A remarkable illaenid trilobite from the Middle Ordovician of Morocco

ISABEL RÁBANO, JUAN C. GUTIÉRREZ-MARCO & DIEGO C. GARCÍA-BELLIDO

Illaenid trilobites were relatively scarce in south-polar peri-Gondwanan areas during the Ordovician, with all their African occurrences restricted to the Middle and Upper Ordovician of Morocco. At a specific level, only the Bohemian form *Ectillaenus benignensis* (Novák) has been positively identified from the Middle Ordovician of that region. In the present work we add the discovery of the new form *Caudillaenus nicolasi* gen. et sp. nov., occurring in a single bed of late Darriwilian 2 age within the Taddrist Formation of the Rahiat region (south of Alnif), in the central Moroccan Anti-Atlas. The new genus is characterized by a large and subtriangular pygidium, a cephalon with relatively large eyes, a broad rostral plate with a short upwardly and forwardly turned posterior flange, and a globose hypostome. It shows a spheroidal enrolment type previously unknown in illaenids, with the pygidium protruding beyond the cephalon, and the cephalic margin fitting into a shallow and wide coaptative furrow on the pygidial doublure. • Key words: Trilobites, Illaenina, enrolment, Ordovician, Gondwana, Anti-Atlas, Morocco.

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Illaenid trilobites are scarce among the Middle and Upper Ordovician assemblages in the African continent, where they have been recorded only from Morocco and are poorly studied. The first mention of an illaenid trilobite from this country was the report of *Illaenus* by Dubois (*in* Moret 1933) from the Imini Inlier on the southern slope of the central High Atlas, later revised by Neltner (1938, p. 163) as *Illaenus* cf. *perovalis* Murchison. The material comes from Llanvirn shales, perhaps equivalent to the upper part of the Tachilla Formation of the Anti-Atlas, as pointed out by Destombes (1963).

Termier & Termier (1950) provided the first illustrations of Moroccan illaenids, collected by L. Clariond and other French geologists in Llandeilo and Caradoc beds of the Anti-Atlas. The material consisted of at least seven specimens, originally identified as *Illaenus perovalis* Murchison (Termier & Termier 1950, pl. 193, figs 15–17), *Illaenus* sp. (Termier & Termier 1950, pl. 193, fig. 23), and *Illaenus zeidleri* Barrande (Termier & Termier 1950, pl. 193, figs 18–22). Based on their illustrations, it is difficult to say whether the first illaenid belongs to *Ectillaenus perovalis* (Murchison, 1839) or even to the similar coarsely ornamented species *E. benignensis* (Novák, 1918), also recorded from Morocco (see below). The second Moroccan form (*Illaenus* sp. of Termier & Termier 1950) is represented by a single cranidium with a broad, barrel-shaped glabella and large eyes, and most likely belongs to *Panderia* Volborth, 1863 (Gutiérrez-Marco *et al*. 2003, p. 167). With regards to the third Moroccan representative, originally assigned to the type species of *Zdicella* Šnajdr, 1957 (= *Delgadoa* Thadeu, 1947; see Gutiérrez-Marco & Rábano 1987, p. 663), it seems to be an oculate form and therefore does not belong to that genus.

During detailed field work on the Ordovician formations of Morocco over about 40 years, the French geologist and palaeontologist Jacques Destombes discovered about 50 localities yielding illaenid trilobites, most of them in the Anti-Atlas and situated in the Tachilla Formation (early to middle Darriwilian), the Taddrist, Guezzart and Ouine-Inirne formations of the First Bani Group (late middle Darriwilian to earliest Sandbian), the entire Ktaoua Goup (Sandbian to Katian) and the Lower Second Bani Formation (late Katian to early Hirnantian). However, the published lists of trilobites mention only "illaenids" or

