An aglaspidid arthropod from the Upper Ordovician of Morocco with remarks on the affinities and limitations of Aglaspidida

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ABSTRACT: A new aglaspidid arthropod, *Chlupacaris dubia* gen. et sp. nov., is described from the Pusgillian (lower Ashgill, Upper Ordovician) Upper Tiouririne Formation near Erfoud, southeastern Morocco. Although disarticulated, careful documenting of the tergites allows a reconstruction of the exoskeleton to be made. Although somewhat trilobite-like in appearance, the lack of facial sutures, a well-defined axis with articulating half-rings and a pygidium clearly prove *Chlupacaris* gen. nov. is not a trilobite. An interesting feature is the presence of a hypostome in this non-trilobite arthropod. In contrast to other aglaspidids usually considered to be carnivorous, a filter-feeding mode of life is proposed for *Chlupacaris* gen. nov., based on the strongly vaulted cephalon, subvertical orientation of the hypostome and less strongly vaulted trunk. *Chlupacaris* gen. nov. is probably most closely related to the atypical aglaspidid *Tremaglaspis unite* from the Tremadoc (Lower Ordovician) of the U.K., but it can also be tentatively linked to the problematic Lower Cambrian arthropods *Kodymirus vagans* and *Kockurus grandis* from the Czech Republic. The relevance and validity of previous definitions and of possibly significant characters used for identifying aglaspidids are evaluated, and as a result, a new combination of characters diagnosing Aglaspidida is proposed. Contrary to previous reports, it is suggested that aglaspidids are probably more closely related to trilobites than they are to chelicerates. This notion may be supported by the shared possession of a mineralised cuticle, a possibly similar number of cephalic appendages, and the presence of a hypostome in some forms, although this last character may alternatively be homoplastic.

KEY WORDS: Chelicerata, *Chlupacaris* gen. nov., hypostome, Trilobita, Upper Tiouririne Formation

Aglaspidids are a poorly known group of rare, Early Palaeozoic, arthropods. Although including a number of clearly distinct core-taxa, Aglaspidida as a clade are rather vaguely defined. Virtually all putative members are known only from dorsal exoskeletons, with just two undisputed specimens preserving ventral appendages in some detail. It is therefore not surprising that the inclusion of several fossils in Aglaspidida is equivocal, and that the wider systematic position of the group as a whole remains unclear. Aglaspidids were originally thought to be chelicerates and grouped together with xiphosurans and eurypterids in the probably paraphyletic 'Merostomata' (Raasch 1939; Størmer 1944, 1955; Novožilov 1962). However, a detailed study by Briggs *et al.* (1979) of the only specimen of *Aglaspis spinifer* Raasch, 1939, preserving appendages prompted their removal from Chelicerata. In recent cladistic analyses, their position tends to be rather fluid, but they consistently resolve as relatively basal arthropods (Wills *et al.* 1995, 1998; Dunlop & Selden 1998; Cotton & Braddy 2004). Although aglaspidids are most diverse in the Cambrian, a few younger putative representatives are known (e.g. Fortey & Rushton 2003). Additionally, a sizeable number of poorly-known, problematic and morphologically disparate Cambrian (e.g. Quilty 1971) and post-Cambrian (Chlupáč 1963, 1965, 1999a, b; Hong & Niu 1981; Hou & Bergström 1997) genera have also been allied with the Aglaspidida on questionable grounds.

This paper describes a new arthropod from the Ashgill (Upper Ordovician) of southeastern Morocco, which on the basis of current knowledge can be assigned to Aglaspidida, making it one of the youngest members of the group.

1. The aglaspidid problem

In part due to the very incomplete knowledge of aglaspidid morphology and anatomy, various authors have applied diverse definitions and characters to identify Aglaspidida. As a result, the aglaspidid concept has become very confused. Therefore, an overview of previous definitions of Aglaspidida is presented. Following this, the various characters applied to this group are evaluated, and this evaluation leads to a new character-set and emended diagnosis for Aglaspidida, which can be applied to test the position of the new arthropod and that of other supposed aglaspidids. Because of the problematic systematic position of aglaspidids and aglaspidid-like arthropods, and the related problem of uncertain homologies, the neutral terms 'cephalon' (or 'cephalic shield'), 'trunk' and 'tailspine', as used by Briggs *et al.* (1979) and Hesselbo (1989, 1992) are preferred over 'prosoma', 'opisthosoma' and 'telson', as used for aglaspidids by some recent authors (Dunlop & Selden 1998; Fortey & Rushton 2003). The terms 'prosoma' and 'opisthosoma' are traditionally reserved for chelicerates, and since close relationships between aglaspidids and chelicerates are far from proven, it seems prudent to reserve these terms for *bona fide* chelicerates only.

1.1. Previous definitions of Aglaspidida
In his monograph on North American Cambrian aglaspidids, Raasch (1939, p. 3) established Aglaspidida as: "... Merostomata having a phosphatic exoskeleton consisting of a longitudinally trilobed dorsal shield and a longitudinally cleft postventral plate". He further considered a pair of compound

