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The trilobite assemblage of the *Declivolithus* Fauna (lower Katian, Ordovician) of Morocco: a review with new data

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Non-technical Summary.—The El Qaid Errami area in the Moroccan Anti-Atlas has become famous in the last 20 years for its spectacular fossil specimens from the Ordovician Period (ca. 485–443 million years ago). However, due to challenges of field access to the sites and the reluctance of Moroccan collectors to reveal precise locality information there is a mismatch between information provided informally through traders, social media, etc. and that available in the formal scientific literature. Verifying exact specimen provenance is particularly difficult, and all these issues hinder resolution of scientifically crucial information concerning phylogenetic lineages, the paleogeography, and faunal connections pertaining at the time of deposition. Here, we formally describe a famous trilobite association from this region of Morocco from the Upper Ordovician (ca. 450 Ma) that is dominated by a bizarre-looking trilobite, *Declivolithus*, which is the most conspicuous element of an assemblage occurring principally in the locality called Bofloss, in the Tizi n'Ounfite area. A decade of our work reveals a level of geological control impossible to obtain by studying materials collected by others, which allows us to properly geographically locate previous published data. We have thus increased the diversity of this assemblage from four to 11 species, including a new species: *Ulugtella*? *biformis* n. sp. A great opportunity offered by this work has been to study conspecific specimens preserved both in 3-D (in sandstones) and flattened (in mudstones), highlighting the importance of preservation of original morphology in taxonomic studies. With this revision, we not only clarify the identity of previously reported species of the *Declivolithus* Fauna from Morocco, but also increased diversity and demonstrated that the famous *Declivolithus titan*, well known among collectors, is a junior synonym of the type species *D. alfredi* erected in the Czech Republic. Links to the Czech assemblages remained strong during the Late Ordovician. These data help improve paleogeographical reconstructions of the Gondwana margin in this time period, as well as provide new information on several phylogenetic lineages endemic to the peri-Gondwana realm.

Abstract.—Intense commercial exploitation of fossils in the famous El Qaid Errami area in the last 20 years has led to the discovery of the interesting *Declivolithus* Fauna in the Moroccan Anti-Atlas. This unusually large trinucleid trilobite, described originally from the Czech Republic, is the most conspicuous element of an assemblage mainly occurring in the Bofloss locality, a local biofacies development of pelagic mudstones and sandstones cropping out in a structurally isolated place in the Tizi n'Ounfite area. Here we revise this *Declivolithus* Fauna trilobite assemblage from Morocco, increasing the known trilobite diversity from four to 11 species: *Ulugtella*? *biformis* n. sp., *Selenopeltis* cf. *S. vultuosa*, *Phacopidina quadrata*, *Eudolatites* cf. *E. bondoni*, *Prionocheilus* cf. *P. verneuili*, *Nobiliasaphus* cf. *N. kumatox*, *Cyclopyge* cf. *C. rediviva*, *Symphysops stevaninae*, *Heterocyclopyge* sp., *Dionide* sp., and *Declivolithus alfredi*. The new data and the very good preservation of specimens in sandstones, clarify the specific identity of previously reported taxa. Although the stratigraphical correlation of the fossiliferous levels remains problematic, it probably corresponds to the upper part of the Lower Ktaoua Formation or to the lower half of the Upper Tiouririne Formation. Most taxa support previous assignment of the Moroccan assemblage to the late Berounian (ca. early Katian, Ka2), although a middle Berounian (ca. Sa2–Ka1) age cannot be excluded. Most of the identified species are known from the Czech Republic (eight out of 11), showing that the strong faunal link between Morocco and the Czech Republic still existed during the Late Ordovician, being stronger than the link with the coeval Ibero-Armorican domain faunas.

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Introduction

In the beginning of the twentieth century, Jan Vratislav Želízko (1874–1938), a Czech geologist and paleontologist, erected the new species *Trinucleus alfredi* Želízko, 1906, based on a label left by the famous fellow Czech paleontologist Ottomar Pravoslav Novák (1851–1883). This author died prematurely and much of his work was not published, being scattered among manuscripts and old labels, including one with the name *Trinucleus alfredi*. The specimens, which were collected from a structurally complex area, the Rožmitál tectonic block (Havlíček, 1977, 1998), were poorly preserved. Later, Chlupáč (1952) described a similar form but from the Prague Basin, in the Bohdalec Formation (upper Berounian, ca. Ka2 stage slice), based on much better-preserved material, erecting a new species, *Tretaspis novaki* Chlupáč, 1952. This was later considered to be a junior synonym of *Trinucleus alfredi* by Přibyl and Vaněk (1967), who erected the new monotypic genus *Declivolithus* Přibyl and Vaněk, 1967. In the important monograph on Trinucleina, Hughes et al. (1975) emphasized the weird appearance of the attractive *Declivolithus*, a “bizarre trinucleid” with harpid-like genal prolongations.

This charismatic trilobite was subsequently found in Morocco for the first time by Jacques Destombes (1971), and later mentioned by Destombes et al. (1985) and Destombes (2006a) but has generally been overlooked. Curiously, Destombes (1971) identified “*Declivolithus* aff. *alfredi*” not in the incredibly fossiliferous Anti-Atlas, but in a small inlier located in the southern border of the central High Atlas, in the Skoura region (Fig. 1.2a). The genus was finally recorded in the Anti-Atlas only in the late 2000s, in the famous El Qaid Errami (= El Caïd Rami) area, as a result of intense commercial extraction of fossils (e.g., Gutiérrez-Marco and García-Bellido, 2022). When *Declivolithus* first appeared in fossil shops, coming from Tifrit n’Ougnaou at Jbel Tijarfaïouine mountain area (Fig. 1.3B; Corbacho et al., 2014; Lebrun, 2018) and preserved in sandstones, the dealers/collectors called it “*Nankinolithus*,” a locally co-occurring trinucleid with a similar arrangement of the outer arcs. Later they amended the classification to “*Declivolithus alfredi*,” the Czech species. It started to be very famous in the Moroccan trade, but it remained unpublished, as is the case with so many Moroccan fossils. Finally, Fortey and Edgecombe (2017) described the Moroccan specimens, which they considered to represent a new species, *Declivolithus titan* Fortey and Edgecombe, 2017, as well as the accompanying assemblage of three additional trilobites.

It may have been the commercial importance of *Declivolithus* that prompted the discovery of correlatable levels at the Bofloss locality, in the Tizi n’Ounfite area, from where most of the *Declivolithus* specimens found subsequently originate. In 2015, one of us (J.C.G.-M.) began studying the stratigraphy and paleontology of this locality, collecting materials of the groups represented. This *Declivolithus* Fauna, so called because this unusually large trinucleid is the most conspicuous element of this assemblage, is composed almost exclusively of trilobites preserved either in gray mudstones or in coarse-grained sandstones, with scattered representatives of biserial graptolites (Gutiérrez-Marco et al., 2022a), disarticulated machaeridians, stylophoran echinoderms, and rhynchonelliform brachiopods.

Here we revise the *Declivolithus* Fauna trilobite assemblage from the Moroccan Anti-Atlas, increasing the known trilobite diversity from 4 to 11 species, clarifying the specific identity of previously reported taxa, enabling a better characterization of several species, and improving the knowledge of endemic trilobite lineages from the high-latitude peri-Gondwana realm. The age and lithostratigraphic positioning of these *Declivolithus*-bearing assemblages are discussed but remain problematic due to the structural setting and the extraordinary variations within the Ktaoua Group in this sector of the north-eastern Anti-Atlas. As stated by Gutiérrez-Marco et al. (2022a, p. 232), this stratigraphical uncertainty cuts across several other important fossil beds and localities in the El Qaid Errami area, most of which have been discovered in the last 20 years and favored by the fossil industry. It is important to describe these diverse fossil assemblages from the Moroccan Ordovician, from new and more diverse collections. These provide information for paleogeographical reconstructions of the Gondwanan margin and contribute to understanding many evolutionary lineages of several groups.

Geographical and geological setting

The studied material comes from the ‘Bofloss’ site (locality 3 of Gutiérrez-Marco et al., 2022a), located west of Erfoud, at the Tizi n’Ounfite area, 9 km SW of Oukhit (or Oukrite: 31° 25′24.7″N, 04°33′59.0″W, locality A in Fig. 1.3). From a tectonostratigraphic point of view, it belongs to the northeastern northern part of the eastern Anti-Atlas (Fig. 1.2b). The site consists of a single trench in the core of a small anticline delimited by faults that exposes a sand-dominated sequence with a total thickness of at least 25 m, defined by alternations of sandstone beds (up to 0.6 m thick) and silty micaceous mudstones, mostly showing oblique and hummocky cross-stratification.

The curved trench was made for commercial extraction by the Moroccan diggers Lahcen and Hamide Ouzemmou for the exploitation of the very peculiar *Declivolithus* trilobite Fauna dominated by this large trinucleid, abundant cyclopygid and some rarer dalmanitids and other groups (illaenids, asaphids, odontopleurids). In the thin bluish-gray mudstones, trilobites are mostly complete or with minimal disarticulation, associated with only rare graptolites (Gutiérrez-Marco et al., 2022a). In the sandstone levels, mainly in the lowermost ones, there are articulated trilobites (*Declivolithus*, rare cyclopygids, and illaenids), several other disarticulated trilobites (e.g., cyclopygids, dalmanitids) and very rare, isolated plates of stylophorans (*Anatifopsis*), machaeridia (*Plumulites*), and a fragment of a juvenile shell of a costulate brachiopod, which all show evidence of transportation.

The first levels to be explored were the sandstones, for which it was necessary to remove the overlying fossiliferous mudstones. Once the sandstones were exhausted, the mudstones were exploited and dug. Two collection campaigns were carried out, one in May 2015 and another in December 2017. Hence, this locality offered the important opportunity to assess the taphonomic variability of specimens of the same species preserved either in full relief (sandstones) or flattened (mudstones).

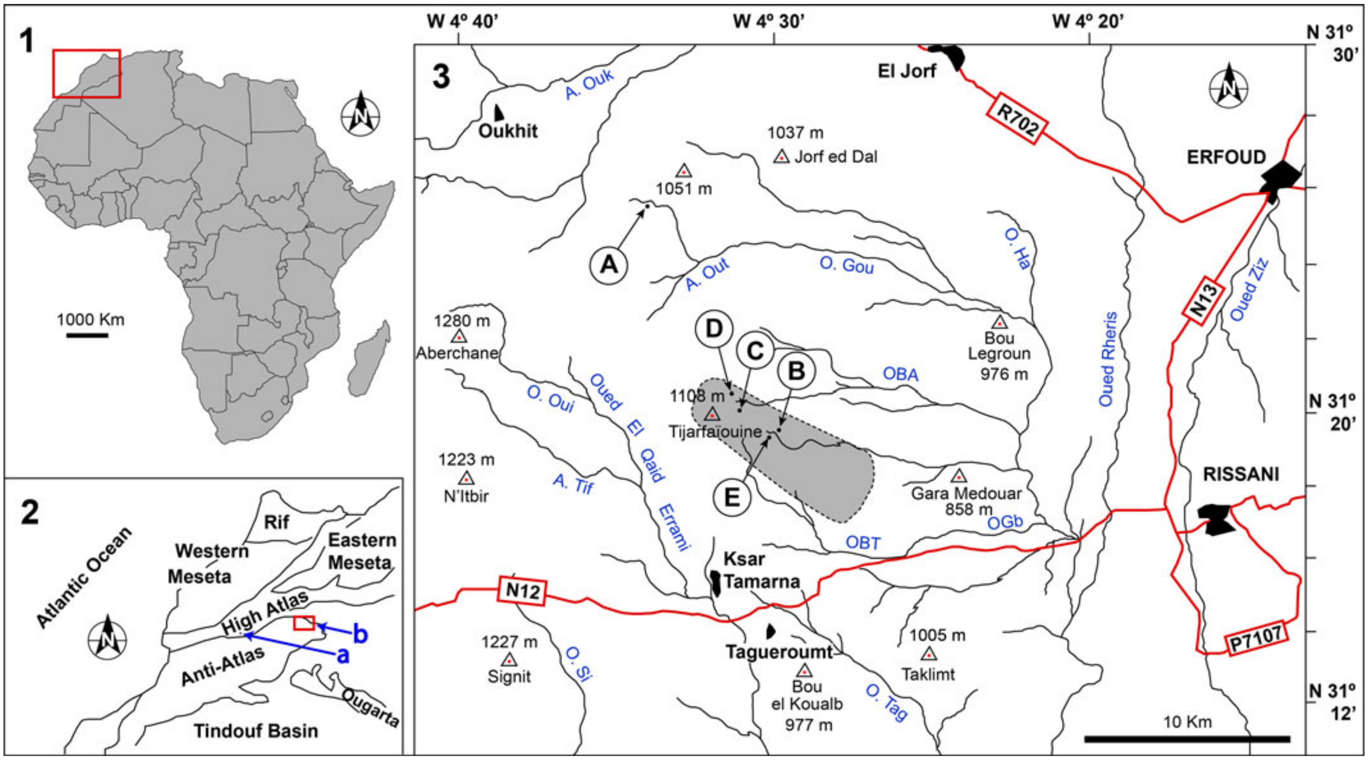

Figure 1. Sketch maps showing the position of the examined localities with reference to the African continent (**1**), the main Moroccan tectonosedimentary basins (**2**), and a local map from the northwestern Tafilalt area, SE Morocco (**3**). Localities (a) and (b) in map (**2**) correspond to the early finds of the trilobite genus *Declivolithus* in the Skoura inlier of the central High Altas (Destombes, 1971) and to the study area, respectively. The map (**3**) is a detail of the position of the fossiliferous localities mentioned in the text with reference to the road and drainage network, main populations, and geodesic vertices. The outline of Jbel Tijarfaïouine, the mountains where *Declivolithus* was first reported in the Eastern Anti-Atlas, is highlighted in gray. Fossil localities: (A) Bofloss; (B) Tifrit n'Ougnaou; (C) erroneous placement of the type locality of *Declivolithus titan* in the Jbel Tijarfaïouine according to Fortey and Edgecombe (2017); (D) Tizi n'Mouri; (E) erroneous placement of the Tifrit n'Ougnaou trilobite and echinoderm locality according to Lebrun (2018, p. 138). Abbreviations for other elements of the hydrological and drainage network: A. Oui = Assif n'Ouinigui; A. Ouk = Assif n'Oukhit; A. Out = Assif n'Outaouch; A. Tif = Assif Tifersiguet; OBA = Oued Bou Azgar; OBT = Oued Bou Terga; OGb = Oued Gbis; O. Gou = Oued Gounat; O. Ha = Oued Hanich; O. Si = Oued Signit; O. Tag = Oued Tagueroumt. Map and place names adapted from the sheets n° NH-30-XX-1, Misissi (published/edited in 1968) and NH-30-XX-2, Erfoud (published/edited in 1970) of the Topographic Map of Morocco at a scale of 1:100,000.

The *Declivolithus* Fauna assemblage described by Fortey and Edgecombe (2017) probably comes from this same locality, although the locality given in that work is 10 km farther south (locality C in Fig. 1.3) This suggestion comes from the fact that the family exploiting Bofloss may be the same one indicated by the authors, but with a different transcription of the father's name—Lahsa Ouzmmou/Lahcen Ouzemmou vs. 'Lahcen Ozammu'. The reluctance of the Moroccan collectors to reveal precisely where are they actively mining fossils also hinders the geological and lithostratigraphic settings of some Moroccan published material.

The stratigraphic placement of the Bofloss locality remains problematic because of its structurally isolated character, corresponding to a local biofacies development. It is very hard to properly correlate these local sequences with the typical Anti-Atlas units. In the El Qaid Errami area, the traditional formations of the Ktaoua Group exhibit great variations in thickness and facies compared with other regions, being generally thicker, much more fossiliferous and dominated by alternations of sandstones and sandy mudstones (with a few quartzites) from the middle part of the Lower Ktaoua Formation to the top of the Upper Tiouririne Formation. According to Gutiérrez-Marco et al. (2022a), the Bofloss fossiliferous beds probably correspond with the upper part of the Lower Ktaoua Formation, although correspondence with the lower half of the Upper Tiouririne Formation cannot be excluded.

The first *Declivolithus* specimens were found in commercial exploitations initiated in 2008 at a site called Tifrit n'Ougnaou (locality B in Fig. 1.3), where they are three-dimensionally preserved in sandstone, together with a few specimens from very thin mudstone intercalations. Lebrun (2018) and Corbacho et al. (2014) *Declivolithus* records came from this mountainous area, the Jbel Tijarfaïouine (Fig. 1.3, highlighted in gray). On a recent trip to the area (February 2023) we noted the occurrence of *Declivolithus* sclerites in the mentioned locality (B in Fig. 1.3: 31°19′50.9″N, 04°30′14.0″W), together with abundant *Cyclopyge* specimens and rare *Nankinolithus* sp. and *Nobiliasaphus* sp., among others. Corbacho and Kier (2011) probably were the first to publish this fossil locality, and in a set of succeeding papers (López-Soriano and Corbacho, 2012; Corbacho and López-Soriano, 2013; Corbacho et al., 2014) they listed about 20 genera of trilobites from there, whose occurrences remain mostly undescribed. In these works, the locality is always referred as "Tizi n'Mouri," which is a different fossil locality that is located a little farther northwest (locality D in Fig. 1.3; see also Lebrun, 2018, p. 138). However, the geographical coordinates given for the site by López-Soriano and Corbacho (2012) and Corbacho and López-Soriano (2013) match exactly with those we obtained for Tifrit n'Ougnaou. And, in turn, they differ from those mentioned by Corbacho and Kier (2011) and Corbacho et al. (2014) for what appears to be the same fossil locality, placed at an identical altitude of 920 m and cited as "Tizi n'Mouri." In any case, both localities—Tifrit n'Ougnaou and Tizi n'Mouri (B and D in Fig. 1.3)—were mapped by Destombes and Hollard (1986) as belonging to the Lower Ktaoua Formation. The record of the solute echinoderm genus *Dendrocystites* in both localities suggests that these outcrops may even be correlated with the upper part of the Lower Ktaoua Formation. This confirms the stratigraphic distribution of *Declivolithus* into sandy facies, where the genus never dominates, and in which the trilobite assemblage reaches a higher diversity than in what we regard as the true *Declivolithus* Fauna, dominated by this trilobite, as recorded in more distal and calm environments at the Bofloss locality. In fact, the occurrence of *Declivolithus* in the Tifrit n'Ougnaou locality is rather sporadic and for this reason the assemblage cannot be correlated with confidence with the *Declivolithus* Fauna described in Bofloss. In addition to this, the sedimentary facies of the upper middle Berounian of Jbel Tijarfaïouine include turbidites with frequent intercalations of conglomerate levels; even the commercial trenches of Tifrit n'Ougnaou are succeeded by sandstone beds rich in trace fossils typical of environments having a particular depth (*Cosmorhaphe*, *Nereites*, and others), including a decimeter-scale layer of great lateral continuity that records the massive appearance of a shallow *Zoophycos* with U-form, centrifugal spiraling spreiten.

Biostratigraphical and paleogeographical remarks

The revision of the *Declivolithus* Fauna trilobite assemblage from Morocco, in the Bofloss locality, led to the identification of 11 species, which are described in detail in the systematic paleontology section: *Ulugtella*? *Biformis* n. sp., *Selenopeltis* cf. *S. vultuosa* Přibyl and Vaněk, 1966, *Phacopidina quadrata* (Hawle and Corda, 1847), *Eudolatites* cf. *E. bondoni* Destombes, 1972 [= *E. cf. E. galafrea* Šnajdr, 1987, in Fortey and Edgecombe, 2017], *Prionocheilus* cf. *P. verneuili* Rouault, 1847, *Nobiliasaphus* cf. *N. kumatox* Šnajdr, 1982a, *Cyclopyge* cf. *C. rediviva* (Barrande, 1846) [= *Cyclopyge sibilla* Šnajdr, 1982a, in Fortey and Edgecombe, 2017], *Symphysops stevaninae* López-Soriano and Corbacho, 2012, *Heterocyclopyge* sp. (Hawle and Corda, 1847), which probably is *H. pachycephala* (Hawle and Corda, 1847) (= *Heterocyclopyge* sp. in Fortey and Edgecombe, 2017), *Dionide* sp. (probably *D. vokaci* Vaněk and Vonka, 2004; = *D. carlottae* Corbacho, Morrison, and Ait Addi, 2014), and *Declivolithus alfredi* (Želízko, 1906) (= *D. titan* Fortey and Edgecombe, 2017).

The previous record of the *Declivolithus* Fauna from the Anti-Atlas of Morocco (Fortey and Edgecombe, 2017) was assigned to "middle Katian" (Ka2) based on trilobite biostratigraphical correlation with the Bohdalec Formation. While this is indeed the most likely biostratigraphic placement, it is not definite either for this Moroccan association or for previous records of *Declivolithus* in Morocco in the High Atlas, or for the type locality of *Declivolithus alfredi* from the Czech Republic.

The only other biostratigraphic data from this locality are based on graptolites by Gutiérrez-Marco et al. (2022a), who identified *Diplograptus*? sp. and *Neodiplograptus*? sp. These are also consistent with a late Berounian age, although the condition of the material and the scarcity of the graptolite record in the Moroccan Upper Ordovician reduce the confidence of this attribution.

