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Atopidae (Trilobita) in the upper Marianian (Cambrian Series 2, Stage 4) of Iberia

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

Introduction

Atopidae Hupé, 1954 is a little investigated trilobite family based on *Atops* Emmons, 1844. Family membership has had a long and contentious history (Howell and Stubblefield, 1950) and constituent genera were regularly included in the Conocoryphidae based on their secondary blindness; this assignment continued beyond Hupe's (1954) erection of the family (Harrington et al., 1959; Korobov, 1973; Jell et al., 1992). In Spain, this genus was doubtfully recognized by Richter and Richter (1941) as *Atops*? *calanus* Richter and Richter, 1941 in the 'Fauna von Cala' from Huelva, and that occurrence has been cited by Lotze (1958, 1961) and Sdzuy (1961, 1962). Herein, we describe several cranidia and fragments that enable positive assignment to *Atops*.

Pseudatops Lake, 1940 is described for the first time in the Iberian Peninsula, with recognition of the Taconic North American species *Pseudatops reticulatus* (Walcott, 1890b). Its presence allows biostratigraphic and paleobiogeographic correlations with other Avalonian and Taconic localities.

Geological setting

The trilobites were collected in northern Huelva Province, southwestern Spain (Fig. 1), in the Sierra de Aracena y Picos de Aroche Natural Park. Cambrian rocks of the Ossa-Morena Zone are placed in distintict belts or 'blocks'—named 'Cubetas' in Spanish—with a notable change of facies and thickness, most likely related to downthrow and tilting along an active growth fault at the time of sediment deposition (Liñán and Quesada, 1990) (Fig. 1).

The stratigraphy of the different Cambrian blocks in northern Huelva has been little studied. Only early Cambrian formations have been established (Collantes et al., 2020) although not formally defined.

In the Cumbres block (Cumbres Cubeta), the siliciclastic sandstones and shales of the Cumbres beds (350–1100 m) are dated as middle–late Marianian, based on the trilobites *Delgadella* Walcott, 1912, *Hicksia* Delgado, 1904, *Rinconia* Hupé, 1953, and *Triangulaspis* Lermontova, 1940 in the lower part and *Serrodiscus* Richter and Richter, 1941 and *Triangulaspis* in the upper part (Liñán and Mergl, 1982; Liñán et al., 2002). The Cumbres fossil site (CU1) is located in the upper Cumbres beds (Collantes et al., 2020). The 24-m section at CU1 is between 38°02′45.74″N, 006°43′07.40″W and 38° 02′43.90″N, 006°43′07.80″W. Atopid trilobites occur 17, 19, and 20 m from the base in association with *Serrodiscus silesius* Richter and Richter, 1941, *Calodiscus ibericus* Sdzuy, 1962, *Triangulaspis fusca* Sdzuy, 1962, *Hicksia*? sp. indet., *Marocella morenensis* (Yochelson and Gil Cid, 1984), brachiopods, and hyoliths.

In the Herrerías block (Herrerías Cubeta), the Herrerías shale (200–500 m) (Schneider in Richter and Richter, 1941) consists of purple shales with spilitic intercalations and has an age ranging from middle to late Marianian, based on *Delgadella*, *Rinconia*, *Atops*, *Gigantopygus* Hupé, 1953, *Hicksia*, *Protaldonaia* Sdzuy, 1961, *Sdzuyomia* Lieberman, 2001, and *Strenuaeva* Richter and Richter, 1940 in the lower part and *Serrodiscus*, *Calodiscus* Howell, 1935, and *Triangulaspis* in the upper part (Richter and Richter, 1941; Sdzuy, 1962; Ruiz López et al., 1979; Liñán and Mergl, 1982). The El Pozuelo fossil site (POZ1) is in the upper level Herrerías shale with *Serrodiscus silesius*, *C. ibericus*, *Protaldonaia morenica* Sdzuy, 1961, *Delgadella* sp. indet., *Strenuaeva* sp. indet., *Marocella morenensis*, and brachiopods. Base and top of the 48-m section at the collecting site are at 37°58′59.17″N, 006°24′18.92″W and 37°58′56.90″N, 006°24′19.93″W, respectively, with atopid trilobites 7 and 9 m from the base (Collantes et al., 2020).

