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Devonian Harpetidae from the central and eastern Anti–Atlas, Morocco

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Abstract

The systematics of 37 new species of Devonian Harpetidae from the central and eastern Anti–Atlas Mountains, Morocco, are described. The new material comes from the Dra—Tafilalet region and the province of Tata. A cladistic study was undertaken involving 138 taxa with the objective of assigning the new taxa to the appropriate genera, which are, as far as possible, monophyletic. In order to identify the widespread homoplasy present amongst harpetid taxa, which has proven so problematical for systematics in the past, many additional morphological characters were coded in the data matrix, totaling 111. In addition to the new material, all those described harpetid species from the Devonian and Silurian in which at least 10% of characters could be reliably coded were included in the study. The parsimony analysis using 20 different seeds identified 636 shortest trees; the consensus tree recognised 10 monophyletic clades to accommodate Devonian species. While the node support was weak the topology of the consensus tree is a substantial improvement on those of previous phylogenetic studies which have tended to be pectinate. The new species were assigned to 10 genera. Four genera (*Harpes*, *Lioharpes*, *Kielania* and *Eskoharpes*) are redefined and *Globoharpes* is reduced to a junior synonym of *Eskoharpes*. Three further genera are recognised, *Declivoharpes*, *Fritchaspis* and *Helioharpes*, which have been misinterpreted in the past and the new genera *Maghroharpes*, *Pinnuloharpes* and *Stoloharpes* established. The new species are assigned as follows:

to *Harpes, H. boudibensis, H. lahceni*, *H. lentigo, H. oudris, H. prescheri*, *H. sphenocephalus* and *H. supercilium;* to *Lioharpes, L. ammari*; *L. galea, L. morocconensis*, *L. saredra,* and *L. scopulum;* to *Fritchaspis*, *F. edgecombei*; to *Helioharpes, H. aougili*; to *Kielania*: *K. tumula*; to *Eskoharpes*, *E. sicarius*; to *Maghroharpes*, *M. azmamarensis, M. forteyi*, *M. hammii*, *M. ihmadii*, *M. laatchanensis*, *M. minutipunctus*, *M. oufatenensis*, *M. terridus*, and *M. zguidensis*; to *Pinnuloharpes*, *P*. *apteros, P. chaperon*, *P. hannabouensis*, *P haustrum, P. igaouii*, *P. merzaneensis*; *P. segaouii*. and *P. torquis; Stoloharpes*, *S. calceolus, S. capricornus, S. retiarius,* and *S. rissaniensis*.

Decllivoharpes, is also recognised as a genus, although no new species has been assigned to it.

The cladogram produced very few synapomorphies and there are no unique diagnostic characters available to determine genera. To assist in the process of assigning species in the future to the correct genera a working guide using combinations of characters and character states used in the study has been prepared.

The name *Helioharpes perradiatus* has been widely used with regard to harpetids from the Anti Atlas. This study shows that this has been a 'portmanteau' name for at least three distinct species. All are very different from the type material of *H. perradiatus*, which was recovered from the Western Meseta to the north of the Atlas Mountains, and has not been found to occur in the Anti-Atlas.

The new material figured herein has provided additional information on the eyes of Devonian harpetids of the Anti-Atlas. Typically, each eye lobe has two lenses which vary considerably in shape from species to species and are very different from the symmetrical multi lensed eyes of other Devonian trilobites. Probably in response to environmental changes a small third eye lens appeared for a short time twice, first in the upper Pragian/lower Emsian and then again in the Eifelian. The shape of the Pragian/Emsian lens was circular whereas that of the Eifelian lens was similar to the shape of the two larger accompanying eye lenses.

Key words: Morocco, Anti-Atlas mountains, Devonian, Harpetidae, taxonomy, phylogenetics

Introduction

This study describes Devonian harpetid trilobites from the central and eastern Anti-Atlas Mountains in southern Morocco. The region is known as having some of the best-preserved Devonian trilobites collected to date. Despite this, however, and the existence of a flourishing trilobite mining industry for nearly 40 years, only two Devonian harpetid trilobites from the region have so far been named and described, and both of those comparatively recently, by Feist & Belka (2018) and Crônier *et al.* (2018). This can be partly explained by the fact that until some 10 years ago, mining activity was concentrated on a relatively few prolific fossil-bearing beds where complete trilobites could be found. However, there were few species of harpetids in these "couches". When these traditional localities were mined out and market demand became focused on new species, trilobite miners found new localities containing a suite of different harpetid species. Nonetheless, while trilobites from other families have attracted the attention of systematists, Devonian Harpetidae have been comparatively neglected, despite their exceptional beauty. This can be partly explained by the problems they pose for classification. Despite their long history, their characters intergrade and are dominated by conservative features.

For this study, the more recent discoveries of the trilobite mining industry have proven invaluable and some 250 specimens were acquired, providing enough new material for 37 new species to be described. To resolve stratigraphic

uncertainties, ten visits to the field were undertaken by the author to identify the particular horizons from which new fauna had been collected. This material was collected by trilobite miners from 14 different localities, from Tata in the southwest to Hamar Laghdad in the northeast. The author has established the stratigraphic occurrence of the species through his own field work and their distribution is described.

The earliest harpetid to be described here, *Kielania tumula* n. sp., was amongst the first to colonise the Devonian shelf area of northeast Gondwana in the first half of the Pragian, in the area that is today the eastern Anti-Atlas. The youngest species to be described herein is from the lower Frasnian. A detailed cladistic study has been undertaken to establish the systematic relationships of the new species described herein within the current family Harpetidae.

Geology

Field occurrence and stratigraphy—For some three decades, well preserved articulated Devonian harpetid trilobites from the Anti-Atlas have been available on the international market. However, information concerning the horizons and localities from which they originated was often unknown or so generalised as to be of little meaning. Over the past 5 years, the author has made ten trips accompanying local trilobite miners into the field to discover more about the occurrence of Devonian Harpetidae, relevant horizons and ranges. The material found on these trips was recorded and subsequently purchased on the international market.

In the Anti-Atlas, harpetid trilobites were amongst the first trilobites to colonise the region in the first half of the Pragian and have been found in many horizons up to the beginning of the Frasnian. The localities from which the present material was collected are shown in Figure 1. Maps of these localities, detailing where the material was mined, together with the surrounding Devonian outcrops, are shown in Figure 2A, 2B and Maps 1–15, with supporting relevant GPS information included in Table 1. Maps 1 and 2 are of areas in the province of Tata in the Souss–Massa region of Morocco. In the region of Dra–Tafilalet, Map 4 is an area in the province of Zagora and Map 3 straddles the border of the provinces of Tinghir and Errachidia, with the trilobite locality being in Errachidia. Maps 5 to 15 are of areas in the province of Errachidia. The maps were based on the "Carte Géologique du Maroc" ("CGM") published by Ministry of Energy and Mines as follows: Map 1, CGM No. 163, Hollard, H. (1970a); Map 2, CGM No. 219, Hollard (1971) and CGM No.138, Hollard, H. (1970b); Map 4, CGM No. 259, Hollard, H. (1982); Map 3 and Maps 5-8, CGN No. 243, Hollard, H. (1988); Maps 10-15, CGM No. 244, Hollard, H. (1986) and Map 9, CGM Nos 243 and 244. Devonian formations in the areas covered by the maps are detailed in Hollard (1981), Figure 3 (Maps 1 to 6), Figure 4 (Maps 7 and 8) and Figure 5 (Maps 9 to 15). The location of the discovery sites indicated by the arrows on the Maps were based on GPS co-ordinates recorded by the author and are categorised in Table 1 as follows:

a) discovery site recorded at the time of discovery;

b) discovery site recorded on being shown the site by the relevant trilobite miner at a subsequent date;

c) position of discovery horizon recorded on information obtained from the relevant trilobite miner.

By inputting the GPS information into Google Earth "search", it is frequently possible to obtain additional positional information concerning the exposure of the discovery horizon. The lack of vegetation in the Anti-Atlas often leaves the rock strata on sloping ground exposed, and the excavations of trilobite miners frequently highlight the discovery horizon.

Correlations between localities were figured by Hollard (1974, figs 1–8). The areas covered by Maps 3, 6, 11 and 15 herein are not included in Hollard's tables or figures. The geology of Hamar Laghdad (Map 11) has most recently been described by Klug *et al.* (2018); the correlations and events of the western Anti-Atlas by Becker *et al*. (2004); and Emsian conodont stratigraphy and correlation of the Anti-Atlas by Aboussalam *et al.* (2015). Other published measured sections are referred to herein, where appropriate, and two new measured sections, Section 1 and Section 2 are shown in Figures 6 and 7, respectively. Section 1, starting in the lower to mid Emsian and extending to the mid Eifelian, is situated on the western edge of the Ma'der basin on the southern flank of Jbel Ou-Driss, 140 km S.W. of Erfoud. Section 2, a much shorter section of mid Eifelian age, is from the north Jbel Issoumour, 80 km W.S.W. of Erfoud. In these sections, harpetid trilobites are found at intervals in limestone ribs rarely exceeding 50 cm thick, which are interbedded with lime argillites. Rare in many localities, they are fairly abundant in certain lower to mid Eifelian beds at the two localities. They are also abundant in some upper Pragian to middle Emsian localities where corals and bryozoans are present. In the region of northwest Tafilalt (Map 6), they are also fairly common in certain upper Eifelian horizons.

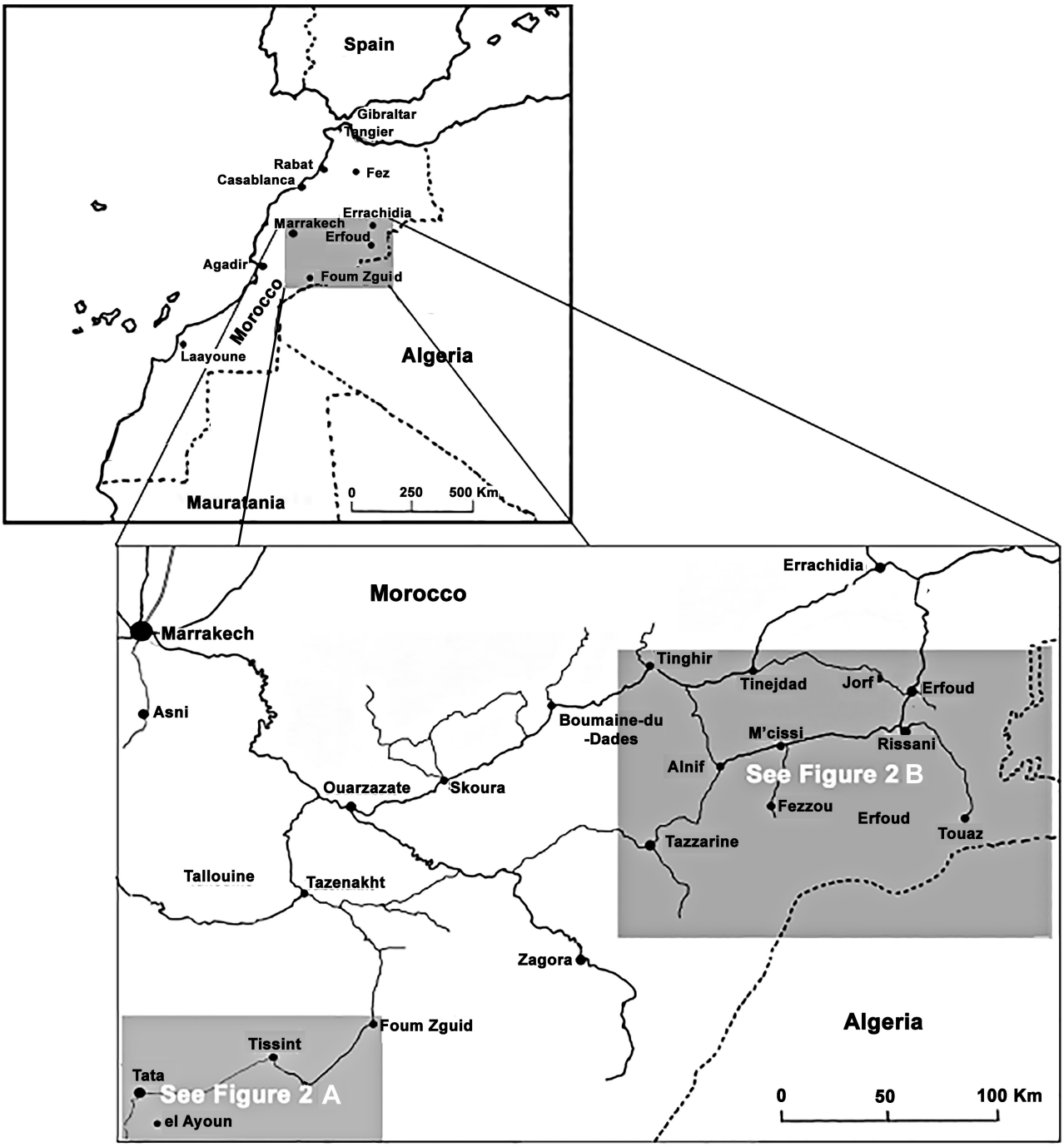


FIGURE 1. Locations of areas of study and collection

Correlating the trilobite beds of Section 2 with the Eifelian trilobite beds of Section 1 can only be done tentatively at this stage but the author considers it likely that the whole of Section 2 is represented by levels 12 to 13 in Section 1. This is suggested by the presence of the same *Thysanopeltis* species as well as *Harpes boudibensis* n. sp. at Jbel Issoumour. *Harpes boudibensis* appears some 35 m above the Eifelian / Emsian boundary (Gibb & Chatterton 2010), whereas at Jbel Ou-Driss, it is only some 13 m above this same boundary.

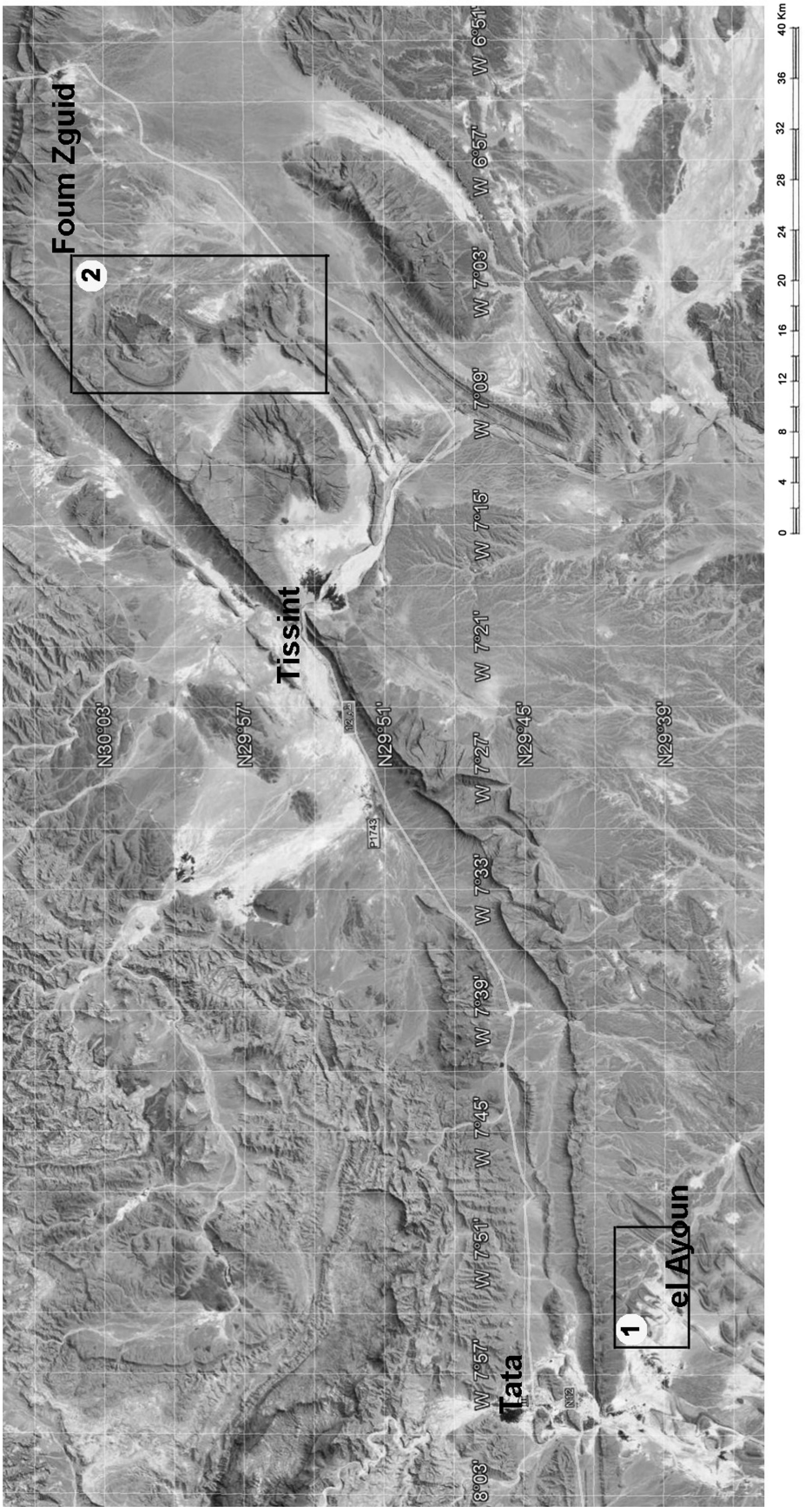


FIGURE 2A. Map locations in the Souss–Massa region

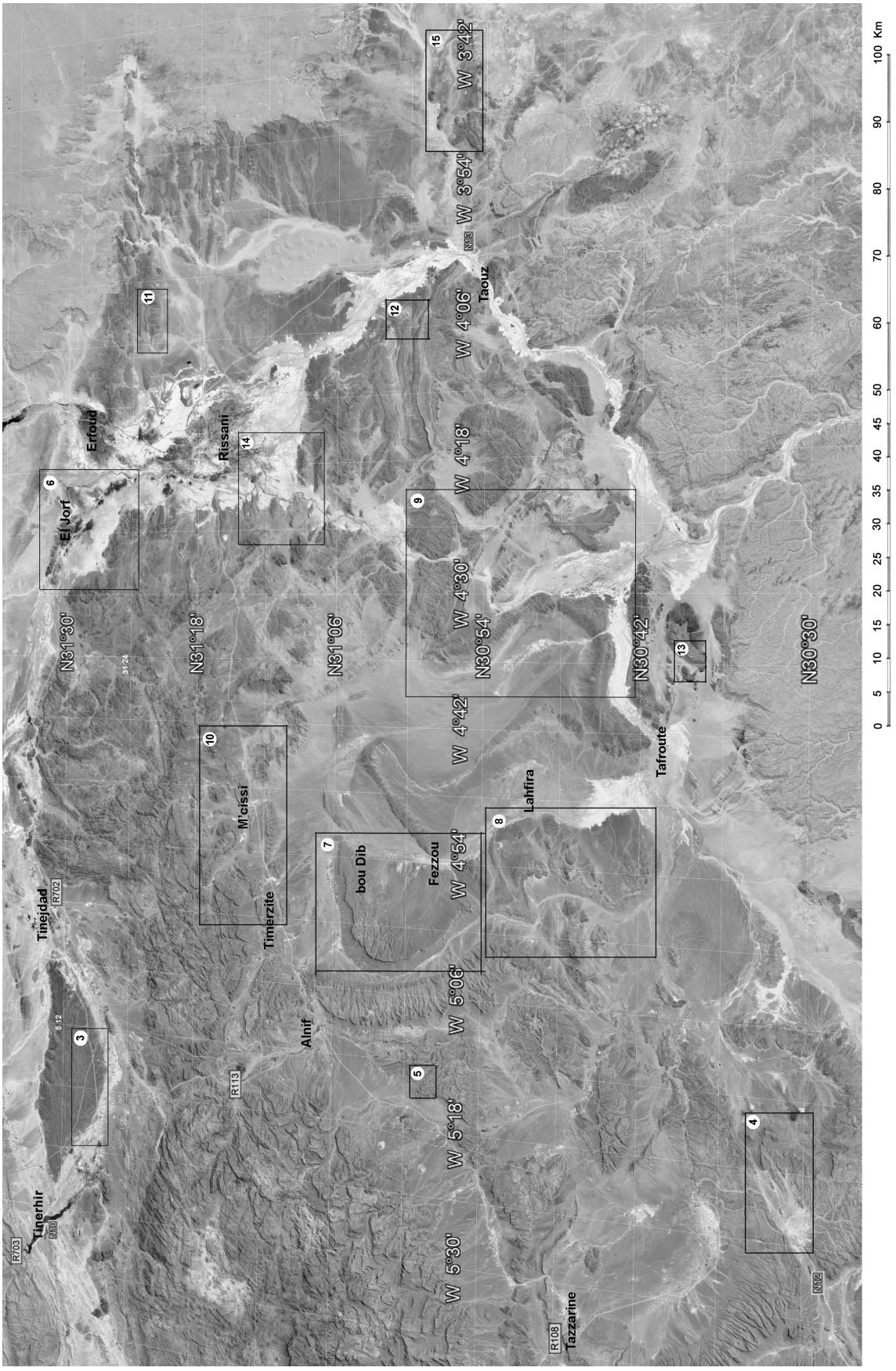


FIGURE 2B. Map locations in the Dra–Tafilalet region

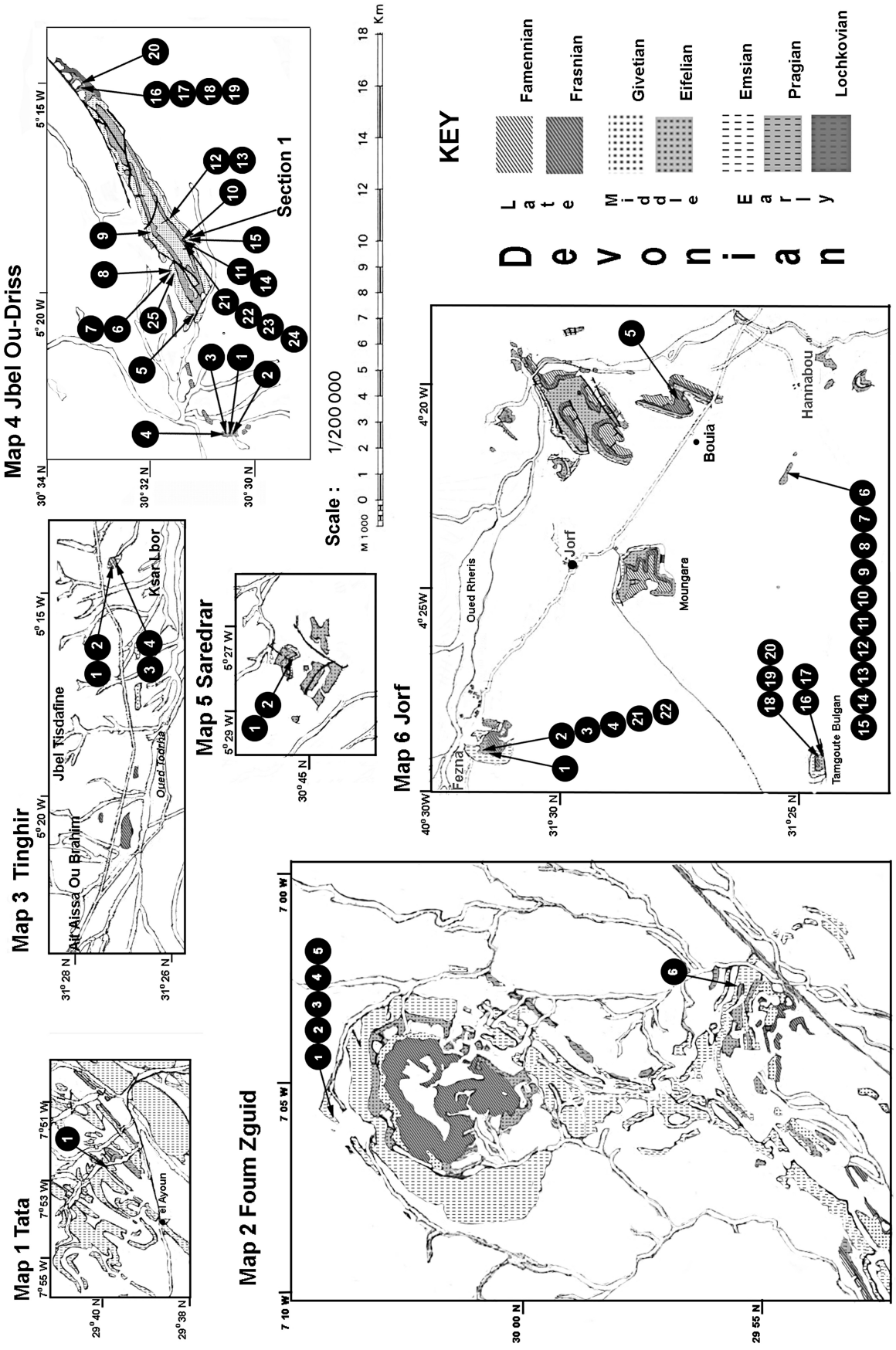


FIGURE 3. Souss–Massa, Tiinghir, West and North Ma'der regions

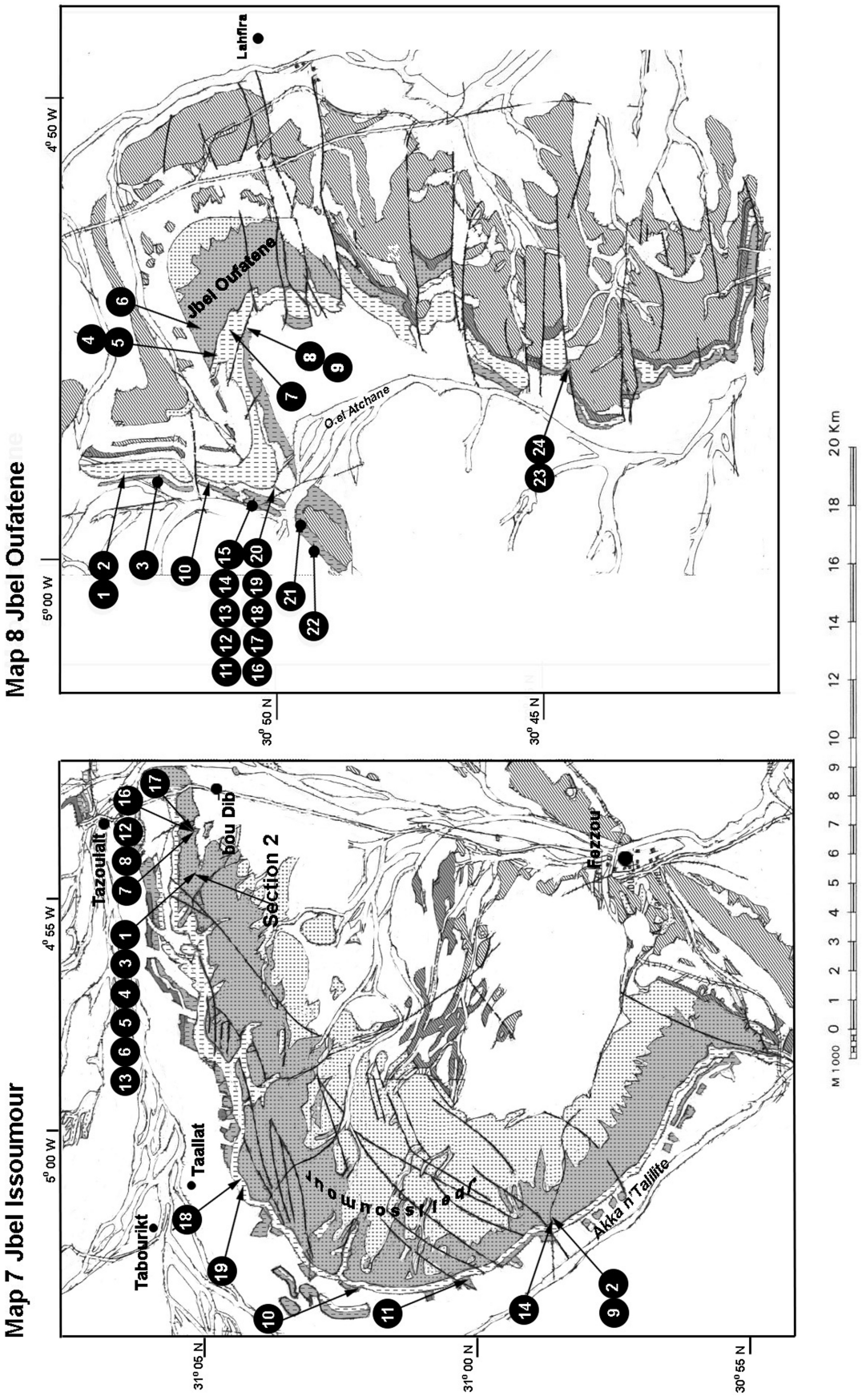


FIGURE 4. Ma'der

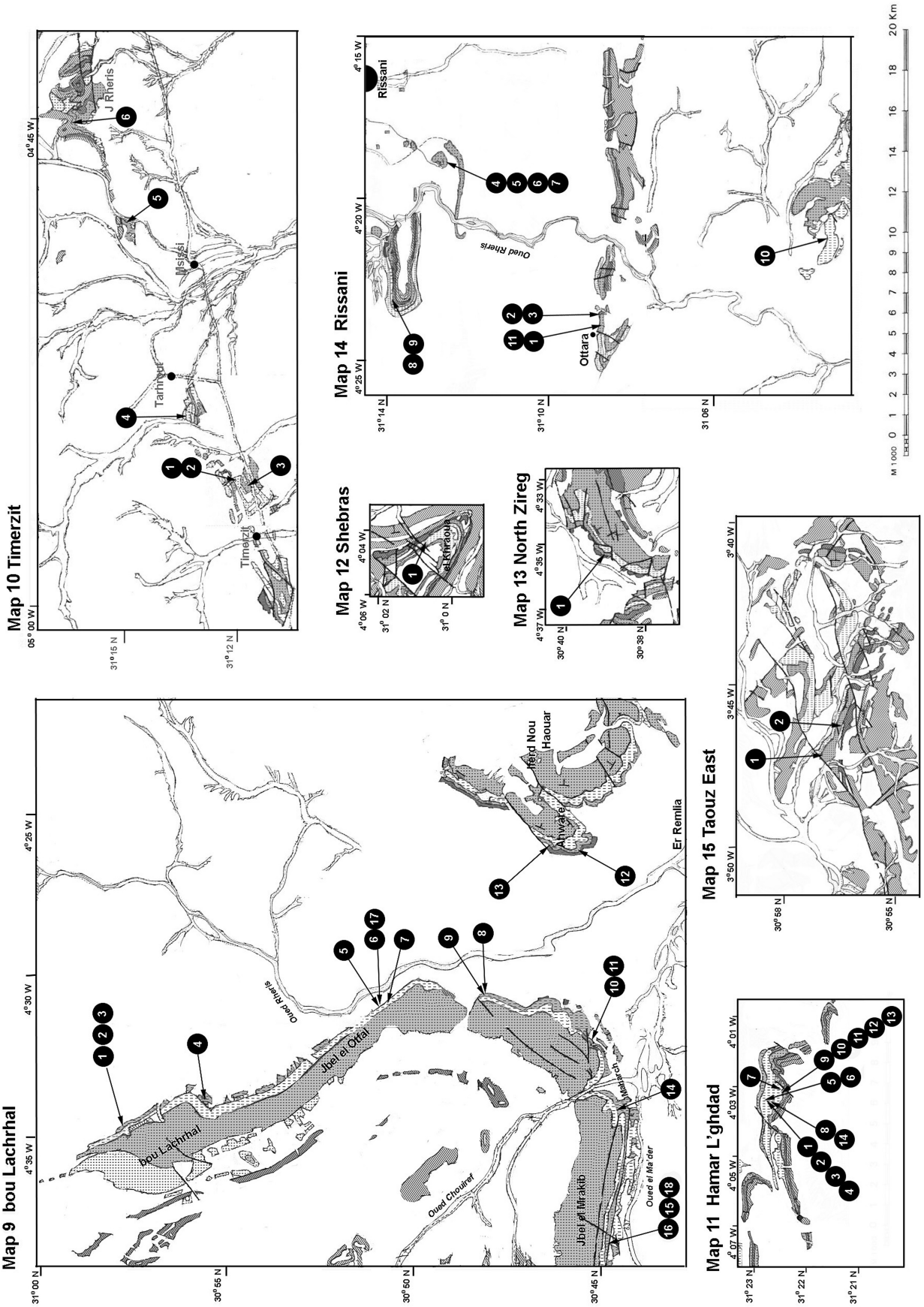


FIGURE 5. East Ma'der, Tafilalt and Taouz

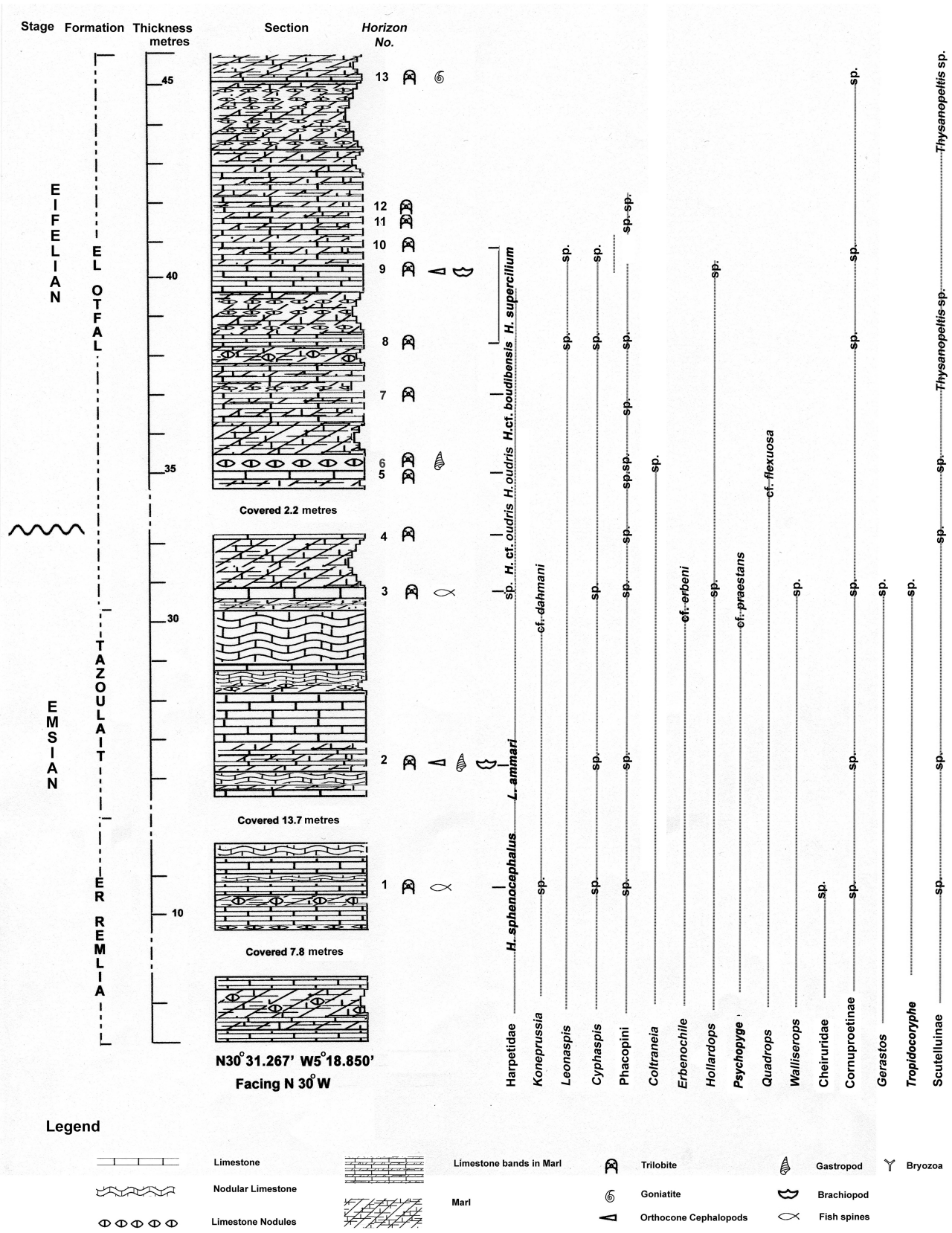
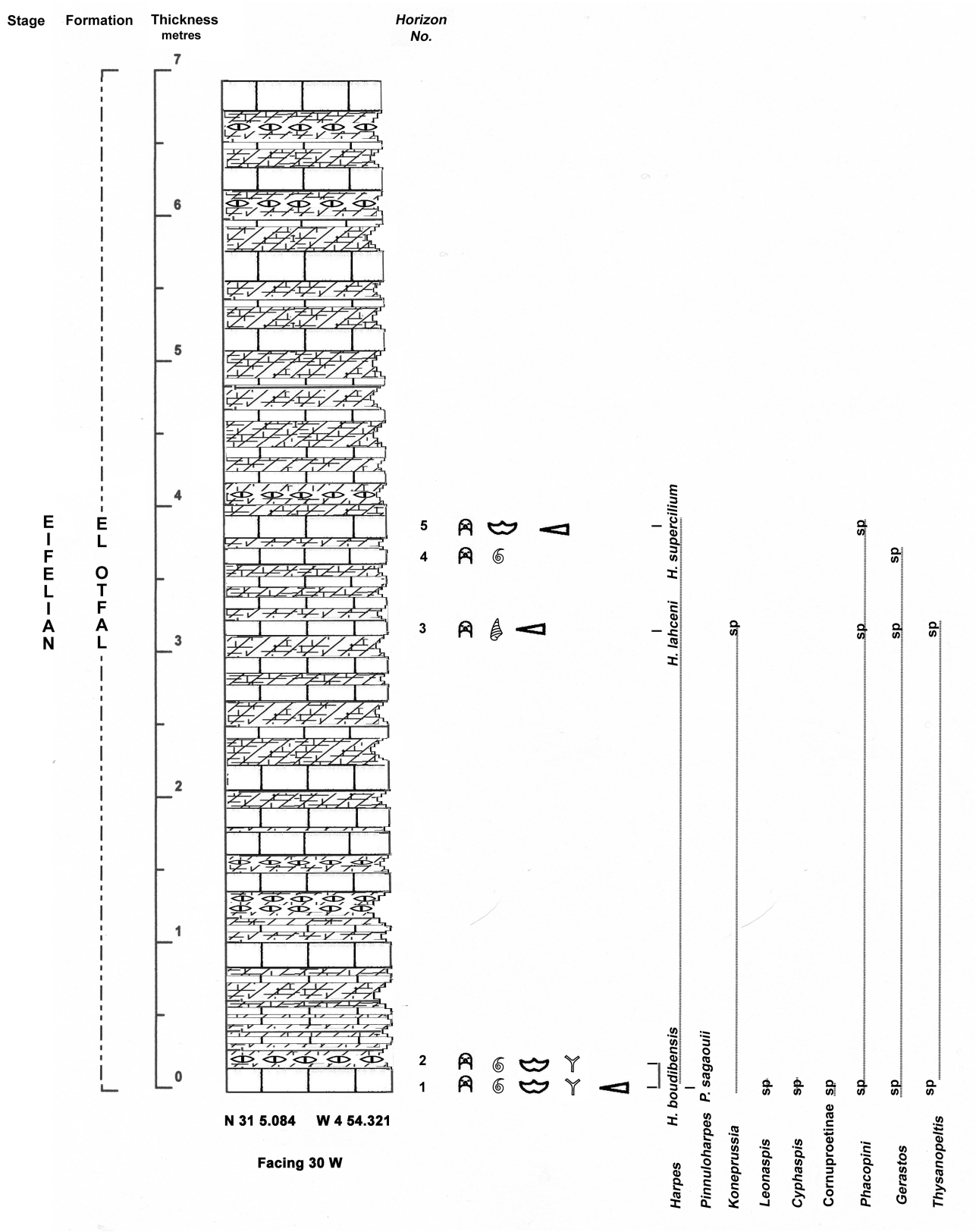


FIGURE 6. Section 1 Jbel Ou-Driss



Legend: see Figure 6

FIGURE 7. Section 2 Jbel Issoumour

Taphonomy

At all localities dating from the early Pragian to the beginning of the Givetian, it is likely that relatively shallow, open marine conditions prevailed during deposition, although there was a rise in sea levels at the end of the Emsian (Morrow & Sandberg 2008). Specimens recovered in the field frequently comprise only cephalic shields, but even when they are articulated they are usually found in a partial state of enrolment. It is reasonable to infer from such articulated trilobites that they were 'frozen' at the point of trying to adopt protective enrolment. The perfect preservation of sculptural details of much of the material figured herein implies that burial was rapid and sclerites were not subject to post-mortem abrasion. It is highly probable that burial involved hyperpycnal flows of flocculated sediment triggered by storms or seismic activity as described by Brett *et al.* (2012). Brett *et al.* divided these flows into two types, the first, the detached flow, rapidly deposited sediment burying the benthos quickly but not instantaneously and leaving the sea floor otherwise undisturbed; the second involved the seafloor sediment, trilobites and other benthic organisms being caught up in the hyperpycnal flow itself, transported and then instantly buried. Typically, trilobite carcasses in the first type of obrution bed are more or less aligned with the bedding plain and often show incipient disarticulation (eg. Pl. 33G). The carcasses in the second obrution bed tend to be well articulated, enrolled or outstretched, and are at set differing angles to each other and the bedding plain (eg. Pl. 43N, N (two carcasses on the same slab)).

Since a majority of specimens comprise only cephala, the implication is that the mechanism attaching the thorax to the cephalon was not particularly strong, quickly decomposing on death or liable to failure if mechanically stressed. This mechanical weakness is evidenced in several specimens figured herein where the thorax and cephalon have separated but the sclerites otherwise remain articulated. (eg. Pls 5A, 7A, 10I). During life, the thorax was elevated above the sediment surface on which the genal prolongations rested, and during enrolment the cephalic/thoracic junction served as a flexible hinge (Bergström 1973) to permit rapid tucking of the thorax beneath the cephalic cavity. It was therefore likely to represent a line of weakness post-mortem. This contrasts with the strong attachment of the lower lamella to the upper lamella. None of the examples figured here shows an upper lamella with a displaced lower lamella. On the other hand, trinucleid trilobites are often found with the lower lamellae separated, proving that the marginal suture was routinely functional.

By contrast, only two moulted harpetid lower lamellae (Pls 29O, 33K) and one upper lamella (Pl.6I–L) are included among the present material, suggesting that the marginal suture was rarely operative, or that moulted exoskeletons were very quickly broken up.

Sorting seems to have occurred as part of the process, as the size range of exoskeletons within a particular horizon is very limited. There are no examples of protaspids and only one example of a possible *meraspid* (Pl. 53A–F) being found together with a holaspid. Even the size range of holaspids is very limited at individual localities where the typical conditions of deposition and preservation prevailed. One rare assemblage of different-sized specimens on a single bedding plane figured herein (Pl. 25H) came from a small, isolated coral colony. The *meraspid* figured here (Pl. 53A–F) came from a similar coral environment, reinforcing the idea that coral interfered with the sorting process at certain localities. The sorting process, however, probably does not explain the total absence of protaspids and small *meraspid*s from these beds as this absence is widespread in the region, involving all families of trilobite, and is probably the result of preservation bias (small forms being more readily resorbed/dissolved post-deposition as they have a much larger surface to volume ratio). To be certain, however, a lot more information is required as taphonomic process vary with paleoenvironmental/sequence stratigraphic setting. (Carlucci, J.R., and Westrop, S.R. 2014.). On the international market, with so many complete Moroccan trilobites available, there is no demand for incomplete specimens, and they are discarded by trilobite miners and preparators whenever found. The author has seen broken cephala in the field but they are unusual. Since harpetid exoskeletons are not thick and robust—in contrast to those of phacopids, for example—the comparative rarity of broken specimens is puzzling, especially if size sorting occurred by selective transport.

History of harpetid classification

Members of the trilobite family Harpetidae, Hawle & Corda, 1847, are easily recognizable by their perforated brims, vaulted genicrania and their genal prolongations. However, the systematics of the family have proved far

from straightforward. For the first hundred years, from 1847 until 1948, systematic treatment of the Harpetidae was limited. The only genera created were *Hibbertia* Jones & Woodward, 1898, and *Eoharpes* Raymond, 1905, the latter replacing *Harpina*, Novák, 1885, a name that was already in use. *Hibbertia* was subsequently made a junior subjective synonym of *Harpes* Goldfuss,1839 by Withers (1929). From 1948, however, the pace of systematic splitting accelerated. The discovery of undescribed species prompted Lamont to establish three new genera: *Scotoharpes* (Lamont 1948a), *Dubhglasina* and *Metaharpes* (both Lamont 1948b), and Whittington (1949a) established *Dolichoharpes*.

Whittington (1950a) undertook the first comprehensive systematic review of the family and established five more new genera of Harpetidae: *Selenoharpes*, *Platyharpes*, *Paraharpes*, *Aristoharpes* and *Lioharpes*. Shortly after this publication, Whittington (1950b) reduced *Platyharpes* to a junior subjective synonym of *Hibbertia*, which he had revived. In the same year, Whittington (1950c) separated out *Harpides* and placed it in a new family Harpididae. Harrington & Leanza (1957) erected *Australoharpes*; Vaněk (1963) erected *Bohemoharpes, Fritchaspis, Kielania* and *Reticuloharpes*; Sheng (1974) erected *Sinoharpes*; and Koroleva (1978) erected *Harpesoides*. *Aristoharpes* and *Selenoharpes* were both made junior subjective synonyms of *Scotoharpes* by Norford (1973). In 1981, Přibyl & Vaněk proposed two new subfamilies, Eoharpetinae and Dolichoharpetinae, leaving those genera not assigned to these subfamilies in Harpetinae Hawle & Corda, 1847. They also proposed three new genera, *Thorslundops, Wegelinia* and *Helioharpes*, and three new subgenera *Bohemoharpes* (*Declivoharpes*), *Bohemoharpes* (*Unguloharpes*) and *Kielania* (*Lowtheria*). The genus *Brachyhipposiderus* was added by Jell (1985), and Owen (1981) who synonymized *Harpesoides* with *Paraharpes* and *Metaharpes* with *Hibbertia*.

The second major comprehensive systematic study was that of Přibyl & Vaněk (1986), by which time the systematics of the family had been greatly developed: three subfamilies, nine new genera and three subgenera had been proposed and two genera made junior synonyms. In contrast to Whittington (1950a), Přibyl & Vaněk's (1986) synopsis of the family proposed few major conceptual changes except that of reducing *Fritchaspis* to a subgenus of *Lioharpes*. *Paraharpes* was later placed in synonymy with *Hibbertia* by Owen & Clarkson (1992), a decision supported by Lespérance & Weissenberger (1998).

The third systematic review of the family Harpetidae was that of Ebach & McNamara (2002). These authors considered that "unnecessary subfamilies, poorly supported genera, subgenera, species and subspecies" had been created previously, and made an attempt to place the systematics of the family on a sounder basis. The division of harpetids into three subfamilies (Dolichoharpetinae, Eoharpetinae and Harpetinae) was not supported. The genera *Australoharpes* and *Sinoharpes* were placed in synonymy with *Dubhglasina*; *Wegelinia* and *Thorslundops* were synonymised with *Hibbertia; Fritchaspis* made a junior subjective synonym of *Lioharpes;* and *Helioharpes* and *Reticuloharpes* junior subjective synonyms of *Harpes*. Also, the subgenera *Kielania* (*Lowtheria*), *Bohemoharpes* (*Declivoharpes*) and *Bohemoharpes* (*Unguloharpes*) were made junior subjective synonyms of their respective genera. This left the family Harpetidae without any subgenera.

Since Ebach & McNamara's (2002) review, only two new genera have been proposed: *Eskoharpes* and *Globoharpes* McNamara *et al.*, 2009. Beech & Lamsdell's (2021) cladistic study was designed to explore the phylogenetic relationship within Harpetida and to understand the relationships between extinction events and disparity, and did not propose any phylogenetic changes. The genera currently included in the family are therefore: *Bohemoharpes* Vaněk 1963*, Brachyhipposiderus* Jell 1985, *Dolichoharpes* Whittington 1950, *Dubhglasina* Lamont 1948b, *Eoharpes* Raymond 1905, *Eskoharpes* and *Globoharpes* McNamara *et al* 2009, *Harpes* Goldfuss 1839, *Hibbertia* Jones & Woodward 1898, *Kielania* Vaněk 1963, *Lioharpes* Whittington 1950a and *Scotoharpes* Lamont 1948a.

The family Harpetidae shows considerable morphological variation but lacks obvious synapomorphies with which to define genera within the group. This has made it difficult to recognise genera on the basis of "presence or absence" characters. Such morphological criteria as have been used often involved describing outlines and profiles, relative dimensions and angles of slopes of brims and genal areas, all of which can vary, albeit slightly, within a single species. Making the task more difficult is the fact that harpetid thoraces, pygidia, hypostomes and moulted lower lamellae are rarely preserved, so most studies have relied on the dorsal surface of the cephalon only.

In the Ebach & McNamara (2002) review at the supraspecific level, genera were assessed on a subjective basis in line with previous practice. However, as regards the Devonian species that are the focus of this paper, the author considers that *Fritchaspis* and *Helioharpes* were incorrectly reduced to junior subjective synonyms of *Harpes*. This may have been the result of an undescribed species of *Harpes* (*H. boudibensis* n. sp.) being mistaken for

the type species of *Helioharpes* (*H. perradiatus*) by Ebach & McNamara (fig. 2, F). The authors had warned that "Because the large degree of morphological variability encompassed by the species within each genus, any cladistic analysis dealing with supraspecific taxonomy must be treated with caution." In the author's view, the problem of morphological variability within species is less important than the lack of synapomorphies and widespread homoplasy that is typical of the family. At the species level, Ebach & McNamara's (2002) review involved a cladistic analysis on a genus-by-genus basis using no more than 26 characters. By using so few characters, their study lacked enough potential synapomorphies to provide meaningful cladograms, which accounts for the many pectinate trees they recovered, which revealed little of the relationships between taxa and highlighted the difficulties peculiar to harpetids.

Morphological terms and morphology

Morphological terms used herein are those used by Whittington & Kelly (1997, pp. 313–329) in the revised version of the Treatise on Invertebrate Paleontology, Part O Arthropoda 1. Figure 8, below, is based on a fig. 1 of Ebach & McNamara 2002, which in turn was based on Whittington's (1950a) fig. 1 and (1959) fig. 85. In the Treatise, the term preglabellar field is defined as the "portion of the cranidium lying between front of glabella and anterior border furrow". In harpetid trilobites, however, the doublure or lower lamella extends up past the border furrow to form the ventral exoskeleton of the inner portion of the fringe. Here, therefore, the term preglabellar field is used to describe the area lying between the preglabellar furrow and the inner margin of the fringe. Also, genicranium is defined in the Treatise as the dorsal cephalic shield of hypoparian forms of Olenellia separated by marginal (or supramarginal in conocoryphids) suture from ventral doublural plate. Here it is used to describe the central part of dorsal cephalic exoskeleton of harpetids which is comprised of the glabella, genal area, genal roll and posterior border. It does not include the brim, girder, prolongations or external and internal rims. Additional terms used in this work include: the cephalic median organ (CMO) described by Lerosey-Aubril and McNamara, 2008; the preaxial furrow, which runs down the sides of the preglabellar boss to the girder; and the dorsal rim suture that runs around the dorsal surface of the exterior rim. Some abbreviations have been used: 'sag.' for sagittal, 'exsag.' for exsagittal, 'tr.' for transverse, 'L0' for occipital ring and 'L1' for preoccipital basal lobe, 'S0' for occipital furrow and 'S1–S4' for other glabellar furrows, 'abax.' for abaxially and 'adax.' for adaxially.

Posterolateral narrowing of brims in dorsal view is expressed as a ratio of the sagittal width of the brim to the width of the brim (tr.) at the level of S0. The lateral positioning of the eyes relative to the glabella is expressed by the ratio of the distance (tr.) of the inner margin of the fringe to the glabella and the distance (tr.) of the eye lens to the glabella. Brim perforation counts have been taken where possible from a 1 sq. millimetre area straddling the axis in the centre of the brim. Where this was not possible due to brim damage or poor preservation, a 1 sq. millimetre from the nearest undamaged area of the brim was selected. To compare perforation counts of brims of different sizes, the count for each specimen was adjusted to a notional sagittal brim width of 5 mm, "a standardised brim". This adjustment being $(n \times sw^2) / 5^2$ where n is the number of perforations and sw is the sagittal brim width. The validity of this adjustment relies on the number of brim perforations remaining constant for each instar. The four species in the current material which display the greatest size range suggest that this is indeed the case. These species are *Lioharpes maroccanensis* n. sp., *L. saredra* n. sp., *L. scopulum* n. sp. and *Maghrohapes oufatenensis* n. gen. and n. sp. Their brim width (sag.), brim perforation size and number per sq. mm, actual and standardised, are shown in Table 2. The values for perforation counts and sizes are approximations only. It was not always possible to select the sample area in the same place, and perforation patterns and shapes vary slightly between specimens. In order to arrive at a more representative perforation diameter for each specimen, the sag. and tr. width of each perforation were measured and averaged and then the resultant values for all the perforations in the sample area were averaged.

Further work is needed to ascertain whether scaling brims of *meraspid*s and very early stage holaspids is valid. For instance, the development of brim perforations close to the sagittal line on the smallest specimen of *Bohemoharpes ungula* (National museum Prague, L 6123; Pl. 54I) is patchy.

All material designated as holotypes herein have a cephalic length (sag.) of 1 cm or more and all appear to be well developed holaspids.

The new material figured herein includes well preserved eye lenses for 18 of the 37 new species, providing additional information on the eyes of Devonian Harpetidae of the Anti-Atlas. The eyes of harpetid trilobites are

very different from the compound holochroal and hyper-compound (Schoenemann, *et al.*, 2021) schizochroal eyes of other trilobite families of this period. They do not have the multiple symmetrically arranged hexagonal lenses of holochroal eyes or the subspherical lenses typical of schizochroal eyes. They generally have only two lenses, long axis horizontal, with shapes that vary considerably: rectangular with rounded corners (Pl. 2M), stadium-shaped (Pl. 36H), sub trapezoidal (Pl. 28M), sub-oval (Pl. 47F) and almost triangular (Pl. 37N–O). These different shapes are species specific rather than genus specific, and shapes and sizes of lenses on the same eye lobe can differ (e.g., Pl. 40M). Distance between the two eye lenses of harpetid species also varies, in many species they are well separated (Pl. 2M), while others are contiguous (Pl. 27H) and occasionally they appear to overlap (Pls 23J, 38D). The orientations of the eye lenses are usually anterolateral and posterolateral and tilted slightly upwards. In cases where the eye lobe is weakly inflated, however, the upwards tilt becomes much stronger. The variability of eye lenses also extends to their convexity from weakly convex (e.g. Pls 4K, 12K) to strongly convex (Pl. 28M).

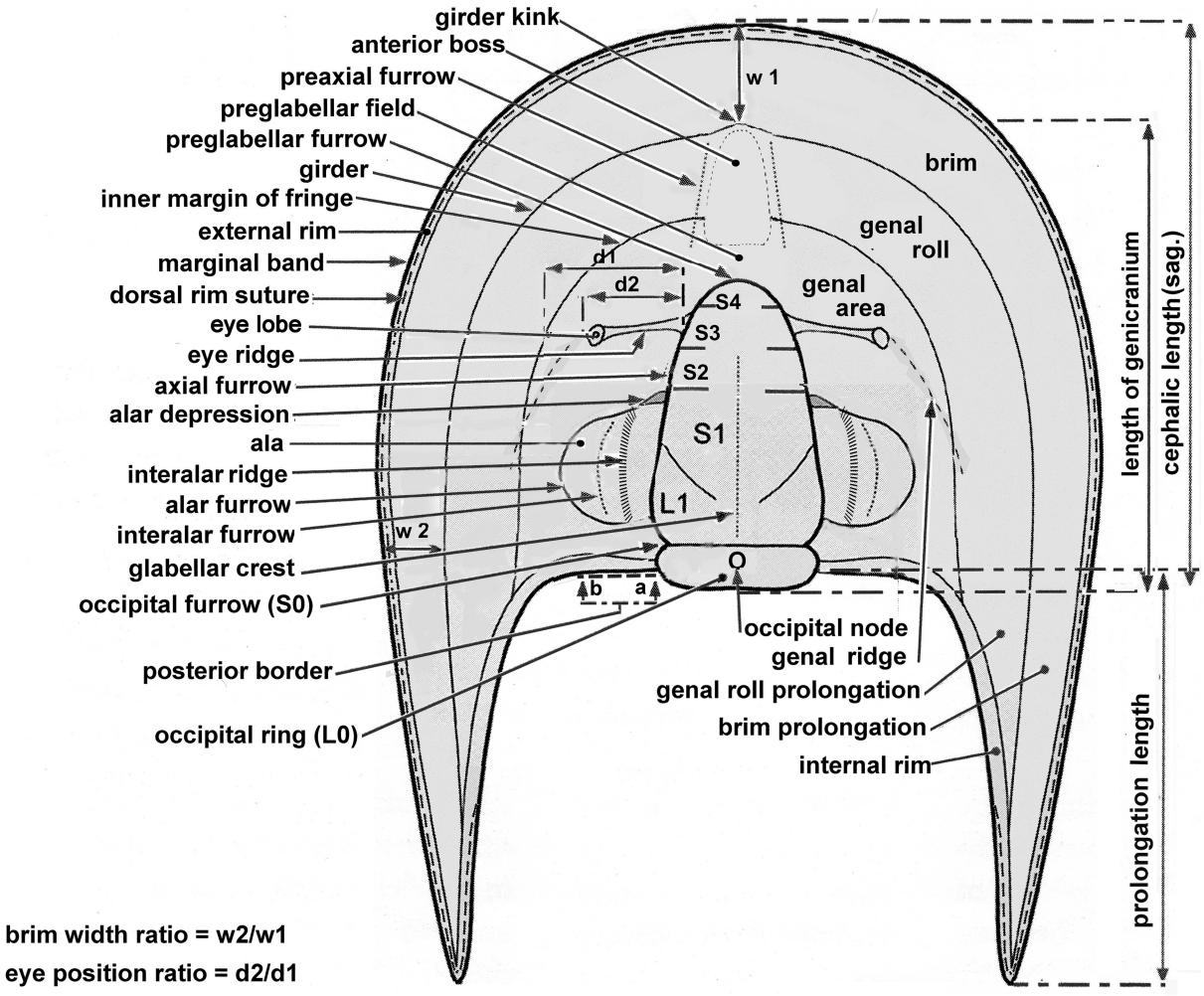


FiGURE 8. Morphology

While typically there are two eye lenses per eye lobe, in the second half of the Pragian some harpetids developed a third, much smaller lens, located high up in between the two other lenses and in at least one case, the lens is set in a cylindrical cavity similar to sublensar alveoli of the schizochroal eye (Pl. 32N). This third lens is found in species of *Fritchaspis* Vaněk, (emend.) 1963, *Kielania* Vaněk, 1963, *Lioharpes* Whittington, 1950a and *Maghroharpes* n. gen. and seems to have existed for a relatively short period disappearing in the lower Emsian. Not all species of these genera carried this third lens during this period, for example *M. oufatenensis* n. sp. and *Lioharpes saredra* n. sp. had only two lenses per eye lobe. On two specimens, denoted as *Maghroharpes* aff.1 *minutipunctus*, the central lens is relatively very large, subtriangular, and upwardly orientated (Pl. 22I) and on another, *M. ihmadii* n. sp., the central lens is apparently split into two separate lenses (Pl.26G) making four lenses per eye lobe in total.

The appearance and disappearance of this third lens coincided with the appearance and disappearance of isolated colonies of corals and stromatoporoids, a habitat that was strongly favoured by several harpetid species, (see Mode

of life and history of harpetids below). The vision provided by the two irregularly shaped main lenses was likely to have been limited but sufficient for relatively sluggish benthic filter feeders (Fortey & Owens 1999; Fortey 2014). The third sub-circular lens of the upper Pragian and lower Emsian might have provided better vision in a more enclosed environment.

It was not until the late Eifelian that a third eye lens reappeared, this time however, it was of a similar shape to the other two accompanying lenses and not circular. This third lens may have involved a response to the marine transgression towards the end of the Eifelian (Morrow & Sandberg 2008) connected with lower light levels in deeper water. The new Moroccan material has two examples of such lenses *Stoloharpes* n. gen. aff. *rissaniensis* (Pl. 49D) and *Stoloharpes retiarius* n. sp. (Pl. 51G). In the case of *S. retiarius* n. sp., the shape of the third lens is not well defined and the other two lenses appear to be no longer convex and partially effaced. In the centre of each of the two largest visual areas there appears to be one small dark tubercle like structure. It is difficult to determine whether this structure is an ommatidium. The visual areas on eye lobes of paratype NHMUK it 29370 are also unclear but this may be a deficiency in preservation.

Cladistic study

Introduction

The purpose of this study is to determine the relationship of the new species described below and to investigate how they might fit into the existing harpetid family structure (and in some cases, modify it). It is not an attempt to re-evaluate the systematics of the whole family Harpetidae, which requires an assessment of many more species. A detailed standard parsimony analysis was undertaken at the species and supraspecific levels, involving predominately the Devonian genera *Harpes*, *Lioharpes*, *Kielania*, *Globoharpes* and *Eskoharpes*, as well as two genera of upper Silurian harpetids, *Scotoharpes* and *Bohemoharpes*. Given the shortage of potential synapomorphies, the strategy of the study was to look for unique combinations of characters which would help identify the different genera. To this end, a total of 111 characters were chosen to be applied to all taxa in the study. This study, being at the supraspecific level, reassessed the existing generic allocations and assisted with the systematic treatment of the new material.

All the species studied were included in one matrix, together with their respective character states. The chosen characters and their different states are defined below. As regards intraspecific variation, details such as sculpture (where preservation allowed) showed virtually no variation. Morphological dimensions did show some variation, but this was catered for by ensuring that the "bin" size was large enough in respect of the relevant character.

Taxa

The number of taxa included in the cladistic analysis totaled 138, including the 37 new species described herein. Eleven harpetid species and two subspecies previously described, and most species in open nomenclature, were excluded from the analysis due to the information on their morphology being unreliable, with no photographs available, or the specimens available being too poorly preserved. These exclusions are as follows: *Harpes altaicus* Weber, 1932*; Bohemoharpes acuminatus* (Lindström 1885)*; Harpes cassinensis* Whitfield, 1897; *H. excavatus* Linnarsson, 1875; *H. fornicatus* Novák, 1890; *H. forojuliensis* Gortani, 1909; *H. gracilis* (Münster, 1840); *H. granti* Billings,1865; *H. koeneni* Wedekind, 1914; *H. pyrenaicus* (Barrois,1866); *H. pygmeaus* Lütke, 1965; *H. radians* Richter, 1863; *Kielania ovalis* Lisogor, 1965; *Lioharpes bischofi* (Roemer, 1852); *L. venulosus alter* Přibyl & Vaněk, 1986; *L. venulosus caillaudi* Pillet, 1972 and *Harpes sinensis* Grabau, 1925. Also excluded are the following unnamed species: *Scotoharpes* sp. (Norford, 1973); *Aristoharpes* sp. (Whittington, 1950a); *Scotoharpes* (?) sp. (Bordet *et al.*, 1960); *Harpes* (?) sp. (Münster, 1840); *H.* (?) sp. (Dean, 1970); *H.* (?) sp. (Kobayashi & Hamada, 1972); *H.* (?) sp. (Owen & Bruton, 1980); *H.* (?) sp. (Thomas, 1978); *H.* (?) sp. (Ingham, 1970); *H.* (?) sp. (Ross, 1972); *H.* (?) sp. (Lane, 1979); *H.* sp. (Ancygin, 1977); *H. sp.* (Alberti, 1981); and *Lioharpes* sp. Rábano & Gutiérrez-Marco, 1993.

All other harpetid species have been included in the study, as listed below. Species already described are listed in their respective genera before any reassignment, which is shown in Fig. 9 and described in systematics below (species to be reassigned marked by *****). New species are listed under the genera assigned by the study.

Harpes Goldfuss, 1839: *Harpes macrocephalus* Goldfuss, 1839; *H. escoti* Bergeron, 1887; *H. hamarlaghdadensis** Crônier *et al*., 2018; H. nymageensis* Fletcher, 1975; *H. ormistoni* Přibyl and Vaněk, 1986; *H. perradiatus** Richter & Richter, 1943; *H. polaris** Maksimova, 1977; *H. pruniformis**, Alberti, 1969; *H. reticulatus* Hawle and Corda, 1847; *H. rouvillei** Frech, 1887; *H. socialis** Hozalpfel, 1895; *H. transiens** Barrande, 1872; *H. whidbornei* Whittington, 1950a; the open nomenclature material *H.* sp.* Alberti, 1969; *H.* sp."1" (Feist 1977, p. 152), *H.* sp. "2"* (Feist, 1977, p. 153), H. sp. "3"* (Feist, 1977, p. 155), and the new species: *H. boudibensis* n. sp., *H.* cf. *boudibensis*, *H. lahceni* n. sp., *H. lentigo* n. sp., *H. oudris* n. sp., *H. prescheri* n. sp., *H. sphenocephalus* n. sp., *H.* cf. *sphenocephalus,* and *H. supercilium* n. sp.

Scotoharpes Lamont, 1948a: *Scotoharpes domina* Lamont, 1948a: *S. aduncus* Fortey, 1980; *S. filiarum* Dean, 1979; *S. lauriei* Jell & Stait, 1985; *S. loma* Lane, 1972; *S. molongloensis* Chatterton & Campbell, 1980; *S. planilimbatus* Lu, 1975; *S. raaschi* Norford, 1973; *S. sombrero* Owen, 1981; *S. vestustus* Zhou & Zhang, 1978; *S. volsellatus* Howells, 1982; *Harpes consuetus* Billings, 1863; *H. judex* Marr & Nicholson, 1888; *H. latior* Poulsen, 1934; *H. lobulatus* Chugaeva, 1975; *H. pansa* Maksimova, 1960; *H. spasskii* Eichwald, 1840; *H. eller* Weller, 1907; *H. trinucleoides* Etheridge & Mitchell, 1917; *H. (Eoharpes) youngi* Reed, 1914; *Eoharpes fragilis* Raymond, 1925; *Aristoharpes rotundus* Bohlin, 1955; *A. taimyricus* Balashova, 1959; *A. willsi* Whittington, 1950a; *Hibertia sanctacrucensis* Kielan, 1960; *Selenoharpes singularis* Whittington, 1965; *S. tatouyangensis* Chang & Fang, 1960; *S. vitilis* Whittington, 1963.

Lioharpes Whittington, 1950a; *Harpes venulosus* Hawle & Corda, 1847; *H. hastatus** Lütke, 1965; *H. montagnei** Hawle & Corda, 1847; *H. perneri** Prantl & Přibyl, 1954; *H. sculptus** Hawle & Corda, 1847; *H. venetus** Gortani, 1915; *Fritchaspis crassimargo* Vaněk ,1963; *Lioharpes vectori** Doubrava, 1991; *Lioharpes wendti** Feist & Belka, 2018 and the new species: *Lioharpes ammari* n. sp.; *L. galea* n. sp.; *L. morocconensis* n. sp.; *L.* cf. *morocconensis*; *L. saredra* n. sp.; and *L. scopulum* n. sp.

Bohemoharpes Vaněk, 1963: *Bohemoharpes naumanni* (Barrande, 1872); *B.* aff. *acuminiatus* Lindström, 1885 (material photographed by M. Zwanzig); *B. buphthalmus* (Bouček, 1935); *B. budovicensis* Přibyl & Vaněk, 1986; *B. hypsipyle* Přibyl & Vaněk, 1986; *B. janae* Doubrava, 1991; *B. naumanni* (Barrande, 1872); *B. ovatus* (Bouček, 1935); *B. ruderalis* (Hawle & Corda, 1847); *B. ungula* (Sternberg,1833); *B. vittatus* (Barrande, 1852) *and B. wilkensii* (Münster, 1840).

Fritchaspis Vaněk, 1963 (emend.): *Fritchaspis edgecombei* n. sp.

Kielania Vaněk, 1963: *Harpes waageni* Prantl & Přibyl, 1954; *H. convexus** Hawle & Corda, 1847; *H. dorbignyanus** Barrande, 1846; *H. dvorcensis** Prantl & Přibyl, 1954; *H. kayseri** Novák, 1890; *H. novaki** Prantl & Přibyl, 1954; *H. praecedens** Prantl & Přibyl, 1954; *Kielania obuti** Přibyl & Vaněk, 1986; *K. stenolimbata* Maksimova, 1977; *K. superna** Maksimova, 1979 and *K. triabsiata* Ormiston, 1971, and the new species described herein: *K. tumula* n. sp. and *K.* aff. *tumula*.

Eskoharpes McNamara *et al.*, 2009 : *Eskoharpes palanasus, E. wandjina, E. boltoni* and *E. guthae* McNamara *et al*., 2009; *E. neogracilis* Richter & Richter, 1924 and *E. sicarius* n. sp.

Globoharpes McNamara *et al*., 2009: *Globoharpes teicherti** and *G. friendi** McNamara *et al*., 2009.

Helioharpes Přibyl & Vaněk, 1981(emend.): *Helioharpes aougili* n. sp.

Maghroharpes n. gen: *Maghroharpes azmamarensis* n. sp.; *M.* cf. *azmamarensis*; *M. forteyi* n. sp.; *M. hammii* n. sp.; *M. ihmadii* n. sp.; *M.* aff. *M. ihmadii*; *M. laatchanensis* n. sp.; *M. minutipunctus* n. sp., *M.* aff1 *minutipunctus* and *M.aff* 2 *minutipunctus*; *M. oufatenensis* n. sp.; *M. terridus* n. sp.; *M. zguidensis* n. sp. and *M.* aff. *zguidensis.*

Pinnuloharpes n. gen.: *Pinnuloharpes apteros* n. sp.; *P*. aff. *apteros*; *P. chaperon* n. sp.; *P. hannabouensis* n. sp.; *P haustrum* n. sp.; *P.* aff. *haustrum; P. igaouii* n. sp.; *P. merzaneensis* n. sp.; *P. segaouii* n. sp.; *P. torquis* n. sp.; and *P.* aff. *torquis.*

Stoloharpes n. gen.: *Stoloharpes calceolus* n. sp. *S*. aff. *calceolus; S. capricornus* n. sp.; *S.* aff. *capricornus; S. retiarius* n. sp.; *S. rissaniensis* n. sp. and *S.* aff. *rissaniensis*.

In Table 1, Figure 9 and Figure 10 the following abbreviations have been used for the purposes of brevity and clarity:

Harpes Goldfuss,1839	= *H.*	*Eoharpes* Raymond, 1905	= *E.*
Scotoharpes Lamont,1948a	= *S.*	*Lioharpes* Whittington, 1950a	= *L.*
Bohemoharpes Vaněk, 1963	= *B*.	*Fritchaspis* Vaněk, 1963	= *F.*

Kielania Vaněk, 1963	= *K.*	*Helioharpes* Přibyl & Vaněk, 1981	= *Hl.*
Declivoharpes Přibyl & Vaněk, 1981	= *D.*	*Eskoharpes* McNamara *et al.*, 2009	= *Es.*
Globoharpes McNamara *et al.*, 2009	= *G.*	*Maghroharpes* n. gen.	= *M.*
Pinnuloharpes n. gen.	= *P.*	*Stoloharpes* n. gen.	= *St.*
Holotype	= Ht	Paratype	= Pt
Other Material	= OM	Not figured	= NF
Systematics	= Syst	New material	= NM
Same as specimen above (where there is more than one specimen on plate)			= SP

Characters and character states for cladistic analysis

All species already described were coded from published material and from the photographs illustrated in Plates 10 and 53 to 59 herein. All new specimens coded are holaspids more than 0.75 cm long (sag.). In the character states set out below, all linear measurements are relative rather than absolute except in the case of standardised brim perforation sizes (character 73), which are measured in microns (μm). Angles of slopes and convergence were measured using the 'rectangular marquee tool' of Adobe Photoshop Elements 13, which gives the horizontal and vertical distance between the relevant two points. These distances were then entered into Cleave Books online right-angle triangle calculator to give the angle required.

Explanations of how other character states were measured are given as footnotes to the relevant character where necessary.

The presence/absence of an occipital node is a character often used in trilobite cladistic studies. All material used in the current study, which was well enough preserved to determine this state, carried an occipital node. The character was therefore not considered phylogenetically relevant and omitted from the study.

A Cephalon:

1. Widest point (tr.) of cephalon:
   - at alae (Pl. 54I) 0
   - aid-point between eyes lobes and alae (Pl. 57A) 1
   - at eye lobes (Pl. 18A) 2
   - posterior to alae (Pl. 55I) 3

   Where the widest point fell between any two of the above positions the character state attributed was that of the closest position.

2. Outline shape of cephalon:
   - sub oval (2 axes of symmetry) (Pl. 53I) 0
   - ovoid (1 axis of symmetry) (Pl. 33A) 1
   - sub circular (Pl. 54I) 2
   - pyriform slightly (Pl. 47A) 3
   - strongly (Pl. 50A) 4

3. Genicranium length (sag.) / width (tr.):
   - very broad, under 0.65 (Pl. 7A) 2
   - broad, 0. 65–0.74 (Pl. 57A) 0
   - narrow, 0.75–0.85 (Pl. 54I) 1
   - very narrow, over 0.85 (Pl. 9A) 3

4. Widest point of genicranium:
   - at alae (Pl. 44A) 0
   - at posterior border (Pl. 14A) 1

between alae and eye lobes (Pl. 51A) 2

Where the widest point falls between any two of the above measuring points, the character state attributed was that of the closest measuring point. In dorsal view, where flanks of the genicranium become parallel and the widest point of the genicranium crosses more than one of the measuring points above, the anterior measuring point is selected.

5. Glabella inset below surface of genal area where genae are strongly inflated (Pl. 7A) 0
Glabella not inset where genae are weakly inflated (Pl. 18H) 1

6. Glabella anterior to S0 width (tr.) at S1 / length (sag.):
< 0.55 (NF) 3
0.55 to 0.65 (Pl. 21A) 1
0.66 to 0.75 (Pl. 5A) 0
> 0.75 (Pl. 54A) 2

7. Crest of glabella rounded (Pl. 5C) 0
Glabella carinate (Pl. 4E) 1

8. Viewed anteriorly glabella flanks convex (Pl. 5C) 0
Viewed anteriorly glabella flanks tectiform (roof shaped) (Pl. 17A) 1

9. On glabella anterior to S0: no ornamentation (Pl. 1K) 0
Present on glabella anterior to S0:
granulation (Pl. 23E) 1
tubercles (Pl. 7a) 2
blisters* (Pl. 50A) 3
very fine reticulation (Pl. 16I) 4
(*Dorsal surface broad and nearly flat, unlike tubercles which are domed or pointed)

10. No small single axial tubercle on anterior of glabella (Pl. 18G) 0
Small single axial tubercle present on anterior of glabella (Pl. 57D) 1

11. On glabella anterior to S0:
pitting (Pl. 3A) 0
no pitting (Pl. 1K) 1

12. S1 on flanks of glabella:
rising vertically out of axial furrow, not curving forward (NF) 0
sloping backwards but not curving forward (Pl. 12G) 1
sloping backwards before curving forward around the top of the muscle insertion area (Pl. 3A) 2
S1 a shallow depression in axial furrow only (Pl. 17A) 4
S1 not evident (Pl. 37F) 3

For the purposes of determining the states of this character, only the dorsal surface of the cuticle was considered. Based on the evidence of the few specimens where the cuticle had been lost, S1 appeared to be much more clearly and completely defined by the inner surface of the cuticle.

13. Other muscle insertion furrows at:

S2 only (Pl. 4E)	1
S 2 & 3 (Pl. 54E)	0
S 2, 3 & 4 (Pl. 14K)	2
No furrows at S2–4 (Pl. 18A)	3

The muscle attachment areas (S0 to S4) were often much more visible as dark areas on the flanks of the glabella. These were not included as characters as the colouring could be influenced by the nature of the matrix.

14. Axial furrows converging anteriorly:

strongly (15^0 or more) (Pl. 4E)	0
weakly (less than 15^0) (Pl. 5A)	1
Axial furrows not converging (Pl. 44A)	2

The angle measured was the angle of the axial furrow to the axis (as seen in dorsal view). The two measuring points used were the axial furrow at junction with S1 and the point at which the curve of axial furrow starts to tighten to join the preglabellar furrow.

15. Preglabellar furrow:

distinct (Pl. 2G)	0
shallow (Pl. 12H)	1
nearly effaced (Pl. 2A)	2

16. Preglabellar furrow in anterior view:

bowed downwards (Pl. 18H)	0
straight (Pl. 12H)	1
bowed upwards (Pl. 2G)	2

17. Occipital furrow shallow (sag.)(Pl. 38B) 0
Occipital furrow deep (sag.) (Pl. 2J) 1

18. Occipital furrow medially: straight (dorsal view) (Pl. 38A) 0

bowed forward (Pl. 16A)	1
bowed posteriorly (Pl. 46A)	2

19. Occipital furrow width (sag.):

same as, or greater than posterior border (exsag.) (Pl. 43C)	1
between half of to almost the same as width (exsag.) of posterior border (Pl. 51A)	0
under half of width (exsag.) of posterior border (Pl. 55L)	2

The width of the posterior border was measured at its widest point.

20. Occipital ring where not medially broadened: very broad, broader (sag.) than posterior border (exsag.) (Pl. 2I) 1
narrow, narrower than posterior border (exsag.) (Pl. 17A) 0
broad, same width as posterior border (exsag.) (Pl. 10E) 2

The width of the posterior border was measured at its widest point.

21. occipital ring:

not medially broadened (sag.) (Pl. 10E)	0
medially broadened (sag.) (Pl. 16A)	1

22. Seen in lateral view top of occipital ring:

higher than glabella anterior to S0 (Pl. 12I)	0
lower than glabella anterior to S0 (Pl. 16B)	1
same height as glabella anterior to S0 (Pl. 26C)	2

23. Occipital ring in lateral view:

near vertical (Pl. 17C)	0
sloping backwards (Pl. 12I)	1

24. No sculptural tubercles or granulations on occipital ring

(Medial occipital node excluded) (Pl. 40E)	0
Sculptural tubercles present on occipital ring (Pl. 5A)	1
Fine granulation on occipital ring (Pl. 32B)	2
Reticulate pattern of very fine raised ridges (Pl. 16A)	3
Pitting on occipital ring (Pl. 44A)	4
Pitting and tubercles on occipital ring (Pl. 32E}	5

25. L1:

inflated (Pl. 11A)	0
not inflated (Pl. 23A)	1

Inflation was determined by whether the axial furrow had been displaced outwards or effaced by L1.

26. Alar size:

small tr. (< 30% of glabella anterior to S0 sag.) (Pl. 40A)	0
large tr. (30% & over of glabella anterior to S0 sag.) (Pl. 1A)	1

27. Alar dimensions: width (tr.) divided by length at axial furrow (exsag.):

very narrow	< 0.65 (Pl. 21A)	4
narrow	0.65–0.80	3
moderately wide	> 0.80–0.95	2
wide	> 0.95–1.10	1
very wide	> 1.10 (Pl. 4L)	0

28. Alar shape:

parabolic (Pl.1A)	0
subtriangular (Pl. 54E)	1

29. Ala direction:

laterally directed (Pl. 14A)	0
anterolaterally directed (see example Pl. 18G)	1

30. Ala:

flat (not rising above genal area) (Pl. 18G)	0
Inflated (Pl. 2C)	1
depressed below genal area (NF)	2

31. Alar furrow:

deep, well-defined (Pl. 7A)	1
shallow, well-defined (Pl. 5A)	0
very shallow and distally effaced (Pl. 36A)	2
effaced (Pl. 38E)	3

32. Interalar furrow:

absent (Pl. 26A)	0
present (Pl. 4E)	1

33. Interalar ridge:

absent (Pl. 28A)	0
present (Pl. 4E)	1

34. Alar depression:

absent (Pl. 9F)	0
present (Pl. 7A)	1

Widening of axial furrow as it meets the anterior alar furrow.

35. Axial furrow effaced where ala joins basal lobe (Pl. 12G) 1
Axial furrow crossing junction of ala with basal lobe (Pl.3A) 0

36. Posterior border:

< 25% of width (tr.) of occipital ring (Pl. 51A)	1
between 25% and 30%	2
between 31% and 40%	3
between 41% and 50%	0
between 51% and 60% (Pl. 35A)	4
> 60% (NF)	5

The junction between the posterior border and the genal prolongations was determined by drawing a line sub-parallel to the posterior edge of the border from the occipital ring (Fig. 7 point a) to where the point where it first touches the border as the border starts to curve posteriorly (Fig. 7 point b).

37. No preglabellar field (Pl. 17A) 1
Preglabellar field (sag.):

very narrow < 10% of width (tr.) (Pl. 18G)	0
narrow 10%–20%	2
wide 21%–30%	3
very wide > 30 % (Pl. 44B)	4

38. Genal area (tr.):

broad (67% and above of length exsag.) (Pl. 35A)	0
narrow (below 54% of length exsag. and under.) (Pl. 1K)	1
medium width (54% to 66% of length exsag.)	2

39. Genal area with:

pronounced caeca (Pl. 54E)	0
faint caeca (Pl. 14A)	1
no caeca (Pl. 1K)	2

40. Genal area with:

fine pits (Pl. 42A)	0
no pits (Pl. 1M,K)	1

41. Genal area with:

no tubercles or granulation (Pl. 1M,K)	0
tubercles or granulation (Pl. 12G)	1
reticulate pattern of very fine raised ridges (Pl. 16I)	2

42. Eye lobes:

very small	< 15% exsag. of glabella width (tr.) at S1 (Pl. 53k)	0
small	15%–31% exsag. of glabella width (tr.) at S1	1
large	32%–45 % exsag. of glabella width (tr.) at S1	2
very large	45%–60% exsag. of glabella width (tr.) at S1 (Pl. 3D)	3

43. Lateral position of eye lobes:

eye location ratio of over 0.80 (Pl. 18G)	1
eye location ratio under 0.80 (Pl. 32A)	0

(For definition of eye location ratio see Figure 6)

44. Eye lobes:

extending to edge of axial furrow (Pl. 7A)	1
not extending to axial furrow (Pl. 40A)	0

45. Eye lobes:

barely developed (Pl. 53K)	0
weakly inflated	1
inflated	2
strongly inflated (Pl. 7A)	3

46. Eye lobe shape (dorsal view):

circular/oval (inner edge of lobe convex) (Pl. 14J)	0
cone shaped (Pl. 5A)	1
reniform shaped (inner edge of lobe concave) (Pl. 40A)	2
eye lobe divided (Pl. 56G)	3

47. Dorsal surface of palpebral lobes with:

no ornamentation (Pl. 2A)	0
tubercles (Pl. 7A)	1
pitting (Pl. 42A)	2
tubercles and pitting (Pl. 29H)	3

48. Eyes with:

a single lens (Pl. 53K)	0
two lenses (Pl. 3K)	1
three lenses (Pl. 11L,D)	2
four lenses (Pl. 26G)	3

49. Genal ridge:

absent (Pl. 12I)	0
present (Pl. 56C)	1

50. Eye lenses relative sizes:
- anterior largest (Pl. 40C) 0
- posterior largest (NF) 1
- central lens largest (Pl. 22I) 2
- anterior and posterior are largest lenses equal in size (Pl. 12K) 3

51. Eye lens location:
- on flanks of eye lobe (Pl. 12I) 0
- on dorsal surface of eye lobe (upwards looking) (NF) 1
- on both dorsal and lateral surfaces (Pl. 22I,J) 2

52. Eye ridge:
- narrow, well defined, curved (Pl. 43C) 0
- well defined, straight (Pl. 14A) 1
- not well defined (Pl. 32E) 2
- absent (Pl. 12G) 3

53. Course of inner margin of fringe across the anterior of genicranium either side of anterior of glabella:
- convex (Pl. 18G) 2
- straight (Pl. 4E) 1
- concave (Pl. 14A) 0

54. Inner margin of fringe:
- not marked by bigger perforations or furrow (Pl. 32 P,G) 0
- marked by:
- bigger perforations across anterior boss only (Pl. 5C) 1
- bigger perforations along all the inner margin (Pl. 54K) 2
- furrow & bigger perforations along whole inner margin (NF) 3
- furrow only along whole inner margin (NF) 4

55. No anterior boss (Pl. 5A) 0
Anterior boss:
- barely inflated (Pl. 4E) 1
- Inflated (Pl. 26A) 2

56. Anterior boss not reaching girder (Pl. 10E) 0
Anterior boss reaching girder (Pl. 26A) 1

57. Anterior boss not joined to glabella (Pl. 10E) 0
Anterior boss joined to glabella (Pl. 49G) 1

58. Preaxial furrows do not converge towards girder (Pl. 4E) 0
Furrows converge (Pl. 12G,H) 1

59. No girder kink (Pl. 1K) 0
Weak girder kink (Pl. 12G) 1
Girder kink Σ shaped (Pl. 21E) 2

60. Genal roll continuing curvature of genal area (Pl. 1M) 0
change of curvature at the inner margin of the fringe (Pl. 56B) 1

61. Genal roll sloping anteriorly (sag.):

gently	30°–40° (Pl. 17C)	1
moderately steeply	41°–50°	0
steeply	51°–60° (Pl. 5B)	2

(in lateral view the angle between the horizontal and a straight line drawn between the top of the girder and inner margin of fringe)

62. Genal roll sloping laterally (tr.):

very gently	< 45° to horizontal (Pl. 54J)	1
gently	45°–55°	2
moderately steeply	56°–65°	3
steeply	66°–75° (Pl. 4F)	0

In anterior view the angle between the horizontal and a straight line drawn between the top of the girder and inner margin of fringe at the widest point of the genicranium.

63. In lateral view narrowing of internal fringe: width of internal fringe,directly below the anterior of eye lobes divided into the width of fringe at its narrowest point on the flanks of the genicranium.

Narrowing:

barely	> 0.90 (Pl. 56B)	0
moderately	0.75–0.90	1
strongly	0.60–0.75	2
very strongly	< 0.60 (Pl. 18D)	3

64. Caeca on genal roll:

absent (Pl. 40G)	0
present (Pl. 11A)	1

65. Genal roll perforations:

same as on brim (Pl. 5C)	0
smaller than on brim (Pl. 4N)	1
bigger than on brim (Pl. 58C)	2

66. Perforations all same size on genal roll

(excluding any row at inner margin of fringe (Pl. 46B)	1
Single row of larger perforations above girder (Pl. 40F)	0
Perforations graduated, becoming smaller away from girder (Pl. 42N)	2
Single row of larger perforations above girder across the anterior of genicranium only (NF)	3
Perforation larger anteriorly and in a single row above the girder (Pl. 51A)	4

67. Width of girder (sag.) x 100 divided by width (tr.) of genicranium:

wide	>3 (Pl. 21B)	0
moderately wide	2.20–3	1
moderately narrow	1.5–2.20	2
narrow	<1.5 (Pl. 14K)	3

68. Girder:

unperforated (Pl. 28B)	0
with large central perforations (Pl. 37G)	1

69. Brim profile:

concave (lateral as well as sagittal) (Pl. 26B)	0
straight (neither concave nor convex) (Pl. 4G,F)	1
concave sag., straight laterally (Pl. 1M)	2
convex (Pl. 51A)	3
concave sag., convex laterally (NF)	4
convex anteriorly close to girder, becoming concave distally (NF)	5
convex anteriorly close to girder, becoming straight distally (NF)	6

70. In dorsal view brim width sag. % of cephalon sag.

Narrow	<29 % (Pl. 40a)	1
moderately wide	29% to 34%	0
wide	35% to 38%	2
very wide	>38% (Pl. 54I)	3

71. Brim sloping:

slightly	<10° (Pl. 40G)	1
moderately	10°–20°	2
moderately steeply	21°–30°	0
steeply	31°–40°	3
strongly	41°–50° (Pl. 58A)	4
very strongly	>50	5

In lateral view the angle between the horizontal of a straight line drawn between the proximal edge of the brim and the junction of the brim with the external rim.

72. Brim width ratio:

1.0 or greater (Pl. 54I)	1
0.95 to 1	0
0.86 to 0.94	2
0.76 to 0.85	3
0.66 to 0.75	4
<0.66 (Pl. 1K)	5

Brim width (tr.) at S0 divided by brim width sag. (see Figure 6).

73. Standardised brim perforations' diameters:

very fine	<100 µm (Pl. 23I)	1
moderately fine	100 µm to 150 µm	2
moderately large	151 µm to 200 µm	3
large	201 µm to 250 µm	0
very large	>250 µm (Pl. 51A)	4

Standard brim width sag. was selected at 5 mm. The diameter of brim perforations (tr. and exsag.) were measured from dorsal view photographs of a 1 sq. mm located across the middle of the brim (sag. and tr.). Where this was not possible, an area as close as possible to this area was selected. The diameters of perforations were measured (exsag. and tr.), averaged and standardised to adjust for brim width as explained above. In the cases where brim perforation could be measured, brim slope did not materially distort the averaged perforation sizes.

74. Row of larger perforations on the brim at:

both the proximal and distal edges (Pl. 1K)	2

distal edge only (Pl. 57G) 1
neither edge (Pl. 53I) 0

75. Perforations:
not graduated outwards from the girder (Pl. 12G) 3
becoming smaller outwards from the girder (Pl. 11A) 1
becoming larger outwards from the girder 2
becoming smaller medially (Pl. 53I) 0

76. No caeca on brim (Pl. 1K) 0
Caeca just reaching onto brim (Pl. 26A) 1
Light caeca reaching across brim (Pl. 11A) 2
Caeca forming strong network on brim (Pl. 17A) 3
Spaces between perforations inflated (Pl. 33B) 4

77. No blister-like tubercles on brim (Pl. 1K) 0
Blister-like tubercles on brim (NF) 1

78. External rim:
stout (10% or more of total brim width (sag.)) (Pl. 12G) 1
fine (under 10% of total brim width (sag.)) (Pl. 14A) 2
undeveloped (Pl. 53I) 0

79. Dorsal surface of external rim:
without sculpture (Pl. 1K) 0
with fine tubercles (Pl. 5A) 1
with granulation (Pl. 57G) 2

80. Dorsal surface of external rim close to horizontal and marginal band near vertical (Pl. 12I) 0
Dorsal surface of external rim tilted outwards and marginal band sloping down and under cephalon:
anteriorly and laterally (Pl. 47D) 1
posterolaterally only (Pl. 2B) 2

81. Marginal band:
concave (Pl. 27N) 1
with a straight profile (Pl. 42C,M) 0

82. Marginal band with:
no ridges (Pl. 4G,F) 0
ridges top and bottom (Pl. 26I) 1
top, bottom and medial ridges (Pl. 39F,J) 2
medial ridge only (NF) 4
dorsal surface of rim overhanging marginal band (Pl. 12C) 3

83. Marginal band with:
no tubercles or granulation (Pl. 40A) 0
Tubercles (Pl. 29B) 1
Granulation (Pl. 17C) 2

84. Prolongations (excluding genal spine) length (exsag.) as % of length of cephalon (sag.).

very long	>100% (Pl. 37E)	4
long	95%–100%	3
moderately long	86%–94%	2
moderately short	76%–85%	0
short	65%–75% (Pl. 22N)	1
very short	<65% (NF)	5

85. Prolongations not strongly tapered in lateral view (Pl. 1M) 0
Prolongations tapered (at mid-point half of height or less at junction with posterior border) (Pl. 17C) 1

86. In dorsal view internal rim:

sub parallel (medially) (Pl. 23E)	0
curving adaxially (Pl. 14A)	1
slanting abaxially before curving adaxially (Pl. 50A)	2
straight slanting abaxially (NF)	3
curving adaxially then abaxially (Pl. 37E)	4

87. In dorsal view external rims on prolongation:

curving adaxially (Pl. 1K)	0
straight slanting adaxially (Pl. 38F)	1
slightly concave (Pl. 38A)	2

88. In lateral view profile of internal rims:

concave (Pl. 4G)	0
straight (until meeting external rim) (Pl. 38B)	1
weak wave-like profile (Pl. 7D)	2
strong wave-like profile (Pl. 2J)	3

89. Internal rim meeting with external rim:

at end of prolongation (Pl. 1M)	0
before end of prolongation but not joining until at end of prolongation (Pl. 38B)	1
joining with external rim before end of prolongation (see example Pl. 51C)	2

90. No genal spine (Pl. 32E) 2
Genal spine:

short, < 10% of length (exsag.) of prolongation (Pl. 3K)	0
Long, > 10% of length of prolongation (Pl. 35A)	1

91. Genal spine following curve of external rim (Pl. 35A) 0
Genal spine not following curve of external rim (Pl. 47C) 1

92. Extension of girder continuing to end of prolongation (NF) 0

meeting internal rim +/- 2/3 of the way down prolongation (Pl. 31M)	1
meeting +/- 1/2 the way down prolongation	2
meeting +/- 1/3 the way down prolongation	3

meeting +/- 1/4 the way down prolongation 4
meeting +/- 1/6 the way down prolongation (Pl. 59G) 5
extension of girder not meeting internal rim (Pl. 18D) 6

93. Tubercles on the dorsal surface of internal rim (Pl. 5A) 1
Dorsal surface of internal rim smooth (Pl. 26A) 0

94. No large perforations under internal rim (Pl. 18D) 0
Row of large perforations beneath all of the internal rim (Pl. 4G) 1
Row of large perforations beneath part of the internal rim (Pl. 4N) 2

95. Brim does not steepen on prolongations (Pl. 21C) 0
Proximal edge of brim steepens posteriorly (Pl. 18J) 1
Whole of brim steepens moderately to less than vertical (Pl. 51A) 2
Brim steepens quickly to near vertical (Pl. 1K) 3

B Thorax:

96. Axis on last thoracic segment as a % of that of the first segment:
50–60% (Pl. 46N) 0
40% – 49% 1
30% – 39% 2
20% – 29% (Pl. 19M) 3

97. Tubercles on anterior axial rings (Pl. 5A) 1
No tubercles or granulation on axial rings (Pl. 1A) 0
Granulation on axial rings (Pl. 17A) 2

98. Pitting on axial rings (Pl. 42A) 1
No pits on axial rings (Pl. 3A) 0

99. Thoracic segments:
16 or less (Pl. 53I) 0
17 to 19 (Pl. 40J) 1
20 to 23 (Pl. 3A) 2
24 to 28 (Pl. 1A) 3
more than 28 (Pl. 55I) 4

100. Pleurae lengthening (tr.) to
5th segment (greater than narrowing of axis) (Pl. 10I) 1
7th segment (greater than narrowing of axis) (Pl. 17A) 2

Pleurae in first 5 thoracic segments
lengthening to compensate for narrowing of axis only (Pl. 42A) 0
not lengthening to compensate narrowing of axis (NF) 3

101. Shortest (tr.) pleura as % of longest pleura (inner portion only)
66–75 (Pl. 46G) 0
56–65 (NF) 1

46–55 (Pl. 10I) 2
35–45 (Pl. 40J) 3
Less than 35 (Pl. 9A) 4

102. Pleural furrows:
broad (>50% width of pleura exsag.) (Pl. 5D) 0
narrow (<50% width of pleura exsag.) (Pl. 42A) 1

103. Pleural furrows:
deep (Pl. 5D) 0
shallow but well-defined (Pl. 42A) 1
shallow almost effaced (see example Pl. 44A) 2
effaced (see example Pl. 40E) 3

104. Pleural furrows U-shaped in cross section (exsag.) (Pl. 53I) 0
V-shaped in cross section (exsag.) (Pl. 21F) 1

105. Pitting on pleurae (Pl. 42A) 1
No pits on pleurae (Pl. 40J) 0

106. Outer portion of pleurae slanting slightly posteriorly from:
junction with inner portion (Pl. 7L) 0
outer portion in line (tr.) with inner portion (Pl. 17J) 1

107. Outer portion of pleurae:
straight (Pl. 33E) 0
Curved anteriorly (Pl. 46F) 1
Curved posteriorly (NF) 2

108. Pleurae terminating in a point (Pl. 46F) 1
Distal ends rounded (Pl. 45E) 0
Distal ends straight (truncate) (Pl. 23M) 2

C Pygidium:

109. Number of axial rings on the pygidium (+ tail piece):
2 (Pl. 33F) 1
3 (Pl. 53I) 0
more than 3 (Pl. 55J) 2

110. No tubercles on posterior axial rings (Pl. 53I) 0
Tubercles on posterior rings (Pl. 33F) 1

111. No borders around posterior edge (Pl. 33F) 0
Borders around posterior edge (NF) 1

Material and methods

The material described herein was acquired on the international market, from Moroccan trilobite miners whom the author accompanied on trips to the many mining localities in the Anti-Atlas of the Dra–Tafilalet and Souss–Massa regions of Morocco. GPS readings were taken of the mining sites and the material found was marked and recorded. The material purchased has been transferred to the collection of the Natural History Museum, London. Although there are some articulated specimens, most of the material consists of disarticulated cephala. Very few lower lamellae, cranidia or hypostomes were found. Prior to photography, the material was coated with ammonium chloride except in certain cases where muscle insertion impressions and eye lenses were more easily seen uncoated. Photographs were processed using Helicon Focus 6.7.1 and edited using Adobe Photoshop Elements 13. For species already described, an attempt was made to locate and photograph holotypes, or failing that, topotype specimens from the type localities. The photographs are refigured in Figures 63 to 69. To carry out a parsimony analysis, a data matrix of the relevant taxa and the chosen characters together with character states, was compiled using the Nexus Data Editor. The data matrix comprised 111 (characters) X 138 (taxa). Of the 111 characters, 95 related to the cephalon, 13 to the thorax, 3 to the pygidium and none to the hypostome, as the new material contained only two specimens with hypostomes visible. The data matrix is shown in Table 3.

For the parsimony analysis, *Eoharpes* Raymond, 1905 (redescribed by Whittington 1949), (Pl. 53 **G**–L) was chosen as an outgroup and the better-known *E. beningensis* (Barrande, 1872) was the species selected to be included in the matrix.

