

# First occurrence of well-preserved Ordovician trilobites of the family Olenidae from Africa

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**Non-technical Summary.**—Some trilobite species lived in deeper-water environments that are not well preserved in the fossil record. There are also intervals of time that are not well represented in some areas. This is the case for the earliest part of the Ordovician in Morocco. Because of this, any well-preserved trilobite specimens from these rocks are important for understanding how they relate to other parts of the world. They are also important for our understanding of migration and evolution of trilobites during this time. Here we present the first well-preserved trilobites of the family Olenidae from Morocco. Species from this family were often restricted to deeper or low-oxygen environments. This is the first discovery of olenid trilobites from Africa that are well preserved enough to be able to identify the species.

**Abstract.**—Here we describe the first articulated olenid trilobite specimens recovered from the lowermost Fezouata Shale Formation (lower Tremadocian, Ordovician) of Morocco. Prior to the discovery of this sample, only two partial olenid trilobite specimens had been found from this part of the rock record. The specimens are well preserved enough to confidently identify as *Leptoplastides salteri* (Callaway, 1877), extending the species geographic range from Avalonia into Gondwana. We argue that the Moroccan occurrences formerly referred to as “*Beltella* sp.” in the literature are likely to be those of *L. salteri*. This species is the only olenid trilobite known from African Gondwana.

## Introduction

The early Paleozoic rock record of Morocco is predominantly marine and highly fossiliferous. Among Ordovician deposits, the Fezouata Shale Formation is notable for its diverse fossil fauna, including two intervals (upper Tremadocian and mid-Floian interval) with exceptional preservation (Lefebvre et al., 2018). In contrast, the lowermost Fezouata Shale Formation (lower Tremadocian) is relatively unfossiliferous: in the last 60–70 years, only a handful of marine invertebrate specimens have been recovered from the lowest 100 meters of the more than 800 m that the formation reaches in the depocenter of the central Anti-Atlas Mountains (Lefebvre et al., 2016a, 2018). The fossil material consists primarily of graptolites and rare trilobite specimens referred to as *Beltella* sp. and *Pharostomina* sp. (Destombes, 1967, 2006c; Destombes et al., 1985; Lefebvre et al., 2016a). Further, across Morocco, the early Tremadocian is represented only by the lowermost Fezouata Shale Formation in the Anti-Atlas area (Destombes et al., 1985). Thus, any new

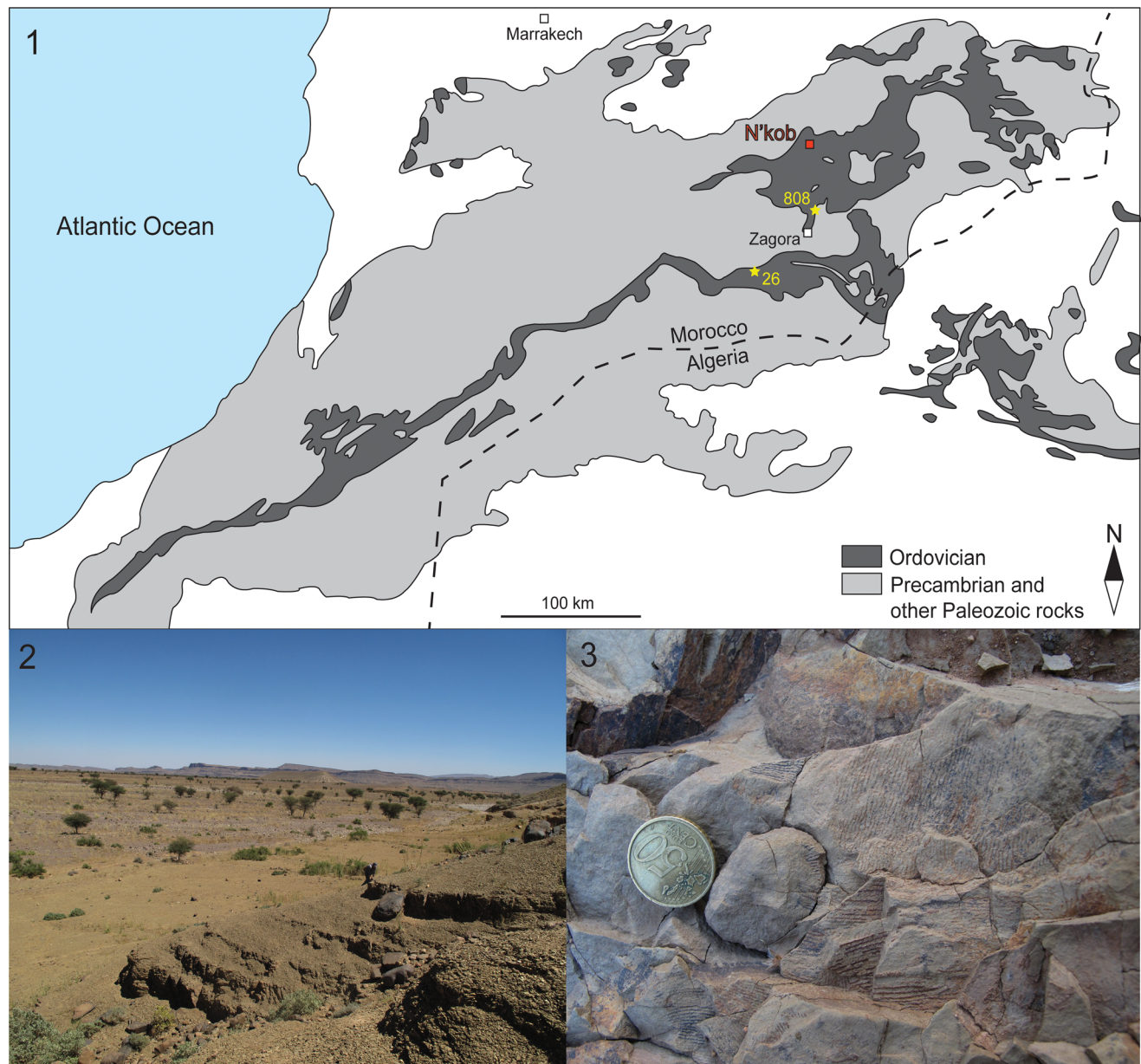
discoveries of well-preserved specimens from this unit can have particular value on our understanding of the earliest Ordovician faunas (e.g., Lefebvre et al., 2016a). In this paper, we describe the first well-preserved olenid trilobite specimens recovered from this unit. These are also the first olenid trilobite specimens well preserved enough to be identified to species level from the African continent.

## Geologic setting

The specimens were found by locals near N’kob village (Fig. 1.1) and acquired in 2019. In the N’kob area, the Fezouata Shale Formation crops out extensively across the southern flank of the Precambrian antiform of the Jbel Saghro (also known as the Saghro Massif), but there are no complete stratigraphic sections because the unit is regularly covered by Quaternary sediments. Partial exposures exist on hillsides, where they are topped with Pleistocene terrace deposits (Fig. 1.2). In the plains, Holocene deposits are thin enough (1 meter or less) that any small excavation has the potential to expose Fezouata Shale Formation layers. Although the exact location where these specimens were found is unknown, outcrops of the Fezouata Shale Formation around

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**Figure 1.** Geographic setting. (1) Simplified geologic map of the Anti-Atlas Mountains and localities of recovered olenid trilobites in Morocco. Previously reported specimens identified as *Beltella* sp. were found at localities 26 and 808 (yellow stars) in the Zagora area (Destombes, 2006c). The specimens described in this paper were found in the N'kob area (red square). Modified from Álvaro et al. (2022). (2) Lower Tremadocian exposures of the Fezouata Shale Formation in the N'kob area. Mountainous area in background represents the First Bani Group. (3) Bedding-plane accumulations of the graptolite *Rhabdinopora* cf. *R. socialis* (Salter) in the Akka n'Ousdidene locality east of N'kob, ~12 m above the base of the Fezouata Shale Formation. Diameter of coin is 24 mm.

