

# A new aglaspidid euarthropod with a six-segmented trunk from the Lower Ordovician Fezouata Konservat-Lagerstätte, Morocco

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**Abstract** – A new euarthropod with an uncommon morphology, *Brachyaglaspis singularis* gen. et sp. nov., is described from the Early Ordovician (middle Floian) Fezouata biota of Morocco. The presence of a pair of postventral plates, widely attached to each other and located under the posterior-most trunk tergite and the base of the tailspine, indicates a phylogenetic relationship with the enigmatic group Aglaspidida. The overall morphology of *Brachyaglaspis* most closely resembles that of the ‘Ordovician-type’ aglaspidids, more specifically the late Cambrian – Early Ordovician genus *Tremaglaspis*. However, the presence of a prominent cephalon and only six trunk tergites in the new genus deviates from the organization of all other known aglaspidid species, notably extending the known range of morphological disparity of the group. A taxonomic revision of this euarthropod group indicates that the most accurate name and authorship combination correspond to Aglaspidida Walcott, 1912.

Keywords: Aglaspidida, Floian, postventral plates, Ordovician-type aglaspidid, *Tremaglaspis*.

## 1. Introduction

Aglaspidida Walcott, 1912 (= Aglaspidida *sensu stricto* cf. Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006; Lerosey-Aubril, Ortega-Hernández & Zhu, 2013; Ortega-Hernández, Legg & Braddy, 2013) represents a major and diverse – yet historically problematic – group of early Palaeozoic euarthropods typified by a biomineralized phosphatic exoskeleton (Briggs & Fortey, 1982). Although aglaspidids are relatively poorly understood, recent studies have produced significant insights into their morphology (e.g. Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006), biostratigraphic range (e.g. Fortey & Rushton, 2003, 2009; Lerosey-Aubril *et al.* 2013), palaeobiogeographic distribution (e.g. Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006; Ortega-Hernández *et al.* 2010; Lerosey-Aubril, Ortega-Hernández & Zhu, 2013) and phylogenetic position within the evolutionary context of Artiopoda Hou & Bergström, 1997, and even the entire phylum Euarthropoda Lankester, 1904 (Ortega-Hernández, Legg & Braddy, 2013; see also Legg, Sutton & Edgecombe, 2013).

It is possible to draw three major conclusions from these findings. (1) The presence of postventral plates (paired sclerotized structures located underneath the posterior trunk tergites and covering the base of the tailspine ventrally) and anterior tergal processes represent the only autapomorphic characters for the clade

(Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006). (2) Aglaspidida is monophyletic and subdivided into two groups: a ‘Cambrian-type’ clade whose overall morphology reflects the ‘traditional’ aglaspidid diagnosis (e.g. 11 trunk tergites, subtriangular glabella, genal and pleural spines, long tailspine) and an ‘Ordovician-type’ clade that includes taxa with derived features (e.g. effaced cephalon, reduction/loss of dorsal eyes, rounded genal angles, reduced tergite count, short tailspine) (Ortega-Hernández, Legg & Braddy, 2013). (3) Most of the evolutionary history of aglaspidids is obscured due to their poor fossil record, most likely as a consequence of their general preference for relatively shallow-water environments (Lerosey-Aubril *et al.* 2013).

Aglaspidid fossils are remarkably rare, and the paucity of well-preserved material often makes it difficult to recognize new species that may provide additional information on the evolutionary history of these enigmatic euarthropods. Here we describe a new aglaspidid from the Lower Ordovician Fezouata Konservat-Lagerstätte in Morocco (see Van Roy *et al.* 2010; Martin *et al.* 2015; Van Roy, Briggs & Gaines, 2015). Despite having an unusual morphology for the group, the new taxon is recognized as an Ordovician-type aglaspidid, and indicates that these problematic euarthropods possessed a greater degree of morphological disparity than previously considered.

## 2. Geological setting and preservation

The new taxon is described based on a single almost-complete individual collected from Bou Chrebeb, an

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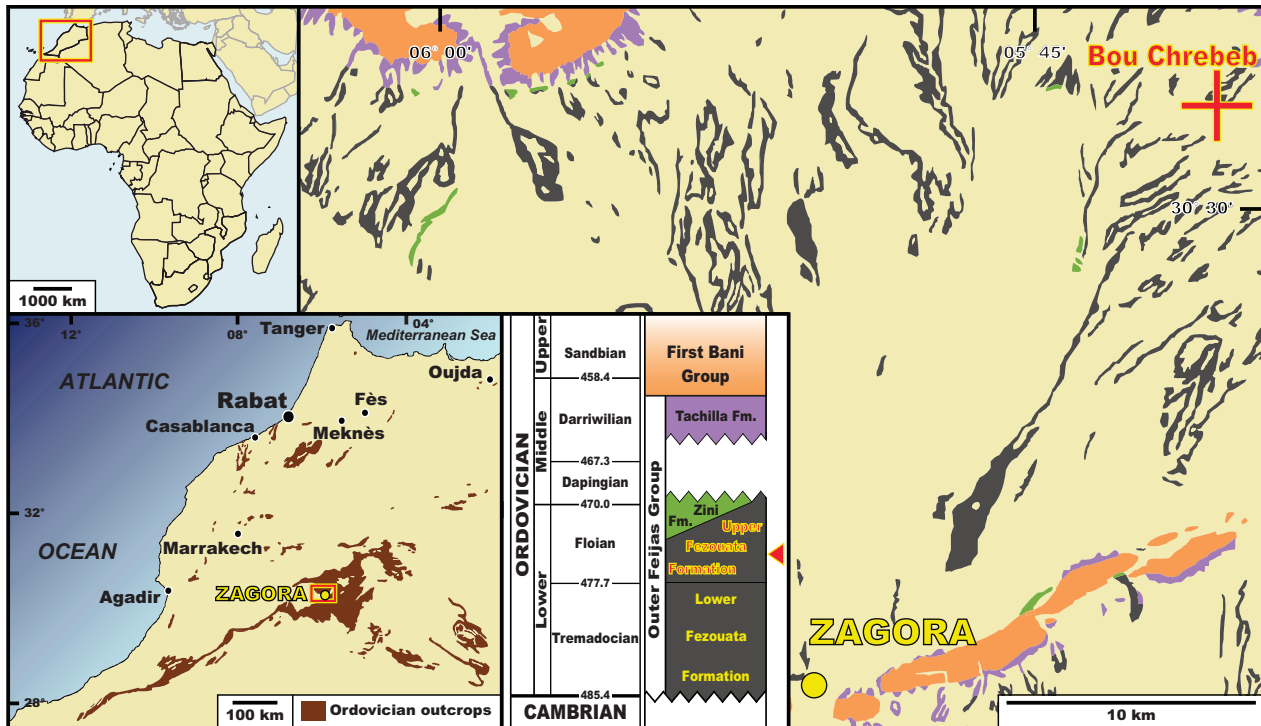