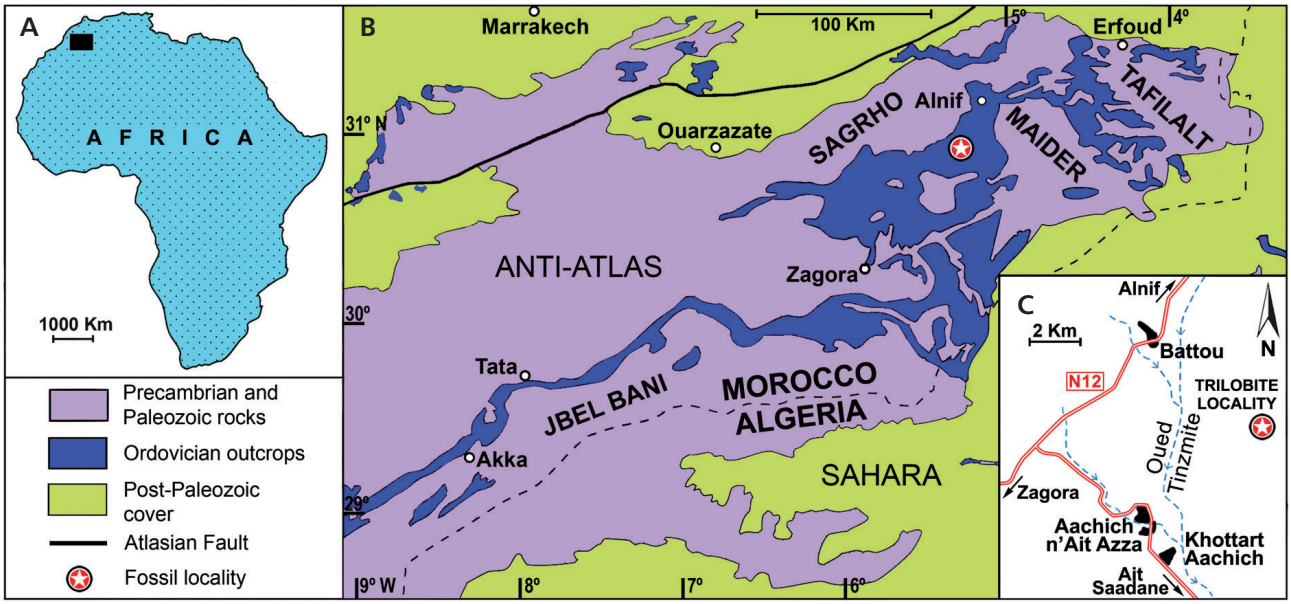


Figure 1. A – map indicating the position of the studied region in Africa. • B – geological sketch map of the central and eastern Anti-Atlas of Morocco (modified from Gutiérrez-Marco *et al*. 2003), showing the position of the fossil locality (star). • C – sketch map of the area around the new trilobite site.

"Illaenidae" from most of these localities, except for *Ectillaenus* sp. and *Dysplanus*? sp. recorded in the Tachilla, Guezzart and Ouine-Inirne formations (see Gutiérrez-Marco *et al*. 2003 for compilation of previous data), and *Octillaenus* sp. in the Upper Ktaoua Formation (Destombes *in* Destombes *et al*. 1985, Destombes 2000 and references therein). Outside the Anti-Atlas, a few other unidentified illaenid remains have been cited from Middle and Upper Ordovician formations of the central and eastern High Atlas, as well as in the Coastal Meseta east of Casablanca (Destombes *in* Destombes *et al*. 1985, with earlier references).

The most recent report of illaenid trilobites from the Anti-Atlas was by Rábano *et al*. (2010), who documented the first Moroccan record of the Bohemian species *Ectillaenus benignensis* (Novák, 1918) from two localities of late Darriwilian age in the Guezzart and Ouine-Inirne formations of the First Bani Group, reinforcing the palaeobiogeographical relationships between Bohemia and Morocco across the peri-Gondwanan platform.

From 2009, a few specimens of a previously unknown illaenid genus from Morocco began to appear at fossil and mineral shows and shops, later being offered on the Internet by fossil traders worldwide. This new illaenid was briefly examined by Rábano *et al*. (2012), who believed that it derived from Upper Ordovician rocks owing to its purported association, according to a Moroccan dealer, with a cyrtolitid tergomyan mollusc characteristic of the Lower Ktaoua Formation (Katian). Recent field work by the second author in Morocco led to the identification of the exact provenance of this particular trilobite, formally described here as a new genus and species of the family Illaenidae, and which comes from Middle rather than Upper Ordovician beds.

Geological setting

The studied fossils come from a previously unknown locality in the central Anti-Atlas of Morocco (Fig. 1B), intensively quarried in the last few years by local inhabitants for commercial exploitation of Ordovician trilobites and echinoderms. The site lies 5.8 km northeast from the town of Aachich n'Ait Azza (Fig. 1C), in the region of Rahiat (= Rihyate). Geographic coordinates for the main trench (Fig. 2) are Lat. 30° 55´ 18˝N, Long. 05° 14´ 51˝W, situated on the Tarhbalt sheet of the 1:50,000 scale topographic map of Morocco (Todrha-Maïder geological map at 1:200,000 scale; Service Géologique du Maroc, Rabat 1988). The fossiliferous bed is restricted stratigraphically to a 40–60 cm-thick interval within a succession of silty shales with decalcified nodules towards the middle part of the Taddrist Formation, the lowermost unit of the First Bani Group, which in this area rests slightly unconformably on shales of the Tachilla Formation. The base of the Taddrist Formation at the studied locality is formed by the so-called Imi-n'Tourza oolitic ironstone bed, still under exploitation in a mine approximately 1 km east of the fossil locality. The fossiliferous horizon lies about 38–40 m above the top of this widespread ironstone.