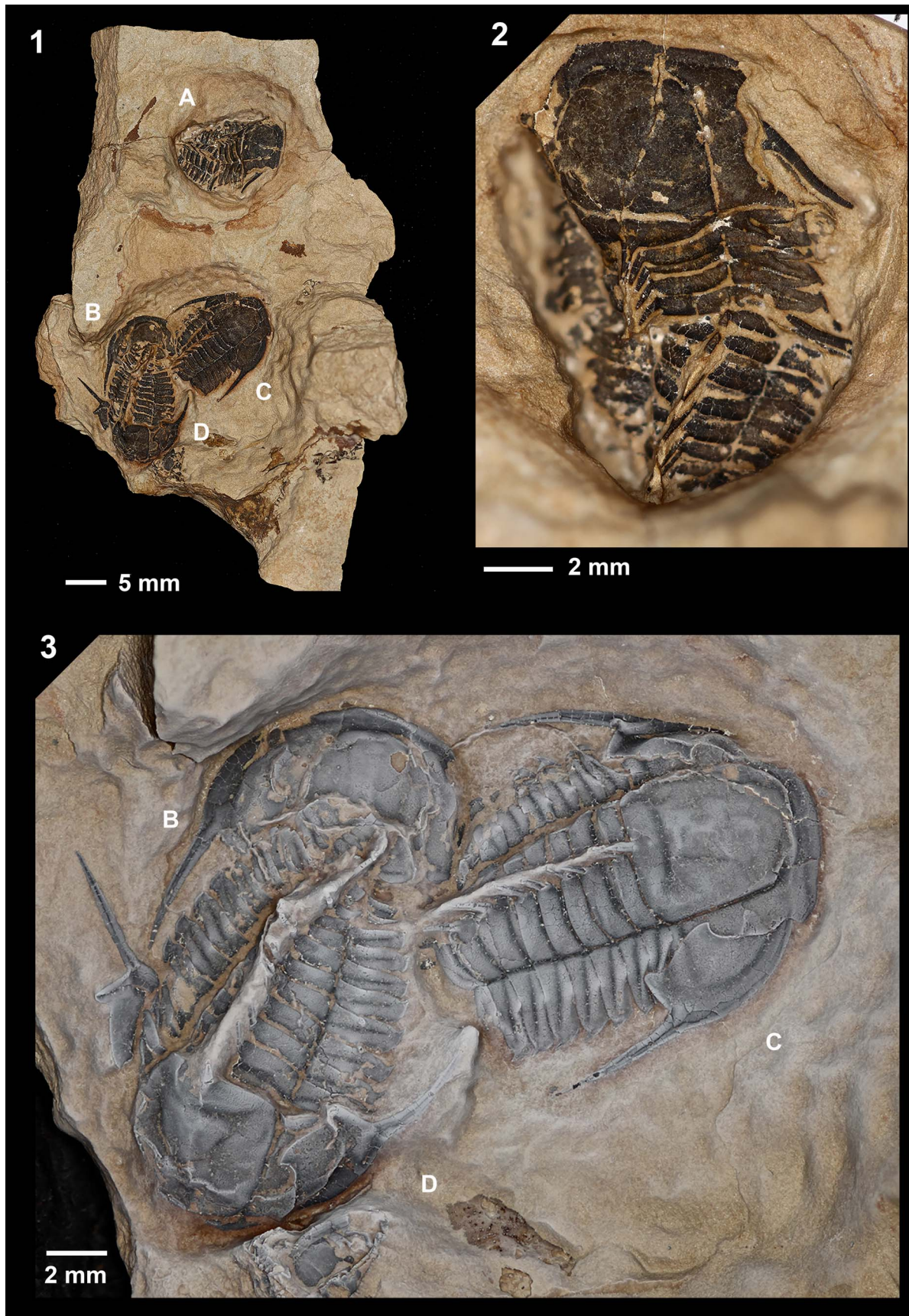
N'kob preserve the graptolites *Rhabdinopora canadensis* (Lapworth, 1898) and *R. socialis* (Salter, 1858), among other graptolites, in the lowermost 6–15 m, followed by sporadic occurrences of *R. flabelliformis* (Eichwald, 1840) in the succeeding 50 meters of the Fezouata Shale Formation (Destombes and Willefert, 1959; reviewed by Gutiérrez-Marco and Martin, 2016; with taxonomy updated according to Maletz et al., 2023).

### Materials and methods

The specimens are preserved in a light tan, non-calcareous, micaceous argillite. The fossil material is likely recrystallized, brown calcite, that strongly stands out visually against the matrix.

While the exoskeletal surface preserves small details of ornamentation, it is also characterized by a network of fine fractures and the exoskeleton fragments easily. The specimens were prepared using air abrasion with a dolomite–calcium–carbonate powder blend. Four exoskeletons of varying completeness were recovered, three of which are clustered on top of one another (Fig. 2). Although mostly articulated, displacement of librigenae indicates that these specimens are molts of roughly the same size (the length of the cranidia varies from 6.8 to 7.7 mm).

*Repository and institutional abbreviation.*—Specimens examined and figured in this study are deposited in the American Museum of Natural History (AMNH), New York,



**Figure 2.** *Leptoplastides salteri* (Callaway, 1877) specimens from N'kob, Morocco. (1) Entire rock sample showing all four specimens labeled A–D to correspond to (2, 3). (2) Part of rock sample showing AMNH-FI-139288 (labeled “A”). (3) Part of rock sample showing AMNH-FI-139289 (labeled “B”), AMNH-FI-139290 (labeled “C”), and AMNH-FI-139291 (labeled “D”); (1, 3) whitened with ammonium chloride. Scale bars below associated images.

USA, under catalog numbers AMNH-FI-139288 to AMNH-FI-139291.

## Results

The Moroccan material fits the diagnosis of the genus *Leptoplastides* Raw, 1908 (Nikolaisen and Henningsmoen, 1985, p. 12) and, among the species defined for the genus, it most closely resembles *Leptoplastides salteri* (Callaway, 1877). Articulated specimens, including meraspides, of *L. salteri* (Callaway, 1877) have been figured and described by Lake (1919, p. 89–93, pl. 11, figs. 2–5), Raw (1925, p. 229–247, pls. 16–18), Fortey and Owens (1991, p. 449–451, fig. 8c–j), and Månsson and Clarkson (2020, p. 2–15, figs. 1–11). Features that align the newly recovered Moroccan specimens with *L. salteri* include the mid-axial spines on the occipital ring and thoracic tergites (Figs. 2.3, 3.1) but not the pygidium (Fig. 3.3), the small anteriorly placed palpebral lobes (Fig. 2.2), the narrow, relatively long genal spines emerging from the lateral margin of the cephalon (Figs. 2.3, 3.2), the spinose thoracic pleura (Fig. 3.2), and the small spinose projection at the antero-lateral angle of pygidium (Fig. 3.3).

The specimens presented here have two axial rings and a terminal piece (Fig. 3.3). This would seem in contrast to the description of *L. salteri* provided by Lake (1919), which stated that the axis is divided into three distinct rings and a terminal portion. However, Lake's illustrations clearly show specimens with two rings and a terminal piece (e.g., Lake, 1919, pl. 11, fig. 3), as do the specimens figured in Raw (1925) and Fortey and Owens (1991), including the lectotype, which is housed in the Birmingham University Collections (BU691, see Fortey and Owens, 1991, fig. 8h).