In the Czech Republic, *Declivolithus alfredi* is known in both the Rožmitál Block and in the Prague Basin. In the Rožmitál Block, type locality of *Declivolithus alfredi*, it is known from the Voltuš Formation, a sequence of monotonous shales. In the current concept of this unit, *Declivolithus* levels are located in the middle–upper part of the succession ("lower parts of the Rožmitál shales" sensu Přibyl and Vaněk, 1969). The stratigraphical correlation of this formation with the Prague Basin units is uncertain due to the isolation of this fault-bounded block, the poor exposure, and the rare fossil levels (Havlíček, 1998). *Declivolithus* co-occurs with *Cyclopyge* cf. *C. rediviva*, *Dionide formosa* (Barrande, 1846), *Eudolatites angelini* (Barrande, 1852), and one putative "undetermined dalmanitid," which could also correspond to *Prionocheilus* (Želízko, 1906; Přibyl and Vaněk, 1972). This assemblage mostly has been assigned to the middle Berounian, due to the presence of the brachiopod *Aegiromena aquila* (Barrande, 1848) and, therefore, correlation with the Zahořany Formation, but an upper Berounian correlation with the Bohdalec Formation cannot be excluded. On the other hand, it is difficult to assure the specific identity of these trilobites, due to the poor preservation state, and they could correspond to another of the closely related species known in the Czech Berounian. The Rožmitál assemblage has several taxa similar to the *Declivolithus* Fauna assemblage from Morocco: the species *D. alfredi* and *Cyclopyge* cf. *C. rediviva*, plus the genera *Dionide* and *Eudolatites* (Přibyl and Vaněk, 1969).

In the Prague Basin, *Declivolithus* was reported in the middle Berounian Zahořany Formation (Přibyl and Vaněk, 1969), mainly in its upper part (although Havlíček and Vaněk, 1966, also mentioned its presence in the middle part). Nevertheless, it is better known and more characteristic in the lower part of the upper Berounian Bohdalec Formation and in the Karlík ore horizon. The Moroccan assemblage shares three species with the Zahořany Formation and the Bohdalec Formation (*Declivolithus alfredi*, *Phacopidina quadrata*, and *Cyclopyge* cf. *C. rediviva*) and one extra with Bohdalec Formation (*Nobiliasaphus* cf. *N. kumatox*). Nevertheless, both *D. alfredi* and *P. quadrata* are much more characteristic of the Bohdalec Formation. The remaining taxa may equally correlate with Bohdalec Formation species, including *Dionide* sp., which may be closer to *D. vokaci* than to *D. formosa* of the Zahořany Formation or to *Ulugtella*? *biformis* n. sp., which could be related to a putative blind illaenid from the Bohdalec Formation ("*Zbirovia vaneki*" Šnajdr, 1958, partim). *Prionocheilus verneuili* is only known from the middle Berounian of Ibero-Armorica, but the poor preservation of our studied material and the very slight differentiation of Berounian species of the genus allow no further considerations. *Eudolatites bondoni* Destombes, 1972, was equally assigned to the middle to upper Berounian ("middle to upper Caradoc" in his sense), with Destombes expressing the same doubts discussed here.

Finally, the first reports of *Declivolithus* from Morocco made by Destombes (1971, 2006a) are also difficult to correlate.

These came from the Skoura region, in the High Atlas, but the stratigraphic sequence of this inlier shows greatest affinity with the Anti-Atlas and not with the northern Moroccan sectors. Additional Upper Ordovician argillaceous facies farther to the west of the Anti-Atlas (e.g., Tagounite, Zagora) continue to the north of the Anti-Atlas and in the central High Atlas, where the Skoura region is located (Destombes et al., 1985). *Declivolithus* was reported from two levels and occurs in association with the trilobites *Prionocheilus* sp., *Actinopeltis* sp., echinoderms, hyolithids, and the brachiopod *Aegiromena* aff. *A. aquila* (curiously, the same species reported in the Czech Rožmitál locality). Destombes et al. (1985), who could not make a confident chronostratigraphic assignment, considered the sequence to represent the middle and, mostly, the "upper Caradoc" and correlated it with both the Lower Ktaoua and the Tiouririne formations.

Notwithstanding the repeated difficulties demonstrated, we consider that the *Declivolithus* Fauna from Morocco shows greater affinity with the Bohdalec Formation of the Czech Republic and, together with the graptolite data of Gutiérrez-Marco et al. (2022a), possibly corresponds to the upper Berounian. We cannot exclude that *Declivolithus* Fauna from Morocco correlates with the middle Berounian. From a lithostratigraphic point of view, the particular facies of this geographical sector complicate the correlation with the classical scheme for the Anti-Atlas. The Bofloss sequence possibly correlates with the uppermost Lower Ktaoua Formation or with the lower part of the Upper Tiouririne Formation, which agrees with a late Berounian age according to the chitinozoan records and the stratigraphic data known from the Anti-Atlas (Loi et al., 2010; Álvaro et al., 2022, fig. 7).

Regardless of the exact age of the association, these rocks represent the middle part of the Katian, and most of the identified species (8 of 11) are known from the Czech Republic. The remaining three species have links to taxa previously known in this region and other high-latitude peri-Gondwanan areas (Ibero-Armorica). The new Moroccan data herein presented improve the knowledge of these previously known species and, most importantly, they support a strong faunal link between Morocco and the Czech Republic (Destombes et al., 1985; Fortey and Edgecombe, 2017; Gutiérrez-Marco et al., 2022b, and references therein), which still existed during the middle Late Ordovician and it seems to have been stronger than the faunal link with the Ibero-Armorican domain during the same interval. This must be considered in paleogeographical reconstructions (e.g., Torsvik and Cocks, 2017) and the Prague Basin (Bohemia; Czech Republic) position in relation to the peri-Gondwanan margin because the faunal links with Morocco were still very strong during early–mid Katian.

Materials

Repositories and institutional abbreviations.—Types, figured, and other specimens examined in this study are deposited in the paleontological collections of the Museo Geominero (CN Instituto Geológico y Minero de España-CSIC/Spanish Geological Survey), Madrid (registration prefix MGM). Specimens with NM labels are housed in the Národní Muzeum, Prague, Czech Republic. Back to the Past Museum (Cancún, México) is designated BPM.

Systematic paleontology

The use of open nomenclature follows Bengtson (1988). The assignment to orders follows Adrain (2011), whereas suprafamiliar arrangement of taxa follows the proposal of Adrain (2013). In the descriptions, the chronostratigraphic record of trilobite species cited from a wide area embracing North Africa, southwestern Europe, and Bohemia uses the regional Bohemo–Iberian scale (Gutiérrez-Marco et al., 2017). Its equivalence to the global scale is normally indicated, but it is as roughly as follows (Bergström et al., 2009): Dobrotivian (upper Dw3–lower Sa1); lower Berounian (ca. Sa1–Sa2); middle Berounian (uppermost Sa2–Ka1); upper Berounian (ca. Ka2); and Kralodvorian (Ka3–Ka4).

Class Trilobita Walch, 1771
Order Corynexochida Kobayashi, 1935
Suborder Illaenina Jaanusson, 1959
Family Illaenidae Hawle and Corda, 1847
?Genus *Ulugtella* Petrunina in Repina et al., 1975

Type species.—*Ulugtella turgida* Petrunina *in* Repina et al., 1975, from the "*Keananella–Tretaspis* beds," upper Katian, Turkestan.

Diagnosis.—See Hammann (1992, p. 75).

Remarks.—Given the uncertainty in the generic assignment of the species *Ulugtella*? *biformis* n. sp., a list of other species of *Ulugtella* will not be given here. For detailed information on the genus, reference is made to the work of Hammann (1992, p. 75–78) and Hammann and Leone (1997, p. 92–97). However, it is important to add a few remarks concerning the current concept of the genus *Ulugtella* and another genus that may be closely related. There are several blind illaenid genera from the peri-Gondwanan realm whose validity needs revision. Among others, these include *Ulugtella* and *Zbirovia* Šnajdr, 1956. The genus *Zbirovia* is represented by a single species—the type species *Zbirovia arata* (Barrande, 1872)—spanning from the Dobrotivian (ca. uppermost Darriwilian) Dobrotivá Formation to the middle Berounian (ca. upper Sandbian–lower Katian) Vinice Formation. This form is characterized by a relatively narrow glabella and ten thoracic segments (at least, in specimens from the older Dobrotivá Formation, where complete specimens are available). It is difficult to understand the origin of *Zbirovia*. It recalls some blind *Ectillaenus* species, such as *E. sarkaensis* (Novák in Perner, 1918) and *E. benignensis* (Novák in Perner, 1918), whose pygidial structure is similar to *Zbirovia arata*.

On the other hand, the type species of *Ulugtella* was defined in the upper Katian of Turkestan, which is younger than *Zbirovia*, bearing only nine thoracic segments, a cephalic anterior border, a strongly convex cephalon, and a well-defined pygidial axis. Nevertheless, the current concept of the genus (sensu Hammann, 1992, and Hammann and Leone, 1997), is based on a group of species that were assigned to *Ulugtella* and not necessarily related to the type species, which is poorly known. In this sense, Hammann (1992, p. 75–76) listed several records that he considered could belong to *Ulugtella*, including material from Spain, Czech Republic, Sardinia (Italy), United Kingdom, Poland, Germany, Turkey, and China. The wide geographical distribution given by Hammann, 1992, to *Ulugtella* makes its monophyly suspect, although in fact many trilobite genera became widespread during the late Katian (e.g., Fortey and Cocks, 2005).

Ulugtella? *biformis* new species
Figure 2

Holotype.—One complete exoskeleton (internal mold; Fig. 2.1–2.3), MGM-7666X housed in the paleontological collections of the Museo Geominero (CN Instituto Geológico y Minero de España, CSIC, Madrid).

Paratypes.—Four exoskeletons (MGM-7667X, MGM-7668X, MGM-7669X, MGM-7670X); one hypostome (MGM-7671X-1).

Diagnosis.—Parabolic cephalic outline; well-defined hourglass-shaped glabella, occupying about one-third of maximum cranidial width; axial reaching up to 40% sagittal cephalic length; facial sutures curving abaxially opposite the anterior ends of axial furrows; facial suture smoothly curving opposite anterior ends of the axial furrows; posterior ends of the facial suture curving abaxially; subtriangular librigenae with broadly rounded genal angles. Pygidium subpentagonal, with parabolic posterior margin; length ∼90% of the maximum pygidial width (tr.); axis poorly defined, with a faint subtriangular outline in flattened specimens, weakly convex, anterior width ∼30% of maximum pygidial width; pygidial doublure broad, ∼50% pygidial sagittal length, anterior margin of doublure slightly convergent with lateral pygidial margin abaxially, medially with posteriorly convex indentation.

Occurrence.—“*Declivolithus* Fauna beds,” upper part of the Lower Ktaoua Formation–?lower half of the Upper Tiouririne Formation, from the middle to upper Berounian boundary beds (ca. lower Katian), Bofloss locality, Tizi n'Ounfite location, 9 km SW of Oukhit (or Oukrite: 31°25′24.7″N, 04°33′59.0″W), northeastern Anti-Atlas, Morocco.

Description.—Cranidium maximum width (at posterior margin) ∼110% of sagittal length in full-relief specimens, with steep librigenae. Cranidium strongly vaulted (sag. and tr.); frontal part overhanging anterior margin. Axial furrows moderately deep, reaching 35–40% of sagittal cephalic length, slightly curved inwards; hourglass-shaped glabella, moderately convex, slightly exceeding height of fixigena in lateral view, merging with fixigenae anteriorly. Posterior glabellar width corresponding to 35% of posterior cephalic width; cranidium width ∼90% cephalic width. Facial suture very hard to observe in most of the specimens; one specimen with displaced librigenae shows divergent posterior end of the facial suture (Fig. 2.7); facial suture then running straight forwards up to opposite the anterior limit of the axial furrows, where it smoothly inflexes adaxially and then runs straight again anteriorly, converging at anterior margin, crossing the anterior border at a distance approximately twice the posterior width of the glabella. Fixigenae maximum width at posterior margin, ∼85% glabellar posterior width. Librigenae subtriangular, with broadly rounded genal angle; maximum width at posterior margin ∼60% glabellar posterior width. Anterior margin defined by a rim, which continues posteriorly into lateral librigenal border, fading backwards (Fig. 2.2, 2.3). Rostral plate subtrapezoidal, posterior width ∼60% anterior width and 150% sagittal length; connective suture converging backwards at 50–55° to sagittal line; surface bearing about 10 well-marked terrace ridges, subparallel to anterior rostral plate margin, being more regular anteriorly and becoming more sinuous posteriorly. Hypostome with semicircular posterior margin. Large subtriangular (almost rectangular) wings, length (exsag.) ∼40% hypostome sagittal length; middle body divided by a shallow middle furrow; anterior lobe convex, suboval, wider (tr.) than long (sag.); posterior lobe sickle-shaped, slightly convex, its sagittal length about half the length of anterior lobe. No maculae. Lateral and posterior border very narrow, limited by a furrow that meets the oblique middle furrow at about half the hypostome length (sag.), forming deep grooves. Three transverse terrace ridges are observed on the anterior lobe of the middle body.

Nine thoracic segments. Axis moderately arched (tr.), about one-third of thoracic width anteriorly, slightly narrowing backwards, more strongly in last five segments. Axial furrow deeper than on cephalon; subcircular axial processes visible on internal molds. Pleurae as wide anteriorly as posteriorly, fulcrum located ∼50% of pleural width. Inner portion of pleurae flattened and smooth; outer portion deflected downwards and slightly backwards, bearing a broad (exsag., tr.) and smooth facet.

Pygidium subpentagonal in full-relief specimens (in flattened specimens pygidium acquires an almost subcircular outline, short, sag.), length/width ratio ∼70% (in full-relief specimens); posterior margin parabolic. Pygidial axis poorly defined, broadly triangular in flattened specimens, weakly convex, anterior width ∼30% of maximum pygidial width. Axial furrow not defined. Doublure very broad, corresponding to 50% of pygidial sagittal length medially; anterior margin of doublure slightly convergent with lateral pygidial margin abaxially, medially with posteriorly convex indentation; the pygidium, both in full-relief specimens and flattened ones, often exfoliates, exposing the medial indentation very prominently (Fig. 2.1, 2.2, 2.4, 2.5); sculpture of terrace ridges running subparallel to pygidial margin, becoming more sinuous medially.

Dorsal surface of exoskeleton densely covered with circular pits, more evident on cephalon and pygidium, obliterated in most specimens, better preserved in a single example (Fig. 2.6). This sculpture is not preserved in full-relief specimens.

Etymology.—From the Latin adjective *biformis*, *bis* (twice) + -*fōrmis* (having form of), meaning having two forms, or two faces (like Janus), reflecting the different morphologies shown by the specimens of this species when preserved in full relief or flattened. *Ulugtella* gender feminine.

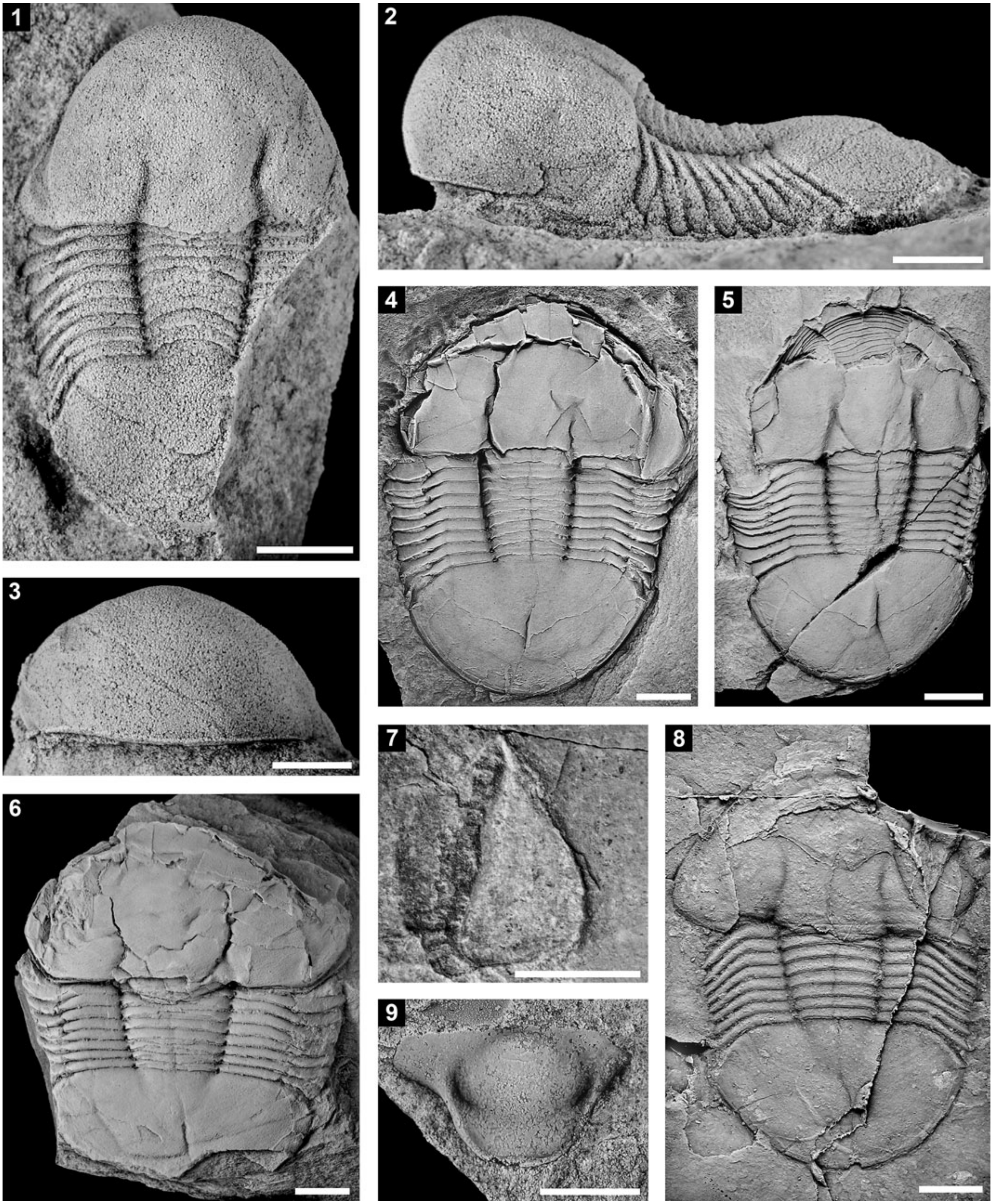

Figure 2. (**1–8**) *Ulugtella*? *biformis* n. sp., from the Bofloss locality, Morocco. (**1–3**) Exoskeleton, internal mold, holotype, MGM-7666X: (**1**) dorsal view; (**2**) left lateral view; (**3**) anterior view. (**4**) Exoskeleton, internal mold, paratype, MGM-7667X: dorsal view. (**5**) Exoskeleton, internal mold, paratype, MGM-7668X: dorsal view. (**6**) Exoskeleton, internal mold, paratype, MGM-7669X: dorsal view. (**7, 8**) Exoskeleton, paratype, MGM-7670X: (**7**) external mold of the left librigena; (**8**) latex cast of the external mold, MGM-7670X-1: dorsal view. (**9**) Hypostome, internal mold, paratype, MGM-7671X-1: ventral view. Specimens (**1–3**) and (**9**) are preserved in full relief (sandstones); the remaining specimens are preserved in mudstones, flattened. Scale bars = 5 mm.

Remarks.—We considered whether a Portuguese species ("*Ulugtella*? *guedesi* n. sp." in the unpublished PhD thesis by Pereira, 2017, p. 268–272, pl. 19, figs. A–K; pl. 20, figs. A–J; pl. 21, figs. A–M) and these Moroccan specimens are conspecific but decided not to assume that to be the case. The very distinct subtrapezoidal morphology of the librigenae of the Portuguese specimens, with sharp right genal angle (90°), the strongly inflected facial suture (suggesting recent loss of the eyes), with posterior branch curving adaxially (and not abaxially as in the Moroccan specimens). and the more heart-shaped pygidium, with no evidence of any indentation on the inner edge of the doublure suggest that although extremely similar, the Portuguese species differs in characters that are significant within Illaenidae.

Ulugtella? *biformis* n. sp. is here only tentatively assigned to *Ulugtella* due to the current unsatisfactory knowledge on Upper Ordovician illaenid lineages from the peri-Gondwana realm. Nevertheless, we think it is closely related to *Zbirovia arata*. The number of thoracic segments has been treated in Illaenidae as being relevant at a genus level. *Zbirovia* bears 10 thoracic segments, and because the new species fits the current diagnosis of *Ulugtella* (Hammann, 1992), we chose to assign it to this genus and not to the former. The current *Ulugtella* diagnosis and concept of *Ulugtella* were established by Hammann (1992) based on the assumption that a group of occurrences from Spain, Sardinia, Sweden, and Poland are congeneric with the type species *U. turgida*. If *U. turgida* is not related to these peri-Gondwanan occurrences and the species described herein, then either a new genus to include this group of nine-segmented blind illaenids related to *Zbirovia* would be appropriate or *Zbirovia* should encompass all of them, regardless of the number of thoracic segments. This awaits detailed revision of this group, and we follow Hammann's (1992) proposal for now.