eyes and twelve trunk segments to have been present, regarding the tailspine as a true somite. In his view, the aglaspidid trunk was subdivided into a preabdomen and a two or three segmented postabdomen. Størmer (1944, p. 135) defines the Order Aglaspidida as: "[X]iphosura with 11-segmented elongate abdomen. Posterior tergites may be anchylosed. Chelicera 4-segmented(?), abdominal telopodites but slightly reduced. Pretelsonic ventral plate present." Størmer (1955, p. 10) later modified his diagnosis of Aglaspidida to: "[X]iphosura with elongate, more or less vaulted body. Prosoma with prominent compound eyes. Opisthosoma with 11 or 12 segments, all free, or the posterior ones ankylosed into a shield; trilobation absent or indistinct. Telson with broad, powerful basal portion. Postventral plates below the posterior portion of the abdomen. ?Chelicera 4-jointed, other 5 prosomal appendages, as well as abdominal appendages, developed as short walking legs. Exoskeleton phosphatic, outer surface with variable granulation." This definition was subsequently adopted by Chlupáč (1965), while Novožilov (1962) also proposed a largely identical diagnosis. Based on their study of a single specimen of *Aglaspis spinifer* and another fossil originally thought to represent *A. barrandei* (Raasch 1939), but later placed in the genus *Flobertia* (Hesselbo 1992), Raasch (1939) and Størmer (1944, 1955) believed that aglaspidids had six pairs of cephalic appendages, the first being a 4-segmented chela. All post-cheliceral appendages were thought to be uniramous walking legs of similar construction. Raw (1957, p. 170) commented that aglaspidids: ". . . have an ovoid outline except for a great tail spine, a semicircular head shield with large posterolateral or genal spines, a pair of compound eyes and absence of facial sutures; but an abdomen of 11 free segments diminishing in width to the rear, and all with large falcate pleura; followed by the tailspine." He believed that the first cephalic appendages were four-segmented chelicerae and speculated that the other cephalic appendages most likely were uniramous walking legs, with the appendages of the trunk being developed into respiratory structures. This author rejected the division of the aglaspidid trunk into a pre- and postabdomen and considered the tailspine to be a true somite, being ". . . the development of the dorsal axial spine of a normal segment" (Raw 1957, p. 172). In his view, the postventral plates represented the moveable pleurae of this somite being folded under the tailspine to support it. Because of the supposed presence of a fused 'tailshield' in *Beckwithia* Resser, 1931, the separate Order Beckwithida was erected by Raw (1957) to contain this genus.

The work by Briggs *et al.* (1979) on the single specimen of *Aglaspis spinifer* preserving appendages showed that probably only four, or at most five appendage pairs were incorporated into the cephalon. The first pair was shown not to be chelate, but probably antenniform. After this first antennal pair, nine pairs of similar uniramous appendages consisting of five podomeres including the coxa, were identified. These findings prompted the removal of Aglaspidida from among the chelicerates. Weygoldt & Paulus (1979a, b) considered aglaspidids to possess chelicerae and preferred to retain the Aglaspidida in Chelicerata, regarding them as primitive sister taxon to all other chelicerates. Bergström (1980) also considered the removal of the aglaspidids from among the chelicerates as premature and regarded the nature of the aglaspidid first appendage pair as unsettled. However, Hesselbo (1992) confirmed the findings of Briggs *et al.* (1979) and further stressed (Hesselbo 1988, 1992) that at least twelve pairs of appendages including antennae were probably present. Like Raw (1957) and Briggs *et al.* (1979), Hesselbo (1992) also failed to find any evidence for the subdivision of the trunk into a pre- and postabdomen, and further showed (Hesselbo 1989) that the last tergites of *Beckwithia typa* Resser, 1931, were not fused into a 'tailshield' as suggested by Resser (1931) and accepted by Raasch (1939), Størmer (1944, 1955) and Raw (1957). In agreement with previous comments made by Raw (1957), Hesselbo (1992) further noted the total lack of cephalic ecdysial sutures in aglaspidids. An important finding by Hesselbo (1992) was the identification of a pair of elongate, protruding cuticular outgrowths on the anterior margins of the tergites of *Aglaspella granulifera* Raasch, 1939, *Aglaspis barrandei* Hall, 1862, *A. spinifer* Raasch, 1939, *Cyclopites vulgaris* Raasch, 1939, *Glyptarthrus vulpes* Raasch, 1939, *G. simplex* (Raasch, 1939) and *Flobertia kochi* Hesselbo, 1992. These so-called 'anterior tergal processes' probably served for muscle attachment and are ". . . seemingly unique to aglaspidids" (Hesselbo 1992, p. 918). Furthermore, as Raasch (1939) did in earlier work, Hesselbo (1992) identified postventral plates in *Aglaspella granulifera*, *Aglaspis spinifer*, *Aglaspoides sculptilis* Raasch, 1939, *Chraspedops modesta* Raasch, 1939, *Cyclopites vulgaris*, *Glyptarthrus simplex* and *Uarthrus instabilis* Raasch, 1939. Hou & Bergström (1997, p. 96) diagnosed a Subclass Aglaspidida, including the similarly-named Order Aglaspidida and the Order Strabopida, as follows: "[A]rtiopodans with mineralised exoskeleton, with eleven overlapping segmental tergites behind the head, and a tail spine. Uropods present. Feeding not through mud ingestion." In the caption to their fig. 4, Bergström & Hou (2003, p. 327) noted the following defining characters for Aglaspidida: "spine shaped telson, possibly 4 cephalic legs, possibly phosphatic exoskeleton". Dunlop & Selden (1998, p. 225) regarded aglaspidids as ". . . a morphologically distinct group characterised by an 11-segmented opisthosoma, postanal plates, a tail spine, and a carapace bearing genal spines", while Selden & Dunlop (1998, pp. 304–306) commented that "[A]glaspidids have a phosphatic exoskeleton and leglike appendages on both prosoma and opisthosoma. The carapace has genal spines and the lateral margins of the tergites curve strongly backward." Cotton & Braddy (2004) also regarded centrally positioned dorsal eyes and the presence of genal spines as indicative of aglaspidid affinity. Finally, Zhang & Shu (2005, p. 185) stated that "[A]glaspidids are characterised by a phosphatic exoskeleton with a pitted texture, 11 trunk tergites and a tail spine; the most distinct structure are the postventral plates (Hesselbo 1992, Dunlop & Selden 1997 [=Dunlop & Seldon 1998])". However, the same authors (Zhang & Shu 2005), believed that twelve tergites might be present in *Aglaspis barrandei* and *Glyptarthrus thomasi* (Walter, 1924).

1.2. Discussion of possible diagnostic aglaspidid characters

1.2.1. Mineralisation of exoskeleton.
Several authors state that the composition of the aglaspidid exoskeleton is phosphatic (Raasch 1939; Størmer 1944, 1955; Briggs & Fortey 1982; Selden & Dunlop 1998). This indeed often seems to be the case, but Fortey & Theron (1995) figured an undescribed aglaspidid-like arthropod with a calcified exoskeleton. It may therefore be too bold to attribute a phosphatic exoskeleton to *all* aglaspidids. Anyhow, the possession of a mineralised exoskeleton, of unspecified composition, seems to be a characteristic of aglaspidids but this character cannot be regarded as an autapomorphy of the clade, as it is shared with a number of other arthropods, such as trilobites, crustaceans and diplopods. It must be noted that *Kwanyinaspis maotianshanensis* Zhang & Shu, 2005, from the Lower Cambrian of Chengjiang, which is tentatively considered to be an aglaspidid by its authors, apparently lacks exoskeletal mineralisation.