Raw (1925) noted that *L. salteri* transitioned to the holaspide stage at a body size of about 5.75 mm and that disarticulated material indicated a maximum size of 60 mm. He reported ongoing ontogenetic changes during the holaspide period, including (1) increasing width-to-length ratio of the glabella; (2) increasing effacement of glabellar furrows; (3) decrease in prominence of the ocular ridge; (4) increasingly posterior position of the genal spine; (5) increase in the number of thoracic segments with “unguiculate” (= spiny or pointed) pleural terminations from anterior to posterior; (6) diminishing size of the pleural projection at the antero-lateral angle of the pygidium; (7) increasing emargination of the posterior border of the terminal piece; and (8) increasingly concave posterior border of the pygidium. The Moroccan specimens are more than twice as large as the previously figured articulated specimens. For example, AMNH-FI-139291 (Fig. 2.3, specimen D) is 16.58 mm in length, while the largest articulated specimens figured by Månsson and Clarkson, 2020, fig. 8e, and Fortey and Owens, 1991, fig. 8j, are 7.1 mm and 6.8 mm, respectively, and the differences between them and previously figured specimens are consistent with the ontogenetic changes described by Raw (1925).

Although displacement complicates comparisons, the genal spines in the Moroccan specimens appear to be relatively longer than those of smaller specimens figured elsewhere. The occipital furrows are more deeply expressed medially than laterally in the Moroccan specimens. It is not clear if this is taphonomic (for example, this is seen in some of the more compressed specimens

from England [e.g., Fortey and Owens, 1991, figs. 8c–e]), ontogenetic, or both.

Additional morphological details that are expressed on the Moroccan specimens include fine pitting on the axial lobes of the cephalon and thorax (Fig. 3.1) and terrace lines along the margin of the pygidium (Fig. 3.3).

Combinations of these features distinguish the UK and Moroccan specimens from other *Leptoplastides* species (see also Table 1).

*Leptoplastides argentinensis* (Kobayashi, 1935) has a longer (sag.) preglabellar field, smaller palpebral lobes, no intergenal angle, and more developed pygidial marginal spines (see Monti, 2018).

*Leptoplastides coniunctus* (Tomczykowa, 1968) has transglabellar furrows, no (apparent) axial spines or nodes on the thorax, shallower intergenal angle, and shorter genal spine (see Żylińska, 2001).

*Leptoplastides depressus* (Salter in Murchison, 1859) has no axial spines or nodes and blunt pleural ends on the thorax (see Fortey and Owens, 1989).

*Leptoplastides dissimulosulcus* (Loch et al., 1993) has a longer (sag.) preglabellar field and wider librigenal field. The thorax is unknown, and the pygidium is too incomplete for adequate comparison, but the occipital ring bears what may be the base of a robust spine (see Loch et al., 1993).

*Leptoplastides granulatus* (Harrington, 1938) has a narrower (sag. and tr.) anterior border, shorter, more anteriorly placed palpebral lobes, shallower genal angle, thoracic axial nodes not developed into spines, and granular ornamentation (see Waisfeld and Vaccari, 2003; Monti, 2018).

*Leptoplastides irae* (Orłowski, 1968) has no intergenal angle, shorter genal spines, no axial spine or nodes, and two short marginal pygidial spines (see Żylińska, 2001).

*Leptoplastides latus* (Tomczykowa, 1968) has an axial node (instead of long spine) on the occipital ring and at least two short marginal pygidial spines; the thorax is unknown although comparable specimens from Norway show nodes only on the anteriormost thoracic tergites (see Nikolaisen and Henningsmoen, 1985; Żylińska, 2001).

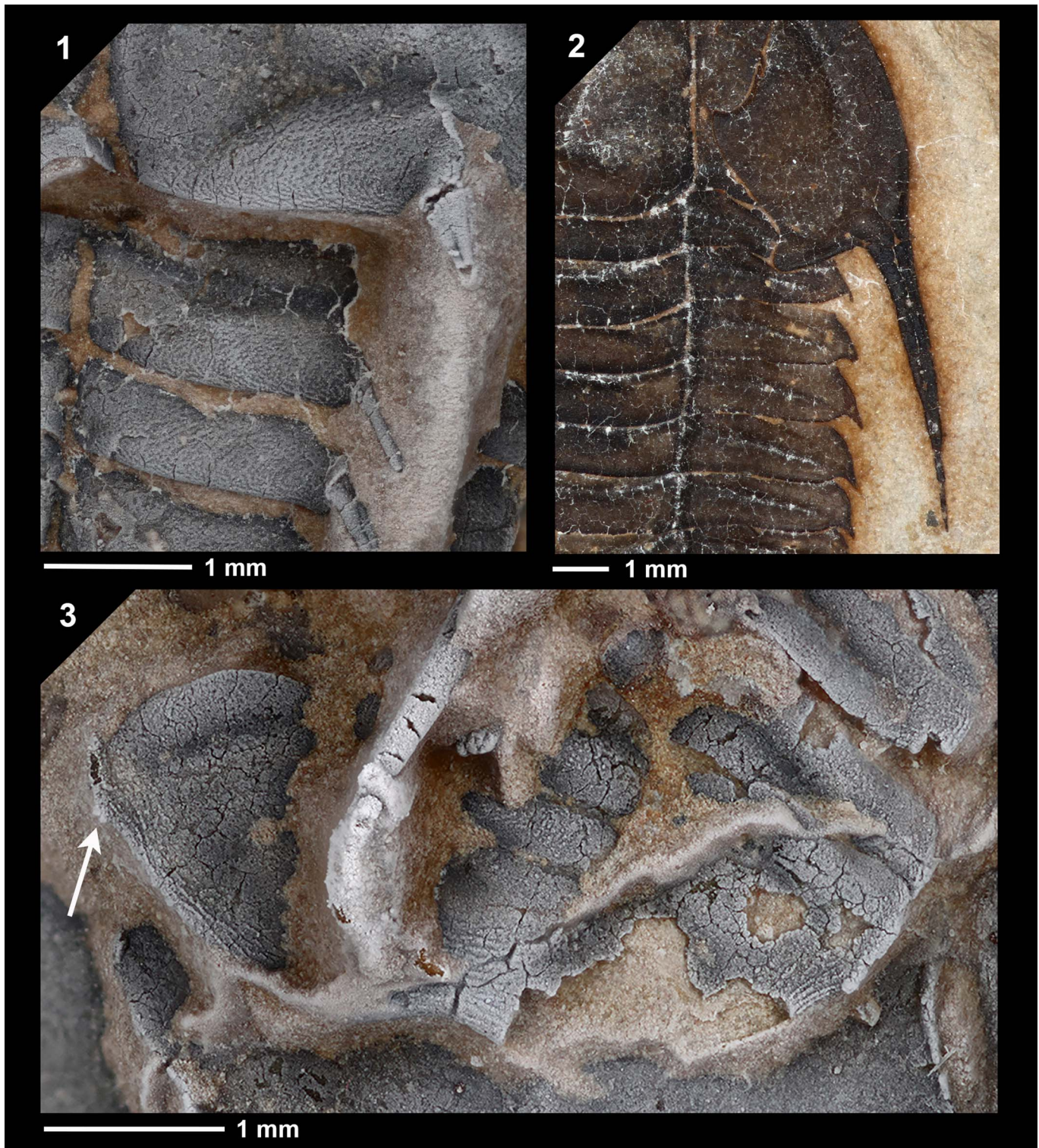
*Leptoplastides marianus* (Hoek in Steinmann and Hoek, 1912) was recently restricted to the type specimens (Monti, 2018), which have no apparent axial spines or nodes and a shallower genal angle. Comparison is hampered by extreme distortion of the specimens, which has resulted in a complicated taxonomic history for this and other Argentinian species (see Waisfeld and Vaccari, 2003; Monti, 2018).