Parsimony analysis was carried out with TNT (Goloboff & Catalano 2016; Cladistics DOI 10.111/cla.12160, a free programme provided by the Willi Hennig Society), using the "New Technology" option. Heuristic searches were undertaken with equal character weights as well as implied weights, with varied concavity constraints, and with the default function set at six different settings, where k = 2, 3, 4, 5, 6 and 7, respectively. Ratchetting, drift and tree fusing available under New Technology were activated. The settings that yielded the shortest cladograms were as follows: for "ratchetting" and "drift", the perturbation phase was stopped when 98 substitutions had been made or 99% of swapping had been completed; for ratchetting, during perturbation, alternate weighting was used with up-weighting and down-weighting probabilities set at 20 and 10, respectively. The number of iterations was 1,000 with one auto constrained iteration. For drift parameters, sub-optimal rearrangements were accepted with maximum fit difference and maximum relative fit difference of 5 and 10, respectively. The rejection factor was set at 45 and the number of cycles at 50, with one auto constrained cycle. Tree fusing parameters were 70 rounds with the options of "Save as equals", "Swap after exchange", "Start from best tree", "Choose best exchanges" and "Use fusing to multiply optimal trees" switched on. Searches were carried out using 20 different random seeds and the trees found were exported to ASad0 Ver. 1.61 TNT-MRBAyES SLAVER (vl 5.30) for editing and further analysis using the optimisation option "unambiguous changes only". Based on this analysis, the first tree of the search that found the most trees (seed 7) was selected and the final editing of this tree, and the consensus tree, was undertaken in Adobe Photoshop Elements 13. Node support was calculated for the selected trees using jackknifing, with character removal probability set at 36, replicates set at 1000 and using the same New Technology settings as described above. Bremer support analysis using suboptimal trees was also calculated. The matrix may be downloaded from http://www.morphobank.org.

Results

The new material does not extend the range of *Scotoharpes* or *Bohemoharpes* to the Devonian of Morocco and therefore a review of these two genera is considered outside the scope of this paper.

The new Moroccan material is included in 10 different clades: *Eskoharpes*, *Fritchaspis*, *Declivoharpes*, *Harpes, Helioharpes, Kielania*, *Lioharpes, Maghroharpes* n. gen., *Pinnuloharpes* n. gen. and *Stoloharpes* n. gen.. *Declivoharpes*, *Fritchaspis* and *Helioharpes* and are reinstated as genera. Using equal character weights, 19 of the 20 different searches found a total of 636 shortest trees with lengths of 1968, CI = 12 and RI =48. One search found shortest trees of 1969. Table 4 shows the search results for each random seed together with the node collapse for the relevant strict consensus tree. The consensus tree for all the shortest trees involved the collapse of 31 nodes and is shown in Figure 9. The most trees found in a single search was 60 using seed 7. The consensus tree of these 60

trees involved the collapse of 20 nodes. Figures 10a–10e map the characters and states on the first tree of the seed 7 search, their location being marked by a white circle if they are homoplastic, or black if they are unique unreversed synapomorphies. As can be seen nearly all character states are homoplastic and very few are unique unreversed synapomorphies. Jackknife analysis provided support of 50 or over for only three nodes. There was no Bremer support for any nodes, even though the less consensus tree has more structure than those of Ebach & McNamara (2002), and the analysis provides a way of defining clades more objectively than Přibyl & Vaněk (1986), on the basis of a much larger range of characters. Beech & Lamsdell's (2021) study was designed to explore the phylogenetic relationship within Harpetida and to understand the relationships between extinction events and disparity, using selected harpetid species to represent the different genera. It included only one third of the existing described species included in the current study and was, therefore, of little assistance in confirming or otherwise the assignment of taxa to existing or new genera. In addition, the author's observations disprove Lamsdell's coding relating to the presence or absence of an occipital node. Of the 24 harpetid species common to both studies, Beech and Lamsdell scored 13 as having no occipital node, namely *Eoharpes benignensis, Bohemoharpes naumanni* (Barrande,1872)*, Fritchaspis montagnei, Harpes macrocephalus* Goldfuss, 1839, *H. whidbornei* Whittington, 1950a, *Lioharpes venulosus, Scotoharpes domina, S. consuetus, S. latior, S. loma, S. raaschi, S. spasskii* and *S. tatouyangensis*. The following clearly do have an occipital node: *Fritchaspis montagnei* (see Pl. 57A), *H. whidbornei* (see Morphobank.org, Beech & Lamsdell 2021, Fig. M595186) *Lioharpes venulosus* (see Lectotype, Prantl & Přibyl 1954, pl 2, fig. 6 and Pl. 10A) and *Harpes macrocephalus* (see Basse & Müller 2004, Figs 314, 665). *Scotoharpes spasskii* would appear to have a small, almost granule-sized node located in a small depression on the anterior edge of the dorsal surface of the occipital ring (see Klikushin *et al.* 2009, Figs 469, 470). As regards other species, the author has seen no material or figures where the occipital ring was sufficiently well-preserved to be able determine whether an occipital node was present or not.

The relevant phylogenetic findings of the current study are discussed in the systematics section below.

The searches with implied weightings yielded topologies that conflict with generic assignments under equal weights, those where k = 2, 3, 4, 5, 6 and 7. All weighting used produced trees in which the genera were non-monophyletic, for instance with Ordovician species being placed between Devonian species. The best score fit values were for K2, 84.05645; K3, 78.98202; K4, 74.69542; K5, 71.02836; K6, 67.74779 and K7, 64.81916. All searches produced only one tree.

In carrying out the cladistics analysis, over 2600 separate analyses were undertaken as the data matrix was being developed and new material added. Often these produced poorly-resolved consensuses, but the Devonian genera that were most stable were *Harpes*, *Eskoharpes*, *Globoharpes* and *Helioharpes*, with *Pinnuloharpes* and *Stoloharpes* merging occasionally. *Maghroharpes* tended to subdivide into two or three separate subgroups; *Kielania* on occasions was reduced to the type species, the other species being in a paraphyletic relationship with *Eskoharpes* and *Globoharpes*. *Lioharpes* was the most unstable.

While *Scotoharpes* or *Bohemoharpes* are not the focus of this study, it should be noted in Figure 9 that the *Scotoharpes* and *Bohemoharpes* clades include several species currently attributed them with all other species either in a paraphyletic relationship or forming small sister groups. Also, a relevant part of the tree has been collapsed in arriving at a consensus and it would be unwise to rely on these results without a full systematic review of the whole Harpetidae family. It was found that *Eskoharpes* comprises a paraphyletic group that contains *Globoharpes*, and *Globoharpes* is reduced here to a junior subjective synonym of *Eskoharpes*. *Lioharpes Crassimargo* is shown as an isolated species in the cladogram Fig. 9 and is of indeterminate genus so remains pro tem in its existing genus.

Table 5 has been drawn up as a practical guide to assist in determining whether a harpetid trilobite belongs to one of the genera reviewed or described herein. It is based on the characters and states of cephala used in the matrix prepared for the cladistic study and described above. For each genus s.s., the characters which had states that were common to at least 70% of taxa of that genus were selected. Those characters where it was not possible to determine states for more than 50% of species were ignored. Taxa of other genera were then checked for the same character states and where a state was found to be shared with less than 30% of the total it was retained on a shortlist. A subjective assessment was then made as regards those character states which were shared more widely (up to 60%), and those which helped to differentiate between genera were added to the short list. From this list, Table 5 was prepared, making a few minor adjustments to some bin sizes and combining two character states where this was helpful. In column 5, the blank "squares" show there is no diagnostic character for that part of the cephalon shown at the head of the column.

Table 5 also gives guidance as to the reliability of the diagnostic characters chosen, in terms of the level of support given by the taxa in each relevant genus (columns 4 and 5), and the extent to which the characters are shared by other genera (columns 7 and 8). Column 4a shows the number of taxa which comply with the character state where compliancy is at its lowest and 4b, the average number of supporting taxa across all chosen character

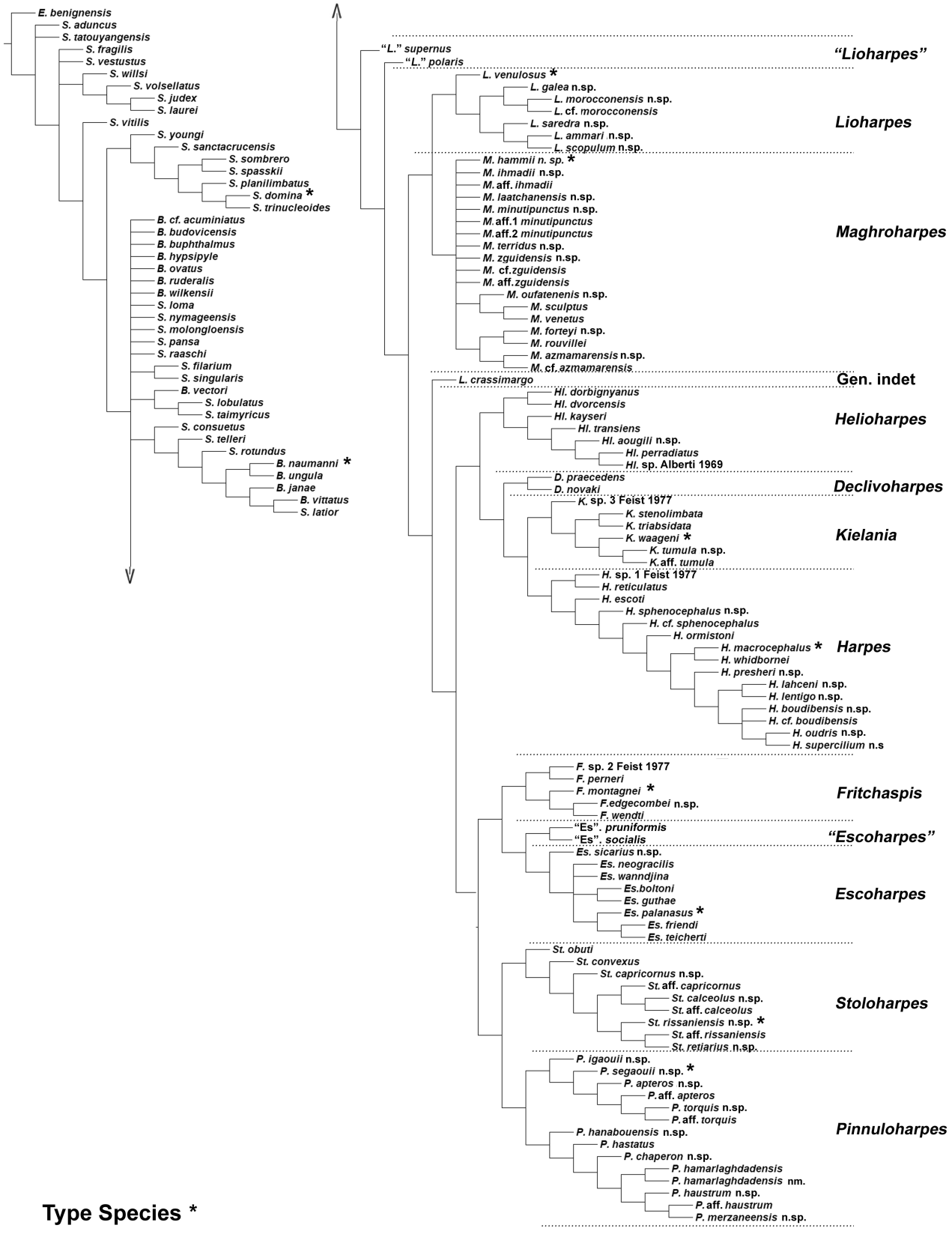


FIGURE 9. Cladogram consensus of 636 trees with a 31 node collapse and each tree L = 1968, Ci = 12 and Ri =48

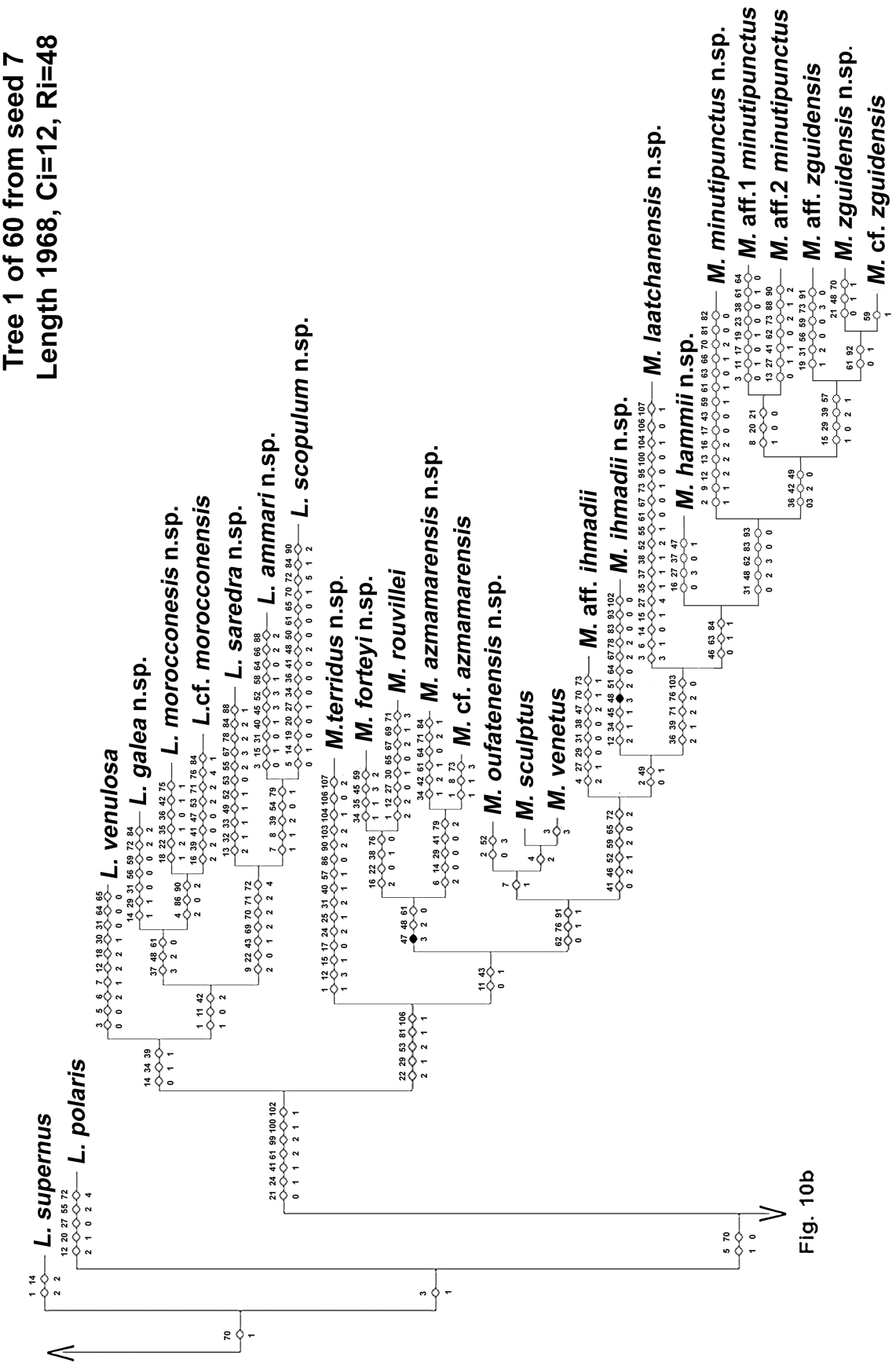


Fig. 10b

FIGURE 10a. *Lioharpes* and *Maghroharpes* from tree 1 of 60 found using seed 7

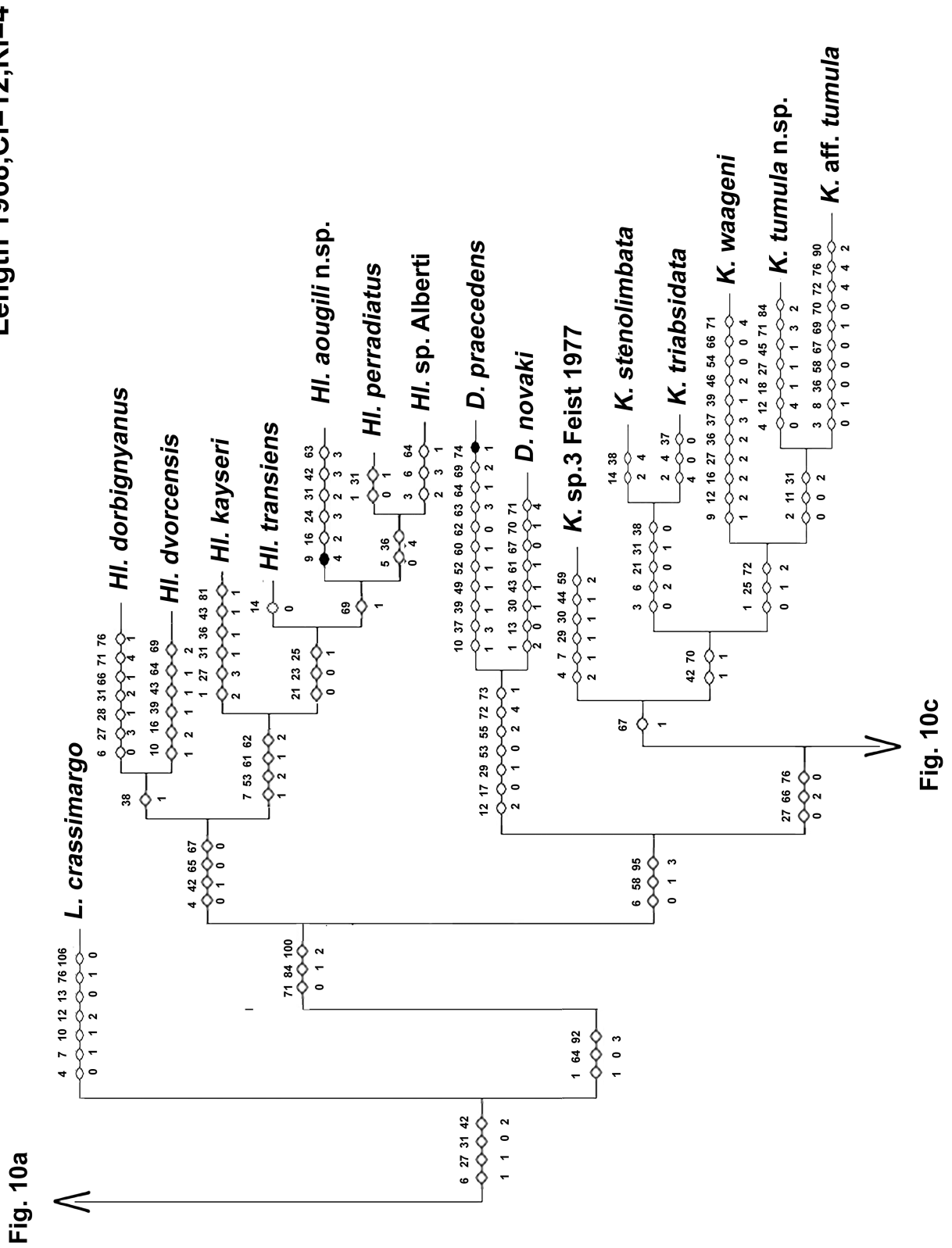


FIGURE 10b. *Helioharpes, Declivoharpes, Kielania* and gen. indet from tree 1 of 60 found using seed 7

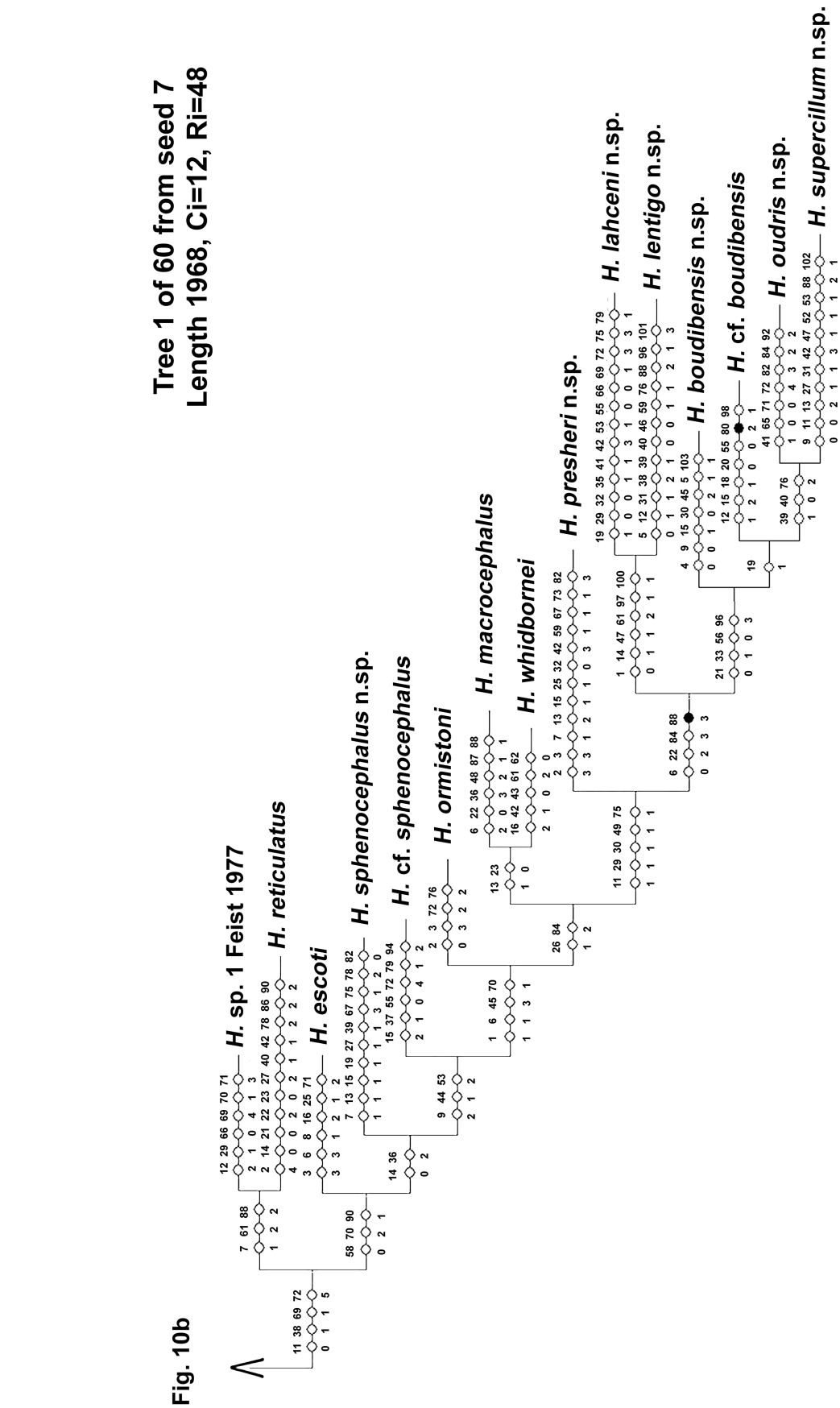


FIGURE 10c. *Harpes* from tree 1 of 60 found using seed 7

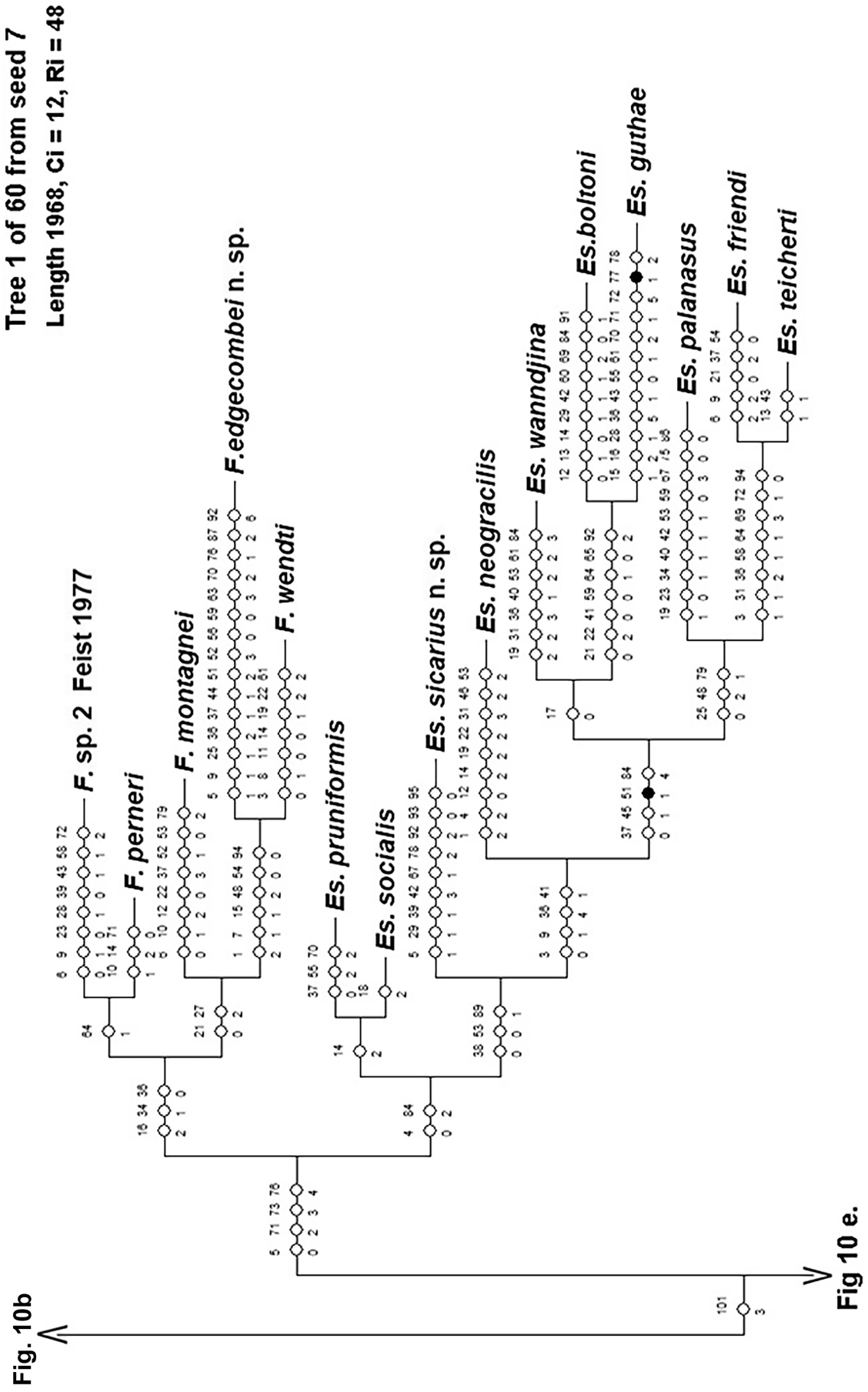


FIGURE 10d. *Fritchaspis* and *Escoharpes* from tree 1 of 60 found using seed 7

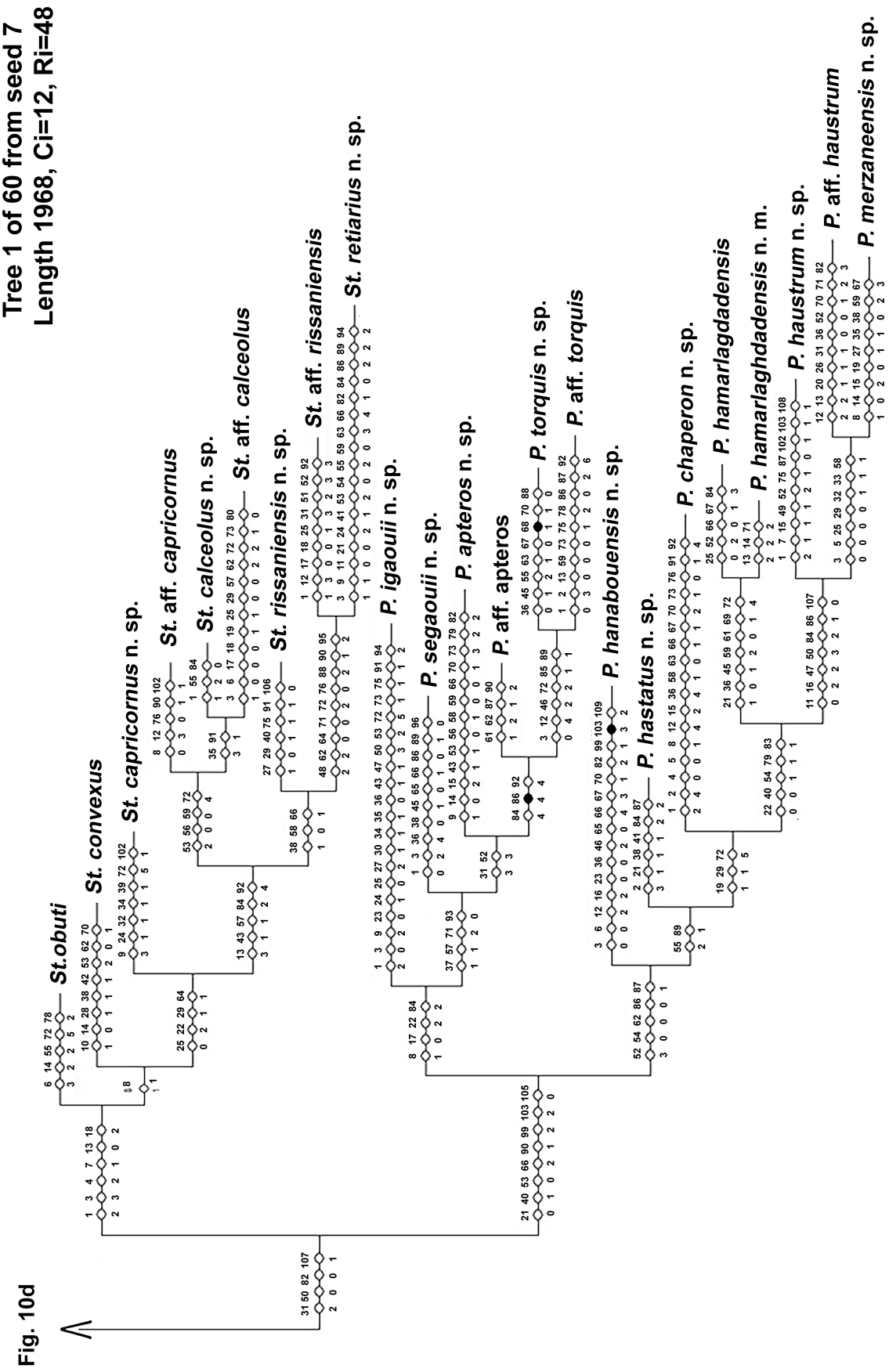


Fig. 10d

FIGURE 10e. *Stoloharpes* and *Pinnuloharpes* from tree 1 of 60 found using seed 7

states for the genus in question. All numbers are expressed as a percentage of taxa where the relevant character state can be determined. Those characters which are fully supported are marked by stars in column 6. Column 5 shows the number of taxa which do not fully comply with the diagnostics listed, according to the number of diagnostic characters they lack. The characters which are missing for each new species described herein are detailed in the systematics section under "remarks". Column 7 shows the number of species belonging to other genera with one or more of the diagnostic characters, analysed according to the number of characters shared. Column 8a shows the extent to which the most widely shared character state is shared with species from other genera. For example, the most widely shared *Harpes* diagnostic character is present in 42% of taxa in other genera included in the cladistic study. Column 8b shows the averaged percentage of taxa in other genera sharing the selected character states of the genera in question (the sum of the percentage of other taxa sharing each character state divided by the total number of character states). For *Harpes*, if the percentage of taxa of other genera sharing a diagnostic character is calculated for all 10 diagnostic characters, the average is 17%.

For the purpose of identifying material, column 9 suggests the minimum number of diagnostic characters that have to be complied with in deciding the generic assignments.

On the basis of Table 5, the generic diagnostics that are the most reliable are those for *Declivoharpes*, with both species having all the diagnostic character states and the character state most widely shared being shared with only 24% of taxa of other genera. For *Frichtaspis* and *Helioharpes*, with five and seven species respectively, the lowest character support for any one species is 87% and 83% respectively and the most widely shared character is shared with 40% and 44% of other genera respectively. Perhaps the least reliable of the diagnostic characters are those for *Kielania,* where the lowest character support for any one species is 57% and the character most widely shared is shared with 60% of species from other genera. The median sharing figure for *Fritchaspis*, *Helioharpes* and *Kieania* is 18%, 23% and 23% respectively.

Fifty-two characters out of the total 95 cephalon characters in the cladistic study were used as diagnostic characters and only 11 were used more than twice. These were as follows:

Used three times: character 4, the widest (tr.) point of genicranium; character 16, the shape of the preglabellar furrow in anterior view; character 38, the width (tr.) of the genal area; character 67, the width (sag.) of the girder; character 69, the profile of the brim; character 72, brim width ratio; character 92, the point at which the extension of the girder onto the prolongations meets the internal rim; and character 95, the steepening of the brim on the prolongations.

Used four times: character 71, the slop of the brim (sag.); and character 76, brim caeca or the lack of it.

Used five times: character 53, course of inner margin of fringe across the anterior of the genal area.

Mode of life and history of harpetids

Whittington (1950a) long ago pointed out the conservative morphology of harpetid trilobites, which remain essentially unchanged from the early Ordovician to their extinction during the Kellwasser Event, at the end of the Frasnian stage of the Upper Devonian. This implies a specialised morphology, well adapted to an environmental niche. It has been suggested that this adaptation may have been connected with the specialised filter feeding technique suggested by Fortey & Owens (1999) and Fortey (2014), involving a ventral filter chamber beneath the cephalon with the thorax suspended while the trilobite rested on its enlarged fringe. The morphology of a few species with hypostomes preserved herein (see Pls 1H, I, 6E, F, 23P, 36J, 43M) prove that the hypostome was affixed well above the cephalic margin in a manner consistent with a ventral chamber. This feeding mode was both conservative and successful within the group, which accounts for its stratigraphic longevity, crossing the end Ordovician extinction event with little change. It is also highly likely that it was the principal cause of parallel and/or convergent evolution in the Harpetidae.

Whittington (1963) noted that harpetids were often found in "coral reef"-like habitats. In the central and eastern Anti-Atlas, small (3 m to over 150 m exposure) isolated colonies of corals and stromatoporoids, often too few to form a proper reef structure, appeared towards the end of the Pragian, coinciding with a minor eustatic regression (Morrow & Sandberg 2008). These colonies became preferred habitats to a number of species of harpetids whose exoskeletons are often found in close proximity to each other. The same species are rarely found in the same horizon away from the colonies. These colonies continued into the second half of the Emsian and became more extensive, particularly at Hamar Laghdad (Map 11), where they are associated with the well-known hydrothermal Kess Kess

mud mounds (Klug *et al.* 2018). Towards the end of the Emsian, the colonies seemed to have disappeared, perhaps prompted by the strong marine transgression (Ouali Mehadji *et al*. 2004 and 2011). It was not until the late Eifelian and early Givetian that the coral and stromatoporoid colonies reappeared, this time becoming much more substantive, forming massive reef-like structures of heliolitid tabulate corals and large stromatoporoids. Two such reefs in the Anti-Atlas have been described, one at Ouihlane (8.5 km north of Jbel Issoumour) (Schröder & Kazmieczak 1999) and the other at Aferdou el Mrakib (Jbel el Mrakib) (Jakubowicz *et al*. 2019). There are, however, no reports of harpetids or any other trilobites being associated with these reefs although crinoid fragments, brachiopods and gastropods have been found. This may be because either these reefs did not provide a suitable habitat for trilobites or possibly that taphonomic conditions for the preservation of trilobites were unsuitable. If the former, it may have been that the Pragian/Emsian colonies provided flat feeding areas around the corals, something that was missing in the Eifelian/Givetian reefs.

If indeed filter feeding and the morphological requirements of a successful feeding chamber gave rise to the widespread homoplasy of the family, perhaps pygidia, being remote from the ventral chamber, might in the future provide synapomorphies. As it is, however, pygidia are rare, being either missing or hidden in enrolment. Pygidia illustrated herein (Pls 5J, 33F, 45G, 46H, 53I) do show distinct differences, but more material is needed before it is possible to determine whether these differences can be of any use in defining genera.

Systematic paleontology

The generic order below follows the order in which the different genera were historically established, and the new genera follow on in alphabetical order.

Species which belong sensu stricto (s.s.) and sensu lato (s.l.) to their respective genera have been included. Typically, s.l. species, which are denoted by the generic name in parentheses, are not so deeply nested within their tree and/or are in a paraphyletic grouping.

Specimens of species described below are in the collections of the Natural History Museum London (NHMUK).

Class Trilobita Walch, 1771

Subclass Libristoma Fortey, 1990

Order Harpetida Whittington, 1959

Family Harpetidae Hawle & Corda, 1847

Genus *Harpes* Goldfuss, 1839

Type species. *Harpes macrocephalus* Goldfuss, 1839, from the Übergangskalk der Eifel (recte Auburgschichten der Crinoidenzone, Devonian), Gerolstein, Eifel, Germany

Emended diagnosis: Cephalon strongly vaulted and ovoid. Preglabellar field narrow (sag.) (20% to 30% of width (tr.)) and posterior border short (tr.) (20% to 30% of width (tr.) of occipital ring). Genal area narrow, width (tr.) under 54% of length (exsag.). Alae large, extending over 60% of way across (tr.) genal area. Eye lobe forms prominent inflated cone or oval extending from edge of axial furrow to near internal margin of fringe. Anterior boss absent or barely inflated and girder without kink. Genal roll and brim free of caeca. Brim slightly concave (sag.), straight laterally, gently to moderately sloping and steepening quickly to near vertical on prolongations. Brim narrowing (tr.) moderately strongly to very strongly posteriorly (brim width ratio <0.68). Extension of girder meeting internal rim one third of the way down prolongation. Thorax up to 31 segments.

Discussion. *Harpes* has been used as a "catch all" for all species of harpetids which cannot be readily assigned to other genera. Supported by the results of the cladistic study, here the author intends to narrow the concept, distinguishing *Harpes* from other genera by their prominent eye lobes and alae and their relatively narrow (tr.) genal area. This genus was re-considered by Ebach & McNamara (2002) but their emended diagnosis was in the author's view overgeneralised and contained inaccuracies, for instance, eyes are not set "anterior to preglabellar furrow", an inaccuracy which was pointed out by Basse & Müller (2004, p. 75). The author has omitted "cephalon semi-

circular to ovate. Brim flat, pitted, rim wide and raised along whole margin" and "genal roll long (sag.), convex and vaulted," as these descriptions are either inaccurate or apply to many other harpetids. No *Harpes* brim is flat, many are straight, but all are sloping to some degree. All harpetid species have pitted brims and nearly all have raised rims and genal rolls with a degree of convexity. No species of *Harpes* has the widest part of its cephalon across (tr.) its posterior border, and therefore their cephala (ignoring the prolongations) cannot be semi-circular.

The holotype of *H. macrocephalus* is lost and the type locality in the Eifel region is uncertain, although it is thought to be near Gerolstein where *H. macrocephalus* is most commonly found (Basse & Müller, 2004). *Harpes macrocephalus* has been recently refigured by Basse & Müller (2004, taf. 25 & 26), who also figured material of *H. macrocephalus* ssp. 1 which was found outside the Eifel region, east of the Rhine, near Wetzlar and is of middle Givetian age. A proper comparison of this subspecies with *H. macrocephalus* requires further material.

It should be pointed out that, while the outline shape of the cephalon of *H. macrocephalus* is described as an inverted "U" (Whittington 1950a) (see Basse & Müller 2004, taf. 25, fig. 320), the outer rims on the prolongations are convergent posteriorly and therefore the cephalon can be considered ovoid in shape. Richter (1920) reported (in addition to two eye lenses per eye lobe) a small tubercle on the dorsal surface of the lobe which he believed was not a third eye lens (taf.17, fig. 10). *Harpes macrocephalus* is the only species of *Harpes* with such a tubercle. All other species of *Harpes* have only two lenses per eye lobe and no "tubercle".

Ebach & McNamara (2002) listed species assigned to *Harpes* which seem arbitrary in the light of this research. As a result of this revision, the following have been reassigned: *H. perradiatus* Richter & Richter (1943), *H. transiens* Barrande (1872) and *H. sp.,* Alberti, 1969, to *Helioharpes* Přibyl & Vaněk (1981), which was considered a junior subjective synonym of *Harpes* by Ebach & McNamara (2002). *Helioharpes* has been re-established, albeit with a much-revised diagnosis. Ebach & McNamara (2002, fig. 2F), figured *H. perradiatus* and *a*lthough the figure is imperfect, the material shown is certainly not *H. perradiatus*, but almost certainly *Harpes boudibensis* n. sp. This clearly renders their coding of characters in their analysis inappropriate. *Harpes pruniformis* Alberti (1969) and *H. socialis* Holzapfel (1895) are reassigned to *"Eskoharpes*" s. l.. *Harpes* sp."2" Feist (1977, p. 153), *H. rouvillei* Frech (1887), *H. polaris* Maksimova (1977) and *H.hamarlaghdadensis* Cronier *et al.* (2018), are reassigned to *Fritchaspis*, *Maghroharpes*, "*Lioharpes"* s.l. and *Pinnuloharpes* respectively. *Harpes nymageensis* Fletcher (1975) from the lower Silurian is reassigned to *"Scotoharpes"* s. l.. However, the material and the photographs illustrating it are of poor quality and it was only possible to complete the character states for 12 of the 111 characters used in the cladistic study. *Harpes* sp. "3" Feist (1977, p. 155) has been reassigned to *Kielania* Vaněk (1963).

Harpes species which were not included in the cladistic study due to lack of reliable information have been assigned pro tem as follows: *H. forojuliensis* Gortani, 1909 to *Bohemoharpes*; *H. fornicatus* Novák, 1890 and *H. pygmeaus* Lütke, 1965 to *Pinnuloharpes* n. gen and *Harpes gracilis* (Münster, 1840), *H. koeneni* Wedekind, 1914, *H. pyrenaicus* (Barrois,1866) and *H. radians* Richter, 1963 to *Helioharpes*.

Apart from any open nomenclature of other species, all *Harpes* species have been included in the study and are shown together with their interspecies relationships in Figs 9 and 10c. Within the genus there is a separate group of six species including *H. boudibensis* that is supported by a character state that is a unique unreversed synapomorphy being in lateral view the wave like profile of the internal rim. The range of the *Harpes* genus is from lower Emsian to upper Eifelian.

***Harpes boudibensis* n. sp.**

Plate 1A–Q

Diagnosis. Narrow cephalon, width (tr.) around 1.2 times sagittal length and widest (tr.) just posterior to eyes. Glabella cone-shaped, anteriorly rounded. Extension of axial furrow across ala distinct. Alae inflated and alar furrows proximally deep, becoming very shallow distally. Alar depression pronounced. Prolongations around same length (exsag.) as cephalon (sag.). In lateral view external rim posteriorly curving upwards and internal rim wave-like in shape and terminated by short genal spine. Over 25 thoracic segments.

Etymology. Named after the village bou Dîb, which is close to the type locality.

Material and occurrence. Holotype: NHMUK It 29227, Pl. 1K–Q, from horizon 1, Section 2 (Fig. 7), El Otfal Formation, Eifelian, Jbel Issoumour (Fig. 2B, Map 7, site 4), enrolled articulated dorsal exoskeleton. Paratypes: NHMUK It 29226, Pl. 1A–D, articulated dorsal exoskeleton and NHMUK It 29228, Pl. 1E–J, dorsal exoskeleton, pygidium enrolled. NHMUK It 29226 and NHMUK It 29228 from the type locality and horizon, site 1 and site 5,

respectively. *Harpes boudibensis* is almost certainly present at other Jbel Issoumour Eifelian localities, many of which have been extensively mined for harpetid trilobites.

Other material: cf. *boudibensis,* NHMUK It 29225 from horizon 7, Section 1 (Fig. 6), El Otfal Formation, Jbel Ou-Driss (Fig. 2B, Map 4, site 11), Pl. 2A–D, an enrolled dorsal exoskeleton. Horizon 7 of a similar age to the *H. boudibensis* horizons on Jebel Issoumour

Description. In dorsal view, cephalon widest just posterior to level of eyes, where length (sag.) ≈ 80% of width (tr.). Cephalon and glabella strongly vaulted. Glabella cone-shaped, rounded anteriorly and sometimes with sparse fine tubercles along posterior two thirds of top of glabella. L1 weakly inflated. S1, S2 and S3 poorly marked by change in tone of cuticle (Pl. 1P). Shallow furrow which rises 2/3 of way up flank of glabella delineates posterior edge of S1 muscle attachment scar area (Pl. 1A). S1 tulip-shaped, S2 and S3 subcircular and about 1/4 size of S1. S0 oval and about two thirds of area of S1. S1 with subparallel intermittent dark vertical stripes and dark edge.

Preglabellar furrow very shallow and preglabellar genal area length (sag.) around 45% of width (tr.) of glabella at S1. Axial furrows deepening posteriorly and alar depression prominent. Alae large, reaching more than 70% of way across (tr.) genal area. Low rounded ridge crosses (exsag.) ala close to axial furrow, visible on holotype in Pl. 1M (lateral view) and in dorsal view on paratype NHMUK It 29226 (Pl. 1A). Alar furrows shallow, well-defined, becoming shallow distally. Occipital furrow broad, occipital ring narrow (sag. and exsag.) and covered with fine granular tubercles. Larger, low axial tubercle located on anterior edge of ring. Posterior border very short (tr.), ≈30% of width (tr.) of occipital ring. Genal area narrow, width (tr.) around 50% of length (exsag.). Eye lobes nearly conical in shape, reaching across to near inner margin of fringe, with eye position ratio about 0.85. Two horizontal oval eye lenses stadium-shape and well separated, face outwards anterolaterally and posterolaterally, respectively (Pls 1Q, 2M). Broad low ridge reaching down from between the two lenses onto genal area, where it narrows and forms a very faint genal ridge, extending posterolaterally to cross inner margin of fringe level with ala. Genal roll convex, wide and sloping gently anteriorly at under 40^0 and laterally more steeply at around 55^0.

Brim sloping moderately anteriorly; width (sag.) about 30% of cephalic length (sag.) and brim width ratio around 0.50. A row of large perforations lie either side of girder, away from which perforations quickly decrease in size to those on main part of genal roll and brim respectively. Average standardised diameter of perforations on central part of brim around 150 μm (Pl. 1D, J, O). Perforations on main part of genal roll finer (Pl. 1N) except where inner margin of fringe crosses in front of glabella, where there is a row of larger perforations. Around external margin of brim, usual row of coarser perforations. External rim raised and broad with dorsal rim suture central. Marginal band straight, vertical and without tubercles. Material described includes one poorly preserved hypostome (Pl. 1H, I), which has an inverted cone shape with no discernible middle furrow and narrow borders.

Prolongations around 1.05 times sagittal cephalic length and internal rims set at about 140^0 to posterior border, curving inwards posteriorly so that distal ends point obliquely adaxially. In lateral view, external brim narrows and curves steadily upwards posteriorly to meet internal rim at end of prolongation. Internal rim rises gently from posterior border then curves down towards distal end, before curving up to meet external rim to form very short stout spine. Lateral profile of internal rim wave-like. In dorsal view, internal rim broad, rounded and covered by small tubercles. Extension of girder on prolongations rises to run just under internal rim before joining it at about midpoint. Perforations on extension of genal roll on prolongation increase in size towards internal rim. Below internal rim a row of large perforations becoming smaller posteriorly.

Thorax has 26 to 28 thoracic segments. Axis strongly vaulted and with axial rings becoming narrower (tr.) posteriorly, last having width (tr.) of about 30% of first. Postannuli wider (sag. and exsag.) than preannuli and not narrowing medially. Pleurae widening (tr.) posteriorly until 7^{th} segment and then narrowing until last segment which is just over 20% of 7^{th}. Pleurae narrow (exsag.) with anterior and posterior bands approximately same width (exsag.) and a relatively deep pleural furrow. Pleural furrows cross onto outer portion of pleurae, which are turned downwards, straight and terminate in rounded end. Pygidium very short (sag.) with two axial rings and pleural furrows extending to distal edge. Terminal piece short (sag.) and rounded.

Remarks. *Harpes boudibensis* differs from *H. macrocephalus* in having a cephalon which is widest (tr.) just posterior to the eye lobes rather than the anterior of the alae and is ovoid rather than U-shaped. Its glabella anterior to S0 lacks tubercles and S1 furrow is shallower, becoming effaced before reaching the top of muscle attachment area. Preglabellar furrow of *H. boudibensis* is very shallow as is the extension of the axial furrow across the ala. Genal area and genal roll not so strongly convex and anterior slope of genal roll is under 40^0 compared with over 50^0 for that of *H. macrocephalus.* The prolongations are a third longer (exsag.) in relation to length (sag.) of cephalon than

those of *H. macrocephalus*. In dorsal view, internal rims curve adaxially rather than being subparallel and in lateral view, their profile is wave-like rather than straight.

Harpes cf. *boudibensis*, NHMUK it 29225, (Pl. 2A–D) is very similar to *H. boudibensis* but differs in having fine tubercles scattered along top of the glabella, a wider occipital furrow which is medially bent forward, an occipital ring which is narrower, a slightly shorter (tr.) posterior border, more inflated alae and a steeper-sloping genal roll (sag.). Some of these features are shared with *H. Lahceni*.

Harpes boudibensis has been widely mistaken for *Helioharpes perradiatus* (Richter & Richter, 1943) in the Moroccan trilobite mining industry, and by Ebach & McNamara (2002) and most likely Beech & Lamsdell (2021). The type locality of *Helioharpes perradiatus,* Dechra-ait-Abdallah, is some 250 km North-North-West of bou Dîb on the southern edge of the Moroccan Central Meseta. *Harpes perradiatus* differs from *H. boudibensis* in having a less vaulted cephalon and less steep genal roll; a less inflated glabella which is subcylindrical rather than oval or cone-shaped and is without tubercles. Eye lobe is small and is not cone-shaped and the brim does not narrow posterolaterally. The brim width of *H. boudibensis* reduces (tr.) posterolaterally to become one half of its sagittal width at posterior border. Also, there is a strong web-like caeca on the brim, forming pseudo perforations and caeca on genal roll, not present on *H. boudibensis.*

***Harpes lahceni* n. sp.**
Plate 5A–N

Diagnosis. Wide cephalon, width (tr.) across alae about 1.4 times length (sag.). Glabella oval and strongly inflated. Brim barely sloping, slightly concave and narrowing moderately strongly posterolaterally. Alae inflated and axial furrows not extending across alae. Alar furrows become shallower distally. Fine pointed tubercles scattered along top of glabella, on dorsal surface of eye lobes and occipital ring and along dorsal surfaces of external and internal rims. Prolongations up to 15% longer (exsag.) than cephalon (sag.). In lateral view, external rim posteriorly curving upwards and internal rim wave-like in shape. Over 25 thoracic segments.

Etymology. For Ait Hssaine Lahcen, a Moroccan trilobite worker who assisted with fieldwork in the Anti-Atlas.

Material. Holotype: NHMUK It 29232, Pl. 5A–J, from horizon 3, Section 2 (Fig. 7), El Otfal Formation, Eifelian, Jbel Issoumour near bou Dîb (Fig. 2B, Map 7, site 6). Paratype: NHMUK It 29233, Pl. 5M, N, from "*Phylonix* Couche", El Otfal Formation, Jbel Oufatene (Fig. 2B, Map 8, site 6). Paratype: NHMUK It 29234, Pl. 5K, L, El Otfal Formation, Eifelian from "*Harpes* Couche" just above the *Acanthopyge* horizon, Timerzit (Fig. 2B, Map 10, site 2). All articulated dorsal exoskeletons with thorax partly enrolled.

Other material: *H.* cf *lahceni*, NHMUK It 29235, Pl. 6I–N, from "*Erbenochile* Couche", Timrhanrhart Formation, Emsian, 24 km S.W. of Foum Zguid (Fig. 2A, Map 2, site 6). Partial dorsal exoskeleton of an upper lamella.

Description. In dorsal view, ovoid cephalon widest at mid-point between level of eye lobes and alae, where length (sag.) is around 70% of width (tr.). Cephalon and glabella particularly strongly vaulted. Glabella anterior to S0 more oval than cone-shaped, rounded anteriorly and with sparse tubercles along posterior two thirds of crest. S1 sloping posteriorly before curving anteriorly near crest. No furrows or visible scars at S2 and S3. Preglabellar furrow shallow and preglabellar genal area narrow, with length (sag. exsag.) ≈20% of width (tr.). Axial furrows convex, weakly convergent and not crossing junction of ala and L1. Alae are large, inflated, laterally directed and reaching more than 70% of way across (tr.) genal area. Alar furrows shallow distally. No interalar furrows or ridges but alar depressions present. Occipital furrow deep, broad and medially straight. Occipital ring narrow (sag. and exsag.) and occipital node small, set back from anterior edge of occipital ring. Posterior border very short (tr.), around 20% of width (tr.) of occipital ring.

Genal area narrow, width (tr.) around 53% of length (exsag.). Eye lobes nearly conical in shape and nearly reach across genal area to near inner margin of fringe. Scattered fine tubercles on dorsal surfaces. Eye position ratio about 0.89. Two horizontal oval eye lenses face outwards anterolaterally and posterolaterally respectively (Pl. 5E). Broad but low ridge from between the two lenses, reaches down onto genal area, where it narrows and forms a very faint genal ridge extending posterolaterally to cross inner margin of fringe level with anterior of ala. Genal roll convex and wide, narrowing moderately posteriorly and steep, sloping anteriorly at over 60^0 and laterally at over 70^0. No anterior boss or girder kink.

Brim gently sloping anteriorly at under 10^0 and with a width (sag.) of about 28% of cephalic length (sag.); brim width ratio around 0.70. Row of large perforations either side of girder. Average diameter of perforations on central part of standardised brim ≈190 μm (Pl. 5H). Above girder, perforations quickly decrease in size to that of perforations on main part of genal roll, which are finer than those of brim. At inner margin of fringe, in front of glabella, a row of larger perforations about the same size as those immediately above girder. Row of coarser perforations around external margin of brim. External rim is raised and broad with dorsal rim suture located closer to outside edge than inside edge. Tubercles on dorsal surface of rim densely packed. Marginal band not visible on material presented here.

Internal rim set at about 150^0 to posterior border and curving adaxially posteriorly so that distal ends point obliquely adaxially. In lateral view, profile of internal rim strongly wave-like and upturned distally. Dorsal surface of internal rim broad with densely-packed tubercles. Row of perforations immediately under internal rim larger than those on brim below. Extension of girder meeting internal rim about one third of the way down prolongation. External rim turning upwards posteriorly to meet internal rim at end of prolongation. Genal spine short and stout.

The thorax has 23 thoracic segments and tapers posteriorly so that last segment is just under 40% of width (tr.) of fifth segment (widest point). Axis strongly vaulted and with axial rings becoming narrower (tr.) posteriorly, width (tr.) of last being about 40% of the first. Anterior and posterior bands of pleura narrow (exsag.) and of the same width (exsag.). Pleural furrow deep, widening distally and extending onto downturned outer portion of pleura, which has rounded distal end.

Pygidium (Pl. 5J) short (sag.) with three axial rings and pleurae and a very short (sag.) terminal piece. Axial rings wide (tr.), first axial ring being over 40% of width (tr.) of anterior of pygidium. Interpleural furrows deep, pleural furrows shallow and pleurae distal ends acute.

Remarks. *Harpes lahceni'*s morphology complies with the genus diagnostics with the exception of the brim width ratio, which is 10% above the range proposed in Table 5a.

Harpes lahceni is similar to *H. whidbornei* (Whittington 1950a, pl. VII, figs 5–12) in the strong vaulting of the cephalon, the steep slope of the anterior of the genicranium and the inflated glabella. The alae of *H. whidbornei* are more weakly-defined and lack the inflation of those of *H. lahceni*. Also, *H. whidbornei'*s prolongations are shorter and the internal rims, which in lateral view are nearly straight, descend steeply to meet the external rims at the distal ends. The internal rims of *H. lahceni* initially arch up from the posterior border before curving down and then, towards the distal ends, curving up again forming a wave-like shape. The poor state of the *H. whidbornei* material makes comparisons of the anatomy of the two species difficult. The thorax of *H. whidbornei* is unknown and the pygidium attributed by Whidborne (1889–1892) to *H. whidbornei* was considered doubtful by Whittington (Whittington 1950a).

H. lahceni is also similar to *H. lentigo* (Pl. F7A–M) but it has: a glabella that is inset with much finer tubercles a furrow at S1 curving around the top of the muscle insertion area; a preglabellar furrow that in anterior view is straight rather than being bowed up; a broader occipital furrow; axial furrows that do not cross the alae and alae that are wider, more inflated with no interalar furrows; a narrower genal area with scattered fine tubercles but no caeca or pits; larger eye lobes that are cone shaped rather than oval; an inner margin of the fringe the course of which across the anterior of the genal areas is straight not convex; no anterior boss or girder kink; a genal roll with perforations that are the same size as those on the brim not smaller as in the case of *H. lentigo*; a brim that slopes less steeply and has a higher brim width ratio, no caeca and perforations that do not become smaller away from the girder; an external rim that has fine tubercles on its dorsal surface; prolongations that are longer and in lateral view have a strong wave like profile; a thorax that is more tapered, inner portion of pleura in line with outer.

A comparison between *H. lahceni* and its sister species, *H. prescheri*, is given in the systematics for *H. prescheri*, below.

Harpes cf. *lahceni* (Pl. F6I–N) differs from *H. lahceni* in having a brim that is significantly wider at S0 and standardised brim perforations that are over 40% larger. The axial furrow is expressed at L1, the alae are less inflated and there are interalar furrows and ridges not present on the alae of *H. lahceni*.

***Harpes lentigo* n. sp.**

Plate. 7A–M

Diagnosis. Cephalon widest (tr.) across anterior of alae. Large ovoid glabella, anteriorly steeply-sloping with

prominent tubercles straddling crest. Tubercles on dorsal surface of eye lobe, occipital ring and internal rim. Alae inflated and moderately large. Alar depression deep and alar and preglabellar furrows well defined. Shallow pitting on post ocular genal area. Narrow (sag.) brim, narrowing moderately posterolaterally (brim width ratio 0.64) with moderately large perforations decreasing in size distally. In lateral view, external rim curves slightly upwards and profile of internal rim weakly wave-like.

Etymology. Lentigo, Latin for freckle. The pronounced tubercles of the glabella and eye lobes give an impression of freckles.

Material and occurrence. Holotype: NHMUK It 29236, Pl. 7A–G, from a coral horizon 5 metres below the "*Morocconites* Horizon" (McKellar & Chatterton 2009, p. 13) (12.2 m down slope), Tazoulait Formation, Emsian, Jbel Oufatene (Fig. 2B, Map 8, site 4), a dorsal exoskeleton with disarticulated thorax. Paratypes: NHMUK It 29237 (1– 3), Pl. 7H–M, from the type horizon and type locality (Fig. 2B, Map 8, site 5), a group of 3 disarticulated and slightly crushed exoskeletons.

Other material: H. cf. *lentigo*, NHMUK It 29239 and NHMUK It 2938 are dorsal cephalic exoskeletons only. NHMUK It 29239, Pl. 8A–H, is from a horizon midway between the "*Lobopyge* Couche" and the "*Phylonix* (*Quadrops*) Couche", El Otfal Formation, Eifelian, Jbel Issoumour (Fig. 2B, Map 7, site 14). NHMUK It 29238, Pl. 8I–L, is from the "*Lobopyge* Couche" (McKellar &Chatterton, 2009, p. 12), El Otfal Formation, Eifelian, Jbel Issoumour (Fig. 2B, Map 7, site 7) and is a specimen with morphological abnormalities. Both "Couches" are close to the Emsian/Eifelian boundary.

Description. Cephalon length (sag.) around 70% of width (tr.). Genicranium widest at posterior border, length (sag.) around 75% of width (tr.). Glabella anterior to S0 broad (width (tr.) 70% of length (sag.)), rounded anteriorly and with pronounced tubercles densely packed along crest. S1 sloping posteriorly before curving anteriorly near crest. No furrows at S2, S3 or S4. Preglabellar furrow distinct and preglabellar genal area length (sag.) 20% of width (tr.). Axial furrows deep, weakly convergent. Occipital furrow deep and broad (sag.) about same width (exsag.) as posterior border. Occipital ring medially broadened and with tubercles. Large moderately inflated occipital node at anterior edge of occipital ring. Posterior border short (tr.), around 30% of width (tr.) of occipital ring. Alae broad, laterally directed and reaching more than 50% of way across (tr.) genal area. Alar furrows deep, well defined. Interalar furrows and alar depressions present.

Genal area width (tr.) around 57% of length (exsag.) and with pits. Eye lobes oval in shape, strongly inflated and with tubercles on dorsal surfaces finer than those on glabella. Eye position ratio about 0.86. Two well separated horizontal oval eye lenses face outwards anterolaterally and posterolaterally respectively (Pl. 7E, F). Genal ridge just discernible on genal area, becoming clearer as it extends posteriorly across genal roll. Genal roll moderately steep (sag. 58^0 and laterally 63^0). Anterior boss barely inflated, girder kink weak. Perforations on genal roll smaller than on brim except for a row of larger perforations immediately above girder and at inner margin of fringe across anterior of glabella.

Brim narrow (sag.), 27% of cephalic length (sag.), sloping (sag.) at around 16^0. Brim width ratio around 0.60. Brim perforations become smaller away from girder and average standardised diameter of perforations on central part of brim is around 190 μm (Pl. 7G, K) with a row of larger perforations around internal and external margins of brim. Caeca just reaching onto brim. External rim broad with no tubercles on dorsal surface. Marginal band near vertical with tubercles and a ridge top and bottom.

Prolongations around 0.96 times sagittal cephalic length, curving adaxially posteriorly so that distal ends point obliquely adaxially. In lateral view profile of internal rim barely upturned distally. Internal rim broad (tr.) and with tubercles on dorsal surface. Below internal rim row of perforations larger than those on rest of prolongation immediately beneath. Extension of girder meeting internal rim about halfway down prolongation. External rim turning upwards posteriorly to meet internal rim at end of prolongation. Genal spine short and stout.

Thorax with at least 23 thoracic segments. Axis strongly vaulted with axial rings becoming narrower (tr.) posteriorly. Anterior and posterior bands of pleura narrow (exsag.) and of equal width (exsag.). Pleural furrow deep and extending onto outer portion of pleura, which slants slightly posteriorly from junction of inner portion before turning down, and has a rounded distal end.

Remarks. *Harpes lentigo's* morphology lacks three of the genus's diagnostic characters shown in Table 5a: the genal area at 57% of its length (exsag.) is wider than the upper limit of 54%, it has a weak girder kink, and caeca reaching onto brim.

Harpes lentigo differs from *H. boudibensis* (Pl. 1A–Q) in having a broader genal area with a width (tr.) 57%

of its length (exsag.) and alae reaching only 60% of the way across compared with more than 70% in the case of *H. boudibensis*. Also, the glabella is narrower, anteriorly steeper and more ovoid. The eye lobes have tubercles on dorsal surface and there is coarse pitting on post ocular genal area, not evident on *H. boudibensis*. There is a preglabellar field, a well-defined preglabellar furrow, a boss and a weak girder kink. The brim width ratio is some 30% greater and standardised brim 20% larger.

The differences between *H* cf. *lentigo* (NHMUK It 29239) (Pl. 8A–L), and *H. lentigo* are that NHMUK It 29239, has a slightly wider (tr.) cephalon with the widest point being across the midpoint of the glabella rather than across the anterior edge of the alae. Also, the eye lobes are set a little closer to the axial furrow and the tubercles on the glabella are fewer and finer and absent on the dorsal surfaces of eye lobes. The brim differs too, having a brim width ratio of about 0.75 rather than 0.65, and the genal area is finely perforated with the cuticle surrounding the perforations being lighter in tone than elsewhere on the genal area (see Pl. 8A, F, G.).

***Harpes oudris* n. sp.**
Plate 2E–M

Diagnosis. Axial furrows are convex and deep, and preglabellar furrow well defined. Tubercles and faint caeca on genal area. Perforations on genal roll same as on brim. Brim is moderately steeply-sloping and brim width ratio is between 0.68 and 0.75. Dorsal surface of external rim overhangs marginal band and carries tubercles. Prolongations over 90% of cephalic length (sag.), extension of girder meeting internal rim about halfway down prolongation. Internal rim in lateral view strongly wave-like in profile and distal end of prolongation sharply upturned.

Etymology. Named after Jbel Ou-Driss, the type locality.

Material and occurrence. Holoptype: NHMUK It 29241, Pl. 2I–M, from Section 1, horizon 5, (Fig. 6), El Otfal Formation, Eifelian, Jbel Ou-Driss (Fig. 2B, Map 4, site 22), dorsal exoskeleton with thorax partially exposed. Paratype: NHMUK It 29323, Pl. 22K–M, from a lower Emsian horizon, Boutiskaouine Formation, Awhare, Iferd Nou Haouar (Fig. 2B, Map 9, site 13), dorsal exoskeleton of partial cephalon. Paratype: NHMUK It 29240, Pl. 2E–H, from type horizon, site 21, dorsal exoskeleton with thorax enrolled.

Other material: *H.* cf. *oudris.* NHMUK It 29242, Pl. 6A–H, from horizon 4, Section 1 (Fig. 6), El Otfal Formation, Jbel Ou-Driss (Fig. 2B, Map 4, site 10), an articulated dorsal exoskeleton with thorax enrolled with ventral surfaces exposed on anterior half of cephalon.

Description. Cephalon ovoid with widest (tr.) point at mid-point between eye lobes and alae. Genicranium narrow, widest at posterior border. Glabella fairly broad, width (tr.) 75% of length (sag.) of glabella anterior of S0, and with rounded crest and tubercles but no pitting. S1 rising out of axial furrow, sloping backwards and curving around top of muscle insertion area. No furrows at S2, S3 or S4 and L1 inflated. Axial furrows converge strongly anteriorly at nearly 20^0 to axis and cross junction between alae and L1. Preglabellar furrow distinct and bowed upwards in anterior view. Occipital furrow deep, wide, wider than posterior border and straight in dorsal view. Occipital ring broad (sag.), broader than posterior border (exsag.) and same height in lateral view as glabella anterior to S0. Occipital node large, alae anterolaterally directed and large (tr.), over 35% of length (sag.) of glabella anterior to S0 and reaching around 70% of way across genal area. Alar furrow shallow, well-defined. Interalar furrow and ridge and alar depression present. Posterior border short (tr.), around 23% of width (tr.) of occipital ring. Preglabellar field narrow, length (sag.) around 17% of width (tr.).

Genal area narrow, width (tr.) about 50% of length (exsag.) with faint caeca and pits and tubercles. Genal ridge present and eye lobes cone-shaped, strongly inflated and large (exsag.), just under 40% of width (tr.) of glabella at S1. Visual surface close to inner margin of fringe with eye lobes extending to edge of axial furrow. Eyes with two lenses, each lens rectangle shape with rounded corners and of approximately same size, and no eye ridge. Course of inner margin of fringe across anterior of genal area, convex. Boss barely inflated and not reaching down to girder. No girder kink and girder moderately narrow. Genal role sloping gently anteriorly at around 47^0 and more steeply laterally at around 63^0. No caeca on genal roll. Perforations are approximately same diameter as those of brim.

Brim slightly concave (sag.), straight laterally, width (sag.) 30% of cephalic length (sag.) and sloping moderately steeply at around 22%. Brim width ratio around 0.75. Standardised brim perforations becoming finer away from girder towards the centre, where they have a standardised diameter of around 145µm. Light caeca reaching across brim. External rim stout with fine tubercles on dorsal surface. Marginal band near vertical, overhung by external rim

and with tubercles. Prolongations moderately long (exsag.) at around 87% of cephalic length (sag.) with extension of brim steepening quickly to near vertical. In dorsal view, internal and external rims curve adaxially and in lateral view, profile of internal rim strongly wave-like. Tubercles on dorsal surface of internal rim, large row of perforations below; and genal spine short. Extension of girder meets internal rim halfway down prolongation.

Thorax with over 20 thoracic segments with no tubercles or pitting on axial rings. Pleural furrows broad (tr.), deep and u-shaped, and outer portion of pleurae straight with rounded distal ends.

Pygidium and hypostome not known.

Remarks. *Harpes oudris* lacks three genus diagnostic characters shown in Table 5a. Its brim width ratio is above the upper limit of 0.68, there are light caeca reaching across brim and the extension of the girder meets the internal rim halfway down the prolongation rather than one third of the way down.

Harpes oudris is similar to but differs from *H. boudibensis* in having faint caeca on genal areas; axial furrows that are convex rather than straight (reflecting on the difference in glabella outline) and a distinct preglabellar furrow. Alae and eye lobes more inflated and posterior border (tr.) shorter, 25% of width (tr.) of occipital ring rather than between 30% and 34% in the case of *H. boudibensis*. Glabella of *H. oudris* not joined to anterior boss, genal roll steeper anteriorly and perforations on genal roll same size as on brim, not smaller. Brim of *H. oudris* steeper and has light caeca reaching across it. Brim width ratio over 0.68, whereas that of *H. boudibensis* is under 0.55. Dorsal surface of rim has fine tubercles and overhangs marginal band. Prolongations of *H. oudris* are shorter and extension of girder meets internal rim halfway down prolongation, not a third of the way down. *Harpes oudris* has 20 to 24 thoracic segments, not the 27 of *H. boudibensis,* and pleural furrows are deeper.

H. cf. *oudris* (Pl. 6A-H) differs from *H. oudris* in having a gently convex brim, a brim width ratio which is just over 10% higher at 0.77, and an internal rim that, in lateral view, is straight rather than wave-like.

The *H.* cf. *oudris* material contains an exposed hypostome (see Pl. 6 F, E) that differs from that of *H. boudibensis* (see Pl. 1H, I) in having a well-defined middle furrow, with raised maculae on the posterior edge of the furrow. These do not appear to be present on the hypostome of *H. boudibensis*.

***Harpes prescheri* n. sp.**

Plate 9A–I

Diagnosis. Cephalon widest across eyes and glabella is narrow, cone-shaped, rounded anteriorly with suppressed tubercles straddling its crest. Brim width ratio low at around 0.50, brim slightly concave (sag.), becoming gently convex close to posterior border, alar furrows effaced distally, perforations on brim very fine. Prolongations shorter (exsag.) than cephalon (sag.). Pleurae shortening (tr.) posteriorly over last fifteen thoracic segments to become very short, giving pointed appearance to thorax.

Etymology. Named in remembrance of Harald Prescher, a trilobite researcher and a good friend.

Material and occurrence. Holotype: NHMUK It 29244, Pl. 9A–E, from a horizon around 100 m upslope of "Couche Rouge" close to the "*Psychopyge* Couche", Er Remlia Formation, Emsian, Jbel Issoumour (Fig. 2B, Map 7, site 9), disarticulated dorsal exoskeleton. Paratype: NHMUK It 29243, Pl. 9F–I, from type horizon and locality (Fig. 2B, Map 7, site 8), cephalic dorsal exoskeleton.

Other material: *H.* cf. *prescheri,* NHMUK It 29245, Pl. 9J–N from the "*Lobopyge* Couche", El Otfal Formation, Eifelian, Issoumour (see Issoumour section, McKellar & Chatterton 2009, p. 12) (Fig. 2B, Map 7, site 2).

Description. Cephalon and genicranium narrow, length (sag.) 86% and 76% of width (tr.), respectively. Widest point of cephalon and genicranium of holotype at midpoint between eye lobes and alae and at posterior border, respectively. Glabella narrow, carinate, and with coarse, barely-inflated tubercles on crest. Width (tr.) of glabella at S1 around 65% of length (sag.) of glabella anterior to S0. S1 sloping posteriorly and curving slightly anteriorly, S2 and S3 very shallow, barely rising out of axial furrow. Axial furrows very gently convex and converging anteriorly at more than 15^0 to sagittal line. Preglabellar furrow shallow and straight (tr.) in anterior view. Occipital furrow deep and straight (tr.). Occipital ring medially broadened and in lateral view, lower than glabella anterior to S0. Occipital node small and barely inflated. L1 not inflated although alae are. Alae large (tr.) and narrow and reaching over 60% of way across genal area. Alar furrow very shallow and distally effaced. No interalar furrows or ridges. Posterior border short (tr.), under 30% of width of occipital ring (tr.).

Genal area narrow, width (tr.) around 50% of length (exsag.) and lacking pits and caeca. Preglabellar genal area narrow (sag.), length (sag.) ≈20% of width (tr.). Eye lobes very large, strongly inflated, cone-shaped and extending to axial furrow. Eye location ratio around 0.83. Two fairly small oval eye lenses (Pl. 9D). Genal ridge barely indicated, becoming a little more visible posterolaterally on genal roll. Anterior boss barely inflated and girder weakly kinked. Genal roll gently sloping anteriorly (≈ 45°) and moderately steeply laterally (≈60°). Perforations on genal roll about same size as those on brim, becoming slightly smaller away from girder. Row of large perforations immediately above girder, and at inner margin of fringe, anterior to glabella, row of perforations a little larger than those on main part of genal roll.

Brim wide, about one third of cephalic length (sag.), sloping moderately (≈17°), gently concave anteriorly, straight laterally and becoming gently convex close to posterior border. Brim width ratio just over 0.50. Brim perforations becoming smaller away from girder to become very fine (standardised diameter of ≈80 μm). Row of larger perforations at proximal and distal edges, no caeca. Rim stout and lacking tubercles on dorsal surface. Marginal band near vertical with dorsal surface overhanging. Prolongations moderately long (exsag.) at 85% of cephalic length (sag.). In dorsal view, internal rim curving smoothly adaxially and concave posteriorly in lateral view. Internal rim wide (tr.), wider than external rim (sag.) and with tubercles on dorsal edge. Genal spine short set slightly obliquely adaxially.

Thorax little known but inner portion of pleurae shortening (tr.) strongly posteriorly, much more than axial rings. (Pl. 9A). Pygidium and hypostome not known.

Remarks. *Harpes prescheri* lacks only one of the diagnostic characters for the genus shown in Table 5a, in having a weak girder kink rather than no girder kink.

Harpes prescheri and *H. lahceni* are similar but have well defined differences. The cephalon, genicranium and glabella of *H. prescheri* are much narrower, the genal roll is more gently-sloping anteriorly and the brim is wider (sag.) and has a brim width ratio of just over 0.50, whereas that of *H. lahceni* is 0.76. Also, the dorsal surface of the rim lacks tubercles, and the length (exsag.) of the prolongations expressed as a percentage of cephalic length (sag.) is 82% and 112% for *H. prescheri* and *H. lahceni,* respectively. In lateral view, the profile of the internal rim of *H. prescheri* is concave and not wave-like as it is in *H. lahceni*.

NHMUK It 29245, designated as *Harpes* cf. *prescheri*, (Pl.9 J–N) is similar to *H. prescheri* in having a steep genal roll anteriorly and a short (sag.) preglabellar field, but differs in having a narrower brim (sag.) and a brim width ratio of 0.73 rather than 0.50.

Harpes sphenocephalus n. sp.

Plate 4E–K

Diagnosis. Cephalon widest across eyes. Glabella narrow anteriorly-rounded cone without tubercles on dorsal surface. Brim broad (sag.), profile straight (neither convex or concave) and moderately steeply-sloping. External border runs straight, slanting adaxially, from point where it passes eyes to two thirds of way down (exsag.) the prolongations. Eyes set close to midway between axial furrow and inner margin of fringe. Perforations on brim moderately large, becoming smaller distally until middle of rim. Perforations on genal roll much finer except proximal to girder, where there are two rows of larger perforations. Terminal spines long, slanting obliquely adaxially.

Etymology. Derived from the word "sphenoeides" ancient Greek for wedge. The cephalon, in lateral view is wedge-shaped.

Material and occurrence. Holotype: NHMUK It 29246, Pl. 4E–K, from the "Cheirurid Couche" horizon 1, Section 1 (Fig. 6), Er Remlia Formation, Emsian, Jbel Ou-Driss (Fig. 2B, Map 4, site 15), dorsal exoskeleton with cephalon articulated, thorax disarticulated and partially hidden.

Other material: NHMUK It 29247, *Harpes* cf. *sphenocephalus,* Pl. 4L–O, from "Cheirurid Couche", Er Remlia Formation, Emsian, Jbel Issoumour (Fig. 2B, Map 7, site 18), dorsal exoskeleton of partial cephalon.

Both *H. sphenocephalus* and *H.* cf. *sphenocephalus* are found with the same cheirurid species but come from two different localities, some 60 km apart.

Description. Cephalon widest at eye lobes and genicranium broad, length (sag.) 78% of width (tr.), widest at posterior border. Width (tr.) of glabella anterior to S0 62% of length (sag.) Glabella crest rounded but flanks tectiform. S1 slanting posteriorly and not turning anteriorly near crest. Shallow muscle attachment impressions not

rising out of axial furrow at S2 and S3. Glabella tapered anteriorly, axial furrows converging anteriorly at ≈18^0 to sagittal line**.** Preglabellar furrow very shallow and straight (tr.) in anterior view. Occipital furrow deep and wide. Occipital ring wide, not medially broadened, lacking tubercles on dorsal surface and in lateral view, lower than glabella anterior to S0. Occipital node moderately large, poorly inflated. L1 inflated with axial furrow crossing at junction with ala. Alae small, width (tr.) ≈25% of length (sag.) of glabella anterior to S0 and reaching ≈50% of way across genal area. Interalar furrow, low interalar ridge and alar depression present. Posterior border short, ≈30% of width (tr.) of occipital ring. Preglabellar genal area narrow (sag.) (Pl. 4E).

Genal area narrow with faint caeca and coarse pitting. Eye lobes large (≈37% (exsag.) of width (tr.) of glabella at S1), oval and with no tubercles on dorsal surface. Two oval eye lenses of equal size (Pl. 4K). No eye or genal ridges present. Course of inner margin of fringe across anterior of genal areas. Anterior boss barely inflated. Genal roll sloping gently (≈47^0) anteriorly, steeply (≈67^0) laterally and narrowing strongly posterolaterally. Row of large perforations above girder and at inner margin of fringe anterior to preglabellar genal area. Perforations quickly become smaller than those on brim away from girder. Girder narrow (sag. and exsag.).

Brim moderately wide (sag.), 33% of cephalic length (sag.) and narrowing strongly posterolaterally (brim width ratio 0.51). Slope of brim moderate. Brim perforations becoming smaller outwards from girder and moderately small in central area of brim. Larger row of perforations at proximal and distal edges. External rim fine and lacking tubercles on dorsal surface. Marginal band near vertical, without ridges but with central row of coarse tubercles and row of very fine tubercles at bottom edge.

Length (exsag.) of prolongations ≈84% of cephalic length (sag.). In dorsal view, external and internal rims curving adaxially; in lateral view, internal rim concave, external rim curving gently up to meet internal rim at end of prolongation. Tubercles on dorsal surface of internal rim and row of larger perforations below. Genal spine long and slanting slightly adaxially. Extension of girder meeting internal rim third of the way down towards distal end. Hypostome, thorax and pygidium not known.

Remarks. *Harpes sphenocephalus* has a weak girder kink rather than no girder kink but otherwise complies with the *Harpes* diagnostics shown in Table 5a.

H. sphenocephalus is very similar to *H. escoti* but differs by having a wider genicranium and glabella; a glabella that is more carinated with rounded flanks and a more inflated L1; axial furrows that converge more strongly; a preglabellar furrow that is straight and not bowed upwards as is in the case of *H. escoti*; a wider occipital furrow and an occipital ring that is much less broadened medially; larger alae (tr.) each with an interala ridge; a brim that slopes more steeply (sag.), has a lower brim width ratio and perforations that become smaller outwards from girder. Also, *H. sphenocephalus* has longer prolongation (exsag.) than *H. escoti*. As regards *H. escoti* the figured material only allowed 65% of the cephalic characters used in the matrix to be determined and it is likely therefore that there are other differences between the two species which are not included here.

Amongst the new Moroccan species *Harpes sphenocephalus* is similar to *H. boudibensis* but differs by having a glabella that is nearly 15% narrower and with no tubercles straddling the crest. The genal area is 20% wider, pitted and the alae stretch less than 60% of the way across it, compared with over 70% in *H. boudibensis.* The brim is 22% broader (sag.) and more steeply-sloping and has brim perforations that are 15% smaller and 60% more densely packed. On prolongations, the brim of *H. sphenocephalus* is less steeply-sloping and, in dorsal view, the external rim is straight rather than curved as it crosses onto the prolongations. The internal rim, in lateral view, is straight for the first two thirds of the way back, then curves gently upwards over the distal third of its length. In the case of *H. boudibensis,* the internal rim has a wave-like profile and the terminal spines are shorter.

Harpes cf. *sphenocephalus* (Pl. 4L–O) differs from *H. sphenocephalus* most noticeably in having a broader (tr.) genicranium, fine tubercles on the glabella anterior to S0, wider (tr.) alae with alar furrows distally effaced, no caeca on genal areas, eye tubercle larger (tr.) and extending to axial furrow, internal margin of fringe across front of the genal area convex rather than straight, no anterior boss, a wider girder, brim slightly convex with a 30% higher brim width ratio and larger perforations, a much more robust external rim and with fine tubercles on the dorsal surface.

The holotype of *H. sphenocephalis* is well preserved complete cephalon of a size that would indicate that it belonged to a well-developed holaspid. The cephalon is symmetrical and without any apparent pathological defects and has significant differences with *H. escoti,* the species it is most similar too. On this basis the species has been erected although without the support of paratypes.

***Harpes supercilium* n. sp.**
Plates 3A–P, 4A–D

Diagnosis. Narrow cephalon, widest (tr.) midway between eyes and alae, width (tr.) is just over 1.1 times sagittal length. Glabella anteriorly rounded cone. Eye lobe with short transverse eye ridge on posterior edge. Alar furrows becoming shallower distally. Prolongations are about same length (exsag.) as cephalon (sag.). In lateral view, internal rim has subdued wave-shaped profile and is terminated by short genal spine. Twenty thoracic segments.

Etymology. Eyebrow in Latin is "*Supercilium*". The short eye ridges of this species resemble small eyebrows.

Material and occurrence. Holotype: NHMUK It 29252, Pl. 3G–K, from horizon 5, Section 2 (Fig. 7), El Otfal Formation, Eifelian, Jbel Issoumour (Fig. 2B, Map 7, site 10). Paratype: NHMUK It 29251, Pl. 3A–F, from type horizon, site 3; paratype: NHMUK It 29250, Pl. 3L–P, from horizon 10, Section 1 (Fig. 6), El Otfal Formation, Eifelian, Jbel Ou-Driss (Fig. 2B, Map 4, site 24); paratype: NHMUK It 29248, Pl. 4A–D, from horizon 8, Section 1 (Fig. 6), El Otfal Formation, Eifelian, Jbel Ou-Driss (Fig. 2B, Map 4, site 14).

Harpes supercilium's range overlaps the top of that of *H. boudibensis* at Jbel Issoumour, extending to at least one later horizon (Fig. 7). It is also present at Jbel Ou-Driss in horizons 8 and 10, as is *H. oudris* in horizon 5 and *H.* cf. *boudibensis* in horizon 7 (Fig. 6).

Description. Cephalon ovoid with widest point midway between eye lobes and alae. Genicranium narrow widest at posterior border. Glabella not inset and fairly broad (tr.), width (tr.) 70% of length (sag.). Glabella crest rounded without tubercles but with fine pitting. S1 rising out of axial furrow, sloping backwards and curving around top of muscle insertion area, which is tulip-shaped with vertical intermittent striations (Pl. 3O). Furrows at S2, S3 and S4 barely rising out of axial furrow. S2 and S3 muscle insertion areas oval and just over 25% of size of S1. S4 smaller still and joined with preglabellar furrow and muscle insertion area crossing anterior of glabella. S0 muscle insertion area oval, covering about 75% of area of S1 and spreading into occipital furrow. Axial furrows converging weakly anteriorly at around 13° to axis. Preglabellar furrow distinct and bowed upwards in anterior view. Occipital furrow broad (sag.), deep and medially straight in dorsal view. Occipital ring broad (sag.), not medially broadened, carrying transverse row of fine tubercles posterior to occipital node, and in lateral view, same height as glabella anterior to S0. Occipital node small and preglabellar field narrow, length (sag.) about 20% of width (tr.). L1 inflated and axial furrow crossing junction of L1 and ala. Alae inflated, anterolaterally directed, wider (tr.) than long (exsag.), large (tr.), just under 40% of width (tr.) of glabella at S0 and stretching over 60% of way across genal area. Alar furrow deep, interalar ridge and furrow and alar depression present. Posterior border short, about 25% of width (tr.) of occipital ring.

Genal area narrow, width 52% (tr.) of length (exsag.) and with faint caeca, pits and tubercles. Eye lobes oval to cone-shaped, strongly inflated, very large (exsag., 47% of width (tr.) of glabella at S0) and with tubercles on dorsal surfaces. Visual surface close to inner margin of fringe and eye lobe nearly extending to edge of axial furrow. Each eye lobe with two oval lenses, anterior lenses the largest. Genal and eye ridges present. Eye ridge well defined, short and straight. Course of inner margin of fringe across anterior of genal areas straight and marked by large perforations across anterior of boss only. Anterior boss barely inflated and not reaching down to girder. Genal roll sloping gently anteriorly at around 42^0, laterally more steeply at around 62^0. Brim perforations becoming smaller for short distance away from girder to become smaller than on brim. Genal roll without caeca. Girder moderately narrow and without kink.

Brim concave (sag.), straight laterally, sloping anteriorly at 12^0, moderately wide (sag.), 32% of cephalic length (sag.). Brim width ratio 0.51. For short distance, brim perforations decrease in size away from girder and standardised width of brim perforations in centre of brim is moderately fine, at just over 125μm. Row of larger perforations around inner and outer edges of brim, and brim and light caeca reaching across the whole brim. External rim stout and without tubercles on dorsal surface. Marginal band near vertical, straight with ridges top and bottom, and without tubercles. Prolongations are long (exsag.), 98% of cephalic length (sag.). In dorsal view, internal and external rims curving adaxially and internal rim with weak wave-like profile in lateral view. Tubercles on dorsal surface of internal rim; genal spine short, under 10% length (exsag.) of prolongation. Extension to girder meeting internal rim 1/3 way down prolongation. Brim steepens quickly to near vertical on prolongations.

Thorax with 20 segments. Width (tr.) of axial ring on last segment 30% of that of first segment. No tubercles or pitting on axial rings. Thoracic segments widening (tr.) posteriorly to 7^{th} segment. Shortest pleura (inner portion only) 55% of longest. Pleural furrows narrow deep and U-shaped. No pitting.

Thorax only partly known, hypostome and pygidium not known.

Remarks. *Harpes supercilium* has light caeca crossing its brim but otherwise complies with the *Harpes* diagnostics shown in Table 5a.

Harpes supercilium is very similar to *H. oudris* but differs in having no tubercles on the glabella, the eye lobe or genal area, and ala which reaches about 60% of the way across the genal area, compared with 70% in case of *H. oudris*. *Harpes supercilium* has more pronounced pitting on the genal area, a short (tr.) eye ridge, and genal roll perforations are smaller than those on the brim rather than being the same size. Also, its brim slopes anteriorly more steeply and it has a brim width ratio of around 0.55, compared to 0.80 for *H. oudris*. In lateral view, its internal rim has a much less strong wave-like profile and the distal ends of the prolongation are not so strongly upturned.

H. supercilium is also similar to *H. boudibensis* but differs by having glabellar furrows at S2-S4, a distinct preglabellar furrow, a well-defined eye ridge, a genal area with faint caeca and a brim with light caeca reaching across it. Also, the thorax of *H. supercilium* has around 20 segements, 5 fewer than that of *H. boudibensis*. *H. boudibensis* has no furrows at S2-S4, a very shallow preglabellar furrow with the anterior boss joined to the glabella, no eye ridge and no caeca on the genal area or the brim.

Genus *Lioharpes* Whittington, 1950a

Type species. *Harpes venulosusus* Hawle & Corda, 1847, Pragian, from the Koněprusy Limestones, Koněprusy, Czech Republic

Emended diagnosis. Cephalon ovoid. Occipital furrow broad (sag.), equal to or wider (exsag.) than posterior border. Width (tr.) of posterior border between 31% to 40% of occipital ring width (tr.). Genal area moderately broad, inner margin of fringe across anterior of genal area straight and Eye lobes with three lenses each. Tubercles on occipital ring, palpebral lobes and dorsal surface of internal rim. Girder narrow (sag. And exsag.), 1.5% to 2.2% of genicranium width (tr.). Brim width ratio between 0.70 and 0.85. Extension of girder meeting internal rim halfway down prolongation. Thorax with 20 to 24 thoracic segments. Pleural furrows shallow and narrow, and distal ends of pleurae rounded.

Discussion. *Lioharpes* species are similar to *Harpes* but differ in having smaller (tr.) alae, broader genal areas with faint caeca, less inflated eye lobes set away from inner margin of the fringe. In addition, brims are concave to straight and do not steepen so strongly on the prolongations. Their brim width ratio is distinctly higher.

The cladogram for *Lioharpes* is shown in Figs 9 and 10a. and shows that *Lioharpes* species are divided into two groups which are separate from the type species. The type species is from Czech Republic then partial covered by northern part of the Rheic Ocean, and two groups from the south part of the Rheic Ocean, now North Africa and in particular Morocco. The first group includes *L. ammari* n. sp., *L. saredrar,* n. sp. and *L. scopulum* n. sp.*,* and the second group, *L. galea* n. sp., *L.* cf. *galea, L. morocconensis* n. sp.*and L.* cf. *morocconensis*. The type species and Group 1 species have brim extensions that steepen along the proximal edges of the prolongations only, while the whole of the brim extensions steepen on Group 2 species. Also, the eye lobes of Group 1 have three lenses while those of Group 3 have only two. The number of eye lenses of the type species is not known. Group 1 species are upper Pragian and Group 2 are Emsian.

On the basis of the cladistic study, *L hastatus* has been reassigned to *Pinnuloharpes* n. gen; and *L. vectori* Doubrava, 1991, from the Silurian, to *Bohemoharpes* s. l.. *Lioharpes montagnei* (Hawle & Corda, 1847), *L. wendti* Feist, 2018 and *L. perneri* (Prantl & Přibyl, 1954) are transferred to *Fritchaspis,* and *Lioharpes sculptus* (Hawle & Corda, 1847) and *L. venetus* (Gortani, 1915) to *Maghroharpes* n. gen.

Harpes polaris (Maksimova, 1977) and *Kielania superna* (Maksimova, 1979) have been reassigned to *Lioharpes*. s.l.. In the case of *Kielania superna,* the illustrated material provides little data, so its reassignment should be treated with caution, especially as its age is upper Eifelian rather than middle Pragian to upper Emsian, from which the other *Lioharpes* species date.

Lioharpes crasimargo (Novák, 1890) is in a sister relationship with *Lioharpes* and *Maghroharpes,* Its position, however, is not well enough supported to justify the erection of a new genus and as a result the species is designated Gen. Indet..

Lioharpes species included in the study and are shown together with their interspecies relationships in Fig. 10a. *L. bischofi* (Roemer, 1852), not included in the study remains pro tem in the genus. The range of the *Lioharpes* is from middle Pragian to upper Eifelian and "*Lioharpes*" from upper Pragian to Emsian.

***Lioharpes galea* n. sp.**
Plate 10E–K

Diagnosis. Cephalon ovoid, nearly oval, with external and internal rims curving strongly adaxially. Glabella broad, crest rounded with fine granulation and pitting, and axial furrows convex. Alae anterolaterally directed and eye lobes located away from axial furrow. Brim straight to slightly concave in profile, gently sloping and with large brim perforations (diameter around 220 μm on standardised brim). Well-developed caeca on brim and genal roll. Length (exsag.) of genal prolongations over 90% of cephalic length (sag.).

Etymology. Galaea, Latin for helmet. In dorsal view, the cephalon resembles a helmet.

Material and occurrence. Holotype: NHMUK It 29268, Pl. 10E–H, from a coral horizon just above the *Kolihapeltis* horizon, upper Pragian, Ihandar Formation, Jbel Otfal (Fig. 2B, Map 9, site 20**),** a partial dorsal exoskeleton of a cephalon and thorax. Paratype: NHMUK It 29269, Pl. 10I–K, from the type horizon and locality, an articulated dorsal exoskeleton.

Description. Cephalon widest halfway between eye lobes and alae, genicranium moderately narrow, widest at posterior border. Glabella broad, only slightly tapered anteriorly and not carinated or inset. Flanks convex with fine granulation and pitting along crest. L1 inflated, S1 slanting anteriorly, effaced before curving forward near crest. Preglabellar furrow distinct and straight in anterior view. Occipital furrow deep and medially straight (tr.). Occipital ring not medially broadened, same width (sag.) as posterior border (exsag.) and, in lateral view, same height as glabella anterior to S0. Tubercles on occipital ring not prominent but closely packed. Occipital node small, located on anterior slope of occipital ring. Alar furrow anterolaterally directed, small, under 30% of glabella (tr.) at S1 and nearly as wide (tr.) as long (exsag.) at axial furrow. Alar furrow shallow but well defined. Alar depression present and axial furrow partly effaced at junction of ala and L1. Posterior border moderately short (tr.) and preglabellar field wide.

Genal area moderately broad with pits and faint caeca. Genal ridge present, reaching posterolaterally across onto genal roll. Eye lobes oval, long (exsag.) and inflated. Eye location ratio over 80. Anterior eye lens slightly larger than posterior lens and central lens, which sits between and slightly higher than other two lenses and is much the smallest. Anterior and posterior eye lenses oval, central lens subcircular. Eye ridge not well-defined. Inner margin of fringe across anterior of genal area straight and marked by larger perforations across anterior boss. Boss barely inflated and not joined to glabella or reaching girder. No girder kink. Genal roll moderately gently sloping anteriorly, laterally steep and with caeca. Perforations smaller than on brim with a single row of larger perforations above girder. Fringe narrowing strongly posterolaterally and girder moderately narrow.

Brim concave, barely sloping but steepening along proximal edge on prolongations. Brim width (sag.) 32% of cephalic length (sag.) and brim width ratio 0.85. Light caeca across brim and standardised brim perforations of around 220μm; larger perforations along distal and proximal edges of brim. External rim stout and marginal band near vertical with straight profile. Rim and marginal band free of tubercles. Length (exsag.) of prolongations around 90% of cephalic length (sag.), not strongly tapered in lateral view. Internal rim gently concave as it slopes down to short genal spine, which follows curve of external rim. Internal rim with row of large perforations below and sparse fine tubercles on dorsal surface. In dorsal view, internal and external rims curve adaxially.

Thorax with at least 23 segments. Width (tr.) of last axial ring around 35% of first. Tubercles on axial rings. Inner portion of pleurae increasing in length (tr.) to 5th segment, before shortening (tr.) until last segment, which is around 40% of 5th segment. Outer portion of pleurae very short, barely downturned, straight, slanting slightly posteriorly from fulcrum. Distal ends rounded except on first three segments, where they are more pointed.

Hypostome and pygidium unknown.

Remarks. *Lioharpes galea* differs from *L. venulosus* (Hawle & Corda, 1847) Pls 10A–D, 54A–D in having the widest (tr.) point of the cephalon at alae rather than at the midpoint between the alae and eye lobes. The glabella is 15% narrower (tr.) and has a crest that is rounded, not carinate. The alae reach less than two thirds the way across the genal area and are anterolaterally directed, whereas those of *L. venulosus* reach 75% of the way across and are laterally directed. Standardised brim perforations are larger in *L. galea*, having a 55% greater diameter. *L. galea's* genal prolongations are longer, having a length (exsag.) of around 90% of cephalic length (sag.), compared with 66% to 75% in *L. venulosus,* and *L. galea's* external and internal rims are more strongly curved adaxially. On the thorax, there are tubercles on the axial rings and pleural furrows are broad and shallow, rather than narrow and deep (Prantl and Přibyl,1954, p.138, para 2) as is the case in *L. venulosus*.

Of all the *Lioharpes* species, *L. galea,* is the most like those of the genus *Maghroharpes* and in particular, *M. oufatenensis*. It differs, however, in having: a more ovoid cephalon; a slightly narrower genicranium; a rounded crest to the glabella; axial furrows which do not converge as strongly, are not as convex and do not cross the junction of alae with L1; wider occipital furrow and a slightly narrower occipital ring; genal area with light caeca; alae anterolaterally directed; eye lobes less inflated and with three eye lenses rather than two; genal ridge and well-defined eye ridge present; course of inner margin of fringe across anterior of genal area straight rather than mildly convex; anterior boss more inflated; genal roll with caeca and less steeply-sloping and narrower girder than that of *M. oufatenensis*. Also, *M. oufatenensis* has bigger standardised brim perforations; more pronounced caeca right across brim and on genal roll; marginal band straight, not concave; and longer prolongations.

Lioharpes venulosus caillaudi (Pillet 1972) from the quarry of Ferronnière, Erbray, Loire-Atlantique, France has similar adaxially-curved external and internal rims as *L. galea,* but it has more in common with *L. venulosus venulosus.*

***Lioharpes morocconensis* n. sp.**

Plate 11A–M

Diagnosis. Glabella anteriorly tapered with no carination and axial furrows convex. S1 sloping backwards, before curving forward. Occipital furrow medially bent forward, eye ridge poorly defined. Genal roll with caeca and brim perforations moderately large and becoming smaller away from girder. Well-developed caeca crossing brim. Genal prolongations moderately short and internal rims subparallel.

Etymology. Country of type locality.

Material and occurrence. Holotype: NHMUK It 29271 (1), Pl. 11F–J, from a lower Emsian horizon Boutiskaouine Formation, Jbel el Otfal (Fig. 2B, Map 9, site 6), a partial dorsal exoskeleton of cephalon. Paratype: NHMUK It 29272, Pl. 11A–E, from type locality and horizon (Fig. 2B, Map 9, site 17), dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29271 (2), Pl. 11K–L), from type locality (site 6), partial dorsal exoskeleton of cephalon.

Other material: *Lioharpes* cf. *morocconensis*, NHMUK It 29273, Pl. 12A–F, from an lower Emsian horizon, Seheb El Rhassel Group, 28.3 km S.S.W. of Rissani (Fig. 2B, Map 14, site 10), dorsal exoskeleton of partial cephalon.