A preliminary faunal list from the locality includes, besides the new illaenid *Caudillaenus nicolasi* gen. et sp. nov.,

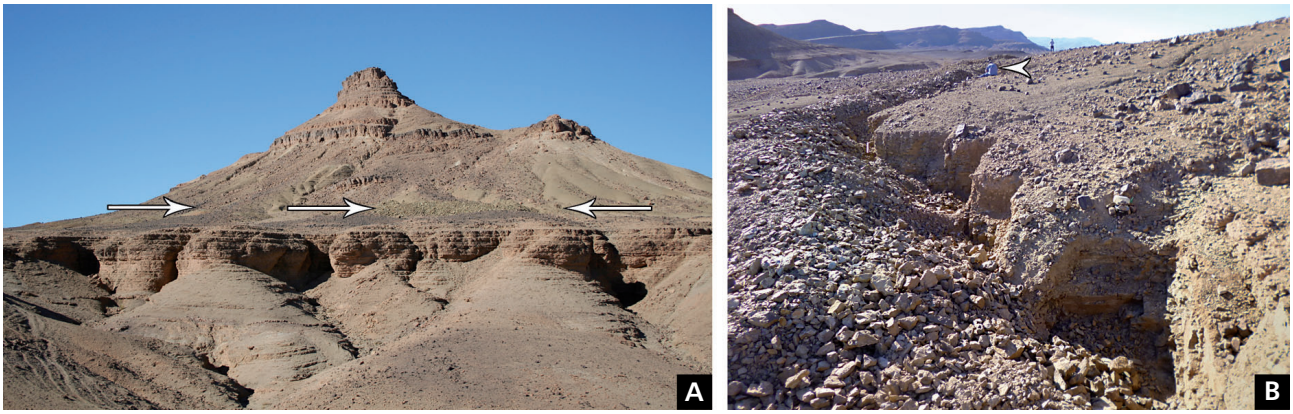


Figure 2. Field views of the fossil locality. • A – fossiliferous bed (arrowed) near the middle part of the Taddrist Formation. • B – detail of trench excavated along the same bed by local inhabitants for commercial prospecting for trilobites and echinoderms; two persons (arrowed and on the skyline) give the approximate scale.

other trilobites such as *Morgatia*? *rochi* (Destombes, 1972), *Placoparia* (*Coplacoparia*) sp. nov., *Colpocoryphe* sp., *Parabarrandia* aff. *crassa* (Barrande, 1872) and an undetermined cheirurid (*Eccoptochile*? sp.). The non-trilobite fossils are represented by some molluscs (a cyrtonellid tergomyan, bivalves such as *Praenucula* sp., orthoconic nautiloids), hyoliths (*Elegantilites* sp.), echinoderms (Diploporita and Asterozoa indet.), conularids (*Exoconularia* sp.) and rare graptolites (*Didymograptus* sp.). The sandy shales above and below the fossiliferous bed contain abundant trace fossils such as *Teichichnus* isp. and *Palaeophycus* isp. Many of the trilobite specimens found in nodules are articulated, outstretched carapaces and complete exuviae, together with numerous enrolled specimens of *Caudillaenus* gen. nov. and *Parabarrandia* aff. *crassa* that are commonly isolated in the silty shales owing to episodes of rapid burial that also prevented the disarticulation of some starfishes recovered in the nodules.

The Taddrist Formation and the other units included in the First Bani Group of the central Anti-Atlas have traditionally been dated as "Llandeilo *sensu lato*" (Destombes 1971, Destombes *et al*. 1985). A later review based on data obtained during completion of the Anti-Atlas geological maps at 1:200,000 scale placed the boundary between the Middle and Upper Ordovician towards the top of this group, whereas the boundary between the traditional "Llanvirn" and "Llandeilo" series was moved up to the middle part of the Bou-Zeroual Formation above the Taddrist Formation. Gutiérrez-Marco *et al*. (2003) assigned the Taddrist Formation to the upper Oretanian, a regional stage division that is roughly equivalent to the upper Darriwilian 2/basal Darriwilian 3 of the global scale (Gutiérrez-Marco *et al*. 2008, Bergström *et al*. 2009). Some of the taxa occurring with *Caudillaenus nicolasi* at its type locality allow precise dating: the trilobite *Morgatia*? *rochi* (Destombes) is restricted to the *Didymograptus murchisoni* graptolite biozone (Gutiérrez-Marco *et al*. 2003), and the occurrence of *Didymograptus* itself (a form with a slender pendent rhabdosome) in a nodule from the same bed reinforces this correlation.