*Leptoplastides nodifer* (Rushton, 1982) has a longer (sag.) preglabellar field, shallower intergenal angle, and axial nodes along the thorax but they are not developed into spines (see Rushton, 1982).

*Leptoplastides ulrichi* (Kayser, 1897) has no apparent axial nodes or spines, short spines on anteriormost thoracic tergites but blunt pleural ends otherwise, and a shallower intergenal angle (see Harrington and Leanza, 1957; Żylińska, 2001).

## Discussion

*Comparison with other Moroccan olenid specimens.*—Previously, the only olenid trilobite to have been reported



**Figure 3.** Close-up images of *Leptoplastides salteri* (Callaway, 1877) specimens, whitened in (1, 3) with ammonium chloride to show sculpture. (1) Close-up of occipital ring and two anteriormost axial rings of the thorax, showing pitting sculpture and axial spines, AMNH-FI-139291 (labeled “D” in Fig. 2A). (2) Close-up of genal spine and pleural region of thorax, AMNH-FI-139288 (labeled “A” in Fig. 2A). (3) Close-up of pygidium, AMNH-FI-139291 (labeled “D” in Fig. 2A). Arrow points to a small spinose projection at the antero-lateral angle. Scale bars below associated images.

from Morocco was *Beltella* sp., which has been mentioned frequently in recent descriptions of the lowermost (lower Tremadocian) Fezouata Shale Formation (e.g., Destombes et al., 1985; Destombes and Feist, 1987; Lefebvre et al.,

2016a, b). However, this occurrence is based on the only two specimens known from extensive collections made by Destombes (Lefebvre et al., 2016b). These specimens include an internal mold of a cranium with four partial thoracic

**Table 1.** Summary of species assigned to the genus *Leptoplastides*, including references supporting current designations, geographic occurrence, and stratigraphic age. The last four rows list species that are not currently assigned to *Leptoplastides* but at one point were designated as *Beltella*.

Current name	Reference	Original name	Synonyms	Type species for	Once assigned to <i>Beltella</i>	Geographic occurrence	Stratigraphic age
<i>Leptoplastides salteri</i>	Månsson and Clarkson, 2020 (p. 2)	<i>Olenus salteri</i> Callaway, 1877	<i>Beltella spinifera</i> Lake, 1932	<i>Leptoplastides</i>		United Kingdom, Morocco	early to late Tremadocian
<i>Leptoplastides argentinensis</i>	Monti, 2018 (p. 186)	<i>Andesaspis argentinensis</i> Kobayashi, 1935		<i>Andesaspis</i>		Argentina	early Tremadocian
<i>Leptoplastides coniunctus</i>	Żylińska, 2001 (p. 360)	<i>Beltella coniuncta</i> Tomczykowa, 1968			X	Poland	<i>Acerocare</i> Zone (Stage 10)
<i>Leptoplastides depressus</i>	Żylińska, 2001 (p. 360)	<i>Ellipsocephalus depressus</i> Salter in Murchison, 1859	<i>Conocoryphe versimilis</i> Salter in Ramsay and Salter, 1866	<i>Beltella</i>	X	United Kingdom, Newfoundland	<i>Rhabdinopora flabelliformis</i> zone (early Tremadocian)
<i>Leptoplastides dissimulosulcus</i>	Jell and Adrain, 2002 (p. 438)	<i>Rampartaspis dissimulosulcus</i> Loch, Stitt, and Derby, 1993		<i>Rampartaspis</i>		Canada	<i>Symphysurina</i> Zone (early Tremadocian)
<i>Leptoplastides granulosis</i>	Monti, 2018 (p. 185)	<i>Protopeltura granulosis</i> Harrington, 1938				Argentina	<i>Bienvillia tetragonalis</i> – <i>Conophrys minutula</i> zone (late Tremadocian)
<i>Leptoplastides irae</i>	Żylińska, 2001 (p. 361)	<i>Beltella irae</i> Orłowski, 1968			X	Poland	<i>Leptoplastides</i> to <i>Acerocare</i> zones (Jiangshanian to stage 10)
<i>Leptoplastides latus</i>	Żylińska, 2001 (p. 363)	<i>Beltella lata</i> Tomczykowa, 1968			X	Poland	<i>Acerocare</i> Zone (stage 10)
<i>Leptoplastides marianus</i>	Monti, 2018 (p. 194)	<i>Parabolinopsis mariana</i> Hoek in Steinmann and Hoek, 1912				Bolivia	Cambrian stage 10 to Tremadocian
<i>Leptoplastides nodifer</i>	Żylińska, 2001 (p. 360)	<i>Beltella nodifer</i> Rushton, 1982			X	United Kingdom	<i>Acerocare</i> Zone (Age 10) to <i>Rhabdinopora flabelliformis</i> Zone (early Tremadocian)
<i>Leptoplastides ulrichi</i>	Żylińska, 2001 (p. 364)	<i>Liostracus ulrichi</i> Kayser, 1897	<i>Beltella rotundata</i> Tomczykowa, 1968; <i>Beltella convexa</i> Tomczykowa, 1968		X	Poland, Argentina, Bolivia	<i>Parabolina (N.) frequens argentina</i> Zone (Jiangshanian) to Tremadocian
<i>Parabolinoides bucephalus</i>	Rushton, 1968 (p. 410)	<i>Conocoryphe? bucephala</i> Belt, 1868			X	United Kingdom	<i>Parabolina spinulosa</i> Zone (Jiangshanian)
<i>Angelina latifrons</i>	Henningsmoen, 1957 (p. 268)	<i>Beltella latifrons</i> Wilson, 1954			X	United States	Tremadocian
<i>Chungkingaspis sinensis</i>	Ghobadi Pour, 2019 (p. 388)	<i>Andesaspis (Parabolinopsis) sinensis</i> Sheng, 1958			X	China, Iran	Tremadocian
<i>Olenus solitarius</i>	Żylińska, 2001 (p. 347)	<i>Beltella solitaria</i> Westergård, 1922			X	Poland, Sweden, United Kingdom	<i>Olenus</i> to <i>Parabolina</i> zones (early Furongian)

tergites and an internal mold of a pygidium and partial thorax (Destombes, 2006c, pl. 1, figs. 1, 2). These two specimens were collected from localities 808 and 26 in the Zagora area (Destombes, 2006b) in 1959 and 1961, respectively (Destombes, personal communication, 2009) (Fig. 1.1), about 50–100 km south of the N’kob area. Although one of us (JCG-M) has been to locality 808, no new olenid trilobites were recovered.

Although the specimens figured by Destombes are not complete, there is no aspect of the preserved exoskeleton that provides conclusive evidence that these are not *L. salteri*. Destombes may have assigned these two specimens to *Beltella* because neither clearly show axial spines. However, previous workers noted that the spines are not well preserved on molds, especially on convex internal molds, and the axial rings can appear smooth (Lake, 1919); the spines also break easily (Månsson and Clarkson, 2020). There is at least one axial ring with what could be the base of a spine on the cranidium with partial thoracic tergites (Destombes, 2006c, pl. 1, fig. 1).

Because he did not find any “*Beltella*” specimens or acritarchs in areas farther north of Zagora, Destombes (2006a, p. 17) suggested that the lowermost Fezouata Shale Formation was missing from those areas, including the region around N’kob. Recent work on graptolites refutes this suggestion (Gutiérrez-Marco and Martin, 2016); furthermore, it is not surprising that Destombes did not find olenid trilobites near N’kob given how rarely they appear in the Zagora area.