1.2.2. Exoskeletal sculpture.
Although many aglaspidids display considerable exoskeletal sculpture, it actually varies

between genera, and aglaspidids without ornament are known (e.g. Fortey & Rushton 2003). Sculpture is also shared with a whole range of other arthropods, and since it was functional and probably related to the mode of life of the arthropod, its value for high-level systematics is questionable.

1.2.3. Absence of visible cephalic ecdysial sutures. This feature is in itself useful, but not always easy to verify in fossil material. Although visible ecdysial sutures are apparently lacking completely in most aglaspidids, the Early Ordovician aglaspidid *Tremaglaspis unite* Fortey & Rushton, 2003, probably has a hypostomal suture. The lack of visible ecdysial sutures is also encountered in extant horsehoe crabs, where during moulting the prosoma splits open along its anterior margin, allowing the new instar to emerge (Shuster & Sekiguchi 2003).

1.2.4. Dorsal eyes. Dorsal eyes are present in a whole range of euarthropods. Moreover, they may become secondarily lost, and therefore this character is of little use in identifying Aglaspidida. The putative aglaspidid *Kwanyinaspis maotianshanensis* may possess ventral eyes.

1.2.5. Genal and pleural spines. These are weak defining characters. Genal spines are present in a large number of arthropods and were repeatedly lost within various groups. Several core aglaspidids, like *Flobertia*, lack these structures. For the same reasons the presence or absence of pleural spines also is uninformative.

1.2.6. Dorsal trilobation. It is not certain that dorsal trilobation is present in all aglaspidids; in any case, it is usually rather weakly developed. Dorsal trilobation is also shared with a large number of other arthropod groups, including early Xiphosura.

1.2.7. Number of trunk tergites. Aglaspidids are generally considered to possess eleven trunk tergites, all with pleurae. However, it must be kept in mind that tergite numbers can vary, even between closely related taxa (Walossek & Müller 1998; Dunlop *et al.* 2004); as noted earlier, Zhang & Shu (2005) believed twelve tergites were actually present in at least some aglaspidids. Although the present author considers the evidence for this inconclusive, it nevertheless seems likely that tergite numbers may vary between different aglaspidid taxa. In any case, the presence of eleven trunk tergites cannot be used in isolation to define Aglaspidida, as other arthropods also exihibit an eleven-segmented trunk, e.g. basal xiphosurans.

1.2.8. Anterior tergal processes. So far, these elongate outgrowths on the anterior tergite margins have only been observed in core aglaspidids, and hence are a very strong synapomorphy for uniting the group. Unfortunately, the anterior tergal processes are relatively delicate structures, normally covered by the preceding tergite, which means that they are difficult to observe, unless the specimen is fragmented or disarticulated. This may be the reason why they have not been found in more aglaspidid-like arthropods.

1.2.9. Tailspine. All aglaspidids described to date have a tailspine. However, possession of a tailspine is a plesiomorphic character, shared with many other groups. It must also be noted that tailspines in different arthropods may not necessarily be homologous. While some tailspines may be genuine telsons, other, similarly shaped structures may have actually arisen in a way similar to the trilobite pygidium, i.e. through fusion of the telson with one or more true somites. Therefore, not every tailspine necessarily is a true telson and the indiscriminate use of 'telson' for all such structures should be avoided. As to the length of the tailspine, it is not believed to be of significant importance, for this attribute is governed by functional demands. It is also subject to intraspecific variation. For example, the extant *Limulus* has a long tailspine, while in many fossil synziphosurine xiphosurans this structure is much shorter. This is probably related to the reduced dorsoventral flexibility of xiphosurids, which, lacking a flexible opisthosoma, need to rely on the long tailspine to right themselves after overturning (Anderson & Selden 1997; Shuster & Anderson 2003).

1.2.10. Postventral plates. These structures are usually considered typical for aglaspidids, but very similar plates are also known from *Emeraldella brocki* Walcott, 1912 (Bruton & Whittington 1983; Hesselbo 1992; Wills *et al.* 1998; Cotton & Braddy 2004). However, this remains one of the better characters available to help in the identification of aglaspidids.

1.2.11. Configuration and organisation of appendages. This is obviously a character of great importance. The problem is, that appendages are only known incompletely from two unequivocal aglaspidids. Neither the number of appendages incorporated into the head tagma, nor the appendage count on the trunk is entirely certain. Furthermore, preservation of the appendages in the specimens is far from ideal, and although they seem to be very similar in both fossils, it cannot be ruled out that Aglaspidida as a whole exhibited more variation in appendage morphology. Whereas the postantennal appendages in *Aglaspis spinifer* and *Flobertia kochi* appear to be uniramous walking legs, the poorly known possible aglaspidids *Kwanyinaspis maotianshanensis* from the Cambrian of China and *Khankaspis bazhanovi* Repina & Okuneva, 1969, from the Cambrian of Siberia may possess filamentous exopods. The significance of these fossils is unclear, and they require further study. In conclusion, it can be said that, although appendage organisation is obviously of great importance, at present its practical diagnostic value for aglaspidids remains limited.

1.2.12. Differentiation of the trunk. Although in dorsal aspect aglaspidids do not exhibit any differentiation of the trunk, it is generally accepted that appendages are missing below the last three or four trunk tergites (Briggs *et al.* 1979; Hesselbo 1992; Cotton & Braddy 2004). This absence of posterior trunk appendages may correlate to the presence of postventral plates, which may actually represent modified appendages (see section 1.4). Although various arthropods, e.g. chelicerates, exhibit a differentiation of the trunk, the combination of an undifferentiated dorsal exoskeleton with a lack of appendages below the last three or four tergites may be unique to aglaspidids.