Description. Cephalon and genicranium widest at mid-point between eye lobes and alae. Glabella anterior to S0 broad, crest rounded with granulation and fine pitting, S1 slanting posteriorly and starting to curve anteriorly near crest, furrows at S2, S3 and S4 not present. Preglabellar furrow distinct and straight (tr.) in anterior view; occipital furrow deep and just broader (sag.) than posterior border (exsag.). Occipital ring same height in lateral view as glabella anterior to S0 and with very fine tubercles on dorsal surface. Occipital node small located on anterior slope of occipital ring. L1 not inflated, axial furrow not crossing junction of ala with L1, ala size (tr.) large, width (tr.) 30% of glabella (tr.) at S1, and moderately wide with width (tr.) 80% of length (exsag.). Alar furrow deep, well defined, interalar ridge, furrow and depression present, alae laterally directed. Posterior border moderately wide (tr.), over 40% of width (tr.) of occipital ring and preglabelar genal area (sag.) 22% of width (tr.).

Genal area moderately broad, width (tr.) 62% of length (exsag.), with caeca and pits. Eye lobes large (exsag.), over 31% of glabella width at S0 and with very fine tubercles on dorsal surface. Anterior and posterior eye lenses ovoid and of equal size, central lens much smaller, subcircular and set in between and slightly higher than anterior and posterior lenses. Eye location ratio 0.78, eye ridge indistinct and no genal ridge. Course of inner margin of fringe across anterior of genal area straight, anterior boss barely inflated, reaching down to weak girder kink. In lateral view, slope (sag.) between inner margin of fringe and girder is gentle (47^0). Genal roll strongly convex, barely sloping at internal margin of fringe but steepening sharply to become near vertical at girder. Laterally, genal roll sloping moderately steeply at 63^0. Genal roll with caeca and perforations smaller than those on brim. Girder moderately narrow.

Brim concave, sloping (sag.) at under 10^0 and moderately wide, width (sag.) 31% of cephalic length (sag.). Brim perforations decrease for short distance away from girder and diameter of standardised brim perforations on central part of brim (sag.) just under 200µm. Brim on prolongation steepening posteriorly along inside edge and brim width ratio 0.82. Rim stout, without tubercles on dorsal surface, and marginal band near vertical with ridge around top and bottom and fine scattered tubercles in between. Prolongations moderately short (exsag.), about 80%

of cephalic length (sag.). In dorsal view, internal rims subparallel; in lateral view, concave. External rim curving gently adaxially (dorsal view) and upwards (lateral view) to meet internal rim at end of prolongation, which lacks genal spine. Dorsal surface of internal rim with tubercles, with row of large perforations below rim.

Thorax, pygidium and hypostome unknown.

Remarks. *Lioharpes morocconensis* complies with all the proposed diagnostic characters of its genus as shown in Table 5a, except that the width (tr.) of its posterior border is about 45% of the width (tr.) of the occipital ring, wider than the upper diagnostic range of 31% to 40%.

Lioharpes morocconensis is also very similar to *L. galea*, but differs in having: the genicranium widest at midpoint between eye lobes and alae rather than at posterior border; alae laterally directed rather than anterolaterally; posterior border wider (tr.);the anterior boss reaches down to the girder that is weakly kinked, unlike in *L. galea*; smaller brim perforations which become smaller towards centre of brim; and shorter prolongations with internal rims subparallel rather than curving adaxially.

Lioharpes cf. *morocconensis* (Pl. 12A–F) differs from *L. morocconensis* in having: an occipital ring whose top in lateral view is lower than the top of the glabella anterior to S0; genal areas more finely pitted; shallower alar furrows ; genal roll much less convex (sag.); brim slightly steeper (sag.) with more pronounced caeca and the whole brim steepening on prolongations, not just along the proximal edge; prolongations shorter with girder extension meeting internal rim a little further down prolongation.

Lioharpes scopulum **n. sp.**

Plate 32E–Q

Diagnosis. Genicranium is narrow (tr.), glabella inset and carinate, axial furrows straight, occipital furrow and occipital ring narrower (sag.) than posterior border (exsag.). CMO on occipital node with four pits arranged in a square, alae longer (tr.) than they are wide (exsag.), no alar depression and genal area without caeca, tubercles or granulation. Inner margin of fringe anterior to glabella not marked by perforations larger than those on genal roll. Brim is concave (sag.), straight laterally and quickly steepening to near vertical on prolongations; brim width ratio under 0.60.

Etymology. Scopulum, Latin for reef, referring to the coralliferous nature of the type locality and horizon.

Material and occurrence. Holotype: NHMUK It 29279, Pl. 32E–L, from coral horizon at the Pragian/Emsian border, Ihandar Formation?, Northern slopes of bou Lachrahl (Fig. 2B, Map 9, site 2), dorsal exoskeleton, cephalon only. Paratypes: NHMUK It 29280 (1– 3), Pl. 32M–N, O–P, Q, respectively, from type locality and type horizon (site 3), partial dorsal exoskeletons of cephala only.

Description. Cephalon ovoid in dorsal outline, widest at midpoint between eyes and alae. Genicranium width (tr.) just under 90% of length (sag.). Glabella inset, moderately narrow, flanks tectiform, crest carinate and with fine pitting. Axial furrows straight, weakly tapering anteriorly. S1 furrows effaced before curving anteriorly and no muscle insertion furrows at S2, S3 or S4. Muscle insertion areas only visible on uncoated glabella (Pl. 32E) as dark patches; S0 oval, S1 tulip-shaped and S2, S3 and S4 subcircular. Occipital furrow deep, narrower (sag.) than posterior border and in dorsal view, straight not bowed. Occipital ring not medially broadened and lower than glabella in lateral view, sloping backwards. Occipital node moderately broad with a CMO of four very fine, symmetrically arranged perforations (Pl. 32L). Alae small, width (tr.) 28% of glabella anterior to S0 (sag.), wider (tr.) than long (exsag.) and laterally-directed. Alar furrow shallow, well defined and no alar depression. Posterior border (tr.) 46% of occipital ring (tr.). Preglabellar furrow well-defined, straight in anterior view and width (sag.) around 25% of width (tr.).

Genal area moderately broad (tr.), around 57% of length (exsag.) and with fine pitting. Eye lobes inflated and moderately long (exsag.) at 41% of glabella width at SO. Each eye lobe with three lenses, anterior and posterior reclined ovals, and central lens circular. (Pl. 32J, K, N). Anterior lens largest and central lens very small. Eye location ratio is 0.78. Eye ridge poorly-defined and no genal ridge. Inner margin of fringe convex across anterior of genal areas. Boss barely inflated, reaching down to weak girder kink and not attached to glabella. Perforations on genal roll same size as those on brim. Girder moderately wide.

Brim sloping at around 15^0 (sag.), concave (sag.), straight laterally and moderately wide, being around 32% of cephalic length (sag.). Brim width ratio around 0.60. Standardised brim perforations between 100µm and 150µm in

diameter, with no graduation in size across brim. Caeca on genal roll and across brim. External rim stout with fine tubercles on dorsal surface. Length (exsag.) of prolongations 72% of cephalic length (sag.) and genal spine short. In dorsal view, internal rims curving adaxially to continue into genal spine. On prolongations, extension of girder meeting internal rim just under halfway down and brim steepening quickly to near vertical.

Hypostome, thorax and pygidium unknown.

Remarks. *Lioharpes scopulum* lacks two of the genus' 8 diagnostic characters shown in Table 5a: the occipital furrow is narrower (sag.) than the posterior border (exsag.) and the width (tr.) of its posterior border is about 46% of the width (tr.) of the occipital ring, wider than the upper diagnostic range of 31% to 40%.

Lioharpes scopulum is similar to *L. saredra,* which has been found at the same locality (Pl. 15K–N), but it has the following differences: widest (tr.) point of the cephalon is posterior to the eye lobes rather than at the eye lobes; glabella is inset, carinate and finely pitted; muscle attachment areas at S2, S3 and S4 are not visible; there is no interalar ridge or alar depression and the axial furrow crosses the junction of the ala and L1; there are 3 eyes lenses per eye tubercle, not two, with the anterior lens being larger than the posterior lens; the course of the fringe inner margin across the anterior of the genal areas is convex not concave, and as it crosses below the preglabellar field, its path is not marked by perforations bigger than those on the main part of the genal roll; the perforations on the genal roll are the same size as those on the brim, not smaller; and the genal prolongations are shorter, some 70% of the cephalic length (sag.), rather than just under 90% in the case of *L. saredra*.

The small central eye lens is difficult to discern on the holotype. In Pl. 32J (dorsal view), the lens appears to be a gentle dome in shape, but in Pl. 32K (lateral view), the lens appears flat and is defined by a subcircular furrow which is intersected by a smaller subcircular furrow below. In Pl. 32N (dorsal view), the small lens which is from the paratype NHMUK It 29280 (1) is much clearer.

The occipital node, with a CMO with four small pits arranged symmetrically in a square pattern, is similar to that found on *Pinnuloharpes hamarlagdadensis* (new material, Pl. 44E)*, P.* aff. *haustrum* (Pl. 43J) and described by McNamara *et al.* (2009, p. 27, text fig. 4) in *Eskoharpes friendi*.

Lioharpes ammari n. sp.

Plates 12G–M, 13A–J

Diagnosis. Glabella is conical, carinate and with tectiform flanks and tubercles along crest. S1 short and shallow. Eye lobes inflated, tall, subcircular and with two eye lenses each. Brim is wide (sag.) and steepens strongly on prolongations. Brim width ratio is around 0.70. In lateral view, internal rim nearly horizontal with slightly wave-like profile. Pleural furrows narrow and well defined.

Etymology. For Ammar Ait Hssain, a trilobite worker and preparator who prepared, together with his brother Hammi, much of the material presented herein.

Material and occurrence. Holotype: NHMUK It 29263, Pl. 12G–M, from an upper Emsian horizon, Tazoulait Formation, north flank of Jbel Ou-Driss (Fig. 2B, Map 4, site 9), dorsal exoskeleton with pygidium enrolled. Paratype: NHMUK It 29264, Pl. 13A–E, from horizon 2, Section 1 (Fig. 6), Tazoulait Formation, upper Emsian, South flank of Jbel Ou-Driss (Fig. 2B, Map 4, site 12), dorsal exoskeleton with pygidium missing; Paratypes: NHMUK It 29265 (1), Pl. 13F–H, and NHMUK It 29265 (2), Pl. 13I–J, from same location and horizon as NHMUK It 29264 (site 13). NHMUK It 29265 (1), dorsal exoskeleton of a partial cephalon, and NHMUK It 29265 (2), a ventral exoskeleton of upper lamella.

Other material: *Lioharpes ammari*? (meraspis / early holaspid), NHMUK It 29266, Pl. 53A–F, from the type horizon and location, north flank of Jbel Ou-Driss (Fig. 2B, Map 4, site 25).

Description. Cephalon widest at midpoint between eyes and alae, genicranium broad (tr.) with width about 1.4 x length (sag.) and widest at posterior border. Glabella anterior to S0 carinate, with pronounced tubercles along crest and broad with width (tr.) over 75% of length (sag,). S1 slanting posteriorly, not reaching halfway up flank of glabella, no muscle insertion furrows at S2, S3, S4. Axial furrows convex, converging at around 17^0 to axis and not crossing junction between F1 and ala. Preglabellar furrow shallow and straight (tr.) in anterior view. Occipital furrow deep, straight (tr.) and medially broader (sag.) than posterior border (exsag.). Occipital ring same width (sag.) as posterior border (exsag.), higher than crest of glabella in lateral view and with pronounced tubercles on dorsal surface. Occipital node large and strongly inflated. L1 inflated, alae laterally directed, large at over 30% of width

(tr.) of glabella at S1 and over 85% of length (exsag.). Alar furrow shallow and alar depression present. Posterior border short width (tr.), just under 30% of width of occipital ring (tr.) and preglabellar genal area narrow.

Genal area moderately broad with width (tr.) over 60% length (exsag.). Eye lobes strongly inflated, tall, oval in dorsal view, tubercles on dorsal surface and with two eye lenses. Eye lenses of about equal size and elongated, recumbent rectangles with rounded corners in shape (Pl. 12K). Eye lobes close to internal margin of fringe; eye location ratio over 0.80. No eye ridge or genal ridge. Anterior boss barely inflated but reaching down to weak girder kink. Genal roll sloping gently, at just under 50^0 anteriorly and about 55^0 laterally. Row of large perforations above girder and across anterior boss at internal margin of fringe. Above row of large perforations at girder, perforations smaller than those on brim and decrease in size upwards away from girder. Genal roll without caeca.

Brim sloping moderately at over 10^0, concave (sag.) straight laterally and width (sag.) over 35% of cephalic length (sag.). Brim width ratio 0.70 and standardised brim perforations moderately fine at around 140μm with larger row of perforations at distal and proximal edges. Light caeca reaching across brim. External rim stout with a few scattered fine tubercles on dorsal surface. Marginal band near vertical and without tubercles. Brim steepens quickly to near vertical on prolongations.

Prolongations moderately short (exsag.), around 80% of cephalic length (sag.). Internal and external rims curving adaxially posteriorly and internal rims with weak wave-like profile in lateral view. Extension of girder meeting internal rim about 45% of way down prolongation. Tubercles on dorsal surface of internal rim and genal spine short, under 10% length (exsag.) of prolongation.

Thorax with 20 segments and axis tapering posteriorly with width (tr.) of last axial ring being under 40% of first.

Remarks. *Lioharpes ammari* lacks one of the diagnostic characters of its genus as shown in Table 5a: it has two eye lenses per eye lobe, not three.

Lioharpes ammari sister species is *L. scopulum* and differs in that *L. ammari* has: a broader genicranium and glabella; axial furrows that converge more strongly; a broader occipital furrow; larger alae (tr. and exsag.); eye lobes that are more strongly inflated and have two lenses each; no caeca on the genal roll; and internal rims on the prolongations that have a weak wave-like profile in lateral view.

Lioharpes ammari is similar to certain *Pinnuloharpes* species and in particular *P. haustrum*. *Lioharpes ammari*, however, has a number of differences, the most important of which are: a wider (tr.) genicranium and glabella; a glabella that is more tapered anteriorly and has tubercles along the crest; a wider occipital furrow and an occipital ring that is higher than the glabella anterior to S0. *Lioharpes ammari* also has an axial furrow that does not cross the junction of L1 with ala; deeper alar furrows; taller eye lobes that are set much closer to the inner margin of fringe; there is no genal ridge or eye ridge, both of which are just visible on *Pinnuloharpes haustrum*; inner margin of fringe across the anterior of genal area is straight, not concave; and the genal roll is not so steeply-sloping. Brim of *Lioharpes ammari* is wider (sag.), steeper-sloping and with a higher brim width ratio at 0.70, rather than 0.56 in the case of *Pinnuloharpes haustrum.* Internal rim and external meet at the end of prolongations, whereas those of *P. haustrum* meet and run together for a short distance posteriorly before joining. The genal spine of *Lioharpes ammari* is shorter and there are no larger perforations under the internal rim. The thorax of *L. ammari* has a more tapered axis, lacks pitting on the axial rings and pleurae, and the distal ends of the pleurae are rounded, not pointed.

The *meraspid* or perhaps early holaspid (Pl. 53A–F), coming as it does from the type horizon, is most likely *L. ammari*. It has the same brim width ratio and other morphological features. However, the eye lobes are not as tall, the glabella is not carinated and the tubercles on the glabella and eye lobes appear not to be so well developed. It may be that some of these features have been lost in the preparation of such a small specimen (cephalon sag. length = 7.5 mm) or that they may have developed in later instars.

***Lioharpes saredra* n. sp.**

Plates 14A–N, 15A–N

Diagnosis. Cephalon widest at eye lobes. Muscle attachment scars on glabella visible at S2, S3 and S4 barely reaching out of axial furrow. Alae well-defined and with alar furrow and ridge. Eye lobes close to inner margin of fringe; eye ridge and genal ridge present and inner margin of fringe concave across the anterior of genal areas. Genal roll sloping anteriorly moderately steeply (just under 60^0) down to narrow girder with prominent oval recesses beneath, formed by caecal ridges radiating down from girder. Brim wide (sag.) (between 25% and 38% of cephalic

length (sag.)), external rim narrow (less than 10% of width (sag.) of brim). In lateral view, internal rim is straight and slopes down posteriorly at a shallow angle.

Etymology. Named after type locality, Jbel Saredrar.

Material and occurrence. Holotype: NHMUK It 29274, Pl. 14A–I, from "*Odontochile* Couche", upper Pragian—lower Emsian, Boutiskaouine Formation?, Jbel Saredrar (Fig. 2B, Map 5, site 2), a dorsal exoskeleton, thorax disarticulated and enrolled. Paratype: NHMUK It 29275, Pl. 14J–N, from type locality and horizon (site 1), a dorsal exoskeleton with pygidium enrolled. Paratype: NHMUK It 29276, Pl. 15A–C, from "*Odontochile* Couche" Taganant, Boutiskaouine Formation, Emsian, Jbel Oufatene (Fig. 2B, Map 8, site 7), dorsal exoskeleton of a partial cephalon only. Paratype: NHMUK It 29278, Pl. 15D–J, from the "*Destombina"* Horizon, Amerboh Group (Upper), base of upper Emsian, el Khraoua, Jbel Shebras (Fig. 2B, Map 12, site 1), disarticulated dorsal exoskeleton. Paratype: NHMUK It 29277, Pl. 15K–N, from a coral reef at the Emsian / Pragian boundary at the base of the northern slope of Jbel bou Lachrhal (Fig. 2B, Map 9, site 1), dorsal exoskeleton of a cephalon only.

Description. Cephalon widest posterior to eye lobes, close to mid-point between eye lobes and alae; genicranium widest at posterior border, width (tr.) nearly 135% of length (sag.). Glabella width (tr.) anterior to S0 ≈ 67% of length (sag.), flanks convex and crest rounded with tubercles and very fine pitting. S1 sloping posterolaterally, becoming effaced before curving anteriorly near crest; S2, S3, S4 depressions barely reaching out of axial furrow and L1 inflated. Axial furrows convex, converging anteriorly at over 15^0 and not crossing junction between L1 and alae. Preglabellar furrow distinct and straight (tr.) in anterior view. Occipital furrow deep medially, straight (tr.) and about same width (sag.) as posterior border (exsag.). Occipital ring has tubercles on dorsal surface and its width (sag.) is about same as occipital furrow and, in lateral view, its height same or little higher than glabella anterior to S0. Occipital node small, barely inflated and located on anterior slope of occipital ring. Alae laterally directed, small (tr.) and moderately wide (exsag.). Alar furrow deep, well-defined, interalar ridge and furrow and alar depression present. Preglabellar genal area narrow, with width (sag.) 14% of width (tr).

Genal area moderately broad with width (tr.) ≈55% of length (sag.) and dorsal surface with faint caeca, pits and tubercles. Caeca more evident on ventral surface of genal areas, as evidenced by impressions on matrix under cuticle (Pl. 15G). Eye lobes large (exsag.), oval, with coarse tubercles on dorsal surface and located close to internal margin of fringe. Each lobe with two recumbent oval eye lenses of roughly equal size. Eye ridge straight (tr.), well defined. Anterior boss reaching down to girder kink; girder very narrow. (sag. and exsag.). Genal roll sloping moderately steeply anteriorly at just under 60^0, steeply laterally at just under 70^0, and with caeca and row of large perforations immediately above girder and across anterior boss at inner margin of fringe; other perforations smaller than on brim.

Brim wide, width (sag.) in dorsal view ≈37% of cephalic length (sag.), concave (sag.), straight laterally and sloping moderately at ≈17^0. Brim width ratio around 0.70. Brim perforations moderately large with diameter over 190 μm and row of larger perforations around distal and proximal edges; caeca reaching onto brim. External rim fine, under 10% (sag.) of brim width (sag.) and external band near vertical with ridge top and bottom and scattered tubercles in between. Brim steepens quickly to near vertical on prolongations. Prolongations moderately long (exsag.), just under 90% of cephalic length (sag.) and in dorsal view, internal and external rims curving adaxially posteriorly. In lateral view, profile of internal rim concave and external rim curving smoothly upwards to meet internal rim. Extension of girder meeting internal rim nearly halfway down prolongation. Row of large perforations below internal rim. Genal spine short and carried on lower lamella.

Thorax with 20 thoracic segments with pleurae widening (tr.) more than reduction in width (tr.) of axis until third segment. Pleural furrows narrow, shallow but well defined. Outer portion of pleurae straight with rounded ends and not offset against inner portion. Pygidium has 3 weakly vaulted axial rings with first two pleural ribs reaching edge of pygidium, and interpleural furrows defining posterior rib petering out on pleural field. Terminal piece gently curved with slight medial indentation (Pl. 15I).

Hypostome not known.

Remarks. *Lioharpes saredra* lacks three of the diagnostic characters of the genus shown 5a: it has two eye lenses per eye lobe rather than three, the course of the inner margin of the fringe across the anterior of the genal areas is concave and not straight, and the girder is particularly narrow.

Paratype NHMUK It 29278 has tubercles on the dorsal surface of the rim (Pl. 15J) not present on the holotype or other paratypes, which are earlier, from lower Emsian horizons. The pygidium of NHMUK It 29278, the only pygidium figured here, may also have small insignificant differences with pygidia from the lower Emsian.

Lioharpes saredra is most similar to *L. ammari* but has a number of differences, the most important of which are that it has a narrower glabella, which is less tapered anteriorly, has convex flanks and a rounded crest with fine scattered granules, rather than the carinate crest with coarse tubercles found on the glabella of *L. ammari*. Also, the glabella has shallow muscle insertion pits at S2, S3 and S4, which are not visible on the glabella of *L. ammari*; The occipital ring in lateral view is lower than that of *L. ammari,* being close to the same height of glabella anterior to S0; eye lobes are less tall and located a little further from internal margin of fringe and eye ridges that are not present on *L. ammari*. Also not present on *L. ammari* are the pitting, fine caeca and scattered granulation present on the dorsal surface of genal areas (Pl. 14E) of *L. saredra*. The course of the fringe inner margin across the anterior of the genal of area of *L. saredra* is concave rather than straight; it has a more inflated anterior boss and a well-defined girder kink; its genal roll is much steeper with caeca and perforations that do not decrease away from the girder as in the case of *L.ammari;* its external rim is finer, its width (sag.) being ≈8% of width (sag.) of brim, compared to ≈11% in the case of *L. ammari*. On the thorax, the axis is broader anteriorly and tapers more strongly posteriorly in *L. saredra*; pleural furrows are broader and pleurae do not shorten (tr.) posteriorly until the 8th segment, whereas those of *L. ammari* start to shorten (tr.) at the 6th segment.

Genus *Fritchaspis* Vaněk, (emend.) 1963

Type species. *Harpes montagnei* Hawle & Corda, 1847 from *Acanthopyge* Limestones, Chotec formation, (Eifelian), Koněprusy area, Czech Republic (exact location unknown).

Diagnosis. Genicranium narrow, length (sag.) between 75% and 85% of width (tr.). Glabella inset and preglabellar furrow bowed upwards in anterior view. No tubercles on occipital ring. Posterior border moderately wide (tr.), between 41% and 50% of width (tr.) of occipital ring. Alar depression present and course of inner margin of fringe across anterior of genal area straight. Genal roll sloping moderately anteriorly (sag.) at between 42^0 and 50^0 to horizontal. Brim wide (sag.) >35% of cephalic length (sag.) and steepening to less than vertical on prolongations. Brim width ratio between 0.86 and 0.94. Spaces between brim perforations inflated. Prolongations moderately short (exsag.), between 76% and 85% of cephalic length (sag.).

Discussion. *Fritchaspis* was established by Vanek in 1963, reduced to a subgenus of *Lioharpes* by Přibyl & Vaněk in 1986 and in 2002 Ebach & McNamara (2002) made it a junior subjective synonym of *Lioharpes,* on the basis that the then diagnosis of *Fritchaspis* was synonymous with that of Whittington's *Lioharpes*. Here, the author re-establishes *Fritchaspis* as a genus on the basis of revised diagnoses for both *Fritchaspis and Lioharpes*. *Fritchaspis perneri*, and *F. wendti* are assigned from *Lioharpes* and *Fritchaspis* sp. 2 (Feist, 1977) from *Harpes*. *Fritchaspis* differs from *Lioharpes* in having: a glabella that is less tapered anteriorly; the dorsal surface of its brim between the brim perforation is inflated, whereas *Lioharpes* species have a caeca network across the brim which is light to moderate; a girder that extends onto the prolongation to meet the internal rim one third of the way down the prolongation, rather than halfway down as in the case of *Lioharpes*. *Fritchaspis* is shown (Figs 9 and 10d) to be more closely related to *Eskoharpes* and a comparison is given in the systematics of *Eskoharpes* below.

The two representative species from Czech Republic, *Fritchaspis montagnei* (Pl. 57A–F) and *Fritchaspis perneri* (Pl. 56G–K), have the additional differences from *Lioharpes* of having a small axial tubercle on the anterior quarter of the glabella. The glabella is otherwise free of tubercles, as are the genal areas. Also, they have a broader (tr.) posterior border. These two species are the only ones which were included in the former subgenus *Lioharpes* (*Fritchaspis*). All species of the genus have been included in the study and are shown in Fig. 10d. The range of the genus is from Emsian to Eifelian.

Fritchaspis edgecombei n. sp.

Plate 18A–F

Diagnosis. Cephalon widest at eyes; glabella not inset; L1 not inflated or barely inflated; occipital ring broader (sag.) than posterior border; posterior border moderately short; no preglabellar field; eye lobes large, extending to axial furrow; and no eye ridge. Course of inner margin of fringe across anterior of genal areas slightly convex; anterior boss barely inflated, attached to glabella but not reaching down to girder. No girder kink. Brim wide (sag.; 35% of cephalic length (sag.)).

Etymology. For Greg Edgecombe who provided guidance during the cladistic study and assisted in analysing the results of the parsimony analysis.

Material and occurrence. Holotype: NHMUK It 29224, Pl. 18A–F, from "Cheirurid Couche", Er Remlia Formation, lower Emsian, Jbel Issoumour (Fig. 2B, Map 7, site 19), a dorsal exoskeleton of cephalon only.

Description. Cephalon ovoid, genicranium narrow, widest at posterior border. Glabella has rounded flanks and slightly carinate crest, fine pitting and tubercles, and is broad with width (tr.) at S0 being around 70% of length (sag.). S1 sloping backwards and becoming effaced before curving anteriorly; no muscle attachment scar furrows at S2, S3 or S4. Axial furrows cross junction of L1 with ala and converge weakly anteriorly. Preglabellar furrow indistinct and bowed upwards in anterior view. Occipital furrow deep, straight (tr.) and broad (sag. and exsag.), broader than posterior border. Occipital ring not as broad as occipital furrow, and in lateral view, is lower than glabella anterior to S0. It has fine tubercles and pitting like that of glabella. Occipital node large, poorly inflated and located on dorsal surface rather than anterior slope. Alae laterally directed, moderately large with width (tr.) around 27% of length (sag.) of glabella anterior to S0 and length (exsag.) at axial furrow same as width (tr.). Alar furrows shallow and alar depression present. Posterior border short (tr.), just under 30% of width of occipital ring (tr.), broadening distally before joining internal rim. No preglabellar field.

Genal area broad (tr.) and without caeca or tubercles, but with fine pits. Eye lobes are oval, large (tr. and exsag.), set away from inner margin of fringe and extend to edge of axial furrow. Three eye lenses per eye lobe, anterior and posterior lenses oval and of equal size and third lens much smaller, subcircular, positioned high up between other two lenses (Pl. 18F). No eye or genal ridge. Inner margin of fringe convex across anterior of genal areas, and across anterior boss, its path not marked by perforations larger than those on genal roll directly below. Anterior boss barely inflated, joined to glabella and only just reaches down to girder, which is narrow and without kink. Genal roll sloping gently anteriorly (49^0) and laterally (55^0). Perforations on genal roll smaller than those on brim, and genal roll lacks caeca. Brim very broad (sag.), 35% of cephalic length (sag.), straight in profile, gently sloping (12^0) and with caeca reaching on to edge of brim posterolaterally. Standardised diameter of brim perforations larger, at nearly 200 μm. Brim width ratio is 0.66. External rim stout, dorsal surface near horizontal and marginal band vertical, rather than sloping down under cephalon. Dorsal surface of rim overhangs marginal band. Prolongations moderately short (exsag.), around 80% of cephalic length (sag.). In dorsal view, exterior and internal rims curve adaxially posteriorly and in lateral view, internal rim in lateral view concave and meets external rim at end of prolongation. Extension of girder meets internal rim about one third of way down prolongation. Whole brim steepens gently on prolongations to less than vertical and no row of larger perforations below internal rim. Internal rim and external rims on prolongations have tubercles on dorsal and distal surfaces, respectively. Genal spine short.

Hypostome, thorax and pygidium unknown.

Remarks. *Fritchaspis edgecombei* lacks two of the genus's diagnostic characters shown in Table 5a: the posterior border is narrower (tr.) being about 30% of the width(tr.) of the occipital ring and the spaces between the brim perforations are not inflated.

Fritchaspis edgecombei differs from *F. wendti* (Feist 2018) in having a slightly narrower genicranium, a glabella which is not inset and has rounded not tectiform flanks; no furrows at S2 or S3; a base lobe which is not inflated or barely inflated; axial furrows less tapered anteriorly; a narrower (sag.) occipital ring, which is narrower than posterior border and, in lateral view, higher than glabella anterior to S0. Also, *F. edgecombei* has a shorter (tr.) posterior border; no preglabellar field; eye lobes which extend to axial furrow and no eye ridge. Inner margin of fringe across the anterior of genal area is convex rather than straight or concave, and the anterior boss does not reach down to girder, there is no weak girder kink and the girder is narrower. The genal roll, both anteriorly and laterally, is not so steeply sloping and the brim much wider (sag.), without caeca and with larger brim perforations.

The main differences between *F. edgecombei* and the type species *F. montagnei* are that *F. montagnei*'s cephalon is widest at the alae, not at the eyes, and the glabella is inset and has a small central tubercle towards its anterior. Also, the glabella is not carinate, S1 is not effaced before curving anteriorly near the crest, and it has muscle insertion scars at S2 and S3. Its preglabellar furrow is distinct and it has a wide preglabellar field, unlike *F edgecombei*, which has none. In lateral view, *F. montagnei*'s occipital ring is higher than the glabella anterior to S0. Eye lobes do not extend to the axial furrow and have two eye lenses each, not three. *F. montagnei* has a narrow eye ridge, and the inner margin of fringe across the anterior of the genal area is straight not convex and its path across anterior boss is marked by perforations that are bigger than those on the boss immediately below. The anterior boss is not joined to the glabella, is more inflated and reaches down to the girder, which is weakly kinked. The girder of *F. montagnei* is

wider, the brim concave (sag.) straight laterally and 20% narrower (sag.) than that of *F. edgecombei*. The brim of *F. montagnei* also has caeca, with inflated spaces between the brim perforations.

The holotype of *F. edgecombei* is a well preserved complete cephalon despite the damage to the anterior of the exterior rim across the sagittal line. It is also of a size that would indicate that it belonged to a well-developed holaspid and appears to be symmetrical. Differences with *F. wendti,* the species it is most similar to are significant. On this basis the species has been erected without the support of paratypes.

Genus *Kielania* Vaněk 1963

Type species. *Harpes waageni* Prantl & Přibyl, 1954 from Prokop Limestone, (Pragian) Praha-Malá Chuchle, Czech Republic.

Emended diagnosis. Cephalon strongly vaulted. Occipital furrow medially straight (tr.). Alae depression absent. Eye lobe short (exsag.), between 15% and 31% width (tr.) of glabella at S0. Course of inner margin of fringe across anterior of genal area convex. Girder moderately wide (sag. and exsag.), between 2.2% and 3% of width (tr.) of genicranium. Brim barely convex to moderately convex and sloping steeply at between 25^0 and 45^0. Standardised brim perforations moderately fine, less than 150 μm. Exterior rim fine and marginal band sloping down under cephalon. Thorax of up to 16 segments.

Discussion. *Kielania* has been used as a genus for nearly all species of harpetids with convex brims, with little attention being paid to other morphological features. Here, the genus has been reduced to include seven species and Prantl & Přibyl's (1954) original diagnosis has been emended to reflect this. The former members of *Kielania* that have been transferred are as follows: *K. superna* Maksimova, 1979 to *"Lioharpes*" s. l.*; K. convexa* (Hawle & Corda, 1847) and *K. obuti* Přibyl and Vaněk, 1986 to *Stoloharpes* n. gen; *K. kayseri* (Novák,1890) to *Helioharpes*. *K. novaki* (Prantl & Přibyl, 1954) and *K. praecedens* (Prantl & Přibyl, 1954) to *Declivoharpes.*

Kielania is similar to Stoloharpes n. gen. in that most of its species have convex brims, but differs in having a cephalon that is widest posterior to the midpoint between the eyes lobes and the alae, rather than at the alae, and which is not pyriform in outline; a glabella that has a rounded rather than carinate crest; a broader genicranium; a distinct preglabellar furrow; a preglabellar field; a genal roll that is more steeply-sloping anteriorly; a brim that does not steepen strongly on the prolongations and up to 16 thoracic segments, not 24 as is the case in *Stoloharpes*.

Kielania species included in the study and are shown together with their interspecies relationships in Fig. 10b. *Kielania ovalis* Lisogor, 1965 is not included in the study but remains in the genus. The range of the *Kielania* genus is from Lochkovian to upper Emsian.

Kielania tumula n. sp.

Plate 16A–L

Diagnosis. Cephalon sub oval, widest (tr.) at alae. Axial furrows broad and shallow. No muscle insertion furrows at S2, S3 or S4, and S1 only shallow depression in axial furrow. Alar furrows almost effaced. Eye lobes barely inflated and eye ridge indistinct. Genal roll gently sloping. Brim convex and brim width ratio around 0.90. No caeca on brim, and perforations around outside of brim large and widely spaced. External rim tilted outwards with marginal band sloping under cephalon. In lateral view, internal rim only slightly concave and steeply declining to terminal spine.

Etymology. *Tumulus*, Latin for mound. Cephalon in lateral view has a mound-like shape.

Material and occurrence. Holotype: NHMUK It 29259, Pl. 16A–E, from a horizon some 11.5 m below the "*Dicranurus* Couche" exposed in the bed of Oued Agourizi, West of Jbel Ou-Driss near the village Iminwaseif (Fig. 2B, Map 4, site 1), Ihandar Formation, Pragian, a partial cephalon. Paratype: NHMUK It 29260, Pl. 16F–L, from the type horizon and locality (site 2), cephalon and enrolled thorax.

Other material: *K*. aff. *tumula*, NHMUK It 29262, Pl. 36P–R, from an upper Pragian horizon, Ihandar Formation, Timerzit (Fig. 2B, Map 10, site 5), dorsal exoskeleton of a partial cephalon; and NHMUK It 29261, from type horizon and locality (Fig. 2B, Map 10, site 3), a partial cephalon lacking bisymmetry and not figured herein or included in the cladistic study.

Description. Sub oval cephalon, narrow genicranium, widest at alae. Glabella wide, not inset and bullet-shaped, with shallow axial furrows tapering slightly anteriorly. S1 shallow depression in axial furrow and no furrows at S2,

S3 or S4. L1 not inflated and occipital furrow bowed anteriorly. Sculptural tubercles on occipital ring and occipital node fairly large, moderately inflated and at edge of anterior slope of occipital ring. Posterior border wide (tr.) compared with width (tr.) of occipital ring.

Genal area moderately broad, without tubercles or genal ridge. Alae laterally directed and alar furrows very shallow. Eye lobes oval and very small with three eye lenses, anterior and posterior lenses oval and central lens subcircular and very small. Course of inner margin of fringe across anterior of area barely convex. Anterior boss barely inflated, reaching down to girder and with preaxial furrows converging gently. Girder kink weak. Genal roll sloping gently anteriorly at around 45^0 and moderately steeply laterally at over 60^0 and in lateral view, fringe narrowing only slightly posterolaterally. Perforations on genal roll fine and not densely packed.

In lateral profile, brim convex and sloping almost as steeply as anterior boss, at around 35^0. In dorsal view, brim width (sag.) 28% of cephalic length (sag.). Standardised brim perforations fine at around 110 μm in diameter, and about same size as those on genal roll but more densely packed. External rim stout and slightly arched medially in anterior view. Marginal band near vertical and straight, with ridge at top and bottom. Slope of marginal band down under cephalon decreases laterally. Prolongations on holotype short (exsag.), just over 70% of cephalic length (sag.). Long genal spine carried on lower lamella. Internal rims curving adaxially and with tubercles on dorsal surface. Only a few segments of thorax known. Pygidium and hypostome not known.

Remarks. *Kielania tumula,* resembles the type species *K. waageni* Prantl & Přibyl (1953, Fig. K4 1-3), from the Prokop Limestone (Pragian), Praha-Malá Chuchle, Czech Republic which is refigured herein (Pl. 58 A–F). It differs, however, in having a less vaulted cephalon and a less steeply-sloping brim and genal roll; a glabella that is narrower and tapered anteriorly, rather than being subcylindrical as in the case of *K. waageni*; perforations on the genal roll the same size as those on the brim, not bigger, and the brim is convex whereas that of *K. waageni* is straight.

The paratype has a broader genicranium, longer prolongations and an internal rim which curves much more strongly adaxially. Also, there is evidence of a straight eye ridge and caeca on the brim. As the surface of the genal area of the holotype and paratype are not well preserved, it is difficult to compare the holotype and paratype.

Kielania aff. *tumula* NHMUK It 29262 (Pl. 36P–R) differs from the holotype NHMUK it 29259 in having: a cephalon which is widest halfway between the alae and eye lobes, rather than at the alae; a glabella which is more tectiform; a genal roll that is more steeply-sloping anteriorly; and a brim which is wider (sag.), less steeply-sloping and straight in profile, rather than convex. Also, the brim has a lower brim width ratio and steepens more strongly on the prolongations.

Genus *Helioharpes* Přibyl & Vaněk (emend.), 1981.

Type species. *Harpes perradiatus* Richter & Richter 1943, Lower Eifelian, from the *Phacopidella (Denckmannites) micromma* zone, Dechra-ait-Abdullah, Western Meseta, Morocco.

Emended Diagnosis. Cephalon not strongly vaulted and genicranium widest at alae. Glabella wholly or partly carinate and narrow (tr.), at S1 between 54% and 66% of length (sag.) of glabella anterior to S0. Eye lobes weakly inflated, genal area moderately wide, width (tr.) between 54% and 66% of length (exsag.). Brim sloping moderately steeply at between 21^0 and 30^0 and strong network of caeca across whole brim.

Discussion. *Helioharpes* was established in 1981 by Přibyl & Vaněk, but was reduced to a junior synonym of *Harpes* by Ebach and McNamara in 2002 and the author now reinstates the genus. In the original diagnosis of the genus, an important element and the basis for the name of the genus was the "radial ridges and pits forming polygonal network" on the brim. The radial arrangement of the caecal ridges on the brim of the type species are not present on the brims of the three other species originally assigned to the genus: *H. pyranicus* (Barrois, 1866), *H. radians* (Richter, 1863) and *H. transiens* (Barrande, 1872), and is therefore not diagnostic of the genus. *Helioharpes transiens* has caeca on the brim but it does not form a radial pattern. The illustrative drawings of *H. radians* and *H. pyranicus* are not clear enough to determine the extent to which brim caeca is present although *H*. aff *radians* (Erben 1950) does have brim caeca similar to *H. perradiatus* . As regards radial brim "pits", *H. radians* is the only species to have such an arrangement and therefore radial brim "pits" also are not a genus diagnostic. The brim "pits" of *H. perradiatus* are difficult to determine as the holotype cannot be located and in the original description (Richter & Richter, 1943), there is only a drawing (abb. 2) and a poor photograph (taf. 4, fig. 12–13) to rely on. In the case of *H. aougili* n. sp., the brim perforations, which are visible in the gaps between the caeca, are not aligned (Pl. 17F).

Given similarity of the arrangement of the brim caeca of *H. perradiatus* with that of *H. aougili* n. sp., particularly immediately anterior to the girder (Pl. 17D, E), it is likely that the brim perforations of *H. perradiatus* also do not form a radial pattern.

The cladogram in Beech & Lamsdell's (2021) cladistic study showed *H. perradiatus* as belonging to *Harpes*. Based on Beech & Lamsdell's coding, it seems quite probable that the same misidentification that was made in Ebach and McNamara, 2002 has been made again, namely that the species coded is different to the *H. perradiatus* holotype and is one of the harpetid species from the Anti-Atlas.

Helioharpes is similar to *Stoloharpes* but has wider genicranidium, widest at the level of the alae rather than between eye and alae; a wider (tr.) posterior border, a more distinct preglabellar furrow and an occipital furrow that is medially straight rather than being bowed posteriorly. Also, *Helioharpes* has no girder kink, the course of the inner margin of the fringe across the anterior of the genal area is convex not straight, the brim does not slope so steeply and has pronounced caeca. On the prolongation the brim does not steepen so quickly and the internal rim slants abaxially before curving adaxially, rather than just curving adaxially as in the of *Stoloharpes*.

Helioharpes is also similar to *Pinnuloharpes,* but differs in having a less vaulted cephalon, more tapered prolongations, a strongly developed caecal network on the brim, no preglabellar field and a higher brim width ratio. In species of *Eskoharpes,* the prolongations are strongly tapering and have rims that meet and join 2/3 of the way down, rather than running side by side to join at the end. Also, the cephalon of *Eskoharpes* is more vaulted and the caeca on the brim much more developed.

The species of *Helioharpes* included in the study and their interspecies relationships are shown in Figs 9, 10b. Species not included in the study are *H. gracilis* (Münster, 1840), *H. koeneni* Wedekind, 1914, *H. pyrenaicus* (Barrois,1866) and *H. radians* Richter, 1863 which pro tem are reassigned from *Harpes*. The range of the genus is from the lower Eifelian to the Eifelian-Givetian boundary.

***Helioharpes aougili* n. sp.**

Plate 17A–K, M–P

Diagnosis. Cephalon mildly piriform. Genicranium moderately vaulted, glabella more strongly vaulted, tectiform and carinate. Occipital ring in lateral view near vertical. Eye lobes long (exsag.), reniform in shape and eye ridge low and broad. Internal rim slanting abaxially over first 2/3 before curving strongly adaxially. In lateral view, prolongations strongly tapered and external and internal borders converge posteriorly to run adjacent to each other along final third of prolongation. External and internal rim very robust. First five thoracic axial rings with axial tubercle. Pleural furrows narrow (exsag.), deepening posteriorly.

Etymology. Named for the trilobite worker, Youssef Aougil, who found the holotype.

Material and occurrence. Holotype: NHMUK It 29254, Pl. 17A–K, from the "*Basseiarges* Couche", Tamgoute Bulgan,11.5 km S.W. of the village of El Jorf, Eifelian (Fig. 2B, Map 6, site 16), articulated dorsal exoskeleton with pygidium folded under. Paratype: NHMUK It 29255, Pl. 17M–P, from the type locality and horizon (Fig. 2B, Map 6, site 17), dorsal exoskeleton of cephalon only.

Description. Cephalon piriform in outline, length (sag.) around 65% of width (tr.) and length (exsag.) of prolongations just under cephalon length (sag.). Glabella length (sag.) 45% of cephalic length (sag.) and subcylindrical in dorsal view, gently tapered anteriorly. Glabella flanks tectiform, crest carinate and in lateral view, anterior gently sloping. S1 barely rising out of axial furrow, S2, S3 and S4 shallow depressions remaining in axial furrow. Alae reach less than halfway across (tr.) genal area and alar furrows shallow, becoming effaced distally. Occipital ring narrow, not medially broadened and with pronounced occipital node located at edge of occipital furrow. In lateral view, near vertical and higher than glabella anterior to S0. Posterior border furrows are deep and axial furrows moderately deep. No preglabellar field. Genal area gently convex, anteriorly narrow (tr.) but quickly broadening posteriorly. Eye lobe mildly inflated, long (exsag., just under 50% of width (tr.) of glabella at S1), reniform and located away from inner margin of fringe (Pl. 17A, J). Eye location ratio 0.73. Each eye lobe with two lenses, one orientated laterally, the other anterior laterally, and ill-defined eye ridge which runs from posterior edge of eye tubercle, slanting adaxially forward into axial furrow. Glabella and genal area covered by very fine disjointed caeca-like sculpture (Pl. 17I). Genal area sparsely covered by fine pitting. Posterior border short, just under 40% of occipital ring width (tr.).

Genal roll convex, broad anteriorly (sag., exsag.) but narrowing (tr.) posteriorly to about 50% of its sagittal width at S0. Anterior slope of genal roll about 40^0 but laterally steeping to about 50^0. Anterior boss gently convex (sag. and tr.), deflating as it reaches down from preglabellar furrow to girder. Preaxial furrows shallow and subparallel. Perforations on genal roll fine (Pl. 17E, F), posteriorly increasing in size as they extend on to prolongations. Short row of larger perforations at inner margin of fringe where it crosses anterior boss. Girder narrow and girder kink barely discernible.

Brim width (sag.) is 33% of cephalic length (sag.). Brim flat, slightly sloping downwards and outwards. Brim width ratio 0.91. Dorsal surface covered with strongly developed caeca in a polygonal net-like structure. Perforations on brim are fine and densely packed in spaces between caeca (Pl. 17H). Row of much larger perforations at distal edge of brim but not at proximal edge. Standardised perforation density in central part of brim is around 25 per sq. mm. External rim is robust, dorsal surface slopes outwards and is covered with fine granules. Dorsal rim suture is pronounced and located over two thirds of way across dorsal surface towards distal edge of rim. Marginal band near vertical, with slight lip on dorsal edge and granular sculpture.

Length of prolongations (exsag.) nearly same as length of cephalon (sag.). In lateral view, prolongations strongly tapered, their height at midpoint being just half their height at junction with posterior border. In dorsal view, external rim slants adaxially until about two thirds of way down its length (exsag.), where it meets internal rim, narrows and flexes slightly abaxially. Internal rim curves adaxially posteriorly from posterior border, before slanting obliquely abaxially to meet with external rim, and then curves adaxially with external rim to end of prolongation where both rims join. Both rims are robust with granulated dorsal surfaces. Brim on prolongation barely steepens. Girder extends onto prolongations but quickly slopes up to meet internal rim, close to junction with posterior border. Brim sculpture on prolongations similar to that on rest of brim, however, row of larger perforations runs beside the two rims and merges into single line of four perforations where the two rims meet. Prolongations terminate in spine.

Thorax has at least 17 segments. Axial rings narrow (sag.) slightly medially and first five have medial tubercle on anterior edge (Pl. 17L), which becomes progressively less inflated posteriorly. Inner portion of pleura of first 7 segments lengthen (tr.) progressively posteriorly slightly more than axial rings narrow (tr.), and on next 10 segments shorten (tr.) progressively posteriorly. Pleural furrows narrow, deepen posteriorly and terminate at start of outer portion of pleurae (Pl. 17J). Outer portion of pleurae cylindrical, short and curve sharply downwards (Pl. 17K).

Hypostome and pygidium unknown.

Remarks.Unfortunately, the *H. perradiatus* material presented by Richter & Richter (1943; abb. 2 and taf. 4, figs 12–13) is incomplete, consisting only of a partial cephalon with a damaged brim and the prolongations largely missing. From this, however, it is possible to note that *H. perradiatus* differs in having smaller eye lobes, a genal area which is broader anteriorly, a longer (tr.) posterior border and an occipital ring that appears not to rise as high as the top of the glabella. Also, the pattern of the caeca on the brim is more radial.

Helioharpes aougili is also quite closely related to *H. kayseri,* however, *H. aougili* differs in having: a cephalon widest at eye lobes and not at midpoint between eye lobes and alae; a glabella that has tectiform flanks rather than convex; an occipital ring that is not medially broadened and, in lateral view, near vertical and slightly higher than glabella anterior to S0 (occipital ring of *H. kayseri* is lower than the glabella anterior to S0); alae anterolaterally rather than laterally directed and alar furrows distally effaced; eye lobes set further from inner margin of fringe; the brim with a straight profile and barely sloping, compared to that of *H. kayseri* which is convex and sloping at nearly 30^0; brim width ratio of 0.93 compared with 0.81 for that of *H. kayseri*; on the prolongations, the internal rim in dorsal view slanting abaxially from junction of posterior border before curving adaxially, while that of *H. kayseri* curves adaxially down its entire length (exsag.).

As in the case of *H. perradiatus*, the *H. kayseri* material available comprised drawings and a poorly photographed exoskeleton of an incomplete cephalon, so that only the limited number of morphological features compared above could be used.

Genus *Declivoharpes* (Prantl & Vaněk emend., 1981).

Type species. *Harpes dvorcensis praecedens* Prantl & Přibyl, 1954, Lochkovian, from the Radotin Limestones, Černá rokle gorge, Praha-Radotin, Czech Republic. (Refigured Pl. 59A–D)

Emended Diagnosis. Furrow at S1 curves around top of muscle insertion area on glabella. Relatively large and wide (tr.) ala, anterolaterally directed; course of inner margin of fringe across anterior of genal area concave,

anterior boss inflated and preaxial furrows converging towards girder. Brim width ratio between 0.66 and 0.75, standardized brim perforations fine (<100μm) and exterior rim with fine granulation

Discussion. *Declivoharpes* was established in 1981 by Přibyl & Vaněk, as a subgenus of *Bohemoharpes* and was reduced to a junior synonym by Ebach and McNamara, 2002 when they reassigned *B.* (*Declivoharpes*) *praecedens,* the sole species of the subgenus, to *Kielania*. The reassignment was on the basis that the strongly raised and gently convex brim and the fineness of brim perforations were more characteristic of *Kielania*. The brim of *Declivoharpes praecedens* is in fact slightly concave anteriorly and straight laterally (Pl. 57 I,H) and differs from *Kielania* especially as regards the genal roll which is steeper laterally and inflated anteriorly and has caeca. Also, the inner margin of the fringe is concave across the anterior of the genal areas not convex and the occipital furrow is shallower.

Declivoharpes differs from *Harpes*, its sister genus, in having: a wider genal area; shallower occipital furrow; an inner margin of the fringe with a course across the anterior of the genal area that is concave rather than convex or straight; has a more inflated anterior boss; a well-defined girder kink; perforations on the genal roll that become gradually smaller away from the girder; and granulation on the outer edge of the exterior rim. The brim width ratio of *Harpes* is typically lower than that of *Declivoharpes* species, at between 0.50 and 0.60.

Declivoharpes, a former subgenus of *Bohemoharpes*, differs from it *Bohemoharpes* in having a narrower genicranium, wider alae which are anterolaterally directed, a more inflated anterior boss, preaxial furrows that converge towards the girder and a brim that is not concave laterally. Also, the brim width ratio of between 0.65 and 0.75 is lower than that of *Bohemoharpes* species, which are typically over 0.80 and can be greater than 1.

The type species *Declivoharpes praecedens* was described clearly by Prantl & Přibyl, 1954, and the author would only make the comment that the cephalon is more ovoid than oval.

The relationship between *Declivoharpes* and other genera is shown in Figs 9, 10b. The range of the genus is Lochkovian to Pragian.

Genus *Eskoharpes* McNamara, Feist & Ebach, 2009

Type species. *Eskoharpes palanasus* McNamara, Feist & Ebach, 2009, from *linguiformis* conodont zone (Frasnian), Calyx Corner, Mc Whae Ridge, Lawford Range, Canning Basin, Western Australia

Emended diagnosis. Glabella inset and narrow, width (tr.) being less than 67% of length (sag.). Preglabellar furrow straight in anterior view. Alae small, posterior border wide (tr.). Fine granulation on glabella, occipital ring and genal area. Inner margin of fringe marked by narrow, faint furrow. Genal roll sloping gently anteriorly, at under 50^0, more steeply laterally at over 55^0. Perforations on genal roll smaller than brim perforations. On brim, spaces between perforations strongly inflated. In lateral view, prolongations are strongly tapered, with internal and external rims joining to form long genal spines.

Discussion. The original diagnosis included morphological characters that are widely shared with other genera. The emended diagnosis focuses on features that are less widely shared so as to provide a practical guide for identifications to be made. Apart from the reduction in the number of characters included, the original diagnosis stated "…genal roll steep and convex". Many of the species do have strongly convex genal rolls, which are steeply sloping where they reach the girder, however, if the average slope is measured by drawing a straight line between inner margin of the fringe and the girder, the slope is gentle.

Based on the results of the cladistic study shown in cladogram (Fig. 9) *Globoharpes* is made a junior synonym of *Eskoharpes*. As can be seen *E. friendi* and *E. teicherti*, formerly assigned to *Globoharpes,* are shown at the end of the *Eskoharpes* tree and if *Globoharpes* continued to stand *Eskoharpes* would be paraphyletic. *Harpes pruniformis* (Alberti, 1969) and *Harpes socialis* (Holzapfel, 1895) are in monophylic relationship with the Eskoharpes species but they there are a significant number of characters that could not be coded from the figures available. Because of the uncertainty that this creates and the fact that *H. pruniformis* (Alberti, 1969) and *H. socialis* (Holzapfel, 1895) are from the upper Eifelian and Givetian respectively, rather than the Frasnian where all Eskoharpes species come from, *H. pruniformis* (Alberti, 1969) and *H. socialis* (Holzapfel, 1895) are designated *Eskoharpes* s. l..

McNamara *et al.* (2009) observed that the former two *Globoharpes* species, had a steeply sloping brim a strongly vaulted cephalon similar *Kielania* and in particular the type species *K. waagoni*. The brims of *K. waagoni* and *Eskoharpes teichertiI,* the former *Globoharpes* slope at an angle of ≈ 50^0, the steepest brim angle of any harpetid described so far. Apart from the angle of slope the brims have little else in common. *Kielania waagenii*'s brim

is barely convex anteriorly and straight laterally, whereas *Eskoharpes teicherti* is strongly convex anteriorly and convex laterally. Also, *Kielania waageni* has smaller brim perforations and no caeca whereas the spaces between the brim perforations of *Eskoharpes teicherti* are inflated. Apart from the steep brims and vaulting *E. teicherti*, and *Kielania wagonii* are very dissimilar. McNamara *et al.* (2009), comparing *Globoharpes* with Kielania wagonii, stated that "*Globoharpes* possess a much smaller glabella, well developed, more incised S1, more pronounced alae a much wider genal roll, eye lobes more anteriorly positioned, the absence of a median glabellar tubercle, the lack of a pronounced occipital spine, and longer prolongations." The strong cephalic vaulting and steep incline of brim are perhaps good examples of convergent evolution. It may have been that a tall feeding chamber, inferred by the strongly vaulted cephalon and steep brim, proved a useful for *Kielania* species in the Early Devonian of what is now Czech Republic and Morocco and once again for *Globoharpes* species in the Late Devonian of the Canning basin, Western Australia.

As can be seen in Fig. 9 the cladistic study shows that the reinstated genus of *Fritchaspis* is a sister genus to *Eskoharpes* and has more in common with *Eskoharpes* than does *Kielania. Eskoharpes* is quite similar to the genus *Fritchaspis* but differs from it in having: genicranium widest at alae or between alae and eye lobes, not at posterior border; preglabellar furrow is straight in anterior view and not bowed upwards; granulation on the occipital ring; L1 inflated; no alar depression; the inner margin of fringe marked by a shallow furrow and its course across anterior of genal field either side of glabella is concave, not straight as in the case of *Fritchaspis;* higher brim width ratios at above 0.85, rather than below 0.75 in the case of *Fritchaspis;* and prolongations around 10% shorter (exsag.).

All species of *Eskoharpes* have been included in the study and are shown in their interspecies relationships in Figs 9, 10d. *Eskoharpes* species are all of Frasnian age except for "E" *pruniformis* (Alberti, 1969) and *"E" socialis* (Holzapfel, 1895) are from the upper Eifelian and Givetian respectively.

The node between *E. teicherti* and *E. friendi* has Jackknife support of 72% and the node between *E. guthae* and *E bolotoni* 52%.

***Eskoharpes sicarius* n. sp.**

Plates 33A–K, 34A–I

Diagnosis. Cephalon ovoid with widest point across or just anterior to alae. Brim strongly convex, less steeply-sloping than genal roll; S1 furrow narrow and deeply incised. Alae anterolaterally directed, eyes lobes small (exsag.) and reniform. Course of inner margin of fringe across anterior of genal area concave. Brim not steepening on prolongations and inner rims subparallel. Prolongations long, pointed, dagger-like in shape, with long terminal spine carried unusually on upper lamella (Pl. 34G).

Etymology. Named after sicarius, a "dagger-man" (a zealot assassin who used a dagger (sica)), for the species' long, pointed, dagger-like prolongations and genal spines.

Material and occurrence. Material comprises 7 dorsal exoskeletons and one lower lamella (Pl. 33G), from the horizon where ammonoids (gephuroceratid family (Frech, 1897)) are mined, lower Frasnian, Achguig Group, Bouia, 7 km S.E. of Jorf (Fig. 2B, Map 6, site 5). Holotype: NHMUK It 29256 (1), Pl. 33D–F, a partially articulated exoskeleton. Paratypes: NHMUK It 29256 (6), Pl. 33A–C, a partial cephalon; NHMUK It 29256 (8), Pl. 33H, a partial cephalon and thorax; NHMUK It 29256 (2), Pl. 34A–E, dorsal exoskeleton of partial cephalon; NHMUK It 29256 (5), Pl. 34F–G, partial cephalon; NHMUK It 29256 (4), Pl. 34H, partial cephalon and thorax; NHMUK It 29256 (7), Pl. 34I, partial cephalon; NHMUK It 29256 (3), Pl. 33I–K, a partial lower lamella.

Description. Cephalon ovoid, and genicranium narrow and moderately vaulted. Both widest at alae. Glabella narrow, width (tr.) around 60% of cephalic length (sag.). L1 not inflated and S1 furrow deep, narrow and slanting posteriorly to reach two thirds of way up flank of glabella, curving slightly anteriorly and becoming effaced. Muscle insertion furrows at S2, S3 and S4 not visible. Axial furrows straight and converging weakly anteriorly. Preglabellar furrow well defined and straight in anterior view. Occipital ring broadened medially and in lateral view, lower than glabella anterior to S0. Presence or absence of occipital node not known. Alae, well defined by shallow alar furrows, are close to subcircular, small (tr.) and anterolaterally directed, to reach a third of way across genal area.

Genal area broad to very broad, gently convex and covered by dense faint caeca and fine pitting. Eye lobes are reniform, large (exsag.) and located longitudinally just behind preglabellar furrow and laterally, halfway between inner margin of fringe and axial furrow. Each eye lobe has two lenses. Eye ridges not well defined, moderately wide (ex., sag.) and reaching into axial furrow. Preglabellar field wide (sag.) and course of inner margin of fringe across

anterior of genal areas mildly concave. Anterior boss barely inflated, reaching down to very weak girder kink. Genal roll gently sloping anteriorly, moderately steep laterally and in lateral view, narrows very strongly posterolaterally. Perforations on genal roll are smaller than on brim and of uniform size except for row of slightly larger perforations above girder. Genal roll lacks caeca. Girder moderately narrow.

Brim strongly convex, moderately wide (sag.) (32% of cephalic length (sag.)) and steeply sloping at 30^0. Brim width ratio is just over 0.85. Perforations on standardized brim are moderately large, between 160 μm and 190 μm in diameter, and at density of around 18 per sq. mm. Both perforation size and density vary considerably between individuals. No caeca on brim and external rim fine and slightly raised with inside edge sloping, dorsal surface rounded and dorsal rim suture close to outside edge. Marginal band narrow and sloping downwards and slightly inwards.

Prolongation (excluding genal spine) nearly same length (exsag.) as cephalon and strongly tapered in lateral view. Girder extending almost horizontally onto prolongations to meet internal rim about one third of way down its length (exsag.). Internal rim slightly concave in lateral view; declining at an angle of around 20°, before flattening out slightly just before meeting with external rim and running short distance with it until the two join at end of prolongation. Terminal spine carried on upper lamella, very long and curved slightly adaxially (Pl. 34G). In dorsal view, internal borders run subparallel to each other until near their distal ends, where they curve slightly adaxially. External rims curving gently adaxially.

Thorax with at least 15 segments, with width (tr.) of axial rings and inner portion of pleurae reducing progressively posteriorly, by two thirds and 70%, respectively. Pleural furrow shallow and continuing a little way onto outer portion of pleurae. Outer portion of pleura short, slanting slightly posteriorly from fulcrum and on 8 posterior pleurae, terminating in a rounded end. Outer portion of anterior pleurae terminate in short spine, curving posteriorly.

Pygidium (Pl. 33F) short, axis consisting of two segments and a terminal piece. Second axial ring comprises four small tubercles arranged across (tr.) axis. Terminal piece comprises a pair of large tubercles close to, but not at, the margin. On pleural field, first pleural furrow is deep, second much shallower and shorter.

Hypostome not known.

Remarks The glabella of *Eskoharpes sicarius* is not inset but otherwise the species complies with the other 7 diagnostic characters of its genus as set out in Table 5b. The inter-species variations in key morphological ratios of the paratypes is limited and are shown in Table 6.

Eskoharpes sicarius is similar to *Eskoharpes wanndjiana* but differs in having: a slightly narrower genicranium; a glabella that is not inset and which has no granulation or pitting anterior to S0; a wider (sag.) and deeper occipital furrow; alar furrows that are well defined, not partially effaced; a genal area with faint fine caeca and pitting but no granulation; more inflated and larger (exsag.) eye lobes; an inner margin of the fringe that is concave across the anterior of the genal area either side of the glabella and not convex; a fringe that, in lateral view, narrows more strongly posteriorly; a brim that is wider (sag.) and has a profile that is convex rather than straight; a finer external rim; longer and broader (tr.) prolongations that, in lateral view, do not curve as strongly adaxially as those of *E. wanndjiana* and an extension to the girder that meets the internal rim half of the way down the prolongation rather than a third of the way down. Also, the brim of *E. sicarius* does not steepen on the prolongations while that of *E. wanndjiana* steepens along its proximal edge.

Eskoharpes sicarius is also similar to the type species *Eskoharpes palanasus* but differs from it in having: the widest point of the cephalon a little further back at the alae rather than at the midpoint between alae and eye lobes; a slightly narrower genicranium; a glabella that is not inset and which has no granulation or pitting anterior to S0; a narrower and deeper occipital furrow; L1 not inflated; alae narrower and anterolaterally directed and no alar depression present, as there is in , *E. palanasus* a posterior border that is nearly half the length of that of *E. palanasus*; a wider (sag.) preglabellar field; a narrower genal area is narrower with faint fine caeca and pitting, while that of *E. palanasus* is granulated; larger (exsag.), more elongated eye lobes with 2 eye lenses on their outside flanks, while those of *E. palanasus* are located more on the dorsal surface of the eye lobe; the inner margin of the fringe concave across the anterior of the genal area either side of the glabella and not straight as in the case of *E. palanasus*; no shallow furrow marking the inner margin of the fringe; a wider girder whose brim is more steeply-sloping and convex rather than straight; a finer external rim that lacks sculpture; and internal rims that also lack sculpture and curve adaxially over the whole of their length (exsag.) in dorsal view, rather than being subparallel over the first two thirds.

Genus *Maghroharpes* n. gen.

Type Species: *Maghroharpes hammii* n. sp.

From the Ihandar Formation, Pragian,10metres below the "*Dicranurus* Couche", Oued el Atchane, Jbel Oufatene near Fezzou, Errachidia, Morocco

Diagnosis. Cephalon sub oval, widest (tr.) at alae. Genicranium widest (tr.) at posterior border. Glabella anterior to S0 moderately broad (width (tr.) 0.66 to 0.75 of length (sag.)) and with no furrows at S2, S3 or S4. Alae small (tr.) and well defined, and no alar depression. Eye lobes set close to internal margin of fringe. Inner margin of fringe across anterior of genal area convex. Girder broad (sag.) (>2.3% of width (tr.) of genicranium), meeting internal rim one half or little over one half of way down prolongation. Brim concave, gently sloping with proximal edge steepening slightly on prolongations. Brim width ratio between 0.77 and 0.95. Marginal band concave with ridges top and bottom. 20 to 24 thoracic segments with inner and outer portions of pleurae aligned (tr.).

Etymology. el Maghreb (Arabic meaning "place where the sun sets") is the name given in pre-modern times by Arab writers to the northern part of Africa, particularly Morocco.

Remarks. *Maghroharpes* species are very similar to those of its sister genus *Lioharpes*, but differ in having: cephala that are sub oval and widest at alae, or just anterior thereto, rather than ovoid and widest at the eyes; glabellae anterior to S0 lacking the granulation or tubercles typical of *Lioharpes;* genal areas lacking faint caeca; the course of inner margin of fringe across anterior of genal areas convex rather than straight; the anterior boss more inflated; girder kink more pronounced; marginal band concave rather than straight; finer brim perforations; and distal ends of pleurae rounded rather than pointed.

M. rouvillei (Frech 1887) and *M. sculptus* (Hawle & Corda, 1847) have been assigned from *Harpes* and *Lioharpes* respectively. All species are included in the study (Figs 9, 10a) and the genus range is from the Pragian to upper Emsian.

The cladogram for *Maghroharpes* has been partially collapsed in the formation of a consensus (Fig. 9). There is, however, two sister groups, one five species supported by a character state that is a unique unreversed synapomorphy: tubercles and pitting on the palpebral lobes.

***Maghroharpes hammii* n. sp.**

From the Ihandar Formation, Pragian,10metres below the "*Dicranurus* Couche", Oued el Atchane, Jbel Oufatene near Fezzou, Errachidia, Morocco

Plates 18G–N, 19A–O, 20A–P, 27L–O

Diagnosis. Genicranium broad, glabella subcylindrical, rounded anteriorly and preglabellar furrow well defined. Eye lobes with two lenses, and eye and genal ridges well defined. Whole of inner margin of fringe marked by row of bigger perforations. Anterior boss mildly inflated, genal roll steeply inclined (sag. and tr.) and girder kink Σ-shaped. Brim barely concave and width ratio around 0.95. Fine perforations on brim (around 100μm) and finer on genal roll. Internal rims subparallel. Thorax with 20 segments. Blister-like tubercular granulation on dorsal surfaces of external and internal rims, occipital ring and first 5 axial rings of thorax (Pls 18G, 19L).

Etymology. For Hammi Ait H'ssainne who prepared the holotype and much of the material presented in this publication.

Material and occurrence. Holotype: NHMUK It 29292, Pl. 18G–N, from 10 m below the "*Dicranurus* Couche", Ihandar Formation, Pragian, Oued el Atchane, Jbel Oufatene (Fig. 2B, Map 8, site 21), a partially articulated dorsal exoskeleton, enrolled with pygidium missing or folded under. Paratype: NHMUK It 29296, Pl. 19A–F; and Paratype NHMUK It 29295, Pl. 19M–O, from main trilobite 'couche' (Johnson & Fortey, 2012, fig. 2, Section 2, horizon 2, 17.5 m above bottom of section), Ihandar Formation, Pragian, southern flank of Jbel el Mrakib (Fig. 2B, Map 9, sites 16 and 15 respectively), dorsal exoskeletons with pygidium missing or hidden. Paratype: NHMUK It 29294, Pl. 19G–L, from a *Ceratonurus* horizon, Ihandar Formation, Pragian, Ahware (South), Iferd Nou Haouar (Fig. 2B, Map 9, site 12). Paratypes: NHMUK It 29290, Pl. 20A–D; NHMUK It 29291, Pl. 20J–M, from 12.5metres below the "*Dicranurus* Couche" (Johnson and Fortey, 2012, fig. 1, Section 1, 14.5 metres above bottom of section, top horizon of range indicated by " Harpidae sp. 1"), Ihandar Formation, Pragian, Jbel Oufatene (Fig. 2B, Map 8, sites 8 and 9 respectively); NHMUK It 29290, dorsal exoskeleton cephalon and disarticulated thorax, and NHMUK

It 29291, dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29293 Pl. 20N–P, from a horizon between the "*Dicranurus* Couche" and the "*Kolihapeltis* Couche", Talhadjate, Oufatene South (Fig. 2B, Map 8, site 22), dorsal exoskeleton of upper lamella only. Paratype: NHMUK It 29300, Pl. 20E–I, Ihandar Formation, North Zireg (Fig. 2B, Map 13, site1), dorsal exoskeleton with pygidium enrolled, from a Pragian horizon. Paratype: NHMUK It 29297, Pl. 27L–O, from a horizon some 5 metres below the "*Dicranurus* Couche", 26 metres above base of the Pragian, Ihandar Formation, Iminwasief (Fig. 2B, Map 4, site 4), dorsal exoskeleton comprising disarticulated thorax and pygidium.

Other material: *M.* cf. *hammii*, NHMUK It 29299 (Fig. 2B, Map 10, site 6), partial dorsal cephalon from a Pragian horizon, Jbel Rheris and NHMUK It 29298 (Fig. 2B, Map 4, site 19), a crushed dorsal exoskeleton with pygidium enrolled, from a Pragian horizon east of Jbel Ou-Driss. Other material is not figured herein.

Description. Cephalon sub oval, widest at alae, genicranium broad, width (tr.) 1.4 X length (sag.) and glabella anterior to S0 broad (width at S0 0.70 x length), crest rounded and with fine pitting. L1 inflated and muscle attachment scars S0 and S1 tulip-shaped, reaching over 40% and 60% of way up occipital furrow and flank of glabella, respectively. S2 and S3 appear as dark oval areas rising from axial furrow and S4 as dark line at preglabellar furrow (Pls 18N, 19F). Posterior and top of S1 is delineated by very faint hook-like furrow. There are no furrows associated with S2, S3 and S4. Occipital furrow broad and occipital ring medially broadened (sag.). Occipital node on anterior edge of occipital ring, moderately inflated. Occipital ring same height as glabella and carries blister-like tubercles. Alae small (tr.), narrow (width (tr.) 77% of length (exsag.), well defined, parabolic in shape, and are anterolaterally directed to reach nearly 40% across (tr.) genal areas. Alar furrows deep. Connecting L1 to occipital ring small, rounded ridge that crosses S0 where occipital ring begins to broaden (sag. and exsag.). Posterior border short (tr.) and with tubercles.

Dorsal surface of genal area barely convex, with faint caeca and fine pits. Eye location ratio is around 0.90, with eye lobe located on anterolateral slope of genal area at a level one fifth from anterior of glabella. Eye lobe small (exsag.), subcircular, inflated and with two ovoid eye lenses (Pl. 18K), latero-anteriorly and latero-posteriorly orientated, respectively. Low transverse eye ridge runs from eye tubercle to meet axial furrow at right angles and, on well preserved specimens, a genal ridge that crosses obliquely onto fringe (Pl. 18J). In dorsal view, inner margin of fringe is convex where it crosses (tr.) anterior of genal areas. Anterior boss mildly inflated, extends from preglabellar furrow to Σ-shaped girder kink. Girder moderately wide (sag. and exsag.). Genal roll sloping moderately steeply anteriorly and steeply laterally. Perforations on genal roll are fine, with row of bigger perforations above girder and along inner margin of fringe, which are slightly bigger than those below, becoming much bigger where they cross anterior boss. Caeca well-spaced, forming narrow, subparallel ribbon-like strips, which run down from inner margin of fringe to girder. In lateral view, inner fringe narrows only moderately posteriorly.

Brim slightly concave, sloping gently downwards, width (sag.) around 30% of cephalic length (sag.). Brim width ratio 0.95 +/- 6%. At proximal edge of brim, row of large perforations separated by light caeca, which stretches down from girder and across brim. Standardised perforations on brim, at 100μm, are a little larger than those on central part of genal roll and are moderately densely packed, at around 25 per sq. mm (Pl. 18G, L). Row of coarse perforations runs along outside edge of brim. External rim raised and robust, with slightly rounded dorsal surface and dorsal rim suture located at about mid-point on rim. Outside edge of marginal band close to vertical, slightly concave with a ridge top and bottom and fine tubercles.

Prolongations short (exsag.), at around 70% of sagittal cephalic length. External rims on prolongations curve strongly adaxially, while internal rims are subparallel. Internal rim thicker (tr.) in dorsal view than exterior rim. Brim steepens slightly on prolongations, and girder extension meets internal rim about halfway along prolongation. Terminal spine carried on lower lamella, short and slanted slightly adaxially. Perforations on brim and extension of genal roll increase in size posteriorly. Row of pits below girder extend from where girder meets internal rim to near end of prolongation, becoming smaller posteriorly and running just below row of larger pits immediately below internal rim. Small blister-like tubercles present on dorsal surface of internal rim.

Thorax consists of 20 or more segments, widening (tr.) to 5th segment. Axis strongly tapering. Shortest pleurae (inner portion) one third length (tr.) of longest. Pleural furrows narrow, well defined and shallow. Outer portion of pleurae straight and not offset to inner portion. Fine blister-like tubercles on first four axial rings (Pl. 19L).

Hypostome and pygidium not known.

Remarks. *Maghroharpes hammii* is similar to *M. minutipunctus* but differs in having: a cephalon that is sub oval rather than ovoid; a slightly broader (tr.) genicranium; a glabella that lacks granules on its dorsal surface; anS1

furrow that slopes backwards but does not curve forward around the top of the muscle insertion area; no muscle insertion furrows at S2, S3, or S4, as there are on the glabella of *M. minutipunctus*; a deeper occipital furrow; narrower (tr.) alae; deeper and better-defined alar furrows; a preglabellar field that is only visible in dorsal view and is much narrower than that of *M. minutipunctus;* eye lobes with small blister-like tubercles on their dorsal surface and two lenses per eye lobe. not three, an anterior boss that is more strongly inflated, reaching down to a well-defined girder kink, while *M. minutipunctus* is without a kink although the girder is slightly bowed in anterior view; a genal roll that slopes more steeply; an internal fringe that narrows more posterolaterally in lateral view; perforations on the genal roll that are smaller and more densely packed, except immediately above the girder where there is a row of larger perforations, absent on the genal roll of *M. minutipunctus*; a narrower brim (sag.) with slightly larger brim perforations and a brim width ratio (0.88) that is 10% higher than that of *M. minutipunctus*; a concave marginal band that has a ridge at the top and bottom and fine tubercles in between, while the marginal band of *M. minutipunctus* is straight and lacks ridges and tubercles; and internal rims that are much more concave in lateral view.

Maghroharpes hammii is reminiscent of some *Bohemoharpes* species from the Silurian and, in particular, *B. (B.) ungula* (*H. ungula* Sternberg,1833; Pl. 54G) from the Kopanina Limestone (Ludlow stage), Mt. Dlouhá Hora, Králův Dvůr, Central Bohemia. The cephalic outline and shape of the genicranium and glabella are similar, albeit the cephalon and genicranium of *B. (B.) ungula* are around 10% wider. Other differences include *B. (B.) ungula* having an inner margin of the fringe that, in dorsal view, is concave across the anterior of the genicranium rather than convex; thinner rims and posterior border which lack tubercles on their dorsal surfaces. *Bohemoharpes ungula* has an eye location ratio of 0.65, some 30% less than that of *Maghroharpes hammii*, and finer and more densely packed perforations on the brim and genal roll.

Variation in the morphological ratios of the *M. hammii* material figured herein is shown in Table 7. Brim perforation size and density show the greatest variability. There are also other variations, for instance, specimens from Jbel Mrakib (south) have larger muscle insertion scars at S2, S3 and S4 on the glabella. (see Pl. 19F) compared with those of *M. hammi* (see Pl. 18N).

Maghroharpes azmamarensis n. sp.

Plates 29E–J, O, 30A–E

Diagnosis. Cephalon nearly ovoid; glabella inset, broad, strongly vaulted and with convex axial furrows, converging anteriorly. Genal roll gently sloping (sag. and exsag.) and without caeca. Axial and alar furrows deep; preaxial furrows forming circular depressions, crossing inner margin of fringe. Eye lobes inflated and with three eye lenses each. Brim width ratio 0.80 to 0.85, and diameter of standardised brim perforations moderate to large (>145 μm).

Etymology. Named from type locality: Azmamar.

Material and occurrence. Holotype: NHMUK It 29281, Pl. 29E–J, from coral horizon at or near the "Couche Rouge" horizon at the top of the Pragian, Ihandar Formation, Azmamar, Oued el Atchane, Jbel Oufatene (Fig. 2B, Map 8, site 18), dorsal exoskeleton of cephalon only. Paratypes: NHMUK It 29282 (1 and 2), Pl. 30A–E and 39O, from type locality and horizon (Fig. 2B, Map 8, site 19), A–E dorsal exoskeleton of cephalon and, O, lower lamella on same slab.

Other material: *Maghroharpes* cf. *azmamarensis*: NHMUK It 29285, Pl. 30F–K, from coral horizon at or near the "Couche Rouge" horizon at the top of the Pragian, Ihandar Formation, Azmamar, Oued el Atchane, Jbel Oufatene (Fig. 2B, Map 8, site 17), dorsal exoskeleton of cephalon. NHMUK It 29286, Pl. 30L–O, from an upper Pragian horizon, Ihandar Formation, Maharch, Jbel Mrakib (Fig. 2B, Map 9, site 14), dorsal exoskeleton of partial cephalon.

Description. Cephalon ovoid, widest at midpoint between eyes and alae. Genicranium broad, widest at posterior border. Glabella inset, strongly vaulted, very broad with convex flanks, rounded crest and tubercles. Axial furrows convex and converging strongly anteriorly. L1 inflated, S1 sloping posteriorly and effaced before curving anteriorly near crest. No furrows at S2–S4. Preglabellar furrow straight in anterior view, and preglabellar field narrow and well defined. Occipital furrow narrow and medially straight. In lateral view, occipital ring sloping posteriorly and same height as glabella anterior to S0; not medially broadened and has sculptural tubercles. Occipital node large and well inflated. Alae small (tr.) and laterally directed. Alar depression present and posterior border moderately short.

Genal area moderately broad, with no caeca or tubercles. Large eyes (exsag.), set close to inner margin of

fringe. Eye location ratio around 0.90, and tubercles and pitting on eye lobes. Each eye lobe with 3 eye lenses, anterior and posterior largest and small central lens located high up between other two lenses. Eye ridge not well defined and internal margin of fringe convex across anterior of genal area. Preaxial furrows broad, not converging and forming depressions where they cross at inner margin of fringe. Glabella, preglabellar field, genal area and dorsal surface of eye lobes have fine, dense pitting. Anterior boss barely inflated, reaching down to weak girder kink. Genal roll sloping very gently anteriorly (≈ 35^0) and moderately steeply laterally (≈ 55^0). In lateral view, fringe narrows strongly posteriorly. Perforations on genal roll smaller than on brim, with row of larger perforations immediately above girder and across anterior boss at inner margin of fringe. No caeca. Girder moderately wide (≈ 2.6% of width (tr.) of genicranium).

Brim concave, not steeply sloping (≈15%) and with width (sag.) 30% of cephalic length (sag.). Brim width ratio 0.80. Standardised brim perforations 147µm, with row of larger perforations at proximal and distal edges of brim. Density of perforations on brim around 15 per square mm on standardised brim. Light caeca across brim. External rim stout, with rim suture running around centre of dorsal surface. Marginal band near vertical, concave, with tubercles and ridge around top and bottom. Length (exsag.) of prolongations around 75% of cephalic length (sag.). Internal and external rims curve adaxially and internal rims are concave in lateral view. Posterior border and internal rims thicker than exterior rim in dorsal view. Dorsal surface of internal rim sparsely covered by small tubercles. Girder extends onto prolongation, to meet internal rim halfway down prolongation. Proximal edge of brim steepening on prolongations, and prolongations terminate in spine carried on lower lamella.

No hypostomes, thoracic or pygidial sclerites are known.

Remarks. *Maghroharpes azmamarensis* lacks one of the diagnostic characters of its genus as shown in Table 5b, having an alar depression, which is lacking in most other members of the genus.

NHMUK It 29282 is very similar to the holotype but lacks bilateral symmetry, with one prolongation longer than the other, which may be the result of a teratological fault.

Maghroharpes azmamarensis closely resembles *M. oufatenensis* but differs in having: an ovoid rather than oval cephalon, which is widest at midpoint between the eye lobes and the alae, not at the alae as in the case of *M. oufatenensis;* an inset, carinate glabella with tubercles on its dorsal surface; eye lobes with pitting and tubercles on their dorsal surfaces and 3 lenses each the anterior and posterior lenses of equal size and the third lens between the other two, much smaller, while *M. oufatenensis*'s eye lobes lack tubercles and pitting and have only two lenses, the anterior lens being the largest; a low poorly defined eye ridge, which is absent on *M. oufatenensis;* a genal roll that slopes gently anteriorly at around 36^0 and laterally at around 54^0, compared to 55^0 and 72^0 respectively, in the case of that of *M. oufatenensis*; the brim sloping at around 15^0 with caeca that stretch right across it, while the brim of *M. oufatenensis* slopes at 7^0 and has caeca does not reach far across it; internal rims that curve adaxially and are not subparallel; and genal spines that follow the curve of external rim rather than being set at an oblique angle, as they are in the case of *M. oufatenensis*.

Maghroharpes cf.1 *azmamarensis* (Pl. 40 A–E) specimen NHMUK It 29285 differs from *M. azmamarensis* in having a wider (tr.) cephalon and genicranium, and shorter (exsag.) prolongations. The exoskeleton is not well preserved but otherwise seems similar to the holotype.

Maghroharpes cf.2 azmamarensis (Pl. 30L–O) specimen NHMUK It 29286 is similar to *M. azmamarensis*, but differs in having a broader and less vaulted glabella that is not inset and has more tectiform flanks. Also, it lacks alar depressions and has a brim that is wider (sag.) and has slightly bigger perforations.

***Maghroharpes ihmadii* n. sp.**

Plates 26A–Q, 27A–D

Diagnosis. Glabella subcylindrical, rounded anteriorly, and S1 curving anteriorly near crest. Alar depression present and ala close to axial furrow is inflated to rise slightly above level of genal area. Eye lobe weakly inflated with four lenses, two very small contiguous central eye lenses (Pl. 26G) dorsolaterally orientated. Anterior boss inflated and girder moderately narrow (just over 1.5% of width of genicranium). Brim barely sloping but steepening slightly posteriorly along inside edge on prolongations. Brim width ratio ≈ 0.95. External rim fine (< 10% of width sag. of brim). Thorax with 20 segments.

Etymology. Named after the trilobite worker, Ihmadi Hssaine, who found the holotype and paratypes.

Material and occurrence. Holotype: NHMUK It 29301, Pl. 26A–G, from the "*Lanceaspis* Couche" Ihandar Formation, Pragian, Jbel Ou-Driss East (Fig. 2B, Map 4, site 16), dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29302, Pl. 26 H–Q, from type locality and horizon (Fig. 2B, Map 4, site 17), partially articulated dorsal exoskeleton with pygidium missing and right prolongation with pathological defect. Paratype: NHMUK It 29303, Pl. 27A–D, from type locality and horizon (Fig. 2B, map 4, site 18), dorsal exoskeleton of cephalon only.

Other material: *Maghroharpes* cf. *ihmadii*: NHMUK It 29304, Pl. 27E–K, from "*Kolihapeltis* Couche" (Johnson & Fortey 2012, fig. 2, Section 1, horizon 3), Oued el Atchane, Ihandar Formation, Pragian, Jbel Oufatene (Fig. 2B, Map 8, site 14), dorsal exoskeleton pygidium enrolled. *Maghroharpes* aff. *ihmadii*: NHMUK It 29305, Pl. 31A–E, from an upper Pragian Couche below Tizinmarzelaghman, Ihandar Formation, bou Lachrhal (Fig. 2B, Map 9, site 4), dorsal exoskeleton of a partial cephalon.

Description. Cephalon length (sag.) just over two thirds its width (tr.). Glabella broad anterior to S0, width (tr.) just under 70% of length (sag.)), flanks and crest rounded and finely pitted, and axial furrows tapering slightly anteriorly. L1 inflated, and muscle attachment scars of S1, S2, S3 and S4 appear as dark oval areas rising from axial furrow, and S0 rising from base of occipital ring and spreading across L1 (Pl. 26O, P). S0 and S1 tulip-shaped, reaching over 50% and 70% of way up occipital furrow and flank of glabella, respectively. Posterior and top of S1 delineated by very faint hook-like furrow. S2 and S3 oval and about one third size of S1, and S4 only just discernible across junction of axial furrow and preglabellar furrow. No furrows associated with S2, S3 and S4. Occipital furrow broad and occipital ring broadened slightly medially. Occipital node small, well inflated, located towards anterior edge of L0. Occipital ring same height as glabella, and free of tubercles. Alae well defined, small (tr.) (22% of width of glabella at S0) and narrow (length (exsag.) being nearly 1.20 times width (tr.)), parabolic in shape and anterolaterally directed to reach nearly 45% across (tr.) genal areas. Alar furrows deep. Posterior border moderately short (tr.) (≈ 33% of width (tr.) of occipital ring) and without tubercles on dorsal surface.

Dorsal surface of genal area with fine pits but no caeca. Eye lobe located on anterolateral slope of genal area, with eye location ratio being just under 0.90. Eye lobe small (exsag.), subcircular, inflated and with what appears to be four eye lenses (Pls 26E, F, G, 27H, I), Two large ovoid lenses latero-anteriorly and latero-posteriorly orientated, respectively, and small subcircular furrow around two small contiguous lenses (Pl. 26G). Low transverse eye ridges gently arch into axial furrows and, on well preserved specimens, faint genal ridge that crosses obliquely onto fringe and reaches posteriorly to prolongations (Pl. 26C). In dorsal view, inner margin of fringe strongly convex across anterior of genal areas. Anterior boss extends from preglabellar furrow to Σ-shaped girder kink. Girder moderately narrow (sag. and exsag.), just over 1.5% of width of genicranium. Genal roll sloping moderately steeply anteriorly (≈ 53^0) and steeply laterally (≈ 67^0). Perforations on genal roll fine with row of bigger perforations above girder and along inner margin of fringe, where it crosses anterior boss. Genal roll lacks caeca. In lateral view, inner fringe narrows only moderately posteriorly.

Brim slightly concave, sloping gently downwards, width (sag.) around 32% of cephalic length (sag.). Brim width ratio ≈ 0.93. At proximal edge of brim row of large perforations separated by light caeca, which stretches down from girder onto brim, to occasionally reach outside edge. Standardised brim perforations, at ≈130μm, are a little larger than those on central part of genal roll and are moderately densely-packed, at around 22 per sq.mm (Pls 26D, K, 27D). Row of coarse perforations runs along outside edge of brim. External rim raised and narrow (width (sag.) 9% of brim width (sag.), dorsal surface slightly rounded, with internal dorsal rim suture located at about mid-point on rim. Outside edge of marginal band close to vertical, slightly concave with ridge top and bottom.

Prolongations moderately short (exsag.), at around 78% of cephalic length (sag.). External and internal rims on prolongations curve adaxially. Brim steepens slightly on prolongations, and girder extension meets internal rim about halfway along prolongation. Terminal spine carried on lower lamella, short and slanted slightly adaxially. Perforations on extension of genal roll increase in size posteriorly on prolongations. No tubercles on dorsal surface of internal rim and no row of larger perforations below.

Thorax consists of more than 20 segments, widening (tr.) to 7^{th} segment. Shortest pleurae (inner portion) under 45% of length (tr.) of longest. Pleural furrows moderately broad and well defined. Outer portion of pleurae straight and not offset to inner portion.

Hypostome and pygidium not known.

Remarks. *Maghroharpes ihmadii* lacks two of the diagnostic characters of its genus as shown in Table 5b. It has an alar depression and its girder is narrower than those of other *Maghroharpes* species.

Maghroharpes ihmadii is very similar to *M. laatchanensis* but differs in having: a genicranium that is about 13%

broader; a glabella that is less tapered anteriorly and has a crest that is more rounded than carinate; a shallow muscle insertion furrow at S1 that curves around top of muscle insertion area; a distinct rather than shallow preglabellar furrow; an occipital ring that in lateral view is same height as the glabella anterior to S0, not lower, as is that of *M. laatchanensis*; a wider (tr.) ala; an alar depression and axial furrows that cross the junction between the ala and L1; a wider (tr.) but thinner (exsag.) posterior border; a narrow preglabellar field rather than none; a broader genal area free of the light caeca found on the genal area of *M. laatchanensis*; less inflated eye lobes with four eye lenses each not two; a better-defined curved eye ridge; a more inflated anterior boss; a genal roll that is more steeply sloping and without caeca; a wider girder; a more steeply-sloping brim with bigger perforations and light caeca just reaching on to it, unlike those of *M. laatchanensis* that reach right across the brim; a much finer external rim; no tubercles on the dorsal surface of internal rim and on the thorax; pleurae lengthening (tr.) to widen the thorax to 5th segment and not just lengthening to compensate for the narrowing posteriorly of the axial rings; much broader pleural furrows, pleurae that shorten (tr.) less posteriorly; and outer portions of the pleurae in line with the inner portion, not offset as is the case in *M. laatchanensis.*

Paratype NHMUK It 29302 (Pl. 26H–Q) has a damaged prolongation which, judging from the repair to the external border, may have occurred at an earlier intermoult period.

Maghroharpes cf. *ihmadii* NHMUK It 29304 (Pl. 27E–K) differs from *M. ihmadii* in having a narrower (tr.) genicranium and glabella, alae that are smaller (tr.), and an S1 furrow that is shallower and does not reach as far up the flank of the glabella. Also, the standardised brim perforations are 20% smaller. *Maghroharpes* aff. *ihmadii* NHMUK It 29305 (Pl. 31A–E) also differs from *M. ihmadii* in having a more inflated anterior boss, a narrower (sag.) and more concave brim, and an eye lobe with no third central lens (Pl. 31D).

Maghroharpes zguidensis n. sp.

Plate 24A–L

Diagnosis. Cephalon widest just anterior to alae, glabella carinate, and no eye ridges. Anterior boss barely inflated and joined to glabella by gentle swelling in preglabellar field. Genal roll sloping anteriorly at under 50^0. Brim narrow (sag.), at 28% of length of cephalon (sag.); and very fine brim perforations with standardised diameter of ≈70μm. Prolongations short, ≈ 66% of length (sag.) of cephalon. Internal and external rims robust, curving adaxially on prolongations.

Etymology. Named after the town near the type locality, Foum Zguid.

Material and occurrence. Holotype: NHMUK It 29325, Pl. 24 A–E, from basal limestones of the Merzâ Akhsai Formation?, Pragian, S.W. of Foum Zguid (Fig. 2A, Map 2, site 1), dorsal exoskeleton of cephalon only. Paratypes: NHMUK It 29326, Pl. 24 F–I, and NHMUK It 29327, Pl. 34J–K, both from type locality (Fig. 2A, Map 2, sites 2 and 3, respectively), dorsal exoskeletons of cephala only.

Other material: *Maghroharpes* cf. *zguidensis*, NHMUK It 29328, Pl. 31L–N, from a Pragian horizon, Merzâ Akhsai Formation? el Ayoun, Tata (Fig. 2A, Map 1, site 1).

Maghroharpes aff. *zguidensis*, NHMUK It 29287, Pl. 23A–D, from an upper Pragian horizon, Ihandar formation, at the foot of bou Lachrhal (Fig. B, Map 9, site 5), dorsal exoskeleton of cephalon.

Description. Cephalon sub oval, widest (tr.) just anterior to alae. Genicranium narrow (length 77% of width), widest at posterior border. Glabella carinate; L1 barely inflated; S1 very shallow, becoming effaced before curving anteriorly near crest; and no furrows at S2, S3 or S4. Axial furrows convex and converging weakly anteriorly. Preglabellar furrow barely distinct, occipital furrow deep and medially straight. Occipital ring same width (sag.) as width of posterior border (exsag.), sloping posteriorly and lower than glabella anterior to S0. Occipital node small, at anterior edge of dorsal surface of occipital ring. Alae small (tr.) and laterally directed. Alar furrow shallow and well defined, and no alar depression. Posterior border moderately short (tr.) and preglabellar field narrow (sag.).

Genal area moderately broad (tr.) and without caeca. Eye lobes oval, inflated and located close to inner margin of fringe. There are two eye lenses per eye lobe and no pitting or tubercles on their dorsal surfaces. No genal ridge or eye ridge, and course of inner margin of fringe across anterior of genal area is straight. Boss barely inflated but reaches down to girder, joined to glabella by a ridge narrower than glabella. Genal roll sloping gently anteriorly (≈ 49^0), moderately steeply laterally (≈ 62^0). Inner fringe narrowing moderately in lateral view. Caeca on genal roll and genal roll perforations same size as those on brim. Girder moderately wide and girder kink weak.

Brim concave, narrow (sag.), moderately to moderately steeply sloping (≈ 20^0). Brim width ratio 0.88 and standardised brim perforations very fine, with a diameter around 70μm. Light caeca across brim. Marginal band is near vertical, concave and with ridges top and bottom, but no tubercles. Prolongations short (exsag.), at 65% of cephalic length (sag.). Internal and external rims curving adaxially. Internal rim concave in lateral profile. Genal spine short, following curve of external rim. Extension of girder meeting internal rim nearly two thirds of way down prolongation. No larger perforations under internal rim and rim on prolongation only steepening along proximal edge.

Remarks. *Maghroharpes zguidensis* has two characters which do not comply with the chosen diagnostics of the genus as shown in Table 5b—inner margin of the fringe across the anterior of the genal area is straight rather than convex, and the extension of the girder meets the internal rim two-thirds of the way down the prolongation rather than half-way down.

Maghroharpes zguidensis is similar to *M. minutipunctus* but differs in having: a cephalon that is oval rather than ovoid shaped; a glabella which is carinate and has no muscle insertion furrows at S1, S2, S3 and S4; a much less distinct preglabellar furrow; a deeper occipital furrow; an occipital ring that is not medially broadened (sag.); a wider (tr.) posterior border; alae laterally not anterolaterally directed; the genal area without the faint caeca present on *M. minutipunctus*; larger eye tubercles (exsag.) set close to the inner margin of the fringe, with two rather than three eye lenses each; no genal or eye ridge, unlike *M. minutipunctus* where both ridges are well defined; an anterior boss that is connected to the glabella and reaches down to a well-defined girder kink; perforations on the genal roll the same size as on the brim rather than smaller, and the brim is 20% narrower (sag.) than that of *M. minutipunctus*; a more robust external rim; a marginal band that has a ridge top and bottom rather than none; internal rims which in dorsal view curve adaxially rather than being subparallel; and an extension to the girder that meets the internal rim two thirds of the way down the prolongation, rather than halfway down as in the case of *M. minutipunctus.*

Maghroharpes cf. *zguidensis* (Pl. 31L–N) differs from *M. zguidensis* in having an occipital ring that is medially broadened, eye lobes with three lenses rather than two and a wider brim (sag.) with a 10% lower brim width ratio.

Maghroharpes aff. *zguidensis* (Pl. 23A–D) is similar to *M. zguidensis* but differs in having: a glabella with a rounded rather than carinate crest; a wider occipital furrow; a broadened occipital ring; a very shallow and distally-effaced alar furrow; a posterior border that is 70% wider (tr.) in relation to the width (tr.) of the occipital ring than that of *M. zguidensis*; an anterior boss that does not reach down to the girder; the girder lacking a kink; the genal roll sloping more steeply anteriorly; the perforations on genal roll smaller than those on brim; the brim 18% wider (sag.), the brim width ratio 15% lower and brim perforations more than twice the diameter of those on the brim of *M. zguidensis*; internal rims on prolongations subparallel rather than curving adaxially; genal spine that follows the curve of external rim, and the extension to its girder meeting half way down the prolongation rather than two thirds of the way down, as in the case of *M. zguidensis*.

Maghroharpes terridus **n. sp.**

Plate 32A–D

Diagnosis. Genicranium narrow, glabella very broad without any muscle attachment furrows, and L1 not inflated. Alar furrows and occipital furrows very shallow. Preglabellar furrow barely distinct and anterior boss joined to glabella. Brim barely sloping and with concave profile. Marginal band with three ridges. Internal rims subparallel.

Etymology. Terridus Latin for scared, inspired by the name of type locality Maharch, which is known the "pass of the conflict" after a fight between two tribes that took place there. Maharch is a narrow pass between Jbel el Mrakib and the southern extension of Jbel Otfal, an ideal ambush site and strategically important.

Material and occurrence. Holotype: NHMUK It 29321, Pl. 32A–D, from the narrowly turriculate caenogastropod horizon, (Johnson & Fortey 2012, fig. 2, section 2, horizon 2, 17.5 metres above bottom of section), Ihandar Formation, Pragian, Maharch, Southern flank of Jbel el Mrakib (Fig. 2B, Map 9, site 18), dorsal exoskeleton with thorax disarticulated and pygidium missing.

Description. Cephalon widest at mid-point between eye lobes and alae. Genicranium narrow, length (sag.) 78% of width (tr.) and widest at posterior border. Glabella not inset; very broad (width (tr.) 76% of length (sag.)); flanks convex; crest rounded and with granulation but no pitting. S1 not evident and no furrows at S2, S3 or S4. L1 not

inflated. Axial furrows convex and converging weakly anteriorly. In lateral view, preglabellar furrow barely distinct and straight. Occipital furrow broad, shallow and medially straight. Occipital ring broader (sag.) than posterior border (exsag.), but not medially broadened, and has fine granulation on dorsal surface. In lateral view, it slopes posteriorly and is higher than glabella anterior to S0. Occipital node small and poorly inflated, located on anterior slope of occipital ring. Alae small (tr. and exsag.). Alae anterolaterally directed and alar furrow shallow, distally effaced. Posterior border moderately short (tr.). Narrow (sag.) preglabellar field.

Genal area moderately broad without caeca or pits, but evidence of small tubercles or granulation. Eye lobes inflated, oval, set away from inner margin of fringe (eye location ratio 0.77) and lacking sculpture on dorsal surface. No genal ridge, and eye ridge ill-defined. Inner margin of fringe convex across anterior of genal areas, with row of bigger perforations where it crosses anterior boss. Boss barely inflated, joined to glabella and reaching down to girder. Girder kink very weak. Genal roll moderately steep anteriorly (≈ 57^0) and laterally (≈ 62^0). Fringe narrowing strongly in lateral view. Genal roll with caeca and perforations smaller than on brim; perforations all the same size, apart from row of larger perforations above girder.

Brim barely sloping, concave, moderately wide (32% of cephalic length (sag.)) and with brim ratio of 0.84. Brim perforations moderately fine (≈120μ) with larger perforations around proximal and distal edges. Light caeca across brim. External rim stout. No tubercles on dorsal surface of rim and marginal band vertical, concave, ridge top and bottom, and without tubercles. Length (exsag.) of prolongations nearly 80% of cephalic length (sag.). Internal rims subparallel in dorsal view and concave in lateral view. External rims curving adaxially. No genal spine. Girder extension meeting internal rim halfway down prolongations, tubercles on dorsal surface of internal rim and only proximal edge of brim steepening on prolongation. Thorax widening (tr.) to 5^{th} segment, and no pitting or tubercles on axial rings or pleurae. Pleural furrows broad, very shallow, almost effaced and V-shaped in cross section. Outer portion of pleurae set at an angle to inner portion, curved posteriorly and terminating in a point.