**Taxonomic history of the genus *Leptoplastides*.**—There are currently 11 species assigned to the genus *Leptoplastides* (Table 1). Perhaps the most controversially assigned species are those formerly assigned to the genus *Beltella*. In contrast to *L. salteri*, *Beltella depressa* (Salter in Murchison, 1859), the type species of *Beltella*, was known only from deformed, disarticulated specimens until the end of the twentieth century when well-preserved specimens were described by Fortey and Owens (1989) from material recovered from temporary excavations in Gloucestershire, UK. Fortey and Owens (1989) argued that each genus should be retained, contrary to previous opinions to synonymize the two (Henningsmoen, 1957; Nikolaisen and Henningsmoen, 1985; Morris, 1988). The primary distinctions made were the presence of axial spines or nodes and posterolateral pleural spines on *Leptoplastides* and the absence of both on *Beltella*. However, Żylińska (2001) noted that the presence of these features is not restricted to species of *Leptoplastides* and synonymized them on this basis as well as the observation that pleural spines were lost in some olenid trilobite species during ontogeny (Whittington, 1992, 1996), a view that we share.

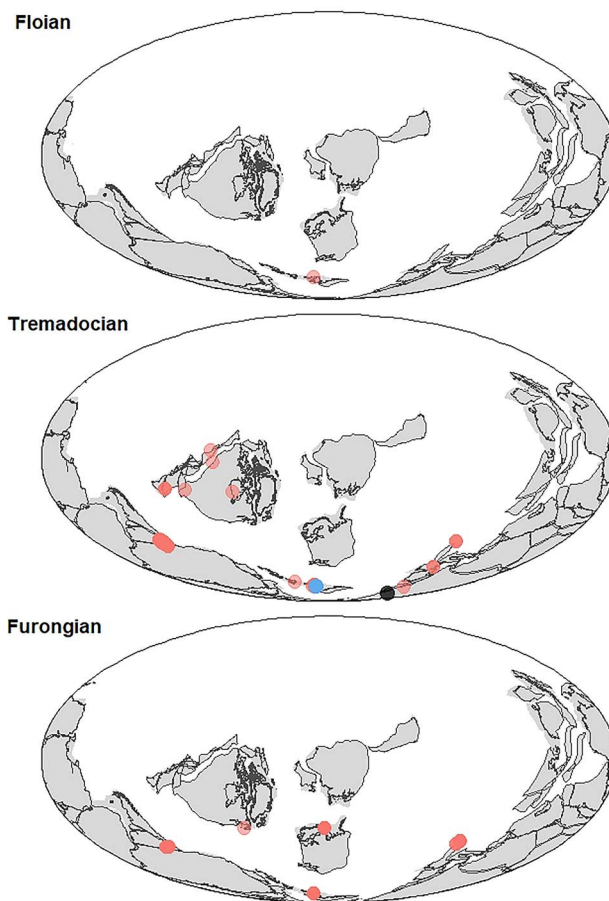
Opinion has varied over whether *Andesaspis argentinensis* Kobayashi, 1935, should be synonymized with *Leptoplastides marianus* (Hoek in Steinmann and Hoek, 1912) or treated as a separate species of *Leptoplastides* (e.g., Henningsmoen, 1957; Waisfeld and Vaccari, 2003; Tortello and Esteban, 2016), with the most recent treatment providing morphometric evidence for their separation with *L. marianus* restricted to the type specimens (Monti, 2018; see also Waisfeld and Vaccari, 2003). Jell and Adrain (2002) synonymized *Rampartaspis* Loch in Loch et al., 1993, with *Leptoplastides* without explanation.

Monti and Confalonieri (2018) published the first attempt at a family-wide phylogenetic analysis of olenid trilobites. The

analysis included 58 species, five of which belong to *Leptoplastides* sensu Żylińska (2001), and the resulting maximum parsimony tree indicated that those species comprise a polyphyletic group. However, recent explorations of the same matrix modified for analysis using a Bayesian approach frequently recovered trees where included *Leptoplastides* species formed a monophyletic clade (Wright and Hopkins, 2021). Nonetheless, different treatments also identified different distributions of trees that vary considerably in their topologies (Wright and Hopkins, 2021), so our understanding of genera and subfamilies within Olenidae remains in flux (see also Monti et al., 2022).

**Spatial and temporal extent of *Leptoplastides*.**—The 11 species currently assigned to *Leptoplastides* range from the Jiangshanian (e.g., *Leptoplastides irae* [Orłowski, 1968] from the Holy Cross Mountains in Poland; see Żylińska, 2001) into the Tremadocian. Species occur in deeper-subtidal to offshore deposits of Gondwana (Argentina, Bolivia, southern Mexico, Morocco, Poland, Spain?), Baltica (Norway), British Avalonia, and Laurentia (Canada, Texas) (Fig. 4). The occurrences of *Leptoplastides* in Laurentia appear to belie previous compilations indicating provincialization of trilobite faunas in the Early Ordovician (Fortey and Cocks 2003; Torsvik and Cocks, 2017, p. 113). Further, the occurrence of *L. argentinensis* in deeper-water basin sequences of Texas is reported alongside at least one other olenid genus (*Angelina*) known from Argentina (Wilson, 1954), implying some connection between South American Gondwana and the southern coast of Laurentia. However, the Mexican occurrences are from the Tiñú Formation (Robison and Pantoja-Alor, 1968), which is considered to belong to a terrane (Oaxaquia) that, although accreted to North America, originally was either an insular area in temperate latitudes or was situated in a Gondwanan or peri-Gondwanan position in pre-Silurian times (Landing et al., 2007; Torsvik and Cocks, 2017, p. 104; Cuen-Romero et al., 2023), even though Mexico is reconstructed adjacent to Laurentia in the PALEOMAP models (Scotese, 2023). Notably the only other trilobite genus reported from the lowermost Fezouata Shale Formation, the phacopide *Pharostomina*, also co-occurs with *Leptoplastides* in the Tiñú Formation (Robison and Pantoja-Alor, 1968), various formations of Argentina (Balseiro et al., 2011), and Wales (Owens et al., 1982).

The genus *Leptoplastides* has been cited by Hammann et al. (2008, p. 154) from the Lower Ordovician sequence of Celtiberia (northwestern Spain), which also yielded other olenid genera (*Angelina* and *Hypermeaspis*). Most probably they come from the lower Tremadocian shales of the Borrachón Formation, from which Hammann et al. (1982, p. 24) previously reported a trilobite assemblage very closely related to early Tremadocian faunas of South America. Several of the genera cited in the last paper (but with no mention of *Leptoplastides*) were illustrated for the Borrachón Formation by Álvaro and Martínez-Benítez (2023), who considered the record of the olenid *Angelina* aff. *A. hyeromimi* (Kayser, 1876) as evidence of direct correlation of these beds with Oaxaca and the Argentinean margin of Gondwana at the Furongian–Tremadocian boundary interval. The premature death of Wolfgang Hammann prevented publication of a monograph, by then almost finished, describing, among other trilobites, the Iberian material of *Leptoplastides* and other olenids. The manuscript is presently in the hands of J.J. Álvaro (personal communication, 2022) with the intent to publish posthumously.



**Figure 4.** Paleogeographic maps with *Leptoplastides* occurrences in the Furongian (lower panel), Tremadocian (middle panel), and Floian (upper panel). Increased opacity of locality dots indicates greater number of occurrences in those areas. Blue = *Leptoplastides salteri*, UK; Black = *Leptoplastides salteri*, Morocco; Red = all other *Leptoplastides* species, including those previously assigned to *Beltella* and *Rampartaspis*. Paleoreconstructions are based on the PALEOMAP reconstruction model (Scotese and Wright, 2018) and plotted using a Mollweide projection. Paleogeographic coordinates were downloaded directly from the Paleobiology Database (PBDB) (7 April 2023) using the URL “[https://paleobiodb.org/data1.2/occs/list.csv?base\\_name=Leptoplastides,Rampartaspis&pgm=Scotese&show=coords,paleoloc](https://paleobiodb.org/data1.2/occs/list.csv?base_name=Leptoplastides,Rampartaspis&pgm=Scotese&show=coords,paleoloc)”. Eighty-six new occurrences and 53 taxonomic names and opinions were entered into the PBDB specifically for this project. Coastlines and polygons for each timeline were reconstructed using GPlates Webservice ([gwsdoc.gplates.org](https://www.gplates.org)) and the R packages rgdal v 1.6-5 (Bivand et al., 2023), ggplot2 v. 3.3.5 (Wickham, 2016), broom v. 1.0.3 (Robinson et al., 2023), ggthemes v. 4.2.4 (Arnold, 2021), and cowplot v. 1.1.1 (Wilke, 2020). See also <https://bcmoon.uk/palaeomap/02-gplates-web-service/> for useful guidelines on using the GPlates Webservice.

