PALAEONTOLOGICAL PUBLICATIONS - VOL. 9

7th International Trilobite Meeting

Abstracts Book

San Emiliano (Spain)
6th–11th July 2026

Esteve, J., Fernández-Martínez, J.,
González-Cloquells, A., Fuertes-Murciego, I. (Eds.)

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Ros-Franch, S., Martínez-Pérez, C.
(Editors of the Series)

Published by:

Sociedad Española de Paleontología

Series: Palaeontological Publications Nº 9

7th International Trilobite Meeting. Abstracts Book. Esteve, J., Fernández-Martínez, J., González-Cloquells, A., Fuertes-Murciego, I. (Eds.). San Emiliano, Spain, 2026.

216 pp, 17x24 cm

ISBN-13: 978-84-09-88472-8

1. Palaeontology - 2. Meeting - 3. Spain - 4. Trilobites - 5. Sociedad Española de Paleontología, ed.

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It is suggested that either of the following alternatives should be used for future bibliographic references to the whole or part of this volume:

Esteve, J., Fernández-Martínez, J., González-Cloquells, A., Fuertes-Murciego, I. (Eds.) (2026). 7th International Trilobite Meeting. Abstracts Book. *Palaeontological publications*, *9*, 216 pp.

Briggs, D. E. G. (2026). Trilobites and their relatives: Fifty years and ongoing. In Esteve, J. *et al.* (Eds.), 7th International Trilobite Meeting. Abstracts Book. *Palaeontological publications*, *9*, 9–15.

Cover:
Trilobite cluster from the Drumian Wheeler Formation of Utah; picture by Rudy Lerosey-Aubril. *Olenoides serratus* from the Burgess Shale; picture by Sarah Losso. *Burmeisteria notica* from the Devonian of Brazil; picture by Gilmar Kerber. La Majúa Member of the San Emiliano Formation; picture by Pablo Suárez-González.

Back cover:
Esla Nappe from the Alto del Pozo; picture by Manuel de Paz.

Chapter title pages:
Calymene sp. (MCZ8284_2_BW), *Calymene blumenbachi* (MCZ8212_M), *Ptychoparia striata* (L37130_1). Pictures by Francesc Pérez-Peris.

Logo:
Designed by María Gabriela Suárez and Jorge Esteve.

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editor@sepaleontologia.es

ISBN-13: 978-84-09-88472-8

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FIELD TRIP

TRILOBITES AND THEIR RELATIVES: FIFTY YEARS AND ONGOING

(Dedicated to the memory of Richard Fortey 1946-2025)

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Keywords: Trilobites, Arthropods, Meeting.

TRILOBITES AND THEIR RELATIVES: THE INAUGURAL MEETING IN OSLO 1973

As we embark on the 7th International Meeting on *Trilobites and their relatives* it seems appropriate to reflect on how the field has progressed since 1973 when the first international meeting took place in Oslo. That meeting was organized by David Bruton of the University of Oslo as a NATO Advanced Study Institute (Bruton, 2019). There were 60 invitees and 32 presentations resulting in a volume published two years later (Martinsson, 1975).

Citations to papers in conference volumes are a crude measure of the impact of the event because attendees may decide to publish elsewhere and critical taxonomic papers may have long term relevance that is not reflected in the attention they garner. The Oslo volume (Martinsson, 1975) is arguably an exception, however, as the 30 papers include the majority of those presented at the meeting. The paper by Richard Fortey (Figure 1), to whose memory this presentation is dedicated, is by far the most cited. He identified trilobite communities at different depths onshore to offshore along the margin of Laurentia based on his field work on the Ordovician Valhallfonna Formation in Spitsbergen (Fortey, 1975). Fortey's results have had far-reaching implications for understanding the environmental preferences of trilobites, their utility for correlating sequences and defining faunal provinces, and ultimately for reconstructing palaeogeography and testing plate configurations. Peter Jell also considered faunal provinces, reconstructing the distribution

Figure 1. Derek Briggs, Richard Fortey and Jorge Esteve, with his daughter, at the North American Paleontological Convention at the University of California, Riverside, in 2019.

of Cambrian continental masses in a paper that was published elsewhere (Jell, 1974). Other highly cited papers include descriptions of trilobite anatomy, particularly the limbs, based on exceptionally preserved examples of *Olenoides* from the Burgess Shale (Whittington, 1975), and *Triarthrus* from Beecher's Trilobite Bed (Cisne 1975), as well as a paper reviewing the evolution of the trilobite eye (Clarkson, 1975). Issues of high-level classification were considered by Fortey and Owens (1975) who proposed a new order Proetida, and Hughes and Ingham (1975) presented a new subfamilial classification of trinucleids, illustrated by multiple stereo pairs. The place of trilobites in the evolution of arthropods was addressed by Hessler and Newman (1975) who concluded that the Trilobitomorpha gave rise to both chelicerates and crustaceans, but these phylogenetic papers predated the widespread adoption of cladistic methods. Important themes at the Oslo meeting, including anatomy (as revealed by exceptional preservation), mode of life and palaeoecology, classification, and evolution, remain central to trilobite research today.

ST. CATHERINES 1997

The second international meeting, *Trilobite paleobiology: Past, present, and future*, was a long time coming. It took place in 1997, organized by Jonathan Adrain and Stephen Westrop at Brock University in St. Catharines, Ontario, Canada, and attracted 85 attendees. Fourteen of the papers were published in 1999 as an issue of the *Journal of Paleontology*. Adrain and Westrop (1999) noted in their introduction to the published papers that the most substantial change in the 25 years since the Oslo meeting was the adoption of cladistic methods. Fortey and Chatterton had been the first to publish a computer-based phylogenetic analysis of trilobites, on Asaphina, in 1988. Advances in computing had also allowed morphometrics to become a new and widely applied tool in investigations of taphonomy, taxonomy, and the evolution of disparity through time. The importance of data on ontogenetic sequences was becoming widely recognized, capitalizing on silicified material and advances in scanning electron microscopy. Trilobite palaeoecology, now informed by taphonomic considerations, was illuminating the macroevolution of the group although Adrain and Westrop (1999) noted, perhaps prematurely, that 'functional morphology ... has ceased to be pursued in any meaningful way'. There was less emphasis on palaeobiogeography, perhaps because plate tectonics was by then a guiding principle in earth sciences. Given increases in computing power it is perhaps not surprising that the two papers in the published volume that have received the most citations are a cladistic analysis of the relationships of Cambrian Arachnata and the position of Trilobita, which applied PAUP (phylogenetic analysis using parsimony) to a matrix of 29 characters (Edgecombe & Ramsköld, 1999) and a consideration of the compaction of Cambrian olenelloids and its implications for morphometric studies, based on a comparison of silicified and shale specimens (Webster & Hughes ,1999). Adrain and Westrop (1999) predicted the continued use of cladistics and morphometrics, and an ongoing emphasis on evolutionary palaeoecology and taphonomy, in looking forward to the next conference.

OXFORD 2001

The third meeting on *Trilobites and Their Relatives*, organized by Derek Siveter at Oxford in 2001, was attended by more than 120 delegates. The abstracts covered 60 talks (and one reserve) and 24 posters, and 22 papers were published in a volume of *Special Papers in Palaeontology* (Lane *et al*., 2003). 'The sessions were broadly divided into themes around trilobite functional morphology, palaeoecology, systematics, evolution and palaeogeography, and stratigraphy, together with a consideration of broader arthropod phylogenetic questions' (Fortey *et al*., 2003). The areas of investigation may have been similar to those covered in the first two meetings but new approaches included the development of computer-aided reconstructions, new morphometric methods, and even the potential for integrating molecular data with morphology in generating a phylogeny of living arthropods (McCormick, 2001). This last topic, an early contribution on the application of

phylogenomics to arthropods presented by Gregory Edgecombe and published in *Nature* (Giribet *et al*., 2001) has attracted an order of magnitude more citations than the other papers presented at the conference. The highest cited papers in the published volume include a detailed report by Terence Fletcher on the role of trilobites in correlating Cambrian sequences based on decades of his fieldwork in Newfoundland (Fletcher, 2003), an important contribution at a time when no subdivisions of the Cambrian were recognized globally. An account of cryptic behaviour in trilobites reported specimens hiding in burrows and in priapulid tubes (Chatterton *et al*., 2003). Papers on other exceptionally preserved arthropods also attracted significant attention including a description of a three-dimensionally preserved Cambrian phosphatocopid crustacean from Shropshire, UK (Siveter *et al*., 2003) and new information on *Offacolus* from the Herefordshire biota (Sutton *et al*., 2002) and *Marrella* from the Burgess Shale (García-Bellido & Collins, 2006), the last two published elsewhere.

TOLEDO 2008

The fourth meeting, organized by Isabel Rábano, was held in Toledo in 2008, and attracted over 100 participants. In contrast to the previous trilobite conferences, a book of the 75 extended abstracts was available at the meeting (Rábano *et al*., 2008) There were 45 presentations and a keynote by Richard Fortey on the life habits of trilobites, a long-term focus of his research, as well as 30 posters. Jonathan Adrain gave a presentation on the *Treatise*. A range of trilobite research was represented: systematics and classification, biostratigraphy, evolution, Lagerstätten (including the Cambrian Emu Bay Shale, Ordovician Beecher's Trilobite Bed, and the Silurian of Herefordshire), palaeobiogeography, morphometrics, and mode of life (Clarkson & Schoenemann, 2008).

PRAGUE 2012

The fifth meeting, organized by Oldrich Fatka and Petr Budil, took place in Prague in 2012 and was dedicated to the memory of Harry Whittington. About 60 participants attended and the 50 abstracts, 30 of them oral presentations, covered a series of topics: biostratigraphy and palaeogeography, evolution and systematics, taphonomy and lagerstätten, non-trilobite arthropods, palaeobiology and palaeoecology (Budil *et al.,* 2014a). The published volume contains 17 papers reflecting the themes addressed (Budil *et al.,* 2014b). Those attracting the most citations all deal with Cambrian topics: The biostratigraphy of the Pribram Jince basin in the Czech Republic (Fatka & Szabad, 2014), the early ontogeny of the Cambrian trilobite *Sao hirsuta* from the Barrandian of the Czech Republic (Laibl *et al*., 2014), and the appendages of a radiodont and an arthropod from the Cambrian Weeks Formation Lagerstätte in Utah (Lerosey-Aubril *et al*., 2014). Other presentations on exceptionally preserved fossils, published elsewhere, attracted multiple citations including a report on the nature of the limbs of a horseshoe crab from the Silurian Herefordshire Lagerstätte (Briggs *et al*., 2012) and the morphology of *Anomalocaris* from the Burgess Shale and Emu Bay Shale (Daley & Edgecombe, 2014).

TALLINN 2017

The most recent meeting was organized by Helje Pärnaste in 2017 in Tallinn in Estonia. More than 80 participants attended and there were 55 oral and poster presentations (Pärnaste, 2019). The published volume (Owen & Bruton, 2019) comprised just 7 papers, most with a focus on stratigraphy and systematics. The conference sessions, however, covered a much wider range of topics: Lagerstätten, functional morphology, early arthropod evolution, systematics and phylogeny, Cambrian trilobites, the Great Ordovician Biodiversification Event, and Devonian trilobites (Pärnaste, 2019). Among the many presentations, subsequent publications on the

development and evolution of facial sutures (Drage *et al*., 2018) and the evolution of cranidial shape (Hopkins, 2017) have attracted particular attention.

RECENT HIGHLIGHTS

New discoveries, techniques and analyses have propelled trilobite research forward since the 2017 meeting in Tallinn. Concretions in a volcanic ash from Morocco yielded previously unknown 3-dimensional details of the limbs and digestive system of a Cambrian ellipsocephaloid to microtomography (El Albani *et al*., 2024). Reexamination of specimens of *Olenoides* from the Burgess Shale and *Triarthrus* from Beecher's Trilobite Bed indicate that five appendages were present in the trilobite cephalon (Hou & Hopkins, 2024). Hypotheses about relationships within trilobites and their position among arthropods (including the place of Agnostina, for example) continue to be tested (Paterson, 2020). Development and changes through ontogeny in different trilobite taxa are being documented, and not just via silicified material (Dai *et al*., 2023, Wang *et al*., 2025). Function is being analysed using biomechanical and other quantitative approaches including computational fluid dynamics (Esteve & López-Pachón, 2023). The role of extinction in trilobite macroevolution is being explored using morphometric data (Balseiro *et al*., 2025).

ONGOING

Richard Fortey wrote an introduction, appropriately entitled Trilobites: an ongoing story (Fortey 2024), to a recent issue of the *Journal of Paleontology* devoted to trilobites. He notes the importance of trilobites in stratigraphy, particularly in the Cambrian, and the need to link them to other methods of calibrating time, including isotope excursions. His last paper on trilobites, on rare occurrences of deeper water biofacies (Fortey *et al*., 2024), is published in the same issue and confirms the biostratigraphic utility of Olenidae as they exhibit 'biogeographic independence'. The fundamental importance of phylogenetic analyses to understanding trilobite evolution is illustrated by a paper on the convergence of the fringe in trinucleids and harpetids (Beech *et al*., 2024). Fortey (2024) emphasizes the value of 'old-fashioned' fieldwork, including careful collecting of logged sections, as a means of identifying extinction events (Westrop *et al*., 2024), for example, as well as the importance of museum specimens as a resource for future research. While noting our recent 'preoccupation with Konservat-Lagerstätten', he exhorts future researchers to appreciate the value of trilobites with their readily preserved calcified skeletons, noting that their morphological complexity and abundance allow quantitative data through time to be used to address a range of scientific questions. No doubt this 7th international meeting on trilobites will include testament to the wisdom of his views.

REFERENCES

Adrain, J. M. & Westrop, S. R. (1999). Trilobite paleobiology: Past, present and future. *Journal of Paleontology*, *73*, 161–163. doi: 10.1017/S0022336000027682

Balseiro, D., Serra, F. & Bignon, A. (2025). Extinction drives both expansion and contraction of morphological disparity in trilobites. *Proceedings of the Royal Society B: Biological Sciences, 292*, 2055. doi: 10.1098/rspb.2025.1418

Beech, J. D., Bottjer, D. J. & Smith, N. D. (2024). Parallel evolution of unusual 'harpiform' morphologies in distantly related trilobites. *Journal of Paleontology*, *98*, 732–743. doi: 10.1017/jpa.2024.47

Briggs, D. E. G., Siveter, D. J., Siveter, D. J., Sutton, M. D., Garwood, R. J. and Legg, D. (2012). Silurian horseshoe crab illuminates the evolution of arthropod limbs. *Proceedings of the National Academy of Sciences*, *109*, 15702–15705. doi: 10.1073/pnas.1205875109

Bruton, D. L. (2019). From Oslo to Prague - the Trilobite meetings 1973-2012. *Fossils and Strata*, *64*, 5–16. doi: 10.1002/9781119564249.ch2

Budil, P., Fatka, O., Holloway, D. J. & Hughes, N. (2014a). From J. Barrande to H.B. Whittington. *Bulletin of Geosciences*, *89*, 201–450.

Budil, P., Fatka, O., Holloway, D. J. & Hughes, N. (2014b). From J. Barrande to H.B. Whittington (Introduction). *Bulletin of Geosciences*, *89*, 201–202. doi: 10.3140/bull.geosci.1510

Chatterton, B. D., Collins, D. H., Ludvigsen, R. & Lane, P. (2003). Cryptic behaviour in trilobites: Cambrian and Silurian examples from Canada, and other related occurrences. *Special Papers in Palaeontology*, *70*, 157–174.

Cisne, J. L. (1975). Anatomy of *Triarthrus* and the relationships of the Trilobita. *Fossils and Strata*, *4*, 45–64. doi: 10.18261/8200049639-1975-03

Clarkson, E. & Schoenemann, B. (2008). 4th International Conference of trilobites and their relatives. *Palaeontological Association Newsletter*, *69*, 46–48.

Clarkson, E. N. K. (1975). The evolution of the eye in trilobites. *Fossils and Strata*, *4*, 7-32. doi: 10.18261/8200049639-1975-01

Dai, T., Zhang, X. & Peng, S. (2023). Developmental traits and life strategy of redlichiid trilobites. *Biological Reviews*, *98*, 63–80. doi: 10.1111/brv.12895

Daley, A.C. & Edgecombe, G.D. (2014). Morphology of *Anomalocaris canadensis* from the Burgess Shale. *Journal of Paleontology*, *88*, 68–91. doi: 10.1666/13-067

Drage, H.B., Laibl, L. & Budil, P. (2018). Postembryonic development of *Dalmanitina*, and the evolution of facial suture fusion in Phacopina. *Paleobiology*, *44*, 638–659. doi: 10.1017/pab.2018.31

Edgecombe, G.D. & Ramsköld, L. (1999). Relationships of Cambrian Arachnata and the systematic position of Trilobita. *Journal of Paleontology*, *73*, 263-287. doi: 10.1017/S0022336000027761

El Albani, A., Mazurier, A., Edgecombe, G. D., Azizi, A., El Bakhouch, A., Berks, H. O., Bouougri, E. H., Chraiki, I., Donoghue, P. C., Fontaine, C. & Gaines, R. R. (2024). Rapid volcanic ash entombment reveals the 3D anatomy of Cambrian trilobites. *Science*, *384*, 1429–1435. doi: 10.1126/science.adl4540

Esteve, J. & López-Pachón, M. (2023). Swimming and feeding in the Ordovician trilobite *Microparia speciosa* shed light on the early history of nektonic life habits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *625*, p.111691. doi: 10.1016/j.palaeo.2023.111691

Fatka, O. & Szabad, M. (2014). Cambrian biostratigraphy in the Pøíbram-Jince Basin (Barrandian area, Czech Republic). *Bulletin of Geosciences*, *89*, 411–427. doi: 10.3140/bull.geosci.1456

Fletcher, T. P. (2003). *Ovatoryctocara granulata*: the key to a global Cambrian stage boundary and the correlation of the olenellid, redlichiid and paradoxidid realms. *Special Papers in Palaeontology*, *70*, 73–102.

Fortey, R. A. (1975). Early Ordovician trilobite communities. *Fossils and Strata* 4, 331-352. doi: 10.18261/8200049639-1975-21

Fortey, R. A. (2024). Trilobites: an ongoing story. *Journal of Paleontology*, 98, 449-451. doi: 10.1017/jpa.2024.51

Fortey, R. A. & Chatterton, B. D. E. (1988). Classification of the suborder Asaphina. *Palaeontology*, *31*, 165–222.

Fortey, R. A. & Owens, R. M. (1975). Proetida - a new order of trilobites. *Fossils and Strata*, *4*, 227–240. doi: 10.18261/8200049639-1975-14

Fortey, R. A., Lane, P. D. & Siveter, D. J. (2003). Introduction. *Special Papers in Palaeontology,* 70, 7-8.

Fortey, R. A., Vargas-Parra, E. E. & Droser, M. L. (2024). Trilobites from the Al Rose Formation (Lower Ordovician, Inyo Mountains, California)—faunas marginal to the Great Basin. *Journal of Paleontology*, *98*, 644–657. doi: 10.1017/jpa.2023.57

García-Bellido, D.C. & Collins, D.H., (2006). A new study of Marrella splendens (Arthropoda, Marrellomorpha) from the Middle Cambrian Burgess Shale, British Columbia, Canada. *Canadian Journal of Earth Sciences*, *43*, 721–742. doi: 10.1139/e06-012

Giribet, G., Edgecombe, G. D. & Wheeler, W. C. (2001). Arthropod phylogeny based on eight molecular loci and morphology. *Nature*, *413*, 157–161. doi: 10.1038/35093097

Hessler, R. R. & Newman, W. A. (1975). A trilobitomorph origin for the Crustacea. *Fossils and Strata*, *4*, 437–460. doi: 10.18261/8200049639-1975-29

Hopkins, M. J. (2017). How well does a part represent the whole? A comparison of cranidial shape evolution with exoskeletal character evolution in the trilobite family Pterocephaliidae. *Palaeontology*, *60*, 309–318. doi: 10.1111/pala.12287

Hou, J. B. & Hopkins, M. J. (2024). New evidence for five cephalic appendages in trilobites and implications for segmentation of the trilobite head. *Palaeontology*, *67*, p.e12723. doi: 10.1111/pala.12723

Hughes, C. P., Ingham, J. K. & Addison, R. (1975). The morphology, classification and evolution of the Trinucleidae (Trilobita). *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *272*, 537–604. doi: 10.1098/rstb.1975.0100

Jell, P.A. (1974). Faunal provinces and possible planetary reconstruction of the Middle Cambrian. *The Journal of Geology*, *82*, 319–350. doi: 10.1086/627967

Laibl, L., Fatka, O., Cronier, C. & Budil, P. (2014). Early ontogeny of the Cambrian trilobite Sao hirsuta from the Skryje-Týřovice Basin, Barrandian area, Czech Republic. *Bulletin of Geosciences*, *89*, 293–309. doi: 10.3140/bull.geosci.1438

Lane, P. D., Siveter, D.J . & Fortey, R. A. (eds) (2003). Trilobites and their relatives. Contributions from the Third International Conference, Oxford 2001. *Special Papers in Palaeontology*, *70*, 1–397.

Lerosey-Aubril, R., Hegna, T. A., Babcock, L. E., Bonino, E. & Kier, C. (2014). Arthropod appendages from the Weeks Formation Konservat-Lagerstätte: new occurrences of anomalocaridids in the Cambrian of Utah, USA. *Bulletin of Geosciences*, *89*, 269–282. doi: 10.3140/bull.geosci.1442

Martinsson, A. (ed.) (1975). Evolution and morphology of the Trilobita, Trilobitoidea and Merostomata. *Fossils and Strata*, *4*, 1–467. doi: 10.18261/8200049639-1975

McCormick, T. 2001 Third International Conference of trilobites and their relatives. *Palaeontological Association Newsletter, 47*, 44–51.

Owen, A. W. & Bruton, D. L. (2019). Papers from the 6th International Conference on Trilobites and their Relatives. *Fossils and Strata*, *64*, 1-3. doi: 10.1002/9781119564249.ch1

Pärnaste, H. (2019). The 6th International Conference on Trilobites and their Relatives: Tallinn calling, Estonia celebrating. *Fossils and Strata*, *64*, 17–22. doi: 10.1002/9781119564249.ch3

Paterson, J. R. (2020). The trouble with trilobites: classification, phylogeny and the cryptogenesis problem. *Geological Magazine*, *157*, 35–46. doi: 10.1017/S0016756819000426

Rábano, I., Gozalo, R. & García-Bellido, D. (eds.) (2008). Advances in trilobite research. *Cuadernos del Museo Geominero* 9. Inst. Geol. y Minero de España, Madrid, 448 pp.

Siveter, D., Waloszek, D. & Williams, M. (2003). An early Cambrian phosphatocopid crustacean with three-dimensionally preserved soft parts from Shropshire, England. *Special Papers in Palaeontology*, *70*, 9–30.

Sutton, M. D., Briggs, D. E. G., Siveter, D. J., Siveter, D. J. & Orr, P.J. (2002). The arthropod *Offacolus kingi* (Chelicerata) from the Silurian of Herefordshire, England: computer based

morphological reconstructions and phylogenetic affinities. *Proceedings of the Royal Society B: Biological Sciences*, *269*, 1195–1203. doi: 10.1098/rspb.2002.1986

Wang, Y., Esteve, J., Wang, D., Ren, G., Zhang, H., Luo, X. & Yang, X. (2025). Moulting behaviors in oryctocephalid trilobites reveal ontogenetic shifts in ecdysial strategies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *684*, 113527. doi: 10.1016/j.palaeo.2025.113527

Webster, M. & Hughes, N. C. (1999). Compaction-related deformation in Cambrian olenelloid trilobites and its implications for fossil morphometry. *Journal of Paleontology*, *73*, 355–371. doi: 10.1017/S0022336000027827

Westrop, S. R., Welch, K. F., Engel, M. H. & Adrain, J. M. (2024). Faunal and paleoenvironmental changes at a Cambrian (Jiangshanian; Steptoean–Sunwaptan boundary interval) trilobite extinction event, in contrasting deep-and shallow-subtidal settings, Nevada and Oklahoma. *Journal of Paleontology*, *98*, 584–611. doi: 10.1017/jpa.2023.75

Whittington, H. B. (1975). Trilobites with appendages from the Middle Cambrian, Burgess Shale, British Columbia. *Fossils and Strata*, *4*, 97–136. doi: 10.18261/8200049639-1975-06

KEYNOTES

TRILOBITE APPENDICULAR MORPHOLOGY: INSIGHTS INTO MATING, LOCOMOTION, DEFENSIVE BEHAVIORS, AND RESPIRATION

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Keywords: Trilobite, appendage preservation, biomechanics, enrollment.

Trilobites are an abundant and diverse part of the Paleozoic macroscopic fossil record mainly known from their readily fossilized calcitic exoskeletons. To date, 41 species are known with preserved appendages ranging from the early Cambrian to Early Devonian, revealing morphological and functional variability in this clade (Losso *et al*., 2026). Trilobites bore a pair of uniramous antennae followed by a series of biramous ventral appendages, the latter composed of a protopodite (appendage base), endopodite (walking leg) and exopodite (gill). Only 14 trilobite species show evidence of well-preserved and nearly complete appendage series (Losso *et al.*, 2026). Comparisons between the biramous appendages suggest modular evolution between the endopodite and exopodite. Whereas endopodite organization is largely stable between trilobite groups of different ages, exopodite morphology is highly variable in number and width of articles, number and size lamellae and size relative to endopodite, likely in response to selective pressures from their environment and function (respiration vs. swimming) (Losso *et al.*, 2026). Detailed study of the appendicular morphology from different clades and preservation styles can provide insights into behavior and functional morphology of these extinct animals, including the mating style of *Olenoides serratus* based on the presence of supposed claspers.

Olenoides serratus from the Cambrian Burgess Shale is one of the best-known trilobites with preserved appendages is (Fig. 1A). Over 60 specimens of *O. serratus* preserve limbs (Losso *et al.*, 2025, 2026; Whittington, 1975, 1980). The abundant specimens of *O. serratus* allowed for study on limb flexure and extension through measurement of the angles between podomeres (Losso *et al.*, 2025). The limbs exhibit flexure proximally and a greater ability to extend distally unlike modern horseshoe crabs which display an alternating pattern of joints (Fig. 1C). A three-dimensional, articulating model of the limbs in *O. serratus* shows how the limbs could move to create common variations of *Rusophycus* and *Cruziana*.

Unlikely the highly compressed Burgess Shale fossils, the trilobites from the Walcott-Rust Quarry preserve non-biomineralize ventral anatomy as calcite filled external casts (Brett *et al.*, 1999; Losso *et al*., 2023). Specimens are prepared as thin sections, allowing the three-dimensional morphology to be seen. In *Ceraurus pleurexanthemus* and *Flexicalymene* sp., thin sections through the proximal part of the pleural lobes display wedge-shaped protopodites narrowing ventrally (Fig. 2A; Losso *et al*., 2023). The wedge-shaped protopodites facilitated enrollment by allowing the limbs to fit snuggly together to be completely protected by the exoskeleton.

Exopodites are well-known in 11 species of trilobites, with variation in number and shapes of articles and lamellae, and lamellar cross section (Fig. 2E; Losso *et al.*, 2026). To calculate surface area of the lamellae, 3D models of exopodites in *O. serratus* and *T. eatoni* were created. The surface area (SA) of 9 additional trilobites was calculated through measurement of lamellae and scaled to the number of limbs and size along the body. This shows a large SA for *O. serratus* at 16,589 mm^2 compared to the 2,159 mm^2 for the much smaller *T. eatoni*. The results indicate that lamellae SA of trilobites increased exponentially with overall body size. Trilobite data follows the

same trendline of gill SA/biomass observed in extant species and thus supports the interpretation of their exopodites as respiratory structures despite substantial variation in morphology (Fig. 2F).

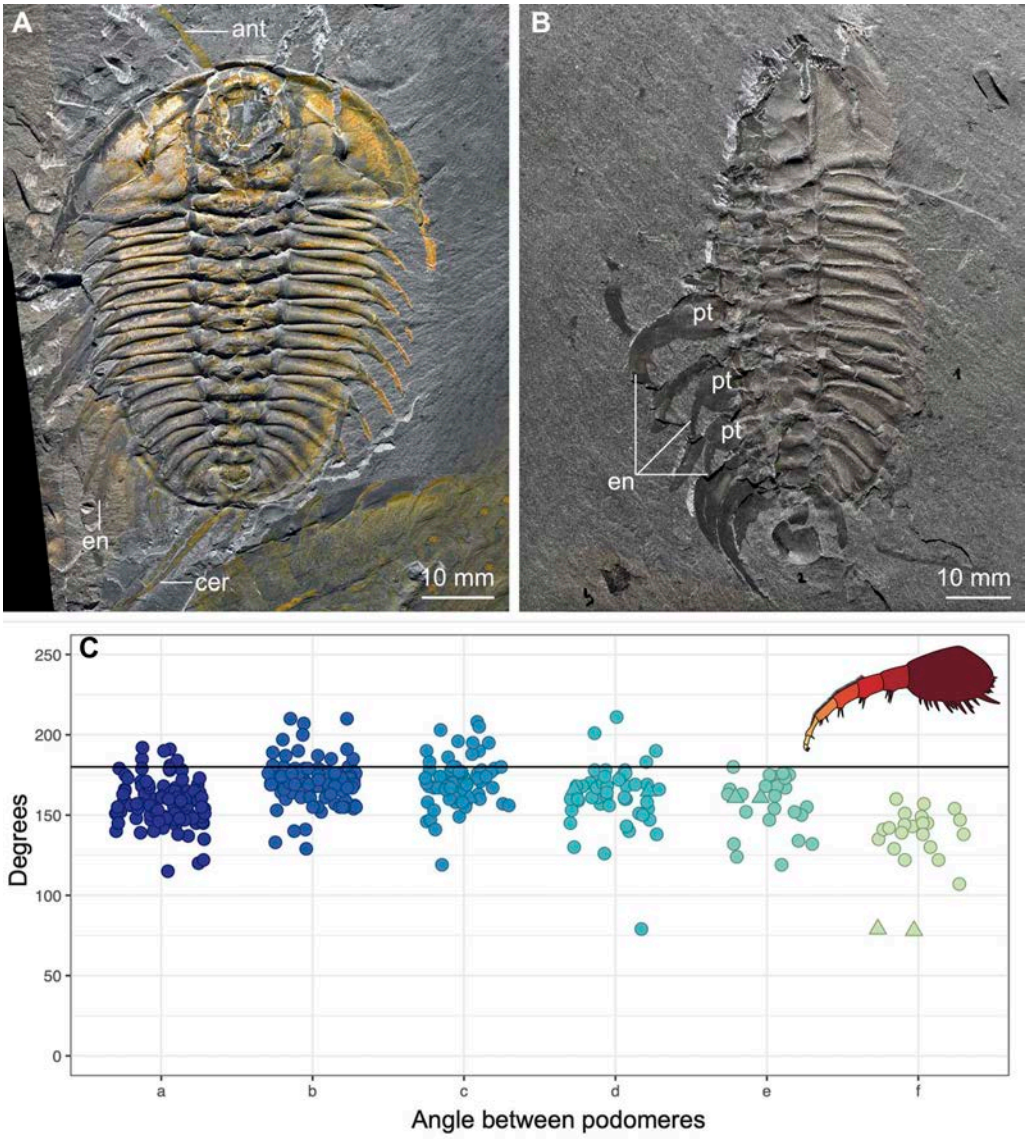

Figure 1. Olenoides serratus from the Burgess Shale (Cambrian; Wuliuan) in British Columbia, Canada. **A,** Dorsal view of complete specimen with antennae, biramous appendages and cerci (USNM PAL 65510); **B,** ventral view of partial specimen missing right pleural lobe show claspers at back of thorax and front of pygidium (ROMIP 66299; (Losso & Ortega-Hernández, 2022); **C,** variability of flexure and extension in endopodites from *O. serratus* measured on 138 limbs from 28 specimens (Losso *et al*., 2025). Institutional abbreviations: **USNM,** Smithsonian Institution; **ROMIP,** Royal Ontario Museum. Abbreviations: **ant,** antenna; **cer,** cerci; **en,** endopodite; **pt,** protopodite.

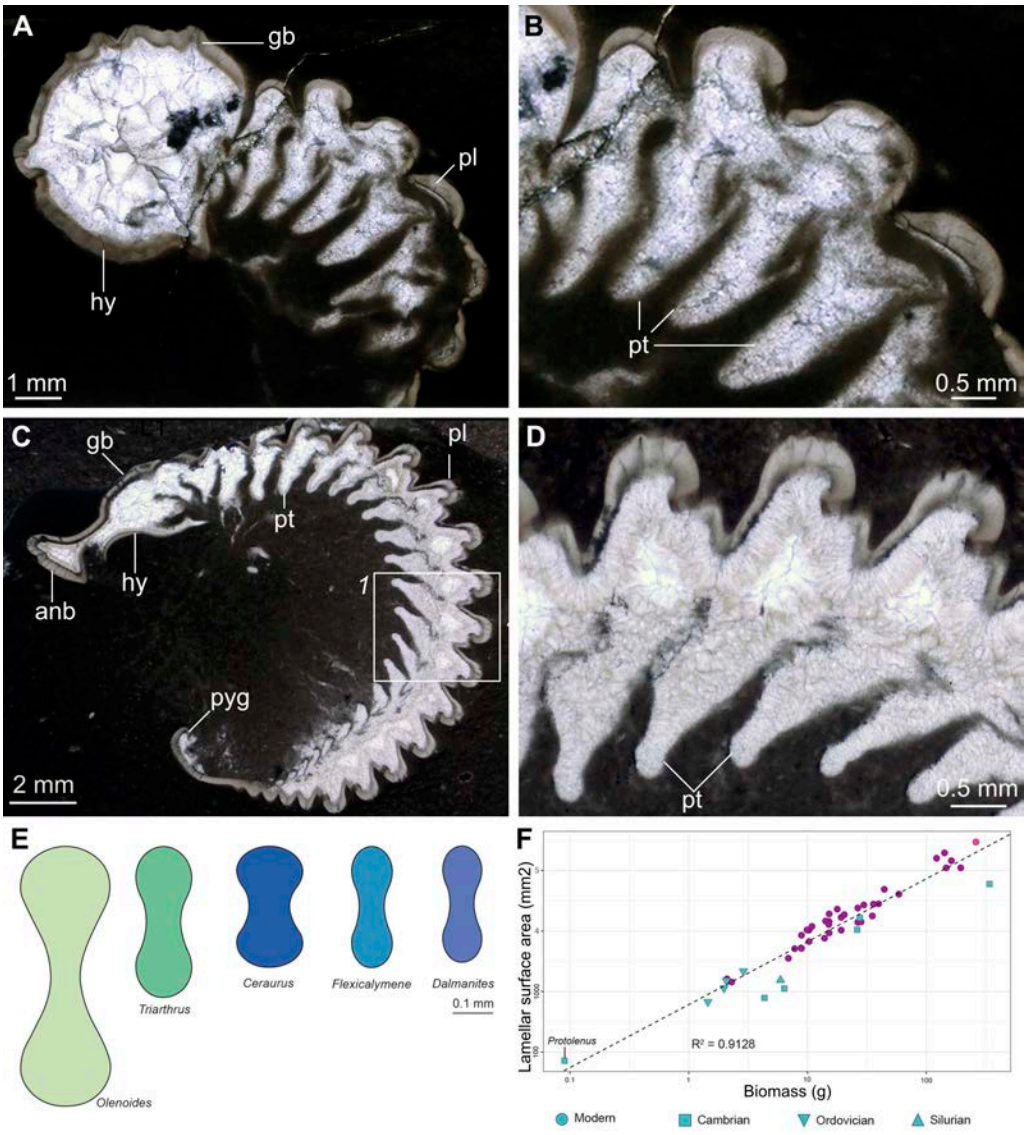

Figure 2. Wedge-shaped protopodites in partially enrolled trilobites from the Walcott-Rust Quarry (Ordovician; Katian) in New York, USA. A – D modified from (Losso *et al.*, 2023). **A,** Photomicrograph of *Ceraurus pleurexanthemus*, an exsagittal thin section of showing protopodites in cross section from a lateral view (MCZ: IP:158240); **B,** magnification of protopodites; **C,** photomicrograph of *Flexycalymene* sp., an exsagittal thin section of showing protopodites in lateral view (MCZ:IP:104956); **D,** magnification of protopodites in box 1 of c; **E, F** modified from (Losso, Vallefuoco, *et al*., 2026); **E,** cross section of lamellae in five trilobites; **F,** lamellar surface area compared to biomass in trilobites (geen), marine brachyurans (purple) and xiphosuran (pink). Institutional abbreviations: **MCZ,** Museum of Comparative Zoology, Harvard University. Abbreviations: **gb,** glabellae; **hy,** hypostome; **pl,** pleural lobe; **pt,** protopodite; **pyg,** pygidium.

REFERENCES

Brett, C. E., Whiteley, T. E., Allison, P. A., & Yochelson, E. (1999). The Walcott-Rust Quarry: Middle Ordovician Trilobite Konservat-Lagerstätten. *The Paleontological Society*, *73*(2), 288–305.

Losso, S. R., Affatato, P., Nanglu, K., & Ortega-Hernández, J. (2023). Convergent evolution of ventral adaptations for enrolment in trilobites and extant euarthropods. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2013), 20232212. doi: 10.1098/rspb.2023.2212

Losso, S. R., Hegna, T. A., & Ortega-Hernández, J. (2026). These legs were made for walking: 150 years of trilobite appendage morphology and evolution. *PaleoRxiv.* doi: 10.31233/osf.io/6u3pk_v1

Losso, S. R., Nanglu, K., Weyland, W. C., & Ortega-Hernández, J. (2025). Quantification of leg mobility in the Burgess Shale *Olenoides serratus* indicates functional differences between trilobite and xiphosuran appendages. *BMC Biology*, *23*, 238. doi: 10.1186/s12915-025-02335-3

Losso, S. R., & Ortega-Hernández, J. (2022). Claspers in the mid-Cambrian *Olenoides serratus* indicate horseshoe crab–like mating in trilobites. *Geology*, *50*(8), 897–901. doi: 10.1130/G49872.1

Losso, S. R, Thines, J. E., & Ortega-Hernández, J. (2023). Taphonomy of non-biomineralized trilobite tissues preserved as calcite casts from the Ordovician Walcott-Rust Quarry, USA. *Communications Earth & Environment*, *4*(1), 330. doi: 10.1038/s43247-023-00981-5

Losso, S. R., Vallefuoco, F., Foglia, I., Laborieux, L., Belén Muñoz-García, A., & Ortega-Hernández, J. (2026). Surface area calculations of lamellae support respiratory function of trilobite exopoites. *BioRxiv*. doi: 10.64898/2026.02.02.702636

Whittington, H. B. (1975). Trilobites with appendages from the Middle Cambrian, Burgess Shale, British Columbia. *Fossils and Strata*, *4*, 97–136. doi: 10.18261/8200049639-1975

Whittington, H. B. (1980). Exoskeleton, moult stage, appendage morphology, and habits of the Middle Cambrian Trilobite *Olenoides serratus*. *Palaeontology*, *23*(1), 17–22.

QUANTITATIVE REASSESSMENT OF CLASSICAL TRILOBITE MORPHOTYPES

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Keywords: Richard Fortey, Trilobita, morphospace, disparity.

INTRODUCTION

Morphological classifications are widely used to infer ecological strategies in the fossil record. With the aim of linking morphology to function and ecology, Fortey and Owens (1990) proposed a framework in which trilobite diversity was organized into a series of morphotypes, based on recurrent morphological traits and their inferred environmental preferences. The authors qualitatively recognized eight distinctive morphotypes and described their adaptive significance and temporal distribution. Despite their widespread use, these morphotypes have not been rigorously tested using quantitative approaches, raising questions about their reproducibility and biological meaning. It remains unclear whether morphotypes represent natural groupings or simplified descriptive constructs. In recent decades, the evolutionary history and ecological roles of trilobites have been progressively addressed through the development of taxonomically broad morphometric datasets for trilobites, encompassing multiple anatomical structures and a variety of data acquisition methods (Foote, 1993; Suárez & Esteve, 2021; Vargas-Parra & Hopkins 2022; Bault *et al*., 2022; 2023; Serra *et al*. 2023a; Drage & Pates, 2024). In this context, geometric morphometrics allows morphospace structure to be quantitatively evaluated rather than inferred qualitatively, providing a framework to explicitly test long-standing morphological classifications (*e.g*., Cole & Hopkins 2021; Holmes 2023; Esteve & Suárez, 2022; Serra *et al.,* 2025).

Qualitative classifications have proposed a conceptual framework of polyphyletic groups corresponding to distinct ecological–functional strategies; however, this remains theoretical and it is not grounded in a quantitative perspective. We therefore revisit the classical morphotype concept of Fortey and Owens (1990) from a morphospace approach under the hypothesis that trilobite cephalic morphospace is structured into broad, overlapping regions rather than discrete categories, reflecting recurrent ecological strategies across lineages. We explore whether morphotypes originally defined on qualitative grounds can be recovered within empirical morphospaces derived from quantitative data. Specifically, we test whether classical morphotypes emerge as distinct clusters or instead show substantial overlap within morphospace.

MATERIALS AND METHODS

Data preparation. Specimens selected for digitization were compiled from published sources and correspond to previously described material housed in public institutional repositories, each specimen is associated with a unique repository code that ensures traceability and reproducibility. This approach ensures full transparency and reproducibility of the dataset and allows all specimens to be traced back to their original descriptions. All selected specimens

were incorporated into TriloMorph, an online, open-access, and dynamic repository designed to integrate trilobite morphometric data and specimen-level metadata (see Serra *et al.,* 2023b for a detailed description of database assembly, and TriloMorph: https://github.com/balsedie/trilomorph for the complete specimen list, raw morphometric data, and original references). Additionally, cephalic data of 198 specimens originally published by Suárez and Esteve (2021), were added to TriloMorph and adjusted to its landmark and semilandmark template. Specimens were analyzed following the TriloMorph landmarking template that summarizes cephalic shape with three outline curves: glabellar, facial suture, and cephalic curves. These curves capture the main axes of cephalic shape variation and maintain comparability across phylogenetically diverse taxa. The focus on cephalic morphology is justified by its central role in trilobite functional ecology, including vision, feeding, and environmental interaction, making it particularly informative for testing ecological–morphological hypotheses.

A second database was constructed based on the digitized specimens (N = 624), in which each specimen was individually examined, and subsequently assigned a morphogroup (**MG**) tag corresponding to the MGs defined by Fortey and Owens (1990): *Pelagic, Phacomorph, Illaenimorph, Atheloptic, Marginal cephalic spines (***MCS***), Pitted fringe*, and *Olenimorph*. The "*Miniaturization*" morphotype was excluded from the analysis, since our approach targets shape variation and does not account for size differences. Importantly, MG assignment was performed at the specimen level rather than at the generic level, as individual genera may encompass more than one MG. This specimen-level approach allows intra-generic variability to be explicitly captured and avoids masking morphological diversity within broadly defined taxa. Each specimen was independently classified by seven trilobite specialists. A final morphotype was assigned only to specimens for which at least five classifiers agreed on the same morphotype. Applying this consensus threshold resulted in 386 specimens being retained for further analysis, which were subsequently used for morphospace plotting.

Construction of the morphospace. Generalized Procrustes Analysis (**GPA**) was applied to standardize the data by removing non-shape variation. Principal component analyses (**PCA**) were then performed on the aligned coordinates to identify the principal axes of shape variation and to construct the empirical morphospace. This approach allows morphological variation to be represented in a reduced-dimensional space in which patterns of clustering and overlap can be explicitly evaluated. Both GPA and PCA were implemented using the geomorph package (Adams *et al*., 2022) in R (R Core Team, 2018).

Optimal cluster analysis. To assess the presence of MGs in morphospace, we performed a K-means analysis, a non-hierarchical partitioning of morphospace. We explored two approaches: (i) testing a partition into seven clusters (k = 7), corresponding to the number of morphogroups originally defined, and (ii) determining the optimal number of clusters objectively using the Gap Statistic method (Tibshirani *et al*., 2001). This dual approach allows both direct comparison with the classical morphotype framework and an independent assessment of the underlying structure of morphospace. The gap statistic compares the total variation within a given number of clusters in the real dataset with the expected values for that same number of clusters in a reference dataset that lacks clustering. The optimal number of clusters is the number that maximises the gap statistic (Tibshirani *et al*., 2001). These analyses were performed in R using the functions *kmeans*() and *clusGap*() from the cluster package (Maechler *et al*., 2022).

RESULTS

Principal Component Analysis captured shape variation across 386 trilobite specimens, with the first two principal components accounting for 54.68% and 10.81% of the total variance,

respectively. These axes define a morphospace in which the distribution and potential clustering of morphotypes can be evaluated.

The seven morphotypes considered are shown in Figure 1A. Classical morphotypes are not recovered as discrete partitions in morphospace under clustering (k = 7). Instead, each cluster comprises a heterogeneous mixture of morphotypes, indicating substantial overlap among them. Figure 1B further depicts how morphotypes are distributed across the seven clusters. The most abundant morphotypes are *Olenimorphs* and *Phacomorphs*. Interestingly, these span clusters located toward opposite ends of PC1 (Fig. 1A): *Olenimorphs* are most abundant in clusters 1, 3, and 5, whereas *Phacomorphs* predominate in clusters 2 and 6; both groups also show high representation in the central cluster (cluster 4 in Fig. 1A). This distribution further highlights the lack of discrete separation, as dominant morphotypes occupy broad and overlapping regions of morphospace. All morphotypes show variable degrees of association within different regions, under this partition, cluster membership shows partial but incomplete segregation: *Phacomorph* is mostly represented in cluster 2, *Illaenimorph* and *Pelagic* in cluster 6, *Atheloptic* in cluster 3, *Olenimorph* in cluster 5, *MCS* in cluster 4, and *Pitted fringe* in cluster 7 (Fig. 1A). However, this segregation is partial and does not result in clearly bounded groupings (Fig. 1B). Although k = 7 allows direct comparison with classical morphotypes, an independent model selection approach using the Gap statistic indicates a more parsimonious structure (k = 4), which we interpret as reflecting broad morphological domains rather than strict equivalents of traditional morphotypes, suggesting that classical categories may over-partition morphological variation.

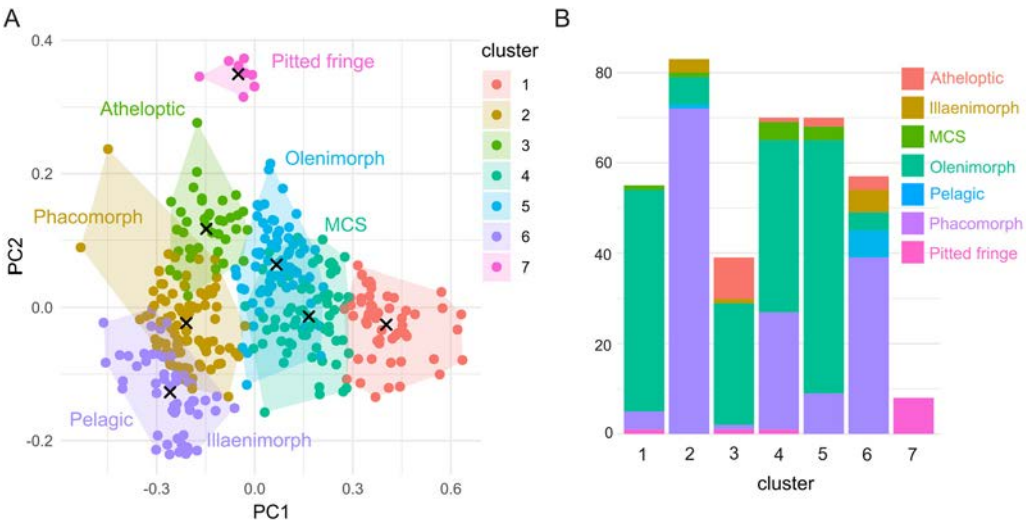

Figure 1. A, Clusters in trilobite morphospace (K=7), the first two principal components are shown accounting for 54.68% and 10.81% of the total variance, respectively; **B,** Distribution of morphotypes across clusters.

CONCLUSIONS

We identify four main groups across Trilobita, with additional internal structure emerging at finer resolutions (*e.g.*, k = 7). Under this partition, dominant morphotypes such as *Olenimorphs* and *Phacomorphs* largely define the morphospace, while more distinctive groups, such as *Illaenimorph, Pelagic, Pitted fringe* and *Atheloptic*, appear as subgroups associated with clearly differentiated ecological strategies (Fig. 1A, 1B).

This study provides a quantitative reassessment of the classical morphotype framework proposed by Fortey and Owens (1990), offering both support and reinterpretation of their model. Our results indicate that trilobite morphospace exhibits limited, non-discrete structuring, being organized into a small number of broad morphological domains with partial overlap. These domains do not map directly onto traditional morphotype categories. While classical morphotypes capture recurrent aspects of the morphological variation, morphospace structure instead reflects broad morphological groupings within which multiple ecological strategies coexist. This reinterpretation has important implications for how morphological diversity and ecological patterns are analyzed in trilobites and other fossil groups.

Acknowledgements: We thank the Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (PICT-2021-I-A-00968) and CONICET (PIP 1220200103192CO, PIBAA 28720210101292CO) for financial support. This work is also a contribution to projects PID2021-125585NB-I00 and CNS2024-154147 of the Ministerio de Ciencia e Innovación de España.

REFERENCES

Adams, D. C., Collyer, M. L., Kaliontzopoulou, A., & Baken, E. (2026). *geomorph: Software for geometric morphometric analyses* (R package). https://cran.r-project.org/package=geomorph

Bault, V., Crônier, C., & Monnet, C. (2022). Morphological disparity trends in Devonian trilobites from North Africa. *Palaeontology, 65*(5), e12623. doi: 10.1111/pala.12623

Bault, V., Crônier, C., Monnet, C., Balseiro, D., Serra, F., Waisfeld, B. G., Bignon, A., & Rustán, J. J. (2023). Rise and fall of the phacopids: The morphological history of a successful trilobite family. *Palaeontology, 66*(5), e12673. doi: 10.1111/pala.12673

Cole, S. R., & Hopkins, M. J. (2021). Selectivity and the effect of mass extinctions on disparity and functional ecology. *Science Advances, 7*(19), eabf4072. doi: 10.1126/sciadv.abf4072

Drage, H. B., & Pates, S. (2024). Distinct causes underlie double-peaked trilobite morphological disparity in cephalic shape. *Communications Biology, 7*(1), 1–18. doi: 10.1038/s42003-024-07221-2

Esteve, J., & Suárez, M. G. (2023). Ecomorphological datasets: Comment on Hopkins (2022). *Lethaia, 56*(2), 1–5. doi: 10.18261/let.56.2.2

Foote, M. (1993). Contributions of individual taxa to overall morphological disparity. *Paleobiology, 19*(4), 403–419.

Fortey, R. A., & Owens, R. M. (1990). Trilobites. In Evolutionary Trends, ed. K. J., McNamara, pp. 121–42. London: Belhaven

Holmes, J. D. (2023). Contrasting patterns of disparity suggest differing constraints on the evolution of trilobite cephalic structures during the Cambrian “explosion”. *Palaeontology, 66*(2), e12647. doi: 10.1111/pala.12647

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2022). *cluster: Cluster analysis basics and extensions* (R package, version 2.1+).

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Serra, F., Balseiro, D., & Waisfeld, B. G. (2023a). Morphospace trends underlying a global turnover: Ecological dynamics of trilobite assemblages at the onset of the Ordovician radiation. *Palaeogeography, Palaeoclimatology, Palaeoecology, 615*, 111448. doi: 10.1016/j.palaeo.2023.111448

Serra, F., Balseiro, D., Monnet, C., Randolfe, E., Bignon, A., Rustán, J. J., Bault, V., Muñoz, D. F., Vaccari, N. E., Martinetto, M., Crônier, C., & Waisfeld, B. G. (2023b). A dynamic and collaborative database for morphogeometric information of trilobites. *Scientific Data, 10*(1), 841. doi: 10.1038/s41597-023-02724-9

Serra, F., Balseiro, D., Allaire, N., Waisfeld, B. G. (2025). Trilobite cranidial and pygidial disparity patterns: two sides of the story. *Historical Biology,* 38(3), 698–712. doi: 10.1080/08912963.2025.2506093

Suárez, M. G., & Esteve, J. (2021). Morphological diversity and disparity in trilobite cephala and the evolution of trilobite enrolment throughout the Palaeozoic. *Lethaia, 54*(5), 752–761. doi: 10.1111/let.12437

Tibshirani, R., Walther, G., & Hastie, T. (2001). Estimating the number of clusters in a dataset via the gap statistic. *Journal of the Royal Statistical Society: Series B, 63*(2), 411–423.

Vargas-Parra, E. E., & Hopkins, M. J. (2022). Modularity in the trilobite head consistent with the hypothesized segmental origin of the eyes. *Evolution & Development, 24*(6), 177–188. doi: 10.1111/ede.12418

ABSTRACTS

MIDDLE FURONGIAN (LATE CAMBRIAN) TRILOBITES FROM THE *QUADRATICEPHALUS* ZONE OF THE HWAJEOL FORMATION, TAEBAEK DISTRICT, KOREA

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Keywords: Trilobites, *Quadraticephalus*, Late Cambrian, Taebaeksan Complex, Biostratigraphy.

The international correlation of the Furongian of Sino-Korea remains a challenging task, owing to the low number of cosmopolitan trilobites. The Hwajeol Formation of the Taebaek Group in Korea extends from the Jiangshanian Stage to Cambrian Stage 10. This study documents silicified trilobites from the middle part of the Hwajeol Formation in the Sagundari section that belong to the *Quadraticephalus* Zone, which is well correlated with the *Changia* (or *Quadraticephalus*) Zone of North China and attributed to the late Jiangshanian Stage. This interval yields at least eleven polymerid species belonging to nine genera: *Akoldinioidia*, *Baikadamaspis*, *Hamashania*, *Haniwa*, *Lophosaukia*, *Pagodia*, *Pseudokoldinioidia*, *Quadraticephalus*, and *Shergoldia*. *Quadraticephalus elongatus* occurs throughout the interval, hence the biozone is named as the *Quadraticephalus* Zone. This new trilobite assemblage thus not only support a strong palaeogeographical link between the Taebaeksan Complex and North China but also a solid connection with other peri-Gondwanan terranes such as South China, Australia, and Sibumasu.

SOME GEOPHYSICAL CONSTRAINTS ON THE PALAEOZOIC

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Keywords: Palaeozoic, Trilobita, rotation rate, Earth-Moon.

We present an overview of changes in the length of day and equivalently, the Earth-Moon distance, over geological time and suggest what it may imply about conditions in the Palaeozoic under which trilobites lived and evolved. We give estimates of the decrease in rotation rate of the Earth since the Precambrian and associated changes in length of day and the lunar cycle as well as implications for tidal amplitudes, shifts in large scale weather structures and a possible link to volcanism. Using recent global circulation model studies of the Palaeozoic era, we also compare the impacts of changes in the length of day with other effects, for example the greenhouse effect due to changes in atmospheric composition. This provides a platform for discussions on the possible links between changes in trilobite morphology, abundance and diversity and these long-term drivers of environmental conditions.

TRILOBITE BIOSTRATIGRAPHY AND REGIONAL CORRELATION OF LOWER CAMBRIAN NANGAOAN (CHIUNGCHUSSUAN) IN CHINA, IMPLICATIONS FOR THE SUBDIVISION OF GLOBAL SERIES 2

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Keywords: China, Cambrian Series 2, Trilobita, Biostratigraphy.

Cambrian Series 2 encompasses the peak of the Cambrian Explosion and is marked by rapid diversification of marine metazoans. Trilobites are the most diverse and abundant biomineralized Cambrian arthropods and provide the principal high-resolution biostratigraphic framework for this interval (Geyer, 2019; Peng *et al*., 2020). However, strong faunal provincialism among early Cambrian trilobite assemblages hampers interregional correlation, and no global consensus has yet been reached on the subdivision of Cambrian Series 2 or its index taxa (Palmer, 1998; Zhang *et al*., 2017; Zhu *et al*., 2019).

In China, lower Cambrian Trilobite zonation in shallow water facies was originially established in eastern Yunnan, where the Chiungchussuan, Tsanglangpuan, and Lungwangmiaoan stages were defined (Luo *et al*., 1994). However, eastern Yunnan lacks trilobite records across the transition between Cambrian Stage 3 and 4 (between the *Drepanuroides* and *Palaeolenus* zones), limiting broader correlations (Zhu *et al*., 2019; Fig. 1). More recently, the Nangaoan and Duyunian stages were established in Jiangnan slope zone and are considered equivalent to international Stage 3 and 4 (Peng, 2000; Peng *et al*., 2020). Additional zonations have been proposed in central Guizhou, the Three Gorges, and the Tarim Block (Zhou & Lin, 1978; Zhou *et al*., 1980; Zhou & Yuan, 1980; Lin *et al*., 2001) but remain poorly constrained. Based on new field investigations and taxonomic studies, this study refines the trilobite biostratigraphy of the Nangaoan (Chiungchussuan) in Guizhou and the Tarim Block, providing a basis for improved correlation of Cambrian Series 2.

In shallow water facies of Guizhou (Middle Yangtze Platform), the Nangaoan trilobite fauna generally comprises five zones, in ascending order: the *Tsunyidiscus niutitangensis*, *Kueichowia liui*, *Yinites typicalis*, *Ushbaspis constrictus* and *Paokannia-Szechuanolenus* zones (Fig. 1). Our study confirms the concepts and stratigraphic ranges of the *Kueichowia liui* and *Ushbaspis constrictus* zones, replaces the previously recognized *Drepanuroides* Zone with the *Yinites typicalis* Zone in Guizhou, and documents the occurrence of *Metaredlichia cylindrica*, providing the first direct evidence for correlation between the *Yinites typicalis* Zone of Guizhou and the *Hunanocephalus-Hupeidiscus* Zone in the eastern Three Gorges region (Sun *et al*., 2025).

Along the platform margin of Guizhou (Wengan and Yuqing areas), the Nangaoan trilobite assemblages closely resemble those of the Three Gorges region (Fig. 1). Here, slope-affiliated taxa (*e.g*., Tsunydiscida and Cheiruroididae) occur together with shallow water groups (e.g., Metaredlichinae, Estaingiidae, and Palaeolenidae), forming mixed platform-slope assemblages that provide a promising basis for broader interregional correlations.

The Nangaoan trilobite fauna of the Tarim Block was previously subdivided into the *Shizhudiscus sugaitensis*, *Metaredlichioides kalpinensis*, *Kepingaspis-Tianshanocephalus* and *Paokannia* zones (Lin *et al*., 2001). Recent taxonomic revisions indicate that *S. sugaitensis* and *M. kalpinensis* are junior synonyms of *Tsunyidiscus niutitangensis* and *Ushbaspis hubeiensis*, respectively, requiring

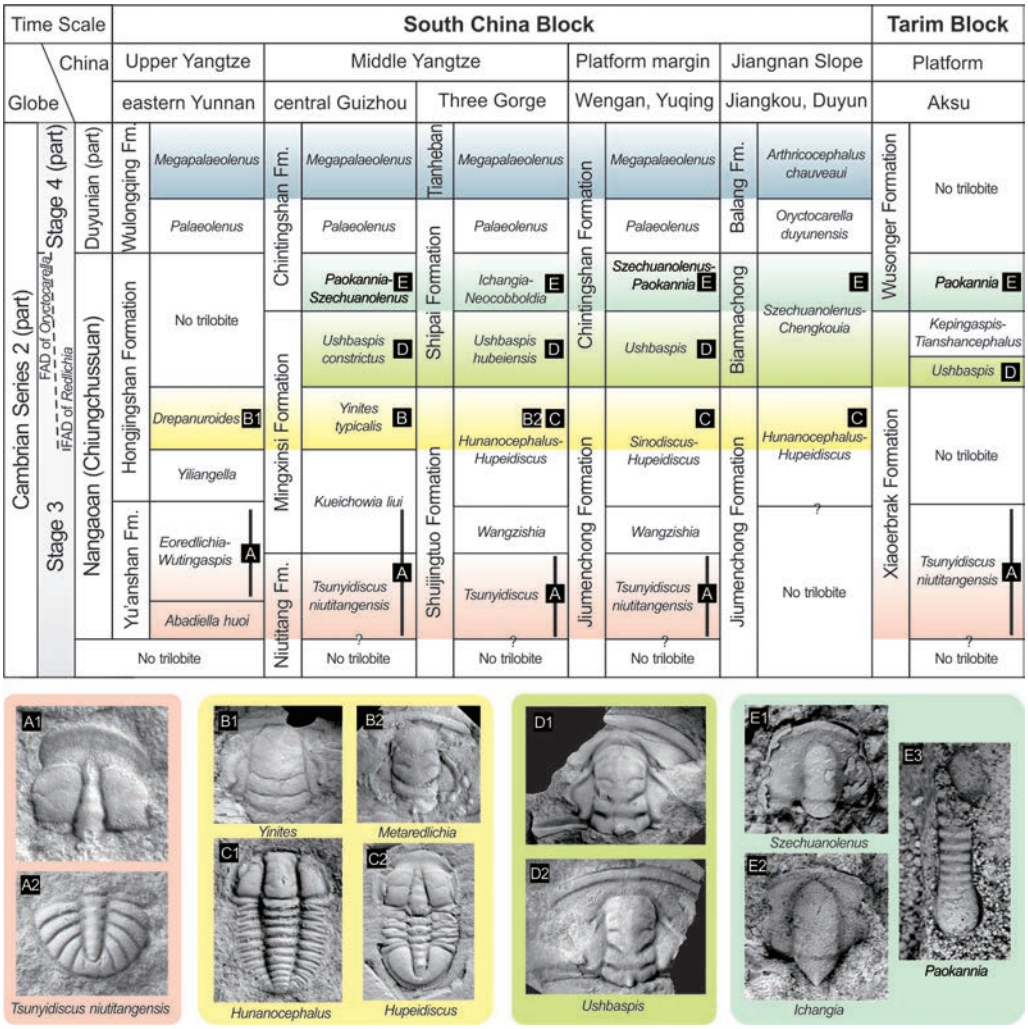

Figure 1. Trilobite biostratigraphic correlation of the lower Cambrian Nangaoan (Chiungchussuan) across the South China and Tarim blocks. Colored bands indicate key correlatable horizons within the Nangaoan recognized in this study. Representative trilobites from these horizons are illustrated below, with colors and labels corresponding to the correlation chart. **A,** *Tsunyidiscus niutitangensis*; **B,** *Yinites* and *Metaredlichia*; **C,** *Hunanocephalus* and *Hupeidiscus*; **D,** *Ushbaspis*; **E,** *Szechuanolenus-Paokannia* assemblage. Trilobite specimens are not to scale.

corresponding revision of the zonation. Together with the occurrence of the characteristic Shuijingtuo Formation trilobite *Zhenbaspis similis* within the *T. niutitangensis* Zone, these results demonstrate close affinities between the Nangaoan trilobite faunas of Tarim and the Three Gorges region (Xiang *et al*., 1987).

In the Jiangnan Slope Zone, the FAD of *Oryctocarella duyunensis*, which defines the base of the Duyunian Stage, has been proposed as a potential standard for the Stage 4 (Peng *et al*., 2020). However, this level is considered higher than other candidate indexes (Geyer, 2019) and trilobites are extremely rare below it in slope zone (Zhang *et al*., 1979; Peng & Babcock, 2001). It is therefore

necessary to focus on lower intervals in China (upper Nangaoan) and on regions with richer trilobite assemblages, such as margin platform rather than slope facies. In this study, four horizons within the Nangaoan are recognized that allow broad correlation across China (Fig. 1). Although the horizon of the *T. niutitangensis* appears too low, the other three show considerable potential for further investigation. In margin platform, these zones contain widely distributed eodiscoid trilobites, such sa *Sinodiscus* (Mongolia), *Hebediscina* (Italy and Australia) and *Neocobboldia* (cosmopolitan), as well as taxa enabling intercontinental correlation (*Ichangia*, *Estaingia*, *Pararaia* with South Australia; *Ushbaspis* and *Paokannia* with Kazakhstan and the Himalaya) (Zhang *et al*., 1979, 1980). Future studies should therefore focus on the evolution and stratigraphic distribution of key trilobite taxa in the upper Nangaoan of platform-margin settings, which may provide critical evidence for defining Cambrian Stage 4.

REFERENCES:

Geyer, G. (2019). A comprehensive Cambrian correlation chart. *Episodes Journal of International Geoscience*, *42*(4), 321–332. doi: 10.18814/epiiugs/2019/019026

Lin, H., Chen, T., Yuan, J., Yuan, W., Zhang, Y., Yuan, X., & Zhang, S. (2001). Cambrian. In: Zhou, Z. (ed.). *Stratigraphy of the Tarim Basin*. Beijing: Science Press. 1–359 (in Chinese with English abstract).

Luo, H., Jiang, Z., & Tang, L. (1994). *Stratotype Sections for Lower Cambrian Stages in China*. Kunming: Yunnan Science and Technology Press, 1–183 (in Chinese).

Palmer, A. R. (1998). Why is intercontinental correlation within the Lower Cambrian so difficult?. *Spanish Journal of Palaeontology*, *13*(3), 17–21. doi: 10.7203/sjp.23974

Peng, S. (2000). Cambrian of slope facies of China. In Nanjing Institute of Geology and Palaeontology (ed.), *Stratigraphical Studies in China (1979-1999)*. Hefei: Anhui Science and Technology Publishing House, 23–38 (in Chinese).

Peng, S., & Babcock, L.E. (2001). Cambrian of the Hunan-Guizhou Region, South China. *Palaeoworld*, *13*, 3–51.

Peng, S., Babcock, L. E., & Ahlberg, P. (2020). The Cambrian Period. In *Geologic Time Scale 2020. Volume 2*: 565–629. doi: 10.1016/B978-0-12-824360-2.00019-X

Sun, Z., Wang, D., Zeng, H., & Zhao, F. (2025). Biostratigraphy and regional correlation of trilobite zones from the Mingxinsi Formation of the Cambrian Series 2, Guizhou Province. *Journal of Stratigraphy*, *49*(2), 142–159 (in Chinese with English abstract). doi: 10.19839/j.cnki.dcxzz.2025.0011

Wang, X. F., Xiang, L. W., Zhou, T. M., Ni, S. Z., Zeng, Q. L., Xu, G. H., Lai, C., & Li, Z. (1987). *Cambrian. In: Biostratigraphy of the Yangtze Gorge Area (2) Early Palaeozoic Era*. Beijing: Geological Publishing House. 4–42 (in Chinese with English summary).

Zhang, W. T., Lu, Y. H., Zhu, Z. L., Qian, Y. Y., Lin, H. L., Zhou, Z. Y., Zhang, S. G., & Yuan, J. L. (1980). Cambrian trilobite faunas of southwestern China. *Palaeontologia Sinica, B*, 16, 1–497.

Zhang, W., Yuan, K., Zhou, Z., Qian, Y., & Wang, Z.Z. (1979). Cambrian of southwestern China. In: *Carbonate Biostratigraphy of Southwest China*. Nanjing Institute of Geology and Palaeontology Beijing: Science Press, 39–107 (in Chinese).

Zhang, X., Ahlberg, P., Babcock, L. E., Choi, D. K., Geyer, G., Gozalo, R., Hollingsworth, J. S., Li, G., Naimark, E. B., Page, T., Steiner, M., Wotte, T. & Zhang, Z. (2017). Challenges in defining the base of Cambrian Series 2 and Stage 3. *Earth-Science Reviews*, 172, 124–139. doi: 10.1016/j.earscirev.2017.07.017

Zhou, T., & Lin, T. (1978). Early Cambrian trilobites. In *Sinian to Permian stratigraphy and palaeontology of eastern Yangtze Gorges*. Beijing: Geological Publishing House. 143–154 (in Chinese).

Zhou, Z., & Yuan, J. (1980). Lower Cambrian trilobite succession in southwest China. *Acta Palaeontologica Sinica*, *19*(4), 331–339 (in Chinese with English abstract).

Zhou, Z., Yuan, J., Zhang, Z., Wu, X., & Yin, G. (1980). Classification and correlation of Cambrian in Guizhou. *Journal of Stratigraphy*, *4*(4), 273–281 (in Chinese).

Zhu, M., Yang, A., Yuan, J., Li, G., Zhang, J., Zhao, F., Ahn, S. Y. & Miao, L. (2019). Cambrian integrative stratigraphy and timescale of China. *Science China Earth Sciences*, *62*(1), 25–60. doi: 10.1007/s11430-017-9291-0

TEMPO AND MODE OF COORDINATED TRILOBITE TURNOVER IN SHALLOW WATER FAUNAS OF THE EARLY ORDOVICIAN NORTHERN LAURENTIAN PALEO-MARGIN: MASS EXTINCTIONS AND FRENZIED RATES OF FAUNAL REPLACEMENT

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Keywords: Diversity, Ordovician, extinction, Trilobites, Laurentia.

Samples made over more than a quarter century of intensive annual fieldwork have revealed many unexpected features of patterns of species level duration and turnover, heretofore unknown or underappreciated mass extinction, unprecedented rates of evolution, and a surprising decoupling of biotic patterns from low (fourth to sixth order) level stratigraphic cyclicity. The patterns documented persist throughout the entire Lower Ordovician across the region.

Work has been concentrated in the classic field areas of the Bear River Range, southeastern Idaho, and the Ibex area of western Utah. Complementary fieldwork has been carried out in California, Nevada, and Alberta, Canada. The history of study of the faunas was reviewed by Adrain *et al*. (2009), and until the present field program began in the late 1990s, it consisted chiefly of two monographs, one on southeastern Idaho faunas by Ross (1951) and one on western Utah faunas by Hintze (1953). A biostratigraphic and chronostratigraphic work published nearly half a century later (Ross *et al*., 1997) used trilobite data almost entirely based on these monographs.

Ross (1949, 1951) introduced a series of lettered (ostensible) assemblage zones which were adopted by Hintze (1953) and widely cited in the late 20th century literature for the Laurentian Lower Ordovician. Ross's (1951) and Hintze's (1953) taxonomic work was good for its time, but it became evident during the current work that they studied relatively few horizons, and the letter based zones (given names based on genera by Ross *et al*., 1997) were mostly extrapolations over substantial stratigraphic intervals with very little published supporting data. On reinvestigation, they usually turned out to contain multiple intervals with completely different faunas (i.e., multiple zones). The letter-based scheme has now been entirely replaced by a species level system based on new sampling, with zonations for the upper Skullrockian (lower Tremadocian) (Adrain *et al*., 2025), Stairsian (mid-Tremadocian) (Adrain *et al*., 2014), Tulean and Blackhillsian (upper Tremadocian through Floian) (Adrain *et al*., 2009) and Dapingian to lower Darriwilian (Adrain *et al*., 2012).

An intensive, field-based program sampling the shallow water trilobite faunas of the late Cambrian to early Middle Ordovician northern Laurentian paleo-margin in what is now the Great Basin, western USA, has been underway since 1996, spurred by the recognition that most of the trilobite diversity of the region had yet to be described. Facies are mostly shallow water (above storm wave base), and the region formed part of the northern tropical margin of Laurentia. The rocks are mainly lime mudstones, calcisiltites, and intrarudites, with intervals of microbial buildups. All of the classic sections in the region were remeasured and new stratigraphic logs made. Many new sections were also logged and collected.

Globally, the Tremadocian is poorly sampled for trilobites. There are few areas with continually fossiliferous records over a substantial stratigraphic interval. In many cases there reasonably well known, but stratigraphically isolated, faunas which are often termed "lower" or "upper" Tremadocian with only broad understanding of what that might mean and limited means to

correlate with other terranes or paleocontinents. The northern Laurentian paleo-margin has one of the most complete stratigraphic records of the entire Lower Ordovician known from anywhere in the world. The overall composite section is some 655 m thick. Importantly, the trilobite fossils have mostly been secondarily replaced by silica across the region, permitting large, three dimensional, and exquisitely well preserved samples to be obtained via hydrochloric acid dissolution. These faunas are widespread and pervasive. The 655 m composite section includes nearly 200 horizons yielding silicified trilobites. While there is temporal variation in the distribution of horizons, this yields a sampling density on average of samples around every three to four meters.

Sampling thousands of kilograms of rock from 19 main sections has yielded better knowledge of previously named species, but also a vast body of new taxa, including dozens of new genera and hundreds of new species. Systematic work is well underway (see references in the above-cited zonation papers) but many papers and monographs await publication. Nevertheless, all species from all sections and horizons have been digitally imaged and their species- and genus-level taxonomy worked out, if not formally published. This permits synthesis of patterns of diversity and distribution at a low meter scale across the northern Laurentian margin throughout the entire Lower Ordovician. This presentation provides a brief and preliminary summary of some of the most surprising large scale results. It is worth explaining that this knowledge has not previously been available largely because most of the taxonomy of these trilobite faunas simply did not exist prior to the current project. To take one example, Ross (1951) and Hintze (1953) classified many aulacopleuride species in a single genus, *Hystricurus* Raymond, 1913. These taxa are now assigned to five different families, and each comprise multiple genera and dozens of species.

Some of the results include:

Lockstep, coordinated species turnover is the rule throughout the Lower Ordovician. With no preconceptions about stratigraphic distribution, a null expectation about the stratigraphic distribution of trilobite species would usually involve stochastic origination and extinction, overlapping ranges, and relatively weak (if any) patterning. Along the northern Laurentian margin, trilobite faunas show nothing like this. Instead, they exist for meters or tens of meters mostly in taxonomic and morphological stasis, then turn over completely or almost completely in coordinated fashion, abruptly replaced by a new set of species, often of the same genera. This has made biostratigraphic zonation very easy. The zonal boundaries are not impervious - it is possible for some species to range through two or more zones. However, most boundaries feature no crossers or only one or two.

The tempo of turnover is much higher than expected. The rate of faunal turnover is extreme. At its slowest, zones are on average 15–20 m in thickness. At its most extreme, faunas replace each other on a 2–3 m scale. The pace of turnover appears to be related to major biotic events (see below).

Overprinting the pattern of turnover are two obliterating Tremadocian mass extinctions which nearly completely reset continental trilobite faunas. The notion of a trilobite mass extinction at the end of the Tremadocian Skullrockian Stage was ingrained in the literature of "biomeres" as the end of the "Symphysurinid Biomere." Actual evidence for the nature and scale of the event was scant. A later extinction at the end of the mid-Tremadocian Stairsian Stage was not previously suspected. Each extinction removed most of the dominant pre-extinction trilobite families and paved the way for a mostly new set of families in post-extinction strata. In either case, only a small number of lineages appear to have survived the event. These events essentially represent a fourth and fifth "biomere" mass extinction, with timing and scope very similar to the better known Cambrian events in the Marjuman, Steptoean, and Sunwaptan stages.

Trilobite turnover is not apparently driven by sequence stratigraphic architecture but seems largely decoupled from stratigraphic cyclicity. When confronted with a series-long pattern of rigid, coordinated stratigraphic turnover of trilobite faunas, the immediate suspicion is that the excellent sampling is revealing a pattern of cyclical control of the stratigraphic distribution of species ranges. This was the starting hypothesis that we approached the study of the integration of biotic and stratigraphic patterns. With so many boundaries to consider, some certainly do fall at stratigraphically significant surfaces. The end-Skullrockian mass extinction, for example, is clearly associated with a major transgressive event. Other boundaries do coincide with lower level surfaces. Overall, though, a strong majority of zonal boundaries fall in strata where there is no clear signal of significant surfaces. The end-Stairsian event, which extinguished nearly 100% of genera, falls within the highstand of a nondescript fifth- or sixth- order cycle. In short, the turnover appears more likely to be a biotic phenomenon and not a stratigraphic artifact.

Variation in turnover rate is tied to significant biotic events. While for much of the 655 m composite section zones average 15–20 m in thickness, immediately below levels of major change (the two Tremadocian mass extinctions and the large-scale faunal upheaval at the Floian-Dapingian boundary) turnover is greatly accelerated. Through the final 20–40 m of strata beneath the events, zonal thicknesses decrease to 2–5 m. Accelerated turnover is also seen in the wake of the events. The end-Stairsian event is captured in well exposed strata in the southern House Range in western Utah. Here, the extinction level is constrained to somewhere between Section C 172.4 m and 174.5 m. In the lowest Tulean strata immediately above the event (uppermost Section C and stratigraphically contiguous Section D) at least seven nearly completely distinct faunas replace each other in 23 m of section. At that point more protracted turnover is returned to, with trilobites of the *Psalikilus spinosum* Zone represented in stasis at multiple horizons though a 14 m interval, a zonal thickness typical of intervals not in proximity to major biotic events.

Obvious questions that arise from these patterns and which we are seeking funding to address are: 1) what caused the severe mass extinctions? 2) what caused the coordinated species level turnover; and 3) given that this is one of the best continuous trilobite records ever found, does it tell us something about the fundamental nature of the fossil record, or is the overall phenomenon something that is unique to the northern Laurentian margin? In response to the latter, some examples of similar turnover documented with silicified faunas in different environments, ages, and geographic regions hint that the answer may be that such patterns are more the norm than the exception.

REFERENCES

Adrain, J. M., McAdams, N. E. B. & Westrop, S.R. (2009).Trilobite biostratigraphy and revised bases of the Tulean and Blackhillsian Stages of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Palaeontologists*, *37*, 541–610.

Adrain, J. M., McAdams, N. E. B. & Karim, T. S. (2012). The Middle Ordovician bathyurid trilobite *Pseudoolenoides*, with a revised trilobite biostratigraphy of the Dapingian and lower Darriwilian of western Laurentia. *Zootaxa*, *3467*, 1–97. doi: 10.11646/zootaxa.3467.1.1

Adrain, J. M., Karim, T. S., Westrop, S. R. & Landing, E. (2014). Trilobite biostratigraphy of the Stairsian Stage (upper Tremadocian) of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Palaeontologists*, *45*, 167–214. doi: 10.3316/informit.343657705520848

Adrain, J. M., Westrop, S. R., Landing, E., Karim, T.S., Losso, S.R., Ng, R. Y., Bradley, A. B. & Pérez-Peris, F. (2025). Trilobite biostratigraphy of the upper Skullrockian Stage (Lower Ordovician; lower Tremadocian) on the northern Laurentian margin, western United

States. *Australasian Palaeontological Memoirs*, *57,* 397–432. doi: 10.3316/informit.T202506190000269008302715 4

Hintze, L. F. (1953). Lower Ordovician trilobites from western Utah and eastern Nevada. *Utah Geological and Mineralogical Survey Bulletin*, *48*, 1–249. (for 1952)

Raymond, P. E. (1913). A revision of the species which have been referred to the genus *Bathyurus*. *Bulletin of the Victoria Memorial Museum*, *1*, 51–69.

Ross, R.J., Jr. (1949). Stratigraphy and trilobite faunal zones of the Garden City Formation, northeastern Utah. *American Journal of Science*, *247*, 472–491. doi: 10.2475/ajs.247.7.472

Ross, R. J., Jr. (1951). Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. *Peabody Museum of Natural History, Yale University, Bulletin*, *6,* 1–161.