Figure 1. Ordovician outcrop map of the area north of Zagora, southeastern Morocco. Crosshairs indicate the position of the Bou Chrebeb locality where *Brachyaglaspis singularis* gen. et sp. nov. was found. Insets show the position of the map below in Africa, the study area within Morocco and the stratigraphic context with the position of the Fezouata biota (arrow).

outcrop ca 35 km NE of Zagora in south-eastern Morocco (Fig. 1). This locality was originally considered to belong to the Upper Fezouata Formation, having a Floian age (Vidal 1998a, b; Destombes 2006; P. Van Roy, unpub. thesis, Ghent University, 2006; Van Roy *et al.* 2010). However, in a recent study, Martin *et al.* (2015) situated this locality at the top of the Lower Fezouata Formation, claiming a latest Tremadocian age (*Hunnegraptus copiosus* biozone) for the site. This attribution, however, has now been shown to be incorrect, based on an erroneous stratigraphic correlation to another site in the wider area; Bou Chrebeb in fact does fall within the Floian of the Upper Fezouata Formation, and has a middle Floian age, as considered previously (J.C. Gutiérrez Marco, pers. comm.). The Lower and Upper Fezouata Formations represent a globally transgressive sequence of mudstone and siltstone, except for the upper part of the Upper Fezouata Formation, which records a substantial shallowing of the depositional environment. The Fezouata Formations have yielded rich assemblages of non-biomineralised organisms including a wide range of iconic Burgess Shale-type elements co-occurring with forms typical for the post-Cambrian Palaeozoic. These non-biomineralised biotas are accompanied by diverse classical ‘shelly’ faunas, including abundant trilobites and echinoderms (Van Roy *et al.* 2010; Van Roy & Briggs 2011; Van Roy, Briggs & Gaines, 2015; Van Roy, Daley & Briggs, 2015; Vinther *et al.* 2008; Martin *et al.* 2015; Fortey 2009, 2011, 2012; Lefebvre & Fatka 2003; Sumrall & Zamora 2011; Kröger & Lefebvre 2012). The Fezouata biota is

preserved essentially *in situ* and is considered to have lived in fairly shallow water, near storm-wave base (Martin *et al.* 2015); the biomineralised taxa are typical for an Early Ordovician fauna living in a normal, open-marine environment (Sepkoski, 1979, 1984).

The holotype (YPM 226552) represents a dorsoventrally flattened individual exposed from its dorsal side, as evidenced by the pattern of trunk tergite overlap and degree of convexity (Fig. 2). The specimen exhibits the typical vivid colouration usually associated with Fezouata fossils. The yellowish and reddish colours are related to the presence of iron oxides; these minerals are the result of pyrite oxidation, the precipitation of which permitted the preservation of soft tissues (Vinther, Van Roy & Briggs, 2008; Van Roy *et al.* 2010; Gaines *et al.* 2012; Van Roy, Briggs & Gaines, 2015; Van Roy, Daley & Briggs, 2015). The more restrained brownish colour of parts of the trunk is typical of originally biomineralized structures that have been replaced by clay minerals (Vinther, Van Roy & Briggs, 2008; Van Roy *et al.* 2010), suggesting that YPM 226552 originally had a lightly biomineralized exoskeleton. The light-coloured mineralization in the cephalic region probably results from the presence of further authigenic clays.

### 3. Materials and methods

The specimen was mechanically prepared using PaleoTools MicroJack1 and 5 air scribes, needles and scalpels. It was glued with Paraloid B-72 dissolved in acetone, after which it received a protective coat