*Leptoplastides salteri* (Callaway, 1877) is one of the youngest species in the genus. In Morocco “*Beltella* sp.” is known from the *Anisograptus matanensis* to *Rhabdinopora anglica* graptolite zones of the early Tremadocian (Lefebvre et al., 2016a); in the UK *Leptoplastides salteri* occurs somewhat above the *Adelograptus tenellus* graptolite Zone, which places it in the later Tremadocian (Fortey and Owens, 1991). A single occurrence of *Leptoplastides* sp. is from either the very latest Tremadocian or the very earliest Floian (*Paratetraraptus approximatus* graptolite Zone) of Wales (Fortey and Owens, 1992). The occurrence of *L. salteri* in the early Tremadocian of Morocco followed by the later Tremadocian occurrence in the UK indicates a possible equatorward immigration of the species during the Early Ordovician, at a time when other closely related clades were dispersing equatorward from other areas of Gondwana (Monti et al., 2023). These occurrences are also consistent with previous paleobiogeographic analyses indicating a close association of faunas from western Gondwana and Avalonia (e.g., Álvaro et al., 2003, 2007; Gutiérrez-Marco et al., 2017), and similarly, support post-Tremadocian rifting of

Avalonia from Gondwana (Murphy et al., 2006; Cocks and Fortey, 2009).

Olenid trilobites are frequently abundant and diverse where they occur (e.g., Spitsbergen, Fortey, 1974; Argentina, Balseiro et al., 2011; Scandinavia, Terfelt et al., 2011), but because they are usually restricted to deeper-water sediments, their fossil record is geographically and temporally discontinuous (see for example the distribution of *Cloacaspis* species; Hopkins, 2019). The rarity of olenid trilobites in Morocco is likely due to the relative rarity of deeper-water sediments in an already sparse Furongian and early Tremadocian record (Álvarez et al., 2007; Álvaro and Vizcaíno, 2018). The occurrence of well-preserved *Leptoplastides salteri* in the N’kob area, however, provides a promising precedent for further fossil discoveries from the earliest Tremadocian of Morocco.

### Acknowledgments

Thank you to B. Hunda for inviting us to submit this manuscript to the special issue and to S. Pereira and K. Månsson for



thoughtful reviews that improved the quality and relevance of this work. Thank you also to A. Rashkova for minor additional preparation work and to B. Moon for making guidelines for using the GPlates Web Service available online (<https://bcmoon.uk/palaeomap/02-gplates-web-service/>). This paper is a contribution to projects IGCP 735 (Rocks n'ROL) of the IUGS–UNESCO and PDI2021-125585NB-100 of the Spanish Ministry of Science and Innovation (to JCG-M). This is Paleobiology Database publication 476.

### Declaration of competing interest

The authors declare none.

### Data availability statement

There are no supplementary data associated with this paper.