Ross, R. J., Jr, Hintze, L. F., Ethington, R. L., Miller, J. F., Taylor, M. E. & Repetski, J. E. (1997). The Ibexian, lowermost series in the North American Ordovician. *United States Geological Survey Professional Paper*, *1579*, 1–50. doi: 10.3133/pp1579

IS ONE SAMPLE ENOUGH TO DESCRIBE LATERAL VARIABILITY OF TRILOBITE DIVERSITY? A CASE-STUDY ANALYSIS FROM THE MURERO FM (DRUMIAN, IBERIAN CHAINS)

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Keywords: Cambrian, sampling effort, bias, representativeness, homogeneity.

INTRODUCTION

As one of the most representative groups of the Paleozoic fauna, trilobites are essential for studying biodiversity changes during the Cambrian. Their ability to form taxonomic assemblages adapted to highly diverse environmental conditions and latitudes, as well as their exceptional preservation due to their calcified carapaces, makes them an exceptional tool for understanding the evolution of marine communities during this period.

Biodiversity parameters are fundamental for describing interspecific interactions and community structure. However, differences in biodiversity can arise across temporal or spatial scales if individual beds present a patchy structure. Therefore, environmental heterogeneity must be studied and controlled to avoid confounding spatial and temporal patterns when sampling a single stratigraphic column.

CONTEXT OF THE STUDY AND LATERAL SAMPLING

Diversity patterns in Cambrian trilobite communities were assessed in sections Pur3 and Pur6, located near the village of Purujosa within the Moncayo Natural Park, in the Iberian Chains, northeastern Spain (Fig. 1A–1B). Twenty beds, labelled Pur/1 to Pur/20, were sampled across the stratigraphic column. Additionally, lateral sampling was performed at ten points within beds Pur/4 and Pur/20. Each point was separated by 10 m from the next and labelled with the bed name followed by a consecutive letter (Pur/4A to Pur/4J and Pur/20A to Pur/20J; Fig. 1C).

Assemblages in these strata have been interpretated as autochthonous, based on mud-rich deposition on an outer platform and a uniform, low-energy depositional environment, as described for different horizons of the Murero Formation (Esteve *et al*., 2011; Zamora, 2011).

METHODOLOGY AND RESULTS

Despite the depositional characteristics suggesting relatively homogeneous strata, the aim of this analysis is to evaluate whether the stratigraphic points (Pur/4 and Pur/20) are representative of their respective beds and to assess the degree of heterogeneity within each bed. Since only a single point is available for each bed in the vertical section, variance-based inferential statistical methods are not appropriate, and so a descriptive statistical approach was adopted. Given that the dataset is based on abundances, the Bray-Curtis index was selected as a dissimilarity measure (Bray & Curtis, 1957). Bray-Curtis distances were calculated between the stratigraphic samples (Pur/4 and Pur/20) and their corresponding lateral samples. These distances were then averaged and transformed into a novel operational similarity measure in this study, termed “Representativeness” and defined in Equation 1:

$$Representativeness = 1 - mean\ distance \quad (1)$$

where values approaching 1 indicate higher representativeness and, therefore, greater compositional similarity.

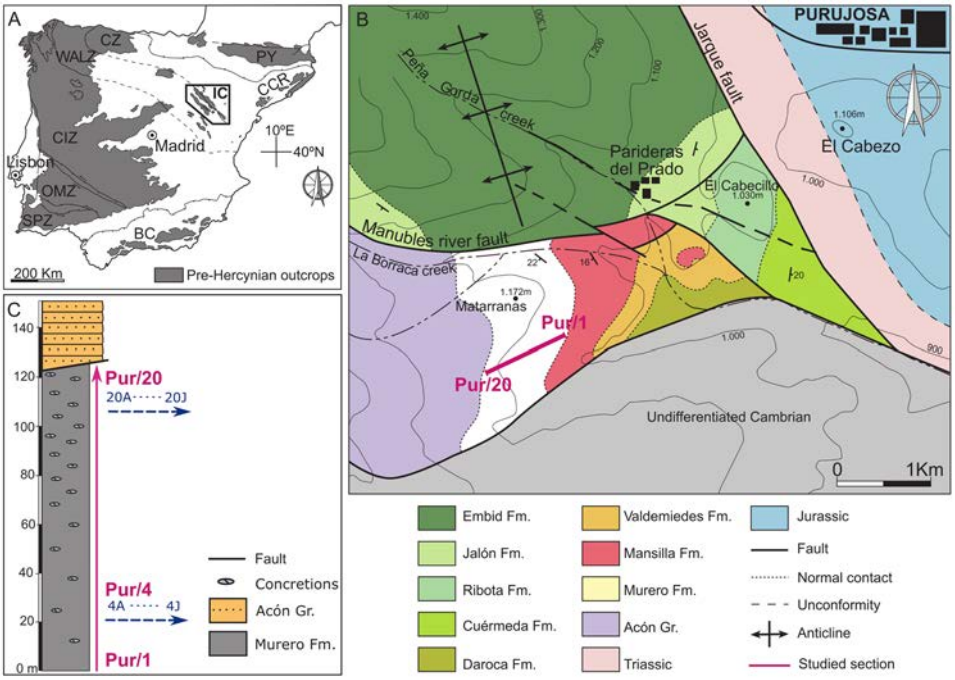

Figure 1. A, Pre-Hercynian outcrops in the Iberian Peninsula; **B,** Murero Formation (Drumian), near Purujosa locality; **C,** stratigraphic column of the investigated succession.

To assess lateral homogeneity, we treated the lateral points as a reference population, excluding the stratigraphic samples to avoid introducing bias by including the sample that we want to evaluate. To this end, the Bray-Curtis distance was calculated for all possible pairs and then averaged. This yielded 45 pairwise comparisons among the ten lateral samples for each bed. Since Bray-Curtis values range from 0 to 1, values closer to 0 indicate higher homogeneity, and vice versa.

Standard deviation (**SD**) was calculated for both the distances between stratigraphic and lateral points and the distances among the lateral points. Since Bray-Curtis values range from 0 to 1, the SD values are also constrained by this range. Values closer to 0 indicate that the variation is distributed uniformly across the samples rather than being driven by extreme values in the pairwise distance distribution. All calculations and figures were generated using R (R Core Team, 2025).

The results for Representativeness are 0.563 for Pur/4 and 0.581 for Pur/20, with SD values of 0.091 and 0.077 respectively. These values indicate moderate compositional dissimilarity between stratigraphic and lateral samples with a dispersion below 0.1, suggesting low variability in taxonomic composition across lateral sampling points. This indicates a relatively consistent level of similarity across lateral comparisons, with stable compositional patterns for the stratigraphic samples with respect to lateral samples.

Regarding homogeneity, the mean Bray-Curtis distance for the lateral samples was 0.291 for Pur/4 and 0.359 for Pur/20, with SD values of 0.093 and 0.094 respectively. These values indicate higher variability in the Pur/20 bed compared to Pur/4, although both remain far from a value of 1, suggesting a relatively low compositional dissimilarity across lateral samples within the beds.

The SD values below 0.1 suggest that the results are not strongly influenced by extreme pairwise values.

To visualize the distribution and density of dissimilarity values, combined violin and box plots were generated (Fig. 2). The violin plots indicate concentrated density distribution. The box plots show no values beyond the whiskers, indicating an absence of extreme values. The median and mean values are closely aligned in both strata, particularly in Pur/20 where they overlap. This supports the suggestion of no strong influence of extreme pairwise values and relatively homogeneous distributions within the strata.

A Non-metric Multidimensional Scaling (**NMDS**) analysis was carried out including all sampled points (20 stratigraphic and 20 lateral samples; Fig. 3B). This NMDS was compared with the previous one calculated with only 20 stratigraphic samples (Fig. 3A). Both analysis yielded stress values below 0.1 (0.073 and 0.066 respectively) indicating a robust ordination with minimal risk of drawing false inferences (Clarke, 1993; Kruskal, 1964). We observed that all lateral points fall within similar multivariate space occupied by the corresponding stratigraphic cluster. Although the inclusion of lateral samples causes minor shifts in the NMDS coordinates due to the iterative nature of the ordination, the overall grouping remains stable. Because NMDS configurations are arbitrary with respect to rotation, reflection and scale, emphasis was placed on the preservation of relative grouping patterns rather than on the absolute position of samples. Therefore, it is unlikely that the use of any other sampling point would have affected the original results.

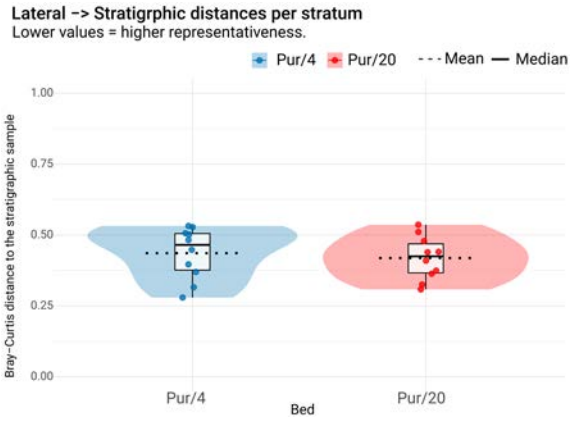

Figure 2. Combined violin and box plots showing the distribution of the Bray-Curtis distances between stratigraphic samples Pur/4 and Pur/20 and their respective lateral samples.

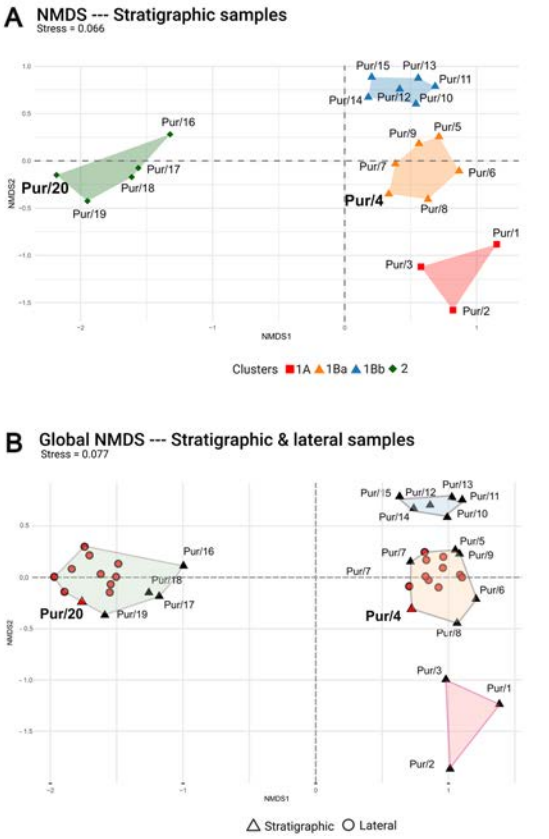

Figure 3. A, NMDS from the previous study, including the calculated clusters and based exclusively on stratigraphic samples; **B,** NMDS plot including all sampled points.

CONCLUSION

While sampling performed across the stratigraphic column only included a single sampled point per bed, limiting the use of variance-based inferential statistical methods, our results indicate that the studied strata are relatively homogeneous at the lateral scale. The stratigraphic samples show moderate compositional similarity to lateral assemblages, with no evidence of marked heterogeneity. Thus, the unique stratigraphic points sampled for beds Pur/4 and Pur/20 capture a reasonable portion of the community spatial variability, supporting their use for the characterization of their respective beds. These results are consistent with the depositional characteristics of the studied area and suggest that lateral heterogeneity is unlikely to have strongly biased the diversity patterns recovered from the stratigraphic samples in this section, at least for the beds tested. Overall, our findings highlight the importance of carrying out a preliminary study to determine the sampling effort and mitigate bias when assessing a new outcrop.

Acknowledgements: This paper is a contribution to project PID2021-125585NB-I00 and CNS2024-154147 of the Spanish Ministry of Science and Innovation.

REFERENCES

Bray, J. R., & Curtis, J. T. (1957). An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs*, *27*(4), 325–349. doi: 10.2307/1942268

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117–143. doi: 10.1111/j.1442-9993.1993.tb00438.x

Esteve, J., Hughes, N. C., & Zamora, S. (2011). Purujosa trilobite assemblage and the evolution of trilobite enrollment. *Geology*, *39*(6), 575–578. doi: 10.1130/G31985.1

Kruskal, J. B. (1964). Multidimensional Scaling by Optimizing Goodness of Fit to a Nonmetric Hypothesis. *Psychometrika*, *29*(1), 1–27. doi: 10.1007/BF02289565

R Core Team. (2025). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Zamora, S. (2011). Equinodermos del Cámbrico de España: Situación actual de las investigaciones y perspectivas futuras. *Estudios Geológicos*, *67*(1), 59.

TRILOMORPH: A COLLABORATIVE EFFORT TO CONSTRUCT THE TRILOBITE MORPHOSPACE.

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Keywords: Trilomorph, geometric morphometrics, landmarks.

INTRODUCTION

Modern approaches offer valuable metrics for quantifying and understanding macroevolutionary and macroecological patterns and processes. A crucial step in most analyses is the construction of empirical morphospaces, which enables the evaluation of morphological diversity (disparity). Evaluating disparity is a powerful method for exploring evolutionary and ecological patterns and processes. Furthermore, many studies have demonstrated that patterns of morphospace occupation over time serve as a robust tool for investigating diversification trends in the fossil record. Geometric morphometrics are a major tool that aids in the quantification of morphology and morphospace construction. The construction of empirical morphospace using geometric morphometrics, however, imposes three major challenges, (1) the time and effort involved in collecting the data, (2) the compromise between morphological detail and taxonomic breadth and (3) the selection of the single structure as reference for the whole morphology.

We here describe how Trilomorph (Serra *et al*., 2023a), a database for geomorphometric information of trilobites, partially solves some of these problems. While the original version of Trilomorph did not fully address two of the three aforementioned key issues, current developments have come to help solve them and made significant progress in its applicability.

TRILOMORPH

There are multiple taxonomically-broad trilobite geometric morphometric datasets that have been assembled, but most (if not all) of them are static dataset in the sense that they are not open to include new data (*e.g*., Foote 1993, Suárez & Esteve, 2021, Drage & Pates, 2024), or sometimes the original raw data is not part of the dataset as to reanalyze it partially. Serra *et al.* (2023) developed an open database for geomorphometric information of trilobites called Trilomorph. The database consists of pictures and landmark data files of each specimen and an easy-to-read yaml-formatted file that contains all relevant metadata for all included specimens. Trilomorph is currently hosted in Github (github.com/balsedie/trilomorph), while stable releases are available in Zenodo (doi: 10.5281/zenodo.17308187) and the official repository of the Universidad Nacional de Córdoba (https://rdu.unc.edu.ar/handle/11086/547753).

Trilomorph was designed not only to be an open access database, but also to be dynamic (Serra *et al*., 2023a), meaning that anyone can contribute with new data as long as it conforms to a simple protocol. This characteristic allows the database to keep growing by collaborative effort, which overcomes the first major problem recognized above relative to the time-consuming work of gathering data. However, it adds another potential problem; it is well known that geometric morphometric analyses are sensitive to quality of the data, and allowing for many different contributors to obtain landmark data can significantly increase the error in the dataset. This issue was already noted and tested by Serra *et al.* (2023), who showed that between contributors'

errors is statistically insignificant relative to the inter-generic variability. Serra *et al.* (2023) further showed that even an intentionally small misplacement of a landmark does not result in significant error. Although these tests suggest that the data is robust for collaborative contributions, to further ensure data robustness, database maintainers (DB and FS) occasionally check uploaded datafiles for precision in landmark positioning and specimen quality.

LANDMARKING PROTOCOL AND ANALYSES FLEXIBILITY

Although not mandatory, the structure of the data is designed to be analyzed in the R (R core). The database, therefore, includes a series of R functions to facilitate data reading and analysis. The two main functions are shapRead() and shapFix().

The shapRead() function allows to integrate data from different original landmarking softwares (essentially TPS, geomorph or Stereomorph) and thus facilitates collaborative contribution. In order to have enough data homogeneity, when creating Trilomorph, Serra *et al.* (2023) developed a general landmarking protocol (Fig. 1A). The template consists of 16 landmarks and 3 curves and is used for landmark data acquisition.

The shapFix() function, on the other hand, allows defining the actual landmark template to analyze. While the Trilomorph landmark template is the basis for the data, it also imposes important limitations, as many trilobites cannot be fully landmarked, due to missing landmarks or curves (semilandmarks). Moreover, in several cases a complete cephalon is simply lacking and the species is only known from cranidiums. Establishing a rigid, detailed landmarking protocol, therefore, constrains the number of taxa to be analyzed (note that it does not prevent their digitization). To overcome this problem, we have improved the shapFix() function. The current version of the function now allows to select any landmark and curve independently (Fig. 1A). Moreover, it further allows to join or split marginal curves (curve C3 and C4) of the cephalon. While any combination of curves and landmarks can be chosen, for the ease of the analyses we have pre-defined templates (Tab. 1, Fig. 1B, following Randolfe et al., in press).

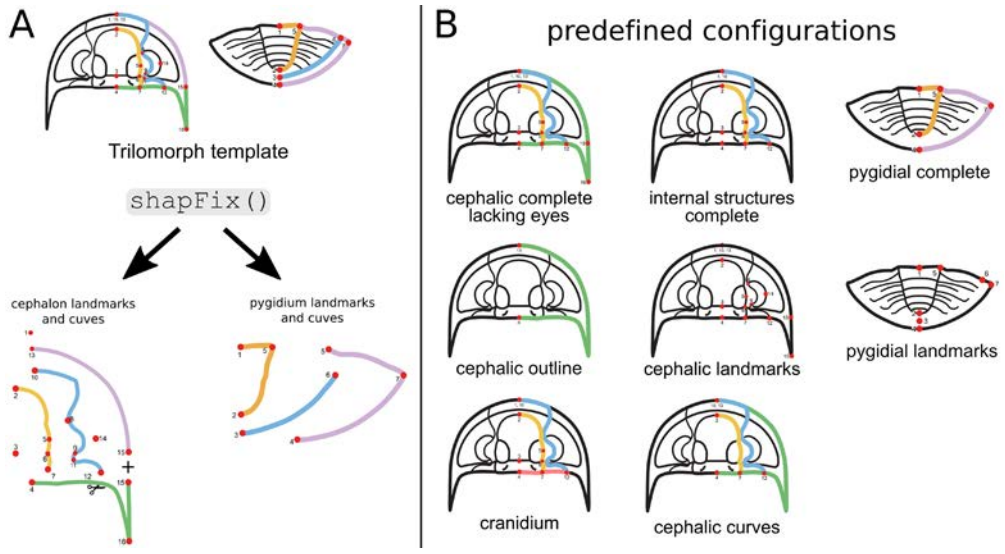

Figure 1. A, The Trilomorph landmarks and semilandmark templates. The shapFix function allows selecting any combination of the landmarks or curves; **B,** The predefined configurations in the shapFix function, predefined configurations facilitate analysis as there is no need to explicitly list the selected landmarks o semilandmarks.

Importantly, the shapFix() function now allows the direct analysis of cranidia (Fig. 1B, Tab. 1). By choosing the cranidium template, the function now creates a new curve starting on landmark 4 and finishing on landmark 12. One of the main improvements of this functionality is that Trilomorph now accepts cranidium data: shapFix() will exclude these specimens when using cephala templates but will automatically include them if analyzing cranidia.

SELECTING THE "BEST" TEMPLATE

A relevant issue relative to the different possible templates (Fig. 1B, Tab. 1) is which one is the more adequate for analysis. While this choice ultimately depends on the objectives of each study, Randolfe *et al.* (in press) addressed this issue in detail by assessing the amount and nature of the morphological information provided by different templates, particularly in relation to the trade-off between taxonomical broadness vs morphological detail. From such a perspective, the "cephalic laking eyes" and "pygidial complete" are the best options to include a large number of taxa with high morphological detail. But even the cephalic and pygidial curves (Tab. 1) seem to capture enough morphological detail (Randolfe *et al*., in press).

Table 1. List of pre-defined configurations in shapFix (L= fixed landmarks; C= curves). 3+4 refers to the single cephalon outline curve joining curves 3 and 4. Curve 5 refers to the new curve defined between landmarks 4 and 12.

Configuration	Landmarks and curves
Cephalic lacking eyes	L= 1-7, 10, 12-13, 15-16. C= 1-2, 3+4
Cephalic landmarks	L= 1-10, 12-16.
Cephalic outline	L= 4, 13. C= 3+4
Internal structure complete	L= 1-7, 10, 12. C= 1-2
Internal structure curves	L= 2, 7, 10, 12. C= 1-2.
Cephalic curves	L= 2, 4, 7, 10, 12, 13. C= 1, 2, 3+4
Cranidium	L= 1-7, 10, 12. C= 5 (new curve)
Pygidial complete	L= 1-2, 4-5, 7. C= 1, 3.
Pygidial landmark points	L= 1-2, 4-5, 7

SELECTING A MORPHOLOGICAL STRUCTURE

While most studies evaluate a single morphological structure, there is ample evidence that at least the cephalon and pygidium capture different morphological information (Oudot *et al*., 2019; Bault *et al.*, 2022, 2023; Esteve & Suárez, 2023; Serra *et al*., 2025; Randolfe *et al*., in press). The pygidium landmarking template was originally defined in Trilomorph (Serra *et al*., 2023a), although only limited pygidial data were available at the time. Trilomorph, however, currently includes pygidium landmark data for more than 100 genera. Moreover, the current version of the shapFix() function allows the evaluation of the cranidium. Therefore, Trilomorph lets one analyze the pygidium, cranidium or cephalon independently. This versatility allowed the first attempts to evaluate the differential morphological signal of the cephalon, cranidium and pygidium (Serra *et al*., 2025; Randolfe *et al*., in press). While it is not easy to generalize, our previous studies suggest that cephalic structures (both the whole cephalon and the cranidium) record ecological information while pygidial morphological diversity seems to mirror taxonomy (Serra *et al*., 2025; Randolfe *et al*., in press). These results indicate that evaluating cephalic morphospace will be highly informative for evolutionary/ecological studies, while the analysis of pygidial patterns will most likely indicate phylogenetic constraints.

FUTURE PROSPECTS

We envisage two main agendas that can be addressed using Trilomorph. On the one hand, beyond traditional disparity studies, the flexibility of the shapFix function can be utilized to address the covariation of different structures. An initial approach was explored by Randolfe *et al*. (in press), but this framework can be extended to evaluate such patterns through time and within and between clades. In turn, this opens the door to analyses of large-scale dynamics of modularity and integration allowing us to improve our understanding of the role of evolutionary trade-offs shaping phenotypic diversification, and ultimately explore the connection between modularity and the structure of morphological disparity (*e.g*., Gerber & Hopkins, 2011).

Furthermore, the broad taxonomic scope of the database provides an opportunity to investigate how disparity is structured across spatial scales, including its hierarchical partitioning through time (*e.g.*, Serra *et al*., 2023b). The integration of morphometric and occurrence data also enables the exploration of the geographic structure of disparity (*e.g*., Parry *et al*., 2025), including the identification of regional patterns and potential hotspots of morphological innovation.

More broadly, Trilomorph provides a framework to address many macroevolutionary questions; however, realizing this potential will depend on continued collaborative efforts to expand and refine the database.

Acknowledgements: We thank the Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (PICT-2021-I-A-00968) and CONICET (PIP 1220200103192CO, PIBAA 28720210101292CO)for financial support.

REFERENCES

Bault, V., Crônier, C., & Monnet, C. (2022). Morphological disparity trends in Devonian trilobites from North Africa. *Palaeontology, 65*(5), e12623. doi: 10.1111/pala.12623

Bault, V., Crônier, C., Monnet, C., Balseiro, D., Serra, F., Waisfeld, B. G., Bignon, A., & Rustán, J. J. (2023). Rise and fall of the phacopids: The morphological history of a successful trilobite family. *Palaeontology, 66*(5), e12673. doi: 10.1111/pala.12673

Drage, H. B., & Pates, S. (2024). Distinct causes underlie double-peaked trilobite morphological disparity in cephalic shape. *Communications Biology, 7*(1), 1–18. doi: 10.1038/s42003-024-07221-2

Esteve, J., & Suárez, M. G. (2023). Ecomorphological datasets: Comment on Hopkins (2022). *Lethaia, 56*(2), 1–5. doi: 10.18261/let.56.2.2

Foote, M. (1993). Contributions of individual taxa to overall morphological disparity. *Paleobiology, 19*(4), 403–419.

Gerber, S. & Hopkins, M. J. (2011). Mosaic heterochrony and evolutionary modularity: The trilobite genus Zacanthopsis as a case study. *Evolution*, *65*, 3241-3252. doi: 10.1111/j.1558-5646.2011.01363.x

Oudot, M., Neige, P., Laffont, R., Navarro, N., Khaldi, A. Y., & Crônier, C. (2019). Functional integration for enrolment constrains evolutionary variation of phacopid trilobites despite developmental modularity. *Palaeontology*, *62*(5), 805–821. doi: 10.1111/pala.12428

Parry, S. L., Balseiro, D., & Waisfeld, B. G. (2025). The geographic structure of trilobite disparity within the Middle Ordovician of Laurentia. *69th Annual Meeting of the Palaeontological Association Programme and Abstracts*, 112.

Randolfe, E., Serra, F., Balseiro, D., María Dorado, J., Aquino, D. F., Parry, S. L., Monti, S. D., Handkamer, N. M., Vaccari, N. E., Rustán, J. J., Waisfeld, B. G. (In press). Building the trilobite

morphospace: the influence of different morphological structures. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Serra, F., Balseiro, D., Monnet, C., Randolfe, E., Bignon, A., Rustán, J. J., Bault, V., Muñoz, D. F., Vaccari, N. E., Martinetto, M., Crônier, C., & Waisfeld, B. G. (2023a). A dynamic and collaborative database for morphogeometric information of trilobites. *Scientific Data*, *10*(1), 841. doi: 10.1038/s41597-023-02724-9

Serra, F., Balseiro, D., & Waisfeld, B. G. (2023b). Morphospace trends underlying a global turnover: Ecological dynamics of trilobite assemblages at the onset of the Ordovician radiation. *Palaeogeography, Palaeoclimatology, Palaeoecology, 615*, 111448. doi: 10.1016/j.palaeo.2023.111448

Serra, F., Balseiro, D., Allaire, N., Waisfeld, B. G. (2025). Trilobite cranidial and pygidial disparity patterns: two sides of the story. Historical Biology, *38*(3), 698–712. doi: 10.1080/08912963.2025.2506093

Suárez, M. G., & Esteve, J. (2021). Morphological diversity and disparity in trilobite cephala and the evolution of trilobite enrolment throughout the Palaeozoic. Lethaia, *54*(5), 752–761. doi: 10.1111/let.12437

BEYOND FLAT IMAGES: IS 3D ANALYSIS CRUCIAL FOR MEASURING TRILOBITE DISPARITY?

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Keywords: Phacopida, geometric morphometrics, 3D shape analysis, Lower Devonian.

Phacopid trilobites, well-documented throughout the Paleozoic, provide an excellent model for investigating morphological variation, phylogenetic relationships, and evolutionary mechanisms across spatial and temporal scales. Most quantitative studies have relied on 2D analyses, which effectively capture dorsal morphology. While 2D geometric morphometrics has advanced our understanding of trilobite shape variation, 3D analyses remain scarce despite their potential to capture complex morphologies, particularly in phacopid trilobites.

This study presents the first direct comparison of 2D and 3D morphometric approaches applied to phacopid trilobites to evaluate: (1) intra- and interspecific morphological variation; (2) shared allometric patterns among species; (3) how phylogenetic relationships shape morphological variation; and (4) differences in accuracy between 2D and 3D approaches (see Crônier et al. 2024).

We analyzed eight well-preserved Lower Devonian species from Algeria, including 60 cephala and 41 pygidia. Specimens were digitized using structured-light 3D scanning for 3D analysis and traditional photography for 2D analysis. Cephalic shape was assessed using 15 landmarks in 2D and 19 landmarks in 3D, whereas pygidial shape was assessed using 8 landmarks in both 2D and 3D, covering their bilateral symmetry. Incomplete specimens were reconstructed by mirroring landmarks relative to the individual symmetry plane. Landmark configurations were standardized using a Generalized Procrustes Analysis (**GPA**). Individual shape variation was visualized using a principal component analysis (**PCA**) based on aligned Procrustes configurations. Procrustes ANOVA and linear models were used to assess allometric variation, and phylomorphospaces were constructed to explore shape variation within a phylogenetic framework (modified from Oudot *et al*., 2018). The congruence between shape spaces from 2D and 3D data was evaluated using Mantel tests performed on PCA individual scores.

Results show that both 2D and 3D analyses reveal broadly similar patterns. For cephala, principal components primarily distinguish taxa, with *Austerops legrandi* being the most clearly differentiated species, whereas other species show partial overlap. 3D data better capture glabellar inflation and genal angles. For pygidia, morphological variation largely reflects taxonomy, though overlap is greater than for cephala; 3D analyses better capture transverse and sagittal elongation.

Allometric analyses reveal consistent patterns in both 2D and 3D datasets. For cephala, both species and size significantly affect shape: glabellar length decreased during growth, resulting in relatively wider cephala across species. *Austerops legrandi* is morphologically distinct, whereas *A. menchikoffi* and *A. speculator* are highly similar. Pygidial shape variation shows significant species effects but no size effect.

Phylomorphospace analyses suggest phylogenetic constraints on cephalic morphologies, supporting *Austerops* and *Morocops* as sister clades with distinct evolutionary trajectories. In contrast, pygidial shape variation exhibits a low phylogenetic signal (quantified by K_{mult} statistics; see Adams, 2014), likely reflecting lower functional and morphological complexity.

Comparisons between 2D vs 3D approaches show strong correlations in centroid sizes and overall shape distances. However, 3D data provide additional morphological details along the third dimension that is not captured by 2D approach, allowing more precise genus-level discrimination, particularly for cephala. For example, *Adrisiops fabrei* and *Austerops legrandi* are better separated in 3D morphospace. Three-dimensional morphometrics enhance the detection of lateral expansion, glabellar inflation, and other cephalic traits, providing deeper insights into developmental constraints and evolutionary patterns. The third dimension also reveals evolutionary constraints not detectable using 2D data. Whereas *Morocops* shows moderate and evenly distributed variation within phylomorphospace*, Austerops* explores a broad range of morphospace in 2D but a more restricted range in 3D.

These results support the continued use of 2D morphometrics for rapid assessments and macroevolutionary studies, while highlighting the added value of 3D approaches for detailed taxonomic and evolutionary analyses, particularly for highly convex or complex structures. Three-dimensional analyses capture evolutionary constraints and phylogenetic information that may remain undetected in 2D datasets.

Integrating 2D and 3D approaches therefore provides a powerful framework for investigating trilobite evolution, functional morphology, and macroevolutionary trends. The results demonstrate that both 2D and 3D morphometrics are effective for quantifying phacopid shape variation, with congruent patterns of allometry and taxonomic differentiation. Moreover, combining 2D and 3D data can reveal developmental constraints, phylogenetic patterns, and potential ecological or environmental influences on morphological evolution in trilobites. While 2D remains a rapid and practical tool, 3D approaches are recommended for highly convex or complex structures to fully capture shape variability. Future studies should expand sample sizes to refine evolutionary inferences.

REFERENCES

Adams, D. C. (2014). A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. *Systematic Biology*, *63*, 685–697. doi:10.1093/sysbio/syu030

Crônier, C., Couette, S. & Laffont, R. (2024). Is 3D, a more accurate quantitative method than 2D, crucial for analyzing disparity patterns in extinct marine arthropods (Trilobita)? *Paleobiology*, *50*, 563–581. doi:10.1017/pab.2024.44

Oudot, M., Crônier ,C., Neige, P., & Holloway, D. (2018). Phylogeny of some Devonian trilobites based on morphological characters and consequences to the systematics of *Austerops* (Phacopidae). *Journal of Systematic Palaeontology*, *17*, 775–790. doi:10.1080/14772019.2018.1471105

THE CAMBRIAN EMU BAY SHALE LAGERSTÄTTE OF KANGAROO ISLAND: ALMOST TWO DECADES OF RESEARCH INTO EARLY ARTHROPOD EVOLUTION

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Keywords: Trilobites, Cambrian, Lagerstätte, Australia.

September 2007 saw the start of the Emu Bay Shale Research Project, in South Australia's Kangaroo Island. The project included a team of scientists from the University of Adelaide, University of South Australia, South Australian Museum, University of New England, Natural History Museum–London and the Spanish Research Council (CSIC), to which many collaborators and volunteers joined from institutions across the world. The project has been funded by Australian Research Council, National Geographic Society, South Australian Museum, Beach Petroleum Ltd. and the Spanish Ministry of Education & Science, among others.

Almost 20 years ago, the assemblage included about a dozen animal taxa, but has since increased by 1 new family, 9 new genera and 15 new species, of which the family, 8 of the genera and 12 of the species are arthropods. The described panarthropod taxa at EBS include a luolishaniid lobopodian (the "EBS monster"), 2 radiodonts (*Anomalocaris* and *Echidnacaris*), 4 bivalved arthropods (2 each of *Isoxys* and *Tuzoia*), 2 megacheirans (*Oestokerkus* and *Tanglangia*), 1 retifaciid (*Squamacula*), 1 habeliid (*Wisangocaris*), 1 aglaspidid (*Eozetetes*), 1 xandareliid (*Austroxandarella*), 2 indeterminate artiopodans (*Squamacula* and *Australimicola*), 2 nektaspids (*Emucaris* and *Kangacaris*), and 6 trilobites (*Estaingia*, *Balcoracania*, *Holyokia*, *Megapharanaspis* and 2 *Redlichia*), plus 8 others still pending formal description and *Myoscolex ateles* which can be considered *incertae sedis*. There are over 25,000 EBS specimens in the South Australian Museum Palaeontological Collections, of which almost 95% are arthropods (mostly *Estaingia bilobata*, with 83%) and from a total of 50 species in the assemblage, 60% (30 taxa) are panarthropods (Gaines *et al*., 2024).

The project has so far produced 32 refereed journal articles, 10 popular articles and other non-specialist publications, and 40 national and international conference presentations. The most significant discoveries, both published in *Nature* in 2011, were the exquisitely preserved compound eyes of the two radiodonts, with up to 13,000 ommatidia in *Echidnacaris briggsi* and about 25,000 ommatidia for *Anomalocaris daleyae*. Besides the systematic palaeontology of the panarthropods in the assemblage, the team has also addressed ontogenetic series and moulting patterns of the trilobites, as well as malformation and evidence in trilobites of durophagous predation, identifying the culprits behind the latter: the large *Redlichia rex* on the larger trilobites, including its own relatives, and *Wisangocaris* on the smaller trilobites, predominantly *Estaingia*.

An interesting, but not totally unexpected, development is the recent extension of the EBS Family Emucarididae in both time range and geographical distribution with *Tafilocaris ordovicica* from the Tafilalt Biota of Morocco: extends by almost 60 million years into the Late Ordovician, and expands from the circum-tropical waters of Eastern Gondwana and South China to the high-latitude environments of Western Gondwana, making the emucaridids a peri-Gondwanan clade (García-Bellido & Gutiérrez-Marco, 2025).

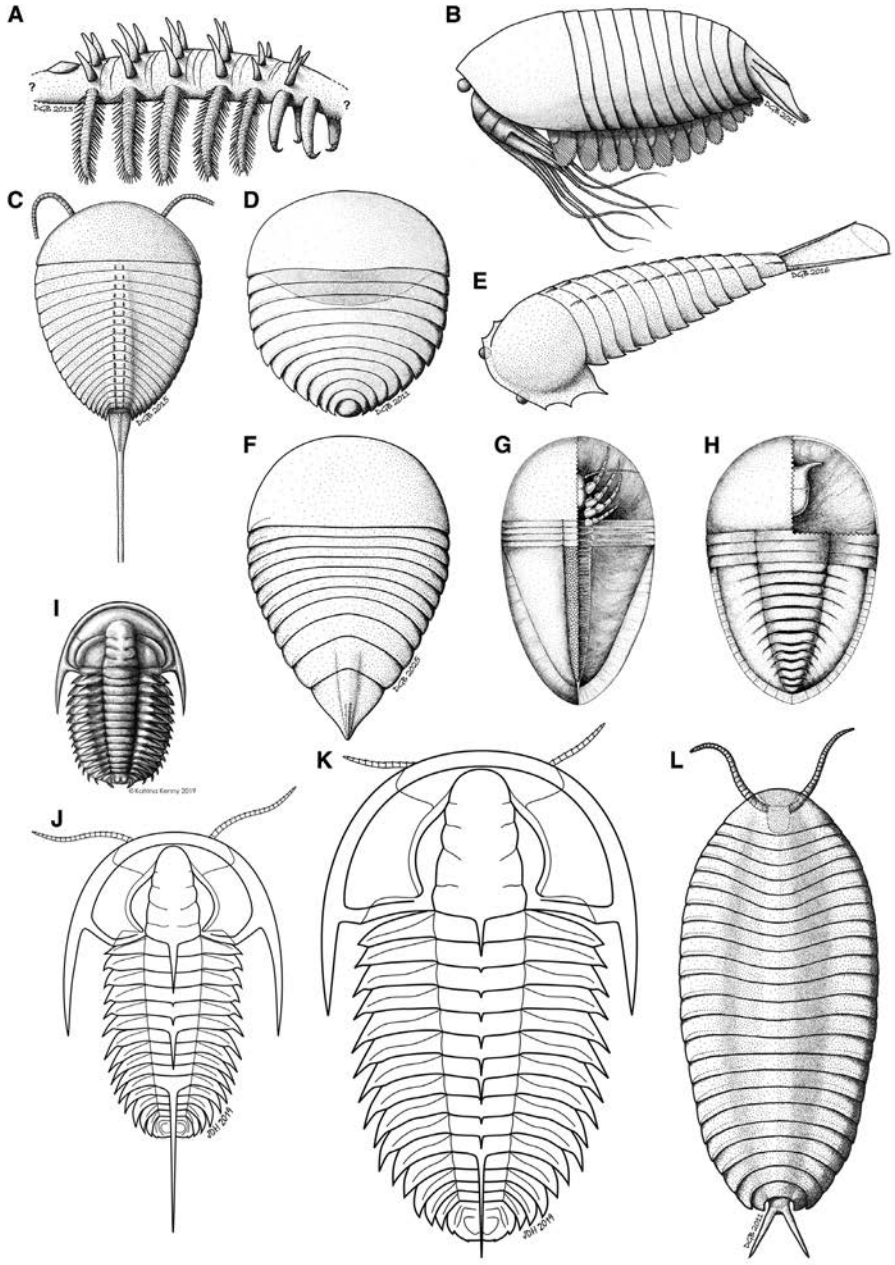

Figure 1. Published reconstructions of panarthropods from the Emu Bay Shale (Cambrian Series 2, Stage 4) of Kangaroo Island, South Australia, since 2007. **A,** "Emu Bay Shale Monster" (García-Bellido *et al*., 2013); **B,** *Oestokerkus megacholix* gen. et sp. nov. (Edgecombe *et al*., 2011); **C,** *Eozetetes gemmelli* gen. et sp. nov. (Edgecombe *et al*., 2017); **D,** *Squamacula buckorum* sp. nov. (Paterson *et al*., 2012); **E,** *Wisangocaris barbarahardyae* gen. et sp. nov. (Jago *et al*., 2016); **F,** *Austroxandarella poikar* gen. et sp. nov. (Edgecombe *et al*., 2025); **G,** *Emucaris fava* gen. et sp. nov. (Paterson *et al*., 2010); **H,** *Kangacaris zhangi* gen. et sp. nov. (Paterson *et al*., 2010); **I,** *Estaingia bilobata* (Holmes *et al*., 2021a); **J,** *Redlichia takooensis* (Holmes *et al*., 2020); **K,** *Redlichia rex* sp. nov. (Holmes *et al*., 2020); **L,** *Australimicola spriggi* gen. et sp. nov. (Paterson *et al*., 2012).

The list below includes all the panarthropod-focused publications of the Emu Bay Shale Research Project since 2007 in chronological order:

REFERENCES

Paterson, J. R., Jago, J. B., Gehling, J. G., García-Bellido, D. C., Edgecombe, G. D., & Lee, M. S. Y. (2008). Early Cambrian arthropods from the Emu Bay Shale Lagerstätte, South Australia. In I. Rábano, R. Gozalo, & D. García-Bellido, (Eds.), *Advances in Trilobite Research*, (pp. 313–320). Instituto Geológico y Minero de España.

García-Bellido, D. C., Paterson, J. R., Edgecombe, G. D., Jago, J. B., Gehling, J. G., & Lee, M. S. Y. (2009). The bivalved arthropods *Isoxys* and *Tuzoia* with soft-part preservation from the lower Cambrian Emu Bay Shale Lagerstätte (Kangaroo Island, Australia). *Palaeontology*, *52*(6), 1221–1241. doi: 10.1111/j.1475-4983.2009.00914.x

Paterson, J. R., Edgecombe, G. D., García-Bellido, D. C., Jago, J. B., & Gehling, J. G. (2010). Nektaspid arthropods from the lower Cambrian Emu Bay Shale Lagerstätte, South Australia, with a reassessment of lamellipedian relationships. *Palaeontology*, *53*(2), 377–402. doi: 10.1111/j.1475-4983.2010.00932.x

Edgecombe, G. D., García-Bellido, D. C., & Paterson, J. R. (2011). A new leanchoiliid megacheiran arthropod from the lower Cambrian Emu Bay Shale, South Australia. *Acta Palaeontologica Polonica*, *56*(2), 385–400. doi: 10.4202/app.2010.0080

García-Bellido, D. C. (2011). Un ojo de más de 500 millones de años. *Investigación y Ciencia*, *420*, 38–39.

Lee, M. S. Y., Jago, J. B., García-Bellido, D. C., Edgecombe, G. D., Gehling, J. G., & Paterson, J. R. (2011). Modern optics in exceptionally preserved Early Cambrian arthropod eyes from Australia. *Nature, 474*(7353), 631–634. doi: 10.1038/nature10097

Lee, M., & Paterson, J. (2011). Rapid evolution? The eyes have it. *Australasian Science*, *32*(10), 28–30.

Paterson, J. R., García-Bellido, D. C., Lee, M. S. Y., Brock, G. A., Jago, J. B., & Edgecombe, G. D. (2011). Acute vision in the Cambrian predator *Anomalocaris* and the origin of compound eyes. *Nature*, *480*(7376), 237–240. doi: 10.1038/nature10689

Daley, A., & Paterson, J. (2012). The Earth's first super-predators. *Australasian Science*, *33*(6), 16–19.

Paterson, J. R., García-Bellido, D. C., & Edgecombe, G. D. (2012). New artiopodan arthropods from the Early Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia. *Journal of Paleontology*, *86*(2), 340–357. doi: 10.1666/11-077.1

Daley, A. C., Paterson, J. R., Edgecombe, G. D., García-Bellido, D. C., & Jago, J. B. (2013). New anatomical information on *Anomalocaris* from the Emu Bay Shale Konservat-Lagerstätte (Cambrian; South Australia) and a reassessment of its inferred predatory habits. *Palaeontology*, *56*(6), 971–990. doi: 10.1111/pala.12029

García-Bellido, D. C., Paterson, J. R., Edgecombe, G. D., & Ma, X. (2013). A "Collins' monster"-type lobopodian from the Emu Bay Shale Konservat-Lagerstätte (Cambrian), South Australia. *Alcheringa*, *37*(4), 474–478. doi: 10.1080/03115518.2013.792456

Paterson, J. R., Edgecombe, G. D., & Jago, J. B. (2015). The 'great appendage' arthropod *Tanglangia*: Biogeographic connections between early Cambrian biotas of Australia and South China. *Gondwana Research*, *27*(4), 1667–1672. doi: 10.1016/j.gr.2014.02.008

Jago, J. B., García-Bellido, D. C., & Gehling, J. G. (2016). An early Cambrian chelicerate from the Emu Bay Shale, South Australia. *Palaeontology*, *59*(4), 549–562. doi: 10.1111/pala.12243

Edgecombe, G. D., Paterson, J. R., & García-Bellido, D. C. (2017). A new aglaspidid-like arthropod from the early Cambrian Emu Bay Shale of South Australia. *Geological Magazine*, *154*(1), 87–95. doi: 10.1017/S0016756815001053

Drage, H. B., Holmes, J. D., García-Bellido, D. C., & Daley, A. C. (2018). An exceptional record of Cambrian trilobite moulting behaviour preserved in the Emu Bay Shale, South Australia. *Lethaia*, *51*, 473–492. doi: 10.1111/let.12266

Holmes, J. D., García-Bellido, D. C., & Paterson, J. R. (2020). The trilobite *Redlichia* from the lower Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia: Systematics, ontogeny and soft-part anatomy. *Journal of Systematic Palaeontology*, *18*(4), 295–334. doi: 10.1080/14772019.2019.1605411

Paterson, J. R., Edgecombe, G. D., & García-Bellido, D. C. (2020). Disparate compound eyes of Cambrian radiodonts reveal their developmental growth mode and diverse visual ecology. *Science Advances*, *6*(49), eabc6721. doi: 10.1126/sciadv.abc6721

Holmes, J. D., Paterson, J. R., & García-Bellido, D. C. (2021a). The post-embryonic ontogeny of the early Cambrian trilobite *Estaingia bilobata* from South Australia: Trunk development and phylogenetic implications. *Papers in Palaeontology*, *7*(2), 931–950. doi: 10.1002/spp2.1323

Holmes, J. D., Paterson, J. R., & García-Bellido, D. C. (2021b). Complex axial growth patterns in an early Cambrian trilobite from South Australia. *Proceedings of the Royal Society B: Biological Sciences*, *288*, 20212131. doi: 10.1098/rsbp.2021.2131

Bicknell, R. D. C., Holmes, J. D., Pates, S., García-Bellido, D. C., & Paterson, J. R. (2022). Cambrian carnage: Trilobite predator-prey interactions in the Emu Bay Shale of South Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *591*, 110877. doi: 10.1016/j.palaeo.2022.110877

Bicknell R. D .C., Holmes, J. D., Pates S., García-Bellido, D. C., & Paterson, J.R. (2023). Malformed individuals of the trilobite *Estaingia bilobata* from the Cambrian Emu Bay Shale and their palaeobiological implications. *Geological Magazine*, *160*(4), 803–812. doi: 10.1017/S0016756822001261

Drage, H. B., Holmes, J. D., García-Bellido, D. C., & Paterson, J. R. (2023). Associations between trilobite intraspecific moulting variability and body proportions: *Estaingia bilobata* from the Cambrian Emu Bay Shale, Australia. *Palaeontology*, *66*, e12651. doi: 10.1111/pala.12651

Paterson, J. R., García-Bellido, D. C., & Edgecombe, G. D. (2023). The early Cambrian Emu Bay Shale radiodonts revisited: Morphology and systematics. *Journal of Systematic Palaeontology*, *21*(1), 2225066. doi: 10.1080/14772019.2023.2225066

Edgecombe, G. D., García-Bellido, D. C., & Paterson, J. R. (2025). A new xandarellid euarthropod from the lower Cambrian Emu Bay Shale, South Australia. *Journal of Paleontology*, *99*(4), 905–913. doi: 10.1017/jpa.2025.10138

MORPHOLOGICAL ALTERATION IN LATE PALEOZOIC PROETID TRILOBITES

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Keywords: trilobite, proetid, Paleozoic, geometric morphometrics.

Trilobite diversity and disparity peaked early in the Cambrian and declined for the remainder of the Paleozoic. Trilobite diversity was significantly reduced following the Late Devonian extinction pulses, and only one order, Proetida, persisted until the end of the Permian. Proetid trilobites, in comparison with other orders, are considered morphologically conservative, with few evolutionary novelties throughout the clade's history. This hypothesis has not yet been quantitatively tested. Therefore, this study examined morphological patterns and possible alteration of proetids from the Ordovician to the Permian. Using geometric morphometrics, we found that a significant alteration in proetid morphology occurred in the Devonian Period, where two morphotypes became distinct. This division into two morphotypes, one bulbous and one streamlined, was lost in the Carboniferous Period. Other factors, such as family, age, or site, were generally not determinative of changes in proetid morphology. Additionally, morphologies for the Late Paleozoic returned to a more primitive proetid state. This study demonstrates that proetids did undergo periods of morphological change across their history, which may have been in response to ecological restructuring or possible expansion of niche space.

REDLICHIA NEEDS REVISION: CRANIDIAL MEASUREMENTS SHOW SUBSTANTIAL OVERLAP BETWEEN TRILOBITES OF THE GENUS *REDLICHIA*

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Keywords: Cambrian, Gondwana, disparity, *Redlichia*.

BACKGROUND

Trilobites of the genus *Redlichia* Cossmann, 1902 are found in many early Cambrian rocks from modern-day Australia, China, Iran, Korea, Morocco, Pakistan and Spain. *Redlichia* is an important index taxon, and is often considered an informal marker of the base of (as yet unnamed) Cambrian Series 2, Stage 4. Despite this, the systematics of *Redlichia* are problematic and in great need of revision. In Australia (and elsewhere), many *Redlichia* species have been described from fragmentary or distorted specimens, and it is likely that the genus has been substantially "oversplit". In Australia, 22 species of *Redlichia* have been described (Bengtson *et al*., 1990; Holmes *et al.*, 2020, 2021; Jago *et al.*, 1997; Kruse, 1990, 1991, 1998; Kruse *et al*., 2004; Laurie, 2016; Öpik, 1958, 1970; Smith *et al.*, 2026; Whitehouse, 1939) is an abundant element of the lower Cambrian (Series 2, Stage 4, eleven of those based on single digit specimen counts and only five that have more than fifty specimens attributed to the species, two of which still could not be confidently assigned to a species (Holmes *et al*., 2021; Kruse, 1998). One major issue is the sizeable number of species described using mostly or exclusively cranidial material.

This contribution focuses on better documenting the occurrence of *Redlichia* in the upper Stage 4 Wirrealpa Limestone in the Flinders Ranges, South Australia (Fig. 1). Fragmentary *Redlichia* specimens from this unit have previously been described by Jell in Bengtson *et al.* (1990) as *Redlichia guizhouensis* Zhao in Lu *et al.* (1974), although this attribution is uncertain as *Redlichia guizhouensis* is known from limited published material from China, and may be synonymous with *Redlichia nobilis* Walcott, 1905 (Bengtson *et al.*, 1990; Zhang, 1985, 2003). Here, we document abundant new material from the Wirrealpa Limestone, and compare this with other Australian *Redlichia* species.

OBJECTIVES

This project has two major aims:

1. Determine the taxonomic affinities of *Redlichia* from the Wirrealpa Limestone based on newly collected material.

2. Determine if this (and other) Australian *Redlichia* species can be differentiated based on ratios of cranidial measurements (i.e. lengths, angles) as used in previous studies.

METHODS

One hundred forty-one new *Redlichia* specimens were collected from the Wirrealpa Limestone from two localities in the Bunkers Range area (Flinders Ranges, South Australia). These are

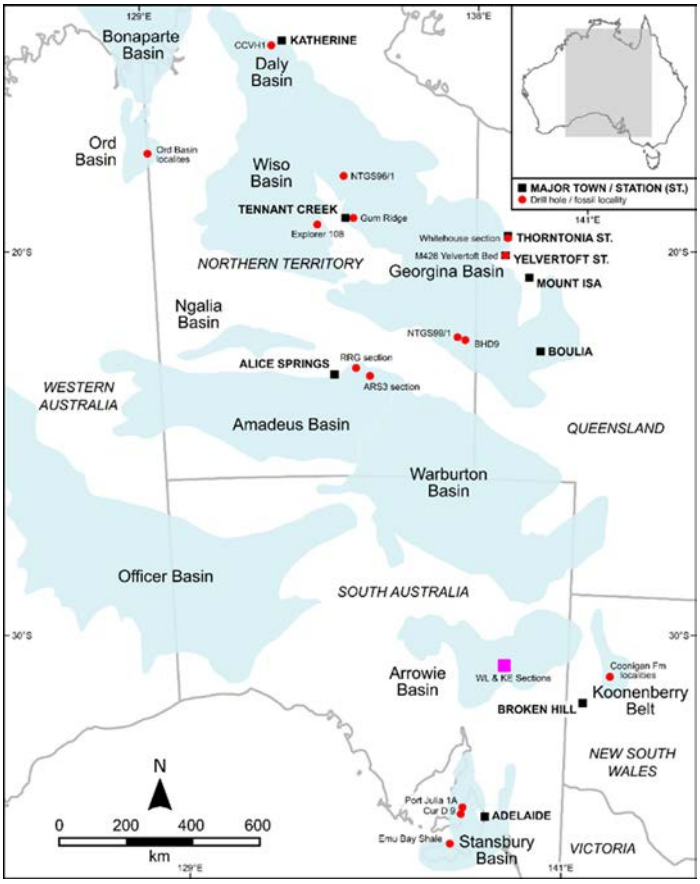

Figure 1. Map of central Australia showing major Cambrian basins and localities where *Redlichia* has been found. Purple square shows location where specimens for this study were collected.

mostly disarticulated cranidia and librigenae, but include some partially articulated specimens. Specimens were collected from grey-green calcareous siltstone in the lower part of the WL Section of Paterson and Brock (2007) and at a new locality approximately 14 km to the south. The second locality is mentioned briefly in Jago *et al*. (2020; p. 937) and occurs in the middle part of a section through the Wirrealpa Limestone in a small fault block just east of Ten Mile Creek, east of Section 6 of Youngs (1977) (31°16'19.7"S 138°56'27.8"E).

Based on ratios used in previous literature to taxonomically diagnose species of *Redlichia*, measurements were taken of the 48 best cranidia from the newly collected material (out of a total of 88). For comparison, measurements were also taken from a total of 80 cranidia from different Australian *Redlichia* species described in the literature, mainly from the Ordian (upper Stage 4). Ratios of these measurements were then compared both within and between species.

MAIN RESULTS

As *Redlichia guizhouensis* is poorly documented, comparisons with the new material instead focused on Australian *Redlichia.* The general measurements and ratios of the Wirrealpa Limestone cranidia are close to several other Ordian *Redlichia* species (except the notably different *R. chinesis* Walcott, 1905 described in Öpik, 1970)(Fig. 2B–2D). As expected, the Wirrealpa Limestone material shows considerable similarity to *R*. cf. *versabunda* from the Ramsay Limestone (Holmes *et al*., 2021), sharing a wide anterior border, strongly divergent anterior facial sutures, and strongly

advanced genal spines (Fig. 2E, 2G). Thoracic spine arrangement is difficult to determine due to the fragmentary nature of the thoracic material, but a thoracic spine is evident on the fourth thoracic segment (Fig. 2A), matching the placement with other Australian Ordian *Redlichia* for which thoracic material has been described. A large spine also occurs on the eleventh or twelfth

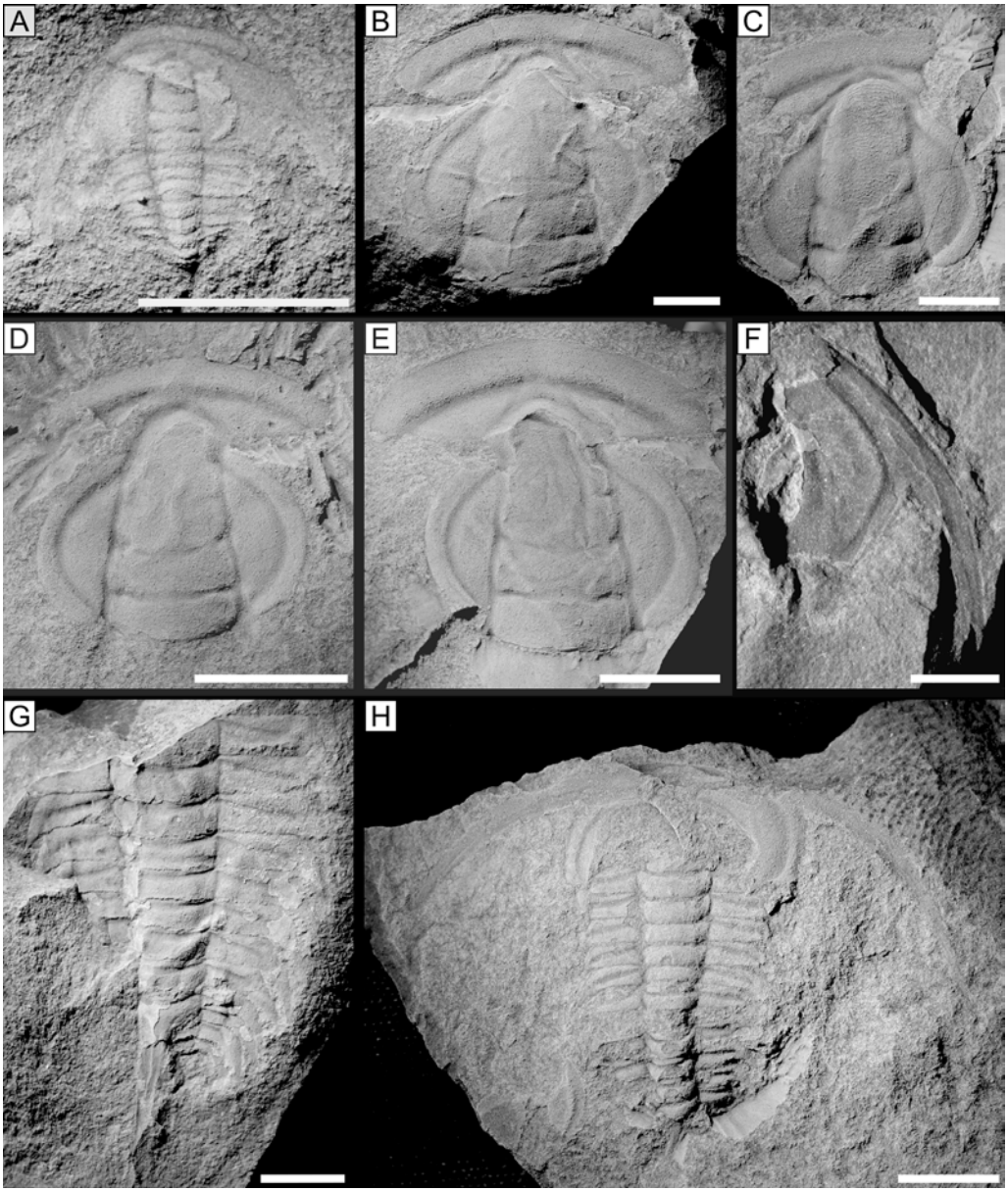

Figure 2. Selection of specimens collected from the Wirrealpa Limestone. **A,** KE-44. Almost complete early holaspid; **B–E,** KE-X3, WL-X4, KE-48 & KE-38. Cranidia, with WL-X4 showing ornamentation; **F,** KE-52. Librigina. **G,** KE-6. Partial thorax, consisting of 11 segments; **H,** WL-X5. Partial thorax with partially articulated libregenae, showing extreme length of librigenal spines; scalebar = 5 mm.

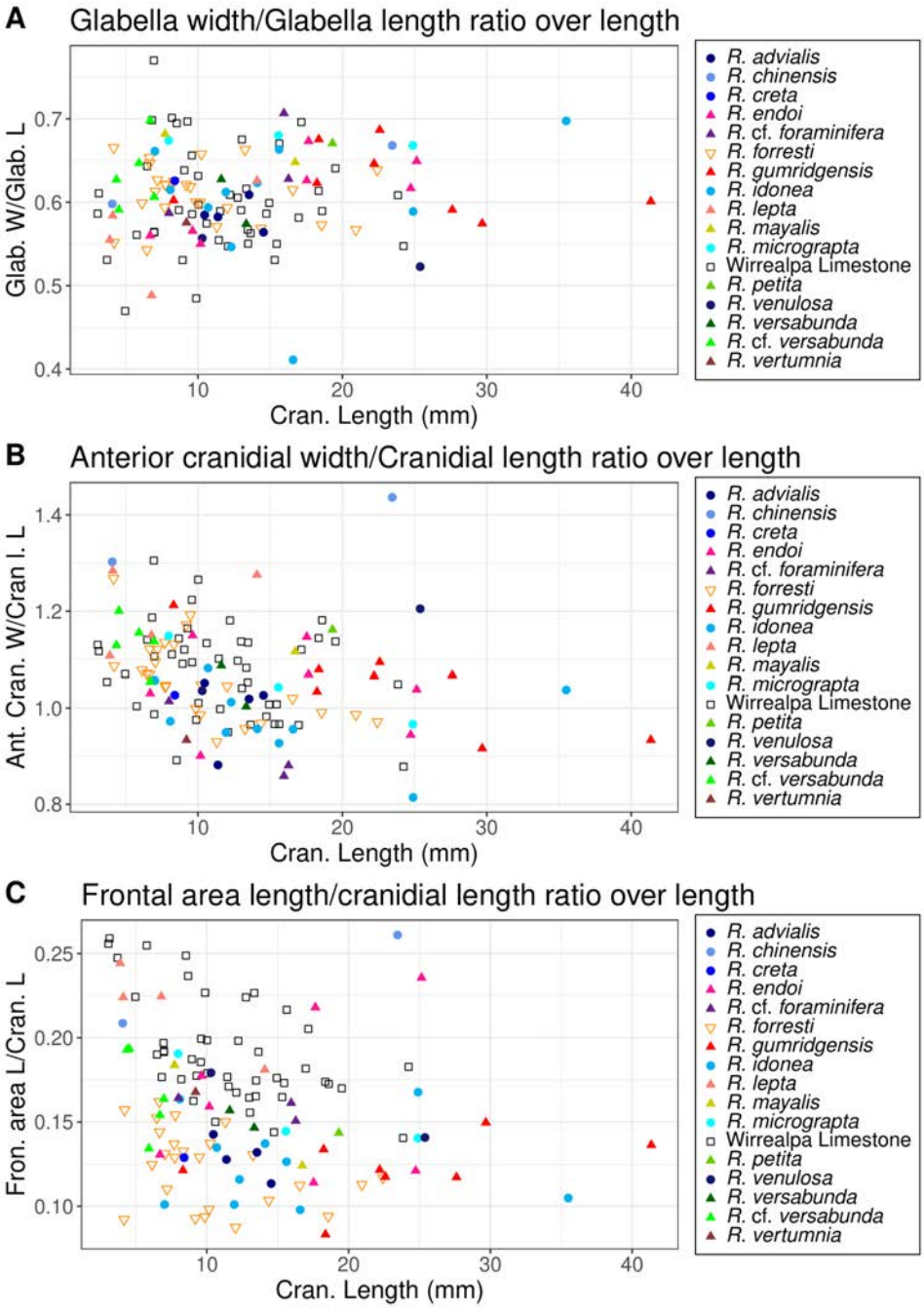

Figure 3. Ratios of different cranidial measurements plotted against cranidial length for most Australian *Redlichia*. **A,** Glabellar length/with ratio over length; **B,** Anterior cranidial width/cranidial length ratio over length; **C,** Frontal area length/cranidial length ratio over length. Black squares show *R.* cf. *versabunda* from the Wirrelapa Limestone, orange hollow triangles show *R. forresti*. Blue circles of different shades show all species from Yelvertoft bed, upwards triangles show all other species.

segment (Fig. 2F). In Australia, an apparent geographic trend occurs in terms of thoracic spine placement, in that eastern Ordian *Redlichia* (from the Yelvertoft bed (Öpik, 1970)1958) have a thoracic spine on the tenth or eleventh segment, whereas the western Ordian *Redlichia* (*R. forresti* and *R. gumridgensis* (Kruse *et al*., 2004; Öpik, 1970)*Rosewood and Argyle Synclines. The Hardman Syncline is the most extensive of these, and preserves the most complete stratigraphic record, including Middle? Upper Cambrian Goose Hole Group and Upper Devonian Mahony Group, resting on LowerCambrian Antrim Plateau Volcanics.\nThe Goose Hole Group consists of two subgronps, the Negri Subgroup and overlying Elder Subgroup. The Negri Subgroup includes in ascending order the Headleys Limestone, Nelson Shale, Linnekar Limestone and Panton Formation. It is predominantly a peritidal succession, with brief marine episodes represented by the Linnekar Limestone and Panton Formation (mainly between and including the Shady Camp and Corby Limestone Members in the medial part of the formation*) have the spine on the twelfth segment. Better preserved material from the Wirrealpa Limestone is required to confidently assess a taxonomic affinity to either of these groups.

Comparison of cranidial measurements within the well sampled Ordian species (*R. forresti* and the newly collected Wirrealpa Limestone material) show large ranges of ratios previously used as diagnostic for species of *Redlichia* (Fig. 3). In the newly collected material there also seems to be a clear ontogenetic trend of decreasing frontal area length relative to cranidial length, suggesting that allometric growth may be complicating the description of (and comparisons between) species. Further, when plotting all species there is no clear clustering in any of the previously used ratios, with ranges of species overlapping greatly. The only notable exception is the lone measurable specimen of *R. chinensis* described from Australia, which is isolated in terms of ratios associated with the frontal area and the anterior cranidial width.

CONCLUSIONS

The newly collected material shows many similarities to *Redlichia* cf. *versabunda* from the Ramsay Limestone (Holmes *et al.*, 2021), with only slight differences associated with the occipital ring, glabellar furrows and facial suture angles, possibly caused by taphonomic deformation. Yet, the lack of postcranidial material besides the pygidium from the Ramsay Limestone does not allow for complete comparison. At present, the Wirrealpa Limestone specimens are best described as *Redlichia* cf. *versabunda,* and may be conspecific with the Ramsay Limestone *Redlichia*.

Comparison of cranidial measurements between different Australian Ordian *Redlichia* suggest these are not sufficient by themselves to differentiate between species. There is major overlap between different species that are known to be separate due to differences in other sclerites (*e.g*., pygidial morphologies or the presence of thoracic axial spines on different segments). This overlap is suggested to be mainly caused by the large intraspecific and ontogenetic variation seen in the best sampled species, in particular *R.* cf. *versabunda* from the Wirrealpa Limestone and *R. forresti*. This calls into question the validity of species described only on cranidial characteristics, and puts further weight behind the assertion that *Redlichia* is oversplit in Australia. Further research will be required on this genus to address these ongoing taxonomic issues. Future work should focus on collecting more specimens of the poorly sampled species from their type localities, especially from the “Yelvertoft Bed” (within the Thorntonia Limestone) in Queensland. This will likely result in the synonymising of a number of poorly known taxa, and make it easier to assign more recently described material to existing species with confidence. In turn, this will provide a clearer view of the variation within and between species of *Redlichia*, and will help to identify which traits are best to confidently differentiate between species.

REFERENCES

Bengtson, S., Conway Morris, S., Cooper, B. J., Jell, P. A., & Runnegar, B. N. (1990). *Early Cambrian fossils from south Australia*. Association of Australasian Palaeontologists, *9*, 1–364

Cossmann, M. (1902). Rectification de la nomenclature. *Revista Critica Paleozoologie*, *16*, 52.

Holmes, J. D., Paterson, J. R., & García-Bellido, D. C. (2020). The trilobite Redlichia from the lower Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia: Systematics, ontogeny and soft-part anatomy. *Journal of Systematic Palaeontology*, *18*(4), 295–334. doi: 10.1080/14772019.2019.1605411

Holmes, J. D., Paterson, J. R., Jago, J. B., & García-Bellido, D. C. (2021). Ontogeny of the trilobite Redlichia from the lower Cambrian (Series 2, Stage 4) Ramsay Limestone of South Australia. *Geological Magazine*, *158*(7), 1209–1223. doi: 10.1017/S0016756820001259

Jago, J., Tian-Rui, L., Davidson, G., Stevens, B., & Bentley, C. (1997). A late Early Cambrian trilobite faunule from the Gnalta group, MT Wright, NSW. *Transactions of the Royal Society of South Australia*, *121*, 67–74.

Kruse, P. D. (1990). Cambrian palaeontology of the Daly Basin. *Northern Territory Geological Survey, Report*, *7*, iv+58 p.

Kruse, P. D. (1991). Cambrian fauna of the Top Springs Limestone, Georgina Basin. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, *8*, 169–188. doi: 10.5962/p.262819

Kruse, P. D. (1998). Cambrian palaeontology of the eastern Wiso and western Georgina Basins. *Northern Territory Geological Survey, Report*, *9*, iv+68 p.

Kruse, P. D., Laurie, J. R., & Webby, B. D. (2004). Cambrian geology and palaeontology of the Ord Basin. *Association of Australasian Palaeontologists Memoirs*, *30*, 1–58.

Laurie, J. R. (2016). Whitehouse's Redlichia (Trilobita) specimens from the Georgina Basin, western Queensland. In J. R. Laurie, I. G. Percival, J. B. Jago, J. R. Paterson, & G. A. Brock (Eds), *Cambro-Ordovician studies VI* (pp. 75–81). Association of Australasian Palaeontologists.

Lu, Y., Chang, W., Chien, Y., Chu, C., Lin, H. L., Zhou, Z. Y., Qian, Y., Zhang, S. G., & Yuan, J. L. (1974). Cambrian trilobites. In *Handbook of stratigraphy and palaeontology of southwest China* (pp. 82–107). Science Press.

Öpik, A. A. (1958). The Cambrian Trilobite Redlichia: Organization and Generic Concept. *Product Catalogue*, *42*.

Öpik, A. A. (1970). Redlichia of the Ordian (Cambrian) of Northern Australia and New South Wales. *Product Catalogue*, *114*. https://ecat.ga.gov.au/geonetwork/srv/api/records/a05f7892-fd8c-7506-e044-00144fdd4fa6

Smith, P. M., Jell, P. A., Leu, M. R., & Zhen, Y. Y. (2026). Trilobites from the Ordian (Cambrian Series 2, Stage 4) First Discovery Limestone Member in western New South Wales, Australia. *Alcheringa: An Australasian Journal of Palaeontology*, *0*(0), 1–61. doi: 10.1080/03115518.2026.2633798

Walcott, C. D. (1905). Cambrian faunas of China. *Proceedings of the United States National Museum*, *29*(1415), 1–106. doi: 10.5479/si.00963801.1415

Whitehouse, F. W. (1939). The Cambrian faunas of north-eastern Australia, Part 3: The polymerid trilobites (with supplement no.1). *Memoirs of the Queensland Museum*, *21*(3), 179–282.

Zhang, W. (1985). Current biostratigraphic scheme of the Chinese Cambrian. *Palaeontologia Cathayana*, *2*, 73–75.

Zhang, W. (2003). Cambrian biostratigraphy of China. In *Biostratigraphy of China eds W-T Zhang, P-J Chen and AR Palmer* (pp. 55–119). Science Press.

EXPLORING MORPHOSPACE IN REMOPLEURIDIDAE HAWLE & CORDA (1847): EARLY EXPANSION AND SUBSEQUENT MORPHOLOGICAL RESTRICTIONS

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Keywords: Remopleurididae, morphospace, morphological disparity, ecological specialization, Ordovician Radiation.

INTRODUCTION

The early Paleozoic was a critical interval in the history of life. Marine communities underwent profound structural changes during the Cambrian and Ordovician, including a marked increase in global diversity driven by both alpha and beta diversity, as well as a progressive increase in ecological complexity (Sepkoski, 1997; Webby *et al*., 2004; Servais *et al*., 2010). Within this context, the family Remopleurididae constitutes an intriguing group for investigating macroevolutionary patterns of diversification and ecological innovation. Representatives of this family occupied a wide range of marine environments across multiple paleocontinents and were important components of Ordovician ecosystems.

Remopleuridids first appeared during the Furongian (late Cambrian) and persisted until the Hirnantian (Late Ordovician) (Adrain, 2013). Their evolutionary history was characterised by two major diversification phases: an early radiation during the Tremadocian and a second global expansion during the Darriwilian, with pronounced morphological changes involving this second propagation. Tremadocian assemblages include forms traditionally regarded as morphologically plesiomorphic within the group (namely "richardsonellines" or/and "kainellids"), which display a near-cosmopolitan distribution. Toward the end of the Tremadocian, however, remopleuridids disappeared from most regions and became restricted to Laurentia and Baltica during the Floian. It is within these regions that more derived forms (namely "remopleuridines") appeared, subsequently dispersing worldwide during the Darriwilian radiation.

These two evolutionary episodes appear to be accompanied by a drastic shift in ecological strategies. Early representatives are commonly interpreted as benthic taxa, whereas later remopleuridids show morphological traits suggesting a more active swimming lifestyle (Shiino *et al.,* 2012, 2014). However, the causes underlying this transition remain poorly understood. One possibility is that the ecological shift reflects the survival and subsequent diversification of a single derived lineage following the decline of early remopleuridid groups. Alternatively, the emergence of more pelagic morphologies may represent a broader ecological response involving multiple lineages adapting to changing Ordovician marine ecosystems. Here we explore these alternatives by examining for the first time morphospace occupation in Remopleurididae across the Cambrian-Ordovician interval. We focus on cranidial morphology, a complex and functionally informative structure that captures key features related to sensory systems, feeding and

hydrodynamic performance, and is therefore closely linked to ecological strategies. By doing so, we aim to explore ecological shifts associated with the two main radiation phases of the family.

METHODS

Specimens selected for digitisation were compiled from published sources and correspond to previously described material housed in public institutional repositories. Morphometric data of 53 genera were obtained. To maximise sample size and ensure consistency across specimens, the cranidium was selected as the primary structure for analyses. Within the cranidium, the dorsal suture captures key morphological features related to ecological strategies (Foote, 1991), and taking into account that remopleuridids have librigenae that closely mirror cranidial morphology; the use of cranidium structures captured by morphometric data is enough to explore shifts in ecological strategies within the family. Specimens were analysed following the TriloMorph landmarking template that summarises cranidial shape (11 fixed landmarks and 3 semilandmark curves for glabella and cranidial outline) (see Randolfe *et al*. in press for full description). Landmark placement was performed using the Stereomorph package (Olsen & Westneat, 2015) in R (R Core Team, 2025). Generalized Procrustes Analysis (**GPA**) was applied to standardise the data by removing non-shape variation. Principal Component Analyses (**PCA**) were then performed on the aligned coordinates to identify the principal axes of shape variation and to construct the empirical morphospace of Remopleurididae. GPA and PCA were implemented using the geomorph package (Adams *et al*., 2026) in R (R Core Team, 2025).

We carried out a K-means cluster analysis to explore the morphospace structure, namely if it is uniformly occupied, or on the contrary, it shows some clustering. We applied the gap statistic method to determine the optimal number of clusters. This method compares the total variation within a given number of clusters in the real dataset with the expected values for that same number of clusters in a reference dataset that lacks clustering. The optimal number of clusters is the number that maximises the gap statistic (Tibshirani *et al*., 2001). These analyses were performed in R using the function clusGap from the cluster package (Maechler *et al*. 2026) and kmeans function from the stats package respectively (R Core Team, 2025).

RESULTS

Figure 1 shows the empirical morphospace of representatives of the family Remopleurididae during their lifespan. The first two principal components account for 64% of the total variation, 49% and 15% respectively. The use of the First Appearance Datum (**FAD**) for each genus allowed us to trace the temporal distribution of morphologies and explore their sequential occurrence through time. Furongian and Early Ordovician taxa are broadly distributed across the morphospace showing substantial overlap, indicating high diversity during the early history of remopleuridids. By contrast, Middle to Late Ordovician taxa cluster towards the other extreme of morphospace, showing a more restricted range of morphologies consistent with the high specialisation of these more derived groups. Notably, morphospace data show that highly derived forms of the group were present early in its history, as evidenced by the genera *Artokephalus* (Furongian) and *Robergiella* (Early Ordovician). However, these forms were rare compared to more intermediate morphologies that appear at this time.

Additionally, the gap statistic analysis indicates that the morphospace is optimally partitioned into two clusters (Fig. 2). These clusters group genera with similar morphologies associated with distinct life habits. A first cluster, which occupies most of the morphospace, includes genera from the Furongian and the Lower Ordovician and accommodates taxa with a more epibenthic morphology. By contrast, a second smaller cluster includes genera with a more pelagic-type cranidia, including some Furongian and Early Ordovician taxa, as well as all representatives from

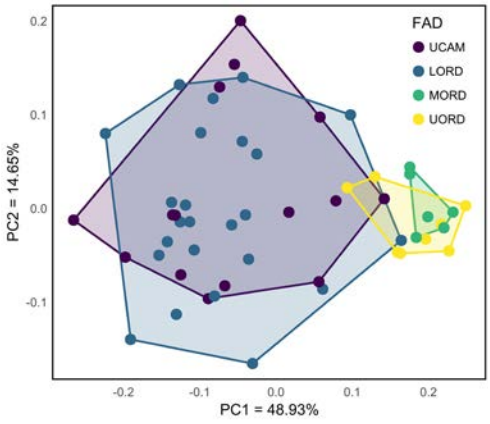

Figure 1. Remopleurididae morphospace coded by First Appearance Datum (FAD). Abbreviations: **UCAM:** Upper Cambrian, **LORD:** Lower Ordovician, **MORD:** Middle Ordovician, **UORD:** Upper Ordovician.

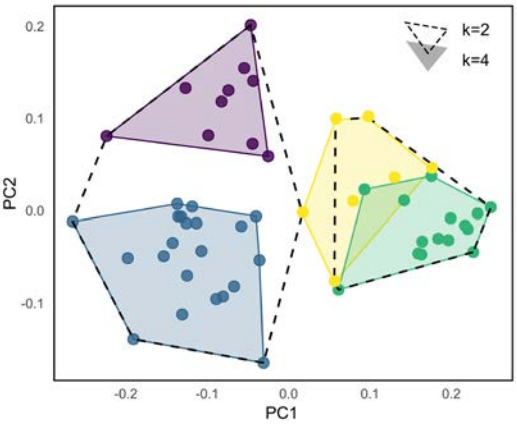

Figure 2. Optimal cluster distribution in the two major axes of the morphospace (accounting for 48.93% and 14.65% respectively). Dashed lines indicate two optimal clusters (method = "Tibs2001SEmax"), whereas solid colored lines indicate 4 optimal clusters (method = "firstSEmax").

the Middle and Upper Ordovician. Each of these clusters can be further subdivided into two additional subgroups, yielding a total of four morphologically distinct groups. A clear subgroup is segregated across the PC2 axis, which includes epibenthic taxa characterised by a rather horizontal anterior branch of the suture, usually referred to as a "kainellid"-type cranidium. A less clearly delimited subgroup occurs within the "pelagic" cluster, composed by taxa that could be regarded as intermediate forms between epibenthic and pelagic morphologies, such as *Arator, Elkanaspis, Eorobergia, Hastiremopleurides, Oculeus, Portentosus* and *Spinacephalus*.

CONCLUSIONS

Our results indicate that the evolutionary history of Remopleurididae was characterised by an early expansion and extensive occupation of morphospace, followed by a sharp restriction associated with increasing specialization. The clear differentiation between early and late forms in morphospace reveals high initial disparity in life habits, with diversification strongly concentrated in the early radiation of the family. Interestingly, the presence of "pelagic" type morphologies as early as the late Cambrian, although rare, supports the idea that functional morphologies associated with derived ecological strategies for this family were already explored early in the history of the clade.