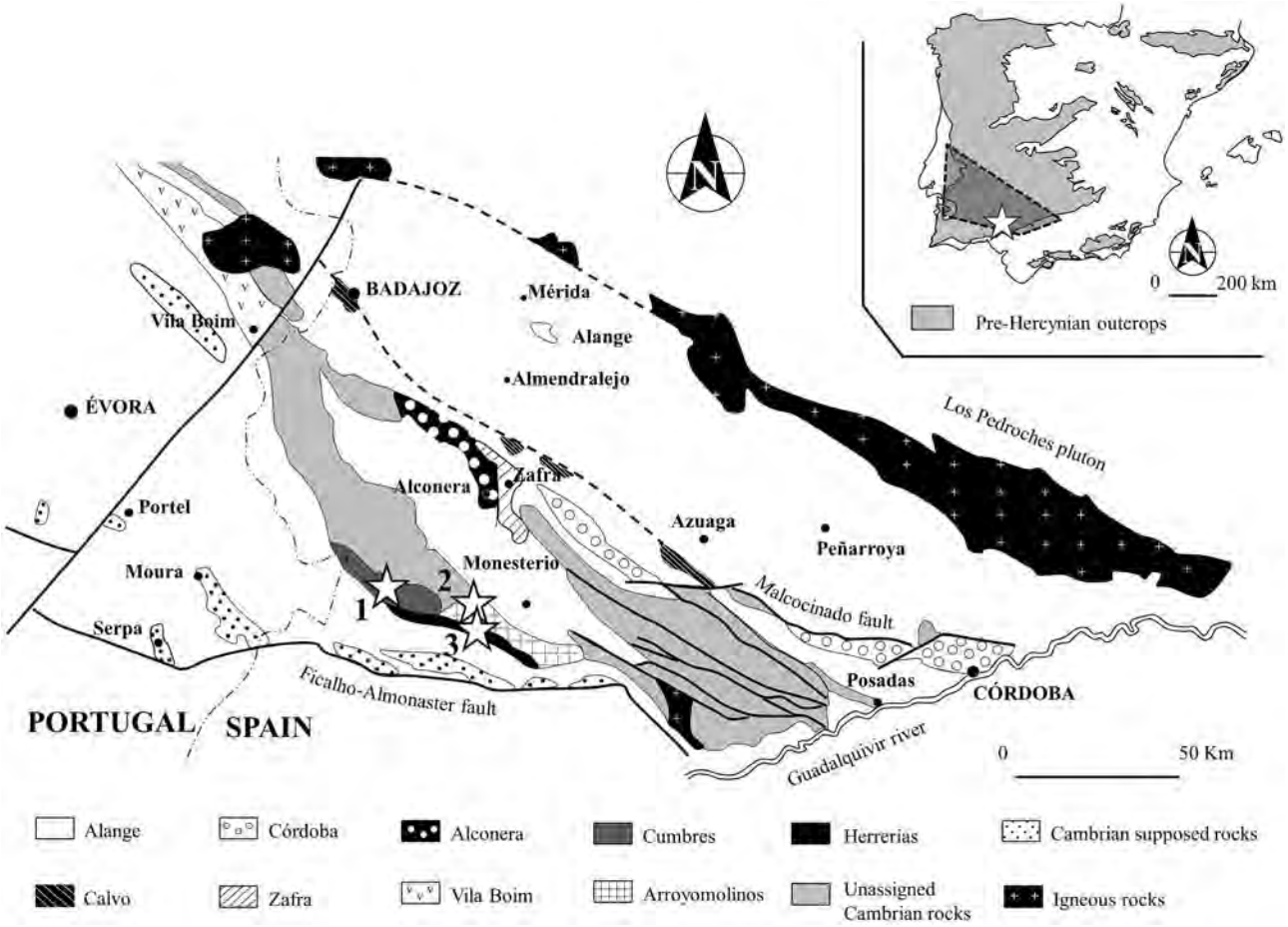

Figure 1. Geological setting of fossil sites in the Cambrian Cubetas (fault-bounded blocks) of the Ossa-Morena Zone, with white stars indicating the positions of the studied fossil sites in each Cubeta. 1 = Cumbres de San Bartolomé site (CU1); 2 = Arroyomolinos de León site (AM1-2); 3 = El Pozuelo site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

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

Materials and methods

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

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

Systematic paleontology

Class Trilobita Walch, 1771
Order uncertain
Family Atopidae Hupé, 1954

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

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

Remarks.—Cotton (2001) carried out a systematic review and a phylogenetic proposal of several blind ptychoparid trilobites, which had been previously included in Conocoryphidae, concluding that it was a polyphyletic group. Within that review, he amended the diagnosis of Atopidae, which he included within the superfamily Ellipsocephaloidea. Given the classification problems, Adrain (2011) proposed not to assign it to any order until a complete revision of the trilobite basal groups was carried out.