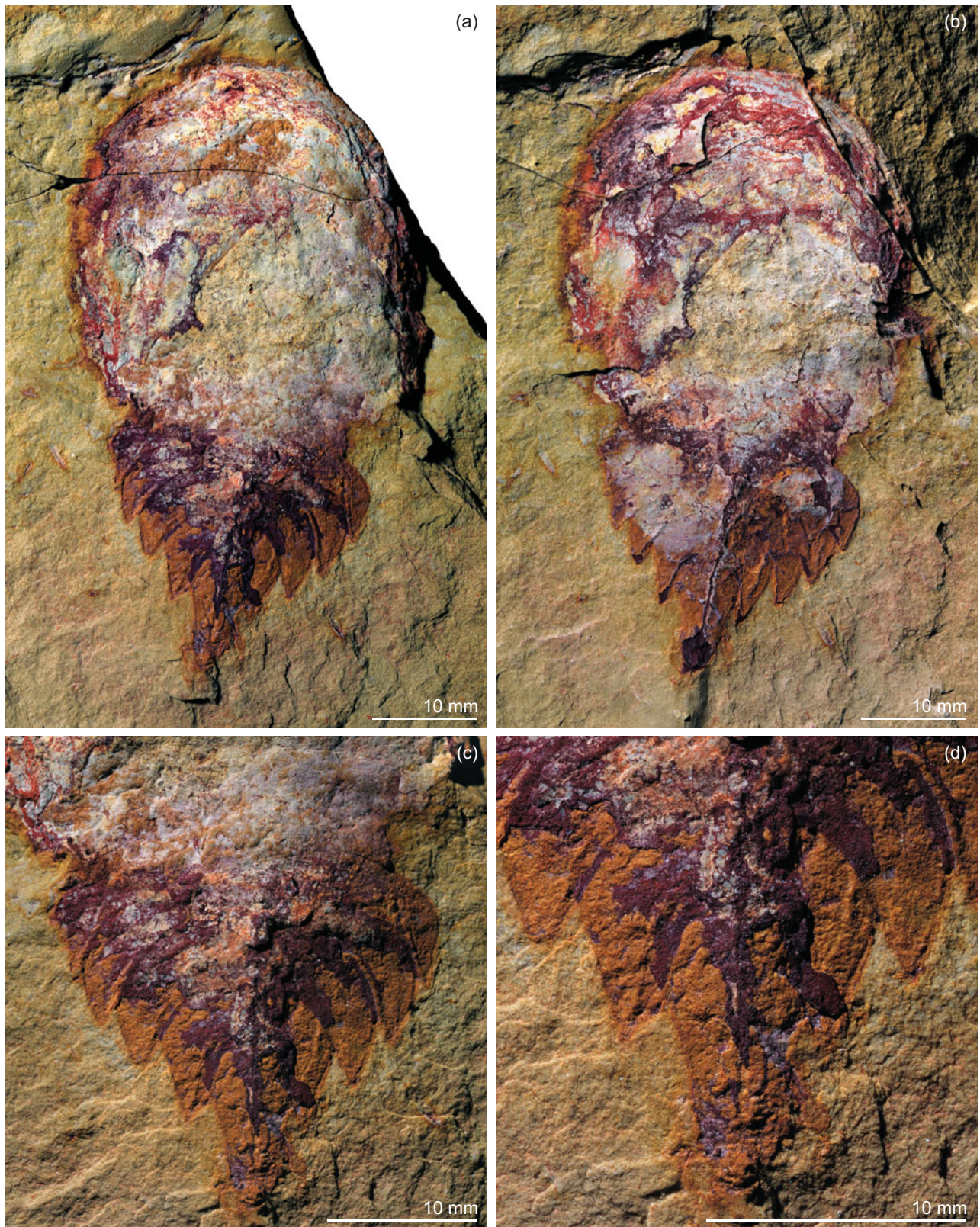


Figure 2. *Brachyaglaspis singularis* gen. et sp. nov., holotype and only specimen YPM 226552, Upper Fezouata Formation, middle Floian (Lower Ordovician), Bou Chrebeb, Morocco: (a) part; (b) counterpart, inverted lighting and mirrored to create false positive relief image; (c) part, close-up of trunk; and (d) part, close-up of postventral plates and tailspine.

of consolidant, consisting of a 5% solution of Butvar B-98 in ethanol. For photography of the complete specimen, the fossil was illuminated by a 500 W tungsten floodlight with an Aflash Photonics linear polarizer in front; for close-up imaging, a Schott KL2500 cold light

source was used with polarizers attached to the tips of the goosenecks. A Cokin XPro X164 circular polarizer was mounted on the camera lens and crossed with the polarizer of the light source to enhance contrast. The part was lit from the NW while the counterpart was

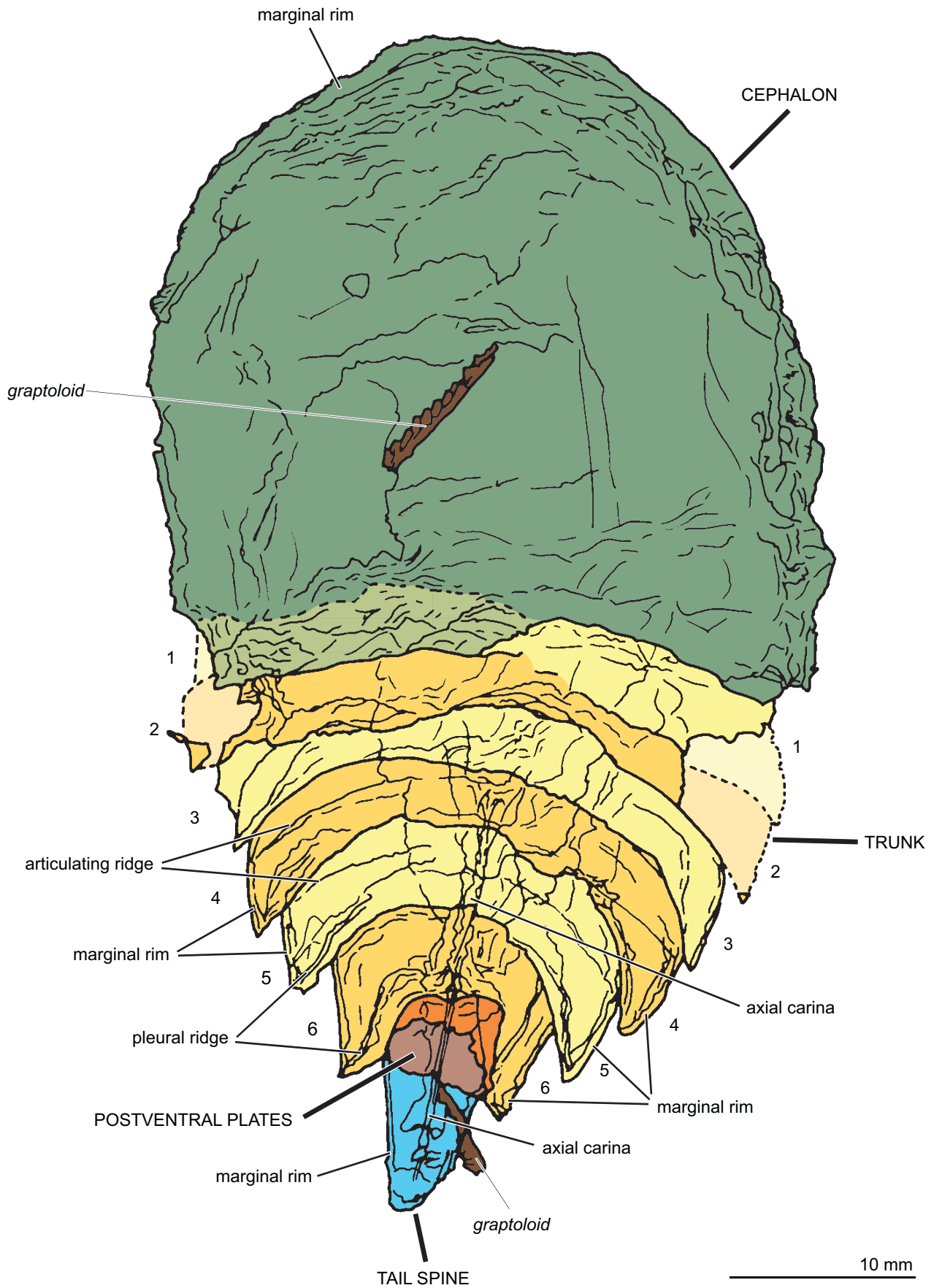


Figure 3. Composite *camera lucida* drawing combining information from both part and counterpart of *Brachyaglaspis singularis* gen. et sp. nov., holotype and only specimen YPM 226552, Upper Fezouata Formation, middle Floian (Lower Ordovician), Bou Chrebeb, Morocco. Numbers indicate trunk tergites.

illuminated from the SW and mirrored in Adobe Photoshop CC 2014 to create a false positive relief image and facilitate direct comparison of part and counterpart. The specimen was photographed dry. All photographs were taken with a Hasselblad H4D-200MS medium frame digital SLR connected to a computer and operated remotely in 6-shot mode through Hasselblad Phocus 8.2.1 software to acquire images of 200 MP resolution. A Hasselblad HC Macro 4/120 mm II lens stopped down to f/9.5 was employed for photography. Lens distortion was corrected using Hasselblad Phocus 8.2.2 software. Stacks of between 26 and 38 images were taken in aperture priority mode, with manual focusing through the focal plane. After exporting the FFF format digital negatives to TIFF from Hasselblad Phocus 8.2.2, the photographs were stacked in Zerene Stacker Pro 1.04 (64 bit) using the PMax pyramid stack algorithm. The stacked images were then post-processed in Adobe Photoshop CC 2014, first applying the ‘Sharpen more’ and ‘Sharpen’ functions, followed by removal of the background. Levels were then manually balanced while holding down the ‘alt’ key to prevent clipping of pixels in the specimen; the grey level was always retained at 50%. The high-resolution images were down-sampled in Adobe Photoshop CC 2014 to lower-resolution TIFF files for use in the plates.

