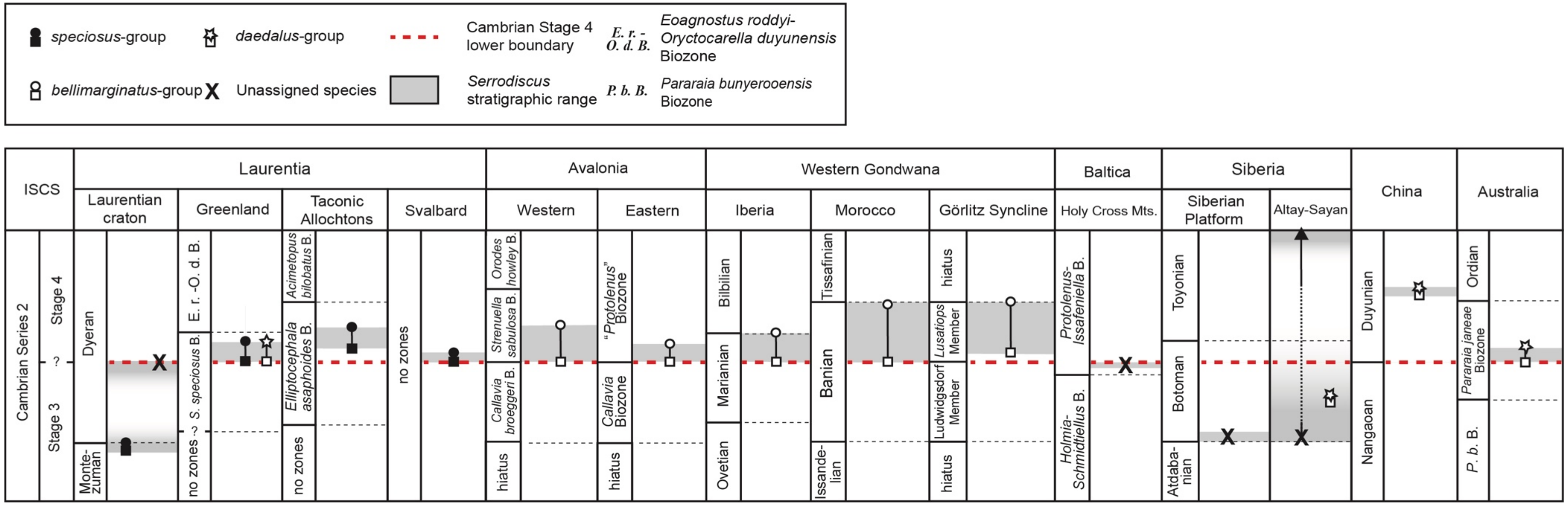


Figure 25: Correlation chart showing the stratigraphical occurrence of *Serrodiscus*. Based on Sundberg et al. (2016), Zhang et al. (2017), and Geyer (2019).

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 Formation, 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)

5.3.6. Palaeobiogeography

The palaeobiogeographical distribution of *Serrodiscus* is discussed in this section and summarized in Figure 26. Different groups and their palaeobiogeographical distribution are justified in the Discussion section.

Laurentia: While many Laurentian polymerid (and especially 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 palaeogeographical 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 characterised by new links between Avalonia and West Gondwana, including some eodiscides (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 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).

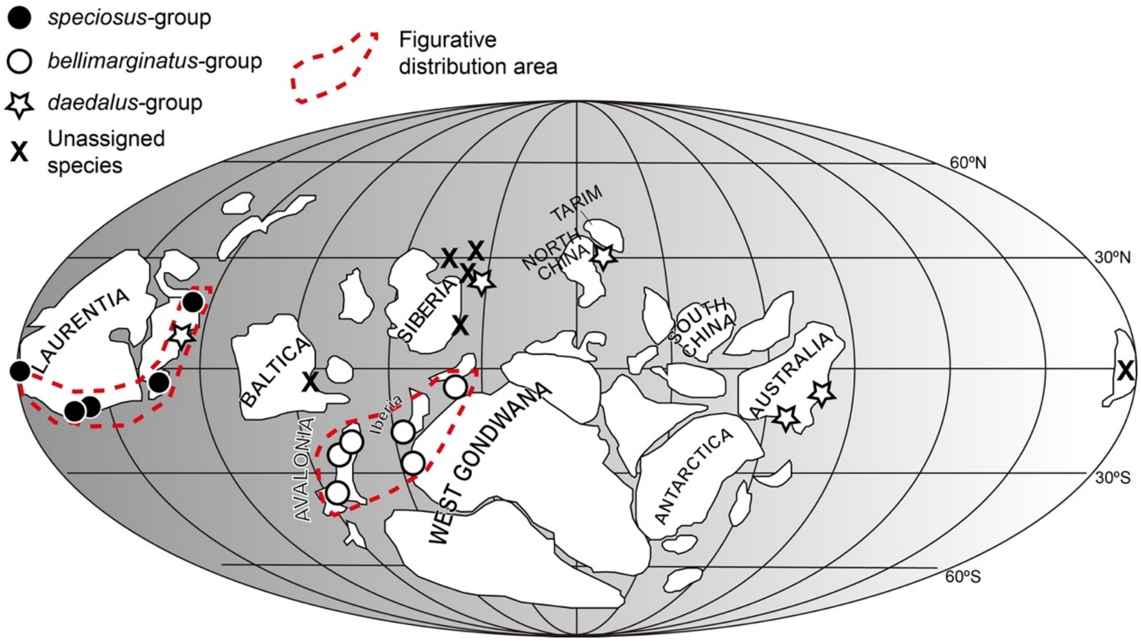


Figure 26: Distribution of *Serrodiscus* plotted on the Cambrian palaeogeographical map. Modified from Scotese & McKerrow (1990), McKerrow et al. (1992), Dalziel (1997), and Malinky & Geyer (2019).

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 upper 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 Görlizt region together with *Serrodiscus*.

Baltica: Baltica has been traditionally subdivided into two tectonostratigraphical 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 Epoch 2 also include

Strenuaeva, *Atops*, *Calodiscus*, and *Protolenus* (Cederström et al., 2009, 2011; Żylińska & Szczepanik, 2009; Żylińska, 2013a, b).

Siberia: The Siberian 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 Altai-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 (Álvaro 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 stratigraphical position is lower Botomian (Datsenko et al., 1968).

In the Altai-Sayan Foldbelt, representatives of *Serrodiscus* are found in several regions, including Tuva (Tannu-Ola), Eastern Sayan, Altai 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 biogeographical 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 odyssei* 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 palaeogeographical 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 stratigraphical record, palaeogeographical affinities, and regional tectonics. Álvaro 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).

5.3.7. Taphonomical and morphological variation remarks

Serrodiscus includes about thirty species, representing a high diversity for a few characters-bearing genus. Unfortunately, many of these species are poorly documented (e.g., *S. asiaticus* Pokrovskaya, 1959, *S. communis* Pokrovskaya, 1959), based on few or even a 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* Orlowski, 1985b). 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 morphological characters of *Serrodiscus* (Figs. 27–29). This variability applies mainly to fossils preserved as moulds, but some features must also be considered for mineralizations since 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. 28.2 and 28.16). 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. 28.13 and 28.16), which seems to be related to compression, since 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 cephala suggest intraspecific variability (Figs. 27.19; 28.16, 28.19).

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. 28.15, 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. 28.8, 28.9).

6) The pre-occipital tubercle is preserved in only two specimens (Fig. 28.16, 28.19), 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., 28.13) and obliterated (e.g., Fig. 28.18). Moreover, smaller specimens bear unfurrowed glabellae with no traces of SO or LO (Fig. 27.1–20.20).

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. 28.1, 28.17). 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.) postaxial region. Nevertheless, in a significant number of specimens, a post-axial area is absent (e.g., Fig. 29.11–14), 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. 29.10) to the merest hint of segmentation (Fig. 29.1), 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. 29.14, 29.16), 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. 29.1). 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. 29.4, 29.5) to laterally (e.g., 29.6–29.8) directed, being easily deformed and obliterated.

5.3.8. 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 taxonomical 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 Bigotinidae 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 & Thekritoff, 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 characterised 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 *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. areolosus* Zhou, 1982 in Zhou et al. (1982); *S. primarius* Orlowski, 1985b; *S. gravestocki* Jell, 1990 in Bengtson et al. (1990).

Serrodiscus bellimarginatus (Shaler & Foerste, 1888)

Figures 27–31

1888 *Microdiscus bellimarginatus* – Shaler & Foerste, p. 35, pl. 2, figs. 19, 19a.

1890 *Microdiscus bellimarginatus* – Vodges, p. 125.

1891 *Microdiscus bellimarginatus* – Walcott, p. 630, pl. 81, figs. 2, 2a, b.

1896 *Microdiscus bellimarginatus* – Matthew, p. 29.

1899 *Microdiscus bellimarginatus* mut. *insularis* – Matthew, p. 75.

1905 *Microdiscus bellimarginatus* – Gorham, pl. 2, figs. 19, 19a.

1907 *Microdiscus speciosus* – Lake, p. 33, pl. 3 fig. 7.

1913 *Eodiscus bellimarginatus* – Raymond, p. 103, fig. 7.

1923 *Eodiscus bellimarginatus* – Clark, p. 476.

1924 *Eodiscus* cf. *speciosus* – Richter & Richter, pp. 732, 733, fig. 14.

1931 *Eodiscus bellimarginatus* – Cobbold, p. 460, pl. 38, figs. 12–14.

1932 *Eodiscus speciosus* – Schwarzbach, pp. 452–454.

1933 *Eodiscus* cf. *speciosus* – Richter, p. 851, fig. 13.

1933 *Eodiscus speciosus* – Schwarzbach, p. 586, 591.

1934 *Eodiscus speciosus* – Schwarzbach, p. 15, 16, 18, 19, 30, 32, 33, pl. 2, fig. 17.

1934 *Eodiscus* sp. – Schwarzbach, p. 18.

1936 *Eodiscus speciosus* – Schwarzbach, p. 34.

1939 *Eodiscus speciosus* – Schwarzbach, p. 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* – Richter & Richter, p. 27, pl. 1, figs. 17–21; pl. 4, fig. 61.

1941 *Eodiscus* (*Serrodiscus*) cf. *speciosus* – Richter & Richter, p. 29, pl. 1, figs. 15, 16.

1944 *Eodiscus bellimarginatus* – Kobayashi, p. 52, pl. 1, fig. 5b.

1950 *Eodiscus* (*Serrodiscus*) *bellimarginatus* – Shaw, p. 582, pl. 79, figs. 19–23.

1952 *Serrodiscus bellimarginatus* – Rasetti, p. 445, pl. 52, figs. 12–17.

1953a *Paradiscus* (*Serrodiscus*) *coloi* nov. sp. – Hupé, p. 110, 111, fig. 13.2.

1953a *Paradiscus* (*Serrodiscus*) cf. *speciosus* – Hupé, p. 110.

1953a *Paradiscus* (*Serrodiscus*) cf. *speciosus* – Hupé, p. 111, fig. 13.1.

1953b *Paradiscus* (*Serrodiscus*) cf. *speciosus* – Hupé, p. 43.

non 1955 *Serrodiscus bellimarginatus* – Major & Winsnes, p. 1314, pl. 1, figs. 6–9.

1958 *Eodiscus* cf. *speciosus* – Lotze, p. 743, 744.

1960 *Serrodiscus silesius* – Sdzuy, p. 105.

1960 *Serrodiscus* cf. *speciosus* – Sdzuy, p. 105.

1961 *Eodiscus* (*Serrodiscus*) cf. *speciosus* – Lotze, p. 164, 169, 171.

1961 *Serrodiscus* cf. *speciosus* – Sdzuy, p. 229, 237, 238, pl. 1, figs. 6–8.

1961 *Serrodiscus* cf. *speciosus* – Sdzuy, pl. 1, figs. 1–5, 9.

1961 *Eodiscus* (*Serrodiscus*) cf. *speciosus* – Schwarzbach, p. 64.

1961 *Eodiscus* (*Serrodiscus*) *silesius* – Schwarzbach, p. 64.

1962 *Serrodiscus speciosus silesius* – Sdzuy, p. 187, 188, pl. 18, fig. 6.

1962 *Serrodiscus bellimarginatus* – Hutchinson, p. 58, pl. 1, figs. 1, 2.

1966 *Serrodiscus* cf. *speciosus* – Rushton, p. 12, pl. 1, fig. 1.

1966 *Serrodiscus bellimarginatus* – Rushton, p. 13, pl. 1, figs. 2–5.

1966 *Ladadiscus llarenai* – Rushton, p. 24–26, pl. 3, figs 16–20, fig. 9a.

1972 *Serrodiscus bellimarginatus* – Fletcher, p. 35, pl. 7, figs 11–18; pl. 8, figs. 1–14; pl. 9, fig. 1.

1972 *Serrodiscus* sp. – Aparigio Yagüe & Gil Cid, p. 107, 108, pl. 1, figs. 1, 3–5.

1972 *Serrodiscus* aff. *speciosus* – Aparigio Yagüe & Gil Cid, pl. 1, fig. 2.

1981 *Serrodiscus speciosus* – Gil Cid, p. 31, pl. 1, figs 4–6; pl. 2, fig. 1, 2, 6–9.

1981 *Serrodiscus speciosus silesius* – Gil Cid, p. 31.

1981 *Serrodiscus* sp. – Gil Cid, pl. 1, fig. 12.

1981 *Serrodiscus* – Gil Cid, pl. 2, figs. 3, 4.

1981 Eodíscido – Gil Cid, pl. 2, fig. 5.

1981 *Serrodiscus* cf. *speciosus* – 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* – Prescher, p. 61.

1988a *Serrodiscus speciosus* – Gil Cid, p. 582, figs. 4, 5, 8.

1988 *Serrodiscus speciosus* – Gómez-Alba, p. 526, pl. 260, fig. 3.

1988 *Serrodiscus coloi* – Geyer, p. 116, figs. 55–58.

1990a *Eodiscus speciosus* – Christian, p. 10.

1990b *Eodiscus speciosus* – Christian, p. 3.

1992 *Serrodiscus* (*Eodiscus*) *silesius* – Elicki & Schneider, pl. 15, fig. 5.

1992 *Eodiscus* (*Serrodiscus*) *speciosus* – Scheibe, p. 299–302, fig. 4.

1992 *Eodiscus* (*Serrodiscus*) *speciosus silesius* – Scheibe, p. 300–302.

1993 *Serrodiscus speciosus silesius* – Liñán et al., p. 824.

1993 *Ladadiscus llarenai* – Liñán et al., p. 824.

1995 *Serrodiscus silesius* – Geyer & Elicki, p. 93–97, figs. 3.1–3.9, 5.1, 5.3.

1998 *Serrodiscus speciosus silesius* – Álvaro et al., 502.

2000 *Serrodiscus silesius* – Elicki, pl. 1, fig. 18

2003 *Serrodiscus silesius* – Elicki, fig. 16.

2005 *Serrodiscus silesius* – Geyer, fig. 6.4.

2006 *Serrodiscus bellimarginatus* – Fletcher, pl. 27, figs. 15–17.

2008 *Serrodiscus bellimarginatus* – Fletcher & Theokritoff, p. 315, 316, figs. 4.26–4.30.

2010 *Serrodiscus silesius* – Elicki & Geyer in Heuse et al., p. 107, figs. 2.1, 2.5.

2011 *Serrodiscus speciosus* – Gil Cid et al., p. 48, pl. 3.

2011 *Serrodiscus bellimarginatus* – Bullock et al., pl. 2, fig. 3.

2011 *Serrodiscus* (s.l.) "*bellimarginatus*" – Westrop & Landing, p. 222–234, figs. 4–12.

Material: Studied specimens are housed in the palaeontological collections of the Department of Earth Sciences (Laboratory of Tectonics and Palaeontology) 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, UHU–CSB255B–273, MPZ2021/326, 128 cephala; UHU–CSB182–189, UHU–CSB191–248A, MPZ2021/325, MPZ2021/327, 81 pygidia. Sierra de El Bujo, Huelva: MPZ2021/320–321, MPZ2021/323, three cephala, 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 cephala, 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–l, SMF X 1234l–2, SMF X 1239–1, SMF X 1239–4, SMF X 1239–5, twelve cephala, 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 cephala, MPZ2021/316–319, four pygidia. Alconera (A3 section), Badajoz: MPZ2021/328–330, three cephala, MPZ2021/331, one pygidium, MPZ2021/332, one complete specimen. Viar fossil site, Llerena-Pallares road, Badajoz: MPZ2021/334, MPZ2021/336, two cephala, 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 cephala, 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 welldefined axial pygidial rings and evident axial nodes.

Description: Semi-elliptic cephalon, semi-circular in smaller specimens (compare Figs. 27 and 28), 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. 28.16), being weak or absent in the smaller ones (e.g., Fig. 27.2). Smallest specimens bearing a pair of laterally projected tubercles (Fig. 27.6, 27.12, 27.14, 27.16) 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. 27.19; 28.19, 28.21; 31.6) 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. 27.6, 27.9). 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. 27.18, 28.17). 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. 28.16, 28.19). SO subtle, shallowing abaxially. LO convex, rectangular to trapezoidal, about 5% cephalic length (sag.), bearing a short occipital spine medially. Genae domed, smooth and homogeneous. Posterior border continuous with lateral border, widening adaxially to

Figure 27: *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), ‘Cumbres beds’, upper Marianian, Cumbres de San Bartolomé, Huelva (**1**–**18**); ‘Alanís beds’, upper Marianian, Camino de la Dehesilla, Seville (**19**); La Hoya Member, upper Marianian, Alconera Formation, Alconera, Badajoz (**20**). **1**) UHU–CSB121. **2**) UHU–CSB126. **3**) UHU–CSB152. **4**) UHU–CSB153. **5**) UHU–CSB155 (latex). **6**) UHU–CSB156. **7**) UHU–CSB157. **8**) UHU–CSB160. **9**) UHU–CSB164. **10**) UHU–CSB165. **11**) UHU–CSB167. **12**) UHU–CSB218 (latex). **13**) UHU–CSB249 (latex). **14**) UHU–CSB250. **15**) UHU–CSB253. **16**) UHU–CSB255 (latex). **17**) UHU–CSB259. **18**) UHU–CSB265. **19**) MPZ2021/324. **20**) MPZ2021/329. Scale bars = 5 mm (**1**), 3 mm (**2**–**3**, **18**, **20**), 2 mm (**9**, **13**, **17**, **19**), 1 mm (**4**–**8**, **10**–**12**, **14**–**16**). Arrows in **6**, **12**, **14** and **16** indicate lateral tubercles.

posterior cephalic corner. Genal spines are small, rarely preserved, abaxially and posteriorly directed, located immediately anterior to the posterior cephalic corner (Fig. 28.15, 28.16).
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 1.3–13.2mm in length and 1.5–11.5mm 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 postaxial 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. 29.3–29.5; 31.1, 31.2).

Remarks: The erection of *Serrodiscus serratus* by Richter & Richter (1941) was based on very poorly preserved material (Fig. 31.1–31.8) 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

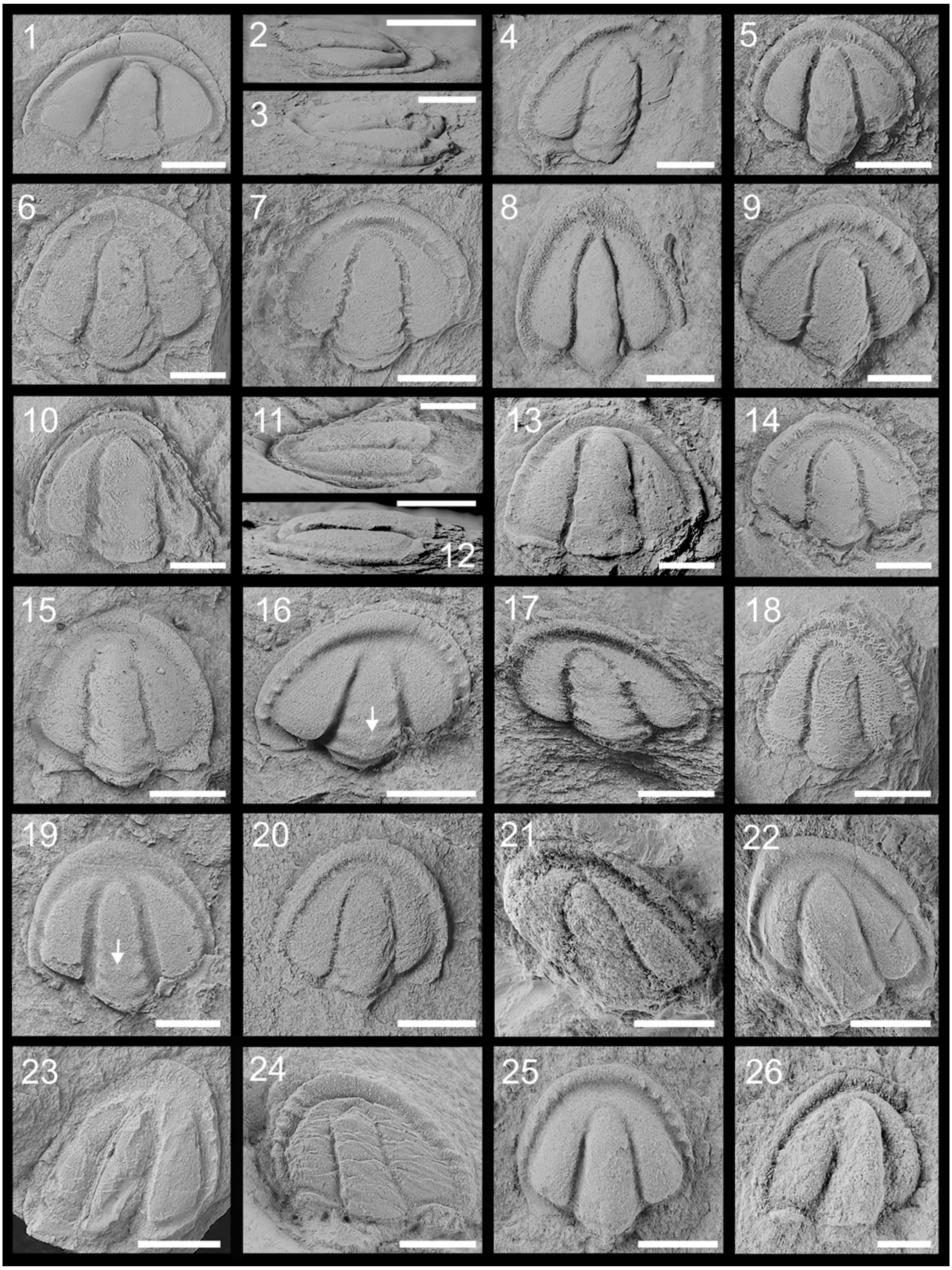

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Figure 28: *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), 'Cumbres beds', upper Marianian, Cumbres de San Bartolomé, Huelva (**1**–**20**, **23**); 'Alanís beds', Viar fossil site, upper Marianian, Llerena-Pallares road, Badajoz (**21**); La Hoya Member, upper Marianian, Alconera Formation, Alconera, Badajoz (**22**); 'Herrerías shale', upper Marianian, Arroyomolinos de León (**24**) and Sierra de El Bujo (**25**), Huelva; Soleras Formation, upper Marianian, Pico Noez, Totanés, Toledo (**26**). **1**–**2**) UHU–CSB103; **1**) dorsal view; **2**) lateral view. **3**–**4**) UHU–CSB119; **3**) lateral view; **4**) dorsal view. **5**) UHU–CSB120. **6**) UHU–CSB124. **7**) UHU–CSB125. **8**) UHU–CSB129 (latex). **9**) UHU–CSB137. **10**–**11**) UHU–CSB104, dorsal view; **11**) lateral view. **12**–**13**) UHU–CSB112; **12**) lateral view; **13**) dorsal view. **14**) UHU–CSB138. **15**) UHU–CSB162 (latex). **16**) UHU–CSB180. **17**) UHU–CSB161. **18**) UHU–CSB111. **19**) UHU–CSB116. **20**) UHU–CSB134. **21**) MPZ2021/334. **22**) MPZ2021/328. **23**) UHU–CSB109. **24**) MPZ2021/314. **25**) MPZ/2021/321. **26**) MPZ2021/338. Scale bars = 5 mm (**1**–**2**), 3 mm (**3**–**4**, **6**–**8**, **10**–**14**, **16**, **18**, **22**–**25**), 2 mm (**9**, **15**, **17**, **19**–**21**, **26**). Arrows in **16** and **19** indicate preoccipital glabellar tubercles.

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 representaive 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. 29.14, 29.15 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. 29, Fig. 31.11, 31.12 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.