Remarks. One character does not comply with the selected diagnostics for the genus shown in Table 5b, the location ratio of eye lobes being further from the internal margin of fringe than is the case with other species of the genus. Also, it is not possible to determine the girder width from the material presented here.

Maghroharpes terridus is unusual amongst maghroharpids, in having a glabella without furrows and L1 that is not inflated. These characters are more typical of *Pinnuloharpes* species. The narrow genicranium, caeca on genal roll, the concave brim and the lack of the steepening of the brim on the prolongations are, however, more typical of *Magroharpes* species.

Maghroharpes terridus is similar to *M. oufatenensis*, but differs in having: an ovoid cephalon that is widest at the mid-point between the eye lobes and the alae, rather than being sub oval and widest at the alae; a genicranium that is around 10% narrower; a glabella that has granulation and pitting on its dorsal surface, and a crest which is rounded not carinate; no muscle insertion furrows at S1; an uninflated L1; shallow preglabellar and occipital; fine granulation rather than tubercles on the occipital ring; alar furrows that are very shallow and distally effaced; genal areas with pitting; eye lobes that are located further from the inner margin of the fringe; an eye ridge, albeit ill-defined, that is missing on the cephalon of *M. oufatenensis*; the anterior boss joined to glabella; the genal roll sloping less steeply laterally; the brim with perforations that are 25% finer than those of *M. oufatenensis*; light caeca on the genal roll and caeca covering the whole of the brim, while *M. oufatenensis* has caeca crossing onto the inner part of the brim only and none on the genal roll; the dorsal surface of the external rim overhanging the marginal band, which lacks tubercles or a ridge around its base; internal rims which, in dorsal view, are subparallel rather than curving adaxially; and no genal spines, unlike *M. oufatenensis* which has short spines.

The holotype of *M. terridus* displays an unusual combination of characters as outlined above. Also, it is well preserved complete cephalon and partial thorax of a size that would indicate that they belonged to a well-developed holaspid. The cephalon is symmetrical and without any apparent pathological defects and has significant differences with *M. oufatenensis*, the species it is most similar too. On this basis the species has been erected although without the support of paratypes.

***Maghroharpes oufatenensis* n. sp.**
Plates 25H, 28A–O

Diagnosis. Genicranium broad and strongly vaulted. Glabella crest carinate, anteriorly rounded and free of tubercles or granulation. Axial furrows converging strongly towards well-defined preglabellar furrow. Occipital node barely inflated; tubercles on genal area. Eye lobes small (exsag.), moderately strongly inflated and with two lenses each, anterior lens being largest. Shape of lenses rectangular with rounded corners to subtriangular. Eye ridge absent. Prominent small tubercles on occipital ring, posterior border and internal rims. No caeca on genal roll. Brim width ratio 0.80, and standardised brim perforations around 170μm.

Etymology. Named after the locality where it was first collected and where it is most abundant.

Material and occurrence. Holotype: NHMUK It 29320 (1), Pl. 28A–E, from Hamar Laghdad, upper Pragian (Fig. 2B, Map 11, site 8), dorsal exoskeleton of cephalon only. Paratypes: NHMUK It 29316, NHMUK It 29319 and NHMUK It 29318 (1–9) from coral horizon at top of Pragian, Ihandar Formation; NHMUK It 29316, Pl. 28F–I, from Bid er Ras in south of Oufatene (Fig. 2B, Map 8, site 23); NHMUK It 29319 and NHMUK It 29318 (1–9), Pls 28J–O, 25H, respectively, from Oued el Atchane west Oufatene (Fig. 2B, Map 8, site 24 and site 2, respectively). All paratypes dorsal exoskeletons of cephala only.

Description. Cephalon sub oval, widest at alae. Genicranium broad, widest at posterior border. Glabella not inset, broad (width (tr.) 75% of length (sag.)), crest slightly carinate and flanks convex. Fine pits but no other sculpture. S1 slanting posteriorly, becoming effaced about halfway up flank of glabella; no furrows at S2, S3 or S4. Axial furrows convex, converging strongly anteriorly (17^0); preglabellar furrow distinct, straight in anterior view. Occipital furrow broad, deep and medially straight. Occipital ring in dorsal view not broadened medially, but broader (sag.) than posterior border (exsag.). In lateral view, sloping posteriorly and at its highest point, same height as glabella anterior to S0. Occipital node small, barely inflated (Pl. 28B), and prominent tubercles on dorsal surface of occipital ring. L1 inflated. Alae laterally directed, slightly inflated and small (tr.) in relation to length of glabella (sag.). Axial furrow crossing at junction of L1 and ala. Posterior border moderately short. Narrow preglabellar field.

Genal area moderately broad, without caeca but with small, low tubercles and very fine pits only visible on paratypes. Eye lobes small (exsag.), oval in shape and located close to inner margin of fringe. Each lobe has two lenses of equal size and without tubercles on its dorsal surface. No genal or eye ridges. Course of inner margin across anterior of genal area convex. Inner margin of fringe marked by bigger perforations across anterior boss only. Anterior boss, barely inflated, not joined to glabella and reaches down to weak girder kink. Genal roll moderately steep anteriorly (sag.) ($\approx 54^0$) and steep laterally ($\approx 72^0$). In lateral view, inner fringe narrowing strongly posteriorly. Genal roll lacks caeca, and has smaller perforations than on brim. Single row of larger perforations above girder. Girder moderately wide.

Brim concave, barely sloping and moderately wide (sag.), being 32% of cephalic length (sag.). Brim width ratio 0.83, and standardised brim perforations moderately large at ≈167μm. Row of larger perforations at distal and proximal edges, and caeca just reaching onto brim. External rim stout and without sculpture on dorsal surface. Marginal band near vertical, concave with ridges around top and bottom, and with tubercles. Prolongations around 80% of cephalic length (sag.). In dorsal view, internal rim subparallel to slightly curved adaxially, with concave profile in lateral view. Genal spine short, not following curve of exterior rim. Extension of girder meeting internal rim halfway down prolongation and with tubercles on dorsal surface. Proximal edge of brim steepening on prolongations.

Remarks. *Maghroharpes oufatenensis* complies with all the diagnostic characters of the genus shown in Table 5b. It is similar to *M. ihmadii* but differs in having: a broader (tr.) glabella which is carinate; a furrow at S1 that does not curve over the top of the muscle insertion scar; axial furrows that converge more strongly anteriorly; a broader genal area with tubercles; eye lobes that are much more inflated, oval rather than reniform and have only two eye lenses each, compared to four lenses in *M. ihmadii*; no genal or eye ridges; a less inflated anterior boss; a girder that is 70% wider (sag. and exsag.); a weak girder kink that is not Σ-shaped like that of *M.ihmadii*; standardised perforations on the brim that are some 50% bigger than those of *M. ihmadii*; a brim width ratio around 0.80, rather than 0.93; a stout rather than fine external rim; a marginal band with tubercles; and tubercles on occipital ring and on the dorsal surfaces of the posterior borders and internal rims.

NHMUK It 29318 is an assemblage of 9 dorsal exoskeletons of cephala of differing sizes, the smallest having a length (sag.) 37% of the largest. In the Devonian of the Anti-Atlas, it is very rare to find such a wide intraspecies size range in trilobite specimens at the same locality. For some yet to be explained reason, differing holaspid development stages are poorly represented. The Upper Ordovician, Silurian and Devonian assemblages in obrution

deposits figured by Brett *et al.* 2012, also show limited size ranges. Of the 8 assemblages figured it would appear that in only one is the sagittal length of the smallest exoskeleton under 70% of the largest.

Maghroharpes minutipunctus n. sp.

Plate 23E–P

Diagnosis. Broad (sag.) brim, around 37% of cephalic length (sag.), with moderately high density of fine perforations. Eye tubercles set well away from inner margin of fringe. Transverse eye ridges, which turn anteriorly in axial furrow. Preglabellar boss barely inflated and no median girder kink. Each eye lobe with three contiguous eye lenses.

Etymology. Minuiti punctus, Latin for small holes. Named after the small brim perforations of the species.

Material and occurrence. Holotype: NHMUK It 29312, Pl. 23E–J, from "*Dicranurus* Couche", Ihandar Formation, Pragian, Oued el Atchane, Jbel Oufatene (Fig. 2B, Map 8, site 11); dorsal articulated exoskeleton with pygidium, enrolled. Paratype: NHMUK It 29313, Pl. 23K–P, from type locality (Fig. 2B, Map 8, site 12), a partial dorsal exoskeleton with dorsal surface of hypostome partly exposed. Paratype: NHMUK It 29323, Pl. 22K–M, from a lower Emsian horizon, Boutiskaouine Formation, Awhare, Iferd Nou Haouar (Fig. 2B, Map 9, site 13), dorsal exoskeleton of partial cephalon.

Other material designated *M.* aff. 1 *minutipunctus,* NHMUK It 29322, Pl. 22F–J, from the "*Ceratocephala* Couche", Boutiskaouine Formation?, lower Emsian, Jbel Ou-Driss north (Fig. 2B, Map 4, site 7), dorsal exoskeleton of cephalon only. *M.* aff 2 *minutipunctus*, NHMUK It 29324, Pl. 22N–Q, from coral horizon below "*Lanceaspis* Couche", Ihandar Formation, Pragian, Jbel Ou-Driss (West) (Fig. 2B, Map 4, site 20), a dorsal exoskeleton of partial cephalon.

Description. Cephalon ovoid and genicranium narrow, length 75% of width. Both are widest at alae. Glabella not inset, broad (width 70% of length), subcylindrical, anteriorly rounded, with granulation on dorsal surface. Axial furrows straight, barely converging anteriorly. S1 backward-sloping and starting to curve anteriorly near crest, before becoming effaced. Other muscle insertion furrows at S2, S3, and S4. Preglabellar furrow bowed upwards in anterior view. Occipital furrow shallow and medially straight in dorsal view. Occipital ring medially broadened and in lateral view, sloping posteriorly and lower than glabella anterior to S0. Occipital node small, located on anterior edge of occipital ring. L1 inflated. Alae small (tr.), parabolic in outline and anterolaterally directed. Alar furrow shallow but well-defined and axial furrow crossing junction of ala with basal lobe. Posterior border short (tr.); narrow preglabellar field (sag.).

Genal area moderately broad with faint caeca and fine pits. Eye lobes small (exsag.) (27% of width of glabella at S1); positioned away from inner margin of fringe; oval in shape; no ornamentation on dorsal surface and with three lenses each, anterior, middle and posterior lens, all contiguous or overlapping. Eye ridge narrow, curved and well-defined. Genal ridge stretching posterolaterally almost to girder. Course of inner margin of fringe across anterior of genal areas convex and marked with larger perforations across anterior boss. Anterior boss barely inflated, not joined to glabella and not reaching down to girder. No girder kink. Genal roll sloping very gently anteriorly (43^0), becoming a little steeper laterally (57^0). Faint caeca present on genal roll. Genal perforations smaller than on brim. Perforations all the same size and no row of larger perforations above girder. Girder moderately wide.

Brim profile gently concave. Brim wide (sag.), 36% of cephalic length (sag.), and moderately steeply sloping at around 22^0. Brim width ratio 0.86. Standardised brim perforations very fine, around 85μm in diameter. Row of larger perforations at distal and proximal edges and light caeca reaching across brim. Rim fine (under 10% of width (sag.) brim). External rim without sculpture on dorsal surface, and marginal band near vertical, with straight profile and no ridges or tubercles. Prolongations short, at around 70% of cephalic length (sag.). Internal rims subparallel in dorsal view, exterior rims curving adaxially. In lateral view, internal rims concave, with no tubercles on dorsal surface. Genal spine short. Extension of girder meeting internal rim halfway down prolongations, and dorsal surfaces of internal rim smooth. Proximal edge only of brim steepens on prolongations.

Thorax with at least 20 segments; no pits or tubercles on axial rings; pleurae not lengthening beyond compensating for narrowing (tr.) of axis posteriorly. Thorax tapering quite strongly, with shortest pleura (inner portion) being around 35% of longest. Pleural furrows U-shaped, deep and narrow. Outer portion of pleurae in line with inner. Outer portion straight with straight distal ends.

Remarks. *Maghroharpes minutipunctus* lacks three maghroharpid diagnostic characters shown in Table 5b. It

has muscle insertion scars on the glabella at S2, S3 and S4, not present on other *Maghroharpes* species, the eye lobes are closer to the axial furrows and the marginal band has a straight profile rather than being concave.

Maghroharpes minutipunctus is similar to *M. hammii* and *M. zguidensis* and comparisons are given in the systematics of both species above.

M. minutipunctus aff.1 (Pl. 22F–M) is similar to *M. minutipunctus* but it has: a cephalon that in dorsal view is more oval than ovoid; a glabella that is carinate with tectiform flanks rather than rounded; a preglabellar furrow that is straight and not bowed upwards; a genal area and posterior border that are slightly wider (tr.); larger (ex sag.) eye lobes that are located close to the inner margin of the fringe, and a central lens located on the dorsal surface of the eye lobe that is larger than the other two lenses located on the lateral surface of the eye lobe. *M. minutipunctus*'s anterior and posterior lenses are of equal size and all lenses are located on the lateral surface of the eye lobe. *M. minutipunctus* aff. 1 also has no genal ridge, no caeca on the genal roll and a brim that is narrower (sag.) and with a higher brim width ratio.

M. minutipunctus aff. 2 (Pl. 22N–Q) differs from *M. minutipunctus* by having: a glabella that has a carinate crest, tectiform flanks and a furrow at S1 that does not curve over the top of the muscle attachment area; axial furrows that converge weakly rather than being sub parallel; a preglabellar furrow that is straight in anterior view; a wider (tr.) posterior border; an inflated anterior boss and a girder kink. The genal roll of *M. minutipunctus* aff. 2 slopes anteriorly and laterally more steeply, there is a single row of larger perforations above girder and a narrower (sag,) brim with larger perforations and a higher brim width ratio. Also, the internal rim curves more strongly adaxially than that of *M. minutipunctus*.

Maghroharpes laatchanensis n. sp.

Plate 21A–O

Diagnosis. Genicranium very narrow. Glabella narrow, with mildly carinate crest and convex flanks. Axial furrows do not cross junction of ala and L1, and converge strongly anteriorly. Preglabellar furrow indistinct and preglabellar field absent. Genal area narrow, width (tr.) around half the length (exsag.). Alae also narrow (tr.) and genal roll moderately sloping (sag.). Brim strongly concave and not steepening on prolongations. Thorax with over 21 segments.

Etymology. Named after the type locality Oued el Atchane.

Material and occurrence. Holotype: NHMUK It 29308, Pl. 21A–G, from "*Kolihapeltis* Couche" (McKellar & Chatterton, 2009, text fig. 5D), Ihandar Formation, Oued el Atchane, west Jbel Oufaten (Fig. 2B, Map 8, site 15); an articulated dorsal exoskeleton with pygidium, enrolled. Paratypes: NHMUK It 29307 and NHMUK It 29306, Pl. 21H–K, L–O, respectively, type locality and horizon (Fig. 2B, Map 8, site 13 and site 3, respectively), dorsal exoskeletons of cephala only.

Other material: *Maghroharpes* cf. 1 *laatchanensis*: NHMUK It 29311, Pl. 22A–E, from Pragian couche below Tizzinydo, Ihandar Formation, Jbel el Oftal (Fig. 2B, Map 9, site 8), dorsal exoskeleton of cephalon only; M. cf. 2 *laatchanensis*, NHMUK It 29310 (1) and NHMUK It 29310 (2), Pl. 25A–G, from Merzâ Akhsai Formation?, Pragian, Foum Zguid (Fig. 2B, Map 1, site 4), dorsal exoskeleton of cephalon only, and a dorsal exoskeleton of cephalon with disarticulated thorax.

Description. Cephalon sub oval, widest at alae. Genicranium widest at posterior border and very narrow, length (sag.) around 90% of width (tr.). Glabella not inset; narrow, with width (tr.) at S1 of around 65% of glabellar length (sag.) anterior to S0; mildly carinate, with convex flanks; and finely pitted. S1 effaced, before curving forward near crest, and no furrows at S2, S3 or S4. Axial furrow convex, tapering strongly anteriorly (angle of convergence just over 15^0). Preglabellar furrow shallow, and straight in anterior view. Occipital furrow deep and in dorsal view, medially straight. Occipital ring same width (sag.) as posterior border, without ornamental tubercles and in lateral view, lower than glabella anterior to S0. Occipital node moderately inflated. L1 inflated, alae small (tr. and exsag.) and laterally directed. Alar furrow deep, and axial furrow not crossing junction of ala and L1. Posterior border short (tr.), 20% of occipital ring width (tr.). No preglabellar field.

Genal area narrow (tr.), just under 50% of length (exsag.), finely pitted and with no caeca or tubercles. Eye lobes reniform; inflated and small (exsag.), under 30% of width (tr.) of glabella at S1; located close to internal margin of fringe; each lobe has three lenses, anterior and posterior oval lenses approximately the same size and small central

subcircular lens located high up between the two larger lenses. Eye ridge broad, short and not well-defined, and no genal ridge. Inner margin of fringe across anterior of genal areas convex. Anterior boss barely inflated, reaches down to girder. Genal roll gently sloping anteriorly (≈ 45^0), more steeply laterally (≈ 70^0). In lateral view, fringe on genal roll narrowing strongly posteriorly. Genal roll with caeca and perforations same size as those on brim, except for row of larger perforations above girder and across anterior boss, where internal margin of fringe crosses it. Girder wide (sag.), ≈ 3% of width (tr.) of genicranium.

Brim concave, moderately wide (sag.), ≈ 34.0% of cephalic length (sag.) and sloping at ≈11^0. Brim width ratio 0.91. Standardised brim perforation very fine, ≈90 μm, and light caeca across brim. Rim stout with no sculpture on dorsal surface and marginal band near vertical, concave with tubercles and ridge at top and bottom. Prolongations (exsag.) 80% of cephalic length. Internal and external rims curving adaxially posteriorly. Internal rim with concave profile in lateral view, extension of girder meets rim nearly halfway down prolongation and it has tubercles on dorsal surface. Brim not steepening on prolongations. Genal spine short.

Thorax with more than 21 segments. Axis tapering quite strongly posteriorly. No pitting or tubercles on axial rings, and pleurae lengthening to compensate for narrowing of axes until 5th segment. Pleurae strongly tapering, width (tr.) of inner portion of smallest being under 40% of longest. Pleural furrows narrow, deep and V-shaped. Outer portion, set at an angle to inner portion, curves anteriorly, terminating in a point (Pl. 21F).

Remarks. *Maghroharpes laatchanensis* has a slightly wider girder than other *Maghroharpes* species and its brim does not steepen along the proximal edge of the prolongations. It otherwise has all the diagnostic characters of its genus shown in Table 5b.

Maghroharpes laatchanensis differs from *M. hammii* in having: a genicranium and glabella which are 25% and 15% narrower, respectively; a carinate glabella which is more tapered anteriorly; axial furrows which do not cross the junction of alae and L1; a shallower preglabellar furrow, which in anterior view is straight and not bowed up as is that of *M. hammii*; an occipital ring that is not medially broadened and lower in lateral view than glabella anterior to S0, rather than being the same height; no preglabellar field; its genal area around 10% narrower than that of *M. hammii*; its eyes lobes reniform rather than oval; its eye ridge shorter (tr.) and not as well defined as that of *M. hammii;* its boss less inflated; a genal roll that is less steeply-sloping (sag.); a slightly wider girder (sag.); an inner fringe that in lateral view narrows more strongly posteriorly; a brim which is 12% wider (sag.); and prolongations that are slightly longer (exsag.) relative to the cephalic length (sag.) ; a thorax with more than 21 thoracic segments (*M. hammii* has at least 20); pleural furrows that are narrower (exsag.) and more V-shaped than U-shaped; and pleurae that lengthen (tr.) sufficiently, anteriorly, to compensate for the narrowing of axial ring but not to increase the overall width (tr.) of the thorax.

Maghroharpes cf.2 *laatchanensis* NHMUK It 29310 (1 and 2) (Pl. 25A–G) is very similar to *M. laatchanensis* but has a broader genicranium, a glabella crest that is rounded and not carinate, a shallower but wider occipital furrow and an occipital ring that is higher than glabella anterior to S0, rather than lower. Also, *M.* cf. *laatchanensis* has a shallower alar furrow; a genal roll that is less strongly sloping, anteriorly and laterally; no caeca on the genal roll or the brim; and internal rims that are subparallel in dorsal view, rather than curving adaxially.

Specimen NHMUK It 29311 of *M.* cf. 1 *laatchanensis* (Pl. 22A–E) differs from *M. laatchanensis* in having: a broader (sag.) brim and genicranium (tr.); a broader glabella with a more rounded crest; a lower brim width ratio; shorter prolongations; narrow preglabellar field; and a row of seven tubercles across (tr.) occipital ring behind occipital node. There are no other tubercles on the ring.

Maghroharpes forteyi n. sp.

Plate 29A–D, K–N

Diagnosis. Cephalon nearly ovoid; genicranium moderately vaulted; genal roll without caeca and sloping gently anteriorly and laterally. Glabella narrow, very strongly vaulted, inset and with fine tubercles and pitting. Axial furrows deep and straight; preglabellar furrows bowed upwards in anterior view; and preaxial furrows forming circular depressions across inner margin of fringe. Occipital ring higher than glabella anterior to S0. Genal area very narrow, and genal ridges present. Eye tubercles tall, with three lenses and fine tubercles and pits on dorsal surface. Brim width ratio high, at 0.87.

Etymology. For Richard Fortey, without whose advice and support this paper would not have been written.

Material and occurrence. Holotype: NHMUK It 29288, Pl. 29A–D, from a horizon at or near the "Couche Rouge" horizon at the top of the Pragian, Ihandar Formation, Azmamar, Oued el Atchane, Jbel Oufatene (Fig. 2B, Map 8, site 16), dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29289, Pl. 29K–N, from horizon close to the top of the Pragian, Ihandar Formation, Jbel Otfal (Fig. 2B, Map 9, site 7), dorsal exoskeleton of a partial cephalon.

Other material: *Maghroharpes* cf. *forteyi,* NHMUK It 29284, Pl. 31F–K, from type horizon and location (Fig. 2B, Map 8, site 20), dorsal exoskeleton of cephalon only.

The material from both the above localities was found in small coral and stromatoporoid colonies with a lateral exposure of around 4 metres.

Description. Cephalon ovoid, widest at anterior of alae; genicranium narrow, width (tr.) 1.3 times length (sag.), widest at posterior border. Glabella broad, width (tr.) 2/3 length (sag.) of glabella anterior to S0, and with rounded crest and flanks and fine tubercles and pits. S1 sloping posteriorly, not curving anteriorly around top of muscle attachment area. L1 inflated. Axial furrows straight, crossing junction of L1 and alae, and weakly converging anteriorly. Preglabellar furrow clearly defined and bowed upwards in anterior view. Occipital furrow deep, narrower (sag.) than posterior border (exsag.) and medially straight in dorsal view. Occipital ring not medially broadened, with fine tubercles and, in lateral view, higher than glabella anterior to S0. Occipital node small and located on swelling on anterior slope of occipital ring. Alae anterolaterally directed and small (tr.), 33% of length (sag.) of glabella anterior to S0 and moderately wide (tr.), being 0.83 of length (exsag.) at junction with axial furrow. Alar furrow deep and with alar depression. Posterior border moderately short (tr.), 35% of width (tr.) of occipital ring. Preglabellar field narrow (sag.), ≈ 13% of width (tr.).

Genal area narrow (tr.), width ≈50% of length (exsag.), and with fine tubercles and pits. Eye lobes large (exsag.), over 35% of width (tr.) of glabella at S0, strongly inflated and located at internal margin of fringe. Each lobe with 3 eye lenses, anterior and posterior oval in shape and of equal size and the third, much smaller, subcircular lens located high up between the two larger lenses. Eye ridge not well defined, genal ridge reaching posterolaterally to prolongation. Inner margin of fringe convex across anterior of genal area and marked by bigger perforations across anterior boss. Anterior boss barely inflated and reaching down to weak girder kink. Genal roll sloping anteriorly at ≈ 45^0, laterally at ≈ 55^0. In lateral view, internal fringe strongly narrowing posterolaterally (by ≈35%). Perforations on genal roll smaller than on brim and all approximately same size, except for row of larger perforations next to girder. Caeca present on genal roll.

Brim concave, barely sloping and with width (sag.) 29% of cephalic length (sag.). Brim perforations moderately fine, with standardised diameter of ≈ 145 μm and larger perforations around distal and proximal edges. Caeca reaching onto brim, and brim width ratio ≈0.87. External rim stout (width (sag.) > 10% of brim width (sag.)), and without sculpture on dorsal surface. Marginal band near vertical, concave and with ridges around top and bottom and scattered tubercles in between. Prolongation length (exsag.) 80% of cephalic length (sag.). Internal and external rims curving adaxially, and profile of internal rim is concave in lateral view. Genal spine short (exsag.), following curve of external rim. Tubercles on dorsal surface of internal rim and row of large perforations below.

Remarks. *Maghroharpes forteyi* has an alar depression but otherwise complies with all the diagnostic characters of its genus shown in Table 5b. *Maghroharpes forteyi* differs from its sister species *M. rouvillei* in having: a cephalon that is widest at anterior edge of alae not at the eye lobes; a glabella which is longer, narrower and pitted; a furrow at S1 which does not curve around the top of the muscle attachment area; narrower (exsag.) alae, which do not reach as far across the genal area and are not as inflated as those of *M. rouvillei*; an alar depression (not present on *M. rouvillei*); eye lobes that are more inflated and larger (exsag.) in relation to width (tr.) of glabella anterior to S0; a genal roll that slopes laterally more gently, at around 55^0 as opposed to 62^0 in *M. rouvillei*; a wider (sag.)girder with a much more pronounced girder kink; a brim that is concave, rather than having a straight profile, and slopes at around 5^0 rather than at over 30^0, with a brim width ratio of around 0.87, compared to 0.61 in *M. rouvillei*.

Only photographs of partial cephala o*f M. rouvillei* were available for comparison. *M. forteyi* is also similar to *M. azmamarensis* and the holotypes of the two species were found in the same small coral colony. *Maghroharpes forteyi* differs from *M. azmamarensis* in having: a much narrower and more vaulted glabella; axial furrows which are straight, converging weakly anteriorly, whereas the axial furrows of *M. azmamarensis* are convex and more strongly convergent; a narrower preglabellar field; the occipital ring higher than the glabella anterior to S0, rather than being the same height; its alae anterolaterally not laterally directed*;* more inflated eye lobes; a much narrower genal area, with tubercles and more pronounced perforations; caeca that just reach onto the brim of *M. forteyi* and

not right across it as they do on the brim of *M. azmamarensis;* a brim width ratio of 0.87, 10% higher than that of *M. azmamarensis;* and the external rim without granulation on its dorsal surface.

Specimen NHMUK It 29284 of *M.* cf. *forteyi* (Pl. 31 F–K) is very similar but differs in having shorter (exsag.) prolongations, and alae that are slightly wider (tr.) and laterally directed.

Genus *Pinnuloharpes* n. gen.

Type species. *P. segaouii* n. sp.

El Otfal formation, Eifelian, from Tarhroat, the Anti-Atlas, Morocco

Diagnosis. Cephalon ovoid, glabella joined to anterior boss, L1 not inflated, occipital furrow shallow and occipital ring not medially broadened. Alar furrows very shallow or effaced; eye lobes set away from inner margin of fringe and with two lenses each, anterior being largest. Course of inner margin of fringe across anterior of genal area concave. Marginal band profile straight and internal rim meeting external rim before joining at end of prolongation. Genal spines long.

Etymology. From the Latin word "pinnula", a little wing, feather or fin, referring to the small alae of the genus.

Discussion. The genus is closely related to *Stoloharpes* n. gen. and is comprised of two sister groups and two separate species. One group comes from Eifelian horizons close to Jorf (Figure 3 Map 6) and neighbouring Timerzite (Figure 5 Map 10) and the other has one species from the Eifelian of Jorf, the rest coming from the upper Emsian horizons of Hamar Laghdad and Ksar Lbour (Figure 5 Map 11 and Figure 3 Map 3 respectively).

Species of *Pinnuloharpes* differ from species of *Stoloharpes* in having an ovoid rather than pyriform cephalon; a broader (tr.) genicranium that is widest at the posterior border rather than anterior to alae; an occipital furrow which is straight in dorsal view and not medially bowed posteriorly; an inner fringe margin which is concave across the anterior of genal areas and not straight or convex; a genal roll that slopes more steeply anteriorly; a brim that is not convex; a marginal band that is near vertical and does not slope down under the cephalon; and, in lateral view, an external rim that meets internal rim before joining at the end of the prolongation. In the case of *Stoloharpes* species, the two rims meet and join at the end of the prolongation.

All species included in the study are shown in Figs 9, 10e. *P. fornicates* (Novak, 1890) and *P. pygmeaus* Lütke, 1965, which not in the study, are assigned pro tem from *Harpes* to *Pinnuloharpes*. The range of *Pinnuloharpes* is Upper Emsian to upper Eifelian.

Pinnuloharpes segaouii n. sp.

Plate 35A–P

Diagnosis. Genicranium wide, length (sag.) 1/3 width (tr.). Glabella with tectiform flanks, rounded crest and joined to anterior boss. Occipital ring length (sag.) same as posterior border length (exsag.); posterior border wide (tr.), half width of occipital ring (tr.). Alae subtriangular and genal roll sloping gently anteriorly. Brim width ratio just under 0.80; brim gently sloping anteriorly, steepening laterally to over 60^0 on prolongations. Perforations on brim moderately fine and internal rims are subparallel.

Etymology. For Hmad Segaoui, who assisted in field work in the Anti-Atlas**.**

Material and occurrence. Holotype: NHMUK It 29351, Pl. 35A–G, from an upper Eifelian horizon, El Otfal Formation, Tarhroat (Fig. 2B, Map 10, site 4), dorsal exoskeleton partially enrolled. Paratype: NHMUK It 29352, Pl. 35H–K, from horizon 1, Section 2 (Fig. 7), El Otfal Formation, upper Eifelian, Taboumakhloûf, Jbel Issoumour (Fig. 2B, Map 7, site 11), dorsal exoskeleton enrolled. Paratype: NHMUK It 29350, Pl. 35L–P, from the main "*Harpes*" horizon, 2 m upslope of the "*Acanthopyge*" horizon, El Otfal Formation?, Eifelian/Givetian boundary, Timerzit (Fig. 2B, Map 10, site 4), dorsal exoskeleton of incomplete cephalon.

Description. Cephalon is ovoid, widest at alae. Genicranium very broad, width (tr.) 1.40 times length (sag.). Glabella broad (width (tr.) 70% of length (sag.)), not inset and with tectiform flanks and rounded crest. No sculpture or pitting, and S1 short, sloping posteriorly. Axial furrows convex, converging weakly anteriorly. Occipital furrow shallow and medially straight in dorsal view. Occipital ring without sculpture, not medially broadened, same width

(sag.) as posterior border (exsag.) and, in lateral view, higher than glabella anterior to S0. Occipital node small and moderately inflated. Alae small (tr.) and subtriangular in shape. Alar furrows shallow and no alar depression. Posterior border wide (tr.), 55% of occipital ring width (tr.). No preglabellar field. Genal area very broad and without caeca or tubercles. Eye lobes oval; barely inflated but large, length (exsag.) 40% of width (tr.) of glabella at S1; and located away from inner margin of fringe. Each lobe has two lenses of equal size. No genal ridge, and eye ridge not well defined. Genal roll sloping gently anteriorly, moderately steeply laterally. Perforations on genal roll same size as those on brim, except for bigger perforations at inner margin of fringe as it crosses anterior boss. No row of larger perforations above girder. In lateral view, inner fringe narrowing very strongly posterolaterally. Brim straight, sloping slightly and moderately wide (sag.), 34% of cephalic length (sag.). Brim width ratio 0.77. Brim perforations moderately fine, with a diameter of just over 100 μm. Exterior rim stout and without sculpture on dorsal surface. Marginal band near vertical, straight and with no ridges or tubercles. Length of prolongations (exsag.) just under 90% of cephalic length (sag.). Internal rims subparallel in dorsal view and lack tubercles on their dorsal surfaces. Genal spines long, over 10% of length of prolongations and following curve of external rim. Extension to girder meeting internal rim about 1/3 of way down prolongation. Whole brim steepens to less than vertical on prolongation.

Thorax with at least 22 segments. Axis not strongly tapering, width (tr.) of last axial ring being 53% of first. Axial rings without tubercles or pits. Thorax widening posteriorly to 5th segment, thereafter width (tr.) of pleurae reducing posteriorly, particularly towards distal end of thorax. Pleural furrows narrow, almost effaced. Outer portion set at an angle to inner portion, slanting posteriorly before curving anteriorly as it turns down. Distal ends rounded (Pl. 35E).

Hypostome and pygidium unknown.

Remarks. *Pinnuloharpes segaouii* is similar to *P. torquis* but differs in having: a cephalon that is widest at the alae and not at the midpoint between the alae and the eye lobes; a genicranium that is 15% wider; a furrow at S1 that curves around the top of the muscle insertion area and a very shallow alar furrow, while in *P. torquis* the S1 furrow is a shallow depression in the axial furrow and the alar furrow is effaced; a broader genal area; eye lobes that are more oval than reniform; an ill-defined eye ridge, which is absent in *P. torquis*; a row of larger perforations at the inner margin of the fringe where it crosses the anterior of the boss; perforations on the genal roll that are the same size as those on the brim, whereas those of *P. torquis* are smaller; a much narrower girder without the central row of large perforations, but with a row of perforations above it that are larger than those on the genal roll immediately above; a wide (sag.) brim, 33% of cephalic length (sag.), and a brim width ratio of 0.76, versus 26% and 0.86, respectively in *P. torquis;* no caeca on the brim (very light caeca on brim of *P*. cf. *torqui*s); much shorter (exsag.) prolongations in relation to cephalic length (sag.), which are less strongly tapered in lateral view; internal rims subparallel in dorsal view, rather than curving adaxially, and straight not concave in lateral view. Girder extension meets internal rim 1/3 way down the prolongation, not 1/4 as in *P. torquis*.

***Pinnuloharpes apteros* n. sp.**

Plates 38J–O, 39A–M

Diagnosis. Glabella strongly vaulted and subcylindrical, tapering anteriorly (axial furrows 15^0 to axis). Preglabellar furrow very shallow, glabella joining with narrow, moderately inflated anterior boss that does not continue down to girder. Alar furrow very shallow and often effaced. Eye lobes slightly inflated, long (exsag.) and reniform. Brim straight, gently sloping and steepening moderately strongly on prolongations. Brim width ratio between 0.7 and 0.8. Perforations over 150 μm on standardised brim. Marginal band with three lateral ridges.

Etymology. Greek for wingless, referring to absence of alae.

Material and occurrence. Holotype: NHMUK It 29358, Pl. 38J–O, from an upper Eifelian horizon, Tamgoute Bulgan (Fig. 2B, Map 6, site 18), dorsal exoskeleton. Paratype: NHMUK It 29356, Pl. 39A–D, from an upper Eifelian horizon, Ksar Hannabou (Fig. 2B, Map 6, site 8), dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29359, Pl. 39E–K, from type locality and horizon (Fig. 2B, Map 6, site 19), dorsal exoskeleton with thorax and pygidium disarticulated. Paratype: NHMUK It 29357, Pl. 39L–M, from "*Harpes* Couche", upper Eifelian, Ksar Hannabou (Fig. 2B, Map 6, site 15), dorsal exoskeleton of a partial cephalon.

Other material: *Pinnuloharpes* aff. *apteros*: NHMUK It 29379, Pl. 38F –I, from an outcrop 3.8 km west of Ksar Hannabou and 8.3 km S.S.W. of El Jorf, Eifelian (Fig. 2B, Map 6, site 6), a dorsal exoskeleton of a cephalon.

Description. Cephalon ovoid, widest at mid-point between eye lobes and alae. Genicranium narrow, with length (sag.) 80% of width (tr.). Glabella not inset, narrow, width being just over 60% of length (sag.) of glabella anterior to S0; crest rounded; flanks tectiform; some fine granulation on dorsal surfaces but no pitting; S1 effaced. Axial furrows are convex and converge strongly anteriorly, at an angle to axis of just over 15°. Preglabellar furrow indistinct but straight in anterior view. No preglabellar field. Occipital furrow deep and medially straight, and occipital ring lacks sculptural tubercles. In lateral view, height of occipital ring same as height of glabella anterior to S0. Width (sag.) of both occipital furrow and occipital ring greater than width of posterior border (exsag.). Occipital node small located on anterior edge of occipital ring. Alar furrow effaced and no alar depression. Posterior border moderately short (tr.), being 35% of occipital ring width (tr.).

Genal area moderately broad with no caeca or pitting but some granulation. Eyes large (exsag.) but barely inflated, reniform and set away from inner margin of fringe. Each eye lobe has two lenses. No genal ridge, and eye ridge ill-defined. Course of inner margin of fringe across anterior of genal areas straight. No bigger perforations across anterior boss. Boss barely inflated, not reaching girder but joined to glabella. No girder kink. Genal roll sloping gently anteriorly, moderately steeply laterally. Perforations on genal roll smaller than on brim and becoming progressively smaller away from girder. No larger perforations across boss at inner margin of fringe, and genal roll caeca free. Girder moderately narrow (sag.) and with no kink. Brim straight; sloping (sag.) at just under 15^0; narrow (sag.) with width (sag.) being 27% of cephalic length (sag.). Standardised brim width ratio just under 0.80. Standardised brim perforation diameter 155μm–180μm, and light caeca across brim. Exterior rim stout with granulation on dorsal surface. Marginal band near vertical, straight and with three ridges but no tubercles. Prolongations long (exsag.), being 90% of cephalic length (sag.). In dorsal view, external and internal rims curve adaxially. In lateral view, internal rim straight, sloping down to end of prolongations where it meets and joins with external rim. Genal spine short. Dorsal surface of internal ring tubercle-free. Extension of girder meets internal rim about 1/3 way down prolongation. Brim steepens to near vertical on prolongations.

Thorax with 24 segments. Axis tapers posteriorly, so that width (tr.) of last axial ring just over 30% of first. Thorax widens posteriorly to 5^{th} segment, then tapers posteriorly so that inner portion of pleura on last segment 35% of longest pleura. Pleural furrow is narrow and almost effaced. No pitting on pleurae, and on last 11 thoracic segments, outer portion of pleurae slightly offset posteriorly to inner portion. Outer portion turns down, curves anteriorly and distal ends pointed. Outer portion less than vertical anteriorly and becoming less steep on each segment posteriorly from 12^{th} segment. Pygidium has 3 axial rings and lacks border and tubercles.

A disarticulated pygidium is shown in Pl. 38O, with three axial rings and terminal piece. Interpleural furrows shallow and reach to distal edge of pygidium. Pleural furrows very shallow on first and second pleural bands. Terminal piece short (sag.), wide (tr.) and rounded.

Remarks. *Pinnuloharpes apteros* has an inner margin of the fringe which is straight across the anterior of the genal areas, not concave. Otherwise, *P. apteros* has the diagnostic characters of *Pinnuloharpes* s.s. shown in Table 5c.

Pinnuloharpes apteros is unusual amongst harpetids in having alar furrows that are largely effaced. It is otherwise similar to material presented by Feist in his doctoral thesis (1977, pl. XII, fig. 10–11), in having a relatively short (sag.), strongly vaulted cephalon, no girder kink and a brim covered by fine caeca. This material, however, has a preglabellar furrow and a short preglabellar field. It also has an eye ridge and a rounded dorsal surface to the eye lobe. The dorsal surface of *P. apteros'*s eye lobe is straight and sloping adaxially.

P. apteros is similar to *P. segaouii* but has: a cephalon that is widest (tr.) between eyes and alae rather than at the alae; a narrower genicranium; no furrow at S1 whereas P. segaouii has a shallow S1 furrow; a broader occipital ring; a more robust but narrower (tr.) posterior border; alar furrows that are effaced whereas those of *P. segaouii* are just discernible; a genal area that is not as broad; eyes lobes that are closer to inner margin of the fringe and no eye ridge; an inner margin of the fringe that has a course across the anterior of the genal area which is straight not concave and across the anterior of the boss that is not marked by a row of large perforations; an anterior boss that does not reach down to the girder; preaxial furrows that converge, perforations on the genal roll that are smaller than those on the brim, not the same size, and which become smaller away from girder; a narrower brim with larger perforations and light caeca across the whole surface; marginal band with top, bottom and medial ridges rather than just a ridge around the top, and internal rims that in dorsal view curve adaxially rather than being sub parallel and in lateral view meet the external rims at the end of the prolongations and not before, as in the case of *P. segaouii*. Also, *P. apteros* has a thorax that tapers more posteriorly, and the distal ends of pleura terminate in a point are not rounded.

P. aff. *apertos* (Pl. 38F–I) differs from *P. apteros* by having: axial furrows that do not converge anteriorly so strongly; an anterior boss that reaches down to the girder; a genal roll that slopes less steeply anteriorly and laterally; a slightly broader (sag.) brim that slopes more steeply, has a convex rather than straight profile and finer brim perforations; a marginal band that is without ridges; much longer prolongations with the internal rims curving adaxially and then abaxially, and external rims straight slanting adaxially rather than curving adaxially; no genal spine and an extension of the girder that meets the internal rim just over 1/5 of the way down compared to 1/3 in the case of *P. apteros*.

***Pinnuloharpes chaperon* n. sp.**
Plate 41A–J

Diagnosis. Cephalon pyriform, strongly vaulted and widest at eye lobes. Glabella inset and joined to anterior boss. S1 not rising out of axial furrow. Genal areas are strongly convex (sag. and exsag.) and genal roll is steeply sloping, over 60^0 anteriorly and over 70^0 laterally. Brim wide (sag.), 35% of cephalic length (sag.), barely sloping and brim width ratio very low, at 0.52. Perforations on brim very fine (< 80 μm) and even finer on genal roll. Brim steepens quickly to near vertical on prolongations. In dorsal view, genal spine not following curve of exterior rim and curving upwards in lateral view.

Etymology. Similar to the shape of the chaperon hat worn in the Middle Ages.

Material and occurrence. Holotype: NHMUK It 29332, Pl. 41G–J, from "*Basseiarges* Couche", Eifelian, Fezna (Fig. 2B, Map 6, site 4), dorsal exoskeleton of cephalon only. Paratypes: NHMUK It 29331 (1 and 2), Pl. 41A–F, from type locality and type horizon (Fig. 2B, Map 6, site 2), NHMUK It 29331 (1), dorsal exoskeleton of cephalon only, and NHMUK It 29331 (2), ventral exoskeleton of cephalon only.

Other material: *Pinnuloharpes* cf. *chaperon*: NHMUK It 29330, Pl. 41K–N, from *P. chaperon* type locality and type horizon (Fig. 2B, Map 6, site 21), dorsal exoskeleton of cephalon only.

Description. Cephalon widest at eye lobes and pyriform in shape. Genicranium narrow, width (tr.) 1.25 times length (sag.), strongly vaulted and widest at alae. Glabella inset, narrow, with rounded crest and tectiform flanks, no sculpture or pitting. S1 barely rising out of axial furrow. Axial furrows convex and weakly convergent anteriorly. Preglabellar furrow indistinct. Occipital furrow is broad, shallow and medially straight in dorsal view. Occipital ring same width (sag.) as posterior border (exsag.), and in lateral view, sloping posteriorly and same height as glabella anterior to S0. No sculpture or pitting on dorsal surface. Occipital node poorly inflated. Alae large (tr.), over 40% of width (tr.) of glabella at S0, just broader (tr.) than long (exsag.) and anterolaterally directed. Alar furrow shallow, well-defined. Posterior border moderately wide (tr.), and no preglabellar field.

Genal area moderately broad and without caeca, pits or tubercles. Eye lobes oval, large (exsag.), barely inflated and located away from inner margin of fringe. Each eye lobe with two lozenge-shaped eye lenses (Pl. 41D). No genal ridge, and eye ridge poorly defined. Inner margin of fringe not marked by bigger perforations as it crosses anterior boss. Anterior boss inflated, reaching down to weak girder kink and joined to glabella. Preaxial furrows converge. Genal roll steeply sloping 62^0 anteriorly, and over 72^0 laterally, and in lateral view, narrowing strongly posteriorly. Perforations on genal roll are smaller than those on brim and no row of larger perforations above girder. Genal roll without caeca; girder moderately wide and brim wide (sag.), barely sloping and concave anteriorly, straight laterally. Brim width ratio low, at around 0.50. Brim perforations very fine, around 70μm, and no caeca on brim. Rim stout, dorsal surface not tilted outwards and without sculpture. Marginal band near vertical, straight, with tubercles but without ridges. Prolongations moderately short (exsag.), at around 80% of cephalic length (sag.). In lateral view, prolongations strongly tapered and internal rims concave. Internal rims subparallel in dorsal view, external rims curve adaxially posteriorly. Internal and external rims separated by a row of perforations from where they meet to end of prolongation, where they join. Genal spine long and set at an angle to curve of external rim. Tubercles on dorsal surface of internal rim, and extension of girder meeting internal rim 1/3 way down prolongation. Brims quickly steepen to near vertical on prolongations.

Thorax, pygidium and hypostome unknown.

Remarks. *Pinnuloharpes chaperon* has cephalon that has a pyriform profile, a genicranium that is broadest at the alae rather than the posterior border and the course of the inner margin of the fringe cannot be determined from the material presented here, otherwise it has the other 8 diagnostic characters of the genus shown in Table 5c.

Pinnuloharpes chaperon is quite similar to *P. hastatus* (Lütke 1965) but differs in having: a cephalon that is widest opposite eye lobes, not mid-point between the eye lobes and alae, and is more pyriform in shape; its genicranium widest at the alae and not the posterior border; the glabella inset and joined with the anterior boss; the axial furrows convex rather than straight; a wider occipital furrow; the occipital ring in lateral view the same height as the glabella anterior to S0, while that of *P. hastatus* is lower; a very shallow preglabellar furrow and no preglabellar field; alae with a width (tr.) 1.05 times their length (exsag.), while those of *P. hastatus* have a width of only around 0.75 times their length; a much broader (tr.) genal area, at 58% of its length (exsag.), rather than 47% as in *P. hastatus*; a wider (sag.) brim, being 36% of cephalic length (sag.), rather than 32% in *P. hastatus*; a much lower brim width ratio (0.49 rather than 0.76); shorter (exsag.) prolongations, which have a length (exsag.) that is 81% of cephalic length (sag.), compared with 89% in *P. hastatus*; the extension of the brim on the prolongations steepening to near vertical, not just along their proximal edge.

Pinnuloharpes chaperon is different to other species of *Pinnuloharpes*, in having a pyriform cephalon and a low brim width ratio. The pyriform cephalon is similar to the cephala of *Stoloharpes* species, however, the brims of these species are sloping and convex, whereas that of *P. chaperon* is almost flat.

Pinnuloharpes cf. *chaperon* (Pl. 41K–N) differs from *P. chaperon* in that its cephalon is not pyriform and its prolongations are shorter than those of *P. chaperon*.

Pinnuloharpes hamarlaghdadensis Cronier *et al.* 2018

Plate 44A–M

Discussion. The new material figured here is similar to *P. hamarlaghdadensis* (Crônier *et al.*, 2018) which was described from 18 more or less fragmented cephala, one nominated as holotype but only five as paratypes. That material was from the same locality as that figured here. The description of this material is as full and complete as the material allows, and the author would only comment that the length (exsag.) of the prolongation of the holotype is probably around 80% of the cephalic length (sag.), not 50% as stated by Crônier *et al.* (2018, p. 257).

New Material. NHMUK It 29337, Pl. 44A–F, from a horizon containing *Morocops granulops*? (Chatterton *et al.*, 2006), at the base of the "Red Cliff" (Klug *et al.*, 2002 & 2009), upper Emsian, Hamar Laghdad, Errachidia southeastern Morocco (Fig. 2B, Map 11, site 1), dorsal exoskeleton with pygidium enrolled. NHMUK It 29338, Pl. 44G–J, from type horizon and location (Fig. 2B, Map 11, site 2), dorsal exoskeleton of cephalon and the first two thoracic segments. NHMUK it 29339, Pl. 44K–M, from type horizon and location (Fig. 2B, Map 11, site 3), crushed dorsal exoskeleton of cephalon and disarticulated thorax. NHMUK 29336 from an Emsian horizon at Timerzite (Fig. 2B Map 10, site 3), dorsal exoskeleton and partial thorax.

Description. Exoskeletons figured here are similar those of *P. hamarlaghdadensis* but differ in having: glabella that slopes less steeply anteriorly; shallower furrow at S1; less inflated basal lobe (L1); 20% wider (tr.) preglabellar field; less steeply-sloping genal roll, anteriorly and laterally; perforations on genal roll which become progressively smaller for short distance away from girder; and finer external rim, being just under 10% of brim width (sag.), as opposed to around 18% of brim width (sag.) in the case of holotype.

The new specimens are more complete than fragmentary cephala of holotype and paratypes of *P. hamarlaghdadensis* and cannot be described on a comparative basis alone. The author therefore expands the description of material figured herein, as set out below.

Cephalon ovoid, widest (tr.) at mid-point between eye lobes and alae. S1 very shallow, becoming effaced halfway up glabella. Occipital node weakly inflated, not prominent, appearing as circular swelling stretching from occipital furrow to close to posterior edge of occipital ring. It has a CMO with four tiny, symmetrically-placed perforations (Pl. 44E) similar to those noted in *P.* cf. *haustrum* below. Preglabellar furrow shallow but clear. Alae hardly conspicuous, anterolaterally directed to reach about 45% of way across genal area.

Genal areas broad (tr.) and slightly convex. Eye lobe reniform, large (exsag.), ≈ 38 % of width (tr.) of glabella at S1; barely inflated; narrow (width 2/3 of length (exsag.)), and located at a level just behind preglabellar furrow and halfway between inner margin of fringe and axial furrow at start of anterolateral slope. Eye lobes weakly-inflated with two eye lenses each; anterior lens largest in shape of elongated rectangle with rounded corners; posterior lens oval and much smaller (Pl. 44F). Preglabellar field broad (sag.), width (tr.) being over 40% of length (sag.). Anterior boss narrow, width (tr.) around 60% of length (exsag.), and gently convex, reaching from preglabellar furrow down to girder kink. Genal roll inclined moderately anteriorly (≈43^0), much more steeply laterally (≈70^0);

narrow in anterior view; and reaching about two-thirds of way up from girder to eye lobe. Posterolaterally, genal roll steepens and narrows by about 40%. Row of large perforations above girder, above which size of perforation quickly decreases over bottom third of genal roll to become a little finer than those on brim. Short row of larger perforations at inner margin of fringe, where it crosses anterior boss. Girder has Σ-shaped kink. Brim straight in profile, gently sloping (≈10^0) downwards and outwards, and has width (sag.) equal to about 30% of cephalic length (sag.). Brim width ratio around 0.70. Perforations on standardised brim number 20 per mm^2 and are moderately fine (just over 100 μm). Marginal band near vertical, straight and without tubercles. Brim on prolongations quickly steepens posteriorly, until reaching near vertical two-thirds of way back. Girder extends on to prolongations, curving gently upwards to meet internal rim about one third of way down its length (exsag.). In dorsal view, external rims on prolongations are straight, slanting obliquely posteromedially. Internal rims subparallel (exsag.) and in lateral view, nearly straight, sloping posteriorly gently downwards, before flattening out to meet external rim at an angle of around 15°, and running for a short distance to end of prolongation, separated by a row of large perforations. Genal spines are long, following curve of external rim.

Thorax has 22 or more segments. Axis narrow and tapering posteriorly, so that width (tr.) of last axial ring just under 40% of that of first. At 7th segment, where thorax is broadest, axis comprises 25% of thoracic width. Postannulus narrows (sag.) medially and pleurae are flat (tr.) and lengthen (tr.) slightly posteriorly until the ninth segment, where they start to shorten (tr.) posteriorly. Pleural furrows are broad (tr.), very shallow and extend onto outer portions of pleurae, which are short and have rounded distal ends (Pl. 44M).

The pygidium and hypostome are unknown.

Remarks. There is a significant size difference between the partial cephala described by Crônier *et al.* (2018) and those figured here. For instance, NHMUK It 29337 has a cephalic length (sag.) that is over 2.5 times that of the *P. hamarlaghdadensis* holotype. This suggests that it is likely the two sets of material came from different horizons. It is less likely that they came from the same horizon as the two groupings would have been in close proximity to each other, the base of the "Red Cliff" measures about 40metres. Nevertheless, morphological differences could be ontogenetic especially as the jackknife support at the node between the holotype and the new material is 69%. The author therefore considers that the erection of a new species is not justified.

There is little literature on the ontogeny of Devonian harpetids. McNamara *et al*. (2009, pp. 16–19) described the ontogeny of *Eskoharpes palanasus* and *E. wandjina* from the Frasnian of the Canning Basin, Western Australia. *Eskoharpes palanasus* showed much greater ontogenetic development than *E. wandjina* and "with increasing size in later *meraspid*s and early holaspids (the size at which transition occurs not being known) the following trends are continued: brim widens; external rim becomes relatively narrower; glabella becomes less vaulted and less steeply inclined anteriorly and wider; genal areas less swollen; genal roll becomes less steeply inclined; axial and posterior furrows become shallower; alar furrows become evident." (McNamara *et* al. 2009, p. 18, para 3). If *Pinnuloharpes* had a similar ontogeny to that of *Eskoharpes*, it could be expected that the material described by Crônier *et al.* (holaspid fragments) would reflect many, if not all, the *meraspid* growth changes observed by McNamara and colleagues. It may be, however, that the narrowing of the external rim and the change in the anterior slope of the glabella and genal roll continued during early holaspid development. This would explain many of the morphological differences between the two sets of material.

Pinnuloharpes hamarlaghdadensis complies with the diagnostics shown in Table 5c, except that it has a medially broadened occipital ring, L1 is a little inflated and the genal roll is without caeca. The diagnostic characters 9 and 10 in Table 5c, cannot be confirmed in respect of the holotype and paratypes but the new material would suggest that the species is compliant with these 2 characters.

NHMUK 29336 from an Emsian horizon at Timerzite which is a poorly preserved specimen is designated as *Pinnuloharpes* cf. *hamarlaghdadensis*.

***Pinnuloharpes hannabouensis* n. sp.**

Plate 40A–N

Diagnosis. Cephalon inverted U in shape, and genicranium strongly vaulted. Occipital ring not medially broadened and in lateral view, nearly upright and lower than glabella anterior to S0. Course of inner fringe across anterior boss not marked by row of large perforations. Anterior boss barely inflated. Brim very narrow, 25% of cephalic length

(sag.), and nearly flat. Marginal band with three ridges. Internal and external rims meeting and joining at end of prolongations. Anterior of thorax not broadening posteriorly and pleural furrows effaced.

Etymology. Named after the village of Ksar Hannabou, close to the type locality.

Material and occurrence. Holotype: NHMUK It 29333, Pl. 40E–I, from horizon 5 m down slope of "*Radiaspis* Couche", Eifelian/Givetian boundary, in an outcrop 3.8 km West of Ksar Hannabou and 8.3 km S.S.W. of El Jorf. (Fig. 2B, Map 6, site 11), dorsal exoskeleton with pygidium missing. Paratype: NHMUK It 29334, Pl. 40A–D, from type horizon and type locality (Fig. 2B, Map 6, site 12), dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29335, Pl. 40J–N, from type horizon and type locality (Fig. 2B, Map 6, site 13), dorsal exoskeleton with pygidium incomplete.

Description. Cephalon inverted U in shape, widest at mid-point between eye lobes and alae. Genicranium broad, widest at posterior border. Glabella anterior to S0 narrow, width (tr.) 65% of length (sag.), and with rounded crest and flanks. Dorsal surface without sculpture. S1 sloping backwards, before curving forwards near crest, and L1 very slightly inflated in some individuals. Axial furrows convex, converging gently anteriorly. Preglabellar furrow distinct and bowed upwards in anterior view. Occipital furrow broad, deep, and medially straight. Occipital ring not medially broadened, same width (tr.) as posterior border and in lateral view, lower than glabella anterior to S0. Alae small (tr.), nearly as wide (tr.) as long (exsag.), and laterally directed. Alar furrow shallow but well-defined. Border moderately short (tr.), just under 40% of occipital ring width (tr.). Narrow preglabellar field, and genal area fairly broad with width (tr.) just under 60% of length (exsag.).

Genal area without sculpture or pits. Eye lobes large (exsag.) (50% of width of glabella at S0), inflated, reniform, without tubercles on dorsal surface and located away from inner margin of fringe. Each eye lobe with two eye lenses of equal size. No eye ridges or genal ridges. Course of inner margin of fringe across anterior boss not marked by larger perforations. Anterior boss not joined to glabella and reaches down to moderately narrow girder, which has weak kink. Genal roll sloping moderately steeply anteriorly ($\approx 57^0$), and steeply ($\approx 68^0$) laterally. In lateral view, fringe on genal roll narrowing strongly posteriorly. Perforations on genal roll same size as those on brim, and no row of larger perforations above girder.

Brim straight, barely sloping, narrow, with its width (sag.) being 26% of cephalic length (sag.). Brim width ratio around 0.80. Brim perforations moderately fine, with a diameter of just under 150 μm. Light caeca, reaching across brim. Exterior rim is stout and without sculpture on dorsal surface. Marginal band straight, with ridge at top and bottom but no tubercles. Length (exsag.) of prolongation just over 80% of cephalic length (sag.). In dorsal view, internal rims are subparallel, external rims straight, slanting adaxially. In lateral profile, internal rims straight and meeting external rim at end of prolongations. Dorsal surface of internal rim smooth. Genal spine long, following curve of external rim. Extension of girder meeting internal rim one third of way down. Brim steepening quickly to near vertical on prolongations.

Thorax has 17 segments, axis is tapered moderately posteriorly, and axial rings are without sculpture or pitting. Thorax not strongly tapered and maintains its width (tr.) posteriorly to 5th thoracic segment. Inner portion of pleurae only start to shorten (tr.) significantly posteriorly from 9th segment. Pleural furrows effaced. Outer portion of pleurae offset slightly to inner portion, curved anteriorly and terminating in a point. Three axial rings on pygidium.

Hypostome unknown.

Remarks. *Pinnuloharpes hannabouensis* has a deep occipital furrow but otherwise complies with the other 9 diagnostic characters of the genus shown in Table 5c.

Pinnuloharpes hannabouensis differs from the type species *P. segaouii*, in having: a cephalon which is widest at mid-point between eye lobes and alae, rather than at alae; a genicranium that is 15% narrower, more vaulted and widest at alae, rather than at the posterior border; a glabella that is narrower and has convex rather than tectiform flanks; a shallow preglabellar furrow that is bowed upwards, while that of *P. segaouii* is nearly effaced; a narrow preglabellar field, which is absent in *P. segaouii*; a deep occipital furrow; the occipital ring in lateral view lower than the glabella anterior to S0 and more upright than that of *P. segaouii*; alae which are parabolic in shape rather than subtriangular; a posterior border that is 30% shorter (tr.) than that of *P. segaouii*; a genal area that is 20% narrower (tr.); eye lobes which are more inflated and reniform rather than oval in dorsal view; no eye ridges; the anterior boss less inflated, and there is no row of larger perforations across the top of the boss to mark the inner margin of the fringe, as there is in the case of *P. segaouii*; the genal roll sloping around 20% more steeply anteriorly and laterally; the girder is narrower; the fringe, in lateral view, narrows less posterolaterally; the brim less steeply sloping, with a width (sag.) nearly 40% narrower than that of *P. segaouii,* light caeca reaching across it, and a marginal band that

has three ridges rather than none; slightly shorter prolongations, with the extension of the brim on the prolongations steepening more strongly; the external rims in dorsal view slanting rather than curving adaxially and in lateral view, the internal rims meeting at end of prolongations rather than before; the thoracic pleural furrows erased; and the outer portion of pleurae terminating in a point rather than being rounded, as they are in *P. segaouii*.

***Pinnuloharpes haustrum* n. sp.**
Plates 42A–M, 43A–B

Diagnosis. Genicranium strongly vaulted and narrow, width (tr.) 1.3 times length (sag.); preglabellar field wide, length (sag.) 16% of width (tr.); and preglabellar furrow bowed up in anterior view. Alae wide (tr.), 45% of glabella width (tr.) at S0, slightly wider than width (exsag.) of ala at axial furrow. Alar depression and faint genal ridge present. Eye lobes oval, inflated and anterior and posterior eye lenses of equal size. Genal roll sloping steeply anteriorly at ≈60^0 and laterally at ≈70^0. Brim narrow (sag.), 29% of cephalic length, and brim width ratio low, at 0.54. Marginal band near vertical anteriorly, increasingly sloping down under cephalon posterolaterally. Tubercles on occipital ring, posterior border, internal rims and marginal band, and fine pitting on glabella, genal areas, axial rings and pleurae.

Etymology. Latin for a scoop: inverted the exoskeleton of cephalon is scoop-like.

Material and occurrence. Holotype: NHMUK It 29341, Pl. 42A–F, from an upper Emsian horizon in an outcrop 10 km west of Ksar Lbour, (Fig. 2B, Map 3, site 3), dorsal exoskeleton with pygidium enrolled. Paratype: NHMUK It 29342, Pl. 42G–M, from type locality and horizon (Fig. 2B, Map 3, site 4), dorsal exoskeleton with pygidium enrolled. Paratype: NHMUK It 29345, Pls 42N–O, 43A–B, from upper Emsian horizon, Hamar Lahgdad (Fig. 2B, Map 11, site 13), dorsal exoskeleton with pygidium enrolled.

Other material: *Pinnuloharpes* aff. *haustrum*: NHMUK It 29347 (1 and 2), Pl. 43C–L, M–P, respectively, both from *Destombesina tafilaltensis* horizon, at base of the Upper Emsian, (Morzadec 2001), Hamar Laghdad (Fig. 2B, Map 11, site 7). NHMUK It 29347 (1), dorsal exoskeleton enrolled; NHMUK 29347 (2), ventral exoskeleton.

Description. Cephalon ovoid in shape, widest just posterior to eye lobes. Genicranium narrow, widest at alae. Glabella inset, flanks tectiform. S1 very shallow and L1 not inflated. Axial furrow convex, converging weakly anteriorly. Preglabellar furrow bowed upwards in anterior view. Occipital furrow deep, medially straight in dorsal view, and very broad (sag.), broader than posterior border (exsag.). Occipital ring same width (sag.) as posterior border (exsag.) and, in lateral view, same height as glabella anterior to S0. Tubercles present on dorsal surface. Alae laterally directed, broad, width (tr.) same as length (exsag.) at axial furrow. Alar furrow shallow, well defined and alar depression present. Preglabella furrow wide; genal area with fine pits. Eye lobes oval, large (exsag.), ≈43% of width of glabella at S1, and inflated. Genal ridge present, and narrow eye ridge well defined. Anterior boss inflated and joined to glabella. Inner margin of fringe barely concave across anterior of genal areas.

Genal roll moderately steep anteriorly (60^o) and steep laterally (70^o). In lateral view, internal fringe narrowing strongly posterolaterally. Perforations smaller than on brim, and decrease in size away from girder. Girder moderately narrow.

Brim barely sloping, concave (sag.), straight laterally and with width (sag.) of 30% of cephalic length (sag.). Brim width ratio low, at 0.57, and brim perforations moderately large, with a diameter of just below 180µm. Light caeca across brim. Rim with fine tubercles on dorsal surface and marginal band straight, vertical anteriorly, sloping under cephalon posterolaterally and with tubercles but no ridges. Brim steepens quickly on prolongations.

Length (exsag.) of prolongations 93% of cephalic length (sag.). Internal and external rims curving adaxially. Internal rim concave in lateral view. Rims meet before joining at end of prolongations. Genal spine long, following curve of exterior rim. Internal rim with tubercles on dorsal surface. Extension to girder meeting internal rim 1/3 way down prolongations.

Thorax with at least 18 segments, widens posteriorly to 5^{th} segment, and then tapers posteriorly so that width (tr.) of last segment is about 45% of 5^{th} segment. Pitting on axial rings and pleurae. Pleural furrows narrow, shallow but well defined. Outer portion of pleurae straight, slanting slightly posteriorly to inner portion, and distal ends pointed.

Remarks. The eye lenses on each eye lobe of *Pinnuloharpes haustrum* are of the same size and the occipital furrow is deep but otherwise the species complies with the diagnostic characters set out in Table 5c.

Pinnuloharpes haustrum is similar to *P. merzaneensis*, but differs in having: a cephalon that is broadest close to eye lobes, not at the midpoint between eyes and alae; a genicranium and genal area which are over 10% narrower than those of *P. merzaneensis;* a shallow but slightly more pronounced preglabellar furrow; L1 not inflated; no interalar ridges or furrows; a slightly weaker girder kink; larger brim perforations; brim width ratio around 0.52, 10% lower than that of *P. merzaneensis*; and the external rims on the prolongations curved rather than straight, as in *P. merzaneensis*.

Pinnuloharpes haustrum is quite similar to the material included on pl. XII, figures 10–11 of Feist's (1977) doctoral thesis, but it has no S1 furrow, eye ridge or caeca on the genal roll, and it has a much lower brim width ratio. Also, the inner margin of the fringe passes well away from the eye lobe, while in the case of the material described in the thesis, the inner margin of the fringe passes immediately below the eye lobe.

The ventral exoskeleton and hypostome of *P. haustrum* is unknown, but other material (NHMUK It. 29347 (1 and 2), designated as *P.* cf. *haustrum* (Pl. 43 C–P), does include a ventral exoskeleton with hypostome. This material is very similar to *P. haustrum* but differs in having: a cephalon that is widest a little further back at the midpoint between eye lobes and alae; a 5–15% wider (tr.) genicranium; a 20% wider (tr.) posterior border; a glabella that is anteriorly more rounded; a much deeper preglabellar furrow; a preaxial furrow depression; a well-defined eye ridge; an occipital node which has a CMO with four regularly-spaced perforations on dorsal surface (Pl. 43J); Laterally-directed alae are; deeper, well-defined alar furrows; a shallow interalar furrow; axial furrows effaced at junction of alae and L1; genal roll with caeca and finer perforations; the brim more steeply sloping; and in lateral view, the profile of the internal rim is straight, rather than concave as in *P. haustrum.*

The ventral exoskeleton of *P.* cf. *haustrum* (Pl. 43M) shows that the ventral surface of the rim is ridged and tuberculate (Pl. 43P), and the perforations on the ventral surface of the lower lamella (Pl. 43I) are finer than those on the dorsal surface of the upper lamella's brim (Pl. 43F). The girder, which forms a narrow brim-like structure around the inside of the genicranium, has an embayment corresponding to the girder kink. The hypostome (Pl. 43O) has a large egg-shaped anterior lobe of the middle body, with a very short (sag.) posterior lobe. The lateral border, which is narrow anteriorly, broadens very slightly two-thirds of the way back, before narrowing again. Posterior border narrow; anterior border even narrower. Shoulders broad close to the anterior of the hypostome, lateral distal edge sloping abaxially. Surfaces are tubercle-free.

The occipital node with a CMO of four very fine perforations found on *P.* cf. *haustrum* (Pl. 43J), may have been present on all harpids, but they are rarely found even in the best preserved of specimens. The only other material presented in this paper with such an occipital node is that of *P. hamarlaghdadensis* (new material) (Pl. 44E) and *Lioharpes scopulum* (Pl. 32L). McNamara (2009) (text fig. 4) described such an occipital node on *Globoharpes friendi*.

***Pinnuloharpes igaouii* n. sp.**

Plate 36A–K

Diagnosis. Cephalon is moderately vaulted, glabella strongly vaulted. Alae are inflated proximally, and alar furrows erased distally. Eye lobes pronounced. Slope of genal roll is moderate, anteriorly continuing anterior slope of glabella. Anterior boss is barely inflated. Perforations on genal roll decrease in size upwards, away from girder. Brim barely sloping; brim perforations widely spaced, decrease rapidly distally to become very fine, before becoming larger again close to rim.

Etymology. For Hssaine Igaoui, a Moroccan trilobite worker who found the holotype.

Material and occurrence. Holotype: NHMUK It 29360, Pl. 36A–H, from a coral horizon 500 m to the N.W. of Jbel Ou-Driss, Boutiskaouine Formation?, lower Emsian (Fig. 2B, Map 4, site 5), dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29361, Pl. 36 I–K, from lower Emsian coral horizon, "*Ceratocephala* Horizon", Boutiskaouine Formation?, North Jbel Ou-Driss (Fig. 2B, Map 4, site 8), dorsal and ventral exoskeleton of damaged cephalon and partial thorax. Paratype: NHMUK It 29267, Pl. 13K–O, from a lower Emsian coral horizon, 20 m below *Lioharpes ammari* horizon, Boutiskaouine Formation?, north Jbel Ou-Driss (Fig. 2B, Map 4, site 6), dorsal exoskeleton of cephalon only.

Other material: *Pinnuloharpes* aff. *igaouii*, NHMUK It 29362, Pl. 36L–O, from "*Struveaspis* Couche", Fezna, Eifelian (Fig. 2B, Map 6, site 1), partial dorsal exoskeleton of cephalon only.

Description. Cephalon ovoid, widest at eye lobes. Genicranium broad, widest at posterior border. Glabella

broad, with rounded crest, tectiform flanks and tubercles, but no pitting. S1 short, very shallow and slopes posteriorly. L1 inflated. Axial furrows slightly convex, moderately convergent anteriorly and effaced at junction of alae and L1. Preglabellar furrow indistinct, straight in anterior view. Occipital ring broader (sag.) than posterior border (exsag.); tubercles on dorsal surface; nearly vertical in lateral view and same height as glabella anterior to S0. Occipital node barely inflated most noticeable on paratype. L1 inflated. Alae small (tr.) and laterally directed, alar furrows shallow, almost effaced. Posterior border moderately wide (tr.), just over 40% of occipital ring width (tr.), and preglabellar field narrow.

Genal area moderately broad, very finely pitted and without tubercles. Eye lobes inflated; large (tr.), 35% of width (tr.) of glabella at S1; elongated oval in shape; and located close to inner margin of fringe. Each eye lobe has 2 lenses of approximately equal size. Eye ridge is poorly defined. Inner margin of fringe across anterior of genal areas convex and its course across anterior boss marked by row of large perforations. Anterior boss barely inflated and not connected to glabella. Genal roll sloping gently anteriorly and moderately steeply laterally; internal fringe does not narrow strongly posteriorly in lateral view; perforations smaller than on brim, decreasing in size away from girder over bottom third of genal roll. Girder moderately wide, and girder kink barely present.

Brim wide, 34% of cephalic length (sag.); barely sloping; concave (sag.), becoming straight laterally and steepening quickly on prolongations. Brim width ratio 0.63. Brim perforations moderately fine, decreasing in size away from girder over inner third of brim. No caeca. Dorsal surface of rim lacks sculpture. Marginal band straight and near vertical. Length (exsag.) of prolongations around 87% of cephalic length and, in lateral view, prolongations not strongly tapered, height at midpoint being 55% of height at junction with posterior border. Internal rim concave. In dorsal view, both rims curve adaxially and internal rim has tubercles on dorsal surface. Genal spine short and does not follow curve of external rim. Extension of girder on prolongations meets internal rim halfway down. Thorax with at least 20 segments; not widening anteriorly and not strongly tapered posteriorly. Pleural furrows very shallow and broad. Outer portion of pleurae at an angle to inner portion and curving anteriorly.

Hypostome (Pl. 36J) has a large egg-shaped anterior lobe of the middle body, with a very short (sag.) posterior lobe. The lateral border, which is narrow anteriorly, broadens very slightly two-thirds of the way back, before narrowing again. Posterior border narrow; anterior border even narrower. Shoulders broad close to the anterior of the hypostome, lateral distal edge sloping abaxially. Surfaces are tubercle-free, very similar to that of *P. haustrum* described above, but middle furrow not present. Pygidium not known.

Remarks. *P. igaouii* has an inflated L1, an anterior eye lens that is the same size as the posterior lens rather than being bigger and an inner margin of the fringe the course of which across the anterior of the genal areas is convex rather than concave. Otherwise *P. igaouii* has the other eight diagnostic characters of the genus shown in Table 5c.

P.igaouii is similar to *P. segaouii* but differs by having: a cephalon that is widest (tr.) at the level of the eye lobes rather at the alae; a narrower (tr.) genicranium, genal area and posterior border; tubercles on the glabella including the occipital ring, on the eye tubercles and on the internal rim; a broader (sag.) occipital ring; an LI and ala that are inflated with the axial furrow not crossing the junction of the two; a narrow preglabellar field that is absent in the case of *P. segaouii*; an inner margin of the fringe the course of which across the anterior of the genal area is convex rather than concave; eye lobes that are more inflated and have two equal sized lenses rather than two different sized lenses; an anterior boss that is not joined to glabella; perforations on the genal roll and the brim that decrease in size away from the girder; a brim that has a lower brim width ratio, is less steeply sloping and in lateral view has a profile that is slightly concave (sag.) rather than being straight. Also, *P. igaouii* has genal spines that do not follow the curve of the exterior rims and internal rims that in lateral view have a concave profile unlike the weak wave profile of those of *P. segaouii*.

P. aff. *igaouii* (Pl.36L–O) has affinities to *P. igaouii* but has: a much more strongly sloping brim, which does not steepen to the same degree on prolongations; a 20% higher brim width ratio, and an occipital ring that, in lateral view, slopes more strongly posteriorly.

The genus of *P. igaouii* has proven to be one of the hardest of the new species to determine. During the development of the cladogram (Fig. 9) *P. igaouii* has been in a paraphyletic relationship with *Pinnuloharpes* and more recently allocated to the harpid genus. Coming from a lower Emsian horizon *P. igaouii* fits into the beginning of the harpid range whereas the earliest *Pinnuloharpes* species described herein is from an upper Emsian horizon. While on the bases of information currently available *P. igaouii* is correctly allocated to *Pinnuloharpes*, it maybe that if new data is added to the cladogram *P. igaouii* may be reallocated once again to *Harpes*.

***Pinnuloharpes merzaneensis* n. sp.**
Plate 45A–L

Diagnosis. Cephalon ovoid, glabella with tectiform flanks. S1 short, sloping backwards. L1 weakly inflated and axial furrows effaced at junction of L1 and alae. Occipital furrow shallow, occipital ring pitted and in lateral view, higher than glabella anterior to S0. Genal area very broad (tr.). Anterior boss joined to glabella and preglabellar furrow effaced. Perforations becoming smaller for a short distance away from girder. Girder kink pronounced. Brim narrowing strongly posterolaterally. Marginal band with ridge top and bottom. Tubercles on dorsal surface of internal rims. Pygidium with four pleurae and tubercles on terminal piece.

Etymology. Named after Merzane, the region of the type locality.

Material and occurrence. Holotype: NHMUK It 20349, Pl. 45A–H, from a horizon 7.5 m below (15 m down slope in a North Easterly direction) the *Morocops granulops*? (Chatterton *et al.*, 2006; van Viersen *et al.* 2017) horizon at the base of the "Red Cliff" (Klug *et al.*, 2009.), Hamar Laghdad (Fig. 2B, Map 11, site 6), articulated dorsal exoskeleton. Paratype: NHMUK It 29348, Pl. 45I–L, from 2.5 m above type horizon (Fig. 2B, Map 11, site 5), dorsal exoskeleton of a partial cephalon only.

Description. Cephalon ovoid, widest at mid-point between eye lobes and alae. Genicranium broad; glabella not inset, pitted and with tectiform flanks. S1 short, slopping backwards. Axial furrows convex, converging anteriorly at just over 15° to axis and not crossing junction of alae and L1. L1 mildly inflated, preglabellar furrow almost effaced and occipital furrow shallow. Occipital ring pitted, not medially broadened (sag.), about same width (sag.) as posterior border (exsag.) and in lateral view, higher than glabella anterior to S0. Occipital node moderate in size and weakly inflated. Alae laterally directed, alar furrows shallow and poorly defined. Posterior border is moderately short (tr.), being around 30% of width (tr.) of occipital ring.

Genal area without pitting and very broad (tr.), with width (tr.) over two-thirds its length (exsag.). Eye lobes large (exsag.), and there is no genal ridge or eye ridge. Anterior boss inflated and joined to glabella. Genal roll moderately steep anteriorly (≈ 55^0 to horizontal), steep laterally (≈ 70^0 to horizontal). Inner fringe narrowing strongly in lateral view, to nearly 60% of its width (tr.) at eye lobes. Perforations on genal roll smaller than those on brim and becoming smaller for a short distance away from girder. Girder narrow (1.4% of genicranium width (tr.)).

Brim moderately wide, gently concave (sag.), straight laterally, barely sloping but quickly steepening to near vertical on prolongations. Brim width ratio very low for genus, at 0.60. Brim without caeca and brim perforations moderately fine, with a standardised diameter of under 130μm. Dorsal surface of external rim without sculpture; marginal band near vertical, straight with tubercles and ridge at top and bottom.

Length (exsag.) of prolongations 88% of cephalic length (sag.). Internal and external rims curve adaxially in dorsal view, and internal rim straight in lateral view. Genal spine extends curve of external rim. Extension of girder meets internal rim 1/3 way down prolongations. There are two rows of fine tubercles forming subparallel ridges on ventral surface of external rim (Pl. 45D).

Thorax with at least 22 segments. Inner portion of pleurae lengthening (tr.) to 5^{th} segment, then tapering so that at last segment it is 25% of 5^{th}. Axis tapering moderately, with width (tr.) of last axial ring being just over 40% of width of first. Pleural furrows broad, shallow, almost effaced and barely extend beyond fulcrum. Outer portion of pleurae set at shallow angle to inner portion, slanting slightly posteriorly from fulcrum and running distally for a short distance before bending near vertically downward; finger-like, straight with rounded ends (Pl. 45E). Pitting on axial rings and pleurae.

Pygidium with at least 3 axial rings and terminal piece. There are four pairs of pleural ribs, inner portions of which are at right angles to axis, but outer portion slants posterolaterally from fulcrum, and distal ends are rounded. Interpleural furrows are fully developed, except those defining fourth rib, which are very shallow. Terminal piece short (sag.) and broad (tr.) with slightly rounded distal edge. There are no pleural furrows. Fine tubercles on axial rings and terminal piece.

Hypostome not known.

Remarks. *P. m*erzaneensis has a slightly inflated L1. Also, from the available material (see Pl. 5) it is not possible to determine with any certainty the number of the eye lenses on each eye lobe or the course of the inner margin of the fringe across the anterior of the genal areas. Otherwise, *P. merzaneensis* complies with the diagnostic characters of the genus shown in Table 5c.

A comparison between *Pinnuloharpes merzaneensis* and *P. haustrum* is given in the systematics of *P. haustrum* above. *P. merzaneensis* is also similar to *P. hamarlaghdadensis* but differs in having: a glabella with flanks that are

tectiform not rounded; axial furrows that are convex not straight, converge more strongly anteriorly and do not cross at the junction of the ala and L1; an almost effaced preglabellar furrow, whereas that of *P. hamarlaghdadensis* is well-defined as is the preglabellar field; the occipital ring not medially broadened; its alae laterally directed a shorter (tr.) posterior border; the anterior boss joined to glabella; the genal area 10% wider than that of *P. hamarlaghdadensis*; a genal roll that is less steeply-sloping laterally and has perforations which are graduated, becoming smaller away from girder; a narrower (sag.) girder; a brim that is slightly concave (sag.), straight laterally and with a brim width ratio of around 0.60, some 12% lower than that of *P. hamarlaghdadensis*; and in dorsal view, the internal rim of *P. merzaneensis* curves adaxially rather than being subparallel.

Although the cephalic length (sag.) of the holotype of *P. hamarlaghdadensis* is just under 9 mm, a third smaller than that of *P. merzaneensis,* it does not seem that any differences are ontogenetic. The genal roll of *P. merzaneensis* is steeper-sloping anteriorly, and the brim and rim width (sag.) relative to cephalon length (sag.) are the same.

***Pinnuloharpes torquis* n. sp.**

Plate 37A–O

Diagnosis. Genicranium broad (width (tr.) 1.2 times length (sag.)), and genal roll gently sloping anteriorly. Glabella mildly tectiform, and S1 small depression in axial furrow. Alar furrows effaced. Girder very broad (sag., exsag.) and with central row of large perforations. Prolongation long (exsag,), 1.2 times cephalic length (sag.); external and internal rims flexing abaxially close to distal end of prolongation.

Etymology. Named for the necklace-like perforated girder. Torquis, Latin for collar or neckless.

Material and occurrence. Holotype: NHMUK It 29354 (1), Pl. 37E–J, from an upper Eifelian horizon, in an outcrop 3.8 km west of Ksar Hannabou and 8.3 km S.S.W. of El Jorf (Fig. 2B, Map 6, site 9) a dorsal exoskeleton of a cephalon which largely overlies another cephalon, Paratype NHMUK It 29354 (2), Pl. 37E. Paratype: NHMUK It 29353, Pl. 37A–D, from type locality and horizon (Fig. 2B, Map 6, site 7), dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29355 (1), Pl. 37K–O, from type locality and horizon (Fig. 2B, Map 6, site 10), dorsal exoskeleton of partial cephalon. Paratype NHMUK It 29355 (2) not figured.

Other material: *Pinnuloharpes* aff. *torquis:* NHMUK It 29329, Pl. 38A–E, from an upper Eifelian horizon, Tamgoute Bulgan (Fig. 2B, Map 6, site 20)**,** dorsal exoskeleton of cephalon only.

Description. Cephalon ovoid, widest at mid-point between alae and eye lobes. Glabella narrow, width (tr.) under 60% of length (sag.) of glabella anterior to S0, with rounded crest, tectiform flanks and no sculpture. L1 not inflated, and S1 shallow depression in axial furrow only. Axial furrows straight, converging anteriorly at an angle to axis of just under 15°. Preglabellar furrow shallow and bowed upwards in anterior view. Occipital furrow shallow, medially straight. Occipital ring not medially broadened, same width (sag,) as posterior border (exsag.), without sculpture and, viewed laterally, same height as glabella anterior to S0. Occipital node of moderate size, barely inflated and located on anterior slope of occipital ring. Posterior border moderately wide (tr.), at around 45% of occipital ring width (tr.). No preglabellar field and alar furrow effaced.

Genal area broad, width (tr.) around 65% of length (exsag.). Eye lobes large (exsag.) (50% of width of glabella at S1); barely inflated; reniform; without sculpture on dorsal surfaces and with two subtriangular (Pl. 37N, O) lenses per eye lobe. No eye ridge or genal ridge. Inner margin of fringe not marked by bigger perforations. Anterior boss inflated and joined to glabella. Genal roll sloping very gently anteriorly (≈43^0), moderately steeply laterally (≈60^0), and genal roll perforations smaller than on brim and becoming smaller away from girder. Girder very wide (sag., exsag.), nearly 4% of width (tr.) of genicranium, with central row of big perforations. Brim narrow (sag.), around 28% of cephalic length (sag.), sloping moderately at just under 20^0 and with straight profile. Brim width ratio around 0.90. Standardised brim perforations large, with diameter of over 200 μm and no caeca on brim. External rim stout and without sculpture on dorsal surface. Marginal band near vertical, lacking ridges and tubercles. Prolongations very long (exsag.), around 1.2 times cephalic length (sag.) and in lateral view, height at midpoint less than half height of prolongation at junction with posterior border. In dorsal view, internal and external rims curving adaxially., Profiles of internal rims concave in lateral view, and meet exterior rim before joining at end of prolongations. Dorsal surfaces of internal rim smooth and genal spines long, following curve of exterior rim. Extension of girder meeting internal rim one third of way down prolongation. Whole brim steepens moderately on prolongations.

Thorax, pygidium and hypostome unknown.

Remarks. *Pinnuloharpes torquis* is similar to *P. apteros* but differs by having: axial furrows that are less convergent anteriorly and are straight not gently convex; a preglabellar furrow that in anterior view is bowed upwards not straight; eye lobes located further from the inner margin of the fringe; wider (tr.) posterior border and an inner margin of the fringe which is concave across the anterior of the genicranium either side of the glabella, rather than being straight as the case of *P. apteros*; an anterior boss that is more inflated and reaches down to girder; a wider (sag. and exsag.) girder that has a weak girder kink and central row of large perforations not found on the girder of *P. apteros;* a brim width ratio of over 0.86 compared to 0.77 for that of *P. apteros*; a marginal band without ridges; brim extensions on the prolongations that steepen less strongly. Prolongations that are longer (exsag.) than the length (sag.) of the cephalon length and over 15% longer than those of *P. apteros*; and internal rims which in lateral view, have a concave rather than straight profile and which meet before the end of the prolongations, rather than at the end as those of *P. apteros* do.

Pinnuloharpes torquis differs from *P.* aff. *torquis* (Pl. 38A–E) in having: a cephalon that in dorsal view is ovoid and widest at the mid-point between the alae and eye lobes, while that of *P*. aff. *torquis* is mildly pyriform and widest at the alae; a glabella with no muscle insertion furrows at S2, S3 or S4, whereas *P.* aff. *torquis* has furrows at S2 and S3; a more inflated boss, but no bigger perforations marking the inner margin of the fringe as it crosses the boss; a wide girder with a central row of large perforations, which are absent in *P.* aff. *torquis;* a weak girder kink, rather than none; a less steeply-sloping brim, which has a straighter, less convex profile and standardised brim perforations some 36% smaller at ≈220 μm; much stouter external rims; internal rims that curve adaxially in dorsal view, rather than being subparallel, and in lateral profile, are concave not straight; the extension of girder on the prolongations meets the internal rim a quarter of the way down, rather than dissipating before reaching the internal rim as it does in *P.* aff. *torquis*; and in lateral view, the internal and external rims of *P. torquis* meet closer to the end of the prolongations than those of *P.* aff. *torquis*.

Genus *Stoloharpes* n. gen.

Type species. *Stoloharpes rissaniensis* n. sp.

From a horizon near the top of the Eifelian, Rissani, Anti-Atlas, Morocco

Diagnosis. Cephalon is pyriform, and genicranium narrow to very narrow (width (tr.) over 85% of length (sag.)). Glabella carinate and joined medially to barely-inflated anterior boss. Preglabellar furrow very shallow and bowed upwards in anterior view. Occipital furrow medially bowed posteriorly. Genal roll gently sloping anteriorly (at under 42^0 with horizontal). Brim convex, sloping steeply at between 31^0 and 40^0 and quicky steepening to near vertical on prolongations. External rims tilted outwards and marginal band sloping down under cephalon. Internal rim has straight profile in lateral view. Thorax with over 24 segments. Outer portion of pleurae in line with inner portion and curving anteriorly distally.

Etymology. From the Greek word στολή (stolē). The shape of the convex brim around the genicranium resembles a stole.

Discussion. *Stoloharpes* sister genus is *Pinnuloharpes* and the two genera are compared in the systematics for *Pinnuloharpes* above.

Amongst the species described below, *Stoloharpes retiarius* may possibly belong to another unnamed genus. Eifelian Material figured by Lebrun, P. (2018, Page 229 Fig. A) from Jorf, Errachidia, Morocco and Basse and Müller (2004, tafel 26, Fig. 340) from Wissenbach-Schiefer, Schiefergebirge, Harz, Germany have similar morphologically features but more material is required to determine whether they form a separate clade with *S. retiarius* and justify the erection of a new genus.

Stoloharpes obuti and *S. convexus* have been reassigned from *Kielania*. *S. obuti* is of Lochkovian age whereas all other species of *Stoloharpes* are from the middle to upper Eifelian and it may be on more material becoming available that *S. obuti* will be found to belong to another genus.

Cladogram Figs 9, 10e show all the species included in the genus.

Stoloharpes rissaniensis n. sp.

Plates 46A–O, 47A–J, 48A–M

Diagnosis. Cephalon mildly pyriform, genal area narrow (width (tr.) 34% of length (exsag.)). Alae are as wide (tr.) as they are long (exsag.). Genal area narrow. Inner margin of fringe across anterior of genal area straight, and anterior boss barely reaching down to girder. Caeca present on genal roll. Brim sloping at 30^0, narrow (sag.) (27% of cephalic length (sag.) in dorsal view) and has brim width ratio of just over 0.75. Perforations on brim become smaller for short distance away from girder. Exterior rim curves sharply upwards at posterior of prolongation, to join with internal rim at near right angle. Genal spine short, slanting obliquely upwards and adaxially.

Etymology. Named after the town of Rissani, which is close to the type locality.

Material and occurrence. Holotype: NHMUK It 29373, Pl. 46A–M, from an upper Eifelian horizon, Bou Tchrafine Group (lower corniche), Ksar Gaouz, 9.5 km S.W. of Rissani (Fig. 2B, Map 14, site 4), dorsal exoskeleton partially enrolled. Paratype: NHMUK It 29376, Pl. 46N–O, from type locality and type horizon (Fig. 2B, Map 14, site 7), partly crushed dorsal exoskeleton with pygidium enrolled. Paratype: NHMUK It 29374, Pl. 47A–F, from type locality and type horizon (Fig. 2B, Map 14, site 5), dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29375, Pl. 47G–J, from type locality and type horizon (Fig. 2B, Map 14, site 6), dorsal exoskeleton of incomplete cephalon with disarticulated thorax. Paratypes: NHMUK It 29371 and NHMUK It 29372, from "*Basseiarges* Couche", Eifelian, Fezna (Fig. 2B, Map 6, site 3 and 22, respectively). NHMUK It 29371, Pl. 48A–D, is a dorsal exoskeleton of cephalon only, and NHMUK It 29372, Pl. 48E–J, a cephalon and disarticulated thorax. Paratype: NHMUK It 29377, Pl. 48K–M, from Ighas, Bou Tchrafine Group (lower corniche), Eifelian (Fig. 2B, Map 14, site 8), dorsal exoskeleton of cephalon only.

Other material: *Stoloharpes* aff. *rissaniensis*, NHMUK It 29380, Pl. 49A–F, from an outcrop 3.8 km west of Ksar Hannabou and 8.3 km S.S.W. of El Jorf, Eifelian (Fig. 2B, Map 6, site 14), a dorsal exoskeleton of a cephalon and partial thorax.

Description. Cephalon weakly pyriform, widest posterior to eye lobes. Genicranium very narrow (width (tr.) > 85% of length (sag.)). Glabella narrow (width (tr.) at S1 just over 60% of glabella length (sag.) anterior to S0); with tectiform flanks; no pitting and S1 sloping posteriorly, but not curving forward over top of muscle attachment area. Muscle attachment areas at S2, S3 and S4 discernible from dark patches in cuticle (Pls 46L, M, 47E). L1 is barely inflated, and axial furrows converge weakly anteriorly, at just over 10^0 to axis. Occipital furrow deep and in dorsal view, moderately bowed posteriorly. Occipital node strongly inflated and occipital ring without sculpture. Alae laterally directed, small (tr.) and as wide (tr.) as it is long (exsag.). Alar furrow very shallow. Posterior border moderately short (tr.), at around 21% width (tr.) of occipital ring.

Genal area narrow, width (tr.) 34% of length (exsag.). Eye lobes oval, large (exsag.), inflated and with two equal-sized lenses each (Pls 46M, 47F). Eye ridge straight, poorly defined. Anterior boss barely inflated, reaching down to moderately narrow girder with weak girder kink. Genal roll sloping on sagittal line at an angle of around 31^0 and laterally at around 55^0; narrowing posteriorly in lateral view by around 65%. Caeca on genal roll and perforations smaller than on brim. No row of larger perforations immediately above girder. Hypostome unknown.

Brim convex, sloping moderately steeply at just over 31^0 and narrow, brim width (sag.) of holotype is 27% of cephalic length (sag.). Brim width ratio 0.86. Brim with light caeca and perforations that decrease in size away from girder, to become very fine at under 100µm. No tubercles or granulation on dorsal surface of rim. Marginal band straight, sloping down under cephalon anteriorly and laterally, and lacking tubercles or ridges. Brim steepens quickly to near-vertical on prolongations.

Prolongations moderately long (exsag.), being 87% of cephalic length (sag.), and wide in lateral view, tapering moderately posteriorly. Height of prolongation at midpoint is 65% of height at junction with posterior border. Internal rim straight, gently sloping downwards posteriorly, and external rim straight over 2/3 of its length, before curving strongly upwards to meet internal rim at near right angle. In dorsal view, both rims on prolongations curve adaxially. Genal spine short, continuing curve of external rim. Internal rim lacks tubercles on dorsal surface and extension of girder meets internal rim 1/4 of way down prolongation.

Thorax with 24 segments, not widening anteriorly and not strongly tapered posteriorly. Axis width (tr.) of last segment about 48% of width (tr.) of first. Pleural furrows broad, shallow, U-shaped and well-defined. No pits or tubercles on axial rings or pleurae. Outer portion of pleurae curved anteriorly, tapered and with distal ends rounded. Pygidium short, with 3 axial rings and two pairs of pleural ribs. Terminal piece short (sag.) and subtriangular.

Remarks. The brim of the paratype shown in Pl. 47A-J is different from that of the holotype, being 20% wider, 10% less steeply-sloping and with a brim width ratio of 0.65 (25% lower than that of the holotype). While some of the difference in width and slope could be explained by flattening of the dorsal exoskeleton of the paratype, difference in brim width ratio cannot and is an example of significant intraspecies variation.

The Anti-Atlas harpetid that *S. rissaniensis* resembles the most is *S. calceolus*. *S. rissaniensis* differs, however, in having: a cephalon that is widest at the eye lobes rather than at the midpoint between the eye lobes and the alae; wider (tr.) alae which are laterally directed not anterolaterally directed; an eye ridge, which is absent in *S. calceolus*; a genal roll that slopes anteriorly at around 32^0 rather than 25^0; a less inflated anterior boss that reaches down to the girder, which has a weak girder kink; preaxial furrows which do not converge as those of *S. calceolus* do; a narrower brim; a higher brim width ratio; and brim perforations which become smaller towards the centre of the brim. The differences in brim width (sag.) and brim width ratios are much less in the case of the *S. rissaniensis* paratypes that have brims wider than those of the holotype.

NHMUK It 29380 (Pl. 49A-F) has been designated as *Stoloharpes* aff. *rissaniensis* and differs from *S. rissaniensis* in having: a cephalon that is widest at mid-point between eye lobes and alae, rather than at the eye lobes: a glabella with flanks that are rounded rather than tectiform; a shallow occipital furrow that is not bowed posteriorly medially; L1 that is not inflated; alar furrows that are effaced whereas *S. rissaniensis* has alar furrows, albeit very shallow; eye lobes with three lenses each, the anterior lens being the largest and the middle lens the smallest and orientated upwards, while *S. rissaniensis* has two lenses with the anterior being the largest; no eye ridge; no caeca on the genal roll or the brim; brim perforations which do not become smaller towards the centre and which have a standardised diameter of over 200µm, more than twice the diameter of those of *S. rissaniensis*; an internal rim that has a shallow wave-like profile in lateral view, whereas that of *S. rissaniensis* is concave; long genal spines, which follow the curve of the exterior rims; an extension to the girder which meets the internal rim a third of the way down the prolongation; and a brim that does not steepen so strongly on prolongations. *Stoloharpes rissaniensis* has genal spines that are smaller and set at an oblique angle to the exterior rim and an extension to the girder that meets the internal rim a quarter of the way down the prolongation.

***Stoloharpes calceolus* n. sp.**

Plate 49G–K

Diagnosis. Cephalon mildly pyriform; glabella sloping gently anteriorly and narrow, width (tr.) just over 50% of length (sag.) of glabella anterior to S0. Axial furrows nearly straight and weakly converging anteriorly. Preaxial furrows also converging and initially deep, becoming shallower anteriorly as anterior boss deflates to disappear close to girder. Occipital ring with prominent occipital node. Alar furrow well-defined and eyes elongated (exsag.). Genal roll sloping anteriorly at same angle as anterior of glabella, just under 25^0. Laterally, slope steepens strongly to around 55^0. Brim strongly convex, moderately broad (sag.) and steeply sloping at around 35^0.

Etymology. Named after the species' slipper-like lateral profile.

Material and occurrence. Holotype: NHMUK It 29363, Pl. 49G–K, from **"***Basseiarges* Couche", Eifelian, Ksar Lbor (Fig.2B, Map 3, site 3), dorsal exoskeleton with pygidium enrolled.

Other material: *S.* aff. *calceolus*, NHMUK It 299381, Pl. 49L–P, from **"***Basseiarges* Couche", Eifelian, Ksar Lbor, 28 km E of Tinghir, at the base of Jbel Tisdafine (Fig. 2B, Map 3, site 4), dorsal exoskeleton of cephalon and partial thorax only.

Description. Cephalon weakly pyriform, narrow, length (sag.) 85% of width (tr.) and widest at mid-point between eye lobes and alae. Genicranium very narrow, width (tr.) being same as length (sag.), widest at posterior border. Glabella strongly carinate, sloping very gently anteriorly and narrow, width (tr.) at S1 being about half sagittal length of glabella anterior to S0. S1 rises obliquely from axial furrow, before fading halfway up glabella. Other lateral glabellar impressions are missing and L1 inflated. Axial furrows straight and converging weakly anteriorly. Occipital ring slightly broadened medially and with prominent occipital node, base of which reaches down into occipital furrow. Top of occipital node only just lower than crest of glabella anterior to S0. Alae nearly as broad (tr.) as long (exsag.), anterolaterally directed and not quite reaching halfway across genal area. Alar furrows are well-defined. Posterior border short (tr.), around 35% of occipital ring width (tr.).

Eye lobes large (exsag.), and no eye ridge. Anterior boss narrow, inflated, strongly connected to glabella but not reaching down to girder. Preaxial furrows slightly convergent anteriorly. Genal roll wide and sloping very gently at just under 25^0 anteriorly, steepening to about 55^0 posterolaterally. In lateral view, inner fringe narrows strongly posterolaterally. Fine perforations, relatively sparsely distributed, increase in size on extensions to genal roll on prolongations. Girder narrow and lacking girder kink.

Brim convex in profile, steeply-sloping at around 34^0 and moderately broad (sag.), being just over 30% of cephalic length (sag.). Brim width ratio 0.70. Brim crossed by light caeca, with a high density of perforations in spaces in between (34 per sq. mm). Diameter of standardised brim perforations averaging just under 95 μm.