YPM 226552 is deposited at the Yale Peabody Museum of Natural History in New Haven, Connecticut (USA). Abbreviations: dia. – diameter; sag. – sagittal; T1–6 – trunk tergites 1 to 6; t.l. – total length; t.w. – total width; tr. – transverse.

#### 4. Systematic palaeontology

Phylum Euarthropoda Lankester, 1904 (see Ortega-Hernández, 2014)  
Order Aglaspida Walcott, 1912

*Emended diagnosis:* Euarthropods with a primarily phosphatic biomineralized cuticle. Except for a possible hypostomal suture, cephalon completely devoid of visible ecdysial sutures. Eyes primarily dorsal and sessile; may be lost in derived taxa. Four, or possibly five, cephalic appendages present. All trunk tergites freely articulating, with pleurae carrying a pair of anterior tergal processes. Paired postventral plates located beneath posterior-most one, two or three tergites and base of tailspine, possibly resulting in the loss of appendages associated with those otherwise undifferentiated terminal tergites (emended from Van Roy, 2006, p. 341).

*Remarks:* There is considerable disagreement regarding the spelling and authorship of the higher taxonomic units (i.e. order and family) that encompass the genus *Aglaspis* Hall, 1862 and its allies (Table 1). The order Aglaspina Walcott, 1912 was the first taxonomic unit to be proposed above the family level, but all later mentions of it have erroneously cited Walcott (1911). According to Walcott (1912, p. 199), the taxa included

in this group are characterized by: an elongate and trilobed exoskeleton; a head with or without sessile eyes and bearing a hypostome (‘epistoma’) and five pairs of appendages; a trunk with 8–11 appendage-bearing segments; and an ‘abdomen’ with 1–3 segments. This order was originally composed of the sole family Aglaspidae (then called ‘Aglaspidae’; see discussion below), which included the genera *Aglaspis*, *Emeraldella* Walcott, 1912, *Habelia* Walcott, 1912 and *Molaria* Walcott, 1912. Clarke (1913) agreed with the grouping of these taxa, but proposed a subordinal rank for the Aglaspina Walcott, 1912. This was not followed by Raymond (1920, p. 149), who agreed with Walcott’s concept of Aglaspina except for his exclusion of the genus *Emeraldella*. Later on, Raasch (1939) discussed the applicability of this concept of Aglaspina and considered that, as initially defined, this group did not adequately represent its constituent taxa. Instead of simply emending the diagnosis, Raasch (1939, p. 3) proposed to abandon Walcott’s Aglaspina and created a new order called Aglaspida which included *Aglaspis*, *Beckwithia* Resser, 1931 and *Strabops* Beecher, 1901, along with the new taxa described in his monograph; *Emeraldella*, *Molaria* and *Habelia* were excluded. Interestingly, Raasch’s diagnosis of Aglaspida acknowledged for the first time the presence of a phosphatic exoskeleton and postventral plates, two characters that are now regarded as critical to the definition of the clade (Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006; Ortega-Hernández, Legg & Braddy, 2013). Despite Raasch’s recommendation (1939, p. 3), Walcott was recognized as the author of this taxon by most subsequent workers (Table 1) until Hesselbo (1989, 1992) re-described *Beckwithia* and the aglaspidid fauna from the upper Cambrian deposits of the Mississippi Valley; here, Raasch was credited the authorship of the order grouping all the known aglaspidid species, a practice that has been adopted in most recent studies (Table 1).

For the last three decades, the order has been referred to not as ‘Aglaspina’ or ‘Aglaspida’, as proposed by Walcott (1912) and Raasch (1939), respectively, but rather ‘Aglaspida’. This spelling was introduced by Bergström (1971, p. 397) probably for the sake of consistency, after Størmer (1955, p. xiii, P12) had replaced the family name Aglaspidae Miller, 1877 with Aglaspididae Miller, 1877. This change was justified on the grounds of complying better with the International Code of Zoological Nomenclature (ICZN), but its article 29.3.1.1 clearly states that if the stem of a family name ends in -id (e.g. aglaspid-), those two letters may be elided before adding the family-group suffix -idae. In other words, replacing ‘Aglaspidae’ by ‘Aglaspididae’ and ‘Aglaspida’ by ‘Aglaspidida’ might have been unnecessary, especially since those spellings were in prevailing usage at that time. Since ‘Aglaspidida’ has been widely used since 1971, regardless of whether Walcott or Raasch was regarded as the author of the taxon, we recommend maintaining this spelling over ‘Aglaspina’ or ‘Aglaspida’.

Table 1. Evolution of the names and authorships of the taxonomic units comprising the euarthropod genus *Aglaspis* and allies. The first mention of the family name Aglaspidae Clarke is found in Clarke (1900), but it is unclear whether this marks the creation of the family or if the author was referring to an unknown contribution published by him a few years earlier. In any case, a family Aglaspidae comprising the sole genus *Aglaspis* had already been created by Miller (1877). See text for further explanations concerning our recommendations.