Ulugtella? *biformis* n. sp. shows more similarities to a group of occurrences assigned by Hammann (1992) and Hammann and Leone (1997) to *U. angelini* (Holm, 1883, p. 120, pl. 4, fig. 29), defined in the "Red *Tretaspis* Mudstone" (Upper Jonstorp Formation) of the upper Katian of Sweden by Holm (1883). These came from the Cystoid Limestone Formation (Kralodvorian, ca. upper Katian) of Spain (Hammann, 1992, p. 75–77, pl. 14, figs. 1–10) and from the Domusnovas Formation (Kralodvorian, ca. upper Katian) of Sardinia (Hammann and Leone, 1997, p. 93–95, pl. 16, figs. 1–16). Despite their similar overall appearance, the Baltic *U. angelini* differs from *U.*? *biformis* n. sp. by having a marginal, posteriorly transverse, facial suture, a simple cephalic border, a definite narrower (tr.) thoracic and pygidial axis, and a simple, shorter (sag./exsag.) pygidial doublure, with no evidence of indentation of its anterior margin. These are significant characters within the group (Jaanusson, 1954). Both in the facial suture and in pygidial doublure outline, Sardinian and Spanish specimens seem to be more similar to *U.*? *biformis* n. sp., but it is very difficult to conduct further analyses due to the poor state of preservation. All the other species assigned to *Ulugtella,* and other material classified as congeneric (listed exhaustively by Hammann, 1992, p. 75, 76, and Hammann and Leone, 1997, p. 94–95) are very distinct from *U.*? *biformis* n. sp. in having much narrower glabella and/or long genal spines (e.g., group *U. bornholmiensis* [Kielan, 1960] sensu Hammann and Leone, 1997, p. 95).

Ulugtella? *biformis* n. sp. shares some important features with *Zbirovia arata*, namely the pygidial morphology, including the typical doublure (see Šnajdr, 1957, pl. 3, fig. 12), the rostral-plate configuration (see Šnajdr, 1957, pl. 3, fig. 9), the cranidium overhanging the anterior margin, which is defined by a rim (see Klouček, 1913, fig. 3a), and a densely pitted sculpture. Nevertheless, *Zbirovia arata* has a simple facial suture, with no inflexion, its thorax being composed of 10 thoracic segments and the pygidial doublure being longer (sag.). The difference in the length of the doublure would, however, be expected, given the reduction in the number of thoracic segments (paedomorphism?), but we do not know whether the suture could, by the same process, present these changes connected to an ancestor of both that had eyes. Furthermore, a specimen recently figured by Lebrun (2018, p. 117, fig. A) from the Lower Ktaoua Formation of Morocco suggests *Zbirovia arata* is also present in Morocco, in beds older than *U.*? *biformis* n. sp.

The discovery of this new species and its possible relationship with *Zbirovia arata*, entails another species, *Zbirovia vaneki* Šnajdr, 1958, from the Bohdalec Formation of the Czech Republic, later assigned to *Vysocania* (see Pereira et al., 2017, and references therein) based on additional cephala bearing eyes and the same typical pygidial morphology. But according to the doubts already expressed by Šnajdr (1958) whether this species was blind or not, it is possible that two very similar illaenids occur in the Bohdalec Formation, one with eyes (*Vysocania*) and another without eyes. This was also mentioned by Bruthansová (2003), but she considered these specimens with eyes to be *Vysocania panderi* (Barrande, 1852), which differs from the Bohdalec specimens in bearing librigenae with rounded genal angles. The holotype of "*Zbirovia vaneki*" (Šnajdr, 1958, pl. 2, fig. 10) corresponds to the eyed-illaenid form (*Vysocania*), but other specimens described under the same name may in fact represent a blind form, justifying Šnajdr's (1958) concerns and original generic assignment. Whether or not this blind illaenid of the Bohdalec Formation that led Šnajdr to the erection of "*Zbirovia vaneki*" is conspecific with the new Moroccan species is hard to say, but the cephalic axial furrows of the Czech types repeatedly appear to be more curved and closer together. Similar thoughts were expressed by Pereira (2017, p. 272) to differentiate *Vysocania iberica* (Hammann, 1976) from "*Ulugtella*? *guedesi* n. sp." (*Ulugtella*? *guedesi* Pereira, 2017) when occurring in the same fossil locality.

Finally, the hypostome morphology of *U.*? *biformis* n. sp. is very similar to "illaenid hypostome B" documented by Hammann (1992, pl. 18, figs. 5, 6) from the Cystoid Limestone Formation of Spain. It is an *Ectillaenus*-type specimen (e.g., Bruthansová, 2003, fig. 2e), but differs in having a more developed posterior lobe of the middle body. Although the hypostome is unknown in many illaenids, this morphology also points to *Ulugtella*? *biformis* n. sp. being connected to a group of endemic illaenids from peri-Gondwana.

Order Odontopleurida Whittington in Moore, 1959
Family Odontopleuridae Burmeister, 1843
Subfamily Selenopeltinae Hawle and Corda, 1847
Genus *Selenopeltis* Hawle and Corda, 1847

Type species.—*Odontopleura buchii* Barrande, 1846, Letná Formation, lower Berounian (ca. Sandbian, Sa2), Czech Republic.

Other species.—See Bruton (2008, p. 4).

Diagnosis.—See Bruton (2008, p. 4).

Occurrence.—Lower (Floian) to Upper Ordovician (topmost Katian) of Europe (Czech Republic, Great Britain, France, Portugal, Spain, Italy, Turkey), North Africa (Morocco), and the Middle East (Iraq).

Remarks.—*Selenopeltis* was revised by Bruton (2008) and partially also by Gutiérrez-Marco et al. (2022b), to whom we refer for further information.

Selenopeltis cf. *S. vultuosa* Přibyl and Vaněk, 1966
Figure 3.1, 3.2

cf. 1966	*Selenopeltis buchi vultuosa* Přibyl and Vaněk, p. 292, pl. 4, fig. 2, pl. 8 figs. 1–3.
?p 2008	*Selenopeltis vultuosa* Přibyl and Vaněk; Bruton, p. 10, fig. 3 A–J, M, N.

Materials.—One cranidium (MGM-7673X); one librigena (MGM-7674X-1).

Remarks.—*Selenopeltis* is a genus that has captured the attention of several researchers, with special emphasis on the works of Bruton (1968, 2008), Přibyl and Vaněk (1973), Bruton and Henry (1978), Romano (1982), Šnajdr (1984), Hammann and Rábano (1987), and Ramsköld (1991). The revision of *Selenopeltis* by Bruton (2008) included material from Morocco, supplemented by the review of a purported endemic Moroccan species (Gutiérrez-Marco et al., 2022b). Given the existence of these works, we have chosen to follow here the considerations of Bruton (2008) to identify Bofloss *Selenopeltis*. Only two fragmentary specimens (one cranidium and one librigenal; Fig. 3.1, 3.2) were collected, but complete exoskeletons coming from *Declivolithus* beds are relatively common in Moroccan trade. Thus, we include some characters observed in those in this discussion.

Following Bruton's (2008) revision, the Bofloss specimens are more similar to *Selenopeltis vultuosa* from the Lower Ktaoua and Upper Tiouririne formations of Morocco, based solely on the presence of pygidial true major border spines overpassing the pygidial border. This character is stable in all the large holaspides observed and has been shown to be the only consistently assessable character unaffected by deformation, preservation, or ontogeny, if in mature holaspides (Šnajdr, 1984; Pereira, 2017). All the Berounian species of *Selenopeltis* defined for high-latitude peri-Gondwana realm (*Selenopeltis buchi* group) have supramarginal true major spines. Other characters that have been used to differentiate several *Selenopeltis* species, namely the external sculpture, are shown to be highly variable within the same locality and dependent on the size of the specimens, even in the holaspid stage (see Pereira, 2017, p. 334–336, pls. 39–41). Nevertheless, if the Moroccan specimens are compared with the type material of *S. vultuosa* from the Králův Dvůr Formation in the Czech Republic, a specific difference is probable. The Moroccan specimens do not show a sharp bend in the thoracic pleural ridge like the Czech types (see Shaw, 2000, pl. 2, figs. 15, 20), which is the most distinctive and persistent character of *Selenopeltis vultuosa* according to Šnajdr (1984) and Shaw (2000, p. 380). Here, we maintain the identification based on Bruton's (2008) work, but the current state of knowledge of *Selenopeltis* species is not satisfactory.

Suborder Phacopina Struve in Harrington et al., 1959
Infraorder Dalmanitiformes Eldredge, 1979
Superfamily Acastacea Delo, 1935
Acastacea s.l. sensu Edgecombe (1993)
(= Kloucekiinae Destombes, 1972)

Remarks.—The systematic position of the basal Acastacea (= Acastoidea) remains unsolved. We follow the proposal of Edgecombe (1993), which is possibly also the ongoing one for the revision of the Treatise on Invertebrate Paleontology (see Adrain, 2011, p. 105). According to Edgecombe (1993), Acastacea s.l. includes genera that present the apomorphies of the superfamily Acastacea but lack the derived characters defining Siluro–Devonian Acastacea s.s. Edgecombe (1993) considered these basal acastaceans to have evolved from Dalmanitoidea through a shift in feeding mechanisms. Although we have chosen to follow the most recent proposal, we express doubts in excluding this Ordovician group or, at least, some of its members from Dalmanitidae.

Genus *Phacopidina* Bancroft, 1949

Type species.—*Phacopidina harnagensis* Bancroft, 1949, from the Smeathen Wood Formation, Aurelucian (ca. lower Sandbian) of Shropshire, England.

Other species.—*Portlockia*? *apiculata* M'Coy in Sedgwick and M'Coy, 1851, Burrellian/Cheneyan, Shropshire, England; *Dreyfussina armoricana* Pillet, 1990, upper part of the Sangsurière Formation ("Schistes d'Angers"), middle Berounian, La Meinanne, Maine et Loire, France; *Phacopidina micheli couyerensis* Henry, 1980, Andouillé Formation, Dobrotivian, France; *Phacopidina makina* Šnajdr, 1987, Zahořany Formation, middle Berounian, Czech Republic; *Dalmanites micheli* Tromelin, 1877, Dobrotivian, France; *Zeliszkella* (*Zeliszkella*) *neltneri* Destombes, 1972, Ouine-Inirne Formation, Dobrotivian, Morocco; *Phacops quadratus* Hawle and Corda, 1847, Bohdalec Formation, upper Berounian, Czech Republic (= *P. rebeka* Šnajdr, 1982b, junior synonym).

Diagnosis.—See Henry (1980, p. 126).

Occurrence.—Middle to Upper Ordovician (Darriwilian to Katian) of Portugal, Spain, France, Czech Republic, Morocco, and United Kingdom.

Remarks.—Regardless of the arguments used by Henry (1980, p. 123–127) to differentiate *Kloucekia* Delo, 1935, from *Phacopidina*, he questioned their independence. The cephalic

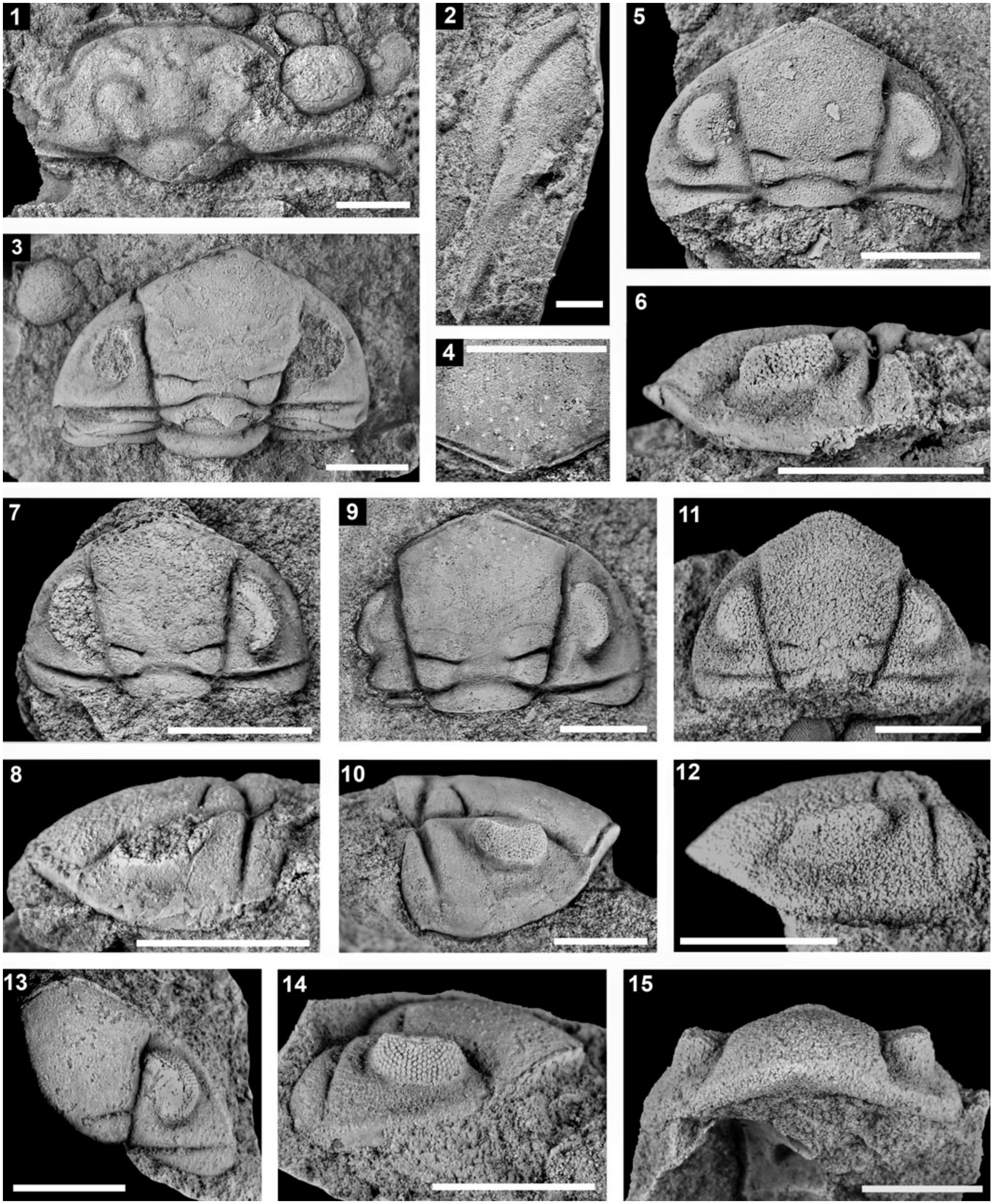

Figure 3. (**1, 2**) *Selenopeltis* cf. *S. vultuosa* Přibyl and Vaněk, 1966, from the Bofloss locality, Morocco. (**1**) Cranidium, internal mold, MGM-7673X: dorsal view; (**2**) left librigena, latex cast of the external mold, MGM-7674X-1. (**3–15**) *Phacopidina quadrata* (Hawle and Corda, 1847) from the Bofloss locality, Morocco. (**3**) Cephalon, internal mold, MGM-7675X: dorsal view; (**4, 9, 10**) cephalon, internal mold, MGM-7676X: (**4**) frontal view showing frontal lobe auxiliary impressions; (**9**) dorsal view; (**10**) right lateral view; (**5, 6**) cephalon, internal mold, MGM-7677X: (**5**) dorsal view; (**6**) left lateral view; (**7, 8**) cephalon, internal mold, MGM-7678X: (**7**) dorsal view; (**8**) left lateral view; (**11, 12, 15**) cephalon, internal mold, MGM-7679X: (**11**) dorsal view; (**12**) left lateral view; (**15**) anterior view; (**13, 14**) cephalon, latex cast of the external mold, MGM-7680X: (**13**) dorsal view; (**14**) right lateral view. All specimens are preserved in full relief (sandstones). Scale bars = 5 mm.

differences listed are questionable because of the existence of species showing intermediate features. Henry (1980) assigned a few species to *Phacopidina* in which the facial suture is not separated from the preglabellar furrow (*P. harnagensis* and *P. apiculata*). In addition, *Kloucekia robertsi* (Reed, 1904), from the Redhill Mudstones and Sholeshook Limestone (upper Katian, Wales, United Kingdom) shows at the same time the cephalic diagnostic features of *Phacopidina* (broad preglabellar area) but pygidia lacking medial spine (one of the diagnostic characters of *Kloucekia* used by Henry, 1980). On the other hand, the genus *Dreyfussina* Hupé in Choubert et al. (1956) may fall within the compass of *Kloucekia*. The diagnostic characters usually mentioned for *Kloucekia*—presence of genal spines, strong pygidial segmentation, and existence of a concave pygidial border (Destombes, 1972; Hammann, 1974, 1976; Henry, 1980)—are absent in its type species, *Dalmania exophtalma* Dreyfuss, 1948 (see Henry, 1980, pl. 44, figs. 5, 6, 8, 10). The current systematic classification of these genera is not satisfactory, but for the moment we follow previous authors who recognized three genera (e.g., Henry, 1980; Hammann and Leone, 2007), and retain *Phacopidina* as a separate genus.

On the other hand, *Phacopidina* is a good example of the concerns in excluding these Ordovician "acastaceans" from Dalmanitidae. These concerns were expressed by Henry (1980, p. 127), who detailed several significant characters shared by *Phacopidina* and some Zeliszkellinae and Dalmanitininae. Accepting the detailed discussion provided by Destombes and Henry (1987) about Calmoniidae versus Dalmanitidae, it is difficult to conceive that several species currently assigned to *Phacopidina* are not closely related to the dalmanitid *Crozonaspis* Henry, 1968 (see Remarks on the different species that follow).

Phacopidina quadrata (Hawle and Corda, 1847)
Figures 3.3–3.15, 4.1–4.6

1847	*Phacops quadratus* Hawle and Corda, p. 99.
1972	*Kloucekia* (*Phacopidina*) aff. *solitaria*; Destombes, p. 60–63, pl. 14, figs. 1–16.
1987	*Phacopidina makina* Šnajdr, p. 276, pl. 2, fig. 8.
1997	*Phacopidina quadrata*; Vaněk and Vokáč, p. 39–40, pl. 7, figs. 7–9, pl. 8, figs. 4–10, pl. 10, figs. 5, 6 (and synonymy therein).
p1997	*Sokhretia solitaria*; Vaněk and Vokáč, pl. 7, figs. 10–15, pl. 8, figs. 15, 16.
2006b	*Kloucekia* (*Phacopidina*) aff. *solitaria*; Destombes, pl. 36, figs. 1, 2.

Holotype.—A holotype was not indicated by Hawle and Corda (1847). The lectotype selected by Šnajdr (1983, pl. 12, figs. 7, 8) is an internal and corresponding external mold of a cephalon (NM L5395–L5396) housed in the Národní Muzeum (Prague, Czech Republic).

Description.—See Destombes (1972, p. 60–63).

Materials.—Fifteen cephala (MGM-7675X to MGM-7688X; MGM-7689X-1); one cephalic doublure (MGM-7689X-2); two pygidia (MGM-7674X-3; MGM-7690X).

Remarks.—The taxonomic problems surrounding *Phacopidina quadrata* and *Dalmanites solitaria* Barrande, 1852, later established as the type species of *Sokhretia* Hupé, 1956, have been discussed by previous authors (e.g., Šnajdr, 1984; Vaněk and Vokáč, 1997) and will not be discussed further here. We should clarify that the identification of "*Kloucekia* (*Phacopidina*) aff. *solitaria*" by Destombes (1972, 2006b) in Morocco, which we consider conspecific with the new Bofloss specimens, is due to this error and in fact the Moroccan cephala are conspecific with the "cephalon" used to define *Sokhretia* (a genus erected based on sclerites belonging to more than one species, including *Phacopidina quadrata*). Hence, the previous assignment by Destombes to Barrande's species "*Kloucekia solitaria*". We consider that the Moroccan specimens are entirely comparable to *Phacopidina quadrata* from the Bohdalec Formation of the Czech Republic, a name that has nomenclatural priority. Similarly, we consider that several specimens figured as "*Sokhretia solitaria*" by Vaněk and Vokáč (1997), either cephala or pygidia, may belong to *Phacopidina quadrata* (see synonymy).

Our material adds little to the very good documentation of *Phacopidina quadrata* in Morocco by Destombes (1972), except perhaps the morphology of the cephalic doublure (Fig. 4.2, 4.4). Destombes and Henry (1987) considered "*Kloucekia* (*Phacopidina*) aff. *solitaria*" (= *P. quadrata*) to be closely related to *Baniaspis globosa* Destombes, 1972. Nevertheless, several characters used by these authors as evidence of a Calmoniidae relationship for *Baniaspis* (e.g., the small anteriorly located eye, the absence of palpebral lobe, the frontal glabellar lobe not limited anterolaterally and merging with genae) are not present in *P. quadrata*. In all these characters, *P. quadrata* differs from *B. globosa* and is entirely comparable to *Crozonaspis*. However, the organized pattern of frontal lobe auxiliary impressions is similar in *B. globosa* and *P. quadrata*, and this morphological detail can be seen both in the Moroccan specimens (Destombes and Henry, 1987, fig. 7) and in the Czech specimens from the Bohdalec Formation (Šnajdr, 1982b, pl. 2, figs. 6–9). Nevertheless, it is doubtful that they are very different from the pattern observed in some specimens of *Crozonaspis* (e.g., Pereira, 2017, pl. 56, fig. K) or *Zeliszkella* (Henry, 1980, fig. 25, fig. 7b). The pygidium of *P. quadrata* is extremely similar to the typical structure of younger *Crozonaspis* species (e.g., Henry, 1980, pl. 42, figs. 2, 3). The pygidium of *P. quadrata* differs from *B. globosa* because the pygidial spine arises from the border instead of the rachis. Regarding the ventral structures, the hypostome of *P. quadrata* (Destombes, 1972, pl. 14, fig. 11) is indistinguishable from that of *Crozonaspis struvei* Henry, 1980, bearing uniform narrow posterior and lateral borders, and middle body not overhanging the lateral border as in *Baniaspis globosa* (Destombes and Henry, 1987, fig. 5). The cephalic doublure is simple, with no auxiliary impressions, and has a convex anterior border, not flattened as in *B. globosa* (see Destombes and Henry, 1987, fig. 3C and 3D). However, these details strongly depend on preservation, and observation in one single specimen of each species is not representative.