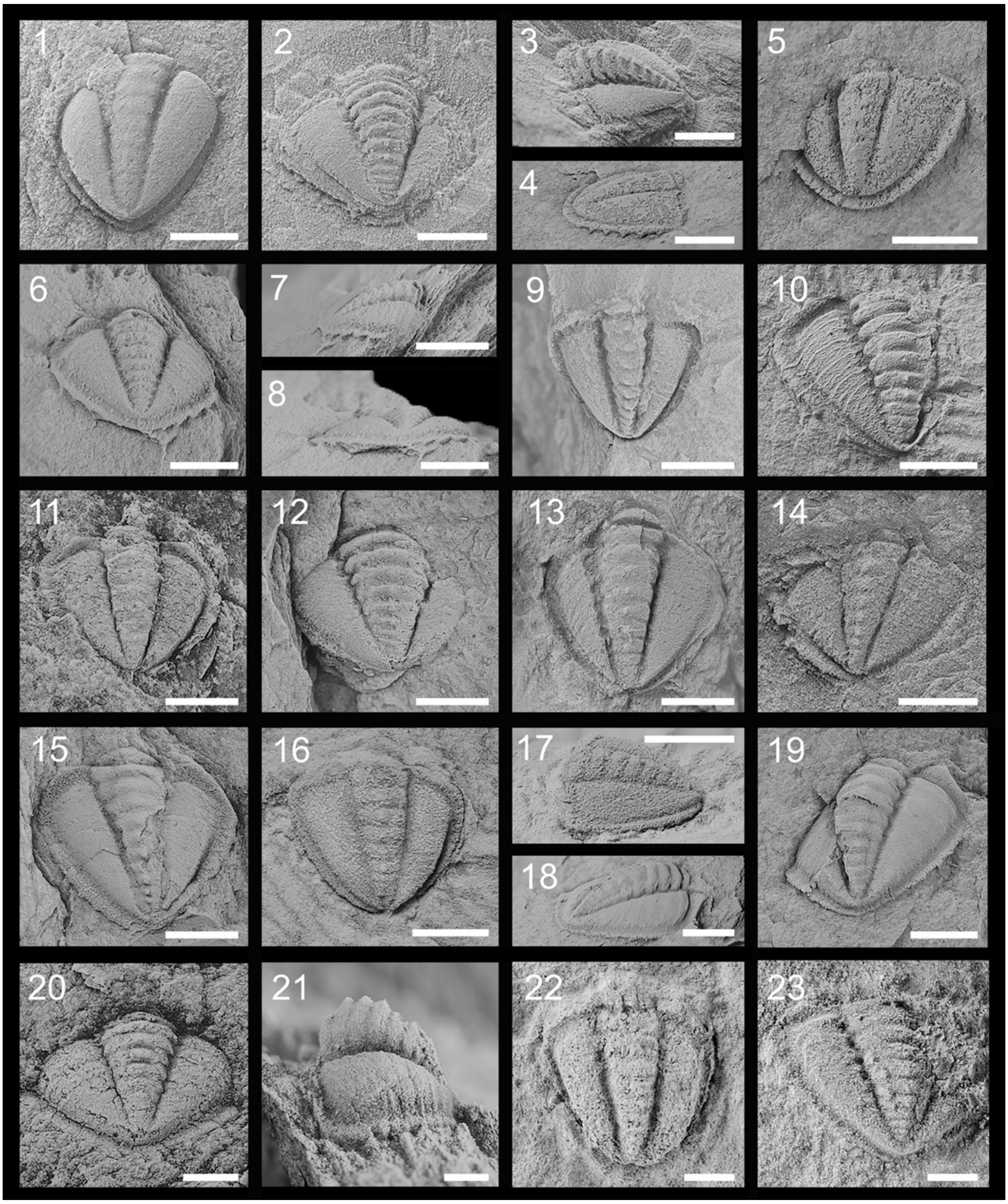

Figure 29: *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), ‘Cumbres beds’, upper Marianian, Cumbres de San Bartolomé, Huelva (**1**–**21**); Soleras Formation, upper Marianian, Pico Noez, Totanés, Toledo (**23**); La Hoya Member, upper Marianian, Alconera Formation, Alconera, Badajoz (**24**). **1**) UHU–CSB229. **2**–**3**) UHU–CSB230; **2**) dorsal view; **3**) lateral view. **4**–**5**) UHU CSB215B (latex); **4**) lateral view; **5**) dorsal view. **6**–**8**) UHU–CSB232; **6**) dorsal view; **7**) lateral view; **8**) post-lateral view. **9**) UHU–CSB236. **10**) UHU–CSB245. **11**) UHU–CSB200 (latex). **12**) UHU–CSB184 (latex). **13**) UHU–CSB187B. **14**) UHU–CSB204. **15**) UHU–CSB238. **16**–**17**) UHU–CSB244; **16**) dorsal view; **17**) lateral view. **18**–**19**) UHU–CSB212B (latex); **18**) lateral view; **19**) dorsal view. **20**) UHU–CSB310 (latex). **21**) UHU-CSB213, lateral view. **22**) MPZ2021/339. **23**) MPZ2021/331. Scale bars = 2 mm (**1**, **5**–**8**, **14**–**15**, **22**), 3 mm (**2**–**3**, **9**–**13**, **16**–**19**), 1 mm (**4**, **20**, **21**, **23**).

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, 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 Formation 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 geographical and lithostratigraphical 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*.

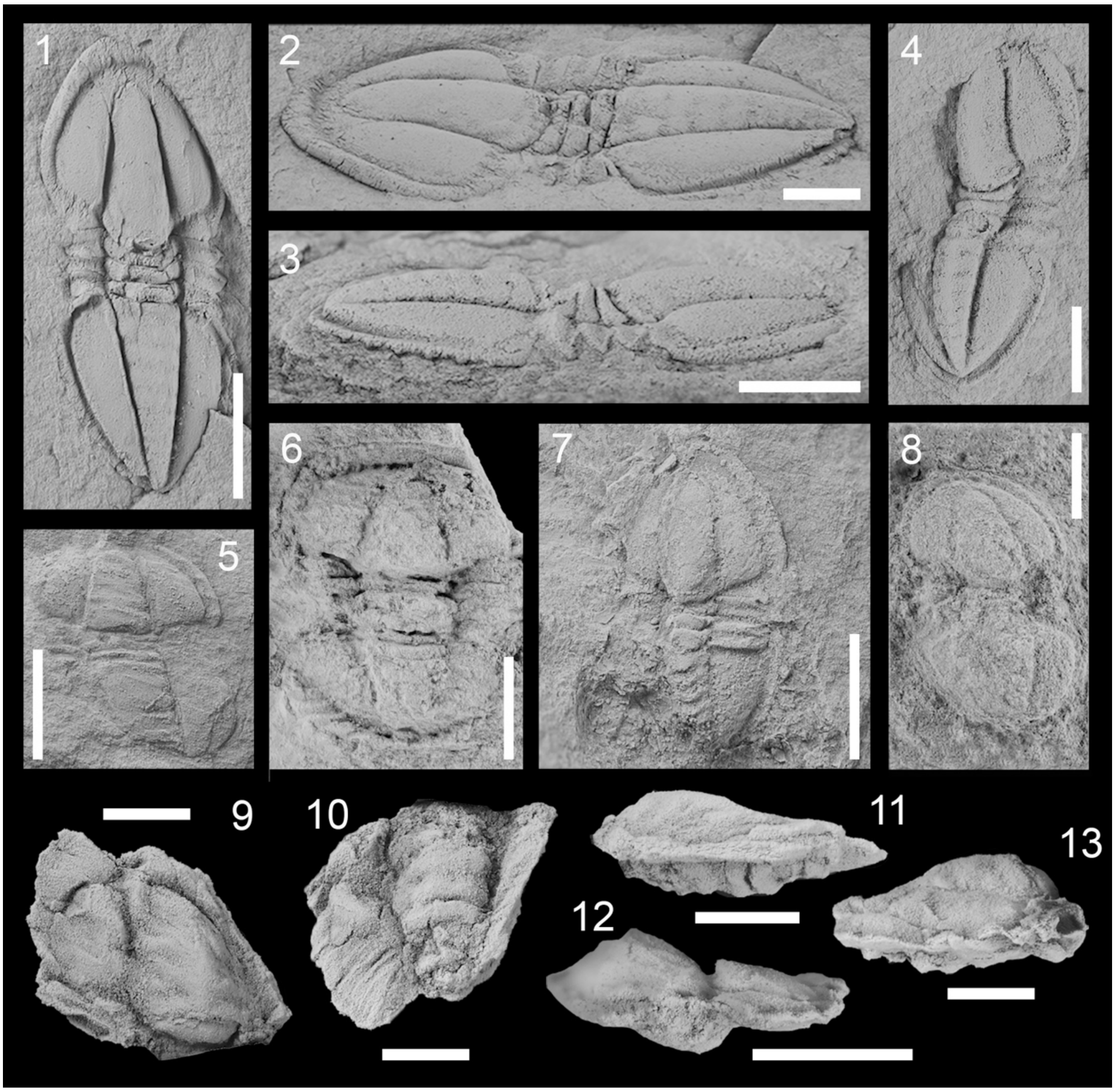

Figure 30: *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), 'Cumbres beds', upper Marianian, Cumbres de San Bartolomé, Huelva (**1**–**4**, **7**, **9**–**13**); 'Herrerías shale', upper Marianian, El Pozuelo, Arroyomolinos de León, Huelva (5); Soleras Formation, upper Marianian, Pico Noez, Totanés, Toledo (**6**); La Hoya Member, upper Marianian, Alconera Formation, Alconera, Badajoz (**8**). **1**–**2**) UHU–CSB100 (latex); **1**) dorsal view; **2**) lateral view. **3**–**4**) UHU–CSB101 (latex); **3**) lateral view; **4**) dorsal view. **5**) UHU–POZ100. **6**) MPZ2021/337. **7**) UHU–CSB190. **8**) MPZ2021/332. **9**–**13**) UHU–CSBsn; **9**) dorsal view; **10**) ventral view; **11**) lateral view (left); **12**) post-lateral view; **13**) lateral view (right). Scale bars = 5 mm (**1**, **5**), 2 mm (**2**–**4**, **6**–**11**, **13**), 3 mm (**12**).

5.3.9. 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 that seem to represent minor morphological changes within an isolated *Serrodiscus* community. Even if we had direct access to the existing material, it would be complicated to make synonymy decisions for several of these species, as these are based on poorly preserved and very limited number of species. For this reason, and 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 morphological, stratigraphical and palaeobiogeographical 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 stratigraphical and palaeobiogeographical provenance):

1) *bellimarginatus* group (Fig. 32.1–32.5): 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 from a palaeogeographical 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 morphological difference is present in *S. subclavatus* from the Shodack Formation, North Chatham (Columbia County, Georgia), which co-occurs with standard "tapered forwards"

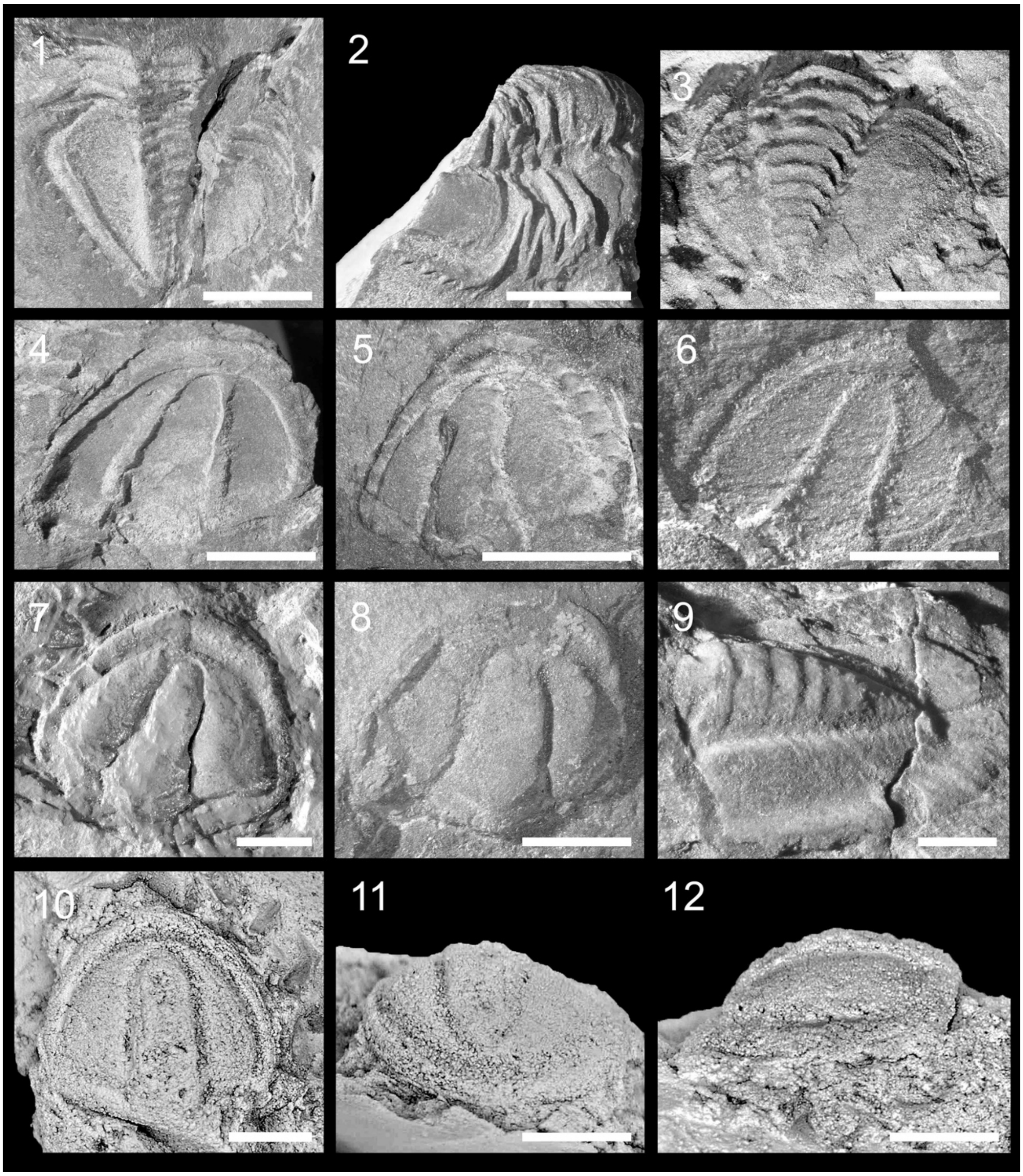

Figure 31: **1**–**8**) Type material of '*Serrodiscus serratus*' Richter & Richter, 1941 [=*S. bellimarginatus* (Shaler & Foerste, 1888)], 'Herrerías shale', upper Marianian, Minas de Cala, Huelva. **1**) SMF X 1234a-1, dorsal view. **2**) SMF X 1234a-3, dorsal view. **3**) SMF X 1234c-1, dorsal view. **4**) SMF X 1234h-1, dorsal view. **5**) SMF X 1234a-2, dorsal view. **6**) SMF X 1234h-2, dorsal view. **7**) SMF X 1234l-2, dorsal view. **8**) SMF X 1234e-1, dorsal view. **9**) type material of '*Eodiscus llarenai*' Richter & Richter, 1941 (=*S. bellimarginatus*), 'Herrerías shale', upper Marianian, Minas de Cala, Huelva, SMF X 1237a-1, lateral view. **10**–**12**) type material of *S. bellimarginatus* (Shaler & Foerste, 1888), Hoppin limestone, lower Cambrian, North Attleborough, Massachusetts, MCZ 105035. Scale bars = 5 mm (**1**–**5**, **7**–**8**), 2 mm (**6**, **9**), 1 mm (**10**–**12**). Credits: Robin Kunz, Senckenberg Museum (**1**–**9**) and Mark D. Renczkowski, Museum of Comparative Zoology (**10**–**12**).

glabella forms (e.g., *S. spinulosus*). Thus, we regard this morphological 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*.

2) *speciosus* group (Fig.32.6–32.10): 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 morphological differences but sharing stratigraphical and palaeogeographical 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 Formation, 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) showed that *S. mackenziensis* is closely related to both *S. speciosus* and *S. bellimarginatus*. Given *S. mackenziensis* palaeogeographical 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

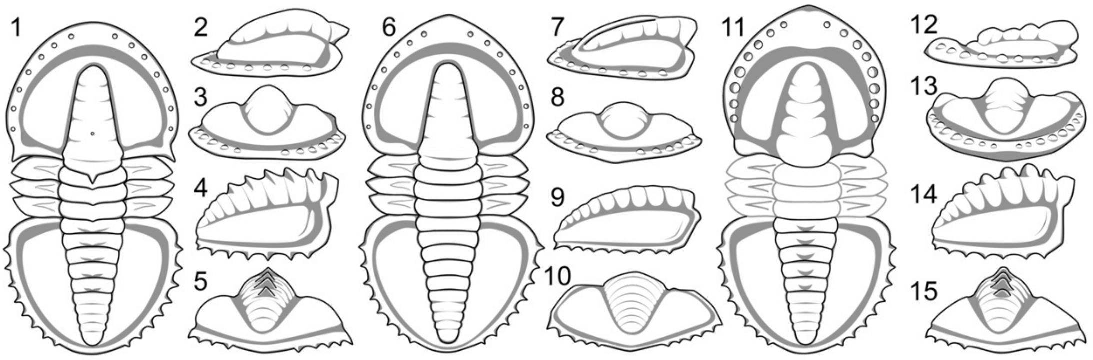

Figure 32: Schematic illustrations of the represeventative dorsal characters of the *Serrodiscus* groups. **1**–**5**) *bellimarginatus* group; **1**) dorsal view; **2**) lateral view of the cephalon; **3**) frontal view of the cephalon; **4**) lateral view of the pygidium; **5**) posterior view of the pygidium. **6**–**10**) *speciosus* group; **6**) dorsal view; **7**) lateral view of the cephalon; **8**) frontal view of the cephalon; **9**) lateral view of the pygidium; **10**) posterior view of the pygidium. **11**–**15**) *daedalus* group; **11**) dorsal view; **12**) lateral view of the cephalon; **13**) frontal view of the cephalon; **14**) lateral view of the pygidium; **15**) posterior view of the pygidium. Credits: Bernat Vázquez.

species came all from the same locality and showed subtle morphological variations, which may be due to taphonomical processes. 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 morphological 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.

3) *daedalus* group (Fig. 32.11–32.15): This group includes *S*. *daedalus* Öpik, 1975, *S*. *fossuliferus* Repina, 1964 in Repina et al. (1964), *S*. *gravestocki* Jell, 1990 in Bengston et al. (1990), and *S*. *areolosus* 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 Formation (New South Wales, Australia) and later reported by Blaker & Peel (1997) from the Aftenstjemesø Formation (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 Formation (North Greenland) shows fine marginal spines, and we cannot exclude the possibility of S. *daedalus* and S. *gravestocki* being conspecific.

Finally, S. *areolosus* 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. *areolosus* 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).

4) *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 cephala and six pygidia (see also Repina & Romanenko, 1978, pl. 1, figs. 1–4) and the later based on solely two cephala (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. *coniformis* Korobov, 1980 from Prikhubsugulye (northern Mongolia) was defined based on four well-preserved cephala (Korobov, 1980, pl. 9, figs. 12–14), although its diagnosis lacks unambiguous characters (Korobov, 1980, p. 98). The species *Serrodiscus primarius* Orlowski, 1985b from Kamieniec, Poland, is based on a single complete specimen initially assigned to *S. speciosus* by Samsonowicz (1962, fig. 6). Orwloski 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 Orlowski 1985b, 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 *Serrodiscus* species (e.g., *S. speciosus*).

The established groups of *Serrodiscus* species, based primarily on morphology, present distinct palaeobiogeographical distributions (Fig. 26). The *specious* 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 characterised 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 biostratigraphical point of view, it is remarkable that the FAD of most species belonging to both the *speciosus* and the *bellimarginatus* groups approximately coincides with a tentative Cambrian Stage 4 lower boundary, with the exceptions of MacKenzie Mountains (Laurentia) (Fig. 25). 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; Shergold & Geyer, 2003). The *daedalus* group has a broader distribution: although it characterises Australia (*S. daedalus* and *S. gravestocki*) and China (*S. areolosus*), it also occurs in Siberia (*S. fossuliferus*) and Laurentia (*S. daedalus*). This group shows a certain disparity: regarding its biostratigraphical 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. 25). However, members of the *daedalus* group from Greenland and Australia depict a closer position to a tentative Cambrian Stage 4 lower boundary.

5.3.10. 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 the Pico Noez fossil site. Given the stratigraphical 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 reassigned 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 morphological variability of studied specimens from at the same locality and horizon, a taphonomical 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 morphological, stratigraphical and palaeobiogeographical 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 biostratigraphical range through the Cambrian Series 2, the palaeobiogeographical 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.

5.4. First report of *Chelediscus* Rushton, 1966 (Trilobita) from Western Gondwana, with description of a new species from the Cambrian Series 2 of Spain (Collantes et al., 2023 in Historical Biology, 35)

5.4.1. Abstract

Chelediscus is reported for the first time from the Cambrian of Western Gondwana. This eodiscide genus is known from the Cambrian Series 2 of England, Newfoundland, New York, Sweden and Russia. An emended diagnosis for the genus is provided, which is here assigned to Calodiscidae, and a new species, *Chelediscus garzoni* Collantes, Pereira, Mayoral & Gozalo, 2023, is described. The species comes from Cumbres de San Bartolomé municipality, northern Huelva Province (Spain), in the upper part of the 'Cumbres beds' formation. This horizon is assigned to the regional upper Marianian Stage based on the trilobite assemblage (*Serrodiscus* Zone), correlating with the lowermost Cambrian Stage 4. *Chelediscus carus* Repina from the Botoman of Siberia and this Spanish occurrence are the earliest appearances of the genus. The new species suggests that a smooth, unlobed glabella is primitive for the genus. *Chelediscus* in Spain strengthens faunal links with Avalonia, Baltica, Siberia and Laurentia.

5.4.2. Introduction

Eodiscida (*sensu* Adrain, 2011) represents one of the most widespread and biostratigraphical-reliable groups for the upper Cambrian Series 2 to the Miaolingian (Robison et al., 1977; Jell, 1997; Geyer & Shergold, 2000; Geyer, 2005; Axheimer et al., 2007; Álvaro et al., 2013; Sundberg et al., 2016; Peng et al., 2020). This group is characterised by small forms (few millimetres to centimetres), frequently isopygous, with two or three thoracic segments and mostly deprived of eyes (Jell, 1997). Their relationship with Agnostida; and an eventual monophyly of both (grouped classically as Agnostida, e.g., Fortey, 1997), has become contentious (e.g., Müller & Walossek, 1987; Bergström & Hou, 2005; Cotton & Fortey, 2005; Adrain, 2011; Legg et al., 2013; Moysiuk & Caron, 2019; Paterson, 2020).

In Western Gondwana, eodiscide trilobites occur widely in Morocco, Iberia, France, Sardinia, Germany and Bohemia (e.g., Howell, 1935; Richter & Ricther, 1941; Šnajdr, 1958; Sdzuy, 1962, 1969, 1995; Aparicio Yagüe & Gil Cid, 1972; Rasetti, 1972; Courtessole, 1973; Geyer, 1988; Pillola, 1991; Geyer & Elicki, 1995; Sepúlveda et al., 2022). In Iberia, six Eodiscida genera have been reported from the Cambrian Series 2: *Delgadella* Walcott, 1912, *Serrodiscus* Richter & Richter, 1941, *Calodiscus* Howell, 1935, *Hebediscus* Whitehouse, 1936, *Chelediscus* Rushton, 1966 and *Neocobboldia* Rasetti, 1952. Among these, *Neocobboldia* and *Chelediscus* were only previously listed, in works of another scope, without the specimens ever having been described (Liñán, 1984b, fig. 3; Liñán & Quesada, 1990, fig. 3; Gozalo et al., 2016).

Herein, we document for the first time *Chelediscus* from Western Gondwana, representing a new species, *Chelediscus garzoni* Collantes, Pereira, Mayoral & Gozalo, 2023, from Spain. This genus was first described from the Cambrian Series 2 of Warwickshire, England (*Chelediscus acifer* Rushton, 1966) and it is distributed across Avalonia (United Kingdom, eastern Newfoundland) throughout Baltica (Sweden), Siberia and Laurentia (Taconic Allochthon, New York). Its presence in Iberia expands the palaeogeographical distribution of *Chelediscus* and reinforces the faunal links between Western Gondwana and the palaeogeographical domains located northwest of Gondwana during the early Cambrian.

5.4.3. Geological setting

The studied area is located on the southern flank of the Ossa-Morena Zone (OMZ). 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 OMZ outcrop in distinct belts or 'blocks', with a notable change of facies and thicknesses, most likely related to downthrow and tilting along an active growth fault at the time of sediment deposition (Liñán & Quesada, 1990). The studied material comes from the Cumbres Block (Spain), from the Cumbres de San Bartolomé fossil site, located at 38°02'43.90" N, 6°43'02.11" W (Figs. 33.1, 33.2). Stratigraphically, the studied specimens come from the uppermost 'Cumbres beds' (Figs. 3.3.3, 3.3.4). This informal unit comprises siliciclastic sandstones and shales, with a total thickness varying between 350 and 1100 meters. It is dated as middle–late Marianian, based on the trilobites *Delgadella souzai* (Delgado, 1904), *Callavia choffati* (Delgado, 1904) and *Atops calanus* Richter & Richter, 1941 in the lower part of the unit (middle Marianian, see Collantes et al., 2021a, 2021b), and *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), *Triangulaspis fusca* Sdzuy, 1962, *Pseudatops reticulatus* (Walcott, 1890b), the mollusc *Marocella morenensis* (Yochelson & Gil Cid, 1984), brachiopods, and hyoliths in the upper part of the formation (*Serrodiscus* Zone, upper Marianian, see Collantes et al., 2020, 2021a, 2021b, 2022). *Chelediscus garzoni* comes from these upper levels.

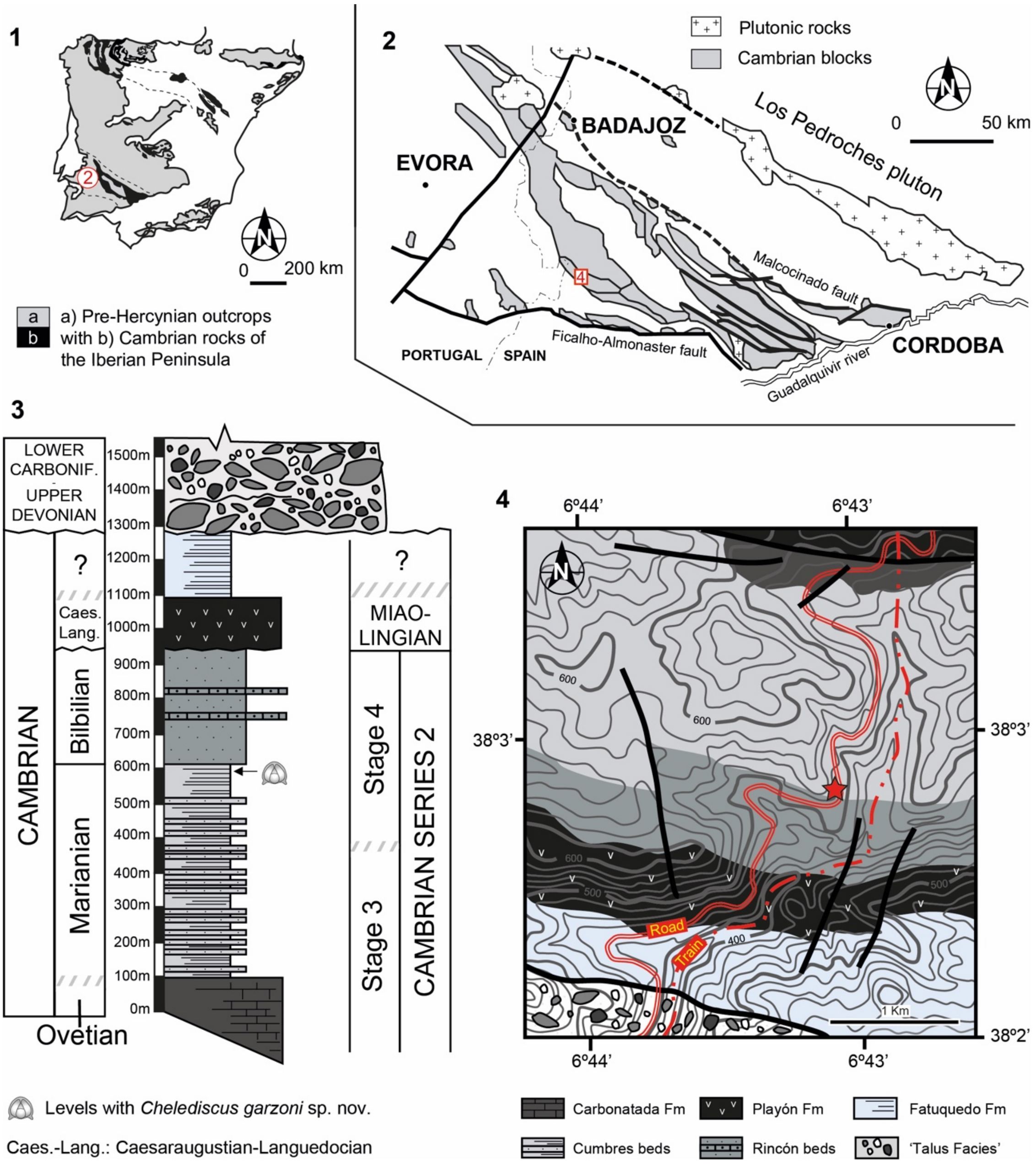

Figure 33: **1**) Pre-Hercynian outcrops in the Iberian Peninsula. **2**) Geological setting of fossil site in the Cambrian sectors (fault-bounded blocks) of the Ossa-Morena Zone, indicating the position of the studied fossil site (modified from Liñán & Quesada 1990). **3**) Stratigraphical column of the Cumbres Block. **4**) Geological map of the Cumbres de San Bartolomé section.