Jell et al. (1992) included *Ivshiniellus nikolai* Korobov, 1966, *I. patulus* Korobov, 1966, and *I. briandailyi* Jenkins

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and Hasenohr, 1989 in *Atops*. Cotton (2001) pointed out that in *I. briandailyi*, the tapering of the glabella represented in their reconstruction (Jenkins and Hasenohr, 1989, fig. 4) is not matched by that of the specimens, and the species closely resembles the other Australian species, *Atops rupertensis* Jell, Jago, and Gehling, 1992. We accept that *Ivshiniellus* is a junior subjective synonym of *Atops* as proposed by Jell et al. (1992) and Cotton (2001).

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

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

Genus *Atops* Emmons, 1844

Type species.—*Atops trilineatus* Emmons, 1844.

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

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

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

Atops calanus Richter and Richter, 1941
Figure 2

1941 *Atops*? *calanus* Richter and Richter, p. 55, pl. 3, fig. 41, pl. 4, fig. 63.
1958 *Atops*? *calanus*; Lotze, p. 743.
1961 *Atops*? *calanus*; Lotze, p. 164.
1961 *Atops*? *calanus*; Sdzuy, p. 230.
1962 *Atops*? *calanus*; Sdzuy, p. 212, pl. 23, figs. 14, ?15, 16.
2018 *Atops* sp. cf. *calanus*; Collantes et al., p. 567, fig. 4.7.

Holotype.—SMF X 1227.

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

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

Description.—Cranidium subtrapezoidal, of pronounced relief, wider than long, 12.9–22.3 mm long, 19.4–41.8 mm wide. Opistoparian facial suture close to the lateral margin, cutting the gena near the lateral furrow. Straight or slightly curved anterior margin. Anterior border short (sag.), homogeneous, sloping upward from the anterior border furrow, turning upward. Anterior furrow pronounced, deep. Pregrablellar field short, laterally extended, subtrapezoidal. Preglabellar furrow slightly pronounced. Glabella conical, with rounded frontal lobe, gradually widened toward the posterior, with length equivalent to 4/5 of the cephalon, with three pairs of deep, narrow, nontransglabellar furrows (S1–S3), slightly curving toward the posterior, all equal in length. Axial furrows narrow, deep, with a slightly convergent tendency toward the anterior area. Occipital furrow (S0) deep. Occipital lobe subtrapezoidal, planoconvex. Preocular field reduced, triangular. Preocular furrow deep, thin. Ocular ridge pronounced, connected between the frontal lobe of the glabella and the lateral furrow, presenting a slight curvature with convexity toward the front. Subtrapezoidal palpebral area wide, with slightly convex relief. Posterior furrow wide, deep, slightly curved. Posterior border thin (sag.), slightly curved. Subtriangular genal area, exsagital extension. Ornamentation composed of coarse granules with massive structure, more pronounced in the preocular and palpebral aresa and softer in the glabella. For reconstruction of the cephalon, see Figure 3.

Materials.—Seven partially preserved cranidia (UHU-CU1001-20, CU1010–CU1013-20, POZ020-20, AM1002-20). Additional fragments assigned to *Atops calanus* are deposited in the same collection.

Remarks.—The description above is based solely on the material collected for this study. Richter and Richter (1941) differentiated *Atops*? *calanus* from *Atops trilineatus* according to the distance between the anterior border furrow and the frontal lobe of the glabella, with a longer glabella reaching the anterior border in *Atops trilineatus* and a shorter, tapered glabella in *Atops*?