Length of prolongations (exsag.) 88% of cephalic length (sag.). External rim narrow, dorsal surface convex. In dorsal view, external rim flares almost imperceptibly outwards as it crosses onto prolongation and then, slanting gently adaxially, continues in a straight line posteriorly for about two-thirds of length (exsag.) of prolongation, where it curves adaxially.

The internal rim, leaving posterior border slanting abaxially at an angle of around 40^0 to axis, curves steadily adaxially until it meets external rim, where it is again at an angle of around 40^0 to axis. In lateral view, external rim curves up distally to meet internal rim at an angle of around 60^0. Internal rim straight in profile, slopes downwards gently from posterior border. Girder, on crossing onto prolongation, slopes sharply upwards, before curving posteriorly to join internal rim about one fifth of its way down prolongation (exsag.). Tubercles on dorsal surface of internal rim. Brim on prolongations quickly steepens posteriorly, to an angle to horizontal of around 80°. Perforations and caeca on brim of prolongations are same as on rest of brim, except for line of slightly bigger perforations which runs just below internal rim. Genal spine short and slanting adaxially.

Thorax has at least 24 segments. Interpleural furrows moderately deep. Distally, pleurae turn down and curve sharply forward, terminating with rounded end (Pl. 49K). Pygidium enrolled and hidden.

Hypostome not known.

Remarks. *Stoloharpes calceolus* is similar to *S.* aff. *capricornus* but differs in having: a cephalon that is not so strongly pyriform, and widest at the mid-point between the eye lobes and the alae not at the eye lobes; the genicranium widest at the eye lobes and not at the mid-point between the eye lobes and the alae; the flanks of the glabella more tectiform than rounded; the muscle insertion furrow at S1 slanting posteriorly, reaching two thirds of the way up the flank of the glabella, whereas the S1 furrow on *S.* aff. *capricornus* is effaced; an anterior boss and light caeca reaching across brim, while the anterior boss of *S.* aff. *capricornus* is effaced and the brim lacks caeca; prolongations that are about 10% shorter in relation to cephalic length (sag.) than those of *S.* aff. *calceolus;* and shorter genal spines that are set at an oblique angle to the exterior rim rather than following its curve.

Other material, NHMUK It 299381 (Pl. 49L–P), is designated as *S.* aff. *calceolus* differs from *S. calceolus* by having: the widest point of the cephalon at the level of the eyes rather than halfway between the eye lobes and alae; a wider glabella and a L1 that is not inflated; a shallower and wider (sag.) occipital furrow that is medially straight; alae that are laterally rather than anterolaterally directed; a poorly defined eye ridge rather than none; preaxial furrows that do not converge anteriorly; an anterior boss that is less inflated and not joined to the glabella; a higher brim width ratio and a marginal band that is near vertical rather than sloping down under the cephalon.

The holotype of *M. calceolus* is well preserved complete cephalon and thorax of a size that would indicate that they belonged to a well-developed holaspid. The cephalon is symmetrical and without any apparent pathological defects and has significant differences with *S.* aff. *calceolus*, the species it is most similar too. On this basis the species has been erected although without the support of paratypes.

***Stoloharpes capricornus* n. sp.**

Plate 50A–F, K–O

Diagnosis. Cephalon strongly pyriform and vaulted. Glabella with blister-like tubercles, slopes gently anteriorly at $< 20^0$. Alae with interalar furrow and alar depression. Pits and faint caeca on genal area. Narrow preglabellar furrow, anterior boss barely inflated and not joined to glabella. Brim very broad and sloping steeply anteriorly at 35^0, increasing to over 47^0 laterally and becoming near vertical on prolongations. In lateral view, in line with eye lobe, brim makes up half the height of cephalon. Brim width ratio low, at around 0.60, no row of larger perforations at proximal edge.

Etymology. Named for the goat horn shape of the prolongations.

Material and occurrence. Holotype: NHMUK It 29364, Pl. 50A–F, from the "*Thysanopeltis* Couche" at the top of the Eifelian, in an outcrop 21 km east of Touaz (Fig. 2B, Map 15, site 1), a dorsal exoskeleton of cephalon only. Paratype: NHMUK It 29365, Pl. 50K–O, from type horizon and locality (Fig. 2B, Map 15, site 2), a dorsal exoskeleton with thorax and pygidium enrolled.

Other material: *Stoloharpes* aff. *capricornus*, NHMUK It 29366, Pl. 50G–J, from a up Eifelian horizon, Hamar Laghdad (Fig. 2B, Map 11, site 14), dorsal exoskeleton of cephalon only.

Description. Cephalon strongly pyriform and vaulted, its height being nearly 60% of sagittal length. Its width (tr.) is 1.22 times length (sag.), and length (exsag.) of prolongation (excluding genal spine) is just over 80% of cephalic length (sag.). Glabella moderately narrow, with width (tr.) just over 60% of length (sag.); flanks tectiform. Large, flat, blister-like tubercles along crest. L1 inflated, and furrows at S1, S2 and S3 are shallow, being discernible by darker colouring of cuticle (Pl. 50E). S1 slopes adaxially backwards. S2 and S3 subcircular, barely rising out of axial furrow. Axial furrows convex, taper slightly anteriorly and cross junction of L1 and ala. L1 is inflated, alae small and alar furrows shallow. Interalar furrow and ridge on each ala, and alar depressions also present. Occipital ring slanting posteriorly in lateral view; narrow, broadens at junction with posterior border and inflates as it curves adaxially. Occipital node broad, barely inflated and appearing as swelling reaching back from occipital furrow to near posterior edge of ring. Posterior border very short (tr.), 23% of occipital ring width (tr.). Preglabellar field narrow, length (sag.) being about 12% of width (tr.). Genal area convex and moderately narrow, with width (tr.) 55% of length (exsag.). Eye tubercle at edge of anterior lateral slope of genal area, just above inner margin of fringe and just posterior to preglabellar furrow. Eye location ratio 0.78. Each eye lobe has two lenses (Pl. 50D), anterior lens being the largest and almost bean-shaped, posterior one more oval. Eye ridge indistinct but extends into axial furrow. Genal area covered by faint caeca and fine pitting.

Anterior boss barely inflated, not joined to glabella and deflating before reaching girder. Preaxial furrows converge slightly anteriorly. Genal roll convex, broad at sagittal line and sloping anteriorly at about 40^0. Laterally, it steepens to over 60^0 and posteriorly, narrows to about two-thirds its width (sag.). Perforations on genal roll are fine and densely-packed, increasing in size as they extend onto prolongations and becoming more spaced out. Intermittent line of bigger perforations at inner margin of fringe, which is particularly noticeable as it crosses anterior boss. Subparallel caeca strands extend down from inner margin of fringe to girder. Caeca also stretch across brim, in places reaching external rim. Girder moderately narrow (sag.), at 2% of width of genicranium, and girder kink very weak.

Brim broad (sag.), being just over 30% of cephalic length (sag.); convex; and sloping anteriorly at an angle of over 35^0, increasing laterally to over 47^0 and to near vertical on prolongations. Brim width ratio just over 0.60. Brim perforations densely-packed and slightly coarser than those covering genal roll. On outside edge of brim, row of coarse pits against rim. External rim is fine, its dorsal surface convex and without tubercles. Extension of genal roll and brim on prolongations quickly steepens posteriorly to near vertical. Girder turns gently upwards on prolongations, to meet internal rim nearly halfway down. Row of larger perforations below internal rim. Viewed dorsally, external rim flexes slightly abaxially as it crosses onto prolongation, straightens, and then curves adaxially to meet internal rim, which points obliquely adaxially. Internal rim is angled about 30° to posterior border, pointing obliquely abaxially, and then curves steadily adaxially posteriorly, to join with external rim at end of prolongation. Prolongation terminated by long genal spine, which extends from lower lamella and points adaxially at an angle of about 50° to exsagittal line. Viewed laterally, internal rim declines steadily posteriorly to meet external rim, which is slightly upturned at its distal end. Dorsal surface of internal rim is initially flat but becomes rounded close to junction with external rim. Intermittent row of fine tubercles runs along outside edge of flat surface.

Only one enrolled thorax, with poorly-preserved surface, has been found (Pl. 50M). It is not strongly tapered posteriorly and its pleural furrows are broad and shallow.

Hypostome and pygidium not known.

Remarks. *Stoloharpes capricornus* is similar to *S. calceolus* but differs in having: a cephalon that is more pyriform and widest at the eye lobes rather than at the mid-point between the eye lobes and alae; a genicranium widest at mid-point between the eye lobes and the alae not at the alae; a glabella with blister-like tubercles on its dorsal surface, rather than being tubercle free; muscle insertion furrows at S2 and S3 rather than none; interalar furrows; alar depressions; a shorter (tr.) posterior border; a genal area with faint caeca and ill-defined eye ridges, which are lacking in *S. calceolus*; a less inflated anterior boss that is not joined to the glabella and does not reach down to the girder; a weak girder kink; a brim width ratio of 0.62, which is 20/% lower than that of *S. calceolus*; genal spines that follow the curve of external rim rather than being set at an oblique angle; and a girder extension that meets the internal rim one third of the way down the prolongation, not one quarter as in *S. calceolus*.

The cephalon of *S. capricornus* is much the same shape in dorsal view as that of *Kielania triabsidata* Ormiston, 1971, but differs from it in having: the glabella 27% longer (sag.) in relation to its width (tr.); no glabellar lobation

like that of *K. triabsidata*; the alae much less prominent; the genal roll narrower in lateral view in relation to the brim than in *K. triabsidata*; longer genal prolongations which in lateral view have an external rim that only starts to curve upwards two-thirds of the way down the prolongation, while that of *Kielania triabsidata* curves upwards over most of its length and terminates in a longer and more robust genal spine, which is not tilted adaxially; the genal spine carried solely on the lower lamella whereas that of *K. triabsidata* appears to be at least partly carried on the upper lamella.

Stoloharpes aff. *capricornus* (Pl. 50G–J) differs from *S. capricornus* by having glabellar flanks that are more convex than tectiform; no tubercles or blisters on the glabella or internal rim; no light caeca on the genal areas or brim; no eye ridges; no preglabellar field; the anterior boss is joined to the glabella but does not reach down to the girder; there is no girder kink and the prolongations are some 12% longer than those of *S. capricornus.*

***Stoloharpes retiarius* n. sp.**

Plates 51A–L, 52A–L

Diagnosis. Cephalon widest at eye lobes, width (tr.) being over 1.46 times length (sag.). Flanks of glabella convex and axial furrows tapered anteriorly. Occipital furrow narrow and occipital ring not medially broadened. Posterior border short (tr.), equal to 25% of occipital ring width (tr.). Perforations on genal roll becoming smaller posterolaterally and no row of larger perforations at the inner margin of fringe across the anterior boss. Brim width ratio high, at around 0.92. Perforations on brim very large and forming net-like web across the dorsal surface. External rim very fine. In dorsal view, internal rim slanting diagonally abaxially, before curving strongly adaxially. No row of larger perforations under internal rim, and brim steepens only moderately on prolongations.

Etymology. Retiarius, Latin for a Roman net fighter, referring to the net like structure of the brim.

Material and occurrence. Holotype: NHMUK It 29368, Pl. 51A–G, from close to Eifelian/Givetian boundary, Bou Tchrafine Group (lower corniche), Ottara (Fig. 2B, Map 14, site 2), dorsal exoskeleton of a cephalon only. Paratype: NHMUK It 29369, Pl. 51H–L, from type horizon and type location (Fig. 2B, Map 14, site 3), dorsal exoskeleton of an incomplete cephalon. Paratype: NHMUK It 29367, Pl. 52A–F, from type horizon and type location (Fig. 2B, Map 14, site 1), dorsal exoskeleton of an incomplete cephalon. Paratype: NHMUK It 29370, Pl. 52G–L, from type horizon and type location (Fig. 2B, Map 14, site 11), dorsal exoskeleton of cephalon.

Description. Cephalon ovoid, widest at eyes lobes. Genicranium narrow, width (tr.) 1.24 times length (sag.), widest just anterior to alae. Glabella strongly vaulted, not inset, pitted and with convex flanks. S1 furrow effaced, before curving forward, and L1 inflated. Axial furrows shallow, convex and converging strongly anteriorly. Occipital furrow narrow, medially bowed posteriorly. Occipital ring is broad (sag.) but not medially broadened and occipital node broad, moderately inflated. Posterior border 40% of occipital ring width (tr.).

Genal area broad, width (tr.) 0.56 times length (exsag.), and faint pitting on central to outer regions similar to fine perforations present on fringe. These traces are more apparent on internal mould, exposed where small patch of cuticle is missing on holotype (Pl. 51F). Alae are anterolaterally directed and reach about halfway across genal area. Eye lobes with two equal-sized, roughly rectangular-shaped lenses and third smaller sub oval lens high up in between. Eye lenses on holotype not clearly defined and appear to have single small tubercle on surface of each lens. Eye ridges not well defined, inner margin of fringe convex across anterior of genal areas, and not marked by row of bigger perforations across anterior boss. Anterior boss inflated, barely reaching girder. Genal roll gently sloping, anteriorly at 42^0, laterally at 50^0 and in lateral view broad (sag.) anteriorly, narrowing by more than 40% posterolaterally. Perforations on genal roll are fine and decrease in size posterolaterally and anteriorly upwards away from girder, for some four rows. Genal roll without caeca, and girder very narrow (sag.), at 1.9% of width (tr.) of genicranium, and without kink.

Brim is steeply-sloping ($\approx 27^0$); moderately wide (sag.), being one third of cephalic length (sag.); and has high brim width ratio of 0.92. Standardised brim perforations are large, at over 300 μm, and are densely-packed at around 10 per sq. mm, forming net-like pattern across brim with around 90% of area being perforated. Brim caeca-free. External rim is fine, and there are ridges at top and bottom of marginal band. Prolongations moderately short (exsag.), at under 80% of cephalic length (sag.). In dorsal view, internal rim slanting abaxially at angle of around 45^0 to posterior border, before curving strongly adaxially. In lateral view, it has weak wave-like profile. Rims meeting just before joining at end of prolongations, to form long genal spine curving adaxially and upwards to follow curve

of external rim. Extension of girder meets internal rim 1/3 of way down prolongations. There is no row of large perforations immediately below internal rim. Brim steepens moderately on prolongations to an angle of around 60^0.

Hypostome, thorax and pygidium not known.

Remarks. *Stoloharpes retiarius* is the least compliant with the diagnostic characters set out for *Stoloharpes* in Table 5c. *S. retiarius*'s genicranium is slightly wider, its brim is not so steeply sloping, its internal rims in lateral view the have a wave like profile rather than being straight and its brim steepens less on the prolongations. *S. retiarius* has the other 7 diagnostic characters of its genus shown in Table 5c.

Intraspecies variation shown by the paratypes include variations in perforation sizes, which range from 300 μm to 370 μm, and in the slope of the brim from nearly flat to moderately steep. Brim width ratios are between 0.90 and 1.06.

Stoloharpes retiarius most resembles *S. rissaniensis* but differs by having: a wider cephalon and genicranium; a glabella that is not so strongly carinated and has a granulated surface; an occipital ring with a granulations; ala anteriorly directed; genal areas with fine pits and granulation; eye lobes with three lenses rather than two; an inner margin of the fringe with a course across the anterior of the genal areas that is more convex than straight and across the anterior of the boss lacks a row of large perforations; an anterior boss that is slightly more inflated; a genal roll sloping more gently laterally, without caeca and perforations that are larger anteriorly; a wider brim that slopes less steeply, has a higher brim width ratio, no caeca, and much larger brim perforations that do not decrease in size away from the girder; a marginal band with ridges top and bottom rather than none; shorter prolongations that in dorsal view slant abaxially before curving adaxially; internal rims that in lateral view have a weak wave like profile rather than a straight profile; an internal rim that meets and joins the external before end of the prolongation; longer genal spines that follow the curve of exterior rim and an extension to the brim that steepens less strongly posteriorly on the prolongations.

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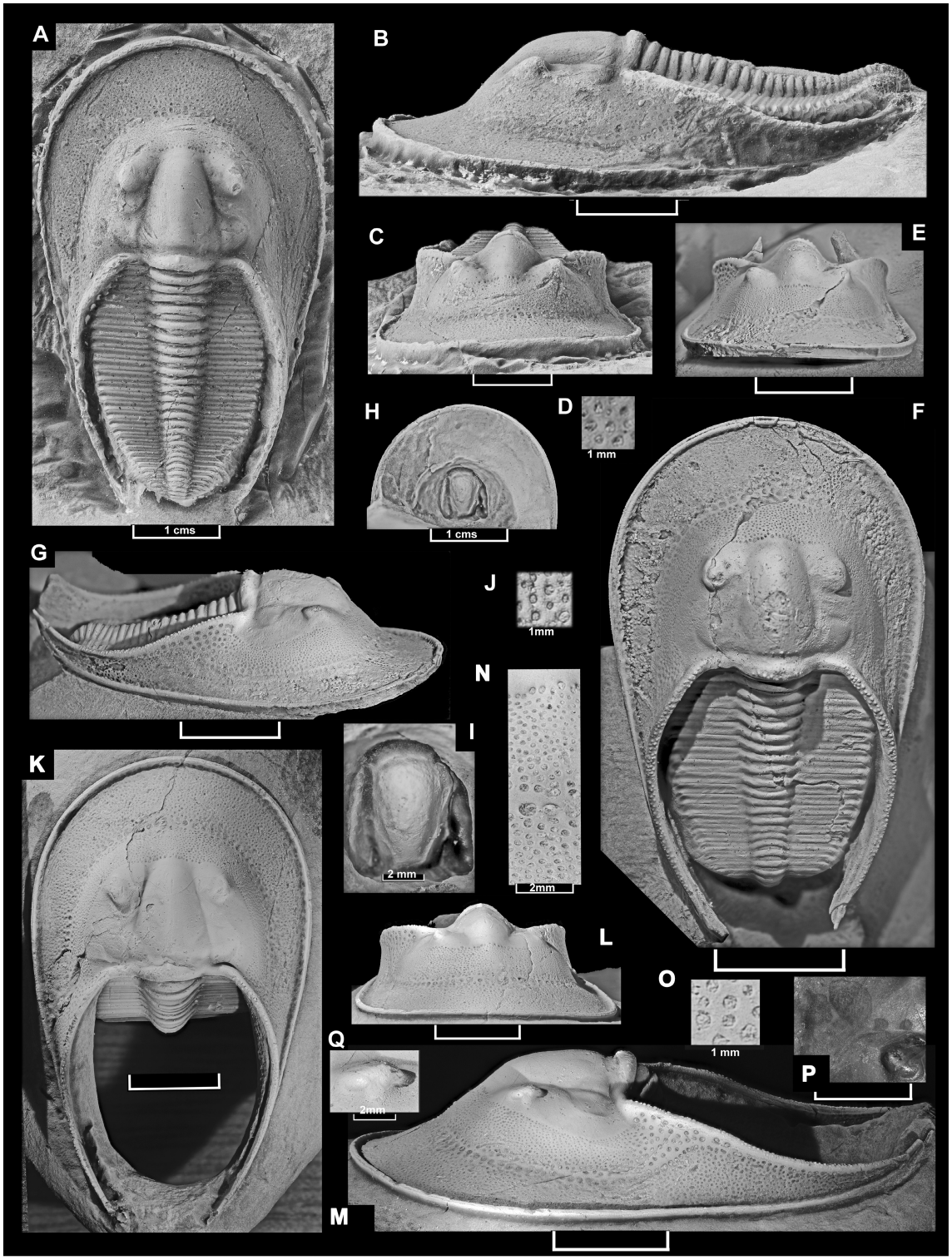


PLATE 1. A–Q *Harpes boudibensis* n. sp., El Otfal Formation, Eifelian. **A–D**, articulated dorsal exoskeleton, **paratype,** NHMUK It 29226, type locality horizon 1 (site 1). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations. **E–J**, dorsal exoskeleton, pygidium enrolled, **paratype**, NHMUK It 29228, type locality, horizon 2 (site 5). E, anterior, F, dorsal and G, lateral view. H, ventral view of anterior part of cephalon, I, hypostome and J, dorsal view of brim perforations. **K–Q**, enrolled articulated dorsal exoskeleton, **holotype,** NHMUK It 29227, horizon 1, Section 2 (Fig. 7), Jbel Issoumour (Fig. 2B, Map 7, site 4). K, dorsal, L, anterior, M, lateral view, N, anterior dorsal view of genal roll and brim perforations, O, dorsal view of brim perforations, P, lateral dorsal view of eye lobe and muscle impression areas at S0, S1, S2 and S3, and Q, lateral view of eye lobe.

Scale bars shown represent 1 cm unless otherwise indicated.

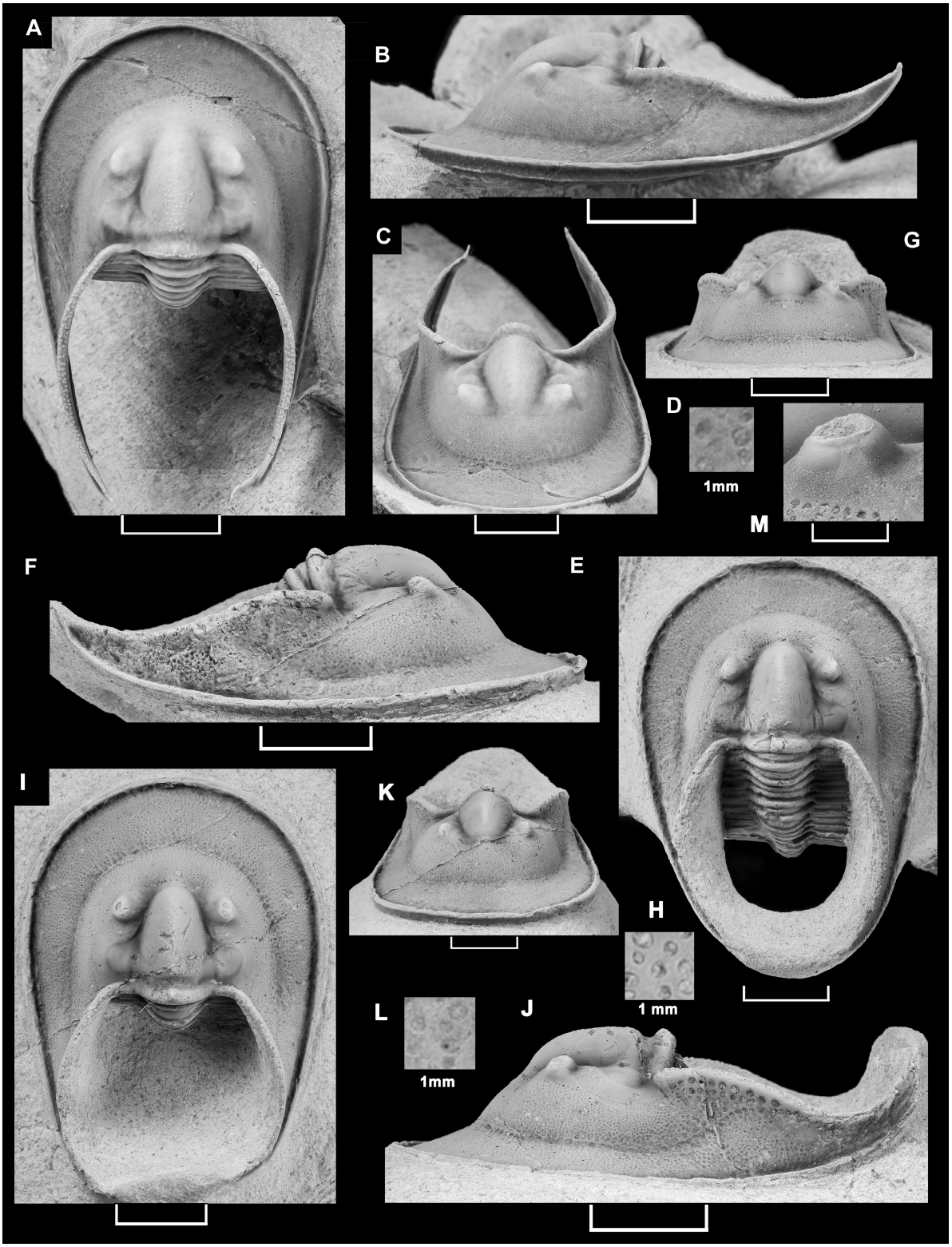


PLATE 2. A–D *Harpes* cf. *boudibensis*, from horizon 7, Section 1 (Fig. 6), El Otfal Formation, Eifelian, Jbel Ou-Driss (Fig. 2B, Map 4, site 11). An enrolled dorsal exoskeleton NHMUK It 29225. A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations.

E–M *Harpes oudris*, from horizon 5, Section 1 (Fig. 6), El Otfal Formation, Eifelian, Jbel Ou-Driss (Fig. 2B, Map 4). **E–H**, enrolled dorsal exoskeleton, **paratype,** NHMUK It 29240 (site 21). E, dorsal, F, lateral and G, anterior view. H, dorsal view of brim perforations. **I–M *Harpes oudris***, enrolled dorsal exoskeleton, **holotype,** NHMUK It 29241 (site 22). I, dorsal, J, lateral and K, anterior view. L, dorsal view of brim perforations and M, lateral view of eye lobe.

Scale bars shown represent 1 cm unless otherwise indicated.

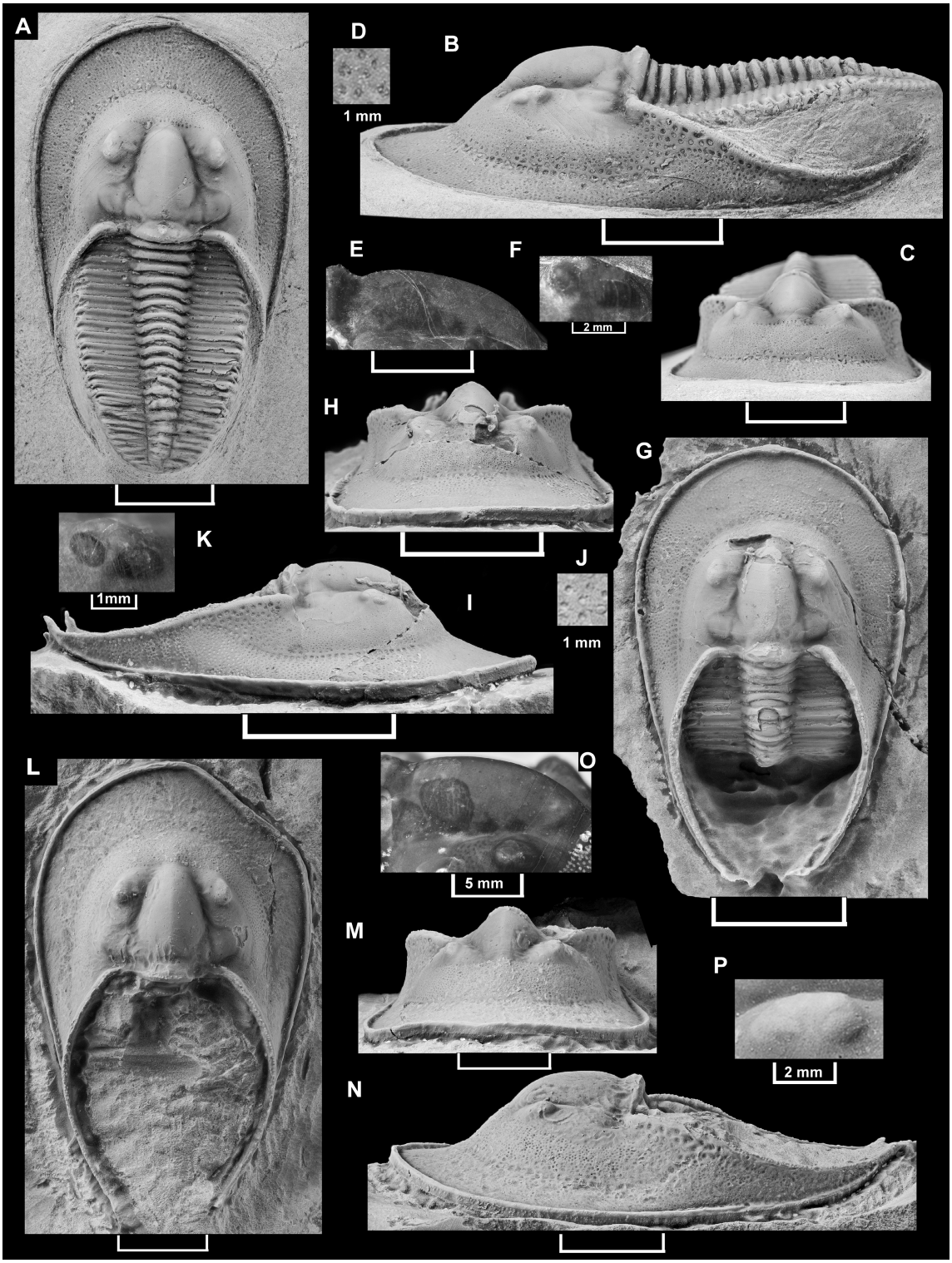


PLATE 3. A–K *Harpes supercilium* n. sp., from horizon 5, Section 2 (Fig. 7), El Otfal Formation, Eifelian, Jbel Issoumour (Fig. 2B, Map 7). **A–F**, articulated dorsal exoskeleton, **paratype**, NHMUK It 29251 (site 3). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations, E, lateral view of glabella muscle insertion scars and F, lateral view of eye lobe. **G–K**, dorsal exoskeleton thorax enrolled, **holotype,** NHMUK It 29252 (site 10). G, dorsal view, H, anterior view, I, lateral view, J, dorsal view of brim perforations, K, lateral view of eye lobe.

L–P *Harpes supercilium* n. sp., from horizon 8, Section 1 (Fig. 6), El Otfal Formation, Eifelian, Jbel Ou-Driss (Fig. 2B, Map 4, site 24), dorsal exoskeleton of cephalon, **paratype,** NHMUK It 29250. L, dorsal, M, anterior and N, lateral view. O, lateral view of muscle insertion scars on glabella, P, lateral view of eye lobe.

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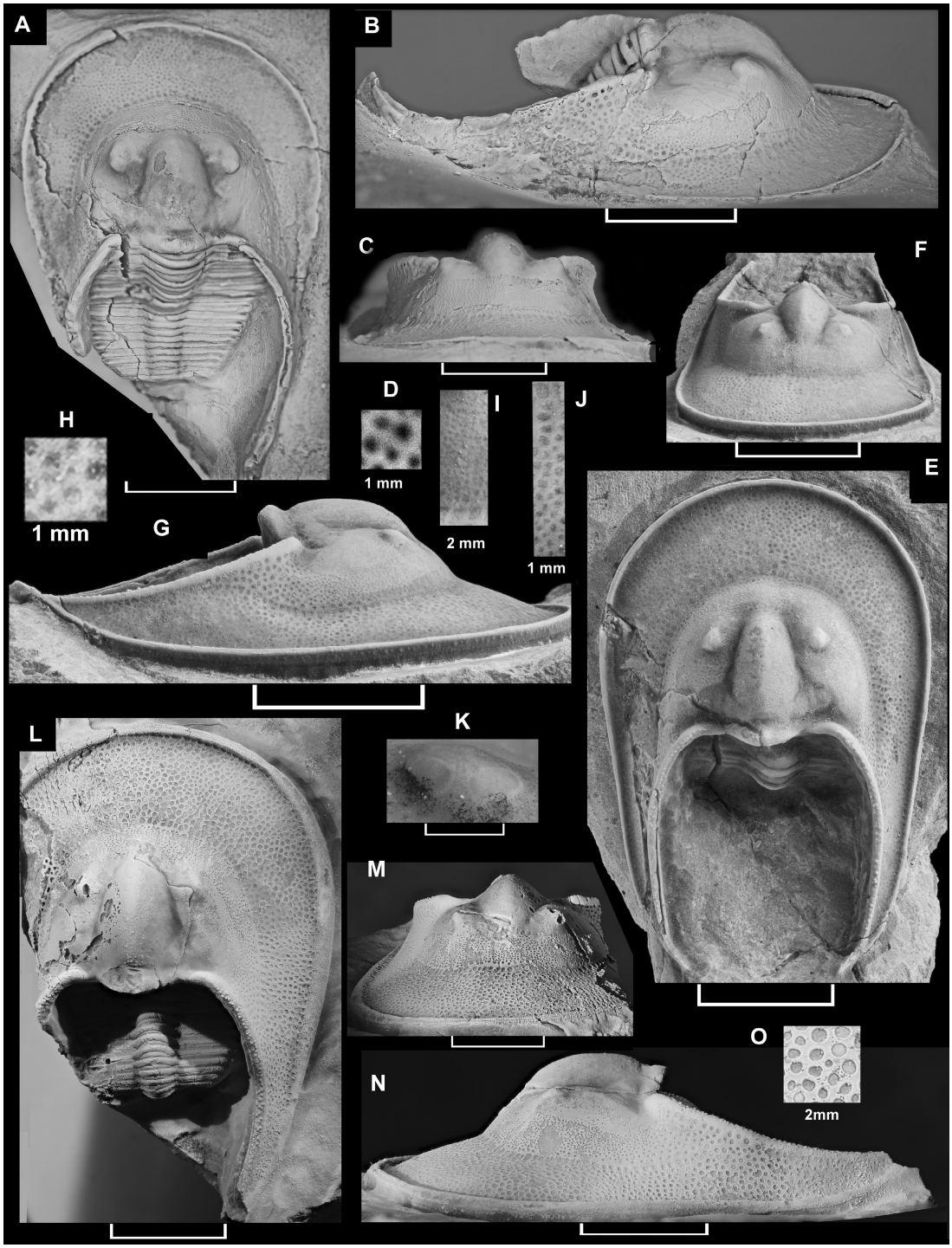


PLATE 4. A–D *Harpes supercilium* n. sp., partial dorsal exoskeleton, **paratype**, NHMUK It 29248, horizon 10, Section 1 (Fig. 6), El Otfal Formation, Eifelian, Jbel Ou-Driss (Fig. 2B, Map 4, site 14). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations.

E–K *Harpes sphenocephalus* n. sp., dorsal exoskeleton and partial thorax enrolled, **holotype**, NHMUK It 29246, horizon 1, Section 1 (Fig. 6), Er Remlia Formation, lower Emsian, Jbel Ou-Driss (Fig. 2B, Map 4, site 15). E, dorsal, F, anterior and G, lateral view. H, dorsal view of brim perforations, I, anterior view of genal roll, J, anterior-dorsal view of perforations across brim, exsag. K, lateral view of eye lenses.

L–O *Harpes* cf. *sphenocephalus*, partial dorsal exoskeleton, NHMUK It 29247, "Cherurid Couche", Er Remlia Formation, lower Emsian Jbel Issoumour (Fig. 2B, Map 7, site 18). L, dorsal, M, anterior and N, lateral view. O, dorsal view of brim perforations.

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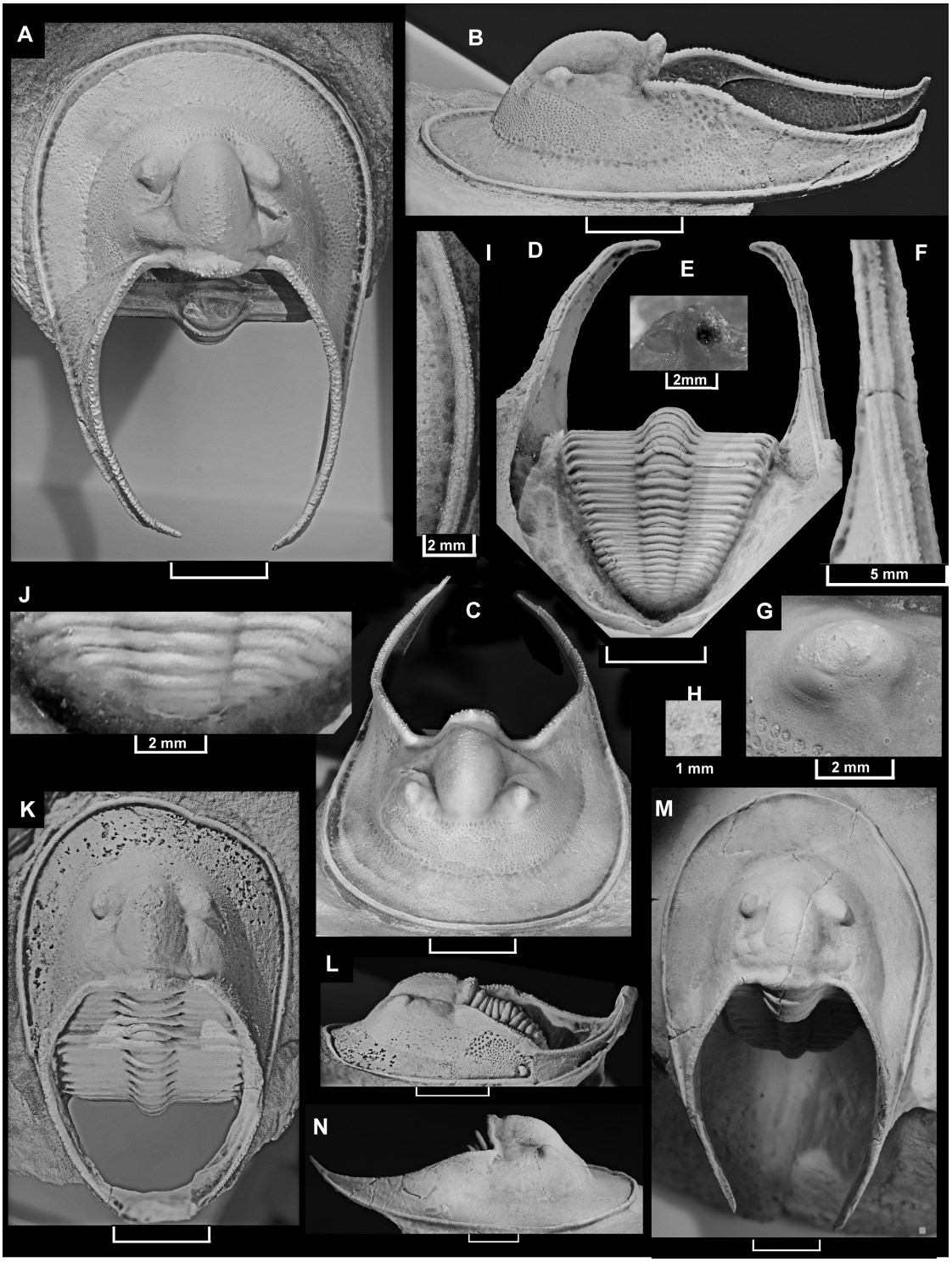


PLATE 5. A–J *Harpes lahceni*, dorsal exoskeleton partially enrolled, **holotype**, NHMUK It 29232, from El Otfal Formation, Eifelian, Horizon 3, Section 2 (Fig. 7), Jbel Issoumour (Fig. 2B, Map 7, site 15). A, dorsal, B, lateraland C, anterior view. D, posterior view, showing dorsal surface partially enrolled thorax and pygidium, and ventral surface of prolongations, E, lateral view of eye lobe, F, ventral view of prolongations, G, dorsal lateral view of eye lobe, H, dorsal view of brim perforations, I, dorsal view of dorsal surface of rim and J, dorsal view of pygidium.

K–L *Harpes lahceni*, dorsal exoskeleton partially enrolled, **paratype**, NHMUK It 29234, from El Otfal Formation, Eifelian, "Harpes Couche" above *Acanthopyge* horizon, Timerzit (Fig. 2B, Map 10). K, dorsal view and L, lateral view.

M–N *Harpes lahceni*, dorsal exoskeleton partially enrolled, **paratype,** NHMUK It 29233, from El Otfal Formation, "*Phylonix* Couche", Jbel Oufatene (Fig. 2B, Map 8). M, dorsal and N, lateral view.

Scale bars shown represent 1 cm unless otherwise indicated.

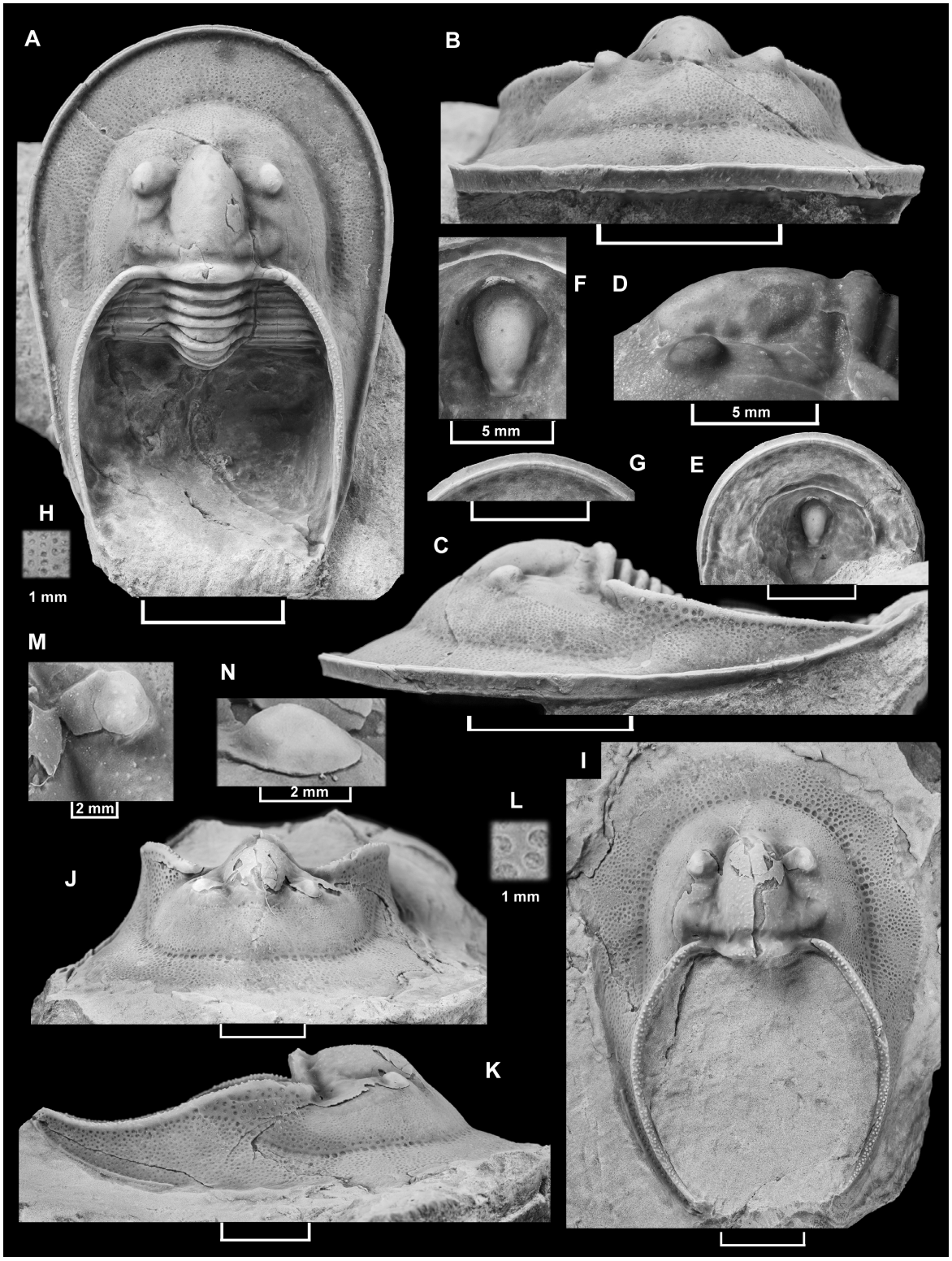


PLATE 6. A–H *Harpes* cf. *oudris*, dorsal exoskeleton with ventral surfaces exposed on anterior half of cephalon, NHMUK It 29242; from El Otfal Formation, Eifelian, horizon 4, Section 1 (Fig. 6), Jbel Ou-Driss (Fig. 2B, Map 4, site 10). A, dorsal, B, anterior and C, lateral view. D, lateral view of glabella (uncoated) and muscle insertion scars, E, ventral view of anterior half of cephalon, F, ventral view of hypostome in place, G, ventral view of anterior of rim, H, dorsal view of brim perforations.
I–N *Harpes* cf. *lahceni*, dorsal exoskeleton of partial cephalon only, NHMUK It 29235, from "*Erbenochile* Couche", Timrhanrhart Formation, Emsian, 23.8 km SW of Foum Zguid (Fig. 2A, Map 2, site 6). I, dorsal, J, anterior and K, lateral view. L, dorsal view of brim perforations and M and N, dorsal and lateral view of eye lobe respectively.
Scale bars shown represent 1 cm unless otherwise indicated.

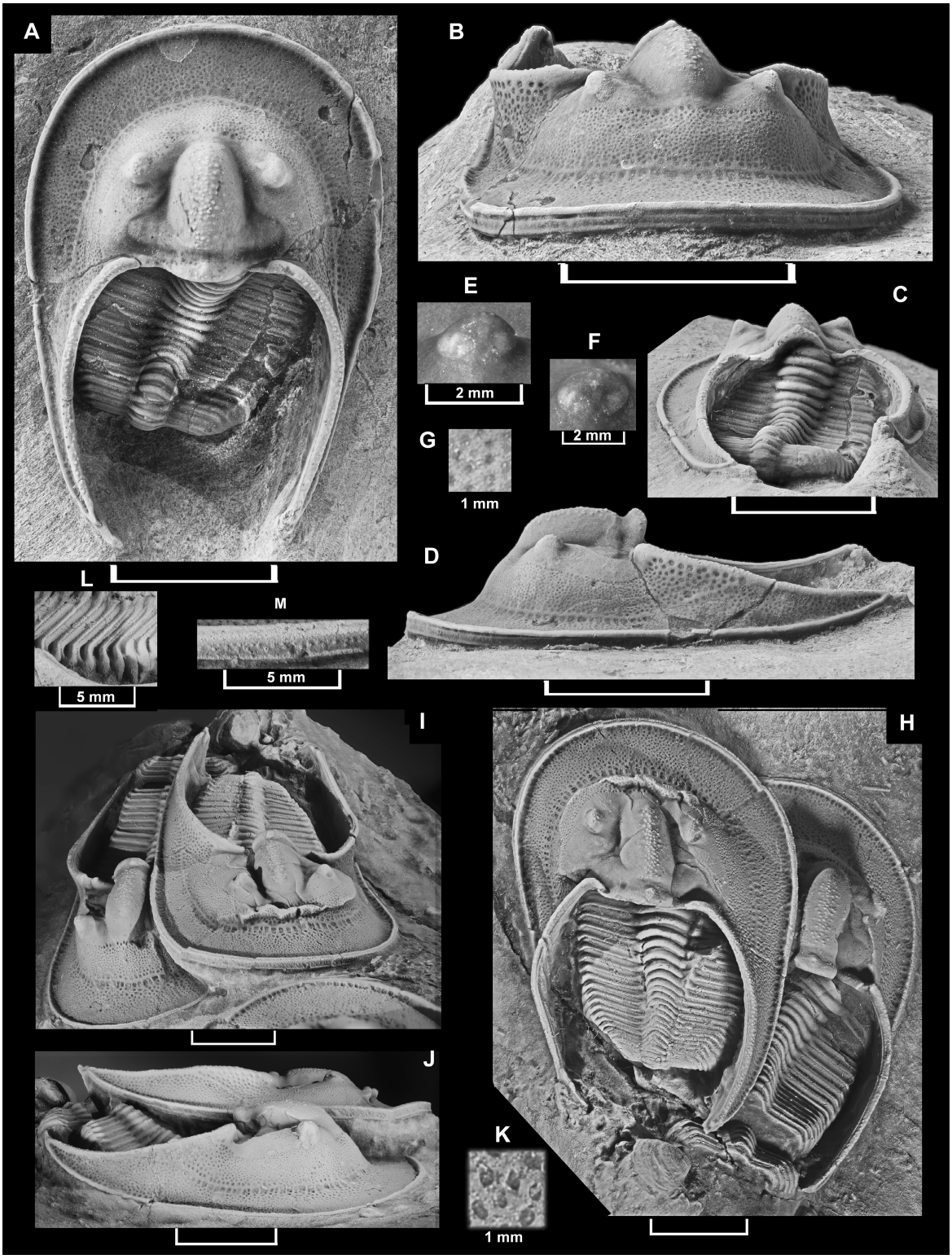


PLATE 7. A–M *Harpes lentigo* n. sp., from a coral horizon 5 m (12.2 m down slope) below the "Morocconites Couche", Tazoulait Formation, Emsian, Jbel Oufatene (Fig. 2B, Map 8, site 4). **A–G** dorsal exoskeleton, thorax disarticulated and partially rolled, **holotype**, NHMUK It 29236. A, dorsal, B, anterior, C, posterior and D, lateral view. E, lateral view of eye lobe (uncoated), F, laterodorsal view of eye lobe (uncoated) and G, dorsal view of brim perforations.

H–M *Harpes lentigo* n. sp., plate of three disarticulated dorsal exoskeletons, **paratypes**, NHMUK It 29237 (1 to 3) (Fig. 2B, Map 8, site 5). H, dorsal, I, anterodorsal and J, lateral view. K, dorsal view of brim perforations, L, lateral view of pleurae and M, anterior view of rim.

Scale bars shown represent 1 cm unless otherwise indicated.

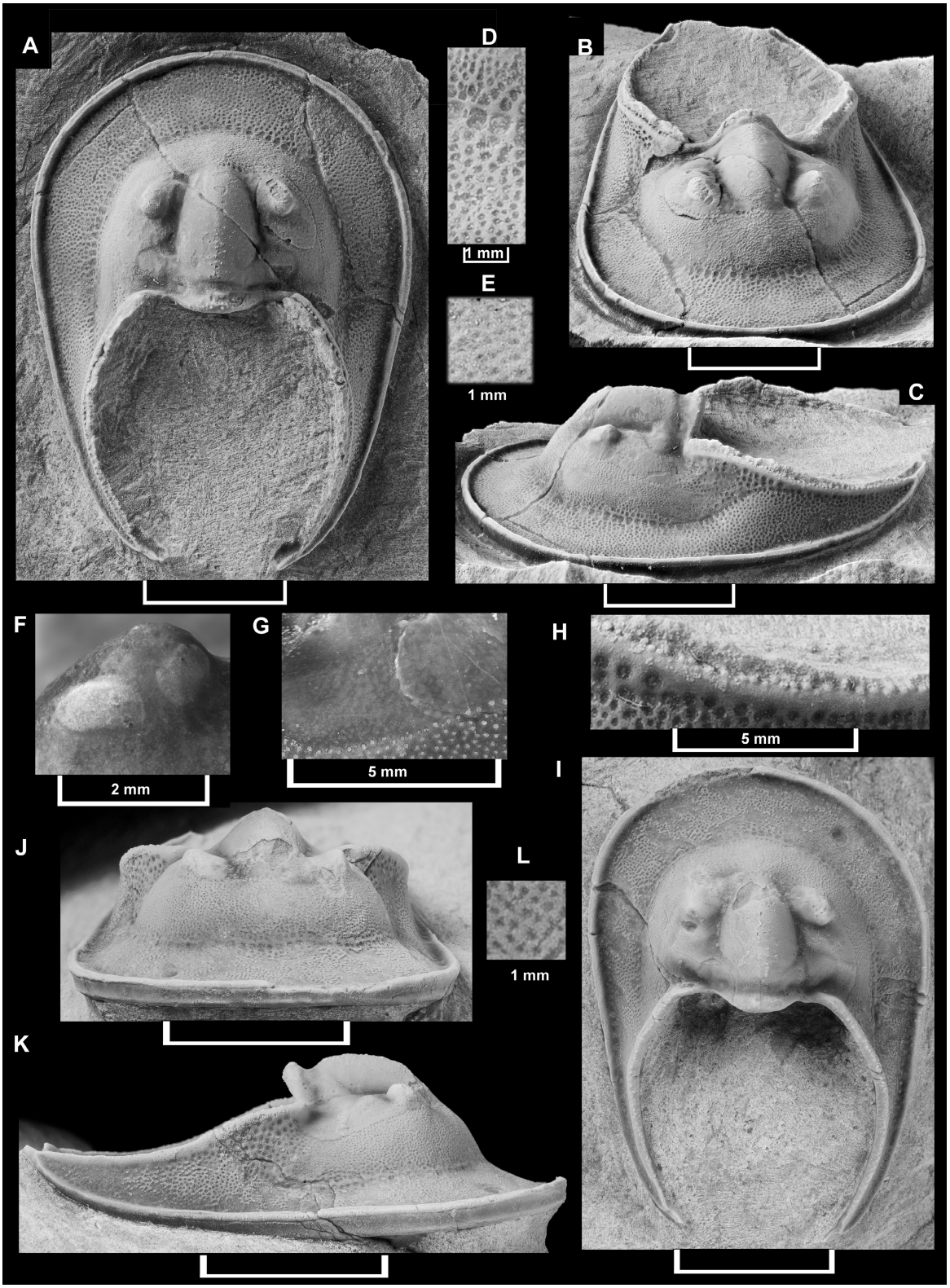


PLATE 8. A–L *Harpes* cf. *lentigo*, El Otfal Formation, Eifelian, Jbel Issoumour. **A–H** from an horizon halfway between "*Lobopyge* Couche" and "*Phylonix* Couche", dorsal exoskeleton of cephalon, NHMUK It 29239 (Fig. 2B, Map 7, site 14). A, dorsal, B, anterior and C, lateral view. D, anterior view of perforations on brim and genal roll, E, dorsal view of perforations on brim, F, lateral view of eye lobe (uncoated), G, lateral view of genal area (uncoated) and H, lateral view of the internal rim. **I–L** from the "*Lobopyge* Couche", dorsal exoskeleton of cephalon, NHMUK It 29238 (Fig. 2B, Map 7, site 7). I, dorsal, J, anterior and K, lateral view. L, dorsal view of brim perforations.
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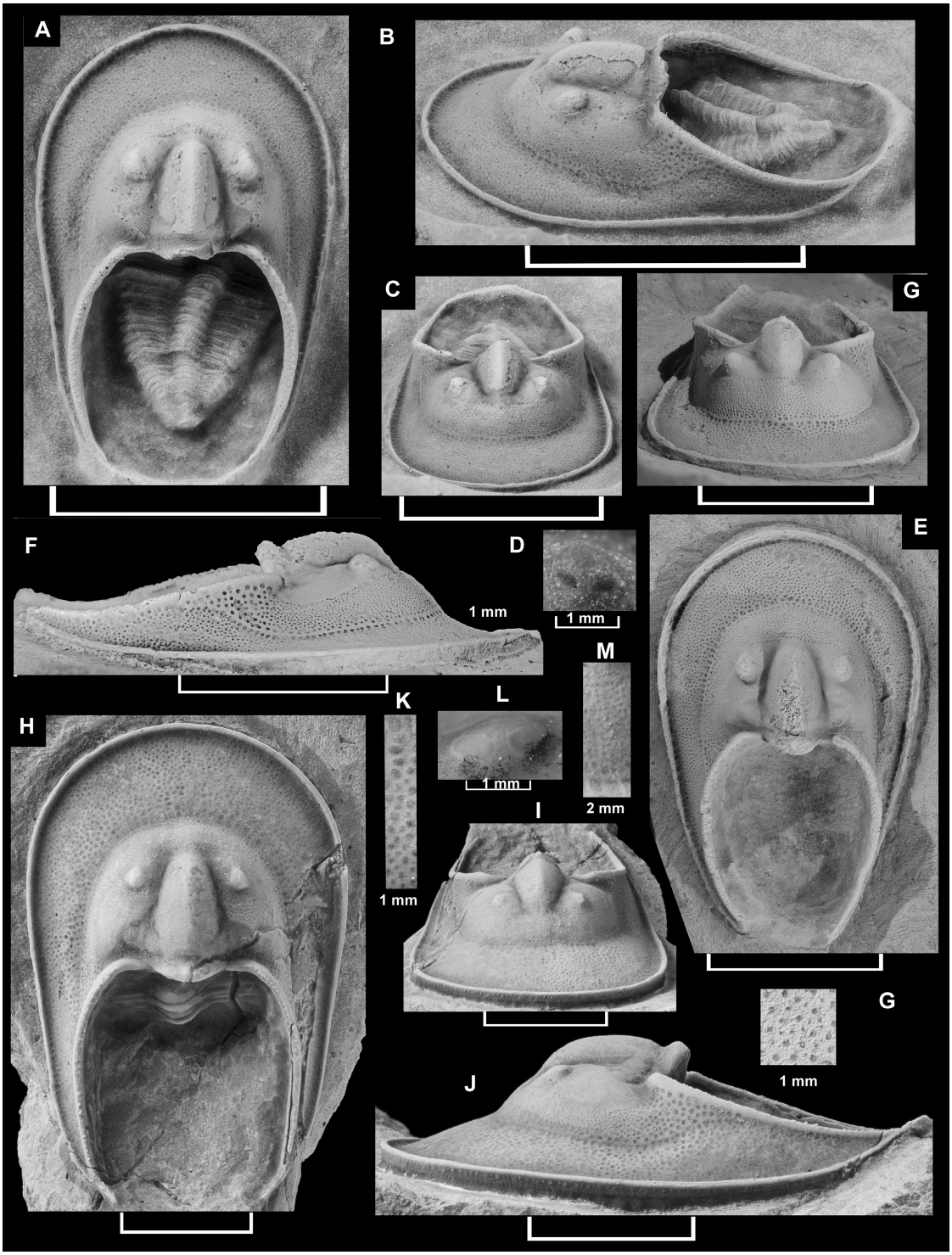


PLATE 9. A–I *Harpes prescheri* n. sp., from an horizon 100 m upslope of "Couche Rouge", close to the *Pyschopyge* horizon, Er Remlia Formation, Emsian, Jbel Issoumour (Fig. 2B, Map 7).

A–E dorsal exoskeleton of cephalon and disarticulated thorax, **holotype**, NHMUK It 29244 (site 9). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations, E, lateral view of eye lobe (uncoated).

F–I dorsal exoskeleton of cephalon, **paratype,** NHMUK It 29243 (site 8);, F dorsal, G, anterior and H, lateral view. I, dorsal view of brim perforations.

J–N *Harpes* cf. *prescheri*, dorsal exoskeleton of cephalon, NHMUK It 29245, from "*Lobopyge* Couche", El Otfal Formation, Emsian/Eifelian boundary, Jbel Issoumour (Fig. 2B, Map 7, site 2). J, dorsal, K, anterior and L, lateral view. M, lateral view of glabella (uncoated) and N, dorsal view of brim perforations.

Scale bars shown represent 1 cm unless otherwise indicated.

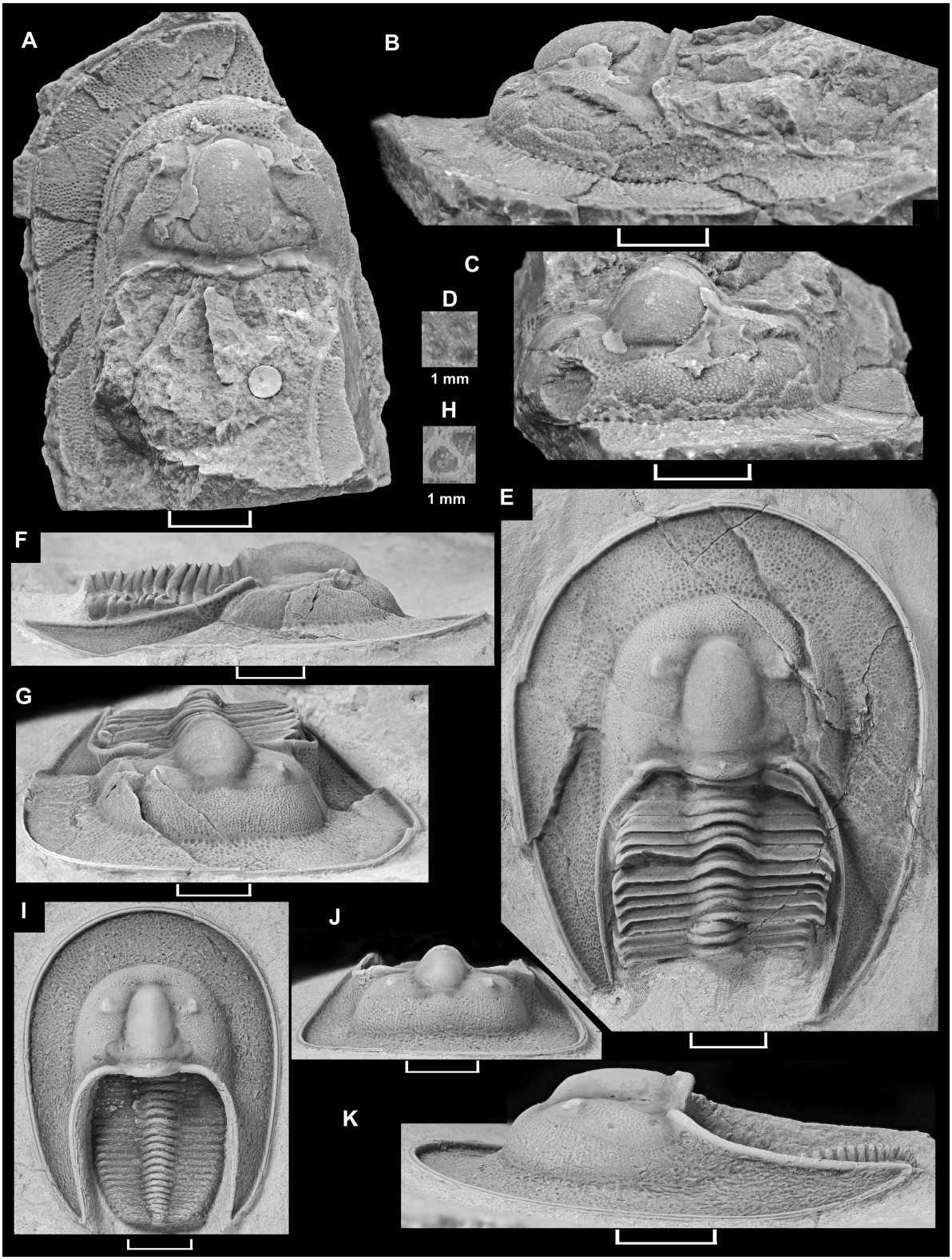


PLATE 10. A–D *Lioharpes venulosa*, from the Natural History Museum London collection, NHMUK In 4180**.** A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations.

E–K *Lioharpes galea* n. sp., from coral in an upper Pragian horizon, Ihandar formation, Jbel Otfal (Fig. 2B, Map 9, site 10**).** **E–H** partial dorsal exoskeleton, **holotype**, NHMUK It 29268, E, dorsal, F, lateral and G, anterior view. H, dorsal view of brim perforation.

I–K dorsal exoskeleton, **paratype,** NHMUK It 29269, from type locality (site 11), I, dorsal, J, anterior and K, lateral view. Scale bars shown represent 1 cm unless otherwise indicated.

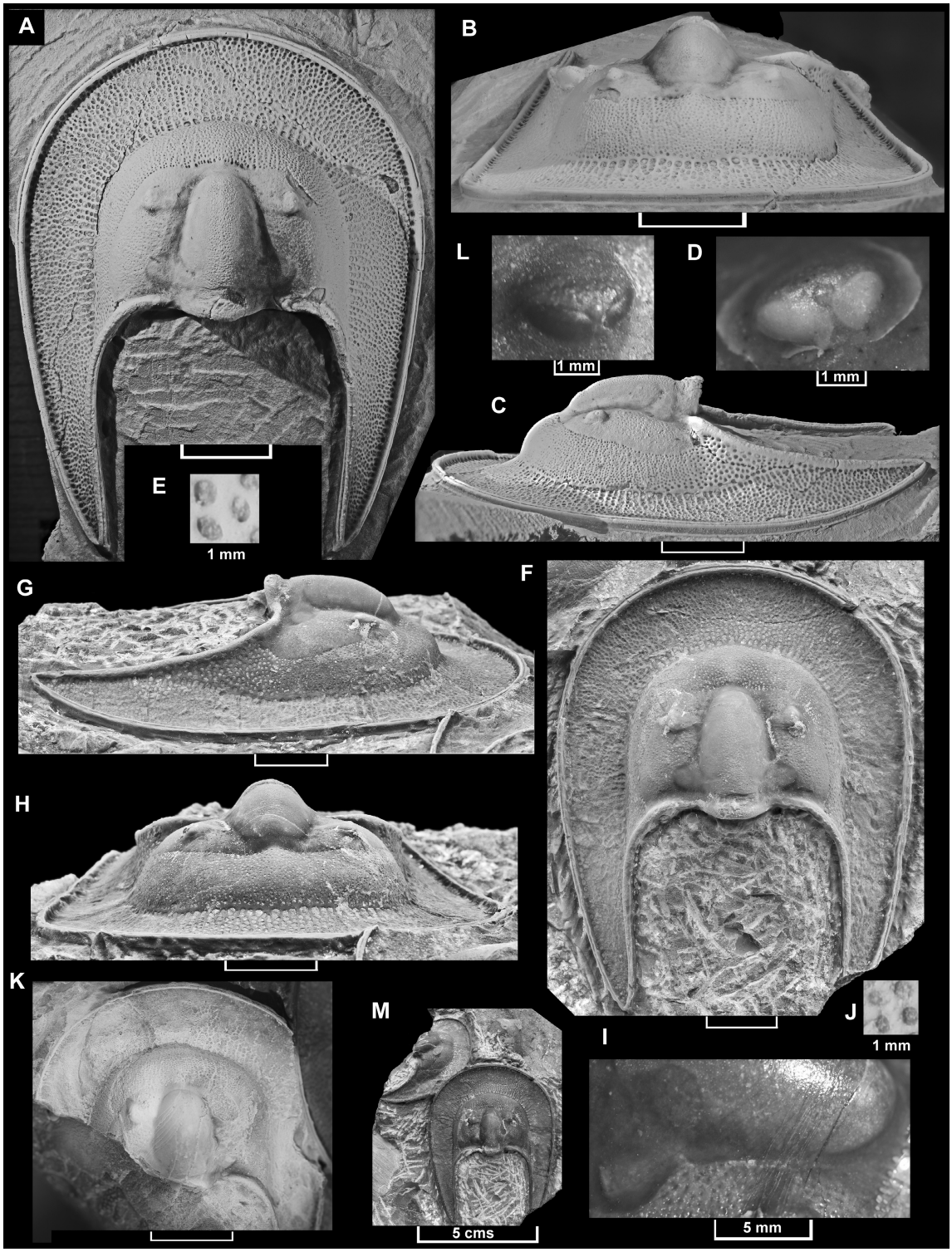


PLATE 11. A–M *Lioharpes morocconensis* n. sp.

A–E dorsal exoskeleton of cephalon only, **paratype**, NHMUK It 29272, from a lower Emsian horizon, Boutiskaouine Formation, Jbel el Otfal (Fig. 2B, Map 9, site17). A, dorsal, B, anterior and C, lateral view. D, lateral view of eye lobe and E, dorsal view of brim perforation.

F–J dorsal exoskeleton of cephalon only, **holotype**, NHMUK It 29271 (1), from type locality and horizon (Fig. 2B, Map 9, site 6). F, dorsal, G, lateral and H, anterior view. I, dorsal view of glabella and J dorsal view of brim perforation.

K–L dorsal exoskeleton of a partial cephalon, paratype, NHMUK It 29271 (2)), on same plate as holotype, K, dorsal view and L, lateral view of eye lobe. M, dorsal view of NHMUK It 29271 (1 and 2) plate.

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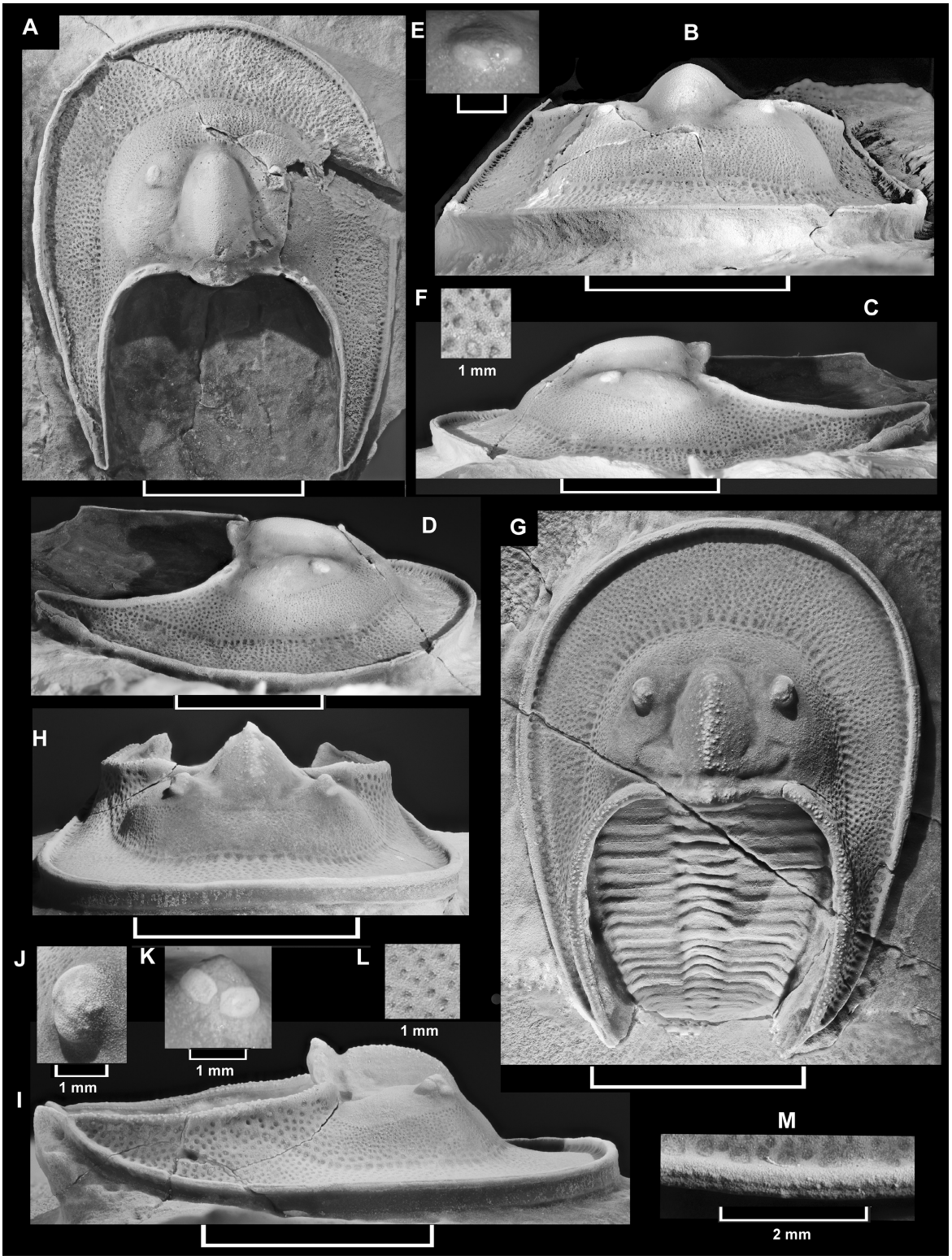


PLATE 12. A–F *Lioharpes* cf. *morocconensis*, from a lower Emsian horizon, Boutiskaouine Formation, 28.3 km SSW of Rissani (Fig. 2B, Map 14, site 10), dorsal exoskeleton of partial cephalon, NHMUK It 29273. A, dorsal, B, anterior and C and D, lateral view. E, lateral view of eye lobe and F, dorsal view of brim perforation.

G–M *Lioharpes ammari* n. sp., from an upper Emsian horizon, Tazoulait Formation, North flank of Jbel Ou-Driss (Fig. 2B, Map 4, site 9), dorsal exoskeleton with pygidium enrolled, **holotype,** NHMUK It 29263. G, dorsal, H, anterior and I, lateral view. J and K, dorsal and lateral views, respectively, of eye lobe. L and M, dorsal view of brim perforations and exterior rim, respectively.

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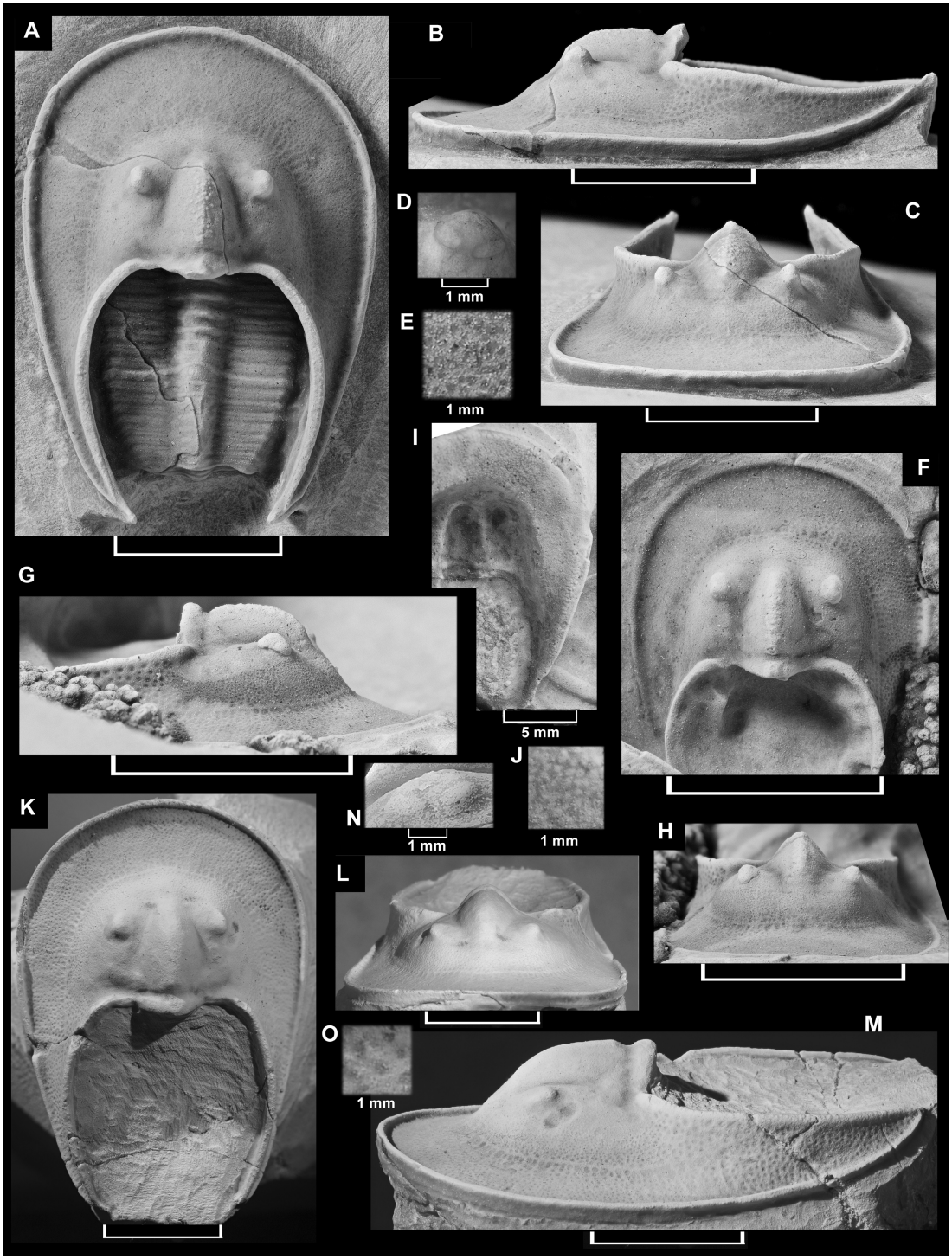


PLATE 13. A–J *Lioharpes ammari* n. sp., from horizon 2, Section 1 (Fig. 6), Tazoulait Formation, upper Emisian, South flank of Jbel Ou-Driss (Fig. 2B, Map 4). **A–E** dorsal exoskeleton, pygidium missing, **paratype,** NHMUK It 29264 (site 12). A, dorsal, B, lateral and C, anterior view. D, lateral view of eye lobe and E, dorsal view of brim perforations.

F–H dorsal exoskeleton of partial cephalon, **paratype**, NHMUK It 29265 (1) (site 13). F, dorsal, G, lateral and H, anterior view.

I–J ventral exoskeleton of a partial upper lamella, **paratype**, NHMUK It 29265 (2) (site 13). I, ventral view and J, lateral view of ventral surface.

K–O *Pinnuloharpes igaouii* n. sp., from a horizon 20 metres down slope from type horizon of *Lioharpes ammari* **n. sp.** Boutiskaouine Formation?, lower Emsian North flank of Jbel Ou-Driss (Fig. 2B Map 4 site 6). Dorsal exoskeleton of cephalon only, **paratype** NHMUK it 29267. K dorsal, L anterior and M lateral view. N lateral view of eye lobe and O dorsal view of brim perforations.

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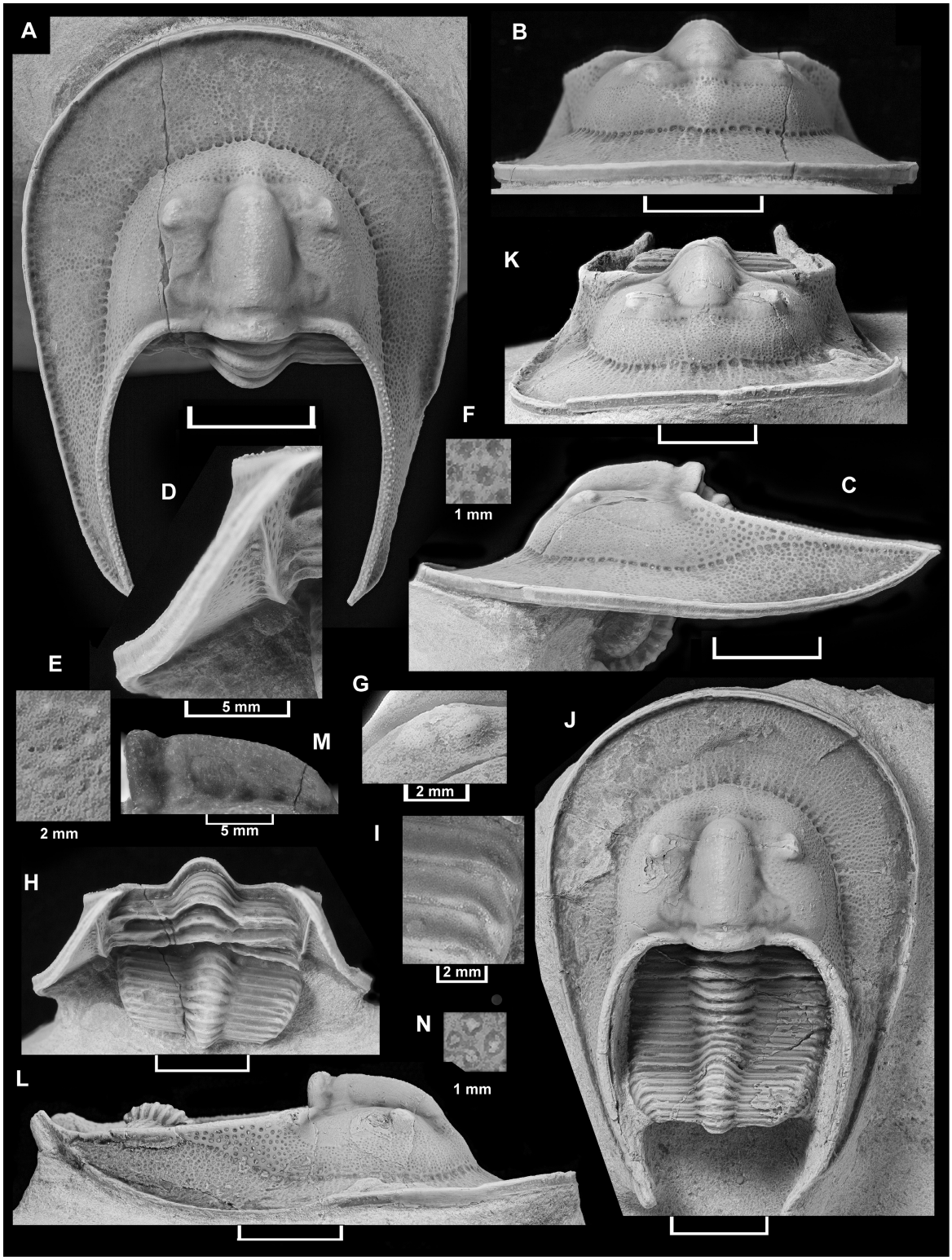


PLATE 14. A–N *Lioharpes saredra* n. sp., from "*Odontochile* Couche", Boutiskaouine Formation, Emsian, Jbel Saredrar (Fig. 2B, Map 5).

A–I dorsal exoskeleton, thorax disarticulated and enrolled, **holotype,** NHMUK It 29274 (site 1). A, dorsal, B, anterior, C, lateral and H, posterior view. D, posteroventral view of prolongation, E, dorsal surface of genal area. F, dorsal view of brim perforation, G, lateral view of eye lobe, I, dorsal lateral view of pleurae.

J–N dorsal exoskeleton with pygidium enrolled, **paratype,** NHMUK It 29275 (site 2). J, dorsal, K, anterior and L, lateral view. M, lateral view of glabella (uncoated) and N, dorsal view of brim perforations.

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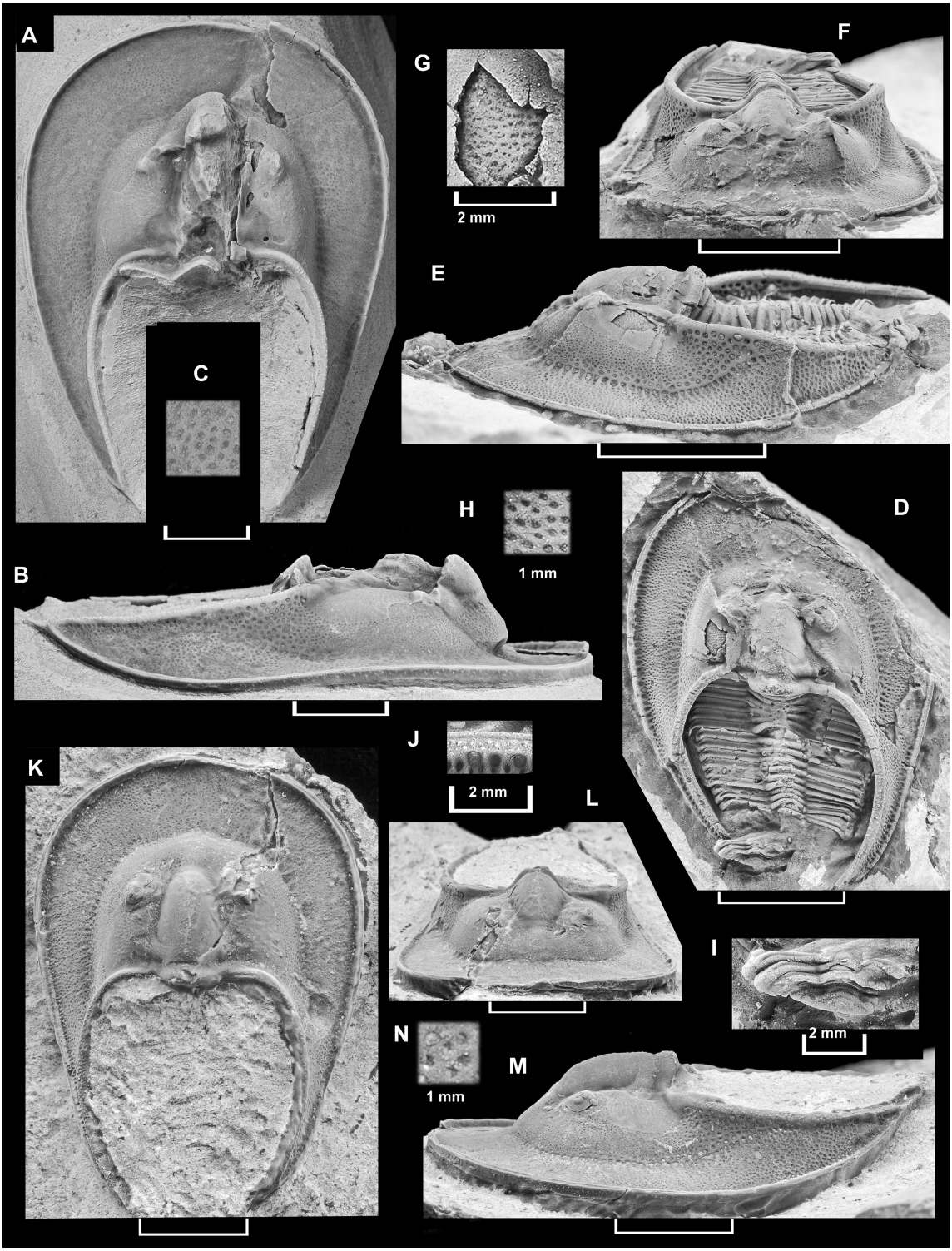


PLATE 15. A-N *Lioharpes saredra* n. sp.

A–C partial dorsal exoskeleton of cephalon from "*Odontochile* Couche" Boutiskaouine Formation, Emsian, Jbel Oufatene (Fig. 2B, Map 8, site 7), **paratype**, NHMUK it 29276. A, dorsal and B, lateral view. C, dorsal view of brim perforations. **D–J** disarticulated dorsal exoskeleton, from the *Destombina* Horizon, Tazoulait Formation, upper Emsian,Jbel Shebras (Fig. 2B, Map 12, site 1), **paratype**, NHMUK It 29278. D, dorsal, E, lateral and F, anterior view. Dorsal view of: G, genal area showing internal mould, H, brim perforations, I, pygidium and J external rim.

K–N dorsal exoskeleton of cephalon only, from coral at the top of the Pragian, Ihandar Formation, bou Lachrhal (Fig. 2B, Map 9, site 1), **paratype**, NHMUK It 29277. K, dorsal, L, anterior and M, lateral view. N, dorsal view of brim perforations. Scale bars shown represent 1 cm unless otherwise indicated.

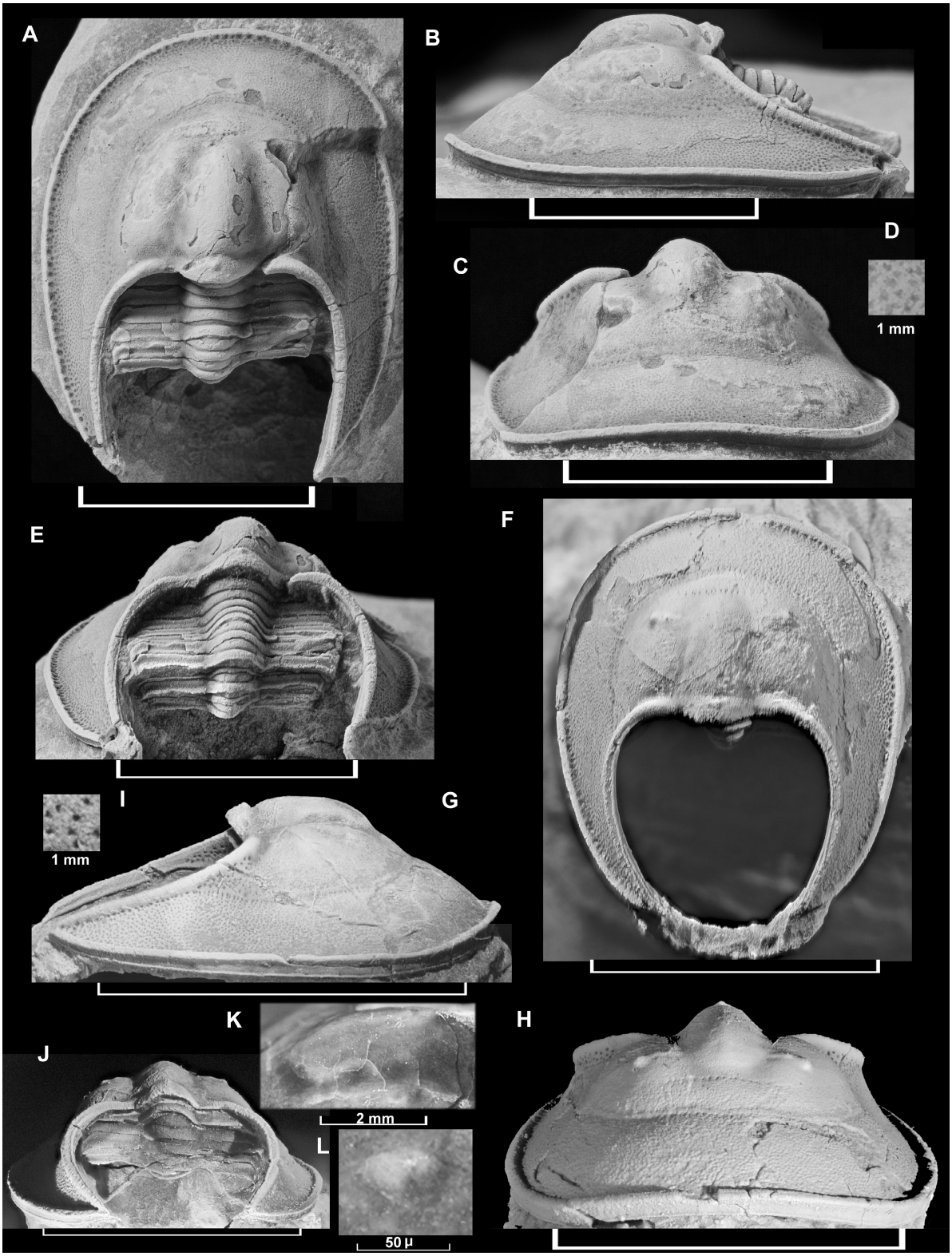


PLATE 16. A–L *Kielania tumula* n. sp., from a lower Pragian horizon, Ihandar Formation, Iminwasief, 4.6 km W of Jbel Ou-Driss (Fig. 2B, Map 4).

A–E dorsal exoskeleton, thorax disarticulated and enrolled, **holotype**, NHMUK It 29259 (site 1). A, dorsal, B, lateral, C, anterior and E, posterior view. D, dorsal view of brim perforations.

F–L dorsal exoskeleton, thorax disarticulated and enrolled, **paratype**, NHMUK It 29260 (site 2). F, dorsal, G, lateral, H, anterior and J, posterior view. I, dorsal view of brim perforations, K, lateral view of glabella (uncoated) and L, lateral view of eye lobe. Scale bars shown represent 1 cm unless otherwise indicated.

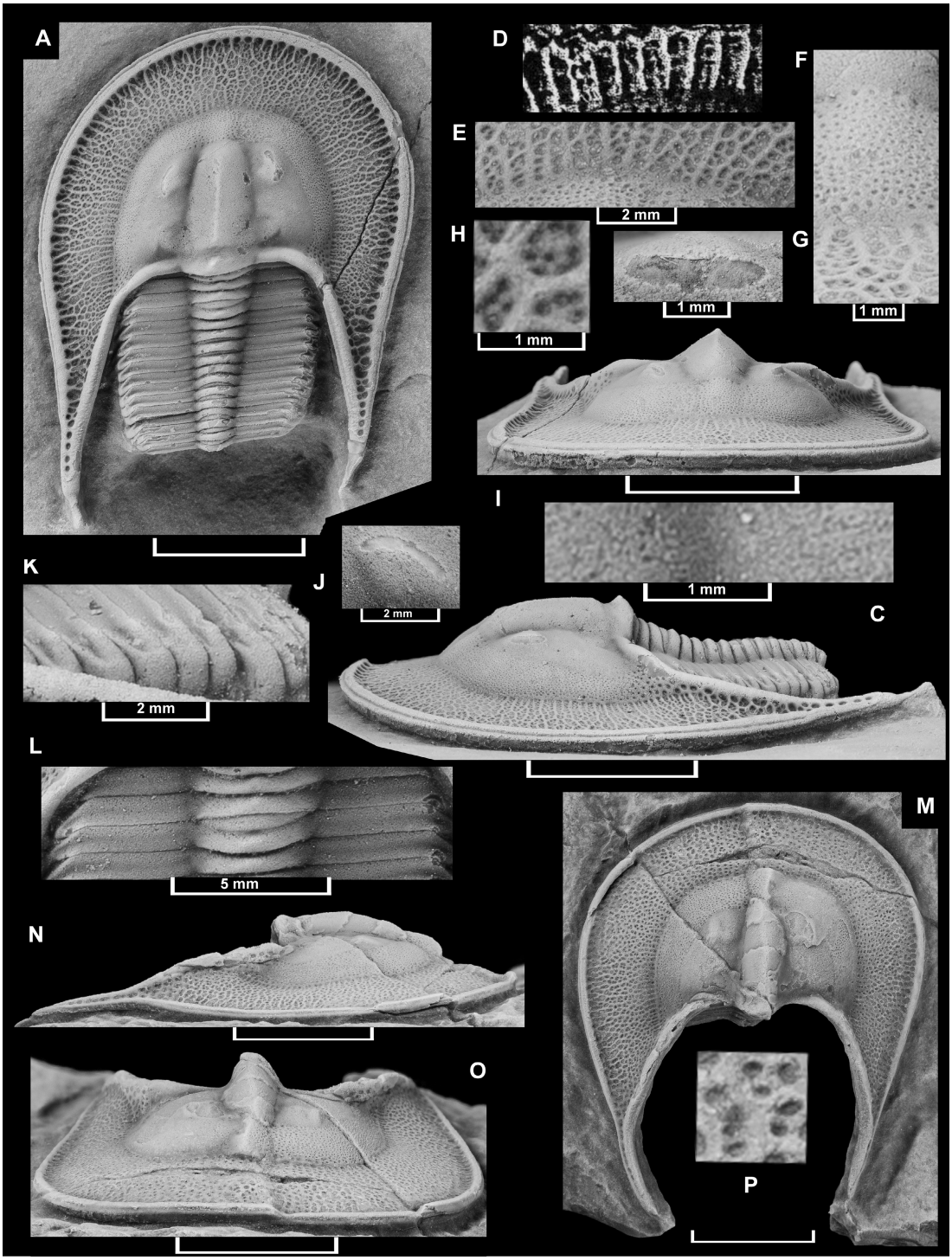


PLATE 17. A–K and **M–P *Helioharpes aougili* n. sp.**, from an Eifelian horizon, El Otfal Formation, Tamgoute Bulgan, 11.6 km SWt of El Jorf (Fig. 2B, Map 6).

A–K dorsal exoskeleton, pygidium missing, **holotype**, NHMUK It 29254 (site 16). A, dorsal, B, anterior and C, lateral view. D, dorsal view of brim proximal to girder across the anterior of genicranium, E, anterior view of perforations on brim and genal roll, F, dorsal view of brim perforations. G and H, lateral and dorsal view of eye lobe, respectively. I, dorsal view of cuticle on glabella and genal area. J and K, lateral and dorsal view of pleurae, respectively.

M–P dorsal exoskeleton of cephalon only, **paratype**, NHMUK It 29255 (site 17). M, dorsal, N, lateral and O, anterior view. P, dorsal view of brim perforation.

L, **H. *perradiatus***, dorsal view of brim proximal to girder across the anterior of genicranium (reprint), Richter & Richter, 1943, abb 2.

Scale bars shown represent 1 cm unless otherwise indicated.

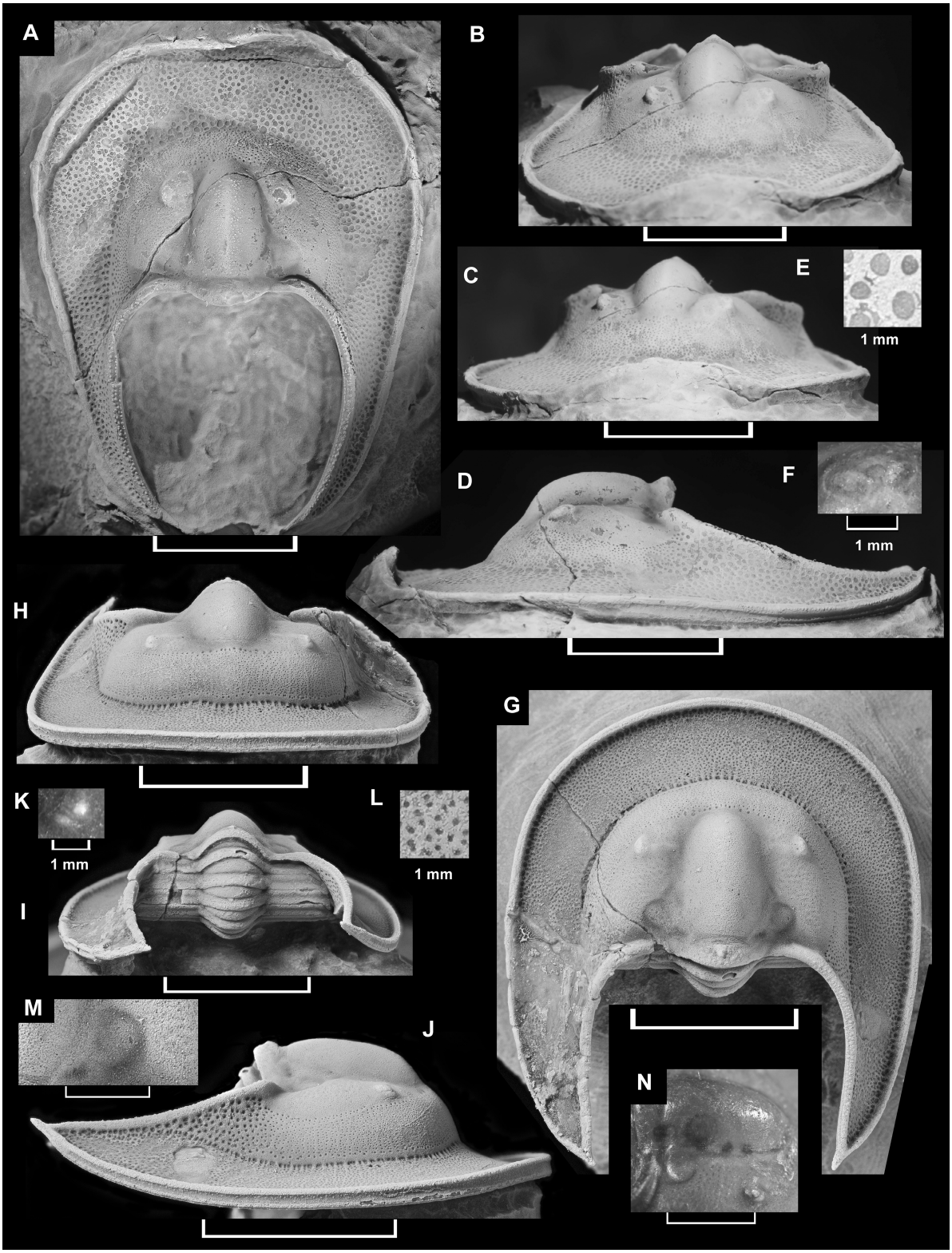


PLATE 18. A–F *Fritchaspis* edgecombei n. sp., dorsal exoskeleton of cephalon only, NHMUK It 29224, from "*Cherurid* Couche", Er Remlia Formation, lower Emsian, Jbel Issoumour (Fig. 2B, Map 7, site 19). A, dorsal, B, antero-dorsal, C, anterior and D, lateral view. E, dorsal view of brim perforation and F, lateral view of eye lobe.