1.2.13. Feeding strategy. The fact that it is often very difficult to determine the mode of feeding and diet of a fossil arthropod means that this character is dubious, because it is based on interpretations rather than directly observable morphological characters. Moreover, this character is of very doubtful phylogenetic value at any rate: various feeding strategies exist in the same group of closely related arthropods, whilst similar feeding strategies may have arisen homoplastically.

1.3. A new aglaspidid character-set

From the discussion above, and pending a much-needed revision of aglaspidid-like arthropods, it is provisionally proposed that the best combination of character states to identify an aglaspidid are: (1) the possession of a mineralised exoskeleton; (2) the total absence of visible cephalic ecdysial sutures, with the possible exception of a hypostomal suture in some forms; (3) the possession of anterior tergal processes; (4) the presence of four or five pairs of cephalic appendages, the first pair being antenniform, and all postantennal appendages of similar construction and probably consisting of five podomeres including the coxa; (5) the absence of appendages below the undifferentiated final three or four trunk tergites;

Table 1 List of taxa that have been considered aglaspidids at some point, provisionally recognising three groups: (1) the aglaspidid core taxa or 'Aglaspidida *s.s.*'; (2) the 'aglaspidid-like arthropods', an informal group of arthropods showing similarities to Aglaspidida *s.s.*, but for which definite proof of their Aglaspidida *s.s.* affinity is lacking; (3) 'non-aglaspidid arthropods' containing all fossils definitely rejected from the Aglaspidida *s.s.* and not considered to be directly related to any of the aglaspidid-like arthropods. For further explanations see text.

Aglaspidida *s.s.*	Aglaspidid-like arthropods
Aglaspella granulifera, Cambrian, Wisconsin	*Aglaspella eatoni*, Cambrian, Wisconsin
Aglaspis barrandei, Cambrian, Wisconsin	*Aglaspis? dorsetensis*, Cambrian, Wisconsin
Aglaspis spinifer, Cambrian, Wisconsin	*Aglaspis? franconensis*, Cambrian, Wisconsin
Aglaspoides sculptilis, Cambrian, Wisconsin	*Aglaspoides semicircularis*, Cambrian, Wisconsin
Chlupacaris dubia, Ordovician, Morocco	*Angarocaris angarensis*, Ordovician, Siberia
Chraspedops modesta, Cambrian, Wisconsin	*Angarocaris? exculptus*, Ordovician, Siberia
Cyclopites vulgaris, Cambrian, Wisconsin	*Angarocaris? nodus*, Ordovician, Siberia
Flobertia kochi, Cambrian, Wisconsin	*Angarocaris padunensis*, Ordovican, Siberia
Glyptarthrus simplex, Cambrian, Wisconsin	*Angarocaris? spinosus*, Ordovician, Siberia
Glyptarthrus vulpes, Cambrian, Wisconsin	*Angarocaris tschekanowskii*, Ordovician, Siberia
Tremaglaspis unite, Ordovician, Wales	*Angarocaris* sp. 1, Ordovician, Siberia
Uarthrus instabilis, Cambrian, Wisconsin	*Angarocaris* sp. 2, Ordovician, Siberia
	Angarocaris sp. 3. Ordovician, Siberia
	Beckwithia? daubikhensis, Cambrian, Siberia
	Beckwithia? major, Cambrian, Wisconsin
	Beckwithia typa, Cambrian, Utah
	Caryon bohemicum, Ordovician, Bohemia
	Chacharejocaris punctatus, Ordovician, Siberia
	Chacharejocaris? novaki, Ordovician, Bohemia
	Drabovaspis complexa, Ordovician, Bohemia
Non-aglaspidid taxa	*Emeraldella brocki*, Cambrian, British Columbia
	Girardevia musculus, Ordovician, Siberia
Lemoneites ambiguus, Ordovician, New Mexico (glyptocystitid echinoderm)	*Girardevia tungussensis*, Ordovician, Siberia
Lemoneites gomphocaudatus, Ordovician, New Mexico (glyptocystitid echinoderm)	*Glyptarthrus thomasi*, Cambrian, Wisconsin
Lemoneites cf. *gomphocaudatus*, Ordovician, New Mexico (glyptocystitid echinoderm)	*Intejocaris maximus*, Ordovician, Siberia
Lemoneites mirabilis, Ordovician, New Mexico (glyptocystitid echinoderm)	*Khankaspis bazhanovi*, Cambrian, Siberia
Lemoneites cf. *mirabilis*, Ordovician, New Mexico (glyptocystitid echinoderm)	*Kockurus grandis*, Cambrian, Bohemia
Lemoneites simplex, Ordovician, New Mexico (glyptocystitid echinoderm)	*Kodymirus vagans*, Cambrian, Bohemia
Neostrabops martini, Ordovician, Ohio (cheloniellid arthropod)	*Kwanyinaspis maotianshanensis*, Cambrian, China
Schamanocaris? sp. 1, Ordovician, Siberia (problematic arthropod, retifaciid?)	*Obrutschewia sergeji*, Ordovician, Siberia
Schamanocaris? sp. 2, Ordovician, Siberia (problematic arthropod, retifaciid?)	*Parapaleomerus sinensis*, Cambrian, Yunnan
Triopus draboviensis, Ordovician, Bohemia (cheloniellid arthropod)	*Paleomerus hamiltoni*, Cambrian, Sweden
Unnamed arthropod, Quilty (1971), Cambrian, Tasmania (problematic arthropod)	*Paleomerus makowskii*, Cambrian, Poland
	Quasimodaspis brentsae, Cambrian, Nevada
	Schamanocaris krascheninnikowi, Ordovician, Siberia
	Setaspis spinulosis, Cambrian, Wisconsin
	Setaspis regularis, Cambrian, Wisconsin
	Sinaglaspis xiashanensis, Carboniferous, Shanxi
	Strabops thacheri, Cambrian, Missouri
	Tuboculops fragilis, Cambrian, Wisconsin
	Zonozoe drabowiensis, Ordovician, Bohemia
	Zonoscutum solum, Ordovician, Bohemia
	Unnamed arthropod, Jago & Baillie (1992), Cambrian, Tasmania
	Unnamed arthropod, figure 6 in Fortey & Theron (1995), Silurian, China

(6) the possession of postventral plates. Although generally less informative, to this set may be added: (7) all trunk tergites with pleurae; and (8) the trunk terminating in a tail spine. With the probable exception of anterior tergal processes and the lack of appendages below the undifferentiated terminal tergites, none of these characters taken separately is unique to aglaspidids. Hence, a more or less reliable indication of aglaspidid affinity requires a combination of at least part of this set. Applying this provisional aglaspidid character-set enables a group of aglaspidid core taxa, the Aglaspidida *sensu stricto*, to be tentatively recognised. These Aglaspidida *sensu stricto* are listed in Table 1.