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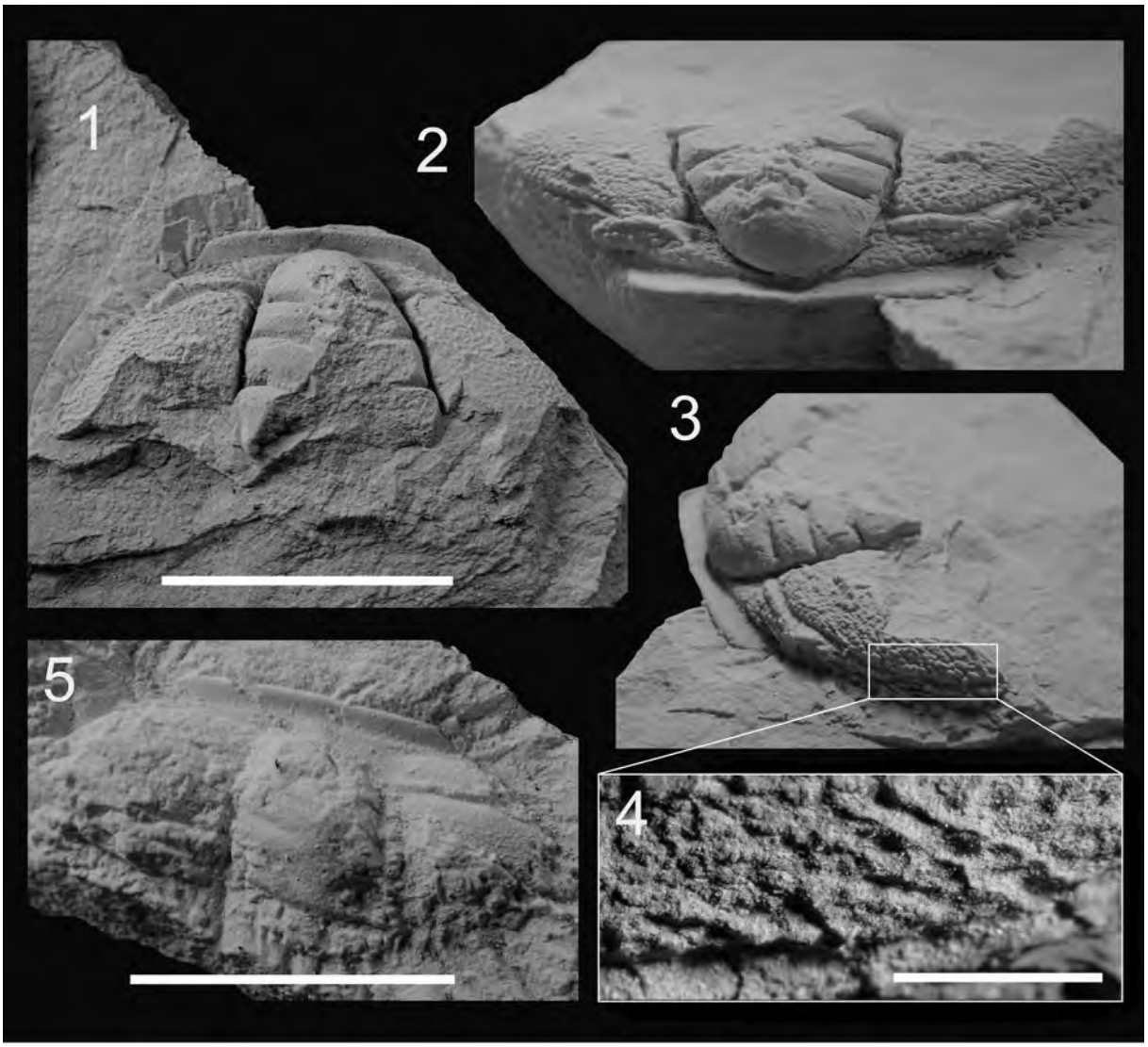

Figure 2. *Atops calanus* Richter and Richter, 1941: (**1–4**) UHU-CU1001-20, Cumbres de San Bartolomé, Cumbres beds, late Marianian: (**1**) dorsal view; (**2**) frontal view; (**3**) anterolateral view; (**4**) detail of the granular ornamentation; (**5**) UHU-CU1002-20, Cumbres de San Bartolomé, Cumbres beds, late Marianian, dorsal view. Scale bars = 20 mm; scale bar for subfigure 4 is 5 mm.

calanus, with a subtle ridge between anterior border furrow and preglabellar furrows. In Huelva specimens, these differences could be due to deformation and are not necessarily taxonomic characters (Fig. 2.1–2.3, note that the frontal lobe of the glabella invades the preglabellar field and reaches the anterior border due to deformation).

Atops rupertensis and *Atops briandailyi* from Australia are differentiated by the proportions of the cephalon, prominent parafrontal band, and a wide anterior border becoming narrower at the sides. Moreover, the glabella is considerably narrower and shorter with four pairs of thin, lateral, nontransglabellar furrows pointing backward and giving rise to less-pronounced glabellar lobes, and shallower, less-pronounced axial furrows. The palpebral area of both *Atops rupertensis* and *Atops briandailyi* is more extensive in proportion to the cephalon than in *Atops calanus*. In *Atops rupertensis,* the posterior furrow is shallower and broader

Figure 3. Reconstruction of the cephalon of *Atops calanus* Richter and Richer, 1941, in (left to right) dorsal, frontal, and lateral views.

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than in *Atops calanus*, becoming thicker at the sides. The posterior border is thin and uniform in both *Atops calanus* and *Atops rupertensis*.

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

Atops korovobi from Russia is similar to *Atops calanus* but is distinguished by its more tapered frontal glabella lobe.