Taxonomic rank	Name and authorship	Reference	Recommendation
Subclass	Aglaspida	Bergström, 1968	To be abandoned
	Aglaspidida Bergström, 1968	Bergström, 1971	
	Aglaspidida (Walcott, 1911) Bergström, 1968	Hou & Bergström, 1997	
Order	Aglaspidida Bergström, 1968	Ortega-Hernández <i>et al.</i> 2013	Order Aglaspidida Walcott, 1912
	Aglaspina	Walcott, 1912	
	Aglaspina Walcott	Raymond, 1920	
	Aglaspina Walcott	Fedotov, 1924	
	Aglaspina Walcott	Henriksen, 1928	
	Aglaspina Walcott, 1912	Raasch, 1939	
	Aglaspida	Raasch, 1939	
	Aglaspida Raasch	Størmer, 1944	
	Aglaspida Raasch, 1939	Caster & Macke, 1952	
	Aglaspida Walcott, 1911	Størmer, 1952	
	Aglaspida Raasch, 1939	Waterlot, 1953	
	Aglaspida Walcott, 1911	Størmer, 1955	
	Aglaspida Raasch, 1939	Raw, 1957	
	Aglaspida Walcott, 1911	Chlupáč & Havlíček, 1965	
	Aglaspida Walcott, 1911	Chlupáč, 1965	
	Aglaspida Walcott, 1911	Radwański & Roniewicz, 1967	
	Aglaspida Raasch, 1939	Fage, 1968	
	Aglaspida Walcott, 1911	Repina & Okuneva, 1969	
	Aglaspidida Walcott, 1911	Bergström, 1971	
	Aglaspida Walcott	Quilty, 1972	
	Aglaspida Walcott, 1911	Eldredge, 1974	
	Aglaspida Walcott, 1911	Hong & Niu, 1981	
	Aglaspidida Raasch, 1939	Hesselbo, 1989	
	Aglaspidida Raasch, 1939	Hesselbo, 1992	
	Aglaspidida Walcott, 1911	Hou & Bergström, 1997	
	Aglaspidida Walcott, 1911	Chlupáč, 1999	
	Aglaspidida Raasch, 1939	Fortey & Rushton, 2003	
	Aglaspidida Raasch, 1939	Waggoner, 2003	
	Aglaspidida Raasch, 1939	Zhang & Shu, 2005	
	Aglaspidida Raasch, 1939	Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006	
	Aglaspidida Walcott, 1911	Rak <i>et al.</i> 2009	
	Aglaspidida Raasch, 1939	Ortega-Hernández, Braddy & Rak, 2010	
	Aglaspidida Raasch, 1939	Ortega-Hernández <i>et al.</i> 2010	
Aglaspidida Raasch, 1939	Ortega-Hernández, Legg & Braddy, 2013		
Aglaspidida Raasch, 1939	Lerosey-Aubril, Ortega-Hernández & Zhu, 2013		
Aglaspidida Raasch, 1939	Lerosey-Aubril <i>et al.</i> 2013		
Suborder Family	Suborder Aglaspina Walcott	Clarke, 1913	To be abandoned Family Aglaspididae Miller, 1877
	Aglaspidae	Miller, 1877	
	Aglaspidae Clarke	Clarke, 1900	
	Aglaspidae Miller, 1877	Beecher, 1901	
	Aglaspidae Clarke	Clarke, 1913	
	Aglaspidae Clarke	Walcott, 1912	
	Aglaspidae Clarke	Raymond, 1920	
	Aglaspidae Clarke	Fedotov, 1924	
	Aglaspidae Clarke	Henriksen, 1928	
	Aglaspidae Walcott (sic!)	Walter, 1925	
	Aglaspidae Miller, 1877	Raasch, 1939	
	Aglaspidae Miller, 1877	Størmer, 1952	
	Aglaspididae Miller, 1877	Størmer, 1955	
	Aglaspididae Miller, 1877	Chlupáč, 1965	
	Aglaspididae Miller, 1877	Bergström, 1968	
	Aglaspididae Miller, 1877	Repina & Okuneva, 1969	
	Aglaspididae Miller, 1877	Briggs, Bruton & Whittington, 1979	
	Aglaspididae Miller, 1877	Hesselbo, 1989	
	Aglaspididae Miller, 1877	Hesselbo, 1992	
	Aglaspididae Miller, 1877	Ortega-Hernández, Braddy & Rak, 2010	
	Aglaspididae Miller, 1877	Ortega-Hernández <i>et al.</i> 2010	
	Aglaspididae Miller, 1877	Ortega-Hernández, Legg & Braddy, 2013	
	Aglaspididae Miller, 1877	Lerosey-Aubril, Ortega-Hernández & Zhu, 2013	
Aglaspididae Miller, 1877	Lerosey-Aubril <i>et al.</i> 2013		

The question of the authorship is more delicate. Walcott (1912) was the first to create and tentatively diagnose an order including and named after the genus *Aglaspis* Hall, 1862. Conversely, Raasch's (1939) monograph describing the aglaspidid fauna from Wisconsin is traditionally regarded as the most significant contribution ever published on this enigmatic group. Walcott's (1912) choice of *Aglaspis* as the type genus of his new order may seem surprising, considering the fact that it is the only genus initially included in this order that he had not created himself. In all likelihood, this decision was dictated by the pre-existence of the family Aglaspidae (see below). Also, Raasch (1939, p. 83) is probably correct in stating that Walcott might have mostly considered *Emeraldella*, *Habelia* and *Molaria* (rather than *Aglaspis*) when defining his order Aglaspina. However, it remains that Walcott's diagnosis of this order (imperfect as it was) is in accordance with the morphology of *Aglaspis*. Because of that, Raasch's order Aglaspida cannot be regarded as a new concept totally distinct of Walcott's order Aglaspina. Instead, it was a significantly improved version of it, both quantitatively (two aglaspidid species were known in 1912 and almost 20 after Raasch's publication 27 years later) and qualitatively (significance of postventral plates and phosphatic cuticle for defining the group). However, because it is priority and not merit that prevails when determining the authorship of a taxon according to the rules defined by the ICZN (albeit for lower taxonomic units), we believe that Walcott (1912) should be regarded as the author of the order Aglaspida.

Finally, the subclass Aglaspida Bergström, 1968 was proposed to treat aglaspidids, xiphosurans and eurypterids at equivalent taxonomic ranks within a new classification scheme of the Merostomata Dana, 1852. The spelling was later replaced by 'Aglaspida' by Bergström (1971, p. 397; Table 1), again most likely to follow the nomenclature introduced by Størmer (1955). The subclass Aglaspida Bergström, 1968 has virtually the same definition and composition as the order Aglaspida Walcott, 1912 (as redefined by Raasch, 1939). Given the fundamental synonymy between these classifications, we recommend abandoning the subclass Aglaspida Bergström, 1968 as it offers no added practical systematic value and contributes to a greater confusion about this name.

#### Family Aglaspidae Miller, 1877

*Remarks:* Family Aglaspidae Miller, 1877 represents the earliest confirmed record of a suprageneric classification for aglaspidid euarthropods (Table 1). A few early publications referred to Clarke as the author of this family (e.g. Clarke, 1900, 1913; Walcott, 1912; Raymond, 1920). It is not clear whether the first of them (i.e. Clarke 1900) represents the publication where this family was supposedly created or whether it refers to an older work from the same author. In any case, it cannot be older than Miller's work as the first publication by Clarke dates precisely from 1877

and dealt with a different topic (Schuchert 1926). Despite Beecher's (1901) clear statement about Miller's priority, this fact was only acknowledged by all after the publication of Raasch (1939). As already discussed above, the spelling of the family name was (unnecessarily) changed to Aglaspidae by Størmer (1955) and, since then, all the publications discussing this family referred to it as the Aglaspidae Miller, 1877 (Table 1). Accordingly, we recommend maintaining the spelling 'Aglaspidae' in line with Article 29.5 of the ICZN and referring to the family as the Aglaspidae Miller, 1877.