### References

- Álvaro, J., and Martínez-Benítez, B., 2023, Advances in the Lower Ordovician of the western Iberian Chain, NE Spain: *Estonian Journal of Earth Sciences*, v. 72, p. 6–9.
- Álvaro, J.J., and Vizcaíno, D., 2018, The Furongian break-up (rift/drift) unconformity in the central Anti-Atlas, Morocco: *Journal of Iberian Geology*, v. 44, p. 567–587.
- Álvaro, J.J., Elicki, O., Geyer, G., Rushton, A.W.A., and Shergold, J.H., 2003, Palaeogeographical controls on the Cambrian trilobite immigration and evolutionary patterns reported in the western Gondwana margin: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 195, p. 5–35.
- Álvaro, J.J., Ferretti, A., González-Gómez, C., Serpagli, E., Tortello, M.F., Vecoli, M., and Vizcaíno, D., 2007, A review of the late Cambrian (Furongian) palaeogeography in the western Mediterranean region, NW Gondwana: *Earth-Science Reviews*, v. 85, p. 47–81.
- Álvaro, J.J., Benharref, M., Destombes, J., Gutiérrez-Marco, J.C., Hunter, A.W., Lefebvre, B., van Roy, P., and Zamora, S., 2022, Ordovician stratigraphy and benthic community replacements in the eastern Anti-Atlas, Morocco, in Hunter, A.W., Álvaro, J.J., Lefebvre, B., van Roy, P., and Zamora, S., eds., *The Great Ordovician Biodiversification Event: Insights from the Tafiltalt Biota, Morocco*: The Geological Society, London, Special Publication, v. 485, p. 37–67.
- Arnold, J.B., 2021, ggthemes: Extra themes, scales, and geoms for “ggplot2” v. 4.2.4. <https://CRAN.R-project.org/package=ggthemes>.
- Balseiro, D., Waisfeld, B.G., and Vaccari, N.E., 2011, Paleocological dynamics of Furongian (late Cambrian) trilobite-dominated communities from northwestern Argentina: *Palaio*, v. 26, p. 484–499.
- Belt, T., 1868, III.—On the “Lingula Flags,” or “Festiniog Group” of the Dolgelly District. Part III: *Geological Magazine*, v. 5, p. 5–11.
- Bivand, R., Keitt, T., and Rowlingson, B., 2023, rgdal: Bindings for the “Geospatial” data abstraction library v. 1.6-5. <https://CRAN.R-project.org/package=rgdal>.
- Callaway, C., 1877, On a new area of upper Cambrian rocks in south Shropshire, with a description of a new fauna: *Quarterly Journal of the Geological Society*, v. 33, p. 652–672.
- Cocks, L.R.M., and Fortey, R.A., 2009, Avalonia: a long-lived terrane in the lower Palaeozoic?, in Basset, M.B., ed., *Early Palaeozoic Peri-Gondwana Terranes: New Insights from Plate Tectonics and Biogeography*: Geological Society, London, Special Publications, v. 325, p. 141–155.
- Cuen-Romero, F.J., Buitrón-Sánchez, B.E., Beresi, M.S., Palafox-Reyes, J.J., Monreal, R., 2023, Ordovician stratigraphy and biota of Mexico, in Servais, T., Harper, D.A.T., Lefebvre, B., and Percival, I.G., eds., *A Global Synthesis of the Ordovician System: Part 2*: Geological Society, London, Special Publications, v. 533, p. 115–132.
- Destombes, J., 1967, Distribution et affinités des genres de trilobites de l'Ordovicien de l'Anti-Atlas (Maroc): *Compte Rendu Sommaire des Séances de la Société Géologique de France*, v. 1967, p. 133–134.
- Destombes, J., 2006a, Carte géologique au 1/200000 de l'Anti-Atlas Marocain. Paléozoïque Inférieur. Cambrien moyen et supérieur–Ordovicien–base du Silurien. Feuille Zagora–Coude du Dra. Mémoire explicatif. Chapitre C (Haut Atlas central, Sillon Sud–Atlasique et Anti-Atlas oriental): *Notes et Mémoires du Service Géologique de Maroc*, v. 161bis, 41 p.
- Destombes, J., 2006b, Carte géologique au 1/200000 de l'Anti-Atlas Marocain. Paléozoïque Inférieur. Cambrien moyen et supérieur–Ordovicien–base du Silurien. Feuille Zagora–Coude du Dra. Mémoire explicatif. Chapitre A: *Notes et Mémoires du Service Géologique de Maroc*, v. 273bis, 36 p.
- Destombes, J., 2006c, Carte géologique au 1/200000 de l'Anti-Atlas Marocain. Paléozoïque Inférieur. Cambrien moyen et supérieur–Ordovicien–base du Silurien. Sommaire général sur les mémoires explicatifs des cartes géologiques au 1/200000 de l'Anti-Atlas Marocain: *Notes et Mémoires du Service Géologique de Maroc*, v. 515, 149 p.
- Destombes, J., and Feist, R., 1987, Découverte du Cambrien supérieur en Afrique (Anti-Atlas central, Maroc): *Comptes Rendus de l'Académie des Sciences de Paris*, v. 304, p. 719–724.
- Destombes, J., and Willefert, S., 1959, Sur la présence de *Dictyonema* dans le Tremadoc de l'Anti-Atlas (Maroc): *Comptes Rendus de l'Académie des Sciences de Paris*, v. 249, p. 1246–1247.
- Destombes, J., Hollard, H., and Willefert, S., 1985, Lower Palaeozoic rocks of Morocco, in Holland, C.H., ed., *Lower Palaeozoic of North-Western and West-Central Africa. Lower Palaeozoic Rocks of the World*, vol. 4: New York, John Wiley & Sons, p. 91–336.
- Eichwald, E.J., 1840, Ueber das Silurische Schichtensystem in Esthland. Aus dem ersten und zweiten Hefte der “Zeitschrift für Natur- und Heilkunde” der Medizinischen Akademie zu St. Petersburg besonders abgedruckt: *St. Petersburg*, 210 p.
- Fortey, R.A., 1974, The Ordovician trilobites of Spitsbergen. I. Olenidae: *Norsk Polarinstittut Skrifter*, v. 160, 129 p.
- Fortey, R.A., and Cocks, L.R.M., 2003, Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions: *Earth-Science Reviews*, v. 61, p. 245–307.
- Fortey, R.A., and Owens, R.M., 1989, The Early Ordovician trilobite *Beltella*: *Proceedings of the Bristol Naturalists' Society*, v. 49, p. 69–79.
- Fortey, R.A., and Owens, R.M., 1991, A trilobite fauna from the highest Shireton Shales in Shropshire, and the correlation of the latest Tremadoc: *Geological Magazine*, v. 128, p. 437–464.
- Fortey, R.A., and Owens, R.M., 1992, The Habberley Formation: youngest Tremadoc in the Welsh borderlands: *Geological Magazine*, v. 129, p. 553–566.
- Ghobadi Pour, M., 2019, Ordovician trilobites from Deh-Molla, eastern Alborz, Iran: *Alcheringa*, v. 43, p. 381–405.
- Gutiérrez-Marco, J.C., and Martin, E.L., 2016, Biostratigraphy and palaeoecology of Lower Ordovician graptolites from the Fezouata Shale (Moroccan Anti-Atlas): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p. 35–49.
- Gutiérrez-Marco, J.C., Sá, A.A., García-Bellido, D.C., and Rábano, I., 2017, The Bohemo–Iberian regional chronostratigraphical scale for the Ordovician System and palaeontological correlations within South Gondwana: *Lethaia*, v. 50, p. 258–295.
- Hammann, W., Robardet, M., and Romano, M., 1982, The Ordovician System in Southwestern Europe (France, Spain, and Portugal). Correlation Chart and Explanatory Notes: *International Union of Geological Sciences, Publication no. 11*, 47 p.
- Hammann, W., Álvaro, J.J., and Vizcaíno, D., 2008, Early Ordovician trilobites from the Iberian Chains, NE Spain: a tribute to Wolfgang Hammann, in Rábano, I., and García-Bellido, D., eds., *Advances in Trilobite Research: IGME, Cuadernos del Museo Geominero*, v. 9, p. 153–156.
- Harrington, H.J., 1938, Sobre las faunas del Ordoviciano inferior del norte Argentino: *Revista del Museo de La Plata (nueva serie)*, v. 1, p. 109–289.
- Harrington, H.J., and Leanza, A.F., 1957, Ordovician trilobites of Argentina: *Department of Geology, University of Kansas Special Publication 1*, 276 p.
- Henningsmoen, G., 1957, The trilobite family Olenidae: with description of Norwegian material and remarks on the Olenid and Tremadocian Series: *Skrifter Utgitt av det Norske Videnskaps-Akademi i Oslo, I, Matematisk-Naturvidenskabelig Klasse*, v. 1957, p. 1–303.
- Hopkins, M.J., 2019, Phylogenetic analysis and revision of the trilobite subfamily Balnibarbiinae (Olenidae): *American Museum Novitates*, v. 3928, p. 1–20.
- Jell, P.A., and Adrain, J.M., 2002, Available generic names for trilobites: *Memoirs of the Queensland Museum*, v. 48, p. 331–553.
- Kaysers, E., 1876, Ueber primordiale und untersilurische Fossilien aus der Argentinischen Republik, in Stelzner, A.W., ed., *Beiträge zur Geologie und Palaeontologie der Argentinischen Republik, II. Palaeontologischer Theil: Palaeontographica, Supplementum* v. 3, n. 2, p. 1–33.
- Kaysers, E., 1897, Beiträge zur Kenntniss einiger Paläozoischer faunen Süd-Amerikas: *Zeitschrift der Deutschen Geologischen Gesellschaft*, v. 49, p. 274–317.
- Kobayashi, T., 1935, On the *Kainella* fauna of the basal Ordovician age found in Argentina: *Japanese Journal of Geology and Geography*, v. 12, p. 59–67.
- Lake, P., 1919, A monograph of the British Cambrian Trilobites. Part V: *Monographs of the Palaeontographical Society*, v. 71, n. 343, p. 89–120.
- Lake, P., 1932, A monograph of the British Cambrian trilobites. Part VII: *Monograph of the Palaeontographical Society*, v. 99, n. 385, p. 149–172.