Ivshinellus nikolai and *I. patulus*, now both assigned to *Atops* (Jell et al., 1992), are based on distorted material (Korobov, 1973), but in comparison with *Atops calanus*, they show a subelliptical outline of the cephalon and a wider anterior border (especially in *Atops nikolai*). Furthermore, these Russian species have more narrowly triangular glabellae. Both Russian species also have subtler granular ornament.

Rushton (1966) described *Atops*? sp. indet. from the Purley Shales, England. The partial cranidium (Rushton, 1966, pl. 5, fig. 19) resembles *Atops trilineatus* especially in glabellar shape and suture configuration.

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

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

Genus *Pseudatops* Lake, 1940

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

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

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

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

Pseudatops reticulatus (Walcott, 1890b)
Figure 4

1890b *Conocoryphe reticulata* Walcott, p. 649, pl. 95, fig. 6, 6a.
1936 *Atops reticulatus* var. *comleyensis* Cobbold, p. 231, pl. 15, fig. 1a–e.
1940 *Pseudatops reticulatus*; Lake, p. 291, pl. 2, figs. 1–3.
2001 *Pseudatops reticulatus*; Cotton, pl. 2, figs. 1–3.
2006 *Pseudatops reticulatus*; Fletcher, pl. 27, fig. 21.
2018 *Pseudatops* n. sp.; Collantes et al., p. 567, fig. 4.8.

Holotype.—USNM 18431.

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

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

Description.—Cranidium trapezoidal, wider than long, ranging 8.5–26.8 mm in length, 19.5–51 mm in width. Marginal facial suture only cutting the lateral border of the cephalon and not affecting the lateral furrow. Anterior margin slightly curved. Anterior border narrow (sag.), homogeneous, planoconvex, slightly turned downward. Anterior furrow shallow, sagittally invaginated toward the front due to the intrusion of the glabella, with a fairly broad and well-defined subtriangular shaped area originating on each side of the frontal lobe of the glabella. Glabella elongated, extending all along the cranidium, subrectangular, with rounded frontal lobe and deep axial furrows. Three pairs of nontransglabellar furrows with slight curvature pointing toward the posterior area. Occipital furrow deep, curving toward the front (convexity toward the posterior area). Occipital lobe narrow, trapezoidal, slightly curved with convexity toward the posterior area and subtle occipital tubercle. Preocular field slim, convex. Ocular ridge slightly pronounced, inserting toward the frontal lobe of the glabella and reaching the lateral furrow. Palpebral area flat, wide, trapezoid, with slight slope toward the posterior area. Posterior furrow well marked, wide. Posterior border narrow, flat, thickened near the genal area due to an incurved posterior border. Lateral border narrow, homogeneous. Genal angle ~ 90°, with a minimal genal spine. Surface of the cephalon subtly reticulated. For reconstruction, see Figure 5.

Materials.—A total of 13 cranidial fragments were available (UHU-CU1002–CU1009-20, CU1014–CU1016-20, POZ021-20, AM2001-20). Additional fragments are deposited in the same collection.

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

The differences between North American *Pseudatops reticulatus* (New York and Newfoundland) and Spanish specimens