Phacopidina quadrata shows many characters typical of Dalmanitidae and is reminiscent of *Crozonaspis*, whose younger species (Late Ordovician) also have obsolete S2 and S3. It is

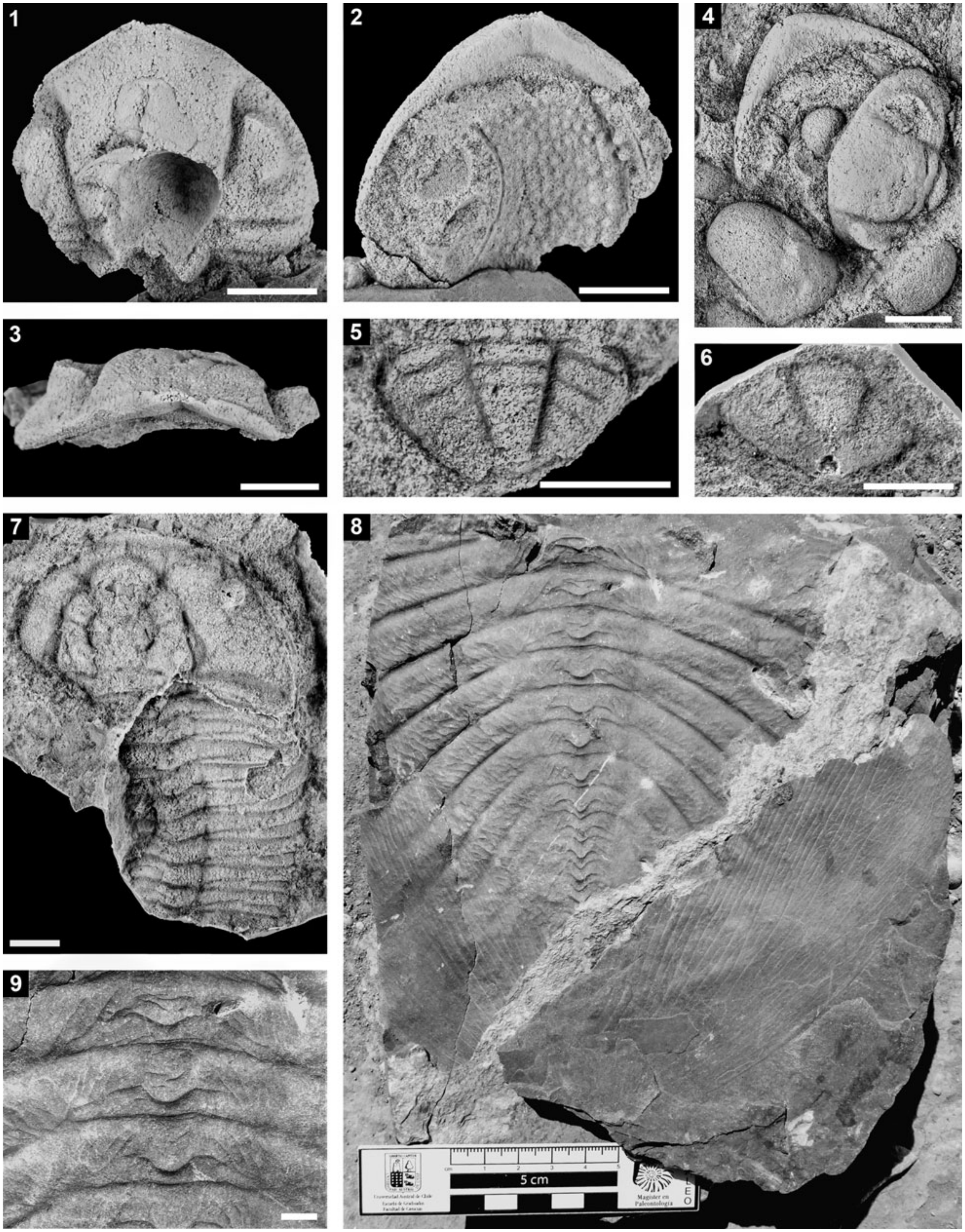

Figure 4. (**1–6**) *Phacopidina quadrata* (Hawle and Corda, 1847) from the Bofloss locality, Morocco. (**1–3**) Cephalon, internal mold, MGM-7681X: (**1**) dorsal view; (**2**) ventral view; (**3**) anterior view; (**4**) cephalon and cephalic doublure, internal molds, dorsal and ventral views, MGM-7689X-1 and 7689X-2, respectively; (**5**) pygidium, internal mold, MGM-7690X: dorsal view; (**6**) pygidium, latex cast of the external mold, MGM-7674X-3: dorsal view. (**7**) *Prionocheilus* cf. *P. verneuili* Rouault, 1847, incomplete cephalon with thorax, latex cast of the external mold, MGM-7703X: dorsal view. (**8, 9**) *Nobiliasaphus* cf. *N. kumatox* Šnajdr, 1982a, pygidium, internal mold (field photograph): (**8**) dorsal view; (**9**) detail of the axis. All specimens are preserved in full relief (sandstones), except specimen (**8, 9**), preserved in mudstone. Scale bars = 5 mm.

possible that *P. quadrata* could be more closely related to this group of dalmanitids than to Calmoniidae, independently of the relationship and systematic position of *Baniaspis globosa*.

Superfamily Dalmanitoidea Vodges, 1890
Family Dalmanitidae Vodges, 1890
Subfamily Eudolatitinae Tomczykowa, 1991
Genus *Eudolatites* Delo, 1935
(= *Eudolatites* [*Destombesites*] Šnajdr, 1987; ? = *Eudolatites* [*Banilatites*] Destombes, 1972)

Type species.—*Dalmanites angelini* Barrande, 1852, from the Bohdalec Formation, upper Berounian (ca. lower Katian, Ka2), Czech Republic (? =*E. galafrea* Šnajdr, 1987, Bohdalec Formation, upper Berounian, Czech Republic).

Other species.—*Eudolatites bondoni* Destombes, 1972, Lower Ktaoua Formation, middle Berounian, Morocco; *Phacops dubius* Barrande, 1846, Zahořany Formation, middle Berounian, Czech Republic (? = *E. sumptuosus* Přibyl and Vaněk, 1972, Vinice Formation, lower Berounian, Czech Republic); *E. flavus* Rábano in Gutiérrez-Marco and Rábano, 1987, "Lumaquelas Terminales" Member, Bancos Mixtos Formation, upper Berounian, Spain; *E. hastatus* Přibyl and Vaněk, 1972, Letná Formation, lower Berounian, Czech Republic (? = *E. promura* Šnajdr, 1987, Letná Formation, lower Berounian, Czech Republic); *E. inflatus* Destombes, 1972, Upper Tiouririne Formation, middle Berounian, Morocco (= ?*E. karmina* Šnajdr, 1987, Zahořany Formation, middle Berounian, Czech Republic).

Diagnosis.—Modified from Rábano in Gutiérrez-Marco and Rábano (1987, p. 71). Exoskeleton fairly convex. Anterior cephalic border absent, with well-marked lateral and posterior furrows; genal spines present or absent. Glabella claviform, with prominent frontal lobe; S1 and S2 parallel or slightly convergent adaxially. Eyes small to large (A/G = 25–35%; A/Gn = 25–40%). Hypostome with long (sag.), complete, and rounded posterior border. Thorax composed of 11 segments; pleural furrows rectilinear and distal tips pointed. Pygidium of parabolic to subcircular outline, length (sag.) similar to that of cephalon, with rounded to pointed posterior margin. Pygidial border simple or defined by a rim, with variable convexity/length. Axis well defined, narrow (tr.; ∼25% of pygidial width at anterior border), with 10–15 axial rings. Pleurae with 8–12 pleural furrows (defining up to 13 ribs); pleural and interpleural furrows well marked.

Occurrence.—Upper Ordovician (Sandbian to Katian) of Portugal, Spain, France, Czech Republic, Italy (Sardinia) and Morocco.

Remarks.—The current state of the systematics of *Eudolatites* was detailed by Hammann and Leone (2007). We follow these authors considering the subgenera *Banilatites* Destombes, 1972, and *Destombesites* Šnajdr, 1987, as junior synonyms. The characters previously considered for distinction of these subgenera, including definition of the pygidial border and pygidial axial length/width ratios, have not proved unequivocal.

Eudolatites cf. *E. bondoni* Destombes, 1972
Figure 5

1972	cf. *Eudolatites bondoni* Destombes, p. 42–43, pl. 4, fig. 1, text-fig. 12.
?2014	*Eudolatites* sp. Lawrence and Stammers, p. 264.
2017	*Eudolatites* cf. *E. galafrea* Šnajdr; Fortey and Edgecombe, p. 320, fig. 4A, 4B.
2018	*Eudolatites* (*Eudolatites*) sp. Lebrun, p. 143.

Description.—Cephalon sub-ogival in outline, sagittal length ∼60% maximum cephalic width (at posterior margin). Glabella flattened in its posterior half, anterior lobe sloping downwards anteriorly; posterior glabellar width corresponding to 30–35% maximum cephalic width (at posterior margin) and 50–60% glabellar width (at frontal lobe). Axial furrows deep, narrow, diverging more strongly anterior to S1, slightly convex and deeper against L3, strongly convex anterior to S3 to surround the enlarged frontal lobe; frontal lobe width ∼50–55% maximum cephalic width, bearing a median pit. Adaxial edges of glabellar furrows almost located at the same exsagittal line, simple, non-bifurcated; S3 shallower, oblique. Eyes with anterior edge opposite S3, touching the axial furrow; posterior edge varying from opposite S2 to slightly posterior to S2 (anterior third of L2), located at a distance from the axial furrow about the width (tr.) of L1; visual surface subvertical, with a regular arrangement of the lenses in about 50 dorsoventral rows, with a maximum of 14 lenses per row. Genal angle enlarged (tr., exsag.) but devoid of spine. Genae sculpture of uniformly distributed pits, absent in the palpebral lobe.

Hypostome typical of Dalmanitidae, particularly elongated (sag.), with broad (sag.), flattened and rounded (not polygonal) posterior margin and middle body with faint ornamentation.

Pygidium sub-triangular in outline; axis moderately convex, protruding pleurae; abaxial half of the pleurae flat, with the adaxial part subvertical due to a sharp bend of the pleurae. Pygidial anterior width ∼80–85% of pygidial length in full-relief specimens (∼70–75% in flattened ones); pygidial axis ∼35% pygidial width at the anterior margin (∼25% in flattened specimens); pygidial axis narrowing backwards to ∼20% of anterior width (∼10% in flattened specimens), ending before it reaches the pygidial margin; its posterior limit is defined by a change in its convexity, which follows the general bend of the pygidial abaxial region. Thirteen axial rings, poorly defined posteriorly (from seventh on); terminal piece rounded, almost indistinct. Nine pairs of pleural and interpleural furrows, defining nine ribs (eighteen bands with a similar length, exsag.); pleural and interpleural furrows equally deep, sub-parallel; pleural furrows end immediately abaxial to the sharp bend in the pygidial pleurae; interpleural furrows longer than pleural furrows, almost reaching the pygidial margin (a very short, tr., abaxial surface of the pygidium that is unfurrowed, but it is not defined as a rim). Outline of posterior pygidial margin gently pointed medially (it is not a true pygidial spine, just a pointed curvature).

Materials.—Five cephala (MGM-7692X to MGM-7695X; MGM-7696X-1); one hypostome (MGM-7702X); six pygidia (MGM-7696X-2; MGM-7697X to MGM-7701X).

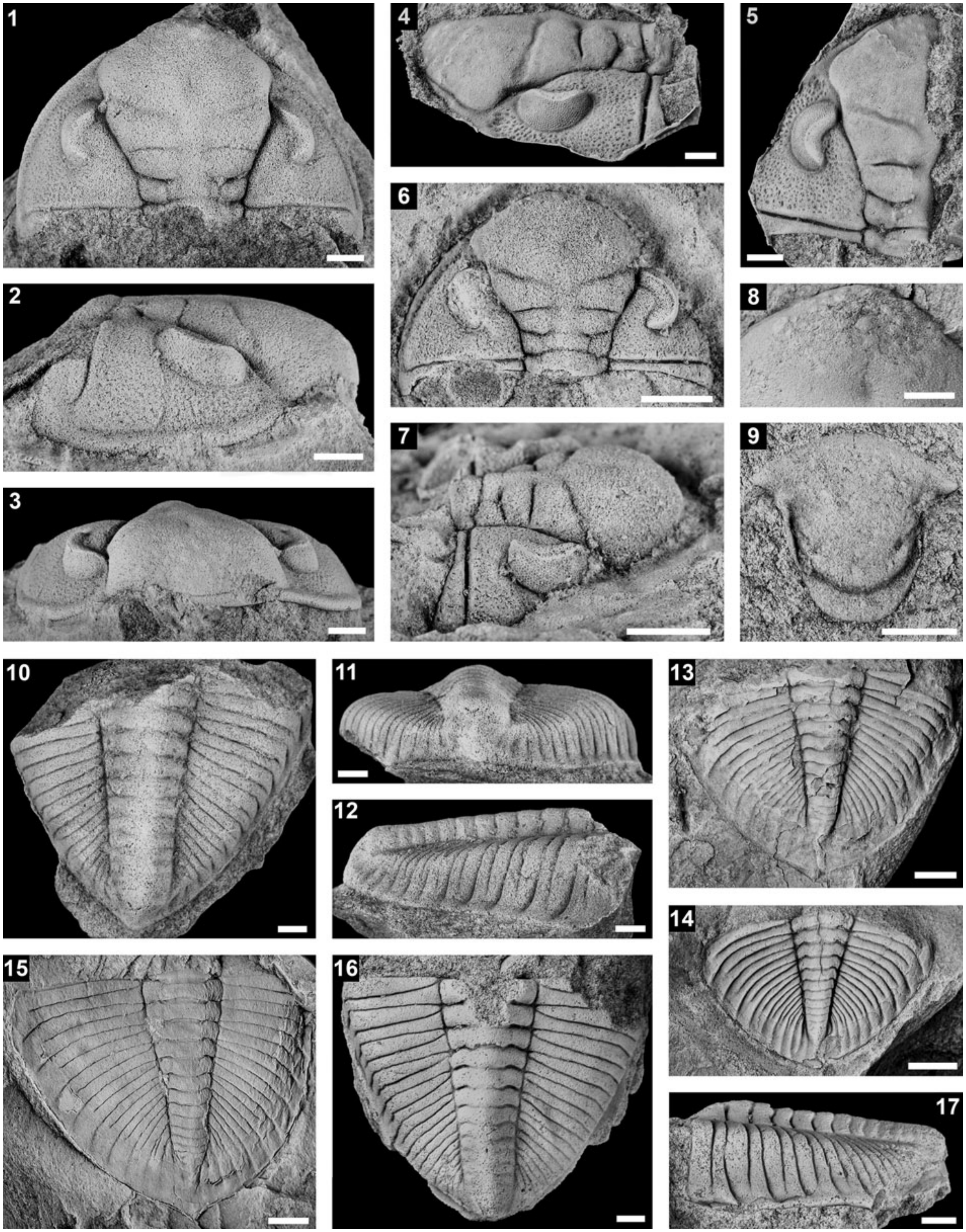

Figure 5. (**1–17**) *Eudolatites* cf. *E. bondoni* Destombes, 1972, from the Bofloss locality, Morocco. (**1–3**) Cephalon, internal mold, MGM-7692X: (**1**) dorsal view; (**2**) right lateral view; (**3**) anterior view; (**4, 5**) incomplete cephalon, latex cast of the external mold, MGM-7696X-1: (**4**) left lateral view; (**5**) dorsal view; (**6, 7**) cephalon, internal mold, MGM-7693X: (**6**) dorsal view; (**7**) right lateral view; (**8**) cephalon, internal mold, MGM-7694X: detail of the frontal lobe showing auxiliary impressions; (**9**) hypostome, internal mold, MGM-7702X: ventral view; (**10–12**) pygidium, internal mold, MGM-7697X: (**10**) dorsal view; (**11**) posterior view; (**12**) right lateral view; (**13**) pygidium, internal mold, MGM-7699X: dorsal view; (**14**) pygidium, internal mold, MGM-7700X: dorsal view; (**15**) pygidium, latex cast of the external mold, MGM-7701X: dorsal view; (**16, 17**) pygidium, internal mold, MGM-7696X-2: (**16**) dorsal view; (**17**) left lateral view. All specimens are preserved in full relief (sandstones), except specimens (**13–15**), which are preserved in mudstones (flattened). Scale bars = 5 mm.

Remarks.—Currently, there is a great diversity of species described for *Eudolatites*, despite the relatively short stratigraphic (Berounian) and geographic (high-latitude peri-Gondwana) distribution. The genus appears to have undergone rapid speciation, with several of the defined species being reliable.

Among the Bofloss material, we have flattened specimens and specimens in full relief. Due to the sharing of very particular and significant characters by both sets of specimens (the small size and the anterior position of the eyes, the number of pygidial rings and pleural/interpleural furrows, the length and direction of pleural/interpleural furrows pairs, and the pointed pygidial margin), we assume they represent the same species. However, this is one of those cases in which flattening gives the specimens a very distinctive overall morphology, especially with regard to the pygidial axis, which appears much more imposing (sag. and tr.) in specimens in full relief than in flattened ones (compare Fig. 5.10–5.12, 5.16, 5.17 with Fig. 5.13–15.15). This is due to the "widening of the pleural areas" when their abaxial margins collapse since they were originally vertical. Hence, what most characterizes Bofloss *Eudolatites* species is (1) the relatively small (for this genus) and anteriorly located eyes; (2) the existence of 13 pygidial axial rings and nine pairs of pleural and interpleural furrows (defining 9 ribs/18 pleural bands), (3) the subparallel relationship between the pleural and interpleural furrows (even abaxially) and the greater length of the interpleural ones, (4) the absence of a pygidial inflated rim/border, and (5) the tipped medial termination of the pygidium. These are the only characters we judge to be useful within this genus. A sixth character, the apparently rounded genal angle (as opposed to species with a pointed genal angle), is poorly understood, but could provide an additional feature.

Among defined *Eudolatites* species, we can exclude a conspecific relationship with *Eudolatites* aff. *E. dubius* (documented by Destombes, 1972, pl. 3, fig. 1, pl. 4, figs. 2–7) because the pleural/interpleural furrows have the same length. We can exclude a conspecific relationship with *Eudolatites maiderensis* Destombes, 1972, and *E. inflatus* Destombes, 1972. because of the same character (equal pleural/interpleural length) plus the presence of a highly inflated and broad pygidial rim (Destombes, 1972, pl. 2, fig. 6, pl. 3, fig. 6). In addition, *Eudolatites* (*Eudolatites*) sp. described by Destombes (1972, p. 43, 44, pl. 5, figs. 1–7) from the Lower Ktaoua Formation in Morocco and considered potentially conspecific with Bofloss specimens by Fortey and Edgecombe (2017), differs in having bigger (exsag.) eyes, fewer pygidial rings and pleural/interpleural furrows, rounded posterior pygidial margin, and, hypothetically, pointed genal angles.

The only previous occurrence of *Eudolatites* from Morocco that can be conspecific with Bofloss specimens is *Eudolatites bondoni* Destombes, 1972, which shares the same short and anteriorly located eyes (Destombes, 1972, pl. 4, fig. 1), but no pygidium is known. Given current knowledge of the genus *Eudolatites*, it is known that the pygidium is more diagnostic and has greater morphological variability than the cephalon. Until pygidia are documented in the type locality of *E. bondoni*, it is a risk to assign any other material to this species.

Therefore, to justify our assignment to *Eudolatites* cf. *E. bondoni*, it is important to clarify the relationships with species that have been defined in the Czech Republic. Šnajdr (1987) briefly defined three new species of *Eudolatites*. He erected *E.* (*Destombesites*) *promura* from the Letná Formation, but did not differentiate it from the coeval *E. hastatus* because he did not include that species in his new subgenus *Destombesites* (to embrace species whose pygidia do not bear a posterior border). As explained in the remarks of the genus, and discussed by Hammann and Leone (2007), the pygidial border is strongly affected by compaction and preservation, and there is no difference between the holotype of *E. promura*, figured by Šnajdr (1987, pl. 1, fig. 1), and that of *E. hastatus*, figured by Přibyl and Vaněk (1972, pl. 5, fig. 5). The cephala are not known or, at least, have never been figured. Therefore, *E. promura* is possibly a junior synonym of *E. hastatus*, sharing not only the same morphology, number, and configuration of pleural and interpleural furrows, but also the slightly pointed posterior pygidial margin, observed in the holotype of *E. promura* and described for *E. hastatus* by Přibyl and Vaněk (1972, p. 19).