G–N *Maghroharpes hammii* n. sp., dorsal exoskeleton, thorax enrolled, **holotype**, NHMUK It 29292, from an horizon below the "*Dicranurus* Couche", Ihandar Formation, Pragian, Jbel Oufatene (Fig. 2B, map 8, site 21). G, dorsal, H, anterior, J, lateral and I, posterior view. L, dorsal view of brim perforation, N, lateral view of glabella and muscle insertion scars and M, dorsal view of cuticle on glabella, genal area, ala, occipital ring and posterior border.

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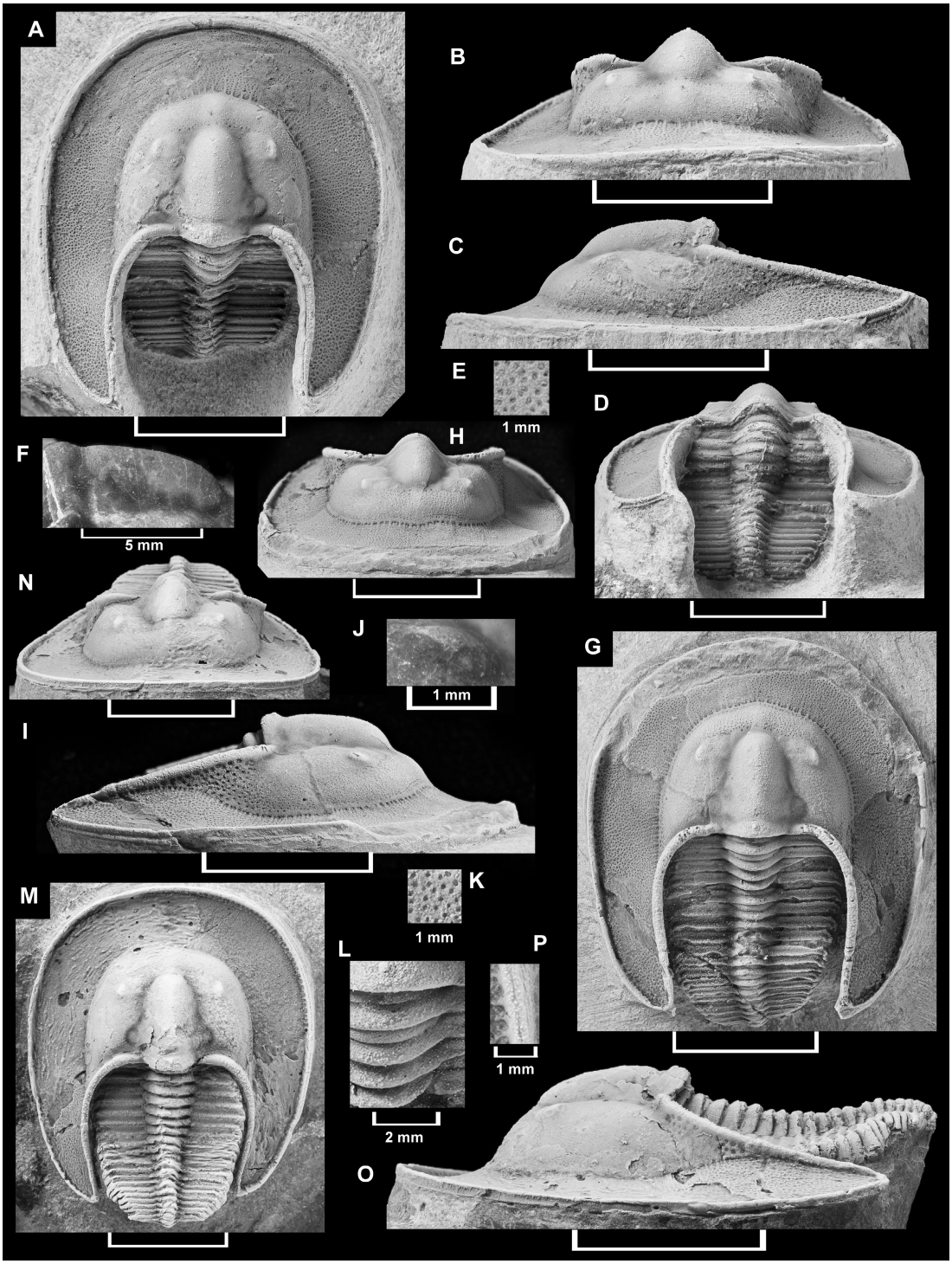


PLATE 19. A–O *Maghroharpes hammii* n. sp.

A–F dorsal exoskeleton with pygidium enrolled, **paratype**, NHMUK It 29296, from main trilobite 'couche' Ihandar Formation, Pragian, southern flank of Jbel el Mrakib (Fig. 2B, Map 9, site 16). A, dorsal, B, anterior, C, lateral and D, posterior view. E, dorsal view of brim perforations and F, lateral view of muscle insertion scars on glabella (uncoated).

G–L dorsal exoskeleton with pygidium enrolled, **paratype**, NHMUK It 29294, from a *Ceratonurus* horizon, Ihandar Formation, Pragian, Jbel Remlia (Fig. 2B, Map 9, site 12). G, dorsal, H, anterior and I, lateral view. J, lateral view of eye lobe (uncoated), K, dorsal view of brim perforations, dorsal view of tubercles on axial rings.

M–O dorsal exoskeleton with pygidium missing, **paratype**, NHMUK It 29295, from main trilobite 'couche', Ihandar Formation, Pragian, southern flank of Jbel el Mrakib (Fig. 2B, Map 9, site 15). M, dorsal, N, anterior and O, lateral view. P, dorsal view of tubercles on rim.

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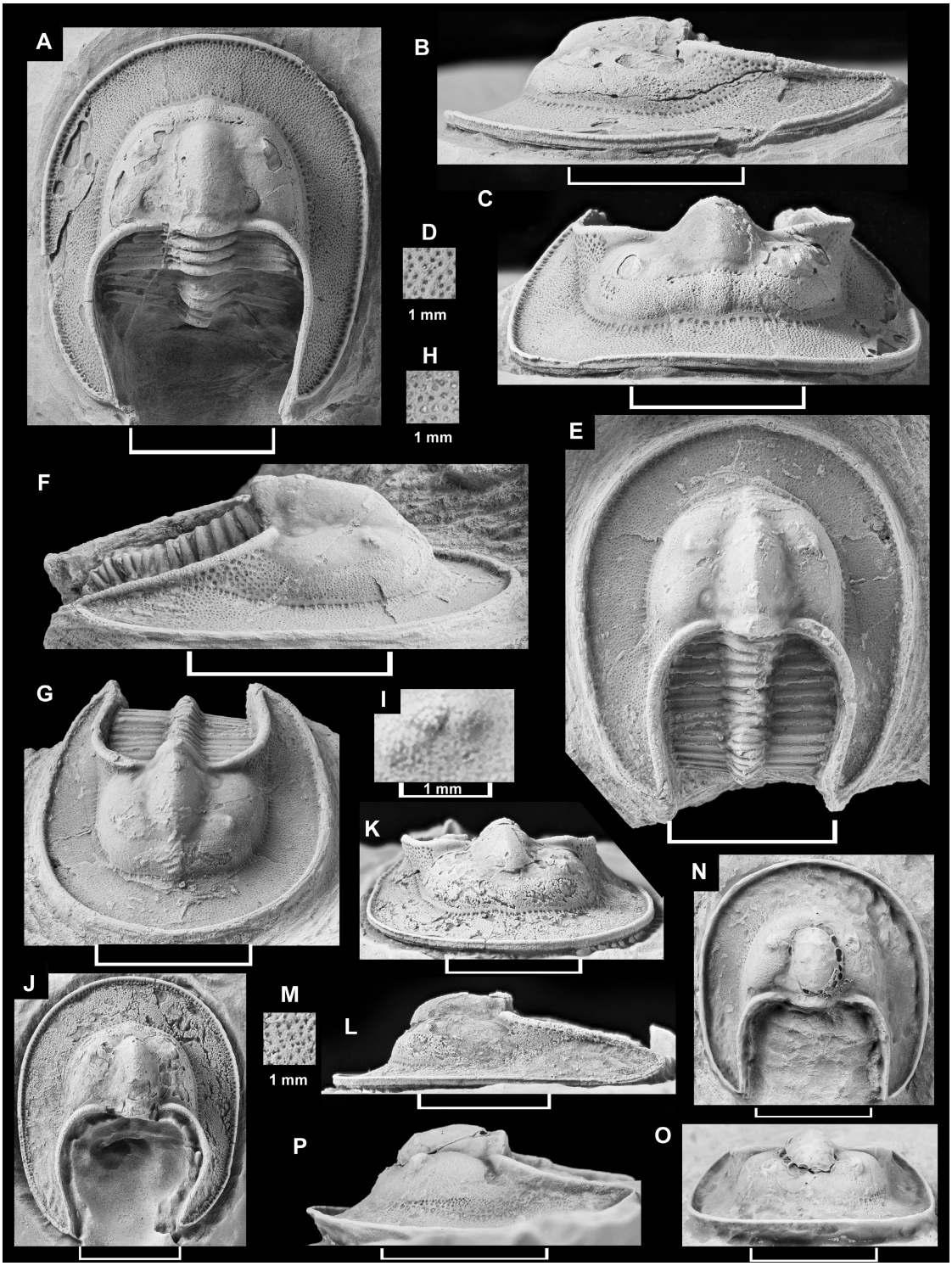


PLATE 20. A–O *Maghroharpes hammii* n. sp., from Ihandar Formation, Pragian. **A–D** dorsal exoskeleton, cephalon and disarticulated thorax, **paratype**, NHMUK It 29290, from Jbel Oufatene (Fig. 2B, Map 8, site 8). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations and F, lateral view of muscle insertion scars on glabella (uncoated).
E–I dorsal exoskeleton with pygidium enrolled, **paratype**, NHMUK It 29300, from North Zireg (Fig. 2B, Map 13, site 1). E, dorsal, F, lateral and G, anterior view. H, dorsal view of brim perforations, I, lateral view of eye lobe.
J–M dorsal exoskeleton of cephalon, **paratype**, NHMUK It 29291, from Jbel Oufatene (Fig. 2B, Map 8, site 9). J, dorsal, K, anterior and L, lateral view. M, dorsal view of brim perforations.
N–P upper lamella only, **paratype**, NHMUK It 29293, from an horizon between the "*Dicranurus* Couche" and the "*Kolihapeltis* Couche", Talhadjate, Jbel Oufatene (Fig. 2B, Map 8, site 22). N, dorsal, O, anterior and P, lateral view.
Scale bars shown represent 1 cm unless otherwise indicated.

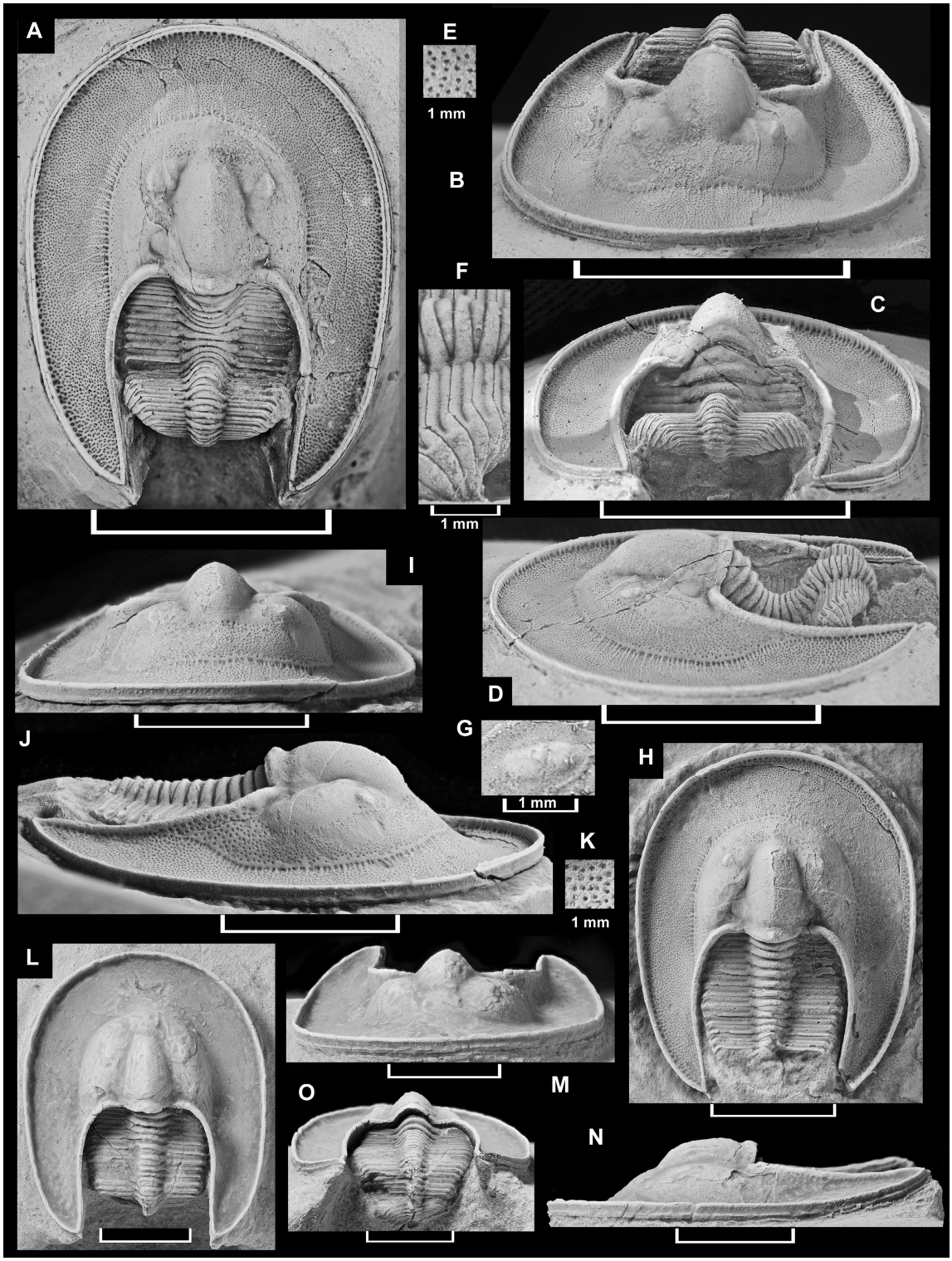


PLATE 21. A–O *Maghroharpes laatchanensis* n. sp., from Ihandar Formation, Pragian.

A–G dorsal exoskeleton pygidium enrolled, **holotype**, NHMUK It 29308, from "*Kolihapeltis* Couche" ,Oued el Atchane Jbel Oufatene (Fig. 2B, Map 8, site 15). A, dorsal, B, anterior, C, posterior and D, lateral view. E, dorsal view of brim perforations and F, lateral view of axial rings and pleurae.

H–K dorsal exoskeleton with pygidium missing, **paratype**, NHMUK It 29307 from type locality (Fig. 2B, Map 8, site 13). H, dorsal, I, anterior and J, lateral view. K, dorsal view of brim perforations.

L–O dorsal exoskeleton with pygidium disarticulated, **paratype**, NHMUK It 29306, from type locality (Fig. 2B, Map 8, site 3). L, dorsal, M, anterior, N, lateral and O, posterior view.

Scale bars shown represent 1 cm unless otherwise indicated.

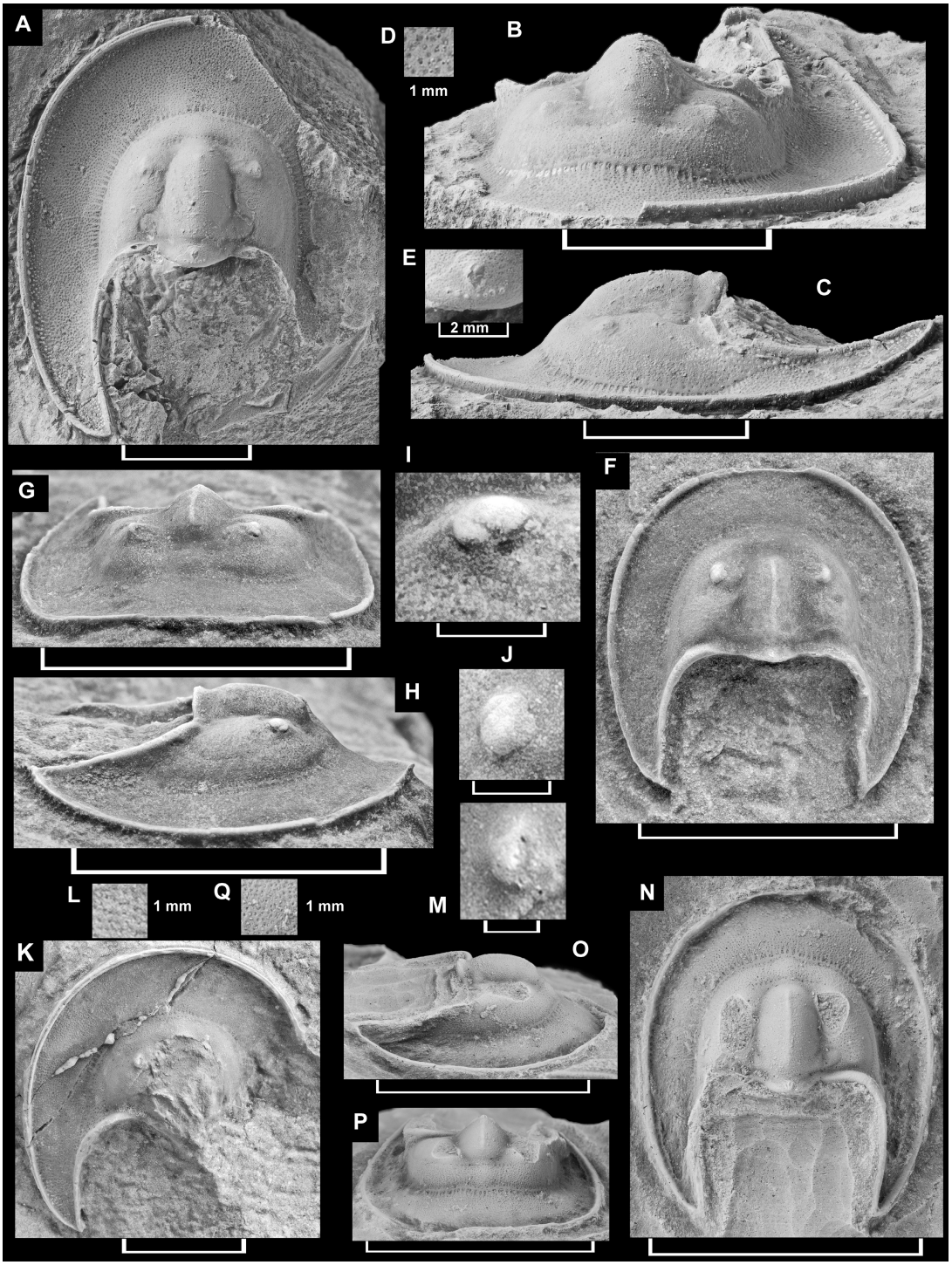


PLATE 22. A–E *Maghroharpes* cf. 1 *laatchanensis*, Ihandar Formation, Pragian, Jbel el Otfal (Fig. 2B, Map 9, site 8), dorsal exoskeleton of partial cephalon, NHMUK It 29311. A, dorsal, B, anterior and C, lateral view. D and E, dorsal view of brim perforations and occipital node and tubercles, respectively.

F–M *Maghroharpes* aff.1 *minutipunctus*, Boutiskaoine Formation? lower Emsian. **F–J** dorsal exoskeleton of partial cephalon, NHMUK It 29322, Jbel Ou-Driss (North) (Fig. 2B, Map 4, site 7). F, dorsal, G, anterior and H, lateral view. I, lateral and J, dorsal view of eye lobe.

K–M dorsal exoskeleton of partial cephalon, **paratype**, NHMUK It 29323, Boutiskaouine Formation, lower Emsian, Ahware (Fig. 2B, Map 9, site 13). K, L and M, dorsal view of cephalon, brim perforations and eye lobe, respectively.

N–Q *Maghroharpes* aff. 2 *minutipunctus*, Ihandar Formation Jbel Ou-Driss (West) (Fig. 2B, Map 4, site 20), dorsal exoskeleton of partial cephalon, NHMUK It 29324. N, dorsal, O, lateral and P, anterior view. Q, dorsal view of brim perforations.

Scale bars shown represent 1 cm unless otherwise indicated.

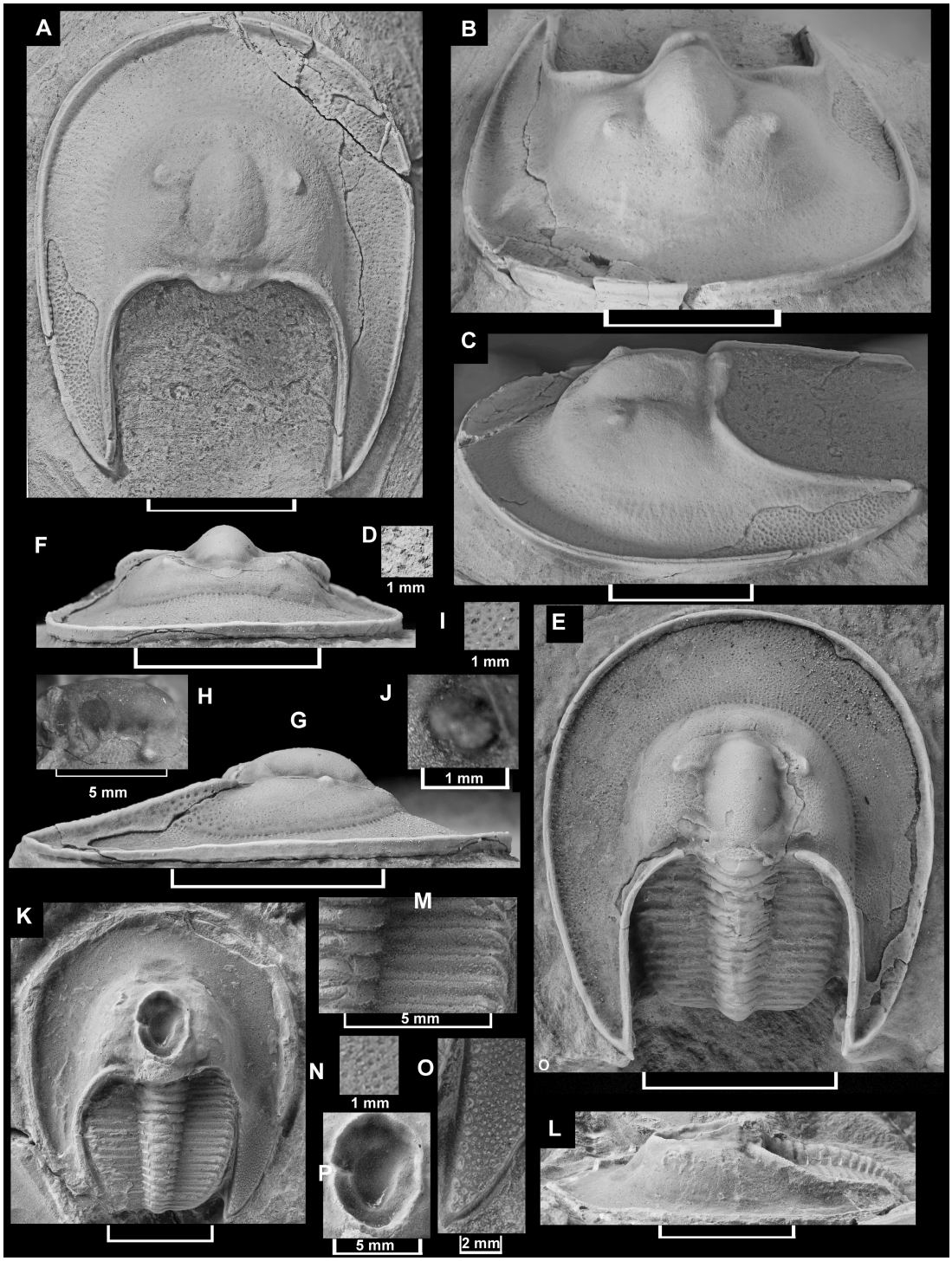


PLATE 23. A–D *Maghroharpes* aff. *zguidensis*, dorsal exoskeleton of partial cephalon, **holotype**, NHMUK It 29287, from Ihandar Formation, bou Lachrhal (Fig. 2B, Map 9, site 5). A, dorsal, B, anterior and C, lateral view. D, dorsal view of brim perforations.

E–P *Maghroharpes minutipunctatus* n. sp.

E–J holotype, NHMUK It 29312, from "Dicranurus Couche", Ihandar Formation, Pragian, El Atchane, Jbel Oufatene (Fig. 2B, Map 8, site 11), dorsal exoskeleton. E, dorsal, F, anterior and G, lateral view. H, lateral view of glabella (uncoated), I, dorsal view of brim perforations and J, lateral view of eye lobe.

K–P paratype, NHMUK It 29313, from type locality (Fig. 2B, Map 8, site 12), partial dorsal exoskeleton with pygidium enrolled. K, dorsal and L, lateral view. M, N, O, and P, dorsal view of pleurae, brim perforations, lower lamella and hypostome, respectively.

Scale bars shown represent 1 cm unless otherwise indicated.

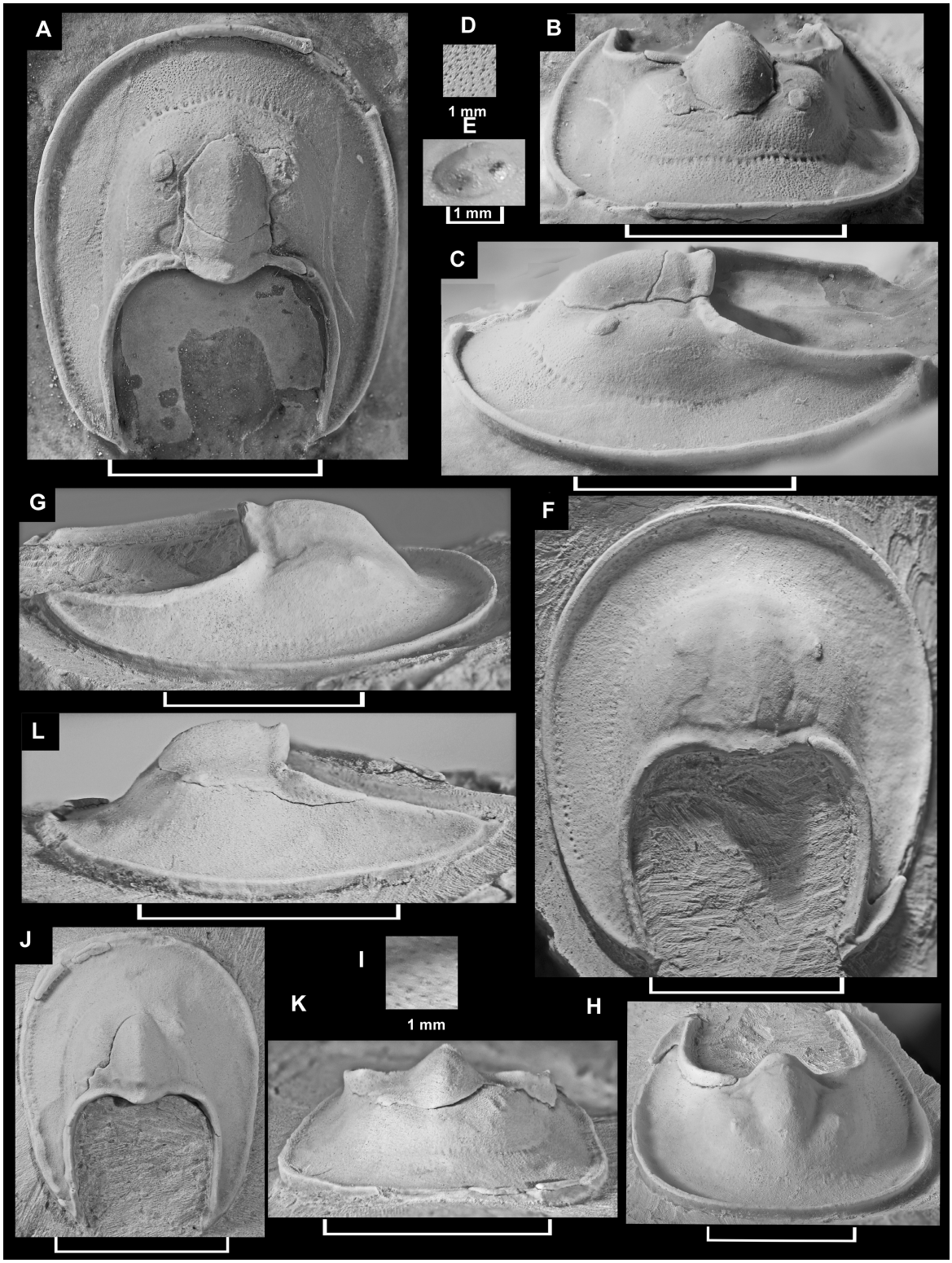


PLATE 24. A– L *Maghroharpes zguidensis* n. sp., Merzâ Akhsai Formation?, Pragian, Foum Zguid.

A–E dorsal exoskeleton of partial cephalon, **holotype**, NHMUK It 29325 (Fig. 2A, Map 2, site1). A, dorsal, B, anterior and C, lateral view. D, dorsal view of brim perforations.

F– I dorsal exoskeleton of cephalon, **paratype**, NHMUK It 29326, from type locality (Fig. 2A, Map 2, site 2). F, dorsal, G, lateral and H, anterior view. I, dorsal view of brim perforations.

J–L dorsal exoskeleton of cephalon, **paratype**, NHMUK It 29327, from type locality (Fig. 2A, Map 2, site 3). J, dorsal, K, anterior and L, lateral view.

Scale bars shown represent 1 cm unless otherwise indicated.

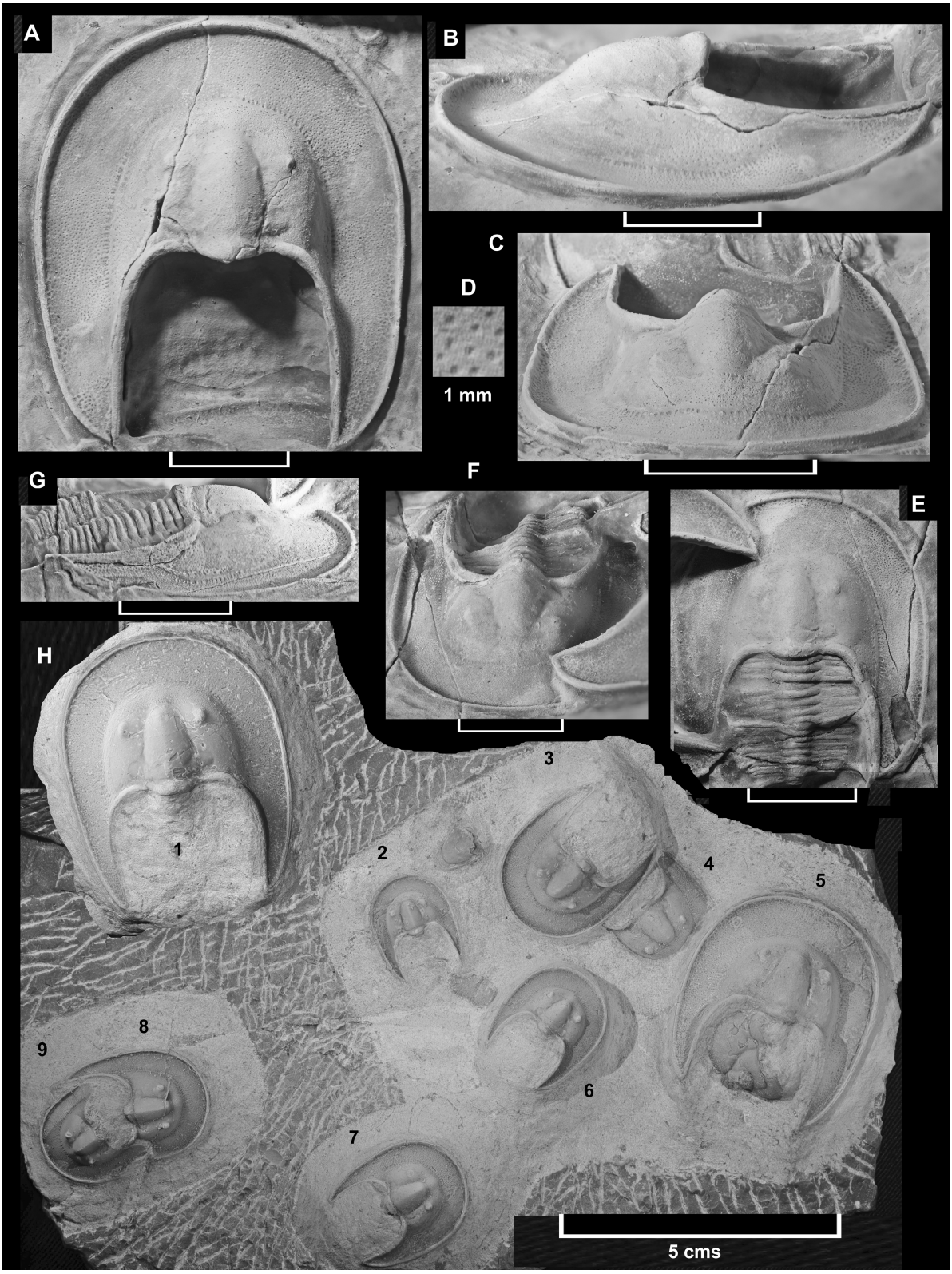


PLATE 25 A–G *Maghroharpes* cf. 2 *laatchanensis*, Merzâ Akhsai Formation?, Pragian, Foum Zguid.
A–D dorsal exoskeleton of cephalon only, NHMUK It 29310 (i), from Foum Zguid (Fig. 2A, Map 1, site 4). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations.
E–G dorsal exoskeleton of cephalon and disarticulated thorax, NHMUK It 29310 (ii), on the same plate as NHMUK It 29310 (i). E, dorsal, F, anterior and G, lateral view. **H *Maghroharpes oufatenensis* n. sp.**, from coral at top of Pragian, Ihandar Formation, Oued el Atchane**,** Jbel Oufatene (Fig. 2B, Map 8, site 2), 9 cephala only, **paratypes**, NHMUK It 29318 (1 to 9), dorsal view of cephala. Scale bars shown represent 1 cm unless otherwise indicated.

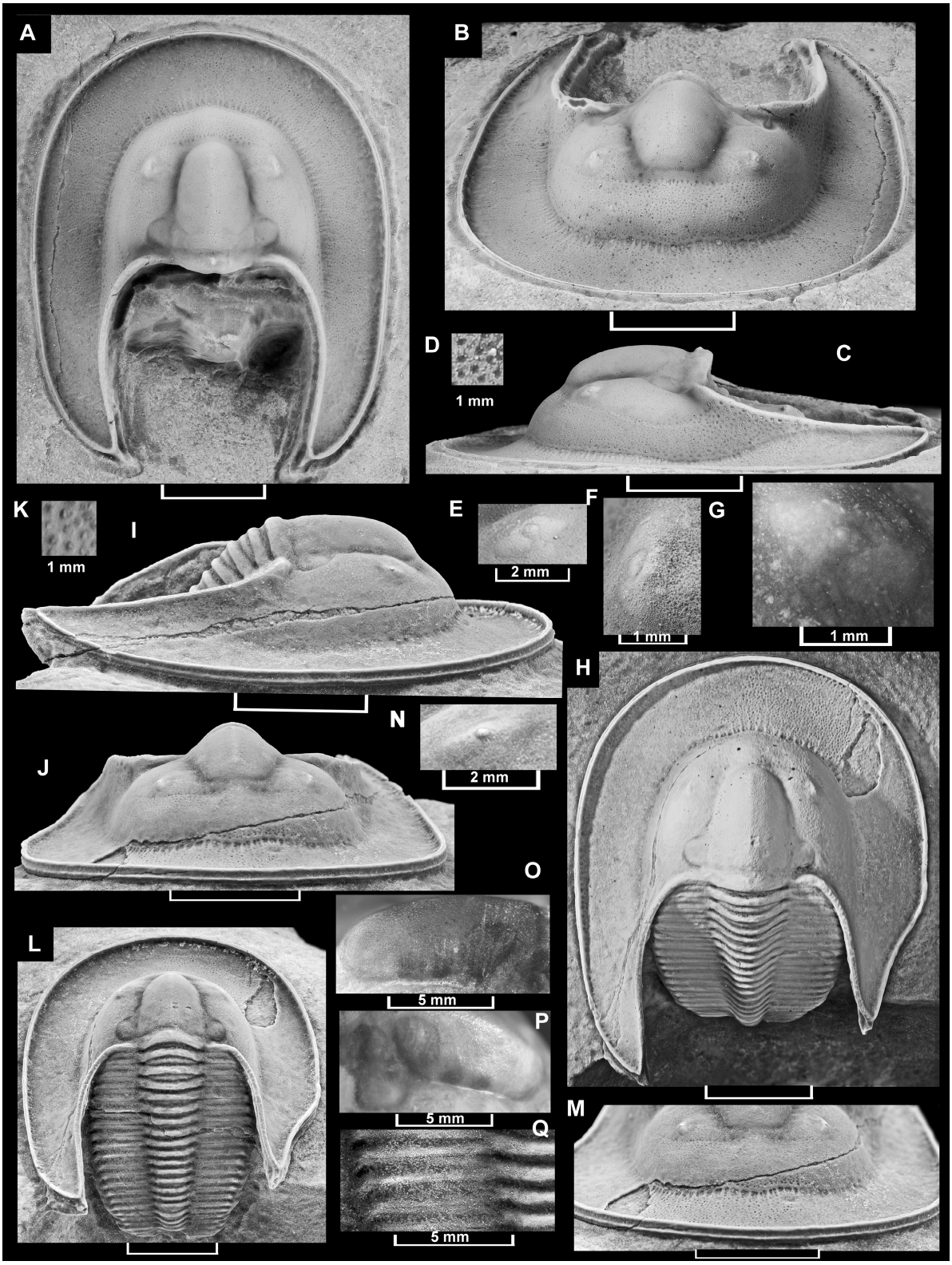


PLATE 26. A–Q *Maghroharpes ihmadii* n. sp., Ihandar Formation, Pragian, Jebl Ou-Driss.

A–G dorsal exoskeleton of cephalon, **holotype**, NHMUK It 29301 (Fig. 2B, Map 4, site 16). A, dorsal, B, anterior and C, lateral view. D, dorsal view of brim perforations. Eye lobe in lateral view E and G, and in dorsal view, F.

H–Q dorsal exoskeleton with pygidium enrolled, **paratype**, NHMUK It 29302 (Fig. 2B, Map 4, site 17). H, dorsaI, I, lateral, J, anterior and L, posterior-dorsal view. K and Q, dorsal view of brim perforations and pleurae, respectively, M, anterior dorsal view, O and P, lateral views of muscle insertion scars on glabella. N, lateral view of eye lobe.

Scale bars shown represent 1 cm unless otherwise indicated.

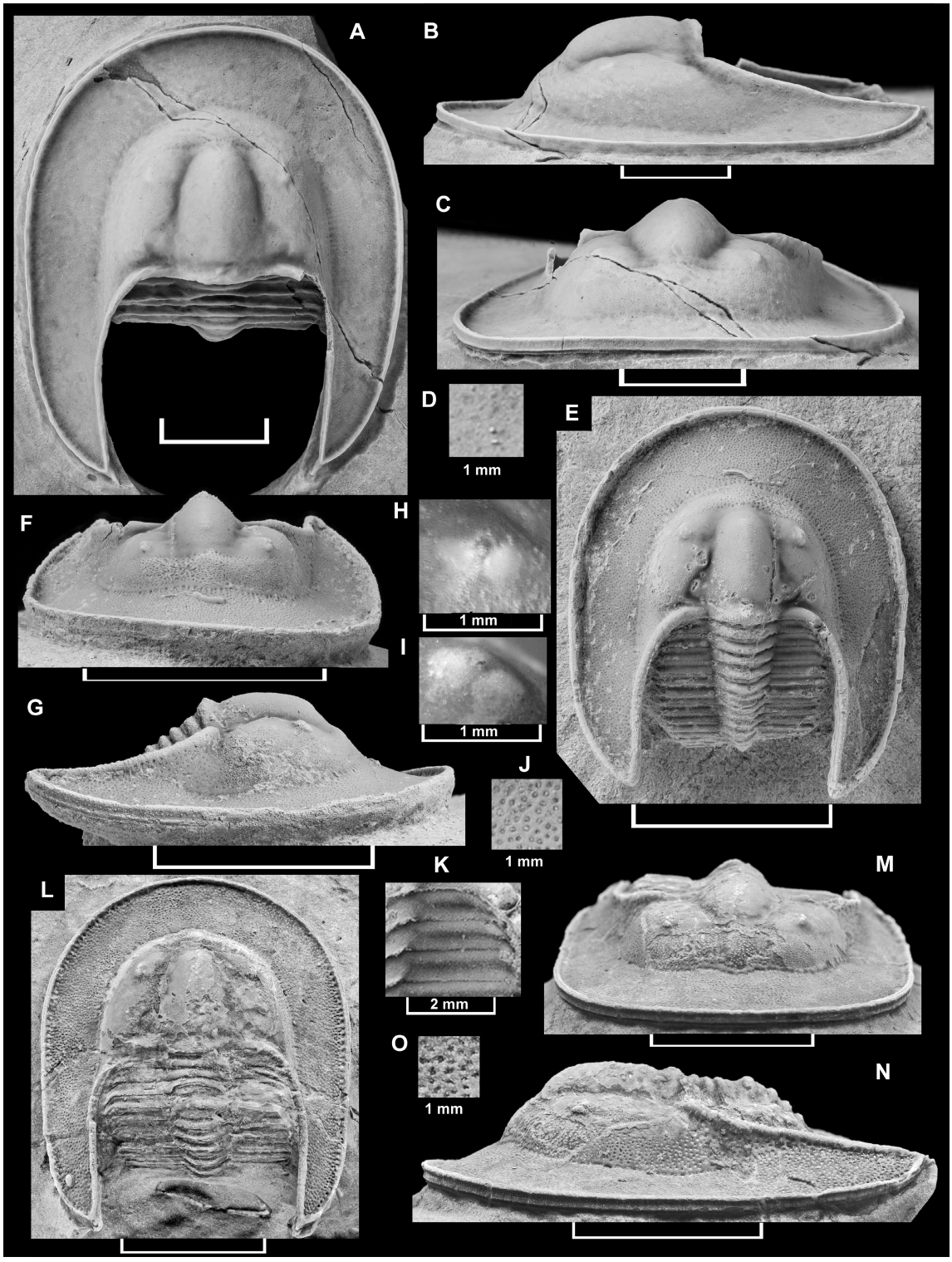


PLATE 27. A–D *Maghroharpes ihmadii* n. sp., dorsal exoskeleton of cephalon and disarticulated thorax, **paratype**, NHMUK It 29303, from type horizon and locality, Ihandar Formation, Pragian. Jbel Ou-Driss (Fig. 2B, Map 4, site 18). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations.

E–K *Maghroharpes* cf. *ihamadii*, dorsal exoskeleton pygidium enrolled, NHMUK It 29304, from "*Kolihapeltis* Couche", Ihandar Formation, Pragian, Jbel Oufatene (Fig. 2B, Map 8, site 14). E, dorsal, F, anterior and G, lateral view. H, dorsal and I, lateral view of eye lobe. J and K, dorsal view of brim perforations and pleurae, respectively. **L–O *Magroharpes hammii***, dorsal exoskeleton, thorax and disarticulated pygidium, NHMUK It 29297, from Ihandar Formation, Iminwasief (Fig. 2B, Map 4, site 4). L, dorsaI, M, anterior, N, lateral view. O, dorsal view of brim perforations.

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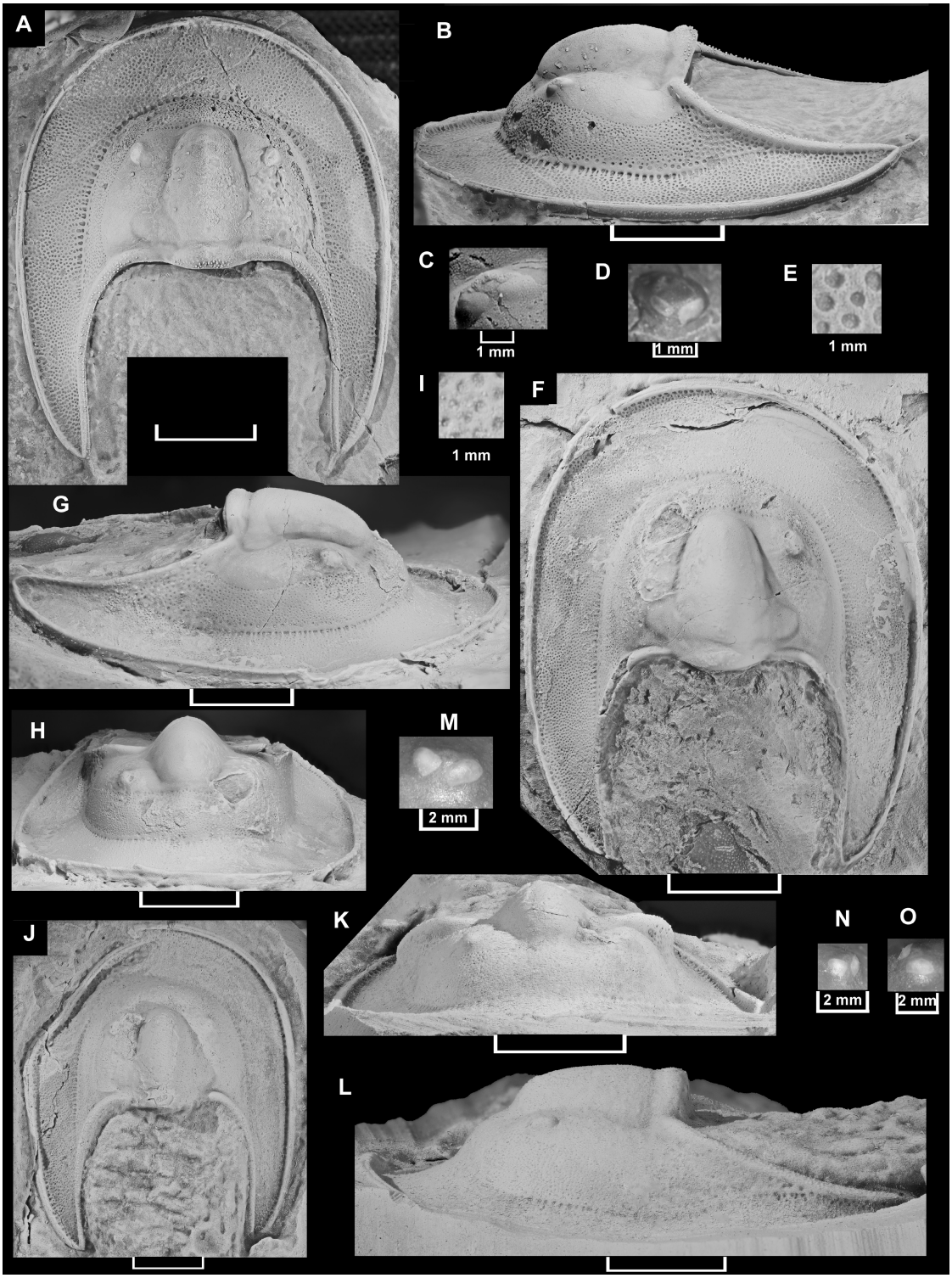


PLATE 28. A–O *Maghroharpes oufatenensis* n. sp.,

A–E dorsal exoskeleton of cephalon, **holotype**, NHMUK It 29320 (1), from lower Pragian horizon, Hamar Laghdad (Fig. 2B, Map 11, site 8). A, dorsal and B, lateral view. C, lateral view and D, (uncoated) dorsal-lateral view of eye lobe, respectively. E, dorsal view of brim perforations.

F–I dorsal exoskeleton of partial cephalon, **paratype**, NHMUK It 29316, Ihandar Formation, Jbel Oufatene (Fig. 2B, Map 8, site 23). F, dorsal, G, lateral and H, anterior view. I, dorsal view of brim perforations.

J–O dorsal exoskeleton of partial cephalon, **paratype**, NHMUK It 29319, Ihandar Formation, Jbel Oufatene (Fig. 2B, Map 8, site 24). J, dorsal, K, anterior and L, lateral view. M, N and O, eye lobe in lateral, anterior lateral and posterior lateral view, respectively.

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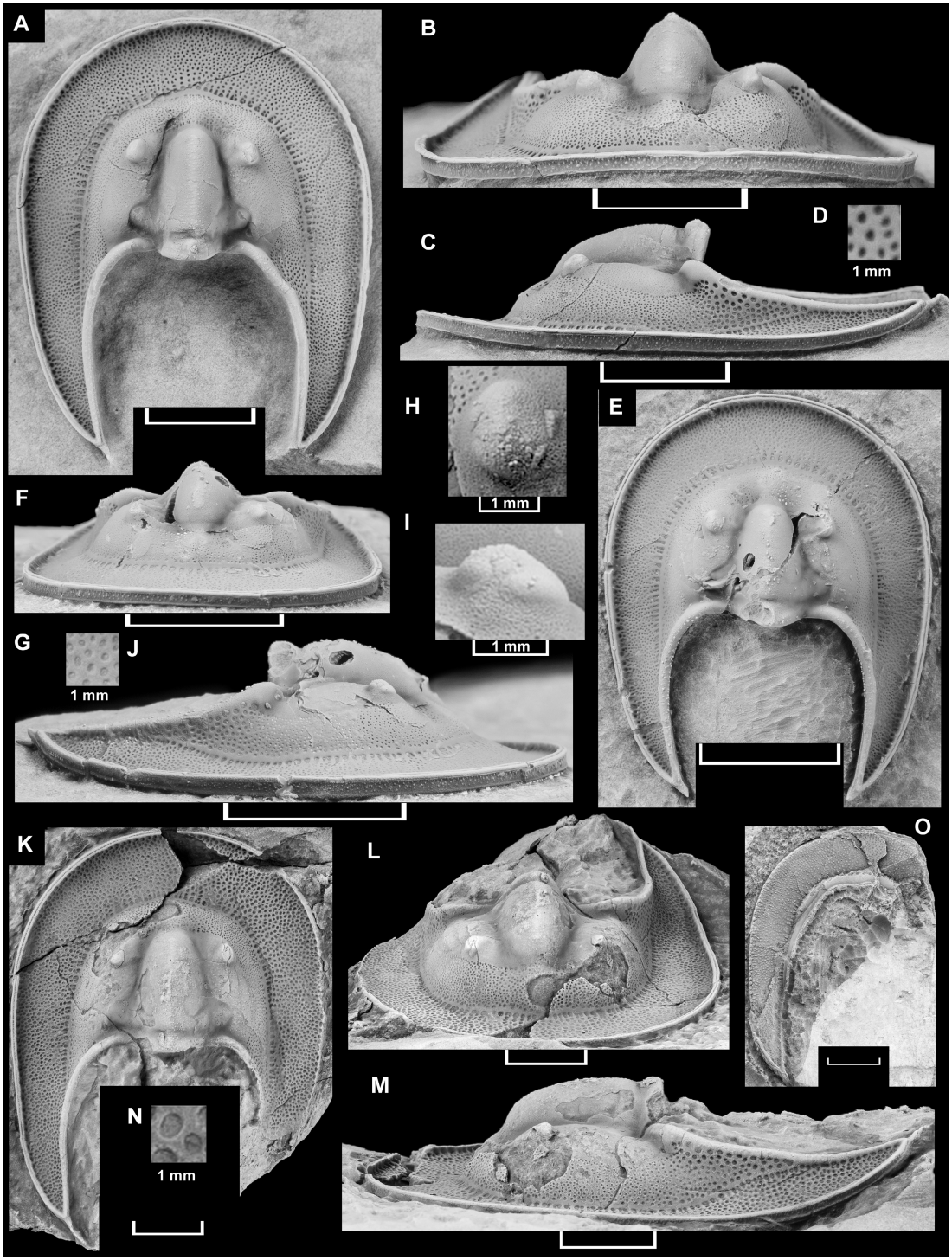


PLATE 29. A–D *Maghroharpes forteyi* n. sp., from top of Pragian, Ihandar Formation, El Atchane Jbel Oufatene, dorsal exoskeleton of cephalon, **holotype**, NHMUK It 29288 (Fig. 2B, Map 8, site 16). A, dorsal B, anterior and C, lateral view. D, dorsal view of brim perforations.

E–J,O *Maghroharpes azmamarensis* n. sp., from top of Pragian, Ihandar Formation, Oued el Atchane Jbel Oufatene, dorsal exoskeleton of cephalon, **holotype**, NHMUK It 29281 (Fig. 2B, Map 8, site 18). E, dorsal, F, anterior and G, lateral view. H, dorsal and I, lateral view of eye lobe, respectively. J, dorsal view of brim perforations. O, from type locality partial dorsal exoskeleton of lower Lamella, **paratype** NHMUK It 29283 (Fig. 2B, Map 8, site 19)).

K–N *Maghroharpes forteyi,* from top of Pragian, Ihandar Formation, bou Lachrhal, dorsal exoskeleton of partial cephalon only, **paratype**, NHMUK It 29289 (Fig. 2B, Map 9, Site 7). K, dorsal, L, anterior and M, lateral view. N, dorsal view of brim perforations.

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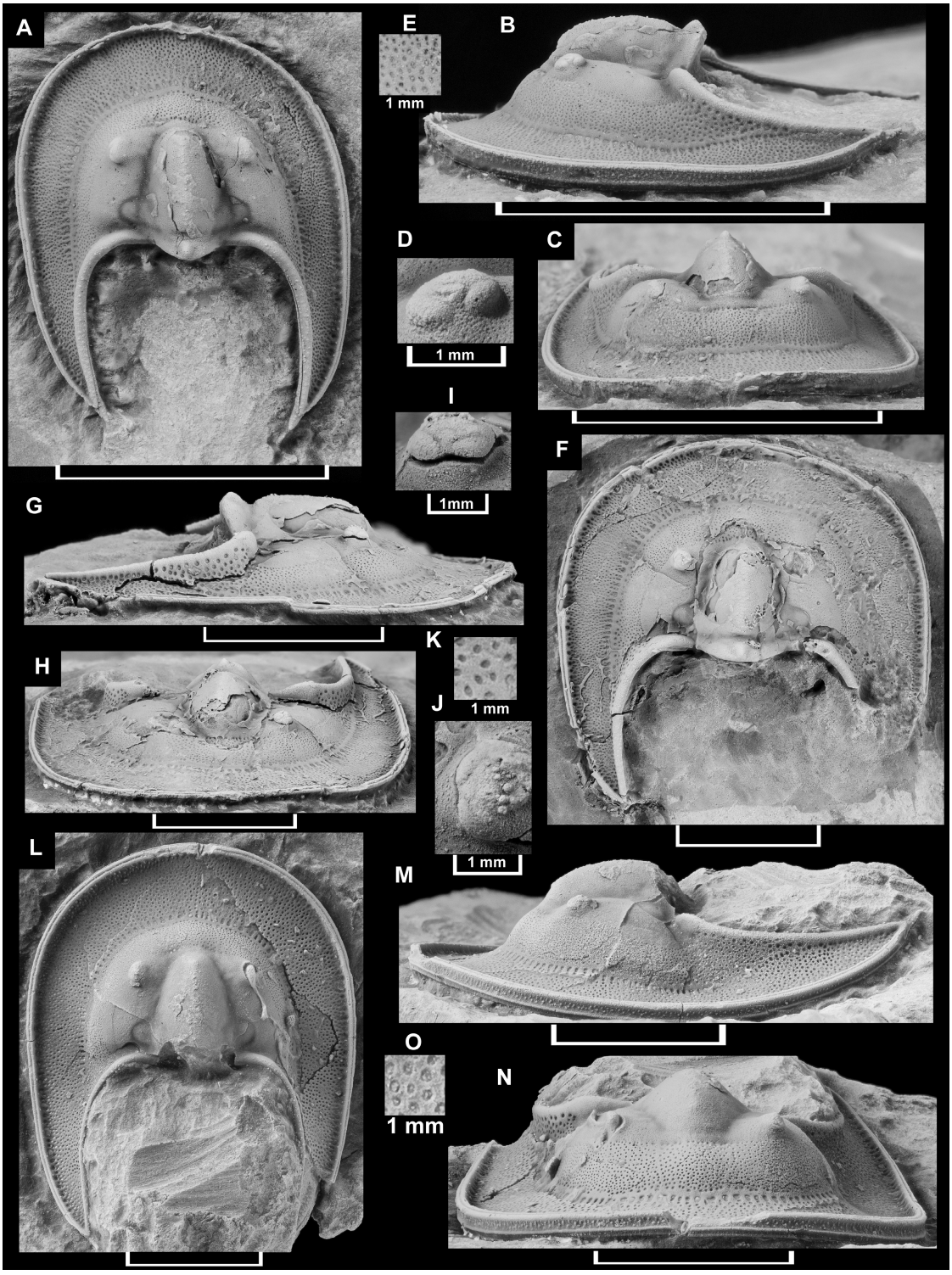


PLATE 30. A–E *Maghroharpes azmamarensis* n. sp., from type locality and horizon, Ihandar Formation, Pragian, dorsal exoskeleton of cephalon, **paratype**, NHMUK It 29282 (Fig., 2B, Map 8, site 19). A, dorsal, B, lateral and C, anterior view. D, lateral view of eye lobe and E, dorsal view of brim perforations.

F–K *Maghroharpes* cf. 1 **azmamarensis**, from top of Pragian, Ihandar Formation, El Atchane Jbel Oufatene, dorsal exoskeleton of partial cephalon, NHMUK It 29285 (Fig. 2B, Map 8, site 17). F, dorsal, G, lateral and H, anterior view. I, lateral and J, dorsal view of eye lobe, respectively. K, dorsal view of brim perforations.

L–O *Maghroharpes* cf. 2 *azmamarensis*, from an upper Pragian horizon, Ihandar Formation, Maharch, Jbel Mrakib, dorsal exoskeleton of partial cephalon, NHMUK It 29286 (Fig. 2B, Map 9, site 14). L, dorsal, M, lateral and N, anterior view. O, dorsal view of brim perforations.

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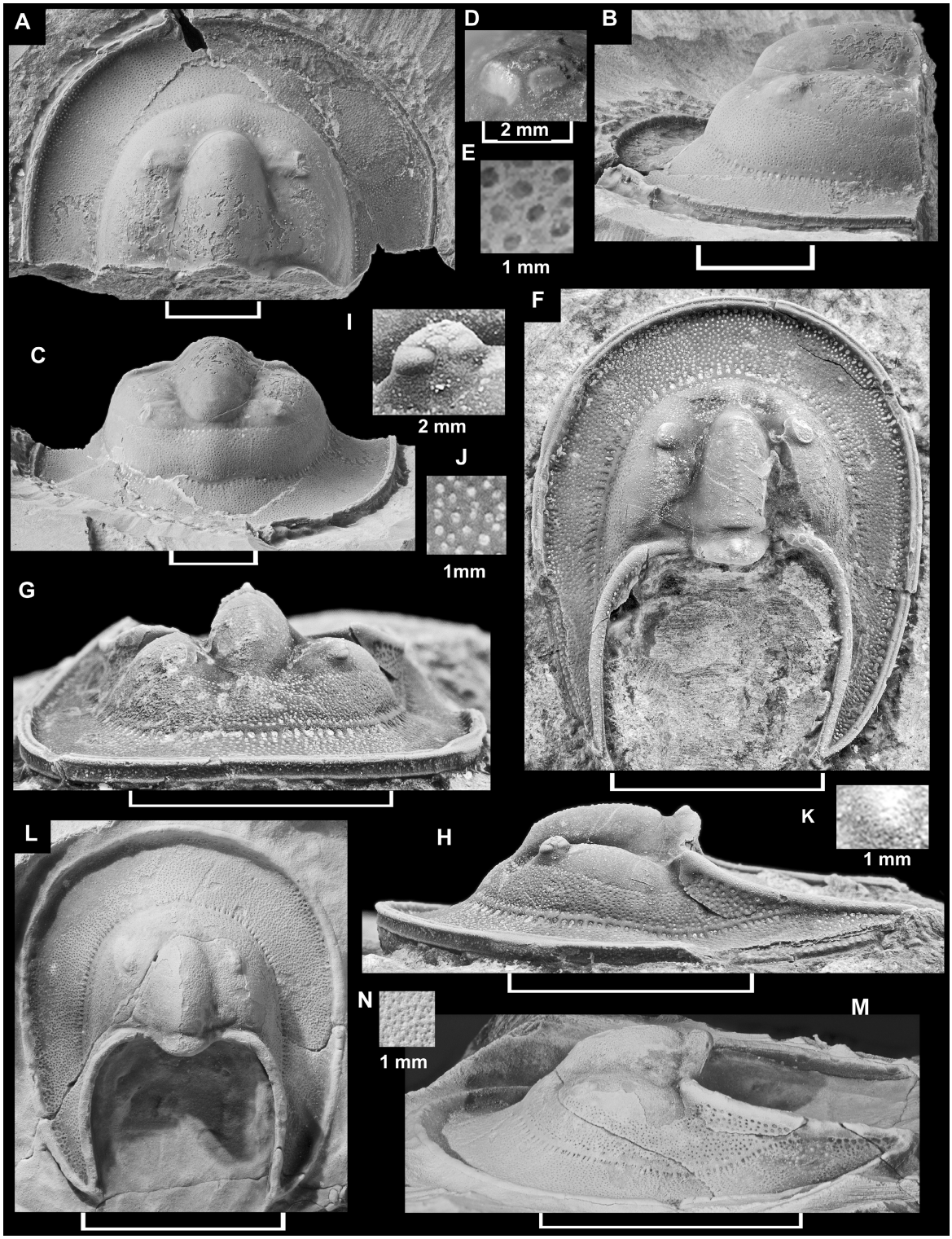


PLATE 31. A–E *Maghroharpes* aff. *ihmadii*, dorsal exoskeleton of partial cephalon, NHMUK It 29305, from an upper Pragian horizon, Ihandar Formation, bou Lachrhal (Fig. 2B, Map 9, site 4). A, dorsal, B, lateral and C, anterior view. D, lateral view of eye lobe and E, dorsal view of brim perforations.

F–K *Maghroharpes* cf. *forteyi*, dorsal exoskeleton of partial cephalon, NHMUK It 29284, from top of the Pragian, Ihandar Formation, Oued el Atchane, Jbel Oufatene (Fig. 2B, Map 8, site 20). F, dorsal, G, anterior and H, lateral view. I, lateral view of eye lobe, J, dorsal view of brim perforations and K, pits on axial node.

L–N *Maghroharpes* cf. *zguidensis*, dorsal exoskeleton of cephalon, NHMUK It 29328, from Merzâ Akhsai Formation?, Pragian, Douar Laayoune, Tata (Fig. 2B, Map 1, site 1). L, dorsal and M, lateral view. N, dorsal view of brim perforations.

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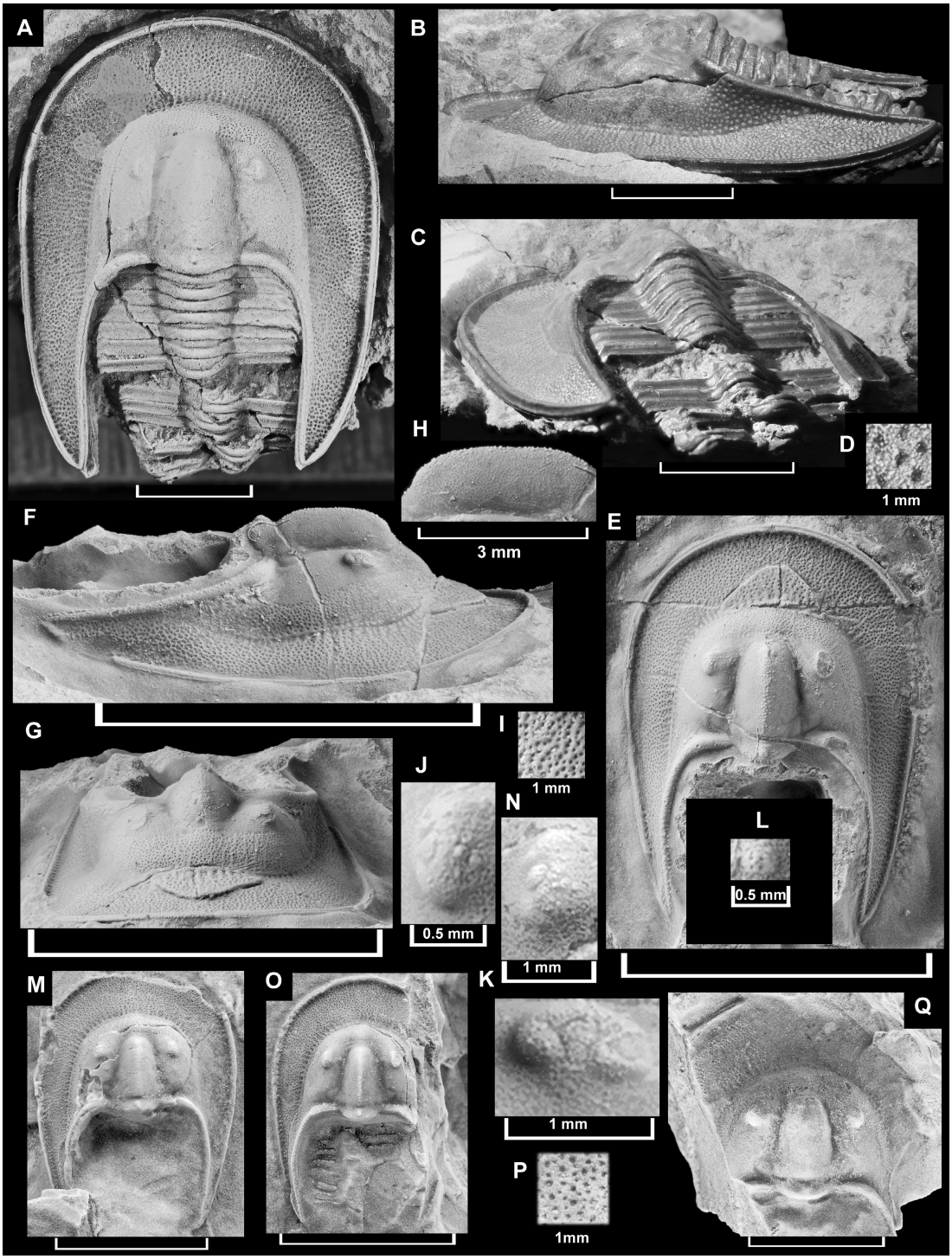


PLATE 32. A–D *Maghroharpes terridus* n. sp., Ihandar Formation, Pragian, Maharch, dorsal exoskeleton, thorax and pygidium disarticulated, **holotype**, NHMUK It 29321 (Fig. 2B, Map 9, site 18). A, dorsal, B, lateral and C, posterior view. D, dorsal view of brim perforations.

E–Q *Lioharpes scopulum* n. sp., Ihandar Formation, bou Lachrhal.

E–L dorsal exoskeleton of cephalon only, **holotype**, NHMUK It 29279 (Fig. 2B, Map 9, site 14). E, Dorsal, F, lateral and G, anterior view. H, lateral view of glabella (uncoated), I, dorsal view of brim perforations. J, and K, dorsal and lateral view of eye lobe respectively. L, dorsal view of occipital node.

M–Q dorsal exoskeletons of partial cephala only, from type locality and horizon, **paratypes**, NHMUK It 29280 (1 to 3) (Fig. 2B, Map 9, site 3). M–N NHMUK It 29280 (1). M, dorsal view and N, dorsal view of eye lobe. **O–P** NHMUK It 29280 (2). O, dorsal view and P, dorsal view of brim perforations. Q, NHMUK It 29280 (3), dorsal view.

Scale bars shown represent 1 cm unless otherwise indicated.

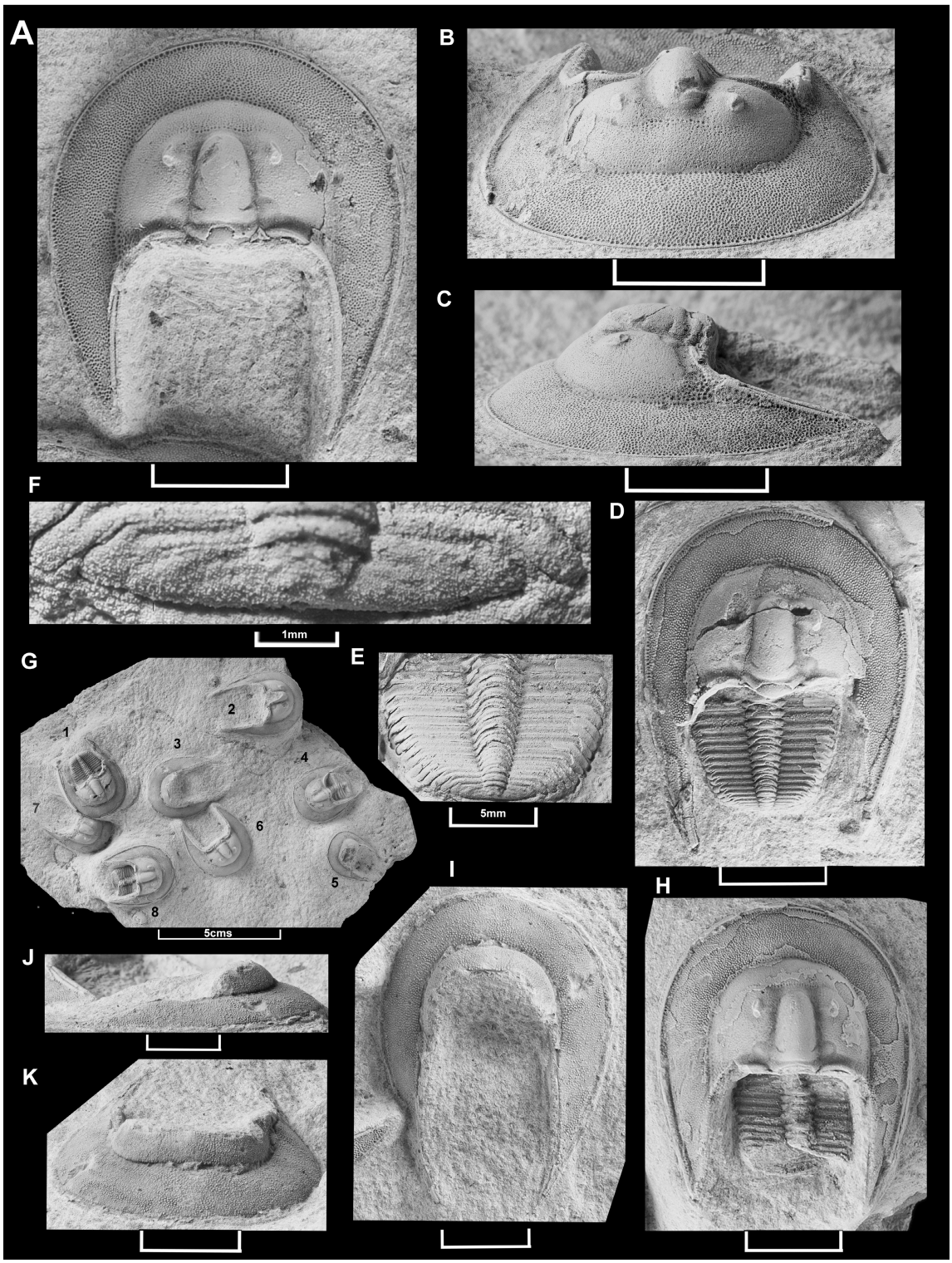


PLATE 33. A–K *Eskoharpes sicarius* n. sp., from the ammonoid mining horizon, Achguig Formation Group, lower Frasnian, Bouia, 7 km SE of Jorf (Fig., 2B, Map 6, site 5).

A–C paratype, NHMUK It 29256 (6), dorsal exoskeleton of cephalon. A, dorsal view, B, anterior view and C, lateral view.

D–F holotype, NHMUK It 29256 (1), dorsal exoskeleton partial cephalon and thorax, and a complete pygidium. D, dorsal view of whole exoskeleton, E, dorsal view of thorax and pygidium and F, dorsal posterior view of pygidium.

G assemblage of partial dorsal exoskeletons of material shown in Figs 43 and 44.

H paratype, NHMUK It 29256 (8), partial dorsal exoskeleton of cephalon and thorax, dorsal view.

I–K paratype, NHMUK It 29256 (3), dorsal exoskeleton of lower lamella. I, dorsal, J, lateral and K, anterior view.

Scale bars shown represent 1 cm unless otherwise indicated.



PLATE 34. A–I *Eskoharpes sicarius* n. sp., from Type horizon, lower Frasnian, Bouia, 7 km SE of Jorf (Fig. 2B, Map 6, site 5).

A–E paratype, NHMUK it 29256 (2), dorsal exoskeleton of partial cephalon only. A, dorsal view, B, lateral view, C, anterior view, D, dorsal view of eye lobe and eye ridge and E, anterior dorsal view of brim perforations.

F–G paratype, NHMUK it 29256 (5), dorsal exoskeleton partial cephalon. F, dorsal, G, lateral view of posterior of prolongation including genal spine.

H paratype, NHMUK it 29256 (4), dorsal exoskeleton of partial cephalon and disarticulated thorax, dorsal view.

I paratype, NHMUK it 29256 (1&7), dorsal exoskeleton of partial concealed cephalon, dorsal view.

Scale bars shown represent 1 cm unless otherwise indicated.

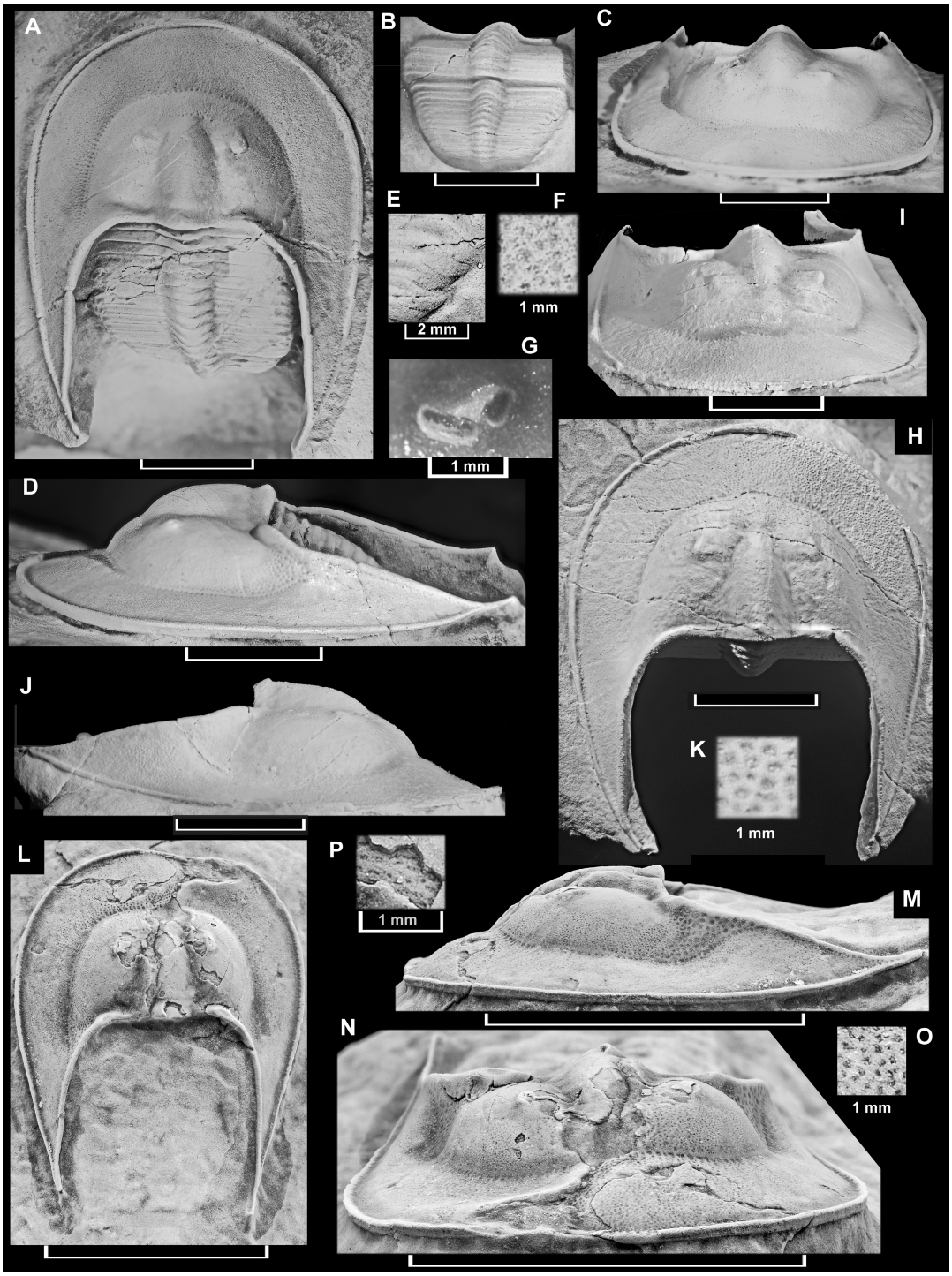


PLATE 35. A–P *Pinnuloharpes segaouii* n. sp., El Otfal Formation, upper Eifelian.

A–G dorsal exoskeleton partially enrolled, **holotype**, NHMUK It 29351, from Taghroute near Timerzit (Fig. 2B, Map 10, site 4). A, dorsal, B, posterior, C, anterior and D, lateral view. E and F, dorsal view of pleurae and brim perforations, respectively. G, lateral view of eye lobe (uncoated).

H–K dorsal exoskeleton enrolled, **paratype**, NHMUK It 29352, the lower "*Harpes* Couche" (Fig. 7), Jbel Issoumour (Fig. 2B, Map 7, site 11). H, dorsal, I, anterior and J, lateral view. K, dorsal view of brim perforations.

L–P dorsal exoskeleton of an incomplete cephalon, **paratype**, NHMUK It.29350 from the main "*Harpes*" horizon, 2 m upslope of the "*Acanthopyge*" horizon, El Otfal Formation? Eifelian/Givetian boundary, Timerzit (Fig. 2B, Map 10, site 1). L, dorsal, M, lateral and N, anterior view. O and P, dorsal view of and brim perforations and impression of ventral surface cuticle on genal area, respectively.

Scale bars shown represent 1 cm unless otherwise indicated.

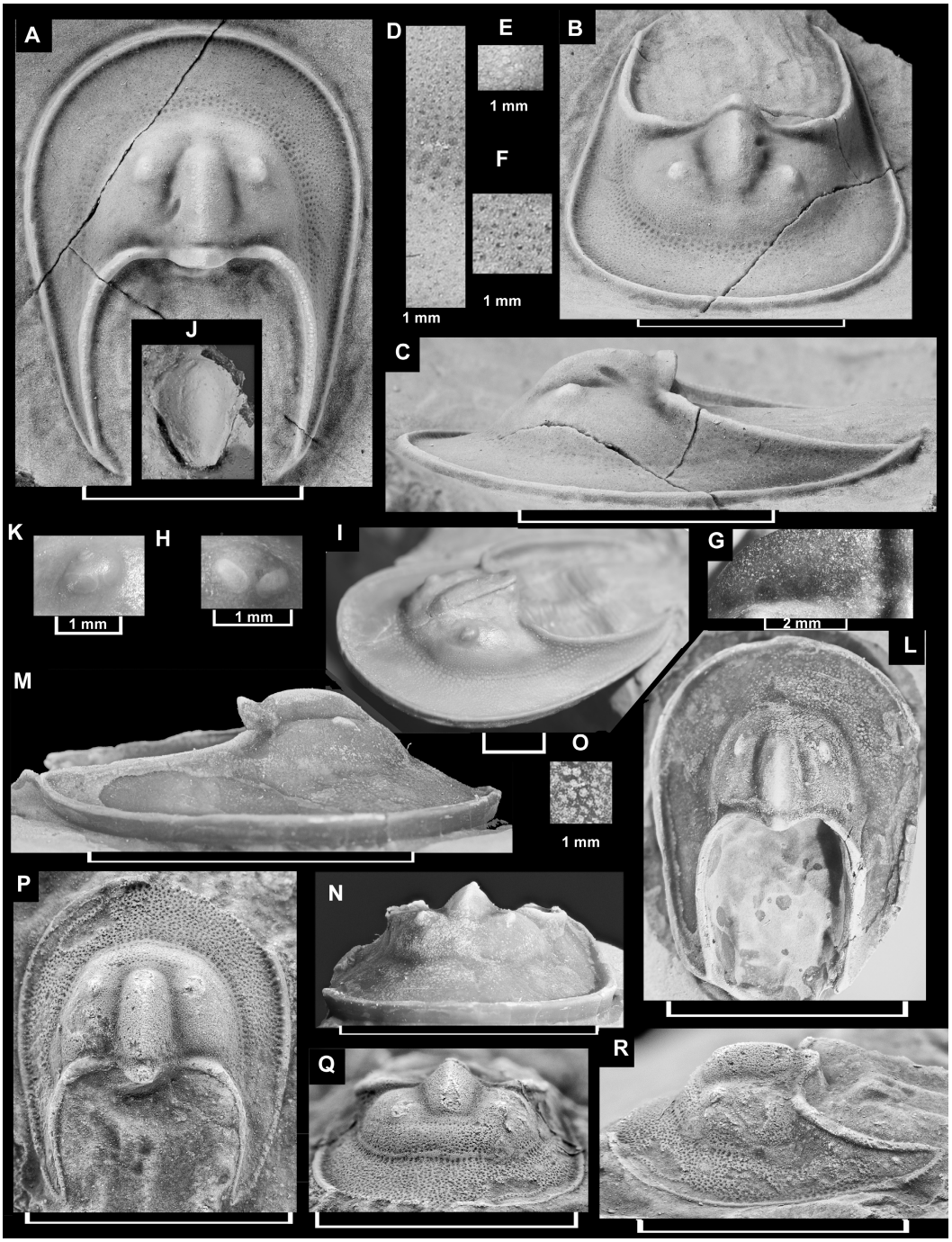


PLATE 36. A–K *Harpes igaouii* n. sp., Ihandar Formation, Pragian-Emsian boundary.

A–H dorsal exoskeleton of cephalon only, **holotype**, NHMUK It 29360, from coral NW of Jbel Ou-Driss (Fig. 2B, Map 4, site 5). A, dorsal, B, anterior and C, lateral view. D, dorsal anterior view of perforations on genal roll and brim. E, dorsal view of glabellar tubercles, F, dorsal view of brim perforations, G, lateral view of glabellar muscle insertion scars (uncoated) and H, lateral view of eye lobe (uncoated).

I–K dorsal exoskeleton of cephalon and partial thorax, **paratype**, NHMUK It 29361, from *Ceratocephala* horizon, North Jbel Ou-Driss (Fig. 2B, Map 4, site 8). I, dorsal anterior lateral view (uncoated). J, ventral view of hypostome and K, lateral view of eye lobe (uncoated).

L–O *Harpes* **aff. *igaouii***, dorsal exoskeleton of cephalon only, NHMUK It 29362, from Fezna, "*Struveaspis* Couche", El Otfal Formation, Eifelian.(Fig. 2B, Map 6, site 1). L, dorsal, M, lateral and N, anterior view. O, dorsal view of brim perforations.

P–R *Kielania* aff. *tumula*, Ihandar Formation, upper Pragian (Fig. 2B, Map 10, Site 5) dorsal exoskeleton of a partial cephalon, NHMUK It 29262. P, dorsal, Q, anterior and R, lateral view.

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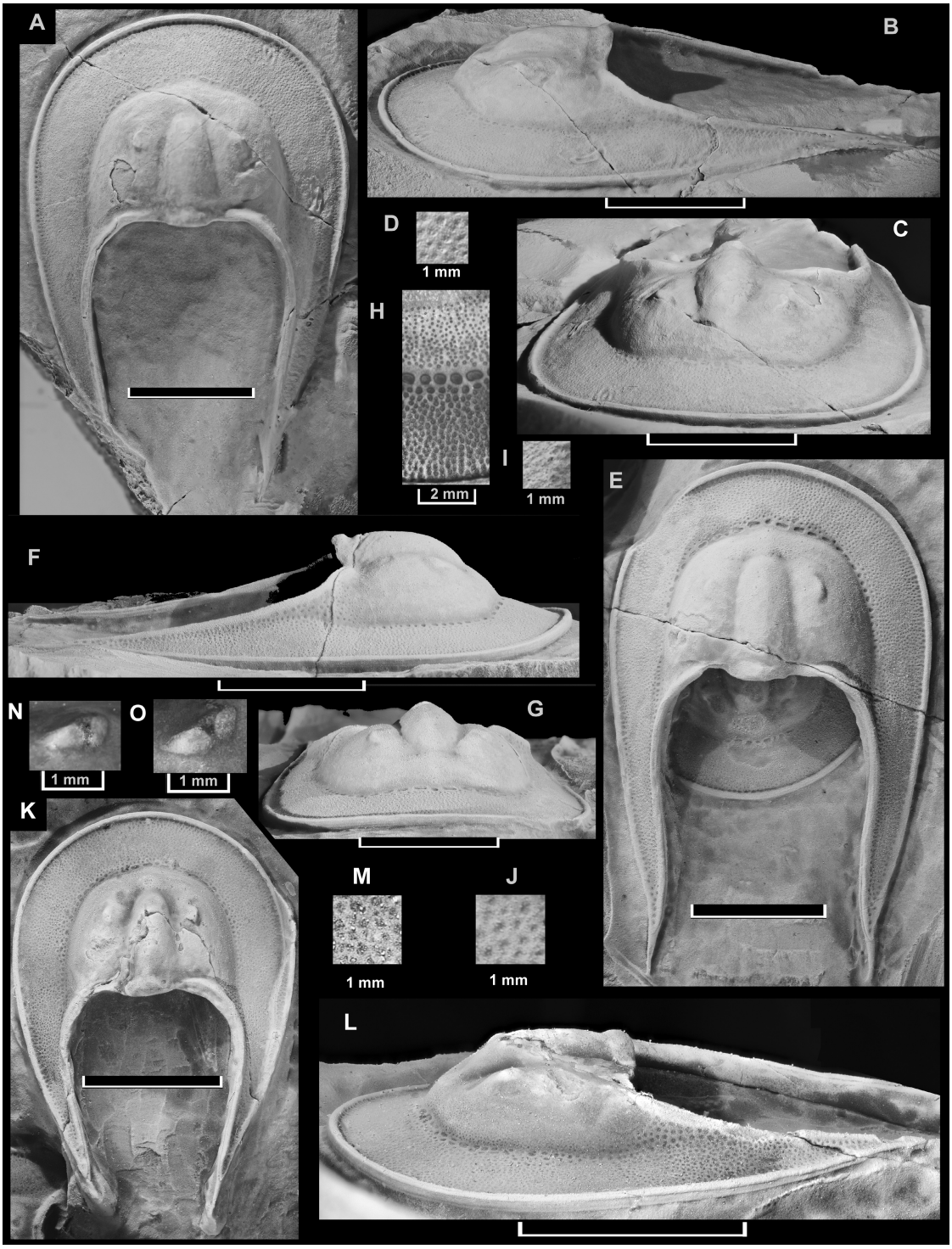


PLATE 37. A–O *Pinnuloharpes torquis* n. sp., from "*Harpes* Couche", El Otfal Formation, upper Eifelian**,** Ksar Hannabou.
A–D dorsal exoskeleton of cephalon only, **paratype**, NHMUK It 29353 (Fig. 2B, Map 6, site 7). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforation.
E–J 2 dorsal exoskeletons of cephala only (one cephalon largely covering the other), **holotype**, NHMUK It 29354 (1) and **paratype** NHMUK It 29354 (2) (Fig. 2B, Map 6, site 9). NHMUK It 29354 (1) E, dorsal view, F, lateral and G, anterior view. H, anterior dorsal view of perforations on genal roll and brim. I and J, dorsal view of impression of ventral surface of cuticle in genal area and brim perforations, respectively. NHMUK It 29354 (2) E, dorsal view.
K–O dorsal exoskeleton of partial cephalon, **paratype**, NHMUK It 29355 (1) (Fig. 2B, Map 6, site 10). K, dorsal and L, lateral view. M, dorsal view of brim perforations, N and O, lateral view of eye lobes (uncoated).
Scale bars shown represent 1 cm unless otherwise indicated.

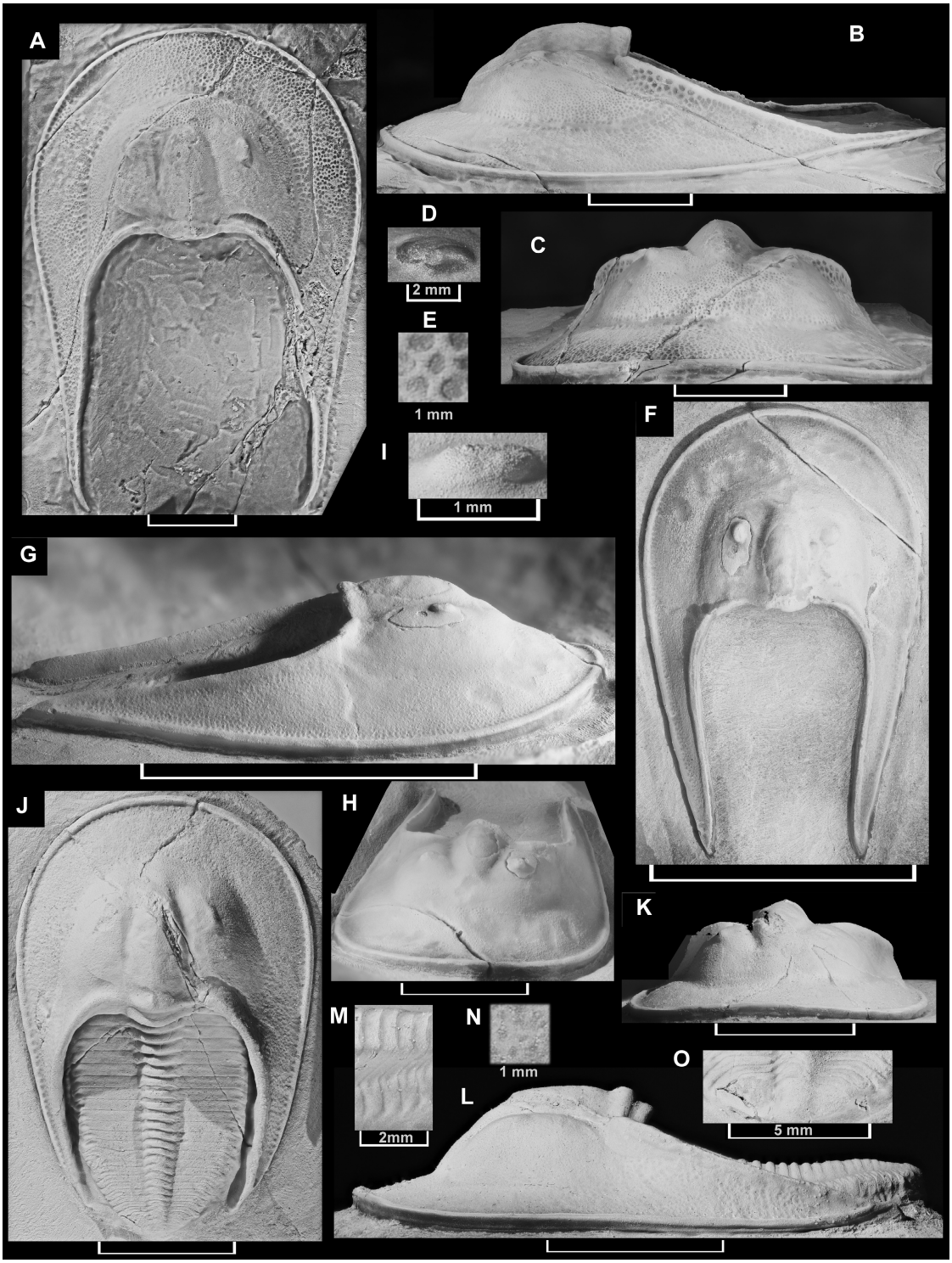


PLATE 38. A–E *Pinnuloharpes* aff. *torquis*, dorsal exoskeleton of cephalon only, El Otfal Formation, upper Eifelian, Tamgoute Bulgan (Fig. 2B, Map 6, site 20)**,** NHMUK It 29329. A, dorsal, B, lateral and C, anterior view. D, lateral view of eye lobe (uncoated) and E, dorsal view of brim perforations.

F–I *Pinnuloharpes* aff. *apteros*, dorsal exoskeleton of cephalon only, El Otfal Formation, upper Eifelian, "*Harpes* Couche", Ksar Hannabou (Fig. 2B, Map 6, site 6), NHMUK It 29379. F, dorsal, G, lateral and H, anterior view. I, lateral view of eye lobe.

J–O *Pinnuloharpes apteros* n. sp.,dorsal exoskeleton, El Otfal Formation, upper Eifelian, Tamgoute Bulgan (Fig. 2B, Map 6, site 18), **holotype**, NHMUK It 29358. J, dorsal, K, anterior and L, lateral view. M, lateral view of pleurae, N, dorsal view of brim perforations and O, posterior view of pygidium.

Scale bars shown represent 1 cm unless otherwise indicated.

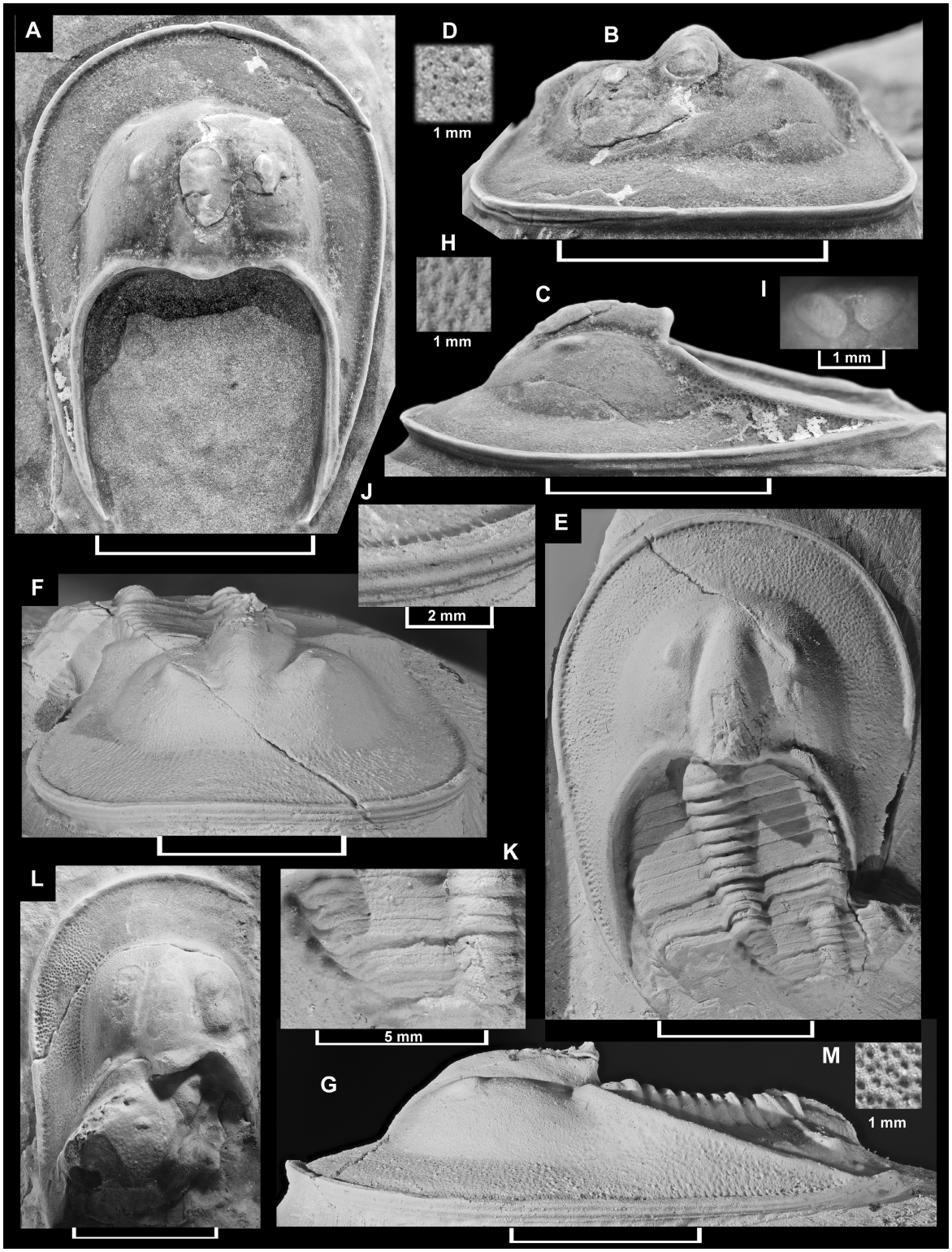


PLATE 39. A–M *Pinnuloharpes apteros* n. sp., El Otfal Formation, upper Eifelian.

A–D dorsal exoskeleton of cephalon only, **paratype**, NHMUK It 29356 from Ksar Hannabou (Fig. 2B, Map 6, site 8). A, dorsal, B, anterior and C, lateral view. D, dorsal view of brim perforations.