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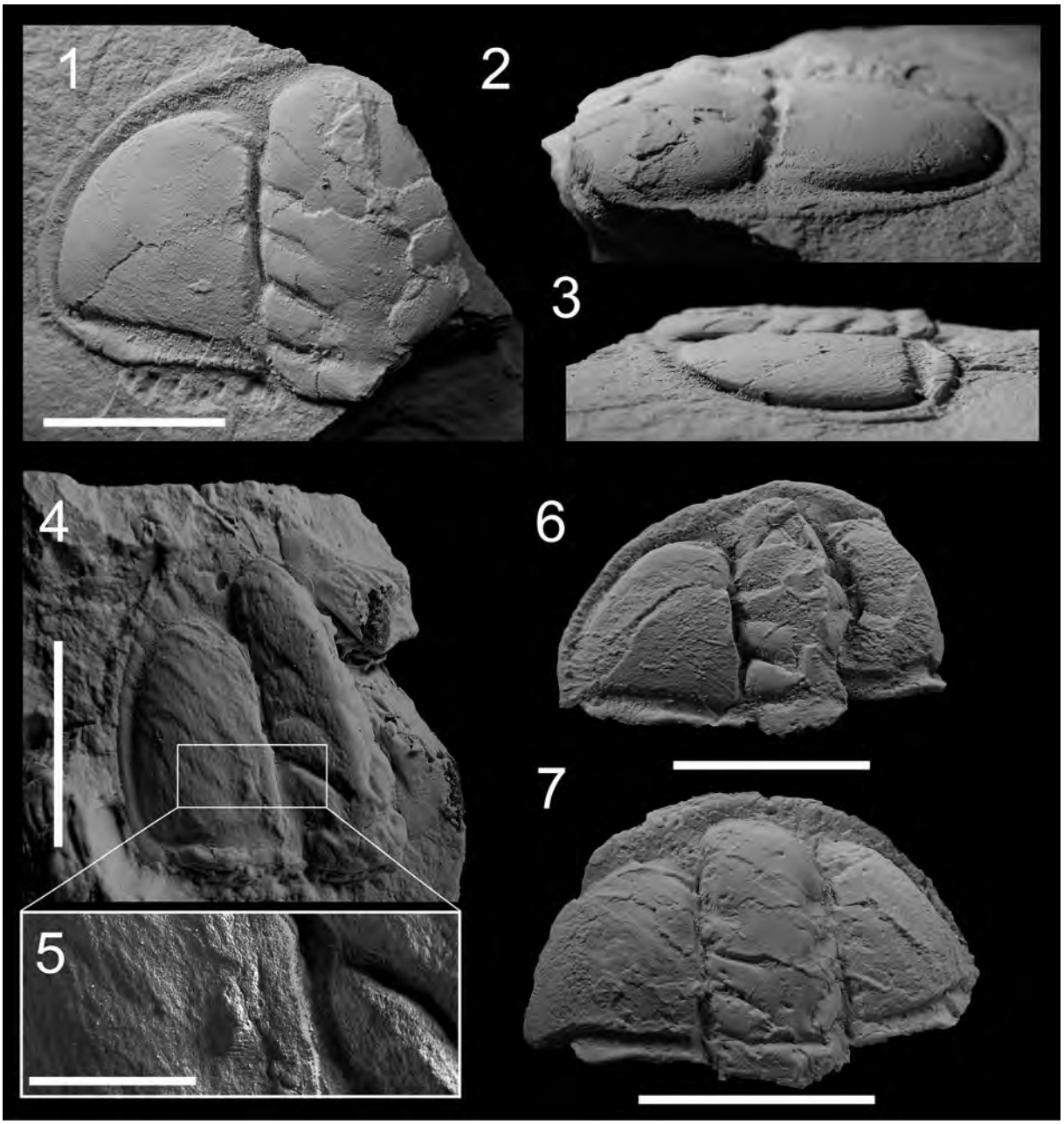

Figure 4. *Pseudatops reticulatus* (Walcott, 1890b): (**1–3**) UHU-CU003-20, Cumbres de San Bartolomé, Cumbres beds, late Marianian: (**1**) dorsal view; (**2**) frontal view; (**3**) lateral view; (**4, 5**) UHU-AM2001-20, Arroyomolinos de León, Herrerías shale, middle-late Marianian: (**4**) dorsal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

are minimal: the cephalon, especially the frontal lobe of the glabella, presents a more significant relief in the North American specimens. This could be taphonomic because the American specimens are preserved in limestone and the Spanish ones in shales.

Pseudatops viola has a cephalon with a semiovate outline, in contrast with the trapezoidal to semicircular cephalon of *Pseudatops reticulatus*. In *Pseudatops viola*, the facial suture crosses the lateral border furrow and a narrow sliver of the cheek, whereas in *Pseudatops reticulatus*, it is confined to the lateral border. The more marginal facial suture also occurs in numerous conocoryphids (see Sdzuy, 1961; Liñán and Gozalo, 1986).

Korobov (1973) erected *Pseudatops perantiquus* from the Ishim River, comparing it with *Pseudatops viola* and *Pseudatops reticulatus*. *Pseudatops perantiquus* differs from *Pseudatops viola* by a wider anterior border, wider anterior and posterior border furrows, and a subtriangular fixigena (Korobov, 1973). *Pseudatops perantiquus* has a wider cranidium, posterior border furrows running directly into the occipital furrow, a wider anterior border, and wider anterior and posterior furrows than *Pseudatops reticulatus*. Korobov (1973) noted that the Russian specimens have a wider, more uniform border in comparison with that of *Pseudatops reticulatus*. The smaller, conical glabella pointing forward and the three pairs of deep, wide lateral

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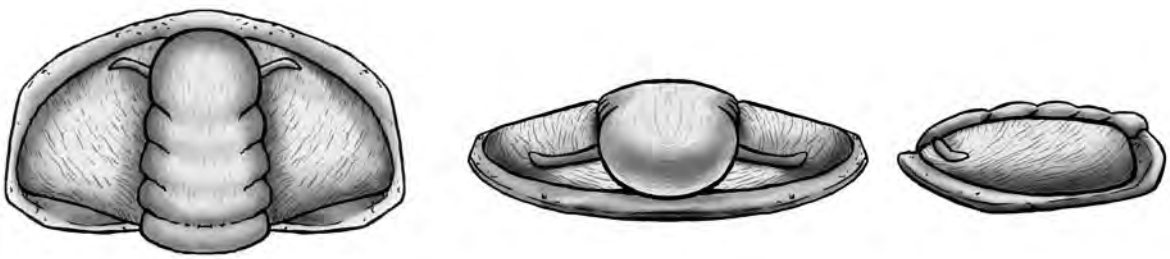