- Landing, E.D., Westrop, S.R., Keppie, J.D., 2007, Terminal Cambrian and lowest Ordovician succession of Mexican West Gondwana: biotas and sequence stratigraphy of the Tiñu Formation: *Geological Magazine*, v. 144, p. 909–936.
- Lapworth, C., 1898, *An Intermediate Text-book of Geology* (13th Edition): Edinburgh and London, Blackwood and Sons, 436 p.
- Lefebvre, B., Allaire, N., Guensburg, T.E., Hunter, A.W., Kourais, K., Martin, E.L., Nardin, E., Noailles, F., Pittet, B., and Sumrall, C.D., 2016a, Palaeoecological aspects of the diversification of echinoderms in the Lower Ordovician of central Anti-Atlas, Morocco: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p. 97–121.
- Lefebvre, B., El Hariri, K., Lerosey-Aubril, R., Servais, T., and Van Roy, P., 2016b, The Fezouata Shale (Lower Ordovician, Anti-Atlas, Morocco): a historical review: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p. 7–23.
- Lefebvre, B., Gutiérrez-Marco, J.C., Lehnert, O., Martin, E.L., Nowak, H., Akodad, M., El Hariri, K., and Servais, T., 2018, Age calibration of the Lower Ordovician Fezouata Lagerstätte, Morocco: *Lethaia*, v. 51, p. 296–311.
- Loch, J.D., Stitt, J.H., and Derby, J.R., 1993, Cambrian–Ordovician boundary interval extinctions: implications of revised trilobite and brachiopod data from Mount Wilson, Alberta, Canada: *Journal of Paleontology*, v. 67, p. 497–517.
- Maletz, J., Wang, X.-F., and Wang, C.-S., 2023, Early Tremadocian (Ordovician) graptolite biostratigraphy and correlation: *Palaeoworld*, v. 32, p. 44–62.
- Månsson, K., and Clarkon, E.N.K., 2020, A revised ontogeny of the early Ordovician trilobite *Leptoplastides salteri* (Callaway, 1877): *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, v. 111, p. 1–16.
- Monti, D.S., 2018, Morphometrics of *Leptoplastides marianus* (Hoek) (Trilobita, Olenidae) from the Tremadocian of north-western Argentina: taxonomic implications: *Journal of Systematic Palaeontology*, v. 16, p. 179–197.
- Monti, D.S., and Confalonieri, V.A., 2018, First cladistic analysis of the trilobite family Olenidae from the Furongian and Ordovician: *Lethaia*, v. 52, p. 304–322.
- Monti, D.S., Tortello, M., and Confalonieri, V.A., 2022, A phylogenetic approach to the study of the evolution of Hypermeccaspididae (Olenida, Trilobita): *Papers in Palaeontology*, v. 8, e1433, <https://doi.org/10.1002/sp2.1433>.
- Monti, D.S., Confalonieri, V.A., and 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*, v. 618, 111519, <https://doi.org/10.1016/j.palaeo.2023.111519>.
- Morris, S., 1988, A review of British trilobites, including a synoptic revision of Salter's monograph: *Monographs of the Palaeontographical Society*, v. 140, n. 574, p. 1–292.
- Murchison, R.I., 1859, *Siluria. The History of the Oldest Fossiliferous Rocks and Their Foundations; with a Brief Sketch of the Distribution of Gold Over the Earth*, 2nd edition: London, John Murray, 592 p.
- Murphy, J.B., Gutiérrez-Alonso, G., Nance, R.D., Fernández-Suárez, J., Keppie, J.D., Quesada, C., Strachan, R.A., and Dostal, J., 2006, Origin of the Rheic Ocean: rifting along a Neoproterozoic suture?: *Geology*, v. 34, p. 325–328.
- Nikolaisen, F., and Henningsmoen, G., 1985, Upper Cambrian and lower Tremadoc olenid trilobites from the Digermul peninsula, Finnmark, northern Norway: *Norges Geologiske Undersøkelse Bulletin*, v. 400, p. 1–49.
- Orłowski, S., 1968, Upper Cambrian fauna of the Holy Cross Mts: *Acta Geologica Polonica*, v. 18, p. 257–292.
- Owens, R., Fortey, R., Cope, J., Rushton, A., and Bassett, M., 1982, Tremadoc faunas from the Carmarthen district, South Wales: *Geological Magazine*, v. 119, p. 1–38.
- Ramsay, A.C., and Salter, J.W., 1866, *The Geology of North Wales, and an appendix on the fossils, with plates: Memoirs of the Geological Survey of Great Britain and of the Museum of Practical Geology*, v. 3, 381 p.
- Raw, F., 1908, The trilobite fauna of the Shineton Shales: *Reports of the British Association for the Advancement of Science*, v. 1907, p. 511–513.
- Raw, F., 1925, The development of *Leptoplastus salteri* (Callaway), and of other trilobites (Olenidae, Ptychoparidae, Conocoryphidae, Paradoxidae, Phacopidae, and Mesonacidae): *Quarterly Journal of the Geological Society*, v. 81, p. 223–324.
- Robison, R.A., and Pantoja-Alor, J., 1968, Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico: *Journal of Paleontology*, v. 42, p. 767–800.
- Robinson, D., Hayes, A., and Couch, S., 2023, broom: Convert statistical objects into tidy tibbles v. 1.0.3. <https://CRAN.R-project.org/package=broom>.
- Rushton, A.W.A., 1968, Revision of two upper Cambrian trilobites: *Palaeontology*, v. 11, p. 410–420.
- Rushton, A.W.A., 1982, The biostratigraphy and correlation of the Merioneth–Tremadoc Series boundary in North Wales, in Bassett, M.G., and Dean, W.T., eds., *The Cambrian–Ordovician Boundary: Sections, Fossil Descriptions, and Correlations*, Volume 3: National Museum of Wales, Geological Series 3, Cardiff, p. 41–59.
- Salter, J. W., 1858, On *Graptopora*, a new genus of Polyzoa, allied to the graptolites: *Proceedings of the American Association of the Advancement of Science for 1857*, v. 11, p. 63–66.
- Scotese, C.R., 2023, Ordovician plate tectonic and palaeogeographical maps: *Geological Society, London, Special Publications*, v. 532, p. 91–109.
- Scotese, C.R., and Wright, N., 2018, PALEOMAP paleodigital elevation models (PaleoDEMs) for the Phanerozoic PALEOMAP project: <https://www.earthbyte.org/paleodem-resource-scotese-and-wright-2018/>
- Sheng, S.F., 1958, [The Ordovician trilobites of southwestern China]: *Acta Palaeontologica Sinica*, v. 6, p. 169–204. [in Chinese with English summary]
- Steinmann, G., and Hoek, H., 1912, Das Silur und Cambrium des Hochlandes von Bolivia und ihre Fauna: *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, v. 34, p. 176–252.
- Terfelt, F., Ahlberg, P., and Eriksson, M.E., 2011, Complete record of Furongian polymerid trilobites and agnostids of Scandinavia—a biostratigraphical scheme: *Lethaia*, v. 44, p. 8–14.
- Tomeczkova, E., 1968, Stratigraphy of the uppermost Cambrian deposits in the Świętokrzyskie Mountains: *Prace Instytutu Geologicznego*, v. 54, p. 5–85.
- Torsvik, T.H., and Cocks, L.R.M., 2017, *Earth History and Palaeogeography*: Cambridge, UK., Cambridge University Press, 317 p.
- Tortello, M.F., and Esteban, S.B., 2016, Early Ordovician trilobites from the Iruya area (Cordillera Oriental, northwestern Argentina) and their stratigraphic significance: *Journal of Paleontology*, v. 90, p. 923–958.
- Waisfeld, B.G., and Vaccari, N.E., 2003, Trilobites, in Benedetto, J.L., ed., *Ordovician Fossils of Argentina: Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba*, p. 295–410.
- Westergård, A.H., 1922, *Sveriges Olenidskiffer: Sveriges Geologiska Undersökning series C*, v. 18, p. 1–205.
- Whittington, H.B., 1992, *Trilobites: Suffolk, Great Britain*, The Boydell Press, 145 p.
- Whittington, H.B., 1996, Sphaeroidal enrolment and thoracic characters in *Beltella depressa* and other olenid trilobites: *Palaeontology*, v. 39, p. 377–388.
- Wickham, H., 2016, *ggplot2: Elegant graphics for data analysis*: New York, Springer-Verlag.
- Wilke, C.O., 2020, cowplot: Streamlined plot theme and plot annotations for “ggplot2” v. 1.1.1. <https://CRAN.R-project.org/package=cowplot>.
- Wilson, J.L., 1954, Late Cambrian and Early Ordovician trilobites from the Marathon Uplift, Texas: *Journal of Paleontology*, v. 28, p. 249–285.
- Wright, D.F., and Hopkins, M.J., 2021, A catch-22 or siren of Titan? Assessing the impact of character evolution models on phylogenetic and macroevolutionary inferences of fossil data: *Geological Society of America Abstracts with Programs*, v. 53, n. 6, <https://doi.org/10.1130/abs/2021AM-367338>.
- Zylińska, A., 2001, Late Cambrian trilobites from the Holy Cross Mountains, central Poland: *Acta Geologica Polonica*, v. 51, p. 333–383.

Accepted: 30 August 2023