E–K dorsal exoskeleton with thorax and pygidium disarticulated, **paratype**, NHMUK It 29359, from type locality and horizon (Fig. 2B, Map 6, site 19). E, dorsal, F, anterior and G, lateral view. H, dorsal view of brim perforations, I, lateral view of eye lobe, J, anterior lateral view of rim and marginal band, and K, dorsal view of pleurae close to pygidium.

L–M dorsal exoskeleton of a partial cephalon, **paratype**, NHMUK It 29357, from Ksar Hannabou (Fig. 2B, Map 6, site 15). L, dorsal view and M, dorsal view of brim perforations. Scale bars shown represent 1 cm unless otherwise indicated.

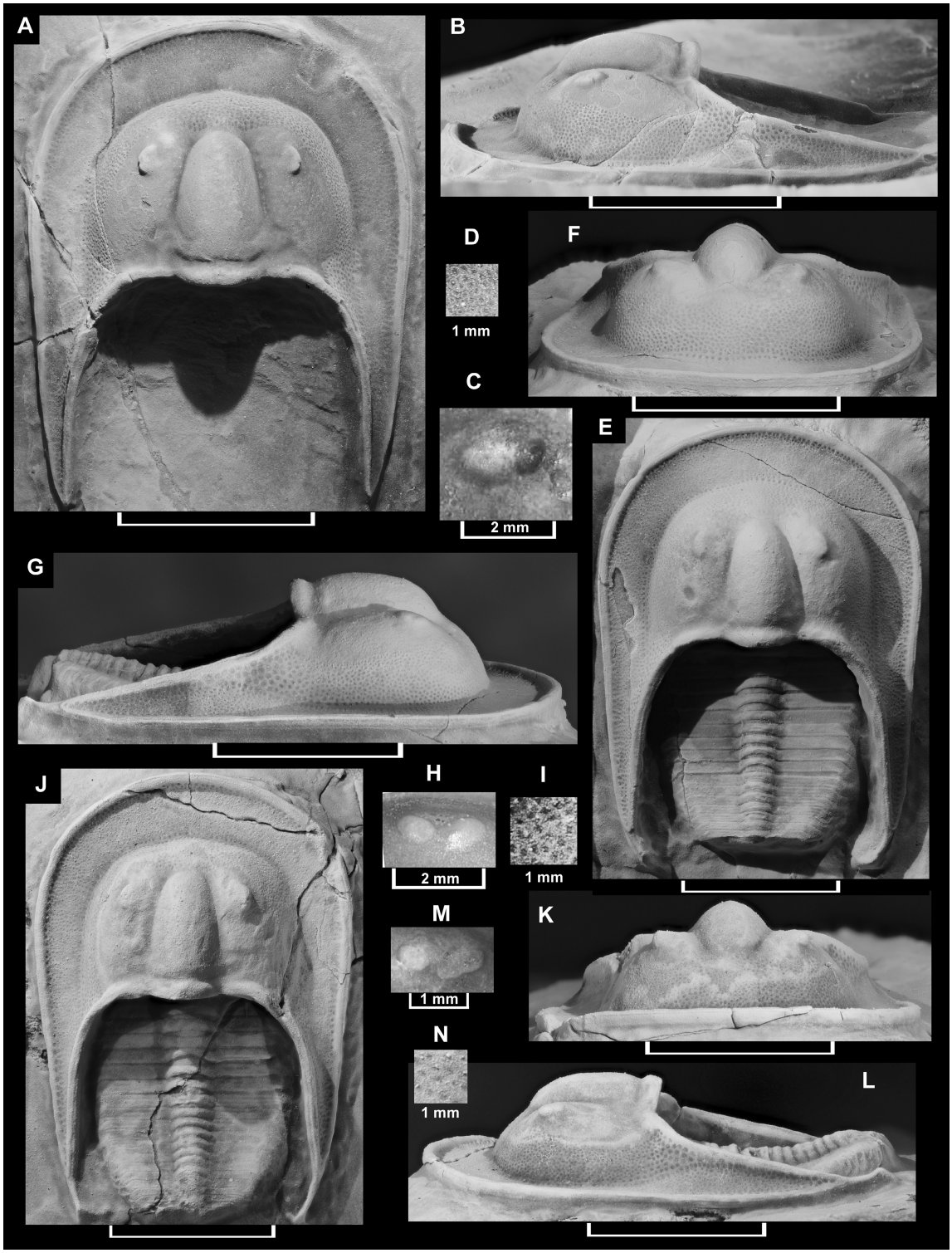


PLATE 40. A–N *Pinnuloharpes hannabouensis* n. sp., from an horizon 5 m down slope of "*Radiaspis* Couche"**,** upper Eifelian/Givetian boundary, Ksar Hannabou.

A–D dorsal exoskeleton of cephalon only, **paratype**, NHMUK It 29334 (Fig. 2B, Map 6, site 12). A, dorsal and B, lateral view. C, lateral view of eye lobe (uncoated) and D, dorsal view of brim perforations.

E–I dorsal exoskeleton cephalon and thorax only, **holotype**, NHMUK It 29333 (Fig. 2B, Map 6, site 11). E, dorsal, F, anterior and G, lateral view. H, lateral view of eye lobes, I, dorsal view of brim perforations.

J–N dorsal exoskeleton pygidium incomplete, **paratype**, NHMUK It 29335 (Fig. 2B, Map 6, site 13). J, dorsal, K, anterior and L, lateral view. M, lateral view of eye lobe and N, dorsal view of brim perforations.

Scale bars shown represent 1 cm unless otherwise indicated.

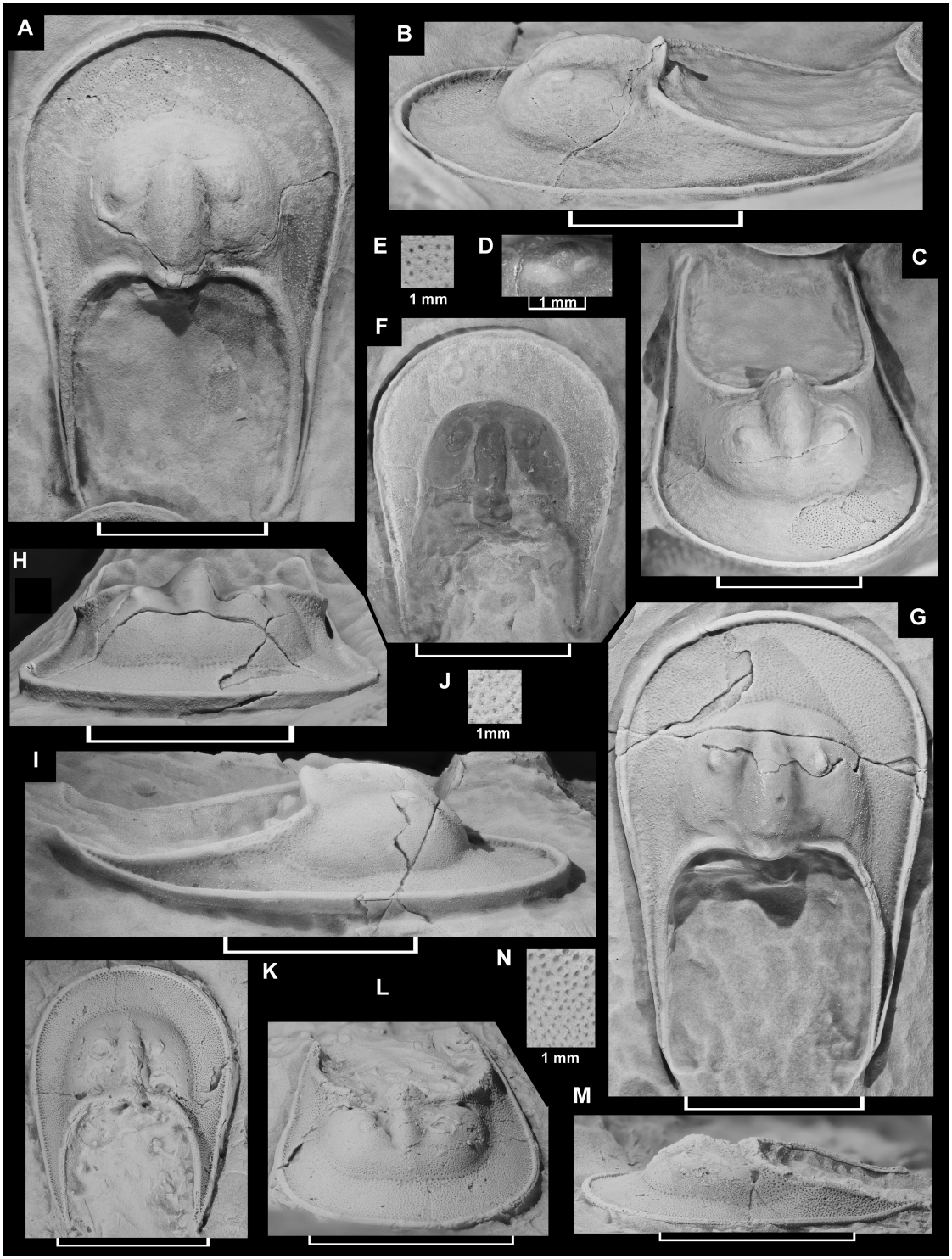


PLATE 41. A–J *Pinnuloharpes chaperon* n. sp., "Basseiarges Couche", El Otfal Formation, Eifelian, Fezna.

A–F exoskeleton of cephalon only, **paratypes**, NHMUK It 29331 (1 and 2), (Fig. 2B, Map 6, site 2).

A–E NHMUK It 29331 (1). A, dorsal, B, lateral and C, anterior dorsal view. D, lateral view of eye lobe (uncoated) and E, dorsal view of brim perforations.

F, NHMUK It 29331 (2)**,** ventral exoskeleton of upper lamella.

G–J dorsal exoskeleton of cephalon, **holotype**, NHMUK It 29332 (Fig. 2B, Map 6, site 4). G, dorsal, H, anterior and I, lateral view. J, dorsal view of brim perforations. **K–N *Pinnuloharpes* cf. *chaperon***, "Basseiarges Couche", El Otfal Formation, Eifelian, Fezna. Dorsal exoskeleton of partial cephalon only, NHMUK It 29330 (Map 2B, site 21). K, dorsal, L, anterior and M, lateral view. N, dorsal view of brim perforations.

Scale bars shown represent 1 cm unless otherwise indicated.

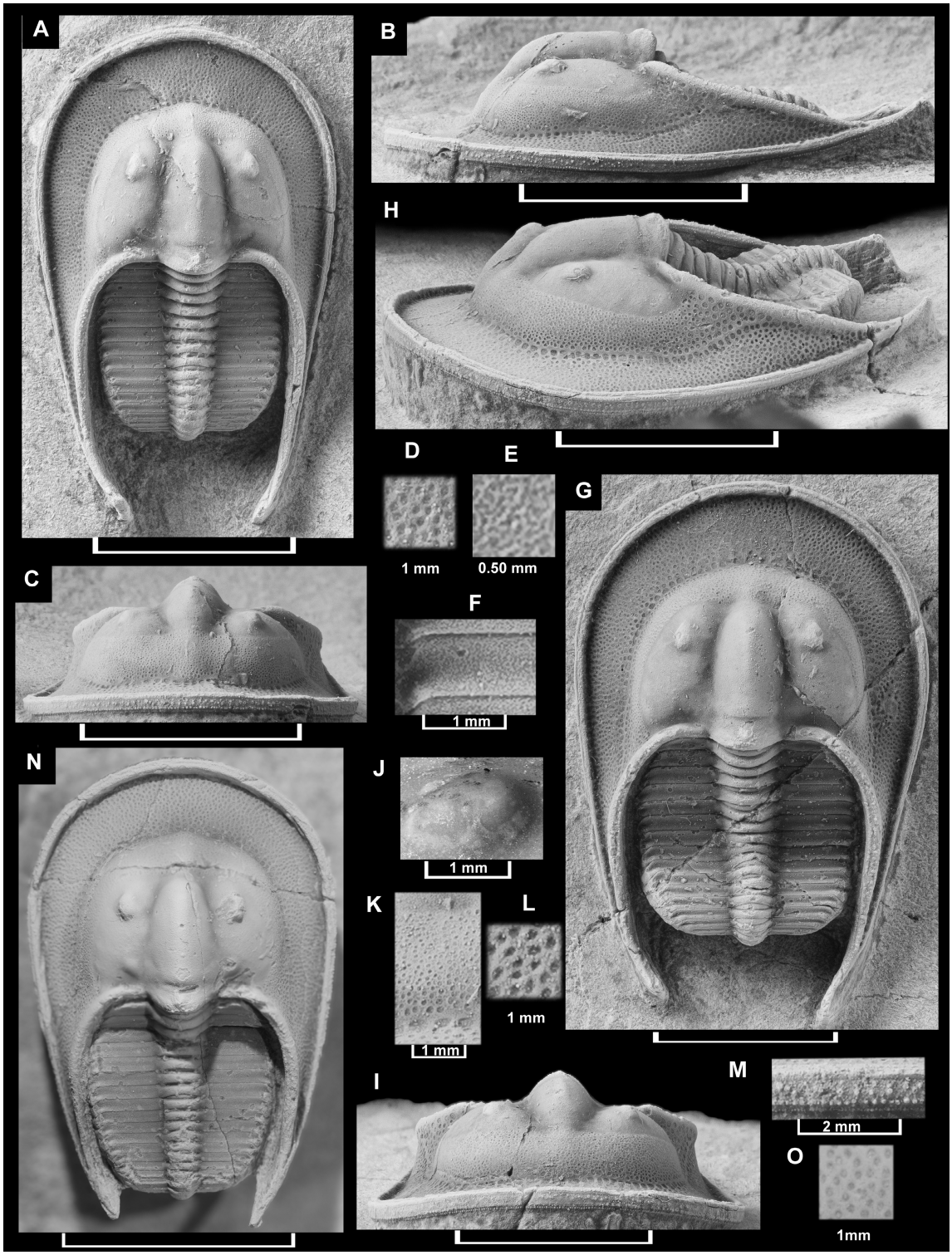


PLATE 42. A–M *Pinnuloharpes haustrum* n. sp., upper Emsian, Ksar Lbour. **A–F** dorsal exoskeleton pygidium enrolled, **holotype**, NHMUK It 29341 (Fig. 2B, Map 3, site 3). A, dorsal, B, lateral and C, anterior view. D, and E, dorsal view of brim perforations and genal area sculpture respectively.

G–M dorsal exoskeleton pygidium enrolled, **paratype**, NHMUK It 29342 (Fig. 2B, Map 3, site 4). G, dorsal, H, lateral and I, anterior view. J, lateral view of eye lobe (uncoated), K, anterior view of genal roll perforations and L, dorsal view of brim perforations. M, anterior view of marginal band.

N–O *Pinnuloharpes haustrum* n. sp., upper Emsian, Hamar Laghdad, dorsal exoskeleton with pygidium enrolled, **paratype**, NHMUK It 29345 (Fig. 2B, Map 11, site 13). N, dorsal view. O, dorsal view of brim perforations.

Scale bars shown represent 1 cm unless otherwise indicated.

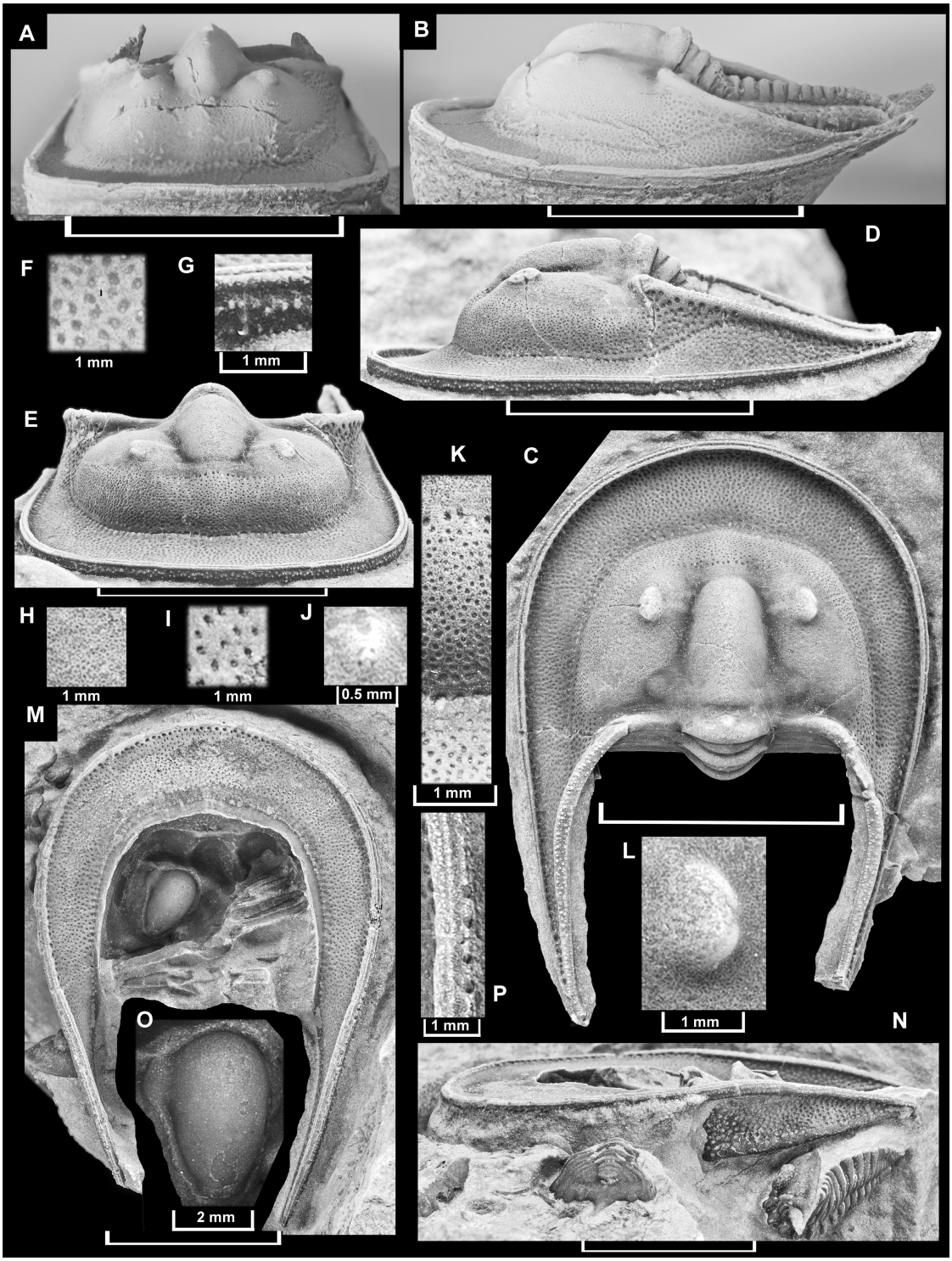


PLATE 43. A–B *Pinnuloharpes haustrum* n. sp., upper Emsian, Hamar Laghdad, dorsal exoskeleton with pygidium enrolled, **paratype**, NHMUK It 29345 (Fig. 2B, Map 13, site 11). A, anterior and B, lateral view.

C– P *Pinnuloharpes* aff. *haustrum*, from base of upper Emsian, Hamar Laghdad.

C–L dorsal exoskeleton with thorax enrolled, NHMUK It 29347 (1) (Fig. 2B, Map 11, site 7). C, dorsal, D, lateral and E, anterior view. F, dorsal view of brim perforations, G, anterior view of external rim. H, I and J dorsal view of sculpture on dorsal surface of genal area, brim perforations and occipital node, respectively. K, anterior view of perforations on the genal roll and L dorsal view of eye lobe.

M–P ventral exoskeleton of cephalon only, NHMUK It 29347 (2), from same site as NHMUK It 29347 (1). M, ventral and N, lateral view. O and P, ventral view of hypostome and external rim, respectively.

Scale bars shown represent 1 cm unless otherwise indicated.

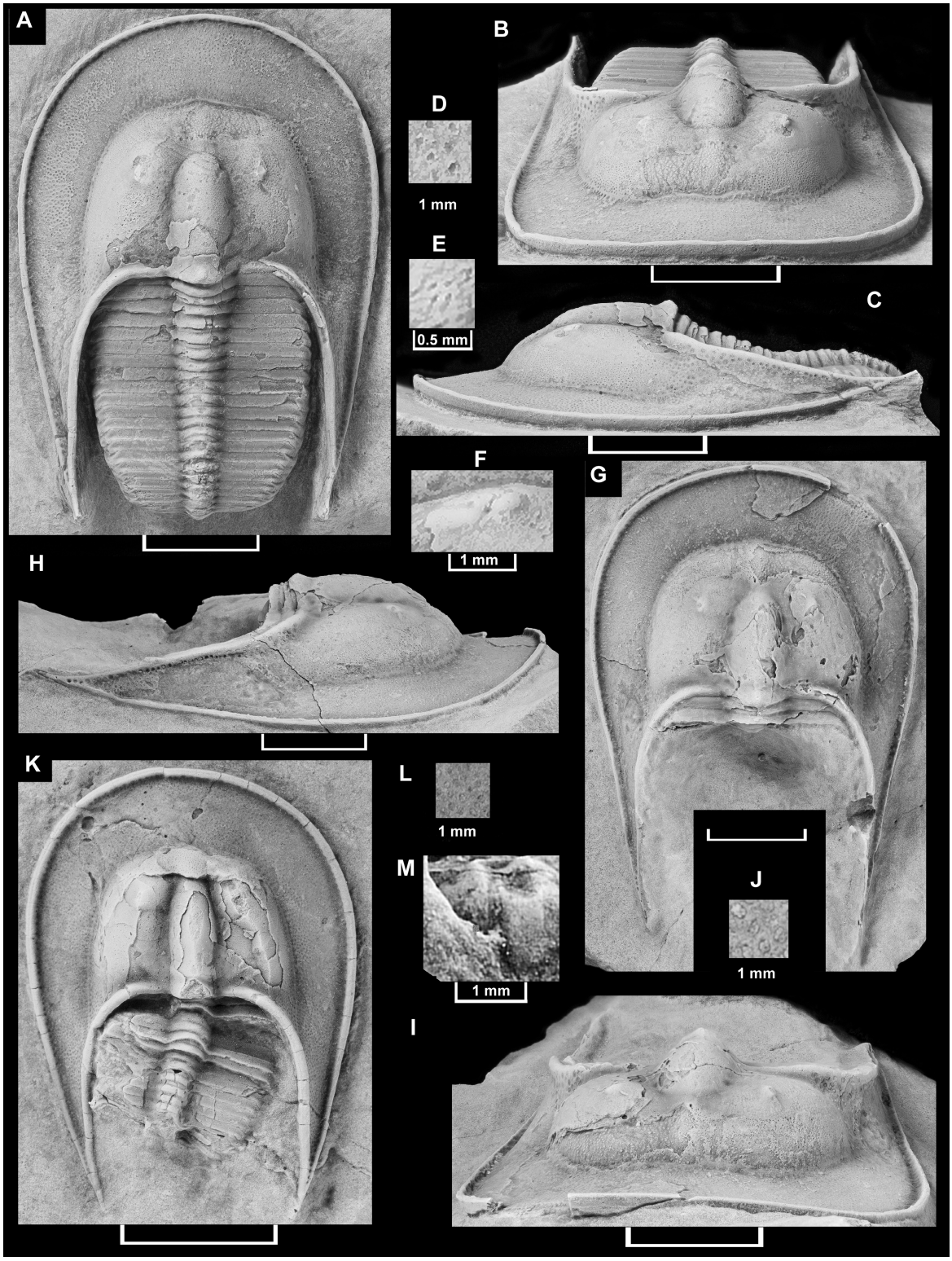


PLATE 44. A–M *Pinnuloharpes hamarlaghdadensis* (Cronier *et al.* 2018), from Hamar Laghdad, upper Emsian.
A–F dorsal exoskeleton with pygidium enrolled, NHMUK It 29337 (Fig. 2B, Map 11, site 1) A, dorsal, B, anterior and C, lateral view. D, dorsal view of brim perforations, E, dorsal view of occipital node and F, lateral view of eye lobe.
G–J dorsal exoskeleton of cephalon and 2 pleural segments of thorax, NHMUK It 29338 (Fig. 2B, Map 11, site 2) G, dorsal, H, lateral and I, anterior view. J, dorsal view of brim perforations.
K–M dorsal exoskeleton with thorax disarticulated and pygidium absent, NHMUK It 29339 (Fig. 2B, Map 11, site 3) K, dorsal and I, anterior view. L, dorsal view of brim perforations and M, lateral view of distal ends of pleurae.
Scale bars shown represent 1 cm unless otherwise indicated.

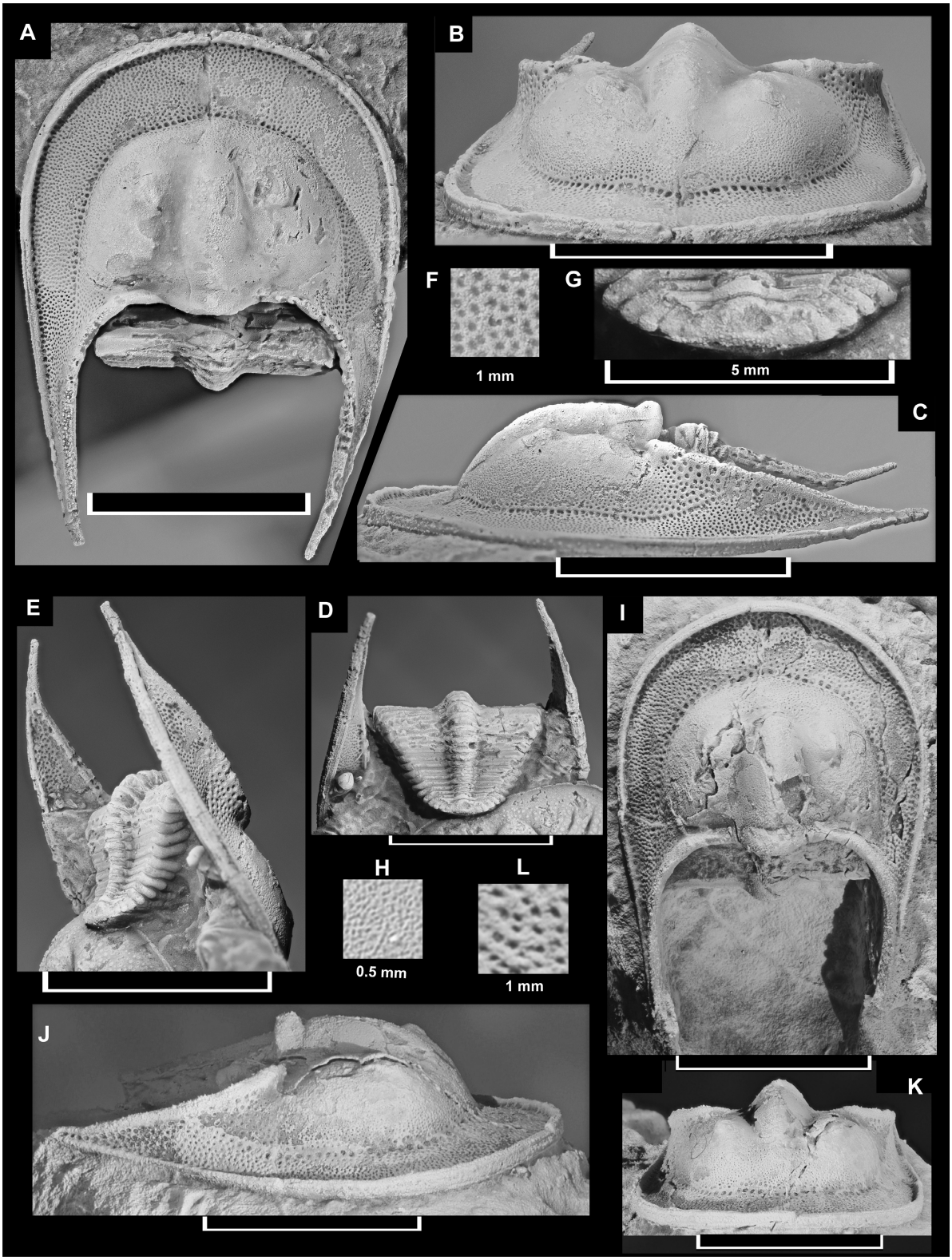


PLATE 45. A–L *Pinnuloharpes merzanensis* n. sp., upper Emsian, Hamar Laghdad.

A–H dorsal exoskeleton partly enrolled, **holotype**, NHMUK It 29349 from 7.5 m below *P. hamarlaghdadensis* horizon (Fig. 2B, Map 11, site 6). A, dorsal, B, anterior, C, lateral, D, posteroventral and E, posterolateral view. F, dorsal view of brim perforation, G, dorsal view of pygidium and H, dorsal view of pitting on genal area.

I–L dorsal exoskeleton of a partial cephalon only, **paratype**, NHMUK It 29348 from 2.5 m above type horizon (Fig. 2B, Map 11, site 5). I, dorsal, J, lateral and K, anterior view. L, dorsal view of brim perforations.

Scale bars shown represent 1 cm unless otherwise indicated.

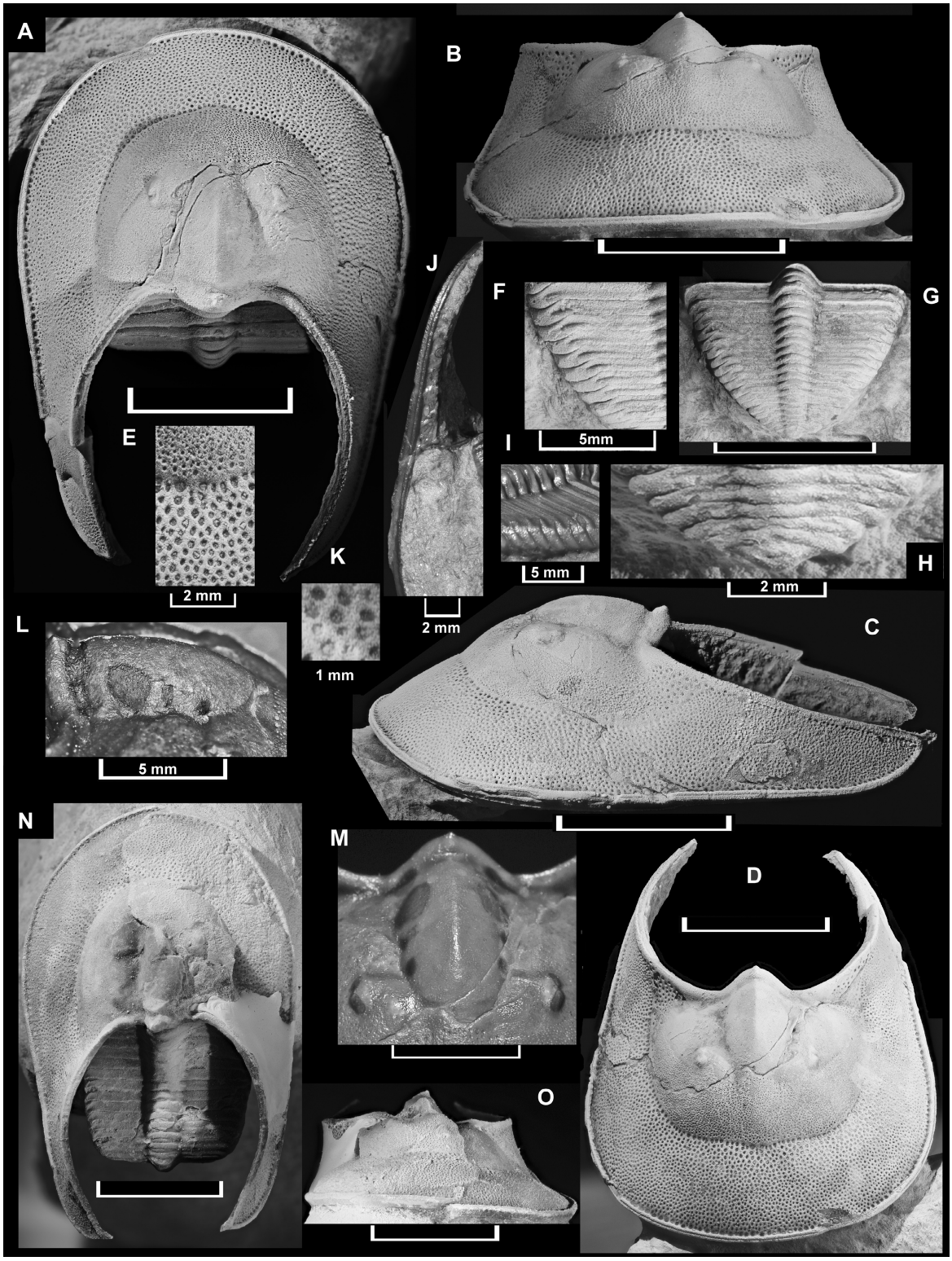


PLATE 46. A–O *Stoloharpes rissaniensis* n. sp., El Otfal formation, South Rissani, Eifelian**.**

A–M articulated dorsal exoskeleton with thorax partly enrolled, **holotype**, NHMUK It 29373 (Fig. 2B, Map 14, site 4)**.** A, dorsal, B, anterior, C, lateral and D, antero-dorsal view**.** E, Antero-dorsal view of perforations on genal roll and brim, F, G and H, dorsal view of pleurae thorax and pygidium, respectively. I, lateral view of thorax and J, ventral view of exterior rim. K, dorsal view of brim perforations, L, lateral view and M, anterior view of glabella muscle insertion scars (uncoated).

N–O partial dorsal exoskeleton with pygidium enrolled, **paratype**, NHMUK It 29376 (Fig. 2B, Map 14, site 7). N, dorsal view and O, anterior view.

Scale bars shown represent 1 cm unless otherwise indicated.

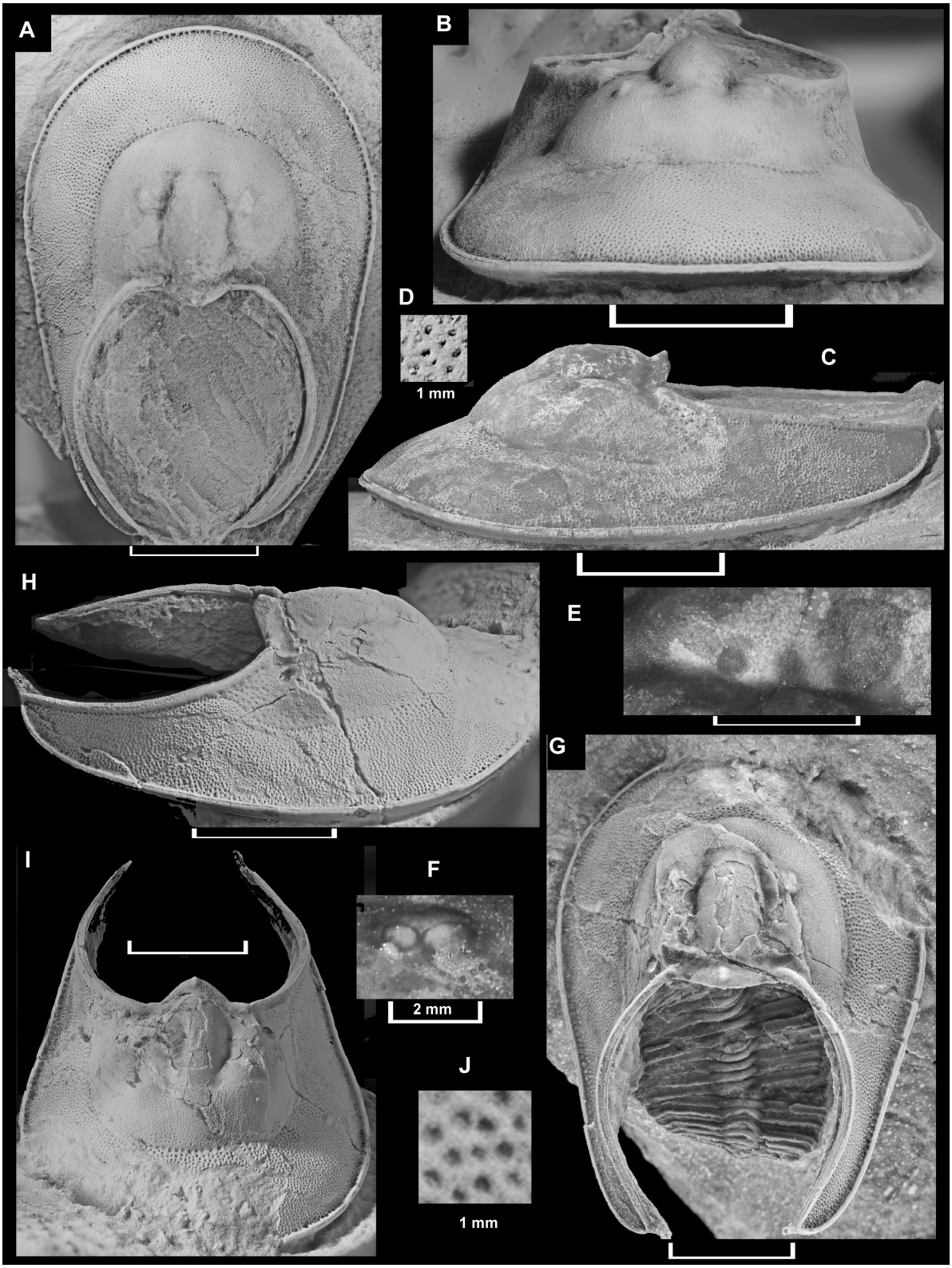


PLATE 47. A–J *Stoloharpes rissaniensis* n. sp., El Otfal formation, Eifelian, South Rissani**.**

A–F dorsal exoskeleton of cephalon only, **paratype**, NHMUK It 29374 (Fig. 2B, Map 14, site 5)**.** A, dorsal, B, anterior, C, lateral view**.** D, dorsal view of brim perforations. E, lateral view of glabella muscle insertion scars (uncoated) and F, lateral view of eye lobe (uncoated).

G–J disarticulated dorsal exoskeleton, **paratype**, NHMUK It 29375 (Fig. 2B, Map 14, site 6)**.** G, dorsal, H, lateral and I, antero-dorsal view. J, dorsal view of brim perforation.

Scale bars shown represent 1 cm unless otherwise indicated.

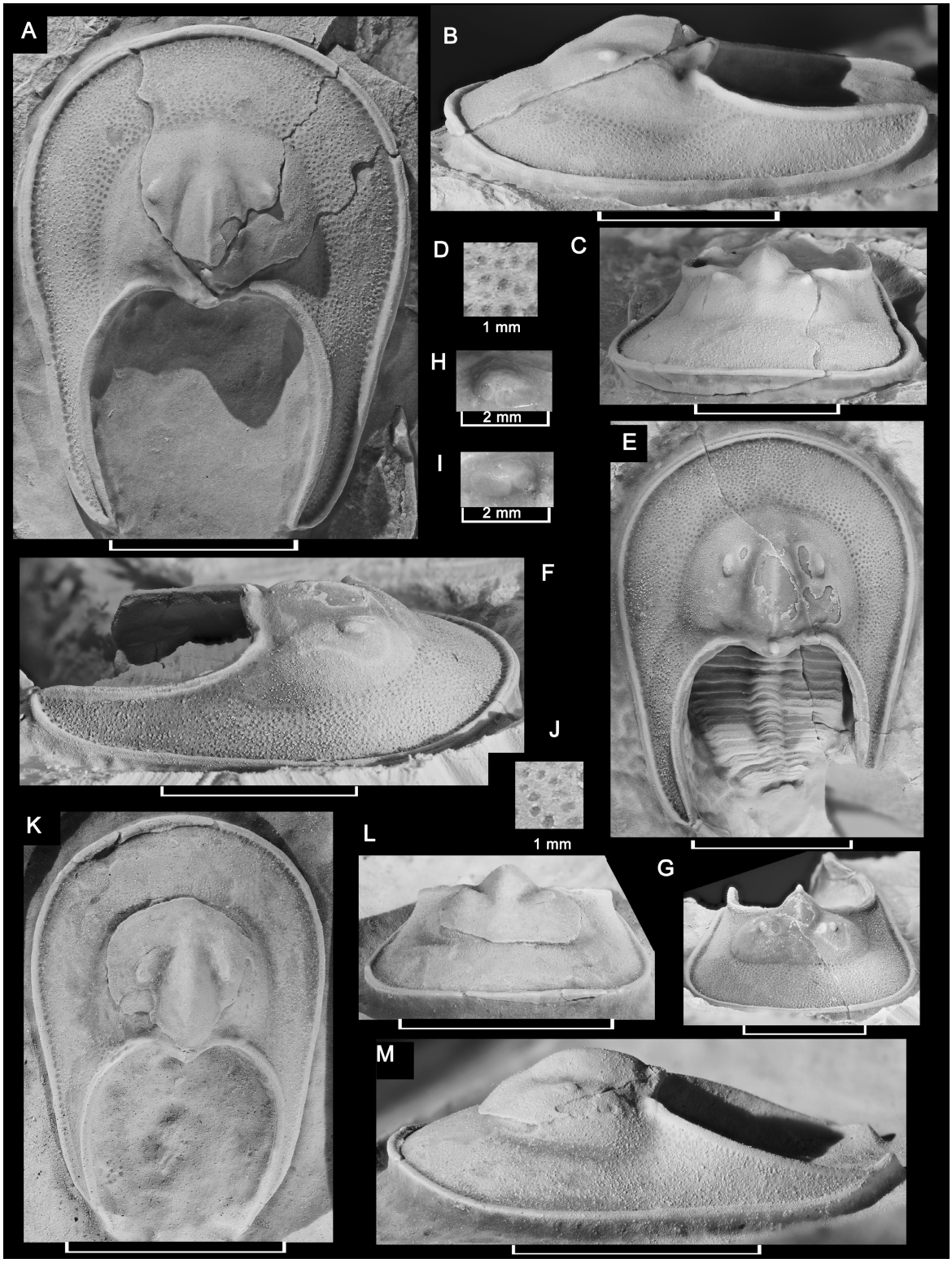


PLATE 48. A–M *Stoloharpes rissaniensis* n. sp., **"***Basseiarges* Couche", Fezna, Eifelian.

A–D dorsal exoskeleton cephalon only, **paratype**, NHMUK It 29371 (Fig. 2B, Map 6, site 3). A, dorsal, B, lateral and C, anterior view. D, dorsal view of brim perforations.

E–J dorsal exoskeleton cephalon and disarticulated thorax, **paratype**, NHMUK It 29372 (Fig. 2B, Map 6, site 22). E, dorsal, F, lateral and G, anterior view. H and I, lateral view of eye lobes. J, dorsal view of brim perforations.

K–M Ighas El Otfal Formation, Eifelian (Fig. 2B, Map 14, site 8), dorsal exoskeleton of cephalon only, **paratype**, NHMUK It 29377. K, dorsal, L, anterior and M, lateral view.

Scale bars shown represent 1 cm unless otherwise indicated.

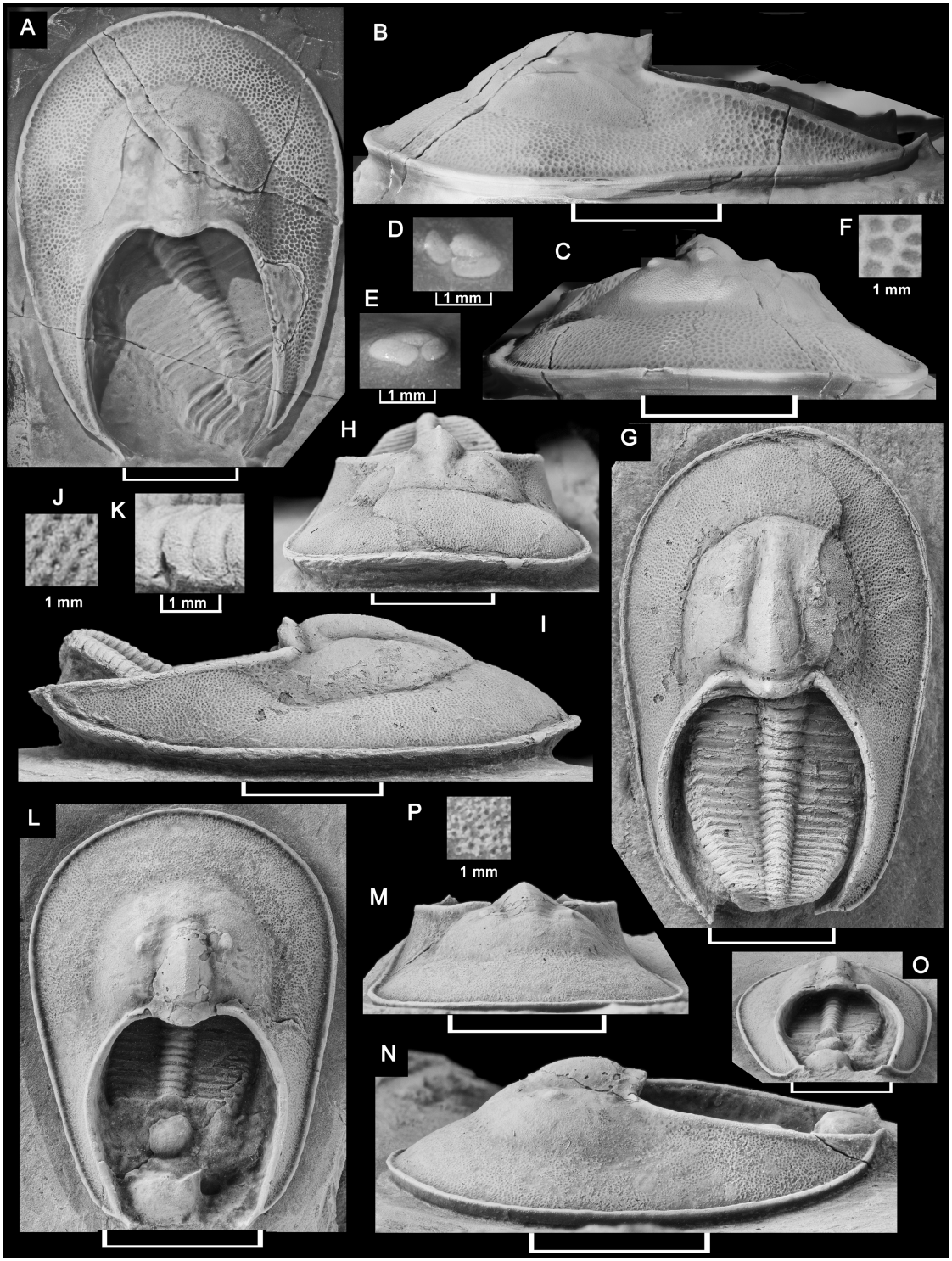


PLATE 49. A–F *Stoloharpes* aff. *rissaniensis*, El Otfal formation, upper Eifelian, Ksar Hannabou (Fig. 2B, Map 6, site 14), dorsal exoskeleton, thorax disarticulated and pygidium missing, NHMUK It 29380. A, dorsal B, lateral and C, anterior view. D, dorsal and E, lateral view of eye lobe (uncoated). F, dorsal view of brim perforations.

G–K *Stoloharpes calceolus* n. sp., **"***Akantharges* Couche", Eifelian, Ksar Lbor (Fig. 2B, Map 3, site 4), dorsal exoskeleton pygidium enrolled, **holotype**, NHMUK It 29363. G, dorsal, H, anterior and I, lateral view. J, dorsal view of brim perforations and K, lateral view of pleurae.

L–P *Stoloharpes aff. calceolus*, **"***Akantharges* Couche", Eifelian, Ksar Lbor (Fig. 2B, Map 3, site 5), dorsal exoskeleton, thorax disarticulated pygidium enrolled, **holotype**, NHMUK It 29381. L, dorsal, M, anterior, N, lateral and O, posterior view. P, dorsal view of brim perforations.

Scale bars shown represent 1 cm unless otherwise indicated.

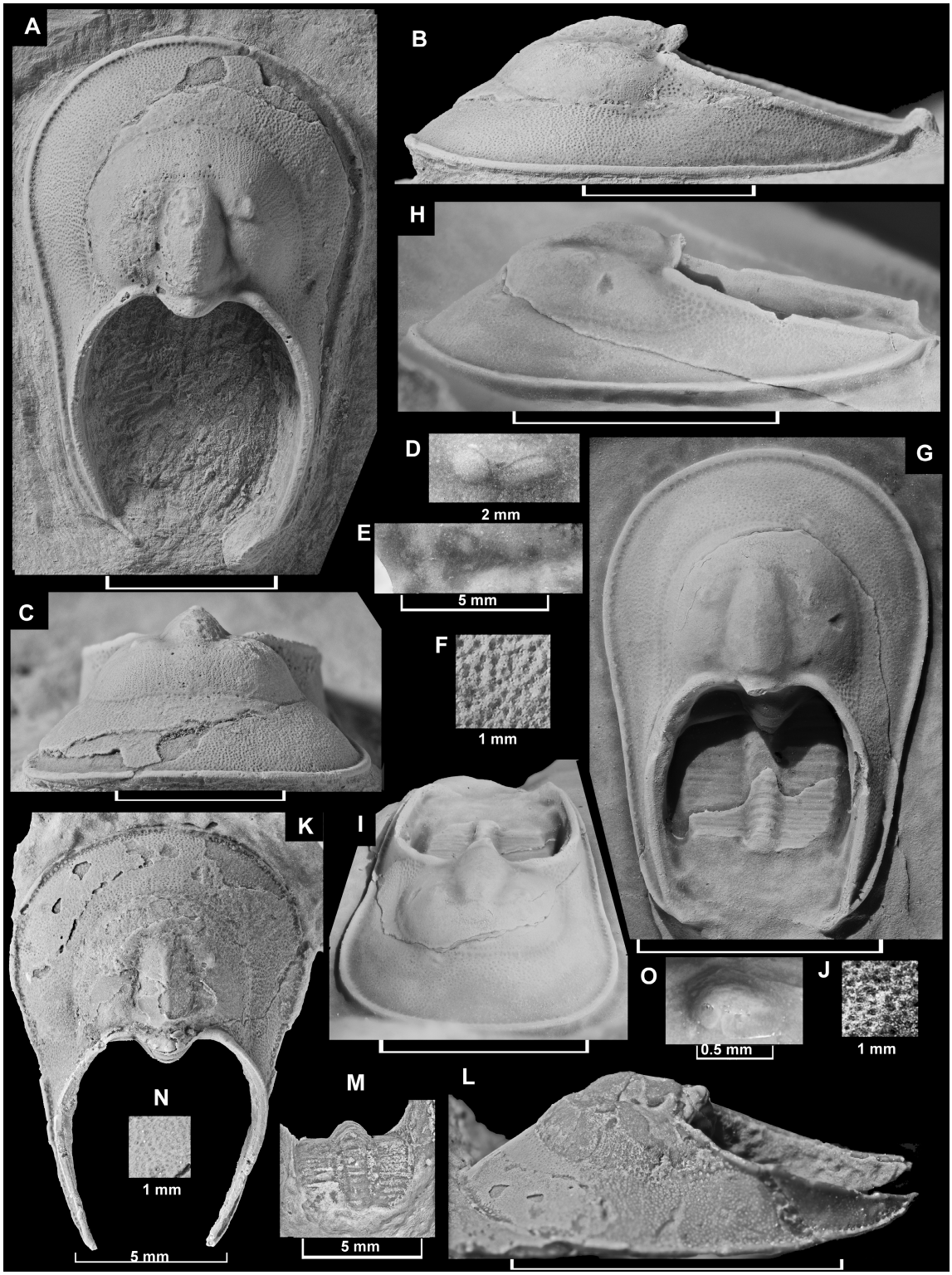


PLATE 50. A–F *Stoloharpes capricornus* n. sp., El Otfal Formation, upper Eifelian, Taouz East (Fig. 2B, Map 15, site 1), dorsal exoskeleton of cephalon only, **holotype**, NHMUK It 29364. A, dorsal, B, lateral and C, anterior view. D, lateral view of eye lobe (uncoated) E, lateral view of muscle insertion scars on glabella (uncoated). F, dorsal view of brim perforations.
G–J *Stoloharpes* aff. *capricornus*, upper Eifelian, Hamar Laghdad (Fig. 2B, Map 11, site 14), dorsal exoskeleton of cephalon only, NHMUK It 29366. G, dorsal, H, lateral and I, anterior view. J, dorsal view of brim perforations.
K–O *Stoloharpes capricornus* n. sp., El Otfal Formation, upper Eifelian, Taouz East (Fig. 2B, Map 15, site 2), dorsal exoskeleton thorax enrolled, **paratype**, NHMUK It 29365. K, dorsal, L, lateral and M, posterior view. N, dorsal view of brim perforations and O, lateral view of eye lobe.
Scale bars shown represent 1 cm unless otherwise indicated.

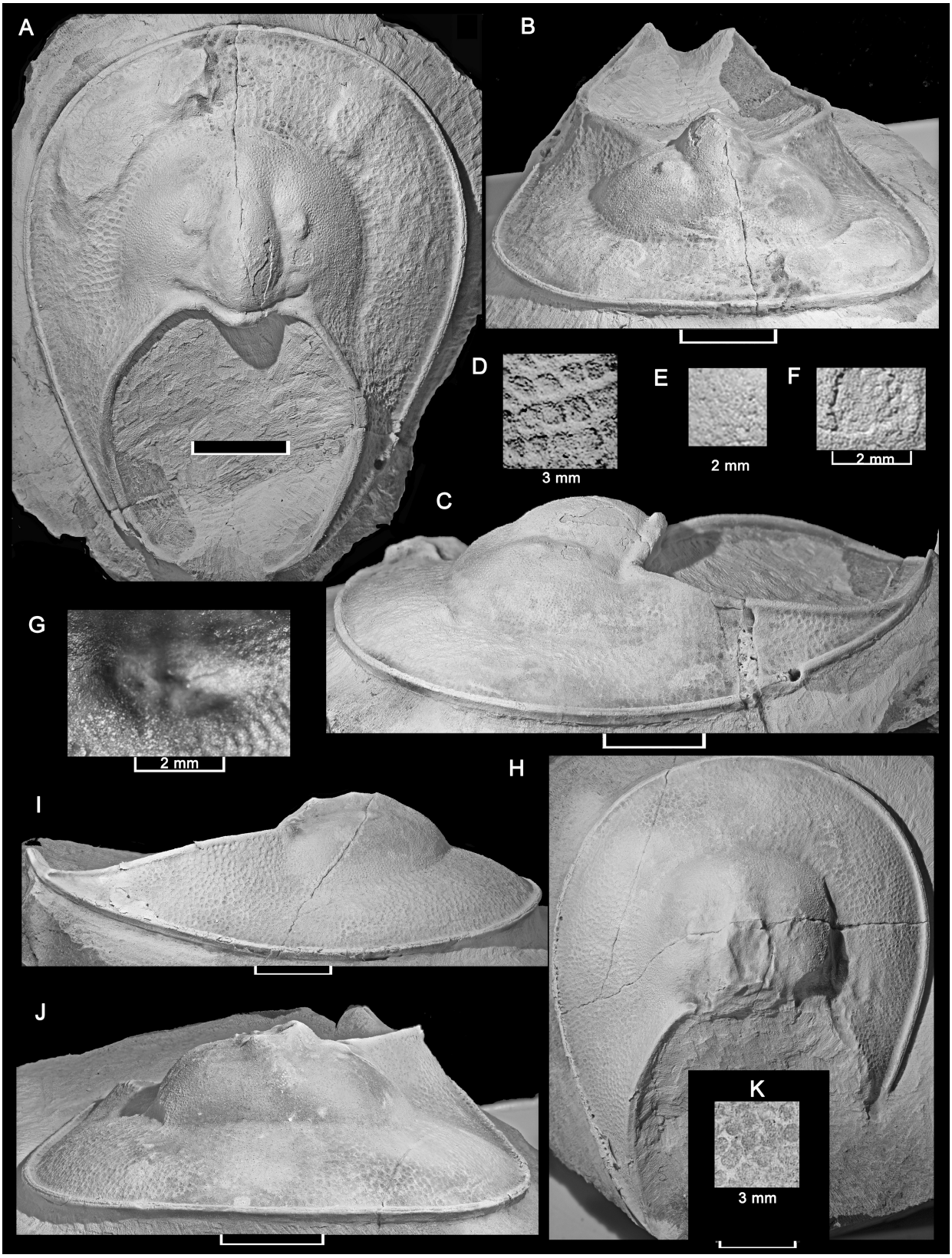


PLATE 51. A–L *Helioharpes retiarius* n. sp., El Otfal Formation, upper Eifelian, Ottara.

A–G dorsal exoskeleton of cephalon only, **holotype**, NHMUK It 29368 (Fig. 2B, Map 14, site 2). A, dorsal, B, anterior and C, lateral view. Dorsal view of brim perforations: E, F and G lateral view of eye lobe.

H–L dorsal exoskeleton of cephalon only, **paratype**, NHMUK it 29369 (Fig. 2B, Map 14, site 3). I, dorsal, J, lateral and K, anterior view. L, dorsal view of brim perforations.

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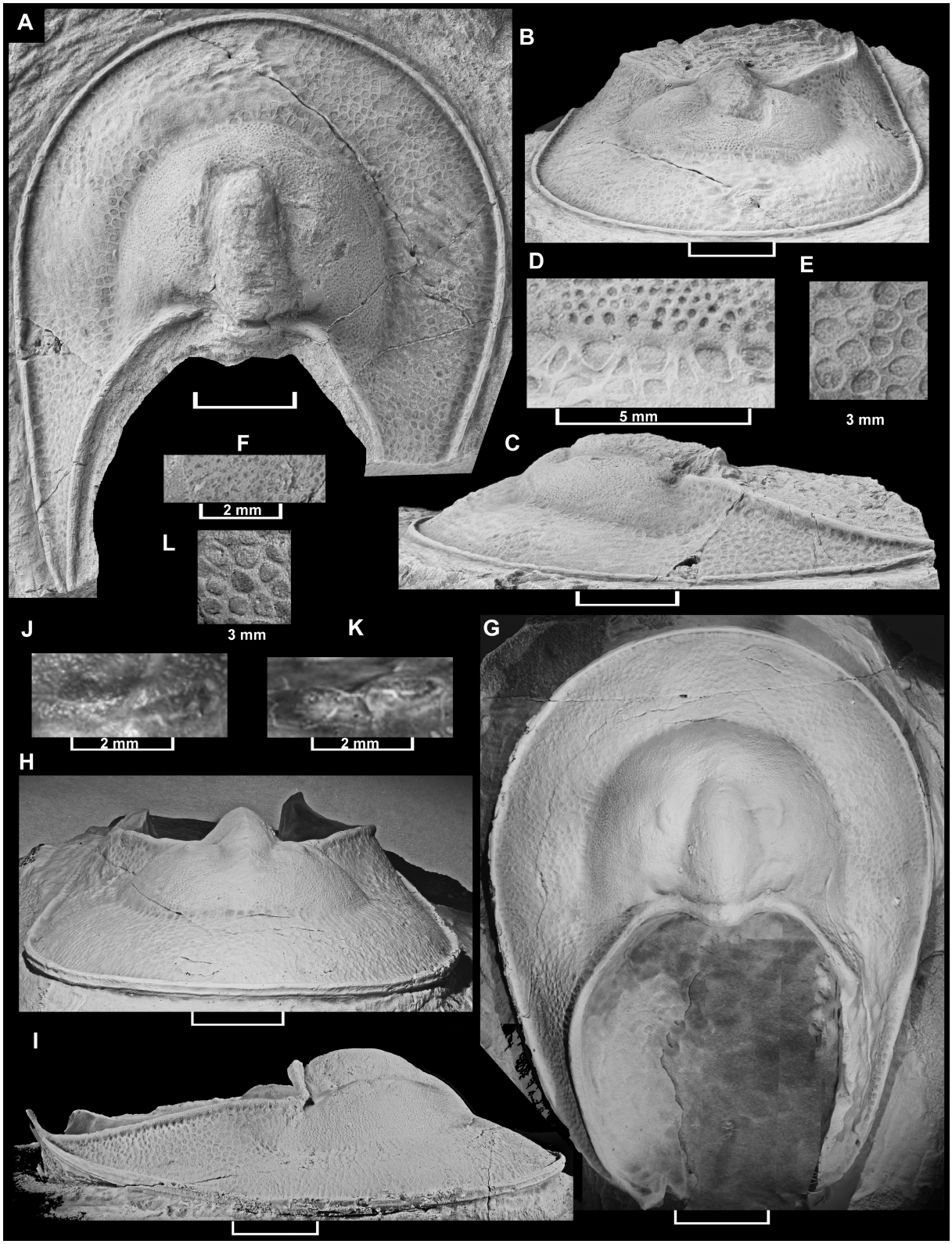


PLATE 52. A–L *Helioharpes retiarius* n. sp., El Otfal Formation, upper Eifelian, Ottara.

A–F dorsal exoskeleton of a partial cephalon only, **paratype**, NHMUK It 29367 (Fig. 2B, Map 14, site 1). A, dorsal, B, anterior and C, lateral view. D, antero-dorsal view of genal roll and brim perforations. Dorsal view of E, brim perforations and F, perforations on genal area.

G–L dorsal exoskeleton of cephalon only, **paratype**, NHMUK It 29370 (Fig. 2B, Map 14, site 11). G, dorsal, H, anterior and I, lateral view. J and K, lateral view of eye lobes and L, dorsal view of brim perforations.

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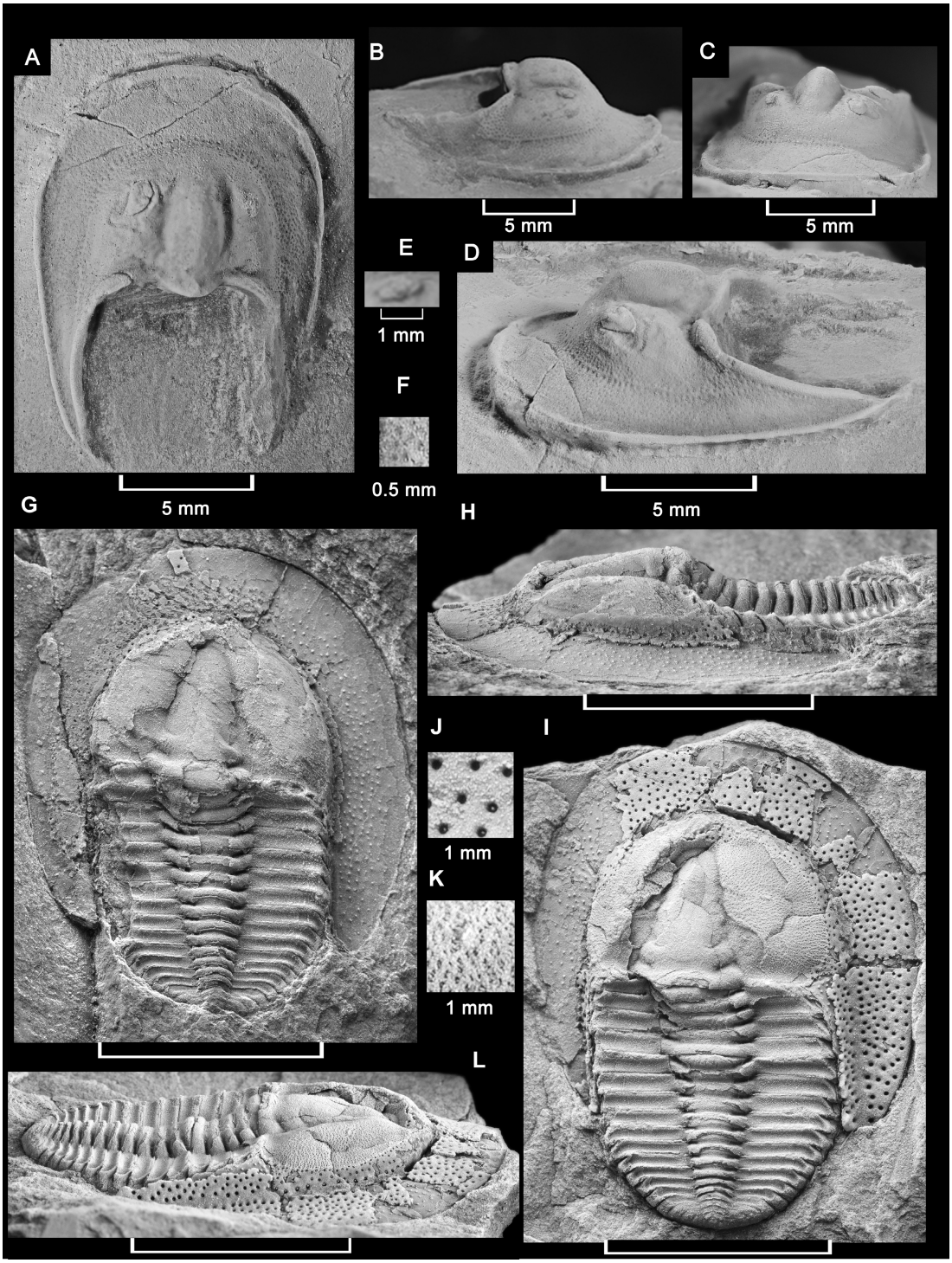


PLATE 53. A–F *Lioharpes ammari* n. sp. (?), a small holaspid or late *meraspid* from an upper Emsian horizon, Tazoulait Formation, North flank of Jbel Ou-Driss (Fig. 2B, Map 4, site 25), dorsal exoskeleton of partial cephalon, NHMUK It 29266. A, dorsal view, B anterior view and C and D lateral views. E, dorsal view of brim perforations and F, laterodorsal view of eye lobe**.**

G–L *Eoharpes beningensis* (Barrande 1872), from Dobrotivá beds, Llandeilo, Lower Ordovician Svatá Dobrovtivá central Bohemia.

G–H partial dorsal exoskeleton, Museum of Comparative Zoology Harvard University, IP 173331. G dorsal view and H, lateral view.

I–L partial dorsal exoskeleton, Museum of Comparative Zoology Harvard University, IP 173316. I, dorsal view and L, lateral view. J, dorsal view of brim perforations and K, lateral view of eye lobe and caeca on genal area.

Scale bars shown represent 1 cm unless otherwise indicated.

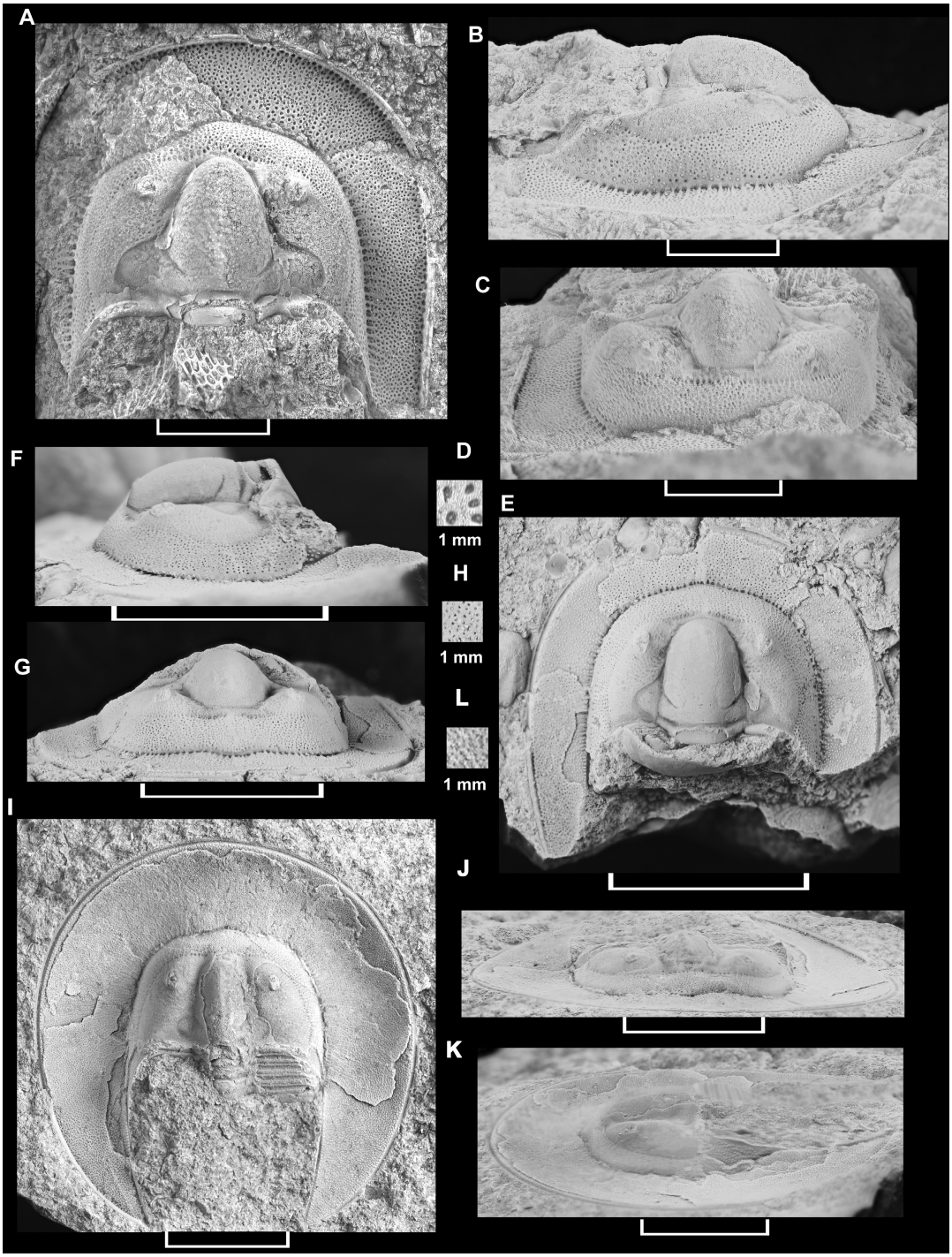


PLATE 54. A–D *Lioharpes venulosus* (Hawle & Corda, 1847); type locality Upper Koněprusy Limestones, (Pragian) Koněprusy, Czech Republic, a dorsal exoskeleton of a partial cephalon, Museum of Natural History, Prague L12545. A dorsal view, B lateral view, C anterior view and D dorsal view of brim perforations.

E–H *Bohemoharpes buphthalmus* (Bouček, 1935). Type locality the horizon with Ananaspis fecunda (Ludlow stage), Dlouhá hora near Beroun, Czech Republic, a dorsal exoskeleton of a partial cephalon, Museum of Natural History, Prague L17145. E, dorsal view, F lateral view, G anterior view and H dorsal view of brim perforations.

I–L *Bohemoharpes naumanni* (Barrande 1852); type horizon and zone *Cyrtograptus lundgreni* zone (Upper Wenlock) Lodenice near Beroun, Czech Republic; dorsal exoskeleton of a partial cephalon, Museum of Natural History, Prague, lectotype (subsequent designation, Prantl and Přibyl, 1954) L6127, IT 48. I dorsal view, J anterior view, K lateral view and L dorsal view of brim perforations. This specimen was illustrated by Prantl and Přibyl,1954 pl. iv fig. 1 and Ebach and McNamara, 2002 Fig 2A.

Scale bars shown represent 1 cm unless otherwise indicated.

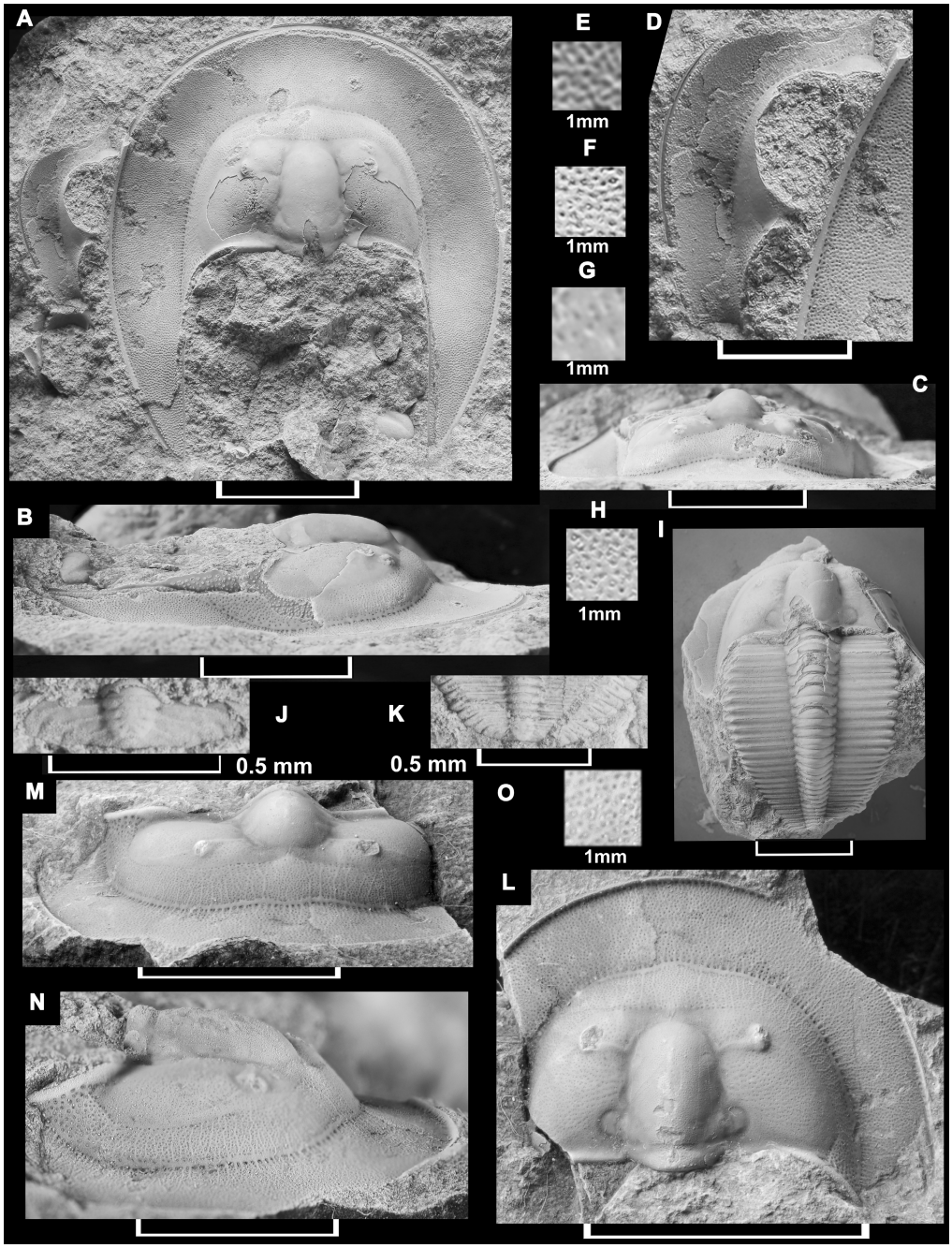


PLATE 55. A–K *Bohemoharpes ungula* (Sternberg, 1833); Type horizon uncertain, Kopanina Formation (Ludlow), type locality Dlouhá hora, near Beroun, Czech Republic, Natural History Museum Prague, Nos L 6123, 6124 and Czech Geological Survey, Nos JV 508, and JV 1390.

A–H L 6123 a dorsal exoskeletons of a large cephalon and a small partial cephalon; A, dorsal view of the two cephala, B lateral view and C anterior view of large cephalon and D dorsal view of small partial cephalon. Dorsal views of brim perforations: G and H, close to the sagittal line and E and F, on the lateral part of brim just anterior to the alae. E and G are from the brims of smallest cephalon and F and H from that of the largest cephalon. **I,** L 6124, a dorsal exoskeleton of partial thorax and cephalon, thorax slightly enrolled, dorsal view.

J–K, JV 508 and JV 1390, dorsal view of a detached and attached pygidium respectively.

L–O *Bohemoharpes ruderalis* (Hawle & Corda 1847) type horizon and locality, upper layers, Praha-Dvorce(?),Lochkov Formation (Lochkovian), Czech Republic, dorsal exoskeletons of a cephalon, the Natural History Museum Prague No. L 19112. L dorsal view, M anterior view, N lateral view and O dorsal view of brim perforations. This specimen was first figured by Prantl & Přibyl 1954 on pl 4, fig. 3.

Scale bars shown represent 1 cm unless otherwise indicated.

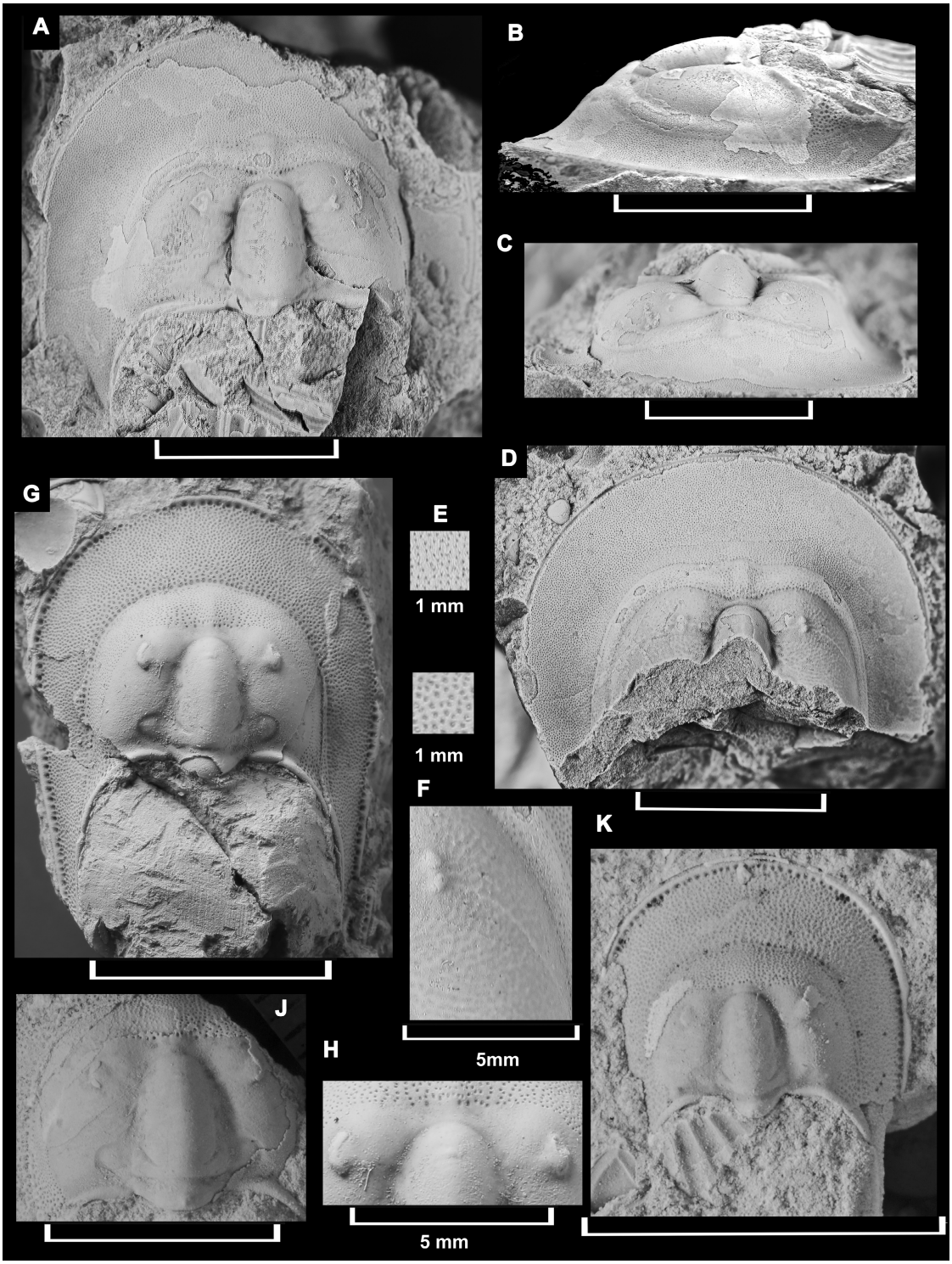


PLATE 56. A–F *Bohemoharpes vittatus* (Barrande 1852); type horizon and locality with *Prionopeltis archiaci*, Kopanina Formation (Ludlow) Praha-Lochkov, dorsal exoskeletons of 2 partial cephala, Natural History Museum Prague Nos L 12549 and L 12565.

A–C, L 12549, A dorsal view, B lateral view and C anterior view.

D–F, No. L 12549, D dorsal view of cephalon, E brim perforations and F genal area including eye lobe and genal ridge.

G–K *Fritchaspis perneri,* Prantl & Přibyl,1954 type horizon and locality Třebotov Limestones, Praha-Holyně Czech Republic, three dorsal exoskeletons of three partial cephala, Natural History Museum Prague No. L6140 and Czech Geological Survey Nos JV15912 and JV15897. **G–I**, No. L6140 holotype, G dorsal view of partial cephalon, H anterior of glabella with axial tubercle and I brim perforations. J, No. JV15912 dorsal view of genicranium and K, No. JV 15897 dorsal view of partial cephalon. Scale bars shown represent 1 cm unless otherwise indicated.

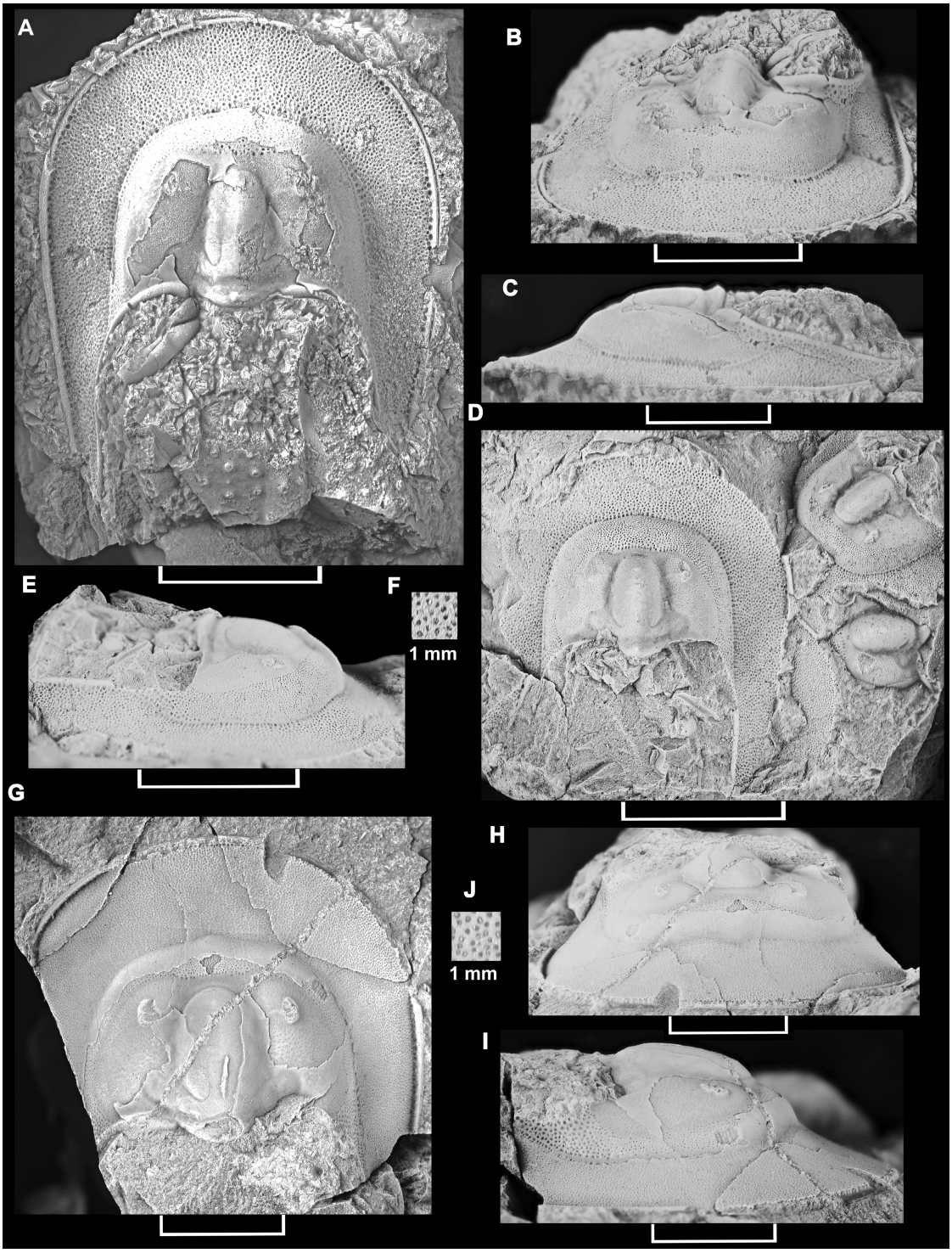


PLATE 57. A–F *Fritchaspis montagnei* (Hawle and Corda, 1847) type horizon and locality *Acanthopyge* Limestones (Eifelian), Koněprusy area, Czech Republic, five dorsal exoskeleton of partial cephala, Museum of Natural History, Prague, syntype Nos L 2996 (one of four syntypes) and L 2990.

A–C, L 2996, a partial cephalon, A dorsal view, B anterior view and C lateral view. L 2990,

D–F a plate with four partial cephala, D dorsal view, E lateral view of largest cephalon and F dorsal vie of brim perforations.

G–J *Declivoharpes praecedens* by (Prantl and Přibyl 1954,) type horizon and locality Radotín Limestones (Lochkovian), praha-radotín (Černá rokle gorge) dorsal exoskeleton of partial cephalon, Museum of Natural History, Prague holotype No. L19103. G dorsal view, H anterior view, I lateral view and J dorsal view of brim perforations. This specimen was illustrated by Prantl and Přibyl (1954, pl. 8 fig.2).

Scale bars shown represent 1 cm unless otherwise indicated.

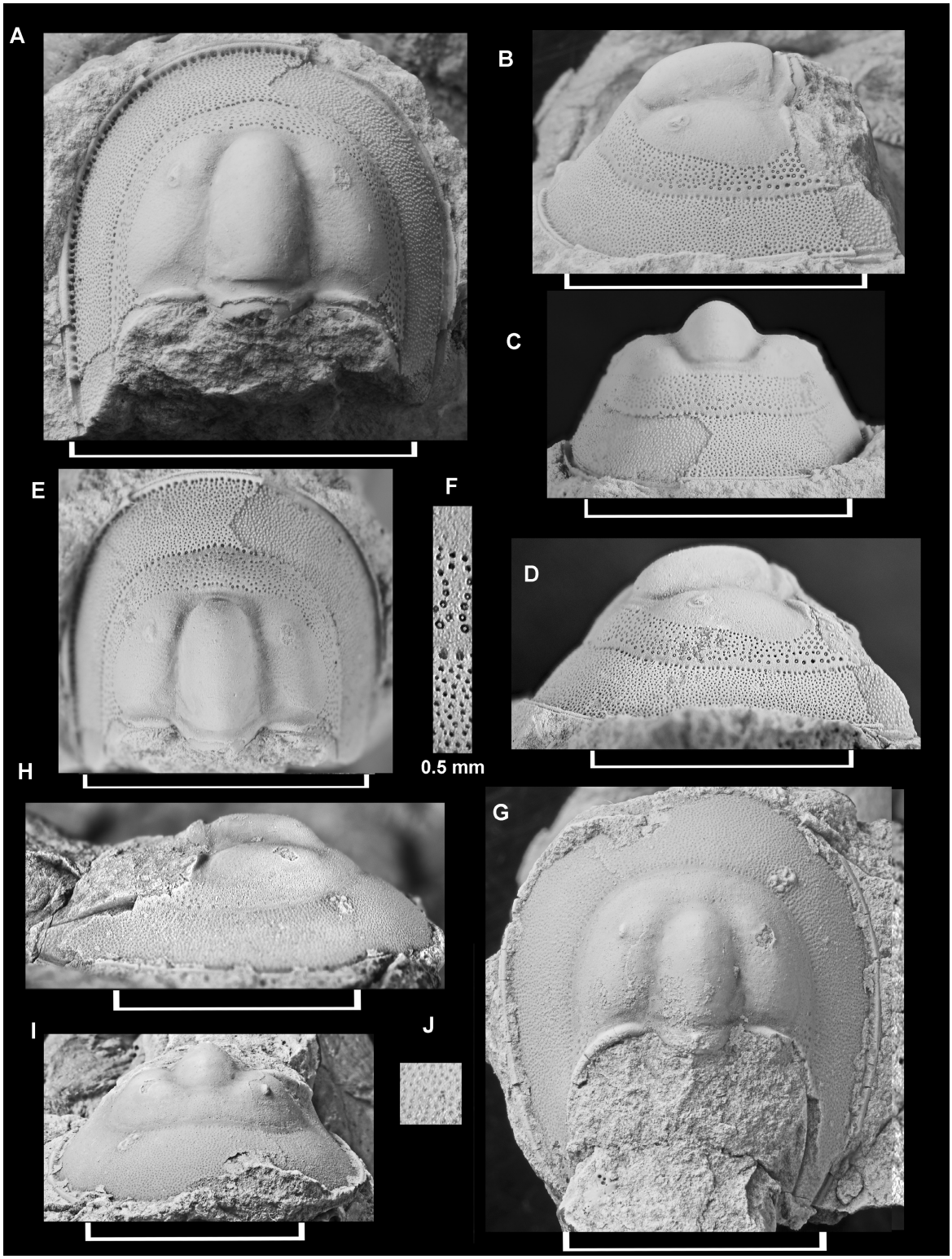


PLATE 58. A –F ***Kielania waageni*** (Novák MS) Prantl and Přibyl, 1954 type horizon and locality Prokop Limestones (Pragian), Praha-Malá Chuchle, Czech Republic, dorsal exoskeleton of a partial cephalon Museum of Natural History, Prague, holotype No. L6141. A dorsal view, B lateral view, C anterior view, D anterolateral view, E anterodorsal view and F lateral view of girder and perforations on genal roll and brim. This specimen was illustrated by Prantl and Přibyl (1954, pl. 9 fig.2).
G–J ***Helioharpes dorbignyanus*** (Barrande 1846) type horizon and locality Dvorce Limestones (Pragian), Praha-Brank ("Za Branickou skalou" locality), Czech Republic, dorsal exoskeleton of a partial cephalon Natural History Museum Prague, No. L12563; G dorsal view, H lateral view, I anterior view and J dorsal view of brim perforations.
Scale bars shown represent 1 cm unless otherwise indicated.

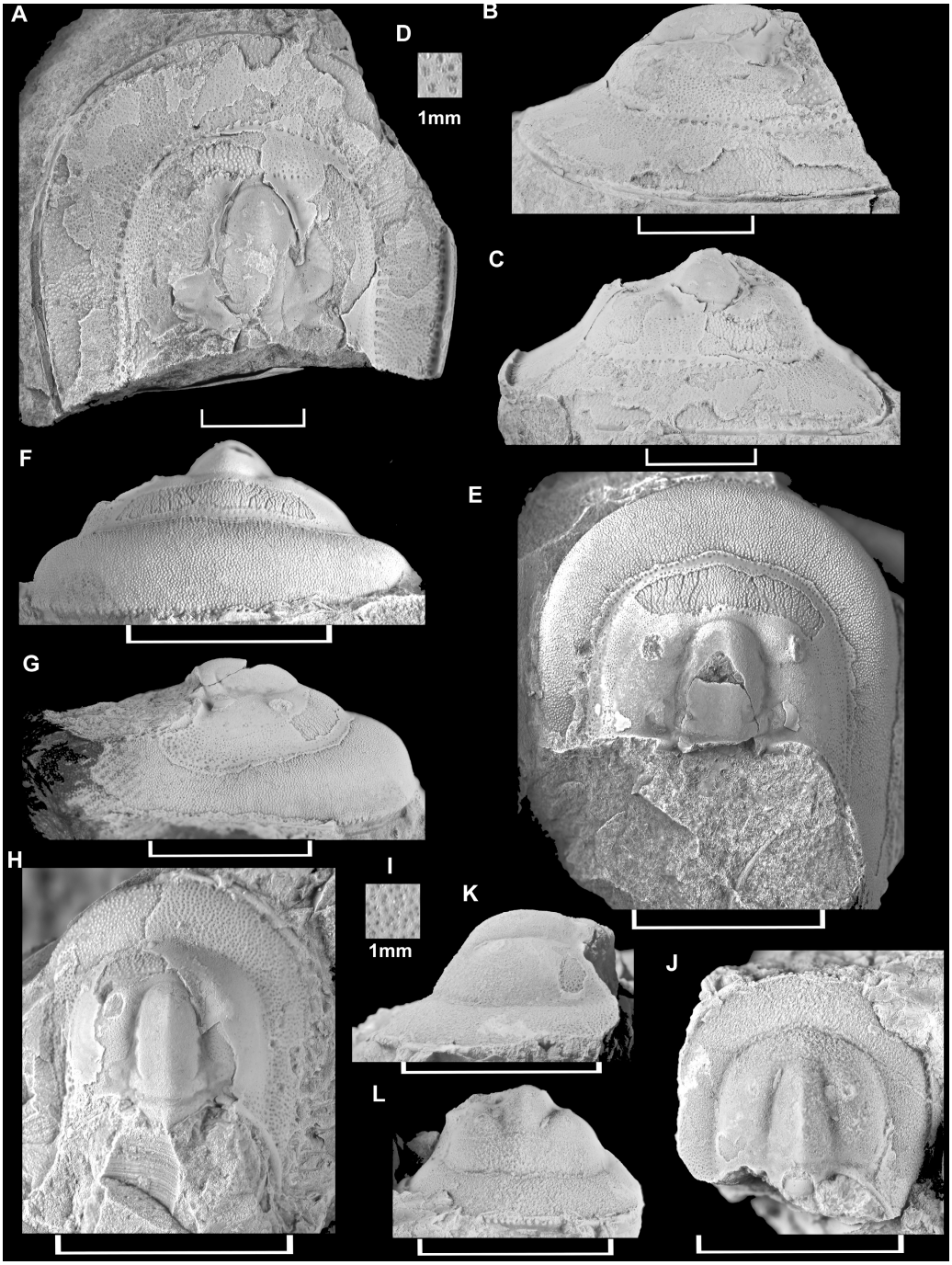


PLATE 59. A–D ***Helioharpes dvorcensis*** (Prantl and Přibyl, 1954), type horizon and locality Dvorce Limestones (Pragian), Praha-Podoli (formerly Dvorce), Czech Republic, dorsal exoskeleton of a partial cephalon from the Natural History Museum Prague No. L19105 holotype. A dorsal view, B lateral view, C anterior,view and D dorsal view of brim perforations. This specimen was illustrated by Prantl and Přibyl (1954, pl.8 fig. 5).

E –G ***Declivoharpes novaki*** (Prantl and Přibyl 1954). Type horizon Prokop Limestone (Pragian), St. Prokop quarry, Praha-Hlubocepy, Czech Republic, dorsal exoskeleton of a partial cephalon from the Natural History Museum Prague holotype No. L6120, E dorsal view of exoskeleton, F anterior view and G lateral view. This specimen was illustrated by Prantl and Přibyl (1954, pl.9 fig. 1).

H–L ***Stoloharpes convexus***. (Hawle and Corda 1847) Suchomasty Limestones (Eifelian), Měňany, Czech Republic, dorsal exoskeletons of two partial cephalon from the Natural History Museum Prague Nos L 6138 and L 6139. H, L 6139, dorsal view of exoskeleton. I–L, L 6138, J dorsal view of exoskeleton, K lateral view, L anterior view and I dorsal view of brim perforations. L 6138 and L 6139 were illustrated by Prantl and Přibyl (1954, pl. 9 figs 3 and 4 respectively).

Scale bars shown represent 1 cm unless otherwise indicated.