1.4. The postventral plates, tailspine and posterior differentiation of the aglaspidid trunk

Although Raw's (1957) interpretation of the postventral plates as the moveable pleurae of the tailspine is quite clearly untenable, there continues to exist some confusion about the construction of these structures. They are usually believed to be composed of two separate plates joined by arthrodial membrane (e.g. Briggs *et al.* 1979; Hesselbo 1992), but Fortey & Rushton (2003) argued that this structure in fact consists of only one single, rigid plate. Still, even if this ventral structure represents only a single plate, the present author considers it to

have arisen from the fusion of two, originally separate plates. Therefore, the term 'postventral plates', in plural, is used here for the entire structure.

The function of the postventral plates is problematic. They may have served for muscle attachment, possibly associated with musculature of the tailspine, and even a respiratory function has been contemplated (Hesselbo 1992; Raasch 1939).

The great similarity of the aglaspidid postventral plates to those of *Emeraldella* was noted by various authors (e.g. Bruton & Whittington 1983; Briggs 1990; Briggs & Fortey 1992; Hesselbo 1992; Wills *et al.* 1998; Cotton & Braddy 2004). Briggs & Fortey (1992) considered this to be due to homoplasy, but Wills *et al.* (1998) believed that both structures might be homologous. Edgecombe & Ramsköld (1999) further considered the postventral plates of *Emeraldella* to be homologous to the uropods of *Sidneyia*. Cotton & Braddy (2004) in turn suggested that all these structures may be homologous with the cheloniellid furcae. The homology of the cerci of the trilobite *Olenoides serratus* Walcott, 1912 (Whittington 1980) is unclear and complicated by the fact that in trilobites cerci are known *only* from *Olenoides*. Therefore, the homology of these cerci to the other caudal structures discussed here was considered dubious by Cotton & Braddy (2004).

It seems likely that the postventral plates were derived from the transformation and subsequent fusion of the appendage pair of the last trunk somite. Usually, the aglaspidid postventral plates are considered to have arisen from the modification of the appendage pair belonging to the last tergite with pleurae (e.g. Cotton & Braddy 2004). However, the potentially homologous postventral plates of *Emeraldella* (Bruton & Whittington 1983), the uropods of *Sidneyia* (Bruton 1981) and the cheloniellid furcae (Stürmer & Bergström 1976; Cotton & Braddy 2004) all belong to the terminal *cylindrical* somite of the trunk, present in these arthropods. If the homology of the aglaspidid postventral plates with these structures is accepted, the aglaspidid postventral plates would probably not belong to the last tergite with pleurae, but originate from a cylindrical somite succeeding these tergites. Because aglaspidids seemingly lack such cylindrical somites, this may indicate that the pair of cylindrical somites of *Emeraldella* may have actually become incorporated into the aglaspidid tailspine. As a consequence, the tailspine of aglaspidids would have formed through the fusion of the tailspine (possibly a true telson) of *Emeraldella* with the preceding cylindrical sclerites. This proposal is not entirely new: Raasch (1939) already suggested that the aglaspidid tailspine may be the result of the fusion between the telson and the preceding trunk somite. A parallel example of the fusion of trunk somites with the telson into a single structure is provided by the trilobite pygidium.

If the postventral plates played a role as attachment points for musculature of the tailspine, the fusion of the cylindrical somites of an *Emeraldella*-like arthropod into the tailspine in aglaspidids would require the postventral plates to be moved forward, to a position partially under the last tergites with pleurae. This displacement would necessitate the reduction of the appendages of the somites immediately in front of the fused tailspine. The number of appendage pairs that would be affected by the displacement is not entirely clear. Hesselbo (1988) argued for the presence of at least twelve pairs of appendages in aglaspidids. Because a maximum of five pairs of appendages belong to the cephalon (Briggs *et al.* 1979; Hesselbo 1992), in an aglaspidid with a trunk composed of eleven somites, this means that at most the last four appendage pairs of the trunk were lost. If, however, Walossek & Müller's (1998) argument for the presence of only four pairs of appendages in the aglaspidid head is accepted, at most only the

three last appendage pairs may be lost in aglaspidids with an eleven-segmented trunk.