5.4.4. Materials and methods

Available material consists of seventeen isolated cephala, preserved as internal and external moulds, and two isolated pygidia. Samples were collected during several visits held from 2018 to the present by the authors. Specimens were prepared using a pneumatic hammer, coated with ammonium chloride and photographed using a Canon EOS 77D coupled with a macro lens Canon MPE 65 mm f/2.8 1–5x. Figured specimens are housed in the Departamento de Ciencias de la Tierra (Laboratorio de Tectónica y Paleontología) of the Facultad de Ciencias Experimentales, Universidad de Huelva (UHU).

5.4.5. Systematic palaeontology

Order Eodiscida Kobayashi, 1939 (*sensu* Adrain, 2011)

Family Calodiscidae Kobayashi, 1943

Genus ***Chelediscus*** Rushton, 1966

Type species: *Chelediscus acifer* Rushton, 1966, Purley Shales (upper Comley Series, Cambrian Stage 4), Warwickshire, United Kingdom.

Included species: *C. chathamensis* Rasetti, 1967, *C. carus* Repina, 1972.

Emended diagnosis (from Jell 1997, p. 390): Glabella conical, highly elevated posteriorly and sloping anteriorly, smooth or bilobed; when bilobed, may bear a transglabellar furrow and the anterior lobe is much smaller; LO depressed, forming basal lobes or simple, median preglabellar furrow present; border furrow with a line of pits; border may bear a pair of marginal spines laterally; genal spines present or absent, with genal angles bearing a small tumescence solely. Thorax with two segments. Pygidium strongly convex; axis wide, tapering strongly in posterior half, of five or six rings; pleural areas with rudimentary furrows; border narrow.

Remarks: The suprageneric classification of Eodiscida is far from stable and consensual, and some particular genera remain difficult to assign to higher taxa. Jell (1975) and Öpik (1975) considered the structure of the glabella and, in particular, modifications of the occipital area to be key features in the classification of Eodiscida. Assigned initially to Calodiscidae by Rushton (1966), *Chelediscus* was later regarded as a very particular eodiscide related to Weymouthiidae by Cotton & Fortey (2005). We prefer to follow the original and Jell's (1997) assignment of *Chelediscus* to Calodiscidae because it does not present most of the diagnostic characters of the Weymouthiidae and, as stated by Rushton (1966), among Eodiscida genera, *Chelediscus* is more closely related to *Calodiscus* Howell, 1935. Cotton & Fortey (2005) argued that *Chelediscus* differs from the other taxa in the Calodiscidae in having a pointed glabella, a larger number of pygidial segments, genal spines and an occipital furrow that slopes backwards.

Nevertheless, *Chelediscus* has a significantly reduced size (weymouthiids are typically oversized for the order), the glabella strongly tapers forwards (it is parallel-sided or tapers gently in Weymouthiidae), S0 is clearly impressed, the fixigenae are not confluent in front of glabella, the thorax bears only two segments (all weymouthiids known thoraxes have three segments), and the pygidium has five to six pygidial rings (Weymouthiidae has typically more than nine) and it has a wide axis. Finally, the anterior configuration of glabella stressed by Cotton & Fortey (2005) is quite variable among all the families established for Eodiscida (see Jell, 1997); the occipital ring configuration may not be that significant (see remarks on *Chelediscus garzoni*). The genal spines in *Chelediscus* may be interpreted as spine-like tubercles, besides being a character that has developed widely and independently in different trilobite groups and commonly present in juvenile stages of species that do not retain them in holaspid stages. *Chelediscus* also resembles Eodiscidae members in some characters, particularly in the configuration of the preglabellar area and the fixigenae. However, it lacks an occipital spine; it bears an evident complete occipital ring and has a different pygidial structure, with a wide axis and a reduced number of pygidial rings (an apomorphy of Calodiscidae, although not exclusive of that family). These characters, together with *Chelediscus* resemblance to *Calodiscus*, justify its assignment to Calodiscidae. Nevertheless, it is interesting to note the presence of reminiscent traces of possible scrobicules in *Chelediscus* (see Rushton, 1966, pl. 3, fig. 11), a character typical of Eodiscidae. An emended diagnosis is provided to encompass the morphological variability of the species currently included in *Chelediscus*: the bilobed glabella does not seem to be a diagnostic character for *Chelediscus* (absent in *C. carus* and *C. garzoni*), nor is the presence of cephalic marginal and genal spines (the former absent in *C. chathamensis* and both absent in *C. carus*), as well as the differentiation of the occipital ring into basal lobes (absent in *C. chathamensis* and *C. garzoni*).

Chelediscus garzoni Collantes, Pereira, Mayoral & Gozalo, 2023

Figure 34

Etymology: Named after Ignacio Garzón González, a geologist and enthusiastic palaeontologist from Puerto Moral (Huelva, Spain) who has contributed remarkably to the study, conservation and dissemination of the geological and palaeontological heritage from the Sierra de Aracena and Picos de Aroche Natural Park.

Holotype: Internal mould of a cephalon, UHU-CSB514, Figures 34.1, 34.2.

Paratypes: Sixteen cephala (internal moulds: UHU–CSB500, 505–507, 509–510, 512–513, 515–516; internal moulds with corresponding external moulds: UHU–CSB501, 502, 504, 508, 511; external mould: UHU–CSB518); two pygidia (internal moulds: UHU–CSB517, 519).

Type locality: ‘Cumbres beds’, upper Marianian (lowermost Cambrian Stage 4), Cumbres de San Bartolomé (38°02’43.90” N 6°43’02.11” W), Huelva, Spain.

Diagnosis: Glabella smooth, progressively decreasing in convexity anteriorly; L0 transverse, simple and complete; cephalic border bearing a pair of small spines/tubercles opposite the anterior quarter of the glabella; genal spines abaxially directed. Pygidium with axis of five rings plus a terminal piece; with smooth pleurae.

Description: Cephalon semicircular of low convexity in frontal and lateral views, 0.9–2.2 mm in length and 1.1–2.6 mm in width. Flat to subtly domed anterolateral border, about 12% of the total cephalic length (exsag.), sagittally elongate, occupying about 18% of the total cephalic length (sag.). Anterolateral border sculptured with numerous short, elongated, shallow pits with longitudinal arrangement (Figs. 34.9, 34.12), rarely preserved due to mineraliation. A pair of lateral border spines are situated anteriorly to the widest (tr.) part of the cephalon (Figs. 34.1, 34.2, 34.5, 34.14), directed abaxially, although commonly missing (Figs. 34.3, 34.6, 34.12). Deep, continuous anterolateral border furrow. Median preglabellar furrow present. Conical to subconical glabella, convex, showing higher relief than the genae, extending about 62% of the total cephalic length (sag.) and progressively decreasing in convexity anteriorly (Figure 34.7, 34.8). Anteriormost part of glabella pointed anteriorly. Posteriormost part of the glabella is strongly convex and with a higher relief, with a maximum width about 38% of the total cephalic width, rounded posteriorly. Deep, narrow axial furrows, frontally convergent and merging with the median preglabellar furrow. Genae is domed, smooth and

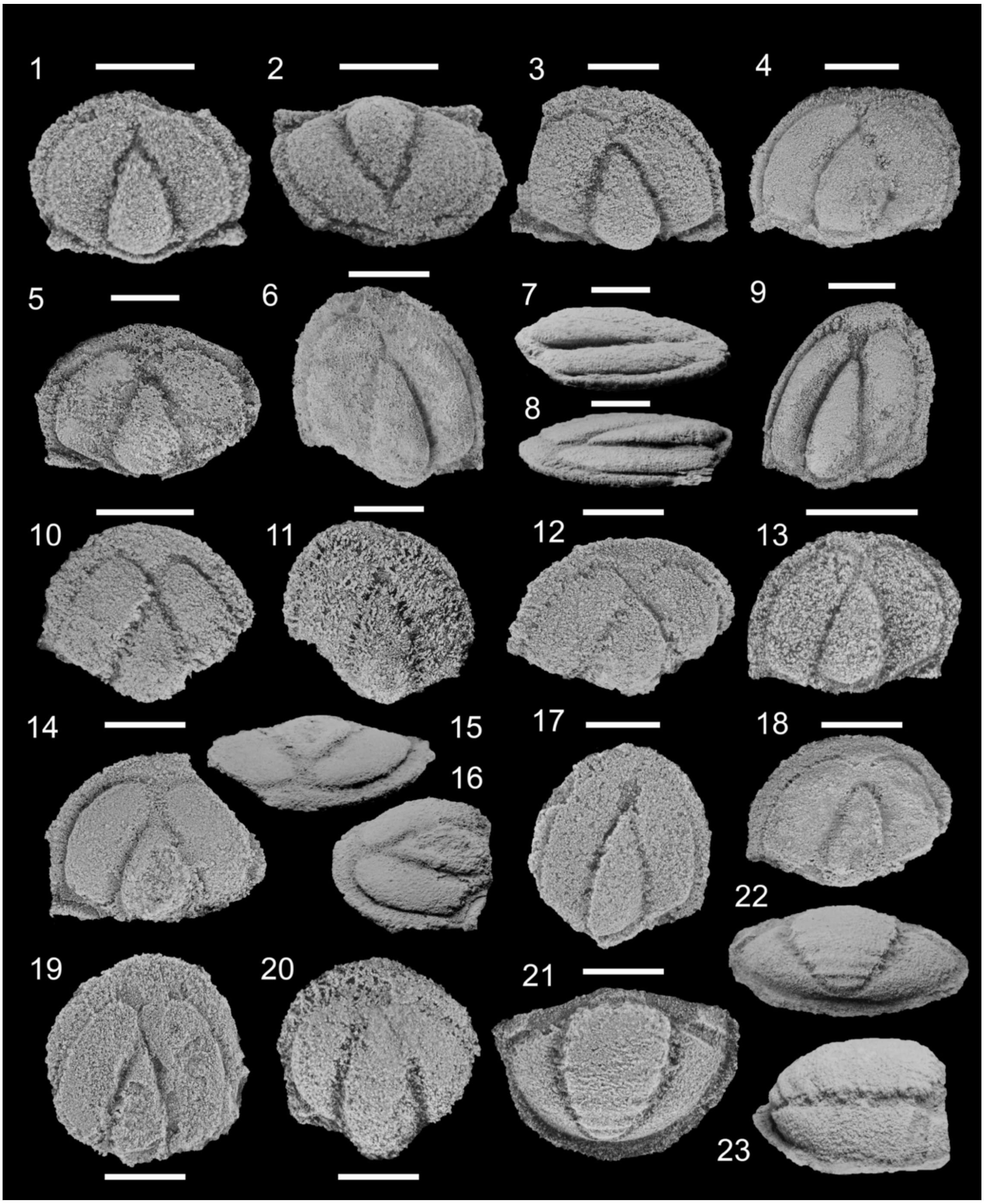

Figure 34: *Chelediscus garzoni* Collantes, Pereira, Mayoral & Gozalo, 2023, 'Cumbres beds', upper Marianian, Cumbres de San Bartolomé, Huelva. **1**–**2**) UHU–CSB514, holotype; **1**) dorsal view; **2**) frontal view. **3**) UHU–CSB500. **4**) UHU–CSB518. **5**) UHU–CSB507. **6**–**7**) UHU–CSB502; **6**) dorsal view; (**7**) lateral view. **8**–**9**) UHU–CSB505; **8**) lateral view; **9**) dorsal view. **10**) UHU–CSB504. **11**) UHU–CSB501. **12**) UHU–CSB506. **13**) UHU–CSB513. **14**–**16**) UHU–CSB508; **14**) dorsal view; **15**) frontal view; **16**) lateral view. **17**) UHU–CSB516. **18**) UHU–CSB509. **19**) UHU–CSB503. **20**) UHU–CSB511. **21**–**23**) UHU–CSB519; **21**) dorsal view; **22**) posterior view; **23**) lateral view. Scale bar = 1 mm.

homogeneous, with low convexity, slightly sloping antero-laterally (Figs. 34.7, 34.8); max-width (opposite the anterior quarter of the glabella) occupying 62% of the total cephalic width. Deep, wide posterior furrow, with max-width (sag.) at the genal corner and narrowing adaxially, with the oblique posterior end of the genae converging backwards. Posterior border continuous with lateral border, narrowing adaxially to posterior cephalic corner. Short, conical genal spines, pointing posterolaterally. The occipital ring is simple, with uniform length and slightly convex backwards (Figs. 34.1, 34.9).

Semicircular pygidium, high relief and convexity in posterior and lateral views (Figs. 34.22, 34.23). Maximum length 1.9 mm and width 2.9 mm. The pygidial axis is subconical, prominent and highly convex, with greater relief than the adjacent pleurae; length (sag.) is about 94% of total pygidial length, max-width (tr.) opposite second axial ring, about 55% of the total pygidial width. Five axial rings plus one terminal piece. Pygidial axial furrows are narrow and deep. Pleurae are moderately convex, smooth and homogeneous. Border furrow is broad, deep and continuous. Deep, wide and oblique articular furrow. The posterolateral border is continuous with the anterior one and homogeneous posteriorly.

Remarks: *Chelediscus garzoni* differs from the type-species *C. acifer* in having a glabella without transglabellar furrow, in having a simple transverse occipital ring lacking basal lobes and in having smooth pygidial pleurae, with no rudimentary pleural or interpleural furrows (although its absence is not definite, taking into account the poor preservation of the two available pygidia) (Fig. 35). Among species of *Chelediscus*, *C. garzoni* is most similar to *C. carus* from the Shumnoy Formation of Shukharikha section, Russia, in having a simple and smooth glabella. Nevertheless, *C. carus* has a smooth cephalic border, lacking lateral spines; it has only a faint tumescence on the genal angles rather than genal spines; and it has a deeply incised furrow on the pygidial pleural areas. *Chelediscus chathamensis* from the *Leptochilodiscus punctulatus* beds of East Chatham, New York (Rasetti 1967, pl. 3, figs. 11–14), is very poorly preserved. The only characters that can be compared appropriately and used to differentiate this species from *C. garzoni* are broad, very shallow depression in front of the elevated posterior of the glabella and the absence of lateral spines on the cephalic border. Rasetti (1967, p. 47) did not describe their presence, and there is no clear evidence of such structures in the figured material. The few available specimens of *C. chathamensis* are silicified and were extracted from limestones, preserving the original relief. Thus, among the differences mentioned by Rasetti (1967, pp. 47–48) to differentiate *C. chathamensis* and *C. acifer*, the only one we consider reliable is the absence/presence (respectively) of a transglabellar furrow. Fletcher & Rushton (2007) figured a Calodiscid pygidium, that they compared with *Cheledíscus* because it has the most similar morphology, but its generic identity remains extremely uncertain.

Taking into account the systematic significance that has been given to the occipital ring in the Eodiscida (e.g., Jell, 1997), it is important to discuss the fact that *Chelediscus garzoni* lacks the basal occipital lobes described for the type-species *C. acifer* (see Rushton 1966, pl. 2, fig. 17d) and also present in the Siberian species *C. carus* (see Repina 1972, pl. 31, figs. 3, 5). A simple transverse occipital ring is also present in *C. chathamensis* and in *Chelediscus* specimens documented by Axheimer et al. (2007, fig. 4l) from the Torneträsk Formation of Sweden. Apart from the occipital ring, both these two occurrences and *C. garzoni* share (individually or all together) a group of significant morphological characters with *C. acifer* and *C. carus* that, in our opinion, supports their congeneric relationship, namely a pitted cephalic border furrow, the lateral and posterolateral spines, the glabellar structure, the indifferentiable pygidium with a pair of pygidial pleural furrows located in the same position (compare Rushton, 1966, pl. 2, fig. 19a, Repina, 1972, pl. 31, figs. 2, 4; Axheimer et al., 2007, fig.4p). According to Jell (1997), *C. garzoni* shows a primitive structure of the occipital ring, being transverse and of more or less uniform depth and length. This feature, together with the absence of a glabellar transglabellar furrow and its stratigraphical slightly lower position to the type-species *C. acifer*, may justify these differences within the *Chelediscus* lineage.

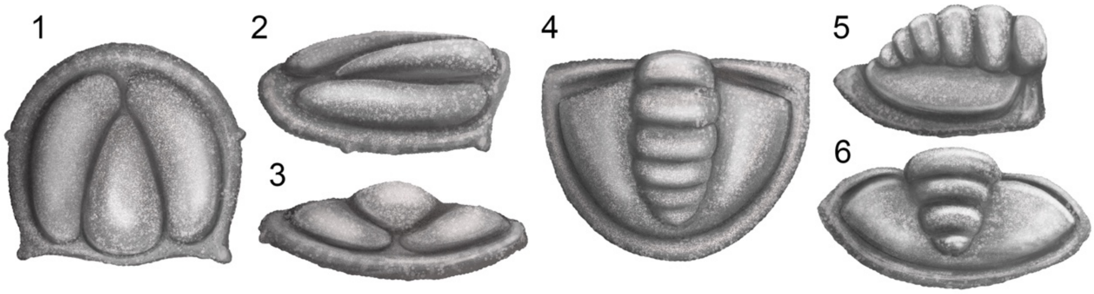

Figure 35: Schematic illustrations of the representative dorsal characters of *Chelediscus garzoni* Collantes, Pereira, Mayoral & Gozalo, 2023. **1**–**3**) Cephalon; **1**) dorsal view; **2**) lateral view; **3**) frontal view. **4**–**6**) Pygidium; **4**) dorsal view; **5**) lateral view; **6**) posterior view. Illustration by Nia Schamuells.

Regarding other reports of the genus, we do not think *Chelediscus* specimens documented by Axheimer et al. (2007, fig.4, k-p) from the Torneträsk Formation of Sweden belong to *C. acifer*. The glabella is not bilobed, and the occipital ring is simple, like in *C. garzoni*. However, the pygidium shows a well-incised pair of pleural furrows (like in *C. carus*), although, as previously stated, the absence of this furrow is not definite in *C. garzoni* due to the poor preservation of the pygidia. *C. acifer* also occurs in Brigus Formation, Newfoundland (Fletcher, 2003, pl. 1, figs. 25–26).

5.4.6. Discussion

Chelediscus garzoni adds to the known fauna of Western Gondwana and helps understanding evolution within *Chelediscus*. *C. garzoni* from Iberia and *C. carus* from Siberia are the oldest species of the genus, suggesting that the unlobed glabella is primitive for holaspides and the transglabellar furrow in later species (*C. acifer* and *C. chathamensis*) is derived. This circumstance could be inferred from the second transglabellar furrow in the meraspis of *C. acifer* (Rushton, 1966, text.-fig. 7), suggesting that younger species of *Chelediscus* may have evolved through neoteny.

Chelediscus shows a widespread geographical distribution and a restricted chronostratigraphical range, broadly coincident with the Cambrian Stage 4 (Fig. 36). In Iberia, *C. garzoni* in the *Serrodiscus* Zone, which correlates with the lowermost Cambrian Stage 4 (Sundberg et al., 2016). Regarding *C. acifer* type material, coming from Warwickshire (eastern Avalonia), it occurs in the middle *Protolenus* Zone of the so-called Comley Series, and conspecific specimens from Newfoundland (western Gondwana; Fletcher, 2003) are assigned to *the Orodes howleyi* Zone. In addition, the stratigraphical position of the Luobákti trilobite fauna from Sweden, where Axheimer et al. (2007) documented *Chelediscus*, indicates that it belongs to the top of the '*Ornamentaspis*' *linnarssoni* Zone (or *Chelediscus acifer* Zone according to the new division of interval-zones proposed by Ahlberg et al., 2016), uppermost Vergalian-Rausvian Stage in Baltica. On the other hand, *C. chathamensis* was erected from the *Leptochilodiscus punctulatus* beds, East Chatham, New York, which is assigned to the lower *Acimetopus bilobatus* Zone of the Taconic Allochthon. Finally, *C. carus* was reported from the Shumnoy Formation, in the Shukharikha river section, assigned to the upper *Triangulaspis annio–Bergeroniellus micmacciformis–Erbiella* Zone, corresponding to the lower Botomian Stage. All these occurrences of *Chelediscus* are broadly coincident with the lower to middle Cambrian Stage 4, being the species C. *carus* and *C. garzoni* slightly older than the remaining occurrences.

From a palaeobiogeographical view (Fig. 37), *Chelediscus* is distributed across the Laurentian Taconic Allochthon (New York), western Avalonia (Newfoundland), eastern Avalonia (Warwickshire, United Kingdom), Baltica (Sweden), Siberia and, for the first time, western margin of Gondwana (Iberia).

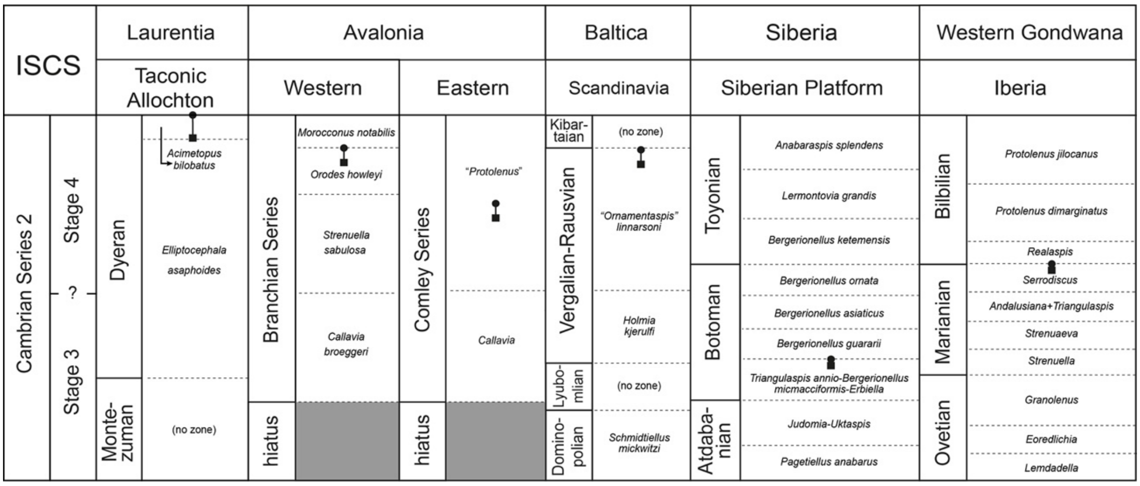

Figure 36: Correlation chart showing the stratigraphical occurrence of *Chelediscus*. Based on Sundberg et al. (2016), Zhang et al. (2017) and Geyer (2019).

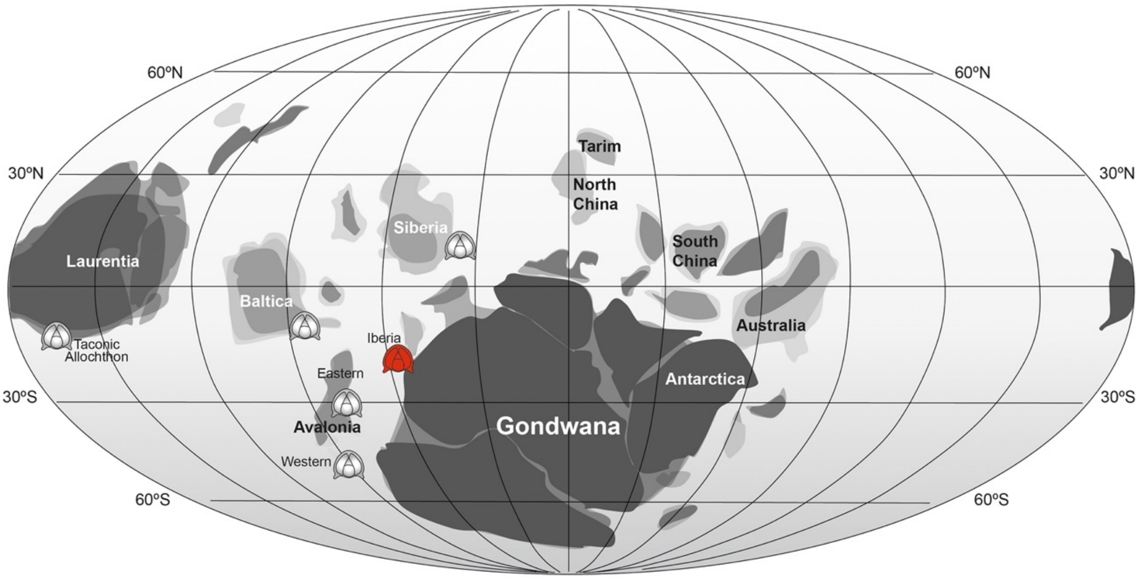

Figure 37: Distribution of *Chelediscus* plotted on the Cambrian palaeogeographical map, with red specimen indicating the new report from Western Gondwana. Modified from Scotese & McKerrow (1990) McKerrow et al. (1992), Dalziel (1997) and Malinky & Geyer (2019).

5.4.7. Conclusions

Chelediscus garzoni is reported from the upper Marianian 'Cumbres beds' formation of the Cumbres de San Bartolomé fossil site, representing the first occurrence of *Chelediscus* in Iberia and, therefore, the first report from Western Gondwana, where the genus was previously unknown. Although relatively rare, this genus is widely distributed worldwide, extending across the Cambrian rocks of Taconic Allochthon, Baltica, Siberia, western and eastern Avalonia, and western Gondwana margin. Its biostratigraphical distribution is restricted to the Cambrian Series 2, Stage 4, with the Siberian and the new Iberian representatives being the oldest occurrences of the genus. These species provide information on the morphology and evolutionary trends within *Chelediscus* lineage, suggesting an unlobed glabella as a primitive character state and the transglabellar furrow as derived.