Figure 5. Reconstruction of the cephalon of *Pseudatops reticulatus* (Walcott, 1890b), in (left to right) dorsal, frontal, and lateral views.

furrows are especially remarkable. The frontal lobe of the glabella reaches the anterior furrow without invading the anterior border, but it has the characteristic reticulated ornament of *Pseudatops*.

Discussion

Biostratigraphy.—The Atopidae has a worldwide distribution. The stratigraphic distributions of *Atops* and *Pseudatops* are summarized in Figure 6.

Atops trilineatus occurs in the Taconic Allochthon, in the 'Lower Faunule' of the *E. asaphoides* Zone (Lochman, 1956; Rasetti, 1967). In Baltica, *Atops granulatus* occurs in the Holy Cross Mountains (Poland), in the middle *Holmia-Schmidtiellus* Biozone (Orlowski, 1985; Żylinska, 2013). *Atops calanus* occurs in the middle to late Marianian (Cambrian Stage 4) with *Serrodiscus*, *Calodiscus,* and *Triangulaspis* (Richter and Richter, 1941; Sdzuy, 1962; Collantes et al., 2018). In Australia, *Atops rupertensis* and *A. briandailyi* occur in the *Pararaia janeae* Biozone (Jell et al., 1992; Jago et al., 2006). *Atops korobovi* occurs in the Sanashtykgol Horizon of the Botomian stage in the Altai-Sayan Fold Belt (Repina et al., 1999). *Atops nikolai* and *Atops patulus* from Tuva Republic are from the upper Aldan Stage or, possibly, lowermost Lenan Stage (Korobov, 1973, table 1). Because the Lenan is now assigned to the Toyonian Stage (Astashkin et al., 1991), this species is likely upper Botomian. *Atops*? sp. indet. of Rushton (1966) from the Purley Shales (locality 2A) occurs with *Serrodiscus ctenoa* Rushton, 1966 of the *Cephalopyge* Biozone in the upper Cambrian Stage 4 (Rushton et al., 2011; Williams et al., 2013). Conocoryphidae gen. indet. sp. indet. of Fritz (1973) in the Mackenzie Mountains, northwestern Canada, assigned here to *Atops*, occurs in the lower Sekwi Formation, dated as *Nevadella* Biozone (upper Cambrian Stage 3 to lower Stage 4). Although Cotton (2001) did not offer information about the stratigraphic position of his *Atops* sp. indet., Murray studied the Salt Water Pond Series in 1864 (Murray and Howley, 1881; Schuchert and Dunbar, 1934) and the first three levels are included in the Forteau Formation (Betz, 1939, table 2), the horizon of which is assigned to the *Bonnia-Olenellus* Biozone, Dyeran Stage (Skovsted and Peel, 2007; Stouge et al., 2017).