1.5. The status of aglaspidid-like arthropods

The limited knowledge of aglaspidid morphology and anatomy, and the resulting vague definition of this group made Aglaspidida a bucket taxon for various problematic arthropods. This is exemplified by an unnamed Middle Cambrian arthropod from Tasmania briefly described by Quilty (1971). This small fossil has a sharp trapezoidal to triangular cephalon, a trunk composed of eight tergites and a spinose tailshield. Although this arthropod does not show even a superficial resemblance to any known aglaspidid, Quilty (1971, p. 21) considered it as "... probably belonging to the Order AGLASPIDA Walcott." The Late Ordovician cheloniellid arthropods *Neostrabops martini* Caster & Macke, 1952, and *Triopus draboviensis* Barrande, 1872 (Chlupáč 1965) were in the past also placed in Aglaspidida. Several other problematic fossils are also included in Aglaspidida on the basis of a superficial resemblance rather than a more or less reliable character combination; a classic example is the Carboniferous *Sinaglaspis xiashanensis* Hong & Niu, 1981. However, the evidence for aglaspidid affinity is also somewhat circumstantial for *Aglaspella eatoni* (Whitfield 1880), *Aglaspoides semicircularis* Raasch, 1939, *Beckwithia typa*, *Glyptarthrus thomasi* (Walter 1924), *Quasimodaspis brentsae* Waggoner, 2003, an unnamed Late Cambrian Tasmanian arthropod (Jago & Baillie 1992), and fossils known only from isolated, often fragmentary sclerites, such as *Aglaspis? dorsetensis* (Raasch 1939), *A? franconensis* (Raasch 1939), *Beckwithia? major* (Graham 1931), *Setaspis spinulosis* Raasch, 1939, *S. regularis* Raasch, 1939, *Tuboculops fragilis* Hesselbo, 1992, and the more tentatively assigned problematic cephala of *Caryon bohemicum* Barrande, 1872, *Chacharejocaris? novaki* Chlupáč, 1963, *Drabovaspis complexa* (Barrande 1872), *Zonozoe draboviensis* Barrande, 1872 (Chlupáč 1963, 1965, 1999b) and *Zonoscutum solum* Chlupáč, 1999a. Other, extremely poorly known arthropods often considered as aglaspidids (e.g. Hou & Bergström 1997) on the basis of a very general resemblance include the Ordovician genera *Angarocaris* Černyšev, 1953, *Chacharejocaris* Černyšev, 1945, *Girardevia* Andreeva, 1957, *Intejocaris* Černyšev, 1953, *Obrutschewia* Černyšev, 1945 and *Schamanocaris* Černyšev, 1945. *Schamanocaris krascheninnikowi* Černyšev, 1945 was described on the basis of isolated cephala only. Černyšev (1945) further attributed a number of isolated trunks to *Schamanocaris* in a questionable, and rather arbitrary, way. These trunks show a very large, probably fused, shield-like terminal sclerite that possibly preceded a long, moveable, styliform telson. Such an arrangement would seem to preclude an aglaspidid affinity for these specimens, possibly allying them with *Retifacies abnormalis* Hou, Chen & Lu, 1989, from the Lower Cambrian of Chengjiang. Novožilov (1962) considered *Angarocaris* to be a paleomerid, whilst regarding the other poorly-known genera *Obrutschewia*, *Chacharejocaris* and *Intejocaris* as Aglaspidida *incertae sedis*. The same author placed *Girardevia*, known only from its isolated cephalon, in the Aglaspidida. Although some of the mentioned Russian arthropods may have had mineralised exoskeletons (Hou & Bergström 1997) and may belong to the Aglaspidida, the present author considers that none of them is presently known well enough to allow any further systematic placement. Although more completely preserved, this also holds true for the aglaspidid-like Cambrian arthropods *Khankaspis bazhanovi* and *Beckwithia? daubikhensis* Repina & Okuneva, 1969. Cotton & Braddy (2004) regarded *Khankaspis* as a probable aglaspidid, because this taxon possesses central dorsal eyes and genal spines, but, as shown above, these

characters are useless as indicators of aglaspidid affinity. Of the putative aglaspidids from Russia, *Khankaspis* is by far the most important, because it may possibly show the presence of filamentous exopods on the trunk appendages. In this regard, restudy of the available material is urgently needed. Another arthropod deserving separate mention is the recently described *Kwanyinaspis maotianshanensis* Zhang & Shu, 2005, from the Lower Cambrian of Chengjiang. This fossil, which was tentatively regarded by the authors as an aglaspidid, is particularly significant because it shows exceptionally well-preserved biramous appendages. These consist of a gnathobasic basis carrying a seven-segmented endopod and a large, trilobite-like, flap-shaped exopod. The distal part of the endopod is similar to the incompletely preserved walking legs of the aglaspidids *s.s. Aglaspis spinifer* and *Flobertia kochi*. If *Kwanyinaspis* indeed proves to be an aglaspidid, the unequivocal presence of trilobite-like exopods is highly significant. However, as Zhang & Shu (2005) themselves admit, the assignment of *Kwanyinaspis* to Aglaspidida is based on a general resemblance to *Aglaspis* only. The evidence for the presence of postventral plates in *Kwanyinaspis* is highly tenuous at best; additionally, it does not show any evidence of anterior tergal processes and lacks exoskeletal mineralisation. Therefore, *Kwanyinaspis* is best regarded as an arthropod of uncertain affinity. The possession of ventral eyes in *Kwanyinaspis* is likely a plesiomorphic character state (Hou & Bergström 1997; Edgecombe & Ramsköld 1999), and this arthropod therefore may occupy a position basal to the Aglaspidida *s.s.*

Whilst some authors were happy to accept aglaspidid affinities for certain fossils on a sometimes questionable basis, others have excluded taxa on equally tenuous grounds. Bergström (1971) excluded *Paleomerus* Størmer, 1956 and *Strabops* Beecher, 1901 from the Order Aglaspidida on the basis that the head tagma was too short to accomodate the six pairs of appendages then assumed to be present in aglaspidids. Tetlie & Moore (2004) argued that even the maximum number of appendages considered possible by Bergström (1971) was probably too high. Since nothing is known about the appendages of either genus, this argument is speculative. In *Cheloniellon calmani* Broili, 1932, for example, five pairs of appendages are crowded together under a very short cephalon (Stürmer & Bergström 1978). Briggs *et al.* (1979) and Hesselbo (1992) have shown that less appendages are incorporated into the head of the aglaspidid *Aglaspis spinifer* than originally thought, which further weakens Bergström's (1971) argument. Hou & Bergström (1997) included *Paleomerus* and *Strabops* in their Subclass Aglaspidida, but excluded them from the Order Aglaspidida, placing them in their Order Strabopida on the same equivocal basis. Dunlop & Selden (1998, p. 229) removed *Paleomerus* and *Strabops* from Aglaspidida because ". . . they lack aglaspidid apomorphies (e.g. genal spines)." The criteria used by these authors have been discussed previously, and if rigorously applied, for example, *Flobertia*, one of only two undoubted aglaspidids preserving appendages, would have to be removed from Aglaspidida. Nevertheless, Tetlie & Moore (2004, p. 197) apparently accepted Dunlop & Selden's (1998) argument, noting that "[T]his conclusion is supported by the presence of a short, triangular telson in *Paleomerus*, which is in contrast to the long styliform telson of aglaspidids (Hesselbo 1992)". As shown above, the length of the tailspine is in no way a reliable indicator for aglaspidid affinity. Whilst Tetlie & Moore (2004) place *Paleomerus* and *Strabops* in Hou & Bergström's (1997) Order Strabopida, they do not mention that the same authors placed this order in their Subclass Aglaspidida; in the end Tetlie & Moore (2004) conclude that the phylogenetic position of strabopids is uncertain. Shuster & Anderson (2003), on the other hand, did consider *Paleomerus*

to be an aglaspidid. The present author does not want to argue that *Paleomerus* and *Strabops* are aglaspidids; the point made here is that these fossils are very poorly known and that there are as many (weak) arguments for including these genera in the Aglaspidida as there are for excluding them. They are currently best regarded as aglaspidid-like arthropods of further uncertain affinity.