After demonstrating the absence of fused posterior trunk tergites in *Beckwithia typa* Resser, 1931, the family Beckwithiidae Raasch, 1939 was regarded as a subjective junior synonym of Aglaspidae Miller, 1877 by Hesselbo (1989). However, Hou & Bergström (1997, p. 96) considered this decision as premature, arguing that it should await the availability of further data on the morphology of this species and the chemical composition of its cuticle. Lerosey-Aubril, Ortega-Hernández & Zhu (2013) detected phosphorus in the exoskeleton of *B. typa*, but also stated that new material of this species confirms that its morphology cannot be accommodated within the current definition of the Aglaspida. Likewise, the recent phylogenetic analysis of Ortega-Hernández, Legg & Braddy (2013) suggests that *B. typa* is particularly close to, but definitely outside the Aglaspida *sensu stricto* (*sensu* Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006). This position likely stems from the absence of postventral plates in this species, a feature that remains uncertain considering the paucity of material described to date. As a result, we concur with Hou & Bergström (1997) that the fate of the family Beckwithiidae should await the description of new material of its type species.

The so-called 'Ordovician-type' aglaspidids with their distinct morphology (see Ortega-Hernández, Legg & Braddy, 2013) may represent another suprageneric group within Order Aglaspida Walcott, 1912. We nevertheless consider it premature to formally erect a new family to accommodate these forms, and prefer to retain them within Aglaspidae Miller, 1877 for now, pending detailed study of additional post-Cambrian forms.

#### Genus *Brachyaglaspis* gen. nov.

*Type species:* *Brachyaglaspis singularis* sp. nov. (by monotypy).

*Derivation of name:* Conflation of the Latin 'brachy' (short) and *Aglaspis*, referencing the peculiarly short trunk that typifies the new taxon.

*Diagnosis:* Aglaspida characterized by a large cephalon, both longer (sag.) and wider (tr.) than the trunk region, without apparent dorsal eyes. Trunk composed of six overlapping tergites. Paired postventral plates small, subrectangular and broadly attached to one another sagittally. Postventral plates located underneath

the last trunk tergite and base of tailspine. Tailspine short and almond-shaped, with a rounded termination.

*Brachyaglaspis singularis* sp. nov.

Figures 2–5

*Derivation of name:* *singularis*, from Latin, referring to the unusual morphology for an aglaspidid.

*Diagnosis:* as for genus.

*Description:* Holotype (YPM 226552) is a complete, mostly articulated individual consisting of part and counterpart, with a total original articulated length (sag.) of *c.* 69.6 mm. Cephalon large (*c.* 52% t.l., sag.), *c.* 36.0 mm long and 37 mm wide, with a rounded and convex anterior margin, almost straight lateral margins and slightly concave posterior margin. No dorsal eyes or ecdysial sutures visible. Marginal rim widest anteriorly (*c.* 1 mm), gradually narrowing towards the posterior. Axial region poorly differentiated (Figs 2a, b, 3); dorsal convexity moderate. Trunk short (*c.* 23.4 mm t.l., sag., excluding telson, i.e. *c.* 33% t.l. sag.), composed of six freely articulating tergites and preserved rotated *c.* 10° clockwise relative to cephalon (Figs 2a–c, 3). Axial region weakly developed, approximately one-third to one-quarter of t.w. (tr.). Median carina present on at least T3–6, becoming more pronounced rearwards. Trunk width (tr.) decreasing posteriorly, due to width reduction and increasing backwards curvature of pleurae. Pleural tips point sharply backwards. Each pleura bears a rather large articulating facet anterolaterally, the posterior margin of which is bordered by a faint articulating ridge which is situated just ahead of the midline (tr.) of the tergites. In their posterior third, the pleurae exhibit a ridge running towards pleural tip and vanishing abaxially. The lateral margins of the pleurae show a very narrow marginal rim of constant width (*c.* 0.5 mm). Overlap between adjacent tergites is broad (tr.) but limited (sag.). T1–5 roughly similar in length (sag.), but T6 is *c.* 50% longer. T1 and T2 poorly preserved medially and their lateral margins are missing, leaving only faint impressions. T1 covered by cephalon on the left and *c.* 31.5 mm in width (tr.). T2 is *c.* 30.5 mm in width (tr.). Exposed length (sag.) and width (tr.) of T3, T4, T5 and T6 are: *c.* 3.7 mm and *c.* 25.1 mm; *c.* 3.3 mm and *c.* 20.5 mm; *c.* 4.4 mm and *c.* 16.0 mm; and *c.* 6.8 mm and *c.* 9.1 mm, respectively. Strongly recurved pleurae of T6 point almost straight backwards, and form an embayment for the base of the tailspine. Tailspine short (*c.* 10.2 mm exposed length, i.e. *c.* 15% t.l., sag.), almond-shaped and terminating in a rounded, blunt tip (Figs 2, 3). Dorsal median carina and narrow marginal rim (*c.* 0.3 mm wide) present. Postventral plates small (*c.* 4.5–5 mm long sag., 5.8 mm wide tr.), subrectangular in outline, slightly tapering towards the anterior and with rounded corners; they seem to be broadly attached to one another, form a median notch anteriorly and posteriorly and cover ventrally posterior region of T6 and base of tailspine medially (Figs 2b, c, 3, 4).

*Remarks:* *Brachyaglaspis* is recognized as a member of Aglaspidida Walcott, 1912 based on the presence of paired postventral plates, which are autapomorphic for the group (Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006; Ortega-Hernández, Legg & Braddy, 2013, character 74). This assignment is further supported by the presence of articulating facets on the pleural regions (see Hesselbo, 1992; Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006), although similar features also occur in a few other Cambrian non-trilobite arthropods such as *Emeraldella* and *Molaria* (see Stein & Selden, 2012).

Although the large cephalon and trunk composed of only six tergites make *Brachyaglaspis* rather unusual compared to other aglaspidids, the new taxon also exhibits characters found in more orthodox members of this group. An effaced cephalon, apparent absence of dorsal eyes, trunk with less than 11 tergites and short tailspine make *Brachyaglaspis* most similar to the Ordovician-type aglaspidid species *Tremaglaspis unite* Fortey & Rushton, 2003 (see also Fortey & Rushton 2009) (Fig. 5). The new taxon is mainly distinguished from *T. unite* in the comparatively larger proportions of the cephalon, the presence of only six trunk tergites and apparently unfused postventral plates. Given that these morphological features are not observed in any similarly sized specimens of *Tremaglaspis* sp., which represents the only other aglaspidid known from the Fezouata Biota (e.g. P. Van Roy, unpub. thesis, Ghent University, 2006; Van Roy *et al.* 2010, fig. 2a), or any congeneric species (Fortey & Rushton, 2003, 2009; Lerosey-Aubril, Ortega-Hernández & Zhu, 2013), it can be concluded that YPM 226552 does not represent a juvenile specimen of any known species of *Tremaglaspis*. *Brachyaglaspis* also shares similarities with the Late Ordovician aglaspidid *Chlupacaris dubia* from Morocco (Van Roy, 2006), including an effaced cephalon and a short tailspine; because *Chlupacaris* is only known from disarticulated material, the exact tergite count for this taxon is uncertain but was probably larger than that of the new taxon (Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006). In any case, *Brachyaglaspis* is easily differentiated from *Chlupacaris* by the overall shape of the cephalon, absence of medially placed dorsal eyes and the different organization of the postventral plates.