Systematic palaeontology

Figured and cited specimens are housed in the Museo Geominero of Madrid, Spain (MGM), except one specimen (Fig. 3D, E) which remains in the private collection of Mr Nicolás Mesas (Cadrete, Spain). Over a hundred additional specimens of *Caudillaenus nicolasi* have been examined, including specimens in various Moroccan shops, and international fossil shows and websites.

Order Corynexochida Kobayashi, 1935
Suborder Illaenina Jaanusson, 1959
Superfamily Illaenoidea Hawle & Corda, 1847
Family Illaenidae Hawle & Corda, 1847

Genus *Caudillaenus* gen. nov.

Type species. – *Caudillaenus nicolasi* gen. et sp. nov., from the Taddrist Formation (upper Oretanian regional stage, in beds equivalent to upper Darriwilian 2 global substage) of the Moroccan Anti-Atlas.

Etymology. – The name refers to the pygidium (L. *cauda*, tail), which has a unique morphology among illaenid genera, thus the suffix *-illaenus*.

Diagnosis. – Cephalon parabolic in outline, with moderately large eyes situated about 1.5 times their own length from posterior margin; glabella wide, about half the width of cephalon posteriorly, axial furrows subparallel to slightly curved inwards in vicinity of the lunette (*ca* opposite posterior end of the palpebral lobes), genal angles

rounded. Librigenae with weak subocular furrow. Rostral plate broad (tr.), weakly convex (sag.), posterolaterally defined by almost transverse connective sutures and with a short upwardly and forwardly turned flange on the posterior edge. Hypostome with a narrow and globose middle body. Thorax of ten segments with well-defined axis that is broader than pleurae in dorsal view; axial furrows subparallel; pleurae adaxial to fulcrum successively increasing in width (tr.) posteriorly. Pygidium subtriangular in outline, larger than cephalon; axis weakly defined, subconical; pleural region concave posteromedially. Pygidial doublure broad, divided into convex outer half and flattened or weakly concave inner half by a shallow vincular furrow running approximately parallel to the inner margin. Dorsal surface of carapace almost smooth, with sculpture of fine terrace lines and small pits only developed on the anteriormost part of cephalon and the lateral borders of pygidium.

Remarks. – With the exception of some Silurian and Devonian scutelluids, typical illaenimorph trilobites have a pygidium that is semicircular to parabolic in outline. The pygidium of *Caudillaenus* is unique among illaenid trilobites in shape and in the presence of a vincular furrow. However, the cephalic and thoracic morphology is rather conservative, with the exception of the rostral plate which is somewhat reminiscent of that of some *Cybantyx*, *Liolalax* and *Bumastus*? species (Lane & Thomas 1978, 1983; Holloway & Lane 1998) in its almost triangular shape in ventral view. However, the rostral plates of those genera differ from that of *Caudillaenus* in that the connective sutures are oblique rather than almost transverse and approach the midline posteriorly.

The spheroidal mode of enrolment of *Caudillaenus nicolasi*, with the posterior end of the pygidium projecting beyond the glabella, resembles the "pseudomegalaspis type" of Harrington (1959, fig. 75A, p. O104). However, in *Pseudomegalaspis* Jaanusson, 1953 the anterior margin of the cephalon fits against the inner edge of the pygidial doublure on enrolment, whereas in *C. nicolasi* the anterior margin of the cephalon abuts the middle (sag., tr.) of the pygidial doublure, fitting into the shallow vincular furrow that serves to stabilize the enrolment (Figs 3K, 4H–L). A different kind of closing mechanism resulting in the projection of the pygidium beyond the cephalon was developed in an apomorphic group of Devonian homalonotids that includes *Digonus* Gürich, 1909, but in this case a pointed process on the rostral plate fits against the inner edge of the pygidial doublure (Wenndorf 1990, fig. 13). The enrolment mode of *C. nicolasi* should not be confused, either, with the taphonomic effect resulting in the so-called "discoidal hyper-enrolment type" described by Pillet (1982), where compactional flattening of specimens of *Ectillaenus* with a normal spheroidal enrolment of the "asaphid type", with the cephalic and pygidial doublures facing each other (see Harrington 1959, fig. 75B, p. O104), has caused the pygidium and thorax to be displaced posteriorly, so that the pygidium projects beyond the front of the cephalon.

Occurrence. – As for type and only known species.

Caudillaenus nicolasi sp. nov.

Figures 3, 4

2012 *Caudillaenus nicolasi* gen. et sp. nov. (*nomina nuda*); Rábano *et al.*, p. 49.
2012 Illaenidae nov.?; Lebrun, p. 9 (photograph).