Two other arthropods that deserve to be mentioned are *Kodymirus vagans* Chlupáč & Havlíček, 1965, and the very similar but less well-known *Kockurus grandis* Chlupáč, 1995, from the Lower Cambrian of Bohemia. Both these arthropods have a ventral plate attached to the cephalic doublure that is remarkably similar to the hypostome of trilobites. Because the homologies between the trilobite hypostome and the labrum in other arthropods are largely unresolved, the term hypostome is here used in a broad sense as defined by Cotton & Braddy (2004), i.e. indicating any posteroventral extension of the pre-segmental acron into a sclerotised plate covering the mouth. Chlupáč & Havlíček (1965), interpreting the hypostome as an epistoma, considered *Kodymirus* an aglaspidid, with possible affinities to eurypterids. These authors also figured an isolated incomplete subcircular structure which they considered to belong to *Kodymirus* and which they believed might represent a metastoma or possibly a postventral plate. Hesselbo (1992) questioned the aglaspidid affinity of *Kodymirus* because of the presence of a hypostomal plate. After the discovery of slender, spinose appendages superficially resembling eurypterid legs in *Kodymirus*, Chlupáč (1995) considered this arthropod to be a 'protostylonuroid' eurypterid. The support provided by Chlupáč & Havlíček (1965) and Chlupáč (1995) for a eurypterid affinity for *Kodymirus* is extremely weak: although a large quantity of material of *Kodymirus* has been collected, not one single convincing metastoma, genital operculum or genital appendage has been found. Therefore, the assignment of *Kodymirus* to the Eurypterida is rejected. Likewise, the presence of a very large attached hypostome in the atypical Early Ordovician aglaspidid *Tremaglaspis* (Fortey & Rushton 2003), and in the new Late Ordovician Moroccan aglaspidid described here, shows that Hesselbo's (1992) objections against the inclusion of *Kodymirus* in the Aglaspidida are unjustified. The shared possession of a single row of median dorsal spines in *Kodymirus*, *Kockurus* and *Beckwithia* is also noteworthy. However, for the moment, the importance of this shared possession of spines is unclear, while the presence of twelve or more (Dunlop & Selden 1998) somites in *Kodymirus* and *Kockurus* and the appendage morphology of these taxa could militate against an aglaspidid affinity. Pending further study, *Kodymirus* and *Kockurus* are for now best regarded as closely-related aglaspidid-like arthropods of uncertain affinity.

A striking similarity between aglaspidids and *Emeraldella* is the shared presence of postventral plates and, as already discussed, it seems very likely that these structures are homologous. If the argument presented earlier that the tailspine of aglaspidids is homologous to the tailspine + the two cylindrical sclerites of *Emeraldella* is accepted, it significantly further reduces the perceived morphological gap between *Emeraldella* and Aglaspidida. Still, important differences exist between the appendages of *Emeraldella* and aglaspidids. *Emeraldella* has six pairs of cephalic appendages, with all postantennal appendages being biramous. The endopods appear to consist of six podomeres, and the exopods are of different construction in the cephalic and trunk appendages. Hou & Bergström (1997) questioned the reconstruction of the appendages of *Emeraldella* by Bruton & Whittington (1983), whilst Edgecombe & Ramsköld (1999) presented a new reconstruction of the trunk exopods of this arthropod. For the purpose of this discussion, it must be kept in mind that our

knowledge of aglaspidid appendages is very limited. *Khankaspis* (Repina & Okuneva 1969), and possibly *Kwanyinaspis*, leave open the possibility that aglaspidid appendages were biramous, the apparent lack of exopods in *Aglaspis* and *Flobertia* possibly being a taphonomic artefact. Because of the uncertain affinities of *Kwanyinaspis*, the significance of the differences between the exopods of this arthropod and those of *Emeraldella* is unclear. Therefore, the appendages of *Emeraldella* may be more like those of aglapidids than generally realised.

Concluding this discussion, and applying the provisional aglaspidid character-set presented in the previous section, an informal group of 'aglaspidid-like arthropods', summarised in Table 1, can be recognised. These aglaspidid-like arthropods are considered to include any arthropod resembling Aglaspidida *s.s.* in general aspect, but this does not automatically imply a close relationship to this clade. The group of aglaspidid-like arthropods may contain taxa that belong in the Aglaspidida *s.s.* but for which definite evidence of their affinity is lacking, and similar forms that may be, but not necessarily are, closely related. Table 1 further lists the fossils that are unequivocally rejected as aglaspidids.