The trunk of *Brachyaglaspis* is composed of only six overlapping tergites, and is therefore unusually short for an aglaspidid euarthropod (sag.; see Discussion section below); however, the broad (tr.) tergite overlap and the trend towards an increased curvature and a reduction of tergite pleurae rearwards are two characters reminiscent of the morphology of several Cambrian-type aglaspidid genera (e.g. *Aglaspis*, *Glypharthrus*, *Aglaspella*; see Ortega-Hernández, Legg & Braddy, 2013, characters 44 and 61; Fig. 5). Finally, the small postventral plates, which are widely attached to each other medially and display straight posterior margins, somewhat recall those of the late Cambrian *Australaglaspis stonyensis* Ortega-Hernández *et al.* 2010 from Tasmania. In



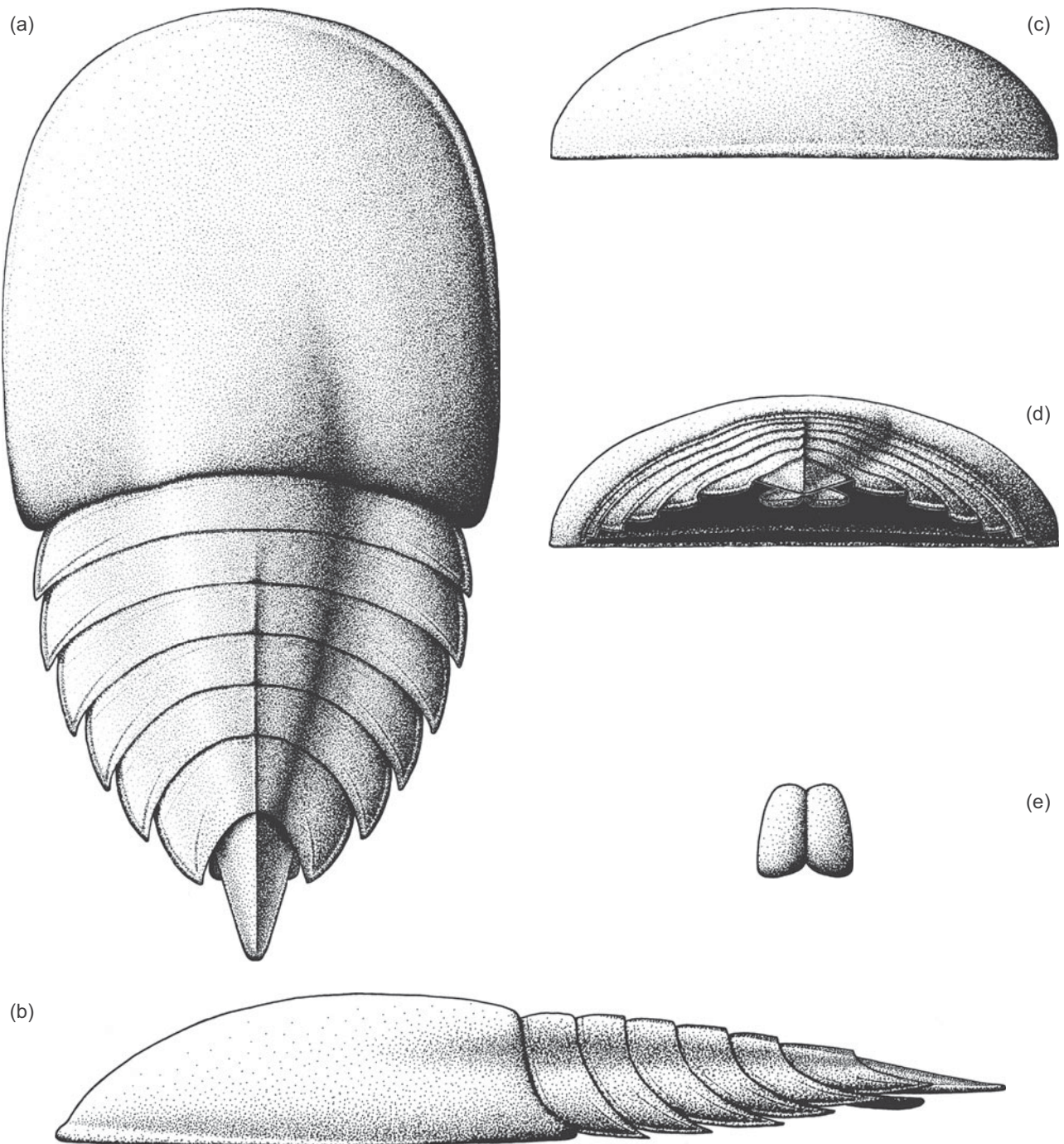


Figure 4. Morphological reconstruction of the dorsal exoskeleton and postventral plates of *Brachyaglaspis singularis* gen. et sp. nov.: (a) dorsal; (b) left lateral; (c) frontal; (d) rear; and (e) ventral view of postventral plates.

this regard, the new taxon strongly differs from *T. unite* (Fortey & Rushton 2003, 2009); the latter species exhibits long postventral plates that are apparently fused medially and possess straight anterior and pointed posterior margins.