Rapid shifts from predominantly epibenthic to more pelagic strategies coincide with the decline of primitive morphologies within the group, suggesting an ecologic filtering process. This transition coincides with environmental changes during the Early Ordovician that could have caused a selective turnover within the family, limiting the persistence and further diversification of deeper-water, epibenthic lineages.

REFERENCES

Adams, D., Collyer, M., Kaliontzopoulou, A. & Baken, E. (2026). *Geomorph: Software for geometric morphometric analyses* [R-Packages]. https://cran.r-project.org/package=geomorph

Adrain, J. M. (2013). Chapter 20. A synopsis of Ordovician trilobite distribution and diversity. *Geological Society, London, Memoirs, 38*, 297–336. doi: 10.1144/m38.20

Foote, M. (1991). Morphologic patterns of diversification: examples from trilobites. *Paleontology*, 34, 461–485.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. (2026). *cluster: Cluster Analysis and Extensions* [R-Packages]. https://cran.r-project.org/package=cluster

Olsen, A. & Westneat, M. (2015). StereoMorph: an R package for the collection of 3D landmarks and curves using a stereo camera set-up. *Methods in Ecology and Evolution, 6*, 351–356.

Randolfe, E. A., Serra, F., Balseiro, D., María-Dorado, J., Aquino, D. F., Parry, S. L., Monti, D. S., Handkamer, N. M., Vaccari, N. E., Rustán, J. J. & Waisfeld, B. G. (2026) [in press]. Building the trilobite morphospace: the influence of different morphological structures. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh.* [Special volumen] *"A Palaeontological Odyssey: A tribute to Euan Clarkson DSc, FRSE (1937-2024)"*.

R Core Team (2025). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing https://www.R-project.org

Sepkoski, J. J., Jr. (1997). Biodiversity: past, present, and future. *Journal of Paleontology, 71*, 533–539. doi: 10.1017/s0022336000040026

Servais, T., Owen, A.W., Harper, D.A.T., Kröger, B. & Munnecke, A. (2010). The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension. *Palaeogeography, Palaeoclimatolology, Palaeoecology, 294*, 99–119.

Shiino, Y., Kuwazuru, O., Suzuki, Y. & Ono, S. (2012). Swimming capability of the remopleuridid trilobite Hypodicranotus striatus: hydrodynamic functions of the exoskeleton and the long, forked hypostome. *Journal of Theoretical Biology, 300*, 29–38.

Shiino, Y., Kuwazuru, O., Suzuki, Y., Ono, S., & Masuda, C. (2014). Pelagic or benthic? Mode of life of the remopleuridid trilobite *Hypodicranotus striatulus*. *Bulletin of Geosciences, 89*, 207–218.

Tibshirani, R., Walther, G. & Hastie, T. (2001). Estimating the number of clusters in a data set via the gap statistic. *Journal of the Royal Statistical Society, Series B, 63*, 411–423. doi: 10.1111/1467-9868.00293

Webby, B.D., Droser, M.L., Paris, F. & Percival, I.G. 2004. *The Great Ordovician Biodiversification Event.* Columbia University Press, New York, 484 pp.

3D APPENDAGE PRESERVATION OF *YUNNANOCEPHALUS YUNNANENSIS* (TRILOBITA:REDLICHIIDA) FROM THE CHENGJIANG BIOTA AND ITS IMPLICATIONS FOR THE TRILOBITE VENTRAL ANATOMY

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Keywords: Trilobita, micro-CT, Chengjiang biota, appendage morphology.

In the last two decades, our knowledge about the ventral anatomy of trilobites has substantially increased. This improvement is due, among other factors, to the use of new methodologies such as X-ray microcomputed tomography, which provides unprecedented resolution for the visualization and description of the trilobite appendages. In the case of the Chengjiang biota (Early Cambrian, Yunnan province, China), these advances in micro-computed tomography have produced insights into the non-biomineralized morphology of different artiopodans, but have not previously been applied to trilobites. Here, the three-dimensional ventral anatomy of the trilobite *Yunnanocephalus yunnanensis* is presented for the first time, by means of micro-CT and computer-based 3D rendering. Application of this technique to *Y. yunnanensis* reveals well-preserved three-dimensional morphology, including the appendages and the labrum. Specimens of *Y. yunnanensis* show a well-preserved first postantennal appendage, which is not frequently visible in trilobites. In other redlichiid trilobites, this appendage has a reduced endopodite and flagelliform exopodite. However, in *Y. yunnanensis*, the first postantennal appendage has a well-developed endopodite and exopodite, demonstrating the great variability of the appendage morphology within trilobites. The well-developed endopodite and exopodite of the first cephalic appendage in *Y. yunnanensis* could aid in respiration, feeding, and locomotion. This broad range of appendage morphology in trilobites may reflect selective pressures of feeding, sensory functions, and locomotion. Redlichiid trilobites also exhibit a broad range of glabellar morphology, coupled with the appendicular variability which reflects a diversity of feeding behaviours and lifestyles.

INSIDE A TRILOBITE GUT: NEW INSIGHTS INTO THE DIGESTIVE ANATOMY AND PHYSIOLOGY IN *DEANASPIS GOLDFUSSI* FROM SYNCHROTRON DATA

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Keywords: digestive system, crop, paleophysiology, feeding strategy, peritrophic membrane.

In the first volume of *Systême silurien du centre de la Bohême*, Joachim Barrande (1852) illustrated two specimens of *Deanaspis goldfussi* (pl. 30, figs. 38–39) from the Upper Ordovician Letná Formation with a discernible digestive tract. This tract, preserved as sediment infill and/or voids, extends beneath the axial lobe and exhibits a conspicuously swollen region beneath the glabella. A similar specimen was reported several years earlier by Beyrich (1846). Subsequently, Šnajdr (1991) re-examined Barrande's specimens and described additional material from the same strata. He demonstrated that the gut infill may consist of fecal pellets and suggested that *D. goldfussi* was likely a deposit feeder. Here, we present new data based on high-resolution synchrotron microtomography of the original specimens, scanned at the European Synchrotron Radiation Facility (**ESRF**) in Grenoble, allowing a refined interpretation of the anatomy and functional morphology of the trilobite digestive system.

The digestive tract of *D. goldfussi* is reconstructed as a relatively simple, continuous tube extending from the posterior region of the glabella to the terminal axial piece of the pygidium. Along its length, the gut infill is partitioned into short, pellet-like segments with a distinct concentric internal structure. This organization is strikingly reminiscent of gut contents in extant mandibulates possessing a peritrophic membrane.

Beneath the glabella, the tract expands into a voluminous crop of unusual, bell-shaped morphology that departs markedly from previous hypotheses. This structure is connected to the mouth via a markedly narrow oesophagus; the mouth itself is positioned slightly posterior to the hypostome. A pair of large digestive caeca is attached dorsally to the posterior portion of the crop. Both the crop and the intestine contain remnants of hard-shelled organisms, providing direct evidence for feeding strategies in trinucleid trilobites. Trinucleids were apparently non-selective feeders that, in addition to deposit feeding, also consumed small animals.

Overall, these findings not only refine our understanding of feeding mechanisms in trinucleids but also offer rare insight into the physiological organization of the trilobite digestive system. More broadly, the observed gut architecture and its similarities to extant mandibulates open new perspectives on the evolution of digestive strategies in early euarthropods and contribute to ongoing discussions about their phylogenetic affinities.

REFERENCES

Barrande, J. (1852). *Systême silurien du centre de la Bohême: lère partie, Crustacés: Trilobites*. 935 pp. Published by the author, Prague & Paris.

Beyrich, E. (1846). *Untersuchungen über Trilobiten. Zweite Stück als Fortsetzung zu der Abhandlung "Ueber einiger böhmische Trilobiten"*. 37 pp. G. Reimer, Berlin.

Šnajdr, M. (1991). *Zažívací trakt trilobita Deanaspis goldfussi (Barrande). Časopis Národního muzea, Řada přírodovědná* 156, 8–16.

A LIVELY TRILOBITE REUNION ON THE CAMBRIAN SEAFLOOR: INSIGHTS INTO EXCEPTIONAL PRESERVATION IN THE DRUMIAN WHEELER FORMATION OF UTAH

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Keywords: Cambrian, Wheeler Formation, exceptional preservation, oxygen-poor environment, Trilobites.

The Wuliuan–Drumian Wheeler Formation of western Utah is renowned worldwide for the remarkable quality and abundance of its palaeontological record (Robison *et al*., 2015). This includes a high diversity of trilobites, often preserved fully articulated, as well as a wide range of soft-bodied organisms. A classic example of Burgess Shale-type (**BST**) fossil assemblage (Gaines, 2014), these carbonaceous compression macrofossils were preserved in the deepest parts of a basin – the House Range Embayment – which encroached onto the offshore margin of a carbonate platform (Hintze & Robison, 1975; Rees, 1986). In this low-energy, wave-protected environment, calcareous clay was deposited under geochemical conditions conducive to the preservation of organic remains, particularly under sustained anoxia (*e.g.* Gaines *et al*., 2005, 2012). This setting has led to the recognition of two subcontemporaneous (lower Drumian) but taxonomically distinct BST biotas from the Wheeler Formation – those of the House Range and the Drum Mountains – comprising approximately 95 and 85 species, respectively, about half of which are associated with exceptional preservation (Robison, 1991; Robison *et al*., 2015; Lerosey-Aubril & Skabelund, 2018).

According to the most widely accepted taphonomic model (Gaines, 2014; Foster & Gaines, 2016), the severe oxygen depletion that enabled the preservation of BST biotas in the deepest parts of the House Range Embayment also precluded the establishment of benthic animal communities, with the possible exception of some sponges. Consequently, it is assumed that the non-poriferan remains composing the Wheeler BST assemblages were either transported from better-oxygenated, shallower benthic settings or settled from more oxygenated portions of the water column (Gaines & Droser, 2010). Found in non-bioturbated beds at the transition between laminated and bioturbated intervals, the *Elrathia* Biofacies, characterized by monospecific accumulations of carcasses and moults of *Elrathia kingii*, has been interpreted as representing a marginal environment – the exaerobic zone – at the edge of oxygenated bottom waters and, therefore, benthic animal life (Gaines & Droser, 2003).

In this contribution, we describe a remarkable association of 69 fossils preserved on the surface of a small slab originating from the Wheeler Formation (unknown locality) and housed at the Natural History Museum of Utah. This assemblage is largely dominated by trilobites (n=58), particularly *Jenkinsonia varga* (n=52), but also includes agnostids (n=8), an indeterminate arthropod, a fragment of a non-biomineralized scalidophoran(?) tube, and the large phosphatized body of an annelid. The trilobites, especially *J. varga*, are interpreted as primarily representing carcasses, based on the predominance of fully articulated exoskeletons (84%), *in situ* preservation of the hypostome (89%), and gut preservation (64%). The azimuthal orientation of the trilobite carcasses is random, suggesting that they were not transported with the sediment that buried them. Likewise, the hypothesis that these carcasses settled from the water column can be ruled out based, as 91% are orientated dorsum-up and more than a quarter display moderate flexure

of one body extremity – usually the posterior one – whereas complete enrolment is exceedingly rare. It can also be statistically demonstrated that these trilobite remains are positioned closer to the large annelid carcass than would be expected under a random distribution on the slab surface. Taken together, these observations suggest that an abrupt depositional event caused the death of this large group of *J. varga* (and at least one other trilobite species, *Brachyaspidion sulcatum*), which were buried alive while clustered on the seafloor, likely attracted to and feeding in the vicinity of a large annelid carcass.

Figure 1. Trilobite-dominated cluster of 69 fossils from the Drumian Wheeler Formation of western Utah (UMNH.IP.6188). **A,** Close-up of the area with the densest distribution of fossils, including a large phosphatized annelid body (arrowhead); **B,** close-up of a group of variously sized carcasses of *Jenkinsonia varga* Robison, 1971 with preserved guts (arrowheads); **C,** a rare specimen of *J. varga* preserved dorsum-down with its hypostome in *in situ* position (arrowhead).

The association of *J. varga*, *B. sulcatum* (and/or the closely related *B. microps*), and exceptionally preserved fossils in strata representing the deepest and distalmost environments of the basin has previously been reported from the House Range and the Drum Mountains (Gaines, 2003, his "Soft-Bodied Biofacies" or "**SBF**"; Gaines & Droser, 2005; Brett *et al*., 2009, their "calcareous gray shale facies"; Halgedahl *et al*., 2009). The occurrence of these trilobites in environments reconstructed as permanently anoxic led to the inference of a pelagic lifestyle for these species (Gaines, 2003; Gaines & Droser, 2010; Robison *et al*., 2015), a hypothesis challenged by the biostratinomic characteristics of the Wheeler slab described above and, earlier, by Brett *et al*.

(2009) based on similar observations (*i.e*., high degree of articulation, random to preferentially dorsum-up orientation, and the presence of moult ensembles). These authors proposed to regard that the *Jenkinsonia-Brachyaspidion* (and agnostid) association constitutes a distinct biofacies representative of "even lower benthic oxygen levels than those dominated by *Elrathia*" (Brett *et al*., 2009).

A review of Fortey's (1985) criteria for identifying pelagic trilobites confirms that *J. varga* is an unlikely candidate for such a lifestyle: 1) Functional design – its body is not streamlined and includes a cephalic shield with wide genal fields bearing small, centrally positioned eyes; 2) Analogy – this flat body morphology is reminiscent to extant epibenthic dwellers, such as serolid isopods; 3) Geological occurrence – this species has a limited stratigraphic and palaeogeographic distribution, being solely known from the Wheeler Formation in the House Range and Drum Mountains (Robison, 1971; Robison *et al*., 2015), and is strongly facies-dependant, occurring abundantly in the non-bioturbated strata preserving organic remains (*i.e*., the deepest and distalmost parts of the basin; Gaines, 2003; Brett *et al*. ,2009; Halgedahl *et al*., 2009).

In conclusion, we reconstruct *J. varga*, and possibly *B. sulcatum* and *B. microps*, as opportunistic epibenthic, detritus-feeding trilobites adapted to life in severely and recurrently – though perhaps not permanently – oxygen-depleted environments, where they may have temporarily thrived near decomposing, transported carcasses of larger animals. Such an ecological niche could account for the limited taxonomic diversity and occasional high abundance of these trilobite assemblages, the small size of the individuals, as well as certain morphological traits of these species (e.g., the narrow thoracic pleurae of *J. varga*). The repeated occurrence of this *Jenkinsonia-Brachyaspidion* Biofacies in the Wheeler Formation indicates that even in the deepest parts of the House Range Embayment, oxygen levels fluctuated sufficiently to permit the intermittent reappearance of a specialized, taxonomically and size-limited benthic fauna.

REFERENCES

Brett, C. E., Allison, P. A., DeSantis, M. K., Liddell, W. D., & Kramer, A. (2009). Sequence stratigraphy, cyclic facies, and lagerstätten in the Middle Cambrian Wheeler and Marjum formations, Great Basin, Utah. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *277*(1-2), 9–33. doi: 10.1016/j.palaeo.2009.02.010

Fortey, R. A. (1985). Pelagic trilobites as an example of deducing the life habits of extinct arthropods. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, *76*(2–3), 219–230. doi: 10.1017/S0263593300010452

Foster, J. R. & Gaines, R. R. 2016. Taphonomy and Paleoecology of the "Middle" Cambrian (Series 3) Formations in Utah's West Desert: recent finds and new data. In Comer, J. B., Inkenbrandt, P. C., Krahulec, K. A. & Pinnell, M. L. (eds). *Resources and Geology of Utah's West Desert* (pp. 291–336). Utah Geological Association, Publication, 45, 377 pp.

Gaines, R. R. 2003. *Dissecting a Cambrian Lagerstätte: Insights from the Wheeler Formation, Utah*. [Unpublished Ph.D]. Dissertation, University of California Riverside, 143 pp.

Gaines, R. R. (2014). Burgess Shale-type preservation and its distribution in space and time. *The Paleontological Society Papers*, *20*, 123–146. doi: 10.1017/S1089332600002837

Gaines, R. R., & Droser, M. L. (2003). Paleoecology of the familiar trilobite Elrathia kingii: an early exaerobic zone inhabitant. *Geology*, *31*(11), 941–944. doi: 10.1130/G19926.1

Gaines, R. R., & Droser, M. L. (2005). New approaches to understanding the mechanics of Burgess Shale-type deposits: From the micron scale to the global picture. *The Sedimentary Record*, *3*(2). 4–8. http://www.sepm.org/pages.aspx?pageid=37

Gaines, R. R., & Droser, M. L. (2010). The paleoredox setting of Burgess Shale-type deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *297*(3–4), 649–661. doi: 10.1016/j.palaeo.2010.09.014

Gaines, R. R., Kennedy, M. J., & Droser, M. L. (2005). A new hypothesis for organic preservation of Burgess Shale taxa in the middle Cambrian Wheeler Formation, House Range, Utah. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *220*(1–2), 193–205. doi: 10.1016/j.palaeo.2004.07.034

Gaines, R. R., Hammarlund, E. U., Hou, X., Qi, C., Gabbott, S. E., Zhao, Y., Peng, J. & Canfield, D. E. (2012). Mechanism for Burgess Shale-type preservation. *Proceedings of the National Academy of Sciences*, *109*(14), 5180–5184. doi: 10.1073/pnas.1111784109

Halgedahl, S. L., Jarrard, R. D., Brett, C. E., & Allison, P. A. (2009). Geophysical and geological signatures of relative sea level change in the upper Wheeler Formation, Drum Mountains, West-Central Utah: A perspective into exceptional preservation of fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *277*(1–2), 34–56. doi: 10.1016/j.palaeo.2009.02.011

Hintze, L. F., & Robison, R. A. (1975). Middle Cambrian stratigraphy of the House, Wah Wah, and adjacent ranges in western Utah. *Geological Society of America Bulletin*, *86*(7), 881–891. doi: 10.1130/0016-7606(1975)86<881:MCSOTH>2.0.CO;2

Lerosey-Aubril, R., & Skabelund, J. (2018). Messorocaris, a new sanctacaridid-like arthropod from the middle Cambrian Wheeler Formation (Utah, USA). *Geological Magazine*, *155*(1), 181–186. doi: 10.1017/S0016756817000504

Rees, M. N. (1986). A fault-controlled trough through a carbonate platform: the Middle Cambrian House Range embayment. *Geological Society of America Bulletin*, *97*(9), 1054–1069. doi: 10.1130/0016-7606(1986)97<1054:AFTTAC>2.0.CO;2

Robison, R. A. (1971). Additional middle Cambrian trilobites from the Wheeler Shale of Utah. *Journal of Paleontology*, *45*(5), 796–804.

Robison, R. A. (1991). Middle Cambrian biotic diversity: examples from four Utah Lagerstätten. In *The early evolution of Metazoa and the significance of problematic taxa* (pp. 77–98). Cambridge University Press, Cambridge, U.K.

Robison, R. A., Babcock, L. E., & Gunther, V. G. (2015). *Exceptional Cambrian fossils from Utah: a window into the age of trilobites*. Utah Geological Survey. Utah Geological Survey, Salt Lake City, Miscellaneous Publication, 15-1, 97 pp.

THE TRILOBITE NERVOUS SYSTEM AND THE EARLY EVOLUTION OF THE MANDIBULATE CENTRAL COMPLEX

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Keywords: nervous system, evolution, trilobites, Ordovician, Morocco.

Fossil central nervous systems (**CNS**) have illuminated several facets of total-group euarthropod evolution, including their phylogenetic affinities, the origin of the head, and their ancestral neuroanatomical organization. However, the CNS remains unknown in trilobites, the most diverse and earliest group of Palaeozoic euarthropods, but can potentially clarify fundamental questions that remain disputed despite thousands of described species and countless studies spanning over two centuries, such as their affinities relative to modern representatives. Here, we describe the CNS of the cheirurid *Anacheirurus adserai* from the Lower Ordovician Fezouata Shale. *Anacheirurus* features a tri-partite brain with well-developed proto-, deuto- and tritocerebral neuromeres, an anteriomedian protocerebral protrusion, a central complex, an oesophageal foramen, and a ganglionated nerve cord. The CNS is replicated in framboidal iron that differs in texture and composition from the exoskeleton and rock matrix. *Anacheirurus'* CNS resembles that of Cambrian stem-group mandibulates, and shares the presence of an intricate central complex with a protocerebral bridge and lateral accessory lobes with extant pancrustaceans. Our findings consolidate Trilobita as stem-group mandibulates, illuminate the ancestral morphology of the euarthropod central complex, and offer direct anatomical evidence of the sensorimotor system innovations that originated during the Cambrian Information Revolution.

HOW TO DEFINE A METAMORPHOSIS? A CASE STUDY USING PRINCIPAL COORDINATE ANALYSIS IN TRILOBITES

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Keywords: ontogeny, development, metamorphosis, principal coordinate analysis, evo-devo.

Trilobites had hemianamorphic post-embryonic development, characterized by the addition of new segments during early ontogeny followed by a stable segment number in later stages (Hughes *et al*., 2006). Since the seminal works of Speyer and Chatterton (1989) and Chatterton and Speyer (1989), it has also been recognized that some trilobites exhibited direct or gradual development, whereas others underwent indirect development with pronounced metamorphosis condensed into a short interval during the earliest instars. This dichotomy is, however, overly reductionist. As in modern arthropods, developmental strategies in trilobites are better understood as forming a continuum rather than discrete categories, and the boundary between gradual change and true metamorphosis is often blurred. Representatives of some trilobite families show early stages that differ only modestly from later ones, suggesting weak or incipient metamorphosis, in contrast to the pronounced transformations observed in other groups.

To quantify the degree of metamorphosis, we constructed a dissimilarity matrix based on discrete morphological characters for the four earliest ontogenetic stages across 32 Cambrian and Ordovician trilobite species. Each stage was described using 17 characters, including overall exoskeletal shape, convexity, degree of effacement, hypostomal size, and the presence of spines. Species were visualized using pairwise dissimilarities between consecutive stages and ordinated via principal coordinates analysis (**PCoA**). Differences in Euclidean distances between successive stages in the ordination space were used as a proxy for the magnitude of morphological change and thus for the degree of metamorphosis.

Preliminary results support previous observations that the earliest trilobites exhibited direct development without metamorphosis (Laibl *et al.,* 2023). Incipient metamorphosis appears in Middle Cambrian taxa, whereas pronounced metamorphosis becomes characteristic of Late Cambrian and especially Ordovician trilobites. Cambrian taxa also display a broad spectrum of developmental strategies, ranging from fully direct development through intermediate forms of partial metamorphosis to strongly expressed metamorphosis. In contrast, Ordovician trilobites are more polarized, predominantly exhibiting either direct development or well-defined metamorphosis, with rare intermediate strategies. This shift from a continuous to a bimodal distribution suggests a fundamental restructuring of trilobite ontogeny through time. We interpret this pattern as evidence for disruptive selection acting on developmental strategies, potentially linked to ecological differentiation between juvenile and adult niches.

REFERENCES

Chatterton, B. D., & Speyer, S. E. (1989). Larval ecology, life history strategies, and patterns of extinction and survivorship among Ordovician trilobites. *Paleobiology*, *15*(2), 118–132. doi: 10.1017/S0094837300009313

Hughes, N. C., Minelli, A., & Fusco, G. (2006). The ontogeny of trilobite segmentation: a comparative approach. *Paleobiology*, *32*(4), 602–627. doi: 10.1666/06017.1

Laibl, L., Saleh, F., & Pérez-Peris, F. (2023). Drifting with trilobites: the invasion of early post-embryonic trilobite stages to the pelagic realm. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *613*, 111403. doi: 10.1016/j.palaeo.2023.111403

Speyer, S. E., & Chatterton, B. D. (1989). Trilobite larvae and larval ecology. *Historical Biology*, *3*(1–2), 27–60. doi: 10.1080/08912968909386512

MICROANATOMY AND FUNCTIONAL MORPHOLOGY OF TRILOBITE EXOSKELETON: A CASE STUDY OF *MOROCOPS*? *DEGENER* (BARRANDIAN AREA, CZECH REPUBLIC)

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Keywords: exoskeleton, microanatomy, Devonian, phacopidae, Barrandian.

Despite the extensive research focussed on trilobites, the internal and external microanatomy and functional morphology of their exoskeletons still remains understudied. Some key unexplored aspects in this topic include:

1) the original chemical composition of trilobite exoskeleton
2) function of observed structures
3) homology of different structures with those known in extant arthropods
4) the impact of diagenesis on commonly observed features.

Addressing these gaps in our knowledge is essential for a more comprehensive understanding of trilobite palaeobiology and evolution. Several techniques have been previously applied to study the internal microscopic structure of trilobite exoskeletons. Among them, a method involving careful etching of oriented sections of the exoskeleton using the **EDTA** (ethylenediaminetetraacetic acid) has proven to be particularly effective (Dalingwater *et al*., 1993). This method creates a topography based on differential acid resistance of different subdivisions and microstructures, thus allowing observation of the section in a scanning electron microscope.

In our study, this method was for the first time applied to trilobite samples collected from various Silurian and Devonian carbonates in the classical Barrandian area. Cephala of *Morocops*? *degener* (Barrande, 1852) from the Lower Devonian Zlíchov Formation were then selected as the most suitable for a detailed study. Microanatomical features observed in etched sections were documented and compared with surface structures using both institutional specimens and newly collected material.

Furthermore, other methods such as element mapping using electron microprobe analysis as well as thin section observations were used to supplement the information obtained by EDTA etched samples.

Our analysis revealed that several microanatomically distinct structures are present in the glabellar exoskeleton of *Morocops*? *degener*. Comparisons with extant arthropods suggest that some of them are functionally analogous to specialized sensory and defensive structures, while others appear to be unique and without obvious modern counterparts. These results provide new perspectives on the functional significance of exoskeletal microanatomy in trilobites and highlight the potential of microanatomical studies not only to clarify the biology of trilobites themselves, but also to broaden our understanding of the evolutionary disparity of exoskeletal adaptations in arthropods.

Acknowledgements: MŠ and OF were supported by project GAUK 32124 of Charles University.

REFERENCES

Barrande, J. (1852). *Systême Silurien du centre de la Bohême. 1ère partie. Recherches paléontologiques, vol. I. Crustace`s, Trilobites*. Chez l'auteur et éditeur, Prague, Paris.

Dalingwater, J. E., Hutchinson, S. J., Mutvei, H., & Siveter, D. J. (1993). Cuticular ultrastructure of some Silurian calymenid trilobites from the Welsh Borderland and Gotland. *Palaeontographica Abteilung A*, *229*, 37–49.

MOULTING BEHAVIORS IN ORYCTOCEPHALID TRILOBITES REVEAL ONTOGENETIC SHIFTS IN ECDYSIAL STRATEGIES

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Keywords: Trilobita, South China, ecdysis, functional morphology, evolution.

Similar to other arthropods, trilobites periodically underwent ecdysis in order to grow, and this life history strategy had a profound effect on their ontogeny and morphological evolution. Previous paleontological studies of moulting behavior in trilobites are based on few exuviae within late-stage meraspides and holaspides; thus, little is known about ontogenetic moulting behavior in trilobites. Here, we analyse abundant exuviae across relatively complete ontogenetic sequences of the trilobites *Arthricocephalus chauveaui*, *Arthricocephalites xinzhaiheensis*, *Duyunaspis duyunensis* and *Changaspis elongata* from the Cambrian Stage 4 Balang Formation (South China). The results indicate two clear trends of ontogenetic moulting behavior in oryctocephalid trilobites during development. *A. chauveaui* utilized a single Somersault moulting approach, which allows opening of the cephalic (facial and rostral) sutures by the lower cephalic unit (**LCU**) somersaulting anteriorly and lying beneath the trunk in moult assemblages. However, a gradual transition of moulting behavior during development—from Somersault to Henningsmoen's moulting pattern, i.e., from inverting the LCU to disarticulating the cranidium—is observed in *Ar. xinzhaiheensis*, *D. duyunensis* and *C. elongata*. This change may reflect an evolutionary shift towards different moulting behaviours, possibly representing a significant transition with macroevolutionary implications. The moulting mode may be canalized by structures that develop or change with growth, meaning that the change in strategy is not optional, but rather a consequence of morphological constraints and developmental pathways.

PALEOBIOGEOGRAPHY, HABITAT AFFINITY, AND EVOLUTIONARY CONVERGENCE IN HARPIFORM TRILOBITES

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Keywords: harpetid, trinucleid, paleobiogeography, paleoecology, convergent evolution.

BACKGROUND

Definitions of convergent evolution are generally either pattern-based or process-based (Speed & Arbuckle, 2017; Stayton, 2015). A pattern-based definition might be as simple as "distantly related lineages independently evolving similar phenotypes" (Speed & Arbuckle, 2017; Stayton, 2015). A process-based definition requires that similar phenotypes evolve due to some particular process; adaptation to a similar niche or environment is the process most frequently invoked (Moen *et al.,* 2016; Stayton, 2015; Wiens, 2003). Failing to distinguish between these two categories of convergence can lead researchers to draw poorly supported conclusions. This risk is increased when the convergently similar taxa are known only from the fossil record and lack clear modern analogues.

This is the scenario that confronts researchers studying trilobites in the order Harpetida Ebach & McNamara, 2002 and the superfamily Trinucleioidea Hawle & Corda, 1847. Harpetida is an order of small-bodied trilobites that originated in the Middle Cambrian and persisted into the Late Devonian (Adrain *et al*., 2004; Ebach & McNamara, 2002; Hughes, 2007; McNamara *et al.*, 2009). At present, paleontologists recognize three families of harpetid trilobites and approximately 30 genera (Beech & Lamsdell, 2021; Ebach & McNamara, 2002). Derived harpetids are easily recognized by their reduced eyes, small pygidium, forward narrowing glabella, long flat genal prolongations, and the characteristic 'harpiform brim' (Beech *et al.*, 2024; Fortey & Owens, 1997). This last is a broad, horseshoe-shaped brim, generally flattened and pitted, that encircles the cephalon (Fig. 1).

Trinucleioidea is a superfamily of trilobites usually placed within the order Asaphida (Beech *et al.,* 2024; Fortey & Chatterton, 1988) but sometimes reconstructed as an independent order (Bignon *et al.*, 2020). Like harpetids, trinucleids are generally quite small, with a vaulted cephalic chamber flanked by long genal prolongations, a thorax suspended above the sediment's surface, and greatly reduced eyes (Adrain *et al*., 2004; Fortey & Owens, 1999). Most strikingly, trinucleids belonging to the families Trinucleidae and Dionididae exhibit a so-called 'lace collar' (Pearson, 2017), a flattened fringe or headshield with many pits or holes that surrounds the cephalon: in other words, a harpiform brim (Beech *et al*., 2024) (Fig. 1). These morphological similarities led some early authors to suppose that harpetids and trinucleids were closely related (Swinnerton, 1919; Warburg, 1925), but most subsequent studies have instead assumed that these similar traits evolved independently in both groups (Beech & Lamsdell, 2021; Bignon *et al.*, 2020; Fortey & Chatterton, 1988). A recent phylogeny of harpetid and trinucleid trilobites (Beech *et al*., 2024) confirmed this second hypothesis and further demonstrated that the harpiform brim evolved in both groups through a series of parallel evolutionary innovations.

OBJECTIVES

Although harpetid and trinucleid trilobites evolved their harpiform morphologies independently (pattern-based convergence), it is still unknown whether they evolved them in response to similar

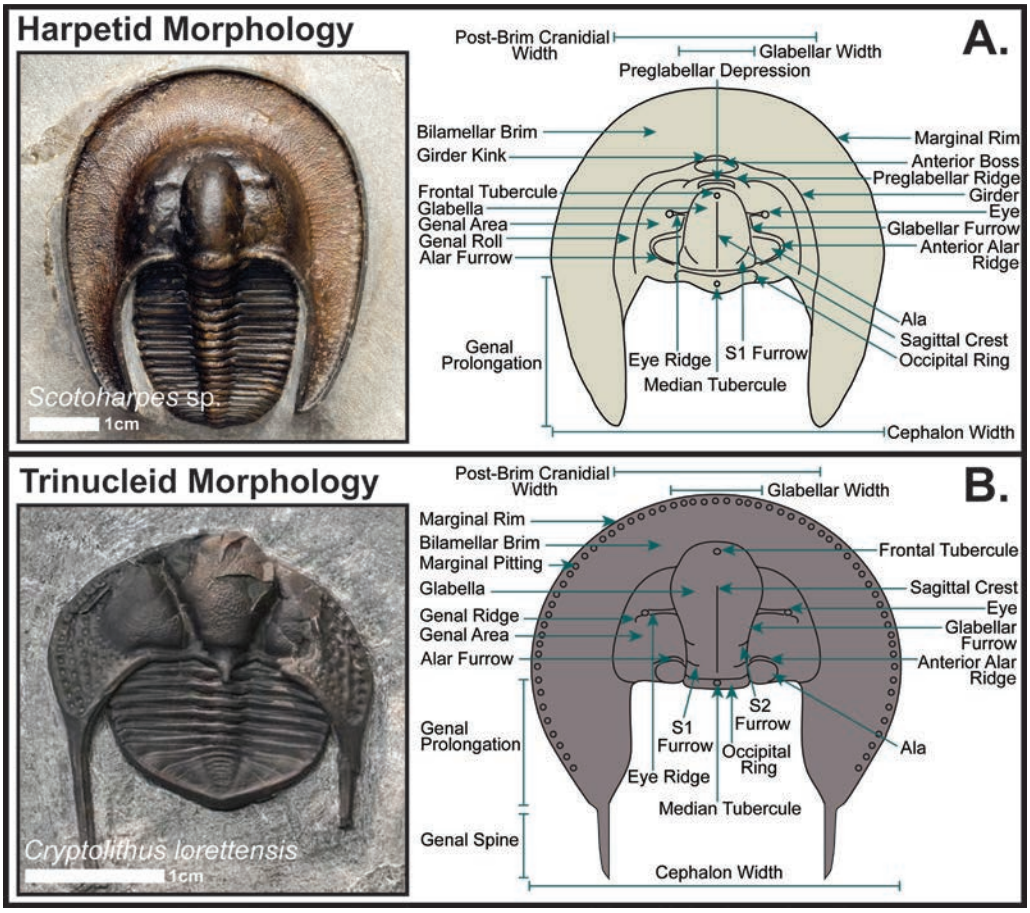

Figure 1. General dorsal cephalic morphology of harpetid (**A**) and trinucleid (**B**) trilobites, including cephalic brim. Adapted from Beech *et al.* (2024); scale bars are 1 cm.

ecological pressures (process-based convergence). Part of the issue is that the ecological function of the harpiform brim is still not well constrained. Although many functional hypotheses have been proposed (Bergström, 1972; Dollo, 1909; Ebach & McNamara, 2002; Fortey & Owens, 1999; McNamara *et al*., 2009; Schoenemann, 2021; Stubblefield, 1959), we know of only one published, peer-reviewed study (Beech *et al*., 2026) that has yet tested any of these hypotheses empirically.

Despite this limitation, it is still possible to address the question of whether harpetid and trinucleid trilobites were subject to similar ecological pressures by studying their paleobiogeographic and paleoecological distributions. If harpetids and trinucleids were living in similar environments, this would support the idea that they convergently developed their harpiform morphologies in response to similar environmental pressures. Conversely, if harpetid and trinucleid trilobites show little biogeographic or ecological overlap, this would suggest that they do not meet a process-based definition of convergent evolution and may instead have evolved their similar morphologies to perform quite different ecological functions.

Studying the paleobiogeography and paleoecology of harpiform trilobites may also help to explain why harpetid and trinucleid trilobites fared so differently during the end-Ordovician mass

extinction. Harpetids specifically do not appear to have been strongly affected by the mass extinction, with no discernable changes to their morphological diversity or increase in the rate of generic diversity loss (Beech & Lamsdell, 2021). This contrasts strongly with the fate of the trinucleids. Trinucleid trilobites suffered severe losses during the end-Ordovician mass extinction (Chatterton & Speyer, 1989). Only a single genus, *Raphiophorus*, extends the fossil record of the order into the Silurian (Adrain *et al*., 2004).

Although part of this discrepancy seems to be attributable to differences in developmental strategy (Chatterton & Speyer, 1989), biogeographic and bathymetric factors also appear to have been significant for end-Ordovician survivorship. Finnegan *et al.* (2012) found that the maximum paleolatitude at which a genus had been previously sampled, a macroecological trait linked to thermal tolerance, strongly influenced extinction risk during the Late Ordovician. In addition, Finnegan *et al.* (2016) found that the first pulse of the extinction event preferentially affected genera restricted to deeper waters or to relatively narrow paleolatitudinal ranges. As such, understanding the paleolatitudinal and paleoecological affinities of harpiform trilobites may be key to interpreting their divergent responses to the end-Ordovician mass extinction.

METHODS

A broad taxonomic sample of both harpetid and trinucleid taxa was selected, with a total of 39 harpetid species represented from 47 distinct occurrences and 24 trinucleid species represented from 75 distinct occurrences. The putative basal harpetid *Baikadamaspis jikdongensis* Park & Choi, 2011 was also included. For the trinucleid taxa, locality and occurrence information was obtained exclusively from the Paleobiology Database (accessed February 2025). In order to increase the sampling of harpetid occurrences, data taken for the Paleobiology Database were supplemented with locality descriptions taken from the primary literature. From this geospatial data, the current global distribution of harpiform trilobite fossils was assessed.

A record of the stratigraphic range of each taxon in the analysis was assembled, likewise using information obtained from the Paleobiology Database or from the primary literature. Where precise dates were unavailable, ranges were constrained to at least the stage level. The next task was to use paleogeographic reconstruction software to combine the age and locality data that have been collected into a series of paleogeographic distribution maps. For this the PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program (Müller *et al*., 2018; Scotese, 2016) was used. The PaleoAtlas itself consists of 91 paleogeographic maps spanning the Phanerozoic and late Neoproterozoic, while the PaleoData Plotter Program allows researchers to plot point data defined by modern latitude and longitude coordinates on these maps (Scotese, 2016). Maps of harpetid paleobiogeographic distribution during the Cambrian, Ordovician, Silurian and Devonian were thus created, allowing changes in the distribution of harpetids over time to be tracked. The distribution of harpetids during the Ordovician period was also compared to the distribution of trinucleid trilobites during the same interval.

Various measures of paleogeographic affinity were tracked across a recent phylogenetic tree of both harpetid and trinucleid trilobites (Beech *et al*., 2024). Species were labelled both in terms of latitude (*i.e*., do members of this species appear at high, low, or mid latitudes?) and paleocontinental association (*i.e*., do members of this species appear along the coasts of particular geohistorical landmasses?), the latter metric being directly related to the evolutionary concepts of cosmopolitism and endemism. Where such reconstructions could be unambiguous, the branches and nodes leading to the labelled species were likewise labelled. In addition, the tree included information about a series of morphological innovations leading to the evolution of the harpiform brim, allowing the emergence of this important morphological trait to be related to shifts in the biogeography of harpiform trilobites.

A three-dimensional habitat affinity space was created for harpiform trilobites with the ecospatial axes of latitude, depth, and lithology. Sampling was carried out at the generic rather than the species level in order to increase the statistical power of each data point. The final sample consisted of 20 harpetid genera and 46 trinucleid genera, as well as the putative basal harpetid genus *Baikadamaspis* Ergaliev, 1980. For all of these genera, occurrence data was collected from the Paleobiology Database (**PBDB**)(accessed August 2024).

For each genus in the sample, the total number of occurrences, the number of occurrences from low (< 30°) rather than high or mid paleolatitudes, the number of occurrences from shallow water depositional settings (including reef settings) rather than deep water settings, the number of occurrences from carbonate rather than siliciclastic settings, and the genus' stratigraphic range were recorded. For each of these binary habitat variables (low vs. high-mid, shallow vs. deep, carbonate vs. siliciclastic) the total number of PBDB occurrences recorded from these habitats during the time interval represented by each genus' stratigraphic range was also recorded. This allowed for the correction of a bias towards more heavily sampled habitat types. The corrected affinities of the trilobite genera were then calculated for each of the three habitat variables using the following equation:

$$k_{gh}/n_g - p = A_{gh}$$

...where n_g is the total number of occurrences of genus g, k_{gh} is the number of occurrences of genus g known from habitat h, and p is the expected probability of sampling genus g from habitat h rather than habitat i. If all habitats were equally well-represented in the Paleobiology Database, p would always be 0.5, but in reality, it is best calculated as...

$$p = Total_h/(Total_h + Total_i)$$

...where $Total_h$ is the total number of PBDB collections over genus g's stratigraphic range collected from habitat h and $Total_i$ is the total number of PBDB collection over genus g's stratigraphic range collected from habitat i. A_{gh} is the corrected affinity of genus g for habitat h. A greater A_{gh} represents a stronger affinity for habitat h, while a smaller A_{gh} represents a weaker affinity. Note that because these habitat variables are constructed as binary categories, a negative A_{gh} indicates that a genus instead has an affinity for the opposing habitat, with a more negative value representing a stronger affinity for habitat i. By plotting the taxa according to their affinities for the three habitat variables, the habitat preferences of harpetid and trinucleid trilobites could be visually compared. In addition, the significance of these affinities was calculated by means of exact one-sided binomial tests. Given that the absence of strictly significant affinities is primarily due to low sample sizes, affinities were evaluated based on marginal significance ($p \leq 0.1$) (Kiessling & Aberhan, 2007).

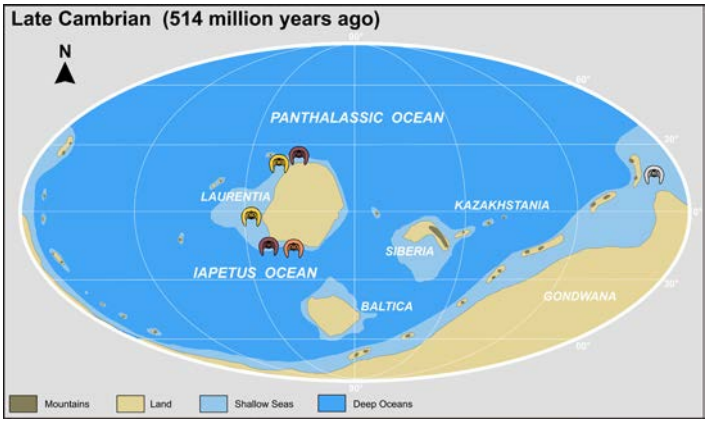

Figure 2. Cambrian distribution of sampled harpetid occurrences. Yellow: Entomaspididae. Brown: Heterocaryonidae. Orange: Harpididae. Grey: *Baikadimaspis jikdongensis*.

MAIN RESULTS

The modern distribution of the harpetid and trinucleid occurrences in this analysis demonstrates a strong bias towards Europe and North America. While this may reflect biases either in paleontological sampling or the rock record (Alison & Briggs, 1993; Benton, 2008; Bernard *et al.,* 2010; Benton, 2015), these data nevertheless support a Laurentian origin for harpetid trilobites. The earliest harpetid fossils in this analysis are all associated with the Cambrian of Laurentia (Fig. 2). These early harpetids were quite diverse, including members of the multiple families. Notably, *Baikadimapsis jikdongensis*, once thought to be a basal harpetid, appears thousands of kilometers away from these taxa in northern Gondwana. This supports the phylogenetic assessment of Beech *et al.* (2024) who concluded that *Baikadimapsis jikdongensis* was better classified as a ptychopariid outgroup to a unified Harpetida. The only putatively Cambrian-age trinucleid occurrence in the analysis also appears in tropical Laurentia, suggesting that even during their earliest days, trinucleids and harpetids may have experienced some level of geographic overlap.

The Ordovician saw significant changes for Harpetida. A new family, the Harpetidae, emerged, likely from an *Entomapsis*-like ancestor living in the shallow seas around Laurentia. Harpetidids quickly began to invade other paleocontinents, including Baltica, Avalonia, and Gondwana. Harpetidae would continue to have a cosmopolitan distribution until its final extinction. Harpididae also dispersed more widely, reaching southern Gondwana by the Tremadocian (Fig. 3A). Their Ordovician geographic dispersals brought harpetids to considerably higher latitudes than seen during the Cambrian, possibly as a result of a changing climate.

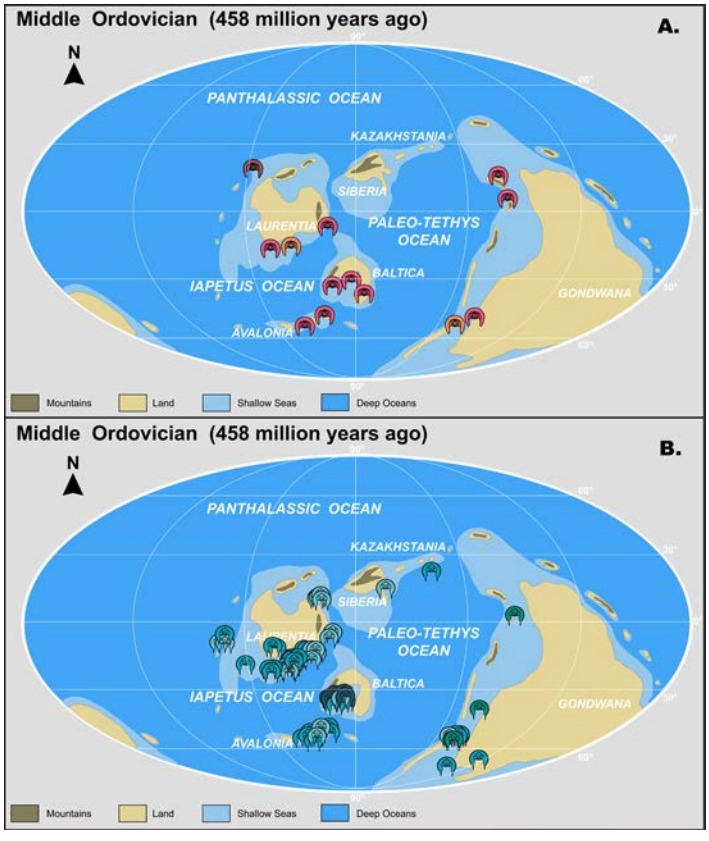

Figure 3. Ordovician distributions of sampled harpetid (**A**) and trinucleid (**B**) occurrences. Yellow: Entomaspididae. Brown: Heterocaryonidae. Orange: Harpididae. Pink: Harpetidae. Light Blue: Raphiophoridae. Medium Blue: Trinucleidae. Dark Blue: Alsatataspidae. Green: Dionididae.

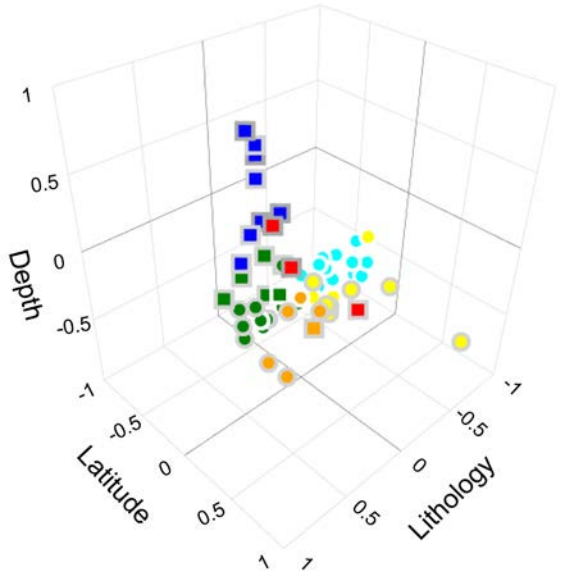

Figure 4. Habitat affinity space of harpiform trilobites. Circular data points represent trinucleid taxa. Square data points represent harpetid taxa. Data points have been colored according to the octant of the three-dimensional space in which they appear. Border around each data point denotes its statistical significance. Dark grey border indicates that the data point is statistically significant with respect to two of three habitat variables. Light grey border indicates that the data point is statistically significant with respect to one of three habitat variables. Data points with white borders are not statistically significant with respect to any individual habitat variables. The farther a data point appears from the origin along any given axis, the stronger its apparent bias or affinity with respect to that environmental variable.

Trinucleid trilobites were also widespread during the Ordovician, with representatives on every major Ordovician paleocontinent (Fig. 3B). They were found not only at low and mid paleolatitudes, but also at high paleolatitudes, perhaps indicating a greater tolerance for cold-water environments than the harpetids. The two largest trinucleid families, Trinucleidae and Raphiophoridae, in particular appear widely dispersed, while the alsataspidids in the analysis are limited to the paleocontinent of Baltica and the dionidids appear only in Gondwana. Importantly, there is no clear geographic separation between harpetid and trinucleid trilobites during the Ordovician period. All regions inhabited by harpetids were also inhabited by trinucleids. This is consistent with the idea that harpetid and trinucleids were subject to the same environmental pressures but also suggests that although these trilobites were morphologically similar, they were not competitively excluding one another from particular geographic areas.

Trinucleids during the Ordovician were somewhat more widely distributed than their harpetid counterparts and significantly more speciose, a finding consistent with a pattern of non-adaptive radiation (Gittenberger, 1991; Rundell & Price, 2009; Erwin, 2015). It is interesting to note, however, that individual trinucleid species also seem to have been more inclined towards cosmopolitanism than individual harpetid species, with multiple examples of a single trinucleid species being distributed across multiple paleocontinents and/or a wide range of different paleolatitudes. This may imply a faster rate of dispersal among trinucleids than among harpetids and can likely be at least partially explained by differences in the ontogenetic strategies of the two groups.

In our habitat affinity space analysis, we find substantial overlap in the kinds of habitats preferred by harpetids as a group and those preferred by trinucleids as a group (Fig. 4). Specifically, deep-water carbonate settings seem to have been preferred both by some trinucleids and by some harpetids. These taxa include some highly derived members of both groups, with well-developed brims, such as the harpetid genus *Harpes* Goldfuss, 1839 and the trinucleid genus *Cryptolithus* Green, 1832. This is consistent with the idea that these taxa are truly convergent from both a pattern and process-based perspective, two distantly related groups adapting to similar environmental conditions by evolving similar morphologies. However, it is also notable that not all harpetid genera show an affinity for deep-water settings. Likewise, not all trinucleid genera show an affinity for carbonate settings. (Interestingly, no genus from either group shows

an affinity for shallow siliciclastic settings). These paleoecologically disparate taxa also include highly derived, brimmed genera, such *Scotoharpes* Lamont, 1948 and *Deanaspis* Hughes *et al*., 1975. This indicates additional complexity, suggesting that the full story of the harpiform brim is more complicated than one of mutual adaption to a single shared environment.

These findings may also have a bearing on the markedly differing responses of harpetid and trinucleid trilobites to the end-Ordovician mass extinction. As all of the trinucleid genera in the habitat affinity space analysis show a bias towards deep-water environments, it may be that trinucleids' dependence on these habitats contributed to their relative vulnerability during the end-Ordovican mass extinction (Finnegan *et al.*, 2016), while harpetids—who as a group appear to have been more tolerant of shallow-water environments—proved relatively resilient.

CONCLUSIONS

The paleobiogeography and paleoecology of the order Harpetida and the superfamily Trinucleioidea were explored to improve scientific understanding of convergent evolution in harpiform trilobites. A series of paleobiogeographic maps were generated using data taken from the Paleobiology Database and from the primary literature on harpetid trilobites using the PaleoData Plotter Program (Scotese, 2016). Latitudinal and paleocontinental associations were also tracked across a recent phylogenetic tree of harpiform trilobites. While the fossil record of harpiform trilobites appears biased towards Europe and North America, it seems likely that the earliest harpetids originated in the shallow seas surrounding the paleocontinent of Laurentia. During the Ordovician, harpetids dispersed and diversified, overlapping broadly with the even more diverse and widespread trinucleids. This overlap is consistent with the idea that harpetid and trinucleid trilobites evolved their remarkably similar morphologies in response to similar environmental pressures, meeting both pattern and process-based definitions of convergent evolution. This hypothesis receives mixed support from the results of a habitat affinity space analysis, which shows that although some harpetid and trinucleid trilobites do overlap in terms of their habitat affinities, trinucleids as a group appear to have been less restricted in terms of sedimentary lithology, while harpetids appear to have been less restricted in terms of water depth. These results may also help to explain why the end-Ordovician mass extinction was more lethal for trinucleids than for harpetids, as previous studies have shown that the extinction event preferentially eliminated genera restricted to deeper waters.

REFERENCES

Adrain, J.M., Edgecombe, G.D., Fortey, R.A., Hammer, O., Laurie, J.R., McCormick, T., Owen, A.W., Waisfeld, B.G., Webby, B.D., Westrop, S.R., & Zhou., Z. (2004). Trilobites. In Webby, B.D., Paris, F., Droser, M.L., & Percival, I.G. (Eds.), *The great Ordovician biodiversification event* (pp. 231–254). Columbia University Press, New York.

Alison, P. A. & Briggs, D. E. G. (1993). Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology, 21*(1), 65–68. doi: 10.1130/0091-7613(1993)021%3C0065:PSBPSD%3E2.3.CO;2

Beech, J. D., & Lamsdell, J.C. (2021). Phylogeny, disparity and mass extinction response in the trilobite order Harpetida. *Papers in Palaeontology, 7*(4), 2205–2225. doi: 10.1002/spp2.1399

Beech, J. D., Bottjer, D. J., & Smith, N. D. (2024). Parallel evolution of unusual 'harpiform' morphologies in distantly related trilobites. *Journal of Paleontology, 98*(4), 732–743. doi: 10.1017/jpa.2024.47

Beech, J. D., Hebdon, N., Dorgan, K., Soni, P., Duncan, J. L., & Bottjer, D. J. (2026). Organism–sediment interactions and the evolution of a unique trilobite morphology. *Proceedings of the Royal Society B, 293*(2063), 20252073. doi: 10.1098/rspb.2025.2073

Benton, M. J. (2008). How to find a dinosaur, and the role of synonymy in biodiversity studies. *Paleobiology, 34*(4), 516–533. doi: 10.1666/06077.1

Benton, M. J. (2015). Palaeodiversity and formation counts: redundancy or bias? *Palaeontology, 58*(6), 1003–1029. doi: 10.1111/pala.12191

Bergström, J. (1972). Appendage morphology of trilobite *Cryptolithus* and its implications. *Lethaia, 5*(1), 85–94. doi: 10.1111/j.1502-3931.1972.tb00843.x

Bernard, E. L., Ruta, M., Tarver, J. E. & Benton, M. J. (2010). The fossil record of early tetrapods: worker effort and the end-Permian mass extinction. *Acta Palaeontologica Polonica, 55*(2), 229–239. doi: 10.4202/app.2009.0025

Bignon, A., Waisfeld, B. G., Vaccari, N.E., & Chatterton, B. D. E. (2020). Reassessment of the order Trinucleida (Trilobita). *Journal of Systematic Palaeontology, 18*(13), 1061–1077. doi: 10.1080/14772019.2020.1720324

Chatterton, B. D. E., & Speyer, S. E. (1989). Larval ecology, life history strategies, and patterns of extinction and survivorship among Ordovician trilobites. *Paleobiology, 15*(2), 118–132. doi: 10.1017/S0094837300009313

Dollo, L. (1909). La paleontologie ethologique. *Bulletin de la Societe Belge de Geologie, 23,* 1–377.

Ebach, M. C., & McNamara, K. J. (2002). A systematic revision of the family Harpetidae (Trilobita). *Records of the Western Australian Museum, 21*(3), 135–167. doi: 10.18195/issn.0312-3162.21(3).2002.235-267

Ergaliev, G. K. (1980). *Middle and Upper Cambrian trilobites from Malyy Karatau*. Academy of Sciences of the Kazakh SSR.

Erwin, D. H. (2015). Novelty and innovation in the history of life. *Current Biology, 25*(19), R930–R940. doi: 10.1016/j.cub.2015.08.019

Finnegan, S., Heim, N. A., Peters, S. E., & Fischer, W. W. (2012). Climate change and the selective signature of the Late Ordovician mass extinction. *Proceedings of the National Academy of Sciences, 109*(18), 6829–6834. doi: 10.1073/pnas.1117039109

Finnegan, S., Rasmussen, C. M. Ø, & Harper, D. A. T. (2016). Biogeographic and bathymetric determinants of brachiopod extinction and survival during the Late Ordovician mass extinction. *Proceedings of the Royal Society B, 283*(1829), 20160007. doi: 10.1098/rspb.2016.0007

Fortey, R. A., & Chatterton, B. D. E. (1988). Classification of the trilobite suborder Asaphina. *Palaeontology, 31*(1), 165–222.

Fortey, R. A., & Owens, R. M. (1997). Evolutionary history. In Kaesler, R.L. (Ed.), *Treatise on invertebrate paleontology, part O, Arthropoda 1: Trilobita (revised),* (pp. 250–287). University of Kansas Paleontological Institute and the Geological Society of America.

Fortey, R. A., & Owens, R. M. (1999). Feeding habits in trilobites. *Palaeontology, 42*(3), 429–465. doi: 10.1111/1475-4983.00080

Gittenberger, E. (1991). What about non-adaptive radiation? *Biological Journal of the Linnean Society, 43*(4), 263–272. doi: 10.1111/j.1095-8312.1991.tb00598.x

Goldfuss, G. A. (1839). Beitrage zur Petrefactenkunde. *Verhandlung K. Leopold - Caroline Akademie fur Naturforschung, 19,* 327–364.

Green, J. (1832). *A monograph of the trilobites of North America.* Joseph Brano, Philadelphia.

Hawle, I., & Corda, A. J. C. (1847). Prodrom einer Monographie der bohmischen Trilobiten. *Abhandlungen Kongligischen Bohemischen Gesellschaft der Wiossenschaften, V. Folge, 5,* 1–176.

Hughes, N. C. (2007). The evolution of trilobite body patterning. *Annual Review of Earth and Planetary Sciences, 35,* 401–434. doi: 10.1146/annurev.earth.35.031306.140258

Hughes, C. P., Ingham, J. K., & Addison, R. (1975). The morphology, classification and evolution of the Trinucleidae (Trilobita). *Philosophical Transactions of the Royal Society of London B, 272*(920), 537–604. doi: 10.1098/rstb.1975.0100

Kiessling, W. & Aberhan, M. (2007). Environmental determinants of marine benthic biodiversity dynamics through Triassic–Jurassic time. *Paleobiology, 33*(3), 414–434. doi: 10.1666/06069.1

Lamont, A. (1948). Indications of cephalic structure in Trinucleidae and Harpetidae. *Nature, 162,* 376–377. doi: 10.1038/162376a0

McNamara, K. J., Feist, R., & Ebach, M. C. (2009). Patterns of evolution and extinction in the last harpetid trilobites during the late Devonian (Frasnian). *Palaeontology, 52*(1), 11–33. doi: 10.1111/j.1475-4983.2008.00832.x

Moen, D. S., Morlon, H., & Wiens, J. J. (2016). Testing convergence versus history: convergence dominates phenotypic evolution for over 150 million years in frogs. *Systematic Biology, 65*(1), 146–160. doi: 10.1093/sysbio/syv073

Müller, R. D., Cannon, J., Qin, X., Watson, R. J., Gurnis, M., Williams, S., Pfaffelmoser, T., Seton, M., Russell, S. H. J., Zahirovic, S. (2018). GPlates: Building a virtual Earth through deep time. *Geochemistry, Geophysics, Geosystems, 19,* 2243–2261. doi: 10.1029/2018GC007584

Park, T.-Y. S., & Choi, D. K. (2011). Trilobite faunal successions across the base of the Furongian Series in the Taebaek Group, Taebaeksan Basin, Korea. *Geobios, 44*(5), 481–498. doi: 10.1016/j.geobios.2011.02.003

Pearson, K. K. (2017). *Experimental biomechanics of trinucleid fringe pits (Trilobita)* (Publication No. 184). [Honors thesis, Oberlin College]. Digital Commons at Oberlin.

Rundell, R. J., & Price, T. D. (2009). Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology and Evolution, 24*(7), 394–399. doi: 10.1016/j.tree.2009.02.007

Schoenemann, B. (2021). An overview on trilobite eyes and their functioning. *Arthropod Structure and Development, 61*, e101032. doi: 10.1016/j.asd.2021.101032

Scotese, C. R. (2016). PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project, http://www.earthbyte.org/paleomap-paleoatlas-for-gplates/

Speed, M. P., & Arbuckle, K. (2017). Quantification provides a conceptual basis for convergent evolution. *Biological Reviews, 92*(2), 815–829. doi: 10.1111/brv.12257

Stayton, C. T. (2015). The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution, 69*(8), 2140–2153. doi: 10.1111/evo.12729

Stubblefield, C. J. (1959). Evolution in trilobites. *Quarterly Journal of the Geological Society of London, 115,* 145–162. doi: 10.1144/GSL.JGS.1959.115.01.08

Swinnerton, H. H. (1919). The facial suture of trilobites. *Geological Magazine, 6*(3), 103–110. doi: 10.1017/S0016756800202252

Warburg, E. (1925). The trilobites of the Leptrena Limestone in Dalarne. *Bull. of Geol. Inst. Upsala, 17*(8), 74-376. doi: 10.1017/S0016756800105886

Wiens, J.J., Chippindale, P.T., & Hillis, D.M. (2003). When are phylogenetic analyses misled by convergence? A case study in Texas cave salamanders. *Systematic Biology, 52*(4), 501–514. doi: 10.1080/10635150390218222

EMPHASIZING DIVERSE BEHAVIOURS OF TRILOBITES: INSIGHTS FROM THE UPPERMOST DEVONIAN HANGENBERG SANDSTONE EQUIVALENT OF MOROCCO

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Keywords: Devonian, trace fossils, Anti-Atlas.

BACKGROUND

The Devonian deposits of the eastern Anti-Atlas (Morocco) are increasingly recognized as a major hotspot for the study of both vertebrate (fishes) and invertebrate (trilobites, cephalopods, brachiopods, bivalves, and crinoids) palaeontology (Klug & Pohle, 2018; Frey *et al.,* 2019). The interaction of these organisms with the substrate generated valuable ichnological records. Although the arthropod fossil record is well documented through abundant body fossils—particularly trilobites—ichnological studies remain comparatively underrepresented. Despite the documented richness of vertebrate and invertebrate ichnofossils in the region (Klug *et al.,* 2018), studies focusing specifically on Devonian ichnology are still limited relative to those on body fossils. Only a small number of contributions addressing vertebrate and invertebrate ichnofauna have been published over the past decade (*e.g.*, Klug & Hoffmann, 2018; Lagnaoui *et al*., 2019; Klug *et al*., 2021; Bel Haouz *et al*., 2026a,b). Beyond their palaeobiological significance (Klug *et al*., 2021), Devonian trace fossils provide critical insights into palaeoenvironmental and palaeoecological conditions (Lagnaoui *et al*., 2019; Bel Haouz *et al*., 2026a,b). They are particularly valuable for reconstructing benthic activity and ecosystem dynamics, especially in sedimentary settings where body fossils are scarce or preservation is episodic.

OBJECTIVES

Here, we present a comprehensive ichnotaxonomic analysis of trilobite ichnoassemblages associated with vertebrate and invertebrate trace fossils from the latest Devonian of the eastern Anti-Atlas (Morocco). This study aims to elucidate trilobite ethology through their trace fossil record in the aftermath of the Kellwasser Event and during the Hangenberg Event. In addition, the analysis of these ichnoassemblages provides an independent line of evidence for reconstructing the palaeoenvironmental and palaeoecological conditions prevailing during the formation of these trace-bearing deposits.

MATERIAL AND METHODS

The invertebrate trace fossils investigated in this study occur within the Aoufilal Formation at El Khraouia, Taouz, and Filon 12, all located on the Tafilalt Platform of the eastern Anti-Atlas (Morocco) (Fig. 1A–1B). The material was collected during multiple field campaigns across the Tafilalt region since 2018. In total, more than 60 specimens were documented through photography, morphometric analysis, and detailed measurements. The trace fossils were produced at the sediment–water interface by benthic organisms moving across or within the seafloor. Preservation resulted from rapid burial by overlying, typically coarser-grained sediment, which filled the depressions and produced natural casts on the bases of overlying beds. The

Figure 1. A. The location of the Tafilalt region in the Anti-Atlas of Morocco; **B.** map showing the approximate outlines of the Maïder and Tafilalt basins, as well as the Tafilalt platform, in the Late Devonian of the eastern Anti-Atlas (modified after Wendt & Belka 1991 and Frey *et al*., 2019).

ichnofossil-bearing horizons also contain abundant disarticulated trilobite remains. All described traces are preserved as convex hyporeliefs within fine- to medium-grained sandstones.

Specimens were photographed under natural light and using a spotlight to enhance morphological details. Morphometric measurements were taken from the best-preserved specimens, focusing on key parameters of trace fossil morphology and trackway patterns. All descriptions and measurements follow the standard protocols for the documentation and identification of arthropod trackways proposed by Trewin (1995).

MAIN RESULTS

***Allocotichnus* Osgood, 1970:** Numerous specimens consist of bifid, dimorphic arthropod trackways in which one branch is expressed by long, subparallel, regularly arranged imprints, whereas the opposing branch is weakly preserved or absent. The traces occur as convex hyporeliefs in fine-grained sandstone, with individual trackways individual trackways ranging in length from 20 to over 80 cm' (Fig. 3H).

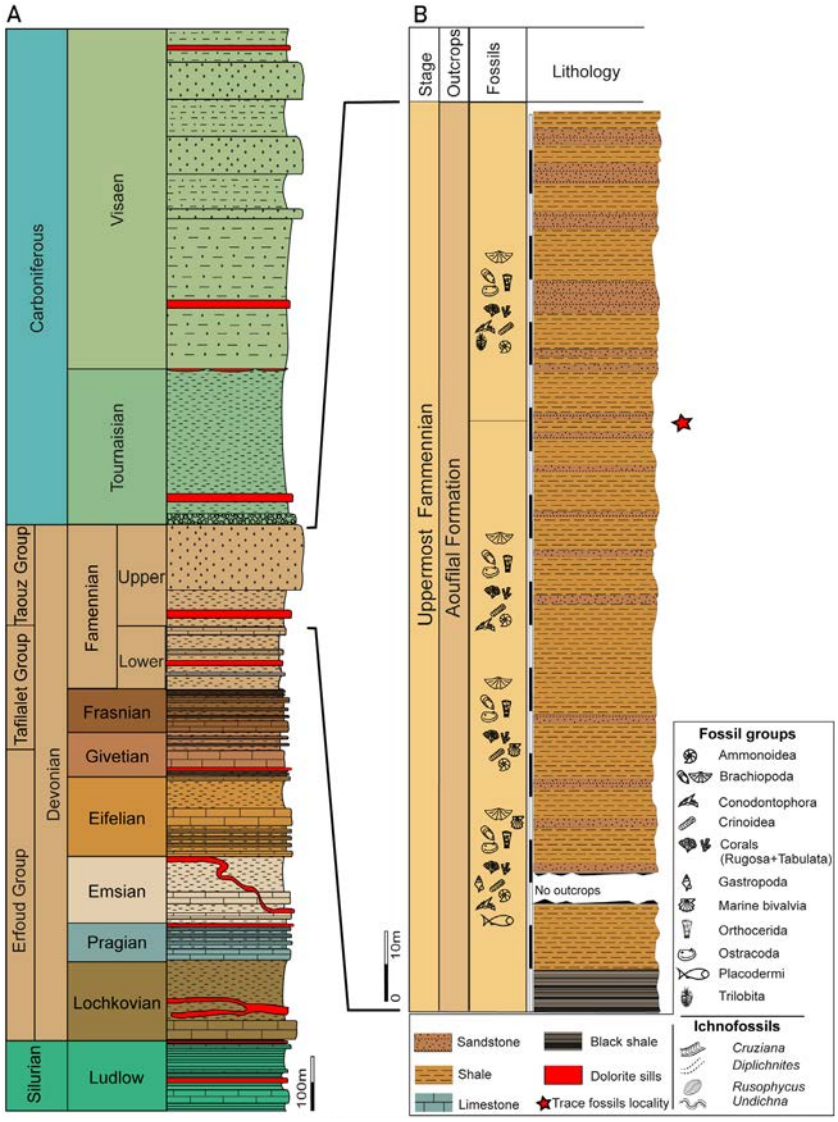

Figure 2. A. Late Paleozoic stratigraphy subdivision of the South Tafilalt region, modified after Álvaro *et al.* (2014) and Najih *et al.* (2019); **B.** lithological section of the late Famennian stage of the Aoufilal Formation, showing the stratigraphic position of the ichnofossiliferous strata (Bel Haouz *et al.*, 2026b).

***Cruziana lobosa* Seilacher, 1970:** Six specimens consist of horizontal trace fossils preserved in curved, sinuous to looping paths as convex hyporeliefs (Fig. 3A–3D). The traces are long, shallow to moderately deep, bilobate, ribbon-like structures separated by a median furrow. They exhibit fine, slightly oblique, blunt-ended transverse scratch marks in the central region, produced by trilobite endopods, flanked by two lateral continuous grooves and ridges corresponding to exopodal activity (Figs. 3A–3D). The holotype of *C. lobosa* originates from the Middle Devonian Aouinet Quenine Formation of Libya (Seilacher, 1970). Therefore, the specimens described herein are regarded as the youngest occurrence of *C. lobosa*.

***Diplichnites gouldi* Gevers in Gevers *et al*., 1971:** more than 20 specimens of straight to gently curved trackways, each comprising two parallel rows of closely spaced and well-organised to unorganised series of tracks in bilateral symmetry (Fig. 3E–3F). The trackways are preserved as convex hyporelief, with lengths between 10 cm and more than 60 cm. The internal width varies between 14 and 16 mm, and the external width between 16 and 24 mm with an external/internal width ratio of less than 1.5. *Diplichnites* has a wide stratigraphic and geographic range. It has been reported from the Cambrian to the recent, while *D. gouldi* is known from the Cambrian to the Permian from the North and South America, Europe, Asia and Africa.

***Rusophycus antiatlasensis* Bel Haouz *et al.*, 2026b:** more than 40 short, bilobate trace fossils which exhibit an oblong to ovate shape; they are well-preserved in convex hyporeliefs and concave epireliefs consisting of two juxtaposed symmetric and parallel lobes (Fig. 3J). These bilobate trace fossils occur as individuals or are arranged in population-like assemblages of up to eleven serially repeated traces, with a preferred orientation within the slab. Distances between burrows are not uniform; sometimes the burrows intersect or overlap locally (Fig. 3J), or occur as traces continuous with *Diplichnites* (Fig. 3E). Lobes are characterised by closely spaced transverse striae, oriented at 70–90° to the median ridge and varying in depth toward the outer margins. The burrows exhibit carapace imprints within moulds of scratches. The specimens described here constitute the only known record of this ichnotaxon.

***Rusophycus* cf. *carleyi* James, 1885:** more than 5 specimens consisting of bilobate, elliptical to ovate trace fossils preserved as convex hyporelief and concave epirelief. Traces consist of two lateral convex lobes, separated anteriorly by a median depression or mesial opening that extends posteriorly (Fig. 3E, 3G). *Rusophycus* specimens occur either isolated or at the end of *Diplichnites* trackways, sometimes interrupting them. The median mesial opening is shallowly impressed. The specimens described herein do not exhibit any exopodal, spinal, cephalic or pygidial traces. Coxal impressions are the only remaining morphological feature.

***Rusophycus* isp.:** Numerous specimens show a short bilobate structure preserved as convex hyporelief depressions with oblong to ovate outlines (Fig. 3E). Lobes are not well separated and the median furrow is either missing or only faintly preserved. Due to their short, oval shape and bilobate character, it is not possible to assign them to the ichnospecific level.

***Monomorphichnus lineatus* Crimes *et al*., 1977:** This group comprises eight unpaired ridges or grooves bearing straight striations. Spacing between successive elements ranges from 3 to 6 mm. The specimens conform to the diagnostic features of *Monomorphichnus*, characterized by parallel, straight to slightly sinuous ridges or grooves. They are assigned to *M. lineatus*, distinguished from *M. bilinearis* by the absence of paired ridge structures. *Monomorphichnus* was originally interpreted as the result of trilobite locomotion under current influence, during which endopodite claws scraped the sediment surface (Crimes, 1970; Crimes *et al*., 1977). Based on ridge spacing, the trackmaker is estimated to have been approximately 4 cm in length.

Unidentified trackways: A series of bilaterally symmetrical, lunate trace fossils is preserved as convex hyporeliefs. Individual imprints reach up to 6 cm in length and 1.5 cm in width, with a total trackway length of approximately 20 cm. Spacing between successive imprints is regular, averaging 4 cm (Fig. 3I). The lunate morphology recalls *Crescentichnus*, although the consistent trackway organization differs from previously described occurrences of that ichnogenus. Comparable Cambrian material from Sweden has been assigned to cf. *Protovirgularia* (McLoughlin *et al*., 2021, fig. 11c). Due to limited material and preservation quality, erection of a new ichnotaxon is not justified at this stage. These specimens are therefore retained for future detailed ichnotaxonomic analysis.

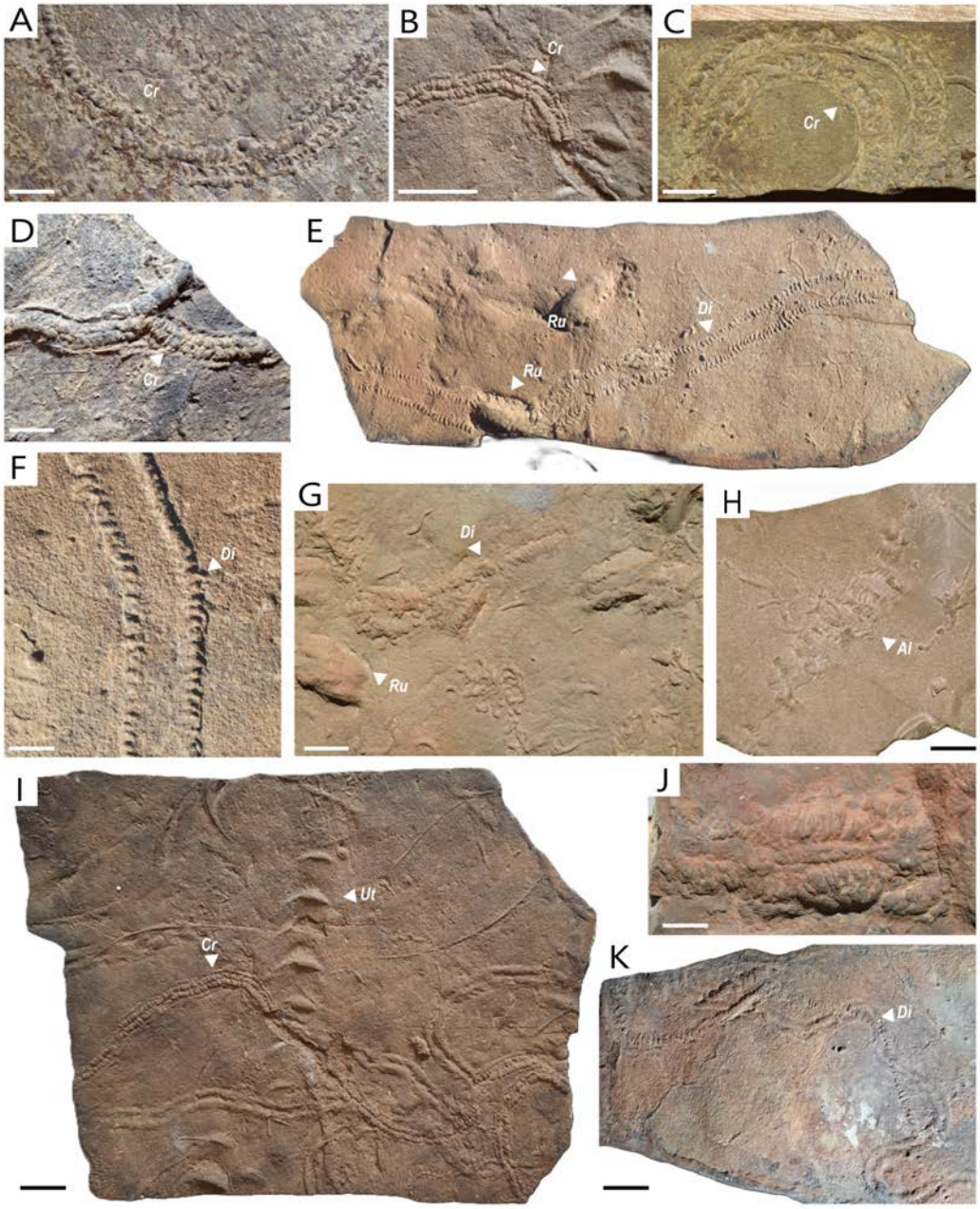

Figure 3. A–D, Slabs showing *Cruziana lobosa*; **E,** slab showing the co-occurrence of *Rusophycus antiatlasensis* and *Diplichnites gouldi*; F, slab showing *Diplichnites gouldi*; **H,** slab showing *Allocotichnus dyeri*; **I, K,** slab displaying multiple overlapping and intersecting bilobate trails preserved in convex hyporelief; **J,** slab showing *Rusophycus antiatlasensis* (Bel Haouz *et al.*, 2026). All specimens are invertebrate trace fossils preserved at the base of sandstone beds. **Cr** = *Cruziana lobosa;* **Di** = *Diplichnites gouldi;* **Ru** = *Rusophycus antiatlasensis;* **Ut** = unidentified trackways; scale bar = 1 cm.

CONCLUSIONS

The Famennian (Upper Devonian) strata of the eastern Anti-Atlas of Morocco yielded a highly diverse trilobite ichnofossils. These are found in association with invertebrate and vertebrate ichnoassemblages that still remain poorly studied. The trilobite trace fossils reported herein are referred to several behavioural aspects, including pascichnia-repichnia (*Cruziana lobosa*), repichnia (*Allocotichnus dyeri*, *Diplichnites gouldi, Mammillichnis* isp., *Undichna* isp.), and cubichnia (*Rusophycus antiatlasensis, Rusophycus* cf. *carleyi,*). Several of these ichnogenera (*Cruziana, Diplichnites, Monomorphichnus, Rusophycus)* are here attributed to proetid and phacopid trilobites as potential tracemakers. The described trilobite ichnoassemblages are ascribed to the archetypal *Cruziana* ichnofacies, indicating a shallow-marine environment with low hydrodynamic-energy settings, stable substrate conditions, and regular organic matter sources. The morphology of *C. lobosa* is strongly influenced by anatomical constraints and behavioural patterns. *D. gouldi* has been made by homopodous trilobites. *Rusophycus antiatlasensis* is regarded as serially repeated resting traces. This could indicate a gregarious behaviour of trilobites, potentially linked to adult migration for mating and spawning, or alternatively, to localized prey abundance.

The association of *Diplichnites, Rusophycus antiatlasensis,* and *Rusophycus* isp. suggests a predatory strategy involving prey stalking. This behaviour was likely interrupted by periods of concealment within the sediment to avoid potential predators such as fishes (evidenced by abundant *Undichna*).

Given its pivotal role in understanding Upper Devonian ecosystem evolution, following a series of biotic crises and culminating in the Hangenberg Event—fossil exploration in eastern Anti-Atlas should be intensified. This region offers a profound record of the events that reshaped marine life on Earth.