5.5. Taxonomy, biostratigraphy and palaeobiogeography of *Strenuaeva* (Trilobita) from the Marianian (Cambrian Series 2) of Iberia (Collantes et al., 2024 in Geobios, 82)

5.5.1. Abstract

Problems surrounding the identification and systematics of taxa belonging to the trilobite family Ellipsocephalidae have been discussed for several decades. The ellipsocephalid genus *Strenuaeva* is revised herein on the basis of material from Spain, including the type material of the identified species together with newly collected specimens from the Ossa-Morena Zone and the Iberian Chains. Two species are recognized as valid for these regions, *S. sampelayoi* and *S. incondita*. The species '*S. melendezi*' and '*Ellipsostrenua alanisiana*' from Spain, as well as '*S. marocana*' from Morocco, are here considered junior synonyms of *S. sampelayoi*. Previous assignment of the Spanish species to *Issafeniella* is here rejected. The abundant available material of *S. sampelayoi* made it possible to evaluate the taphonomical role in the preservation of some characters and to recognize intraspecic variability similar to that described for *S. inflata* from Baltica, reinforcing its assignment to *Strenuaeva*. Biostratigraphically, *Strenuaeva* ranges from uppermost Cambrian Stage 3 to uppermost Cambrian Stage 4. In Iberia, it is restricted to the middle Marianian in the Ossa-Morena Zone, whereas it is known from the lowermost middle Marianian to the lowermost upper Marianian in the Iberian Chains. *Strenuaeva* is known from Baltica (Scandinavia and Holy Cross Mountains, Poland), Iberia (Spain), Morocco and, possibly, western Avalonia (Newfoundland), hence being a characteristic genus of the Acadobaltic faunal Province.

5.5.2. Introduction

Ellipsocephaloidea is one of the problematic superfamilies within the paraphyletic Redlichiina (Paterson & Edgecombe, 2006; Laibl et al., 2015; Paterson et al., 2019), with Fortey (1990) suggesting that some ellipsocephaloids should be placed in Ptychopariina. On the other hand, Adrain (2011) has been drawing attention to the role of Ptychopariina in trilobite phylogeny, being an operational taxon, whose phylogenetic significance is doubtful. The lower-level systematics within Ellipsocephaloidea are not clearer than its higher level relationships. Within Ellipsocephalidae, there have been many proposals for subfamiliar and generic concepts (e.g., Hupé, 1953; Sdzuy, 1961; Ahlberg & Bergström, 1978; Geyer, 1990; Żylińska & Masiak, 2007; Cederström et al., 2022), but again, they have served as operational "drawers" for the authors, but in fact their phylogenetic significance and reliability have never been addressed. One of the main systematic recognition problems for Ellipsocephalidae highlighted by Geyer (1990) is the intraspecific variability of most taxa, but it is possible that the variability to a great extent is due to the taphonomy. Perhaps this is even our greatest limitation: when dealing with a group consisting of very few diagnostic characters, we have almost none of them left in many collections (e.g., Spain, Morocco, Poland; Sdzuy, 1961; Geyer, 1990; Żylińska & Masiak, 2007) due to poor preservation.

Ellipsocephalids from Spain have been known since the pioneer works of Casiano de Prado (1855; also Verneuil & Barrande, 1855), but only since the 1940s has systematic study of this group been undertaken, beginning with the contribution of Richter & Richter (1940). Since then, several genera and species have been described, mostly from Cambrian Series 2, but a few also from the lowermost Drumian, and the family's biostratigraphical and correlation potential has also been highlighted (e.g., Hupé, 1953a; Richter & Richter, 1941; Sdzuy, 1958, 1961, 1962, 1971a, b; Lotze, 1961; Gil-Cid, 1972a, 1975; Liñán, 1978; Liñán & Gozalo, 1986; Gil-Cid & Jago, 1989; Gil-Cid & Bernal Barreiro, 1991a; Liñán et al., 1995b, 2003, 2008b; Dies et al., 1999, 2001, 2013; Álvaro, 2007; Gozalo et al., 2008; Gil-Cid et al., 2009; Álvaro et al., 2019; Sepúlveda et al., 2022).

This work follows on from another set of papers which aim to make a broad and integrated review of Spanish lower Cambrian trilobites, in order to create reliable and updated information that can be used for biostratigraphy and palaeobiogeography. The genus *Strenuaeva* is described herein and its potential for regional and intercontinental correlation is discussed.

5.5.3. Geological setting

5.5.3.1. Ossa-Morena Zone

The Ossa-Morena Zone (OMZ) belongs to the southern branch of the Variscan Orogen of the Iberian Peninsula. It comprises rocks ranging from the uppermost Proterozoic to the Carboniferous, with a general structure of large, recumbent folds with SW vergence, and ductile thrust-faults with the main movement towards SW (Azor, 2004). Cambrian rocks of the OMZ outcrop in distinct belts or 'blocks' with a significant 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). The specimens of *Strenuaeva* studied here come from several localities of the Viar-Benalija Block (belonging to the Sierra Norte UNESCO Geopark, Seville), Alconera Block (Alconera municipality, Badajoz Province) and Herrerías Block (Sierra del Bujo, Huelva) (Fig. 38.1, 38.2).

Specimens of *Strenuaeva sampelayoi* from the Viar-Benalija Block were collected at different levels along the road between Cazalla de la Sierra and Alanís, although most of the material comes from two main localities at 38º 00' 31.70" N 5º 45' 15.55" W (AL05) and 37º 59' 56.72" N 5º 46' 00.34" W (AL08). The material occurs in greenish to greyish shales with carbonate nodules, assigned to the intermediate member of the 'Alanís beds' (~1400 m), dated as middle Marianian (Liñán et al., 2004). *Strenuaeva sampelayoi* frequently occurs together with *Saukianda andalusiae* Richter & Richter, 1940, although the complete trilobite assemblage from that unit is composed of *Alanisia guillermoi* (Richter & Richter, 1940), *Perrector perrectus* Richter & Richter, 1940, *Eops eo* Richter & Richter, 1940, *Gigantopygus* cf. *bondoni* Hupé, 1953a and *Delgadella souzai* (Delgado, 1904) (Fig. 38.3).

The material of *S. sampelayoi* from the Alconera Block comes from La Hoya Member (~400 m), consisting of shales with calcareous nodules, nodular calcilutites, and limestones in the upper part of the Alconera Formation (~900 m; Liñán & Perejón, 1981; Liñán et al., 2004). Specimens were collected from two main localities belonging to the sections 1 and 3 (*sensu* Liñán & Perejón, 1981), both within the Alconera municipality, located at 38º 22' 49.56" N 6º 29' 02.73" W and 38º 23' 50.60" N 6º 28' 55.20" W, respectively. *S. sampelayoi* appears frequently together with *Delgadella souzai*, *Saukianda andalusiae*, and undetermined ellipsocephalid trilobites, in addition to brachiopods and hyoliths (Fig. 38.4).

A single specimen was collected from Sierra del Bujo, Huelva, belonging to the Herrerías Block. The sample is from purple shales with spilitic intercalations, named as 'Herrerías shale' (200–500m). These levels are dated as middle Marianian based on the presence of *Delgadella souzai, Rinconia schneideri* (Richter & Richter, 1941), *Gigantopygus* cf. *bondoni*, *Hicksia elvensis* Delgado, 1904, *Protaldonaia morenica* Sdzuy, 1961, *Callavia choffati* (Delgado, 1904), *Atops calanus* Richter & Richter, 1941, *Calodiscus ibericus* Sdzuy, 1962, and *Triangulaspis fusca* Sdzuy, 1962. For stratigraphical details of this fossil assemblage, see Collantes et al. (2021b).

5.5.3.2. Iberian Chains

The Iberian Chains comprise two NW-SE parallel ranges of Palaeozoic rocks, separated by the Tertiary Calatayud-Teruel Basin, that have suffered major tectonic deformation during the Hercynian and Alpine orogenies. It constitutes the southernmost prolongation of both the Cantabrian and West Asturian-Leonese zones (Gozalo & Liñán, 1988) in the Eastern and Western Iberian Chain respectively, where three tectonostratigraphical units (Badules, Mesones and Herrera Units) have been defined (Lotze, 1929; Carls, 1983; Gozalo & Liñán, 1988). The studied area includes four sections from the Comarca del Aranda, Zaragoza Province, where *Strenuaeva incondita* has been found: the Jarque (J1 and J2) sections are located in the Badules Unit, whereas the Mesones de Isuela (M9) and Minas Tierga (MT1) sections are located within the Mesones Unit (Fig. 38.5). In addition, *Strenuaeva incondita* has been described from four other localities, all of them located in the Badules Unit: Huérmeda Fp. 1 (Jalón valley, Zaragoza, Lotze, 1961; Sdzuy, 1961), Bo1 section (Borobia, Soria; Gámez-Vintaned et al., 1991; Palacios & Mocylowska, 1998), At12 and At15 (Ateca, Zaragoza; Álvaro, 1991; Álvaro et al., 1995) and Purujosa (PU) area (Zaragoza; Zamora et al., 2019) (Fig. 38.6).

Specimens of *Strenuaeva incondita* Sdzuy, 1961 were collected from four studied sections comprising two main stratigraphical units: the Ribota and Huérmeda formations (Fig. 38.6). The Ribota Formation (84–102 m) is a carbonate unit characterised by bedded to massive dolostone with lutite and marl intercalations. The Huérmeda Formation (80–150m) is a siliciclastic unit mainly composed of lutites and siltstones with minor dolostones intercalations. The trilobite association of the Ribota Formation consists of *S. incondita*, *Lusatiops ribotanus* Richter & Richter, 1948, *Kingaspis* (*Kingaspidoides*) *velata* Sdzuy, 1961, *Onaraspis garciae* Álvaro et al., 2019 and *Termierella* sp. (Sepúlveda et al., 2021b, 2022). The trilobite assemblage in the base of Huérmeda Formation consists of *S. incondita*, *Lusatiops ribotanus*, *Kingaspis* (*Kingaspidoides*) *velata*, *Onaraspis garciae*, *Redlichia* (*Redlichia*) *isuelaensis* Álvaro et al., 2019, *Luciaspis matiasi* Álvaro et al., 2019, *Paulaspis tiergaensis* Álvaro et al., 2019, *Andalusiana* cf. *cornuta* Sdzuy, 1961, *Acanthomicmacca* (*A.*) aff. *coloi* Hupé, 1953a, *Triangulaspis* sp. and *Hebediscus*? sp. (Liñán et al., 1993, 1996, 2003, 2008b; Álvaro et al. 2019; Sepúlveda et al., 2021b, 2022). For a precise stratigraphical position of the described fossil assemblages, see Sepúlveda et al. (2022).

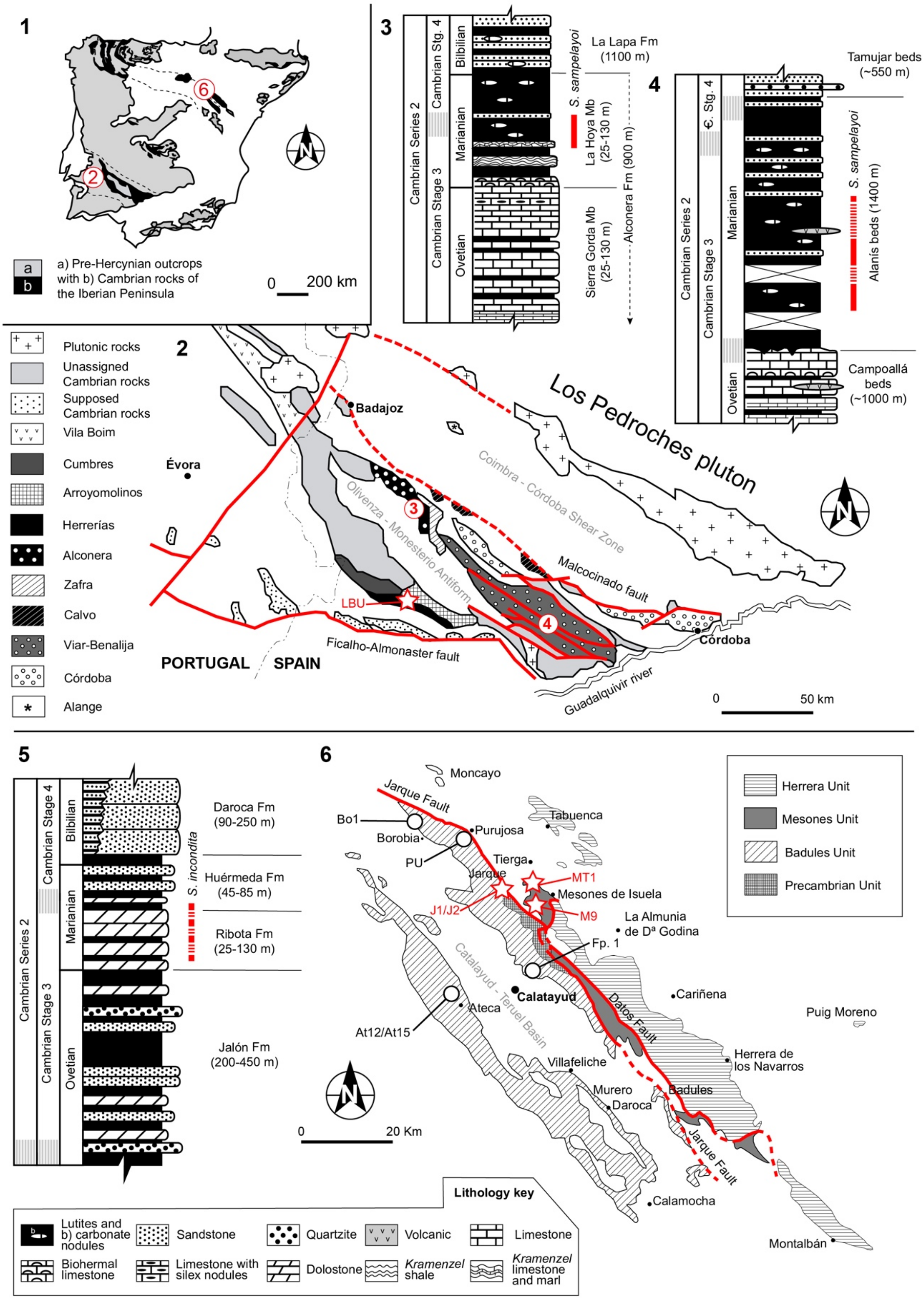

Figure 38: **1**) Pre-Hercynian outcrops in the Iberian Peninsula. **2**) geological setting of fossil sites in the Cambrian sectors (fault-bounded blocks) of the Ossa-Morena Zone, indicating the position of the studied fossil sections, modified from Liñán & Quesada (1990). **3**) Stratigraphical column of the Alconera Block, with stratigraphical range of *S. sampelayoi* (modified from Liñán & Perejón, 1981). **4**) Stratigraphical column of the Viar-Benalija Block, with stratigraphical range of *S. sampelayoi*. **5**) Composite stratigraphical column for the Cambrian Series 2 interval in the Iberian Chains, modified from Liñán et al. (2008b). **6**) Location of the studied sections in the Iberian Chains, modified from Gozalo & Liñán (1988).

5.5.4. Materials and methods

The available specimens are preserved as internal and external moulds and consist mainly of isolated cranidia, in addition to several complete or almost complete exoskeletons. The specimens from Alanís are preserved in shales with carbonate nodules, while those from Alconera are preserved in grey marls and purple shales. Regarding the specimens from Iberian Chains, material from the Ribota Formation was collected from grey marly shales, while specimens from the Huérmeda Formation are preserved in shale.

All specimens were prepared using a pneumatic hammer and then coated with ammonium chloride and photographed using a Canon EOS 77D coupled with a macro lens Canon 100mm f/2.8L.

5.5.5. Systematic palaeontology

Order Redlichiida Richter, 1932

Superfamily Ellipsocephaloidea Matthew, 1887

Family Ellipsocephalidae Matthew, 1887

Remarks: Several subfamilies have been established by previous authors (e.g., Hupé, 1953; Henningsmoen, 1959; Geyer, 1990 and, more recently, Cederström et al., 2022), but the validity of some is doubtful, reflecting a combination of characters that frequently are randomly mixed in other subfamilies. These have been useful as operating units, but their reliability as natural entities has never been addressed. The most comprehensive effort towards a subfamiliar classification was made by Cederström et al. (2022), who based their phylogenetic scheme on a set of characters significant to the group and for which they coded several types. In our opinion, the characters are indeed well chosen, being the ones which vary independently of taphonomy within the group. But if some subfamilies, like Ellipsocephalinae, seem to include a number of genera that share significant characters (e.g., "*Ellipsocephalus*-type" shape of glabella and "kingaspidoidid type" pattern of lateral glabellar furrows *sensu* Cederström et al., 2022), others are based on weak criteria. This is the case for Strenuaevinae, erected to encompass *Strenuaeva* and *Epichalnipsus* Geyer et al., 2004 but whose diagnoses overlap with that of

Antatlasiinae Hupé, 1953a. In defining Strenuaevinae, Cederström et al. (2022) considered that *Strenuaeva* differs from all other genera of Ellipsocephalidae in having a short and distinctively convex glabella, raised fixigenae and the tendency to develop an angulation of the anterior cephalic margin. However, both *Antatlasia* and also *Berabichia* are represented by species with similar glabellae (e.g., *Antatlasia tadakoustensis* Geyer, 1990, pl. 1, figs. 11-14 and *Berabichia vertumnia* Geyer, 1990), and a very similar anterior angulation is found in *Berabichia* species (compare Cederström et al., 2011, text-fig. 8 and Cederström et al., 2022, fig. 19 with *Berabichia vertumnia* Geyer, 1990, pl. 7 and *B. inopinata* Geyer, 1990, pl. 8, figs. 13-16). They also considered that *Strenuaeva* and *Epichalnipsus* share "apomorphic characters" (p. 38), but the phylogenetic value of such characters was not properly addressed. One of those characters represents a different grade of a hypothetical trend (e.g., "slightly inflated fixigenae") and is entirely comparable in Antatlasiinae and Strenuaevaninae genera (e.g., *Issafeniella* and *Strenuaeva*). The other character, the plectrum in front of the glabella, is faintly present in some Antatlasiinae (e.g., *Issafeniella turgida* Geyer, 1990, pl. 12, figs. 1, 2; *Issafeniella modesta* Geyer, 1990, pl. 12, fig. 7; *Antatlasia guttapluviae* Geyer, 1990, pl. 3, fig. 13) and it is as absent in the type species *Strenuaeva primaeva* as in Antatlasiinae (Cederström et al., 2022, fig. 19), absent in other *Strenuaeva* species (e.g., *S. inflata* in Cederström et al., 2011) and in the other genus included in the Strenuaevaninae (see *Epichalnipsus* in Cederström et al., 2022). Finally, *Epichalnipsus rotundatus* (Kiær, 1917) do not bear the putative apomorphies noted by Cederström et al. (2022) and lacks the distinctive convexity of the fixigenae and the preglabellar area. Thus, it is not clear if Strenuaevaninae is a natural group, and it is also very unlikely that *Strenuaeva* is closer to *Epichalnipsus* than, for example, to *Issafeniella*.

Ellipsocephalidae are in need of phylogenetic analysis and for the reasons given above, we prefer to abandon the subfamily division proposed by Cederström et al. (2022).

Genus ***Strenuaeva*** Richter & Richter, 1940

Type species: *Arionellus primaevus* Brøgger, 1878 (p. 58), *Holmia kjerulfi* Zone, middle Ringstrand Formation, Tømten Member, at Tømten, Mjøsa area, SE Norway, by original designation (Richter & Richter, 1940, p. 40).

Included species: *S. primaeva* (Brøgger, 1878), *S. sampelayoi* Richter & Richter, 1940, *S. orlowinensis* Samsonowicz, 1959, *S. incondita* Sdzuy, 1961, *S. inflata* Ahlberg & Bergström, 1978, and *S. nefanda* Geyer, 1990.

Diagnosis: Emended from Cedeström et al. (2022): Moderately raised glabella with subparallel sides to slightly tapering forward; frontal lobe narrow, rounded anteriorly; glabellar furrows indistinct to moderately incised, transverse, about 25% of the glabellar width; fixigenae gently convex (tr. and exsag.); palpebral lobe separated from fixigena by well impressed palpebral furrow; preglabellar field distinctly convex to conspicuously swollen, subtriangular to subtrapezoidal in outline, posterolaterally limited by transverse to abaxially oblique furrows; anterior margin of cephalon rounded to angulate.

Remarks: Richter & Richter (1940) erected *Strenuaeva* as a subgenus of *Strenuella* and included several new ellipsocephalid trilobite species from middle Marianian rocks of Alanís: *Strenuella* (*Strenuaeva*) *sampelayoi*, *S*. (*S*) *insecta* Richter & Richter, 1940 (=*S. sampelayoi*) (Fig. 39), *Camaraspis guillermoi* Richter & Richter, 1940 (=*Alanisia guillermoi*) and *Camaraspis onyx* Richter & Richter, 1940 (=*Alanisia guillermoi*). Subsequently, Richter & Richter (1941) raised *Strenuaeva* to genus level and also included *Strenuaeva* cf. *annio* and *Strenuaeva* cf. *vigilans* from the middle Marianian of northern Huelva. These species were later transferred to *Triangulaspis* Lermontova, 1940 by Sdzuy (1962). Hupé (1953) erected *Alanisia* Hupé, 1953a and *Hindermeyeria* Hupé, 1953a, both closely related to *Strenuaeva*, and assigned some species described by Richter & Richter (1940) to these new genera, namely *Alanisia guillermoi* (Richter & Richter, 1940) and *Hindermeyeria insecta* (Richter & Richter, 1940). Henningsmoen (1958) showed that most of the differences between *S. sampelayoi* and *H. insecta* could have been caused by deformation, and the anterior furrow of *H. insecta* may correspond to a juvenile feature of *S. sampelayoi*, suggesting that *Hindermeyeria* is a subjective junior synonym of *Strenuaeva* (see Sdzuy, 1962). Although the similarities between *Alanisia* and *Strenuaeva* has been previously emphasised (e.g., Henningsmoen, 1958), our newly collected material reinforces the differences between these genera. The cephalic anterior border and the occipital spine of the former (see also Jell, 1990) has never been observed in the abundant material of *Strenuaeva sampelayoi*.

The genus *Alueva* Sdzuy, 1961, from the uppermost lower Cambrian (upper Cambrian Stage 4, see Gozalo et al., 2013) of Murero site (Iberian Chains, Zaragoza Province), shares several characters with *Alanisia* and *Strenuaeva*. Liñán & Gozalo (1986) transferred to *Alueva* the species *Alanisia hastata* Sdzuy, 1958 and *Strenuaeva sampelayoi moratrix* Sdzuy, 1958, both of them occurring in the uppermost Cambrian

Stage 4 and the lowermost Miaolingian (Gozalo et al., 2007, 2013), and suggested that the similarities between *Alueva*, *Strenuaeva* and *Alanisia* may reflect convergent evolution (Dies et al., 2013).

Strenuaeva nefanda Geyer, 1990 from Morocco resembles *Alueva* in the morphology and curvature of the preglabellar area, the configuration of the glabella and the pattern of the lateral glabellar furrows, and the morphology of the occipital lobe and palpebral lobes (see *Alueva moratrix* in Dies et al., 2013, pl. 3, figs. A–J). In addition, *S*. *nefanda* from Morocco is stratigraphically younger than the other *Strenuaeva* occurrences, being closer to uppermost Cambrian Stage 4. Regarding the identification of *S. nefanda* in Newfoundland (Fletcher, 2003, pl. 3, figs. 15–17; 2006), it should be noted that, although some morphological features may fit with those of *Strenuaeva* (e.g., the morphology of the preglabellar area and the glabellar configuration) Newfoundland specimens lack the prominent ocular ridge, bear more developed palpebral lobes and a long, stout occipital spine, which clearly differs from *S*. *nefanda* from Morocco. These specimens from Newfoundland are here identified as *S.* aff. *nefanda.*

Geyer (1990) erected the genus *Issafeniella*, defining two new species, *I. turgida* Geyer, 1990 and *I. modesta* Geyer, 1990, and transferred several species previously assigned to *Strenuaeva* to the new genus, including *S*. *sampelayoi*, *S*. *melendezi* Gil Cid, 1972a, *S*. *orlowinensis* Samsonowicz, 1959, *S*. *trifida* Orlowski, 1985b and, hesitantly, *S*. *marocana* Hupé, 1953a. Subsequently, Geyer (2016) also included *S. incondita* Sdzuy, 1961 in *Issafeniella*. According to Geyer (1990) and Cederström et al. (2022), *Issafeniella* differs from *Strenuaeva* in lacking a plectrum-like structure connecting the anterior margin of the frontal glabellar lobe and the preglabellar field, bearing a semicircular anterior margin without a trend to form an angulation, a wider (tr.) glabella with a broader frontal lobe (not slightly pointed), deeper glabellar furrows and an occipital spine. The plectrum-like structure and the cephalic anterior margin are discussed above (see remarks on Family Ellipsocephalidae), and it has been shown that there are no significant differences in these characters between species included in *Strenuaeva* and *Issafeniella*. In relation to the depth of the glabellar furrows, it is important to state that they are highly dependent on the mode of preservation (mineralization or mould), as suggested by Cederström et al.'s (2022) observations in external and internal moulds and will always be a very subjective and unquantifiable character (e.g., "a little more, a little less"). Differences are observed in conspecific specimens coming from the same level (Figs. 3-4). As for glabellar morphology, *Strenuaeva sampelayoi*, assigned by Geyer (1990) to *Issafeniella*, has the glabella slightly pointed anteriorly, a character he considers to be typical of *Strenuaeva*. The suggestion that *Strenuaeva* and *Issafeniella* cephala are prime examples of convergent evolution (Geyer, 1990) is risky and highly unlikely, not only given the distribution of the two genera (see Palaeobiogeography section below), but also because of the sharing of very specific characters (see remarks of the species *Strenuaeva sampelayoi*). For nomenclatural stability, we treat them together with respect to palaeogeographical analysis because we believe they may be closely related.

In our opinion, *Issafeniella orlowinensis* (Samsonowicz, 1959) from the Holy Cross Mountains (Poland) should be maintained to *Strenuaeva*, in accordance with the original classification of Samsonowicz (1959). Based on the diagnostic characters presented by Geyer (1990) and Cederström et al. (2022) for *Strenuaeva* and *Issafeniella*, the Polish species is much closer to the former (e.g., almost obsolete glabellar furrows, anterior margin of preglabellar area slightly angulated, absence of an occipital spine; Żylińska & Masiak, 2007, fig. 9g, j). *I. trifida* (Orlowski, 1985b), also from the Holy Cross Mountains (Poland), is too poorly known in relevant characters (cephala destroyed medially) for a generic assignment.

Strenuaeva? kiaeri Samsonowicz, 1959 from the Holy Cross Mountains, Poland was considered to possibly represent a distorted specimen of '*Issafeniella' orlowinensis* by Żylińska & Masiak (2007) and Weidner et al. (2015).