What characterizes most of the Letná Formation specimens (whether one or two species) is the configuration of pleural/interpleural furrows, being almost the same length (with interpleural furrows slightly longer anteriorly and curving backwards in their abaxial ends; see Destombes, 1972, pl. 3, fig. 2). The Bofloss specimens clearly differ in this character and since both are preserved in full relief, it is possible to verify that the pygidial profile is very different (*E. hastatus* does not have vertically truncated margins, but instead has a convex, inflated border). In the same work, Šnajdr (1987) also erected *E. galafrea*, but did not differentiate it from the coeval *E. angelini*. Later, Vaněk and Vokáč (1997) tried to differentiate both, finding most of the putative differences on the cephalon, although no well-preserved cephala of *E. galafrea* is figured. The differences listed by Vaněk and Vokáč (1997, p. 38) to differentiate *E. galafrea* from *E. angelini* are seen among different specimens occurring in the same locality, thus, they are possibly not reliable, because (1) frontal lobe "highness" is preservational; (2) the presence/deepness of the frontal lobe median pit is highly dependent on preservation; (3) there is no difference between the distance of the posterior extremities of the eyes to the axial furrows in cranidia attributed to *E. galafrea* or to *E. angelini* (compare Vaněk and Vokáč, 1997, pl. 7, figs. 3, 4, with Struve, 1958, pl. 2, fig. 12) and the anterior eye contact with the axial furrows is exactly the same, with differences probably due to deformation (compare the anterior position of the ocular lobe on the right and on the left of the *E. angelini* cephalon figured by Vaněk and Vokáč, 1997, pl. 6, fig. 8); (4) no free cheek of *E. galafrea* is shown by Vaněk and Vokáč, 1997 (pl. 7, fig. 3, 4) and this feature will depend on the size of the eye (variable within the same population) and on deformation (just as the position of the anterior part of the eye in relation to the axial furrow); (5) the genal angle is often deformed/incomplete and it is comparable in figured cephala of *E. angelini* and *E. galafrea* (compare Vaněk and Vokáč, 1997, pl. 6, fig. 8 and pl. 7, fig. 3); (6) the pygidial "inflated" rim depends on preservation, and the pygidial margin is entirely comparable in both specimens (compare Vaněk and Vokáč, 1997, pl. 10, fig. 7 with Přibyl and Vaněk, 1972, p. 19, pl. 5, fig. 4); (7) the pygidial rachis bear the same number of rings (about 15); (8) the path and relationship between the pleural and interpleural furrows are the same in both "species"; and (9) since the relation between the articulating or inter-ring furrow and the pleural and interpleural furrows of at least half of the pygidial axis is clear, it is very doubtful that *E. galafrea* has five ribs fewer than *E. angelini*, although according to Vaněk and Vokáč (1997) the former has more axial rings than the latter. All figured *E. galafrea* pygidia are incomplete (Šnajdr, 1987; Vaněk and Vokáč, 1997), so we cannot calculate the total number of pygidial furrows, and among specimens documented as belonging to *E. angelini* (e.g., Vaněk and Vokáč, 1997, pl. 7, fig. 2) there are pygidia with the same number of ribs as described by these authors for *E. galafrea*.

Although it is not implausible that there may be more than one species of *Eudolatites* per lithostratigraphic unit in the Czech Republic, so far, the arguments and documentation presented are neither convincing nor reliable. As far as it is possible to ascertain, *E. galafrea* seems to be a junior synonym of *E. angelini*. In any case, specimens from the Bohdalec Formation have a higher number of pygidial axial rings and pleural/interpleural furrows than the specimens from Bofloss. Previously, Fortey and Edgecombe (2017) assigned Bofloss specimens, in open nomenclature, to *E. galafrea*, but admitted major doubts given the need for revision of several species. Nevertheless, the *E. galafrea* holotype, a pygidium with a well-preserved posterior border (Šnajdr, 1987, pl. 1, fig. 2), has no evidence of the medial pygidial point characteristic of the Moroccan specimens. Only a few specimens assigned to *E. angelini* show a very subtle angulate margin (e.g., Barrande, 1952, pl. 23, fig. 21; Přibyl and Vaněk, 1972, pl. 5, fig. 3), but clearly bearing a higher number of pleural/interpleural furrows (12 pairs instead of only 8–9).

Šnajdr (1987) also erected the species *Eudolatites karmina* in the Zahořany Formation of the Czech Republic, considering it to be closely related to *E. inflatus* from Morocco. Although he listed several differences, they are not relevant within the genus because they are all related to preservation (e.g., S3 outline, vaulting of the cephalic border, pitting of the genal field, granulose sculpture), and he did not figure any cephalon. As far as can be observed in the existing figures of *E. karmina*, it is probably a junior synonym of *E. inflatus*.

Finally, there are *E. sumptuosus* and *E. dubius* from the Vinice and Zahořany formations, respectively. When defining *E. sumptuosus*, Přibyl and Vaněk (1972) did not differentiate it from *E. dubius*. Later, Šnajdr (1990, p. 240–241) figured the *E. sumptuosus* holotype as belonging to *E. dubius*, thus, as stated by Hammann and Leone (2007), we assume he considered both to be synonyms. They probably are, but there are not enough published records of specimens from the Zahořany Formation and the Vinice Formation to allow a decision. As far as we can tell, *E. dubius* is quite similar to the Bofloss specimens, and at first analysis we attributed them, in open nomenclature, to the Czech species (Pereira et al., 2020) because they share an equivalent number of pygidial axial rings and pleural/interpleural furrows, with a similar configuration, and, according to Přibyl and Vaněk's (1972, p. 18–19) description for *E. sumptuosus*, the pygidial rachis extends to the pygidial margin, as in Bofloss specimens. However, an important and very characteristic feature of the Moroccan material, which should have significance within the genus since there are species with rounded edges and others with angulate-shaped ones, is the permanent presence of a medial pointed termination of the pygidium. Although remnants of a tendency to develop this tip are present (e.g., in *E. hastatus* of the Letná Formation), and an angular border is present in *E. maiderensis* from the Upper Ktaoua Formation, no known species presents a comparable spine-like margin like the Bofloss specimens. This differentiates the Moroccan material from *E. dubius*, a species that not only has the most subcircular edge, but even flattens out in the medial zone (see Barrande, 1852, pl. 26, fig. 40, and Přibyl and Vaněk, 1972, pl. 4, fig. 1). On the other hand, and although this character is variable and very few specimens of *E. dubius* are known, some have extremely big eyes, their posterior ends reaching S1, a condition never observed in Bofloss specimens.

Finally, the Bofloss specimens are different from the Iberian species *E. flavus*, from the Bancos Mixtos Formation in Spain, the latter having genal spines, a rounded pygidial margin, and pleural/interpleural furrows of same length, converging posteriorly. In addition, a new *Eudolatites* species described in an unpublished PhD thesis by Pereira (2017) in the Cabeço do Peão Formation of Portugal also has a rounded pygidial margin and pleural/interpleural furrows of same length.

In view of the impossibility of a confident assignment of our specimens to defined *Eudolatites* species but wanting as far as possible to avoid erection of new species that might prove to be synonyms later and increase the taxonomic chaos, we decided to identify our material in open nomenclature as *Eudolatites* cf. *E. bondoni*. As previously discussed, only cephala are known, but the cephala agree with our material in all the characters, including the quite small and anterior position of the eyes. This species also occurs in the same geological area of Morocco and, putatively, in coeval levels ("Caradocien moyen–supérieur" sensu Destombes, 1972). It will be necessary to describe pygidia from the type locality of *E. bondoni* to verify if they agree with the morphology of the Bofloss specimens: if so, one can refine the nomenclature and much better characterize the species of Destombes (1972). If not, the Bofloss specimens should be formalized as a new species.

Suborder Calymenina Swinnerton, 1915
Family Pharostomatidae Hupé, 1953
Genus *Prionocheilus* Rouault, 1847
(= *Pharostoma* Hawle and Corda, 1847)

Type species.—*Prionocheilus verneuili* Rouault, 1847, from the Riadan Formation, middle Berounian (ca. upper Sandbian/lower Katian), Armorican Massif, France.

Other species.—See Pereira (2017, p. 453).

Diagnosis.—See Whittard (1960, p. 132).

Occurrence.—Ordovician (Floian–Hirnantian) of Portugal, Spain, France, Italy (Sardinia), Czech Republic, Morocco, Turkey, Sweden, Norway, Estonia, United Kingdom, Uzbekistan, Kazakhstan, China, USA, Canada, and Argentina.

Remarks.—Hammann (1992, p. 94–95) and Hammann and Leone (2007 p. 128–133) made extended remarks on *Prionocheilus* occurrences, to which we refer.

Prionocheilus cf. *P. verneuili* Rouault, 1847
Figure 4.7

1847 cf. *Prionocheilus verneuili* Rouault, p. 320–321, pl. 3, figs. 3, 3a.
?1966 *Prionocheilus pulcher*; Destombes, p. 39–40, pl. 4, figs. 1–6.

Materials.—One incomplete cephalon with thorax (MGM-7703X).

Remarks.—One single incomplete cephalon with thorax (Fig. 4.7) is too poorly preserved to allow a specific identification. Although the glabellar lobation and the external surface sculpture are comparable to those of the species-group from the Upper Ordovician of the high-latitude peri-Gondwanan domain—*P. borni* Vaněk, 1995, from the Bohdalec Formation (upper Berounian) of the Czech Republic, *P. pulcher* (Barrande, 1846) from the Zahořany Formation (middle Berounian) of the Czech Republic, and the type species *P. verneuili* from the Riadan Formation (middle Berounian) of France—it is too poorly preserved for further discussion. For this reason, we also base the discussion and identification of *Prionocheilus* cf. *P. verneuili* on two additional specimens from the same locality that were observed during this work. The presence of six pygidial pleural ribs (instead of seven) excludes *P. borni* and relates the Moroccan occurrences to *P. verneuili* and *P. pulcher*. These species are differentiated by an apparently longer (sag.) preglabellar area in the former, although this character is highly dependent on preservation. The figured specimen does not preserve the preglabellar area, but the remaining observed ones are comparable with those documented by Destombes (1966, p. 39–40, pl. 4, figs. 1–6) from the Upper Tiouririne Formation (upper Berounian, ca. lower Katian, Ka2) of Morocco. Although he assigned these occurrences to *P. pulcher*, he noted that the preglabellar field of the Moroccan specimens is larger (in relation to the anterior border) than in the Czech specimens. For this reason, the Moroccan specimens are here considered to be more closely related to *P. verneuili*, but additional specimens are necessary to strengthen this identification.

Order Asaphida Salter, 1864
Superfamily Asaphoidea Burmeister, 1843
Family Asaphidae Burmeister, 1843
Subfamily Birmanitinae Kobayashi, 1960
Genus *Nobiliasaphus* Přibyl and Vaněk, 1965
(= ?*Ogygites* Tromelin and Lebesconte, 1876; = *Pamirotchechites* Balashova, 1968)

Type species.—*Asaphus nobilis* Barrande, 1846, from the Zahořany Formation, middle Berounian (ca. upper Sandbian–lower Katian, Sa2–Ka1), Czech Republic.

Other species.—See Gutiérrez-Marco et al. (2022b, p. 122).

Diagnosis.—See Hughes (1979, p. 117).

Occurrence.—Occurrence. Middle to Upper Ordovician (Darriwilian to upper Katian) of Portugal, Spain, France, Czech Republic, Morocco, Italy (Sardinia), Turkey, Wales, ? Belgium, Germany, Tajikistan, Afghanistan, and ?Syria.

Remarks.—We follow Fortey et al. (2022, p. 317), who considered that Nobiliasaphinae Balashova, 1971, falls within the Birmanitinae, which is the oldest available name for this asaphid group. Fortey et al. (2022, p. 318) also considered that *Ogygites* Tromelin and Lebesconte, 1876, is the senior synonym of *Nobiliasaphus*, but this is one of those cases that we consider should not follow the rule of nomenclatural priority for reasons of taxonomic stability because *Nobiliasaphus* is has been a very firm and well-documented name in the trilobite nomenclature and bibliography for decades. As was discussed by Rábano (1989), the type species of *Ogygites*, *O. desmaresti* (Brongniart, 1822), is based on an unrecognizable fragment and the species should be restricted to its holotype by monotypy (Rábano, 1989, fig. 9). *Ogygites* originally was proposed as a replacement name for *Ogygia* Brongniart in Desmarest, 1817, a name that was pre-occupied by a lepidopteran. Its original first-named species, "*Ogygia*" *guettardi* Brongniart in Desmarest, 1817 (Brongniart, 1822), clearly shows the characters of *Nobiliasaphus*. Nevertheless, the subsequent designation of *O. desmaresti* as the type species of *Ogygites* (Œhlert, 1903; ICZN, 1983) highlighted the problematic concept of this genus as well, and strongly supports that *Nobiliasaphus* should be considered a nomen protectum.

Nobiliasaphus cf. *N. kumatox* Šnajdr, 1982
Figure 4.8, 4.9

cf. 1982a *Nobiliasaphus kumatox* Šnajdr, p. 229, pl. 1, fig. 5.
cf. 1997 *Nobiliasaphus kumatox*; Vaněk and Vokáč, p. 26–27, pl. 1, figs. 13, 14 (and the synonymy therein).

Materials.—One pygidium (field photograph, Fig. 4.8, 4.9; specimen not collected).

Remarks.—A single pygidium was observed and photographed in the field, but not collected given its large dimensions and weight issues (about 20 cm long, sag.; Fig. 4.8, 4.9). Several species of *Nobiliasaphus* have been proposed and differentiated on the basis of ornamental details, whose taxonomic value is unknown (Hammann and Leone, 1997, p. 53). Nevertheless, we used ornamental details for species-level taxonomy of the genus. The single studied pygidium is complete enough and very well preserved so that it is possible to assign the specimen to *Nobiliasaphus kumatox*, from the Bohdalec Formation of the Czech Republic. We opted for open nomenclature because only one incomplete pygidium is available, thus several other characters relevant for species identification, such as the exact number of pygidial axial rings and pleural ribs and all the cephalic features (e.g., size of the eyes), within the genus were not possible to ascertain. The Moroccan pygidium shows the same pattern of axial transverse ridges and 3–4 diagonal ridges on the axial rings (compare Fig. 4.9 and Vaněk and Vokáč, 1997, pl. 1, fig. 14), distinct interpleural furrows, and, as far as is possible to ascertain, a comparable number of axial rings and pleural furrows.

It is important to point out that *N. kumatox* from the Czech Republic also reaches abnormally large dimensions (Vaněk and Vokáč, 1997, p. 26), although unusually large size has no systematic value per se.

Superfamily Cyclopygoidea Raymond, 1925
Family Cyclopygidae Raymond, 1925
Subfamily Cyclopyginae Raymond, 1925
Genus *Cyclopyge* Hawle and Corda, 1847

Type species.—*Egle rediviva* Barrande, 1846, from the Vinice Formation, middle Berounian, in Trubín, Beroun, Czech Republic.

Remarks.—Hammann and Leone (1997, p. 73–76) widely discussed the current state of knowledge of the genus *Cyclopyge* at that time. As noted by these authors and discussed previously by Zhou et al. (1994), many Middle and Upper Ordovician species defined for *Cyclopyge* may be synonyms. We totally avoid differentiation based on pygidial and cranidial outline, expressed as length/width ratio. As Hammann and Leone (1997, p. 72) stated, it is "… conspicuous fact that in many places several species comprising both glabellar types are described as coexisting in the same bed." Other characters, especially those related to sculpture details or faint furrows/elevations, are very sensitive to deformation or type of preservation and should be avoided for differentiation of species as well. Cyclopygids are very conservative (Fortey and Owens, 1987; Adrain et al., 2004), so it would not be expected for these types of general characters to change reliably at a species level. Differentiating species based solely on different locations/lithostratigraphic units may create a sense of organizational comfort, but it serves no systematic purposes. Ontogeny, on the other hand, may play a relevant role in these characters and even among holaspides, because size can justify slight differences, as demonstrated by Tripp et al. (1989) for *Cyclopyge* occurrences from the Tangtou Formation (China), which led them to conclude that only one extremely variable species was present.

We reject Hammann and Leone's (1997) revival of *Phylacops* Cooper and Kindle, 1936, as a subgenus of *Cyclopyge* to embrace species with frontally fused eyes. As Karim (2009) noted, there is no phylogenetic understanding of the nature of anteriorly fused eyes (synophtalmy sensu Marek, 1961) among cyclopygids and this character is unknown for many of the species. Thus, the supposition that eyes changed from separated to fused through time (e.g., Marek, 1961; Hammann and Leone, 1997), and that this trend has phylogenetic significance, is not possible to verify. Furthermore, it is likely that ontogeny, already in holaspid stages, implies variation in the completeness of optical organs for the same species (see for instance the variation in *Cyclopyge recurva* Lu, 1962, figured by Zhou et al., 2016, pl. 40, figs. 4, 6, pl. 41, fig. 4, and see remarks on *Cyclopyge* cf. *C. rediviva* below). The best way to overcome these difficulties is to have a very large number of co-occurring specimens (not always possible) and start from the assumption that only one single species of the same genus is represented in the same levels/localities (see discussion about *Cyclopyge* species from Kazakhstan in Hammann and Leone, 1997, p. 72). Frequently, even when having several specimens, only a few show the anterior configuration of the eyes. It is therefore difficult to know whether this character is fixed for all adult individuals, or if it has a larger range of morphological variability, as shown by Zhou et al. (2016) for *Cyclopyge recurva* from the Pagoda Formation (China).

Cyclopyge cf. *C. rediviva* (Barrande, 1846)
Figures 6, 7

cf. 1846	*Egle rediviva* Barrande, p. 34.
cf. 1961	*Cyclopyge rediviva* (Barrande); Marek, p. 19–21, pl. 1, figs. 1–6, text-fig. 4.
2017	*Cyclopyge sibilla* Šnajdr; Fortey and Edgecombe, p. 316, 318, fig. 3A–H.
2018	*Degamella sandinoae* Corbacho [sic]; Lebrun, p. 137, fig. C.
2023	*Cyclopyge sibilla* Šnajdr; Schoenemann and Clarkson, figs. i–p.

Addenda to description.—Fortey and Edgecombe (2017, p. 316) described in good detail specimens from the same beds, so we will only add additional morphological details, given the varied, complete, and well-preserved material available to us. Among holaspides, there is a tendency for the cranidium to become progressively more pointed anteriorly. This also led to an increase in the cranidial length/width ratio, which varies from ∼105–110% in smaller holaspides and up to 120% in larger ones. In anterior view, the cranidium is rhomboid-shaped, extremely convex (sag.), and surrounded by the eyes, also very convex (laterally) and vertically positioned. The extreme anterior elongation of the cranidium separates the eyes, so in larger specimens the eyes seem prevented from meeting medially. In anterior–ventral view, the eyes meet medially to form an optical surface with an infinity symbol outline. The completeness of the fusion of the eyes is variable and hard to evaluate: in full-relief specimens, the coarser-grain preservation makes it difficult to see the medial edge of the eyes (e.g., Fig. 7.6. 7.7, 7.10); in the flattened specimens preserved in mudstones, it is not clear if the eyes are conjoined medially or not, if there are missing lenses due to exfoliation, of if they just meet but are not conjoined (e.g., Fig. 6.2). Thus, it seems that in some specimens they barely touch each other, which makes it possible to differentiate the right and the left eye and a very narrow depressed band (groove) between them. Other specimens do seem to have fused eyes, with very few lenses shared (2–3 lenses at the median suture). There are ∼55 gently arched vertical rows of lenses, bearing a maximum of 27 lenses in the middle (widest) part of the eye. The lenses become larger towards the upper part of the eye (Fig. 6.6). Doublure subtriangular, developing a small medial depression at the contact with the eye, its posterior margin (ventrally) is subtransverse, embayed medially (median depression). The pygidium bears a very weak and narrow sagittal ridge, rarely visible, which starts at the posterior end of the pygidial axis, disrupting the axial furrow, and ends at the posterior margin (Figs. 6.2, 7.2, 7.11).