REFERENCES

Álvaro, J. J., Benziane, F., Thomas, R., Walsh, G. J., & Yazidi, A. (2014). Neoproterozoic–Cambrian stratigraphic framework of the Anti-Atlas and Ouzellagh promontory (High Atlas), Morocco. *Journal of African Earth Sciences*, *98*, 19–33. doi: 10.1016/j.jafrearsci.2014.04.026

Bel Haouz W., Lagnaoui, A., Klug, C., Baidder, L. & Maanan, M. (2026a). Middle Devonian ichnofossils from Hamar Laghdad (eastern Anti-Atlas, Morocco). *Swiss Journal of Palaeontology*, *145*, 403–431. doi: 10.3897/sjp.145.188799

Bel Haouz W., Lagnaoui, A., Klug, C., Maanan, M., & Baidder, L. (2026b). An exceptional diverse trilobite ichnofauna from the uppermost Devonian of Anti-Atlas, Morocco. *Acta Palaeontologica Polonica*. Advance online publication.

Crimes, T. P. (1970). Trilobite tracks and other trace fossils from the Upper Cambrian of North Wales. *Geological Journal, 7*, 47–68. doi: 10.1002/gj.3350070104

Crimes, T. P., Legg, I., Marcos, A., & Arboleya, M. (1977). Late Precambrian–Lower Cambrian trace fossils from Spain. In T. P. Crimes & J. C. Harper (Eds.), *Trace Fossils* 2 (pp. 91–138). *Geological Journal Special Issue, 9*.

Frey, L., Pohle, A., Rücklin, M., & Klug, C. (2019). Fossil-Lagerstätten and preservation of vertebrates and invertebrates from the Devonian of Morocco (eastern Anti-Atlas). *Lethaia, 53*(2), 242-266. doi: 10.1111/let.12354

Gevers, T. W., Frakes, L. A., Edwards, L. N., & Marzolf, J. E. (1971). Trace fossils in the lower Beacon sediments (Devonian), Darwin Mountains, Southern Victoria Land, Antarctica. *Journal of Palaeontology, 45*, 81–94.

James, J. F. (1885). The fucoids of the Cincinnati Group, Part. 2. *Journal of the Cincinnati Society of Natural History,* 7,151–166.

Klug, C., & Hoffmann, R. (2018). Trace fossils of Actiniaria (Conichnus) from the Early Devonian of Morocco. In C. Klug & D. Korn (Eds.), *Palaeontology of the Devonian of Hamar Laghdad (Tafilalt, Morocco): Special volume honouring Jobst Wendt. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 290*(1), 65–74. doi: 10.1127/njgpa/2018/0767

Klug, C., & Pohle, A. (2018). The eastern Amessoui Syncline – a hotspot for Silurian to Carboniferous cephalopod research. *Münstersche Forschungen zur Geologie und Paläontologie 110*, 244–260.

Klug, C., Lagnaoui, A., Jobbins, M., Bel Haouz, W., & Najih, A. (2021). The swimming trace Undichna from the latest Devonian Hangenberg Sandstone equivalent of Morocco. *Swiss Journal of Palaeontology*, *140*(1), 19. doi: 10.1186/s13358-021-00233-9

Klug, C., Samankassou, E., Pohle, A., De Baets, K., Franchi, F., & Korn, D. (2018). Oases of biodiversity: Early Devonian palaeoecology at Hamar Laghdad, Morocco. In C. Klug & D. Korn (Eds.), Palaeontology of the Devonian of Hamar Laghdad (Tafilalt, Morocco). Special volume honouring Jobst Wendt. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 290* (1), 9–48. doi: 10.1127/njgpa/2018/0772.

Lagnaoui, A., Bel Haouz, W., & Najih, A. (2019). Trackway and resting traces of trilobites with associated invertebrate ichnofossils from the Early Carboniferous of the Al Atrous region (Eastern Anti-Atlas, Morocco). In *Kazan Golovkinsky Stratigraphic Meeting* (pp. 24-28).

McLoughlin, S., Vajda, V., Topper, T. P., Crowley, J. L., Liu, F., Johansson, O., & Skovsted, C. B. (2021). Trace fossils, algae, invertebrate remains and new U-Pb detrital zircon geochronology from the lower Cambrian Torneträsk Formation, northern Sweden. *GFF, 143*(2–3), 103–133. doi: 10.1080/11035897.2021.1939775

Najih, A., Montero, P., Verati, C., Chabou, M.C., Fekkak, A., Baidder, L., Ezzouhairi, H., Bea, F., & Michard, A. (2019). Initial Pangean rifting north of the West African Craton: Insights from late Permian U-Pb and 40Ar/39Ar dating of alkaline magmatism from the Eastern Anti-Atlas (Morocco). *Journal of Geodynamics 132*, 101670. doi: 10.1016/j.jog.2019.101670

Osgood, R. G., Jr. (1970). Trace fossils of the Cincinnati area. *Palaeontographica Americana 41*, 281–444.

Seilacher, A. (1970). Cruziana stratigraphy of “nonfossiliferous” Palaeozoic sandstones. In T. P. Crimes & J. C. Harper (Eds.), *Trace Fossils* (pp. 447–476). *Geological Journal Special Issue*.

Trewin, N. H. (1995). A draft system for the identification and description of arthropod trackways, *Palaeontology, 37*(4): 811–823.

Wendt, J., & Belka, Z. (1991). Age and depositional environment of Upper Devonian (early Frasnian to early Famennian) black shales and limestones (Kellwasser facies) in the eastern Anti-Atlas, Morocco, *Facies 25*, 51–90. doi: 10.1007/BF02536756

ARTHROPOD TRACE FOSSILS FROM THE BARRIOS QUARTZITE FORMATION OF TORRESTÍO (BABIA, LEÓN, NW SPAIN): IMPLICATIONS FOR ICHNOTAXONOMY AND AGE ASSESSMENT

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Keywords: Spain, Trilobites, *Cruziana*, Biostratigraphy.

We report an assemblage of arthropod trace fossils from Torrestío, more specifically from the western flank of Pico Morronegro, in the Babia region (León, northwestern Spain), within the southwestern sector of the Cantabrian Zone. The studied specimens were recovered from strata assigned to the Barrios Quartzite Formation, a classic Lower Palaeozoic siliciclastic unit of the Cantabrian Mountains composed predominantly of quartz arenites to white quartzites with mudstones interbeds. Although the Los Barrios de Luna–Mallo de Luna section constitutes its classical stratotype in the León area, this formation is widely represented throughout the Cantabrian Zone and commonly forms prominent topographic relief owing to its high resistance to erosion (Castaño de Luis & Fernández Martínez, 2007; Castaño de Luis & Toyos, 2022).

The Torrestío material includes forms preliminarily assignable to *Cruziana*, *Rusophycus*, *Dimorphichnus*, and *Didymaulichnus*, as well as several ichnospecies of *Cruziana*, notably *Cruziana goldfussi*, *C. barriosi*, and *C. semiplicata*. From an ichnotaxonomic point of view, the distinction between *Cruziana* and *Rusophycus* is maintained here on strictly morphological grounds, in accordance with both the classical literature and subsequent revisions, thus avoiding the automatic merging of these morphotypes on purely ethological grounds or based on inferred tracemakers (Crimes, 1975; Keighley & Pickerill, 1996).

The chronostratigraphic interpretation of the outcrop is based primarily on the trace-fossil association itself. In particular, *Cruziana semiplicata* has been regarded as a characteristic taxon of the Upper Cambrian–lower Tremadocian transition, whereas *C. furcifera*, *C. rugosa*, and *C. goldfussi* are frequent in the *Lower Ordovician*, with possible extension into the Tremadocian in some Iberian sectors (Crimes, 1975; Baldwin, 1977b). Accordingly, the co-occurrence at Torrestío of morphotypes comparable to *C. semiplicata* and forms closely related to *C. goldfussi*, together with *Rusophycus* and other arthropod traces, supports a provisional Lower Ordovician age for this outcrop, most likely within a Tremadocian to earliest Arenigian interval. This interpretation is also consistent with the regional assignment of the Barrios Quartzite Formation to the Ordovician in the Cantabrian Zone, even though in some specific sections the unit displays diachronous development and a stratigraphically complex history (Castaño de Luis & Toyos, 2022).

The significance of this occurrence is further enhanced by the fact that the Barrios Formation has previously yielded, elsewhere in northwestern Iberia, an ichnofauna including *Skolithos*, *Teichichnus*, *Arenicolites*, *Corophioides*, *Planolites*, *Rusophycus* Type A, *Cruziana semiplicata*, and *Cruziana barriosi*, among other taxa, particularly in the classical Los Barrios de Luna section (Baldwin, 1977b; Castaño de Luis & Toyos, 2022). The new Torrestío specimens thus expands the record of arthropod trace fossils in the León sector of the Cantabrian Zone and provides additional evidence for discussing ichnotaxonomic diversity, the biostratigraphic significance of *Cruziana–Rusophycus* associations, and the palaeoecological patterns of substrate colonization in shallow siliciclastic settings of the Lower Ordovician.

From a palaeoecological perspective, the Torrestío assemblage suggests a combination of locomotory, shallow-burrowing, and resting/feeding activities on relatively firm substrates. Previous studies on trilobite-related traces have emphasized that many forms of *Cruziana* reflect intrastratal or semi-infaunal production, and that transitions between *Rusophycus* and *Cruziana* may record a behavioural continuum linking resting, excavation, and feeding phases (Goldring, 1985; Boyer & Mitchell, 2017). In this context, the assemblage reported herein is particularly relevant for comparative analyses of trace fossils attributed to trilobites and other Palaeozoic arthropods.

Acknowledgements: This paper is a contribution to project PID2021-125585NB-I00 and CNS2024-154147 of the Spanish Ministry of Science and Innovation.

REFERENCES

Baldwin, C. T. (1977a). *Rusophycus morgati*: an asaphid produced trace fossil from the Cambro-Ordovician of Brittany and northwest Spain. *Journal of Paleontology*, *51*, 411–413.

Baldwin, C. T. (1977b). *The stratigraphy and facies associations of trace fossils in some Cambrian and Ordovician rocks of north western Spain*.

Boyer, D. L. & Mitchell, C. E. (2017). Aligned trace fossils from the Utica Shale: implications for mode of life and feeding in the trilobite *Triarthrus beckii*. *Lethaia*, *50*, 69–78. doi: 10.1111/let.12172

Castaño de Luis, R. & Fernández Martínez, E. (2007). Los Barrios de Luna (León, España): un lugar de interés geológico y didáctico. *De Re Metallica*, *8,* 81–92.

Castaño de Luis, R. & Toyos, J. M. (2022). *El Paleozoico inferior de Los Barrios de Luna: Formaciones y contenido paleontológico*. GeoLaciana 2022. Aula Geológica Robles de Laciana, 39–50

Crimes, T. P. (1975). Trilobite traces from the Lower Tremadoc of Tortworth. *Geological Magazine*, *112*, 33–46. doi: 10.1017/S0016756800045568

Goldring, R. (1985). The formation of the trace fossil Cruziana. *Geological Magazine*, *122*, 65–72. doi: 10.1017/S0016756800034099

Keighley, D. G., & Pickerill, R. K. (1996). Small *Cruziana*, *Rusophycus*, and related ichnotaxa from eastern Canada: the nomenclatural debate and systematic ichnology. *Ichnos*, *4*, 261–285.

CRUZIANA TAPHONOMY AND ECOLOGY FROM SOUTHERN SPAIN

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Keywords: *Cruziana*, taphonomy, epirrelief, preservational morphotypes, quantitative analysis.

Among the ichnogenera commonly attributed to trilobites, *Cruziana* is one of the most extensively studied. However, over the last four decades, research has focused mainly on taxonomic and systematic aspects, whereas taphonomic processes and ecological or ethological interpretations have received comparatively less attention. Most taphonomic studies have addressed the common preservation of *Cruziana* as hypichnial casts on sandstone or quartzite soles, usually interpreted as epibenthic or semi-infaunal grazing traces. By contrast, epirelief occurrences with preserved infill, including meniscate structures, remain poorly understood despite their potential to indicate truly infaunal behaviour.

Here, we present data from several localities in southern Spain where dense associations of epirelief *Cruziana* are preserved on quartzite bedding surfaces. Using photogrammetry and quantitative methods, size classes and geometric parameters are analysed to explore behavioural patterns in the absence of diagnostic ichnospecific features. Three preservational morphotypes are recognized according to infill preservation and trace orientation relative to stratification. These data allow us to propose a formation model linking infaunal activity with early weathering and erosion processes.

Acknowledgements: This paper is a contribution to project PID2021-125585NB-I00 and CNS2024-154147 of the Spanish Ministry of Science and Innovation.

BIOGLYPHS IN THE *CRUZIANA RUGOSA* GROUP: PRELIMINARY RESULTS FROM THE LOWER ORDOVICIAN LOS CABOS SERIES (LEÓN, NW SPAIN)

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Keywords: ichnotaxonomy, morphometrics, substrate consistency, trilobite locomotion.

ABSTRACT

Cruziana is a celebrated ichnogenus of trace fossils produced by arthropods, mainly trilobites, since the lower Cambrian (Jensen, 1997; Seilacher, 2007). They are commonly interpreted as *repichnia* (locomotion) or *pascichnia* (grazing), and record an extremely wide range of morphological variations, which has led to the description of dozens of ichnospecies (*e.g.*, Fillion & Pickerill, 1990; Seilacher, 1970). The present work focuses on the 'Rugosa Group' (Seilacher, 1970), which is regarded as a pivotal proxy for understanding the ethology and palaeoecology of Trilobita (Mángano *et al.,* 2001). Seven specimens of *Cruziana* are examined herein, constituting an advance in the current study of the material hosted at the Geology Museum of the University of Oviedo (Asturias, Spain), which holds nearly 250 specimens.

The study samples were collected by Dr Alberto Marcos (1944–2022) during the 1970s in the surroundings of Palacios del Sil (León, NW Spain). From a stratigraphic point of view, the material was collected from the upper part of Los Cabos Series (Cambrian–Ordovician), corresponding to the lower Arenigian (Floian Stage, Lower Ordovician, c. 477-470 Ma) (Gutiérrez-Marco *et al.,* 2002). Los Cabos Series consists of an alternation of shales and sandstones deposited in a shallow marine setting (Marcos *et al.,* 2004).

Seven specimens were examined for this abstract, chosen on the basis of their exceptional preservation and the variability of their morphological features, such as scratches and corrugations. Indeed, the remarkably fine preservation of the scratches produced by the tracemaker constitutes a relevant source of information for advancing the understanding of trilobite locomotion patterns. Additionally, their wide morphological variations provide a potential proxy for developing and refining *Cruziana* ichnotaxonomy.

The morphology of the study specimens was measured, focusing especially on the size and depth of the lobes, their distribution (contiguous vs separated) and correlation (inter-lobe angle, β), the size of the scratches and their angle with respect to the medial line (α), the size and distribution of the corrugations and their angle with respect to the medial line (γ), and the angle between scratches and corrugations (δ).

Based on these parameters, the study samples were assigned to *Cruziana rugosa* d'Orbigny, 1842 and *Cruziana goldfussi* (Rouault, 1850) Lebesconte, 1883 from the 'Rugosa Group'. *C. rugosa* (n = 4) is characterised by scratches attributed to the endopodites co-occurring with variably marked corrugations, whereas *C. goldfussi* (n = 3) is characterised by grooves parallel to the lobes and the absence of corrugations (Seilacher, 1970).

Based on the distribution of the lobes within each specimen, two morphotypes have been defined and identified within both ichnospecies studied: (A) those in which both lobes are parallel and in contact with each other, and (B) those in which the lobes diverge as the trilobite progressed,

forming a V-shaped pattern. The separation of the lobes can be attributed to low substrate consistency: as the tracemaker advanced through an area characterised by a high-water-content substrate, the organism 'sank' within the sediment, occasionally leaving coxal impressions (*e.g.*, *C. carleyi*) (cf. Seilacher & Gishlick, 2015). This implies that the depth of the lobes should be higher in morphotype B, which was evaluated using a depth:width ratio (n.b. depth itself can be a function of larger tracemakers, thus using the width as a corrective factor potentially limits this bias). However, similar depth:width ratios are observed for both morphotypes: a mean of 0.093 for morphotype A and 0.098 for morphotype B. Albeit the sample size is very low (n = 2 for morphotype B and n = 3 for morphotype A), this result aligns with the fact that discrete features are not commonly preserved in water-saturated substrates. Such conditions typically lead to the preservation of 'biodeformational structures', characterised by the absence of the diagnostic criteria required for ichnotaxonomical classification (Wetzel & Uchman, 1998; Wetzel, 2026), thus, alternative interpretations of these morphotypes may arise with future studies.

Regarding *C. rugosa*, the correlation between scratches and corrugations arises as a promising proxy for studying trilobite locomotion and refining its ichnotaxonomy. Two morphotypes have been described within this ichnospecies: (C) characterised by marked corrugations crosscut by continuous scratches, and (D) distinguished by less marked corrugations, with scratches mostly distributed in sets within each pair of corrugations. Apparently, these two morphotypes of *C. rugosa* are well-supported by their morphological traits; morphotype C exhibits a high angle between scratches and corrugations (δ), ranging from 40° to 70°, whereas morphotype D exhibits a lower δ, ranging from 15° to 20°.

In conclusion, although these preliminary findings are based on a limited subset of samples, they highlight the significant potential of detailed morphometric analyses—specifically regarding lobe dynamics and angular parameters—to refine *Cruziana* ichnotaxonomy. Further advances in this study will validate or refine the presented morphotypes across a larger dataset, promising to provide a more robust proxy for decoding trilobite locomotion strategies.

Acknowledgements: This paper is a contribution to project PID2021-125585NB-I00 and CNS2024-154147 of the Spanish Ministry of Science and Innovation.

REFERENCES

Fillion, D., & Pickerill, R. K. (1990). Ichnology of the Upper Cambrian? To Lower Ordovician Bell Island and Wabana groups of Eastern Newfoundland, Canada. *Palaeontographica Canadiana, 7*, 1–83.

Gutiérrez-Marco, J. C., Robardet, M., Rábano, I., Sarmiento, G. N., San José Lancha, M. A., Herranz Araújo, P., & Pieren Pidal, A. P. (2002). Ordovician. In W. Gibbons & M. T. Moreno (Eds.), *The geology of Spain* (pp. 29–49). Geological Society of London. doi: 10.1144/GOSPP.4

Jensen, S. (1997). Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. *Fossils & Strata*, *42*, 1–111. doi: 10.18261/8200376656-1997-01

Lebesconte, P. (1883). *Oeuvres posthumes de Marie Rouault, publiées par les soins de P. Lebesconte. Suivies de Les cruziana et les rysophycus, connus sous le nom général de bilobites, sont-ils des végétaux ou des traces d'animaux*. Typographie Oberthur.

Mángano, M. G., Buatois, L. A., & Moya, M. C. (2001). Trazas fósiles de trilobites de la Formación Mojotoro (Ordovícico Inferior-Medio de Salta, Argentina): implicancias paleoecológicas, paleobiológicas y bioestratigráficas. *Spanish Journal of Palaeontology*, *16*(1), 9–28. doi: 10.7203/sjp.16.1.21577

Marcos, A., Bastida, F., Martínez-Catalán, J. R., Gutiérrez-Marco, J. C., & Pérez-Estaún, A. (2004). Estratigrafía y paleogeografía de la Zona Asturoccidental-leonesa. In J. A. Vera (Ed.), *Geología de España* (pp. 49–68). SGE-IGME.

Orbigny, A. d' (1842). *Voyage dans l'Amérique méridionale (le Brésil, la République orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivia, la République du Pérou) exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833: Vol. 3, pt. 4 (Paléontologie)*. Pitois-Leverault.

Rouault, M. (1850). Note préliminaire sur une nouvelle formation découverte dans le terrain silurien inférieur de la Bretagne. *Bulletin de la Société Géologique de France, Série 2*, *7*, 724–744.

Seilacher, A. (1970). Cruziana stratigraphy of "non-fossiliferous" Palaeozoic sandstones. In T. P. Crimes & J. C. Harper (Eds.), *Trace fossils* (Geological Journal Special Issues, Vol. 3, pp. 447–476). Seel House Press.

Seilacher, A. (2007). *Trace fossil analysis*. Springer. doi: 10.1007/978-3-540-47226-1

Seilacher, A., & Gishlick, A. D. (2015). *Morphodynamics*. Taylor & Francis. doi: 10.1201/b17557

Wetzel, A. (2026). The diversity of biodeformational structures–their classification, characteristics, and interpretation. *Ichnos*, *32*(1), 1–22. doi: 10.1080/10420940.2026.2630389

Wetzel, A., & Uchman, A. (1998). Biogenic sedimentary structures in mudrocks—an overview. In J. Schieber, W. Zimmerle, & P. Sethi (Eds.), *Shales and mudrocks: Vol. I* (pp. 351–369). E. Schweizerbart'sche Verlagsbuchhandlung.

EXPLORING CAMBRIAN-ORDOVICIAN TRILOBITE CEPHALIC BIOMECHANICS

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Keywords: Finite element analysis, plane models, functional morphology, biomechanics.

INTRODUCTION

Biomechanics aims to assess the movement and the mechanical behaviour of biological systems (Alexander, 2005). This approach enables a deeper understanding of the physical capabilities and limitations of organisms, how they interact with their environment, and the ecological roles they occupy based on these constraints and abilities. To date, such studies have been conducted predominantly on vertebrates (*e.g.*, Ballell & Ferrón. 2021; Cuff *et al*., 2022; Figueirido *et al*., 2014), with comparatively limited research focusing on invertebrates (*e.g.*, Briggs *et al*., 1991; Bicknell *et al*., 2002). Trilobites are no exception, as biomechanical studies on this group remain scarce (*e.g.*, Esteve *et al*., 2021; Gómez- Rodríguez *et al*., 2025).

These arthropods first appeared during the Cambrian Series 2, beginning a specialization process that will culminate during the Ordovician, when they underwent significant diversification, both taxonomically and morphologically, as well as in terms of ecological niches (Adrain *et* al., 2004; Hughes, 2007; Whalen & Briggs, 2018). Trilobite morphology, particularly that of the cephalon, has traditionally been associated with their lifestyle (Fortey, 1985, Fortey & Owen, 1990). Despite its evident ecological significance, the relationship between cephalic morphology and biomechanics remains poorly understood. Therefore, integrating morphological and biomechanical analyses across different trilobite groups could substantially improve our understanding of their evolutionary history and adaptive strategies. Due to the specialization process we hypothesized that during Cambrian there will be small differences regarding the biomechanics between different groups of trilobites, as they are not so differentiated, and that during the Ordovician each group will adquire a caracterhistic biomechanical range.

MATERIAL AND METHODS

We applied the methodology proposed by Marcé-Nogué *et al.* (2016), which employs plane models (2D), Quasi-Ideal Meshes (**QUIM**), and a single Von Mises stress value to represent the relative structural strength of biological forms. This approach has already been successfully applied to both vertebrates and invertebrates, yielding promising results. Although 2D models lack the structural information provided by three-dimensional representations and are less precise for specific comparisons, they allow for the efficient analysis of a large number of specimens, facilitating the identification of evolutionary patterns. Ideally, the mesh generated from a 2D model would consist of elements of uniform size. However, commonly used software cannot produce such ideal meshes, which poses a significant limitation, as Finite Element Analysis (**FEA**) is highly sensitive to element size. By applying the indicators defined by Marcé-Nogué *et al*. (2016), it is possible to generate meshes with an error below a defined threshold, thus obtaining QUIMs whose results are representative of the real structure.

Using this methodology, we analysed 304 trilobite specimens belonging to different Cambrian–Ordovician orders. Finite Element Analysis was applied to the plain models derived from photographs of the specimens' cephalon. A force was applied to the central third of it, scaled according to its total area and width (Marcé-Nogué *et al*., 2013). The fixed displacement was positioned at the articulation between the cephalon and the thorax, specifically in the region defined by the fulcrum. Von Mises stress data was obtained for each specimen and then, was subsequently correlated with taxonomic, ecological, and temporal variables.

RESULTS AND DISCUSSION

Despite the differences observed previously between trilobites with and without dorsal facial suture in the Cambrian (Esteve *et al*., 2021) our results indicate that there is relatively little, although significant, variation in biomechanical performance between Cambrian and Ordovician trilobites. But, Ordovician taxa exhibit a broader overall range. In other words, during the Ordovician there is a greater number of trilobites displaying extreme stress values in both directions compared to those from the Cambrian (Fig. 1). With regard to lifestyle (epibenthic, semiinfaunal, infaunal and pelagic), the Median values of Von Mises stress show no significant differences between epibenthic, semiinfaunal and infaunal groups (Fig. 2). However, these differ significantly from pelagic trilobites, which reach, on average, higher stress values along the cephalon. This pattern is consistent with functional expectations, as pelagic trilobites do not require the same structural resistance as benthic forms, given that the resistance of water is considerably lower than that imposed by sediment. A qualitative analysis of the stress distribution (the colour patterns resulting from FEA) was conducted to further assess whether infaunal, semiinfaunal and epibenthic forms are truly comparable (Fig. 4). The results suggest that epibenthic trilobites

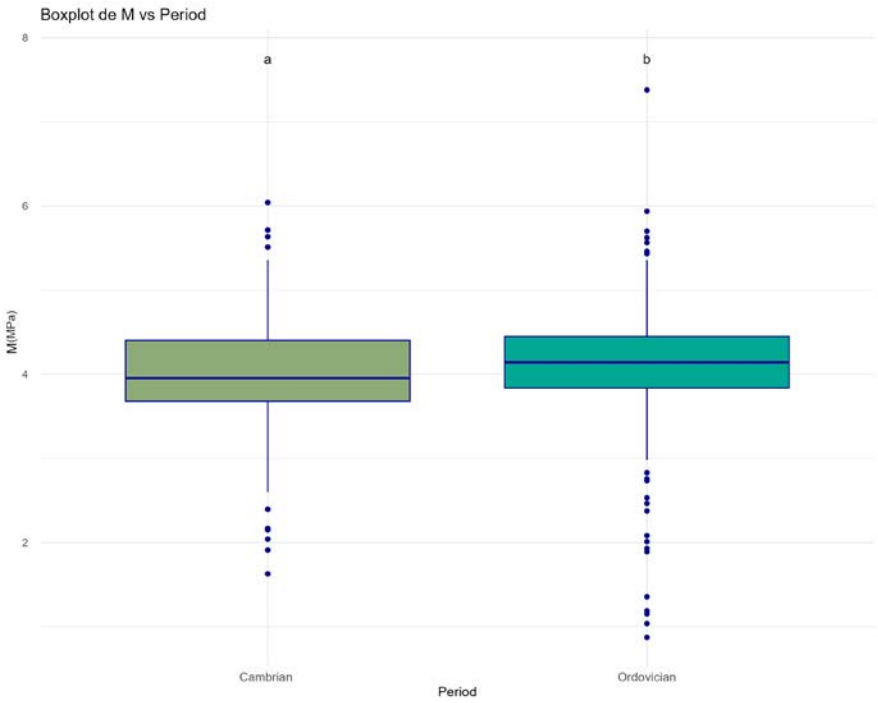

Figure 1. Von Mises Stress Median for each specimen cephalon grouped by the period. Different letters upon the boxplots indicate whether there are significant differences.

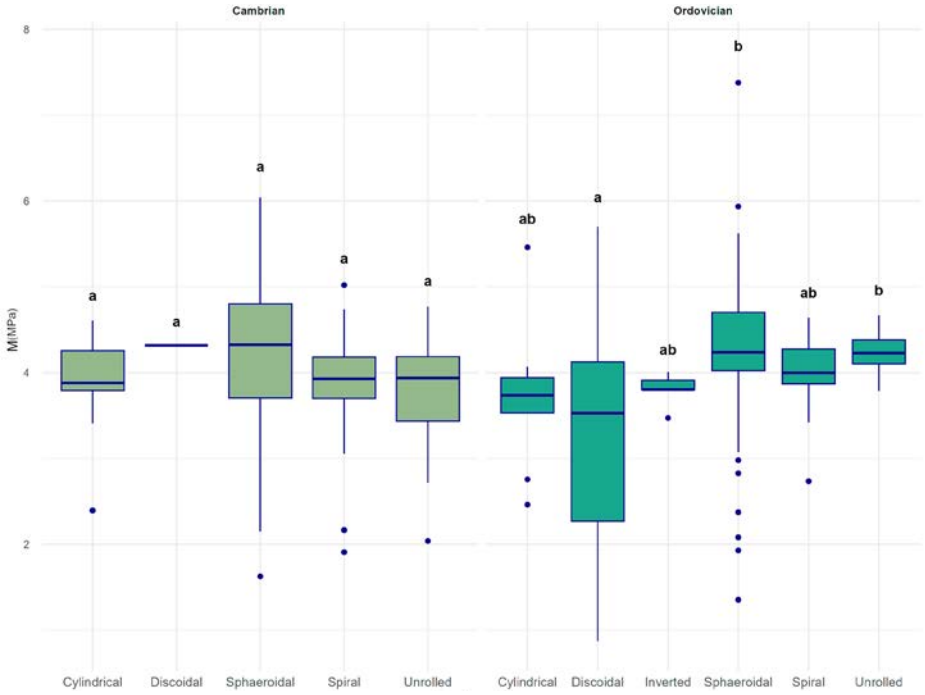

Figure 2. Von Mises Stress Median for each specimen cephalon grouped by the type of enrollment. Diferent letters upon the boxplots indicate wether there are significant differences.

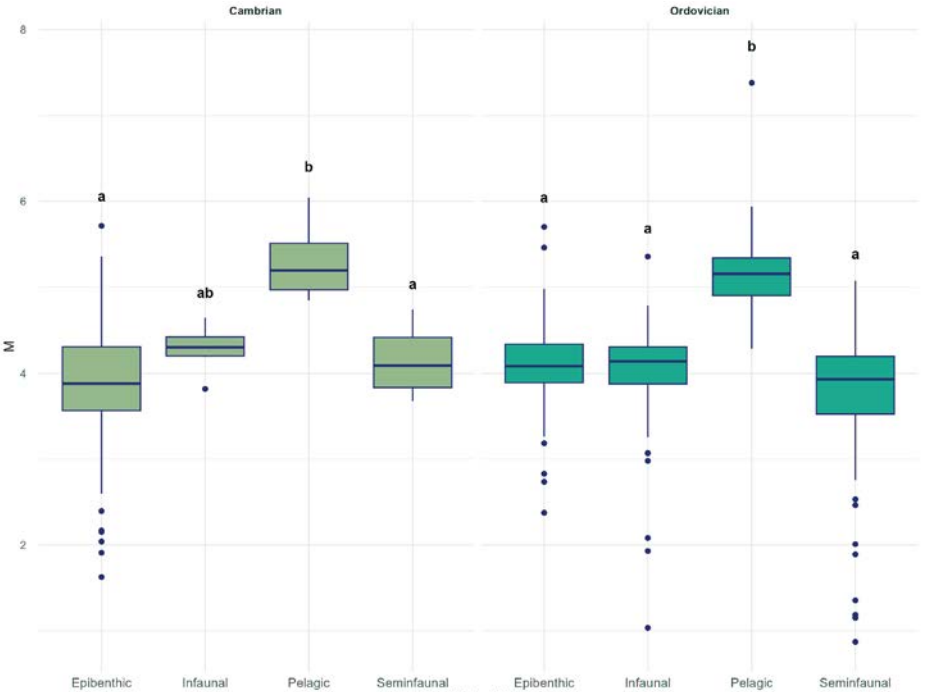

Figure 3. Von Mises Stress Median for each specimen cephalon grouped by the life habit. Diferent letters upon the boxplots indicate wheter there are significant differences.

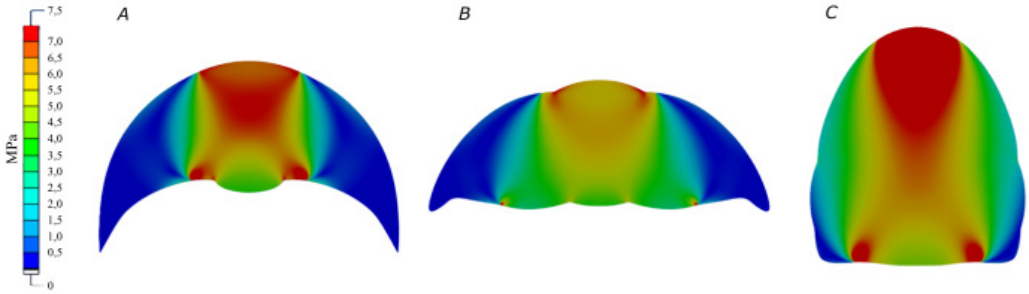

Figure 4. Von Mises Stress distribution across the cephalon. **A,** *Alistocari Harrisi,* a epibenthic taxon. M=3,34 MPa; **B,** *Edmunsonia typa*, an infaunal taxon. M= 3,43 MPa; **C,** *Degamella princeps,* a pelagic taxon. M= 5,56 MPa. Abbreviations: **M**, median.

tend to concentrate stress in specific regions, whereas infaunal and semiinfaunal forms display a more uniform distribution of stress across the body. Nevertheless, numerous exceptions to this trend were identified, indicating that further investigation and potential reassessment of the lifestyle of several taxa would be advisable.

No significant differences were observed in Von Mises stress values between Cambrian and Ordovician trilobites when comparing lifestyles, a finding that is particularly notable in pelagic forms. While epibenthic and infaunal trilobites exhibit relatively wide stress ranges, pelagic trilobites show a more constrained distribution. During the Cambrian, the primary pelagic group was Agnostida, whereas in the Ordovician, phylogenetically independent orders such as Asaphida and Proetida emerged. Despite taxonomic, morphologic and size differences, agnostids being considerably smaller than the latter groups, these trilobites converged on a similar stress values and distribution patterns, likely representing an optimal configuration for efficiency within the water column. Our results provide a new perspective on the evolution of pelagic trilobites and are consistent with the findings of Whalen and Briggs (2018), who show that the conquest of the water column by animals began in the Cambrian, thanks to adaptations that were already present during this period and that were maintained and diversified in the Ordovician.

Regarding trilobite enrollment behavior (Fig. 3), there are no statistically significant differences among the various enrollment types during the Cambrian. In the Ordovician, however, the disparity in median stress among trilobites increases. Discoidal and spheroidal enrollment are particularly noteworthy. Both exhibit a relatively broad distribution; however, the former shows a tendency toward lower stress levels and is characteristic of harpetid trilobites, whereas the latter displays a distribution encompassing both high and low stress levels and is employed by trilobites across multiple orders. It is possible that there is a relationship between the type of enrollment and the capacity to withstand mechanical stress; however, Finite Element Analyses using full three-dimensional models of trilobite bodies are required to obtain conclusive data.

Our results point out certain limitations of the method, since Cambrian and Ordovician trilobites exhibited high morphological disparity (Foote, 1993). FEA captures a broad range of variation, making the resulting patterns difficult to interpret. In addition, many trilobites possess long genal spines, as well as anterior glabellar spines or spines along the cephalic margin. This generates a biomechanical signal that can be challenging to interpret, although case-by-case analyses may be highly useful for understanding the evolution of particular groups.

Acknowledgements: This work is a contribution to projects PID2021-125585NB-I00 and CNS2024-154147 of the Ministerio de Ciencia e Innovación de España. We also thank Stephen Pates for his review.

REFERENCES

Adrain, J. M., Edgecombe, G. D., Fortey, R. A., Hammer, Ø., Laurie, J. R., McCormick, T., Owen, A. W., Waisfeld, B. G., Webby, B. D., Westrop, S. R., & Zhang, Z. (2004). Trilobites. En B. D. Webby, F. Paris, M. L. Droser, & I. G. Percival (Eds.), *The Great Ordovician Biodiversification Event* (pp. 231–254). Columbia University Press.

Alexander, R. M. (2005). Mechanics of animal movement. *Current Biology, 15*(16), R616–R619. doi: 10.1016/j.cub.2005.08.016

Ballell, A., & Ferrón, H. G. (2021). Biomechanical insights into the dentition of megatooth sharks (Lamniformes: Otodontidae). *Scientific Reports, 11*(1), 1232. doi: 10.1038/s41598-020-80323-z

Bicknell, R. D. C., Schmidt, M., Rahman, I. A., Edgecombe, G. D., Gutarra, S., Daley, A. C., Melzer, R. R., Wroe, S., & Paterson, J. R. (2023). Raptorial appendages of the Cambrian apex predator *Anomalocaris canadensis* are built for soft prey and speed. *Proceedings of the Royal Society B: Biological Sciences, 290*(2002), 20230638. doi: 10.1098/rspb.2023.0638

Briggs, D. E. G., Dalingwater, J. E., & Selden, P. A. (1991). Biomechanics of locomotion in fossil arthropods. En J. M. V. Rayner & R. J. Wootton (Eds.), *Biomechanics and Evolution* (pp. 37–57). Cambridge University Press.

Cuff, A. R., Demuth, O. E., Michel, K., Otero, A., Pintore, R., Polet, D. T., Wiseman, A. L. A., & Hutchinson, J. R. (2022). Walking—and running and jumping—with dinosaurs and their cousins, viewed through the lens of evolutionary biomechanics. *Integrative and Comparative Biology, 62*(5), 1281–1305. doi: 10.1093/icb/icac049

Esteve, J., Marcé-Nogué, J., Pérez-Peris, F., & Rayfield, E. J. (2021). Cephalic biomechanics underpins the evolutionary success of trilobites. *Palaeontology, 64*(4), 519–530. doi: 10.1111/pala.12541

Figueirido, B., Tucker, S., & Lautenschlager, S. (2025). Comparing cranial biomechanics between *Barbourofelis fricki* and *Smilodon fatalis*: Is there a universal killing-bite among saber-toothed predators? *The Anatomical Record, 308*(11), 2962–2975. doi: 10.1002/ar.25451

Fortey, R. A. (1985). Pelagic trilobites as an example of deducing the life habits of extinct arthropods. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 76*(2–3), 219–230. doi: 10.1017/S0263593300010452

Fortey, R. A., & Owens, R. M. (1990). Trilobites. En K. J. McNamara (Ed.), *Evolutionary Trends* (pp. 121–142). Belhaven Press.

Gómez-Rodríguez, I. D., López-Pachón, M., & Esteve, J. (2025). Biomechanical assessment and the fossil record suggest a sensory function in the anterior glabellar and genal spines in Ordovician raphiophorid trilobites. *Palaeogeography, Palaeoclimatology, Palaeoecology, 683*, 113331. doi: 10.1016/j.palaeo.2025.113331

Hughes, N. C. (2007). The evolution of trilobite body patterning. *Annual Review of Earth and Planetary Sciences, 35*(1), 401–434. doi: 10.1146/annurev.earth.35.031306.140258

Marcé-Nogué, J., de Esteban-Trivigno, S., Escrig Pérez, C., & Gil, L. (2016). Accounting for differences in element size and homogeneity when comparing finite element models: Armadillos as a case study. *Palaeontologia Electronica, 19*(3), 1–22.

Marcé-Nogué, J., DeMiguel, D., Fortuny, J., de Esteban-Trivigno, S., & Gil, L. (2013). Quasi-homothetic transformation for comparing the mechanical performance of planar models in biological research. *Palaeontologia Electronica, 16*(3), 1–15.

Whalen, C. D., & Briggs, D. E. G. (2018). The Palaeozoic colonization of the water column and the rise of global nekton. *Proceedings of the Royal Society B: Biological Sciences, 285*(1883), 20180883. doi: 10.1098/rspb.2018.0883

CARCAJOU FALLS, NORTHWESTERN CANADA: SEDIMENTOLOGY, TAPHONOMY AND PALEOECOLOGY OF A TRILOBITE REFUGE IN A HOSTILE EMBAYMENT DURING THE MIDDLE CAMBRIAN

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Keywords: brackish, trilobite, taphonomy.

INTRODUCTION

Lower and Middle Cambrian formations in the eastern Mackenzie Mountains of the Northwest Territories, Canada (Fig. 1A–1D), have yielded unique trilobite faunas (Handkamer *et al.*, 2022). On a regional scale, trilobite assemblages from Cambrian Stage 4 strata broadly reflect those found elsewhere in Laurentia, whereas overlying Wuliuan strata gradually become dominated by dolichometopids and zacanthoidids. Furthermore, collections from several outcrops (Handkamer *et al*., 2022) and those in subsurface cores (Fritz, 1969; Sommers *et al.,* 2020) reveal the existence

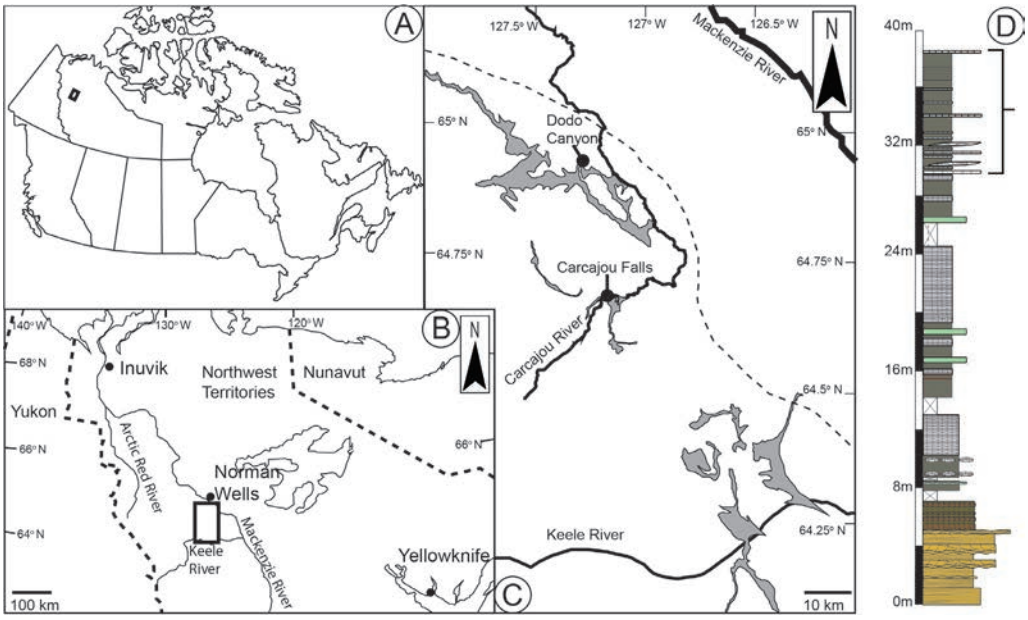

Figure 1. Locality of study area and measured section, in the eastern Mackenzie Mountains. **A,** National map; **B,** location in the Northwest Territories; **C,** location in the eastern Mackenzie Mountains outcrop belt. Outcrops of the Mount Clark, Mount Cap and Saline River formations are present in areas shaded in gray, Carcajou Falls (64.670639°N, 127.161682°W), Dodo Canyon (64.937525°N, 127.265209°W), dashed line roughly delineates the edge of the Mackenzie Arch which is onlapped by Cambrian strata; **D,** measured section of Mount Clark and Mount Cap formations at the section at Carcajou Falls. The lower 5.1 m of sandstone is of the Mount Clark Formation, and the upper 28.2 m of mudstone and limestone is of the Mount Cap Formation. The uppermost 8.7 m of the Mount Cap Formation contains the strata studied here, indicated by the bracket to the right of the stratigraphic column.

of different communities across the Wuliuan shoreline transect. Here, we document one site, Carcajou Falls, which yielded a plethora of fossils from shales and carbonates of the Mount Cap Formation, and explore how the sedimentology, taphonomic conditions and paleoecology may have influenced the development of this trilobite community.

REGIONAL GEOLOGY

During Cambrian Age 4 and the Wuliuan, sedimentary strata present in the northern extension of the Western Canada Sedimentary Basin (**WCSB**) are partly documented from the Sahtu Basin (MacNaughton *et al*., 2025). Deposition occurred in an equatorial, epicontinental embayment that was crisscrossed by a series of arches and grabens (Aitken *et al*., 1973; Aitken & Cook, 1974; Dixon & Stasiuk, 1998; Gabrielse *et al*., 1973; Herbers *et al*., 2016; Pyle, 2012; Sommers *et al*., 2020). The paleotectonics of the region limited connection from the open ocean, as well as produced local lithological and stratigraphic variability. Three formations comprise the bulk of the stratigraphic succession: in ascending order, the Mount Clark, Mount Cap and Saline River formations (Aitken *et al*., 1973; Aitken & Cook, 1974; Dixon & Stasiuk, 1998). The Cambrian Stage 4 to early Wuliuan Mount Clark Formation is composed of sandstone and siltstone and records the initial flooding of the Precambrian basement. It is conformably overlain by siliciclastic mudstone and micritic limestone of the Cambrian Stage 4 to middle Wuliuan Mount Cap Formation. The contact between both units represents a major flooding surface and is diachronous (Dixon & Stasiuk, 1998; Handkamer *et al*., 2022; MacLean, 2011; Sommers *et al*., 2020), indicating that flooding occurred following the initiation of rifting in the Sahtu Basin. The Mount Cap Formation is unconformably overlain by the dolomudstone and evaporite of the Saline River Formation, indicating that basin restriction followed.

The Mount Cap Formation at Carcajou Falls (Figs. 1D, 2A) was deposited in the Mackenzie Plain Depocentre (**MDP**), a relatively stable portion of the basin located between the Mackenzie Arch (**MA**) and the Mackenzie Trough (**MT**). The MA was a positive tectonic element that Cambrian strata onlapped and separated the Sahtu Basin from the open-ocean-facing Selwyn Basin. In contrast, the MT was a regional graben at the centre of the basin where the Mount Cap Formation is anomalously thick (Dixon & Stasiuk, 1998; MacLean, 2011; Sommers *et al*., 2020). Correlation indicates that Carcajou Falls was located in a shallower part of the MPD (Handkamer *et al.,* 2022), and nearer the paleoshoreline than other sections and wells. There, the formation is 28.2 m thick and composed of dark, silty mudstones and dolomitic limestones (Handkamer, 2020). The uppermost 8.7 m, which is composed of dark-grey, fossiliferous silty mudstone with interbedded lime mudstone and lenses of bioclastic grainstone, belongs to the upper part of the *Glossopleura walcotti* Zone (= *Glossopleura boccar* Zone of the southern Canadian Rocky Mountains). The fossils in this interval consist mostly of trilobites, dominantly the corynexochids *Sahtuia carcajouensis* and *Mackenzieaspis parallelispinosa*. Both exhibit novel morphologies for their respective families: a thorax with a relatively low number of segments and a pygidium with a relatively high number of segments (Fig. 2G, 2H). Handkamer and Pratt (2024) partially reconstructed the ontogeny of these species, demonstrating that their cranidial development and segment generation were not unusual. However, segment release was suppressed at a relatively early ontogenetic stage, which may have been due to independent but coincident evolution of heterochronic development (segment generation and release terminology following Hughes *et al*., 2021).

FACIES DESCRIPTION

Mudstone is fossiliferous throughout the section, and occasionally contains shell beds (Fig. 2B, 2D). In thin sections, primary layering is mostly disrupted by bioturbation (Fig. 2E); where preserved,

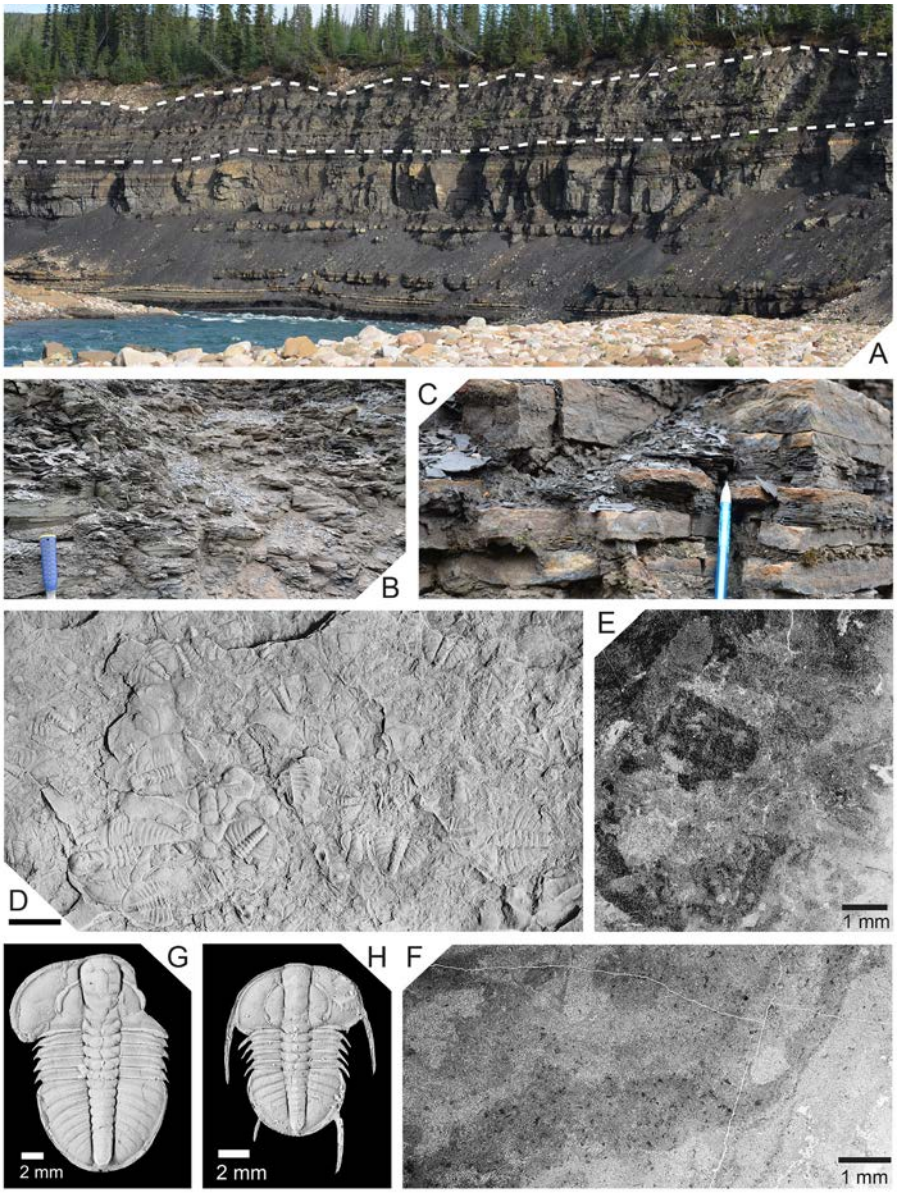

Figure 2. Outcrop, facies and trilobites from Carcajou Falls. **A,** Outcrop view at Carcajou Falls. Stratal thickness is 28.2 m. The contact with the Mount Clark Formation is just below the water level. Interval studied here is between the two dashed, white lines; **B,** example of silty mudstone facies in outcrop, in an interval that lacks carbonate interbeds; **C,** example of interbedded grainstone lenses and silty mudstone; **D,** bedding-plane view of a fossiliferous example of silty mudstone with concentrated trilobite sclerites, moults and a carcass. Scale bar = 10 mm; **E,** optical scan of thin section in bedding-plane view, showing burrow mottling, with examples of *Planolites, Teichichnus* and *Arenicolites*; **F,** thin section in bedding-plane view, showing less-bioturbated interval with some relict bedforms present, dark banding shows clay- and micrite-rich, fine-grained laminae and lighter colored, silt-rich, coarse-grained laminae. A few examples of burrows, possibly *Planolites*, are present; **G,** Holotype of *Sahtuia carcajouensis*; **H,** Holotype of *Mackenzieaspis parallelispinosa*.

it appears to be wavy and alternating between relatively coarse- and fine-grained laminae (Fig. 2F). Coarse-grained laminae are featureless and lack grading. They are composed mostly of quartz silt with minor bioclasts and a matrix which is dominantly clay and micrite. Most bioclasts cannot be discerned, but some are identifiable as fragments of trilobites and linguliformean brachiopods. Fine-grained laminae have a similar composition but contain proportionally more clay, micrite and bioclasts and less silt. Mineralogically, this silty mudstone averages 66% quartz, 9% illite, 5% chlorite, 8% micrite and 9% iron oxide (Kimmig & Pratt, 2016, table 3). Lime mudstone interbeds are thin to medium bedded, planer or wavy bedded, lack internal structures and are composed of micrite and microspar which is partially dolomitic and with minor siliciclastic silt and clay. Sporadic wackestone and floatstone beds have the same composition except that they have more trilobite bioclasts. Bioclastic grainstones are lenticular and wavy (Fig. 2C), composed of trilobite and linguliformean brachiopod bioclasts that are typically fractured or broken. Bioclasts have bladed calcite rinds. Grainstones contain minor micrite, usually preserved under bioclasts. The cement in pores between bladed calcite rinds is blocky spar.

In outcrop, trace fossils are not visible in siliciclastic mudstones, but are present in lime mudstone interbeds, BI=0–1, as simple, horizontal burrows. In thin sections of silty mudstone, trace fossils indicate the presence of vertical and horizontal bioturbation, with the latter being more prevalent (Fig. 2E, 2F). The most common ichnogenera are *Planolites* and *Teichichnus*, with sporadic *Skolithos* and *Arenicolites*. All ichnogenera are generally more common in fine-grained beds, and are infilled by sediment from coarse-grained beds. Trace-element proxies (U/Th, V/Sc, P, U, Ni and Cu enrichment, and Sr/Ba), screened for detrital influence first, indicate that conditions during deposition were well oxygenated, fluctuating between normal-marine and brackish salinities and with occasional high nutrient flux (Fig. 3A).

Characterization of the taphonomy of these beds follows the criteria set by Corrales-Garcia *et al.* (2020). Trilobites are the dominant elements of the fauna, although linguliformean brachiopods, probably acrotretids, are minor components. Disarticulated trilobite sclerites are the most common, but fully articulated and partly articulated exoskeletons and moults are present (n = 339; sclerites =195 (57%); moults = 114 (34%); carcasses = 30 (8%)) (Figs. 2D, 3B). Taxonomic composition is dominated by the paedomorphic species *S. carcajouensis* and *M. parallelispinosa* (84%), along with fewer *Glossopleura youngi* and *Eobathyuriscus mackenziensis* (14%), and *M. divergens, E. macqueeni* and an unknown ptychoparioid which are very rare (2%) (Fig. 3C). The majority of fossils represent holaspides, although some meraspid and protaspid material is present, with the former always disarticulated (Handkamer & Pratt, 2024, figs. 7, 10, 18). Most specimens are preserved dorsal-side up, although there is no preferred orientation to specimens one the bedding plane. No specimens were collected enrolled.

ENVIRONMENTAL INTERPRETATION

The composition and sedimentary structures indicate deposition likely took place under fluctuating conditions: coarse-grained laminae were deposited by relatively high-energy currents, whereas fine-grained laminae were deposited during periods of relative quiescence. Where preserved, wavy laminations suggests that the deposition of a coarse-grained lamina was preceded by partial erosion of the underlying layer, and the lack of grading indicates deposition was relatively rapid. Shell beds of trilobites are interpreted as having been concentrated through low sedimentation rates of clay and silt, indicating sediment bypass. The orientation of the disarticulated material suggest that currents were at times strong enough to flip sclerites into hydrodynamically stable positions, but not enough to orient elongate ones along bedding planes. Most flows were probably strong enough to winnow away most juvenile specimens. Waning conditions allowed more clay and pelagic lime mud to settle, and the higher proportion of bioclasts in fine-grained

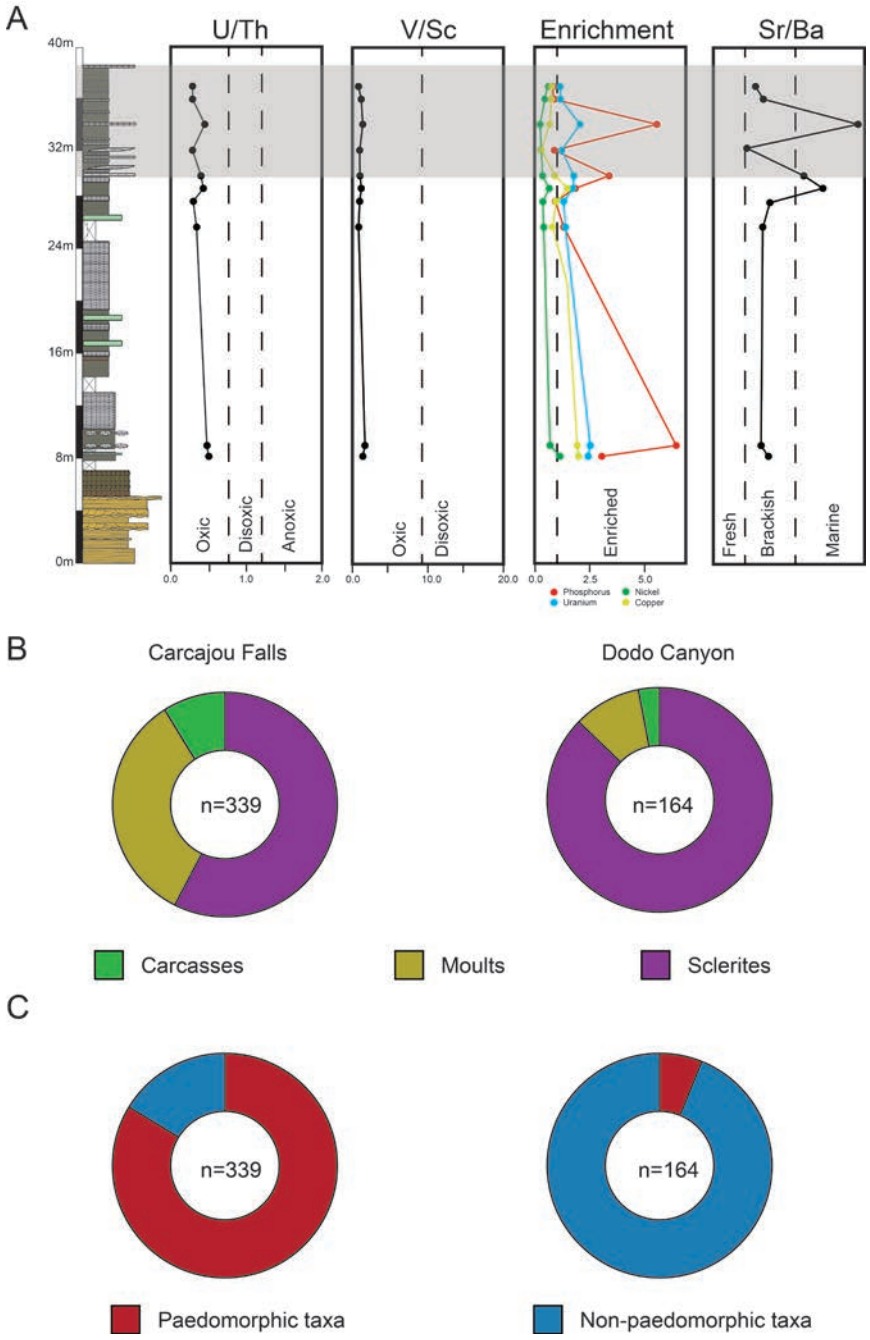

Figure 3. A, Trace-element concentrations from Carcajou Falls. All trace elements were screened for detrital control. U/Th and V/Sc cutoffs for oxic, disoxic and anoxic boundaries, and formula to calculate enrichment of elements, are from Tribovillard *et al.* (2006). Sr/Ba cutoffs of fresh, brackish and marine salinities from Wei and Algeo (2020); **B,** proportion of trilobite fossils as carcasses, moults and sclerites from Carcajou Falls and Dodo Canyon; **C,** comparative compositions of paedomorphic and non-paedomorphic taxa from Carcajou Falls and Dodo Canyon.

laminae could be due to the epibenthos preferring to colonize the sea floor following deposition of coarse laminae. The presence of trilobites and brachiopods throughout the interval indicates a hospitable environment continuously existed at the sediment-water interface, and the latter group of organisms indicates that there was at least enough suspended organic matter to support suspension feeding. Most quartz and some clay minerals are considered detrital, but the lack of correlation between aluminium and other trace elements indicates that at least some proportion of clay minerals are authigenic. Iron oxide is likely from the oxidation of pyrite, although whether pyrite was depositional or diagenetic is not clear. Lime mudstone and wackestone are interpreted as forming under quiescent conditions during low siliciclastic input. By contrast, grainstone lenses suggest that higher-energy deposition occurred, with bioclasts having probably undergone some degree of transportation causing breakage. With subsequent waning, coarse-grained bioclasts settled, but energy was still sufficient to winnow most lime mud, allowing for interparticle calcite cementation. This depositional process was likely intrinsically related to that which formed shell beds scattered throughout the silty mudstone.

The abundance of bioturbation is indicative of relatively oxic conditions in both the water column and in the sediment. The infilling of burrows usually by material present in coarse-grained laminae indicates that most bioturbation reflects quiescent conditions. The mixture of domichnia and fodinichnia substantiates the interpretation of a fluctuating setting, where more turbid conditions supported the filter-feeding ichnofauna by suspending nutrients in the water column, and more tranquil conditions allowed a deposit-feeding ichnofauna to mine organic material which had settled in the sediment. Trace-element ratios from the fossiliferous silty mudstone that reflect bottom-water oxygenation, and are unaffected by organic matter deposition, like U/Th and V/Sc, indicate that conditions were oxic (Tribovillard *et al*., 2006), in agreement with the abundance of the biota. Proxies that are affected by organic matter, such as the enrichment of P, Ni, Cu and U, indicate the occasional input of significant amounts into the sediment. On the other hand, the proxy for salinity, Sr/Ba, suggests that waters during deposition of the section were mostly brackish, but occasionally normal-marine (Wei & Algeo, 2020).

Given the wide range of evidence, these strata are regarded to have been deposited in a fluctuating subtidal setting, akin to the offshore setting of a shallow-marine environment. The most probable depositional mechanisms are the distal expression of storm currents or some type of bottom current, likely transporting siliciclastic sediment from elsewhere, plus lime mud produced in the water column. The absence of obvious grading in the beds suggest that turbidity currents or hyperpycnal flows were unlikely. The setting was conducive to the formation of a healthy epifaunal and infaunal benthos, probably from currents maintaining well-oxygenated conditions and nutrient input. The thinness of coarse-grained laminae and low proportion of carcasses signifies that sedimentation events did not smother the mobile benthos (Speyer & Brett, 1986, see Taphofacies 3B). As a consequence, although this facies could indicate gregarious behaviour in trilobites, such as moulting or mating, the evidence of the concentration of trilobite fossils through low sedimentation rate and probable time-averaging means that this cannot be confirmed.

REGIONAL CORRELATION

The sedimentological and paleoecological conditions during deposition of the upper part of the Mount Cap Formation at Carcajou Falls were in stark contrast to those interpreted for other outcrops in the eastern Mackenzie Mountains, and in the subsurface nearer the centre of the basin. At Dodo Canyon, located northeast of Carcajou Falls, the Mount Cap Formation exhibits different sedimentological and taphonomic characteristics. There, the biostratigraphically equivalent portion of the Mount Cap Formation is more argillaceous and organic rich, has proportionally fewer carbonate beds, few trace fossils and rare trilobites which are mostly non-paedomorphic species

preserved as disarticulated sclerites. Organic material is sourced from alginites and acritarchs (Stasiuk, 2005, fig. 1; Bouchard & Turner, 2017; Handkamer, 2020) (Fig. 3B, 3C). These strata were probably deposited under lower-energy conditions farther from the shoreline (Handkamer *et al*., 2022), allowing more suspended material to settle. The dominance of disarticulated sclerites there indicates consistent scavenging of carcasses and relatively high sedimentation rates (Speyer & Brett, 1986). The entraining currents which deposited these sediments were charged with fine-grained material, and waning of the depositional flow allowed proportionally more of it to settle relative to the facies at Carcajou Falls. Furthermore, the rarity of fossils suggests that conditions were less conducive to the development of the benthos.

Even farther eastward, beyond the deformation front, subsurface wells indicate that where the MPD terminates and the MT begins, biostratigraphically equivalent strata of the MT are composed almost entirely of mudstone, with rare carbonate beds (Pugh, 1993). MacLean (2011, p. 188, fig. 13) proposed that extensional tectonics in this part of the basin, which ultimately formed the MT, increased accommodation space and facilitated net-sediment transport and deposition there, suggesting that this was likely driven by the offshore expression of wave and tidal currents. However, storm-generated bottom flows cannot be ruled out as well. Ultimately, most material generated by these flows were transported into the trough.

A model is proposed here that describes how storm-, wind- and/or tide-generated bottom flows produce the lithologies and paleocommunities present at all three localities. As the flow initiates during the highest energy, in the most-proximal portion of the shoreline transect it causes erosion and sediment bypass of most entrained clay, possibly depositing coarse silt, some clay and lime mud, and concentrating trilobite bioclasts, typified by facies observed at Carcajou Falls. Downslope, the flow begins to lose energy, allowing proportionally more clay to settle, as observed in the facies at Dodo Canyon. Finally, transported sediment is able to reach the MT, likely depositing most of the entrained clay there.

The paedomorphic *S. carcajouensis* and *M. parallelispinosa*, common at Carcajou Falls, are rare in correlative strata from Dodo Canyon (Fig. 3C) (Bouchard & Turner, 2017, fig. 12E; Handkamer *et al*., 2022), and not one has been collected from any of the wells drilled in the MT. However, Dodo Canyon, and the cored well L-04 in the MT, have yielded other trilobites from the *Glossopleura walcotti* Zone (Fritz, 1969). This suggests that the two paedomorphic species preferred to inhabit shallower areas of the MPD and sedimentological and/or paleoecological conditions limited their colonization further offshore. However, other species that do not exhibit paedomorphic features, such as *E. mackenziensis*, tend to be more common farther offshore, and that there, paleoecological conditions were favourable for trilobite colonization. Thus, two synchronous paleocommunities are recognized the shoreline transect along the MPD. The link between environmental conditions and paedomorphosis is cryptic.

REFERENCES

Aitken, J. D., & Cook, D. G. (1974). *Carcajou Canyon map-area, District of Mackenzie, Northwest Territories* (Geological Survey of Canada Paper 74–13, 28 p.). Geological Survey of Canada.

Aitken, J. D., Macqueen, R. W., & Usher, J. L. (1973). *Reconnaissance studies of Proterozoic and Cambrian stratigraphy, lower Mackenzie River area (Operation Norman), District of Mackenzie* (Geological Survey of Canada Paper 73–9, 178 p.). Geological Survey of Canada.

Corrales-García, A., Esteve, J., Zhao, Y., & Yang, X. (2020). Synchronized moulting behaviour in trilobites from the Cambrian Series 2 of South China. *Scientific Reports, 10*, 14099. doi: 10.1038/s41598-020-70858-5

Dixon, J., & Stasiuk, L. D. (1998). Stratigraphy and hydrocarbon potential of Cambrian strata, Northern Interior Plains, Northwest Territories. *Bulletin of Canadian Petroleum Geology, 46*, 445–470.

Fritz, W. H. (1969). *Report on middle Cambrian fossils from Shell Keele I-4 Well, Northwest Territories* (Paleontological Report C32-1969-WHF, 3 p.). Shell Canada.

Gabrielse, H., Blusson, S. L., & Roddick, J. A. (1973). *Geology of Flat River, Glacier Lake, and Wrigley Lake map-areas, District of Mackenzie and Yukon Territory. Part 1: General geology, structural geology, and economic geology* (Geological Survey of Canada Memoir 366, 153 p.). Geological Survey of Canada.

Handkamer, N. M. (2020). *Measured section data, Mount Clark and Mount Cap formations (Cambrian), eastern Mackenzie Mountains, Northwest Territories* (Geological Survey of Canada Open File 8741, 54 p.). Geological Survey of Canada.

Handkamer, N. M., & Pratt, B. R. (2024). Quantified growth and possible heterochronic development of two corynexochid trilobites from the middle Cambrian (Miaolingian Series, Wuliuan Stage) Mount Cap Formation, eastern Mackenzie Mountains, northwestern Canada. *Journal of Paleontology, 98*(3), 504–536. doi: 10.1017/jpa.2023.86

Handkamer, N. M., Pratt, B. R., & MacNaughton, R. B. (2022). Biostratigraphy and paleoecology of the trilobite faunas from the Mount Clark and Mount Cap formations (early and middle Cambrian), eastern Mackenzie Mountains, northwestern Canada. *Journal of Paleontology, 96*(Memoir 89), 1–47. doi: 10.1017/jpa.2022.39

Herbers, D. S., MacNaughton, R. B., Timmer, E. R., & Gingras, M. K. (2016). Sedimentology and ichnology of an Early–Middle Cambrian storm-influenced barred shoreface succession, Colville Hills, Northwest Territories. *Bulletin of Canadian Petroleum Geology, 64*(4), 538–554. doi: 10.2113/gscpgbull.64.4.538

Hughes, N. C., Adrain, J. M., Holmes, J. D., Hong, P. S., Hopkins, M. J., Hou, J. B., Minelli, A., Park, T. S., Paterson, J. R., Peng, J., Webster, M., Zhang, X.-G., Zhang, X.-L., & Fusco, G. (2021). Articulated trilobite ontogeny: Suggestions for a methodological standard. *Journal of Paleontology, 95*(2), 298–304. doi: 10.1017/jpa.2020.88

Kimmig, J., & Pratt, B. R. (2016). Taphonomy of the middle Cambrian (Drumian) Ravens Throat River Lagerstätte, Rockslide Formation, Mackenzie Mountains, Northwest Territories, Canada. *Lethaia, 49*(2), 150–169. doi: 10.1111/let.12121

MacLean, B. C. (2011). Tectonic and stratigraphic evolution of the Cambrian basin of the northern Northwest Territories. *Bulletin of Canadian Petroleum Geology, 59*(2), 172–194. doi: 10.2113/gscpgbull.59.2.172

MacNaughton, R. B., Fallas, K. M., Turner, E. C., Morgan, C. A., Gingras, M. K., & Sommers, M. J. (2025). Sahtu Basin – A replacement name for the Cambrian (Series 2 and Miaolingian) depositional basin underlying the Northern Interior Plains of Canada. *Bulletin of Canadian Energy Geoscience, 72*, 77–82.

Pugh, D. C. (1993). *Subsurface geology of pre-Mesozoic strata, Great Bear River map area, District of Mackenzie* (Geological Survey of Canada Memoir 430, 137 p.). Geological Survey of Canada.

Pyle, L. J. (2012). Cambrian and Lower Ordovician Sauk megasequence of northwestern Canada, northern Rocky Mountains to the Beaufort Sea. En J. R. Derby, R. D. Fritz, S. A. Longacre, W. A. Morgan, & C. A. Sternbach (Eds.), *The Great American Carbonate Bank: The geology and economic resources of the Cambrian–Ordovician Sauk megasequence of Laurentia* (AAPG Memoir 98, pp. 675–723). American Association of Petroleum Geologists. doi: 10.1306/13331506M983502

Sommers, M. J., Gingras, M. K., MacNaughton, R. B., Fallas, K. M., & Morgan, C. A. (2020). Subsurface analysis and correlation of Mount Clark and lower Mount Cap formations (Cambrian), Northern Interior Plains, Northwest Territories. *Bulletin of Canadian Petroleum Geology, 68*(1), 1–29. doi: 10.2113/2020/573668

Speyer, S. E., & Brett, C. E. (1986). Trilobite taphonomy and Middle Devonian taphofacies. *PALAIOS, 1*(3), 312–327. doi: 10.2307/3514694

Stasiuk, L. D. (2005). *Reflected light microscopy and Rock Eval® pyrolysis of Cambrian Mount Cap Formation, Dodo Canyon, Northwest Territories* (Geological Survey of Canada Open File 4888, 7 p.). Geological Survey of Canada.

Tribovillard, N., Algeo, T. J., Lyons, T., & Riboulleau, A. (2006). Trace metals as paleoredox and paleoproductivity proxies: An update. *Chemical Geology, 232*(1–2), 12–32. doi: 10.1016/j.chemgeo.2006.02.012

Wei, W., & Algeo, T. J. (2020). Elemental proxies for paleosalinity analysis of ancient shales and mudrocks. *Geochimica et Cosmochimica Acta, 287*, 341–366. doi: 10.1016/j.gca.2020.08.004

RUSOPHYCUS ANTIATLASENSIS: EVIDENCE OF NEW TRILOBITE BEHAVIOUR FROM THE UPPER DEVONIAN OF THE EASTERN ANTI-ATLAS, MOROCCO

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Keywords: ichnology, trilobites, Anti-Atlas, Devonian.

BACKGROUND

The Moroccan Anti-Atlas is a large NE-SW-oriented anticlinorium that consists mainly of well-exposed basement (Precambrian) and cover (Cambrian to Carboniferous sedimentary successions). Its eastern part is considered as having the world's most complete sedimentary successions from the Precambrian to the Carboniferous (Wendt, 2021a, b), which are outcropping over a 1000 km belt along the western and northern margins of the Tindouf Basin (Fig. 1A–1B). This area also provides an excellent biostratigraphic illustration of the Devonian, exposed mostly in isolated E–W oriented synforms and antiforms consisting of siliciclastics and carbonates (Wendt *et al*., 1984; Baidder *et al*., 2016).

The specimens described herein were collected from the Aoufilal Formation between the villages of El Khraouia and Taouz, situated in the Tafilalt platform. The latter (Tafilalt pelagic ridge) is a palaeogeographic element, extending across the eastern Ougnat–Ouzina Axis and the Ougnat–Erfoud High (Wendt & Belka, 1991; Baidder *et al*., 2016; Lubeseder *et al*., 2010). Its biostratigraphy and palaeontology are well documented (Wendt *et al.,* 1984; Klug *et al*., 2018; Wendt, 2021a, b; Bel Haouz *et al.,* 2026a, b), consisting mainly of carbonatic sediments showing lateral variations (Wendt & Belka, 1991; Lubeseder *et al*., 2010). The succession is characterised by sedimentary stasis above the Frasnian-Famennian boundary. The early Famennian is marked by cephalopod-rich, nodular limestones. During the late Frasnian the succession records a shift from these cephalopod limestones into more massive, fossiliferous limestones (Kellwasser Limestone). Then, the sea level fall during the late Famennian led to clastic-dominated sedimentation. The moderately to highly diverse Famennian marine assemblages indicate normal marine salinity and occasionally well-oxygenated bottom conditions, as well as repeated anoxic pulses (Wendt *et al*., 1984; Klug *et al.,* 2018). The trilobite resting traces reported herein come from the Aoufilal Formation (late Famennian, Fig. 2). This succession consists of a 400 m thick sequence of clastic mudstones and sandstones (Grès d'Aoufilal in the Taouz region), characterised by cross stratification, wave ripple marks, and ferruginous crusts.

OBJECTIVES

The present paper documents and analyses more than 40 slabs bearing trilobite resting trace. It aims to assess the ichnotaxonomy of this material and to provide a comprehensive analysis of trilobite behaviours after the Kellwasser Event and during the Hangenberg Event.

METHODS

The analysed material has been collected from the Aoufilal Formation in the Tafilalt platform of the eastern Anti-Atlas, between 2018 and 2026. More than 40 specimens have been collected

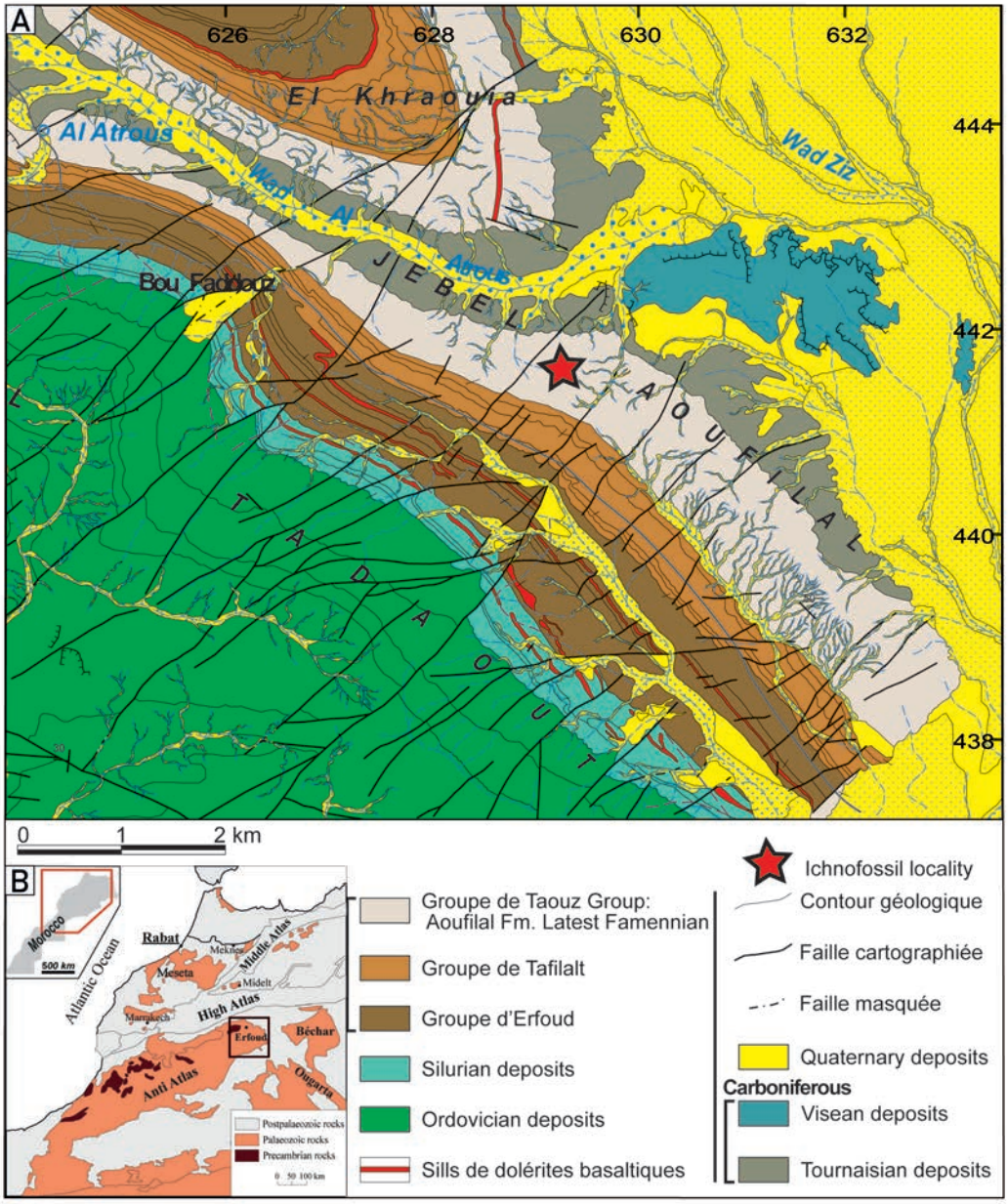

Figure 1. Geological setting of the study area. **A.** Simplified geological map of Taouz region with *R. antiatlasiensis* location (red star) (Najih *et al.*, 2019); **B.** geographic situation of the study area.

and housed at **LTM-ESEFB** collections (Life Traces Museun of Higher School of Education and Training of Berrechid). The material has been studied, analysed, and measured according to standards of description and identification of arthropod trackways in invertebrate ichnology (Trewin, 1995; Bromley, 1996). The best-preserved specimens were photographed under both natural and artificial light. Morphometric parameters were measured to characterise trace fossils morphology and patterns.