Cederström et al. (2022) also transferred *Strenuaeva*? *kullingi* Ahlberg & Bergström, 1978 to *Epichalnipsus* and *Strenuaeva spinosa* Ahlberg & Bergström, 1978 to *Ellipsostrenua*.

Strenuaeva sampelayoi Richter & Richter, 1940

Figures 39–44

1940 *Strenuella* (*Strenuaeva*) *sampelayoi* n. sp. – Richter & Richter, p. 41, pl. 3, figs. 51–53, pl. 5, fig. e.

1940 *Strenuella* (*Strenuaeva*) *insecta* n. sp. – Richter & Richter, p. 42, pl. 3, fig. 58, 56–57?, 59–63? pl. 5, fig. f.

1953a *Strenuaeva sampelayoi* – Hupé, p. 113, 114, 206, 209, 210, fig. 14.1.

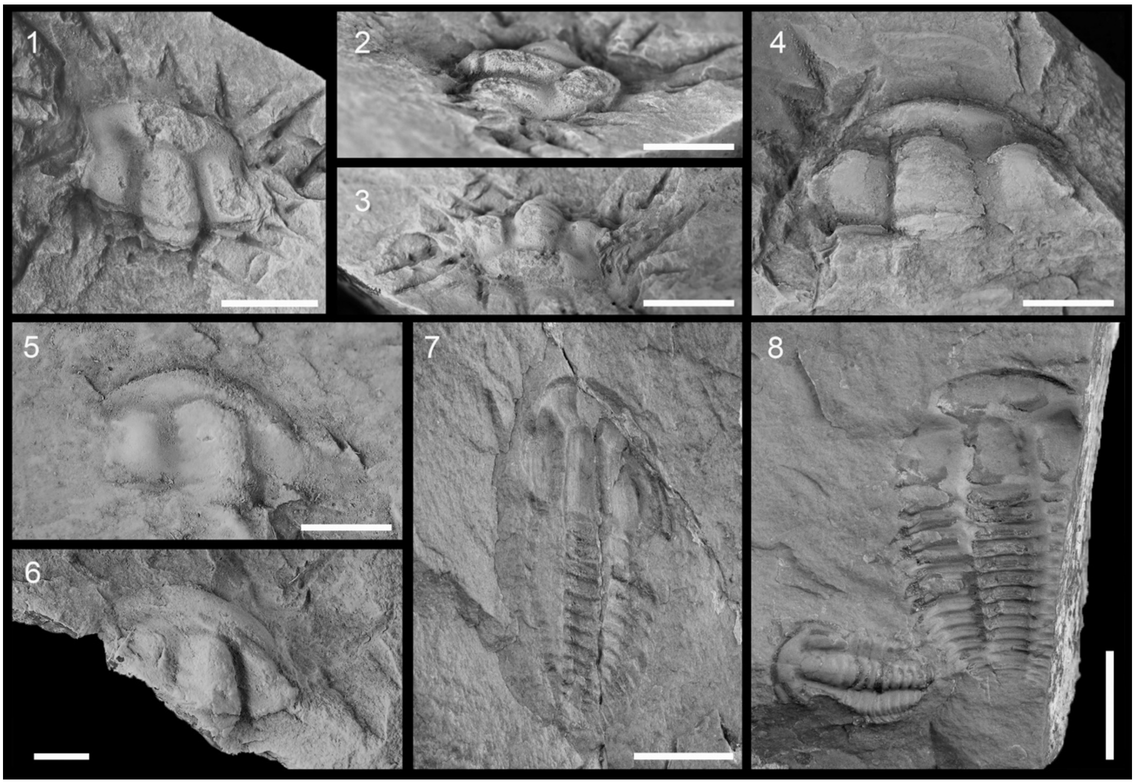

Figure 39: **1**–**4**) *Strenuaeva sampelayoi* Richter & Richter, 1940, 'Alanís beds', Alanís, Spain. **1**–**3**) SMF X 1141a (holotype). **1**) dorsal view; **2**) lateral view; **3**) anterior view. **4**). SMF X 1141f. **5**–**6**). '*Hindermeyeria insecta*' (=*S. sampelayoi*) Richter & Richter, 1940, 'Alanís beds', Alanís, Spain. **5**) SMF X 1142q. **6**) SMF X 1142g. **7**–**8**) '*Strenuaeva melendezi*' Gil Cid, 1972a (=*S. sampelayoi*), 'Alanís beds', Alanís, Spain. **7**) DPM–A231–817–H2 (holotype). **8**) DPM–A232–817–H546b (left) and DPM–A232–817–H546a (right). Scale bar = 5 mm (**1**–**4**, **5**, **8**), 2 mm (**E**, **F**).

1953a *Hindermeyeria insecta* – Hupé, p. 209, 233, 264, figs. 56.21, 63.c.

1953a *Strenuaeva marocana* nov. spec. – Hupé, pl. 7, fig. 12, pl. 11, fig. 25.

1958 *Strenuaeva sampelayoi* – Henningsmoen, p. 265, pl. 38, figs. 4–8.

1959 *Hindermeyeria insecta* – Henningsmoen, p. O207, fig. 149.8.

1961 *Ellipsostrenua alanisiana* n. sp. – Sdzuy, p. 297, pl. 14, figs. 8–15.

1962 *Strenuaeva sampelayoi sampelayoi* – Sdzuy, p. 205, pl. 22, figs. 9?, 10.

1962 *Strenuaeva sampelayoi* – Mingarro Martín, p. 523, fig. 30.

1972 *Strenuaeva melendezi* sp. nov. – Gil Cid, p. 463, pl. 1, figs. 1–3.

1972 *Strenuaeva sampelayoi* – Gil Cid, p. 463, pl. 1, figs. 4–6.

1975 *Strenuaeva sampelayoi* – Gil Cid, pl. 1, figs. 5–6, 8, 10, pl. 2, figs. 8–9.

1975 *Strenuaeva melendezi* – Gil Cid, pl. 1, figs, 7, 9.

2009 *Strenuaeva sampelayoi* – Gil Cid et al., pl. 1, A-C, G–J, pl. 2, A–C, N, pl. 3, B, pl. 4, I–L.

Holotype: Cranidium (SMF X 1141a) from the ‘Alanís beds’, Alanís, Seville, Spain.

Emended diagnosis: Preglabellar area subtrapezoidal, inflated, about 27–30% of the total cephalic length (including occipital lobe), and commonly showing a pair of bulbs separated by a shallower channel, sometimes defined as a faint sagittal furrow; anterior margin of preglabellar area rounded to slightly angulate. Deep w-shaped preglabellar furrow to contour preglabellar bulbs (if present), or gently convex forward medially, continuing into equally deep abaxially oblique furrows, 22 to 26º to sagittal line. Glabella narrowing (tr.) anteriorly, about 70-75% cephalic sagittal length (including occipital lobe), and 30–35 % of cranidial width (across L1). Occipital lobe smooth.

Description: Cranidium subpentagonal, with higher relief of the anterior border, palpebral area, and glabella. Cranidia range from 1.8–19 mm in length and 1.3–15 mm in width. Anterior margin rounded to subtly pointed medially. Preglabellar area subtrapezoidal, inflated, occupying approx. 27–30% of the total cranidial length sagittally (including occipital lobe), and commonly showing a pair of bulbs separated by a shallower channel, sometimes defined as a faint sagittal median furrow. Preglabellar furrow well incised, w-shaped to contour preglabellar bulbs (if present), or gently convex forward medially, and continued into equally deep abaxially oblique furrows, 22 to 26º to sagittal line. Glabellar outline subrectangular to subconical, depending on the deformation/preservation, convex, showing higher relief than the palpebral area, tapered forward and widened posteriorly. Deep, wide (tr.) axial furrows, parallel-sided to slightly convergent depending on the preservation, and connected to the preglabellar furrow and its lateral oblique extensions. Axial furrows are as incised as the preglabellar furrow and the oblique furrows. Glabella about 70-75% cephalic sagittal length (including occipital lobe), and about 30–35 % of the cranidial width (across L1), sloping gently forward. Three pairs of shallow glabellar furrows (a very faint fourth pair rarely observable), shallowing forward from S1 to S3 short (tr.), equidistant, directed backwards adaxially, S1 slightly longer; S1 and S2 slightly more oblique, S3 almost transverse. Glabellar lobes are poorly inflated and subequal in length (sag.), but with L1 slightly longer (exag.) than the others. Deep, wide occipital furrow, straight to slightly convex backwards medially. Occipital lobe is semicircular, widened medially (sag.), convex backwards, inflated, about 15–18% of the cephalic length (sag.) and 38–40% of the cranidial width. Fixigena subtrapezoidal, inflated, with lower relief than the glabella, occupying 40–45% of the total

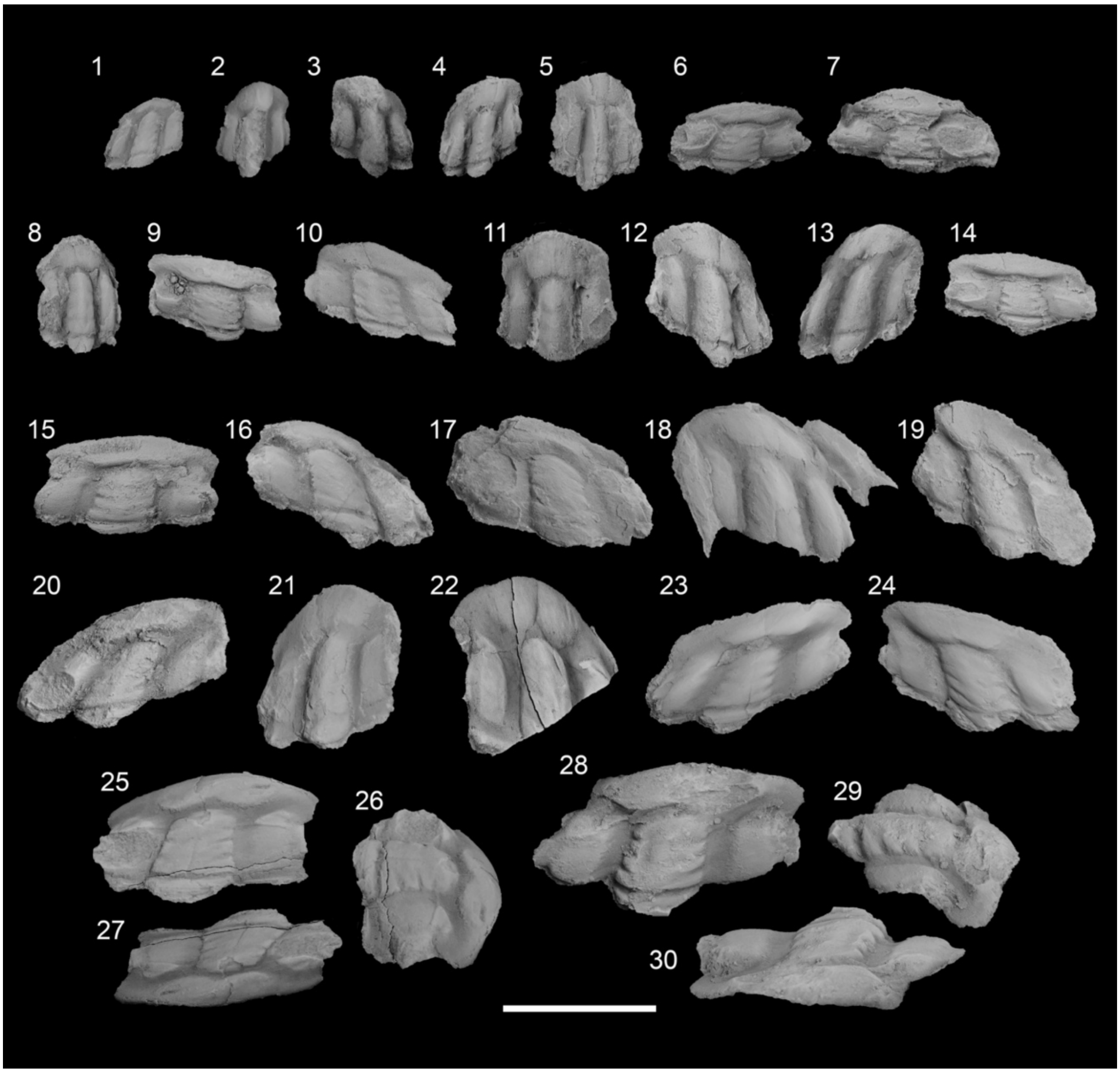

Figure 40: *Strenuaeva sampelayoi* Richter & Richter, 1940, 'Alanís beds', middle Marianian (Cambrian Stage 3), Alanís, Spain. **1**) UHU–AL05–01. **2**) UHU–AL05–40. **3**) UHU–AL05–04. **4**) UHU–AL05–02. **5**) UHU–AL05–03. **6**) UHU–AL05–43. **7**) UHU–AL05–05. **8**) UHU–AL05–06. **9**) UHU–AL05–16. **10**) UHU–AL05–22. **11**) UHU–AL05–07. **12**) UHU–AL05–12. **13**) UHU–AL05–17. **14**) UHU–AL05–18. **15**) UHU–AL05–20. **16**) UHU–AL05–24. **17**) UHU–AL05–25. **18**) UHU–AL05–26. **19**). UHU–AL05–29. **20**). UHU–AL05–28. **21**) UHU–AL05–31. **22**) UHU–AL05–56. **23**) UHU–AL05–32. **24**) UHU–AL05–33. **25**–**26**) UHU–AL05–34; **25**) dorsal view; **26**) lateral view. **27**) anterior view. **28**–**30**) UHU–AL05–36; **28**) dorsal view; **29**) lateral view; **30**) anterior view. Scale bar = 10 mm.

cephalic length (sag.) and 30–35% of the cranidial width (across L1). Eye ridge strongly curved, extending around the outer palpebral area, starting opposite the frontal glabellar lobe (without crossing the axial furrows) to meet the palpebral lobe, getting progressively wider (tr.) backwards. Wide (tr.), pronounced palpebral lobe, same relief as the palpebral area, occupying 5–8% of the cranidial width (across S2), separated of the palpebral area by a deep and wide (tr.) furrow. Palpebral lobe slightly convex outwards. Anterior branch of the facial suture slightly divergent forward, about 15–25° to the sagittal axis. Posterior branch of the facial suture short, slightly divergent backwards around 18–20° to the sagittal line. Posterior border furrow is wide (sag.) and deep, progressively widened abaxially. Posterior border convex, wide (exsag.), with lower relief than the palpebral area and the occipital ring, subtly arched backwards, and, being slightly widened (exsag.) medially, occupying about 8–10% of the total cephalic length (sag.).

Librigena is slightly domed and smooth, approx. 15% of the total cephalic width (at S2), showing a flat, relatively wide (tr.) lateral border (4–6% of the total cephalic width across S2), continuous with posterior border, giving rise to a relatively wide genal angle area. Genal spines variable in length, generally short, straight to slightly curved, and directed outwards. Slight variations are observed in its insertion: in several specimens the insertion is at the posterolateral border, while in others the insertion is at the genal angle. Posterior margin of the librigena subtly convex backwards.

Thorax composed of 14 thoracic segments. Rhachis progressively narrowing (tr.) backwards, from 40% of the total thoracic width to 30%. Narrow (sag.), convex axial rings, with deep axial ring furrows. The pleare are not extended beyond the abaxial end of the genal spine. The first three pleurae are subtly widened (tr.), then progressively narrowing (tr.) posteriorly. Pleurae horizontal adaxially, strongly bent down in its abaxial third (fulcrum), ending in a short, robust pleural spine directed backwards. Deep, wide pleural furrow, extending about 60-70% of total pleural width (tr.). Subtle curvature located approximate at the last third of the pleural width.

Pygidium with oval outline. Length (sag.) represents 40% of width (tr.). Pygidial length (sag.) about 8% of the total body length. Axis semicircular, about 60% of the max. pygidial width (tr.); three subtle, shallow transverse furrows. Very faint pygidial border, defined by shallow lateral and posterior furrows, slightly convex, depressed with respect to the axial area, widened abaxially and reaching about 10% of the max. pygidial width.

Material: All studied specimens are housed in the palaeontological collections of the Departamento de Ciencias de la Tierra (Laboratorio de Tectónica y Paleontología) of the Facultad de Ciencias Experimentales, University of Huelva, Spain (UHU), the Museo de Ciencias Naturales of the University of Zaragoza, Spain (MPZ), the Área de Paleontología of the Complutense University of Madrid (DPM), and the Senckenberg Museum, Frankfurt, Germany (SMF). Alanís, Sevilla: 147 isolated cranidia (UHU-AL05-01 to UHU-AL05-59; UHU-AL08-01 to UHU-AL08-80, SMF X 1141a to SMF X 1141h), 65 articulated specimens (UHU-AL05-100 to UHU-AL05-112; UHU-AL08-100 to UHU-AL08-147, DPM-A231-817-H3, DPM-A232-817-H546a, DPM-A232-817-H546b). Alconera, Badajoz: 18 isolated cranidia (UHU-ALC3-01 to UHU-ALC3-04; MPZ2022/770

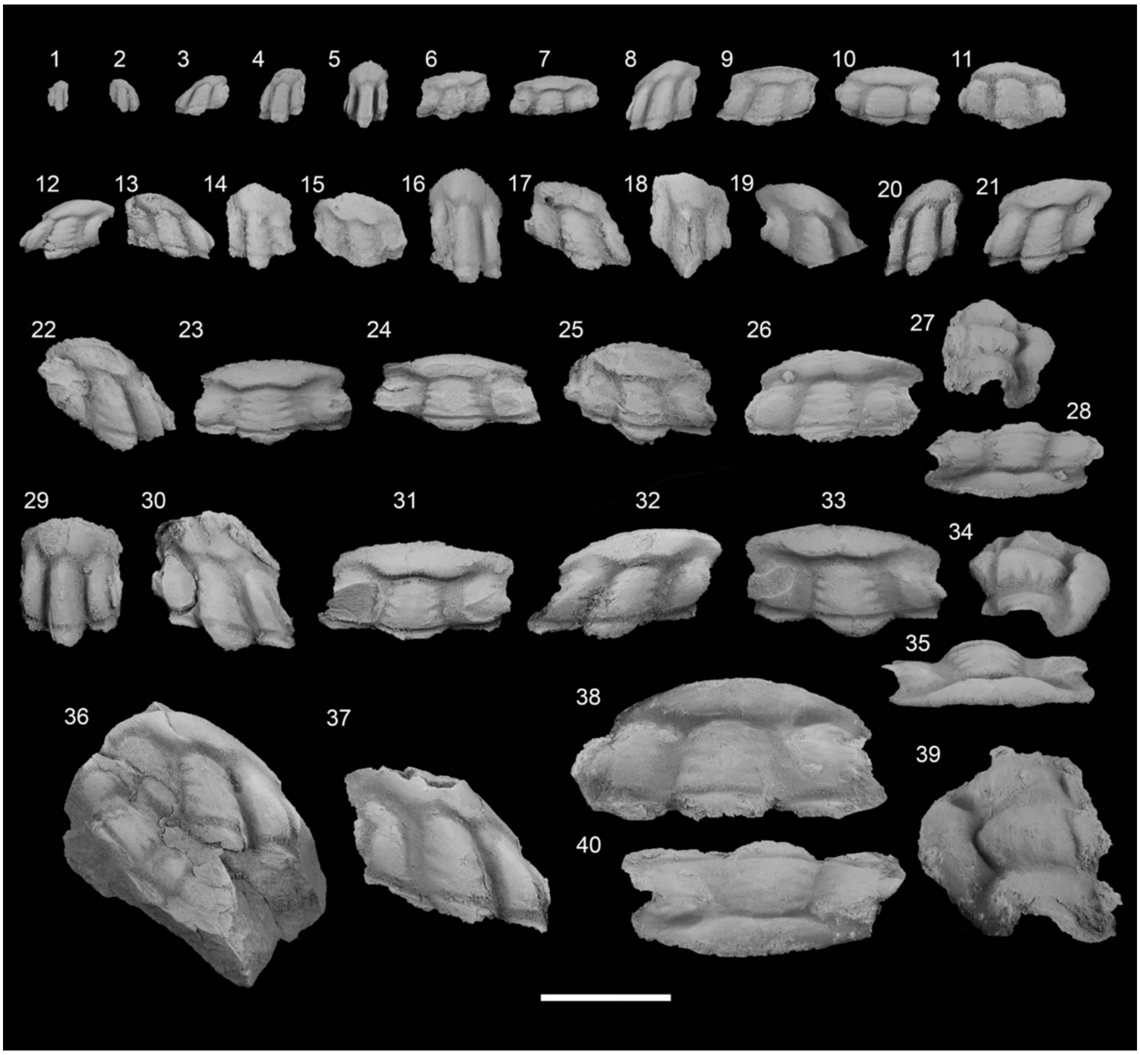

Figure 41: *Strenuaeva sampelayoi* Richter & Richter, 1940, 'Alanís beds', middle Marianian (Cambrian Stage 3), Alanís, Spain. **1**) UHU–AL08–53. **2**) UHU–AL08–54. **3**) UHU–AL08–55. **4**) UHU–AL08–56. **5**) UHU–AL08–58. **6**) UHU–AL08–60. **7**) UHU–AL08–03. **8**) UHU–AL08–59. **9**) UHU–AL08–61. **10**) UHU–AL08–64. **11**) UHU–AL08–65. **12**) UHU–AL08–05. **13**) UHU–AL08–07. **14**) UHU–AL08–08. **15**) UHU–AL08–09. **16**) UHU–AL08–10. **17**) UHU–AL08–12. **18**) UHU–AL08–15. **19**) UHU–AL08–16. **20**) UHU–AL08–17. **21**) UHU–AL08–18. **22**) UHU–AL08–23. **23**) UHU–AL08–26. **24**) UHU–AL08–28. **25**) UHU–AL08–31. **26**–**28**) UHU–AL08–32. **26**) dorsal view; **27**) lateral view; **28**) anterior view; **29**) UHU–AL08–38. **30**) UHU–AL08–39. **31**) UHU–AL08–35. **32**) UHU–AL08–36. **33**–**35**) UHU–AL08–38. **33**) dorsal view; **34**) lateral view; **35**) anterior view. **36**) UHU–AL08–40. **37**) UHU–AL08–47. **38**–**40**) UHU–AL08–50; **38**) dorsal view; **39**) lateral view.; **40**) anterior view. Scale bar = 10 mm.

to MPZ2022/776, DPM-185-700-E40, DPM-185-700-E42, DPM-185-700-T20, DPM-185-700-T23, DPM-185-700-T1245, DPM-185-700-148, DPM-A49-828-A1R1b). Sierra del Bujo, Huelva: one single cranidium (MPZ2022/769).

Remarks: *Strenuaeva sampelayoi* differs from the type species *S. primaeva* by the presence of the strongly incised oblique furrows, defining a subtrapezoidal preglabellar area, whereas in the latter the furrow that limits the preglabellar area abaxially is almost transverse, defining a more subtriangular preglabellar area. *Strenuaeva inflata* Ahlberg

& Bergström, 1978, from the Swedish Lapland and Norway, differs from *S. sampelayoi* in having a subtriangular preglabellar area, defined by a transverse (instead of oblique) pair of furrows, similar to that of *S. primaeva*, and a more angulate anterior margin of the cranidium, and a more strongly tapering glabella with a narrow (tr.) frontal lobe. The thorax of *S. inflata* is very similar to *S. sampelayoi*, and the pygidium differs in the presence of two small spines on the posterior margin (although its absence in our material could be related to preservation). Cederström et al. (2011) described a possible sexual dimorphism in *S. inflata*, differentiating two morphotypes (I and II, assigned to male and female, respectively) co-occurring in the same bed, based on different preglabellar areas (without and with two bulbs, respectively) and different genal spines (more robust and longer versus delicate and short, respectively). Among the studied material, there are specimens of *S. sampelayoi* with a preglabellar area having a distinct pair of bulbs and others with a homogeneously inflated preglabellar area, and also librigenae with shorter and longer genal spines. Although our material is evidently congeneric with Baltic *Strenuaeva* species, we cannot positively identify two distinctive morphotypes in our deformed material, due to the presence of many specimens with intermediate states between the two mentioned morphotypes.