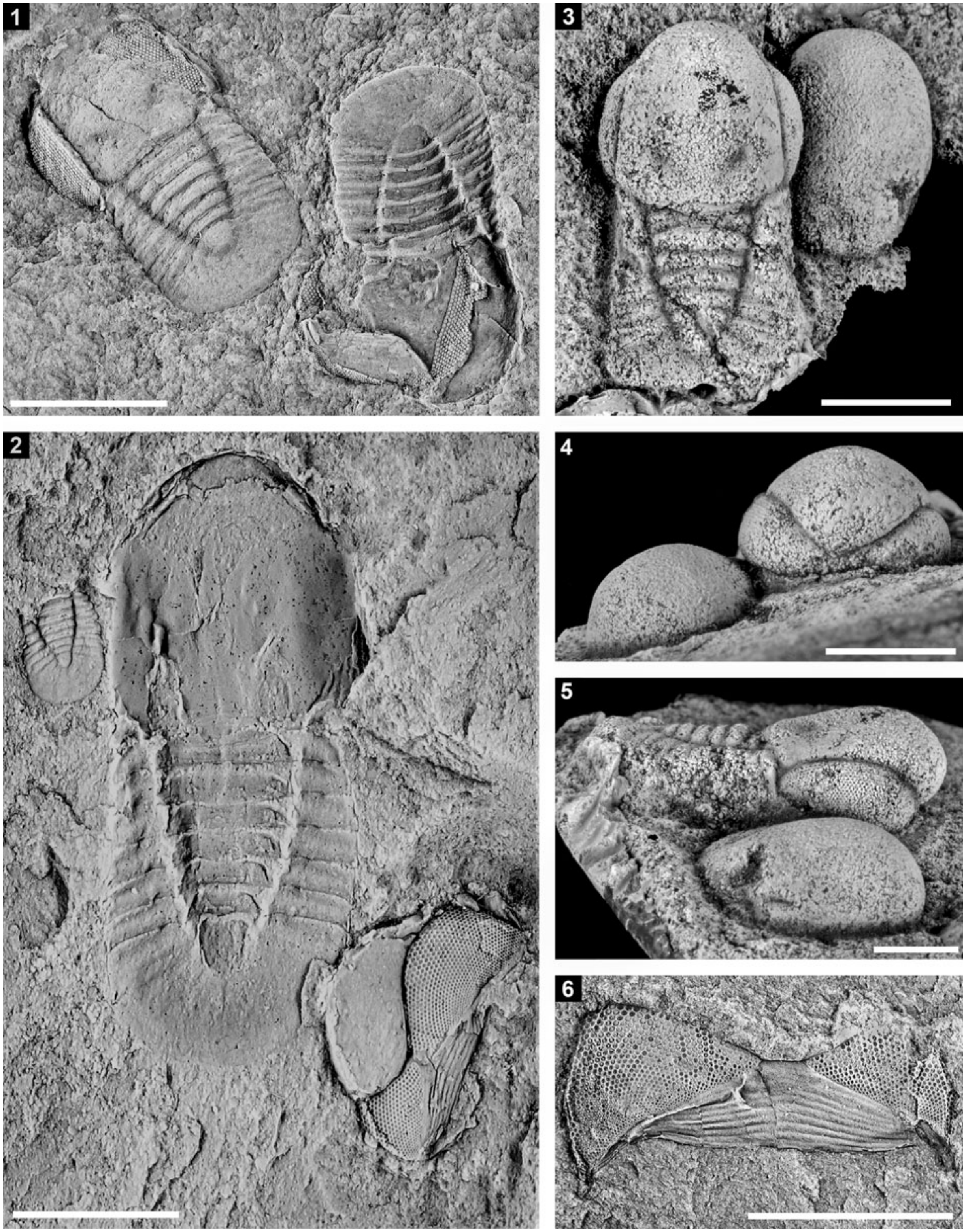

Figure 6. (**1–6**) *Cyclopyge* cf. *C. rediviva* (Barrande, 1846) from the Bofloss locality, Morocco. (**1**) Two exoskeletons, latex cast of internal (MGM-7704X-1a, left) and external (MGM-7704X-2a, right) molds: dorsal view, showing traces of the visual surfaces; (**2**) exoskeleton (center), meraspis thorax with pygidium (upper left) and cephalon (lower right), internal and external molds, MGM-7705X-1, MGM-7705X-3, and MGM-7705X-2, respectively: dorsal and anterior views; (**3–5**) exoskeleton, internal mold, MGM-7706X: (**3**) dorsal view; (**4**) anterior view; (**5**) right lateral view; (**6**) visual surface and cephalic doublure, latex cast of the external mold, MGM-7707Xa: anteroventral view. Specimens (**3–5**) are preserved in full relief (sandstones); the remaining specimens are preserved in mudstones, flattened. Scale bars = 5 mm.

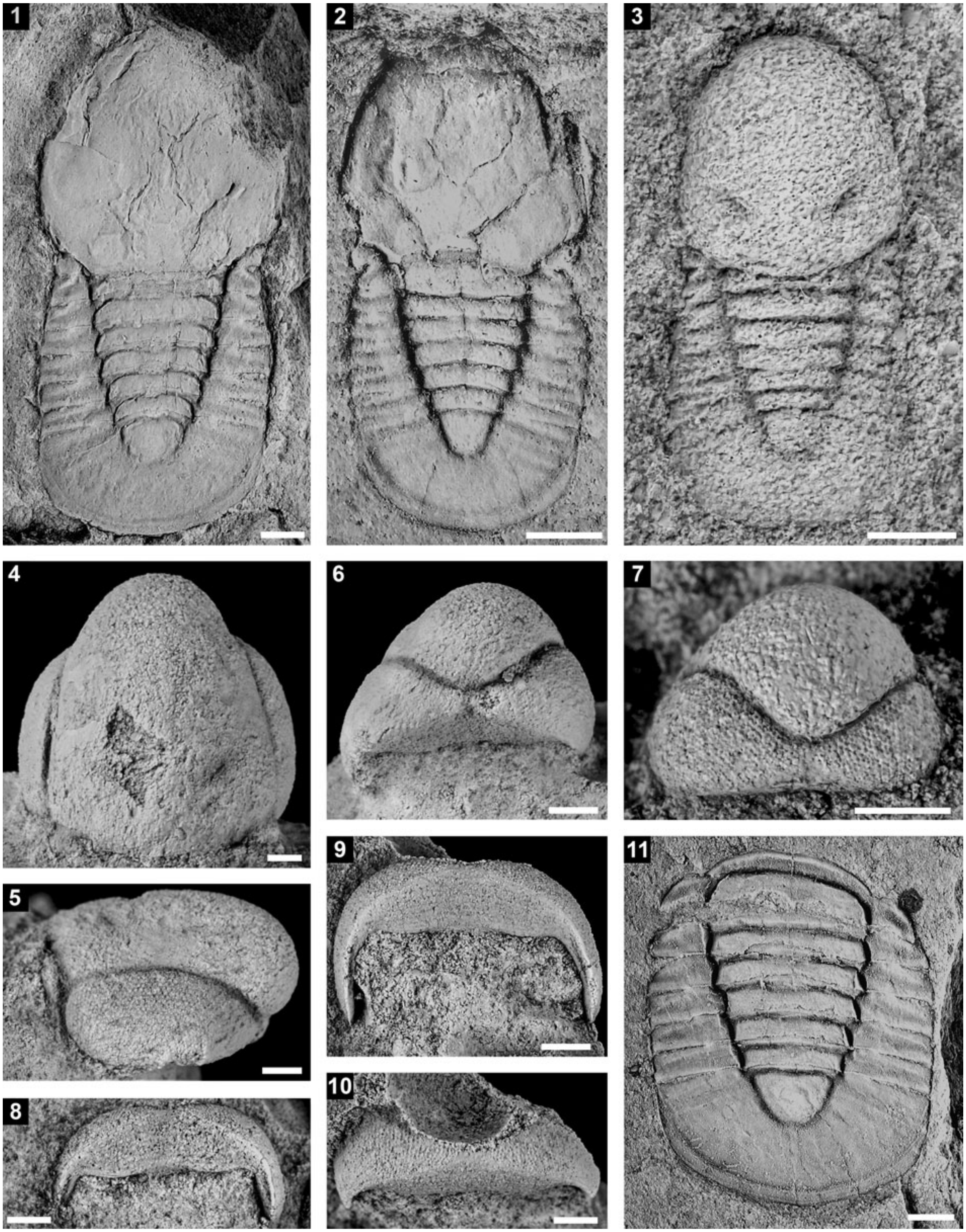

Figure 7. (**1–11**) *Cyclopyge* cf. *C. rediviva* (Barrande, 1846) from the Bofloss locality, Morocco. (**1**) Exoskeleton, internal mold, MGM-7708X: dorsal view; (**2**) exoskeleton, internal mold, MGM-7709X: dorsal view; (**3**) exoskeleton, latex cast of the external mold, MGM-7710Xa: dorsal view; (**4–6**) cephalon, internal mold, MGM-7711X: (**4**) dorsal view; (**5**) right lateral view; (**6**) anterior view; (**7**) cephalon, internal mold, MGM-7712X-1: anterior view; (**8**) visual surface and cephalic doublure, internal mold, MGM-7712X-2: anteroventral view; (**9, 10**) visual surface and cephalic doublure, internal mold, MGM-7713X: (**9**) anteroventral view; (**10**) anterior view; (**11**) thorax with pygidium, internal mold, MGM-7714X: dorsal view. Specimens (**1–2**) and (**11**) are preserved in mudstones, flattened; the remaining are preserved in full relief (sandstones). Scale bars = 2 mm.

Materials.—Eighteen almost complete exoskeletons (MGM-7671X-3; MGM-7704X-1, 7704X-2; MGM-7705X-1; MGM-7706X; MGM-7708X to MGM-7710Xa, b; MGM-7717Xa, b to MGM-7724X; MGM-7725X-1a, b), one of them probably enrolled but flattened (MGM-7730X); two cephalons with thorax (MGM-7712X-3; MGM-7716Xa–b); three cephala (MGM-7705X-3; MGM-7711X; MGM-7712X-1); eight cranidia (MGM-7672X; MGM-7725X-2; MGM-7725X-3; MGM-7726X-1; MGM-7726X-3; MGM-7727X; MGM-7728X-1; MGM-7728X-2); five isolated visual surface +doublure (MGM-7707Xa–b; MGM-7712X-2; MGM-7713X; MGM-7728X-3; MGM-7141X); three thorax with pygidium (MGM-7714X, MGM-7715X; MGM-7726X); one transitory thorax with pygidium (MGM-7705X-2); three pygidia (MGM-7712X-4; MGM-7729X-1; MGM-7729X-2).

Remarks.—The Moroccan material agrees with the description of Barrande (1852) and Marek (1961) for *Cyclopyge rediviva* from the Vinice Formation of the Czech Republic. Fortey and Edgecombe (2017) assigned these Moroccan occurrences to *Cyclopyge sibilla* Šnajdr, 1982a, a species defined in the Bohdalec Formation of the Czech Republic. As previously noted by Hammann and Leone (1997) and Fortey and Edgecombe (2017), this species was erected by Šnajdr (1982a) solely based on a non-diagnostic transitory pygidium, following the dangerous assumption that specimens from a distinct lithostratigraphic unit will potentially be different species. Later, Vaněk and Vokáč (1997) described holaspid specimens from the Bohdalec Formation and proposed a differentiation between *C. sibilla* and *C. rediviva* based on the absence of very fine terrace lines and a post-axial ridge in the pygidium of the former, the Bohdalec Formation form. For all the remaining characters, they largely copied Marek's (1961, p. 19–21) description of *C. rediviva* (Vaněk and Vokáč, 1997, p. 27). As demonstrated for the material studied here, and as is clear from various studies on *Cyclopyge* (e.g., Zhou et al., 1994; Hammann and Leone, 1997), these features strongly depend on preservation and, indeed, the diagnostic characters of *C. sibilla* also are observed in many specimens of *C. rediviva* from the Vinice Formation, including the holotype, which preserves neither the terrace lines nor the pygidial ridge (Horný and Bastl, 1970, pl. 7, fig. 3). Furthermore, two "*C. sibilla*" specimens, a holaspid and a meraspid pygidium figured by Vaněk and Vokáč (1997, pl. 2, figs. 1, 7), bear the pygidial postaxial ridge. Other specimens (Vaněk and Vokáč, 1997, pl. 2, figs. 6, 8) also show the second pair of pygidial ribs, a very characteristic feature of *C. rediviva* described by Marek (1961). Therefore, we consider *C. sibilla* a junior synonym of *C. rediviva*.

One of the major difficulties related to *C. rediviva* is that, despite the existence of abundant specimens from the Vinice Formation, the species is not properly documented. The description presented by Marek (1961) is insufficient for some details, particularly regarding the eye configuration. Marek (1961) indicated that the eyes are not conjoined medially, their anterior ends at a distance of one-third of the total cephalic width from each other. This large distance is highly unlikely. Knowing that even in very well-preserved material it is difficult to observe the contact between the eyes, which occurs ventrally, it is very difficult to know the true morphology of the optical organ of *Cyclopyge rediviva* from its type unit, the Vinice Formation. There is no figured specimen showing the anterior–ventral cephalic view. For this reason, the Bofloss specimens, even if so well preserved and known in detail, have to be left in open nomenclature until the optical organ of *C. rediviva* from the Vinice Formation is properly documented and it is demonstrated to have the same morphology and variability as shown here for the Moroccan specimens.

We agree with Fortey and Edgecombe (2017) that Moroccan specimens may be conspecific with *Cyclopyge* cf. *C. recurva* described by Zhou et al. (1994) from Tarim, China. Both share the same diagnostic characters and differ from *C. recurva* from the Pagoda Formation of China (see Zhou et al., 2016) in having a significantly shorter pygidial axis. This short pygidial axis is very diagnostic within *Cyclopyge*, being a confident character to differentiate *C. rediviva* from several other species, such as the slightly younger *C. marginata* Hawle and Corda, 1847, from the Czech Republic (also described by Hammann and Leone, 1997, in Sardinia). As noted by Fortey and Edgecombe (2017), among the several *Cyclopyge* species defined by Koroleva (1967) in Kazakhstan (see Hammann and Leone, 1997, p. 72–75), there may be synonyms of "*C. sibilla*"/*C. rediviva*, but the latter will always take priority.

Recently, these Moroccan occurrences have come to prominence because Schoenemann and Clarkson (2023) have documented possible median eyes in meraspides, which previously were unknown in trilobites but present in all other arthropods.

Genus *Symphysops* Raymond, 1925

Type species.—*Aeglina armata* Barrande, 1852, from the Králův Dvůr Formation, Kralodvorian (ca. upper Katian, Ka3–4), Czech Republic.

Diagnosis.—See Marek (1961, p. 54).

Remarks.—Except for the older species, *Symphysops mitratus* (Novák, 1883) and *Symphysops sulcatus* (Barrande, 1872), which are known from the Middle Ordovician of the Czech Republic, there is much doubt as to the validity of the various forms described in the upper Katian (see Hammann and Leone, 1997, p. 80, 84–85; Owen and Bruton, 2012, p. 979). This is another of the genera of trilobites that became widespread during the late Katian, which previously seems to have originated and lived in an area that was limited to the peri-Gondwanan realm (see Colmenar et al., 2017, p. 452). *Symphysops* records prior to the late Katian from other than the Czech Republic (and now, Morocco) are doubtful, although some possibly are assignable to the closely related genus *Pricyclopyge* Richter and Richter, 1954 (e.g., Zhou et al., 2016, p. 197, pl. 50, fig. 19). Unfortunately, in the Czech Republic there is a major gap between the oldest records, from the middle–upper Darriwilian Šárka Formation, and those from the upper Katian Králův Dvůr Formation. The genus was reported by Vaněk (1995, pl. 2, fig. 1) in the Dobrotivá Formation (Dobrotivian, upper Darriwilian) as the species *S. psyche* Vaněk, 1995, for which, as far as it is possible to observe, not only is the figured pygidium unobservable and undiagnostic, but it also is doubtful if it could correspond to *Pricyclopyge longicephala* (Klouček, 1916), which is known from the same unit. In the Berounian (Sandbian–lower Katian) the genus was not known before, so the Moroccan record is important for understanding the early history of *Symphysops*.

Symphysops stevaninae López-Soriano and Corbacho, 2012
Figures 8, 9.1–9.4

2012 *Symphysops stevaninae* López-Soriano and Corbacho, p. 2–4, pl. 1, figs. 1–3, pl. 2, figs. 1–6.
2010 *Symphysops* sp. Bonino and Kier, p. 102, figs. b, c.
2018 *Symphysops stevaninae* López-Soriano and Corbacho; Lebrun, p. 137, figs. A–C.

Holotype.—López-Soriano and Corbacho (2012) selected two holotypes, which is contrary to the ICZN recommendation. Here we designate as the lectotype the cephalon, an internal mold (López-Soriano and Corbacho, 2012, pl. 2, fig. 5) housed in the Back to the Past Museum (Cancún, México) with the registration number BPM1029.

Diagnosis.—Smooth glabella, with almost indistinct glabellar impressions; eyes conjoined, with about 17 lenses medially. Pygidial axis with one ring and a subtriangular terminal piece.

Materials.—Two almost complete exoskeletons (MGM-7731X; MGM-7732X); four cranidia (MGM-7733X to MGM-7736X); two visual surfaces+doublure (MGM-7737X; MGM-7738X); one cephalon with thorax (MGM-7739X); one thorax with pygidium (MGM-7691X); two pygidia (MGM-7674X-2; MGM-7740X).

Remarks.—These Moroccan *Symphysops* occurrences were previously considered to represent a new species, *S. stevaninae*, by López-Soriano and Corbacho (2012). Most of the differences pointed out by the authors are not valid, but after a detailed analysis of available specimens as well as the extensive remarks made by previous authors concerning the widespread occurrences of the genus in the upper Katian (e.g. Kielan, 1960; Marek, 1961; Knüpfer, 1967; Owen and Ingham, 1996; Hammann and Leone, 1997; Shaw, 2000; Owen and Bruton, 2012), we consider that, potentially, the upper Sandbian–lower Katian (Sa2–Ka2) Moroccan specimens represent a distinct species, for which the name *S. stevaninae* must be used. However, if there were not an already established name for these occurrences, it would be equally sensible to assign our material to the type species *S. armatus*, which, as discussed by López-Soriano and Corbacho (2012), may even prove to be the only valid species in the upper Katian, as a senior synonym of several others, such as *S. subarmatus* (Reed, 1914), *S. subarmatus elongatus* Kielan, 1959, or *S. spiniferus* Cooper and Kindle, 1936. Other occurrences (e.g., Kolova, 1936; Apollonov et al., 1980; Vaněk, 1995; Ghobadi Pour et al., 2011) are too poorly known to discuss about such a conservative cyclopygid, and we do not think any of those are conspecific with *S. stevaninae*.

Our collection includes specimens in full relief and flattened, that largely support the views of Hammann and Leone (1997) and Owen and Bruton (2012), who considered the features related to the cranidium outline and vaulting to be highly susceptible to distortion and other preservational effects. In body proportions (cephalon/thorax/pygidium/axis), in cephalic and pygidial outline, in the thorax morphology, including the elongated tip of the first thoracic segment as well as in the location of glabellar furrows and the position of the median tubercle, Moroccan specimens are indistinguishable from the type species *S. armatus* from the Králův Dvůr Formation and from *S. subarmatus*/*S. subarmatus elongatus*/*S. spiniferus* from the upper Katian of Girvan, Scotland (Owen and Ingham, 1996), Poland (Kielan, 1960), or Quebec, Canada (Cooper and Kindle, 1936). The Bofloss specimens have two features that differentiate them: (1) the glabellar furrows/impressions are almost imperceptible, rarely observable even in very well-preserved specimens; and (2) the pygidium has only one single ring defined plus a subtriangular terminal piece. We are aware that these characters depend on taphonomy, to a certain extent, but they do seem stable and consistent, especially the obsolete glabellar furrows. It is very rare to observe the glabellar impressions on Moroccan specimens, especially on full relief material. As Marek (1961) noted, *S. armatus* glabellar furrows are quite distinct, and even in highly deformed material, such as that described by Hammann and Leone (1997, pl. 10, figs. 1, 5, 8) from Sardinia, these are very well incised. The older representatives of *Symphysops* (*S. mitratus* and *S. sulcatus*) also have these furrows, albeit much less incised (Marek, 1961, p. 58), and the closely related genus *Pricyclopyge* also has a smooth glabella, with almost imperceptible impressions, suggest this character to be relevant within the lineage. As noted by Fortey and Owens (1987, p. 180), *Symphysops* has well-developed glabellar muscle impressions compared to *Pricyclopyge*. In this sense, *S. stevaninae*, which is older than the widespread *S. armatus*, may indeed represent a different *Symphysops* species.

López-Soriano and Corbacho (2012) described the pygidial axis segmentation in *S. stevaninae* as bearing one single ring and a triangular terminal piece. Nevertheless, one of the specimens figured by these authors (López-Soriano and Corbacho, 2012, pl. 1, fig. 2) clearly shows two axial rings plus a terminal piece. Whether this character is real or resulted from fossil preparation, we do not know. Among our material, no pygidium preserves any traces of a second axial ring, not even well-preserved external molds. Other specimens of *Symphysops* from Morocco, but whose exact geographical and lithostratigraphic provenance is not known, also show two rings (e.g., Bonino and Kier, 2010, pl. 15, fig. c; Lebrun, 2018, p. 137, figs. A, B). But apart from these specimens, which show mechanical preparation, there are several specimens, including our "raw" materials, with no traces at all of a second ring, not even when delicate features, such as fine terrace ridges, are preserved.