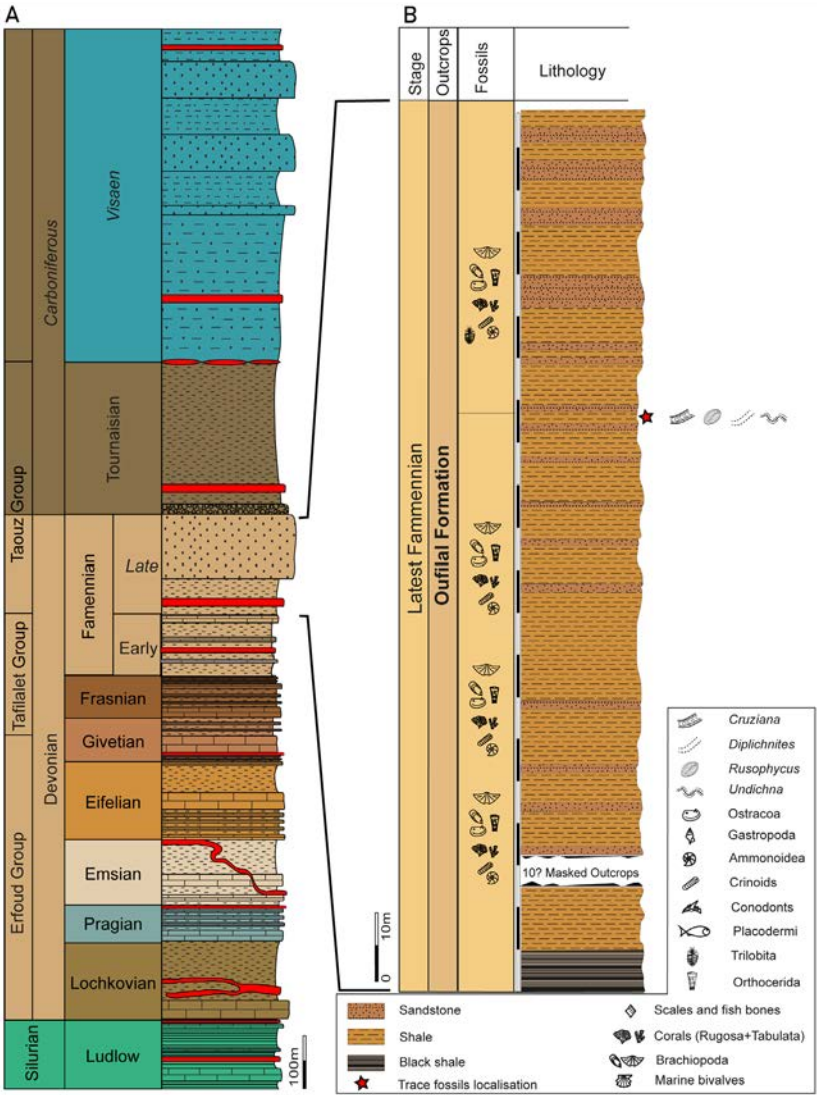

Figure 2. A. Stratigraphic subdivision of the Devonian deposits of the eastern Anti-Atlas of Morocco (after Álvaro *et al.*, 2014 and Najih *et al.*, 2019); **B.** detailed lithostratigraphic section of the ichnosites with stratigraphic position of *R. antiatlasensis* (Bel Haouz *et al.*, 2026b).

MAIN RESULTS

Systematic ichnology

***Rusophycus antiatlasensis* Bel Haouz *et al*. 2026b:** More than 40 slabs bearing short, bilobate trace fossils which exhibit an oblong to ovate shape. They are preserved as convex hyporeliefs (Fig. 3A–3C, 3F–3G, 3I, 3K–3M) and concave epireliefs (Fig. 3D–3E, 3H, 3J). The traces consist of two juxtaposed symmetric and parallel lobes (Fig. 3). These bilobate trace fossils occur as individuals (Fig. 3I–3M) or arranged in group of up to 11 serially repeated traces (Fig. 3A–3F), with a preferred orientation within the slab. Distances between burrows are not uniform; sometimes the burrows intersect or overlap locally (Fig. 3D–3F), or occur as traces continuous

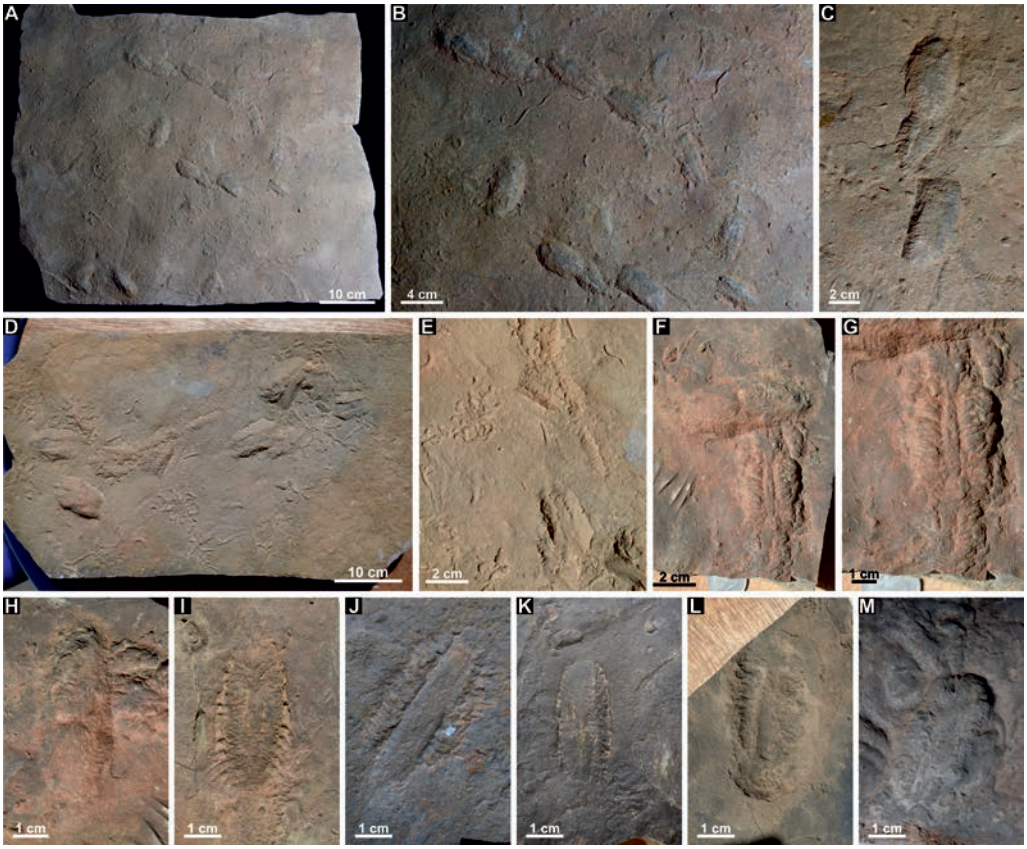

Figure 3. Extramorphological variations of *R. antiatlasensis* preserved as convex epirelief (**A–C, F–G, I, K–M**) and concave hyporief (**D–E, H, J**) in fine-grained sandstone from Aoufilal Formation of the Taouz region.

with *Diplichnites* (Fig. 3A). Lobes are characterised by closely spaced transverse striae, oriented at 70–90° to the median ridge and varying in depth toward the outer margins (Fig. 3G–3M). The burrows exhibit carapace imprints within moulds of scratches. The specimens described here constitute the only known record of this ichnotaxon.

Remarks and discussion

Rusophycus is regarded as a bilobate ovate, elliptical to coffee-bean-shaped trace fossil that is composed of two parallel lobes separated by a median furrow/ridge, occurring isolated or in group within transverse striae or rugae covering the lobes (Osgood, 1970; Häntzschel, 1975; Osgood & Drennen, 1975; Alpert, 1976). It has a widespread geographical distribution as a common Palaeozoic ichnotaxon, recorded from the early Cambrian to the Triassic, and exhibits great morphological variation. Most of *Rusophycus* ichnospecies are sorted into 3 groups (Gibb & Pemberton, 2017; Bel Haouz *et al*., 2026b); which are: (1) The '*biloba* group', characterised by an oval to elliptical outline and a bilobed excavation; the lobes are either entirely or partially separated by a shallow furrow covered in fine or delicate scratches and striations. These include *R. biloba, R. pudicum*, *R. cryptolithi*, *R. unilobus*, *R. latus*, *R. lavonensis, R. crebrus*, *R. magnus*, *R. versans*, and *R. exsilius*. (2) The '*carbonarius* group', characterised by small, oval- to heart-shaped

bilobed traces with two symmetric, posteriorly tapering lobes and an anterior V-shaped gap. This group includes *R. carbonarius*, *R. dispar*, and *R. subnotous*. (3) The '*carleyi* group', including ichnospecies with oval outline and convex hyporelief and two juxtaposed lobes separated by a median furrow, opening mesially at the anterior end with oblique and V-shaped ridges. This group is characterised by trilobite-specific features such as coxal traces, genal spines, pleural impressions, endopodite and exopodite traces. The main ichnospecies are *R. antiatlasensis, R. didymus*, *R. eutendorfensis*, *R. polonicus*, *R. morgati*, *R. carleyi*, *R. moyensis*.

R. antiatlasensis differs from all formerly cited *Rusophycus* ichnospecies by showing a median cylindrical to tube-like ridge/furrow. Other differences in comparison with the '*biloba* group' lie in the transverse to slightly oblique and closely spaced striae covering the lobes, which are mostly deeply to shallowly impressed toward the margins of the trace fossils. However, in comparison with the '*carbonarius* group', which have a heart-shaped outline, *R. antiatlasensis* are characterised by an oblong to elongate elliptical shape. Also, the shape of the ridge/furrow is different; for *R. antiatlasensis* is cylindrical to tube-like structure, while for other ichnospecies is even V- shaped (*R. carbonarius*) or oval (*R. carleyi*). Additionally, we noted that the main difference with the '*carleyi* group' is the absence of the mesial opening, which in that group reveals the impressions of various trilobite morphological features.

Rusophycus antiatlasensis has been described as a new ichnospecies based mainly on its morphological features—including a bilobate oblong to ovate outline with a distinct, cylindrical, shallow median ridge/furrow—and its specific morphometric parameters (Bel Haouz *et al*., 2026b). It has been assigned to the '*carleyi* group'.

Ethology and tracemaker

The Palaeozoic *Rusophycus* is commonly regarded as a resting trace fossil (cubichnion) produced by trilobites, revealing the complete outline of the producer's body (Osgood, 1975). The morphology is dominated by anatomically-controlled features, such as traces made by coxal and genal spines, alongside impressions of the cephalic and pygidial margins formed during burrowing and digging within the substrate (Brandt, 1995, Osgood, 1975). The bilobate shape is produced through the trilobite filter-feeding mechanism, forming a ventral feeding chamber that brushed the sediment towards the median line, where it was washed away by some current (Bel Haouz *et al*., 2026b). The establishment of a feeding chamber represents the main mechanism responsible for transverse striation and ornamentation along its length (Seilacher, 1985). Nevertheless, it can serve as well as a strategy for incubation or egg depository (Fenton & Fenton, 1937), to escaping predators, or as an attempt to remain hydrated (Dawson, 1864; Fenton & Fenton, 1937; Osgood, 1975). However, *R. antiatlasensis* is interpreted as an impression of the digestive tract. This tract typically comprises a tubular structure, beginning with a slit-like mouth that leads to a short, narrow oesophagus, which connects to a J-shaped crop and a long, narrow intestine extending to the posterior most part of the trunk. The transverse to slightly oblique striation in both lobes could have resulted from burrowing and digging activities by the legs; thus, while resting, it could have formed impressions of the exopodites or even the endopodites. The known trilobite groups from the same period characterised by an oblong dorsal shield outline are proetids and phacopids. These could be regarded as the most likely producers of *R. antiatlasensis* Bel Haouz *et al.,* 2026b. The arrangement of *R. antiatlasensis* in population assemblages, of up to 11 serially repeated traces, with an evident preferential orientation at the surface, is interpreted as a gregarious behaviour of trilobites. Thus, it may reflect a mechanical stimulation linked to motion and touch sensors, or seasonal mating behaviour linked to migration of adults to spawning grounds (Vannier *et al.,* 2019).

CONCLUSIONS

The Upper Devonian (Famennian) strata of the eastern Anti-Atlas (Morocco), yielded a new trilobite trace fossil associated with an ichnoassemblage of invertebrate and vertebrate traces. The material is described as *Rusophycus antiatlasensis* isp. nov. As the studied specimens occur as serially repeated traces, *R. antiatlasensis* is interpreted as evidence of gregarious behaviour of trilobites, most probably related to adult migration for mating and spawning. Its cooccurrence with *Diplichnites* is regarded as representing a predation strategy through prey stalking, or alternatively, a means of hiding in the sediment from predators, such as fishes (documented by abundant *Undichna*).

REFERENCES

Álvaro, J. J., Benziane, F., Thomas, R., Walsh, G. J., & Yazidi, A. (2014). Neoproterozoic–Cambrian stratigraphic framework of the Anti-Atlas and Ouzellagh promontory (High Atlas), Morocco. *Journal of African Earth Sciences*, *98*, 19–33.

Alpert, S. P. (1976). *Planolites* and *Skolithos* from the upper Precambrian–Lower Cambrian White-Inyo Mountains, California. *Journal of Paleontology, 49*, 508–521.

Baidder, L., Michard, A., Soulaimani, A., Fekkak, A., Eddebbi, A., Rjimati, E.-C., & Raddi, Y. (2016). Fold interference pattern in thick-skinned tectonics; a case study from the external Variscan belt of eastern Anti-Atlas, Morocco. *Journal of African Earth Sciences, 119*, 204–225.

Bel Haouz, W., Lagnaoui, A., Klug, C., Baidder, L., & Maanan, M. (2026a) Middle Devonian ichnofossils from Hamar Laghdad (eastern Anti-Atlas, Morocco). *Swiss Journal of Palaeontology*, *145*, 403–431. doi: 10.3897/sjp.145.188799

Bel Haouz, W., Lagnaoui, A., Klug, C., Baidder, L., & Maanan, M. (2026b). An exceptional diverse trilobite ichnofauna from the uppermost Devonian of Anti-Atlas, Morocco. *Acta Palaeontologica Polonica, 71*. doi: 10.4202/app.01312.2025 (in press)

Brandt, D. S., Meyer, D. L., & Lask, P. B. (1995). *Isotelus* (Trilobita) “hunting burrow” from Upper Ordovician strata, Ohio. *Journal of Palaeontology*, *69*(6), 1079–1083.

Bromley, R. G. (1996) Trace Fossils: Biology, Taphonomy and Applications, 2nd edition. Chapman and Hall, London, 361 pp.

Dawson, J. W. (1864). On the fossils of the genus *Rusophycus*. *Canadian Naturalist and Geologist*.

Fenton, C. L., & Fenton, M. A. (1937). Trilobite “nests” and feeding burrows. *The American Midland Naturalist, 18*, 446–451.

Gibb, S., & Pemberton, S. G. (2017). *Rusophycus* by any other name is still *Rusophycus carleyi*. Ichnos, 24(1), 19–26. doi: 10.1080/10420940.2016.1257486

Häntzschel, W. (1975). Trace fossils and problematica. *In:* R. C. Moore, (Ed.), *Treatise on Invertebrate Palaeontology, Part W*. Geological Society of America, New York and University of Kansas Press, Lawrence, 269 pp.

Klug, C., Samankassou, E., Pohle, A., De Baets, K., Franchi, F., & Korn, D. (2018). Oases of biodiversity: Early Devonian palaeoecology at Hamar Laghdad, Morocco. *In:* C. Klug, and D. Korn, (eds.), *Palaeontology of the Devonian of Hamar Laghdad (Tafilalt, Morocco)*. Special volume honouring Jobst Wendt. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 290*(1), 9–48. doi: 10.1127/njgpa/2018/0772

Lubeseder, S., Rath, J., Rücklin, M., & Messbacher, R. (2010). Controls on Devonian hemipelagic limestone deposition analysed on cephalopod ridge to slope sections, Eastern Anti-Atlas, Morocco. *Facies, 56*:295–315.

Najih, A., Montero, P., Verati, C., Chabou, M.C., Fekkak, A., Baidder, L., Ezzouhairi, H., Bea, F., & Michard, A. (2019). Initial Pangean rifting north of the West African Craton: Insights from late Permian U-Pb and 40Ar/39Ar dating of alkaline magmatism from the Eastern Anti-Atlas (Morocco). *Journal of Geodynamics, 132*, 101670. doi: 10.1016/j.jog.2019.101670

Osgood, R. G., Jr. (1970). Trace fossils of the Cincinnati area. *Palaeontographica Americana, 41*, 281–444.

Osgood, R. G., Jr. (1975). The history of invertebrate ichnology. *In:* R. W. Frey, (Ed.), *The Study of Trace Fossils: A Synthesis of Principles, Problems, and Procedures in Ichnology.* Berlin, Heidelberg: Springer Berlin Heidelberg, 3-12.

Osgood, R. G., Jr. ,& Drennen, W. T. III. (1975). Trilobite trace fossils from the Clinton Group (Silurian) of east-central New York State. *Bulletins of American Palaeontology*, *67*, 299–349.

Seilacher, A. (1985). Trilobite palaeobiology and substrate relationships: *Transactions of the Royal Society of Edinburgh, 76*(2-3), 231–237.

Trewin, N. H. (1995). A draft system for the identification and description of arthropod trackways. *Palaeontology, 37*(4), 811 – 823.

Vannier, J., Vidal, M., Marchant, R., El Hariri, K., Kouraiss, K., Pittet, B., El Albani, A., Mazurier, A., & Martin, E. (2019). Collective behaviour in 480-million-year-old trilobite arthropods from Morocco. *Scientific Reports, 9*(14941). doi: 10.1038/s41598-019-51012-3

Wendt, J. (2021a). Middle and Late Devonian paleogeography of the eastern Anti-Atlas (Morocco). *International Journal of Earth Sciences, 110*, 1531–1544.

Wendt, J. (2021b). Middle and Late Devonian sea-level changes and synsedimentary tectonics in the eastern Anti-Atlas (Morocco). *Journal of African Earth Sciences, 182*, 104247.

Wendt, J., Aigner, T., & Neugebauer, J. (1984). Cephalopod limestone deposition on a shallow pelagic ridge: the Tafilalt Platform (Upper Devonian, eastern Anti-Atlas, Morocco). *Sedimentology*, *31*, 601–625.

Wendt, J., & Belka, Z. (1991). Age and depositional environment of Upper Devonian (early Frasnian to early Famennian) black shales and limestones (Kellwasser facies) in the eastern Anti-Atlas, Morocco. *Facies, 25*, 51–90.

REASSESSING *DEANASPIS* (TRINUCLEIDAE, UPPER ORDOVICIAN) VARIABILITY IN THE IBERO-ARMORICAN DOMAIN: RANDOM VARIATION OR ECOLOGICAL SIGNAL?

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Keywords: Portugal, Trilobite, Morphological variation, Palaeoecology.

The taxonomy of Upper Ordovician trinucleid trilobites, particularly at the species level, has undergone substantial revision in recent decades, largely driven by the recognition of significant intraspecific variability, especially in the morphology of fringe fossulae (Hughes *et al*., 1975). In the high latitude peri-Gondwanan realm, Shaw (1995) had already synonymized several trinucleid species based on material from the Czech Republic. More recently, the unpublished work of Bowdler-Hicks (2002) on the family Marrolithinae has improved our understanding of the evolution and phylogeny of this group, allowing the identification of more robust diagnostic characters and leading to the synonymization of species previously defined on features now considered to reflect intraspecific variability and/or taphonomic artefacts.

In the Ibero-Armorican domain, Upper Ordovician trinucleids have been known for more than 150 years (*e.g.*, Ribeiro, 1853; Rouault, 1847; Verneuil & Barrande, 1855), and their taxonomy has stabilized in recent decades around four species, here supported: *Marrolithus bureaui* (Oehlert, 1895) [according to Bowdler-Hicks, 2002, a junior synonym of *Marrolithus favus favus* (Salter, 1847)], *Deanaspis grenieri* (Bergeron, 1894), *Deanaspis seunesi* (Kerforne, 1900), and *Onnia? malladai* (Oehlert, 1895). This work focuses on two of these marrolithines: *D. seunesi* and *D. grenieri*, species that characterize the Berounian (ca. Sandbian-lower Katian) of the Ibero-Armorica. Although Bowdler-Hicks (2002) proposed that specimens assigned to *Deanaspis pongerardi* (Rouault, 1847), *D. grenieri*, *D. seunesi*, and *O.? malladai* are all conspecific and should be grouped under *D. pongerardi*, here only the synonymy between the latter and *D. seunesi* is supported. *Deanaspis pongerardi* was originally defined from material of the Riadan Formation (Berounian of France) and distinguished by the bifurcation of the genal spines. This character is a taphonomic artefact (see Lebrun, 1994) and, in fact, *D. seunesi* represents a junior synonym of *D. pongerardi*. Nevertheless, and as previously defended by Pereira *et al.* (2018), given the disuse of the epithet *pongerardi*, the name *Deanaspis seunesi* is retained as a *nomen protectum* for reasons of taxonomic stability.

The distinction between *D. grenieri* and *D. seunesi* has long been problematic. *Deanaspis grenieri* was originally defined by Bergeron (1894) based on the shape of the glabella and fringe, as well as the presence of only two arcs in front of glabella. Bergeron (1894, p. 46) stated that "*aucun échantillon ne porte de pointe sur l'anneau occipital*", but this absence is now interpreted as resulting from the limited number of specimens and their poor preservation. Subsequent studies of trinucleids from Ecalgrain (*e.g.*, Coates, 1967; Lebrun, 1994) demonstrate that specimens from the type locality consistently possess three medial arcs and, importantly, an occipital spine. Likewise, all *Deanaspis* material from the Cotentin Peninsula is characterized by the presence of an occipital spine (Coates, 1967; Pillet & Robardet, 1968, 1969, 1970) and is considered conspecific with the type material of *D. grenieri*.

In contrast, *D. seunesi* (Kerforne, 1900) was defined based on material from several French localities (Raguenez, Morgat, Île de L'Aber, Camaret, Riadan, and Ille-et-Vilaine), including specimens both

with and without an occipital spine. Kerforne (1900, p. 789) noted that "*Le bourrelet occipital porte une pointe relevée assez forte*", but the illustrated material (Kerforne, 1900, est. XIII, figs. 7–13) and most of the specimens discussed originate from Raguenez and Ille-et-Vilaine, where *Deanaspis* specimens lack an occipital spine. Moreover, Kerforne (1900, pp. 383–384) explicitly stated "*Dans les schistes de Raguenez* (…) *j'ai trouvé un* Trinucleus (…)" and "*J'en fais une nouvelle espèce: le* Trinucleus Seunesi", indicating that the Raguenez material should be regarded as the type. Although no holotype or type locality was formally designated, it is therefore clear that comparisons must be based on this material, which is consistently spineless.

The only difference originally proposed between *D. seunesi* and *D. grenieri* was the more inflated glabella of the former, a feature now interpreted as taphonomic, leading Coates (1967) to consider *D. seunesi* invalid. However, the absence of an occipital spine in the Raguenez material provides a consistent morphological distinction between the two forms. At the beginning of the 1990s, Pillet (1990) was the first to suggest that the presence or absence of an occipital spine (a character that J.-L. Henry, in Hughes *et al.*, 1975, admitted not fully understanding) could distinguish two distinct taxa (which he considered subspecies): "*D. grenieri grenieri*", including specimens with an occipital spine, and "*D. grenieri seunesi*", referring to the material from Raguenez lacking an occipital spine. The presence/absence of an occipital spine to distinguish two taxa was also followed by Lebrun (1994). However, Lebrun introduced confusion which, due to the wide dissemination of his work in France (see also Lebrun, 2002), subsequently led to an inversed use of the epithets *grenieri* and *seunesi* (*e.g.*, Crônier *et al.*, 2008; Vidal *et al.*, 2011). But the study was very useful in drawing attention to the interesting distribution of the two morphotypes (with and without an occipital spine) in France, which does not appear to be random (see Lebrun, 1994, fig. 11).

To clarify, *D. grenieri* is characterized by the presence of an occipital spine and has as its type material the *Deanaspis* specimens from the Sangsurière Formation of the Ecalgrain region (Cotentin; these levels are referred to in older literature as the "Vauville" Formation), whereas *D. seunesi* is characterized by the absence of an occipital spine and has as its type material the *Deanaspis* specimens from the Kermeur Formation at Raguenez beach. In other localities of the Crozon Peninsula (*e.g.,* Veryac'h beach), also within the Kermeur Formation, specimens bearing occipital spines have been documented and should therefore be assigned to *D. grenieri* (*e.g.,* Vidal *et al*., 2011).

The Portuguese material further supports this distinction. The genus *Deanaspis* is present in several Berounian formations (Louredo, Cabeço do Peão, and Chão do Amieiral) across multiple regions (Buçaco, Dornes-Amêndoa-Mação, Vila Velha de Ródão, Penha Garcia, and Moncorvo). Specimens from Buçaco, Dornes, Vila Velha de Ródão, Penha Garcia, and Moncorvo consistently lack an occipital spine and are assignable to *D. seunesi*. In contrast, specimens bearing an occipital spine occur in the Queixopêrra Member (Cabeço do Peão Formation, Amêndoa/Mação), where both morphotypes are present. Notably, co-occurrence is restricted to a single outcrop and is strongly dominated by spineless forms, and the exclusive occurrence of the spiny form (*D. grenieri*) is also restricted to a single locality, within a sector considered parautochthonous (Alcaravela), which is interpreted as having had slightly different bathymetric conditions, possibly more distal or more protected (Pereira, 2017).

This distribution is particularly relevant when considering the palaeoecological significance of the occipital spine. The observed pattern is characterized by segregation and only rare overlap (one single locality in Portugal) of the two morphotypes. The rarity of co-occurrence and the apparent segregation of morphotypes across localities and stratigraphic levels both in France and in Portugal indicate that the presence or absence of this structure is not random. Instead, it likely reflects a biologically meaningful character, potentially linked to ecological differentiation.

The hypothesis that the occipital spine represents an environmentally controlled morphotype must therefore be considered.

Accordingly, the presence or absence of an occipital spine in marrolithine trilobites is here regarded as a diagnostic character at the species level, despite known exceptions [e.g., *Hammannaspis nomen nudum ornata* (Sternberg, 1833) in Bowdler-Hicks, 2002]. The Portuguese material, together with the distribution of morphotypes in France, supports the interpretation that *D. grenieri* (with occipital spine) and *D. seunesi* (without occipital spine) represent distinct species rather than environmentally induced variants of a single taxon. Although the precise functional role of the occipital spine remains uncertain, its consistent association with particular populations and its structured distribution suggest that it had ecological relevance and was subject to selective pressures, rather than representing a neutral or incidental feature.

Acknowledgments: This study was supported by Fundação para a Ciência e a Tecnologia, I.P. (Portugal) in the frame of UID/00073/2025, UID/PRR/00073/2025 and UID/PRR2/00073/2025 projects of the R&D unit of Geosciences Center (University of Coimbra, Portugal). This is a contribution to IGCP project 735.

REFERENCES

Arnaud, A., & Pillet, J. (1971). Sur l'existence de caradocien à trilobites dans le synclinal de Saint-Julien-de-Vouvantes-Angers (sud-est du Massif armoricain). *Mémoires du Bureau de Recherches Géologiques et Minières, 73*, 151–161.

Bergeron, M. J. (1894). Description de quelques trilobites de l'Ordovicien d'Ecalgrain. *Bulletin de la Société Linnéenne de Normandie, 15*, 42–47.

Bowdler-Hicks, A. (2002). *The taxonomy and phylogeny of the trinucleid trilobites (Marrolithinae)* (Unpublished PhD thesis). University of Glasgow.

Coates, A. (1967). Stratigraphie et paléontologie des synclinaux de Siouville et de Jobourg dans le Cap de la Hague (Cotentin, Normandie). *Bulletin de la Société Linnéenne de Normandie, 10*(7), 77–103.

Crônier, C., & Delabroye, A. (2008). Ontogeny of an Ordovician trinucleid (Trilobita) from Armorica, France: A morphometric approach. *Journal of Paleontology, 82*(4), 800–810. doi: 10.1666/07-078.1

Henry, J.-L. (1980). *Trilobites ordoviciens du Massif Armoricain*. *Mémoire de la Société Géologique et Minéralogique de Bretagne, 22*, 1–250.

Hughes, C. P., Ingham, J. K., & Addison, R. (1975). The morphology, classification and evolution of the Trinucleidae (Trilobita). *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 272*, 537–604. doi: 10.1098/rstb.1975.0100

Kerforne, M. F. (1900). Description de trois nouveaux trilobites de l'Ordovicien de Bretagne. *Bulletin de la Société Géologique de France, 3*(28), 783–791.

Lebrun, P. (1994). Les Onnia ordoviciens (Trinucleidae, Trilobita) du Massif Armoricain. *Minéraux et Fossiles, 223*, 13–21.

Lebrun, P. (2002). *Trilobites de France. Tome 1. Généralités sur les trilobites, Massif armoricain (Bretagne, Normandie, Vendée). Minéraux & Fossiles, 14*, 1–132.

Mitchell, W. I. (1974). An outline of the stratigraphy and palaeontology of the Ordovician rocks of Central Portugal. *Geological Magazine, 111*, 385–396.

Pereira, S. (2017). *Trilobites do Ordovícico Superior da Zona Centro-Ibérica Portuguesa* [PhD dissertation]. Universidade de Lisboa.

Pereira, S., Gutiérrez-Marco, J. C., Colmenar, J., & Rábano, I. (2018). Trilobites del Ordovícico Superior del Macizo del Tremedal (Rama Castellana de la Cordillera Ibérica). *Geogaceta, 64*, 95–98.

Pillet, J. (1990). Les faunes trilobitiques de l'Ordovicien Supérieur en Anjou. *Mémoires de la Société d'Études Scientifiques d'Anjou, 11*, 1–23.

Pillet, J., & Robardet, M. (1968). Les schistes à *Trinucleus* de la Sangsurière (Manche). *Bulletin de la Société Linnéenne de Normandie, 9*, 66–78.

Pillet, J., & Robardet, M. (1969). Les schistes à *Cryptolithus grenieri* de Saint-Sauveur-le-Vicomte (Manche). *Bulletin de la Société Linnéenne de Normandie, 100*, 15–19.

Pillet, J., & Robardet, M. (1970). Les «schistes à *Trinucleus*» de la tranchée de chemin de fer entre Sottevast et Martinvast (Manche). *Bulletin de la Société Linnéenne de Normandie, 10*, 15–19.

Přibyl, A., & Vaněk, J. (1969). Trilobites of the family Trinucleidae Hawle & Corda, 1847, from the Ordovician of Bohemia. *Sborník Geologických Věd, Paleontologie, 11*, 85–137.

Rábano, I. (1984). Trilobites ordovícicos del Macizo Hespérico español: una visión bioestratigráfica. *Cuadernos de Geología Ibérica, 9*, 267–287.

Ribeiro, C. (1853). On the Carboniferous and Silurian formations of the neighbourhood of Bussaco in Portugal. *Quarterly Journal of the Geological Society of London, 9*, 135–161.

Robardet, M., Henry, J.-L., Nion, J., Paris, F., & Pillet, J. (1972). La Formation du Pont-de-Caen (Caradocien) dans les synclinaux de Domfront et de Sées (Normandie). *Annales de la Société Géologique du Nord, 92*(3), 117–137.

Rouault, M. (1847). Extrait du mémoire sur les trilobites du département d'Ille-et-Vilaine. *Bulletin de la Société Géologique de France, 2*(4), 309–328.

Shaw, F. C. (1995). Ordovician trinucleid trilobites of the Prague Basin, Czech Republic. *Journal of Paleontology, 69*, 1–23.

Verneuil, E. D., & Barrande, J. (1855–1856). Description des fossiles trouvés dans les terrains silurien et dévonien d'Almaden, d'une partie de la Sierra Morena et des montagnes de Tolède. *Bulletin de la Société Géologique de France, 2*(12), 964–1025.

Vidal, M., Loi, A., Dabard, M.-P., & Botquelen, A. (2011). A Palaeozoic open shelf benthic assemblage in a protected marine environment. *Palaeogeography, Palaeoclimatology, Palaeoecology, 306*(1–2), 27–40. doi: 10.1016/j.palaeo.2011.03.021

RAPHIOPHORID TRILOBITES FROM THE MIDDLE AND LATE ORDOVICIAN (LOWER DAPINGIAN TO LOWER SANDBIAN) OF THE PRECORDILLERA OF ARGENTINA, WITH FUNCTIONAL-MORPHOLOGICAL AND PHYLOGENETIC IMPLICATIONS

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Keywords: Raphiophoridae, phylogenetics, taxonomy, cladistic analysis, Argentina.

INTRODUCTION

Trilobites from the family Raphiophoridae Angelin, 1854 comprise a disparate clade that appeared during the Tremadocian and diversified until the Sandbian, reaching peak diversity in the Darriwilian and Sandbian (Adrain, 2013). They subsequently became less diverse during the Katian before going extinct in the early Silurian. Throughout that time period, raphiophorids are typically found in facies of offshore settings (Adrain, 2013; Fortey, 1975). Currently, this family is subdivided into two subfamilies, Raphiophorinae Angelin, 1854 and Endymioniinae Raymond, 1920. The former typically has a long, anteriorly protruding glabella with a spine or tubercle, lacking eyes or ocular structures, usually having long genal spines, and a relatively conservative trunk morphology. By contrast, the latter family always has a shorter glabella, possesses a tubercle but not a spine, occasionally possesses ocular structures, and shares the conservative trunk morphology.

Because of the peculiar morphologies of these two subfamilies, it was suggested that raphiophorids inhabited a unique niche in the ecosystem, where their spines may have functioned as sensory structures (Gómez-Rodríguez *et al*., 2025; Knell & Fortey, 2005; Vannier *et al*., 2019). By forming a queue, this would have enabled raphiophorines to migrate in groups despite their blindness. However, some species of raphiophorines and all species of endymioniines lack glabellar spines and could not have formed queues. Furthermore, new species documented here indicate that some had spines which may have been used in a sensory fashion but not functioned within a queue. Thus, raphiophorid paleoecology is probably more complex than was previously thought.

Niche complexity is further complicated by the poorly understood phylogeny of Raphiophoridae and other closely related groups. The presence of a globular protaspis, pre-occipital tubercle, and ventral media cephalic suture indicate that Raphiophoridae belongs to the order Asaphida. Bignon *et al.* (2020), in their phylogenetic hypothesis, proposed that this family was closely related to the clade Dionididae and together formed a sister group to Trinucleidae (Fig. 1A). These were in-turn closely related to the paraphyletic Alsataspididae, and the monophyletic family, Liostracinidae. However, Yang *et al.* (2022) later demonstrated that a species in Liostracinidae did not possess the three synapomorphies above that unite Trinucleida, calling into question the validity of the order and the topology of tree obtained by Bignon *et al*. (2020). Following this, Beech *et al*. (2024) examined the evolution of the 'harpiform brim' amongst harpetids and trinucleids, demonstrating convincingly that they evolved independently. Their tree produced a polyphyletic clade that included Raphiophoridae, Dionididae, Trinucleidae, and Alsataspididae.

Within this context, raphiophorid evolution and adaptation to their new niches in the Ordovician ecosystem remains unclear. We clarify these ambiguities by analyzing the phylogeny, diversity,

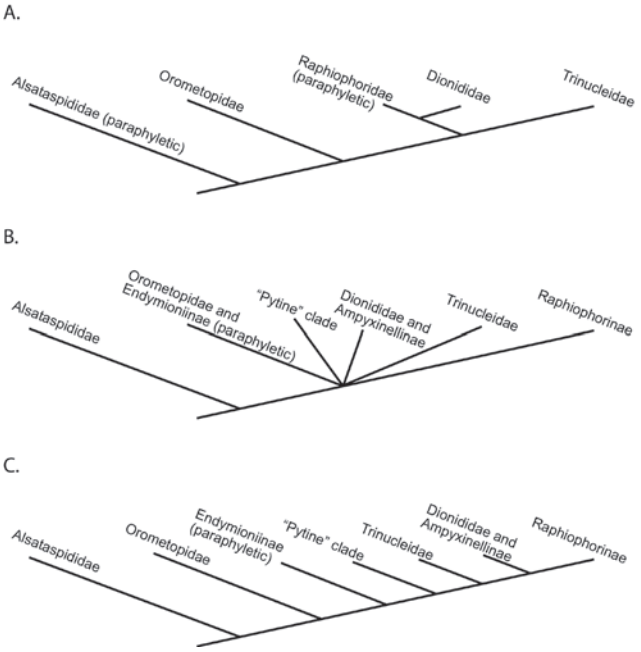

Figure 1. Phylogenetic hypotheses of Raphiophoridae and other closely related clades. **A,** Tree developed by Bignon et al. (2020); **B,** consensus tree of most-parsimonious trees of K = 7–10; **C,** consensus tree of most-parsimonious trees of K = 11–30. The third consensus tree (K = 3–6) has the same topology as that of K = 11–30, although the position of Trinucleidae and the "Pytine" clade are switched.

and disparity of this family, based on specimens from the Precordillera of western Argentina. This presentation will report the diversity of raphiophorids in the Precordillera, and the results of a phylogenetic analysis of the family, with implications for the systematics. The purpose of this study was to determine the relationship of Raphiophoridae relative to other major trilobite clades, to test for monophyly, and resolve internal evolutionary relationships.

METHODOLOGY

This study uses raphiophorid taxa from La Rioja, San Juan, and Mendoza provinces of Argentina as a basis for the analysis. Many specimens have been collected from the Precordillera, including silicified material from the San Juan, Gualcamayo, Las Chacritas, and Las Aguaditas formations (*e.g.*, Waisfeld *et al*., 2011). These formations span several similar depositional environments and range from the early Dapingian to early Sandbian.

A cladistic analysis was used to assess the phylogeny of Raphiophoridae. A dataset of 24 species of 20 genera of raphiophorines, 11 species of 10 genera of endymioniines, three species and genera of dionidids, 14 trinucleids, three orometopids, and six alsataspidids was constructed. A total of 128 characters were included, comprised of 27 continuous characters and 101 discrete characters (11 of which are considered ordered). The characters were selected to codify variation that exists in all parts of the mineralized exoskeleton, except the hypostome due to the lack of known material. Selected characters were those that vary within Raphiophoridae, or those which may discriminate raphiophorids from other clades. For example, the presence of a pitted brim is useful to discriminate Trinucleidae and Dionididae from Raphiophoridae, but the form and style of pitting, while useful to discriminate subfamilies within Trinucleidae (Hughes *et al*., 1975), does not suite any objective here. *Aphelaspis brachyphasis* Palmer, 1962 was chosen as the outgroup taxon, due to the breadth of documented material and its ptychoparid morphology, given the uncertainty of the higher-level taxonomy of raphiophorids and asaphids (Yang *et al*., 2022; Beech *et al.,* 2024). A parsimony analysis was performed (tree bisection and reconnection [TBR]) with 1000 random addition sequences, in the software TNT v. 1.6 (Goloboff *et al.,* 2008).

Implied character weighting was applied to account for the high degree of homoplasy inferred in Trinucleida, and multiple K values were explored to assess sensitivity to weighting parameters. Clade support was evaluated using bootstrap, jackknife, and symmetric resampling methods, each based on 100 replications.

Character evolution was examined by tracing its distribution on the tree for certain traits that are considered important to the development of the raphiophorin morphology. These include: the elevation and advancement of the glabella, the evolution of a glabellar tubercle or spine on the anterior glabellar lobe, the loss of ocular structures, the evolution of dorsal-marginal facial suture, and the development of a relatively large pygidium. This analysis was performed in Mesquite v. 4.02 (Maddison & Maddison, 2025).

REGIONAL GEOLOGY

Studied specimens were collected from the Precordillera, where Cambrian to Carboniferous strata are exposed in thin-skinned, thrust sheets. The lowermost unit that yielded raphiophorids is the San Juan Formation, a thick succession of fossiliferous limestones that were deposited on open carbonate platform that hosted a diverse skeletonized fauna (Keller *et al*., 1994; Cañas, 1999; Cañas & Carrera, 1993). Fossils were collected from nodular, fossiliferous wackestone and lime mudstone of the uppermost portion of San Juan Formation, interpreted as the most outboard region of the platform (Cañas, 1999). These strata are lower Dapingian (*Tripodus precolaevis* Zone, Dapingian slice 1, Mango & Albanesi, 2025).

The San Juan formation is directly overlain by the Gualcamayo, Los Azules, Las Chacritas, or Las Aguaditas formations, depending on the geographic position (Astini, 1994, 1998). In the north Precordillera, and in the central-east Precordillera, the San Juan Formation is overlain by the siliciclastic mudstone and minor lime mudstone of either the Gualcamayo or Los Azules formations (Astini, 1994; Ottone *et al*., 1999). In the central-west Precordillera, the formations overlying the San Juan Formation are either the lime mudstone and minor shale and limestone breccia of the Las Aguaditas Formation (Baldis *et al*., 1982; Keller *et al*., 1993), or the lime mudstone, wackestone, and minor grainstone of the Las Chacritas Formation (Astini, 1998). All four formations are interpreted as deposited in deep-water environments following flooding of the carbonate platform. Biostratigraphy demonstrates that this was diachronous, occurring first during the early Dapingian in the north and later during the early Darriwilian farther south (Albanesi & Barnes, 2000; Feltes *et al.,* 2019; Mango & Albanesi, 2005 Ortega *et al*., 2007; Serra *et al*., 2018). The Gualcamayo and Los Azules formations are interpreted as deposition in a setting that was beyond the carbonate platform and the most outboard, whereas the Las Aguaditas and Las Chacritas formations are interpreted as catch-up of the carbonate platform, with the former representing a deep-water setting and the latter representing remnant shallow-water facies.

PRELIMINARY RESULTS

Taxonomy

At least nine species of raphiophorids have been identified in the Precordillera, *Raphioampyx nunezi* and *Mendolaspis salagastensis* have been described before but five are new, with two new genera, and three others placed in open nomenclature. New species include *Ampyx* n. sp. 1, *Ampyx* n. sp. 2, *Ampyx* n. sp. 3, raphiophorin n. gen. and sp. 1, and raphiophorin n. gen. and sp. 2. Silicified material has revealed novel information about the form and ontogeny of the anterior glabellar spine or tubercle. Diversity is highest during the early Darriwilian of the Precordillera, whereas during the Sandbian, raphiophorid diversity decreases slightly. Their abundance drops significantly at this time, coinciding with an increase in abundance of trinucleids.

Cladistic Analysis

Preliminary analyses exploring different K values (3–30) under implied weighting recovered distinct sets of most-parsimonious trees; strict consensus trees were subsequently evaluated for three K-values ranges. All three consensus trees support the monophyly of Raphiophorinae and Ampyxinellinae subfamilies, and the Dionididae, Trinucleidae, and Alsataspididae families (Fig. 1B, 1C). Two of the consensus trees also support the monophyly of Orometopidae, whereas the remaining hypothesis suggests that orometopids are a paraphyletic family. All three trees indicate that Endymioniinae is paraphyletic. Due to the difference in topologies of the consensus trees, we favor the tree which has the least resolved relationships (Fig. 1B). In this, Alsataspididae is a monophyletic group and sister clade to the large polytomy that includes all other taxa. Within this polytomy, Raphiophorinae, Ampyxinellinae, Dionididae, and Trinucleidae are all monophyletic groups. Due to the high proportion of homoplasious characters, exploring different K values has a direct impact on tree topology; consequently, relationships among families and subfamilies may vary depending on the degree of down-weighting applied of homoplasy. As stated before, internal relationships and subclades within Alsataspididae, Orometopidae, and Trinucleidae should not be considered valid due to the characters used in the analysis (see methods).

DISCUSSION

Taxonomic implications

The development of the anterior spine and tubercle in raphiophorin n. gen. and sp. 1 and raphiophorin n. gen. and sp. 2 suggests that both structures can be considered homologous. In the former taxon, the tubercle develops from an anterior protrusion which is part of the spine and gradually separates from the spine during development. In the latter species, the tubercle develops from the gradual reduction of the spine. This suggests that the spine and tubercle, when present on the frontal lobe of the glabella, as it is in Raphiophorinae, can be considered homologous structures.

Species like *R. nunezi* and raphiophorin n. gen. and sp. 1 have spines that curve dorsally and, in the case of the latter, posteriorly. The shape of their spines could not have been used in a queuing behaviour (Vannier *et al.,* 2019) due to their upward curvature. However, the spines are covered by fine punctae and terrace lines, that likely served a sensory function (Gómez-Rodríguez *et al*., 2025). A dorsally directed mechanoreceptor could have detected movement in the water column, such as from lunging motion by pelagic predators (*e.g.,* nautiloids).

There does not appear to be any correlation between species which possess a spine or tubercle to water depth, and they nearly always co-occur in the same horizon. However, species which possess spines that strongly curve dorsally are typically found only in facies that indicate the shallowest parts of the offshore setting.

Phylogenetic implications

The results of the cladistic analysis performed here broadly agree with the topology obtained by Bignon *et al*. (2020) (Fig. 1A) and is in contrast to that proposed by Beech *et al*. (2024). We recover a paraphyletic Endymioniinae, and our analysis retrieved a monophyletic Raphiophoridae that only contains taxa of Raphiophorinae. Thus, we here recommend restricting the family to contain those of that subfamily. Some taxa, such as *Globampyx* or *Edmundsonia* have unresolved positions among the consensus trees, although given their primitive morphologies, it seems reasonable to speculate that they closely resemble a morphology of a last-common ancestor to all clades, or possibly due to pleiomorphy.

The consensus trees obtained in this analysis provide resolution to the discrepancy of the relationship of Raphiophoridae and Dionididae, the latter hypothesized as either a sister clade to the former, or a subclade within it (Bignon *et al.,* 2020). Our analysis retrieved a clade formed by Dionididae and Ampyxinellinae, which is sister clade to Raphiophoridae. We recommend that Ampyxinellinae be re-adopted and assigned as a subfamily of Dionididae, and the remaining dionidids be placed within a new subfamily, Dionidinae. Also, like Bignon *et al*. (2020), Dionididae is more closely related to Raphiophoridae than Trinucleidae in two of the three consensus trees, whereas the other tree does not resolve this relationship.

The recovery of *Pytine, Damghanampyx*, *Raymondella,* and *Ampyxina* as a clade is unexpected as the latter two genera are conventionally classified as raphiophorines. The ontogeny of both genera has shown that their anterior glabellar spines become tubercles during development (Whittington, 1959). This analysis did not consider ontogenetic characters, and future studies should consider codifying the development of the glabellar spine, and its eventual loss during ontogeny, to test whether that changes support for the phylogenetic position of this group.

By tracing the evolutionary history of the characters interpreted as important to raphiophorines, our analysis shows that relatively early in the history of derived forms of Trinucleida (clade containing Trinucleidae, Raphiophoridae, Dionididae), basal forms have a dorsally inflated glabella, dorsal-marginal facial suture, and glabellar tubercle, while ocular structures were lost. Following this, basal forms of raphiophorids evolved to possess a more-anteriorly advanced glabella, and a spine (derived from the tubercle present on the anterior lobe), a proportionally wider glabella, and significantly larger pygidium. More derived raphiophorids evolved glabellas that overhang the anterior border (advanced), and eventually bulbs.

REFERENCES

Adrain, J. M. (2013). A synopsis of Ordovician trilobite distribution and diversity, In Harper, D.A.T., & Servais, T. (eds.), *Early palaeozoic biogeography and palaeogeography, 38*, 29–336. Geological Society of London, Memoirs. doi: 10.1144/M38.20

Albanesi, G. L., & Barnes, C. R. (2000). Subspeciation within a punctuated equilibrium evolutionary event: Phylogenetic history of the Lower-Middle *Ordovician Paroistodus originalis—P. horridus complex* (Conodonta). *Journal of Paleontology, 74(*3), 492–502. doi: 10.1666/0022-3360(2000)074<0492:SWAPEE>2.0.CO;2

Angelin, N. P. (1854). Pars 1. Crustacea Formationis Transitionis [Part 1: Crustacean formation transition]. In Leizpig &Lund (Eds.) *Fascicle 2: Palæontologia Scandinavica*, 21–22.

Astini, R. A. (1994). Geología e interpretación de la Formación Gualcamayo en su localidad clásica (suroeste de Guandacol y cordón de Perico-Potrerillo), Precordillera septentrional. [Geology and interpretation of the Gualcamayo Formation in its classical outcrop (southwest of Guandacol and Perico-Porterillo range), southern Precordillera]. *Revista de la Asociación Geológica Argentina*, *49*(1–2), 55–70. doi: 10.1144/GSL.SP.1998.142.01.02

Astini, R. A. (1998). Stratigraphical evidence supporting the rifting, drifting and collision of the Laurentian Precordillera terrane of western Argentina. *Geological Society, London, Special Publications*, *142*(1), 11–33.

Baldis, B. A. J., MS, B., Bordonaro, O., & Vaca, A. (1982). Síntesis evolutiva de la Precordillera Argentina [Evolutive synthesis of the Argentinian Precordillera] *Congreso Latinoamericano de Geología* (Buenos Aires), *Actas 4*, 399–445.

Beech, J. D., Bottjer, D. J., & Smith, N. D. (2024). Parallel evolution of unusual 'harpiform'morphologies in distantly related trilobites. *Journal of Paleontology*, *98*(4), 732–743. doi: 10.1017/jpa.2024.47

Bignon, A., Waisfeld, B. G., Vaccari, N. E., & Chatterton, B. D. (2020). Reassessment of the order Trinucleida (Trilobita). *Journal of Systematic Palaeontology*, *18*(13), 1061–1077. doi: 10.1080/14772019.2019.1665480

Cañas, F.L. (1999). Facies and sequences of the Late Cambrian-Early Ordovician carbonates of the Argentine Precordillera: A stratigraphic comparison with Laurentian platforms, In Ramos, V.A. and Keppie J.D. (eds.), *Laurentia-Gondwana Connections before Pangaea* (Special Paper 336, pp. 43–62). Geological Society of America.

Cañas, F., & Carrera, M. (1993). Early Ordovician microbial-sponge-receptaculitid bioherms of the Precordillera, western Argentina. *Facies*, *29*(1), 169-178. doi: 10.1007/BF02536804

Feltes, N. A., Serra, F., Ortega, G., & Albanesi, G. L. (2019). Graptolite and conodont faunas of Upper Ordovician (Sandbian) successions of the Argentine Precordillera: Biostratigraphic implications. *Geological Journal*, *54*(4), 2301–2322. doi: 10.1002/gj.3298

Fortey, R.A. (1975). Early Ordovician trilobite communities. *Fossils and Strata, 4*, 339-360.

Goloboff, P. A., Farris, J. S., & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, *24*(5), 774–786. doi: 10.1111/j.1096-0031.2008.00217.x

Gómez-Rodríguez, I. D., López-Pachón, M., & Esteve, J. (2025). Biomechanical assessment and the fossil record suggest a sensory function in the anterior glabellar and genal spines in Ordovician raphiophorid trilobites. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 113331. doi: 10.1016/j.palaeo.2025.113331

Hughes, C. P., Ingham, J. K., & Addison, R. (1975). The morphology, classification and evolution of the Trinucleidae (Trilobita). *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *272*(920), 537–604. doi: 10.1098/rstb.1975.0100

Keller, M., Eberlein, S., & Lehnert, O. (1993). Sedimentology of Middle Ordovician carbonates in the Argentine Precordillera: evidence of regional relative sea-level changes. *Geologische Rundschau*, *82*(2), 362–377. doi: 10.1007/BF00192232

Knell, R. J., & Fortey, R. A. (2005). Trilobite spines and beetle horns: sexual selection in the Palaeozoic?. *Biology letters*, *1*(2), 196-199. doi: 110.1098/rsbl.2005.0304

Maddison, W. P., & Maddison, D. R. (2025). *Mesquite: a modular system for evolutionary analysis.* (Version. 4.02). https://www.mesquiteproject.org

Mango, M. J., & Albanesi, G. L. (2025). New conodont taxa and correlation of the upper San Juan Formation, Dapingian (Ordovician), at Potrerillos Creek, Argentine Precordillera. *Palaeoworld*, 200994. doi: 10.1016/j.palwor.2025.200994

Ortega, G., Albanesi, G. L., & Frigerio, S. E. (2007). Graptolite–conodont biostratigraphy and biofacies of the Middle Ordovician Cerro Viejo succession, San Juan Precordillera, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *245*(1–2), 245–263. doi: 10.1016/j.palaeo.2006.11.019

Ottone, E. G., Albanesi, G. L., Ortega, G., & Holfeltz, G. D. (1999). Palynomorphs, conodonts and associated graptolites from the Ordovician Los Azules Formation, central Precordillera, Argentina. *Micropaleontology*, *45*(3), 225–250. doi: 10.2307/1486110

Palmer, A. R. (1962). Glyptagnostus *and associated trilobites in the United States. Geological Survey Professional Paper 374-F*. Government Printing Office.

Raymond, P. E. (1920). Some new Ordovician trilobites. *Bulletin of the Museum of Comparative Zoology*, *64*, 273–296.

Serra, F., Feltes, N. A., Ortega, G., & Albanesi, G. L. (2018). Lower middle Darriwilian (Ordovician) graptolites and index conodonts from the Central Precordillera of San Juan Province, Argentina. *Geological Journal, 53*, 2161–2177. doi: 10.1002/gj.3034

Vannier, J., Vidal, M., Marchant, R., El Hariri, K., Kouraiss, K., Pittet, B., El Albani, A., Mazurier, A., & Martin, E. (2019). Collective behaviour in 480-million-year-old trilobite arthropods from Morocco. *Scientific reports*, *9*(1), 14941. doi: 10.1038/s41598-019-51012-3

Waisfeld, B. G., Vaccari, N. E., Edgecombe, G. D., & Chatterton, B. D. (2011). The upper ordovician trinucleid trilobite Bancroftolithus from the Precordillera of Argentina. *Journal of Paleontology*, *85*(6), 1160–1180. doi: 10.1666/11-023.1

Whittington, H.B., (1959). Silicified Middle Ordovician trilobites. *Bulletin of the Museum of Comparative Zoology, 121*, 370–496.

Yang, X., Peng, S., Babcock, L. E., Zhu, X., & Liu, Y. (2022). New species of Liostracina Monke, 1903 (Trilobita, Cambrian) from Yunnan, China: complete holaspid exoskeleton and implications for higher level classification. *Journal of Paleontology*, *96*(6), 1431–1446. doi: 10.1017/jpa.2022.56

Zhang, W. (1980). On the Miomera and Polymera (Trilobita). *Scientia Sinica*, *23*(2), 223–235.

ADVANCES IN BAYESIAN PHYLOGENETIC INFERENCE USING FOSSILS – WITH EXAMPLES FROM TRILOBITES

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Keywords: Bayesian inference, phylogenia, trilobites.

Phylogenetic inference – the construction of hypotheses examining how organisms are related to one another – provides a fundamental framework for evolutionary and paleobiological studies. There is mounting evidence that even a small number of fossils can 1) induce exploration of novel tree space (Mongiardino Koch & Parry, 2020), 2) decrease discrepancies in phylogenetic signal between molecular and morphological analyses (Davesne *et al.,* 2016; Keating *et al*., 2023; Legg *et al*., 2013), 3) improve the quality of inference (Mongiardino Koch *et al*., 2021), and 4) increase the robustness of downstream analyses (Gearty *et al.*, 2024). As a result, there has been renewed broad interest in the performance and expansion of models of morphological evolution (Mulvey *et al*., 2025; Tarasov, 2023; Wright *et al.,* 2016), and methods for accounting for uncertainty or imprecision in age data (Barido-Sottani *et al*., 2019; Barido-Sottani *et al*., 2020). Below we review some of these advancements, specifically for tip-dated Bayesian analyses using the fossilized birth-death process (Heath *et al*., 2014), using examples from trilobites. However, advances are also being made within parsimony frameworks, particularly regarding the inclusion and treatment of different character types (Catalano & Goloboff, 2012; Goloboff & De Laet, 2024; Grams & Richter, 2023; Hopkins & St. John, 2021).

The tip-dated Bayesian approach for phylogenetic inference is "tripartite", meaning that it employs three different types of models: 1) the substitution model, which describes how character may evolve; 2) the clock model, which describes how rates of character evolution can vary across the tree; and 3) the tree model, which describes the process of speciation, extinction, and sampling that generated the tree (Warnock & Wright, 2020).

Substitution model. Subsets, or partitions, of characters may be modeled using different substitution models. This makes it possible to consider discrete, continuous, and meristic characters separately. Discrete characters are currently modeled using the Lewis Mk model (Lewis, 2001), which is analogous to the Jukes-Cantor model used for molecular data. Matrices which describe the transition probabilities from one character state to another are generated based on the number of character states. They may be modified to include asymmetric, ordered, or irreversible transitions between character states (*e.g*., Wright *et al*., 2016). Characters may be further divided into different partitions based on other information, including functional, ecological, or developmental information. These partitions can be set up with the goal of improving the inference itself or to test hypotheses about rates of evolution for different types of characters. For example, Wright and Hopkins (2025) showed that rates of evolution were greater for characters inferred to have ecological importance compared to other characters.

Continuous characters are currently modeled using a Brownian motion model. Characters may share a single rate parameter or have independent rate parameters. Rate parameters may be set a priori or may be drawn from a distribution, for example a bounded uniform distribution (*e.g.,*

Wynd *et al*., 2025). For continuous characters that are ratios, log-transformation is recommended in order to mitigate any differential effect caused by which measurement is chosen for the numerator (Mongiardino Koch *et al*., 2015). Importantly, within the last year, it has become possible to include continuous characters with missing data for at least two popular programs for Bayesian analysis (MrBayes, see Wang & Zhang, in press; RevBayes, see Wynd *et al.,* 2025).

Treatment of meristic characters provides an interesting challenge because they can be treated as unordered-discrete, ordered-discrete, or continuous. Choosing the most appropriate model for any given meristic character may be informed by knowledge about variation within and between character states (Revell, 2025), as well as trait development (Brocklehurst & Haridy, 2021). For trilobites, examples include numbers of thoracic segments and the number and placement of spines.

It is increasingly being recognized that how characters are coded determines the models that may be considered for that data (Khakurel *et al.,* 2024), and likewise, that choices must be made about character coding in consideration of the analytical method that will be applied (Brazeau, 2011; Hopkins & St. John, 2021; Simões *et al*., 2023; Tarasov, 2019, 2023). Past and current practice for character construction and coding was recently examined through meta-analysis of 164 phylogenetic analyses conducted for trilobites over the past 35 years. Trends in matrix size, data type, and coding strategy were evident. Other notable results included 1) that polymorphic characters have been predominantly derived from discretized continuous characters; 2) that characters can have high information content even when data are missing for many tips; 3) that avenues for increasing character quality and quantity may be found in modularity studies, advances in functionally- or developmentally-informed methods for handing character dependence and hierarchy, and computable phenotypic data based on ontologies.

Clock model. Both exponential and lognormal distributions have been used to model the rate of evolution across the tree. Clock models can be strict (one unchanging rate) or relaxed (rates can vary across branches or taxa), and do not necessarily produce the same results. For example, the use of different models may result in the exploration of different parts of tree space (Wright & Hopkins, 2025).

Tree model. The fossilized birth-death process is a powerful tree model and increasingly popular for any inference that includes fossil data. However, decisions about how speciation, extinction, and sampling rates will be sampled are non-trivial (*e.g*., Wright *et al.,* 2021; Wright & Toom, 2017). Similarly to clock models, rates are often sampled from exponential or lognormal prior distributions. Knowledge from fossil occurrence data is useful for determining the parameters that describe the chosen distribution. For example, one can use empirically-derived per-capita speciation rates from fossil occurrence data from the Paleobiology Database to estimate parameters. For Cambrian to Ordovician trilobites, speciation rates are well-characterized by a lognormal distribution with a mean of -0.07 and variance of 0.56.

Similarly, metrics of fossil sampling and/or completeness can be applied to fossil occurrence data to place empirically-informed prior distributions on these important paleontological parameters (Thuy *et al.,* 2022). Fortunately, once sampling distributions for speciation, extinction, and sampling have been characterized for trilobites at different time intervals (or across the entire clade), they can potentially be used repeatedly as priors in later analyses.

Further, it is also possible to collapse branches in order to allow for ancestor-descendent relationships, not just sister species relationships. In our work, we have found that small proportions of taxa are supported as sampled ancestors, particularly in cases where we were attempting to sample densely at lower taxonomic levels (Bapst & Hopkins, 2017; Wright &

Hopkins, 2025). This supports past occurrence-based studies indicating that ancestors are likely to occur in robustly sampled fossil records (Foote, 1996; Liow & Ergon, 2016).

Finally, it is possible to include taxa for which morphological data is not available or has not been coded (Cole *et al*., 2025; Wright *et al.,* 2021; Zamora *et al.,* 2023). Doing so has been shown to increase the quality of the inference (Barido-Sottani *et al*., 2023; Nikolic *et al*., 2025) but because the placement of the taxa is constrained by their affinity, this approach may be best for analyses are at broad taxonomic levels where taxa are selected as exemplars, as opposed to analyses at lower taxonomic levels where generic affinities are being tested.

Because of the resurgence in interest in morphological data, this is an exciting time to be building phylogenies in paleobiology. Developments are occurring at all stages of the process: character construction, taxon selection, model choice and analytical details. Much of this development is about finding out how methodological choices impact results and how we can make the most use out of all the data available to us, both directly (*e.g.,* different types of characters, age information, even biogeographic information) and indirectly (*e.g*., occurrence data for better informed priors). At the frontier, developing biologically informed, internally consistent, comprehensive ontologies for trilobites holds considerable potential for dramatically improving phylogenetic inference at all taxonomic levels, including the most ambitious of goals: the trilobite tree-of-life.

REFERENCES

Bapst, D. W., & Hopkins, M. J. (2017). Comparing cal3 and other a posteriori time-scaling approaches in a case study with the pterocephaliid trilobites. *Paleobiology*, *43*(1), 49–67. doi: 10.1017/pab.2016.34

Barido-Sottani, J., Aguirre-Fernández, G., Hopkins, M. J., Stadler, T., & Warnock, R. (2019). Ignoring stratigraphic age uncertainty leads to erroneous estimates of species divergence times under the fossilized birth–death process. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1902), 20190685. doi:10.1098/rspb.2019.0685

Barido-Sottani, J., van Tiel, N. M. A., Hopkins, M. J., Wright, D. F., Stadler, T., & Warnock, R. C. M. (2020). Ignoring Fossil Age Uncertainty Leads to Inaccurate Topology and Divergence Time Estimates in Time Calibrated Tree Inference [Original Research]. *Frontiers in Ecology and Evolution*, *8*, 2020.00183. doi: 10.3389/fevo.2020.00183

Barido-Sottani, J., Pohle, A., De Baets, K., Murdock, D., & Warnock, R. C. (2023). Putting the F into FBD analysis: tree constraints or morphological data? *Palaeontology*, *66*(6), e12679.

Brazeau, M. D. (2011). Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnean Society*, *104*, 489–498. doi: 10.1111/j.1095-8312.2011.01755.x

Brocklehurst, N., & Haridy, Y. (2021). Do meristic characters used in phylogenetic analysis evolve in an ordered manner? *Systematic Biology*, *70*, 717–718. doi: 10.1093/sysbio/syaa078

Catalano, S. A., & Goloboff, P. A. (2012). Simultaneously Mapping and Superimposing Landmark Configurations with Parsimony as Optimality Criterion. *Systematic Biology*, *61*(3), 392-400. doi: 10.1093/sysbio/syr119

Cole, S. R., Wright, D. F., & Hopkins, M. J. (2025). Phylogenetic position and stratigraphic uncertainty of a new flexible crinoid from the Ordovician–Silurian boundary of Anticosti Island (Québec, Canada). *Journal of Paleontology*, *99*(2), 358–368. doi: 10.1017/jpa.2025.10110

Davesne, D., Gallut, C., Barriel, V., Janvier, P., Lecointre, G., & Otero, O. (2016). The phylogenetic intrarelationships of spiny-rayed fishes (Acanthomorpha, Teleostei, Actinopterygii): fossil taxa increase the congruence of morphology with molecular data. *Frontiers in Ecology and Evolution*, *4*, 2016.00129. doi: 10.3389/fevo.2016.00129

Foote, M. (1996). On the probability of ancestors in the fossil record. *Paleobiology*, *22*(2), 141–151.

Gearty, W., Allen, B., Godoy, P. L., & Chiarenza, A. A. (2024). The impact of tip age distribution on reconstructing trait evolution using phylogenetic comparative methods. doi: 10.32942/X27K79

Goloboff, P. A., & De Laet, J. (2024). Farewell to the requirement for character independence: phylogenetic methods to incorporate different types of dependence between characters. *Cladistics*, *40*, 209–241. doi: 10.1111/cla.12564

Grams, M., & Richter, S. (2023). On the four complementary aspects of hierarchical character relationships and their bearing on scoring constraints, expressed in a new syntax for character dependencies. *Cladistics*, *39*, 437–455. doi: 10.1111/cla.12550

Heath, T. A., Huelsenbeck, J. P., & Stadler, T. (2014). The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences*, *111*(29), E2957-E2966. doi: 10.1073/pnas.1319091111

Hopkins, M. J., & St. John, K. (2021). Incorporating hierarchical characters into phylogenetic analysis. *Systematic Biology*, *70*(6), 1163–1180. doi: 10.1093/sysbio/syab005

Keating, J. N., Garwood, R. J., & Sansom, R. S. (2023). Phylogenetic congruence, conflict and consilience between molecular and morphological data. *BMC Ecology and Evolution*, *23*(1), 30. doi: 10.1186/s12862-023-02131-z

Khakurel, B., Grigsby, C., Tran, T. D., Zariwala, J., Höhna, S., & Wright, A. M. (2024). The fundamental role of character coding in Bayesian morphological phylogenetics. *Systematic Biology*, *73*(5), 861–871. doi: 10.1093/sysbio/syae033

Legg, D. A., Sutton, M. D., & Edgecombe, G. D. (2013). Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications*, *4*, 2485. doi: 10.1038/ncomms3485

Lewis, P. O. (2001). A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, *50*(6), 913–925. doi: 10.1080/106351501753462876

Liow, L. H., & Ergon, T. (2016). Fitting ancestral age-dependent speciation models to fossil data. In W. D. Allmon & M. M. Yacobucci (Eds.), *Species and Speciation in the Fossil Record* (pp. 198–216). University of Chicago Press.

Mongiardino Koch, N., Garwood, R. J., & Parry, L. A. (2021). Fossils improve phylogenetic analyses of morphological characters. *Proceedings of the Royal Society B*, *288*(1950), 20210044. doi: 10.1098/rspb.2021.0044

Mongiardino Koch, N., & Parry, L. A. (2020). Death is on our side: paleontological data drastically modify phylogenetic hypotheses. *Systematic Biology*, *69*(6), 1052–1067. doi: 10.1093/sysbio/syaa023

Mongiardino Koch, N., Soto, I. M., & Ramírez, M. J. (2015). Overcoming problems with the use of ratios as continuous characters for phylogenetic analyses. *Zoologica Scripta*, *44*(5), 463–474. doi: 10.1111/zsc.12120

Mulvey, L. P. A., May, M. R., Brown, J. M., Höhna, S., Wright, A. M., & Warnock, R. C. M. (2025). Assessing the Adequacy of Morphological Models used in Palaeobiology. *Systematic Biology*, *74*(1), 34–52. doi: 10.1101/2024.01.25.577179

Nikolic, M. C., Warnock, R., & Hopkins, M. J. (2025). Combining fossil taxa with and without morphological data improves dated phylogenetic analyses. *Biology Letters*, *21*(8), 20250205. doi: 10.1098/rsbl.2025.0205

Revell, L. J. (2025). Ancestral state reconstruction of phenotypic characters. *Evolutionary Biology*, *52*, 1–25. doi: 10.1007/s11692-025-09645-y

Simões, T. R., Vernygora, O. V., de Medeiros, B. A. S., & Wright, A. M. (2023). Handling logical character dependency in phylogenetic inference: Extensive performance testing of assumptions and solutions using simulated and empirical data. *Systematic Biology*, *72*(3), 662–680. doi: 10.1093/sysbio/syad006

Tarasov, S. (2019). Integration of anatomy ontologies and evo-devo using structured Markov models suggests a new framework for modeling discrete phenotypic traits. *Systematic Biology*, *68*(5), 698–716. doi: 10.1093/sysbio/syz005

Tarasov, S. (2023). New phylogenetic markov models for inapplicable morphological characters. *Systematic Biology*, *72*(3), 681–693. doi: 10.1093/sysbio/syad005

Thuy, B., Eriksson, M. E., Kutscher, M., Lindgren, J., Numberger-Thuy, L. D., & Wright, D. F. (2022). Miniaturization during a Silurian environmental crisis generated the modern brittle star body plan. *Communications Biology*, *5*(1), 14. doi: 10.1038/s42003-021-02971-9

Wang, Z., & Zhang, C. (in press). An implementation of the Brownian motion model for Bayesian phylogenetic inference using continuous traits with missing states. *Paleobiology*. doi: 10.1017/pab.2025.10088

Warnock, R. C., & Wright, A. M. (2020). Understanding the tripartite approach to Bayesian divergence time estimation. *Elements of Paleontology*, *781108954365*. doi: 10.32942/osf.io/4vazh

Wright, A. M., Lloyd, G. T., & Hillis, D. M. (2016). Modeling character change heterogeneity in phylogenetic analyses of morphology through the use of priors. *Systematic Biology*, *65*(4), 602–611. doi: 10.1093/sysbio/syv122

Wright, A. M., Wagner, P. J., & Wright, D. F. (2021). *Testing Character Evolution Models in Phylogenetic Paleobiology: A case study with Cambrian echinoderms*. Cambridge University Press. doi: 10.1017/9781009049016

Wright, D. F., & Hopkins, M. J. (2025). Assessing the impact of character evolution models on phylogenetic and macroevolutionary inferences from fossil data. *Palaeontology*, *68*(5), e70031. doi: 10.1111/pala.70031

Wright, D. F., & Toom, U. (2017). New crinoids from the Baltic region (Estonia): fossil tip-dating phylogenetics constrains the origin and Ordovician–Silurian diversification of the Flexibilia (Echinodermata). *Palaeontology*, *60*(6), 893–910. doi: 10.1111/pala.12324

Wynd, B. M., Khakurel, B., Kammerer, C. F., Wagner, P. J., & Wright, A. M. (2025). Incorporating continuous characters in joint estimation of dicynodont phylogeny. 2025.2003.2003.641281. doi: 10.1101/2025.03.03.641281

Zamora, S., Wright, D. F., & Nohejlova, M. (2023). Phylogenetic position of *Bohemiacinctus* gen. nov.(Echinodermata, Cincta) from the Cambrian of Bohemia: implications for macroevolution and the role of taxon sampling in palaeobiological systematics. *Papers in Palaeontology*, *9*(1), e1482. doi: 10.1002/spp2.1482

PHYLOGENETIC ANALYSIS OF THE LATE CAMBRIAN LAURENTIAN TRILOBITE FAMILY DIKELOCEPHALIDAE MILLER 1889 AND EVOLUTIONARY PATTERNS AMONG SOME OF ITS MEMBERS

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Keywords: Laurentia, Mississippi Valley, Cambrian.

Trilobites belonging to Dikelocephalidae are recognized within Dikelocephalacea by their extended cephalic doublures. These large, exclusively Laurentian trilobites are restricted to an ~ 2.5 million years interval within the Cambrian late Jiangshanian and earlier Stage 10. Phylogenetic analyses of various data partitions using maximum parsimony and Bayesian methods consistently recognise a clade encompassing members of *Dikelocephalus*. The phenetically distinctive *Walcottaspis vanhornei* (Walcott, 1914) roots among St. Lawrence Formation *Dikelocephalus* in all analyses conducted. This is consistent with recent analyses of a different dataset and with C.D. Walcott's original comparison but not with those of other earlier workers. Various iterations of maximum parsimony analyses based on mixed mode data, along with Bayesian analysis using ordered, discretized characters, recognize *Osceolia* as a clade that roots at the base of the *Dikelocephalus/Walcottaspis* clade. Poor node support and placement instability in stem Dikelocephalidae comprising species assigned to *Briscoia* suggests that understanding of evolutionary relationships remains rudimentary in these areas. To the extent that Dikelocephalidae are a typical "family-level" clade of trilobites, current knowledge of their phylogeny is in part both encouraging and cautionary for the proposition of evolutionary scenarios based on such entities. Knowledge is best of those forms well represented in the shoreward deposits of the Upper Mississippi Valley which are discussed below.

Occurrence of *Osceolia osceola* (Hall, 1863) in the early part of a falling stage systems tract shows size-related distinction between smaller holaspid specimens in nearer shore, very fine-grained sandstone deposits, and larger specimens in fine-grained dolomitic mudstones in more distal settings. Along with the variable occurrence of a ledge in the anterior border, this size difference, which we consider likely primarily related to habitat preference, accounts for prior species level taxonomic over-splitting because *O. osceola* shows appreciable holaspid ontogenetic variation in shape. No other geographically or stratigraphically influenced variation is evident within this species, which was represented in the region for some 350,000 years. A new species, *O. tumerispina* Srivastava-Losey & Hughes, 2025, is known only from one unusually dolomite-rich bed at a single locality.

Dikelocephalus from the earlier part of the falling stage systems tract show a complex and continuous landscape of morphological variation with several prominent peaks linked by valleys with elevated floors over an ~1,000,000 year local range. Although this landscape is influenced by compaction-related deformation, its main architecture was biotically determined and we recognize the four principal peaks as named morphotypes among these *Dikelocephalus*. For one pair of these morphotypes, co-occurrence in single bed collections is known in several cases. For the other pair, members of which occur only toward the top of the local range, similar co-occurrence is known in one clear case only. Several specimen-rich single bed collections yield only one *Dikelocephalus* morphotype. Morphotypes may represent species or intraspecific polymorphs (including possible sexual dimorphs). Their morphological variation is consistent

with Darwin's predictions for populous species and the distribution of their form mimics a Sewell Wright (1932) adaptive landscape.

Abundant occurrence of *Walcottaspis vanhornei* may be confined to as little as ~50,000 years towards the end of earlier part of the falling stage systems tract (Srivastava & Hughes 2024). Phylogenetic analysis consistently places one *Dikelocephalus* morphotype as sister taxon to *W. vanhornei,* with which it is not known to co-occur. At Hokah, Minnesota, the locality from which *Walcottaspis* is best known, another *Dikelocephalus* morph occurs in several dolomitic siltstone horizons, including a single cranidium recovered in the bed bearing *Walcottaspis vanhornei*. Occurrence of *Walcottaspis vanhornei* shows several characteristics of the punctuated equilibrium model of speciation, but interpretation is obscured by uncertainty in interpretating the biological entities that the *Dikelocephalus* morphotypes represent.

REFERENCES

Hall, J. (1863). Preliminary notice of the fauna of the Potsdam Sandstone. *Sixtheenth Annual Report of the Regents of the State of New York on the condition of the State Cabinet of Natural History*, 119–226.

Miller, S. A. (1889). *North American Geology and Paleontology*. Cincinnati: Western Methodist Book Concern.

Srivastava, S., & Hughes, N. C. (2024). Morphology, variation, and systematics of the late Cambrian Laurentian dikelocephalid trilobite *Walcottaspis vanhornei* (Walcott, 1914). *Journal of Paleontology, 98*(4), 612–633. doi: 10.1017/jpa.2023.29

Srivastava-Losey, S., & Hughes, N. C. (2025). Occurrence, morphology and taxonomy of the late Cambrian dikelocephalid trilobite *Osceolia* Walcott, 1914. *Journal of Paleontology, 99*(4), 914–947. doi: 10.1017/jpa.2025.10103

Walcott, C. D. (1914). Cambrian Geology and Paleontology. II. No. 13. *Dikelocephalus* and other genera of the Dikelocephalinae. *Smithsonian Miscellaneous Collections, 57*, 345–430.

Wright, S. (1932). *The roles of mutation inbreeding, crossbreeding and selection in evolution.* Paper presented at the Proceedings of the Sixth International Congress on Genetics, *1*(8), 355–366.

DEVONIAN TRILOBITES FROM PARANÁ BASIN – ALTO GARÇAS SUB-BASIN – BRAZIL

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Keywords: Brazil, Biostratigraphy, Devonian, Trilobites.

INTRODUCTION

The Paraná Basin in Brazil has been the subject of research for almost 150 years. Divided into two sub-basins, the Devonian outcrops have been explored more extensively in the southern portion – the southeast of the basin (Apucarana Sub-basin), near the city of Ponta Grossa, with research dating back to the early work of John Mason Clarke in the late 19th and early 20th centuries. In the northern portion, the Alto Garças Sub-basin, studies have intensified in the last decade, leading to an increase in the number of records. It is worth noting that the trilobite composition of the entire Paraná Basin is predominantly of the order Phacopida and is mainly restricted to two families: Homalonotidae and Calmoniidae. The composition of both sub-basins shows some divergences to date. Records of the superfamily Dalmanitoidea Vogdes, 1890, based on the occurrence of *Gamonedaspis* (=*Dalmanitoides) accola* (Clarke, 1913), and although the supposed dalmanitid *Dalmanites gonzaganus* (Clarke, 1890) has also been reported, are restricted to the Apucarana Sub-basin. On the other hand, some taxa occur only in the northern part.

Different what has occurred since early on in the Apucarana Sub-basin, trilobite records in the northern portion of the basin (Alto Garças Sub-basin) have only been known in recent decades and have occurred mainly on the edge of its northernmost part. On the other hand, the northwesternmost portion of that Sub-basin (in Mato Grosso do Sul state – Fig. 1) had its trilobite fauna little explored until recently, although it was known from research such as that of Caster between 1945 to 1947, Almeida, 1948 and Boucot and Caster, 1984. In 1987, with Carvalho *et al.,* the first trilobites were recorded there. At the time, only two species from the Rio Verde region were identified, one of the genus *Burmeisteria* and the other of Calmoniidae with a unique identified species.

CONTEXT

The sedimentites of the Paraná Basin cover an area of 1.6 million km², occurring in regions of Brazil, Argentina, Paraguay and Uruguay. In Brazil, they crop out , in north, in the central-western and southern states of Mato Grosso (**MT**) and Goiás (**GO**), and in northwest of Mato Grosso do Sul (**MS**), meanwhile to the south they extend into the eastern Paraná (**PR**) according several authors (Melo, 1988; Grahn, 1992; Grahn *et al*. 2010, 2013). Devonian records of the Paraná Basin in Brazil, was subdivided into two sub-basins: *Apucarana*, to the south and *Alto Garças*, to the north (Ramos, 1970). Throughout the Basin's evolution, sedimentary deposits were affected by several transgressive-regressive eustatic events that varied giving a pattern of regional unconformities (Melo, 1988; Abe & Lieberman, 2009). Due to distinct tectonic configurations and subsidence rates, the depositional evolution of both sub-basins was different, resulting in distinct lithological and stratigraphic stacking patterns.