TABLE 1. Location of map sites in Figures 3 to 7 cross referenced with material and systematics

Locality	Map No.	Site No.	GPS co-ordinates North	GPS co-ordinates West	GPS Cat.	Genus	*Species*	Type	Ref. Nos. NHMUK	Plate Nos.	
Tata	1	1	029 39.825	007 52.412	b	M.	cf. *zguidensis*	OM	It 29328	31	L–N
Foum Zguid	2	1	030 03.316	007 06.000	b	M.	*zguidensis*	OM	It 29325	24	A–E
		2	030 03.316	007 06.000	b	M.	*zguidensis*	Pt	It 29326	24	F–I
		3	030 03.316	007 06.000	b	M.	*zguidensis*	Pt	It 29327	24	J–K
		4	030 03.316	007 06.000	b	M.	cf. 2 *laatchanensis*	OM	It 29310 (1)	25	A–D
		4	SP	SP	b	M.	cf. 2 *laatchanensis*	OM	It 29310 (2)	25	E–G
		5	030 03.316	007 06.000	b	M.	cf. *minutipunctus*	OM	It 29314	NF	
		6	029 55.671	073 03.1848	b	H.	cf. *lahceni*	OM	It 29235	6	I–N
Tinghir	3	1	031 27.191	005 14.244	c	St.	*calceolus*	OM	It 29363	49	G–K
		2	031 27.191	005 14.244	c	St.	aff. *calceolus*	OM	It 29381	49	L–P
		3	031 27.202	005 14.190	b	P.	*haustrum*	Ht	It 29341	42	A–F
		4	031 27.202	005 14.190	b	P.	*haustrum*	Pt	It 29342	42	G–M
Jbel Ou-Driss	4	1	030 30.399	005 23.089	a	K.	*tumulus*	Ht	It 29259	16	A–E
		2	030 30.418	005 23.092	b	K.	*tumulus*	Pt	It 29260	16	F–L
		3	030 30.424	005 23.099	a	K.	*tumulus*	OM	It 29261	NF	
		4	030 30.412	005 23.092	a	M.	*hammii*	Pt	It 29297	27	L–O
		5	030 31.172	005 20.594	a	P	*igaouii*	Ht	It 29360	36	A–H
		6	030 31.587	005 19.379	a	L.	cf. *ammari*	OM	It 29267	13	K–O
		7	030 31.587	005 19.379	a	M.	aff. 1 *minutipunctus*	Ht	It 29322	22	F–J
		8	030 31.583	005 19.377	a	P	*igaouii*	Pt	It 29361	36	I–K
		9	030 31.901	005 18.854	a	L.	*ammari*	Ht	It 29263	12	G–M
		10	030 31.361	005 18.748	a	H.	cf. *oudris*	OM	It 29242	6	A–H
		11	030 31.352	005 18.774	a	H.	cf. *boudibensis*	OM	It 29225	2	A–D
		12	030 31.621	005 18.311	a	L.	*ammari*	Pt	It 29253	13	A–E
		13	030 31.621	005 18.311	a	L.	*ammari*	Pt	It 29265 (1)	13	F–H
		13	SP	SP	a	L.	*ammari*	Pt	It 29265 (2)	13	I–J
		14	030 31.352	005 18.773	a	H.	*supercilium*	Pt	It 29248	4	A–D
		15	030 31.345	005 18.728	a	H.	*sphenocephalus*	Ht	It 29246	4	E–K
		16	030 33.334	005 15.324	b	M.	*ihmadii*	Ht	It 29301	26	A–G
		17	030 33.334	005 15.324	b	M.	*ihmadii*	Pt	It 29302	26	H–Q
		18	030 33.334	005 15.324	b	M.	*ihmadii*	Pt	It 29303	27	A–D
		19	030 33.334	005 15.324	b	M.	cf. *hammii*	OM	It 29298	NF	
		20	030 33.172	005 15.149	b	M.	aff. 2 *minutipunctus*	OM	It 29324	22	N–Q
		21	030 31.354	005 18.762	c	H.	*oudris*	Pt	It 29240	2	E–H
		22	030 31.354	005 18.762	c	H.	*oudris*	Ht	It 29241	2	I–M
		23	030 31.354	005 18.762	b	H.	*supercilium*	OM	It 29249		NP
		24	030 31.373	005 18.754	a	H.	*supercilium*	Pt	It 29250	3	L–P
		25	030 31.583	005 19.377	a	L.	*ammari meraspid*?	OM	It 29266	53	A–F
Saredrar	5	1	030 45.388	005 27.684	c	L.	*saredra*	Ht	It 29274	14	A–I
		2	030 45.388	005 27.684	c	L.	*saredra*	Pt	It 29275	14	J–N

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TABLE 1. (Continued)

Locality	Map	Site	GPS co-ordinates		GPS	Genus	*Species*	Type	Ref. Nos.	Plate Nos.	
	No.	No.	North	West	Cat.				NHMUK		
Jorf	6	1	031 31.612	004 28.783	a	P.	aff. *igaouii*	OM	It 29362	36	L–O
		2	031 31.653	004 28.763	b	P.	*chaperon*	Pt	It 29331 (1)	41	A–E
		2	SP	SP	b	P.	*chaperon*	Pt	It 29331 (2)	41	F
		3	031 31.653	004 28.763	b	St.	*rissaniensis*	Pt	It 29371	48	A–D
		4	031 31.653	004 28.763	b	P.	*chaperon*	Ht	It 29332	41	G–J
		5	031 27.507	004 20.177	c	K.	*sicarius*	Pt	It 29256 (6)	33	A–C
		5	SP	SP	c	K.	*sicarius*	Ht	It 29256 (1)	33	D– F
		5	SP	SP	c	K.	*sicarius*	Pt	It 29256 (8)	33	H
		5	SP	SP	c	K.	*sicarius*	Pt	It 29256 (3)	33	I–K
		5	SP	SP	c	K.	*sicarius*	Pt	It 29256 (2)	34	A–E
		5	SP	SP	c	K.	*sicarius*	Pt	It 29256 (5)	34	F–G
		5	SP	SP	c	K.	*sicarius*	Pt	It 29256 (4)	34	H
		5	SP	SP	c	K.	*sicarius*	Pt	It 29256 (7)	34	I
		6	031 25.201	004 22.012	a	P.	aff. *apteros*	OM	It 29379	38	F–I
		7	031 25.192	004 22.009	a	P.	*torquis*	Pt	It 29353	37	A–D
		8	031 25.198	004 22.009	a	P.	*apteros*	Pt	It 29356	39	A–D
		9	031 25.192	004 22.009	a	P.	*torquis*	Ht	It 29354 (1)	37	E–J
		9	SP	SP	a	P.	*torquis*	Pt	It 29354 (2)	37	E
		10	031 25.192	004 22.009	a	P.	*torquis*	Pt	It 29355 (1)	37	K–O
		10	SP	SP	a	P.	*torquis*	Pt	It 29355 (2)	NF	
		11	031 25.171	004 21.994	b	P.	*hannabouensis*	Ht	It 29333	40	E–I
		12	031 25.171	004 21.994	b	P.	*hannabouensis*	Pt	It 29334	40	A–D
		13	031 25.171	004 21.994	a	P.	*hannabouensis*	Pt	It 29335	40	J–N
		14	031 25.171	004 21.994	c	St.	aff. *rissaniensis*	OM	It 29380	49	A–F
		15	031 25.201	004 22.012	a	P.	*apteros*	Pt	It 29357	39	L–M
		16	031 24.447	004 28.923	c	Hl.	*aoujili*	Ht	It 29254	17	A–K
		17	031 24.447	004 28.923	c	Hl.	*aoujili*	Pt	It 29255	17	M–P
		18	031 24.534	004 28.843	c	P.	*apteros*	Ht	It 29358	38	J–O
		19	031 24.534	004 28.843	c	P.	*apteros*	Pt	It 29359	39	E–K
		20	031 24.534	004 28.843	c	P.	aff. *torquis*	OM	It 29329	38	A–E
		21	031 31.653	004 28.763	b	P.	cf. *chaperon*	OM	It 29330	41	K–N
		22	031 31.653	004 28.763	b	St.	*rissaniensis*	Pt	It 29372	48	E–J
Jbel	7	1	031 05.099	004 54.333	c	H.	*boudibensis*	Pt	It 29226	1	A–D
Issoumour		2	030 58.419	005 01.749	b	H.	cf. *prescheri*	OM	It 29245	9	J–N
		3	031 05.099	004 54.333	b	H.	*supercilium*	Pt	It 29251	3	A–F
		4	031 05.099	004 54.333	b	H.	*boudibensis*	Ht	It 29227	1	K–Q
		5	031 05.165	004 53.453	a	H.	*boudibensis*	Pt	It 29228	1	E–J
		6	031 05.168	004 53.441	a	H.	*lahceni*	Ht	It 29232	5	A–J
		7	030 58.419	005 01.750	b	H.	cf. *lentigo*	OM	It 29238	8	I–L
		8	031 02.132	005 03.057	b	H.	*prescheri*	Pt	It 29243	9	F–I
		9	031 00.224	005 03.010	b	H.	*prescheri*	Ht	It 29244	9	A–E
		10	031 05.099	004 54.333	a	H.	*supercilium*	Ht	It 29252	3	G–K
		11	031 05.165	004 53.453	a	P	*segaouii*	Pt	It 29352	35	H–K

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TABLE 1. (Continued)

Locality	Map No.	Site No.	GPS co-ordinates North	GPS co-ordinates West	GPS Cat.	Genus	*Species*	Type	Ref. Nos. NHMUK	Plate Nos.	
		12	031 05.099	004 54.333	a	H.	*supercilium*	OM	It 29253	NF	
		13	031 05.099	004 54.333	b	H.	*boudibensis*	OM	It 29229	NF	
		14	030 58.422	005 01.752	b	H.	cf. *lentigo*	OM	It 29239	8	A–H
		15	031 05.168	004 53.441	a	H.	*boudibensis*	OM	It 29230	NF	
		16	031 05.169	004 53.439	a	H.	*boudibensis*	OM	It 29231	NF	
		17	031 04.412	005 00.967	b	H.	cf. *sphenocephalus*	OM	It 29247	4	L–O
		18	031 04.506	005 00.674	b	F	*edgecombei*	Ht	It 29224	18	A–F
Jbel Oufatene	8	1	030 52.767	004 58.041	a	M.	*oufatenensis*	OM	It 29317	NF	
		2	030 52.767	004 58.041	b	M.	*oufatenensis*	Pt	It 29318 (1 to 9)	25	H
		3	030 51.171	004 58.349	b	M.	*laatchanensis*	Pt	It 29306	21	L– O
		4	030 51.156	004 55.825	b	H.	*lentigo*	Ht	It 29236	7	A–G
		5	030 51.156	004 55.825	b	H.	*lentigo*	Pt	It 29237 (1 to 3)	7	H–M
		6	030 51.327	004 55.130	b	H.	*lahceni*	Pt	It 29233	5	M–N
		7	030 50.855	004 55.216	c	L.	*saredra*	Pt	It 29276	15	A–C
		8	030 50.492	004 54.906	a	M.	*hammii*	Pt	It 29290	20	A–D
		9	030 50.492	004 54.906	a	M.	*hammii*	Pt	It 29291	20	J–M
		10	030 51.191	004 58.222	b	M.	cf. *minutipunctus*	OM	It 29315	NF	
		11	030 52.160	004 58.113	b	M.	*minutipunctus*	Ht	It 29312	23	E–J
		12	030 52.160	004 58.113	b	M.	*minutipunctus*	Pt	It 29313	23	K–P
		13	030 52.160	004 58.100	b	M.	*laatchanensis*	Pt	It 29307	21	H–K
		14	030 51.064	004 58.380	b	M.	cf. *ihmadii*	OM	It 29304	27	E–K
		15	030 52.160	004 58.102	b	M.	*laatchanensis*	Ht	It 29308	21	A–G
		16	030 50.010	004 58.395	b	M.	*forteyi*	Ht	It 29288	29	A–D
		17	030 50.010	004 58.395	b	M.	cf. *azmamarensis*	OM	It 29285	30	F–K
		18	030 50.010	004 58.395	b	M.	*azmamarensis*	Ht	It 29281	29	E–J
		19	030 50.010	004 58.395	b	M.	*azmamarensis*	Pt	It 29282	30	A–E
		19	030 50.010	004 58.395	b	M.	*azmamarensis*	Pt	It 29283	29	O
		20	030 50.010	004 58.395	b	M.	cf. *forteyi*	OM	It 29284	31	F–K
		21	030 49.404	004 59.393	c	M.	*hammii*	Ht	It 29292	18	G–N
		22	030 48.895	004 59.916	b	M.	*hammii*	Pt	It 29293	20	N–P
		23	030 44.617	004 55.709	b	M.	*oufatenensis*	Pt	It 29316	28	F–I
		24	030 44.617	004 55.709	b	M.	*oufatenensis*	Pt	It 29319	28	J–O
bou Lachrhal & Ifred Nou Haouar	9	1	030 57.784	004.34.797	a	L.	*saredra*	Pt	It 29277	15	K–N
		2	030 57.784	004.34.797	a	L.	*scopulum*	Ht	It 29279	32	E–L
		3	030 57.784	004.34.797	a	L.	*scopulum*	Pts	It 29280 (1)	32	M–N
		3	SP	SP	a	L.	*scopulum*	Pts	It 29280 (2)	32	O–P
		3	SP	SP	a	L.	*scopulum*	Pts	It 29280 (3)	32	Q
		3	SP	SP	a	L.	*scopulum*	Pts	It 29280 (4)	NF	
		4	030 55.432	004 33.552	a	M.	aff. *Ihmadii*	OM	It 29305	31	A–E

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TABLE 1. (Continued)

Locality	Map No.	Site No.	GPS co-ordinates North	GPS co-ordinates West	GPS Cat.	Genus	*Species*	Type	Ref. Nos. NHMUK	Plate Nos.	
		5	030 50.704	004 30.888	a	M.	aff. *zguidensis*	OM	It 29287	23	A–D
		6	030 50.688	004 30.873	b	L.	*morocconensis*	Ht	It 29271 (1)	11	F–J
		6	SP	SP	b	L.	*morocconensis*	Pt	It 29271 (2)	11	K–M
		7	030 50.323	004 30.589	a	M.	*forteyi*	Pt	It 29289	29	K–N
		8	030 48.040	004 30.529	a	M.	cf. 1 *laatchanensis*	OM	It 29311	22	A–E
		9	030 48.044	004 30.527	a	M.	*laatchanensis*	OM	It 29309	NF	
		10	030 45.039	004 32.051	a	L.	*gallea*	Ht	It 29268	10	E–H
		11	030 45.039	004 32.051	c	L.	*gallea*	Pt	It 29269	10	I–K
		12	030 45.296	004 26.117	a	M.	*hammii*	Pt	It 29294	19	G–L
		13	030 45.767	004 26.012	b	M.	aff. 1 *minutipunctus*	OM	It 29323	22	K–M
		14	030 44.476	004 34.089	a	M.	cf. *azmamarus*	OM	It 29286	30	L–O
		15	030 44.508	004 37.965	b	M.	*hammii*	Pt	It 29295	19	M–O
		16	030 44.508	004 37.965	b	M.	*hammii*	Pt	It 29296	19	A–F
		17	030 50.688	004 30.873	c	L.	*morocconensis*	Pt	It 29272	11	A–E
		18	030 44.508	004 37.960	c	M.	*terridus*	Ht	It 29321	32	A–D
Timerzit	10	1	031 11.962	004 56.083	a	P.	*segaouii*	Pt	It 29350	35	L–P
		2	031 11.962	004 56.083	a	H.	*lahceni*	Pt	It 29234	5	K–L
		3	031 11.559	004 56.091	a	P.	cf. *hamarlaghdadensis*	OM	It 29336	NF	
		4	031 13.374	004 54.003	b	P.	*segaouii*	Ht	It 29351	35	A–G
		5	031 14.867	004 47.961	a	K.	aff. *tumulus*	OM	It 29262	36	P–R
		6	031 16.106	004 44.850	a	M.	cf. *hammii*	OM	It 29299	NF	
Hamar Laghdad	11	1	031 22.784	004 03.426	b	P.	*hamarlaghdadensis* nm	OM	It 29337	44	A–F
		2	031 22.784	004 03.426	b	P.	*hamarlaghdadensis* nm	OM	It 29338	44	G–J
		3	031 22.784	004 03.426	b	P.	*hamarlaghdadensis* nm	OM	It 29339	44	K–M
		4	031 22.786	004 03.424	b	P.	aff. *hamarlaghdadensis*	OM	It 29340	NF	
		5	031 22.791	004 03.419	b	P.	*merzanensis*	Pt	It 29348	45	I–L
		6	031 22.791	004 03.419	b	P.	*merzanensis*	Ht	It 29349	45	A–H
		7	031 22.392	004 03.015	b	P.	cf. *haustrum*	OM	It 29347 (1)	43	C–L
		7	SP	SP	b	P.	cf. *haustrum*	OM	It 29347 (2)	43	M–P
		8	031 22.716	00 4 03.478	b	M.	*oufatenensis*	Ht	It 29320 (1)	28	A– E
		8	SP	SP	B	M.	*oufatenensis*	Pt	It 29320 (2)	NF	
		9	031 22.459	004 03.105	b	P.	*haustrum*	Pt	It 29270	NF	
		10	031 22.459	004 03.105	b	P.	*haustrum*	Pt	It 29343	NF	
		11	031 22.433	004 03.067	b	P.	*haustrum*	Pt	It 29344	NF	
		12	031 22.433	004 03.067	b	P.	*haustrum* ?	Pt	It 29346	NF	
		13	031 22.433	004 03.067	b	P.	*haustrum*	Pt	It 29345	42 43	N–O & A–B
		14	031 22.716	004 03.478	a	St	aff. *capricornus*	OM	It 29366	50	G–J

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TABLE 1. (Continued)

Locality	Map No.	Site No.	GPS co-ordinates North	GPS co-ordinates West	GPS Cat.	Genus	*Species*	Type	Ref. Nos. NHMUK	Plate Nos.	
Shebras	12	1	031 00.297	004 04.043	a	L.	*saredra*	Pt	It 29278	15	D–J
North Zireg	13	1	030 39.068	004 35.274	b	M.	cf. *hammii*	Pt	It 29300	20	E–I
Rissani	14	1	031 08.342	004 23.892	a	H.	*retinarius*	Pt	It 29367	52	A–F
		2	031 08.327	004 23.639	a	H.	*retinarius*	Ht	It 29368	51	A–G
		3	031 08.327	004 23.639	a	H.	*retinarius*	Pt	It 29369	51	H–L
		4	031 12.429	004 18.751	a	St.	*rissaniensis*	Ht	It 29373	46	A–M
		5	031 12.429	004 18.751	a	St.	*rissaniensis*	Pt	It 29374	47	A–F
		6	031 12.429	004 18.751	a	St.	*rissaniensis*	Pt	It 29375	47	G–J
		7	031 12.429	004 18.751	a	St.	*rissaniensis*	Pt	It 29376	46	N–O
		8	031 13.853	004 22.981	b	St.	*rissaniensis*	Pt	It 29377	48	K–M
		9	031 13.853	004 22.981	b	St.	*rissaniensis*	Pt	It 29378	NF	
		10	031 02.147	004 21.252	a	L.	cf. *morocconensis*	OM	It 29273	12	A–F
		11	031 08.342	004 23.892	b	H.	*retinarius*	Pt	It 29370	52	G–L
Taouz East	15	1	030 56.660	003 46.890	b	St.	*capricornus*	Ht	It 29364	50	A–F
		2	030 56.660	003 46.890	c	St.	*capricornus*	Pt	It 29365	50	K–O

TABLE 2. Brim perforations, number and diameter (actual and standardised) of two specimens with differing brim widths (sag.) from four chosen species**.**

	Ref. NHMUK No It	Brim width (Sag.) mm	Perforations Actual No.	Perforations Actual Size µm	Perforations Standardised No.	Perforations Standardised Size µm
Maghroharpes n. gen *oufatenensis* n. sp.	29318(1)	7.50	6	222	14	148
	29318(2)	3.90	21	107	13	138
Lioharpes morocconensis n. sp.	29271(1)	11.55	2.5	471	13	204
	29271(2)	7.22	6	308	13	213
saredra n. sp.	29277	7.10	9	210	18	148
	29274	9.69	5	275	19	142
scopulum n. sp.	29280(1)	5.60	21	149	26	133
	29280(2)	2.70	80	79	23	146
	29279	2.59	80	69	21	134

TABLE 3a. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
E. benignensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. naumanni	0	2	2	1	1	1	1	0	0	?	0	1	1	1	0	1	?	0	?	?	?	1	?	?	1	0	2	0	0	0	0	0	0	0	0	4	2	0
B. cf. *acuminiatus*	3	0	0	1	1	0	0	0	0	0	0	1	0	1	0	?	1	0	2	1	0	1	1	4	0	0	2	0	0	1	1	0	0	1	0	0	2	0
B. budovicensis	3	1	2	0	?	0	0	0	?	?	?	2	1	1	0	?	1	0	?	?	?	?	?	?	1	0	1	0	0	0	1	0	0	0	0	?	2	0
B. buphthalmus	0	0	0	1	0	0	0	0	?	0	?	2	3	1	0	1	1	0	0	-	1	1	1	?	0	0	3	1	0	0	1	0	0	1	0	1	0	2
B. hypsipyle	1	?	0	?	0	0	0	0	?	?	?	1	3	1	1	1	1	0	?	2	0	1	1	?	1	0	2	0	0	0	1	0	0	0	0	0	2	2
B. janae	0	0	2	1	0	1	0	0	0	0	1	1	0	2	0	1	?	0	2	-	1	?	?	?	1	0	2	0	0	0	0	0	0	0	?	5	2	0
B. ovatus	0	2	2	0	1	1	0	0	?	?	?	1	3	1	0	?	1	2	0	2	0	?	0	?	?	0	2	1	0	0	1	0	0	0	0	4	0	0
B. ruderalis	3	1	2	0	1	0	0	0	1	0	0	0	3	1	0	1	0	2	2	-	1	0	0	0	0	0	2	0	1	0	1	0	0	1	0	4	2	0
B. ungula	0	0	2	1	1	1	0	0	0	0	1	1	2	1	0	1	0	2	0	1	0	1	0	0	0	0	2	0	0	0	2	0	0	0	0	4	2	0
B. vectori	0	1	0	1	1	1	0	0	?	?	?	1	3	1	0	?	?	?	?	?	?	?	?	?	0	0	3	0	0	0	0	0	0	0	0	?	?	2
B. vittatus	1	1	2	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	2	2	0	2	0	0	0	0	3	0	0	0	0	0	0	?	0	4	2	0
B. wilkensii	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	?	1	2	2	2	0	2	1	0	0	0	2	0	0	0	1	0	0	?	0	3	2	0
D. praecedens	1	1	1	1	1	0	0	0	0	1	1	2	3	1	0	1	0	?	?	-	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	?	3	2
D. novaki	2	1	1	1	1	0	0	0	0	0	?	2	0	1	0	?	0	?	2	?	?	?	1	?	0	0	1	0	1	1	0	0	0	0	0	3	2	2
Es. palanasus	1	1	0	0	0	1	0	0	1	0	0	1	3	1	0	1	1	0	1	-	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	4	0	0
Es.boltoni	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	2	1	2	1	0	0	0	1	0	0	0	0	0	0	4	0	0
Es. friendi	1	1	1	2	0	2	0	0	2	0	0	1	3	1	0	?	1	0	0	1	0	1	1	2	0	0	2	0	0	0	1	0	0	0	0	2	2	0
Es. guthae	0	1	0	0	0	1	0	0	1	0	1	1	3	1	1	2	0	0	0	1	0	2	1	2	1	0	0	1	0	0	0	0	0	0	0	5	0	0
Es. neogracilis	2	1	0	2	0	1	0	0	1	0	1	0	3	2	0	1	1	0	2	-	1	2	1	2	1	0	?	-	-	0	3	0	0	0	0	4	2	0
"*Es*". *pruniformis*	1	1	1	0	0	1	?	0	?	?	?	?	?	2	0	?	1	0	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	0	2
Es. sicarius n. sp.	0	1	1	0	1	1	0	0	0	0	1	1	3	1	0	1	1	0	0	-	1	1	1	?	1	0	1	0	1	0	0	0	0	0	0	3	2	0
"*Es.*" *socialis*	1	1	1	0	0	1	0	0	?	0	?	?	?	2	0	?	?	2	?	-	1	1	?	?	1	0	?	?	?	0	?	0	0	0	0	?	2	2
Es. teicherti	0	1	1	1	0	1	0	0	1	0	1	1	1	1	0	1	1	0	0	-	1	1	1	2	0	0	2	0	0	0	1	0	0	0	0	2	0	0
Es. wanndjina	0	1	0	0	0	1	0	0	1	0	1	1	3	1	0	1	0	0	2	-	1	1	1	2	1	0	1	1	0	0	2	0	0	0	0	3	?	0
F. montagnei	1	1	1	1	0	0	0	0	0	1	1	2	0	1	0	2	1	0	0	1	0	0	1	0	0	0	2	0	0	0	0	0	0	1	?	0	3	2
F.edgecombei n. sp.	2	1	1	1	1	1	1	0	1	0	1	1	3	1	1	2	1	0	0	1	0	1	1	0	1	0	2	0	0	0	0	0	0	1	0	2	1	2
F. sp. 2 Feist 1977	1	1	1	1	0	0	0	0	1	0	?	1	3	1	0	2	1	0	?	-	1	1	0	?	0	0	1	1	0	0	0	0	0	?	0	0	2	2
F. perneri	1	1	1	1	0	1	0	0	0	1	?	1	3	2	0	?	1	0	0	-	1	?	1	0	0	0	1	0	0	0	0	0	0	1	0	0	2	2
F. wendti	2	1	0	1	0	1	1	1	0	0	0	1	0	0	1	2	1	0	1	1	0	2	1	0	0	0	2	0	0	0	0	0	0	1	0	0	2	2
H. macrocephalus	1	1	0	1	1	2	0	0	2	0	0	2	1	0	0	1	1	0	0	-	1	0	0	?	0	1	0	0	0	0	0	1	0	1	0	3	2	1
H. boudibensis n. sp.	1	1	1	0	1	0	0	0	0	0	1	2	3	0	1	2	1	0	0	1	0	2	1	1	0	1	2	0	1	0	0	1	1	1	0	2	2	1
H. cf. *boudibensis*	1	1	1	1	1	0	0	0	2	0	1	1	3	0	2	-	1	1	1	0	0	2	1	1	0	1	2	0	1	1	0	1	1	1	0	2	2	1
H. escoti	2	1	3	1	1	3	0	1	?	?	?	1	?	1	0	2	1	0	0	-	1	1	1	?	1	0	0	0	0	0	0	?	0	?	0	3	2	1
H. sp. 1 Feist 1977	1	1	1	1	1	0	1	0	0	0	0	2	3	1	0	1	1	0	0	-	1	1	1	0	0	0	0	0	1	0	0	?	0	0	0	1	2	1
H. lahceni n. sp.	0	1	0	1	1	0	0	0	2	0	1	2	3	1	0	1	1	0	1	2	1	2	1	1	0	1	2	0	0	1	0	0	0	1	1	2	2	1
H. lentigo n.sp.	0	1	0	1	0	0	0	0	2	0	1	1	3	1	0	2	1	0	0	-	1	2	1	1	0	1	1	0	1	1	1	1	0	1	0	2	2	2
H. ormistoni	1	0	3	1	?	1	0	0	?	?	?	?	?	?	?	?	1	0	?	?	1	?	?	?	0	0	2	?	?	?	?	?	?	?	?	2	?	?
H. oudris n. sp.	1	1	1	1	1	0	0	0	2	0	1	2	3	0	0	2	1	0	1	1	0	2	1	?	0	1	2	0	1	1	0	1	1	1	0	2	2	1
H. presheri n. sp.	1	3	3	1	1	1	1	0	2	0	1	?	2	0	1	1	1	0	0	-	1	1	1	?	1	1	1	0	1	1	2	0	0	0	0	2	2	1
H. reticulatus	2	4	1	1	1	0	1	?	0	0	0	1	3	0	0	?	1	0	0	1	0	2	0	?	0	0	2	0	0	0	0	0	0	0	0	?	2	1
H. sphenocephalus n. sp.	2	1	1	1	1	0	1	0	0	0	0	1	1	0	1	1	1	0	1	-	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	2	2	1
H. cf. *sphenocephalus*	2	1	0	1	1	0	0	0	2	0	0	1	3	0	2	-	?	0	0	-	1	?	1	?	0	0	0	0	0	0	2	1	1	?	0	2	1	1
H. supercilium n. sp.	1	1	1	1	1	0	0	0	0	0	0	2	2	0	0	2	1	0	1	1	0	2	1	1	0	1	1	0	1	1	1	1	1	1	0	2	2	1
H. whidbornei	?	1	1	?	1	1	0	0	?	?	?	2	1	0	0	2	1	0	0	1	?	1	0	?	0	?	0	0	0	0	2	?	?	0	0	2	2	1

TABLE 3b. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
E. benignensis	?	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. naumanni	1	0	0	1	0	0	2	0	?	1	0	?	?	2	0	2	1	1	0	0	1	0	1	1	1	1	0	?	3	0	0	3	1	1	1	2	3
B. cf. *acuminiatus*	0	0	0	1	0	0	2	0	0	2	1	3	0	0	1	1	1	1	0	0	1	0	?	?	1	1	0	0	?	0	?	0	?	1	2	2	3
B. budovicensis	0	0	?	2	0	0	2	0	?	?	?	?	?	2	0	?	?	?	0	?	?	1	?	?	?	1	?	?	?	0	0	?	?	2	?	?	?
B. buphthalmus	0	0	0	1	1	0	2	0	?	1	1	?	?	2	1	1	1	1	0	0	1	0	2	3	2	1	0	0	2	0	0	1	1	1	2	2	3
B. hypsipyle	0	0	0	1	0	0	2	0	?	?	?	?	?	2	0	2	1	1	0	0	1	0	?	?	?	1	0	0	?	0	0	?	?	2	1	2	3
B. janae	?	0	0	1	0	0	2	0	?	?	1	?	?	?	0	1	1	1	0	0	1	1	?	?	?	1	0	1	?	0	0	2	?	0	?	?	3
B. ovatus	?	?	?	2	0	0	2	0	?	?	?	?	?	2	?	1	0	-	-	0	1	0	?	?	?	?	?	?	?	0	0	0	?	2	?	?	3
B. ruderalis	?	0	0	2	0	0	2	0	?	1	1	0	?	1	0	1	1	1	0	1	1	0	0	3	2	1	0	1	2	0	0	1	0	3	2	2	3
B. ungula	1	0	0	1	0	0	1	0	0	2	0	3	0	1	0	0	2	1	0	0	2	0	0	0	1	1	0	0	2	0	0	2	2	0	1	2	3
B. vittatus	1	1	0	1	0	0	1	3	0	1	1	3	?	2	0	1	2	1	0	0	2	1	1	0	0	0	1	0	2	0	0	2	3	4	4	2	3
B. wilkensii	0	0	0	2	0	0	2	0	?	?	1	?	?	2	0	1	2	1	0	0	1	1	1	?	2	0	2	?	?	0	0	0	5	1	?	2	3
B. vectori	?	0	?	1	0	0	?	0	?	?	?	?	?	3	0	?	1	0	0	0	0	1	?	?	?	?	?	?	?	0	0	2	1	0	?	?	3
D. praecedens	1	0	0	2	0	0	?	0	?	?	1	?	?	1	0	1	2	1	0	1	1	1	0	0	3	1	1	0	2	0	2	0	0	4	1	1	3
D. novaki	2	0	0	2	1	0	2	?	?	?	0	?	0	2	0	1	2	1	0	1	1	0	1	3	2	0	1	0	0	0	3	1	4	4	1	2	?
Es. palanasus	2	1	1	1	0	0	1	0	0	2	0	?	1	2	1	4	1	1	0	0	0	0	0	3	2	0	1	?	3	0	1	0	2	2	?	2	0
Es.boltoni	2	0	0	1	0	0	1	0	0	?	0	?	?	2	0	4	1	1	0	0	0	1	0	?	1	1	0	1	0	0	2	1	2	2	?	2	3
Es. friendi	2	0	1	2	0	0	1	0	0	2	0	3	?	2	0	0	1	1	0	1	1	0	0	3	2	1	1	0	2	0	3	1	4	1	?	2	3
Es. guthae	2	0	0	2	1	0	1	0	0	1	0	?	1	2	0	?	0	-	-	-	0	0	1	2	0	1	0	?	0	0	1	2	1	5	?	2	3
Es. neogracilis	2	0	1	2	0	0	2	2	0	1	0	3	0	2	2	?	1	1	0	0	1	0	0	3	3	0	1	0	2	0	1	0	2	4	?	2	3
Es. teicherti	2	0	1	2	1	0	1	0	0	2	0	?	2	2	0	4	1	1	0	1	1	0	0	3	2	1	1	0	2	0	3	1	5	1	?	2	3
Es. wanndjina	2	1	1	2	0	0	1	0	0	?	0	?	?	2	2	?	1	1	0	0	1	0	2	?	2	0	1	0	?	0	1	1	2	2	?	?	3
"*Es*". *pruniformis*	?	?	?	2	?	0	2	0	?	?	?	?	?	?	1	?	2	1	0	0	?	0	?	?	?	?	1	?	?	0	2	2	2	4	3	?	?
Es. sicarius n. sp.	1	0	0	3	0	0	2	?	0	1	0	?	0	2	0	1	1	1	0	0	1	0	0	3	3	0	1	0	1	0	3	0	2	2	3	2	3
"*Es.*" *socialis*	2	?	?	2	?	0	2	0	?	?	?	?	?	?	1	1	1	1	0	0	1	0	0	?	?	?	1	?	?	0	1	0	2	3	3	2	3
F. montagnei	?	0	0	2	0	0	2	0	?	1	0	?	0	1	0	1	1	1	0	0	1	0	0	0	2	0	1	0	2	0	0	0	2	4	3	2	3
F. sp. 2 Feist 1977	0	?	?	2	1	0	2	0	?	?	0	?	0	?	1	1	1	1	0	1	1	0	0	3	?	1	1	?	3	0	4	0	2	2	3	2	3
F. perneri	2	0	0	2	0	0	2	0	?	1	0	?	0	2	1	1	1	1	0	0	1	0	?	?	?	1	1	0	?	0	3	0	0	4	3	2	3
F. wendti	2	0	0	2	0	0	2	0	0	2	0	3	0	2	1	0	1	1	1	0	1	0	2	0	2	0	1	0	1	0	1	0	2	4	0	2	3
F.edgecombei n. sp.	2	0	0	2	0	1	2	0	0	2	0	3	2	3	1	0	1	0	?	?	0	0	0	3	3	0	1	0	3	0	1	2	2	4	4	2	3
H. macrocephalus	2	1	0	2	1	1	3	1	?	2	0	3	0	3	2	1	1	1	0	0	0	0	0	3	1	0	0	0	3	0	2	1	1	5	?	?	3
H. boudibensis n. sp.	2	1	0	2	1	1	2	1	0	1	1	3	0	3	2	1	1	0	1	0	0	0	0	3	2	0	1	2	2	0	2	0	2	5	2	2	1
H. cf. *boudibensis*	2	1	0	2	1	1	3	1	0	1	1	3	0	3	2	1	0	-	-	-	0	0	0	3	2	0	1	2	2	0	2	0	2	5	2	2	1
H. escoti	?	?	?	2	?	0	2	?	?	?	?	?	?	?	?	?	1	0	0	0	0	0	0	0	?	?	1	?	2	0	1	2	2	5	?	2	3
H. sp. 1 Feist 1977	2	0	0	2	0	0	2	0	?	?	0	?	?	2	1	?	1	0	0	1	0	0	2	3	?	0	1	0	2	0	4	1	3	5	?	2	3
H. lahceni n. sp.	2	1	1	3	1	1	3	1	1	1	1	3	0	3	1	1	0	-	-	0	0	0	2	3	2	0	0	0	2	0	1	1	1	3	3	2	3
H. lentigo n. sp.	1	0	0	2	1	1	3	0	1	1	1	3	0	3	2	1	1	1	0	0	1	0	2	3	2	0	1	2	2	0	2	1	0	5	3	2	1
H. ormistoni	?	?	?	2	?	1	3	1	?	?	?	?	?	?	?	?	1	?	?	?	?	0	?	?	?	?	?	?	?	0	?	1	?	2	?	?	?
H. oudris n. sp.	1	0	1	2	1	1	3	1	0	1	1	3	0	3	2	1	1	0	0	0	0	0	0	3	2	0	0	2	2	0	2	0	0	4	2	2	1
H. presheri n. sp.	2	1	0	3	1	1	3	1	0	1	1	3	0	3	2	1	1	1	0	0	1	0	0	3	2	0	0	2	1	0	2	0	2	5	1	2	1
H. reticulatus	2	1	0	1	0	0	2	0	?	1	0	?	0	?	1	1	1	0	0	1	0	0	2	?	?	0	1	2	?	0	1	0	0	5	3	2	3
H. sphenocephalus n. sp.	1	0	0	2	1	0	2	0	0	1	0	3	0	3	1	1	1	1	0	0	0	0	0	0	2	0	1	2	3	0	1	2	0	5	2	2	1
H. cf. *sphenocephalus*	2	0	0	2	1	1	2	?	0	1	0	?	0	?	2	1	0	-	-	-	0	0	0	3	2	0	1	2	2	0	3	2	0	4	3	2	3
H. supercilium n. sp.	1	0	0	3	1	1	3	1	1	1	1	3	0	1	1	1	1	0	0	0	0	0	0	3	2	0	1	2	2	0	2	0	2	5	2	2	1
H. whidbornei	2	?	?	1	0	1	3	?	?	1	?	?	0	?	2	?	1	1	0	?	?	0	2	0	?	?	?	?	?	0	?	1	?	5	?	?	?

TABLE 3c. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
E. benignensis	0	0	0	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. naumanni	1	0	2	0	?	?	?	?	0	?	1	0	?	0	0	0	?	?	?	0	?	?	?	3	0	?	0	0	0	?	?	?	?	?	?	?
B. cf. *acuminiatus*	2	0	1	1	?	?	?	?	2	0	1	0	0	0	0	1	3	1	0	0	?	0	1	?	?	?	0	0	0	1	1	0	0	?	?	?
B. budovicensis	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. buphthalmus	0	0	1	1	?	?	?	?	2	?	1	0	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. hypsipyle	2	0	1	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. janae	0	0	2	?	?	?	?	?	2	?	0	0	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. ovatus	1	0	1	?	?	?	?	?	2	?	1	0	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. ruderalis	2	0	2	?	?	?	?	?	3	?	?	0	?	0	?	?	?	?	?	2	?	?	?	1	0	?	0	0	?	1	1	?	2	?	?	?
B. ungula	1	0	2	0	?	?	?	?	2	0	0	0	0	0	2	-	2	?	1	0	2	0	0	4	1	4	1	1	0	0	1	0	0	2	0	0
B. vectori	1	0	2	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. vittatus	0	0	2	0	?	?	?	?	?	0	1	0	0	0	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. wilkensii	1	0	2	?	?	?	?	?	?	0	1	0	0	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
D. praecedens	2	0	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
D. novaki	?	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	5	?	?	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Es. palanasus	4	0	1	1	?	?	?	?	?	1	0	0	0	?	0	0	3	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Es.boltoni	4	0	1	?	?	?	?	?	0	1	1	0	0	2	1	1	2	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Es. friendi	4	0	1	1	?	?	?	?	4	1	1	0	0	?	?	?	?	?	0	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Es. guthae	4	1	2	0	?	?	?	?	4	1	1	0	0	1	0	0	2	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Es. neogracilis	4	0	1	0	?	?	?	?	2	1	1	0	0	1	?	0	3	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
"*Es*". *pruniformis*	4	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Es. sicarius n. sp.	4	0	2	0	?	?	?	?	2	1	1	0	0	1	1	0	2	0	1	0	2	?	?	0	0	3	0	0	0	?	1	0	0	1	1	0
"*Es.*" *socialis*	4	0	1	?	?	?	?	?	2	?	1	0	?	0	?	?	3	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Es. teicherti	4	0	1	1	0	?	?	?	4	1	?	0	0	1	?	?	3	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Es. wanndjina	4	0	1	0	?	?	?	?	3	1	1	0	0	2	1	0	3	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
F. montagnei	4	0	1	2	?	?	?	?	0	0	1	0	0	0	?	-	3	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
F.edgecombei n. sp.	1	0	1	0	0	0	1	0	0	0	1	2	0	0	0	0	6	1	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
F. sp. 2 Feist 1977	4	0	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
F. perneri	4	0	1	0	?	?	?	?	0	0	1	0	0	0	?	-	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
F. wendti	4	0	1	?	?	?	?	?	0	0	1	0	0	0	?	?	3	?	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
H. macrocephalus	0	0	1	?	?	?	?	?	2	0	1	1	1	0	?	?	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
H. boudibensis n. sp.	0	0	1	0	?	1	1	?	4	0	1	0	3	0	?	0	3	1	1	3	3	0	0	3	2	4	0	1	0	0	0	?	?	0	?	?
H. cf. *boudibensis*	0	0	1	1	2	1	1	1	3	0	1	0	3	0	0	0	3	1	1	3	?	0	1	?	?	?	0	0	0	0	?	0	0	?	?	?
H. escoti	0	0	1	?	?	?	?	?	5	0	1	0	0	0	1	0	3	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
H. sp. 1 Feist 1977	0	0	1	?	?	?	?	?	1	0	1	0	2	0	0	?	4	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
H. lahceni n. sp.	0	0	1	1	0	?	?	?	4	0	1	0	3	0	0	0	3	1	1	3	2	1	0	3	1	4	0	0	0	0	1	0	0	0	0	0
H. lentigo n. sp.	1	0	1	0	0	0	1	1	3	0	1	0	2	0	0	0	3	1	1	3	1	1	0	?	1	3	0	0	0	0	0	0	0	?	?	?
H. ormistoni	2	0	1	?	?	?	?	?	0	?	1	0	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
H. oudris n. sp.	2	0	1	1	0	?	3	1	2	0	1	0	3	0	0	0	2	1	1	3	?	0	0	2	?	?	0	0	0	0	?	0	0	?	?	?
H. presheri n. sp.	0	0	1	0	0	0	3	?	2	0	1	0	0	0	0	0	3	1	1	3	?	?	?	?	?	4	?	?	?	?	?	0	0	?	?	?
H. reticulatus	0	0	2	0	?	?	?	?	1	0	2	0	2	0	2	-	5	?	0	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
H. sphenocephalus n. sp.	0	0	2	0	0	0	0	1	0	0	1	0	0	0	1	0	3	1	1	3	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
H. cf. *sphenocephalus*	0	0	1	1	0	?	?	?	?	0	1	0	0	?	?	?	3	1	2	3	?	?	?	?	?	?	0	0	0	?	?	?	?	?	?	?
H. supercilium n. sp.	2	0	1	0	0	0	1	1	3	0	1	0	2	0	0	0	3	1	1	3	3	0	0	2	2	2	1	0	0	0	?	?	?	0	0	0
H. whidbornei	?	0	?	?	?	?	?	?	?	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

TABLE 3d. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Hl. perradiatus	0	?	1	0	0	1	1	1	0	0	0	?	?	1	0	1	1	0	0	?	?	?	0	0	1	0	?	?	?	?	1	?	?	?	0	4	1	2
Hl. sp. Alberti 1969	1	3	2	0	0	3	1	?	?	?	?	?	?	1	0	?	?	0	?	?	?	?	?	?	?	1	?	?	?	?	?	0	?	?	?	?	4	?	2
Hl. aougili n. sp.	1	3	1	0	1	1	1	1	4	0	1	4	2	1	0	2	1	0	0	0	0	0	0	3	1	0	1	0	0	0	2	0	0	0	0	3	1	2
Hl. dorbignyanus	1	1	1	0	1	0	0	0	1	0	1	1	?	1	0	1	1	2	0	-	1	1	1	?	0	0	3	1	0	0	2	0	0	?	0	2	2	1
Hl. dvorcensis	1	1	1	0	1	1	0	0	?	1	?	1	0	?	?	2	?	?	?	?	?	?	1	?	0	0	1	0	0	0	0	0	0	?	0	?	2	1
Hl. kayseri	2	3	1	0	1	1	1	0	0	0	?	0	2	1	0	?	1	0	0	-	1	1	1	?	0	0	3	0	0	?	1	0	0	?	0	1	?	2
Hl. transiens	1	1	1	0	?	1	?	?	?	?	?	?	?	0	?	?	1	0	?	?	0	?	0	?	1	?	?	?	?	?	0	?	?	?	?	?	?	?
K. waageni	0	1	1	1	1	0	0	0	1	0	1	2	3	1	0	2	1	0	0	-	1	1	1	?	1	0	2	0	0	0	0	0	0	0	0	2	3	2
K. sp.3 Feist 1977	1	1	1	2	1	0	1	0	0	0	1	1	3	1	0	1	1	0	0	-	1	1	1	?	0	0	0	0	1	1	0	0	0	0	0	3	2	2
K. stenolimbata	1	1	0	1	?	2	0	0	?	?	?	?	?	2	0	?	?	0	?	?	0	?	1	?	0	0	?	?	0	?	1	0	0	?	0	4	2	0
K. triabsidata	1	4	0	0	1	2	0	0	3	0	?	1	0	1	0	1	1	0	0	1	0	1	1	?	0	0	3	0	0	2	1	0	0	1	0	3	0	0
K. tumula n. sp.	0	0	1	0	1	0	0	0	0	0	0	4	3	1	0	1	1	1	0	-	1	1	1	1	1	0	1	0	0	0	2	0	0	0	0	3	2	2
K. aff. *tumula*	0	0	0	1	1	0	0	1	?	0	0	1	3	1	0	1	1	0	0	-	1	1	1	?	1	0	0	0	0	0	2	0	0	0	0	0	2	2
L. venulosus	0	1	0	1	0	2	1	0	1	0	1	2	3	0	0	1	1	2	1	1	0	1	1	1	0	0	2	0	0	1	0	0	0	1	0	3	2	2
L. ammari n. sp.	1	1	0	1	1	0	1	1	2	0	0	1	3	0	1	1	1	0	1	2	0	0	1	1	0	0	2	0	0	0	0	0	0	1	1	3	2	2
L. crassimargo	0	1	1	0	1	1	1	0	1	1	1	2	0	1	0	?	1	0	1	-	1	?	1	?	0	0	1	0	0	0	0	0	0	?	0	3	2	2
L. galea n. sp.	1	1	1	1	1	0	0	0	1	0	0	1	3	1	0	1	1	0	1	2	0	1	1	1	0	0	2	0	1	0	0	0	0	1	0	3	3	2
L. morocconensis n. sp.	1	1	1	2	1	0	0	0	1	0	0	1	3	0	0	1	1	1	1	1	0	2	1	0	0	0	2	0	0	0	1	0	0	1	1	0	3	2
L. cf. *morocconensis*	1	1	1	2	1	0	0	0	1	0	0	1	3	0	0	2	1	0	1	1	0	1	1	?	0	0	2	0	0	0	1	0	0	1	0	3	3	2
"*L.*" *polaris*	0	1	1	1	0	0	0	0	?	0	?	2	?	1	0	?	1	0	1	-	1	1	1	?	0	1	0	0	0	?	1	?	?	?	0	?	2	?
L. saredra n. sp.	1	1	1	1	1	0	0	0	2	0	0	1	2	0	0	1	1	0	1	2	0	0	1	1	0	0	2	0	0	0	1	1	1	1	1	3	2	2
L. scopulum n. sp.	1	1	1	1	0	0	1	1	2	0	0	1	3	1	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	2	2
"*L.*" *supernus*	2	1	0	1	0	0	0	0	?	?	?	?	?	2	0	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
M. hammii n. sp.	0	0	0	1	1	0	0	0	0	0	0	1	3	2	0	0	1	0	0	-	1	2	1	1	0	0	3	0	1	0	1	0	0	0	0	2	0	2
M. azmamarensis n. sp.	0	1	0	1	0	2	0	0	2	0	0	1	3	0	0	1	1	0	0	1	0	2	1	1	0	0	2	0	0	0	1	0	0	1	0	3	2	2
M. cf. *azmamarensis*	1	1	0	1	1	2	0	1	2	0	0	1	3	0	0	1	?	?	?	?	?	?	?	?	0	0	2	0	0	0	1	0	0	0	0	?	2	2
M. forteyi n. sp.	0	1	1	1	0	0	0	0	2	0	0	1	3	1	0	2	1	0	0	1	0	0	1	1	0	0	2	0	1	0	1	0	0	1	1	3	2	1
M. ihmadii n. sp.	0	0	1	1	1	0	0	0	0	0	0	2	3	1	0	1	1	0	0	1	0	2	1	0	0	0	2	0	1	0	1	0	0	1	0	3	2	2
M. aff. *ihmadii*	0	1	0	2	1	0	0	0	0	0	0	1	3	1	0	1	1	0	?	?	?	?	?	?	0	0	1	0	0	0	0	0	0	0	0	?	2	0
M. laatchanensis n. sp.	0	0	3	1	1	1	1	0	0	0	0	1	3	0	1	1	1	0	0	2	0	1	1	0	0	0	4	0	1	0	1	0	0	0	1	2	1	1
M. minutipunctus n. sp.	0	1	1	1	1	0	0	0	1	0	0	2	2	2	0	2	0	0	?	-	1	1	1	?	0	0	2	0	1	0	0	0	0	0	0	2	2	2
M. aff.*1 minutipunctus*	0	0	0	1	1	0	1	1	0	0	1	1	3	1	0	1	0	0	1	0	0	1	0	?	0	0	2	0	1	0	0	0	0	?	0	3	2	0
M. aff.*2 minutipunctus*	0	0	1	1	1	0	1	1	0	0	0	1	0	1	0	1	1	0	0	0	0	1	1	4	0	0	1	0	1	0	0	0	0	0	0	0	2	2
M. oufatenenis n. sp.	0	0	0	1	1	0	1	0	0	0	0	1	3	1	0	1	1	0	0	1	0	2	1	1	0	0	2	0	1	0	1	0	0	0	0	3	2	2
M. rouvillei	2	1	1	1	0	0	?	0	2	0	?	2	3	1	0	2	1	0	0	1	0	0	1	?	0	0	0	0	1	1	1	0	0	0	0	3	2	1
M. sculptus	1	1	0	2	?	0	1	?	?	?	?	1	3	1	0	?	1	0	?	?	?	?	?	?	?	0	?	?	?	?	1	?	?	?	?	?	0	2
M. terridus n. sp.	1	1	1	1	1	0	0	0	1	0	1	3	3	1	1	1	0	0	0	1	0	2	1	2	1	0	2	0	1	0	2	0	0	0	0	3	2	2
M. venetus	?	?	3	2	0	0	1	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	0	?	?	?
M. zguidensis n. sp.	0	0	1	1	1	0	1	0	?	?	?	1	3	1	1	?	1	0	0	2	0	1	1	?	0	0	2	0	0	0	0	0	0	0	?	3	2	2
M. cf. *zguidensis*	0	0	1	1	1	0	1	0	?	?	0	?	3	1	1	?	1	0	0	-	1	1	1	?	0	0	2	0	0	0	0	0	0	0	0	3	2	2
M. aff. *Zguidensis*	0	0	1	1	1	0	0	0	?	0	?	1	3	1	1	-	1	0	1	-	1	?	1	?	0	0	2	0	0	0	2	0	0	0	0	0	2	2
P. segaouii n. sp.	0	1	2	1	1	1	0	1	0	0	1	2	3	1	1	?	0	0	0	2	0	2	1	0	1	0	1	0	0	0	2	0	0	0	0	4	1	0
P. apteros n. sp.	1	1	1	1	1	1	0	1	1	0	1	3	3	0	2	1	0	0	0	1	0	2	1	0	1	-	-	-	-	-	3	-	-	0	0	3	1	2
P. aff. *apteros*	1	1	1	1	1	1	0	1	?	0	?	3	3	1	1	1	0	0	?	1	0	1	1	?	1	-	-	-	-	-	1	-	-	0	0	3	1	?
P. chaperon n. sp.	2	4	1	0	0	1	0	1	0	0	1	4	3	1	2	-	0	0	1	2	0	1	1	0	1	0	0	0	1	0	2	0	0	0	0	4	1	2
P. hamarlaghdadensis	1	1	1	1	1	1	0	0	?	0	?	?	3	1	0	1	0	0	?	-	1	?	1	?	0	0	0	0	1	0	2	0	0	0	0	0	3	2
P. hamarlaghdadensis nm	1	1	1	1	1	1	0	0	0	0	1	1	2	2	0	1	0	0	1	-	1	0	1	4	1	0	0	0	1	0	2	0	0	0	0	0	4	2

TABLE 3e. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Hl. perradiatus	2	0	?	1	0	0	1	0	?	?	?	?	?	2	0	0	1	1	0	0	0	0	1	2	2	0	?	1	?	0	1	0	0	1	?	2	3
Hl. sp. Alberti 1969	?	?	?	1	?	0	1	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	?	?	?	1	?	?	?	0	1	?	?	?	?	?	?
Hl. aougili n. sp.	2	0	2	3	0	0	1	2	0	?	0	?	0	2	2	1	1	1	0	0	0	0	1	2	3	0	0	0	3	0	1	0	0	2	2	2	3
Hl. dorbignyanus	2	0	0	1	0	0	2	0	?	2	0	?	?	0	1	1	0	-	-	0	0	0	0	3	2	0	0	1	0	0	3	0	4	3	?	2	3
Hl. dvorcensis	1	0	0	1	1	0	?	0	?	2	?	?	?	?	1	1	?	?	?	?	0	0	0	3	2	1	0	0	0	0	2	0	0	3	2	2	3
Hl. kayseri	?	?	?	?	1	0	?	2	?	?	0	?	?	?	2	?	0	-	-	-	0	0	1	2	2	?	?	?	0	0	3	0	0	3	?	2	3
Hl. transiens	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	3	0	?	3	?	?	?
K. waageni	1	0	0	1	0	0	2	2	?	2	0	?	?	2	2	0	1	1	0	1	1	0	2	3	1	0	2	0	1	0	3	1	4	2	?	2	3
K. sp.3 Feist 1977	2	0	0	2	0	1	2	0	?	?	0	?	?	?	?	?	1	1	0	1	2	0	0	3	?	0	1	?	1	0	3	0	0	3	?	2	3
K. stenolimbata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	?	?	0	?	0	0	0	?	?	?	?	?	?	0	3	1	0	3	?	?	?
K. triabsidata	?	0	?	1	1	0	?	0	?	?	?	?	?	2	2	1	?	?	0	?	?	0	0	3	1	?	?	2	?	0	3	?	?	?	?	2	3
K. tumula n. sp.	2	0	0	1	0	0	1	0	0	2	?	3	?	2	2	1	1	1	0	1	1	0	0	3	0	0	0	?	1	0	3	1	3	2	2	2	3
K. aff. *tumula*	2	0	?	1	0	0	2	0	?	?	?	?	?	2	2	1	1	1	0	0	1	0	2	3	?	0	0	2	0	0	1	0	0	4	2	2	3
L. venulosus	1	0	1	1	0	0	2	0	?	?	0	?	?	2	1	1	1	1	0	0	1	0	2	0	2	0	0	0	2	0	0	0	1	3	2	2	3
L. ammari n. sp.	2	1	1	2	1	0	3	0	1	1	0	3	0	3	1	0	1	1	0	1	1	0	2	3	2	0	1	2	2	0	2	2	2	4	2	2	3
L. crassimargo	2	0	0	2	?	0	2	0	?	1	?	?	0	2	?	1	1	1	0	?	1	0	0	?	?	1	?	0	2	0	0	0	1	3	?	2	3
L. galea n. sp.	1	0	1	2	0	0	2	0	1	2	0	0	0	2	1	1	1	0	0	0	0	0	0	0	?	1	1	0	2	0	0	0	1	2	0	2	3
L. morocconensis n. sp.	1	0	1	1	0	0	2	0	1	2	0	3	0	2	1	1	1	1	0	0	1	0	0	3	2	1	1	0	2	0	0	0	1	3	3	2	1
L. cf. *morocconensis*	2	0	0	2	0	0	2	0	0	2	0	0	0	2	2	1	1	1	0	0	1	0	0	3	2	1	1	0	2	0	0	0	2	3	3	2	3
"*L.*" *polaris*	?	?	?	?	?	0	2	?	?	?	?	?	?	2	1	1	2	1	0	0	1	0	0	?	?	?	?	?	?	0	0	1	1	4	?	2	?
L. saredra n. sp.	1	0	1	2	1	0	2	0	1	1	1	3	0	1	0	1	2	1	0	0	1	0	2	0	2	1	1	0	3	0	2	2	2	4	2	2	3
L. scopulum n. sp.	2	0	0	2	1	0	2	0	1	2	0	0	0	2	1	0	1	1	0	0	?	0	0	3	2	1	0	0	2	0	2	1	2	5	2	2	3
"*L.*" *supernus*	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	?	1	?	3	?	?	?
M. hammii n. sp.	1	0	0	1	1	0	2	0	1	1	1	3	0	1	2	1	2	1	0	0	2	0	2	0	1	1	1	0	1	0	0	0	2	2	2	2	3
M. azmamarensis n. sp.	2	0	0	2	1	0	2	0	3	2	0	3	0	2	2	1	1	1	0	0	1	0	1	3	2	0	1	0	1	0	0	0	2	3	2	2	3
M. cf. *azmamarensis*	2	0	0	1	1	0	2	0	3	?	0	?	0	2	2	1	1	1	0	0	1	0	0	3	2	1	1	0	1	0	0	0	1	3	3	2	3
M. forteyi n. sp.	2	0	1	1	1	0	3	0	3	2	1	3	0	2	2	1	1	1	0	0	2	0	0	3	2	1	1	0	1	0	0	0	1	2	2	2	3
M. ihmadii n. sp.	2	0	0	1	1	0	1	2	0	3	1	3	2	1	2	1	2	1	0	0	2	0	2	0	2	0	0	0	2	0	0	0	1	2	2	2	3
M. aff. *ihmadii*	2	0	0	1	1	0	2	2	2	?	0	?	0	1	2	1	2	1	0	0	2	0	2	0	2	1	0	0	1	0	0	1	1	2	1	2	3
M. laatchanensis n. sp.	1	0	0	1	1	0	2	2	0	1	1	3	0	2	2	1	1	1	0	0	2	0	0	0	2	1	0	0	0	0	0	0	2	2	1	2	3
M. minutipunctus n. sp.	1	0	?	1	0	0	2	0	0	2	1	3	0	1	2	1	0	-	-	-	1	0	1	3	0	1	1	1	1	0	0	2	2	3	1	2	3
M. aff.*1 minutipunctus*	1	0	0	2	1	0	2	0	0	2	0	2	2	2	2	1	1	1	0	0	?	0	1	3	1	0	0	0	?	0	0	0	2	2	1	2	3
M. aff.*2 minutipunctus*	1	0	1	?	1	0	?	?	?	?	?	?	?	?	2	1	2	1	0	0	2	0	2	0	1	1	0	0	1	0	?	0	?	2	2	2	3
M. oufatenenis n. sp.	2	0	1	1	1	0	2	0	0	1	0	0	0	3	2	1	1	1	0	0	1	0	2	0	2	0	1	0	1	0	0	0	1	3	3	2	3
M. rouvillei	2	0	1	1	1	?	2	0	?	?	?	?	?	?	2	1	1	1	0	0	1	0	0	3	?	?	0	?	2	0	1	0	3	5	?	2	3
M. sculptus	?	?	?	?	?	0	2	0	?	?	?	?	?	2	2	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	?	3	?	?	?
M. terridus n. sp.	2	1	1	1	0	0	2	0	0	?	0	?	0	2	2	1	1	1	1	0	1	0	2	3	2	1	1	0	?	0	0	0	1	3	2	2	3
M. venetus	?	?	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	1	0	?	1	?	?	?	?	?	?	?	?	0	0	0	1	?	?	?	?
M. zguidensis n. sp.	2	?	?	2	1	0	2	0	0	1	0	3	0	3	1	?	1	1	1	0	2	0	0	3	1	1	0	2	1	0	0	1	2	2	1	2	3
M. cf. *zguidensis*	?	?	?	2	1	0	2	0	?	2	?	?	0	3	?	?	1	1	1	0	1	0	0	?	1	?	0	2	?	0	0	0	2	3	1	2	3
M. depraves n. sp.	2	?	?	2	1	0	2	0	?	?	?	?	?	?	?	?	1	0	1	0	0	0	2	3	?	1	1	?	?	0	0	0	2	3	3	2	3
P. segaouii n. sp.	2	1	0	2	0	0	1	0	0	1	0	0	0	2	0	1	1	1	1	0	1	0	0	3	2	0	0	1	2	0	1	0	2	3	2	2	3
P. apteros n. sp.	2	1	1	2	1	0	2	0	0	1	0	0	0	3	1	0	1	0	1	1	0	0	0	3	?	0	1	0	2	0	1	1	2	3	3	2	3
P. aff. *apteros*	2	1	1	2	?	0	2	0	0	1	0	0	0	?	?	?	1	1	?	?	1	0	1	2	?	0	?	?	?	0	3	0	0	3	2	?	?
P. chaperon n. sp.	2	1	0	2	0	0	2	0	0	1	0	0	0	3	?	0	2	1	1	1	1	0	2	0	0	0	1	1	1	0	2	2	1	5	1	2	3
P. hamarlaghdadensis	2	0	0	2	0	0	1	0	0	1	0	0	0	2	0	1	2	1	0	0	2	0	0	0	?	1	?	0	1	0	1	0	1	4	?	2	3
P. hamarlaghdadensis nm	2	0	0	2	0	0	1	0	0	1	0	0	0	3	0	1	2	1	0	0	2	0	0	0	2	?	1	2	2	0	1	0	2	4	2	2	3

TABLE 3f. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Hl. perradiatus	3	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hl. sp. Alberti 1969	3	0	1	?	?	?	?	?	?	?	2	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hl. aougili n. sp.	3	0	1	2	0	0	0	2	2	1	2	0	0	1	0	1	3	1	1	1	?	2	1	?	2	?	1	1	0	1	1	0	0	?	?	?
Hl. dorbignyanus	1	0	1	?	1	?	?	?	1	0	1	0	0	0	2	-	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hl. dvorcensis	2	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hl. kayseri	?	0	1	?	?	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hl. transiens	3	0	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
K. waageni	0	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
K. sp.3 Feist 1977	0	0	1	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
K. stenolimbata	?	0	1	?	?	?	?	?	5	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
K. triabsidata	?	0	1	0	1	?	?	?	?	?	1	0	?	0	0	0	2	?	1	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
K. tumula n. sp.	0	0	1	0	1	0	1	0	2	0	1	0	0	0	0	0	4	1	1	2	?	0	0	?	?	?	0	1	0	0	1	?	?	?	?	?
K. aff. *tumula*	4	0	1	?	1	?	?	?	1	0	1	0	0	0	2	-	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
L. venulosus	2	0	1	?	?	?	?	?	0	0	1	0	0	0	?	?	2	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
L. ammari n. sp.	2	0	1	1	0	0	3	0	0	0	1	0	2	0	0	0	2	1	0	1	2	0	0	2	1	?	1	1	0	0	1	0	0	?	?	?
L. crassimargo	1	0	1	?	?	?	?	?	0	0	1	0	0	0	?	?	2	?	1	1	?	0	0	?	?	?	?	1	?	0	0	?	?	?	?	?
L. galea n. sp.	2	0	1	0	0	0	?	?	2	0	1	0	0	0	0	?	2	1	1	1	?	1	0	?	1	2	1	1	0	0	1	0	?	?	?	?
L. morocconensis n. sp.	2	0	1	0	0	0	1	1	0	0	0	0	0	0	2	-	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
L. cf. *morocconensis*	4	0	1	0	?	?	?	?	1	0	0	0	0	0	2	-	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
"*L.*" *polaris*	?	0	1	?	?	?	?	?	0	0	?	0	?	0	?	?	2	?	?	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
L. saredra n. sp.	2	0	2	0	0	0	1	1	2	0	1	0	1	0	0	0	2	1	1	3	?	?	0	2	1	?	1	1	0	0	1	0	0	?	?	?
L. scopulum n. sp.	2	0	1	1	?	?	?	?	1	0	1	0	0	0	2	-	2	1	?	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
"*L.*" *supernus*	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. hammii n. sp.	2	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	2	1	1	1	3	1	0	2	1	4	1	0	0	0	1	0	?	?	?	?
M. azmamarensis n. sp.	2	0	1	2	0	1	1	1	1	0	1	0	0	0	0	0	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. cf. *azmamarensis*	2	0	1	2	0	1	1	1	0	0	1	0	0	0	0	0	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. forteyi n. sp.	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. ihmadii n. sp.	1	0	2	0	0	1	1	0	0	0	1	0	0	0	0	1	2	0	1	1	2	0	0	2	1	2	0	1	0	0	1	?	?	?	?	?
M. aff. *ihmadii*	1	0	1	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. laatchanensis n. sp.	2	0	1	0	0	1	1	1	0	0	1	0	0	0	0	1	2	1	1	0	2	?	0	2	0	3	1	0	1	0	0	1	1	?	?	?
M. minutipunctus n. sp.	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	1	1	?	?	0	2	1	4	1	0	0	?	1	0	2	?	?	?
M. aff.*1 minutipunctus*	2	0	1	0	?	?	?	?	1	0	1	0	0	0	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. aff.*2 minutipunctus*	2	0	1	?	?	?	?	?	1	0	1	0	1	0	2	-	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. oufatenenis n. sp.	1	0	1	0	0	1	1	1	0	0	1	0	0	0	1	1	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. rouvillei	0	0	1	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. sculptus	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. terridus n. sp.	2	0	1	0	0	1	1	0	0	0	0	0	0	0	2	-	2	1	1	1	?	0	0	?	1	?	1	2	1	0	0	2	1	?	?	?
M. venetus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. zguidensis n. sp.	2	0	1	?	0	1	1	0	1	0	1	0	0	0	0	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. cf. *zguidensis*	2	0	1	?	0	?	?	?	1	0	1	0	0	0	0	?	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. depraves n. sp.	2	0	1	?	0	1	1	0	1	0	0	0	0	0	0	0	2	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. segaouii n. sp.	0	0	1	0	?	0	0	0	2	0	0	0	2	1	1	0	3	0	1	2	0	0	0	2	1	3	1	2	?	0	0	1	0	?	?	?
P. apteros n. sp.	2	0	1	2	0	0	2	0	2	0	1	0	1	0	1	0	3	0	1	2	2	0	0	2	1	4	1	2	?	0	0	1	1	0	0	0
P. aff. *apteros*	?	0	1	0	0	0	0	0	4	0	4	1	1	0	2	-	4	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. chaperon n. sp.	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	4	1	1	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. hamarlaghdadensis	2	0	1	1	?	?	?	?	3	0	0	1	?	?	?	?	?	?	1	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. hamarlaghdadensis nm	2	0	1	?	0	0	0	1	0	0	0	1	1	1	1	0	3	0	1	3	2	0	1	2	2	?	0	2	-	1	0	1	0	?	?	?

TABLE 3g. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
P. hanabouensis n. sp.	1	1	0	1	1	0	0	0	0	0	1	2	3	1	1	2	1	0	0	2	0	1	0	0	1	0	1	0	0	0	2	0	0	0	0	0	2	2
P. hastatus	1	3	1	1	1	1	0	0	?	0	?	1	3	1	0	1	1	0	0	-	1	1	1	?	1	0	2	0	0	0	2	0	0	0	0	3	?	1
P. aff. *haustrum*	1	1	0	1	0	1	0	0	0	0	0	2	2	1	0	2	1	0	1	1	0	0	1	1	0	1	0	0	0	0	1	1	1	1	0	0	3	2
P. haustrum n. sp.	2	1	1	1	1	1	1	0	0	0	0	1	3	1	1	2	1	0	1	2	0	0	1	1	1	0	0	0	1	0	2	0	0	1	0	3	2	2
P. igaouii n. sp.	2	1	0	1	1	1	0	1	2	0	1	1	3	1	1	1	0	0	0	1	0	2	0	1	0	0	2	0	0	1	2	0	0	1	1	0	2	2
P. merzaneensis n. sp.	1	1	0	1	0	1	0	1	?	0	0	1	3	0	2	-	0	?	0	2	0	0	1	4	0	0	1	0	0	0	2	1	1	0	1	3	?	0
P. torquis n. sp.	1	1	0	1	1	1	0	1	0	0	1	4	3	1	1	2	0	0	0	2	0	2	1	0	1	-	-	-	-	-	3	-	-	0	0	0	1	2
P. aff. *torquis*	0	3	0	1	1	1	0	1	?	0	1	4	0	1	1	-	0	0	0	0	0	1	1	0	1	-	-	-	-	-	3	-	-	0	0	3	1	2
S. domina	3	0	2	1	?	2	0	0	?	?	?	?	3	?	0	?	1	?	?	?	?	?	?	?	0	0	?	0	?	?	?	?	?	0	?	?	?	?
S. aduncus	0	1	0	1	0	2	0	0	?	0	?	1	3	0	0	?	1	1	1	0	0	0	0	?	0	0	4	0	0	2	1	0	0	0	0	0	4	0
S. consuetus	3	0	0	1	0	2	0	0	?	?	?	?	?	2	0	?	1	1	1	?	0	1	?	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?
S. filarium	0	0	?	1	1	?	0	0	0	0	0	2	1	0	0	?	0	0	1	?	?	?	0	?	0	0	2	0	0	2	1	1	1	0	0	4	2	0
S. fragilis	3	?	2	1	0	0	0	0	?	?	?	?	?	2	0	0	1	0	0	-	1	0	?	?	?	1	?	0	0	2	?	?	?	?	?	3	4	0
S. judex	3	0	2	0	?	?	0	0	?	?	1	1	?	2	0	?	0	0	0	?	?	?	?	?	0	0	0	0	0	2	0	0	0	0	0	?	?	0
S. latior	?	?	2	1	0	0	0	0	?	0	?	1	?	2	0	?	0	0	?	?	?	1	?	?	0	0	3	?	0	?	0	?	?	?	?	5	4	0
S. laurei	1	0	2	1	0	1	0	0	0	0	1	0	3	0	1	?	0	0	2	0	0	?	0	0	0	0	?	?	?	?	2	0	0	0	0	0	4	0
S. lobulatus	0	1	1	0	0	0	0	0	?	?	?	0	3	2	0	?	1	2	2	?	1	1	1	?	0	1	0	0	1	?	1	0	0	?	0	0	?	2
S. loma	0	0	0	1	0	1	0	0	0	0	0	1	3	1	0	1	1	0	2	?	?	1	1	?	0	0	1	0	0	0	0	0	0	1	0	0	2	2
S. nymageensis	3	?	?	?	?	0	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?
S. molongloensis	3	1	1	1	0	0	0	0	1	0	1	1	?	1	0	?	1	0	0	1	0	?	?	0	0	0	3	0	0	0	1	0	0	0	0	5	2	0
S. pansa	0	0	0	?	0	0	0	0	?	?	?	1	?	2	0	?	1	0	0	?	0	?	0	?	0	0	1	0	0	0	1	0	0	?	0	?	2	2
S. planilimbatus	3	2	2	1	?	2	?	?	?	?	?	?	?	0	0	?	?	?	?	-	1	?	?	?	0	0	?	?	0	?	?	?	?	?	0	5	4	0
S. raaschi	0	?	0	1	0	0	0	0	0	0	1	0	0	0	0	?	1	0	0	-	1	1	1	0	0	0	2	0	0	0	1	0	0	1	0	4	3	0
S. rotundus	0	2	2	1	1	1	0	0	0	0	1	?	3	2	0	1	?	?	?	?	?	?	?	?	0	0	0	0	1	0	0	0	0	0	0	5	?	0
S. sanctacrucensis	3	0	0	0	?	0	0	0	?	?	?	1	?	0	0	?	1	?	?	0	?	?	?	?	1	0	0	0	0	?	1	0	0	?	?	?	?	2
S. singularis	0	0	2	0	0	0	0	0	?	?	0	1	?	1	0	0	0	0	?	-	1	0	1	?	0	0	2	?	1	2	1	?	?	?	0	3	3	0
S. sombrero	3	0	2	1	0	2	0	0	0	0	0	1	2	0	0	1	0	0	0	0	0	?	0	0	0	0	4	0	1	0	1	0	0	0	0	2	3	0
S. spasskii	3	0	2	1	0	2	0	0	1	0	?	2	2	0	0	?	1	0	0	1	0	0	0	2	0	0	2	0	0	1	1	0	0	0	0	4	3	0
S. taimyricus	0	?	1	0	0	0	0	0	?	?	?	0	3	1	0	?	1	0	2	-	1	?	?	?	1	0	3	0	0	?	1	0	0	?	0	0	2	2
S. tatouyangensis	?	0	2	1	1	2	0	0	?	?	?	1	?	0	0	?	1	2	?	?	0	?	?	?	?	0	2	0	0	?	0	0	0	?	0	?	?	0
S. telleri	3	0	0	1	1	0	1	0	?	?	?	?	?	0	0	1	1	2	0	1	0	2	0	?	?	0	3	0	0	0	0	0	0	0	0	3	3	0
S. trinucleoides	3	0	1	1	0	2	0	0	?	?	?	?	?	0	0	?	0	?	?	?	?	?	?	?	0	0	1	0	0	?	?	0	0	?	0	0	?	0
S. vestustus	?	?	2	1	0	0	0	0	?	?	?	?	?	2	0	?	1	?	2	?	?	?	?	?	0	?	?	?	?	2	0	?	?	?	0	?	?	0
S. vitilis	1	0	0	1	0	0	0	0	0	0	0	1	3	2	0	0	1	0	1	-	1	1	1	3	0	0	2	0	0	2	2	0	0	1	0	0	4	2
S. volsellatus	3	0	0	0	?	3	0	0	0	0	0	1	?	2	0	?	?	?	?	?	?	?	?	?	0	?	0	0	2	?	?	?	?	?	?	?	?
S. willsi	3	0	0	0	1	0	0	0	0	0	?	1	?	2	0	?	0	0	2	-	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	3	0
S. youngi	3	0	1	2	0	?	0	0	0	0	0	?	?	2	0	?	1	0	?	?	?	?	?	?	0	?	?	0	0	?	1	?	?	?	0	?	?	2
St. rissaniensis n. sp.	2	3	3	0	1	1	1	1	0	0	1	1	3	1	1	2	1	2	0	-	1	1	1	0	0	0	1	0	0	0	2	0	0	0	0	2	1	1
St. aff. *rissaniensis*	1	3	3	0	1	1	1	1	0	0	1	3	3	1	1	2	0	0	0	-	1	1	1	0	1	?	?	?	?	?	3	-	0	0	0	3	1	1
St. calceolus n. sp.	1	3	3	0	1	1	1	1	0	0	1	1	3	1	1	2	1	2	0	-	1	1	1	?	0	0	2	0	1	0	2	0	0	0	0	3	?	?
St. aff. *calceolus*	2	3	1	0	1	0	1	1	?	0	1	?	?	1	1	2	0	0	1	-	1	1	1	?	1	0	2	0	0	0	2	0	0	0	0	3	1	2
St. capricornus n. sp.	2	4	3	2	1	1	1	1	3	0	?	1	0	1	1	2	1	2	0	-	1	1	1	1	0	0	2	0	1	0	2	1	?	1	0	2	0	2
St. aff. *capricornus*	2	4	3	2	1	1	1	0	0	0	1	3	3	1	1	2	1	?	0	-	1	1	1	?	?	0	2	0	1	0	2	?	0	?	0	2	1	2
St. convexus	2	1	3	2	1	1	1	1	0	1	1	1	0	0	0	?	1	2	0	-	1	1	1	0	1	0	1	1	0	0	2	0	0	0	0	2	2	1
St. obuti	2	1	3	2	?	3	1	0	?	0	?	1	0	2	?	?	1	2	0	?	1	1	1	?	1	0	?	?	0	0	2	0	0	0	0	5	?	2
St. retiarius n. sp.	2	3	1	2	1	1	1	1	1	0	0	1	3	1	1	2	1	2	0	2	0	1	1	2	0	1	2	0	1	0	2	0	0	0	0	1	1	1

TABLE 3h. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
P. hanabouensis n. sp.	2	1	0	2	0	0	2	2	0	1	0	0	0	3	0	0	1	1	0	0	1	0	2	0	2	0	0	4	3	0	1	1	1	3	2	2	3
P. hastatus	?	?	1	2	0	0	2	0	?	?	?	?	?	3	?	0	2	1	0	?	1	0	2	0	2	?	?	?	?	0	2	0	1	3	?	2	?
P. aff. *haustrum*	2	0	0	2	0	0	2	0	2	1	0	3	0	0	0	1	2	1	1	1	1	0	2	0	2	0	1	2	2	0	2	1	2	5	3	2	3
P. haustrum n. sp.	2	0	0	2	0	0	2	0	2	1	1	3	0	2	0	1	2	1	1	0	1	0	2	0	2	0	1	2	2	0	2	0	1	5	3	2	1
P. igaouii n. sp.	2	1	0	2	1	0	2	0	1	1	0	3	0	2	2	1	1	1	0	0	1	0	0	?	?	0	1	2	2	0	2	0	1	5	1	2	1
P. merzaneensis n. sp.	2	0	0	2	0	0	?	?	?	?	?	?	0	3	?	?	2	1	1	1	2	0	2	0	2	0	1	2	3	0	2	0	1	5	2	2	3
P. torquis n. sp.	2	1	0	2	0	0	1	2	0	1	0	0	0	3	0	0	2	1	1	0	1	0	0	3	1	0	1	2	0	1	1	1	2	2	2	2	3
P. aff. *torquis*	2	1	0	2	0	0	2	2	0	1	0	0	0	3	0	1	1	1	1	0	0	0	0	3	2	0	1	2	2	0	3	0	0	2	0	2	1
S. domina	?	0	?	?	0	?	?	?	?	?	1	?	?	?	?	?	1	0	0	?	0	0	?	?	?	?	?	?	?	0	1	0	?	0	?	?	?
S. aduncus	0	0	0	1	0	0	1	0	?	?	0	?	?	0	2	4	0	-	-	-	0	0	1	?	2	1	0	0	?	0	0	0	0	0	?	?	?
S. consuetus	?	0	0	1	0	?	2	0	?	?	?	?	?	?	?	?	1	1	0	?	1	0	?	?	?	1	?	?	?	0	6	2	?	0	?	?	?
S. filarium	0	0	0	?	0	0	?	?	?	?	1	?	?	0	1	?	?	?	?	?	?	0	?	?	?	1	0	?	?	0	?	?	?	?	?	?	?
S. fragilis	0	0	?	?	?	0	?	?	?	?	0	?	?	?	0	0	0	-	-	-	0	0	1	3	?	1	0	0	2	0	0	3	2	?	1	?	?
S. judex	0	0	0	?	0	0	2	0	?	?	?	?	?	2	?	?	?	?	?	?	?	0	?	?	?	1	?	?	?	0	?	0	?	?	?	?	?
S. latior	2	?	?	1	0	0	1	0	?	?	1	?	?	0	0	0	1	1	0	0	1	1	1	?	?	0	?	?	?	0	0	?	?	?	?	?	?
S. laurei	?	?	?	2	0	0	2	0	?	?	0	?	?	2	?	?	0	-	-	-	0	0	1	?	?	0	?	?	?	0	0	0	?	2	?	?	3
S. lobulatus	?	?	?	1	0	0	?	0	?	?	0	?	?	?	0	?	1	0	0	0	0	1	1	?	2	?	?	?	?	0	0	2	1	2	?	?	?
S. loma	0	0	0	1	0	0	1	0	?	?	1	?	?	2	?	0	1	1	0	0	1	0	0	?	?	1	?	?	3	0	5	2	0	3	?	2	3
S. nymageensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
S. molongloensis	1	0	1	1	0	0	2	0	0	1	?	?	0	?	0	0	1	1	0	0	1	0	?	?	1	1	0	1	3	0	1	2	?	0	?	2	3
S. pansa	0	0	?	?	0	0	?	?	?	?	?	?	?	0	1	?	2	1	0	0	1	0	?	?	?	1	?	?	?	0	0	2	?	1	?	?	?
S. planilimbatus	0	0	0	2	0	0	2	0	?	?	?	?	?	0	2	0	0	-	-	-	0	0	?	?	?	1	?	?	?	0	?	3	?	1	?	?	3
S. raaschi	0	0	0	2	0	0	2	0	0	?	1	?	0	2	?	?	1	?	0	0	?	0	?	?	?	1	?	?	?	0	0	?	?	?	?	?	?
S. rotundus	?	?	?	?	?	0	2	0	?	?	?	?	?	2	?	0	1	1	0	0	0	0	2	2	?	0	?	?	1	0	1	2	2	1	?	?	?
S. sanctacrucensis	1	0	0	1	0	0	1	0	?	?	1	?	?	0	2	?	0	-	-	-	0	0	?	?	?	1	?	?	?	0	?	3	?	1	?	?	?
S. singularis	0	0	0	2	0	0	?	0	?	?	1	?	?	0	1	4	1	0	0	0	1	0	0	3	1	1	0	0	2	0	0	0	2	2	?	2	3
S. sombrero	0	0	0	1	0	0	2	0	?	?	1	?	0	0	1	?	2	1	0	0	1	?	?	2	?	1	?	0	2	0	1	2	1	?	?	2	3
S. spasskii	1	0	0	1	0	0	2	0	0	?	?	?	0	1	2	0	0	-	-	0	0	0	0	?	2	1	0	?	?	0	0	3	1	1	1	?	3
S. taimyricus	0	?	?	1	0	0	2	0	?	?	?	?	?	3	0	0	0	-	-	-	0	0	?	?	?	1	?	?	?	0	0	2	?	4	?	?	?
S. tatouyangensis	0	0	0	0	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	1	?	?	?	0	?	?	?	?	?	?	?
S. telleri	?	?	?	1	0	0	2	0	?	?	?	?	?	2	0	?	1	0	0	0	0	0	1	2	?	?	?	?	?	0	0	2	2	2	?	?	?
S. trinucleoides	2	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	0	1	0	1	0	?	2	?
S. vestustus	0	0	0	1	1	0	1	0	?	?	?	?	?	0	?	?	0	-	-	-	0	0	?	?	?	1	?	?	?	0	?	?	?	?	?	?	3
S. vitilis	0	0	0	2	0	0	2	0	?	?	1	?	?	0	0	4	0	-	-	-	0	0	0	0	2	1	?	0	0	0	2	3	2	?	?	2	3
S. volsellatus	0	0	0	1	0	?	2	0	?	?	?	?	?	3	?	?	?	?	?	?	?	0	?	?	?	1	?	?	?	0	0	0	?	2	?	?	?
S. willsi	2	?	0	1	0	0	1	?	?	?	0	?	?	2	0	1	2	1	0	0	1	0	1	?	2	1	?	0	?	0	0	1	2	1	?	2	3
S. youngi	0	0	0	?	0	0	?	?	?	?	1	?	?	0	2	?	0	-	-	-	0	0	?	?	?	1	?	?	?	0	1	3	?	3	?	?	?
St. rissaniensis n. sp.	2	1	0	2	1	0	2	0	0	1	0	0	0	2	1	1	1	1	1	0	1	0	1	3	2	1	1	1	2	0	3	1	3	3	2	2	1
St. aff. *rissaniensis*	2	?	0	2	1	0	2	0	0	2	0	0	2	3	1	1	1	1	1	0	1	0	1	2	2	0	1	1	2	0	3	1	0	2	0	2	3
St. calceolus n. sp.	2	?	?	2	?	0	?	?	?	?	?	?	?	3	?	?	2	0	1	1	0	0	1	3	?	?	?	?	?	0	3	0	3	4	2	2	3
St. aff. *calceolus*	2	?	?	2	1	0	2	0	0	?	?	?	0	2	2	?	1	0	0	?	0	0	1	2	?	?	1	?	?	?	3	0	3	2	1	2	3
St. capricornus n. sp.	1	0	0	2	0	0	2	0	0	?	0	?	0	2	1	1	1	1	0	1	1	0	1	3	2	1	1	0	2	0	3	0	3	5	2	2	3
St. aff. *capricornus*	2	?	0	2	?	0	2	0	?	?	0	?	?	3	2	1	1	0	1	1	0	0	1	?	?	1	1	0	1	0	3	0	3	4	2	2	3
St. convexus	2	0	0	1	0	0	2	0	0	1	0	?	0	2	2	?	1	1	0	1	1	0	2	0	?	0	?	?	2	0	3	1	3	3	?	?	?
St. obuti	?	?	?	2	0	0	2	0	?	1	?	?	0	2	1	?	2	1	?	?	1	0	?	?	?	?	?	?	?	0	3	0	?	5	?	?	?
St. retiarius n. sp.	2	0	1	2	1	0	2	0	0	2	0	?	0	2	2	0	2	1	1	0	0	0	1	2	3	0	1	4	2	0	3	0	0	2	4	2	3

TABLE 3i. Matrix of taxa and characters showing character states used in the cladistic study

Taxa	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
P. hanabouensis n. sp.	2	0	1	0	0	0	2	0	0	0	0	1	1	0	1	0	3	1	1	2	1	0	0	1	0	3	-	3	-	0	0	1	?	2	0	?
P. hastatus	?	?	1	?	?	?	?	?	2	1	0	2	0	1	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. aff. *haustrum*	2	0	1	1	?	0	3	1	2	0	1	1	1	1	1	0	3	1	1	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. haustrum n. sp.	2	0	1	1	?	0	0	1	2	0	1	0	0	1	1	0	3	1	1	3	1	0	1	2	0	?	1	1	?	1	0	0	1	?	?	?
P. igaouii n. sp.	0	0	1	0	0	0	0	0	2	0	1	0	0	0	1	1	3	1	2	2	?	0	?	?	?	?	?	?	?	?	0	1	?	?	?	?
P. merzaneensis n. sp.	2	0	1	1	?	0	0	1	2	0	1	1	1	1	1	0	3	1	1	3	1	?	1	2	?	4	0	2	-	1	0	0	0	1	?	0
P. torquis n. sp.	2	0	1	0	0	0	0	0	4	1	4	0	0	1	1	0	4	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. aff. *torquis*	2	0	2	0	0	0	0	0	4	1	0	2	1	1	1	0	6	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. domina	?	0	1	?	?	?	?	?	3	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. aduncus	2	0	?	?	?	?	?	?	4	0	1	0	0	0	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. consuetus	?	0	1	?	?	?	?	?	4	?	1	0	?	0	0	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. filarium	0	0	?	1	0	?	?	?	2	?	?	0	?	0	0	0	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. fragilis	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. judex	2	0	?	?	0	0	4	?	3	?	1	?	0	0	?	?	5	?	?	0	?	?	?	?	1	?	0	1	?	?	1	0	?	?	?	?
S. latior	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. laurei	2	0	1	?	?	?	?	?	1	?	1	0	0	1	?	0	3	?	?	0	2	0	0	0	3	3	?	?	?	?	?	1	0	2	2	0	1
S. lobulatus	?	0	2	?	?	?	?	?	2	?	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. loma	2	0	2	?	?	?	?	?	5	0	1	0	?	0	?	?	3	?	2	0	?	0	0	?	?	0	1	0	0	0	1	0	?	?	?	?
S. nymageensis	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. molongloensis	2	0	2	0	0	?	?	?	2	0	1	0	?	0	?	?	4	0	1	0	?	?	?	?	?	?	?	0	1	?	?	?	0	2	?	?	?
S. pansa	?	?	?	?	?	?	?	?	0	?	0	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. planilimbatus	2	0	1	?	?	?	?	?	3	?	3	0	?	1	1	1	3	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. raaschi	?	0	?	?	?	?	?	?	?	?	1	0	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. rotundus	0	0	1	0	0	?	?	?	1	1	1	0	0	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. sanctacrucensis	?	0	2	?	?	?	?	?	2	?	1	0	?	0	?	?	5	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. singularis	2	0	2	1	0	1	3	?	4	0	1	0	?	0	0	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. sombrero	0	0	2	?	?	?	?	?	2	?	1	0	0	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. spasskii	2	0	2	0	?	?	?	?	2	1	1	0	0	0	0	1	2	1	0	0	2	0	0	1	0	4	0	1	?	0	1	2	?	1	0	0
S. taimyricus	2	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. tatouyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. telleri	?	0	2	?	?	?	?	?	2	?	1	0	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. trinucleoides	?	0	1	?	?	?	?	?	3	?	1	0	?	0	?	?	?	?	?	0	2	?	?	2	1	2	?	?	?	?	?	?	?	1	?	?
S. vestustus	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. vitilis	2	0	1	?	?	?	?	?	2	0	1	0	0	0	?	?	4	?	?	1	1	?	?	1	0	4	0	0	0	?	1	0	0	2	?	?
S. volsellatus	?	0	2	?	?	?	?	?	4	?	1	0	?	0	?	?	?	?	?	0	?	?	?	?	?	?	0	2	?	?	?	?	?	?	?	?
S. willsi	2	0	1	?	?	?	4	?	4	0	1	0	0	0	?	?	3	?	?	2	?	?	?	?	1	?	0	1	0	?	1	0	0	?	?	?
S. youngi	0	0	2	?	?	?	?	?	?	?	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
St. rissaniensis n. sp.	2	0	2	0	1	0	0	0	2	0	1	0	1	0	0	1	4	0	1	3	0	0	0	3	0	0	0	1	0	0	0	1	1	1	0	0
St. aff. *rissaniensis*	0	0	1	0	1	0	0	0	2	0	1	0	2	0	1	0	3	0	1	2	?	0	0	?	?	?	0	1	0	0	1	?	?	?	?	?
St. calceolus n. sp.	2	0	1	?	1	?	?	?	0	0	1	0	1	0	0	1	4	1	1	3	2	?	?	3	2	3	0	1	1	?	1	1	1	?	?	?
St. aff. *calceolus*	?	0	1	0	0	0	0	0	2	0	1	0	1	0	0	1	4	?	1	3	?	0	0	?	?	?	0	1	1	?	1	?	?	?	?	?
St. capricornus n. sp.	2	0	1	0	1	?	?	?	0	0	1	0	1	0	0	0	3	1	1	3	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
St. aff. *capricornus*	0	0	1	0	?	?	?	?	2	0	1	0	1	0	1	0	4	0	1	3	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
St. convexus	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
St. obuti	2	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
St. retiarius n. sp.	0	0	2	0	1	0	1	0	0	0	2	0	2	2	1	0	4	1	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

TABLE 4. The results of heuristic searches for each random seed

Seed No.	Tree length	Shortest trees (length 1968) No.	Consensus tree Node collapse No.
1	1968	27	19
2	1968	39	16
3	1968	16	5
4	1968	39	9
5	1968	20	15
6	1968	32	8
7	1968	60	20
8	1968	7	14
9	1968	20	7
10	1968	31	10
11	1968	59	30
12	1968	59	20
13	1968	57	20
14	1969	N/A	N/A
15	1968	33	12
16	1968	30	8
17	1968	32	18
18	1968	41	9
19	1968	18	14
20	1968	16	14
		636	31

TABLE 5a. Proposed diagnostic characters for Devonian harpetid genera

1	2	3	4		5				6						7						8		9
Genus s.s.	**No. of taxa**	**Total No. ceph. Chrt.**	**Compliant taxa: Minimum for any one character**		**No. of taxa in genus which have states that do not comply with diagnostics**				**Diagnostic Characters**						**No. of species belonging to other genera with one or more of the diagnostic characters, totalled according to the number of characters shared.**						**% of other species sharing diagnostic characters**		**Suggested Min No. ceph. Chrt**
			No. of species	**% of taxa**	1	2	3	4	**Cephalon and Genicranium shape and dimension**	**Glabella Preglabellar Field Posterior Border**	**Genal area, alae and eye lobes**	**Genal roll, anterior boss and girder**	**Brim and rim**	**Prolongations**	1	2	3	4	5	6	**The most widely shared charater**	**Mean of all charaters**	
			a	b																	a	b	
Harpes	15	10	8	71%	3	4	3	1		**1)** Preglabellar field narrow (sag.) < 20% of width (tr.)	**2)** Genal area narrow (tr.), 54% or less of length (exsag.) **3)** Eye lobes oval to cone shaped and **4)** eye lobe extending to edge of axial furrow	**5)** No girder kink **6)** No ceaca on genal roll	**7)** Brim width ratio below 0.68. **8)** No caeca on brim	**9)** Extension of girder meets internal rim 1/3 of the way down prolongation **10)** Brim steepens quickly on prolongations to near verticle	43	34	20	8	2		42%	17%	2) or 3) + 5 other
Lioharpes	7	8	4	67%	2	2	1			**1)** Occipital furrow wider (sag.) than posterior border (exsag.) **2)** Posterior border tr. between 31% and 40% of width tr. of occipital ring	***3)** Width of genal area tr. 54% to 66% of length (exsag.) **4)** 3 eye lenses per eye lobe **5)** Palpebral lobes with tubercles	**6)** Inner margin of fringe straight across anterior of genal area	**7)** Girder narrow (sag. and exsag.) under 2.2% of width (tr) of genicranium	***8)** Extension of girder meets internal rim half way down prolongation	35	38	18	10			41%	20%	3) + 4 other
Fritchaspis	5	8	4	87%	3	1			**1)** Genicranium narrow, length (sag.) divide by width (tr.) 0.75 to 0.85	***2)** Preglabellar furrow bowed upwards in anterior view **3)** Posterior border moderately wide (tr.) : 41% to 50% of width of occipital ring (tr.)			**4)** Brim sloping moderately between 100 to 200 **5)** Brim width ratio 0.66 to 0.75 **6)** Spaces between brim perforations inflated	***7)** Prolongations moderately short exsag., 76% to 85% of cephalon sag. ***8)** Whole brim steepens moderately to less than 90 deg. on prolongations	32	35	21	6	1		40%	18%	6
Kielania	6	8	3	90%	1	2					**1)** Allar depression absent **2)** Eye lobes small (exsag.) < 30% of width (tr.) of glabella at S1	***3)** Course of inner margin acraoss anterior of genal area convex **4)** Girder moderately wide (sag.) between 2.2% and 3% width (tr.) of genicranium	***5)** Brim profile barely to moderately convex ***6)** Brim sloping (sag.) at > 20^0 **7)** Brim perforations moderately fine , < 150 µm ***8)** Marginal band sloping down under cephalon		34	39	15	14	3		48%	23%	6

TABLE 5b. Proposed diagnostic characters for Devonian harpetid genera (continued)

1	2	3	4		5				6						7						8		9
Genus s.s.	**No. of taxa**	**Total No. ceph. Chrt.**	**Compliant taxa: Minimum for any one character**		**No. of taxa in genus which have states that do not comply with diagnostics**				**Diagnostic Characters**						**No. of species belonging to other genera with one or more of the diagnostic characters, totalled according to the number of characters shared.**						**% of other species sharing diagnostic characters**		**Suggested Min No. ceph. Chrt**
			No. of species	**% of taxa**					**Cephalon and Genicranium shape and dimension**	**Glabella Preglabellar Field Posterior Border**	**Genal area, alae and eye lobes**	**Genal roll, anterior boss and girder**	**Brim and rim**	**Prolongations**							**The most widely shared charater**	**Mean of all charaters**	
			a	b	1	2	3	4							1	2	3	4	5	6	a	b	
Declivoharpes	2	8	2	100						***1)** S1 curving around top of muscle insertion area	***4)** Course of inner margin of fringe across anterior of genal area concave	***5)** preaxial furrows converge towards girder	***6)** Brim width ratio).66 to 0.75		43	34	16	5			24%	16%	6
										***2)** Ala wide, width tr. 0.95 to 1.10 of length sag.			***7)** Standard brim perforations very fine < 100 μm										
										***3)** Ala anterolaterally directed			***8)** Dorsal surface of external rim with granulation										
Helioharpes	7	8	3	83	2		2		**1)** Genicranium widest (tr.) at alae	**2)** Glabella narrow width(tr.) at S1 between 55% and 65% of length o(sag.) of glabella anteior to occipital furrow	**4)** width (tr.) of genal area between 54% and 66% of length (ex sag.)	**6)** No girder kink	**7)** Brim moderately steep (sag.) sloping at between 210 and 300		41	41	22	13			44%	23%	8) + 3 other
										***3)** Glabella carinate	**5)** Eye lobe weakly inflated		***8)** Caeca forming strong network across brim										
Eskoharpes	10	8	6	88	2	1	1			**1)** Glabella inset with genal areas inflated		**5)** Anterior of genal roll gently sloping at <50 deg.	***7)** Spaces between brim perforations inflated	**8)** Prolongations in lateral view strongly tapered	38	37	21	12			36%	23%	7) +4 others
										2) Glabella anterior to S0 narrow, width at S1 / length < 0.65		**6)** Perforations on genal roll smaller than brim perforations											
										3) Preglabellar furrow straight in anterior view													
										***4)** Fine granulation on occipital ring													
Maghroharpes	18	10	9	87	8	4	1		**1)** Genicranium widest at posterior border	**2)** No glabella muscle insertion furrows at S2, S3 or S4	**3)** Alar depression absent	**5)** Course of inner margin of fringe across the anterior of genal areas convex	**7)** Brim profile concave	**9)** Brim steepening on prolongations along proximal edge only	15	34	37	19	12		59%	28%	Ch 7) +6 others
											4) Eye tubercle close to internal margin of fringe (Eye location ratio over 0.8)	**6)** Girder moderately wide (sag. and exsag.) : between 2.2% and 3.0% of the width (tr.) of genicranium	**8)** Marginal band concave	**10)** Extension of girder meeting internal rim halfway down prolongation									

TABLE 5c. Proposed diagnostic characters for Devonian harpetid genera (continued)

1	2	3	4		5				6						7						8		9
Genus s.s.	**No. of taxa**	**Total No. ceph. Chrt.**	**Compliant species: Minimum for any one character**		**No. of species in genus which have states that do not comply with diagnostics**				**Diagnostic Characters**						**No. of species belonging to other genera with one or more of the diagnostic characters, totalled according to the number of characters shared.**						**% of other species sharing diagnostic characters**		**Suggested Min No. ceph. Chrt**
			No. of species	**% of taxa**					**Cephalon and Genicranium shape and dimension**	**Glabella Preglabellar Field Posterior Border**	**Genal area, allae and eye lobes**	**Genal roll, anterior boss and girder**	**Brim and rim**	**Prolongations**							**The most widely shared charater**	**Mean of all charaters**	
			a	b	1	2	3	4							1	2	3	4	5	6	a	b	
Pinnuloharpes	14	11	8	85%	7	1	3		**1)** In dorsal view outline of cephalon ovoid	**3)** Occipital furrow shallow	**6)** Alar furrow very shallow or effaced	**8)** Course of inner margin of fringe across anterior of genal areas concave	* **10)** Marginal band profile straight	**11)** Long (exsag.) genal spines more than 10% of length (exsag.) of prolongation	19	29	29	20	14	6	59%	27%	7
									2) Genicranium widest at posterior border	**4)** Occipital ring not medially broadened	**7)** Two eye lenses per eye lobe, the anterior being the largest	**9)** Caeca on genal roll										
										5) L1 not inflated													
Stoloharpes	9	11	5	85%	1	2	0	2	**1)** Cephalon pyriform	***3)** Glabella carinate		**6)** Genal roll sloping gently anteriorly at under 42 deg.	***7)** Brim profile convex	**10)** Internal rims in lateral view with straight profile	39	31	10				20%	10%	Ch 7) + 5 others
									2) Genicrannium very narrow (tr.) over 0.85 (length (sag.) divided by width (tr.)	**4)** Pregalbella furrow in anterior view bowed upwards			**8)** Brim sloping (sag.) steeply at between 31^0 and 40^0	**11)** Brim quickly steepens to near vertical on prolongations								
										5) Occipital furrow medially bowed posteriorly			**9)** Marginal band sloping down under cephalon									

TABLE 6. Intraspecies comparisons for *Escoharpes sicarius*

	Holotype	All Types		Standard
		Pop.	Mean	Deviation
	Ratio 1:	No.	Ratio 1:	% Mean
1) Cephalon length sag. to width.	0.71	6	0.69	7
2) Glabella length sag. to cephalon sag.	0.43	6	0.42	4
3) Prolongation length to cephalon sag.*	0.93	6	0.99	12
4) Brim width ratio	0.88	8	0.83	7
5) Eye location	0.8	6	0.74	5
	No.		No.	
6) Standardised brim perforation density per sq. mm	18	5	17.57	6
7) Standardised brim perforation diameter	175 µm	4	182 µm	6

* Excluding genal spine

TABLE 7. Intraspecies comparisons for *Maghroharpes hammii*

	Holotype	All Types		Standard
		Pop.	Mean	Deviation
	Ratio 1	No.	Ratio 1:	% Mean
1) Cephalon length (sag.) to width (tr.)	0.66	9	0.64	2.7
2) Glabella length (sag.) to cephalon length (sag.)	0.46	9	0.44	2.8
3) Ala width (tr.) to glabella width (tr.) at S1	0.26	6	0.27	1.2
4) Prolongation length (exsag.) to cephalon length (sag.)	0.78	9	0.81	10.7
5) Brim width (tr.) at S0 to width (sag.)	0.88	9	0.95	6.6
6) Eye location	0.91	8	0.91	10.4
	No.		No.	
7) Brim perforation density per sq. mm	23	7	23	21
8) Brim perforation diameter	105 µm	7	108 µm	24.3