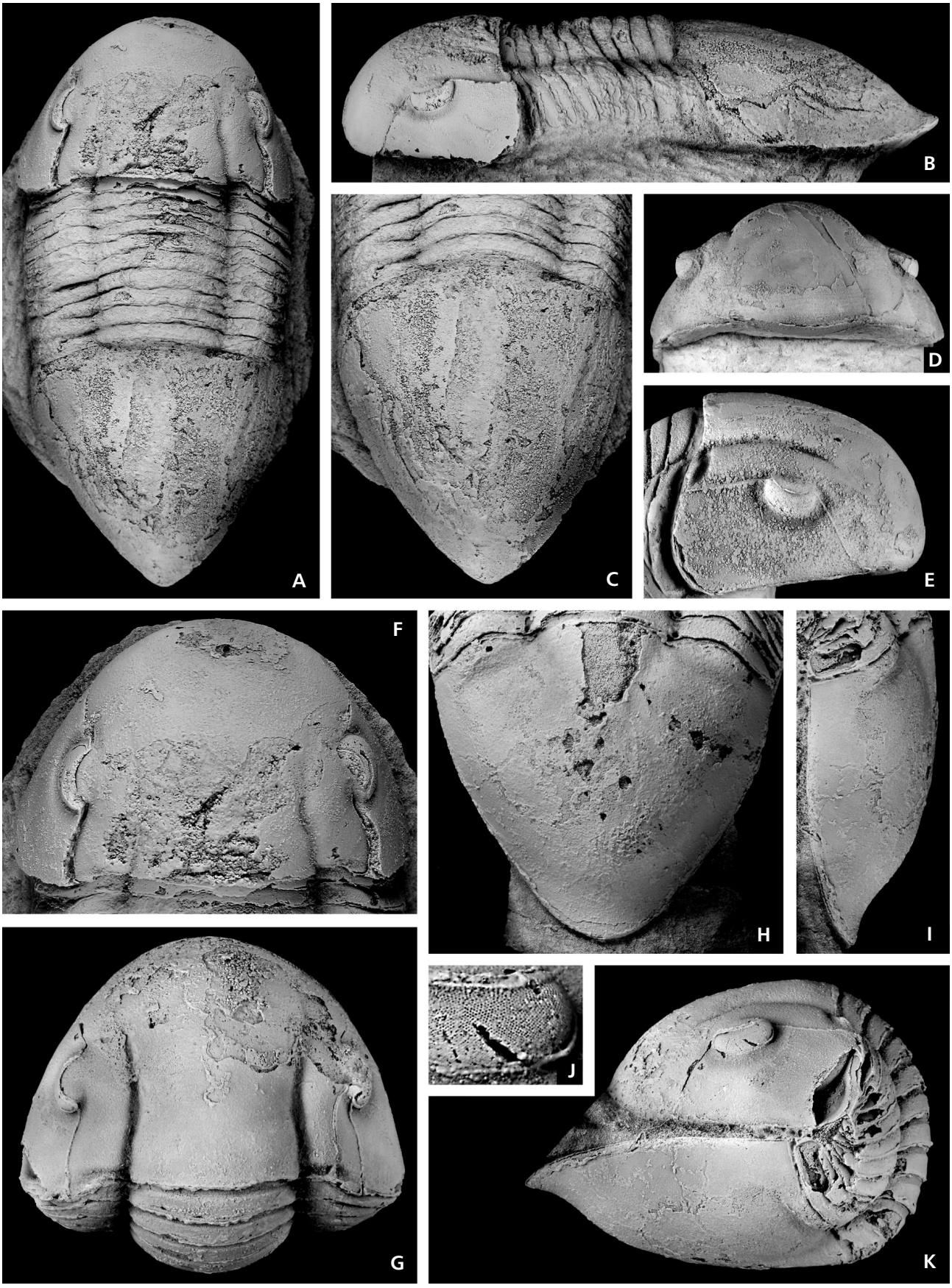
Etymology. – After Mr Nicolás Mesas (Cadrete, Spain), who provided us with the first specimens of this trilobite, making them available for study.

Holotype. – MGM 6729X, internal mould of a complete, undeformed, well-preserved, enrolled specimen (Fig. 3G–K).

Type locality and horizon. – Trench excavated in 2014 (Fig. 2) at an unnamed site in the Rahiat region of the central Moroccan Anti-Atlas, 5.8 km northeast of Aachich n'Ait Azza (Lat. 30° 55´ 18˝ N, Long. 05° 14´ 51˝ W). The fossiliferous bed occurs towards the middle of the Taddrist Formation, about 38–40 m above the top of the Imi-n'Tourza oolitic ironstone bed that constitutes the base of this lithostratigraphic unit. Late Oretanian (= late Darriwilian 2) in age.