The Alto Garças sub-basin is often considered shallower compared to the Apucarana sub-basin due to more abundant coarse-grained facies (Melo, 1988; Grahn *et al*., 2010). In Mato Grosso do

Sul, Devonian sediments extend in a band across the central-western portion of the state (Fig. 1A), trending southwest-northeast (Melo, 1988). The Devonian rocks of the Rio Verde region are correlated with the base (shales) and intermediate portion (sandstones) of the Ponta Grossa Formation of the Apucarana Sub-basin (Pereira, 2000; Grahn *et al*., 2010). An Emsian-Eifelian age for the Devonian outcrops of Rio Verde de Mato Grosso had firstly been suggested by Carvalho *et al.* (1987) based on spores, chitinozoans and achritarcs, based in studies by Daemon *et al.* (1967), Lange (1967b) as also commented by Melo (1982). Subsequently, the presence of the chitinozoan *Ramochitina magnifica* (Pereira, 2000, pp. 23-25 and 72; Grahn *et al*., 2002, 2013) indicated sediments dated from the Pragian-Emsian period.

METHODS

For illustrating details of morphological structures, a Zeiss stereomicroscope with a DF420C camera coupled to a computer running LAS Leica software, was used. For some more proximal images, the macro function of a 50/12/5 MP Samsung A-54 triple camera was used. Macro

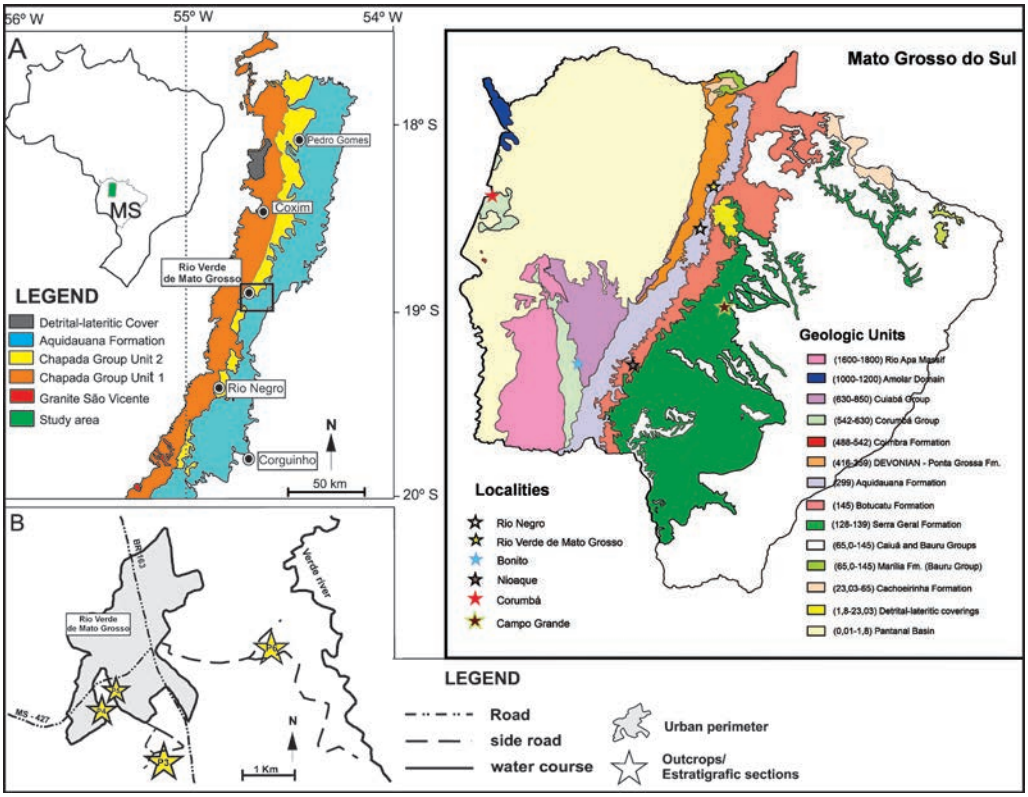

Figure 1. Geological map of the study area. **A,** Brazilian territory, indicating the state of Mato Grosso do Sul, showing the region of Paleozoic outcrops and the study area. Chapada Group, Unit 1 and Unit 2, represents Furnas Formation and Devonian marine sediments, respectively; **B,** Location points of the outcrops in relation to the urban area of the municipality of Rio Verde. Stars indicate some more important outcrops location. On the right, map of Mato Grosso do Sul state, showing the most important geologic units; the relative ages are listed in the column on the left, in parentheses (https://www.semadesc.ms.gov.br/).

functions of Canon PowerShot SX70 HS and an Olympus C-90 digital camera were also used for some images.

Trilobites of this study are deposited in the Coleção Científica do Laboratório de Geologia e Paleontologia da Faculdade de Engenharias, Arquitetura e Urbanismo e Geografia da UFMS-Campo Grande (GeoPaLab/FAENG/UFMS), identified by the acronym CGP/1A or, hereinafter, simply CGP; and in Coleção Zoológica da Universidade Federal de Mato Grosso do Sul, Campo Grande, and identification by the acronym "ZUFMS-FOS" or, in this study, simply "FOS". Fossil collecting were authorized accomplishing legal protocols (fossil extract communications of *Agência Nacional de Mineração* - ANM/COPAL - Brasil): 020/2019; 027/2021; 064/2021; 085/2022; 053/2023; 123/2023; 136/2023; 150/2025.

OBJECTIVES

This study aims to present the latest results due to the increase of research in outcrops nearby Rio Verde city and region.

RESULTS: TRILOBITE RECORDS

Until recently, the Alto Garças sub-basin recorded the following genera: *Burmeisterella* Reed,1918, *Burmeisteria* Salter, 1865, *Calmonia* Clarke, 1913, *Kozlowskiaspis* Braniša & Vaněk, 1973, *Metacryphaeus* Reed, 1907, and *Paracalmonia* Struve 1958, totaling seven identified species. From 2024 onwards, three new species including *Burmeisteria notica* Clarke, 1913 (Fig. 3), *Metacryphaeus meloi* Carvalho, Edgecombe and Lieberman, 1997, and *Bainella* Rennie, 1930, were added. *Bainella sulmatogrossensis* Kerber, Pacheco, Horodyski & Graciolli 2024, is unique among its congenerics, by the presence of two rows of spines with columnar base on the axial axis and the presence of genal and intergenal spines (Fig. 2). Recently, the hypostome of *Burmeisteria notica* was described for the first time, as well as that of *B. sulmatogrossensis*, for which genus only one specimen had been previously recorded by Cooper (1982).

Two species previously unrecorded in the Devonian outcrops of Mato Grosso do Sul are going to be reported (article in preparation): *Paracalmonia cuspidata* Clarke, 1913 and *Metacryphaeus tuberculatus* Kozlowski, 1923, both from the Rio Verde region.

Figure 4 presents the species currently considered valid in the Paraná Basin and its location.

CONCLUSIONS

Over a century of investigations on the Devonian in both sub-basins of the Paraná Basin, seem to indicate that certain taxa remain exclusive to one of the sub-basin, suggesting a decoupled history of paleobiogeographic patterns. However, the increasing searching effort during recent years and the resulting findings, might also suggest a sampling bias. The northwestern portion of the Paraná Basin in Mato Grosso do Sul now encompasses seven genera and nine trilobite species: *Burmeisteria notica, Bainella sulmatogrossensis, Calmonia signifer, Kozlowskiaspis subseciva, Metacryphaeus australis, M. meloi, M. tuberculatus, Paracalmonia cuspidata*, and *Pennaia pauliana*.

In turn, at present, there are no records of Dalmanitidae and *Burmeisteria herschelii* in the Alto Garças Sub-basin, nor, *Metacryphaeus meloi* in Apucarana Sub-basin.

Hence, in spite of the fact that further investigation is needed, evidence indicates these sub-basins represent an ideal study case for testing paleobiogeographical patterns and processes, in a natural laboratory driven by different tectonic and eustatic histories favouring processes of dispersal-vicariance.

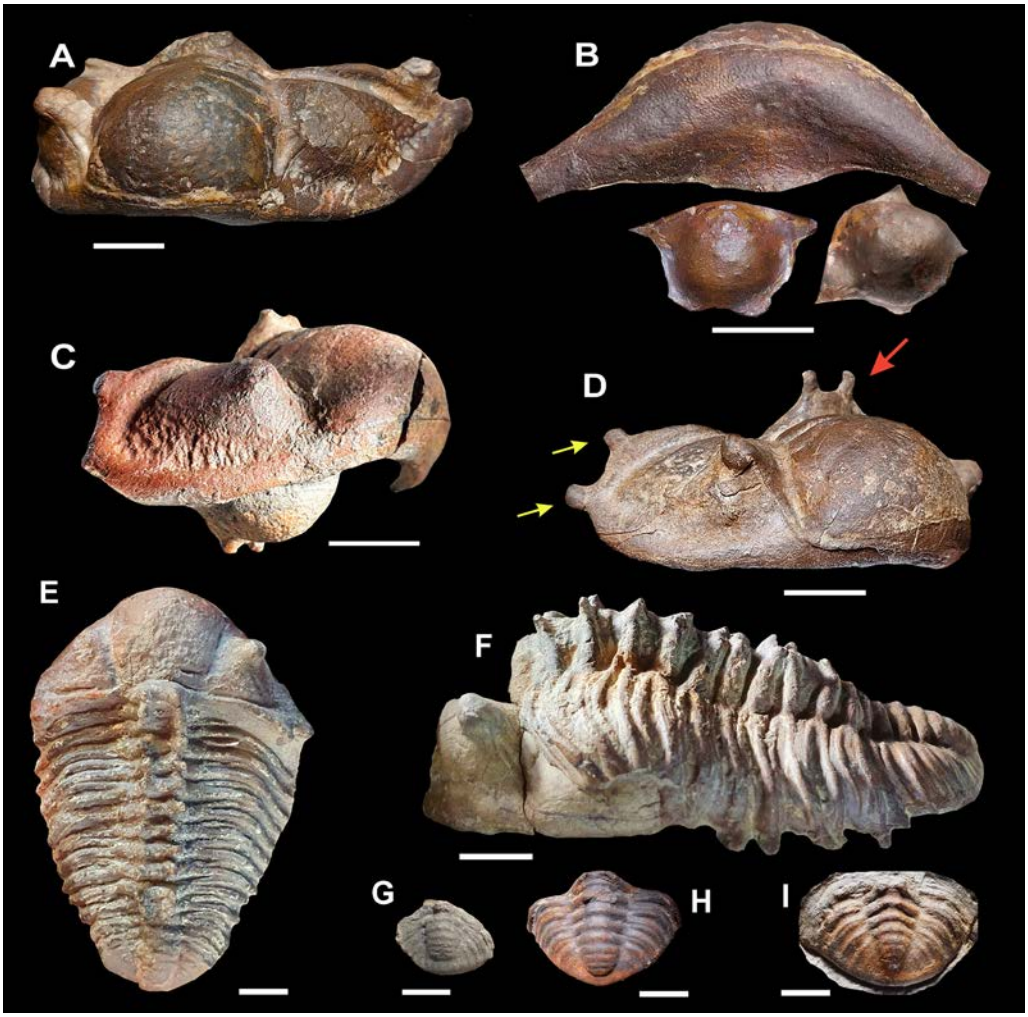

Figure 2. *Bainella sulmatogrossensis* Kerber, Pacheco, Horodyski & Graciolli 2024. Ponta Grossa Formation, Pragian-Emsian age. Locality: Rio Verde de Mato Grosso, Brazil. **A,** Specimen FOS01666 with well-marked characters and ornamentation, broad spines and a strong curvature on the cephalic edge; **B,** portion of the frontal doublure of FOS01666 exhibiting granulosis and respective hypostome, in frontal and lateral view; **C,** Two cephala joined ventrally in opposite positions; view of well-marked and deep characters (curvature of the dishing, broad edges, large intergenal spine and strong dimples); **D,** Cephalon preserved eyes and all spines, in genae and occipital lobe (arrows); **F,** Exuviae skeleton, in an evident post-ecdysis position: glabella and the left eye is hidden under thorax.; **E,** complete specimen, preserved inside pyrite concretion, in horizontal position and constricted thorax sclerites; presence (hidden) of the hypostome under the cephalon; **G**–**I,** Variations of pygidia, from left to right: large and tuberculate axial axis becoming less tuberculate and the axis termination narrow. FOS01666 (A, B); CGP-004 (C); FOS01737 (D); FOS01689 (E); FOS01692 (F); CGP-218 (G); FOS01719 (H); CGP-213 (I); scale bar: 10 mm.

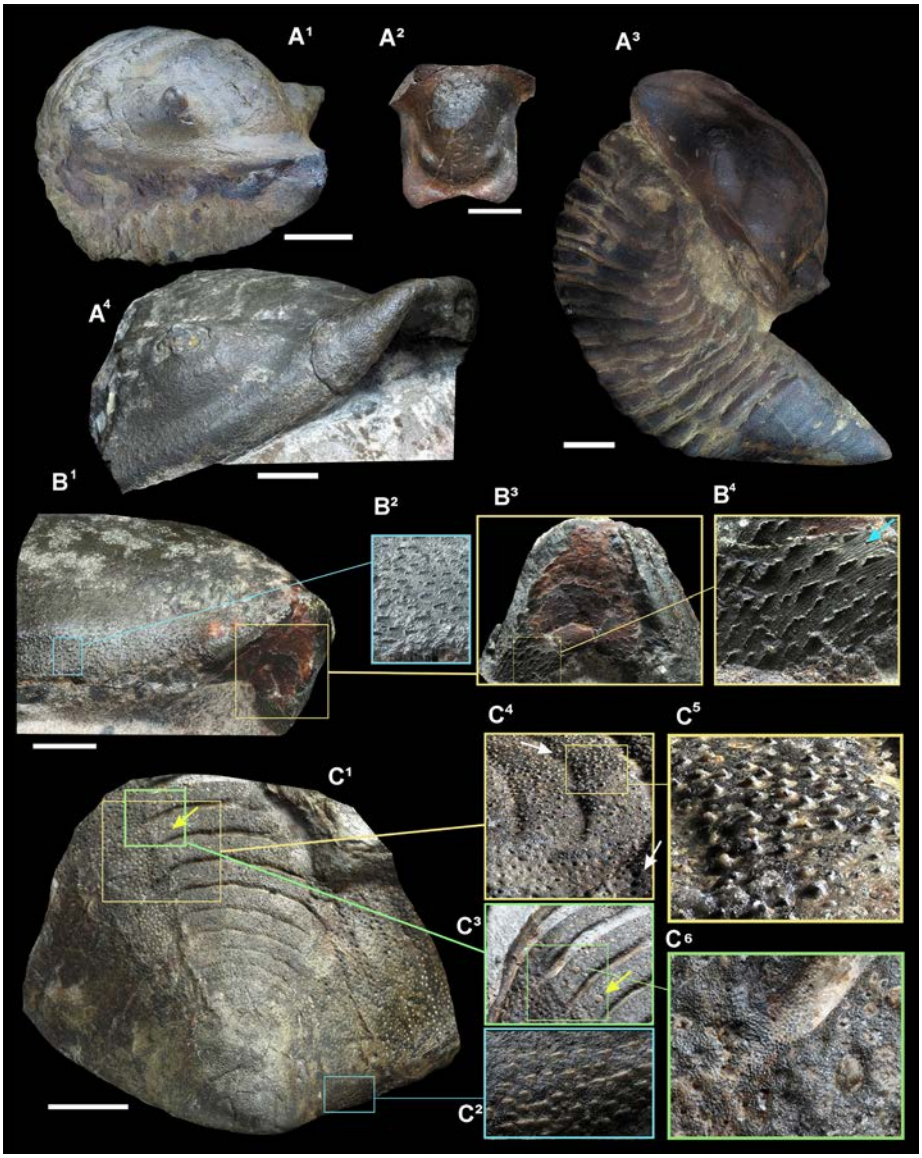

Figure 3. *Burmeisteria notica*. Details of morphology. **A¹,** enrollment specimen, exhibiting shape of eye prominent visual fields. **A²,** Large hypostome; **A³,** complete specimen, cephalon separated from the body (evident exuviae); **A⁴,** View of frontal beak (epistomal and apiculus structures); **B¹- B⁴,** Groove-like structures and terrace ridges (light-blue arrow) arranged in the ventral cuticle of the pygidium; **C¹-C⁶,** Types of ornamentation over carapaces of a thoracopygon. In C¹, C³, C⁶ (yellow arrows): row of little tubercles over thoracic sclerites, a diagnostic character of species (Rustán et al, 2020, p 7; Kerber et al., 2023, fig 3A). C²: Straight grooves on the lateral edge of the pygidium, directed frontal-posteriorly (so as B²). C⁴, C⁵: Granulose scattered across the carapace, with an average grain size of 0.5 mm; originating from fine, filled empty holes (white arrows) on the carapace (C⁵); or, when eroded, they leave small holes. Horizon and age: Ponta Grossa Formation, Early Devonian. Samples: (A¹) FOS01539; (A²) FOS01761 (hypostome); (A³) FOS01537; (A⁴) FOS01774; (B¹- B⁴) FOS01774; (C¹-C⁶) FOS01525; scale bar: 10 mm.

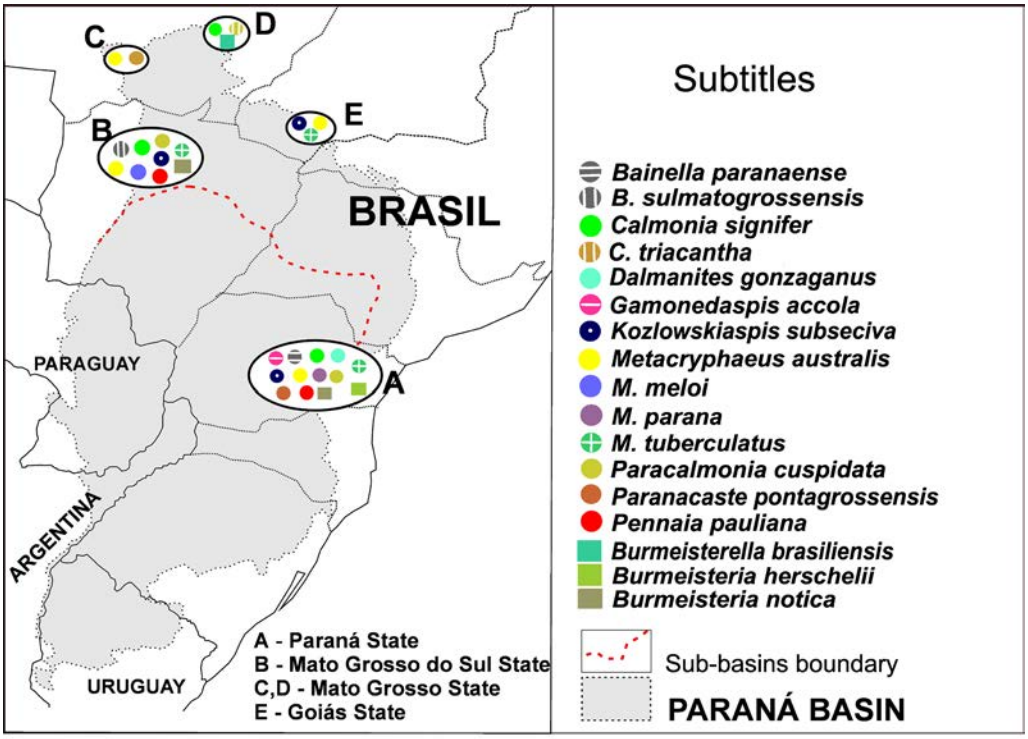

Figure 4. Simplified diagram showing the 17 trilobite occurrences currently valid for the Paraná Basin. On the left, map of southern Brazil highlighting the Basin (gray); in the ellipses, the locations of the most important outcrops and the species recorded therein.

Acknowledgements: This work was carried out with the support of the Federal University of Mato Grosso do Sul – UFMS/MEC – Brazil and the Coordination for the Improvement of Higher Education Personnel – Brazil (Capes) – Funding Code 001.

REFERENCES

Abe, F. R., & Lieberman, B. S. (2009). The nature of evolutionary radiations: a case study involving Devonian trilobites. *Evolutionary Biology*, *36*(2), 225–234.

Carvalho, M. G. P., Melo, J. H. G., & Quadros, L. P. (1987). Trilobitas Devonianos do flanco noroeste da Bacia do Paraná. In *Congresso Brasileiro de Paleontologia* (Vol. 10, p. 36).

Carvalho, M. D. G. P. D., Edgecombe, G. D., & Lieberman, B. S. (1997). Devonian calmoniid trilobites from the Parnaíba Basin, Piauí State, Brazil. *American Museum novitates*; *3192*, 1–13.

Clarke, J. M. (1913). Fósseis devonianos do Paraná. *Monographias do Serviço Geológico e Mineralógico do Brasil. Rio de Janeiro*, *1*, 1–353.

Cooper, M. R. (1982). A revision of the Devonian (Emsian-Eifelian) Trilobite from the Bokkeveld Group of South Africa. *Annals of the South African Museum*, *89*, 1–174.

Daemon, R. F., Quadros, L. P., & Silva, L. C. da, (1967). Devonian palynology and biostratigraphy of the Parana Basin. In: Bigarella, J.J. (Ed.), Problems in Brazilian Devonian geology. *Boletim Paranaense de Geociencias*, *21/22*, 99–132.

Grahn, Y., Mauller, P. M., Pereira, E., & Loboziak, S. (2010). Palynostratigraphy of the Chapada Group and its significance in the Devonian stratigraphy of the Paraná Basin, south Brazil. Journal of South American *Earth Sciences, 29*, 354–370.

Grahn, Y., Mauller, P. M., Bergamaschi, S., & Bosetti, E. P. (2013). Palynology and sequence stratigraphy of three Devonian rock units in the Apucarana Sub-basin (Paraná Basin, south Brazil): additional data and correlation. *Review of Palaeobotany and Palynology*, *198*, 27–44.

Kerber, G., Pacheco, M. L. A. F., Horodyski, R. S., & Graciolli, G. (2024). Revealing new trilobites from the early Devonian alto Garças Sub-basin, Brazil. *Historical Biology*, *36* (7), 1220–1236.

Kozlowski, R. (1923). Faune devonienne de Bolivie. *Annales de Paleontologie, 12*, 1–112

Lange, F. W. (1967b). Biostratigraphic subdivision and correlation of the Devonian in the Parana Basin. In Problems in Brazilian Devonian geology, Bigarella, J. J. (Ed.), *Boletim Paranaense de Geociencias*, *21/22*, 63–98.

Melo, J. H. G. (1988). The Malvinokaffric realm in the Devonian of Brazil. Canadian Society of Petroleum Geologists. *Memoir*, *14*, 669–702

Pereira, E. (2000). Evolução tectono-sedimentar do Intervalo Ordoviciano-Devoniano da Bacia do Paraná, com ênfase na Sub-Bacia de Alto Garças: Unpublished PhD thesis, Universidade de São Paulo, São Paulo.

Rustán, J. J., Waisfeld, B. G., & Vaccari, N. E. (2020). The homalonotid trilobite *Burmeisteria* Salter, 1865 in the Lower Devonian of Argentina: new data in the context of southwestern Gondwana. *Journal of Paleontology*, *94*, 498–512.

PHYLOGENETIC AFFINITIES OF PROBLEMATIC LATE PALAEOZOIC MALACOSTRACANS: THE CASE STUDY OF PYGOCEPHALOMORPHA

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Keywords: Anatomy, Phylogeny, Pancrustacea, Peracarida, Problematica.

Malacostraca is a speciose clade of pancrustaceans, with a great diversity of morphology, lifestyles and habitat. Although morphologically well-defined, the phylogenetic relationships among malacostracans remains controversial. To address these issues, it is necessary to include a source of data that has often been overlooked in phylogenetic analyses: fossils. Malacostracans have an extensive fossil record, dating back to the Cambrian (Collette & Hagadorn, 2010). In the Late Palaeozoic (Devonian-Carboniferous), peculiar groups of eumalacostracans (*e.g.*, Angustidontida, Anthracophausiidae, Belotelsonidae, Palaeocaridacea, Pygocephalomorpha) diversified and became widespread in various regions and environments (Schram, 1977, 1981). However, although they are well-diversified and known since the 19th century, a large proportion of these fossils are rarely included in phylogenetic analyses (Wills *et al*., 2009). This is due to the "problematic" nature of their anatomy, which is either unknown due to poor preservation, or presents a combination of unique character states that prevents a direct assignment to the current malacostracan ingroups.

Among these problematic malacostracans is Pygocephalomorpha. Pygocephalomorphans are eumalacostracans with a shrimp- to lobster-like morphology known from the Late Devonian (Gueriau *et al.,* 2014) to the Cisuralian (Late Permian; *e.g.*, Pazinato *et al*., 2016). In the late Palaeozoic, they were a major component of marginal marine, brackish and freshwater environments (Schram, 1981). Pygocephalomorphans are particularly recognizable by their well-developed shield, their thorax bearing two to three pairs of maxillipeds, and by the oöstegites of the females, i.e. the specialized epipodites of the thoracic appendages, which hold the marsupium (or brood pouch). This last character state is one of the autapomorphies of Peracarida, explaining the assignment of Pygocephalomorpha to this group (Jones *et al.,* 2016). However, their affinities and monophyly are still debated. For example, the Tealliocarididae, a pygocephalomorphan ingroup, has been interpreted as Decapoda (Clark, 2013; Clark & Ross, 2024), based on the presence of three maxillipeds and a cephalothorax and the putative misinterpretation of gills as oöstegites. This could imply that Pygocephalomorpha is polyphyletic or paraphyletic or that it belongs to Decapoda.

Nowadays, pygocephalomorphans are studied only sporadically. For the most part, they have rarely been the subject of "modern" work, despite the question of their phylogenetic affinities. In order to resolve these issues, we restudied pygocephalomorphans from two major Carboniferous Konservat-Lagerstätten: (1) the Coseley Lagerstätte, England, UK (Moscovian, Pennsylvanian), and (2) the Gullane Shrimp Bed, Scotland, UK (Visean, Mississippian). The late Carboniferous Coseley Lagerstätte near Dudley, Staffordshire, contains an important diversity of plant and animals, including arthropods, remarkably preserved in 3D within siderite nodules (Braznell, 2006). One pygocephalomorphan species, *Pygocephalus cooperi*, was reported by Woodward (1907) from the Coseley Lagerstätte. X-ray micro-tomography has proved an efficient approach to reconstructing the anatomy of Coseley arthropods, in particular for arachnids (*e.g.,* Jones *et*

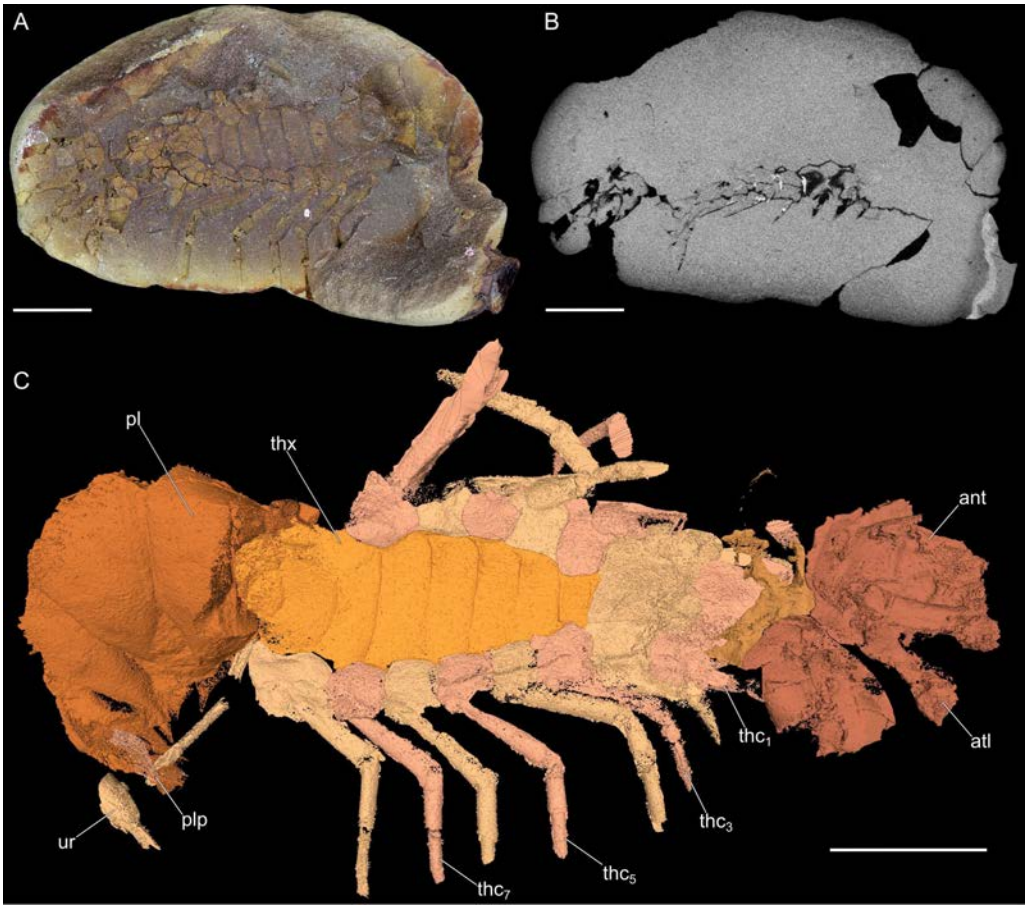

Figure 1. *Pygocephalus cooperi* Huxley, 1857 from the Coseley Lagerstätte, England, UK (Moscovian, Pennsylvanian, Carboniferous; NHMUK In22847). **A,** ventral view; **B,** sagittal virtual section; **C,** 3D rendering (dorsal view). Abbreviation: **ant**, antenna; **atl**, antennula; **plp**, pleopod; **pl**, pleon; **thc**$_{1-7}$, thoracopods 1–7; **thx**, thorax; **ur**, uropod; scales bar = 10 mm.

al., 2014). We therefore decided to apply this technique to a *Pygocephalus cooperi* specimen. The Gullane Shrimp Bed, exposed at Cheese Bay on the East Lothian coast, Scotland, yields almost exclusively the remarkably preserved pygocephalomorphan *Tealliocaris* as well as rare fish and amphibians (Hesselbo & Trewin, 1984). Briggs and Clarkson (1985) described the morphology and anatomy of the Gullane *Tealliocaris* in detail. However, Clark (2013) questioned their interpretation of the epipods of *Tealliocaris* as oöstegites, suggesting that they were actually gills. In order to resolve this debate, we studied undescribed *Tealliocaris* specimens using light (white and luminescence) illumination and scanning electron microscopy.

The revision of the pygocephalomorphans from the Coseley and Gullane Lagerstätten allowed us to redescribe the morphology and anatomy of Pygocephalomorpha in detail. We are in particular able to determine the nature and morphology of their cephalic, thoracic and pleonal appendages. The presence of only two maxillipeds as well as oöstegites is confirmed in both *Pygocephalus* and *Tealliocaris.* The morphology of the pleopods is also reported for the first time in *Pygocephalus cooperi*. Finally, juvenile *Tealliocaris* specimens are described. These new results allow us to discuss their phylogenetic affinities.

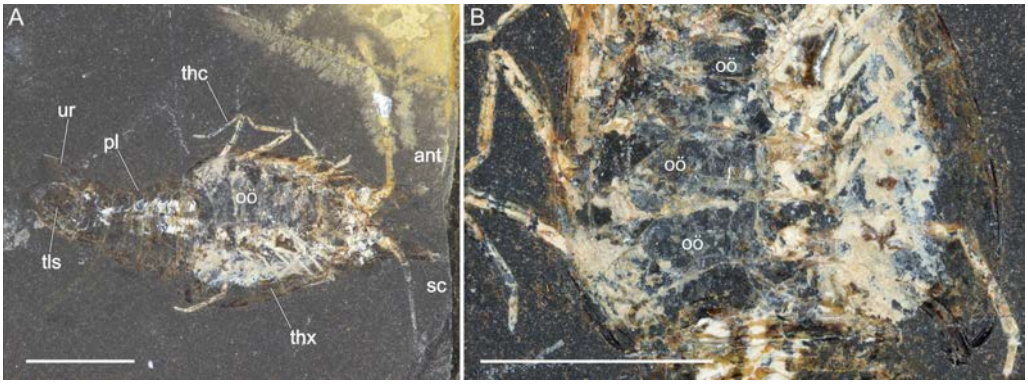

Figure 2. *Tealliocaris* from the Gullane Shrimp Bed Lagerstätte, Scotland, UK (Visean, Mississippian, Carboniferous). **A,** ventral view; **B,** close-up of thorax. Abbreviations: **ant**, antenna; **oö**, *oöstegites;* **pl**, pleon; **sc**, scaphocerite; **thc**, thoracopod; **thx**, thorax; tls, telson; **ur**, uropod; scales bars = 5 mm.

REFERENCES

Braznell, L. J. (2006). *Exceptional preservation in the Upper Carboniferous Coseley Lagerstätte* [PhD Thesis, University of Birmingham]. https://etheses.bham.ac.uk/id/eprint/13336/

Briggs, D. E. G., & Clarkson, E. N. K. (1985). The Lower Carboniferous shrimp *Tealliocaris* from Gullane, East Lothian, Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *76*(2–3), 173–201. doi: 10.1017/S0263593300010439

Clark, N. D. L. (2013). *Tealliocaris*: A decapod crustacean from the Carboniferous of Scotland. *Palaeodiversity*, *6*, 107–133.

Clark, N. D. L., & Ross, A. J. (2024). Caridoid crustaceans from the Ballagan Formation (Tournaisian, Lower Carboniferous) of Willie's Hole, Chirnside, Scottish Borders, UK. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, *115*(1–2), 1–12. doi: 10.1017/S1755691024000045

Collette, J. H., & Hagadorn, J. W. (2010). Three-dimensionally preserved arthropods from Cambrian Lagerstätten of Quebec and Wisconsin. *Journal of Paleontology*, *84*(4), 646–667. doi: 10.1666/09-075.1

Gueriau, P., Charbonnier, S., & Clément, G. (2014). First decapod crustaceans in a Late Devonian continental ecosystem. *Palaeontology*, *57*(6), 1203–1213. doi: 10.1111/pala.12111

Hesselbo, S. P., & Trewin, N. H. (1984). Deposition, diagenesis and structures of the Cheese Bay Shrimp Bed, Lower Carboniferous, East Lothian. *Scottish Journal of Geology*, *20*(3), 281–296. doi: 10.1144/sjg20030281

Jones, F. M., Dunlop, J. A., Friedman, M., & Garwood, R. J. (2014). *Trigonotarbus johnsoni* Pocock, 1911, revealed by X-ray computed tomography, with a cladistic analysis of the extinct trigonotarbid arachnids. *Zoological Journal of the Linnean Society*, *172*(1), 49–70. doi: 10.1111/zoj12167

Jones, W. T., Feldmann, R. M., Schram, F. R., Schweitzer, C. E., & Maguire, E. P. (2016). The Proof is in the pouch: *Tealliocaris* is a peracarid. *Palaeodiversity*, *9*(1), 75–88. doi: 10.18476/pale.v9.a5

Pazinato, P. G., Soares, M. B., & Adami-Rodrigues, K. (2016). Systematic and palaeoecological significance of the first record of Pygocephalomorpha females bearing oöstegites

(Malacostraca, Peracarida) from the lower Permian of southern Brazil. *Palaeontology*, *59*(6), 817–826. doi: 10.1111/pala.12260

Schram, F. R. (1977). Paleozoogeography of Late Paleozoic and Triassic Malacostraca. *Systematic Zoology*, *26*, 367–379. doi: 10.2307/2412793

Schram, F. R. (1981). Late Paleozoic crustacean communities. *Journal of Paleontology*, *55*(1), 126–137.

Wills, M. A., Jenner, R. A., & Dhubhghaill, C. N. (2009). Eumalacostracan evolution: Conflict between three sources of data. *Arthropod Systematics & Phylogeny*, *67*(1), 71–90. doi: 10.3897/asp.67.e31689

Woodward, H. (1907). IV. On the genus *Pygocephalus* (Huxley), a primitive schizopod crustacean, from the Coal-Measures. *Geological Magazine*, *4*(9), 400–407. doi: 10.1017/S0016756800133746

CLASSIFICATION OF REMOPLEURIDIDAE HAWLE & CORDA (1847) (OLENIDA): A CASE OF STUDY

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Keywords: taxonomy, Remopleurididae, Olenida.

Remopleurididae Hawle & Corda, 1847 is a diverse and taxonomically problematic group of trilobites, comprising benthic to pelagic forms recorded from the uppermost Cambrian to the Upper Ordovician, with occurrences dating back to the early Furongian (Palmer, 1968). Information about the family is fragmented and dispersed across numerous publications, some of which are very difficult to access, making their assessment challenging. As a result, its classification remains complex. Additionally, their high morphological disparity (see María-Dorado *et al*. this volume) highlights the need for a comprehensive re-examination of the family as a whole. In light of this issue, we review the principal literature on the classification of Remopleurididae and compile relevant data on the range of morphologies present within the family.

The family was first erected by Hawle and Corda (1847) to accommodate the genera *Remopleurides* Portlock, 1843 and *Amphitryon* Hawle & Corda, 1847. Since then, their complex classification involves multiple groups and subgroups that were broadly used and discussed by many authors (Raymond, 1924; Kobayashi, 1935; Henningsmoen, 1951; Kobayashi, 1953; etc.). Historically, taxa belonging to Remopleurididae (*sensu* Jell & Adrain, 2003) have been assigned to a superfamily comprising a variable number of families, most consistently including Kainellidae Ulrich & Resser, 1930, Richardsonellidae Raymond 1924 and Remopleuridae. The last two have been highly controversial over the years for their similarities in morphology, with Kainellidae being treated ultimately as a junior synonym of Richardsonellidae. The most recent attempt to establish a consensus was provided by Jell and Adrain (2003) in their comprehensive work on trilobite systematics. The authors synonymized the most likely paraphiletic groups Richardsonellidae and Kainellidae, as well as Atratebiinae Shergold, 1980, within the likely monophyletic Remopleurididae (*sensu stricto*) (see Adrain, 2013). However, this proposal has not been consistently adopted in subsequent studies, and classifications have continued to vary considerably among authors, with genera assigned to either families and little consensus regarding their hierarchical classification (see Tortello & Esteban, 2019; Wei *et al*., 2023; Smith & Allen, 2023). In addition to this, many genera are not well defined and/or have been reassigned and synonymized repeatedly, resulting in taxonomically ambiguous groupings that are difficult to track and define.

Remopleurididae is a diverse group encompassing highly disparate morphologies (Fig. 1). Their overall affinity has long been recognized, with *Apatokephalus* Brögger 1896 frequently regarded as the most probable link among its constituent taxa (Kobayashi, 1953; Ross, 1953, Nikolaisen, 1991). In order to avoid the paraphyly inherent in earlier classifications, recent works have treated Remopleurididae as a single family (*e.g*., Adrain *et al.,* 2009; Adrain, 2013). Given the large number

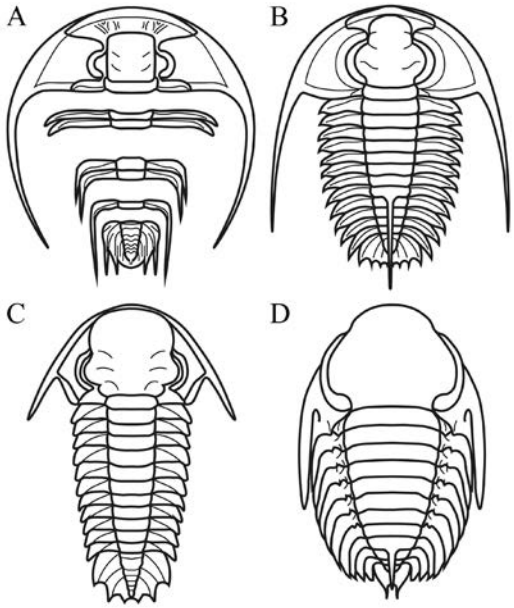

Figure 1. Main general morphologies in Remopleurididae. **A,** *Kainella* (early Tremadocian); **B,** *Apatokephalus* (middle-late Tremadocian); **C,** *Robergia* (Middle - Upper Ordovician); **D,** *Hypodicranotus* (Upper Ordovician).

of taxa involved (over 70 genera and 400 species), comprehensive phylogenetic analyses are still lacking, and thus this classification remains tentative. Subdivisions into major groups should provide a practical approach for studying the family. Within this framework, relationships among the more basal taxa remain poorly resolved. In light of this problem, recently revised collections from the Furongian–Tremadocian of the Cordillera Oriental of Argentina, have revealed a higher taxonomic diversity than previously recognized. These advances offer the opportunity to clarify the basal part of the family, through a comprehensive re-evaluation of Remopleurididae, ultimately contributing to the resolution of these systematic uncertainties and providing new insights for phylogenetic analyses.

REFERENCES

Adrain, J. M., Peters, S. E., & Westrop, S. R. (2009). The Marjuman trilobite Cedarina Lochman: thoracic morphology, systematics, and new species from western Utah and eastern Nevada, USA. *Zootaxa*, *2218*(1), 35–58.

Adrain, J. M. (2013). Chapter 20. A synopsis of Ordovician trilobite distribution and diversity. *Geological Society,* London, *Memoirs*, *38*(1), 297–336. doi: 10.1144/m38.20

Hawle, I., & Corda, A. J. C. (1847). Prodrom einer monographie der bohemischen Trilobiten. Koeniglichen Boehmischen Gesellschaft der Wissenschaften (Prague), *Abhandlungen*, *5,*176.

Henningsmoen, G. (1951). Remarks on the classification of trilobites. *Norsk geologisk tidsskrift*, 29, 174–217.

Jell, P. A., & Adrain, J. M. (2003). Available generic names for trilobites. *Memoirs of the Queensland Museum, Nature*, *48*(2), 331–551.

Kobayashi, T. (1935). The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology, part 3. Cambrian faunas of South Chosen with special study on the Cambrian trilobite genera and families. Journal of the Faculty of Science. *Imperial Tokyo University, Section II, 4*, 49–344.

Kobayashi, T. (1953). On the Kainellidae. *Japanese Journal of Geology and Geography, 23*, 59–67.

Nikolaisen, F. (1991). The Ordovician trilobite genus Robergia Wiman, 1905 and some other species hitherto included. *Norsk geologisk tidsskrift*, *71*, 37–62.

Palmer, A. R. (1968). Cambrian trilobites of east-central Alaska. *US Geological Survey*, 559B, 1–115.

Raymond, P. E. (1924). New Upper Cambrian and Lower Ordovician trilobites from Vermont. *Proceedings of the Boston Society of Natural History, 37*, 389–466.

Ross, Jr, R. J. (1953). Additional Garden City (Early Ordovician) trilobites. *Journal of Paleontology*, 633–646.

Smith, P. M., & Allen, H. J. (2023). Early Ordovician trilobites from Barnicarndy 1 stratigraphic well of the southern Canning Basin, Western Australia. *Alcheringa: An Australasian Journal of Palaeontology*, *47*(3), 234–291. doi: 10.1080/03115518.2023.2226194

Tortello, M. F., & Esteban, S. B. (2019). Trilobites and Sedimentary Settings from the Lower Ordovician (Tremadocian; Bienvillia tetragonalis Biozone) of Iturbe, Jujuy Province, Argentina. *Ameghiniana*, *57*(1), 9–32.

Wei, X., Wang, K., Zhou, Z. Q., Cui, Y. N., Zhang, Z. T., & Liu, J. B. (2023). A new late Katian (Late Ordovician) trilobite association from Zhenxiong, northeastern Yunnan, Southwest China and its palaeoecological implications. *Palaeoworld*, *32*(2), 333–353.

EVOLUTIONARY DYNAMICS OF OLENIDAE THROUGH THE LATE CAMBRIAN AND ORDOVICIAN

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Keywords: Olenidae, phylogenetics, Palaeobiogeography, morphological disparity, diversification.

BACKGROUND

Throughout the Cambrian and Ordovician, global biodiversity increased markedly while ecological interactions and community structure became progressively more complex, leading to a major restructuring of marine ecosystems (Sepkoski, 1997; Webby *et al*., 2004; Servais *et al*., 2010). The Furongian–Early Ordovician interval represents a pivotal phase in this transition, linking the Furongian extinction events with the early stages of the Ordovician radiation (Fan *et al*., 2020). The family Olenidae, one of the most emblematic trilobite groups of the Cambrian–Ordovician, reached its diversity peak during this interval. Olenids crossed the Furongian extinction events, expanded their geographic distribution, and later declined during the early phases of the Great Ordovician Biodiversification Event, as increasingly complex marine communities reshaped global biodiversity patterns.

Traditionally interpreted as highly specialized trilobites associated with dysoxic environments (*e.g*., Fortey, 1985, 1989, 1999, 2000), recent studies reveal greater ecological and morphological variability within the family than previously recognized (*e.g*., Balseiro *et al*., 2011; Mángano *et al*., 2021; Serra *et al*., 2021; Drage & Pates, 2025; Monti & Serra, 2026). At the same time, olenid relationships have begun to be reassessed using explicit morphological datasets and quantitative phylogenetic methods (*e.g*., Monti & Confalonieri, 2017, 2019; Hopkins, 2019; Monti *et al*., 2022), while their palaeogeographic history has started to be explored through the integration of occurrence data and phylogenetic information (*e.g*., Monti *et al*., 2023; Monti & Serra, 2026).

Over the last decade, new analytical approaches and palaeobiological studies have provided fresh insights into phylogenetic relationships, ecological distribution, and palaeogeographic history. Together, these advances provide a framework for exploring the evolutionary dynamics of Olenidae through time.

This contribution synthesizes recent progress on Olenidae evolution, focusing on their phylogenetic relationships, palaeogeographic distribution, and morphological diversification. By integrating phylogenetic, biogeographic, and morphometric evidence, it explores patterns of diversification, dispersal, and survival across the late Cambrian and Ordovician.

METHODS

Previously published morphological matrices were combined and revised (Hopkins, 2019; Monti & Confalonieri, 2019; Monti *et al*., 2022) to obtain a representative sample of olenid diversity and palaeogeographic distribution. The ingroup includes representatives of six olenid subfamilies (Oleninae, Pelturinae, Plicatolininae, Leptoplastinae, Triarthrinae, Balnibarbiinae) and the family Hypermecaspididae. Phylogenetic relationships were analysed using Bayesian inference with

tip-dating approaches. The tree was modelled using a fossilized birth–death (**FBD**) process, with an uncorrelated lognormal relaxed clock used to model among-branch rate variation. Tip ages were sampled uniformly. Mk substitution model and univariate Brownian motion model were used for discrete and continuous characters, respectively. We ran two independent replicates of 100,000 generations, using Markov chain Monte Carlo (**MCMC**) to explore tree space. Convergence to the stationary distribution and acceptable sample sizes were evaluated using the effective sample sizes (**ESS**) in Tracer (Rambaut *et al*. 2018). The consensus tree from the posterior distribution was used to assess palaeogeographic and morphological patterns.

Six areas were defined: Avalonia, Baltica, West Gondwana, East and peri-East Gondwana, Laurentia and Siberia. Palaeogeographic evolution was explored using dispersal-extinction-cladogenesis (**DEC**) models (Ree *et al*., 2005; Ree & Smith, 2008) implemented in RevBayes (Höhna *et al*., 2016), including simple and time-stratified models that incorporate distance matrices and variation in dispersal rates.

In addition, the current geometric morphometric dataset (Monti & Serra, 2026) was expanded and integrated with the phylogeny to examine patterns of morphological variation across key evolutionary intervals. Morphological data for the olenids included in the phylogeny were compiled following the TriloMorph landmarking template, which summarises cranidial shape (Randolfe *et al*., in press). Digitisation was conducted in R (R Core Team 2022), using the StereoMorph package (Olsen & Westneat, 2015). Non-shape variation was removed through Generalized Procrustes Analysis (**GPA**), using geomorph package (Adams *et al*., 2022), and morphospace occupation was quantified using principal components analysis (**PCA**). Morphological disparity was then compared across key evolutionary intervals. Phylogenetic integration of these patterns, through the construction of a phylomorphospace using phytools (Revell, 2012), is currently being explored.

RESULTS

Phylogenetic analyses suggest that the current subfamilial classification of Olenidae requires substantial revision, as several traditionally recognized groups are not recovered as monophyletic. Instead, the analysis yields alternative, mostly weakly supported groupings. Only Balnibarbiinae, Leptoplastinae, and Hypermecaspididae form well-supported monophyletic groups (clade posterior probability > 0.8). While these results differ markedly from previous analyses (Monti & Confalonieri, 2019; Wright & Hopkins, 2025), they agree with Monti and Confalonieri (2019) in questioning the monophyly of the family, owing to the placement of *Olenus gibbosus*. Furthermore, as in Wright and Hopkins (2025), Hypermecaspididae is recovered within Olenidae, although with low support (clade pp < 0.3).

Preliminary palaeogeographic reconstructions suggest episodes of geographic expansion across the Cambrian–Ordovician transition. Dispersal appears to have played a key role in the early spread of the group. Baltica and West Gondwana are the main source areas, with dispersal occurring primarily towards Avalonia and Laurentia. These patterns are consistent with relatively high dispersal capacity, possibly facilitated by stepping-stone pathways among the numerous microcontinents and terranes present at that time. The model also suggests that cladogenetic range subdivision was more common than sympatric range inheritance.

By the end of the Early Ordovician, olenids experienced a marked decline in diversity, a pattern previously linked to the increasing ecological complexity associated with the Great Ordovician Biodiversification Event. However, three phylogenetically separate lineages persisted beyond this decline, corresponding broadly to balnibarbiinids, hypermecaspidids, and triarthrinids. Because these surviving lineages are not recovered as a single closely related group, they may represent

independent evolutionary trajectories that persisted through the ecological restructuring of marine ecosystems during the Ordovician. Ancestral range reconstructions suggest that their diversification was largely associated with Laurentia and West Gondwana.

Morphometric analysis suggests that the geographic expansion and phylogenetic diversification of olenids coincided with a marked expansion of morphospace during the late Furongian (Jiangshanian–Stage 10). Morphological disparity increased during Stage 10, suggesting that morphological diversification accompanied key evolutionary transitions during this interval. During the Middle and Late Ordovician, morphospace occupation shifted toward more extreme morphologies distributed across multiple independent lineages, indicating the emergence of distinct evolutionary trajectories among the surviving clades.

CONCLUSION

These results highlight the evolutionary flexibility of olenids and suggest that their diversification was shaped by the interaction between ecological opportunity, dispersal dynamics, and large-scale environmental changes across the Cambrian–Ordovician transition. Phylogenetic evidence indicates that the current subfamilial classification requires revision, while palaeogeographic patterns suggest that dispersal was an important factor in the early olenid expansion. The subsequent decline by the end of the Early Ordovician was followed by the persistence of a few independent lineages, likely representing distinct evolutionary responses to the restructuring of marine ecosystems during the Ordovician. The integration of morphometric and phylogenetic data further suggests that morphological diversification accompanied these changes, highlighting the ecological flexibility of the group.

REFERENCES

Adams, D. C., Collyer, M. L., Kaliontzopoulou, A. & Baken, E. K. (2022). Geomorph: Software for geometric morphometric analyses. R package version 4.0.4. https://cran.r-project.org/package=geomorph

Balseiro, D., Waisfeld, B. G.,& Vaccari, N. E. (2011). Paleoecological dynamics of Furongian (late Cambrian) trilobite-dominated communities from northwestern Argentina. *Palaios,* 26, 484–499. doi: 10.2110/palo.2010.p10-152r

Drage, H.B., & Pates, S. (2025). Hierarchical importance of factors impacting trilobite cephalic disparity. *BioRxiv*, 2025-07. doi: 10.1101/2025.07.08.663686

Fan, J. X., Shen, S. Z., Erwin, D. H., Sadler, P. M., MacLeod, N., Cheng, Q. M., Hou, X. D., Yang, J., Wang, X. D., Wang, Y., Zhang, H., Chen, X., Li, G. X., Zhang, Y. C., Shi, Y. K., Yuan, D. X., Chen, Q. & Zhao, Y. Y. (2020). A high-resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity. *Science, 367* (6475),272–277. doi: 10.1126/science.aax4953

Fortey, R.A. (1985). Pelagic trilobites as an example of deducing the life habits of extinct arthropods. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh, 76*(2-3), 219–230. doi: 10.1017/S0263593300010452

Fortey, R. A. (1989). There are extinctions and extinctions: examples from the Lower Palaeozoic. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *325*(1228), 327–355. doi: 10.1098/rstb.1989.0092

Fortey, R. A. (1999). Olenid trilobites as chemoautotrophic symbionts. Acta Universitatis Carolinae, *Geologica, 43*, 355–356.

Fortey, R. (2000). Olenid trilobites: the oldest known chemoautotrophic symbionts?. *Proceedings of the National Academy of Sciences*, *97*(12), 6574–6578. doi: 10.1073/pnas.97.12.6574

Höhna, S., Landis, M. J., Heath, T. A., Boussau, B., Lartillot, N., Moore, B. R., Huelsenbeck, J. P., & Ronquist, F. (2016). RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. *Systematic Biology*, *65*(4), 726–736.

Hopkins, M. J. (2019). Phylogenetic analysis and revision of the trilobite subfamily Balnibarbiinae (Olenidae). *American Museum Novitates*, *2019*(3928), 1–20.

Mángano, M. G., Buatois, L. A., Waisfeld, B. G., Muñoz, D. F., Vaccari, N. E., & Astini, R. A. (2021). Were all trilobites fully marine? Trilobite expansion into brackish water during the early Palaeozoic. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1944). doi: 10.1098/rspb.2020.2263

Monti, D. S., & Confalonieri, V. A. (2017). Comparing phylogenetics and linear morphometrics to solve the generic assignment of Parabolinella? triarthroides Harrington (Trilobita, Olenidae). *Journal of Paleontology*, *91*(5), 919–932. doi: 10.1017/jpa.2017.60

Monti, D. S., & Serra, F. (2026). Biogeographical patterns and ecological differentiation of Olenidae across the Cambrian-Ordovician transition. *Lethaia*, *59*(4), 1–17. doi: 10.18261/let.59.4.5

Monti, D. S., Confalonieri, V. A. (2019). First cladistic analysis of the trilobite family Olenidae from the Furongian and Ordovician. *Lethaia, 52* (3), 304–322. doi: 10.1111/let.12313

Monti, D. S., Tortello, M. F., & Confalonieri, V. A. (2022). A phylogenetic approach to the study of the evolution of Hypermecaspididae (Olenida, Trilobita). *Papers in Palaeontology*, *8*(3), e1433. doi: 10.1002/spp2.1433

Monti, D. S., Confalonieri, V. A., & Tortello, M. F. (2023). The Central Andean Basin as a dispersal centre: biogeographic patterns of olenid trilobites during the late Cambrian–Early Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *618*, 111519. doi: 10.1016/j.palaeo.2023.111519

Olsen, A. M., & Westneat, M. W. (2015). StereoMorph: an R package for the collection of 3D landmarks and curves using a stereo camera set-up. *Methods in Ecology and Evolution*, *6*(3), 351–356.

R Core Team. (2022). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, *67*(5), 901–904. doi: 10.1093/sysbio/syy032

Randolfe, E. A., Serra, F., Balseiro, D., María-Dorado, J., Aquino, D. F., Parry, S. L., Monti, D. S., Handkamer, N. M., Vaccari, N. E., Rustán, J. J., Waisfeld, B. G. (2026). Building the trilobite morphospace: the influence of different morphological structures. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh.* [Special volume] *"A Palaeontological Oddyssey: A tribute to Euan Clarkson DSc, FRSE (1937–2024)"*

Ree, R. H., Moore, B. R., Webb, C. O., & Donoghue, M. J. (2005). A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, *59*(11), 2299–2311. doi: 10.1111/j.0014-3820.2005.tb00940.x

Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, *57*(1), 4–14. doi: 10.1080/10635150701883881

Revell, L. J. (2012), phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223. doi: 10.1111/j.2041-210X.2011.00169.x

Sepkoski Jr, J. J. (1997). Biodiversity: past, present, and future. *Journal of Paleontology*, *71*(4), 533–539.

Serra, F., Balseiro, D., Vaucher, R., & Waisfeld, B. G. (2021). Structure of trilobite communities along a delta-marine gradient (lower Ordovician; Northwestern Argentina). *Palaios*, *36*(2), 39–52.

Servais, T., Owen, A. W., Harper, D. A., Kröger, B., & Munnecke, A. (2010). The great Ordovician biodiversification event (GOBE): the palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *294*(3–4), 99–119. doi: 10.2110/palo.2020.013

Webby, B. D., Paris, F., Droser, M. L., & Percival, I. G. (Eds.). (2004). *The great Ordovician biodiversification event.* Columbia University Press.

Wright, D. F., & Hopkins, M. J. (2025). Assessing the impact of character evolution models on phylogenetic and macroevolutionary inferences from fossil data. *Palaeontology*, *68*(5), e70031. doi: 10.1111/pala.70031

A SYSTEMATIC REVISION OF THE TRILOBITE GENUS *CEKOVIA* ŠNAJDR (ILLAENIDAE) FROM THE UPPER ORDOVICIAN OF HIGH LATITUDE PERI-GONDWANA

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Keywords: Gondwana, Ordovicia, Illaenidae.

The smooth exoskeleton that characterizes the trilobite family Illaenidae (and other illaenimorphs) causes considerable difficulties in taxonomic differentiation. A few classical attempts to recognize the structure of the family have been made (*e.g.*, Jaanusson 1954, Lane & Thomas 1983, Whittington, 1997), but we are far from a satisfactory state of knowledge and understanding. More recently, a genus-based strategy has been adopted (*e.g.*, Amati & Westrop, 2004; Carlucci *et al*., 2012; Pereira *et al*., 2017), and this may be the most effective way to deal with this problematic family and move towards a broader systematic framework. After all, fewer than 30 valid genera are currently recognized, making such an approach feasible (as long as classical systematics can stay afloat within current scientific strategies). Within this context, the genus *Cekovia* Šnajdr, 1956 represents a challenging taxon. Since its erection in the Upper Ordovician strata of the Czech Republic, it has frequently been used as a "host" genus for both old and new species lacking clear distinguishing features, leading to a heterogeneous and unstable taxon.

The present work provides a systematic revision of *Cekovia*, based on the reassessment of type material and additional specimens, including new or recent data from Portugal, Spain and Morocco. The main objectives are to redefine the diagnosis of the genus, revise the species currently assigned to it, evaluate its stratigraphic and palaeobiogeographic distribution, and clarify its systematic position within Illaenidae.

The genus is here considered to be restricted to the high-latitude peri-Gondwanan realm, being widely represented in the Upper Ordovician of the Czech Republic, Portugal, Spain, France and Morocco. The oldest known occurrence comes from the basal Sandbian of Morocco (Gutiérrez-Marco *et al*., 2022), and its last unequivocal occurrence from the uppermost Katian (Villas *et al*., 2016; Pereira *et al*., 2025), thus characterizing the Sandbian–Katian interval. *Cekovia* became one of the most characteristic elements of the upper Katian carbonates of this biochorema, associated with the BODA event, even attaining an opportunistic character (*e.g.*, Romero *et al*., 2025).

Cekovia is currently represented by eight species: *C. transfuga* Šnajdr (type-species), *C. goetzi* Šnajdr, *Illaenus loredensis* Thadeu, *I. munieri* Kerforne, *C. perplexa* Hammann, *I. salteri* Barrande, *C. tenuis* Hammann, and one new species from Portugal. All species were revised based on their type material and additional specimens, except *C. munieri*, whose type material could not be accessed. The original documentation of this species is insufficient to establish diagnostic featuress, and current knowledge relies on Spanish material considered conspecific by previous authors. Consequently, *C. munieri*, defined back in 1900, may represent a senior synonym of several subsequently defined species. Only one of the originally illustrated specimens can be confidently attributed to *Cekovia*, whereas part of the remaining ones may belong to another endemic illaenid, *Vysocania*. Resolving this issue requires revision of the original material and new collections from the Rosan Formation. The Moroccan material, only documented in the last decade, highlights the still limited knowledge of many illaenids compared to other trilobites from

the same stratigraphic intervals in Morocco, and it is therefore likely that additional occurrences of *Cekovia* will be identified in this country.

Morphological analysis reveals moderate variability within the genus. At the cranidial level, two main morphotypes are recognized: one with short dorsal furrows and a weakly convex frontal glabellar lobe merging with the anterior cephalic region, and another with longer dorsal furrows that may or may not converge anteriorly, enclosing a more convex, subcircular frontal glabellar lobe. Intermediate forms are also present, and no clear evolutionary trend between these morphotypes is observed. Species such as *C. loredensis,* and *C. salteri* belong to the first morphotype, whereas *C. goetzi*, *C. perplexa*, *C. tenuis* and *C. munieri* belong to the second; *C. transfuga* and the younger Moroccan (*Cekovia* aff. *loredensis*) occurrence represent intermediate morphologies. This pattern suggests diversification rather than a linear evolutionary sequence, which is also supported by the segregated paleogeographical distribution of the species. Because cranidial characters alone are often insufficient, particularly in deformed material, pygidial morphology is essential for species differentiation. The most variable features are the pygidial outline, especially the anterior margin and anterolateral angles, and the morphology of the pygidial axis. Morphologies range from parabolic pygidia with wide anterolateral angles and straight anterior margins (e.g. *C. loredensis*) to sublozenge-shaped pygidia with convex anterior margins and acute anterolateral angles (*e.g., C. transfuga*), with intermediate forms in other species. The pygidial axis may be well defined or fade posteriorly and varies from subtriangular to tapering (funnel-shaped) depending on dorsal furrow curvature. These characters allow reliable species differentiation but do not indicate a clear evolutionary trend.

This work clarifies the controversial systematic position of *Cekovia*. Classically considered an illaenid (*e.g.*, Lane & Thomas, 1983), it has also been assigned to Styginidae (*e.g.*, Jell & Adrain, 2002). While *Cekovia* displays some characters recalling Styginidae (*e.g.*, posterior fixigenal border furrow, strongly divergent axial furrows, pygidial segmentation), these are also present in several illaenids or have been misinterpreted. The pygidial furrows present in *Cekovia perplexa* are interpleural (in styginids they are pleural), the rostral plate and the hypostome – here documented for the first time – lack typical styginid characters (e.g. connective suture inwardly directed). Furthermore, anterior expansion of the glabella, considered typical of Styginidae, may reflect retention of juvenile illaenid traits. Finally, it is suggested that *Cekovia* may have evolved from *Ectillaenus*, based on the indistinguishable morphology of the ventral structures and on several dorsal characters that seem to reflect more than a case of morphological convergence. *Ectillaenus* is the most abundant and diverse illaenid in the high-latitude peri-Gondwanan realm during the Middle Ordovician (Floian-Darriwilian), and its successful lineage likely continued into the Late Ordovician. *Cekovia* raises immediately after *Ectillaenus* disappears, in the same geographic regions in which the latter persisted until the end of the Darriwilian. However, the scenario may be less straightforward, as the oldest record from the Sandbian of Morocco recalls the least consensual species of *Cekovia* (*C. goetzi*), and other genera (*e.g.*, *Zbirovia*), likewise linked to *Ectillaenus* lineage, may be involved.

Acknowledgments: This study was supported by Fundação para a Ciência e a Tecnologia, I.P. (Portugal) in the frame of UID/00073/2025, UID/PRR/00073/2025 and UID/PRR2/00073/2025 projects of the R&D unit of Geosciences Center (University of Coimbra, Portugal). This is a contribution to IGCP project 735.

REFERENCES

Amati, L., & Westrop, S. R. (2004). A systematic revision of *Thaleops* (Trilobita: Illaenidae) with new species from the Middle and Late Ordovician of Oklahoma and New York. *Journal of Systematic Palaeontology, 2*(3), 207–256. doi: 10.1017/S1477201904001439

Carlucci, J. R., Westrop, S. R., Amati, L., Adrain, J. M., & Swisher, R. E. (2012). A systematic revision of the Upper Ordovician trilobite genus *Bumastoides* (Illaenidae), with new species from Oklahoma, Virginia and Missouri. *Journal of Systematic Palaeontology, 10*(4), 679–723. doi: 10.1080/14772019.2011.611268

Gutiérrez-Marco, J. C., Pereira, S., García-Bellido, D. C., & Rábano, I. (2022). Ordovician trilobites from the Tafilalt Lagerstätte: New data and reappraisal of the Bou Nemrou assemblage. *Geological Society, London, Special Publications, 485*, 97–137. (for 2019). doi: 10.1144/SP485-2018-126

Jaanusson, V. (1954). Zur Morphologie und Taxonomie der Illaeniden. *Arkiv för Mineralogi och Geologi, 1*(5-6), 545–583.

Jell, P. A., & Adrain, J. M. (2002). Available generic names for trilobites. *Memoirs of the Queensland Museum, 48*, 331–553.

Lane, P. D., & Thomas, A. T. (1983). A review of the trilobite suborder Scutelluina. *Special Papers in Palaeontology, 30*, 141–160.

Pereira, S., Marques da Silva, C., Sá, A. A., Pires, M., Marques Guedes, A., Budil, P., Laibl, L., & Rábano, I. (2017). The illaenid trilobites *Vysocania* (Vaněk & Vokáč, 1997) and *Octillaenus* (Barrande, 1846) from the Upper Ordovician of the Czech Republic, Portugal, Spain and Morocco. *Bulletin of Geosciences, 92*(4), 465–490. doi: 10.3140/bull.geosci.1647

Pereira, S., Romero, S., Rábano, I., & Gutiérrez-Marco, J. C. (2024). Upper Ordovician (Katian) trilobites from the Upper Ktaoua and Lower Second Bani formations of the Anti-Atlas (Morocco). *4th Annual Meeting of the IGCP 735*, Córdoba, Argentina. *PE-APA*, *24* (5), R36.

Romero, S., Pereira, S., & Gutiérrez-Marco, J. C. (2025). Trilobites de la "Caliza de Pelmatozoos" (Ordovícico Superior) del Geoparque Mundial de la UNESCO Sierra Morena de Sevilla, SO de España. In *XL Jornadas de la Sociedad Española de Paleontología, Aracena*. *Paleontological Publications, 8*, 117.

Šnajdr, M. (1956). Trilobiti drabovských a letenských vrstev českého ordoviku. *Sborník Ústředního ústavu geologického, oddíl paleontologický, 22*, 477–533. (for 1955)

Villas, E., Colmenar, J., Gutiérrez-Marco, J. C., Pereira, S., Álvaro, J. J., García-Bellido, D. C., & Lorenzo, S. (2016). Biostratigraphic assessment of the uppermost Ordovician in the central Anti-Atlas (Morocco). *The PalAss Annual Meeting 2016*, Lyon, France.

Whittington, H. B. (1997). Illaenidae (Trilobita): Morphology of thorax, classification, and mode of life. *Journal of Paleontology, 71*(5), 878–896. doi: 10.1017/S0022336000035812

BAVARILLA ZEMMOURENSIS DESTOMBES, 1969 FROM THE FEZOUATA BIOTA SHEDS LIGHT ON THE CLASSIFICATION OF BAVARILLIDAE SDZUY, 1957 AND THE ORIGIN OF CALYMENINA SWINNERTON, 1915

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Keywords: Calymenina, taxonomy, Fezouata Biota.

The Family Bavarillidae Sdzuy, 1957 is a small trilobite clade composed of three species assigned to the genus *Bavarilla* Barrande, 1868 and currently included within the Suborder Calymenina Swinnerton, 1915 (Adrain, 2013). Although the family is considered one of the most basal clades within Calymenina (*e.g.*, Fortey, 1990), ideas about its affinities have been in constant flux, with the taxon variously considered sister taxon to Homalonotidae Chapman, 1890 (*e.g.*, Sdzuy, 1957; Whittington, 1966; Thomas ,1977), Homalonotidae and Calymenidae Swinnerton, 1915 (Hamman 1983) or the whole of Calymenina (*e.g.*, Fortey, 1990). The family shows morphological similarities with Cambrian taxa, and it has been suggested as critical in the understanding of the Cambrian origin of calymenoids (Fortey, 2001), a group with a cryptogenetic origin. However, the status of *Bavarilla* as part of Calymenina remains unclear (*e.g.*, Warburg, 1925; Přibyl, 1953; Adrain, 2013), a problem partially caused by poor understanding of the morphology of the species assigned to the genus.

Bavarilla zemmourensis Destombes, 1969 is a common species within the late Tremadocian levels of the Fezouata Shale (Morocco; cf. Martin *et al.,* 2016). New material of *Bavarilla zemmourensis* reveals key insights about the morphology of the taxon including information about the appendages. Study of the new material will improve understanding of the phylogenetic affinities of *Bavarilla* and the origin of Calymenina.

The new morphological data reveal a relatively long (sag.) preglabellar field, natant hypostome with a backwardly convex posterior border, squared rostral plate, doublure with raised lines and axial nodes in the eight posterior thoracic axial rings. In addition, the appendages of *Bavarilla* are characterised by an anterior pair of long antennae composed of multiple rectangularly shaped podomeres, followed by a series of homonomous biramous appendages. Little information about the exopodite morphology is revealed, while the endopodites are characterised by robust endites, which become particularly prominent in the most posterior appendages of the thorax. Furthermore, the distalmost podomere of the endopodite is defined by three elongated endites.

The results obtained from the study of the new material challenge the previously assumed affinity of *Bavarilla* with Calymenina. First, none of the morphological features that define *Bavarilla* are characteristic of any member of Calymenina. Second, *Bavarilla* lacks most of the morphological characters that define calymenoids (subparallel course of the anterior branch of the facial suture, upwards lifted anterior border of the cranidium, subtrapezoidal to subtriangular rostral plate, smooth or granulated doublure, paraglabellar fields, small palpebral lobes, conterminant hypostome with forked posterior border of the hypostome, pygidium with several segments). Therefore, the putative affinities of Bavarillidae with Calymenina are tentatively refuted. Possible

affinities of the family with Cambrian taxa are explored, although further work is necessary to establish the relationship of the clade.

Finally, the appendages of *Bavarilla* show a similar overall morphology to that reported in most of trilobites. *Bavarilla* endopodites stand out by the particularly elongated distal claw and the prominent endites of the posterior limbs.

REFERENCES

Adrain, J. M. (2013). A synopsis of Ordovician trilobite distribution and diversity. *Geological Society, London, Memoirs, 38*, 297–336.

Barrande, J. (1868). Silurische Fauna as der Umgebung von Hof in Bayern. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 1868*, 641–696.

Chapman, E. J. (1890). Some remarks on the classification of the trilobites as influenced by stratigraphical relations: with outline of a new grouping of these forms. *Transactions of the Royal Society of Canada* 7 (Section 4), 113–120 (for 1889).

Destombes, J., Sougy, J., & Willefert, S. (1969). Révisions et découvertes paléontologiques (Brachiopodes, Trilobites et Graptolites) dans le Cambro-Ordovicien du Zemmour (Mauritanie septentrionale). *Bulletin de la Société geologique de France* 7, 185–206.

Fortey, R. A. (1990). Ontogeny, hypostome attachment and trilobite classification. *Palaeontology, 33*, 529–576.

Fortey, R. A. (2001). Trilobite systematics: the last 75 years. *Journal of Paleontology 75*, 1141–1151.

Hammann, W. (1983). Calymenacea (Trilobita) aus dem Ordovizium von Spanien; ihre Biostratigraphie, Ökologie und Systematik. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, *542*, 1–177.

Martin, E. L., Vidal, M., Vizcaïno, D., Vaucher, R., Sansjofre, P., Lefebvre, B., & Destombes, J. (2016). Biostratigraphic and palaeoenvironmental controls on the trilobite associations from the Lower Ordovician Fezouata Shale of the central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology, 460*, 142–154.

Přibyl, A. (1953). Seznam ceskych trilobitovych rodu. *Knihovna Ústředního Ústavu Geologického, 25*, 1 – 80.

Sdzuy, K. (1957). Bemerkungen zur Familie Homalonotidae (mit Beschrei-bung einer neuen Art von Calymenella). *Senckenbergiana lethaea, 38*, 275–290.

Swinnerton, H. H. (1915) Suggestions for a revised classification of trilobites. *Geological Magazine 2*, 487–496, 538–545.

Thomas, A. T. (1977). Classification and phylogeny of homalonotid trilobites. *Palaeonlology 20*, 159–178.

Warburg, E. (1925). The trilobites of the Leptaena Limestone in Dalarne with a discussion of the zoological position and the classification of the Trilobita. *Bulletin of the Geological Institution of the University of Uppsala, 17*, 1– 446.

Whittington, H. B. (1966). Phylogeny and distribution of Ordovician trilobites. *Journal of Palaeontology, 40*, 696–737.

MOLARIA SPINIFERA: ARTIOPOD OR CHELICERATE?

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Keywords: Chelicerata, Artiopod, Cambrian, Canada.

Molaria spinifera Walcott, 1912 is an arthropod species from the Burgess Shale that has remained enigmatic since its original description. Walcott (1912) placed *M. spinifera* within the now abandoned chelicerate class Merostomata, although he described a trilobite-like shield and pair of antennae. A century later it was assigned to Artiopoda based on the presence of filiform antennae. However, recent works on early arthropod evolution and new observations of the historical material suggested that previous conclusions might be incomplete.

In this study, more than 100 specimens of *M. spinifera* were photographed and analyzed. The morphology of the dorsal exoskeleton and appendages of the species is described in detail, revealing morphological information previously unknown. With the new information obtained, we tested its phylogenetic relationships using parsimony and Bayesian inference analyses. The results support an early-diverging position within the Chelicerate stem lineage, primarily based on the presence of biramous, tubuliform cephalic appendages that were previously misinterpreted as antennae.

REFERENCES

Walcott, C. D. (1912). Cambrian geology and paleontology II: Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. *Smithsonian Miscellaneous Collections*, 57(6), 145-229.

EVOLUTIONARY MODULARITY OF A TRILOBITE FAMILY OVER THE ORDOVICIAN RADIATION AND LATE ORDOVICIAN MASS EXTINCTION

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Keywords: modularity, radiation, extinction, Ordovician, Silurian.

Animals are organized in packages. These packages, or modules, are composed of traits that have the potential to evolve semi-independently such that change in one module does not necessarily beget change in another. At the macroevolutionary level, this decoupling and relaxation of evolutionary constraints is thought to promote evolvability. Thus, it is thought that modularity facilitates rapid diversification in diverse evolutionary directions as evolutionary rates among modules may vary along phylogenetic branches. Trilobites provide an unmatched fossil record, due to their biomineralized exoskeleton, to examine modularity at the macroevolutionary level in deep time. Specifically, modularity in the trilobite cephalon (head shield) is of interest due to it being a complex structure composed of several fused segments which served multiple functions. The Middle to Late Ordovician trilobite family “Pterygometopidae” well-expresses this segmentation in the glabella, or medial lobe of the cephalon. In this study, phylogenetic relationships within this family and between related taxa are resolved using Bayesian inference showing that Pterygometopidae is paraphyletic with Phacopidae nested within the subfamily Eomonorachinae. The best fit model of modularity in the cephalon is one where the eye constitutes a module with the posterior part of the glabella contrasting with modularity patterns observed at the species level. Rates of evolution vary by subfamily and, along branches, by module particularly in Eomonorachinae. High-disparity/high-rate subfamilies within Pterygometopidae become extinct by the end of the Ordovician. Interestingly, Eomonorachinae has relatively low disparity and low evolutionary rates leading up to the Late Ordovician mass extinction which its descendant Phacopidae survives.

FIELD TRIP

FIELD TRIP:

TRILOBITES AND PALAEOZOIC MARINE ECOSYSTEMS OF THE CANTABRIAN MOUNTAINS: STRATIGRAPHY, DIVERSITY AND PALAEOBIOGEOGRAPHY IN NORTHERN SPAIN

Jorge Esteve[1] (coord.), Antonio Arriola[1], Rodrigo Castaño[2], Gerardo De-Vicente-Muñoz[1], Carlos Fernández-Rodríguez[1], Javier Fernández-Martínez[1], Inés Fuertes-Murciego[1], Alejandro González-Cloquells[1], Lukas Laibl[3], Alfonso Muñoz-Martín[1], Manuel de Paz[4], Francesc Pérez-Peris[5], Isabel Rodríguez-Garcia-de-Castro[1], Sergio Rodríguez[1], Pablo Suarez-Gonzalez[1], José-María Toyos[6], & Samuel Zamora[7]

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Keywords: Cantabrian mountains, Palaeozoic, Cambrian, Ordovician, Devonian, Carboniferous.

INTRODUCTION

Jorge Esteve

Northern Spain contains some of the most extensive and fossiliferous Palaeozoic outcrops in Europe, including trilobite faunas of outstanding international importance for systematics, biostratigraphy, and palaeobiogeography. Within this region, the Cantabrian Zone preserves an exceptionally complete stratigraphic record ranging from the Cambrian to the Carboniferous. Trilobite assemblages from these successions have played a fundamental role in reconstructing the early evolutionary history of arthropods and in establishing biostratigraphic correlations across the Ibero-Armorican domain.

Trilobites from the southern flank of the Cantabrian Mountains have been known since the pioneering studies of Verneuil and Barrande in the mid-nineteenth century. Since then, numerous authors have investigated these classic localities, which have become key reference points for the study of the European Palaeozoic. The abundance of specimens, the remarkable taxonomic diversity, and the excellent preservation observed in many localities allow researchers to address not only systematic and taxonomic questions, but also broader aspects of functional morphology, palaeoecology, and evolutionary dynamics.

This fieldtrip focuses on the Leonese sector of the Cantabrian Mountains, where exceptionally well-exposed successions spanning the Cambrian to the Carboniferous are preserved. The itinerary is organized into two afternoons and two complete days and explores several geologically related areas that record complementary fossil assemblages and a remarkable diversity of geological settings. The main localities shown in the figure 1 include San Emiliano (1), Pinos (2), Truébano (3), Los Barrios de Luna (4), Huergas (5), Barrios de Gordón (6), Colle (7) and Crémenes (8). Localities 1 to 5 belongs to the Somiedo Unit and localities 7 and 8 to the Esla Unit. Together, these localities provide an excellent opportunity to examine the stratigraphic, sedimentological

and palaeontological diversity of the region, the preservation and palaeoecological significance of trilobite communities, and their role within the broader marine ecosystems of the Palaeozoic seas that once covered the northern margin of Gondwana.