On the other hand, Marek (1961) described three pygidial axial rings plus a terminal piece for *S. armatus*, and although only the first ring is distinctively separated, this pygidial segmentation is quite distinct and observed in all the other upper Katian records of the genus (e.g., Kielan, 1960; Owen and Ingham, 1996). Finally, when comparing the detail of the number of

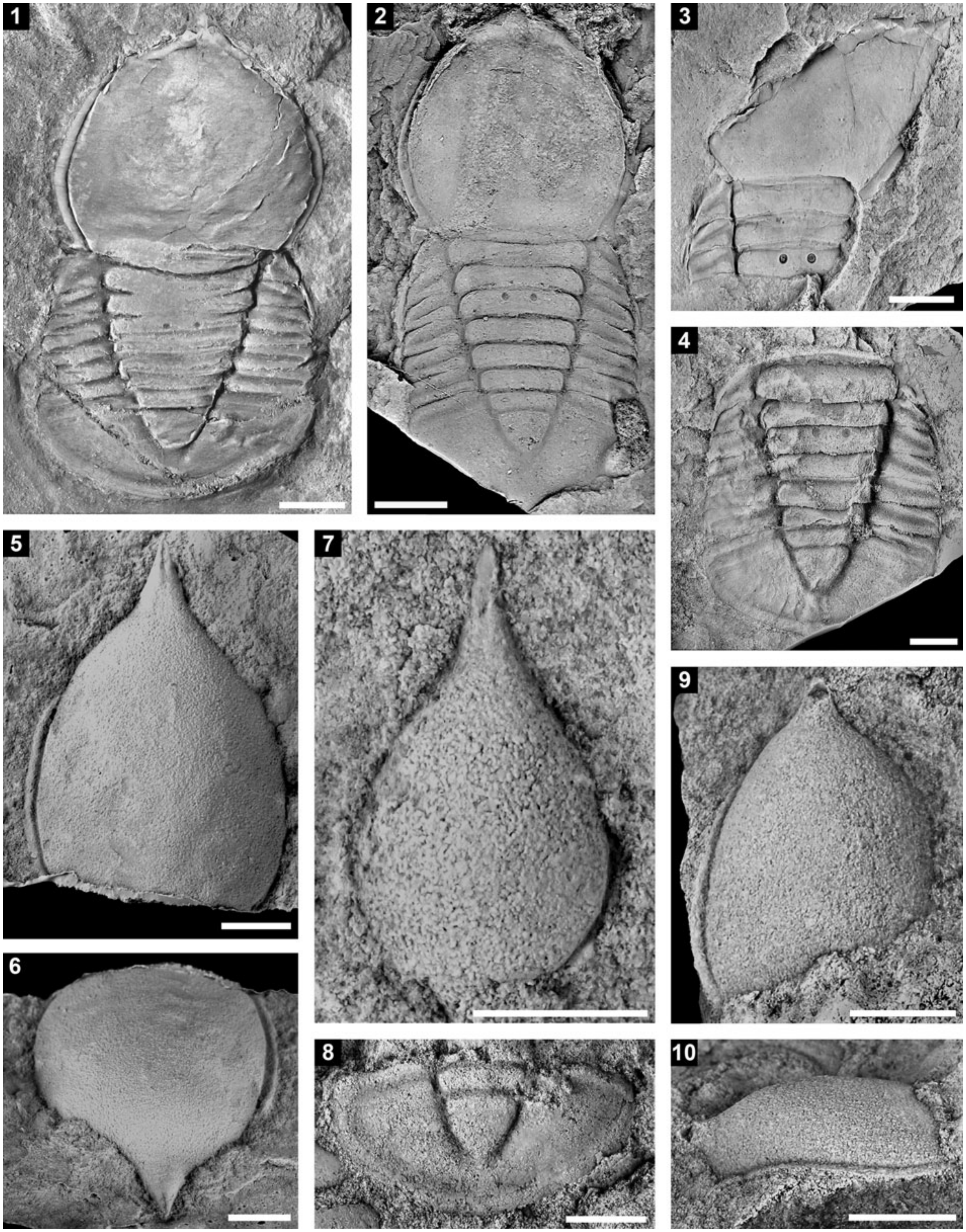

Figure 8. (**1–10**) *Symphysops stevaninae* Lopéz-Soriano and Corbacho, 2012, from the Bofloss locality, Morocco. (**1**) Exoskeleton, internal mold, MGM-7731X: dorsal view; (**2**) exoskeleton, latex cast of the external mold, MGM-7732X: dorsal view; (**3**) incomplete cephalon with thorax, internal mold, MGM-7739X: dorsal view; (**4**) thorax with pygidium, latex cast of the external mold, MGM-7691X: dorsal view; (**5, 6**) cranidium, latex cast of the external mold, MGM-7733X: (**5**) dorsal view; (**6**) anterior view; (**7**) cranidium, internal mold, MGM-7734X: dorsal view, (**8**) pygidium, internal mold, MGM-7740X: dorsal view; (**9, 10**) cranidium, internal mold, MGM-7735X: (**9**) dorsal view; (**10**) left lateral view. Specimens (**1–4**) are preserved in mudstones, flattened; the remaining specimens are preserved in full relief (sandstones). Scale bars = 5 mm.

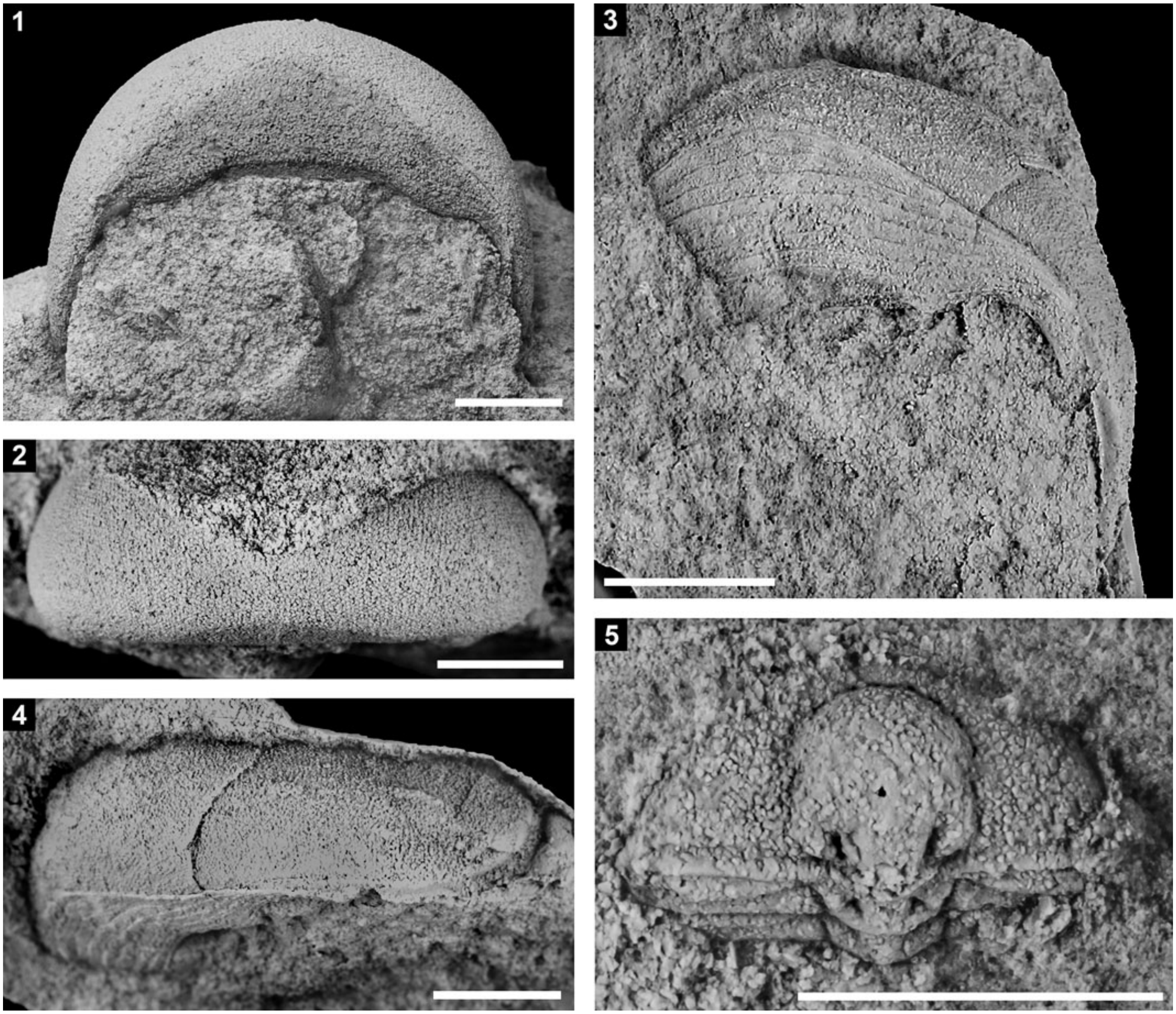

Figure 9. (**1–4**) *Symphysops stevaninae* Lopéz-Soriano and Corbacho, 2012, from the Bofloss locality, Morocco. (**1, 2**) Visual surface and cephalic doublure, internal mold, MGM-7737X: (**1**) ventral view; (**2**) anterior view; (**3, 4**) visual surface and cephalic doublure, latex cast of the external mold, MGM-7738X: (**3**) oblique ventral view; (**4**) oblique left anteroventral view. (**5**) *Dionide* sp. from the Bofloss locality, Morocco. Incomplete cephalon with thorax, internal mold, MGM-7671X-2: dorsal view. All specimens preserved in full relief (sandstones). Scale bars = 5 mm.

lenses in the medial line in Bofloss specimens and, for example, in *S. armatus* from Sardinia (Hammann and Leone, 1997), they both have 17 lenses medially (Fig. 9.2). In *S. armatus* type material, as far as it is possible to count the lenses in the lectotype figured by Marek (1961, pl. 6, fig. 2) and Horný and Bastl (1970, pl. 7, fig. 4), there is also approximately the same number of lenses medially. One specimen from the Upper Ordovician of Morocco, identified as *S. armatus* by Lawrence and Stammers (2014, p. 270), for which the provenance is impossible to identify based on the transliteration of the name (“Kharkhize”), the eyes are not conjoined medially. Whether this represents another, putatively older, *Symphysops* species, or results from poor fossil preparation, is impossible to know. It would not be unlikely, since *Pricyclopyge*, a closely related genus, is characterized by having separate eyes.

To summarize, *S. stevaninae* diagnostic characters are not definite, but considering the knowledge about this particular group of cyclopygids (Pricyclopyginae of Fortey and Owens, 1987, p. 179), we do think they may be relevant. If these differences are real, they could justify the fact that *Symphysops* has not yet been documented in the Berounian (Sandbian–lower Katian) of the Czech Republic, since isolated cephala, without preservation of the stout frontal spine, are unlikely to be identified as belonging to the genus because they are smooth, with no traces of the characteristic glabellar furrows.

Other Cyclopygidae from the *Declivolithus* assemblage

Remarks.—Two other cyclopygid genera possibly occur in the studied *Declivolithus* assemblage of Morocco, but no additional specimens were collected during this work. These are *Heterocyclopyge* Marek, 1961 (type species *Cyclopyge pachycephala* Hawle and Corda, 1847, from the Vinice Formation, middle Berounian of the Czech Republic) and *Degamella* Marek, 1961 (type species *Aeglina princeps* Barrande, 1872, from the Dobrotivá Formation, Dobrotivian of the Czech Republic). These records are based on previous authors. Fortey and Edgecombe (2017, p. 318–319, fig. 3I, J) identified, described, and discussed *Heterocyclopyge* sp. Although only a thorax with pygidium was available, we agree it mainly recalls *Heterocyclopyge pachycephala* (see Horný and Bastl, 1970, pl. 7, fig. 7). Were it not for the adult size (> 1 cm) of the specimen, it would be indistinguishable from meraspides of *Cyclopyge rediviva* (see Fig. 6.2).

Another specimen that hypothetically occurs with *Symphysops stevaninae* from an unknown locality in Morocco, identified as ?*Cyclopyge* sp. by Bonino and Kier (2010, p. 102, fig. e) could also correspond to *Heterocyclopyge*. It seems to bear only five segments, and the pygidial axis looks too long (sag.) and segmented to correspond to *Cyclopyge*. As for the possible presence of *Degamella*, it is based on two specimens figured by Bonino and Kier (2010, p. 102, fig. a), hypothetically coming from the same unknown Moroccan locality as the previous *Heterocyclopyge*, and by Lebrun (2018, p. 137, fig. D), identified as *Cyclopyge* sp. but clearly differing by the short (exsag.) eye, the narrow and elongate glabella, the large thoracic axis, and the smooth pygidium. That specimen came from Jbel Tijarfaïouine where it occurs with *Declivolithus alfredi* and *Symphysops stevaninae*, among other species (see Lebrun, 2018, p. 138). López-Soriano and Corbacho (2012, p. 1) also listed the occurrence of *Degamella* in an assemblage from the same area.

Superfamily Trinucleoidea Hawle and Corda, 1847
Family Dionididae Gürich, 1907
Genus *Dionide* Barrande, 1847
(= *Dionidepyga* Šnajdr, 1981)

Type species.—*Dione formosa* Barrande, 1846, from the Vinice Formation, middle Berounian (ca. upper Sandbian–lower Katian), Czech Republic.

Dionide sp.
Figure 9.5

Material.—One incomplete cephalon with thorax (MGM-7671X-2).

Remarks.—Only a single poorly preserved specimen is available, corresponding to a cephalon articulated to two thoracic segments (Fig. 9.5). No details of fringe pitting are preserved, and the upper lamella of the fringe is missing. On the right side, it is possible to see the marginal facial suture. Despite the poor state of preservation, the subquadrate glabella, with rounded anterior margin and narrowing backwards with two basal lateral lobes, the broad fringe, and the "inflated" first segment clearly indicate this genus.

Destombes (1967) documented the genus in the Upper Ktaoua Formation (upper Katian) of Morocco, but the very incomplete state of the single specimen does not allow further comparison with coeval known species from related geographical regions. Subsequently, Corbacho et al. (2014) erected the new species *Dionide carlottae* Corbacho, Morrison, and Ait Addi, 2014, from beds that should correlate with Bofloss strata, with a trilobite assemblage that shares most of the taxa. This species presents the same significantly reduced number of pygidial rings and pleural furrows as *Dionide vokaci* Vaněk and Vonka, 2004, from the Bohdalec Formation of the Czech Republic, being possibly a junior synonym of the Czech species.

Family Trinucleidae Hawle and Corda, 1847
Subfamily Trinucleinae Hawle and Corda, 1847
Genus *Declivolithus* Přibyl and Vaněk, 1967

Type species.—*Trinucleus alfredi* Želízko, 1906, from the Voltuš Formation, middle–upper? Berounian, Rožmitál pod Třemšínem, in the Rožmitál Block of the Czech Republic.

Remarks.—*Declivolithus* is a very distinctive trinucleid whose strange appearance has been highlighted by previous authors (e.g., Hughes et al., 1975; Shaw, 1995; Fortey and Edgecombe, 2017). It is particularly large for the group, and its extremely wide fringe and long genal prolongations give it an almost harpid-like appearance. *Declivolithus* was placed in Trinucleinae by Hughes et al. (1975) due to its resemblance to *Trinucleus* Murchison, 1839, and *Telaeomarrolithus* Williams, 1948. Later, Tripp et al. (1989) and Zhou and Hughes (1989) suggested that a group of genera closely related to *Nankinolithus* Lu, 1957, including *Declivolithus*, may better be allied with Reedolithinae Hughes, Ingham, and Addison, 1975. At that point, they preferred to maintain these forms in Trinucleinae, but assumed a probable polyphyletic condition for such a subfamily. More recently, Zhou et al. (2016) also discussed this problem and considered that the subfamily systematics for these groups needs revision.

According to Hughes et al. (1975), who revised all Trinucleidae known at the time, *Declivolithus* differs from *Nankinolithus* in having one single external arc (E1) instead of two (E1–2). Nevertheless, as Tripp et al. (1989) stated, "early Ashgill" *Nankinolithus* from China, including the type species of the genus *N. nankinensis* Lu, 1957, only have one external arc, E1, the same condition of *Declivolithus*, making it hard to tie down trustworthy morphological differences between *Nankinolithus* and *Declivolithus*. This ambiguity led to likely misidentifications of several trinucleines that were assigned to *Nankinolithus*, but whose possibly close relationship to *Declivolithus* should be considered.

A group of species currently attributed to *Nankinolithus*, the so-called *granulatus*-group (sensu Zhou and Hughes, 1989), which mainly occur in Europe, resemble *Declivolithus* in having a much wider fringe with more arcs and rows of pits and longer genal prolongation. Nevertheless, they bear a second external arc (E2), although it is often very incomplete, only frontally developed, and may be a character derived from a condition with only one external arc (Zhou and Hughes, 1989). Among these are, for example, "*Nankinolithus granulatus*" (Wahlenberg, 1818) from the Upper Ordovician of Sardinia (Hammann and Leone, 1997, pl. 24) and *Nankinolithus*? sp. from the Şort Tepe Formation in the Upper Ordovician of

Turkey (Dean and Monod, 1990, fig. 8f, i). The E2 is also present in morphologically similar species assigned to *Bergamia* Whittard, 1955, including *Bergamia praecedens* (Klouček, 1916) from the Middle Ordovician of the Czech Republic. Zhou and Hughes (1989) rejected the view of Hughes et al. (1975), who considered that *Bergamia praecedens* should be assigned to *Nankinolithus*, and Shaw (1995) strengthened the assignment to *Bergamia* but suggested that this Czech species may be the predecessor of *Declivolithus*. Another closely related genus is *Kimakaspis* Ghobadi Pour et al., 2011, also bearing an E2 arc but abaxially instead of frontally. Ghobadi Pour et al. (2011, p. 175–176) discussed possible homology between E2 arcs in *Kimakaspis* and the *Nankinolithus granulatus* species-group. In any case, the close relationship between these taxa seems plausible.

The cephalic similarity between *Declivolithus* and *Jianxilithus* Zhang and Zhou in Lu et al., 1976, from the Upper Ordovician of China, has been emphasized by Zhou and Hughes (1989) and Zhou et al. (2016). However, these authors considered that the isolation of the pseudofrontal glabellar lobe by a transglabellar furrow located in the posterior glabellar third, together with a higher number of pygidial furrows in *Declivolithus*, justified retaining both genera as valid. Notwithstanding the very particular characteristics of *Declivolithus*, its phylogenetic relationships certainly should be closely linked to these other taxa. If the development of the cephalic fringe and pygidial segmentation suggests a greater relationship to other undisputed trinucleines such as *Trinucleus* and *Telaeomarrolithus*, it is also possible that these characters could be more related to the large dimensions of *Declivolithus* rather than to a close phylogenetic relationship, its origin being related to this paleogeographically more restricted *Nankinolithus* group.

The first mention of *Declivolithus* in Morocco was made by Destombes (1971) and, curiously, it was not in the Anti-Atlas, but in a small inlier located in the southern border of the High Atlas, in the Skoura region. This information was later reproduced in Destombes et al. (1985) and Destombes (2006a).

Declivolithus alfredi (Želízko, 1906)
Figures 10–12

1906 *Trinucleus alfredi* Želízko, p. 16, pl. 1, figs. 1–6.
1952 *Tretaspis novaki* Chlupáč, p. 183, pl. 1, figs. 1–8, pl. 2, figs. 1–6, pl. 3, figs. 1–2.
1967 *Declivolithus alfredi*; Přibyl and Vaněk, p. 454, pl. 1, fig. 2, pl. 2, fig. 1.
?1971 *Declivolithus* aff. *alfredi*; Destombes, p. 253.
1972 *Declivolithus alfredi*; Přibyl and Vaněk, p. 19, pl. 1, figs. 1–6 (and synonymy therein).
1975 *Declivolithus alfredi*; Hughes et al., p. 557–558, pl. 3, figs. 38, 39.
1975 *D.* sp. Hughes et al., p. 557.
?1985 *Declivolithus* aff. *alfredi*; Destombes et al., p. 227.
1995 *Declivolithus alfredi*; Shaw, p. 7, figs. 10.5, 10.7–10.13, 11.1–11.3.
1997 *Declivolithus alfredi*; Vaněk and Vokáč, p. 29–30, pl. 3, figs 1–5.
?2006a *Declivolithus* cf. *alfredi*; Destombes, p. 11–13, fig. F 5.
2017 *Declivolithus titan* Fortey and Edgecombe, p. 313–314, 316, fig. 2A–F.
2018 *Declivolithus titan*; Lebrun, p. 138–139, figs. A–D.

Holotype.—A holotype was not designated by Želízko (1906). A lectotype was selected by Přibyl and Vaněk (1967), which is a cephalon (old number P 8454; new number NM L17150) figured in Želízko (1906, pl. 1, fig. 1), and figured again in Přibyl and Vaněk (1972, pl. 1. fig. 2) and in Shaw (1995, fig. 10.12).

Addendum to description.—Several authors have described *Declivolithus alfredi* in detail (e.g., Přibyl and Vaněk, 1969, p. 101–102; Shaw, 1995, p. 7; Fortey and Edgecombe, 2017, p. 313, 314). We add here new information and a few remarks concerning some characters that were possible to observe in our material.

Half fringe counts ($N = 17$) of Moroccan specimens are: E_1, 35–43 (39); I_1, 34–38 (36), I_2, 35–37 (36). It is important to note that the number of E_1 pits (1–28) reported by Přibyl and Vaněk (1969) is a typo (it would probably be 38), as can be counted in their figured specimens (e.g., Přibyl and Vaněk, 1969, pl. 4, fig. 2). The I_2 is the innermost of the outer arcs, which is possible to calculate, although it is irregular due to several cut-off points. Inner arcs, adjacent to the genal and glabellar flanks, are organized in radial rows, with I_n varying from 24–29 pits. The adaxially following 1–2 arcs are also radially aligned. Despite the random distribution of pits in the area abaxial to I_2, it is possible to estimate up to 7–8 pseudoarcs (pits in a row) in front of the glabella, and 10–14 pits in a row in the widest part of the fringe. In front of the glabella, the radial outer sulci of the fringe are shared more frequently by E_1 and I_1, but occasionally they also include I_2.

There is a tendency for the number of pits and arcs to increase ontogenetically, with smaller specimens having fewer pits. Surface of the upper lamella concave, more strongly bent anteriorly and flatter laterally. Surface of lower lamella strongly convex, almost subvertical in the inner margin of the fringe, especially at the posterior region, then sloping regularly in anterior and lateral directions. Outer margin of the fringe (E_1 arc) subhorizontal. Frontal margin of the fringe tends to be medially transverse and slightly elevated compared to the lateral margin. Flattening of the fringe produces a subcircular appearance. The pygidium, which is preserved in full relief, shows a very sharp, abrupt, and significantly high external margin, vertical in relation to the dorsal surface.

Materials.—Seven complete or almost complete exoskeletons (MGM-7742X, MGM-7743X; MGM-7744X-R; MGM-7745X to MGM-7748X); eight cephala (MGM-7749X to MGM-7754X; MGM-7759X; MGM-7760X); four isolated lower lamellae (MGM-7761X to MGM-7764X); one thorax with pygidium (MGM-7765X); six pygidia (MGM-7766X; MGM-7767X-1; MGM-7767X-2; MGM-7768X to MGM-7770X); one meraspis cranidium (MGM-7771X).