Strenuaeva nefanda Geyer, 1990 from Morocco is younger than the remaining *Strenuaeva* species (see Biostratigraphy section below) and differs from *S. sampelayoi* in having a stronger angulation of the cranidial anterior margin, and a subtriangular preglabellar area, defined abaxially by transverse furrows and a narrower (tr.) glabella. *Strenuaeva orlowinensis* Samsonowicz, 1959 from the Holy Cross Mountains (Poland) differs from *S. sampelayoi* in the same preglabellar area characters as the Baltic species *S. primaeva* and *S. inflata*. As previously discussed (see genus remarks), we do not agree with Żylińska & Masiak's (2007) assignment of this species to *Issafeniella*. It is most closely related to the Baltic species and should be contrasted with other various species of ellipsocephalids defined in Baltica, from which it cannot be properly differentiated, its diagnosis not being diagnostic. It may be a junior synonym or a senior synonym of other species, for instance *Epichalnipsus anartanus* Geyer et al., 2004 (e.g., compare Żylińska & Masiak, 2007, figs. 9b-e, g-h, j-m, o and Cederström et al., 2022, fig. 21)

'*Strenuaeva melendezi*' Gil Cid, 1972a and '*Ellipsostrenua alanisiana*' Sdzuy, 1961 from Spain, and *S. marocana* Hupé, 1953a from Morocco are here considered junior synonyms of *S. sampelayoi*. '*Strenuaena melendezi*' was erected based on the presence

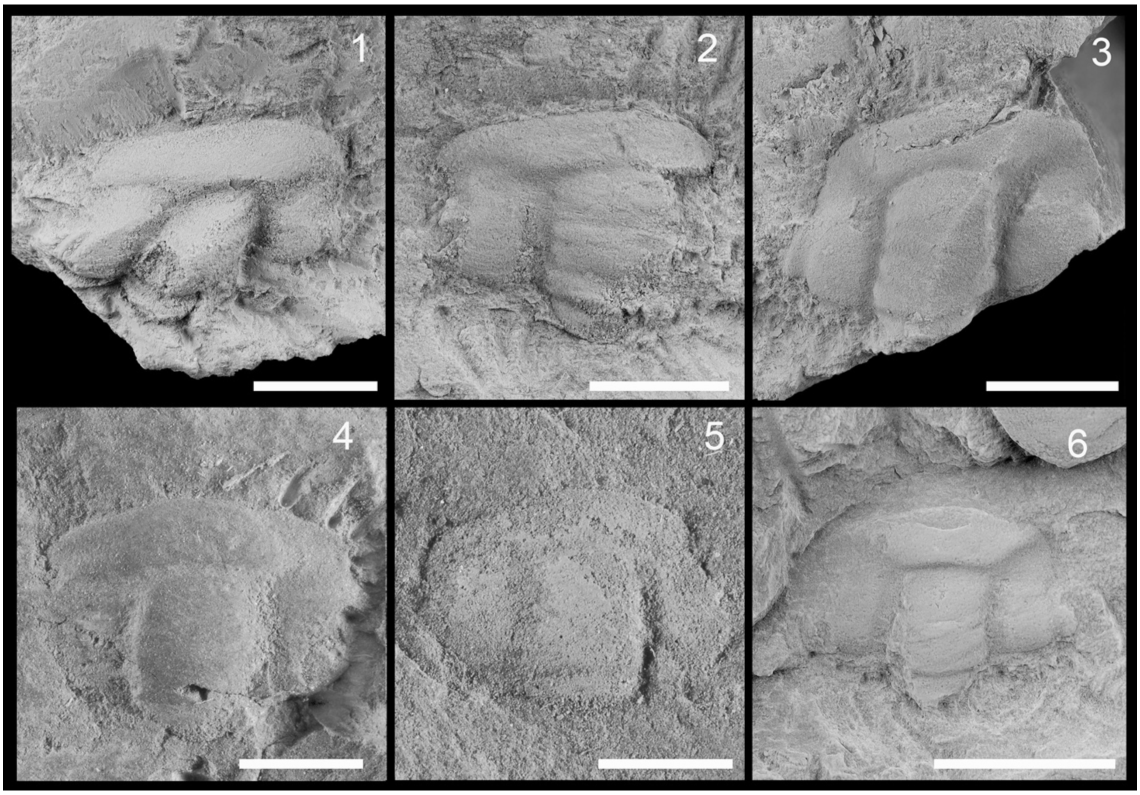

Figure 42: **1**–**5**) *Strenuaeva sampelayoi* Richter & Richter, 1940, La Hoya Member, Alconera Formation, middle Marianian (Cambrian Stage 3), Alconera, Spain. **1**) MPZ2022/776. **2**) DPM–A185–700–T23. **3**) MPZ2022/772. **4**) DPM–A185–700–T20. **5**) DPM–A185–700E42. **6**) 'Herrerías shale', middle Marianian (Cambrian Stage 3), Sierra del Bujo, Huelva, Spain MPZ2022/769. Scale bar = 5 mm.

of a medial furrow dividing the preglabellar area. However, our revision of its type material (Fig. 39.7, 39.8) and the additional collection of *S. sampelayoi* show that this character is present with different grades, dependent on the mode of preservation and/or showing intraspecific variability, not only in this species, but also in other *Strenuaeva* species. As previously mentioned, in describing *Strenuaeva inflata*, Cederström et al. (2011) differentiated one morphotype with a pair of bulbs in the frontal area, that have been interpreted as brood pouches, and, thus, females. Furthermore, it should be noted that *S. melendezi* has the same type locality as *S. sampelayoi*. *Ellipsostrenua alanisiana* Sdzuy, 1961 is based on a rectangular shape of the glabella and the absence (or subtle presence) of ocular ridges. However, among the studied material, there are several specimens showing the same glabellar configuration, together with similar morphology of the ocular ridges, which seem to result from different deformational processes. On the other hand, *S. marocana* was erected solely based on the distinct glabellar furrows and the ocular ridges, both characters being highly dependend of the taphonomy, as shown herein. Finally, it is important to note that *Strenuaeva sampelayoi* is most similar to *Issafeniella turgida* from Morocco, sharing the very characteristic subtrapezoidal configuration of the preglabellar area. However, the Moroccan species differs in having a more parallel-sided glabella (wider anteriorly) and an occipital spine. We believe that *S. sampelayoi* is extremely important for discussing the relationship of *Strenuaeva* and *Issafeniella*, because it brings together the characters taken as diagnostic of one genus and those of the other (see remarks on the genus). Besides the mixed morphology, *S. sampelayoi* shows more or less the same intraspecific variability as that reported by Cederström et al. (2011) for *S. inflata*.

It is worth noting that one of the fossil sites from the Alanís locality (AL08) has provided several articulated specimens of *Strenuaeva sampelayoi*. Among these, some have been found enrolled (Fig. 44.1–44.6), arched (Fig. 44.7–44.11), curved (Fig. 44.13–44.15, 44.18–44.19) and undulated (Fig. 44.15–44.17). These are equivalent positions to those described from the Luobákti section by Cederström et al. (2011) for *S. inflata*.

Strenuaeva incondita Sdzuy, 1961

Figure 45

1961 *Strenuaeva incondita* n. sp. – Sdzuy, p. 300–301, pl. 12, fig. 6–14, text-fig. 21.

1991 *Strenuaeva incondita* – Gámez-Vintaned et al., p. 262, 270, fig. 2.

1991 *Strenuaeva incondita* – Álvaro, p. 73-74, pl. 1, fig. 2.

1998 *Strenuaeva incondita* – Palacios & Moczydłowska, p. 67, 72, 73, figs. 2, 4.

2003 *Strenuaeva incondita* – Liñán et al., p. 11, fig. 2.

2008 *Strenuaeva incondita* – Gozalo et al., p. 140–141, 143, pl. 1, fig. 3.

2018 *Strenuaeva incondita* – Sepúlveda et al., p. 597, fig. 4B–4D.

2019 *Strenuaeva incondita* – Álvaro et al., fig. 3.

2019 *Strenuaeva incondita* – Zamora et al., p. 40, fig. 23E.

2021b *Strenuaeva incondita* – Sepúlveda et al., p. 232, fig. 3B.

2022 *Strenuaeva incondita* – Sepúlveda et al., p. 114, figs. 6M–O, 6R.

Holotype: Cranidium (Münster L 3198) from the Huérmeda Formation, Huérmeda, Zaragoza, Spain.

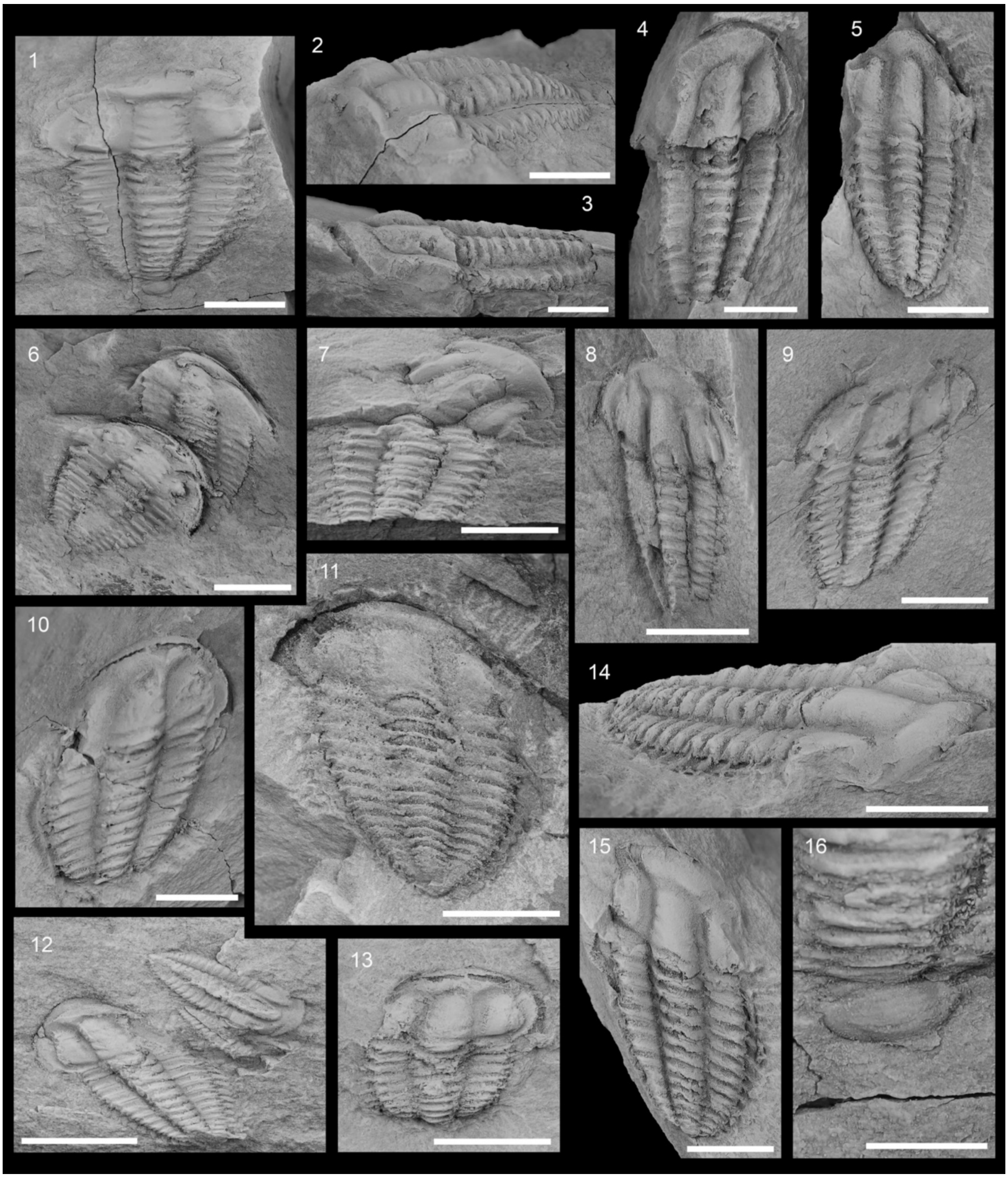

Figure 43: *Strenuaeva sampelayoi* Richter & Richter, 1940, 'Alanís beds', middle Marianian (Cambrian Stage 3), Alanís, Spain. **1**–**2**) UHU–AL05–111; **1**) dorsal view; **2**) anterolateral view. **3**–**4**) UHU–AL08–119. **3**) lateral view; **4**) dorsal view. **5**) UHU–AL08–118. **6**) UHU–AL05–109. **7**) UHU–AL05–105. **8**) UHU–AL05–101. **9**) UHU–AL05–110. **10**) UHU–AL08–143. **11**) UHU–AL08–144. **12**) UHU–AL05–100. **13**) UHU–AL08–133. **14**–**15**) UHU–AL08–117. **14**) anterolateral view; **15**) dorsal view. **16**) detail of the pygidium of UHU–AL05–111. Scale bar = 5 mm (**1**–**15**), 2 mm (**16**).

Emended diagnosis: Preglabellar area subtriangular, low relief, about 20–22% of total cephalic length (including occipital lobe), and commonly with a pair of faint bulbs separated by a shallow, median depressed area/furrow. Anterior margin regular and continuous, subtly pointed adaxially, sub-ogival. Preglabellar furrow shallow and narrow (sag.), connected laterally with an extensive transverse depression in front of the palpebral areas, until reaching the lateral margin of the cranidium, widening laterally. Glabella mostly subconical, gently convex, about 70% cephalic sagittal length (including occipital lobe), and 40–45% of the cranidial width (across L1). Three pairs of shallow, narrow, non-transglabellar glabellar furrows. Glabellar lobes almost effaced. Occipital lobe semicircular, convex and strongly curved medially.

Description: Cranidium subpentagonal, generally with low relief. The cranidia range in length from 3–19 mm and in width from 5.5–2.5 mm in width. Anterior margin subtly pointed adaxially. The preglabellar area is subtriangular, of low relief and occupies approx. 20–22% of the total cranidial length sagitally (including occipital lobe). It shows frequently one pair of bulbs separated by a shallow median furrow. The preglabellar furrow is shallow and narrow (sag.), connected laterally with a wide depression in front of the palpebral areas until reaching the lateral margin of the cranidium, widening laterally. The glabella is generally subconical; gently convex with a slightly higher relief than the palpebral area and tapered forward. Deep and wide (tr.) axial furrows, convergent forward and connected to the preglabellar furrow and its lateral extensions. The axial furrows are deeper than the preglabellar furrow and its lateral extensions. The glabella occupies about 70% of the cephalic sagittal length (including occipital lobe), and about 40–45% of the cranidial width (at the posterior border). Three pairs of shallow lateral glabellar furrows are generally present and directed backwards adaxially. The glabellar lobes are almost effaced in most of specimens. The narrow (sag.) and deep occipital furrow is straight to slightly curved backwards. The occipital lobe is semicircular, strongly curved backwards, convex, and occupies about 15–20% of the cephalic length (sag.) and 35–40% of the cranidial width. The fixigena is semicircular to subtrapezoidal, slightly inflated, occupying 40–45% of the total cephalic length and 25–28% of the cranidial width (across L1). The eye ridge is strongly curved and extends around the outer palpebral area from the frontal lobe of the glabella (without crossing the axial furrows) to the palpebral lobe, getting progressively wider (tr.) backwards. The narrow palpebral lobe is of higher relief than the palpebral area, occupying 4–8% of the cranidial width (across S2) and separated from the palpebral area by a shallow and narrow (tr.) furrow. The anterior branch of the facial suture is oblique and extends slightly

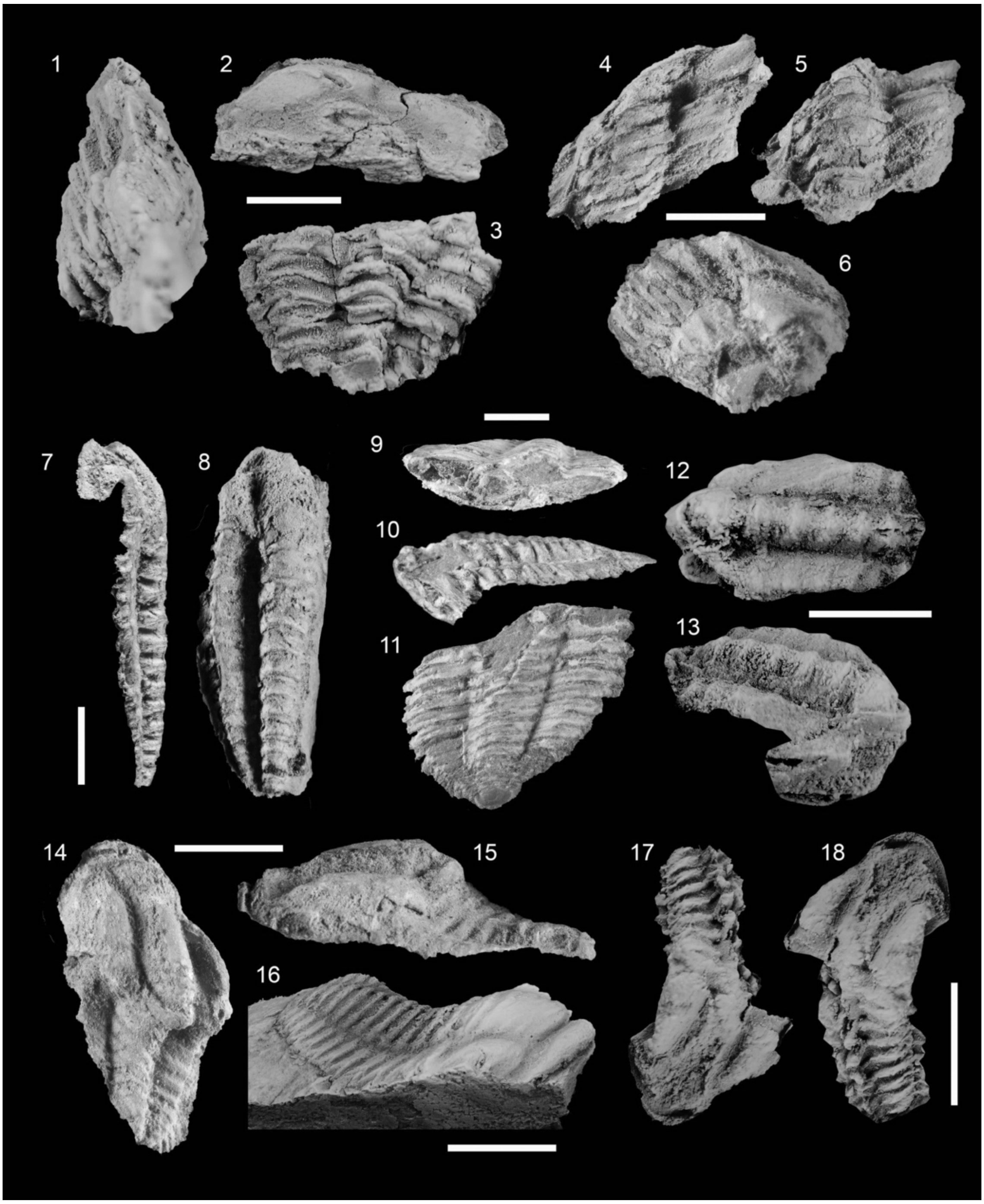

Figure 44: *Strenuaeva sampelayoi* Richter & Richter, 1940, 'Alanís beds', middle Marianian (Cambrian Stage 3), Alanís, Spain. Selected specimens enrolled (**1**–**6**), arched (**7**–**11**), curved (**12**–**13**, **17**–**18**) and undulated (**14**–**16**). **1**–**3**). UHU–AL08–119; **1**) lateral view; **2**) dorsal view; **3**) posterior view. **4**–**6**) DPM–A232–821–HV1; **4**) dorsal view; **5**) posterior view; **6**) lateral view. **7**–**8**) DPM–A232–821–F. **7**) lateral view; **8**) dorsal view. **9**–**11**) DPM–A232–821–HV2. **9**) frontal view; **10**) lateral view; **11**) dorsal view. **12**–**13**) UHU–AL08–134; **12**) dorsal view; **13**) lateral view. **14**–**15**) DPM–A232–821–HT16; **14**) dorsal view; **15**) lateral view. **16**) UHU–AL08–142. **17**–**18**) UHU–AL08–138. **17**) anterolateral view. **18**) dorsal view. Scale bar = 5 mm.

outwards from the anterior end of the palpebral lobe to the anterior margin, with an inclination of 10–15º to the sagittal axis. The central branch of the facial suture is slightly curved outwards, following the outline of the palpebral lobe. The posterior branch of the facial suture is short, straight and slightly oblique, extending from the posterior end of the palpebral lobe to the posterior margin, converging backwards. The posterior furrow is narrow (sag.) and shallow, progressively widened abaxially. The posterior border is flat to gently convex with a lower relief than the palpebral area and the occipital ring, slightly curved backwards and with a width (tr.) occupying about 6–10% of the total cephalic length (sag.).

Material: All studied specimens are housed in the Museo de Ciencias Naturales of the University of Zaragoza, Spain (MPZ). M9 section (Mesones de Isuela, Zaragoza): 3 isolated cranidia (MPZ2023/88–89). J1 and J2 section (Jarque, Zaragoza): 13 isolated cranidia (MPZ 2021/378–379, MPZ2021/380, MPZ2023/82–86). MT1 (Tierga, Zaragoza): 11 isolated cranidia (MPZ2017/741, MPZ2017/744, MPZ2023/89).

Remarks: *Strenuaeva incondita* was originally (Sdzuy, 1961) differentiated from *S. sampelayoi* mainly by different proportions of the glabella. However, after plotting the cranidium/glabella ratio measurements of both species, we do not observe significant differences with respect to this. Taking into consideration the taphonomical parameters and the significative characters among ellipsocephalids (e.g., Cederström et al., 2022), we have found morphological differences between *S. sampelayoi* and newly collected specimens of *S. incondita* coming from the same stratigraphical unit and in locations surrounding the type locality of the latter. We assume that these specimens are conspecific with those of the type material of *S. incondita,* the latter being very poorly preserved and not allowing the evaluation of the characters that are significant to differentiate it from *S. sampelayoi*. S. *incondita* differs from *S. sampelayoi* in having a lower relief of the glabella, the fixigenae and the preglabellar area, a more angulate anterior margin of the cranidium (sometimes almost sub-ogival), in lacking the oblique furrow that laterally limits the preglabellar area in *S. sampelayoi* and, thus, having a subtriangular instead of a subtrapezoidal preglabellar area and shallower (almost obsolete) glabellar furrows.

Compared to the *Strenuaeva* described from Baltica (*S. primaeva*, *S. inflata*, *S. orlowinensis*), Morocco (*S. nefanda*) and Avalonia (*S.* aff. *nefanda*), the most remarkable difference of *S. incondita* is the low relief of the cranidium and the preglabellar area, and the sub-ogival outline of its anterior margin. However, the glabellar morphology, the pre-

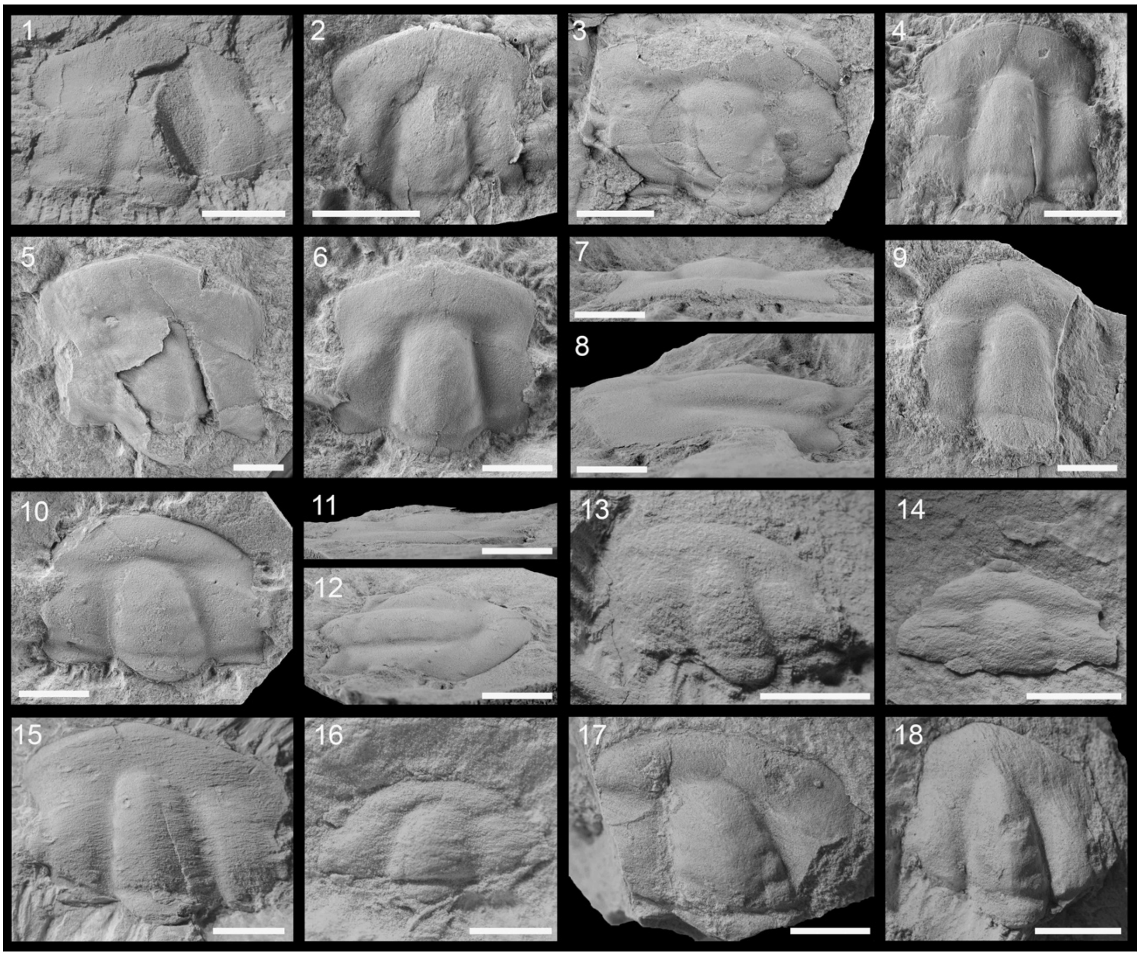

Figure 45: *Strenuaeva incondita* Sdzuy, 1961, Huérmeda and Ribota Formations (Cambrian Stages 3–4), Jarque (**1**–**12**), Mesones de Isuela (**13**–**14**), Minas Tierga (**15**–**18**). **1**) MPZ2023/82. **2**) MPZ2021/378. **3**) MPZ2023/83. **4**) MPZ2023/84. **5**) MPZ2023/85. **6**–**8**) MPZ2021/380; **6**) dorsal view; **7**) frontal view; **8**) lateral view. **9**) MPZ2023/86. **10**–**12**) MPZ2021/379; **10**) dorsal view; **11**) frontal view; **12**) lateral view. **13**) MPZ2023/87. **14**) MPZ2023/88. **15**) MPZ2017/741. **16**) MPZ2023/89. **17**) MPZ2017/748. **18**) MPZ2017/744. Scale bar = 10 mm (**1**), 5 mm (**2**–**15**, **17**–**18**), 2 mm (**16**).

glabellar area (limited abaxially by depressed areas/transverse furrows) and the tendency to develop two anterior preglabellar bulbs, suggest generic relationship with these.

5.5.6. Biostratigraphy

Since its introduction by Sdzuy (1971a), the concept and subdivision of the regional Marianian Stage in Iberia have been subsequently modified by several authors (e.g., Liñán, 1984b; Perejón, 1986, 1994; Liñán et al., 1993, 1996, 2002, 2004; Gozalo et al., 2003; Perejón & Moreno-Eiris, 2006). Nowadays, the most accepted subdivision for the Marianian Stage is that proposed by Liñan et al. (2004): the base of the lower Marianian is placed at the FAD of *Strenuella* and the archaeocyathan zones VIII and IX of Perejón

(1994), the base of the middle Marianian is at the FAD of *Strenuaeva* Richter & Richter, 1940 and the base of the upper Marianian is at the FAD of *Serrodiscus* (see Collantes et al., 2022).

Strenuaeva sampelayoi is relatively common in the middle Marianian of the OMZ (mostly in the northern flank of the Olivenza-Monesterio antiform) and *Strenuaeva incondita* is common in the middle to lowermost upper Marianian of the Iberian Range, having potential as an index taxon for the base of the middle Marianian of Iberia. In the OMZ, the FAD of *Strenuaeva* (represented by *S. sampelayoi*) is located in the middle part of the 'Alanís beds', and in the Iberian Chains (represented by *S. incondita*) it is located in the lower member of the Ribota Formation (Sepúlveda et al., 2022).

The strong provincialism and endemism among trilobite faunas hamper global correlation for the Cambrian Series 2 strata (Peng et al., 2020). Some eodiscide trilobites are geographically widely distributed (e.g., Axheimer et al., 2007; Cederström et al., 2009; Westrop & Landing, 2011; Collantes et al., 2022, 2023), whereas most polymerid trilobite species remain endemic. Ellipsocephalids have some potential for correlation at the regional level and for establishing biogeographical palaeoprovinces, although, and as stated by Cederström et al. (2022, p. 28), the reduced number of recognizable characters, the imperfectly preserved material, and their morphological plasticity makes it very difficult to assure natural entities at genus level.