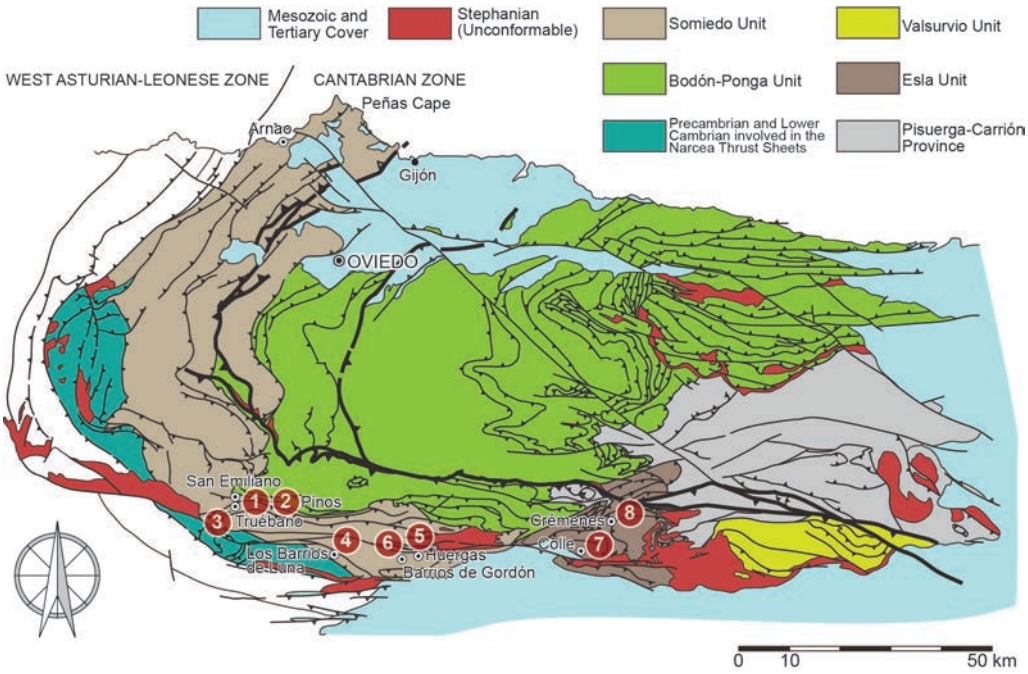

Figure 1. Geological map of the Cantabrian Zone, northern Spain, showing the main structural and stratigraphic units and the location of the field excursion stops in the Leonese sector of the Cantabrian Mountains. 1, San Emiliano; 2, Pinos; 3, Truébano; 4, Los Barrios de Luna; 5, Huergas; 6, Barrios de Gordón; 7, Colle; and 8, Crémenes.

GEOLOGICAL AND TECTONIC FRAMEWORK FOR SAN EMILIANO AREA (CANTABRIAN ZONE, N SPAIN)

Alfonso Muñoz Martín, Gerardo De Vicente Muñoz, & Carlos Fernández Rodríguez

The San Emiliano area is located within the Cantabrian Zone (**CZ**) of the Variscan orogen (NW Spain). The CZ constitutes the external thrust and fold belt of the orogen (Lotze, 1945) and is located at the core of the related orocline that subsequently bent the main previous structures (Fig. 2). It is bound to the west by the Narcea Antiform, a Variscan structure that outcrops Precambrian rocks. The northern, southern, and eastern boundaries of the CZ today are not Variscan limits but correspond to the discordance of the Mesozoic-Tertiary cover, which, together with the Palaeozoic basement, was deformed during the Alpine (Pyrenean) orogeny. The structure of the CZ is therefore the result of the superimposition of the Variscan and Alpine orogenies, between which extensional tectonics were intercalated during the Mesozoic. However, Alpine deformation essentially produced an uplift of the Palaeozoic basement and the reactivation of previous structures, so that most of the currently visible tectonic arrangement in the CZ originated during Variscan deformation.

VARISCAN STRUCTURE

In the CZ, Variscan deformation occurred at the upper tectonic structural level, owing to the lack of widespread internal deformation and metamorphism. Therefore, it is a thin-skinned tectonic style with widespread detachments (Julivert, 1971) and a basal thrust dipping about 3º to the west (Pérez Estaún *et al*., 1995). On the surface, the hanging-wall flat corresponding to the basal thrust of the major allochthonous units is generally located at the base of a Lower-Middle Cambrian carbonate unit (Láncara Formation).

The thrust faults generally have a stepped 3D geometry with ramps and flats at different stratigraphic levels (Fig. 2). Several major allochthonous units can be distinguished, with tectonic transports converging towards the center of the arc (Julivert & Arboleya, 1986). The centripetal arrangement of the structures was caused by the closure of the Asturian arc, with the development of an orocline (Perez-Estaún *et al*., 1988; Hirt *et al*., 1992; Gutierrez Alonso *et al*., 2012). In addition to the thrust faults, there are two systems of folds on a mapping scale, called longitudinal and radial (Julivert & Marcos, 1973), due to their parallel and transverse arrangement to the thrust faults. These two-fold systems are interpreted, respectively, as associated with thrust faults with tectonic transport towards the E, and as folds related to the development of the orocline (N-S shortening) (Bastida *et al.*, 1984; Alonso, 1987; Alvarez Marrón & Perez-Estaún, 1988; Shaw *et al*., 2015). This superimposition produces type 2 (mushroom, half-moon) fold interference patterns. The transverse folds show characteristics of buckling folds caused by N-S shortening (Rodríguez Fernández, 1992). Some important back-thrust structures, such as the Leon fault, complicate matters further in Alpine deformation.

Within the CZ, a series of major thrusting sheets or units can be distinguished (Julivert, 1967) (Somiedo-Correcilla, La Sobia-Bodón, Aramo, Esla, Ponga, Central Carboniferous Basin, Picos de Europa, and Pisuerga–Carrión Units), based on variations in the type of stratigraphic succession or facies, and on their structural homogeneity. The Somiedo-Correcilla, La Sobia-Bodón, and Aramo zones constitute what has been called the 'Fold and Thrust Region', because it is where both types of structures coexist. A more recent division of the CZ has been proposed by Alonso *et al.* (2009: Somiedo, Bodón-Ponga, Esla, Valsurvio and Pisuerga-Carrión Units) which did not fundamentally alter the cartographic trace of the main thrust surfaces. All these structures can be considered a normal sequence of thrust faults directed towards the foreland (the E), with the detachment level in the Láncara Formation (forward-propagation fold-and-thrust belt). However,

the León fault is an out-of-sequence thrust fault that produces apparent palaeogeographic inversions (Alonso *et al*., 2009).

The area where the meeting is held (San Emiliano) is located at the contact between the Sobia-Bodón unit (relatively autochthonous) and the Somiedo nappe (relatively allochthonous), in the vicinity of the León fault.

a) Somiedo-Correcilla Unit (SCU)

This is the CZ unit closest to the Narcea antiform (to the west) and overlies the La Sobia-Bodón unit at its eastern end. It consists of a main thrust sheet (Somiedo nappe) and a multitude of smaller thrust sheets with some differences from the main thrust body. Its south-eastern boundary is the Porma fault, although some authors suggest that the Esla nappe could also be included in this unit on stratigraphic grounds. To the north, the overthrust scales gradually lose displacement, ending in a series of folds that accommodate the deformation (Fold Region). Accompanying this decrease in the thrust slip, the outcrops of the Láncara Formation vanish. The general emplacement direction of the Somiedo nappe is towards the east, and that of Correcilla towards the northeast, although this may vary locally, and they were reworked by N-S Alpine compression. Stratigraphically, this unit is characterized by the most complete pre-Carboniferous series.

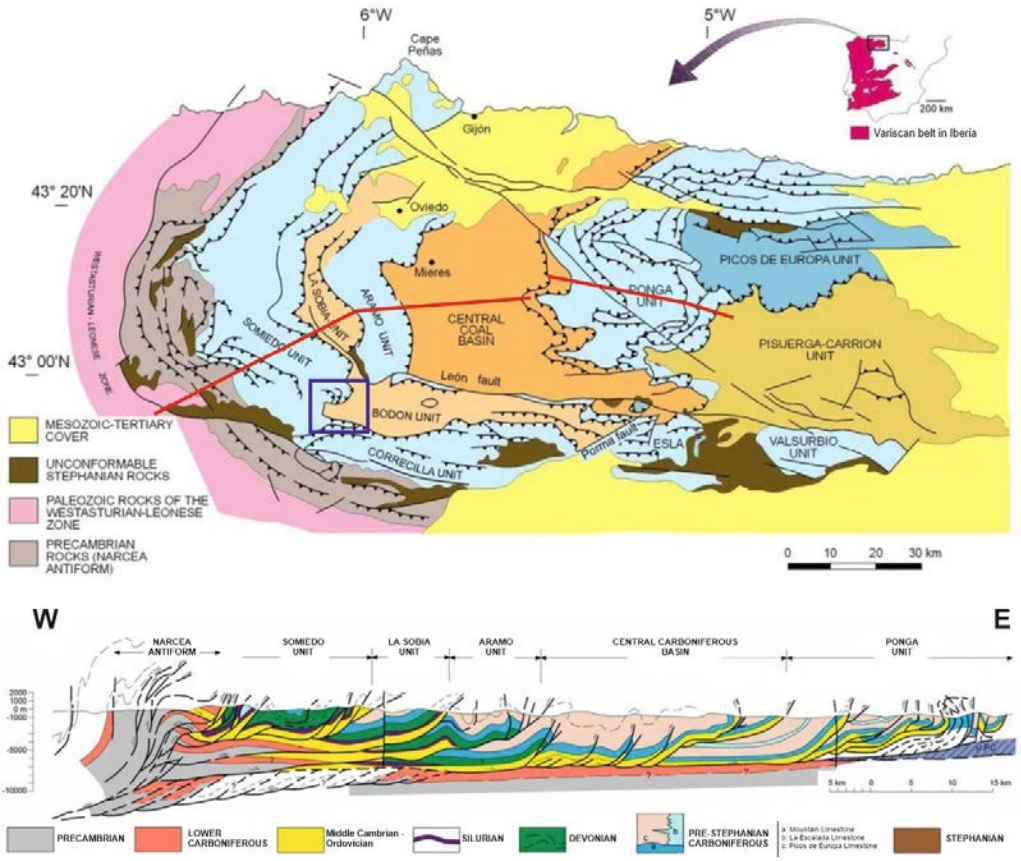

Figure 2. Simplified geological map of the Cantabrian Zone, showing the major thrust units (Julivert, 1967) and the location of the cross-section. Bottom: Longitudinal geological cross-section of the Cantabrian Zone (Pérez Estaún *et al.*, 1988). The blue box indicates the location of the International meeting (San Emiliano).

b) Sobia-Bodón Unit (SBU)

The Sobia-Bodón Unit is bounded to the south by the basal thrust of the Somiedo-Correcilla Unit, to the north by the León Fault, and to the east by the Porma Fault. Within this area, it consists of three major thrust sheets, which from south to north are the Gayo Thrust, the Bodón Thrust, and the Forcada Thrust, all of which show top-to-northeast displacement. The structure of these units is simple, except for the Manto de Bodón, which is somewhat more complex in its westernmost part, where a well-developed lateral structure is present (Villasecino and Cueto Negro). A key feature of this unit is that the basal thrust lies beneath the Herrería Fm (Cambrian).

The age of this unit and that of Somiedo-Correcilla is not known with absolute precision, since the sediments of the Stephanian B, which fossilize the main thrust faults of these units, are, on the scale of the CZ, much later. However, both the Somiedo-Correcilla and Sobia-Bodón units share a very similar Carboniferous sequence prior to their emplacement (the San Emiliano and Cuevas de Correcilla formations), which reaches the Westphalian B in the Bodón nappe. This fact determines that the beginning of the emplacement of both units must be slightly later than that age (Fig. 3).

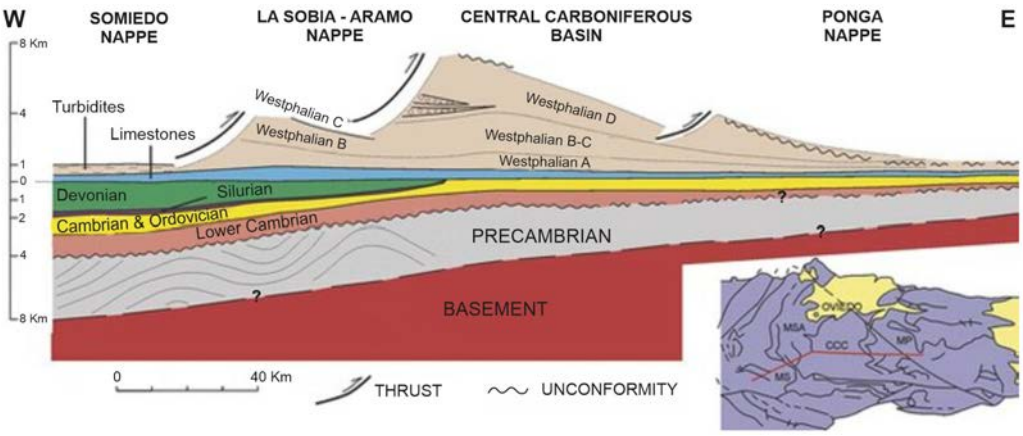

Figure 3. Palinspastic restoration of an E-W cross-section across the Cantabrian Zone (Modified after Marcos & Pulgar, 1982).

ALPINE STRUCTURE

The Cantabrian Mountain Range is, in fact, the westernmost part of the Pyrenean Orogen, whose basement belongs to the CZ of the Variscan Orogen. The cover is composed of Mesozoic and Cenozoic sedimentary rocks, decreasing in thickness towards the south (only the Voznuevo, Utrillas Formation of the Late Cretaceous, outcrops in San Emiliano area). The combination of surface geological data with in-depth geophysical data (particularly from the ESCI project - Seismic Studies of the Iberian Crust) provides information on the structure of the crust in the Cantabrian Zone. Figure 4 shows a crustal-scale section of the Cantabrian Mountain Range and the North Iberian continental margin, integrating geological, seismic, and gravimetric data that reveal the main characteristics of the Variscan and Alpine structures of the Cantabrian Mountain Range.

The Alpine Cycle begins with an extensional Permotriassic stage (Lepvrier & Martinez García, 1990; Espina, 1992) and another from the Upper Jurassic-Lower Cretaceous period. In the Cantabrian Mountains, the Pyrenean orogeny involves the Variscan basement without the Mesozoic cover

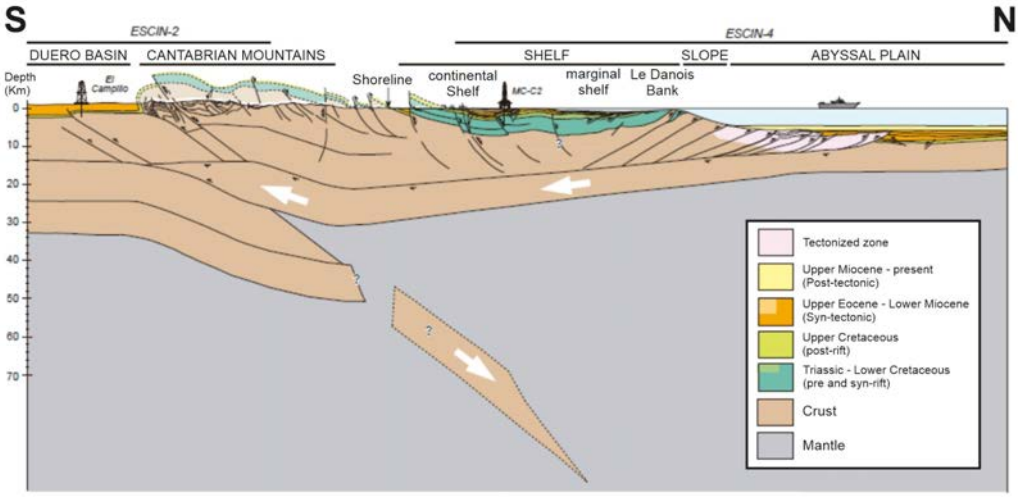

Figure 4. N-S crustal cross-section across the Cantabrian Mountains and the North Iberian continental margin, constructed by Gallastegui (2000) integrating geological, seismic, and gravity data.

appearing detached. The Alpine structure of the Cantabrian Pyrenees can be interpreted in terms of fault-bend folds (Suppe, 1983). Thus, the uplift of the mountain range is explained by a thrust fault with a long ramp, whose displacement is less than the length of the ramp. This displacement would be consumed forward by longitudinal shortening of the sheet (Pulgar & Alonso, 1993). This implies non-rigid behavior of the basement, as evidenced by the structural relationships between the basement and the cover: at a cartographic scale, the Pyrenean deformation consisted mainly of the reactivation of Variscan folds and thrust faults and the inversion of some Mesozoic extensional faults.

The northern margin of Iberia was subject to a period of compression during the Palaeocene-Miocene, because of the partial closure of the Bay of Biscay (Boillot & Malod, 1988; Alvarez-Marrón *et al*., 1997), which opened between 125-118 and 112-80 Ma (Gong *et al*., 2008), accommodating Iberia's counterclockwise rotation. This process is recorded in a well-developed accretionary wedge now buried under post-tectonic sediments (Gallastegui & Pulgar, 2002; Fernández-Viejo *et al.,* 2012). The normal faults inherited from the rifting of the Bay of Biscay were inverted during the Upper Eocene-Middle Miocene compression. A detachment formed in the extension, thinning the crust. During shortening, this plane of weakness allowed delamination of the lower crust relative to the upper crust, thereby penetrating the Cantabrian margin (as a wedge structure, Fig. 4). As a result, the possibility of the formation of a subduction zone diving towards the south was aborted. However, the calculated shortening (90 km) was absorbed by an indentation of the lower crust, while the crust of the Cantabrian Pyrenees thickened as the crust levels doubled (Gallastegui & Pulgar, 2002; Fernández-Viejo *et al.*, 2012). No volcanism related to this process has been documented. The shortening decreased towards the west and disappeared offshore in front of the Galicia Bank, where the Pyrenees ended (Druet *et al*., 2018).

Two continental synorogenic basins were formed in the Cantabrian Mountains during the Pyrenean orogeny (Fig. 5): the northern part of the Cenozoic Duero basin, which represents the 'foreland basin' of the Cantabrian Mountains, and the Cenozoic Oviedo basin, which has the characteristics of a piggyback intramountain basin (Alonso *et al.,* 1996).

The Pyrenean shortening occurred in a north-south direction, similar to that which caused the transverse folds at the end of the Variscan Orogeny, making it difficult to distinguish which structures belong to each stage. It should be noted that the most recent Pyrenean deformation developed at shallower structural levels, resulting in a more brittle tectonic style involving more faulted blocks than folds. In the San Emiliano area, there is ample evidence of Pyrenean deformation, although only fragments of the cover remain, including re-folding of the León Fault (Alonso *et al.,* 2007). In any case, the relief of the area is Alpine.

Therefore, the current landscape visible from San Emiliano—a wide, flat valley through which the River Luna flows, surrounded by mountain peaks aligned east-west—is a Pyrenean pop-down. Between Robledo de Babia and Cospedal (west of San Emiliano), the Alpine thrust, which overlies Mesozoic and Cenozoic strata approximately 250 m thick, runs subparallel to the Variscan thrust of Somiedo, which was reactivated and slightly cut along its trace (Alonso *et al.,* 2024) (Fig. 5).

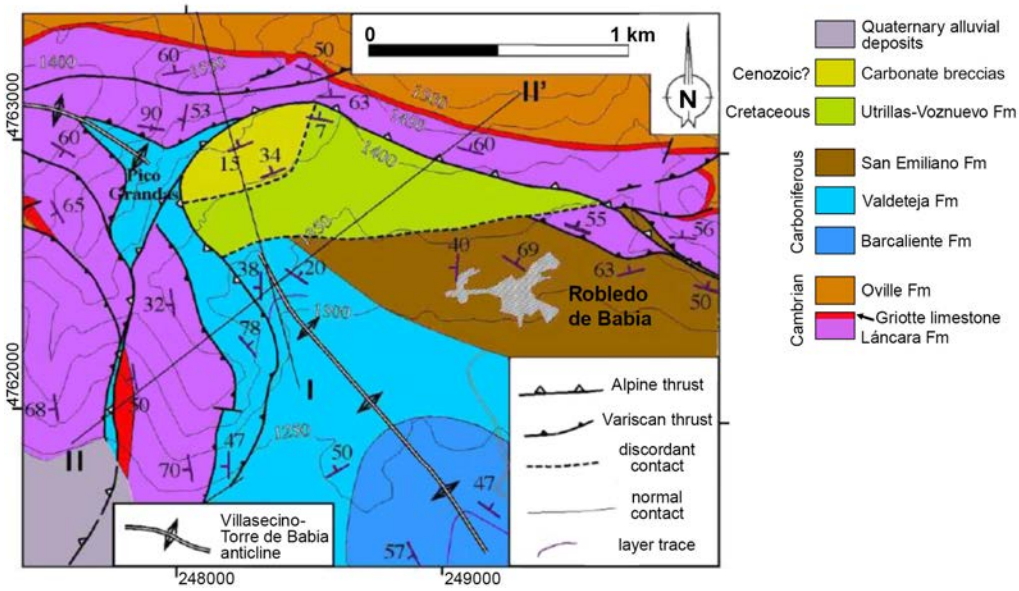

Figure 5. Mesozoic and Cenozoic sediments overlain by Paleozoic materials due to the activity of Alpine faults that cut and reactivated Variscan structures (basal thrust of the Somiedo-Correcilla Unit) during the Pyrenean deformation. Robledo de Babia area (Alonso *et al*., 2024).

THE CAMBRIAN AND CARBONIFEROUS FROM TRUÉBANO

Alejandro González-Cloquells, Isabel Rodríguez Garcia de Castro, Antonio Arriola, Javier Fernández-Martínez, Jorge Esteve & Sergio Rodríguez-García-de-Castro

Location: On the Cuesta del Sol Road, 1.5 km south of Truébano.

Coordinates: 42°56'07.8"N 6°00'18.6"W

Geological Map of Spain: 1:50,000 Los Barrios de Luna sheet (102).

Geological setting: Cantabrian Zone, Somiedo-Correcilla Unit.

Aims

» To recognize the Cambrian Láncara Formation and the Carboniferous Valdeteja Formation exposed in the Cuesta del Sol area at Truébano.

» To collect Cambrian fossil including trilobites, brachiopods, hyolithids, and echinoderms.

» To recognize the main sedimentary structures and fossil assemblages of the Carboniferous deposits at Truébano.

» To take a group photograph from the Carboniferous outcrop, looking at the Palaeozoic successions of Babia.

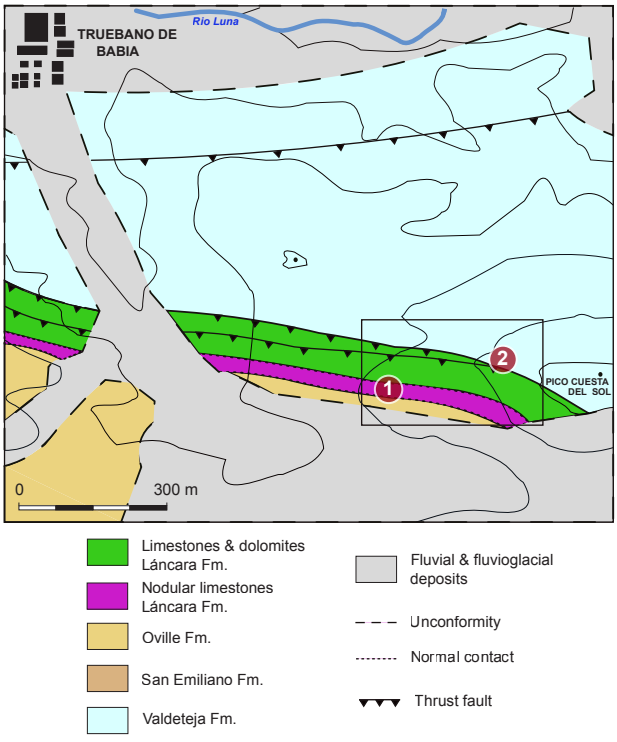

Figure 6. Geological map of the Truébano de Babia area, southern Cantabrian Mountains, northern Spain, showing the distribution of the main Cambrian to Carboniferous lithostratigraphic units. The numbered points indicate the location of the studied stops/outcrops in the Láncara Formation near Cuesta del Sol section.

STOP 1. THE CAMBRIAN FROM TRUÉBANO: THE LÁNCARA FORMATION

At Truébano, the field trip will visit a middle Cambrian outcrop of Miaolingian–Wuliuan age, located in the upper levels of the Láncara Formation at Cuesta del Sol, near Truébano de Babia (Fig. 6). The main section, Cuesta del Sol 1 (**CS1**), offers good access, lateral continuity and a rich fossil record. The Láncara Formation is the main carbonate unit of the Cambro-Ordovician succession in the Cantabrian Zone, lying between the siliciclastic Herrería Formation below and the shale-dominated Oville Formation above (see day 8 of the fieldtrip for more details). At Truébano, the exposed Upper Member is fossil-rich and records a shallow marine carbonate platform on the margin of Gondwana.

The CS1 section is about 37.9 m thick and consists of massive, marly and nodular limestones. It includes the transition between the Beleño Facies and the "griotte" Facies. Lithologically, the succession evolves from glauconitic grainstones to wackestones and packstones, with occasional mudstone intercalations. These changes reflect variations in energy, fine sediment input and benthic communities within the platform.

The fossil assemblage is highly diverse. It includes trilobites, brachiopods, hyolithids, echinoderms, chancelloriids and abundant Small Shelly Fossils. Representative taxa include *Chancelloria*, *Archiasterella*, *Protowenella lancarensis*, *Iberotreta sampelayoi*, *Genetreta trilix*, *Nisusia vaticina*, *Yorkia zafrensis*, *Lignanicystis*, *Tabladocrinus*, *Eccaparadoxides*, *Manublesia*,

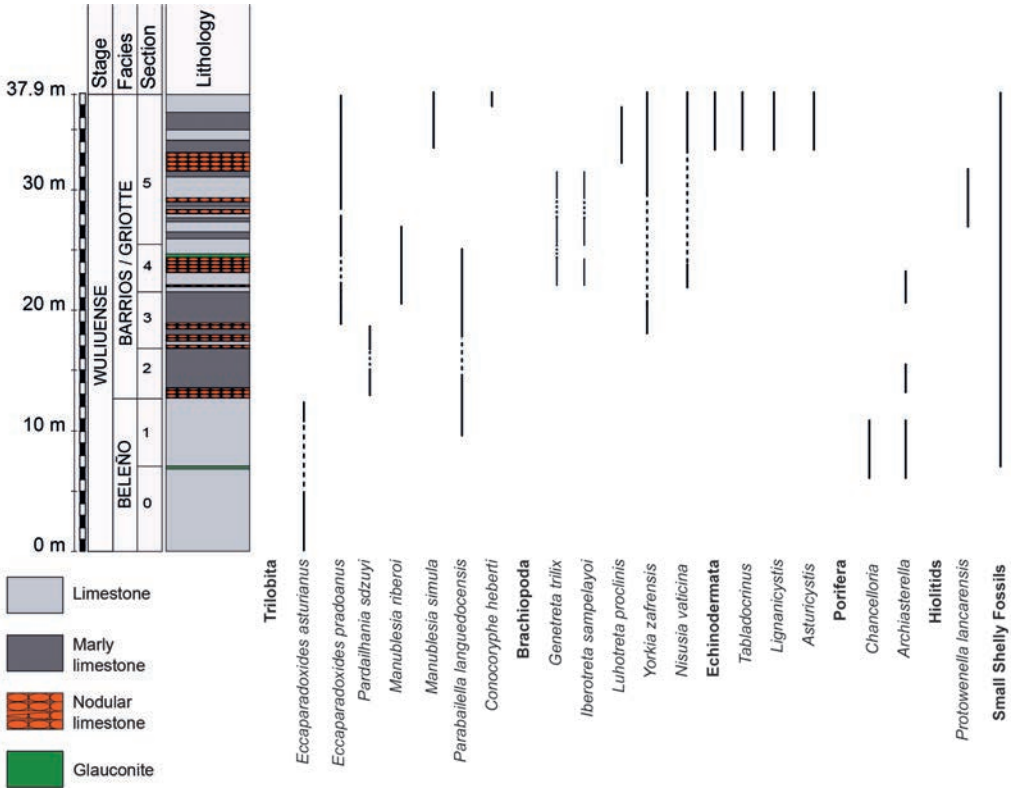

Figure 7. Stratigraphic section of the Barrios/Griotte facies in the Truébano de Babia area, showing the lithological succession, subdivision of the section, and vertical distribution of the recorded fossil assemblages.

Parabailiella and *Conocoryphe* (Figs. 7–8). This diversity indicates a complex benthic community with different modes of life, including sessile and mobile organisms, as well as filter and deposit feeders. Recent studies of Small Shelly Fossils from Truébano have greatly expanded knowledge of these communities, with more than 11,000 fossil remains distributed among 26 taxa. The results show lateral variation within the same levels, indicating that small-scale environmental differences influenced the composition of the microfauna. In addition, biomechanical studies of the phosphatic brachiopods *Iberotreta sampelayoi* and *Genetreta trilix* show that Cambrian diversity was not only taxonomic, but also functional: *Iberotreta* had a lighter, more regular shell structure, whereas *Genetreta* developed a more robust and resistant shell. Overall, the Cambrian of Truébano provides an excellent record of early marine ecosystems, linking the rocks observed in the field with early biomineralization, the diversification of marine invertebrates and the increasing complexity of benthic communities after the Cambrian Explosion.

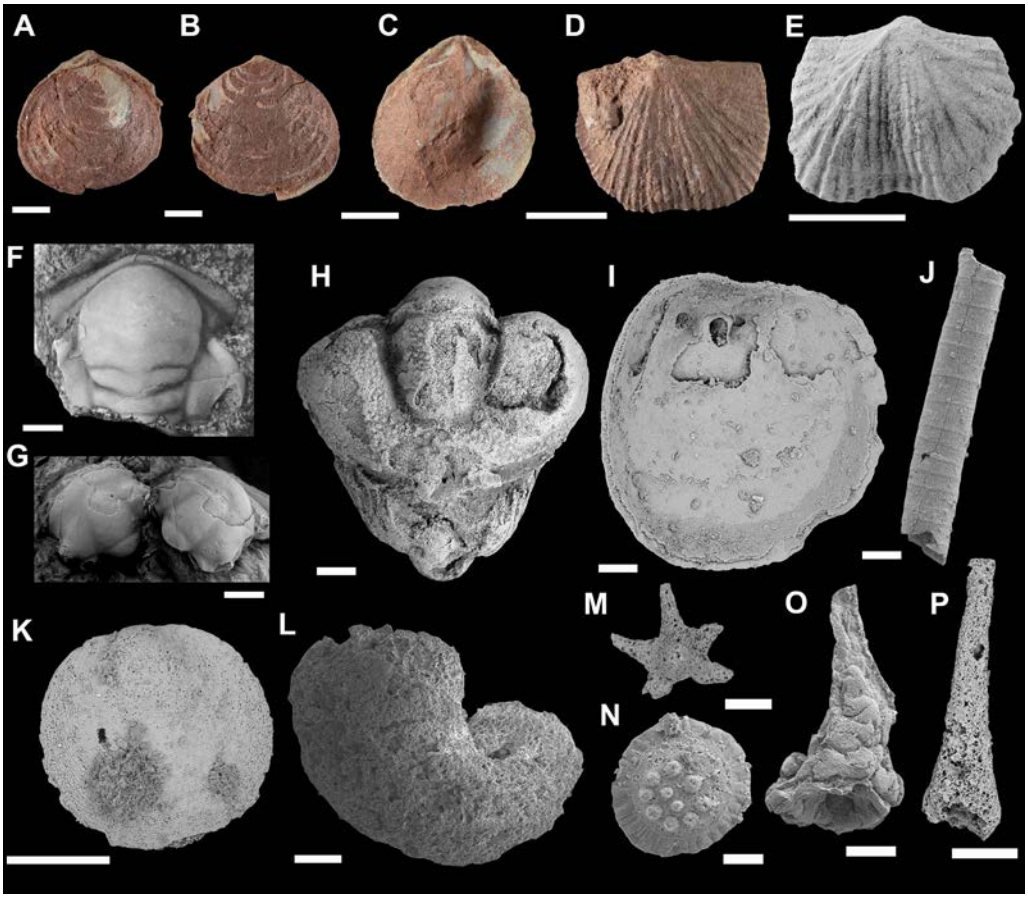

Figure 8. Fossils and microfossils from the Lancara Formation. **A–C,** *Yorkia zafrensis* **D–E,** cf. *Nisusia;* **F,** *Acadoparadoxides mureroensis;* **G,** *Berabichia eslaensis*; **H,** *Manublesia* cf. *thorali*; **I–P,** SEM photographs of small shelly fossils; **I,** phosphatic brachiopod; **J,** fossil of uncertain affinity; **K,** phosphatic brachiopod; **L,** Cambrian mollusc; **M,** internal mould of a sponge spicule; **N–O,** Palaeoscolecid sclerites; **P,** Hyolith; scale bars: **A–E**, 2 mm; **F–G**, 5 mm; **H**, 2 mm; **I**, 200 µm; **J**, 50 µm; **K**, 100 µm; **L**, 50 µm; **M–P**, 20 µm.

STOP 2. THE VALDETEJA FORMATION AT TRUÉBANO: AN EXTRAORDINARY OUTCROP

The Rosario Mine is a small, abandoned coal mine in the location named Cuesta del Sol, south of Truébano (León, Northern Spain). It consists of a Bashkirian carbonaceous shale three meters thick with coal balls that is interbedded in a limestone succession (Valdeteja Formation, Fig. 3). The limestones below and above the coal bed are very different. The basal beds at the west pit of the Rosario Mine consist in a 4.5 metre succession of positively graded sequences. The sequences have irregular bases. They start as grey rudstones and grainstones, gradually change to yellowish-brown packstones and finally to soft marls. The thickness of each sequence varies between 20 centimetres and 1.5 metres. There are centimetric to decimentric intraclasts in the rudstones, containing smaller fossils and micrite. The shapes and borders of these intraclasts

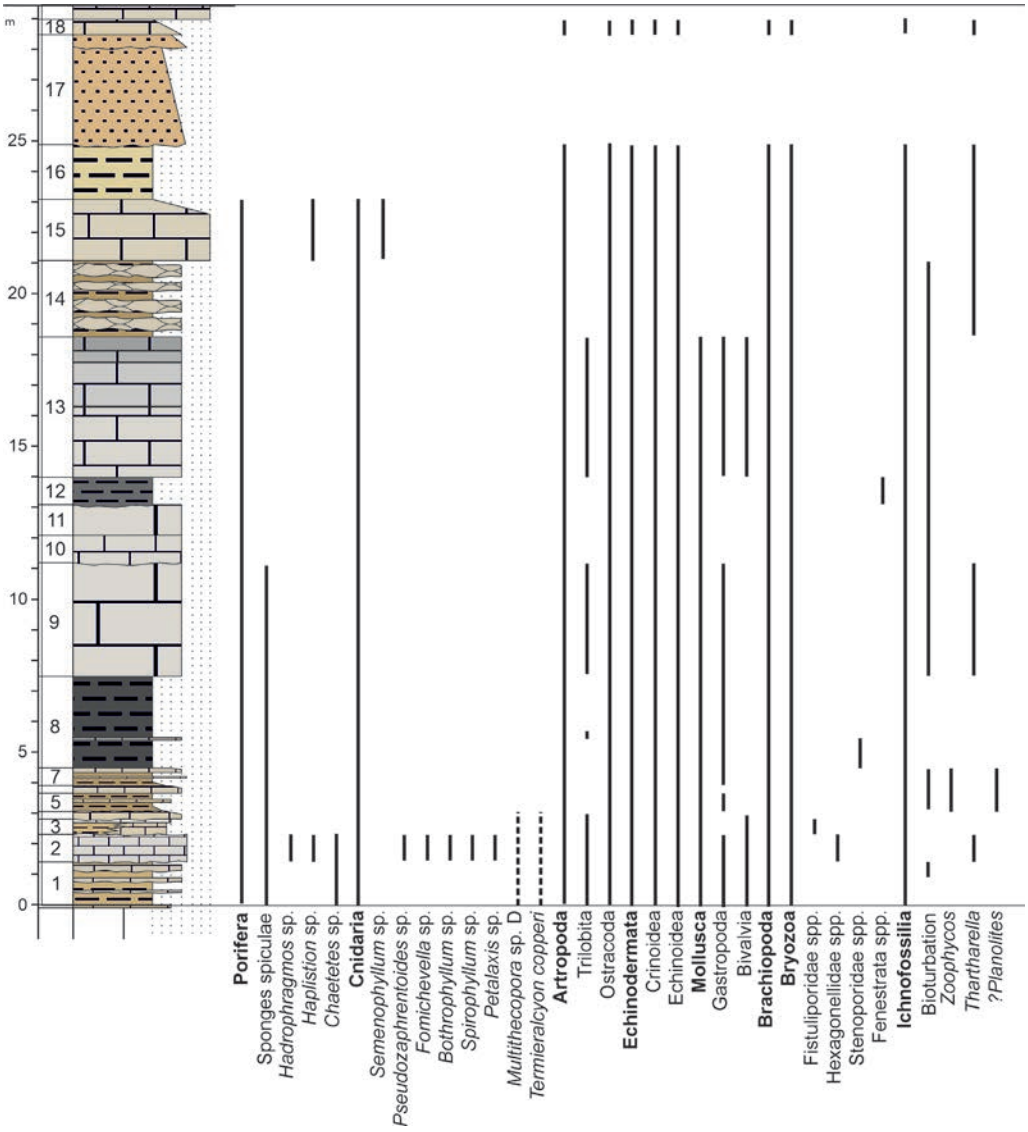

Figure 9. Stratigraphic section at the Rosario mine with the distribution of invertebrates.

are irregular. Large Hummocky cross-stratification (**HCS**) is visible in the sequences, with a wavelength between 50 centimetres and 2.3 metres.

These sequences contain a very diverse and abundant fossil assemblage, dominated by crinoidal plates. Brachiopods, chaetetids, sponges, rugose and tabulate corals, bryozoans, algospongia and foraminifers are also common; molluscs, echinoids, trilobites, ostracods, algae, and plants are also present in some of the sequences. Ichnofossils are abundant and well preserved in the marls at the top of some sequences.

The erosive bases, mass flows and HCS described in this study in the limestones below the carbonaceous shale are further evidence of waves of great wavelengths affecting the sea bottom, provoking mass flows, and producing the sedimentation of these beds. Tsunamis (Dott & Bourgeois, 1982) and storms (Gilbert, 1899) have been suggested as possible origins for HCS. Both events can trigger a variety of transportational and depositional processes such as backwash flows, turbidity currents, mass flows, etc. and both tsunamis and cyclones are possible in the geological context and climate conditions of the Cantabrian Zone during the Bashkirian. An often-overlooked process in tsunamis is the traction, the backwash current from shoreline into deeper waters (Dawson & Stewart, 2007). Coleman (1968) described layers of concentrated vegetation with interbeds of both fine and coarse sediment as one of the characteristics of tsunami-triggered marine deposits. The presence of terrestrial debris, within mass flows or turbidity currents such as present in the Rosario mine (Rodríguez-Castro *et al*., 2023) is a criterion that allows to recognise tsunami induced marine sediments (Dawson & Stewart, 2007).

The limestones of the upper part of the section above the coal are packstones of Donezella in the first meters and boundstones in the upper part. The main components of the boundstones are chaetetids, algospongia and cyanobacteria. They vary from 40 centimetres to a few metres thick. The base of some of the buildups is a continuous framestone of chaetetids, which become less common towards the upper part of the stratum (Rodríguez-Castro *et al.,* 2020, Rodríguez-Castro & Rodríguez, 2025). The gaps between the chaetetids are filled with a framestone composed of *Donezella*, cyanobacteria, and bioclasts. The presence of chaetetids and cyanobacteria (*Girvanella*) indicates that the emplacement of those mounds was shallow water, which is not common in the mounds present in the Bashkirian and Moscovian from the Cantabrian Mountains (Samankassou, 2001; Della Porta *et al*., 2002).

SYN-OROGENIC CARBONATE PLATFORMS AND ASSOCIATED MIXED CLASTIC-CARBONATE DEPOSITS, FROM THE CARBONIFEROUS OF SAN EMILIANO (LEÓN, SPAIN)

Pablo Suarez-Gonzalez, & Jorge Esteve

Location: On the Road LE 482 from San Emiliano to Pinos 2.5 km from San Emiliano.

Coordinates: 42°56'07.8"N 6°00'18.6"W

Geological Map of Spain: 1:50,000 Los Barrios de Luna sheet (102).

Geological setting: Cantabrian Zone, Somiedo-Correcilla Unit.

Aims

- To recognize the Carboniferous syn-orogenic deposits of the San Emiliano area, including the Valdeteja Formation and the San Emiliano Formation.
- To observe the lateral facies relationships between the Valdeteja carbonate platforms and the mixed clastic-carbonate deposits of the Pinos Member.
- To analyse the main sedimentary and palaeontological features of the Carboniferous succession, including turbidites, olistoliths, carbonate beds and skeletal-microbial mounds.

INTRODUCTION

The Cantabrian Zone of the Variscan Iberian Massif consists of Neoproterozoic rocks and an extremely well preserved and continuous Paleozoic sedimentary succession, which includes rocks deposited before, during and after the Variscan Orogeny (Bastida *et al.,* 2004). In particular, the San Emiliano area (León, Spain) is dominated by syn-orogenic Carboniferous deposits, which are tectonically overlain by thrust sheets of early Paleozoic rocks (Fig. 10). In this area, those thrust sheets are located towards the west, their décollement surface is the Cambrian carbonate Láncara Fm, and their transport direction was approximately towards the east (Fig. 10; Bastida *et al*., 2004). This means that during the Carboniferous, the Variscan Orogeny was developing in the west, leading to the deposition of syn-orogenic Carboniferous units in a foreland basin located to the east (Colmenero *et al*., 2002; Bastida *et al.,* 2004; Merino-Tomé *et al*., 2019). These Carboniferous units will be the focus of this fieldtrip, and they include text-book examples of carbonate platforms, clearly showing their vertical evolution and their lateral relationship with both shallower and deeper mixed clastic-carbonate deposits. The Carboniferous of the San Emiliano area consists of the following stratigraphic units (Fernández, 1993, 1995; Colmenero *et al*., 2002; Bastida *et al*., 2004; Merino-Tomé *et al*., 2019):

Alba Fm (Tournaisian-Serpukhovian): up to 30 m of red and fossiliferous nodular limestones (*griotte* facies) with radiolarites and shales, deposited as condensed marine series.

"*Caliza de Montaña*" ("Mountain Limestone") is a popular informal term that groups the two limestone units (often dolomitized) that generate the main peaks of the Cantabrian Mountains, the Barcaliente and Valdeteja Fms. Barcaliente Fm (Serpukhovian-Bashkirian): 150-350 m of black laminated limestones with scarce fossils. Valdeteja Fm (Bashkirian): grey fossiliferous limestones with highly variable thickness (up to 1000 m) because they were deposited as isolated, several-km-wide, microbial-bioclastic carbonate platforms, which were laterally related to the mixed clastic-carbonate deposits of the following unit (Fig. 11; Eichmüller, 1985; Chesnel *et al*., 2016).

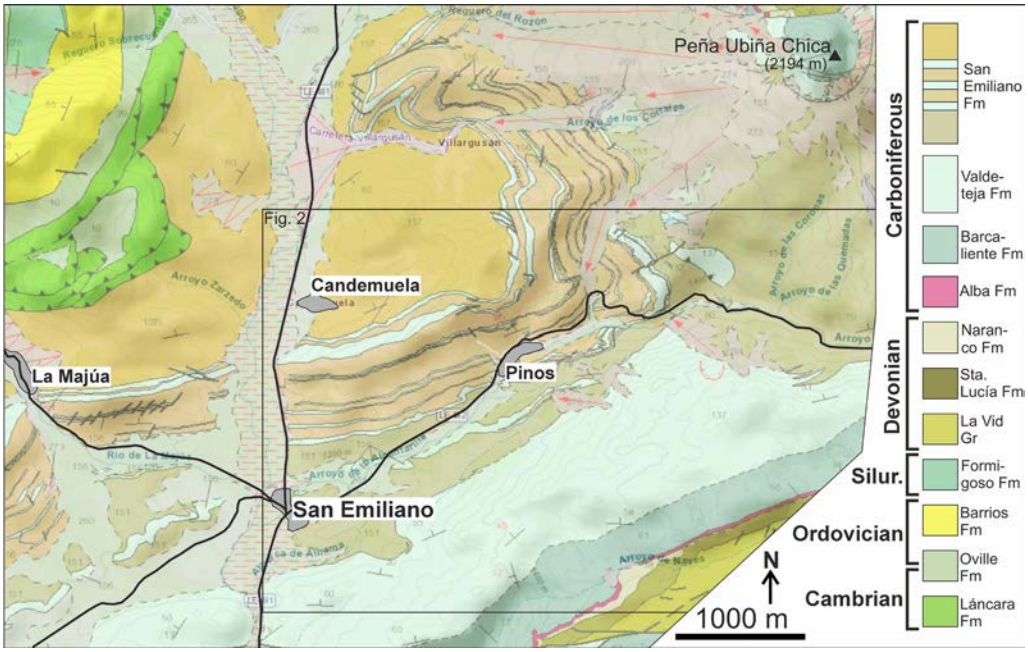

Figure 10: General geological map of the San Emiliano area. Modified after the official Online Geological Map of Spain (Merino-Tomé *et al.*, online: https://info.igme.es/visor/).

San Emiliano Fm. (Bashkirian-Moscovian): is a mainly siliciclastic unit, with interbedded carbonate and coal levels, and a highly variable thickness (>2000 m), which passes laterally to and overlies the Valdeteja Fm (Figs. 10, 11). In general, the unit has a coarsening and shallowing upwards trend, ranging from deep-water turbidite deposits to coastal environments. In the San Emiliano area (type section), the unit was formally divided into three members. The lower Pinos Mb (300-1000 m thick), laterally equivalent of the Valdeteja Fm, consists of siliciclastic and carbonate turbidites, including laterally continuous levels of carbonate olistoliths eroded from the Valdeteja Fm platforms (Fig. 11). The middle La Majúa Mb, ~1000 m of alternating siliciclastic and carbonate beds, overlying the Valdeteja Fm. The siliciclastic deposits are interpreted as prograding deltaic sequences, whereas the carbonate levels were deposited during periods of marine transgression, including very fossiliferous facies and skeletal-microbial mounds (Figs. 11, 12, 13). The upper Candemuela Mb (at least 500 m thick, top not exposed), mainly siliciclastic, with interbedded coal levels, interpreted as more proximal prograding deltaic sequences.

FIELD ITINERARY

STOP 1. WESTERN OVERVIEW

Just outside the town of San Emiliano, at one of the lowermost siliciclastic levels of the San Emiliano Fm in the western part of the study area. Overview of the top of the Valdeteja Fm and of the San Emiliano Fm, which, in this area, mainly corresponds to the alternating siliciclastic and carbonate beds of the La Majúa Mb (Fig. 12). The lateral facies change between these lower beds of the San Emiliano Fm and the upper Valdeteja Fm is observed.

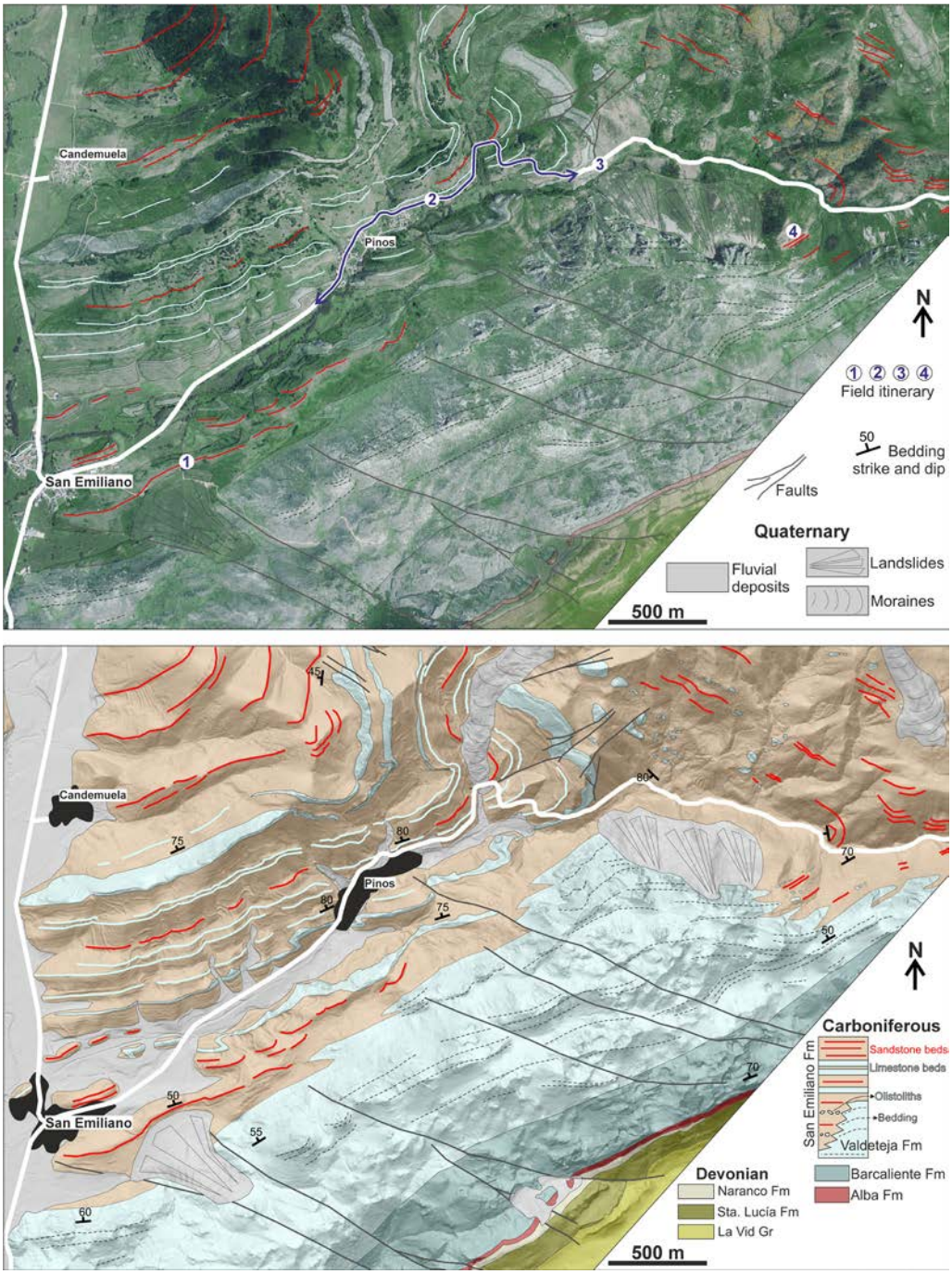

Figure 11: Detailed geological map of the fieldtrip area: above, over the aerial image; below, over the digital surface model. Both base maps obtained from the Spanish National Geographic Institute (IGN: https://centrodedescargas.cnig.es).

Figure 12: Overview of the western part of the fieldtrip area, showing the La Majúa Mb of the San Emiliano Fm, with its characteristic alternation of siliciclastic deposits (vegetated) and carbonate beds (blue arrows). Some of the carbonate beds include isolated mounds (black arrows).

Figure 13: Detail of a carbonate bed from the San Emiliano Fm, showing very abundant phylloid red alga of the genus *Archaeolithophyllum*.

STOP 2. WALK BETWEEN THE TOWNS OF SAN EMILIANO AND PINOS

Several siliciclastic and carbonate beds of the San Emiliano Fm are traversed during this walk. Stratigraphic, paleontological and tectonic observations can be made, including very fossiliferous beds dominated by the phylloid red alga *Archaeolithophyllum* (Fig. 13; Cózar *et al*., 2005; Corrochano *et al*., 2016), as well as skeletal-microbial mounds dominated by the algospongia *Donezella* and sponges (Figs. 3, 5; Bowman, 1979; Samankassou, 2001; Rodríguez-Castro & Rodríguez, 2025).

STOP 3. EASTERN OVERVIEW

Following the road east of Pinos town there is an overview of the eastern part of the study area, where the lowermost part of the San Emiliano Fm (Pinos Mb) is best observed and was originally described. The paleo-slope of the Valdeteja Fm carbonate platform can be observed from here, as well as its lateral relationship with the turbiditic facies of the Pinos Mb (Figs. 11), which include abundant olistoliths eroded from the Valdeteja Fm (Figs. 11, 14, 15).

STOP 4. DETAIL OF THE PINOS MB FACIES

Following the same road to the east, there is an accessible outcrop of the lateral change between the toe-of-slope facies of the Valdeteja Fm carbonate platform and the turbidites and olistoliths of the San Emiliano Fm (Pinos Mb, Fig. 15).

Figure 14: Overview of the eastern part of eastern part of the fieldtrip area, showing the characteristic facies of the Pinos Mb of the San Emiliano Fm, dominated by turbidite deposits, mainly siliciclastic (**S**), with abundant olistoliths (**O**) eroded from the Valdeteja Fm carbonate platforms. At the top left corner, a carbonate bed of the La Majúa Mb is observed, including two isolated mounds (**M**).

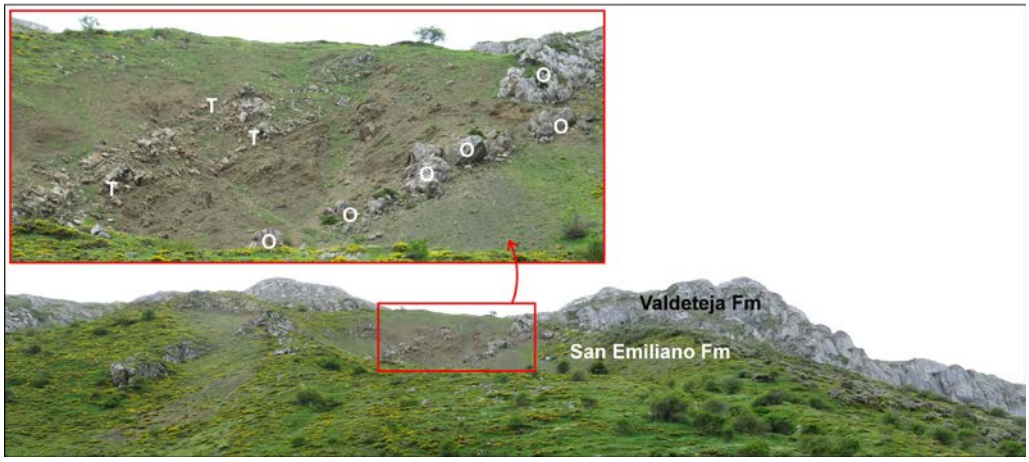

Figure 15: Outcrop 4 of the field itinerary, showing the lowermost San Emiliano Fm (Pinos Mb) laterally changing to the Valdeteja Fm. Insert shows detail of the San Emiliano Fm facies, with turbidites (**T**) and olistoliths (**O**) eroded from the Valdeteja Fm carbonate platforms.

FIRST DAY: LOS BARRIOS DE LUNA AND HUERGAS DE GORDÓN

Jorge Esteve, & Rodrigo Castaño (coords.)

The first day of the excursion will begin with a visit to the complete section of Los Barrios de Luna, which provides an ideal stratigraphic framework for understanding the Cambrian stops that will be examined during the two days of the fieldtrip, as well as for placing into context the brief excursion to the Cambrian of Truébano. Los Barrios de Luna section represents one of the most complete Cambrian–Ordovician successions in the Cantabrian Zone and has played a key role in the study of Lower Palaeozoic stratigraphy and faunas in northern Spain.

The itinerary will then continue to Huergas de Gordón, where the stratotype of the Huergas Formation (Eifelian–Givetian) is exposed. These Devonian levels are characterized by trilobite assemblages dominated by Asteropyginae, including species of *Kayserops*, *Bradocryphaeus* and forms closely related to *Neocalmonia*, together with derived phacopids. These faunas indicate relatively deeper platform environments and show clear affinities with Armorican assemblages, making this locality particularly relevant for palaeobiogeographic analyses of the Middle Devonian of the Cantabrian region.

After Huergas de Gordón, the excursion will visit Los Barrios de Gordón, where trilobite-bearing levels from the Olaja Beds are exposed. These beds represent a key transitional interval at the top of the Alba/Genicera Formation, marking the passage from red nodular limestones to the overlying Olleros / Culm-type deposits. The locality provides an excellent example of the latest Viséan–early Namurian transition in the Cantabrian Zone, with trilobite assemblages that reflect clear facies-related changes in faunal composition.

Despite their stratigraphic and palaeontological significance, the Huergas de Gordón stratotype and the Los Barrios de Gordón Olaja Beds have received comparatively little attention when compared with other classic Palaeozoic localities of the region. One of the aims of this excursion is therefore to introduce these outcrops to the wider scientific community, with the hope of stimulating new lines of research and encouraging interest among younger generations of palaeontologists.

STOP 1. THE CLASSICAL SECTION OF LOS BARRIOS DE LUNA

José María Toyos, Rodrigo Castaño, Inés Fuertes-Murciego, Javier Fernández-Martínez, & Jorge Esteve

Location: Road cut along the LE-3422 between Los Barrios de Luna and Mallo de Luna, in the classical Lower Paleozoic section of the Luna River valley.

Coordinates: 42°50'26.12"N 5°52'11.72"W

Geological Map of Spain: 1:50,000 Los Barrios de Luna sheet (102).

Geological setting: Cantabrian Zone, Somiedo Unit, on the southern limb of the Alba Syncline.

This sector of the Luna River valley belongs to the Somiedo Unit (Alonso *et al.,* 2009), corresponding to the Somiedo–Correcilla Unit of the Fold-and-Thrust Belt Region in the division proposed by Julivert (1971). It is the westernmost unit of the Cantabrian Zone, where a more complete Palaeozoic succession is preserved.

The unit is structured around a broad synformal feature known as the Alba Syncline, whose axis plunges about 20° to the southeast. As a result, in the western sections of the area, such as around Los Barrios de Luna, the succession does not reach the Upper Devonian or Carboniferous,

whereas these intervals are present farther east, in sections located in the eastern third of the Luna River valley and in the Bernesga and Torío valleys. It is also important to note that both limbs of the Alba Syncline are affected by numerous faults and that, locally, the structure is complicated by the presence of small thrust slices.

The Luna River valley contains numerous stratigraphic sections, paleontological localities, and mineral occurrences which, for many decades, have provided data of outstanding value for the understanding of regional geology. Several Geological Sites of Interest have been identified throughout the valley and are included in national and/or provincial inventories. These include stratigraphically significant sites such as the Paleozoic succession at Los Barrios de Luna, tectonically important localities such as the angular unconformity between the Precambrian and the Cambrian at Irede de Luna and the faults in the limestones of Mallo de Luna, as well as paleontological sites such as the trilobite locality at Los Barrios de Luna.

Together, these places highlight the importance of this valley for understanding the geology and palaeontology of the Cantabrian Zone and, more broadly, of the Iberian Massif, as well as of other territories with which it was linked in the geological past. In addition, the Palaeozoic of the Luna River valley is one of the Geological Sites of International Relevance (Global Geosites) recognized in Spain, having been included within the framework Lower and Middle Palaeozoic stratigraphic series of the Iberian Massif. This designation further confirms the importance of the Luna River valley for reconstructing Palaeozoic sedimentary environments.

Lithostratigraphic units: This stop includes part of one of the best-known Palaeozoic sections in the Cantabrian Zone. The road section between Los Barrios de Luna and Mallo de Luna exposes, in structural repetition, rocks ranging from the Lower Cambrian to the Upper Ordovician, including the La Herrería, Láncara, Oville, Barrios, El Ventorrillo beds, and La Serrona formations. Younger Palaeozoic units crop out farther east and north in the valley.

Age: The full section ranges from the Lower Cambrian to the Upper Ordovician, although the most relevant interval for this stop is Middle Cambrian, especially the Caesaraugustian–Languedocian fossiliferous succession.

Aims

- To visit one of the classical Lower Palaeozoic sections of the Cantabrian Zone.
- To examine the geological framework of the Luna River valley within the Somiedo Unit.
- To review the Lower Palaeozoic stratigraphic succession exposed at Los Barrios de Luna.

THE PALAEOZOIC SUCCESSION

The Luna River valley cuts across the Alba Syncline from north to south, producing a number of sections that provide excellent access to the Palaeozoic rocks of this part of the Cantabrian Zone. One of the best known is located west of Los Barrios de Luna, along the road connecting this village with Mallo de Luna (Fig. 16). This is a classic section that has been the subject of numerous studies and in which rocks ranging in age from the Lower Cambrian to the Upper Ordovician are exposed, including the La Herrería, Láncara, Oville, Barrios, El Ventorrillo beds, and La Serrona formations (Fig. 16). In other sections studied along the valley, the La Devesa Formation, of Katian age, occurs between the last two units. Younger Palaeozoic formations crop out well along road C-623, between the dam and Mirantes de Luna. In this section the following formations are exposed: Formigoso, San Pedro, Felmín, La Pedrosa, Valporquero, Coladilla (the last four included in the La Vid Group), Santa Lucía, Huergas, and finally the Portilla Formation, which locally occupies the core of the Alba Syncline (Fig. 16).

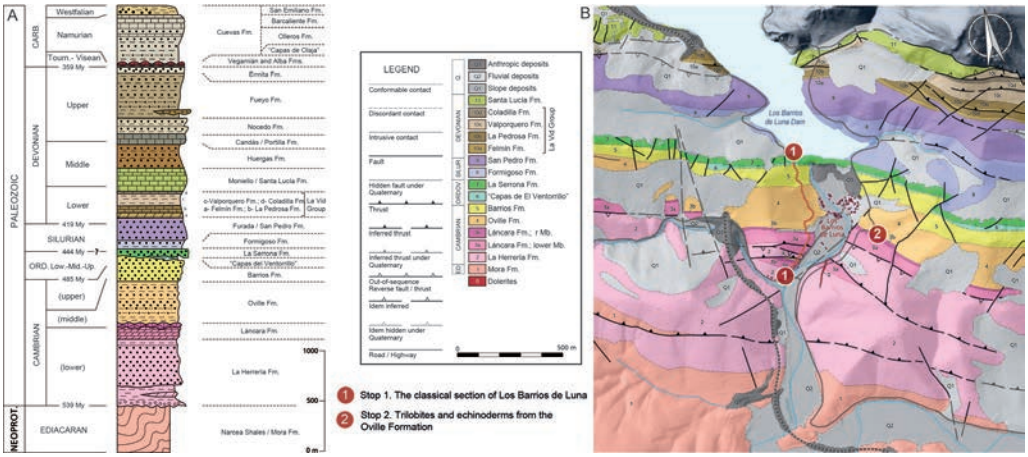

Figure 16. A, Simplified stratigraphic column of the Paleozoic succession exposed in the Los Barrios de Luna area, showing the main lithostratigraphic units from the Ediacaran Mora Formation to the Carboniferous succession; **B,** Simplified geological map of the Los Barrios de Luna sector (Somiedo Unit, Cantabrian Zone), indicating the location of Stops 1 and 2. Modified from Alonso *et al.* (2009), Toyos and Aramburu (2014), and additional field observations.

Mora Formation

The Mora Formation represents the local expression of the Narcea Shales and consists of low-grade Neoproterozoic slates and sandstones belonging to the Narcea Antiform. Sedimentary structures such as flute casts, current lineations and slumps suggest a turbiditic origin. The formation shows folds and axial-plane cleavage related to the Cadomian Orogeny and is separated from the overlying Lower Cambrian La Herrería Formation by a marked angular unconformity, locally associated with rubefied levels.

Fossils and age: The paleontological content of the Mora Formation is very sparse, largely because cleavage has obliterated most fossils. Nevertheless, organic-walled microfossils of Ediacaran age have been reported from the vicinity of Irede de Luna. Absolute ages obtained from equivalent rocks in Asturias range between 640 and 560 Ma.

La Herrería Formation

The La Herrería Formation is the oldest Cambrian unit in the Cantabrian Zone and reaches about 750 m in the Luna valley. It comprises a lower mudstone-dominated member with minor sandstone and carbonate interbeds, a thick middle member dominated by feldspathic sandstones and quartz arenites, and an upper member, the Barrios Beds, made up of alternating mudstones, dolostones and sandstones.

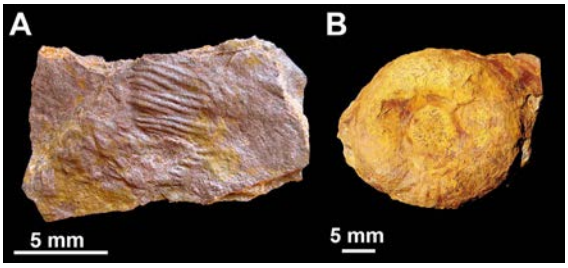

Figure 17. Trace fossils from the Herreria Formation. **A,** *Monomorphichnus* sp.; **B,** *Astropolichnus hispanicus.*

The formation records a transition from deltaic or very shallow-marine environments with strong continental input, through braided fluvial systems, to shallow-marine conditions. It is rich in trace fossils, including *Monomorphichnus* and *Astropolichnus hispanicus* in the Barrios Beds (Fig. 17), and yields trilobites such as *Lunolenus*, *Lunagraulos*, *Dolerolenus*, *Metadoxides* and *Sardaspis?*, indicating a Cordubian–Ovetian age.

Láncara Formation

There are many studies devoted to the Láncara Formation at Los Barrios de Luna, particularly those by van den Bosch (1969), Meer Mohr (1969), and Zamarreño (1972). This unit is in gradual contact with the La Herrería Formation and is subdivided into two members.

Lower member: Near its base there is a 2 m thick level of oolitic dolostones. Above it lies 25 m of dolostones with mudstone interbeds, 3 m of dolostones with stromatolites, and more than 50 m of dolostones with microbial and inorganic lamination. Toward the top of this member there are grey limestones with fenestrae porosity (birdseyes), calcite-filled karst cavities (paleokarst), and some stromatolites.

Upper member: Lies unconformably on the lower member and includes 5 m of grey bioclastic limestones and slightly more than 20 m of red nodular limestones and red marls. It is rich in benthic fossils.

In general, the Láncara Formation was deposited in a tidal-flat setting that later evolved into more open-marine conditions. Thus, the oolitic dolostone represents a high-energy subtidal or intertidal environment, while the stromatolitic levels formed in the intertidal zone. The dolostones of the Láncara Formation are interpreted as primary, meaning that their dolomitic composition is original and not the result of later hydrothermal replacement of earlier limestones.

The limestones with birdseyes formed in the upper intertidal to supratidal zone, where periodic desiccation was common and where karst cavities could develop during episodes of emergence. The red limestones of the upper member were deposited in an open-marine sublittoral setting, where water depth gradually increased and energy and terrigenous input decreased. The red nodular or griotte limestones represent a condensed succession.

Fossils and age: The lower member is generally poor in body fossils, but abundant microbial laminations, stromatolites, and related structures have helped clarify its palaeoecological setting. Archaeocyaths, hyoliths, trilobites, and other benthic organisms found near the top of this member indicate a Bilbilian age (Cambrian Series 2-Miaolingian). The upper member is very fossiliferous and contains echinoderms, molluscs, brachiopods, sponge spicules, and other benthic organisms. Trilobites are particularly abundant and allow precise dating. The basal bioclastic limestone contains *Perenopsella pokrovskajae*, while the griotte limestone has yielded several taxa such as *Badulesia* sp., *Pardailhania* sp., *Solenopleuropsis ribeiroi* and *Eccaparadoxides sequeirosi* indicating deposition during the Caesaraugustian. The upper member of the Láncara Formation is therefore of Miaolingian (Drumian). (See chapter about Truébano).

Oville Formation

The Oville Formation is a siliciclastic succession that at Los Barrios de Luna exceeds 400 m in thickness and overlies the Láncara Formation in relatively sharp contact. It is traditionally subdivided into three members (Aramburu, 1989; Aramburu *et al.,* 1992). The Genestosa Member, historically known as the Paradoxides Beds, ranges from 15 to 100 m in thickness and consists mainly of homogeneous green mudstones locally interrupted by sandstone beds. Above it lies the Adrados Member, 50 to 160 m thick, characterized by intervals dominated by fine-grained

sandstones interbedded with siltstones and mudstones. The uppermost La Barca Member, 8 to 20 m thick, is again dominated by green mudstones with subordinate sandy levels. Overall, the Oville Formation records a shallowing-upward trend linked to the progradation of a braidplain delta system, with the lower part deposited below wave base and the upper part accumulating in littoral to sublittoral environments. The Genestosa Member contains the highest diversity of trilobites and echinoderms known in the Cantabrian Zone. The contact between the Láncara Formation and the Genestosa Member is diachronous, ranging from the late Leonian to the early Languedocian (Sdzuy, 1968; Zamarreño, 1972). This diachronous modification of the sea floor influenced diversity peaks in both trilobites and echinoderms (Zamora & Álvaro, 2010), making this interval particularly suitable for analysing the evolution of Miaolingian benthic communities across changing substrate conditions.

Fossils and age: The mudstones and sandstones at the base of the Genestosa Member are rich in benthic fossils. Trilobites are especially abundant and their occurrence in different horizons has allowed the recognition of several assemblages indicating an age ranging from the upper Caesaraugustian to the lower Languedocian (Miaolingian, Wulian-Drumian). These beds also contain echinoderms, including eocrinoids such as *Ubaghsicystis segurae* and *Lichenoides* sp., as well as carpoids such as *Lignanicystis barriosensis*, *Gyrocystis platessa*, and *Gyrocystis* sp. The Adrados Member has yielded trace fossils typical of deltaic environments, including *Cruziana barbata*, *Trichophycus pedum*, and *Teichichnus* isp., *Psammichnites* and *Skolithos* (Fig. 18). Some forms like *Diplopodichnus* and *Monomorphichnus* have also been found. Some levels of the Adrados and La Barca members also contain acritarchs that have allowed precise dating and indicate that the top of the Oville Formation lies within the Languedocian Stage (Drumian) (see stop 2 below).

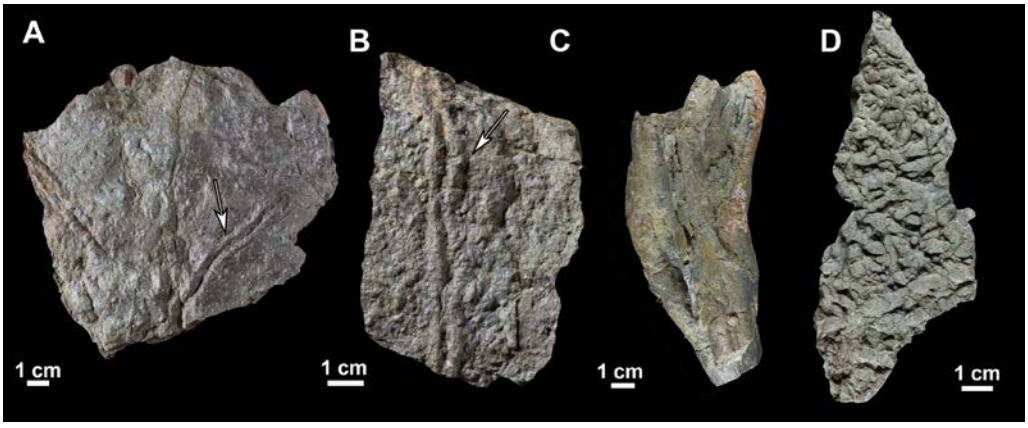

Figure 18. Trace fossils from the Adrados Member at Villar del Puerto. **A**–**B**, *Psammichnites* isp.; **C,** *Teichichnus* isp.; **D,** *Trichophycus pedum*.

Barrios Formation

The type section of this unit is the road cut between Los Barrios de Luna and Mallo de Luna (Bosch, 1969), where it reaches 203 m in thickness. It consists mainly of white quartz-cemented quartz arenites (quartzites) with grey or greenish mudstone interbeds. These lithologies are like those at the top of the Oville Formation. The base of the Barrios Formation is placed at the first thick quartzite bed, from which upward the proportion of quartzite clearly increases relative to mudstone. Other criteria used in the past, such as the absence of glauconite, are now considered unreliable, since glauconite also occurs in the lower and middle parts of the Barrios Formation.

The most common sedimentary structures are parallel and cross lamination, crossbedding, and, less commonly, wave and current ripples. Near the top of the formation there is a 5 m thick interval rich in Skolithos and, immediately above it, a 30 cm kaolinite tonstein. Both are valuable marker horizons for correlating different sections of this unit. Aramburu (1989) subdivided the Barrios Formation into the La Matosa and Tanes members.

From an environmental point of view, the Oville and Barrios formations together represent a braidplain delta system, with the Barrios Formation corresponding to the shallowest, coastal and alluvial parts of the system.

Fossils and age: The Barrios Formation is poor in macrofossils. A level rich in lingulids has been identified about 30 m below the top of the unit. Baldwin (1977) also reported several trace fossils, including *Skolithos*, *Teichichnus*, *Arenicolites*, *Corophioides*, *Planolites*, *Rusophycus*, *Cruziana semiplicata*, and *Cruziana barriosi*, from the lower and middle parts of the section. However, some mudstone levels are rich in acritarchs. Below the base of the formation, acritarchs indicative of the Middle Cambrian have been found, suggesting that the base of the unit lies close to the Middle–Upper Cambrian boundary. Mudstones just below the lingulid-bearing levels contain *Timofeevia* sp. and *Stelliferidae*, which may indicate a Late Cambrian age. A level above the kaolinite tonstein yielded the acritarch *Cardariola glabra*, a taxon common in the early Ordovician. Most of the Barrios Formation in this section is therefore of middle to late Cambrian age, although its top extends into the Ordovician.

El Ventorrillo beds and La Serrona Formation

Overlying the quartzites of the Barrios Formation in sharp contact is a package of dark mudstones and fine-grained sandstones with ferruginous crusts at the base, informally referred to as the El Ventorrillo beds (Toyos & Aramburu, 2014). In the Luna River valley these deposits show considerable thickness variations. On the right bank of the river they reach about 11 m, and about 12 m on the opposite bank near the bar from which the unit takes its name, although across the region their thickness ranges from 0 to more than 120 m.

In the road to Portilla de Luna section, the El Ventorrillo beds consist of a 60–65 m thick succession of black and green shales and fine-grained sandstones, organized into two upward-coarsening sequences located in the upper half of the unit. Sandstone beds display parallel lamination that upward evolve into hummocky cross-stratification, locally associated with trace fossils. These features indicate deposition in a storm-influenced marine environment.

Fossils and age: Fossils from the section exposed in the Luna valley are relatively scarce and occur mainly in two levels. Level A has yielded trilobites (*Scotiella*? cf. *taouzensis*, indeterminate Homalonotidae), ostracods (*Vogdesella* sp.) and brachiopods (*Rafinesquina* sp.), suggesting early Katian age. Level B has provided Ordovician acritarchs and chitinozoans (Fig. 19).

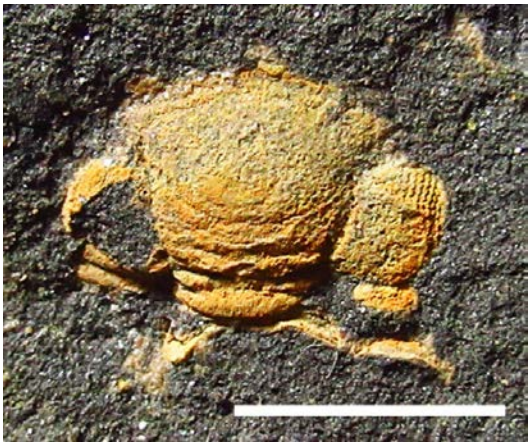

Figure 19. Dalamanitd from El Ventorrillo beds.

In the lower half of the unit at the road to Portilla de Luna section, a different fossil assemblage has been reported, including trilobites, graptolites, ostracods, brachiopods, molluscs, rare echinoderms (including an ophiuroid arm and a plate of

Anatifopsis sp.), and chitinozoans. This association has been reassigned by Gutiérrez-Marco *et al.* (1999) to a late Oretanian (Darriwilian) age. The El Ventorrillo beds are overlain by the quartzites of the La Serrona Formation, which form prominent ridges in the landscape. The type section is located along the Barrios–Mallo road and consists of about 64 m of coarse- to fine-grained quartzites, locally containing lenticular bodies of red mudstone and abundant pyrite nodules. These quartzites have been interpreted as palaeovalley fills incised into the underlying rocks during a phase of sea-level fall associated with the end-Ordovician glaciation. This interpretation explains the scarcity of typical littoral sedimentary structures, which only appear near the top of the unit. Fossils have not been recorded from the La Serrona Formation in this section. However, brachiopods belonging to the Hirnantia Fauna have been reported from equivalent stratigraphic levels elsewhere in the Cantabrian Zone, suggesting that the La Serrona quartzites may correlate with these latest Ordovician deposits.

Getino Beds and Formigoso Formation

Above the quartzites of the La Serrona Formation, visible only around the northern face of the dam when water level is low, there are 26 cm of quartz arenites and intensely bioturbated mudstones with abundant pyrite nodules. These correspond to the Getino beds, an informal unit of highly variable lithology and thickness. It represents a condensed succession that also includes several stratigraphic gaps.

Above the Getino beds lie 6 m of black mudstones, followed by an alternation of mudstones and sandstones, with sandstones becoming increasingly common upward. This is the Formigoso Formation, a widespread unit within the Somiedo Unit that typically gives rise to depressions in the landscape. Traditionally, the Formigoso Formation has been divided into two members, both represented around Los Barrios de Luna: the Bernesga Member, predominantly mudstone, and the Villasimpliz Member, characterized by the alternation of mudstones and sandstones mentioned above.

In this section, the presence of faults, small thrusts, and associated folds complicates the study of these rocks and may locally exaggerate their apparent thickness. The black mudstones formed in a shallow-marine, low-energy, oxygen-poor environment, evolving upward toward shallower and even littoral conditions, as reflected by the increasing abundance of sandstones.

Fossils and age: No fossils have yet been recovered from the Getino beds that would allow direct dating, but their stratigraphic position between the La Serrona and Formigoso formations suggests an age spanning from the Late Ordovician to the earliest Silurian. The basal black mudstones of the Formigoso Formation contain conulariids, bivalves, gastropods, cephalopods, hyoliths, trilobites, and graptolites (Fig. 20). Although no detailed biostratigraphic study has been carried out for this section, Truyols *et al.* (1974) identified five graptolite-bearing levels ranging

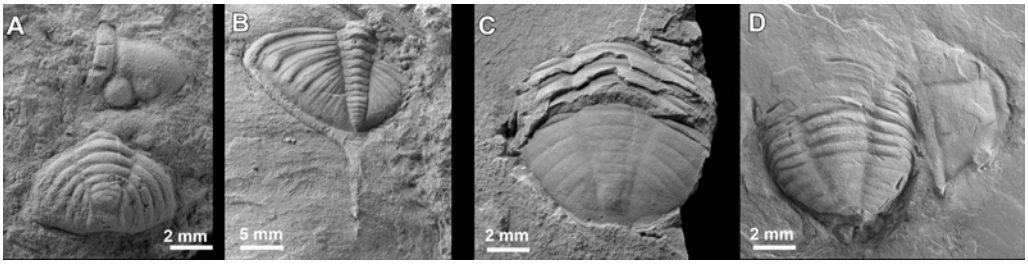

Figure 20. Trilobite assemblage from the Formigoso Formation from Los Barrios de Luna. **A,** Calymene sp.; **B,** Dalamnitd sp; **C**–**D,** Homalonotid sp.

from the Aeronian to the Sheinwoodian. Aramburu *et al*. (2006) later questioned these data and suggested that, pending revision, all the material could be Telychian.