Paratypes. – A complete, outstretched carapace (MGM 6731X; Fig. 3A–C, F); three enrolled specimens (MGM 6730X, Fig. 4H–L; MGM 6919X, not figured; MGM 6920X, with eroded dorsal surface of cephalon, Fig. 4B, C); a complete cephalon (MGM 6921X, Fig. 4A, D, E); seven pygidia (MGM 6922X, internal mould with fragment of external mould, Fig. 4N; MGM 6923X, fragment of external + internal mould, Fig. 4O, P; MGM 6924X, internal

Figure 3. *Caudillaenus nicolasi* gen. et sp. nov., Taddrist Formation (Middle Ordovician), Morocco. • A–C, F – paratype, MGM 6731X, internal mould of dorsal exoskeleton; A, B – dorsal and lateral views, × 1.3; C – detail of the last thoracic segments and the pygidium in slightly oblique posterior view, × 1.5; F – dorsal view of cephalon, × 1.8. • D, E – cephalon of a complete specimen in anterior and right-lateral views, × 0.9 and × 1.3 respectively; original in the private collection of Mr Nicolás Mesas. • G–K – holotype, MGM 6729X, enrolled dorsal exoskeleton; G – cephalon in dorsal view, × 1.4; H – pygidium in dorsal view, × 1.3; I – pygidium in lateral view, × 1.4; J – detail of left eye, × 4; K – specimen in lateral view, × 1.4.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mould with detached doublure, not figured; MGM 6925X, internal mould with well-preserved doublure, not figured; MGM 6926X, Fig. 4F, G; MGM 6927X, fragment of external mould, not figured; MGM 6928X, fragment of internal + external mould, not figured); and a left librigena (MGM 6929X, external mould). All from the type locality.

Other material. – A complete and partially enrolled specimen (Fig. 3D, E) from the type locality is in the private collection of Mr Nicolás Mesas.

Diagnosis. – As for the genus.