In Morocco, *S. sampelayoi* (=*S. marocana*) occurs at the base of the *Antatlasia guttapluviae* Biozone (lower to middle Banian, equivalent to upper Cambrian Stage 3), while the youngest representative of the genus, *S. nefanda*, occurs at the base of the *Morocconus notabilis* Biozone (upper Tissafinian, uppermost Cambrian Stage 4). Given the systematic remarks made regarding *Strenaueva* and *Issafeniella*, we added the records of the latter in Fig. 46. These have a distribution roughly coincident with that of *S. incondita* from Spain (approximately middle Banian and middle Marianian, respectively). *Strenuaeva* aff. *nefanda* from Newfoundland (western Avalonia), is also from the base of the *Morocconus notabilis* Biozone.

In Baltica, the great majority of trilobite species are endemic (Cederström et al., 2022). Regionally, the trilobite biostratigraphical zonation has undergone many changes in recent years (e.g., Nielsen & Schovsbo, 2011; Cederström et al., 2012; Høyberget et al., 2015; Ahlberg et al., 2016). The most recent proposal by Ahlberg et al. (2016) suggests that the Cambrian Series 2 biozonal assemblages in Scandinavia are more

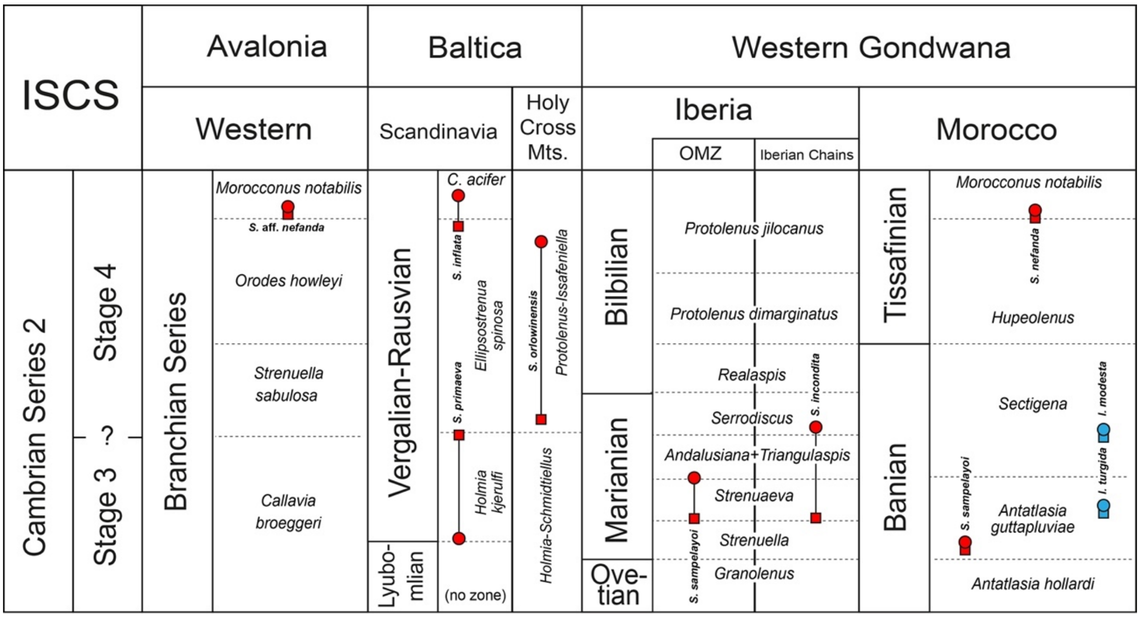

Figure 46: Correlation chart showing the stratigraphical occurrence of *Strenuaeva* and *Issafeniella*. Based on Sundberg et al. (2016), Zhang et al. (2017) and Geyer (2019).

related to biofacies than to temporal divisions. Thus, they proposed reducing the biostratigraphical division of the Scandinavian Series 2 succession into four interval zones: the *Schmidtiellus mickwitzi*, *Holmia kjerulfi*, *Strenuaeva*? (=*Ellipsostrenua*) *spinosa*, and *Chelediscus acifer* zones.

Species of *Strenuaeva* from Baltica (*S*. *primaeva, S. inflata* and *S. orlowinensis*) are relatively common and widespread all over Baltoscandia and show a biostratigraphical range that extends from middle Cambrian Stage 3 to uppermost Cambrian Stage 4 (Fig. 46). Ahlberg et al. (2016) noted that the first appearance of *Strenuaeva primaeva* coincides approximately with the base of the *Holmia kjerulfi* Biozone, whereas the first appearance of *S*. *inflata* occurs slightly before that of *Chelediscus acifer* (see Axheimer et al., 2007).

Strenuaeva and *Issafeniella* range from Cambrian Stage 3 to Cambrian Stage 4, characterising sequences of regional stages that can be correlated intercontinentally (e.g., Banian to Tissafinian in Morocco; Marianian in Iberia; and Vergalian to Rausvian in Baltica).

5.5.7. Palaeobiogeography

Iberia and Morocco, along with other regions, have been traditionally assigned to the so-called 'Mediterranean subprovince' of Western Gondwana (Sdzuy, 1972). Several authors noted that regions belonging to this subprovince show a similar late Neoproterozoic–Cambrian Series 2 depositional record along the margin of Gondwana, associated with the Avalonian–Cadomian active margin (e.g., Doré, 1994; Pereira et al., 2006). Strong faunal links (primarily trilobites) have been previously described by several authors between the territories included in this subprovince (e.g., Álvaro et al., 2003, 2013; Geyer & Landing, 2004). Whereas some palaeogeographical models place Avalonia close to western Gondwana during the Cambrian and Early Ordovician (e.g., Cocks & Torsvik, 2006), others consider it as an independent microcontinent separated from Gondwana by a relatively wide ocean (Landing, 2005; Landing et al., 2013a, b, 2013b, 2022). Regardless of its original position, previous authors (e.g., Álvaro et al., 2013) noted that the end of the Cambrian Epoch 2 is characterised by new links between Avalonia and Western Gondwana, including some eodiscoide trilobites (e.g., *Serrodiscus*, *Calodiscus*, *Hebediscus*, *Chelediscus*) and polymeroid trilobites (e.g., *Strenuella*, *Callavia*, *Pseudatops*, *Protolenus*).

In Western Gondwana, *Strenuaeva* is present in both Iberia and Morocco. In Iberia, *S. sampelayoi* is restricted to the Ossa-Morena Zone, while *S. incondita* is only known from the Iberian Chains. '*S. marocana*' (=*S. sampelayoi*) occurs in the lower Banian of Morocco, with a stratigraphical position slightly lower than the range of *S. sampelayoi* in Iberia. Taking into account the putative relationship of *Issafeniella* from Morocco (represented by *I. turgida* and *I. modesta*) with *Strenuaeva* (see Remarks on the genus and Discussion of *S. sampelayoi*) we added its occurrences to our palaeogeographical reconstruction, and noted that its range is coeval with the Iberian species (Fig. 47). In Morocco, *S. nefanda* was also described from the upper Tissafinian of the Amouslek section (Geyer, 1990), which is the youngest occurrence of the genus *Strenuaeva* so far. Fletcher (2003, 2006) assigned some specimens from Newfoundland (western Avalonia) with an equivalent biostratigraphical position to this species. However, as discussed before, they differ from the Moroccan types (see Remarks on the genus) and are here presented as *S.* aff. *nefanda* and included in this discussion (Fig. 47).

Thus, the putative presence of *Strenuaeva* in Avalonia (*S.* aff. *nefanda*) strengthens the faunal links between Western Gondwana and Avalonia during the Cambrian Epoch 2 as previously noted by, e.g., Sdzuy (1972), Liñán et al. (2002), Álvaro et al. (2003, 2013), Landing et al. (2013a, b, 2022), and Collantes et al. (2021a, b, 2022, 2023), and supports the concept of an Acadobaltic Province (*sensu* Sdzuy, 1972) during Cambrian times.

Baltica has been traditionally subdivided into two tectonostratigraphical domains based on facies associations and trilobite faunas (Nielsen & Schovsbo, 2011). These domains include an inner platform sector (Norway and southern and central Sweden) and an outer platform sector (Holy Cross Mountains and the Digermul Peninsula). *S. primaeva* (upper Cambrian Stage 3 to lowermost Stage 4) and *S. inflata* (upper Cambrian Stage 4) occur in Sweden and Norway, corresponding to the inner platform sector. In addition, other shared trilobite genera between the western Gondwana margin and the inner platform sector of Baltica during Cambrian Series 2 include *Chelediscus*, *Calodiscus* and *Neocobboldia* (Axheimer et al., 2007; Cederström et al., 2009, 2011, 2022; Żylińska & Szczepanik, 2009; Żylińska, 2013a; Gozalo et al., 2016).

To sum up, the genus *Strenuaeva* is distributed across western Avalonia (Newfoundland), the western margin of Gondwana (including Iberia and Morocco), and Baltica (Sweden and Norway), with a biostratigraphical range from the upper Cambrian Stage 3 to uppermost Cambrian Stage 4 (Fig. 47).

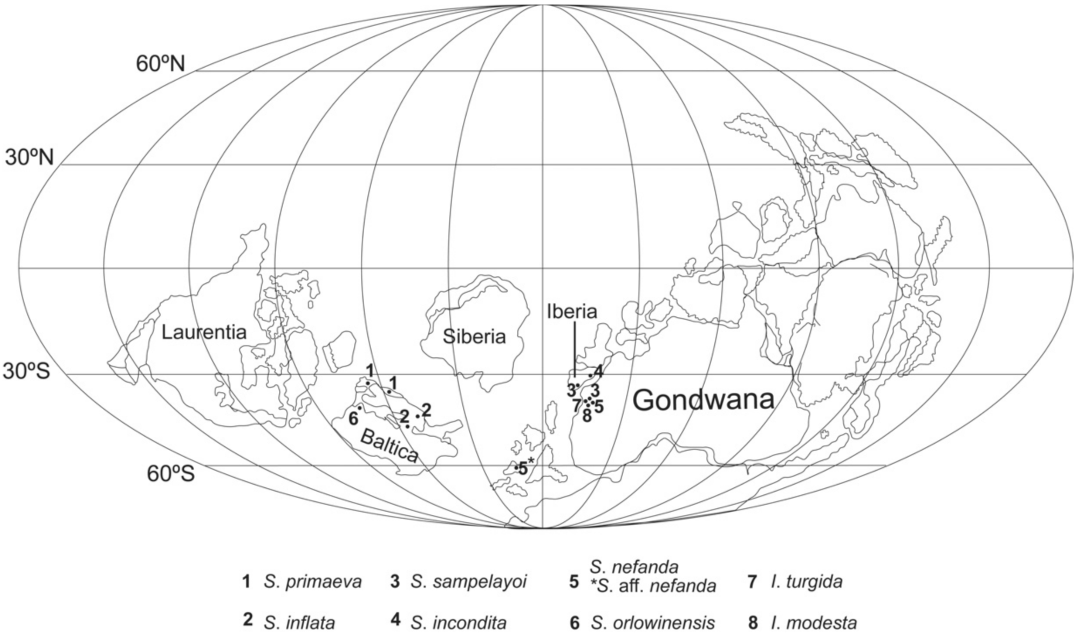

Figure 47: Distribution of *Strenuaeva* and *Issafeniella* plotted on the Cambrian palaeogeographical map. Modified from McKerrow et al. (1992).

5.5.8. Conclusions

Strenuaeva has been reported from several localities in the Ossa-Morena Zone (Viar-Benalija Block, Alconera Block, and Herrerías Block), southwestern Iberia, and the Iberian Chains (Jarque sections, from the Badules Unit; and Mesones 9 and Minas Tierga 1 sections, from the Mesones Unit), northeastern Iberia. Specimens from the Ossa-Morena Zone are identified as *S. sampelayoi*, whereas specimens from the Iberian Chains are recognized as *S. incondita*. Within the Ossa-Morena Zone, the great number of specimens of *S. sampelayoi* from Alanís made it possible to assess the role of taphonomy in the differential preservation of certain characters, which permitted the recognition of some intraspecific variability in this species. Thus, on this basis, the classification of the Spanish species within the genus *Issafeniella* by previous authors is not accepted. In addition, the species '*S. melendezi*' and '*Ellipsostrenua alanisiana*' from Alanís, together with *S. marocana* from Issafen (Morocco), are regarded as junior synonyms of *S. sampelayoi*.

In Iberia, *S. sampelayoi* is known from the middle Marianian in the Ossa-Morena Zone, and *S. incondita* from the lowermost middle Marianian to the lowermost upper Marianian in the Iberian Chains. The genus *Strenuaeva* is known from Baltica (Scandinavia and Holy Cross Mountains), Iberia (Spain), Morocco and, possibly, western Avalonia (Newfoundland) and it ranges from uppermost Cambrian Stage 3 to uppermost Cambrian Stage 4.

6. Complementary results

In addition to the results published in international journals, a short section with additional results is presented below. The additional findings presented herein represent a direct outcome of this PhD project, yet they remain unpublished or are part of ongoing research endeavors.

6.1. Trilobites from the Marianian of the Ossa-Morena Zone: systematic update

The Marianian Stage of the OMZ is characterised by a low diversity and low abundance of trilobites. Previous works have identified 25 species (section 1.4.), although several had never been properly documented and most needed a recent review.

In this work, we studied six species in detail (section 5), but throughout the labour carried out, specimens of other species were also collected and analysed and a review of some of these taxa was begun.

In this subsection, we present short remarks on some Marianian trilobite species which, although they did not resulted in papers for this thesis, were also studied and are of particular relevance because 1) they are reported here for the first time for this territory, 2) they have been listed in previous works but have not been described or illustrated before, 3) they went unnoticed, or 4) they have generated controversy from a taxonomical point of view. An up-to-date taxonomical list of Marianian trilobites from the OMZ is also provided.

6.1.1. Remarks on *Hebediscus* Whitehouse, 1936

The eodiscide *Hebediscus* sp. from the OMZ is illustrated for the first time in the present work (Fig. 48.7). Although this genus has been previously identified in the OMZ (Liñán, 1984b, tab. 3; Liñán & Quesada, 1990, fig. 3, Álvaro et al., 1998, p. 502), no specimens have ever been described or figured. So far, only ten specimens have been reportedly found, collected by Prof. Eladio Liñán during the 1980s. Given their poor preservation state, it is difficult to make a tentative specific identification, although they can be assigned to the genus *Hebediscus*. In the rest of Iberia, beyond OMZ, Sepúlveda et al. (2022) figured three cephala and one pygidium assigned to *Hebediscus*? sp. from level

2 of the Huérmeda Formation of the M9 section (Mesones de Isuela, Zaragoza Province, Iberian Chains). In our opinion, specimens of Sepúlveda et al. (2022) fit the concept of *Hebediscus*. Regarding global distribution, *Hebediscus* is fairly abundant and diverse in several Cambrian sections from Newfoundland (Westrop & Landing, 2011) and also present in Morocco (Hupé, 1953a; Geyer, 1988) and Siberia (Korovnikov, 2007). In addition, according to Sundberg et al. (2016), there are several similar forms that, despite lacking precise taxonomical classification, occur in equivalent stratigraphical positions along Western and Eastern Avalonia, West Gondwana, the Siberian Platform, Australia and South China.

6.1.2. Remarks on *Kingaspis* Kobayashi, 1935

We report for the first time representatives of the genus *Kingaspis* Kobayashi, 1935 from the OMZ (Fig. 48.17). This genus has been previously documented in several Spanish localities belonging to other tectonostratigraphical domains, including the Cantabrian Zone (Valdoré, Crémedes; León Province), the Central Iberian Zone (Los Cortijos de Malagón; Ciudad Real Province), and the Iberian Chains (Murero, Jarque, Ateca and Tierga; Zaragoza Province). The stratigraphical range of these occurrences spans from middle Marianian to lower Leonian (see Liñán et al., 2003; Álvaro, 2007). Specimens of *Kingaspis* from the OMZ have been found in the Alconera A1 section, with a trilobite assemblage indicating a middle Marianian age (Liñán & Perejón, 1984). These specimens are tentatively assigned to *Kingaspis* (*Kingaspoides*) cf. *velata* Sdzuy, 1961, compared with the other Iberian occurrences. Additionally, we identified the genus in the middle Marianian of Alanis. The presence of *Kingaspis* in the OMZ represents additional data to correlate the Marianian sequences of this domain with those of the Iberian Chains, where the genus *Kingaspis* has also been reported in the middle Marianian. Besides Iberia, *Kingaspis* has been documented in Morocco (Geyer, 1990) and Jordan (Rushton & Powell, 1998; Elicki & Geyer, 2013).

6.1.3. Remarks on *Calodiscus* Howell, 1935

Calodiscus Howell, 1935 is an eodiscide trilobite with a wide geographical distribution and of great interest for the international correlation of the Cambrian Series 2 (see Sundberg et al., 2016). Despite its great correlation potential, the presence of *Calodiscus* in Iberia has been overlooked by most of the authors who have worked with this genus (e.g., Ahlberg & Bergström, 1993; Geyer & Elicki, 1995; Cederström et al., 2009; Westrop & Landing, 2011). Sdzuy (1962) described the subspecies *C. schucherti ibericus* Sdzuy, 1962 from the lower levels of the 'Herrerías shale' of the Sierra del Bujo section of northern Huelva Province. The holotype is hereby re-illustrated (Fig. 48.4). Sdzuy differentiated this subspecies from the nominal species based on 1) a less anteriorly narrowed glabella, 2) a long occipital spine and 3) a greater distance between the anterior part of the fixigenae at the frontal lobe (see Sdzuy, 1962, p. 187). Figured specimens (Sdzuy, 1962, pl. 18, figs. 1–5) include both the original internal moulds and casts based on the external ones, the latter showing most of the diagnostic characters of the subspecies, while the formers lack the occipital spine. Subsequently, Geyer et al. (2014) raised *C. ibericus* at a specific level and compared it with the new German occurrences. Nevertheless, the supposed differences between *C. ibericus* and *C. schucherti* (Matthew, 1896) (i.e., the longer occipital spine, widened frontal lobe and greater separation of fixigenae in the former) are unclear, and may represent taphonomical variations of the latter. Therefore, given the scarce material and poor preservation of Spanish specimens, we considered that *Calodiscus ibericus* should be assigned to *Calodiscus* cf. *schucherti* (Matthew, 1896).

6.1.4. Remarks on *Ferralsia* Cobbold, 1935 and *Termierella* Sdzuy, 1961

Regarding *Ferralsia*, one specimen from the A3 section of Alconera (Badajoz, Spain) was reported and figured by Álvaro et al. (1998) and identified as *F. saxonica* Geyer & Elicki, 1995. From the same levels, we recovered *Termierella sevillana* Sdzuy, 1961, represented by well-preserved, indeformed material, which shares a great morphological similarity with *F. saxonica*. Based on what is possible to observe in the figured specimen by Álvaro et al. (1998) and in the new occurrence, it is more likely that it is conspecific with *Termierella sevillana*. Thus, the presence of *Ferralsia* in the OMZ is not verified.

6.1.5. Remarks on *Hicksia* Delgado, 1904

Richter & Richter (1941) erected a new species from the northern Huelva, named '*Boniella*? *hispanica*' Richter & Richter, 1941. Subsequently, this species was transferred to the genus *Hicksia* Delgado, 1904 by Sdzuy (1962). According to Sdzuy (1962, p. 211)

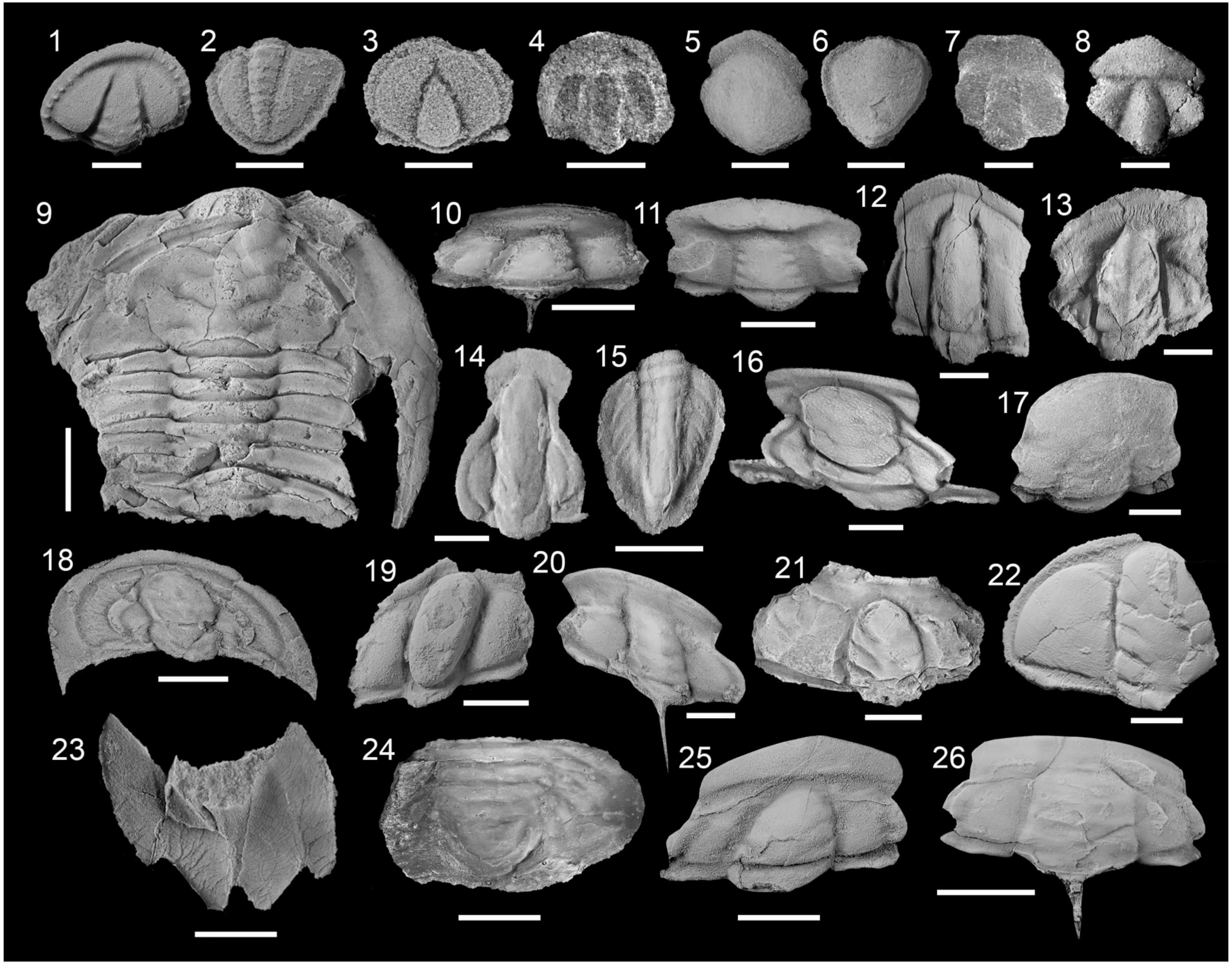
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Figure 48: **1**–**2**) *Serrodiscus bellimarginatus* (Shaler & Foerste, 1888), ‘Cumbres beds’, upper Marianian, Cumbres de San Bartolomé, Huelva; **1**) UHU-CSB180, cephalon, dorsal view; **2**) UHU-CSB191, pygidium, dorsal view. **3**) *Chelediscus garzoni* Collantes, Pereira, Mayoral & Gozalo, 2023, ‘Cumbres beds’, upper Marianian, Cumbres de San Bartolomé, Huelva, UHU-CSB514, cephalon, dorsal view. **4**) *Calodiscus* cf. *schucherti* (Matthew, 1896), ‘Herrerías shale’, middle Marianian, Sierra del Bujo, Huelva, SMF X 16763a1 (paratype of *C. ibericus* Sdzuy, 1962), cephalon, dorsal view. **5**–**6**) *Delgadella souzai* (Delgado, 1904), ‘Herrerías shale’, middle Marianian, Sierra del Bujo, Huelva; **5**) SMF X 16764b1, cephalon, dorsal view; **6**) SMF X 16773, pygidium, dorsal view. **7**) *Hebediscus* sp., La Hoya Member, Alconera Formation, Alconera, Badajoz, MPZ 2022/793, cephalon, dorsal view. **8**) *Triangulaspis fusca* Sdzuy, 1962, ‘Benalija beds’, middle Marianian, Arroyo del Molino, Guadalcanal, Seville, SMF X 16817c, cranidium, dorsal view. **9**) *Andalusiana cornuta* Sdzuy, 1961, ‘Benalija beds’, middle Marianian, Arroyo del Molino, Guadalcanal, Seville, SMF X 16774, cephalon with thorax, dorsal view. **10**) *Alanisia guillermoi* Richter & Richter, 1940, ‘Alanis beds’, middle Marianian, Alanís, Seville, SMF X 1143d, cranidium, dorsal view. **11**) *Strenuaeva sampelayoi* Richter & Richter, 1940, ‘Alanis beds’, middle Marianian, Alanís, Seville, SMF X 1141a (holotype), cranidium, dorsal view. **12**) *Protaldonaia morenica* Sdzuy, 1961, ‘Benalija beds’, middle Marianian, Viar fossil site, Llerena-Pallares, Badajoz, MPZ-2021/302, cranidium, dorsal view. **13**) *Termierella sevillana* Sdzuy, 1961, ‘Benalija beds’, middle Marianian, Arroyo del Tamujar, Guadalcanal, Seville, DPM-A202-727-PM1, cephalon, dorsal view. **14**–**15**) *Perrector perrectus* Richter & Richter, 1940, ‘Alanís beds’, middle Marianian, Alanís, Seville; **14**) DPM-A232-817-H547, cranidium, dorsal view; **15**) SMF X 1154b, pygidium, dorsal view. **16**) *Saukianda andalusiae* Richter & Richter, 1940, ‘Alanís beds’, middle Marianian, Alanís, Seville, SMF X 1034t (holotype), cranidium, dorsal view. **17**) *Kingaspis* (*Kingaspoides*) cf. *velata*, La Hoya Member, middle Marianian, Alconera Formation, Alconera, Badajoz, UHU-ALC-101, cranidium, dorsal view. **18**) *Callavia choffati* (Delgado, 1904), ‘Herrerías shale’, middle Marianian, Cañaveral de León, Huelva, UHU-CVL-46, cephalon, dorsal view. **19**) *Hicksia elvensis* Delgado, 1904, Vila Boim Formation, middle Marianian, Vila Boim, Elvas, Portugal, MG 15713, cranidium, dorsal view. **20**) *Rinconia schneideri* (Richter & Richter, 1941), ‘Herrerías shale’, middle Marianian, Cañaveral de León, Huelva, UHU-CVL-44, cranidium, dorsal view. **21**) *Atops calanus* Richter & Richter, 1941, ‘Herrerías shale’, middle Marianian, Sierra del Bujo, Huelva, SMF X 1227 (holotype), cephalon, dorsal view. **22**) *Pseudatops reticulatus* (Walcott, 1890b), ‘Cumbres beds’, upper Marianian, Cumbres de San Bartolomé, Huelva, UHU-CU003-20, cephalon, dorsal view. **23**–**24**) *Gigantopygus* cf. *bondoni* Hupé, 1953a, ‘Herrerías shale’, middle Marianian, Sierra del Bujo, Huelva; **23**) SMF X 16789, pygidium, dorsal view; **24**) SMF X 1226a, cranidium, dorsal view. **25**) *Strenuella* n. sp., ‘Alanís beds’, lower Marianian, Cerro del Hierro, Seville, UHU-CH-101. **26**) *Acanthomicmacca*? sp., ‘Alanís beds’, lower Marianian, Cerro del Hierro, Seville, UHU-CH-01.