Units from the Upper Silurian to the Middle Devonian

Upstream from the dam, the Palaeozoic succession continues up to the Middle–Upper Devonian, represented by the Portilla Formation (Givetian–Frasnian), which near Peña Cabrones, close to Mirantes de Luna, outlines a clear perisynclinal termination.

Above the Formigoso Formation lies the San Pedro Formation, composed of ferruginous sandstones, mudstones, and quartzites, of Upper Silurian (Wenlock) to Lower Devonian (Lochkovian) age. This is overlain by the Felmín, La Pedrosa, Valporquero, and Coladilla formations. These four units, together forming the La Vid Group, range from the Lochkovian to the Emsian. They are followed by the fossiliferous limestones of the Santa Lucía Formation, of Emsian–Eifelian age, which locally show a strongly reef character. Above them lie the mudstones and sandstones of the Huergas Formation, of Eifelian–Givetian age, and finally the limestones with some sandstone levels of the Portilla Formation, of Givetian-Frasnian age. Despite their reef nature, phacopid trilobites are found in the Santa Lucía and Portilla formations (Fig. 21).

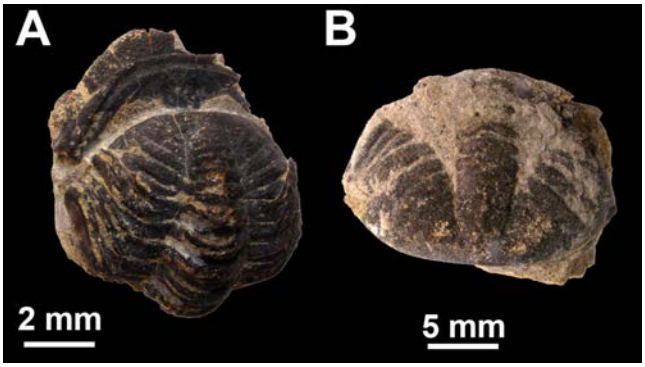

Figure 21. A, Enrolled *Phacops* (*Chotecops*) *zizensis* from the Santa Lucía Formation; **B,** Phacopid sp. from Portilla Formation.

STOP 2. TRILOBITES AND ECHINODERMS FROM THE OVILLE FORMATION

Jorge Esteve, Samuel Zamora, Lukas Laibl, & Francesc Pérez-Peris

Location: Creek 500 m to the southeast of Los Barrios de Luna village, near the Mora-Los Barrios de Luna road.

Coordinates: 42º50'31.26"N, 5º51'22.46"W

Geological map of Spain: 1:50.000, sheet of Los Barrios de Luna (102).

Geological setting: Cantabrian Zone, Somiedo Unit, on the southern limb of the Alba Syncline.

Age: Caesaraugustan-Languedocian (Drumian).

Aims

- To look at the fossiliferous levels of the Genestosa Member of the Oville Formation.
- To analyse the diversity and preservation of trilobites in the Miaolingian of the Cantabrian Zone.
- To discuss the influence of substrate and depositional environments on benthic communities.

Genestosa Member

The Genestosa Member contains the highest diversity of trilobites and echinoderms known in the Cantabrian Zone (Figs. 7-8). The contact between the Láncara Formation and the Genestosa Member of the Oville Formation is diachronous, ranging in age from the late Leonian to the early Languedocian (Sdzuy, 1968; Zamarreño, 1972). This corresponds to Cambrian Series 2-Miaolingian (Stage 4-Drumian) in the international scale. This diachronous shift in the deposit of the rocks corresponding to the Genestosa Member influenced diversity peaks in both trilobites and echinoderms (Zamora & Álvaro, 2010). As a result, this interval provides an excellent opportunity to analyse the evolution of middle Cambrian benthic communities across changing substrate conditions.

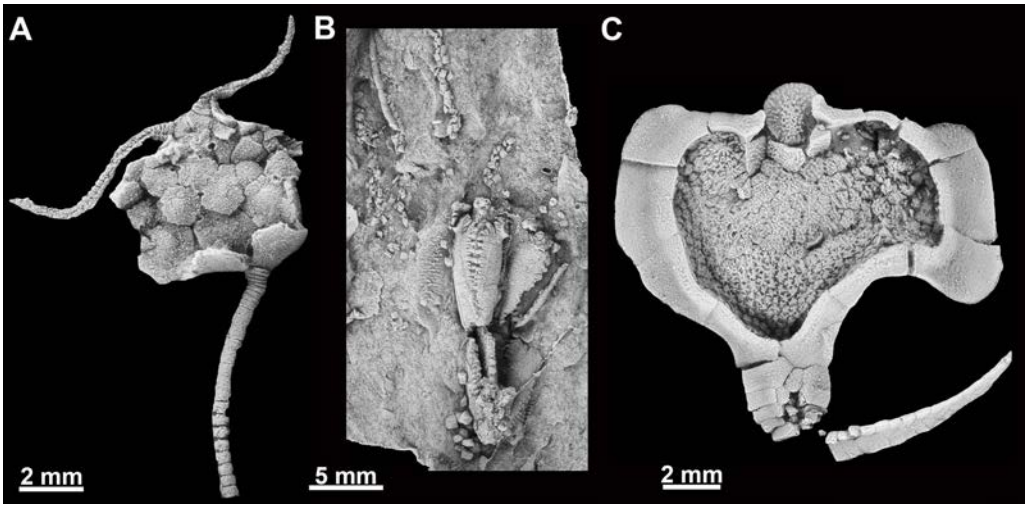

Figure 22. Representative echinoderms from the Genestosa Member. **A,** *Ubaghsicystis segurae*; **B,** *Lichenoides* sp.; **C,** *Lignanicystis barriosensis.*

Paleontological significance

Los Barrios de Luna section provides one of the most complete records of the Miaolingian in the Cantabrian Mountains, spanning the interval from the upper Caesaraugustian to the lower Languedocian (*i.e.*, Wuliuan to Drumian).

Lower levels contain the cinctan *Gyrocystis* platessa, whereas higher levels show an increase in echinoderm diversity, including *Gyrocystis* sp., *Lignanicystis barriosensis*, *Ubaghsicystis segurae*, *Ceratocystis* sp. and the eocrinoid *Lichenoides* (Fig. 22). These taxa illustrate the diversity of benthic echinoderms inhabiting marine environments approximately 510 million years ago. The locality is also well known for its abundance of Miaolingian trilobites, including *Solenopleuropsis thorali*, *Solenopleuropsis marginata*, *Solenopleuropsis rubra, Eccaparadoxides pradoanus*, *Conocoryphe heberti*, *Bailiella levei*, *Occatharia pseudocoulata*, and small agnostids such as *Peronopsis*, *Megagnostus* and *Condilopyge* (Figs. 23-24).

Although the beds of the Genestosa Member may appear rather homogeneous in the field, the fossil record reveals three main types of assemblages: (i) larval and agnostoid assemblages, (ii) horizons enrolled and large trilobite assemblages, and (iii) levels dominated by disarticulated remains.

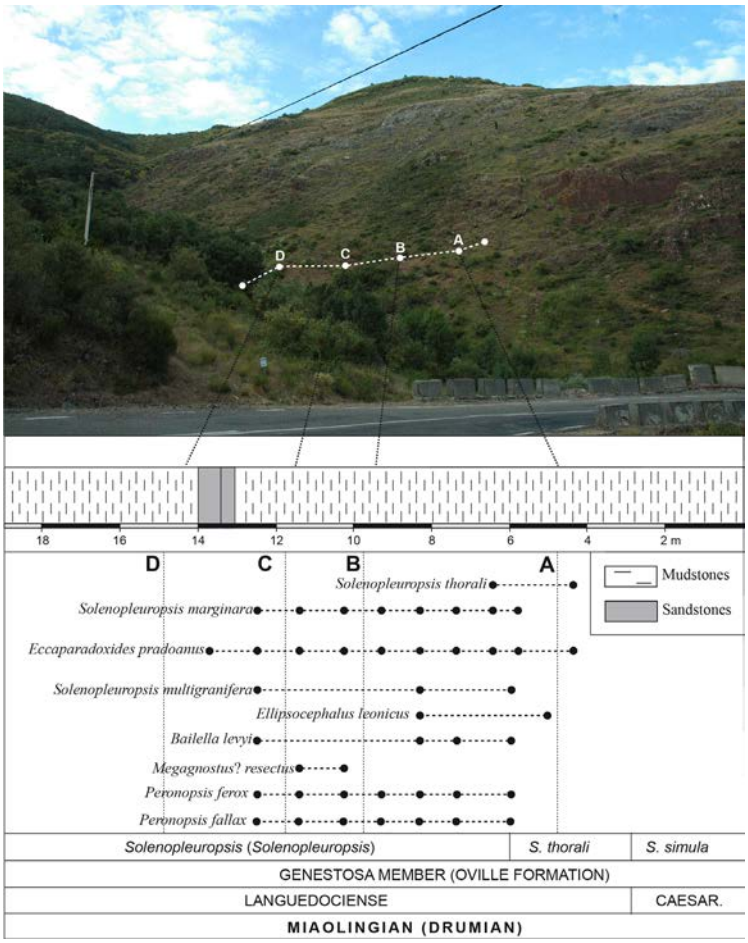

Figure 23. Distribution of trilobites in the different levels with indication of biozones.

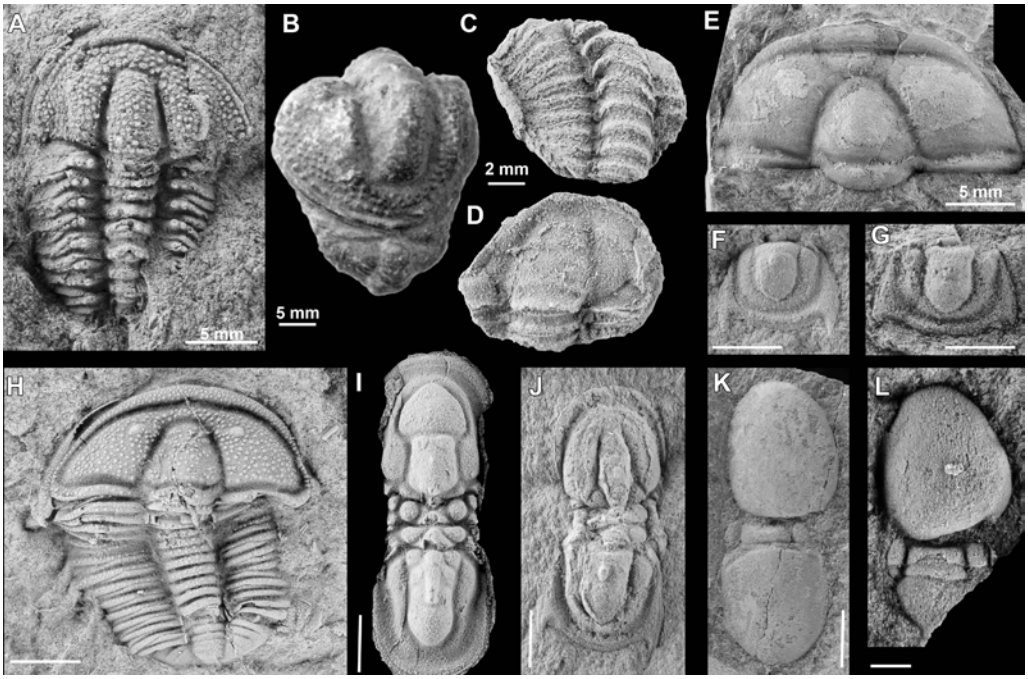

Figure 24. Trilobites from the Oville Formation, Genestosa Member. **A,** *Solenopleuropsis marginata*; **B,** enrolled specimen of *Solenopleuropsis marginata*; **C**–**D,** enrolled specimen of *Ellipsocephalus leonicus*; **E,** *Bailella leveyi*; **F,** *Peronopsis ferox*; **G,** *Peronopsis fallax*; **H,** *Occathara sduyizi*; **I,** *Condylogype* rex from Busdongo; **J,** *Peronopsis fallax*; **K**–**L,** *Megagnostus*? *resectus*; scale bar F-G and I-L = 2mm.

(i) Larval and agnostid assemblages.

The Oville Formation locally contains abundant early developmental stages of trilobites. The most common are protaspides and early meraspid cranidia of the genera *Solenopleuropsis marginata* and *Eccaparadoxides pradoanus* (Fig. 25). Larvae of conocoryphids such as *Bailiaspis* are also relatively common. In some horizons larval forms are especially abundant, and the associated fauna is dominated by small-sized trilobites, particularly agnostids, suggesting concentrations of early developmental stages and possibly nursery environments within the Drumian sea floor.

Solenopleuropsis marginata exhibits two distinct protaspid stages, approximately 0.8–1.01 mm in length. Both are circular in outline and possess a narrow, forwardly expanding glabella. The differences between these stages mainly reflect the progressive development of the trunk region, including an increasing number of segments and a larger overall size. By morphology and size, these developmental stages closely resemble the second and third protaspid instars of the solenopleurid trilobite *Sao hirsuta* from the Drumian strata of Bohemia (Skryje–Týřovice Basin, Buchava Formation; see Laibl *et al.,* 2014). It is likely that the earliest protaspid stage of *S. marginata*, corresponding to the first protaspid stage of *S. hirsuta*, has either not yet been discovered or was not preserved due to the generally coarser sediments of the Oville Formation compared to the Buchava Formation. The early meraspid cranidia of *S. marginata* are subtrapezoidal and display a forwardly expanding to narrowly rectangular glabella.

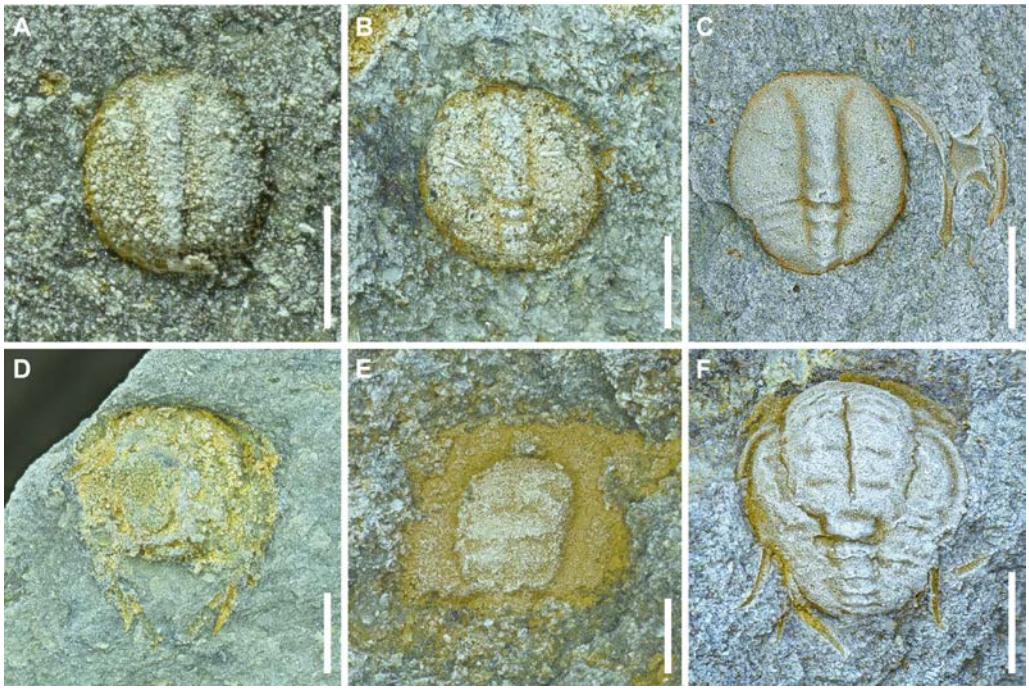

Figure 25. Early developmental stages of trilobites from the Oville (Spain) and Buchava (Bohemia) Formations. **A,** second protaspid stage of *S. marginata* (Oville Fm.); **B,** third protaspid stage of *S. marginata* (Oville Fm.); **C,** third protaspid stage of *S. hirsuta* (Buchava Fm.); **D,** protaspid stage of *E. pradoanus* (Oville Fm.); **E,** meraspid cranidium of *E. pradoanus* (Oville Fm.); **F,** second protaspid stage of *E. pusillus* (Buchava Fm.); scale bar = 0.5 mm.

The early developmental stages of *Eccaparadoxides pradoanus* present in the Oville Formation include rare, relatively large (ca. 1.4 mm wide) protaspides with an elliptical glabella, as well as meraspid cranidia with a more rectangular glabella and long crescentic palpebral lobes. Interestingly, these early stages are relatively large, suggesting that they may have been nourished by substantial yolk reserves within the egg, similarly to the developmental stages of the paradoxidid trilobites *Eccaparadoxides pusillus* and *Hydrocephalus carens* from Bohemia (Laibl *et al*., 2017).

(ii) Enrolled and large trilobite assemblages.

In other horizons numerous specimens are preserved articulated and enrolled, one of the earliest protective mechanisms documented in the fossil record (Esteve *et al*., 2011). Trilobites from Los Barrios de Luna show several types of enrolment, including sphaeroidal and spiral configurations, together with well-developed coaptative structures that allowed the exoskeleton to close tightly. The preservation of enrolled individuals is relatively uncommon and reflects particular taphonomic conditions, such as rapid burial in fine-grained sediments and low-oxygen environments. These beds also contain a relatively higher abundance of echinoderms, emphasizing the importance of this locality not only for trilobites but also for the study of middle Cambrian echinoderm assemblages.

(iii) Disarticulated assemblages.

Other horizons contain strongly disarticulated and resedimented fossil assemblages, characterized by abundant isolated cephala, cranidia, pygidia, and disarticulated echinoderm plates. These concentrations likely reflect resedimentation or transport processes that disrupted the original benthic communities and accumulated skeletal elements within the sediment.

Taken together, these three types of assemblages provide valuable insights into the structure of Miaolingian benthic communities and the taphonomic processes operating in the siliciclastic environments of the Oville deltaic system, where variations in sedimentation rate, oxygenation, and substrate stability strongly influenced fossil preservation.

STOP 3. TRILOBITES AND OTHER INVERTEBRATES FROM THE HUERGAS FORMATION (STRATOTYPE)

Jorge Esteve, Rodrigo Castaño, & Javier Fernñandez-Martínez

Location: Huergas de Gordón

Coordinates: 42°50'37.81"N 5°38'29.13"W

Geological map of Spain: 1:50.000, sheet of La Pola de Gordón (103).

Location: Outcrops located near Huergas de Gordón (León), where the type section of the Huergas Formation is exposed.

Geological setting: Cantabrian Zone, Somiedo Unit.

Age: Middle Devonian (Eifelian–Givetian).

Aims

- To recognize the stratotype of the Huergas Formation and its stratigraphic context within the Middle Devonian of the Cantabrian Zone.
- To study trilobite assemblages dominated by Asteropyginae, including genera such as *Kayserops, Bradocryphaeus, Metacanthina, Treveropyge*, and forms closely related to *Neocalmonia*.
- To analyse the composition of Devonian benthic communities, including brachiopods, crinoids, corals and other marine invertebrates.
- To discuss the palaeoecological and palaeobiogeographic significance of these faunas within the Ibero-Armorican domain.

Huergas Formation

The Huergas Formation was originally defined by Comte (1936) as the *Huergas Sandstones and Shales*, based on outcrops near Huergas de Gordón, which constitute its type locality. In the regional stratigraphic framework, the unit overlies the Santa Lucía Formation, represented by shallow-water carbonate platform deposits, and is overlain by the more massive limestones of the Portilla Formation (Fig. 26). The Huergas Formation is mainly composed of dark, commonly nodular shales and marls, with nodular limestone intercalations, local calcareous sandstone beds and occasional bioclastic limestones. Its base is generally transitional from the Santa Lucía Formation, although it marks a clear lithological change from carbonate to predominantly siliciclastic sedimentation. In the field, the unit commonly forms a topographic depression between the more resistant limestones of the Santa Lucía and Portilla formations.

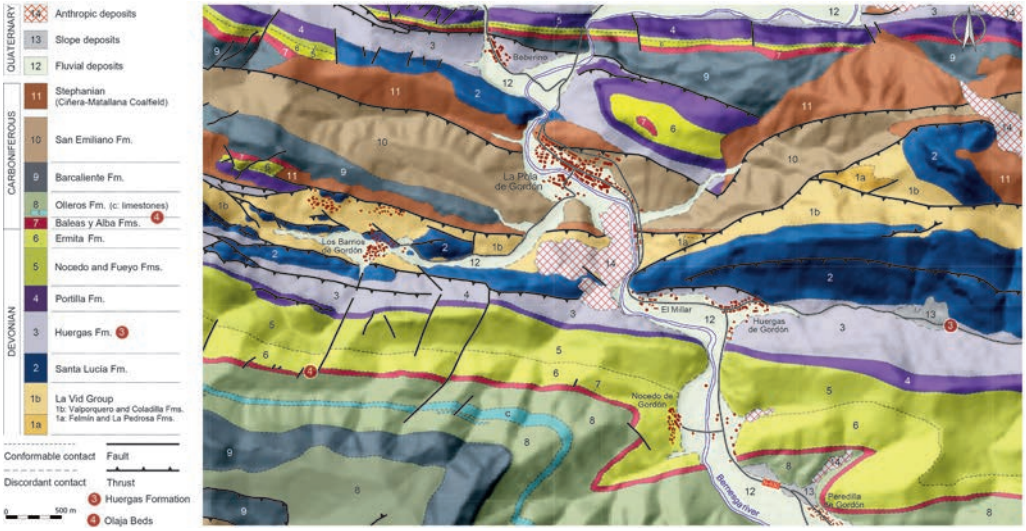

Figure 26. Simplified geological map of the Pola de Gordon sector (Somiedo Unit, Cantabrian Zone), indicating the location of Stops 3 at the Huergas Formation and 4 at the Olaja Beds.

The formation represents a deepening interval within the Devonian succession of the Cantabrian Zone. Sedimentary conditions indicate a distal shelf to outer platform setting, deeper than the carbonate platforms that developed during the Early Devonian. Fine-grained sedimentation, carbonate nodules and occasional bioclastic levels suggest relatively low-energy marine conditions, punctuated by episodic input of skeletal material.

More broadly, the Huergas Formation records the arrival of siliciclastic sediment into the basin, which interrupted the carbonate sedimentation represented by the Santa Lucía Formation. These terrigenous deposits were redistributed across the platform by currents, waves and, locally, storms, producing shale-rich intervals, sandstone beds and bioclastic concentrations. Towards the Leonese sector, the platform became progressively deeper or more restricted, favouring more distal facies and, locally, the replacement of benthic faunas by more pelagic elements. The fossil content is relatively variable but includes brachiopods, trilobites, crinoids, corals, bivalves, goniatites, tentaculitids and other marine invertebrates typical of Devonian shelf ecosystems. Fossils from the lower part of the formation indicate an Eifelian age, whereas higher levels approach or cross the Eifelian–Givetian boundary. This boundary lies within the Huergas Formation, as first suggested by Comte (1959) based on goniatites and later supported by studies of bivalves, ostracods, trilobites and tentaculitids in the Bernesga valley.

Palaeontological and scientific significance

The Huergas Formation is especially significant because its trilobite assemblages are dominated by Asteropyginae, a group that underwent major diversification during the Middle Devonian within the Ibero-Armorican domain. Representative taxa include species of *Kayserops*, *Bradocryphaeus*, *Metacanthina* and *Treveropyge*, together with forms closely related to *Neocalmonia* (Fig. 27). These faunas document an important phase in the evolutionary history of asteropygine trilobites and show clear affinities with other Devonian assemblages from the Armorican Massif, Bohemia and other areas along the northern margin of Gondwana.

In addition to trilobites, the Huergas Formation contains a diverse benthic fauna including brachiopods, crinoids, rugose and tabulate corals, bivalves and other marine invertebrates. These assemblages reflect relatively deep platform environments within the Middle Devonian succession of the Cantabrian Zone. Trilobites are commonly preserved as partially disarticulated remains within shale and marly levels, where isolated cephala and pygidia are frequent, suggesting relatively quiet depositional conditions in which skeletal remains accumulated on the sea floor before final burial.

The Huergas de Gordón section is also a key stratigraphic reference because it corresponds to the stratotype of the Huergas Formation. Its fossil assemblages provide important evidence for regional and interregional correlations within the Ibero-Armorican domain, while the combined study of trilobites and associated benthic invertebrates helps to reconstruct the structure, palaeoecology and taphonomic history of Middle Devonian marine communities.

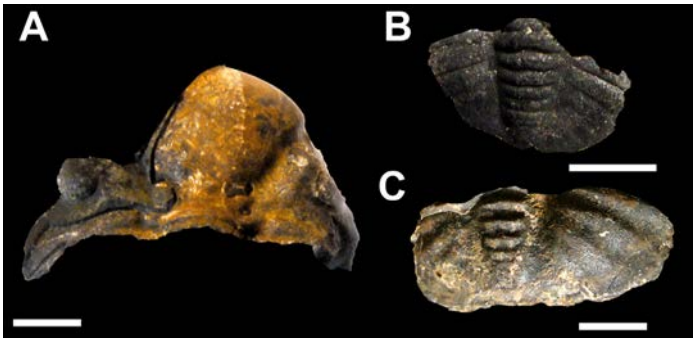

Figure 27. Trilobites from Huergas Formation. **A,** *Kayserops* sp.; **B–C,** Pygidia of phacopids.

STOP 4. TRILOBITES AND OTHER INVERTEBRATES FROM THE OLAJA BEDS AT BARRIOS DE GORDÓN

Jorge Esteve, & Rodrigo Castaño

Location: Los Barrios de Gordón, León

Coordinates: 42°50'26.33"N 5°52'10.94"O

Geological map of Spain: 1:50.000, sheet of La Pola de Gordón (103)

Location: Fossiliferous outcrops located approximately 1.35 km south of Los Barrios de Gordón.

Geological setting: Cantabrian Zone; uppermost Alba/Genicera Formation, represented by the Olaja Beds, transitional to the Cuevas–Olleros / Culm-type facies.

Age: latest Viséan–early Namurian; Namurian A, Eumorphoceras interval.

Aims

- To recognize the Olaja Beds as a transitional interval at the top of the Alba Formation.
- To place the trilobite-bearing levels of Barrios de Gordón within the transition from red nodular limestones to shale- and sandstone-dominated Culm-type deposits.
- To examine the succession of fossiliferous beds A–F described south of Los Barrios de Gordón.
- To discuss how facies changes controlled trilobite diversity, faunal composition and fossil preservation during the latest Viséan–early Namurian transition.

Regional geological framework

The Barrios de Gordón locality lies within the Cantabrian Zone, the external part of the Variscan Belt in north-western Iberia. In the La Pola de Gordón area, the Palaeozoic succession is affected by thrusts and associated folds (Fig. 26). The area records the transition from a relatively stable pre-orogenic marine platform to synorogenic Carboniferous sedimentation related to the development of a foreland basin during Namurian–Westphalian times. This regional context is important because the Olaja Beds represent a key interval between condensed carbonate sedimentation and the onset of more siliciclastic, locally turbiditic sedimentation.

Los Barrios de Gordón section: Olaja Beds and stratigraphic context

At Los Barrios de Gordón, the fossiliferous levels lie about 1.35 km south of the village and are arranged from west to east as F, E, C, B and A. Bed A is located close to a fault affecting the Alba limestones (Fig. 26). The section records the transition from the upper carbonate system of the Alba Formation into the Olaja Beds, making it useful for understanding how sedimentary changes influenced trilobite distribution and assemblage composition. The trilobite-bearing beds belong to the uppermost part of the Alba Formation, regionally characterized by red bedded and nodular “griotte” limestones, rich in ammonoids, conodonts and trilobites. In the Alba Syncline, this unit passes upward into the terrigenous Olleros Formation. The transitional interval is represented by the Olaja Beds, composed of red, green and grey shales and marls, which mark the shift from pelagic or hemipelagic carbonate sedimentation to shale- and sandstone-dominated conditions.

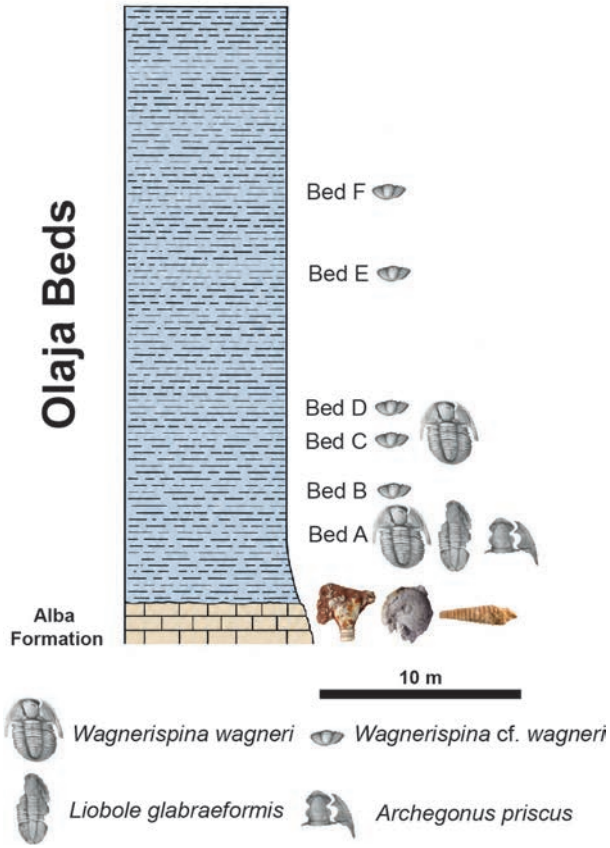

Figure 28. Schematic stratigraphic column of the Olaja Beds above the Alba Formation, showing fossil assemblage of the Alba Formation and the fossiliferous beds A–F and the distribution of the main trilobite taxa in the Olaja Beds. Beds B–F are low-diversity assemblages dominated by *Wagnerispina* cf. *wagneri* and associated with ammonoid-bearing levels of early Namurian age, whereas bed A yields a more diverse benthic fauna including *Archegonus priscus* and *Liobole glabraeformis*. Modify from Gandl (1977).

Palaeontological and scientific significance

The Barrios de Gordón locality is significant because it records trilobite assemblages from the Olaja Beds, a key transitional interval at the top of the Alba Formation. Stratigraphically, the section documents the passage from the red nodular limestones of the Alba Formation to the overlying Olleros/Culm-type deposits, providing a clear field example of the latest Viséan–early Namurian transition in the Cantabrian Zone.

The fossiliferous beds show a marked contrast in faunal composition. Beds B to F are very low in diversity and are dominated almost exclusively by *Wagnerispina* cf. *wagneri* (Fig. 28). These levels are closely associated with ammonoid-bearing beds, supporting an early Namurian age for this part of the succession. In contrast, bed A contains a more diverse trilobite assemblage, including *Archegonus (Phillibole) priscus* and *Liobole glabraeformis*, taxa also known from other important Alba–Olaja localities such as Entrago de Teverga and Santa Olaja de la Varga (Gandl, 1977). The associated fauna in bed A is also richer and includes abundant crinoid stem fragments, ostracods, small pteriomorph bivalves, small chonetid brachiopods and other smooth-shelled brachiopods. This contrast suggests that the faunal differences are not mainly the result of age differences but rather reflect facies-controlled ecological change during the transition from carbonate-dominated to shale-dominated sedimentation. The stop is therefore particularly useful for discussing the links between stratigraphy, facies change, ammonoid biostratigraphy and benthic faunal composition in Carboniferous marine settings.

SECOND DAY: DEVONIAN FAUNAS OF THE ESLA UNIT

Javier Fernández-Martínez, Manuel de Paz, Rodrigo Castaño, & Jorge Esteve

The second day of the excursion will focus on the Devonian successions of the Esla Unit, one of the major tectonostratigraphic domains of the southern Cantabrian Mountains. Compared with the Somiedo Unit visited during the first day, the Esla Unit preserves a somewhat different palaeogeographic and sedimentary evolution, allowing direct comparison between fossil assemblages developed under contrasting environmental conditions.

The morning will begin at Colle, a classical Lower Devonian locality famous for the so-called *"Sabero fossils"*. The section exposes fossiliferous beds of the La Vid Group, yielding diverse benthic faunas including trilobites, brachiopods, corals and echinoderms deposited on a shallow carbonate ramp affected by episodic siliciclastic input. Afterwards, the excursion will continue through several localities within the Esla Nappe, where Cambrian and Devonian successions provide additional insights into the evolution of trilobite-bearing communities along the northern margin of Gondwana. These stops will allow comparison between the faunas previously observed in the Somiedo Unit and those developed in the structurally and palaeogeographically distinct domains of the Esla Unit.

STOP 1. DEVONIAN FOSSIL ASSEMBLAGE OF COLLE

Location: Outcrops near Colle, on the left side of the regional road LE-3143 from Boñar to Sabero. The section to be visited is located on the hill where the main church stands (Fig. 29).

Coordinates: 42º50'38.06"N, 5º15'5.10"W

Geological Map of Spain: 1:50,000 Boñar sheet (104).

Geological setting: Southern slope of the Cantabrian Mountains, Esla Unit.

Lithostratigraphic unit: La Vid Group, upper part of the Valporquero Formation or Sagüera Member of the Esla Formation.

Age: Early Devonian, late Emsian.

Aims

- To examine the fossiliferous Lower Devonian beds from Colle within the Esla Unit.
- To place the trilobites within their broader benthic community, including brachiopods, corals, bryozoans, crinoids and blastoids.

Geological and palaeontological significance

Since the nineteenth century, Colle has been known as an important palaeontological locality because of the abundance and quality of its fossils, commonly referred to in older literature as the "Sabero fossils". Most specimens come from red limestone and marlstone levels cropping out near the top of the hill north of the village. Although the locality is especially well known for its echinoderms, it also contains a diverse Devonian benthic fauna including trilobites, brachiopods, corals, stromatoporoids, bryozoans, nautiloids, gastropods, bivalves, ostracods, tentaculitoids and conodonts (Fig. 30). In this stop, the echinoderm-rich levels provide the ecological background for understanding the trilobites as part of a broader Lower Devonian shelf community.

The visited outcrop consists of a marly interval with limestone intercalations overlying a thick shale succession. Fossils occur mainly in discrete limestone and marlstone beds, where trilobite remains may be found together with other skeletal components. These assemblages record

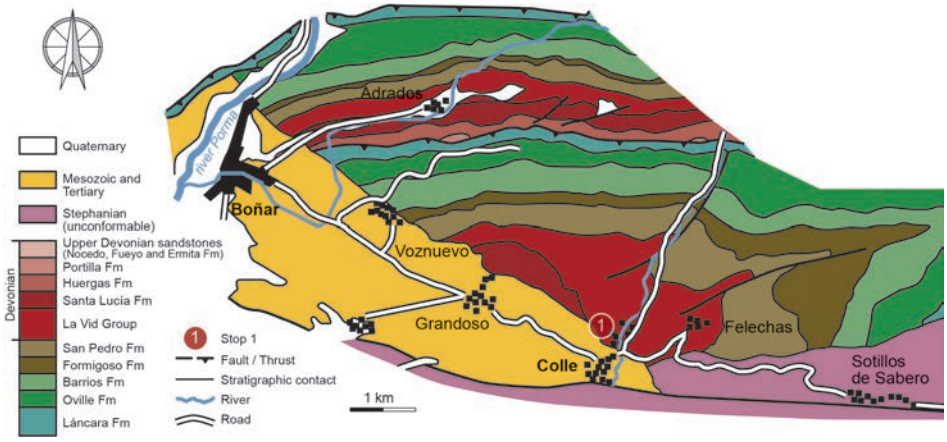

Figure 29. Simplified geological map of the Esla nappe near Colle showing the location of the study area. Modified after Fernández *et al.* (2006).

benthic communities that inhabited a carbonate ramp affected by variations in substrate, water energy and sediment input. Lithostratigraphically, the interval belongs to the Lower Devonian La Vid Group, more precisely to the upper part of the Valporquero Formation (Vilas Minondo, 1971; Vera de la Puente, 1989), also referred to as the Sagüera Member of the Esla Formation by Keller (1988). These beds have been dated as late Emsian on the basis of brachiopods and conodonts.

Depositional setting

The La Vid Group was deposited on a carbonate ramp periodically affected by terrigenous input, represented by shale-rich intervals within the Valporquero Formation. The succession has been interpreted as recording two third-order transgressive–regressive cycles. Within this framework, the shales, marls and limestones of the Valporquero Formation represent highstand deposits of the upper cycle.

For the purposes of this excursion, Colle provides a useful comparison with the Middle Devonian Huergas Formation. Whereas Huergas records deeper and more siliciclastic shelf environments, Colle represents a Lower Devonian carbonate-ramp setting with a diverse benthic fauna (Fig. 30). This contrast allows discussion of how trilobite assemblages changed across different Devonian environments within the Cantabrian Zone.

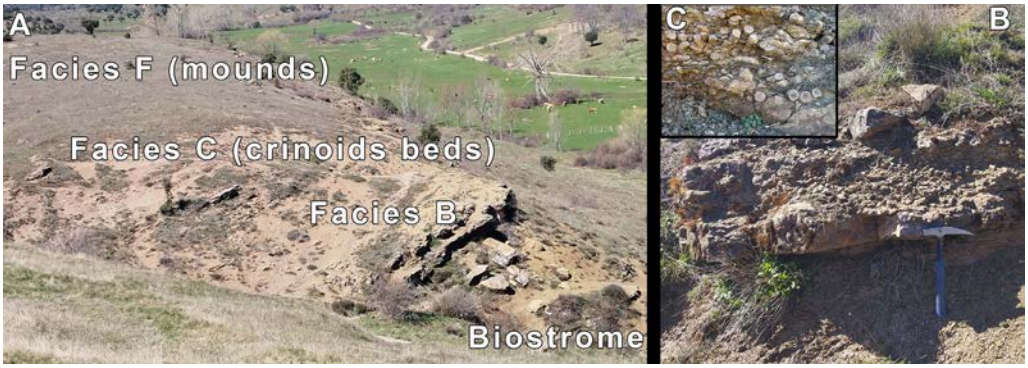

Figure 30. A, Detail of the section with indication of biostromes and crinoids bed and mud mound interval; **B,** general aspect of a biostrome; **C,** detail of a biostrome.

The Esla Unit

Coordinates: 42°52'13.22"N 5° 9'45.78"W (Valdoré)

Geological Map of Spain: 1:50,000 Boñar sheet (104).

Geological setting: Southern slope of the Cantabrian Mountains, Esla Unit.

Age: Cambrian - Carboniferous

Aims

- To understand the structural architecture and tectonic evolution of the Esla Unit, including the relationships between nappes, duplexes, thrust ramps and associated folds.
- To discuss the significance of trilobites and other Palaeozoic faunas from the Esla Unit within the broader stratigraphic and palaeogeographic framework of the Cantabrian Zone.

The Esla Unit, as defined in the most recent Cantabrian Zone subdivision (Alonso *et al.*, 2009), consists of three nappes and three duplexes of kilometre-scale dimensions. In structurally ascending order (bottom to top), they are the Pardominos and Primajas duplexes, the Valbuena and Corniero nappes, the Pico Jano duplex, and the Esla Nappe (Fig. 31; Lobato, 1975; Arboleya, 1981; Alonso, 1987). Their emplacement occurred in a piggy-back sequence, from structurally higher (Esla Nappe) to lower (Pardominos Duplex), forcing the upper units to accommodate to the underlying structures. The Primajas Duplex is composed of several horses involving the Láncara Formation and the lower levels of the Oville Formation. In turn, the Pardominos Duplex consists of horses of the La Herrería Formation and earlier fragments of the Primajas Duplex (Fig. 32).

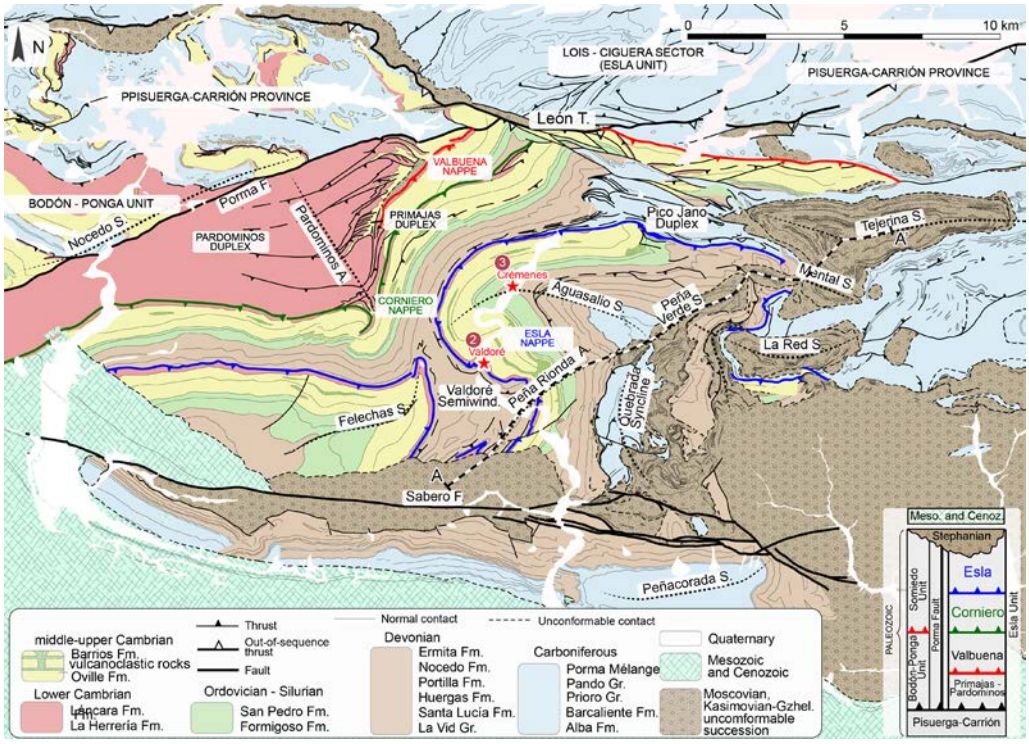

Figure 31. Simplified geological map of the Esla Unit (modified from Merino-Tomé et al., 2014).

From a stratigraphic point of view, the succession becomes progressively thinner in each of the lower thrust sheets, owing to the Upper Devonian unconformity. During the Upper Devonian, the northern Gondwana passive margin started to be influenced by the Variscan deformation. The lithospheric flexure associated to the Orogen modified the palaeogeography of the area and, as a result, the distal areas of the Cantabrian Zone (except the Pisuerga-Carrión Province) were emerged owing to the forebulge uplift (Keller *et al*., 2008). As a result, the earlier Palaeozoic formations were partially eroded, generating a regional-scale unconformity over which the synorogenic formations were deposited. This unconformity resulted in a progressive erosion of Palaeozoic formations towards the foreland. In the Esla Unit, while the Esla Nappe preserves an almost complete Palaeozoic sequence, in the lower Valbuena Nappe the synorogenic succession rests on top of La Vid Group.

The Esla Unit is limited to the east and north by its foreland basin, where a Bashkirian-Moscovian succession was deposited composed of shales, but also sandstones and conglomerates, as well as a well-developed limestone interval in the most distal part (Prioro, Pando and Conjas-Metal groups). The sequence culminates with the unconformable deposition of the Cea Group, of Cantabrian age (equivalent to the upper Myachkovian), which lies unconformably over the Esla Unit in its eastern sector, and the Sabero Group, of Stephanian A–C age, in its southern area (equivalent to Kasimovian–Gzhelian) (Fig. 31) (Alonso, 1987).

The Esla Unit is affected by a series of folds with varying orientations, which have been subdivided into two systems formed in relation to frontal and lateral thrust ramps within the unit (Alonso, 1987) (Fig. 31). Among the frontal structures, the Pardominos Anticline and the Aguasalio Syncline stand out. The Pardominos Anticline formed as a result of the antiformal stacking of its horses, and generates a particular cartographic pattern known as the Valdoré semi-window. The Aguasalio Syncline is a fault-bend fold formed between the Esla Nappe footwall ramp, and the Pardominos Anticline (Fig. 32). The Peña Rionda Anticline is the most important lateral structure, formed as a result of the lateral termination of the Pardominos Duplex below. The folds are readily recognisable on the geological map, and outline the general trends of the Esla Unit.

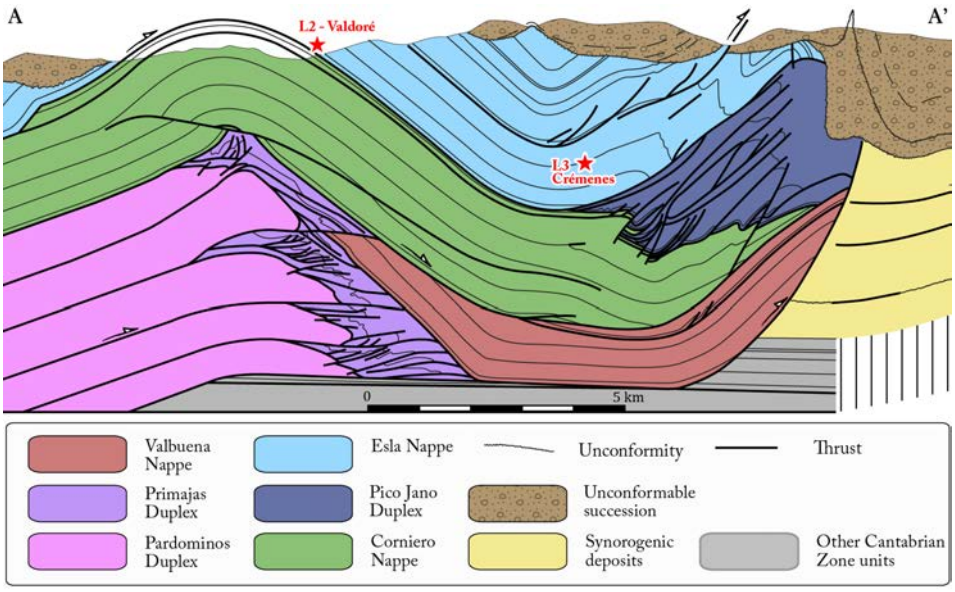

Figure 32. Cross section through the Esla Unit, displaying the three nappes and three duplex that conform it (modified from Alonso, 1987). See location in Figure 31.

After the deposition of the Stephanian synorogenic materials, the Esla Unit underwent a late N–S contraction, which resulted in the tightening of pre-existing thrust-related folds. This tightening is evidenced by the relationships between basement structures and those developed in the unconformable synorogenic deposits (Alonso, 1989): a particular case is the syncline developed in the unconformable Cea Gr. at the summit of Peña Rionda, which paradoxically formed as a result of the tightening of the underlying Peña Rionda Anticline. Part of this deformation has been attributed to the emplacement of other nappes of the Cantabrian Zone (Alonso, 1987), but also to contraction during the Alpine orogeny (Alonso *et al.*, 1996).

Esla Nappe

The Esla Nappe (de Sitter, 1959) is characterised by a regional hangingwall flat developed within the Lower Member of the Láncara Formation, which rests at the base of the nappe in most of the area (*e.g.,* Rupke, 1965; Arboleya, 1981). Towards the NE, a hangingwall ramp develops, cutting upward through the succession until reaching the base of the Devonian Portilla Formation The Esla Nappe is also characterized by several regional footwall flats developed over Devonian formations (*e.g,.* Rupke, 1965; Arboleya, 1981), whereas towards the NE there is a large footwall ramp that reaches the shales of the Carboniferous Prioro Gr.

STOP 2 – CLASSIC LOCALITY OF THE ESLA NAPPE BASAL SHEAR ZONE

Starting at the village of Valdoré, as we follow a path along the western margin of the Esla River, the transition from the Corniero Nappe to the base of the Esla Nappe can be observed (Fig. 33). The hill north of the village offers a good section of the Portilla Fm, which here dips some 30° towards the NE. The base of the formation (Veneros member of Reijers, 1972), not seen in this section, is composed of sandy ooidal limestones and bioclastic grainstones with marl intercalations. As we abandon the village, the first outcrops are part of the B member, which is formed by biostromal limestones with various textures, including packstone, grainstone and reefal boundstones. After some 80 m of outcrop, the hill on our left becomes grassier, marking the presence of the C member, formed by shales with sandstones and limestone intercalations, which is usually readily discernible in the landscape owing to its lower resistance to erosion. After this, the D member follows with limestones with similar facies to those of the B member.

Behind the cemetery, we can observe the base of the Nocedo Formation, which is part of the upper Devonian formations of the Cantabrian Zone. This formation, which is usually constituted by two coarsening-upwards sequences, is here partially eroded by the Upper Devonian unconformity. Thus, the formation, which can be up to 250 m thick, is here restricted to less than 50 m. The base is formed by shales, followed by reddish sandstones formed by hematite-cemented sandstones, with rarely preserved sedimentary structures.

As we approach the basal shear zone, the last formation of the Corniero Nappe is the unconformable Ermita Formation, formed by 2-3 m of sandy bioclastic limestones. After this, the basal shear zone of the Esla Nappe is formed by some 50 cm of ultracataclasites that contain fragments of the overlying Láncara Formation and from the Ermita Formation, which contributes small quartz grains that have been heavily comminuted. These ultracataclasites display a planar fabric (Fig. 34A) that results from variations in the quartz content, solution seams, and variable degrees of internal comminution (Arboleya, 1989; de Paz-Álvarez *et al.*, 2021). On top of the ultracataclasites, we find around 1 m of fault breccias with a particular texture: they are formed by Láncara-derived angular fragments, which are embedded in a quartz-grain matrix cemented by calcite (Fig. 34B). The origin of these quartz grains is considered to be the result of clastic injections into the basal shear zone, sourced from the Upper Devonian sandstone formations (Arboleya, 1989; de Paz-Álvarez, 2021). These injections, in other areas of the nappe, conform

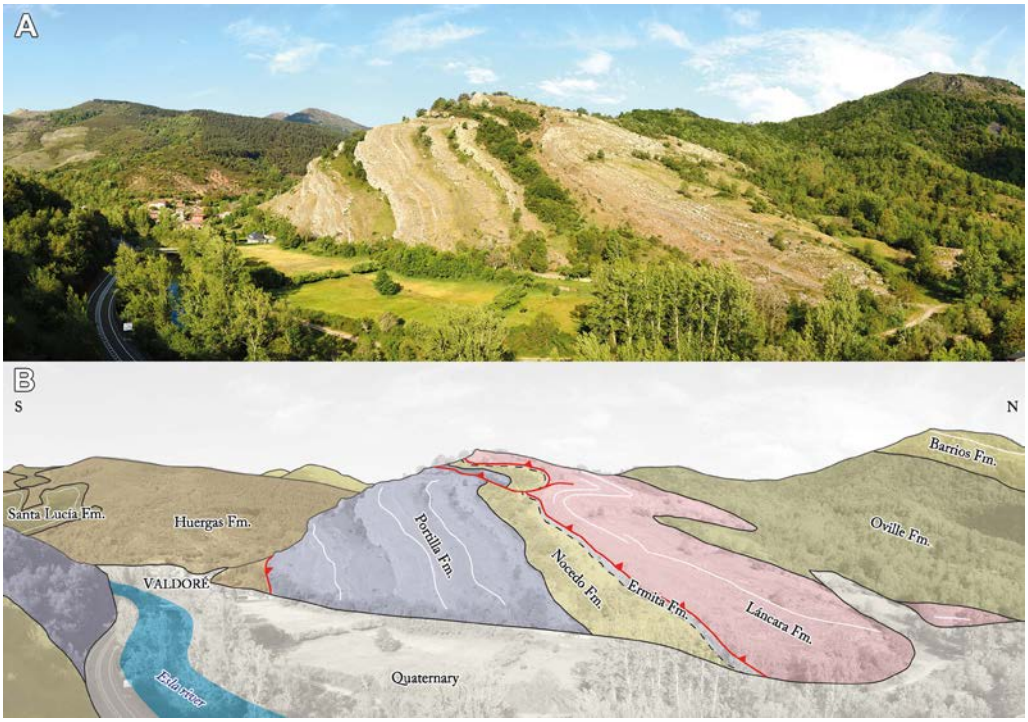

Figure 33. Panoramic view of the base of the Esla Nappe (right), resting on top of the Corniero Nappe (left).

a clastic injection complex formed by interconnected dykes and sills that can reach up to 20 m into the Láncara Formation The lack of deformation recorded by the quartz grains of the matrix, together with the presence of fragments derived from previous cataclasites, led to de Paz-Álvarez *et al*. (2021) to argue that these injections occurred during the final stages of the Esla Nappe emplacement, as a result of the attainment of extreme fluid pressure in the upper formations of the Corniero Nappe.

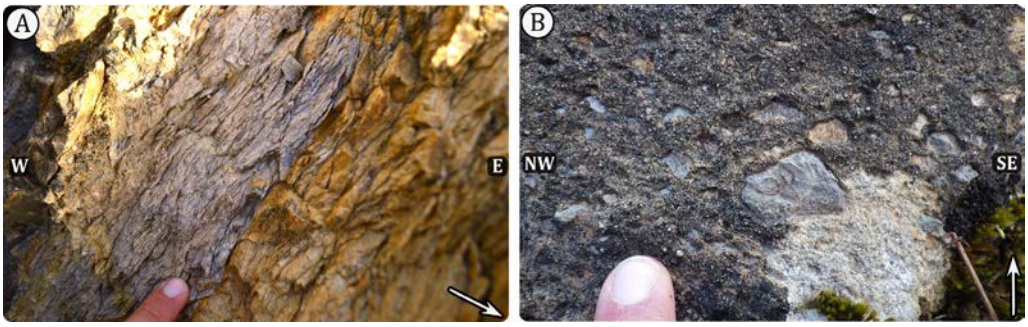

Figure 34. Field photographs of fault rocks at the base of the Esla Nappe. **A,** Ultracataclasites with a pervasive planar fabric (Verdiago); **B,** fault breccias with quartz grains in the matrix (Valdoré).

STOP 3 – AGUASALIO SYNCLINE

In the village of Crémenes, a short path leads to the water deposit, from where several features of the Esla Nappe can be observed. A better view of the area can be obtained walking to the Alto del Pozo, a route of 3,5 km and 200 m elevation gain.

Towards the east, the Aguasalio peak (1707m) rises 600 m over the Esla river valley, exposing the almost complete Palaeozoic sequence of the Esla Nappe (Fig. 35). From this point of view, we can see the alternating siliciclastic and carbonate formations of the Cantabrian Zone, starting with the Láncara Fm. limestones, and culminating in the Barcaliente Formation limestones that constitute the peak. On the background, forming the highest mountains of the ridge, the limestone-derived conglomerates of the Cea Gr. lie unconformably over the rest of the Palaeozoic succession.

A structure easily recognisable from this location, which stands out directly below the Aguasalio summit, is the Aguasalio Syncline (Fig. 35). This is one of the most representative structures of the Esla Nappe, and was formed as a result of the nappe accommodation to underlying structures. Its northern limb, which dips to the south, is the result of the nappe climbing over its

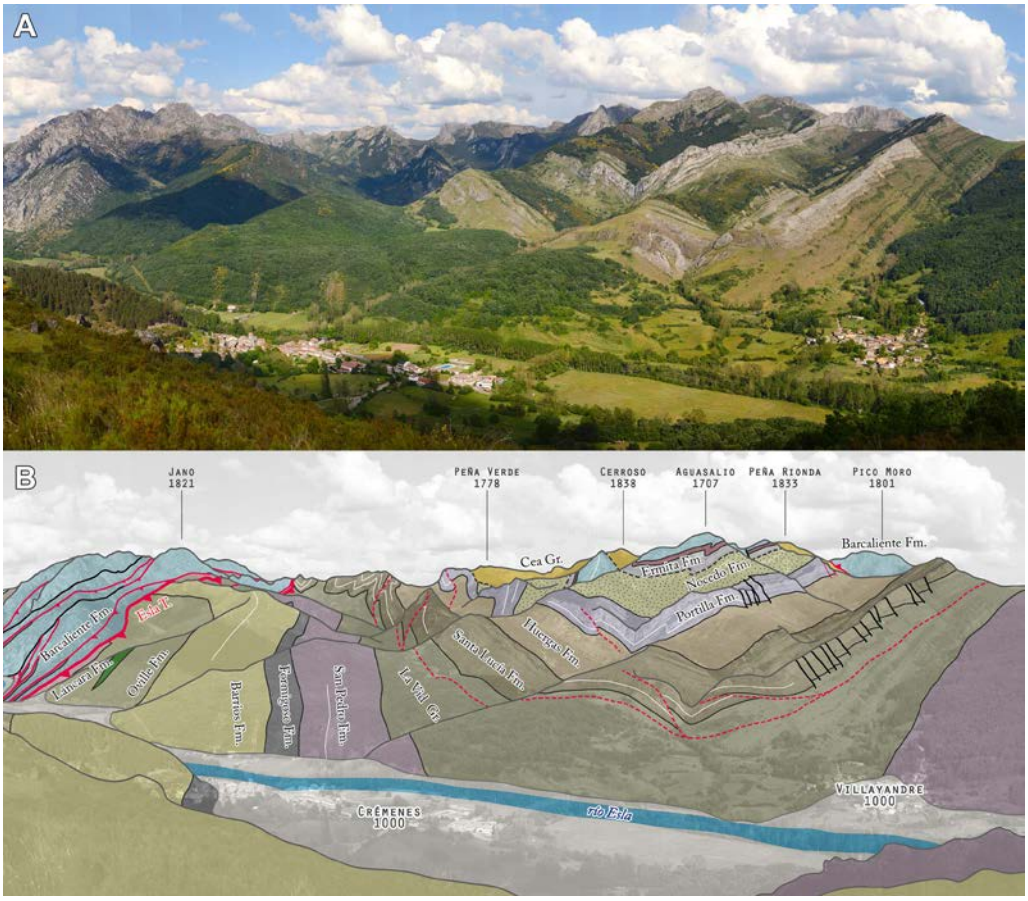

Figure 35. Panoramic view of the Esla Nappe from the Alto del Pozo. On the western slope of the Aguasalio peak, the almost complete Palaeozoic sequence of the Esla Nappe is exposed. The Aguasalio Syncline is seen below the peak. Below the Jano peak, the fault-bend fold associated to the hangingwall ramp can be identified.

footwall ramp, as well as the rotation induced by the emplacement of the underlying Corniero and Valbuena nappes (Alonso, 1987). In contrast, the southern limb, which dips to the NE, was formed as a result of the rotation caused by the emplacement of the Pardominos Duplex horses, organised into an antiformal stack that generated the Pardominos Anticline, a structure that influences the cartographic pattern of the nappe around the Valdoré semi-window. The syncline was subsequently tightened during the late stages of Variscan deformation, and during the Alpine orogeny (Eocene-Oligocene), when the Variscan basement was exhumed, virtually unmodified, along the basal thrust of the Cantabrian Mountains, which was directed towards the Duero Basin (Alonso *et al.*, 1996).

Towards the north, on the southern slope of the Pico Jano, the base of the Esla Nappe can be seen. The Barrios Formation, which is particularly resistant to erosion, conforms a ridge that curves on its upper part towards the mountain, owing to the development of a fault-bend fold related to the accommodation of the hangingwall ramp over the footwall flat (Fig. 35). The Pico Jano is formed by several horses of Barcaliente Formation and Prioro Gr., which constitute the underlying Pico Jano Duplex.

REFERENCES

Alonso, J. L. (1987). Sequences of thrusts and displacement transfer in the superposed duplexes of the Esla Nappe region (Cantabrian Zone, NW Spain). *Journal of Structural Geology, 9*(8), 969–983. doi: 10.1016/0191-8141(87)90005-8

Alonso, J. L., Fernández, L. P., de Paz Álvarez, M. I., de Vicente, G., & Llana-Fúnez, S. (2024). Nota sobre la presencia de una sucesión cretácica-cenozoica bajo el Manto de Somiedo: Implicaciones tectónicas. *Geotemas, 20*, 341–344.

Alonso, J. L., Marcos, A., & Suárez, A. (2009). Paleogeographic inversion resulting from large out-of-sequence breaching thrusts: The León Fault (Cantabrian Zone, NW Iberia). A new picture of the external Variscan Thrust Belt in the Ibero-Armorican Arc. *Geologica Acta, 7*(4), 451–473. doi: 10.1344/105.000001449

Alonso, J. L., Martínez Abad, I., & García-Ramos, J. C. (2007). Nota sobre la presencia de una sucesión cretácica en el Macizo de Las Ubiñas (Cordillera Cantábrica). Implicaciones tectónicas y geomorfológicas. *Geogaceta, 43*, 47–50.

Alonso, J. L., Pulgar, J. A., García-Ramos, J. C., & Barba, P. (1996). Tertiary basins and Alpine tectonics in the Cantabrian Mountains (NW Spain). In P. F. Friend & C. J. Dabrio (Eds.), *Tertiary basins of Spain: The stratigraphic record of crustal kinematics* (pp. 214–227). Cambridge University Press. doi: 10.1017/CBO9780511524851.031

Álvarez-Marrón, J., & Pérez-Estaún, A. (1988). Thin-skinned tectonics in the Ponga region (Cantabrian Zone, NW Spain). *Geologische Rundschau, 77*(2), 539–550. doi: 10.1007/BF01832397

Álvarez-Marrón, J., Rubio, E., & Torné, M. (1997). Subduction-related structures in the north Iberian margin. *Journal of Geophysical Research: Solid Earth, 102*(B10), 22497–22511. doi: 10.1029/97JB01425

Aramburu, C. (1989). *El Cambro-Ordovícico de la Zona Cantábrica (NO de España)* [Doctoral thesis, Universidad de Oviedo].

Aramburu, C., Arbizu, M., Bernárdez, E., Gozalo, R., Gutiérrez-Marco, J. C., & Liñán, E. (2006). *Paleontología y estratigrafía del Paleozoico Inferior en Los Barrios de Luna* (XXII Jornadas de la Sociedad Española de Paleontología, 75 pp.).

Aramburu, C., Arbizu, M., Gutiérrez-Marco, J. C., Méndez-Bedia, I., Rábano, I., & Truyols, J. (1996). Primera identificación de materiales del Ordovícico Medio en la sección de Los Barrios de Luna (Zona Cantábrica, noroeste de España). *Geogaceta, 20*, 7–10. doi: 10.17811/tdg.19.1993.45-75

Aramburu, C., & García-Ramos, J. C. (1993). La sedimentación cambro-ordovícica en la Zona Cantábrica (NO de España). *Trabajos de Geología, 19*, 45–73.

Baldwin, C. T. (1977). The stratigraphy and facies associations of trace fossils in some Cambrian and Ordovician rocks of north western Spain. In T. P. Crimes & J. C. Harper (Eds.), *Trace fossils 2* (*Geological Journal Special Issue*, 9, pp. 9–40).

Bastida, F., Marcos, A., Pérez-Estaún, A., & Pulgar, J. A. (1984). Geometría y evolución estructural del Manto de Somiedo, Zona Cantábrica, N.O. España. *Boletín Geológico y Minero, 95*(6), 517–539.

Bastida, F., Pérez-Estaún, A., Aramburu, C., Méndez-Bedia, I., Arbizu, M., García-López, S., Fernández, L. P., Bahamonde, J. R., Barba, P., Colmenero, J. R., Heredia, N., Rodríguez-Fernández, L. R., Salvador, C., Sánchez de Posada, L. C., Villa, E., Merino-Tomé, O., Motis, K., Aller, J., Álvarez-Marrón, J., Bulnes, M., Marcos, A., & Pulgar, J. A. (2004). Zona Cantábrica. In J. A. Vera (Ed.), *Geología de España* (pp. 25–49). SGE-IGME.

Boillot, G., & Malod, J. (1988). The north and north-west Spanish continental margin: A review. *Revista de la Sociedad Geológica de España, 1*, 295–316.

Bosch, W. J. van den. (1969). Geology of the Luna-Sil region, Cantabrian Mountains (NW Spain). *Leidse Geologische Mededelingen, 44*, 137–225.

Bowman, M. B. J. (1979). The depositional environments of a limestone unit from the San Emiliano Formation (Namurian/Westphalian), Cantabrian Mountains, NW Spain. *Sedimentary Geology, 24*, 25–43. doi: 10.1016/0037-0738(79)90027-7

Chesnel, V., Samankassou, E., Merino-Tomé, O., Fernández, L. P., & Villa, E. (2016). Facies, geometry and growth phases of the Valdorria carbonate platform (Pennsylvanian, northern Spain). *Sedimentology, 63*(1), 60–104. doi: 10.1111/sed.12221

Coleman, P. J. (1968). Tsunamis as geological agents. *Journal of the Geological Society of Australia, 15*, 267–273. doi: 10.1080/00167616808728698

Colmenero, J. R., Fernández, L. P., Moreno, C., Bahamonde, J. R., Barba, P., Heredia, N., & González, F. (2002). Carboniferous. In W. Gibbons & T. Moreno (Eds.), *The geology of Spain* (pp. 93–116). Geological Society.

Comte, P. (1936). La série dévonienne du León (Espagne). *Comptes Rendus de l'Académie des Sciences de Paris, 202*, 337–339.

Comte, P. (1959). *Recherches sur les terrains anciens de la Cordillère Cantabrique*. *Memorias del Instituto Geológico y Minero de España, 60*, 1–440.

Corrochano, D., Vachard, D., & Armenteros, I. (2013). New insights on the red alga *Archaeolithophyllum* and its preservation from the Pennsylvanian of the Cantabrian Zone (NW Spain). *Facies, 59*(4), 949–967. doi: 10.1007/s10347-012-0347-8

Cózar, P., Somerville, I. D., & Medina-Varea, P. (2005). Note on the earliest occurrences of the calcareous algae *Paraepimastopora* and *Archaeolithophyllum* in Mississippian rocks. *Coloquios de Paleontología, 55*, 7–20.

Dawson, A. G., & Stewart, I. (2007). Tsunami deposits in the geological record. *Sedimentary Geology, 200*(3–4), 166–183. doi: 10.1016/j.sedgeo.2007.01.002

Della Porta, G., Kenter, J. A. M., & Bahamonde, J. R. (2002). Microfacies and paleoenvironment of *Donezella* accumulations across an Upper Carboniferous high-rising carbonate platform (Asturias, NW Spain). *Facies, 46*, 149–168. doi: 10.1007/BF02668079

Dott, R. H., Jr., & Bourgeois, J. (1982). Hummocky stratification: Significance of its variable bedding sequences. *Geological Society of America Bulletin, 93*(8), 663–680. doi: 10.1130/0016-7606(1982)93%3C663:HSSOIV%3E2.0.CO;2

Druet, M., Muñoz-Martín, A., Granja-Bruña, J. L., Carbó-Gorosabel, A., Acosta, J., Llanes, P., & Ercilla, G. (2018). Crustal structure and continent-ocean boundary along the Galicia continental margin (NW Iberia): Insights from combined gravity and seismic interpretation. *Tectonics, 37*, 1576–1604. doi: 10.1029/2017TC004903

Eichmüller, K. (1985). The Valdeteja Formation: Environment and history of an Upper Carboniferous platform (Cantabrian Mountains, northern Spain). *Facies, 13*, 45–153. doi: 10.1007/BF02536901

Espina, R. G. (1992). La estructura del borde occidental de la Cuenca Vasco-Cantábrica en el área de Campoo (Cantabria-Palencia, norte de España). *Actas del VIII Congreso Latinoamericano de Geología* (Vol. 8, pp. 294–298).

Esteve, J. (2011). *Sistemática, bioestratigrafía y aspectos paleobiológicos de los trilobites del Caesaraugustiense medio-superior y Languedociense inferior de las Cadenas Ibéricas y Zona Cantábrica (norte de España)* [Unpublished doctoral thesis].

Esteve, J. (2013). Revision of enrolled Cambrian trilobites from Spain and its implications in trilobite evolution. *Estudios Geológicos, 69*, 165–181. doi: 10.3989/egeol.41215.259

Esteve, J., González-Cloquells, A., & Arriola, A. (2026). Microstructural biomechanics underpin Cambrian phosphatic brachiopod diversification. *Proceedings of the Royal Society B: Biological Sciences, 293*, 20260192. doi: 10.1098/rspb.2026.0192

Esteve, J., Hughes, N. C., & Zamora, S. (2011). The Purujosa trilobite assemblage and the evolution of trilobite enrollment. *Geology, 39*(6), 575–578. doi: 10.1130/G31985.1

Fernández, L. P. (1993). La Formación San Emiliano (Carbonífero de la Zona Cantábrica, NO de España): Estratigrafía y extensión lateral. Algunas implicaciones paleogeográficas. *Trabajos de Geología, Universidad de Oviedo, 19*, 97–122. doi: 10.17811/tdg.19.1993.97-123

Fernández, L. P. (1995). El Carbonífero. In C. Aramburu & F. Bastida (Eds.), *Geología de Asturias* (pp. 63–80). Ediciones Trea.

Fernández-Viejo, G., Pulgar, J. A., Gallastegui, J., & Quintana, L. (2012). The fossil accretionary wedge of the Bay of Biscay: Critical wedge analysis on depth-migrated seismic sections and geodynamical implications. *The Journal of Geology, 120*(3), 315–331. doi: 10.1086/664789

Gallastegui, J. (2000). Estructura cortical de la cordillera y margen continental cantábricos: Perfiles ESCI-N. *Trabajos de Geología, 22*, 3–234. doi: 10.17811/tdg.22.2000.3-234

Gallastegui, J., & Pulgar, J. A. (2002). Initiation of an active margin at the North Iberian continent-ocean transition. *Tectonics, 21*(4), 15-1–15-14. doi: 10.1029/2001TC901046

Gandl, J. (1977). Die Karbon-Trilobiten des Kantabrischen Gebirges (NW-Spanien), 2: Die Trilobiten der Alba-Schichten (Unter-Visé bis Namur A). *Senckenbergiana lethaea, 58*(1/3), 113–217.

Gilbert, G. K. (1899). Ripple-marks and cross-bedding. *Geological Society of America Bulletin, 10*, 135–140. doi: 10.1130/GSAB-10-135

Gong, Z., Langereis, C. G., & Mullender, T. A. T. (2008). The rotation of Iberia during the Aptian and the opening of the Bay of Biscay. *Earth and Planetary Science Letters, 273*(1–2), 80–93. doi: 10.1016/j.epsl.2008.06.016

Gutiérrez-Alonso, G., Johnston, S. T., Weil, A. B., Pastor-Galán, D., & Fernández-Suárez, J. (2012). Buckling an orogen: The Cantabrian Orocline. *GSA Today, 22*(7), 4–9. doi: 10.1130/GSATG141A.1

Gutiérrez-Marco, J. C., Aramburu, C., Arbizu, M., Bernárdez, E., Hacar Rodríguez, M., Méndez-Bedia, I., Montesinos López, R., Rábano, I., Truyols, J., & Villas, E. (1999). Revisión bioestratigráfica de las pizarras del Ordovícico Medio en el noroeste de España (zonas Cantábrica, Asturoccidental-leonesa y Centroibérica septentrional). *Acta Geológica Hispánica, 34*, 3–87.

Hirt, A. M., Lowrie, W., Julivert, M., & Arboleya, M. L. (1992). Paleomagnetic results in support of a model for the origin of the Asturian Arc. *Tectonophysics, 213*(3–4), 321–339. doi: 10.1016/0040-1951(92)90461-E

Julivert, M. (1967). Estratigrafía del Cámbrico del oriente de Asturias y estudio petrográfico de las facies carbonatadas. *Trabajos de Geología, Universidad de Oviedo, 1*, 135–163. doi: 10.17811/tdg.1.1967.135-165

Julivert, M. (1971). Decollement tectonics in the Hercynian Cordillera of Northwest Spain. *American Journal of Science, 270*(1), 1–29. doi: 10.2475/ajs.270.1.1

Julivert, M. (1976). La estructura de la región del Cabo Peñas. *Trabajos de Geología, Universidad de Oviedo, 8*, 203–309. doi: 10.17811/tdg.8.1976.203-311

Julivert, M., & Marcos, A. (1973). Superimposed folding under flexural conditions in the Cantabrian Zone (Hercynian Cordillera, northwest Spain). *American Journal of Science, 273*(5), 353–375. doi: 10.2475/ajs.273.5.353

Keller, M. (1988). Die La-Vid-Gruppe: Fazies, Paläogeographie und synsedimentäre Tektonik im Unterdevon des Kantabrischen Gebirges (NW-Spanien). *Erlanger Geologische Abhandlungen, 115*, 77–154.

Lepvrier, C., & Martínez-García, E. (1990). Fault development and stress evolution of the post-Hercynian Asturian Basin (Asturias and Cantabria, northwestern Spain). *Tectonophysics, 184*(3–4), 345–356. doi: 10.1016/0040-1951(90)90447-G

Marcos, A., & Pulgar, J. A. (1982). An approach to the tectonostratigraphic evolution of the Cantabrian foreland thrust and fold belt, Hercynian Cordillera of NW Spain. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 163*(2), 256–260. doi: 10.1127/njgpa/163/1982/256

Meer Mohr, C. G. van der. (1969). The stratigraphy of the Cambrian Láncara Formation between the Luna River and the Esla River in the Cantabrian Mountains, Spain. *Leidse Geologische Mededelingen, 43*, 233–316.

Merino-Tomé, O., Alonso, J. L., Bahamonde, J. R., Fernández, L. P., Marcos, A., Colmenero, J. R., Villa, E., & Suárez, A. (2019). Foreland basin at the Cantabrian Zone: Evolution from the distal foreland basin successions to wedge-top deposition and the tightening of the Ibero-Armorican Arc. In C. Quesada & J. T. Oliveira (Eds.), *The geology of Iberia: A geodynamic approach. Volume 2: The Variscan cycle* (pp. 356–361). Springer.

Merino-Tomé, O., Suárez Rodríguez, A., & Alonso Alonso, J. L. (n.d.). *Mapa Geológico Digital continuo E. 1:50.000, Zona Cantábrica (Zona-1000)*. In *GEODE. Mapa Geológico Digital continuo de España*. Instituto Geológico y Minero de España.

Pérez-Estaún, A., Bastida, F., Alonso, J. L., Marquínez, J., Aller, J., Álvarez-Marrón, J., Marcos, A., & Pulgar, J. A. (1988). A thin-skinned tectonics model for an arcuate fold and thrust belt: The Cantabrian Zone (Variscan Ibero-Armorican Arc). *Tectonics, 7*(3), 517–537.

Pérez-Estaún, A., Pulgar, J. A., & Álvarez-Marrón, J. (1995). Crustal structure of the Cantabrian Zone: Seismic image of a Variscan foreland thrust and fold belt (NW Spain). *Revista de la Sociedad Geológica de España, 8*(4), 307–319. doi: 10.1029/TC007i003p00517

Pulgar, J. A., & Alonso, J. L. (1993). La estructura alpina de la Cordillera Cantábrica. In *Resúmenes XV Reunión de Xeología e Minería do NO Peninsular* (pp. 69–71). Laboratorio Xeolóxico de Laxe.

Rodríguez-Castro, I., Fregenal-Martínez, M. A., Rodríguez, S., & González, F. J. (2024). Taphonomic analysis of the Rosario Mine (Valdeteja Formation, Bashkirian, NW Spain): Evidence of tsunamis or cyclones. *Historical Biology, 36*(8), 1583–1591. doi: 10.1080/08912963.2023.2221298

Rodríguez-Castro, I., & Rodríguez, S. (2025). Intergrowth of chaetetids, *Girvanella* and *Donezella* in Pennsylvanian mounds in the Valdeteja Formation, NW Spain. *Spanish Journal of Palaeontology, 40*(2), 243–252. doi: 10.7203/sjp.31746

Rodríguez-Castro, I., Rodríguez, S., & Fregenal-Martínez, M. A. (2020). *Donezella*-chaetetid mounds in the Valdeteja Formation (Bashkirian, Pennsylvanian) at Truébano, Cantabrian Mountains, northern Spain. *Bollettino della Società Paleontologica Italiana, 59*(3), 247–259. doi: 10.4435/BSPI.2020.19

Rodríguez Fernández, L. R. (1992). *Estratigrafía y estructura de la región de Fuentes Carrionas y áreas adyacentes (Cordillera Cantábrica)* [Doctoral thesis, Universidad de Oviedo].

Samankassou, E. (2001). Internal structure and depositional environment of Late Carboniferous mounds from the San Emiliano Formation, Cármenes Syncline, Cantabrian Mountains, northern Spain. *Sedimentary Geology, 145*(3–4), 235–252. doi: 10.1016/S0037-0738(01)00150-6

Sdzuy, K. (1968). Trilobites del Cámbrico Medio de Asturias. *Trabajos de Geología, Universidad de Oviedo, 1*, 77–133. doi: 10.17811/tdg.1.1967.77-135

Shaw, J., Johnston, S. T., & Gutiérrez-Alonso, G. (2015). Orocline formation at the core of Pangea: A structural study of the Cantabrian orocline, NW Iberian Massif. *Lithosphere, 7*(6), 653–661. doi: 10.1130/L461.1

Suppe, J. (1983). Geometry and kinematics of fault-bend folding. *American Journal of Science, 283*(7), 684–721. doi: 10.2475/ajs.283.7.684

Toyos, J. M., & Aramburu, C. (2014). El Ordovícico en el área de Los Barrios de Luna, Cordillera Cantábrica (NW de España). *Trabajos de Geología, 34*, 61–96. doi: 10.17811/tdg.34.2014.61-96

Vera de la Puente, C. (1989). Revisión litoestratigráfica y correlación de los Grupos Rañeces y La Vid (Devónico Inferior de la Cuenca Astur-Leonesa). *Trabajos de Geología, Universidad de Oviedo, 18*, 53–65.

Vilas Minondo, L. (1971). El Paleozoico Inferior y Medio de la Cordillera Cantábrica entre los ríos Porma y Bernesga (León). *Memorias del Instituto Geológico y Minero de España, 80*, 1–169.

Zamarreño, I. (1972). Las litofacies carbonatadas del Cámbrico de la Zona Cantábrica (NW de España) y su distribución paleogeográfica. *Trabajos de Geología, 5*, 1–118. doi: 10.17811/tdg.5.1972.3-118

Zamora, S., & Álvaro, J. J. (2010). Testing for a decline in diversity prior to extinction: Languedocian (latest mid-Cambrian) distribution of cinctans (Echinodermata) in the Iberian Chains, NE Spain. *Palaeontology, 53*(6), 1349–1368. doi: 10.1111/j.1475-4983.2010.01004.x

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