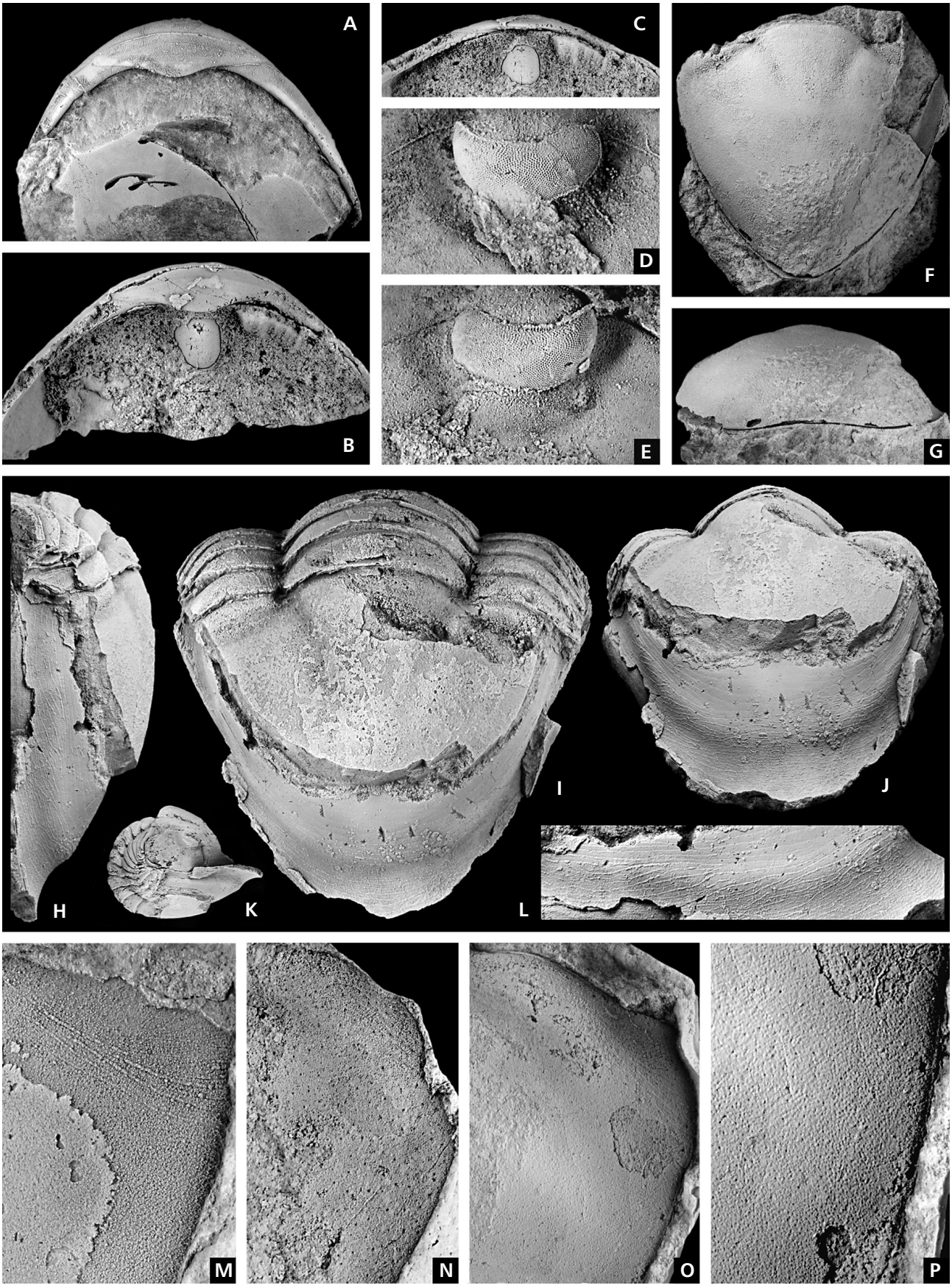
Description. – Cephalon vaulted, slightly more convex transversely than sagittally; sagittal length 25–41 mm, 83–90% of maximum width. Glabella clearly defined only in posterior half of cranidium, comprising 58–64% of cranidial width at posterior margin and 45–50% of the maximum cephalic width. Axial furrows gently diverging anteriorly and posteriorly from lunette. Fixigenae elongated, subrectangular in posterior half of cephalon where it can be distinguished from the glabella, width at posterior margin approximately one-third of the glabellar width. Palpebral lobes large, arched, almost flat in lateral view, with anterior edges situated just in front of cephalic mid-length (sag.) in dorsal view, their length (exsag.) corresponding to 17–20% of cephalic length. Palpebral furrows faint, most distinct posteriorly. Preocular sutures diverging slightly forwards immediately in front of eyes before converging in a broad curve and joining under the anterior edge of the cephalon. Postocular sutures weakly sigmoidal and slightly diverging overall, intersecting the posterior margin of cephalon in line (exsag.) with outer edge of palpebral lobes and at an angle of about 70–75°. A faint posterior furrow, subparallel to the posterior edge of the fixigena, dies out before reaching the facial suture. Librigenae smooth, broader than fixigenae in lateral view, extending slightly farther back than the posterior extremity of cranidium. Visual surface arched (vertical and exsag.) and kidney-shaped, about three times longer than high and covered with numerous very tiny holochroal lenses, bounded below by a broad and shallow subocular furrow that is slightly deeper and wider posteriorly than anteriorly. Doublure of librigenae narrow, with a sharp ridge posteriorly, subparallel to the posterior edge of the cephalon. Rostral plate weakly convex (sag.), broad (tr.), of wide subtriangular outline (Fig. 4A), laterally defined by almost straight connective sutures forming an angle of convergence of 170°. Posterior margin of rostral plate slightly pointed backwards in ventral view, with a short upwardly and forwardly turned flange. General outline of the hypostome unknown, but with a narrow and globose middle body. Its anterior margin must have had a median indentation into which the rostral flange fitted.

Thorax with ten segments. Pleural regions moderately arched (tr.). Pleural tips obtuse, with doublure increasing in width (tr.) on more posterior segments. A single apodeme is present on the posterior part of all the thoracic segments beneath the axial furrows (Fig. 3H).

Pygidium with axis comprising about 39–45% of maximum pygidial width, with an observed maximum width of 63 mm. Axis short, about 23–30% of the sagittal pygidial length in dorsal view; axial furrows almost completely effaced, even less indistinct posteriorly than anteriorly, better defined on internal than external surface. Pleural areas without traces of segmentation except for first pair of pleural furrows that are very shallow and wide (exsag.), run obliquely backwards, and become indistinct distally. Posterior and lateral pleural margins forming sharp edge with doublure. Doublure comprising about 38–40% of the pygidial length sagittally and tapering anteriorly; inner margin with wide, gentle, forwardly-curved deflection medially. In longitudinal section, doublure sigmoidal with broad, weakly concave anterior part and convex marginal part separated by shallow vincular furrow. This furrow weakens on anterior and posteromedian part of the doublure.