Remarks.—When erecting *Declivolithus titan*, Fortey and Edgecombe (2017) stated that they only had flattened specimens. In fact, given the material they had available, it

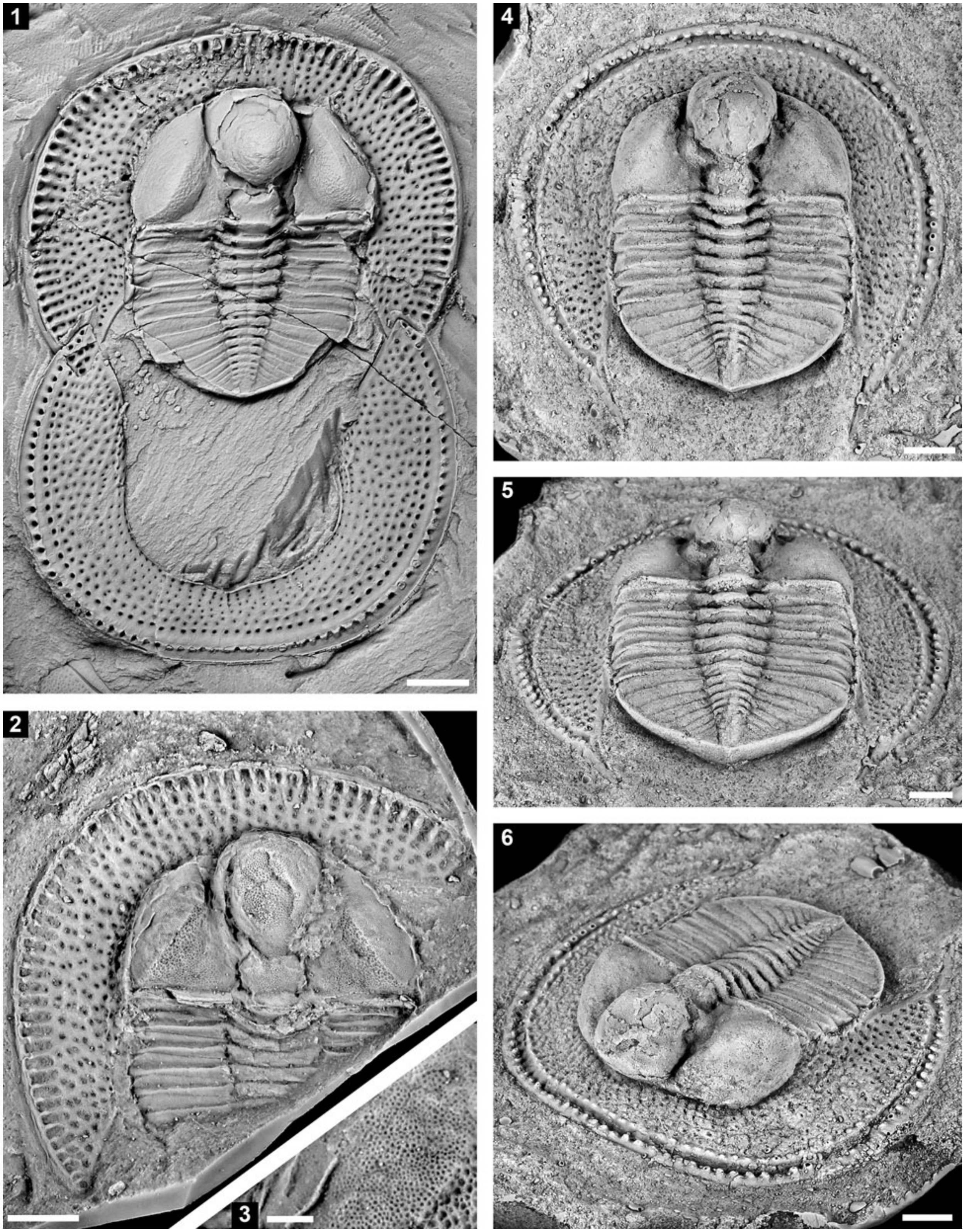

Figure 10. (**1–6**) *Declivolithus alfredi* (Želízko, 1906) from the Bofloss locality, Morocco. (**1**) Exoskeleton (molting configuration), internal mold, MGM-7742X: dorsal and ventral (lower lamella) views; (**2, 3**) incomplete cephalon with thorax, latex cast of the external mold, MGM-7743X: (**2**) dorsal view; (**3**) detail of the external sculpture of the left genal lobe; (**4–6**) exoskeleton (upper lamella missing), dental plaster replica of the internal mold, MGM-7744X-R: (**4**) dorsal view; (**5**) dorsoposterior view; (**6**) oblique left anterolateral view. Specimens (**1, 2**) are preserved in mudstones, flattened; specimen (**4–6**) preserved in full relief (sandstone). Scale bars = 5 mm.

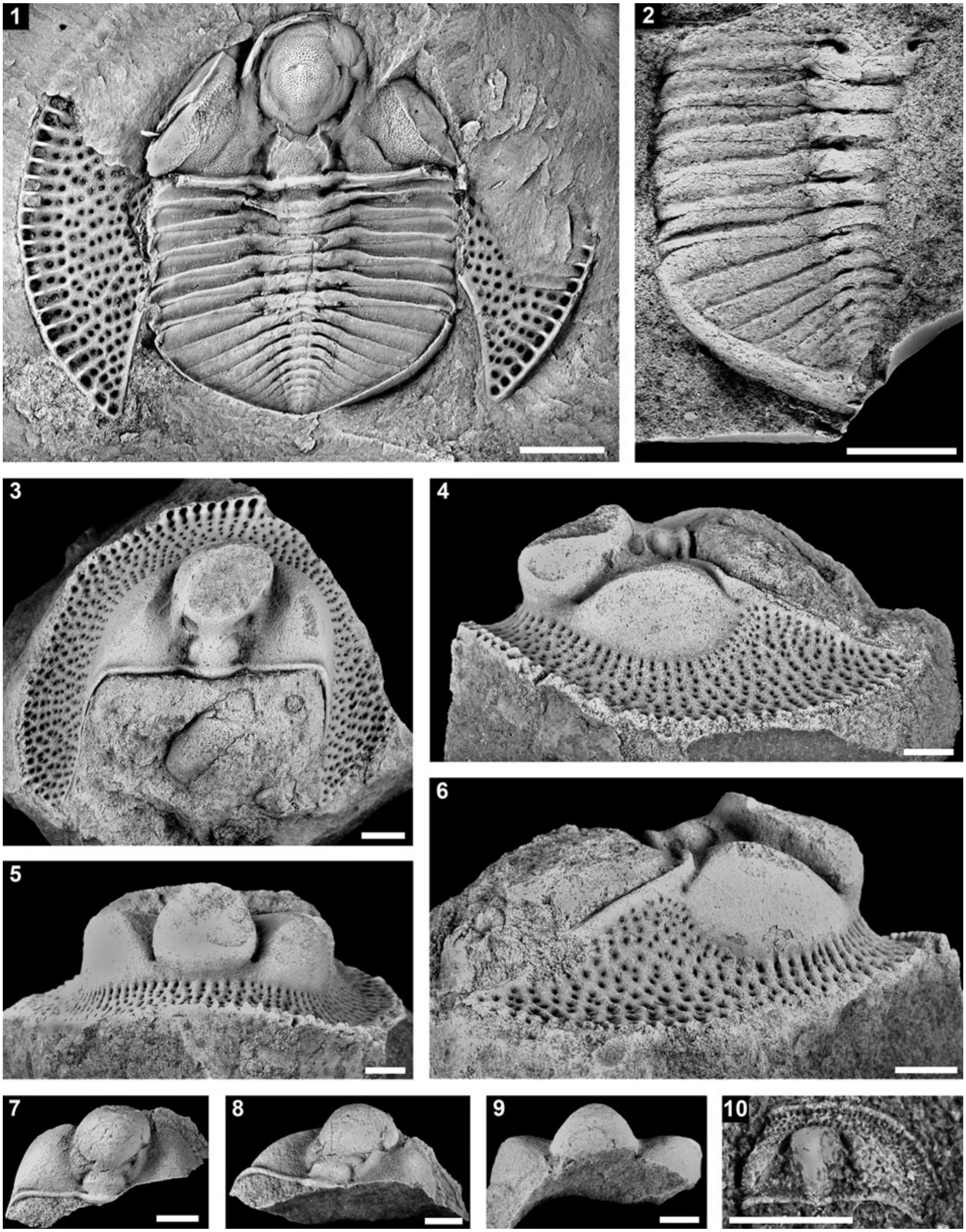

Figure 11. (**1–10**) *Declivolithus alfredi* (Želízko, 1906) from the Bofloss locality, Morocco. (**1**) Exoskeleton, latex cast of the external mold, MGM-7745X: dorsal view; (**2**) incomplete thorax with pygidium, latex cast of the external mold, MGM-7765X: dorsal view; (**3–6**) cephalon, internal mold (lower lamella missing), MGM-7749X: (**3**) dorsal view; (**4**) left lateral view; (**5**) anterior view; (**6**) right lateral view; (**7–9**) cephalon (fringe missing), internal mold, MGM-7750X: (**7**) dorsal view; (**8**) oblique right posterolateral view; (**9**) anterior view; (**10**) meraspis cephalon, latex cast of the external mold, MGM-7771X: dorsal view. All specimens are preserved in full relief (sandstones), except specimen (**1**), preserved in mudstone, flattened. Scale bars = 5 mm, except (**10**) = 2 mm.

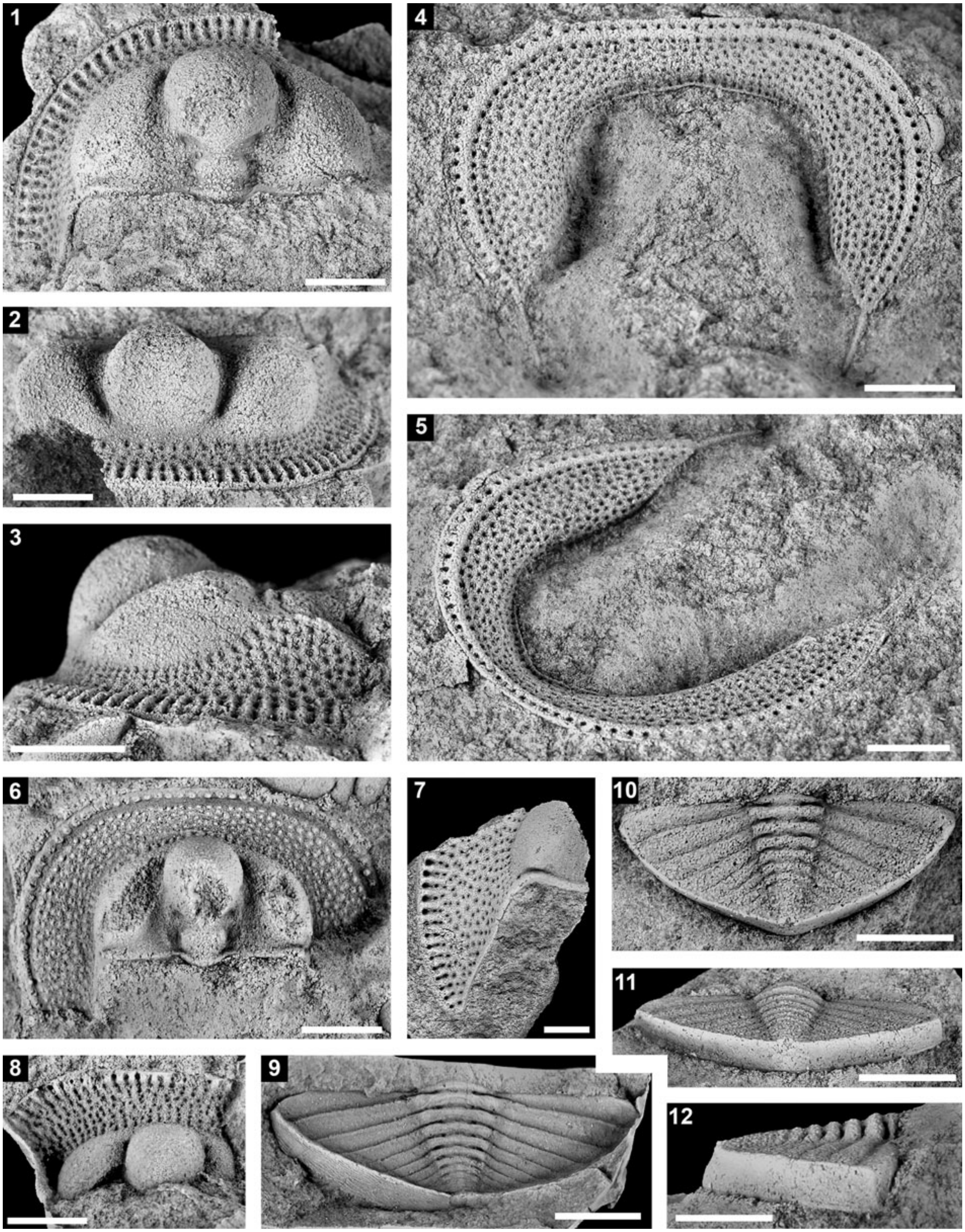

Figure 12. (**1–12**) *Declivolithus alfredi* (Želízko, 1906) from the Bofloss locality, Morocco. (**1–3**) Cephalon, internal mold, MGM-7751X: (**1**) dorsal view; (**2**) anterodorsal view; (**3**) left lateral view; (**4, 5**) lower lamella of the fringe, internal mold, MGM-7761X: (**4**) ventral view; (**5**) oblique right ventrolateral view; (**6**) cephalon (upper lamella missing), internal mold, MGM-7752X: dorsal view; (**7**) incomplete cephalon (left genal lobe and posterior left part of the fringe), internal mold, MGM-7753X: dorsal view; (**8**) incomplete cephalon, latex cast of the external mold, MGM-7754X: anterodorsal view; (**9**) pygidium, latex cast of the external mold, MGM-7768X: dorsoposterior view. (**10–12**) Pygidium, internal mold, MGM-7767X-1: (**10**) dorsal view; (**11**) posterior view; (**12**) right lateral view. All specimens are preserved in full relief (sandstones), except specimen (**9**), preserved in mudstone, flattened. Scale bars = 5 mm.

was not possible to assess the variability of the characters they took as diagnostic. Among our material, there are several specimens in full relief (Figs. 10.4–10.6, 11.3–11.10, 12.1–12.12), allowing comparison of the Moroccan specimens with similar *Declivolithus alfredi* from the Czech Republic. One of the main differences that justified the erection of *D. titan* was the greater organization of the innermost arcs in the Czech species, distributed in radial sulci along the flanks of the genal lobes. In the flattened Moroccan specimens studied by Fortey and Edgecombe (2017) it is not possible to see this arrangement, due to the collapse of the genal lobe over the flank, but in the full-relief specimens, it is possible to verify that the pits of the innermost arcs have the same configuration (radially aligned and organized in fringe sulci) as in *Declivolithus alfredi* from the Czech Republic (compare Shaw, 1995, fig. 10.5, 10.10 with Figs. 11.5, 11.6, and 12.7 herein, respectively). Generally, these sulci are more marked on the anterior half of the fringe, and occasionally they are also present in front of the glabella, with small ridges developed between the sulci (Fig. 11.5). Posteriorly, the sulci are less defined. As in the Czech material, this configuration is not always observed in Moroccan specimens and, sometimes, the same specimen only preserves these sulci and the obvious radial arrangement of the inner pit rows on one side. Although weakly marked, the holotype and another specimen of *D. titan* figured by Fortey and Edgecombe (2017, fig. 2A, B) also show these sulci, but they are visible only on the left side. This character is highly susceptible to taphonomy, but the new material shows it is entirely comparable in *D. titan* and *D. alfredi*. A very small cephalon (Fig. 11.10), probably corresponding to a meraspis, also seems to show these sulci adjacent to the glabella and to the genal lobes.

Another difference described by Fortey and Edgecombe (2017) is the fringe outer sulci, which in *D. titan* barely extend only one-third and includes two pits/arcs (E_1 and I_1) frontally and a third anterolaterally. In some *D. alfredi* specimens the fringe outer sulci are longer (about halfway across the fringe) and include three pits/arcs anteriorly, and sometimes even a fourth posterolaterally. However, not only is this character highly variable from specimen to specimen (even among specimens preserved in full relief) but it is also observed in the new Moroccan specimens (Figs. 10.1, 11.1, 12.1–12.3). Occasionally there are three pits/arcs between the anterior sulci (see also Lebrun, 2018, p. 139, fig. D), and four pits posterolaterally, just as in the Czech specimens. When *Declivolithus* specimens from the famous El Qaid Errami area began to appear very frequently in the Moroccan trade, we observed many specimens for sale that show great variability of fringe characters. There are specimens whose furrowed margin occupies 70% of the width (sag.) of the fringe, others in which the furrows are almost indistinct, and still others whose preservation has exaggerated the sulci to such an extent that there are strong ridges between the sulci, similar to the general appearance of the specimen figured by Hughes et al. (1975, pl. 3, fig. 39). Even within the Czech material, many details of the description, such as this particular character described by Chlupáč (1952), were based on a single specimen from a collection of fragmentary material. As Vaněk and Vokáč (1997, p. 29) noted, the presence of I_2 is common, but it does not always occur.

We consider that *Declivolithus titan* is a junior synonym of *D. alfredi* and that the Czech and Moroccan representatives of this genus are conspecific. We also clarify that two specimens figured by Přibyl and Vaněk (1969, pl. 5, figs. 4, 9) as *Declivolithus alfredi*, which Fortey and Edgecombe (2017, p. 316) considered not to correspond to this species because they “show the dorsal surface of the fringe carrying a prominent ridge parallel to the cephalic margin inside the E arc” were misinterpreted. As Přibyl and Vaněk (1969) indicated in their figure caption, the former is an enrolled specimen, thus showing the lower lamella in ventral view (the prominent ridge is the girder; see also the same specimen figured by Shaw, 1995, fig. 10.13). The second specimen is an exfoliated cephalon exposing the lower lamella as well, but in dorsal view (compare to a specimen with similar exfoliation figured by Shaw, 1995, fig. 10.9).

An interesting detail in some Moroccan material of *Declivolithus* is a characteristic molting configuration. As discussed by Fortey and Owens (1987) and Drage (2019), trinucleids, as well as harpetids, may have molted by opening the marginal suture that separates the upper and lower lamella of the fringe, a mechanism similar to modern xiphosurans, in which a marginal gape opens between the dorsal and ventral parts. In some trinucleids, the molting took place with the lower lamella of the fringe displaced away from the remainder of the exuvia (see also Drage, 2019, fig. 5.1; the displaced lamella is the lower and not the upper one). This is common for *Declivolithus alfredi*, with a frequent 8-shaped molting configuration (see Fig. 10.1 and Fortey and Edgecombe, 2017, fig. 2B) in which the lower lamella appears rotated 180° and overlapped at the posterolateral ends with the upper lamella. However, there are also specimens where it is the upper lamella that is missing but not around (e.g., Fig. 10.4), making it difficult to ensure that this is a molting configuration, and not the result of post-mortem disarticulation. Other trinucleids (e.g., *Deanaspis* Hughes, Ingham, and Addison, 1975) present different molting procedures, through the disarticulation of the cephalon and sometimes the first thoracic segment, which may or may not still be articulated to the cephalon, leaving a typical configuration in which these anterior-separated sclerites are slightly rotated with respect to the sagittal axis of the thorax with pygidium (e.g., Přibyl and Vaněk, 1969, pl. 14, fig. 4; Pereira, 2018, fig. 3G, I–K).

Conclusions

The revision of the *Declivolithus* Fauna trilobite assemblage from the Moroccan Anti-Atlas increases the known trilobite diversity from four (Fortey and Edgecombe, 2017) to 11 species. These include new occurrences for Morocco, including a new species (*Ulugtella*? *biformis* n. sp.), and improves systematic knowledge of several species previously known from the Czech Republic. New light on some lineages of peri-Gondwanan endemic trilobites and new biostratigraphic and paleobiogeographic data are important in discussing the chronostratigraphic and lithostratigraphic positions of several fossiliferous facies. The previous assignment of this assemblage to the upper Berounian due to correlation with the Bohdalec Formation from the Czech Republic (Fortey and Edgecombe, 2017; Gutiérrez-Marco et al., 2022a) is supported, and the relevant beds correspond to the upper part of the Lower Ktaoua Formation or the lower part of the Upper Tiouririne Formation. An extended stratigraphic range can be envisaged on the basis of occurrences of *Declivolithus* in the central High Atlas, where this genus was recorded in two beds separated by ∼500 m of arenaceous shales and sandstones (Destombes, 1971, 2006a; Destombes et al., 1985).

Most of the species identified in Bofloss are known from the Czech Republic (8 of 11), showing that the strong faunal link between Morocco and Bohemia still existed during middle Katian times. The Bofloss assemblage also constitutes a case study for taphonomic variability, making it possible to analyze representatives of the same species preserved either in full relief (sandstones) or flattened (mudstones). For some taxa (e.g., *Eudolatites*) the taphonomical imprint of each type of preservation is extreme and could lead to the establishment of "taphonomical" species if the preservational effects are not critically taken into account.

This study contributes to disseminating among the scientific community the important fossil beds and localities in the El Qaid Errami area, most of which have been discovered in the last 20 years as a result of the intense commercial extraction of fossils. Many of these constitute new associations compared to what was known in the Moroccan Anti-Atlas, with no record of the typical Upper Ordovician Moroccan index taxa and, thus, no obvious correlation with the classical lithostratigraphic scheme erected for this important geological region of Morocco.

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Declaration of competing interests

The authors declare none.

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