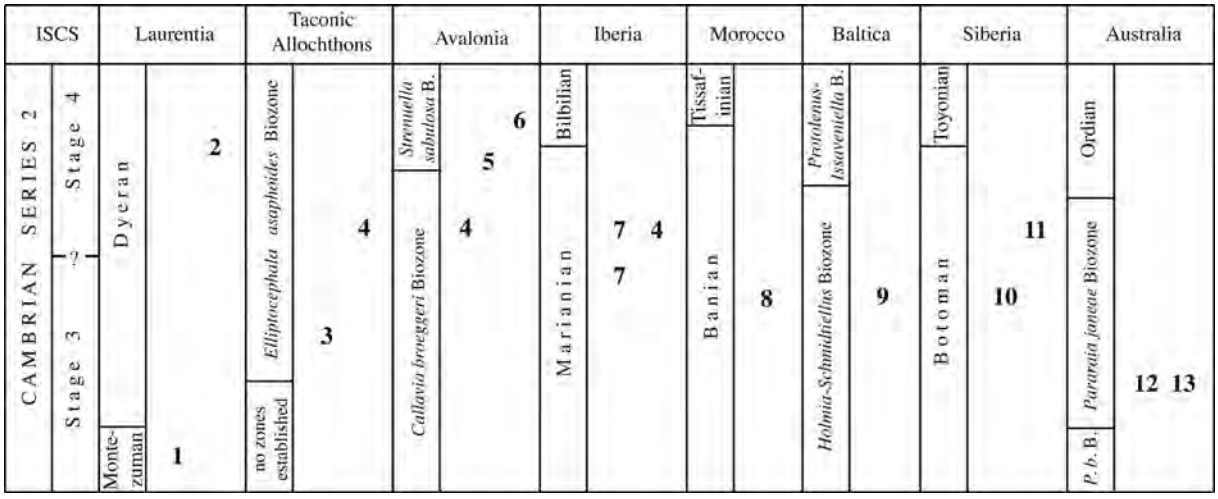

Figure 6. Correlation chart showing the stratigraphic occurrence of Atopidae. 1 = Conocoryphidae gen. indet. sp. indet. of Fritz (1973); 2 = *Atops* sp. indet. of Cotton (2001); 3 = *Atops trilineatus* Emmons, 1844; 4 = *Pseudatops reticulatus* (Walcott, 1890b); 5 = *Pseudatops viola* (Woodward, 1888);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

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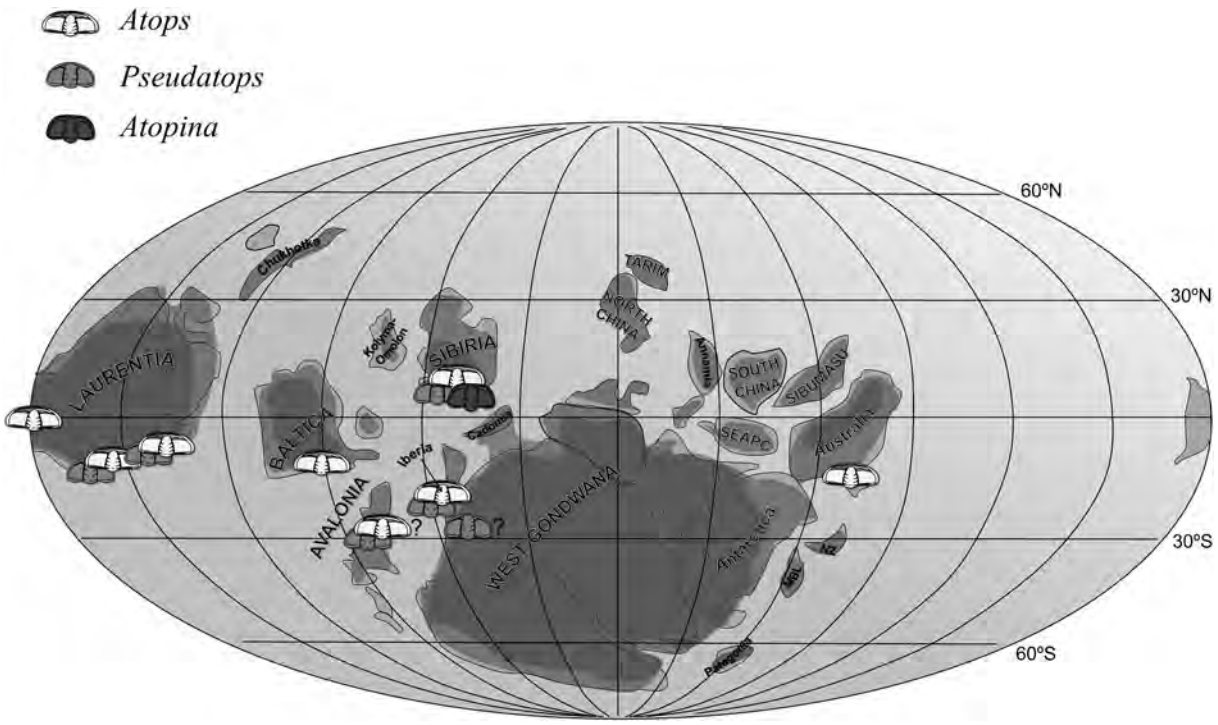

Figure 7. Distribution of the Atopidae, plotted on the Cambrian palaeogeographic map. Based on Dalziel (1997), Scotese and McKerrow (1990), McKerrow et al. (1992), and Malinky and Geyer (2019).

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

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

Paleobiogeography.—The Atopidae is known from Laurentia (northwestern Canada), the Taconic Allochthon (New York), western Newfoundland, western and eastern areas of Avalonia (eastern Newfoundland and the United Kingdom, respectively), Baltica (Poland), Siberia (Tuva Republic), the western margin of Gondwana (Iberia and Morocco), and Gondwana (Australia). Figure 7 shows that the distribution of Atopidae is mainly in the Southern Hemisphere, close to the equator.

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