Dorsal surface of the cephalon is virtually smooth apart from some very fine, long and transverse terrace ridges on the front of the cranidium, not extending laterally onto the librigenae. Rostral plate with sculpture of about seven long, unbranched, relatively faint terrace ridges, running continuously between connective sutures and mainly subparallel to anterior margin of rostral plate. Sculpture on dorsal surface of the pygidium is most pronounced in the

Figure 4. *Caudillaenus nicolasi* gen. et sp. nov., Taddrist Formation (Middle Ordovician), Morocco. • A, D, E – paratype, MGM 6921X, internal mould of cephalon showing ventral details (A, × 1.2), and aspects of right and left eyes (D and E respectively, × 3.8), including the weak subocular furrow on librigenae. • B, C – paratype, MGM 6920X, latex cast of anterior part of cephalon of an eroded specimen showing details of rostral plate, connective sutures and hypostome in ventral (B, × 1.4) and posteroventral (C, × 1.1) views. • F, G – paratype, MGM 6926X, internal mould of pygidium in dorsal (F, × 0.9) and posterior (G, × 1) views. • H–L – paratype, MGM 6730X, internal mould of enrolled dorsal exoskeleton prepared to show external mould of pygidial doublure; H–J – pygidium in lateral, dorsal and oblique posterior views, showing the shape of the broad coaptative furrow on the doublure, × 1.2, × 1.2 and × 1, respectively; K – complete specimen in lateral view, × 0.4; L – detail of H (rotated 90° CCW, showing interfingering, outward branching and diverging terrace ridges), × 1.4. • M – paratype, MGM 6924X, right anterolateral corner of an isolated pygidium, preserved as a natural external mould, showing terrace ridges and fine pits, × 2.5. • N – paratype, MGM 6922X, latex cast of right anterolateral corner of pygidium showing fine pits and larger, randomly arranged pits, × 2.8. • O, P – paratype, MGM 6923X, latex cast of right anterolateral corner of pygidium, showing the faint sculpture (O, × 2.5) and detail of the lower part of the area (P, × 4.1).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anterolateral corners, where a few terrace ridges curve towards the articulating facet. Close to the pygidial margin there are lineations of minute pores, aligned obliquely to the margin, among which a few slightly larger-diameter pits are randomly arranged. Pygidial doublure with fine terrace ridges running subparallel to anterior and posterior margins, more dense on outer than inner part of doublure, and interfingering medially in vincular furrow where they are more oblique to pygidial margin.

Occurrence. – *Caudillaenus nicolasi* gen. et sp. nov. is known from a single locality in the Rahiat region (south of Alnif) of the central Moroccan Anti-Atlas, within the middle part of the Taddrist Formation, First Bani Group, and from beds of late Oretanian age (= late Darriwilian 2 of the global scale).

Conclusions

Illaenid trilobites are apparently rare and of limited diversity in the Ordovician of Morocco, in comparison with the up to 10 genera and 27 species so far recorded from Sandbian–Katian strata of the three areas that share diverse trilobite species in common with Morocco across the peri-Gondwanan realm (Gutiérrez-Marco *et al*. 1999): the Prague Basin (Šnajdr 1957, Bruthansová 2003), Ibero-Armorica (Kerforne 1900; Thadeu 1947; Hammann 1976, 1992) and Sardinia (Hammann & Leone 1997). In Middle Ordovician strata, illaenids are represented by two genera and six species in Bohemia (Šnajdr 1957, Bruthansová 2003) and two genera and species in Ibero-Armorica (Rábano & Gutiérrez-Marco 1983, Rábano 1989 with earlier references, Lebrun 2002). In coeval beds in the Moroccan Anti-Atlas illaenid diversity is greater than in the Upper Ordovician and includes, apart from the new taxon *Caudillaenus nicolasi* in the Taddrist Formation, *Ectillaenus* sp. and *Dysplanus*? sp. in the Tachilla Formation and some beds of the First Bani Group (references in Gutiérrez-Marco *et al*. 2003), the "Bohemian" form *Ectillaenus benignensis* (Novák, 1918) in the Guezzart and Ouine-Inirne formations (Rábano *et al.* 2010), and the preliminary identification of the "southwestern-European" species *Ectillaenus giganteus* (Burmeister, 1843) and *Panderia beaumonti* (Rouault, 1847) from the Tachilla and Guezzart formations by the present authors (unpublished data). The record of *C. nicolasi* adds a new and important element to the palaeobiogeographical knowledge of Ordovician trilobite assemblages from the peri-Gondwanan African margin, and fits well in the so-called "Calymenacean-Dalmanitacean" cratonic fauna (Cocks & Fortey 1990), represented by particular inshore trilobite biofacies developed in southernmost Gondwanan palaeolatitudes and very rich in endemic forms.

From both functional morphological and palaeontological perspectives, the unusual enrolment mode of *Caudillaenus nicolasi* involves a closing mechanism that has not been recorded previously in illaenid trilobites, in which the posterior end of the pygidium projects beyond the front of the cephalon, with the anterior and lateral margins of the cephalon fitting into a shallow and wide coaptative furrow on the pygidial doublure.

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