## 5. Discussion

A reconstruction of the dorsal exoskeleton and postventral plates of *Brachyaglaspis* is given in Figure 4. *Brachyaglaspis singularis* represents the

second confirmed aglaspidid euarthropod in the Fezouata biota (see Van Roy *et al.* 2010, fig. 2a) and, along with *T. unite* and *C. dubia*, the third unequivocal representative of this group formally described for the Ordovician (but see also Fortey & Theron 1994, fig. 6a; Ortega-Hernández, Legg & Braddy, 2013, p. 22). Although *Brachyaglaspis* increases the taxonomic diversity of Aglaspidida for this poorly known time interval of their history, the broader significance of this new euarthropod stems from its unusual morphology within the evolutionary context of the group (Fig. 5);

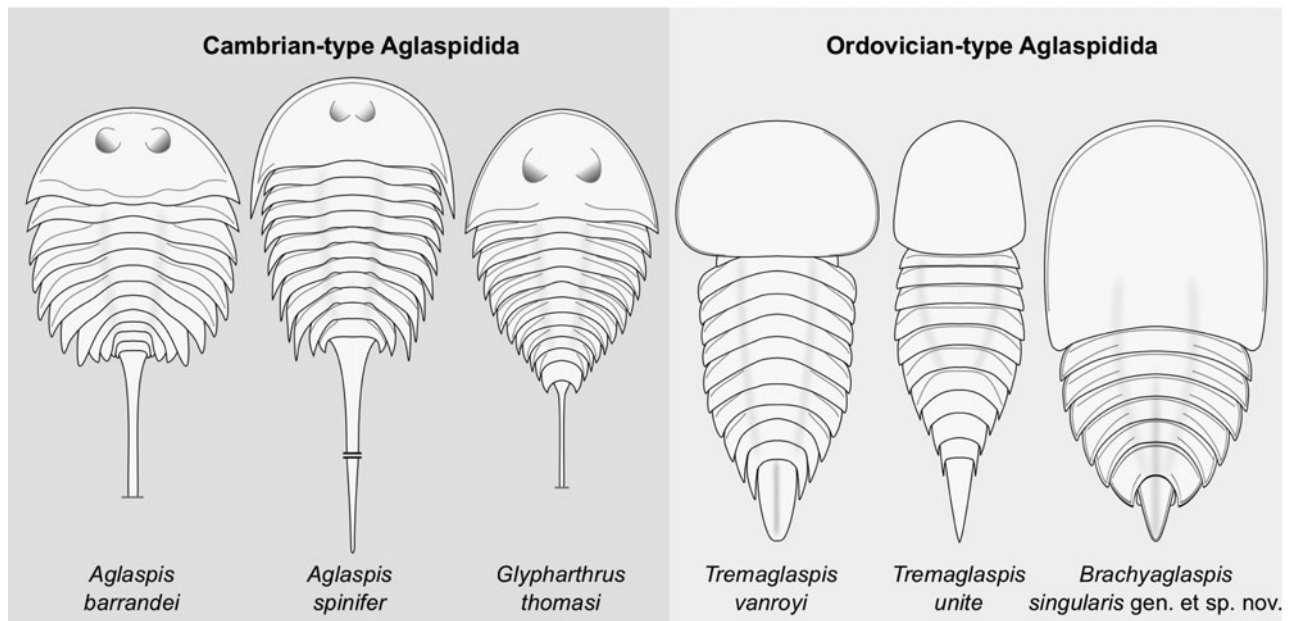


Figure 5. Comparison of aglaspidid euarthropod morphotypes (*sensu* Ortega-Hernández *et al.* 2013). Cambrian-type aglaspidids (left) are typified by the possession of 11 well-developed trunk tergites, dorsal sessile eyes, genal and pleural spines, and an elongate tailspine. By contrast, Ordovician-type aglaspidids (right) are characterized by an effaced cephalon, reduction or loss of dorsal eyes, rounded genal angles, reduced tergite count and a short tailspine (see text for discussion). Note that although *T. vanroyi* possesses 11 trunk tergites (Lerosey-Aubril *et al.* 2013), T1 is substantially reduced. *Brachyaglaspis singularis* gen. et sp. nov. represents the most extreme case of trunk tergite reduction among Ordovician-type aglaspidids known to date.

most aglaspidid species known from complete individuals possess 11 trunk tergites (e.g. Hesselbo, 1992; Ortega-Hernández *et al.* 2010), the exceptions being *T. unite* and *Tremaglaspis* sp. from the Fezouata biota that exhibit 10 trunk tergites only (P. Van Roy, unpub. thesis, Ghent University, 2006; Fortey & Rushton, 2009; Van Roy *et al.* 2010). The late Cambrian *T. vanroyi* Lerosey-Aubril, Ortega-Hernández & Zhu, 2013 possesses 11 trunk tergites, suggesting that this tergite count represents a symplesiomorphy for Aglaspidida, while the lower tergite counts observed in the Ordovician representatives of this genus and *Brachyaglaspis* represent derived conditions. In this regard, it is noteworthy that the presence of 11 trunk tergites is a widespread feature in phylogenetically basal early Palaeozoic euarthropod groups (e.g. Edgecombe, García-Bellido & Paterson, 2011; Lamsdell, 2013; Ortega-Hernández *et al.* 2015). The fact that *T. unite*, *Tremaglaspis* sp. from the Fezouata biota and *Brachyaglaspis* are restricted to Ordovician deposits raises the possibility of a trend towards reduction of the number of trunk tergites in post-Cambrian aglaspidids. However, considering that *T. unite* and the new taxon share other similarities (e.g. shape of cephalon, apparent absence of dorsal eyes), an alternative hypothesis could be that the trend to reduce the number of trunk tergites is restricted to a particular lineage within Aglaspidida. As argued above (see Section 4), it is unlikely that *Brachyaglaspis* represents a juvenile stage of a known aglaspidid species, including the co-occurring *Tremaglaspis* sp. However, the reduced tergite count in this otherwise rather large specimen (t.l. *c.* 6.9 cm) indicates that maturity was reached before the development of the full complement (at least

10) of tergites characterizing the aglaspidid trunk. This suggests that the evolution of this atypical morphology might have involved heterochronic processes – possibly some type of neoteny – considering the large size of the specimen. In the absence of a definite trunk tergite count for *Chlupacaris*, and with virtually no ontogenetic data on these extinct euarthropods, testing any of these evolutionary scenarios will unfortunately have to wait for further discoveries.

Regardless, *Brachyaglaspis* indicates that the body plan of aglaspidid euarthropods was much more variable than previously considered from the study of Cambrian representatives alone (see also Van Roy, 2006; P. Van Roy, unpub. thesis, Ghent University, 2006). This observation mirrors patterns of increased morphological disparity observed in trilobites slightly later during Middle Ordovician time (e.g. Foote, 1991; Hughes, 2007, p. 416–8), which suggests that the complex environmental and palaeoecological conditions resulting in the ‘Great Ordovician Biodiversification Event’ (e.g. Servais *et al.* 2010) also influenced the evolution of aglaspidid euarthropods. Soon after their appearance in the fossil record during the late Cambrian, aglaspidids greatly diversified morphologically and, as evidenced by *Brachyaglaspis*, this dynamic continued until (at least) Floian times. Such a pattern of diversification further underscores the variation in timing among different clades for the onset of a supposedly ‘Ordovician’ radiation event (Webby *et al.* 2004; Harper, 2006), something that has recently also been documented in several non-biomineralized clades (Van Roy *et al.* 2010; Van Roy, Briggs & Gaines, 2015; Van Roy, Daley & Briggs, 2015).

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