‘*Hicksia hispanica*’ differs from the type species *Hicksia elvensis* in 1) a glabella considerably widened frontally, 2) distinct lateral furrows, and 3) a narrow anterior border. However, specimens of ‘*H. hispanica*’ figured by Sdzuy (1962, pl. 23, figs. 8–13) as well as specimens figured by subsequent authors (e.g., Gil Cid, 1971, figs. 3, 4; 1978) consist of partially preserved cranidia that do not allow clear differentiation between species and are considerably deformed. Furthermore, it should be noted that the specimens of *H. elvensis* figured by both Delgado (1904) and Teixeira (1954, pl. 5, figs. 1–8, pl. 6, figs. 1–5, pl. 7, figs. 1–8, pl. 8, figs. 1–11, pl. 9, figs. 1–8, pl. 10, figs. 1–8, pl. 11, figs. 1–9 pl. 12, figs. 3–4) show a considerable degree of flattening, which may explain the differences in the glabellar relief and morphology comparing to the Spanish material. Here, we consider ‘*H. hispanica*’ a junior synonym of *H. elvensis* (Fig. 48.19).

6.1.6. Updated taxonomical list of occurrences

The review of the Marianian trilobites of the Ossa-Morena Zone resulted in a total of 23 species (Tab. 3): *Acanthomicmacca*? sp., *Alanisia guillermoi*, *Andalusiana cornuta*, *Atops calanus*, *Callavia choffati*, *Calodiscus ibericus*, *Chelediscus garzoni*, *Delgadella souzai*, *Eops eo*, *Gigantopygus* cf. *bondoni*, *Hebediscus* sp., *Hicksia elvensis*, *Kingaspis* (*Kingaspoides*) cf. *velata*, *Perrector perrectus*, *Protaldonaia morenica*, *Pseudatops reticulatus*, *Rinconia schneideri*, *Saukianda andalusiae*, *Serrodiscus bellimarginatus*, *Strenuaeva sampelayoi*, *Strenuella* n. sp., *Termierella sevillana* and *Triangulaspis fusca* (Fig. 48). Two genera have been identified for the first time in the Marianian of the OMZ (*Kingaspis* and *Pseudatops*), the presence of *Ferralsia* and *Longianda* is rejected, the presence of *Chelediscus* and *Hebediscus* is confirmed, and the identification of 11 previously reported taxa have been updated.

6.2. Biostratigraphy

The current biostratigraphical scheme for the Marianian Stage is unsatisfactory (see section 1.3.2, “The problem of the Marianian Stage”). The previously proposed subdivisions face two main challenges. On the one hand, there are few stratigraphical sections with a continuous trilobite record, particularly continuous sections where the

Table 3: List of taxa identified by previous authors and updated identification in the present work.

Previous works	This work
Alanisia guillermoi Richter & Richter, 1940	*
Andalusiana cornuta Sdzuy, 1961	*
Atops? *calanus* Richter & Richter, 1941	*Atops calanus* Richter & Richter, 1941
*Callavia choffati (*Delgado, 1904)	*
Calodiscus ibericus Sdzuy, 1962	*Calodiscus* cf. *schucherti* (Matthew, 1896)
Chelediscus sp.	*Chelediscus garzoni* Collantes et al., 2023
*Delgadella souzai (*Delgado, 1904)	*
Eops eo Richter & Richter, 1940	*
Ferralsia saxonica Geyer & Elicki, 1995	*Termierella sevillana* Sdzuy, 1961
Gigantopygus cf. *bondoni* Hupé, 1953a	*
Hebediscus sp.	*
Hicksia elvensis Delgado, 1904	*
Hicksia hispanica (Richter & Richter, 1941)	*Hicksia elvensis* Delgado, 1904
Longianda? sp.	*Saukianda*? sp.
Micmacca? sp.	*Acanthomicmacca*? sp.
Perrector perrectus Richter & Richter, 1940	*
Protaldonaia morenica Sdzuy, 1961	*
Rinconia schneideri (Richter & Richter, 1941)	*
Saukianda andalusiae Richter & Richter, 1940	*
Sdzuyomia lotzei (Richter & Richter, 1941)	*Callavia choffati* (Delgado, 1904)
Serrodiscus silesius Richter & Richter, 1941	*Serrodiscus bellimarginatus* (Shaler & Foerste, 1888)
Strenuaeva sampelayoi Richter & Richter, 1940	*
Strenuella sp.	*Strenuella* n. sp.
Termierella sevillana Sdzuy, 1961	*
Triangulaspis fusca Sdzuy, 1962	*
-	*Kingaspis (Kingaspoides)* cf. *velata* Sdzuy, 1961
-	*Pseudatops reticulatus* (Walcott, 1890b)

index species that characterise the different substages of the current scheme occur, making it difficult to accurately determine the stratigraphical range of those species in relation to each other. On the other hand, we cannot differentiate clear evolutionary lineages within the studied genera, with most genera being represented by one single species (or being monospecific genera). Despite the limitations, it is noteworthy that some of the trilobites are widely distributed within the OMZ, and their stratigraphical range shows the same pattern in the different blocks, as far as can be ascertained by cross-referencing with other data (e.g., lithostratigraphy).

The new data recovered during this study allowed us to overcome some of these issues, studied in detail some of the index species for the Marianian stage of the OMZ (e.g., *Serrodiscus*, *Triangulaspis*, *Strenuaeva*, among others), verifying their geographical distribution and delimiting their stratigraphical range along the different studied sequences. The updated knowledge is presented below. The stratigraphical distribution of all trilobite species from the Marianian of the OMZ is shown in Figure 49.

Lower Marianian

Previous research on this topic considered that the base of the Marianian Stage is characterised by the FAD of *Strenuella*, together with the archaeocyath zone XIII (Liñán et al., 1996, 2002, 2004). Lower Marianian sequence and its typical trilobites are well represented in the lower 'Alanís beds', especially in the old iron quarry at Cerro del Hierro village (San Nicolás del Puerto, Seville), with the trilobites *Strenuaella* n. sp., *Delgadella souzai*, *Acanthomicmacca*? sp. and *Saukianda andalusiae* (see Mayoral et al., 2020). However, it should be noted that the first occurrence of *Strenuella* n. sp. at this locality takes place over a hiatus, interpreted as the so-called Cerro del Hierro Regression (or Cerro del Hierro Event, Liñán & Gámez-Vintaned, 1993), which took place in the late Ovetian (Liñán et al., 1996, fig.3). Besides, *Strenuella* n. sp. co-occurs with *Saukianda andalusiae*, *Acanthomicmacca*? sp. and *Delgadella souzai* in the lower Alconera A1 section, which Liñán et al. (1993) proposed as composite reference section (together with Alconera A3) for the Marianian Stage.

Middle Marianian

Lower boundary of the middle Marianian has been defined by the FAD of *Strenuaeva* (see Liñán et al., 2002, 2004). In the OMZ, it is represented by the species *Strenuaeva sampelayoi* (see section 5.5. in this work). This trilobite is well-represented in the middle 'Alanís beds' between Cazalla de la Sierra and Alanís localities in northern Seville, co-occurring with the trilobites *Saukianda andalusiae*, *D. souzai*, *Alanisia guillermoi*, *Perrector perrectus*, *Eops eo*, and *Gigantopygus* cf. *bondoni*, representing the lower and middle assemblages of the middle Marianian. Since the stratigraphical log of the 'Alanís beds' from the Cazalla de la Sierra-Alanís section is probably duplicated, the exact position of the FAD of *Strenuaeva sampelayoi* in the sequence is not clear. Near Guadalcanal, in the Arroyo del Molino and Arroyo Tamujar sections, there is a slightly younger trilobite assemblage composed of *Andalusiana cornuta*, *Triangulaspis fusca*, and *Termierella sevillana*, assigned to the uppermost middle Marianian as they occur just below the FAD of *Serrodiscus bellimarginatus*. A very similar trilobite assemblage is present in the Alconera A1 section, composed of *S. sampelayoi*, *D. souzai*, *S. andalusiae*, *Kingaspis* (*Kingaspoides*) cf. *velata*, *G.* cf. *bondoni* in the lower and middle part of the middle Marianian sequence, and *T. sevillana*, *T. fusca*, and *Hicksia elvensis* in the uppermost middle Marianian. In the Sierra del Bujo section, northern Huelva, one single specimen of *S. sampelayoi* has been found from the lower 'Herrerías shale', with a trilobite association formed by *D. souzai*, *Callavia choffati*, *Rinconia schneideri*, *Calodiscus ibericus*, *Atops calanus*, and *Hicksia elvensis.*

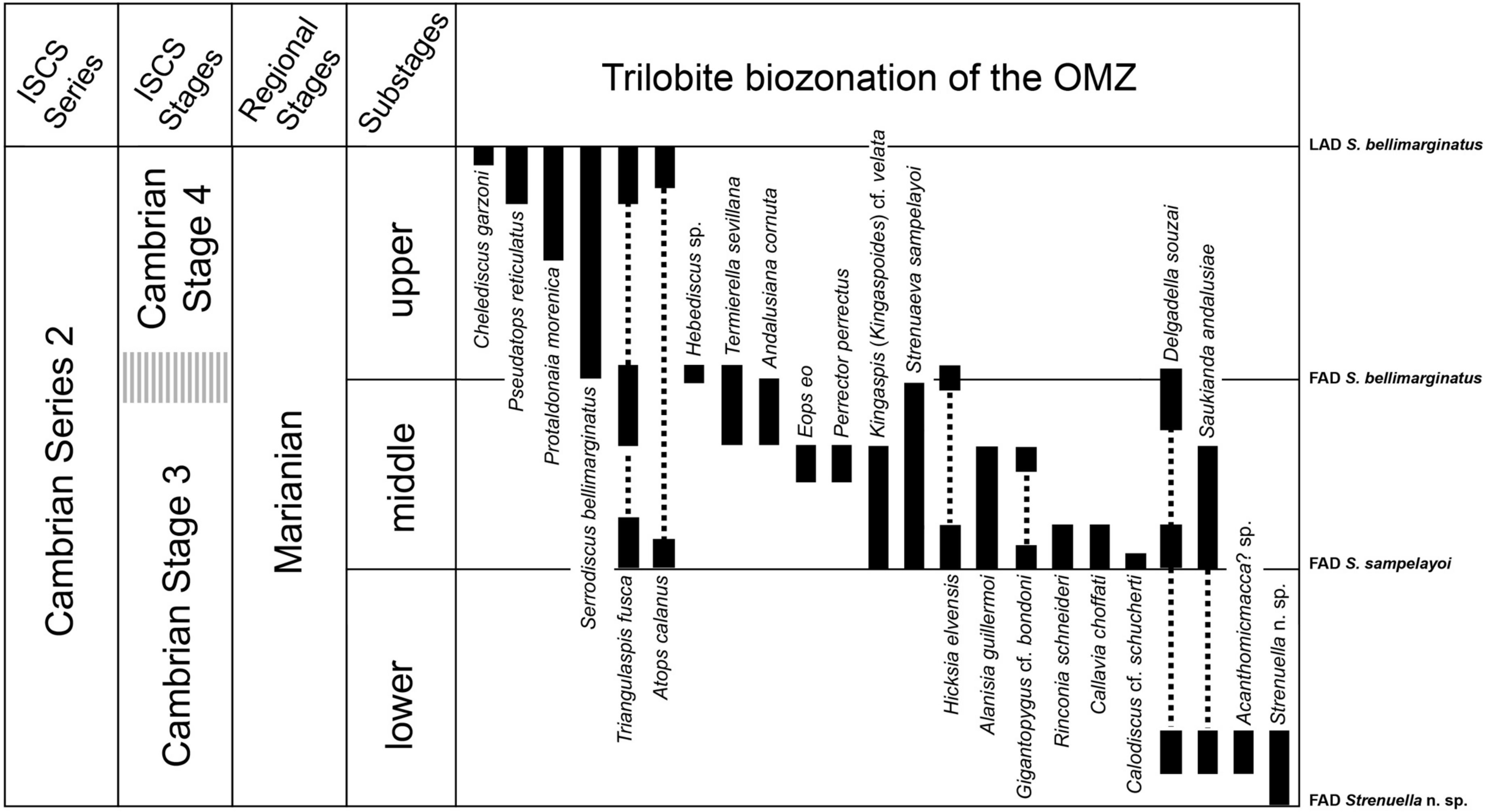

Figure 49: Stratigraphical distribution of Marianian trilobites of the Ossa-Morena Zone.

In the Iberian Chains, the genus *Strenuaeva* is represented by *Strenuaeva incondita* Sdzuy, 1961, which is present in both Huérmeda and Ribota formations in several localities, with a stratigraphical range spanning from lowermost middle Marianian to lowermost upper Marianian (see section 5.5.3. in this work).

Upper Marianian

The base and top of the upper Marianian are marked by the FAD and LAD of *Serrodiscus bellimarginatus*, respectively (see Collantes et al., 2022). This species is widely distributed in the Marianian outcrops of the OMZ: in the Alconera Block, it appears in the A3 section, together with *T. fusca*, *Hebediscus* sp., *Termierella sevillana* and, rarely, *D. souzai*. In the Viar-Benalija Block, this species is present in the Viar river section, together with *Protaldonaia morenica* and *Cheledisus garzoni*, and in the Camino de la Dehesilla fossil site, with no associated trilobites. In the Cumbres Block, it occurs in the uppermost 'Cumbres beds', together with *T. fusca, A. calanus*, *Pseudatops reticulatus* and *C. garzoni*. In the Herrerías Block, *S. bellimarginatus* occurs in different points assigned to El Pozuelo and Minas de Cala fossil sites, with a trilobite assemblage composed of *C. garzoni*, *P. reticulatus, T. fusca, P. morenica*, and *A. calanus*. In the Arroyomolinos Block, *Serrodiscus* occurs in UHU-AM1 and UHU-AM2, reported with *P. reticulatus* and *T. fusca*. In addition, *S. bellimarginatus* has been reported from different points between the Totanés-Noez area, Toledo Province (Central Iberian Zone). To date, no section has been formally selected to delimit the base of the upper Marianian in the OMZ.

6.3. International correlation and palaeobiogeographical affinities

The International Subcommission on Cambrian Stratigraphy (ISCS) initiated in 1999 the "Cambrian Subdivision Project" to establish official international stages and series for the Cambrian System (see Geyer, 2019 for review). However, global biostratigraphical correlations for the Cambrian System are problematic, given the endemic nature of trilobite associations and other fossils. Up to the moment, the Cambrian has been divided into four series (Babcock et al., 2005, 2011): Terreneuvian Series (Landing et al., 2007), Cambrian Series 2 (undefined), Miaolingian Series (Zhao et al., 2019) and Furongian (Peng et al., 2004). Regarding the Cambrian Series 2, some of its major constraints have been the scarcity of taxa with a wide geographical distribution and, in turn, the lack of precise stratigraphical range for those taxa (Peng et al., 2020).

Despite the scarcity of trilobite genera with a wide geographical distribution, the Marianian assemblages from Iberia show several faunal links with the Cambrian Series 2 from other palaeogeographical domains. In the present subsection, we review the different trilobite connections between the Cambrian Series 2 rocks from Iberia and those from other geographical domains to evaluate its hypothetical biostratigraphical potential through this time slice worldwide.

Along the Western Gondwana margin, it is noteworthy that the Marianian rocks of the Ossa-Morena Zone share the vast majority of trilobite genera with the Banian Stage of Morocco (e.g., *Strenuella*, *Acanthomicmacca*, *Saukianda*, *Gigantopygus*, *Perrector*, *Serrodiscus*, *Hebediscus*, *Calodiscus*, *Delgadella*, *Triangulaspis*, *Andalusiana*, *Termierella*, *Kingaspis*, among others; see Hupé, 1953a; Geyer, 1988, 1990; Geyer & Palmer, 1995). Several trilobite genera are also shared with the Cambrian Series 2 of Germany (e.g., *Serrodiscus*, *Calodiscus*, *Lusatiops*, *Acanthomicmacca*) (Geyer & Elicki, 1995; Geyer et al., 2014). Geyer & Landing (2004) introduced a comprehensive chronostratigraphical framework for the western Gondwana region to replace the previous regional stages and series from Morocco and Iberia. The proposed 'Atlasian Series' encompassed the Issendalenian and Banian stages, while the overlying 'Celtiberian Series' included the Agdzian, Caesaraugustan, and Languedocian stages. Despite this effort, this common chronostratigraphical model was never adopted. However, according to it, the Marianian would correspond to the Banian.

Regarding western and eastern Avalonia, the Marianian correlates with upper *Callavia* and lower *Strenuella sabulosa* Biozones (e.g., *Strenuella*, *Callavia*, *Pseudatops*, *Serrodiscus*, *Hebediscus*, *Chelediscus*, *Triangulaspis*) (Rushton, 1966; Fletcher, 2006). Throughout the Cambrian Series 2, and potentially until the end of the Cambrian, Avalonia was strongly linked to the western margin of Gondwana (Cocks & Torsvik, 2006; Pouclet et al., 2007), which is reflected in the similarity of its trilobite associations. According to Courjault-Radé et al. (1992; fig. 5), Iberia represented a peri-Gondwanan terrane located east of Avalonia, possibly belonging to the same biochorema. This view is also supported by Álvaro et al. (2013, p. 285), who considered the existence of new faunal links between Avalonia and West Gondwana at the end of Cambrian Series 2.

In Baltica, the Cambrian biostratigraphical schemes are based mostly on the Scandinavian (interpreted as the "inner-platform" sector) and the Holy Cross Mountains ("outer-platform" sector) sequences. The most consensual biostratigraphical scheme for this domain was outlined by Nielsen & Schovsbo (2011) with posterior modifications (e.g., Cederström et al., 2022). In what respects the Marianian of Iberia, it shows little faunal correlations: with upper *Holmia kjerulfi*–lower *Ellipsostrenua spinosa* Biozones in Scandinavia, given the presence of the trilobites *Strenuaeva*, *Calodiscus,* or *Chelediscus* (Axheimer et al., 2007; Cederström et al., 2009, 2011, 2022); and with the upper *Holmia-Schmidtiellus*–lowermost *Protolenus-Issafeniella* Biozones in Poland, with the shared occurrence of *Strenuaeva*, *Serrodiscus*, or *Atops* (Orlowski, 1985a, b; Żylińska, 2013a; Żylińska & Masiak, 2007; Żylińska & Szczepanik, 2009). Nevertheless, strong faunal links have been established with the Cambrian Series 2 of Morocco, sharing several ellipsocephalid trilobite genera with Baltica (see Álvaro et al., 2013).

Siberian domain (including both the Siberian Platform and the Altai-Sayan Foldbelt) shares abundant trilobite genera known from the Iberian Marianian, which are predominantly dominated by eodiscides (e.g., *Serrodiscus*, *Hebediscus*, *Calodiscus*, *Chelediscus*, *Delgadella*) as well as other groups (e.g., *Triangulaspis*, *Atops*, *Pseudatops*). In summary, the Marianian Stage matches most of the Botoman and lowermost Toyonian stages (Astashkin et al., 1995).

In a complementary way, new biostratigraphical links have been established with further territories belonging to the Laurentian domain (e.g., Laurentian Craton, Greenland, and Taconic Allochthon, among others). Although most polymerid trilobites from Laurentia seem endemic (see Pillola, 1991 for review), small, planktonic trilobites with worldwide distribution are known from this domain; for example, the genera *Serrodiscus*, *Calodiscus*, and *Chelediscus* (see Rasseti, 1952, 1966, 1967). Other trilobites include the genera *Atops* and *Pseudatops* (see Collantes et al., 2021a for review). Consequently, new faunal links were established in this work between the Marianian Stage of Iberia, the Laurentian Dyeran Stage, and the *Elliptocephala asaphoides* Biozone from the Taconic Allochthon.

Concerning South Australia, few trilobite genera are shared with the Cambrian Series 2 of Iberia, namely *Serrodiscus*, *Atops*, and, with plenty of reservations, the genus *Alanisia* (Jenkins & Hasenohr, 1989; Bengtson et al., 1990; Jell et al., 1992). A tentative correlation of the Marianian with the so-called *Pararaia janeae* Biozone from Australia can be suggested.

7. Conclusions

The Marianian Stage is a subdivision of the Cambrian Series 2 of the Iberian Peninsula, characterised by a low diversity and abundance of fossils. Trilobites from the Marianian of the Ossa-Morena Zone (OMZ), southwestern Iberia, have been known for over a century. However, they lacked a comprehensive review and update and have received little attention in recent decades, during which only a few punctual contributions have been made.

Trilobite fossils occur in six tectonosedimentary units: Alter do Chão-Elvas Sector (also known as Vila Boim Block), Alconera Block, Viar-Benalija Block, Cumbres Block, Herrerías Block, and Arroyomolinos Block. Through the new stratigraphical and palaeontological studies on Marianian sequences of the OMZ, it was possible to check, refine and sometimes correct the stratigraphical setting of the Marianian trilobite records. The Marianian sequences of these blocks were correlated using lithostratigraphical and biostratigraphical analysis.

Through bibliographical review and fieldwork, the classic fossil sites originally reported by Franz Lotze, Wilhelm Simon, Rudolf and Emma Richter, and Klaus Sdzuy, among others, were located, and new materials were collected. New fossil sites were also discovered and sampled. About 1300 specimens have been collected and the most relevant collections of Marianian trilobites from the OMZ were visited and reviewed: Museu Geológico de Lisboa (Portugal), the Senckenberg Museum of Frankfurt (Germany), the collections of Prof. María Dolores Gil Cid (Departamento de Palaeontología, Complutense University of Madrid, Spain) and the collections of Prof. Eladio Liñán at the University of Zaragoza (Spain). Among these collections, 585 specimens were selected for study.

The review of the Marianian trilobites of the OMZ to date has allowed us to consider a total of 23 species, four of them left in open nomenclature, belonging to 23 genera (Tab. 3). One new species was erected (*Chelediscus garzoni*), confirming the presence of this genus in the OMZ Marianian. Two genera have been identified for the first time for this age/zone (*Kingaspis* and *Pseudatops*); and the presence of *Ferralsia* and *Longianda* is rejected. Six species were taxonomically studied, described and figured in five indexed published papers (section 5): *Atops calanus*, *Callavia choffati*, *Chelediscus garzoni*, *Pseudatops reticulatus*, *Serrodiscus bellimarginatus* and *Strenuaeva sampelayoi*. The identification of 11 previously reported taxa has been updated. Two case studies *(Serrodiscus* and *Strenueva*) demonstrated the taphonomical role in the preservation of some characters, justifying the previous species splitting for some genera.

A series of conclusions regarding the systematics of some of the studied trilobite groups were made. Specimens from genera *Pseudatops, Kingaspis*, *Chelediscus* and *Hebediscus* are figured for the first time in this territory. *Callavia*? *lotzei* is considered a junior synonym of '*Paradoxides choffati.*'; *Sdzuyomia* is considered a junior synonym of *Callavia*; the species '*S. melendezi*', '*Ellipsostrenua alanisiana*' and '*S*. *marocana*' are considered junior synonyms of *S. sampelayoi*. *Callavia* is here assigned to Judomioidea and *Calodiscus* to Calodiscidae Repina, 1979, and new diagnoses are provided for both genera. The new species *Chelediscus garzoni*, together with *Chelediscus carus* from the Botoman of Siberia, are the earliest appearances of the genus, suggesting that a smooth, unlobed glabella is primitive for the genus. *Serrodiscus* species are grouped into three groups (*bellimarginatus* group, *speciosus* group and *daedalus* group), which shed light on the evolution and distinct lineages within this important genus with a global distribution.

From a biostratigraphical point of view, the Marianian trilobite stratigraphical distribution through the OMZ is updated. The base of the Marianian Stage is characterised by the FAD of *Strenuella*, the boundary with the middle Marianian is defined by the FAD of *Strenuaeva sampelayoi*, and the base and top of the upper Marianian are marked, respectively, by the FAD and LAD of *Serrodiscus bellimarginatus*. Several Marianian trilobite genera have been found in common with the Central Iberian Zone (e.g., *Serrodiscus*, *Chelediscus*, *Triangulaspis*, *Andalusiana*, *Termierella*, *Acanthomicmacca*?) as well as with the Iberian Chains (e.g., *Strenuaeva*, *Andalusiana*, *Termierella*, *Kingaspis*, *Hebediscus*).Their significance demonstrates the potential of this group for the correlation of the Marianian Stage across the Iberian Peninsula, one of the major limitations of the Cambrian of the Iberian Peninsula in recent years.

On a global scale, the new biostratigraphical data reinforced the correlation between the Marianian sequences from southwestern Iberia with other Cambrian Series 2 sequences across various regions. In this sense, along the western margin of Gondwana, the strong correlation between the trilobite associations from the Marianian of the OMZ and those of the Banian Stage in Morocco has been demonstrated, as well as with the Cambrian Series 2 from Germany. In the same line, correspondences of the Marianian trilobites with those of the upper *Callavia* Biozone and the lower *Strenuella sabulosa* Biozone from western and eastern Avalonia (i.e., Newfoundland and United Kingdom, respectively) have been improved, and the faunal links between both regions strengthened. With Baltica, much of the Marianian Stage can be correlated to the lower to middle Vergalian-Rausvian Stages, and more specifically with the upper *Holmia kjerulfi*–lower *Ellipsostrenua spinosa* Biozone in Scandinavia, and with the upper *Holmia-Schmidtiellus*–basal *Protolenus-Issafeniella* Biozone in Poland. In Siberia, a concurrence is evident with most of the Botoman and the lowermost Toyonian stages. Regarding the Laurentian domain, new biostratigraphical correspondences have been established between the former and Iberia, sharing several trilobite genera with the Dyeran Stage of the Laurentian Craton and Greenland, and the *Elliptocephala asaphoides* Biozone of the Taconic Allochthon. Finally, a few trilobite genera (including *Serrodiscus*, *Atops* and, possibly, *Alanisia*) are shared with the lower Cambrian Series 2 of Australia (eastern Gondwana), specifically with the *Pararaia janeae* Biozone.

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