1.6. Systematic position of aglaspidids and aglaspidid-like arthropods

Due to our limited data on aglaspidids and aglaspidid-like arthropods, establishing their systematic relationships has proven problematic and the placement of these fossils shows appreciable mobility in cladistic analyses. The largely pectinate cladogram presented by Briggs & Fortey (1989, 1992) and Briggs (1990) shows *Emeraldella* and *Aglaspis* in a position basal to the chelicerates, trilobites and megacheiran taxa included in the analyis. In a rather contentious paper on chelicerate phylogeny, Starobogatov (1990) included *Beckwithia, Paleomerus* and *Strabops* in the Chelicerata, considering these taxa as 'lower xiphosurans'. In the cladogram proposed by Briggs *et al.* (1992), *Emeraldella* and *Sidneyia* are the most basal arachnomorph taxa, with *Aglaspis* as the sistertaxon of a clade including *Molaria* Walcott, 1912, *Sanctacaris* Briggs & Collins, 1988, *Yohoia* Walcott, 1912, *Sarotrocercus* Whittington, 1981, *Burgessia* Walcott, 1912, and chelicerates. In the 50% majority rule consensus tree including both fossil and extant taxa by Wills *et al.* (1995, 1998), *Emeraldella* is sister to a clade containing *Aglaspis, Cheloniellon*, Chelicerata and megacheiran arthropods. Within this clade, *Aglaspis* is basal to a subclade of *Cheloniellon+* chelicerates. The synapomorphies uniting *Aglaspis* with *Cheloniellon*+Chelicerata are the following: (1) cuticle tuberculate; (2) cuticle trilobed; (3) cardiac lobe present; (4) inner rami of trunk appendages spinose. The support for this grouping is weak: the limited usefulness of the first two characters has already been outlined above, whilst the presence of a cardiac lobe in aglaspidids is questionable; even in early xiphosurans this character is weakly developed or even absent (Selden & Drygant 1987). Endopod spinosity is a functional feature of the appendages and encountered in a whole range of arthropods, as Wills *et al.* (1998) themselves concede. When Wills *et al.* (1998) repeated the analysis, coding only fossil taxa, *Aglaspis* and *Cheloniellon* formed a clade basal to all other included arachnomorph taxa. *Emeraldella* is situated higher up, basal to a clade of *Molaria* Walcott 1912+trilobites. In their analysis of chelicerate origins and relationships, Dunlop & Selden (1998) included *Paleomerus, Strabops* and *Aglaspis*. They favoured a cladogram in which *Aglaspis* is sister to *Paleomerus/Strabops*, these taxa forming a sister group basal to all other taxa in their analysis. They did however concede

that: "[T]he position of Aglaspidida relative to the other taxa in the analysis is difficult to resolve. It is equally parsimonious to place aglaspidids as sister group to either *Paleomerus/Strabops* or the Chelicerata and aglaspidids share no synapomorphies with any of these groups." These authors also regarded *Paleomerus/Strabops* as ". . . a primitive stem group from which Chelicerata, Aglaspidida and Cheloniellida can be derived" and ". . . perhaps the best model of a primitive arachnomorph." (Dunlop & Selden 1998, p. 229). Hou & Bergström (1997) also included *Emeraldella*, Strabopida and Aglaspidida in their own, somewhat controversial analysis, in which they rejected parsimony for reconstructing evolutionary relationships. Apart from the questionable characters and methodology (see e.g. Briggs 1998) used for their analysis, and the fact that they rather confusingly used the name Aglaspidida for *both* a subclass and an order, one thing is noteworthy about their results. Whilst Hou & Bergström (1997) place the Orders Aglaspidida and Strabopida together in the Subclass Aglaspidida, in their cladogram, Aglaspidida (probably referring to the Order?), and Chelicerata are placed as sister taxa to an unresolved clade containing Cheloniellida, Strabopida, *Sidneyia* and *Emeraldella*. Hence, according to their own cladogram, their Subclass Aglaspidida is blatantly paraphyletic. In the cladogram presented by Bergström & Hou (2003), aglaspidids form a clade together with the chelicerates and *Cheloniellon* united by the dubious character 'dorsal eyes fairly close to axis'. *Sidneyia* is the primitive sistertaxon of this group, which in turn is sister to a clade containing *Emeraldella, Retifacies*, the marrellomorphs, trilobites and trilobite-related arthropods. Cotton & Braddy (2004) coded *Emeraldella, Paleomerus* and a generalised aglaspidid for their analysis of arachnomorph phylogeny. Unfortunately, their analysis also includes *Lemoneites* Flower, 1968, which was recently shown to be a fragment of a glyptocystitid cystoid echinoderm (Moore & Braddy 2005). To account for the uncertainty regarding the presence or absence of exopods on the post-antennal appendages in aglaspidids, Cotton & Braddy (2004) employed two codings for the generalised aglaspidid. They found that *Emeraldella, Paleomerus* and the generalised aglaspidid formed a clade with *Sidneyia* and *Cheloniellon* (and the echinoderm fragment *Lemoneites*). Four different, equally parsimonious topologies were found for this clade, causing a collapse into an unresolved polychotomy in the strict consensus of their 27 most parsimonious trees. After eliminating *Paleomerus* and the non-arthropod *Lemoneites* from the analysis and treating characters as unordered, they found only one topology for this clade, regardless of the coding used for Aglaspidida. The same analysis with some characters ordered resulted in three of the six most parsimonious solutions for the clade also yielding the same result. Therefore, Cotton & Braddy (2004) preferred this topology over the three other most parsimonious solutions. This favoured topology for the clade is compatible only with a relationship of the form *Emeraldella* (*Sidneyia* (*Cheloniellon* (Aglaspidida (*Paleomerus+Lemoneites*)))), uniting Aglaspidida and *Paleomerus* on the shared possession of a mineralised cuticle. It forms the sister group to another clade containing the paraphyletic Megacheira and Chelicerata. Synapomorphies uniting these two clades are: (1) exopod of the second segment absent or much reduced; (2) head consisting of five segments; and (3) absence of posterior reduced segments with reduced appendages. Again, the first two characters do not appear to be very robust. As shown previously, the post-antennal appendages of aglaspidids are too poorly known to be sure that exopods are truly lacking, while the number of appendages expressed in the head of an arthropod is an unreliable indication of the true number of segments incorporated into the head; moreover,

only four pairs of appendages may be present on the aglaspidid head (Briggs *et al.* 1979; Walossek & Müller 1998). However, the third character may be phylogenetically significant.

The foregoing discussion shows that, although generally lacking support from robust synapomorphies, aglaspidids and a number of aglaspidid-like arthropods have usually been considered as lying near, or belonging to the chelicerate stem group. This general tendency may in part be a result of the marked influence of the views expressed by Størmer (1944, 1955) and Weygoldt & Paulus (1979a, b) on subsequent authors. However, Chen *et al.* (2004) found evidence for a clade of anomalocaridids, megacheirans and chelicerates, characterised by the possession of a first pair of raptorial 'great appendages', homologous to the first antennae of other arthropods. Scholtz & Edgecombe (2005) also considered the antennae of the mandibulate taxa and of trilobites and the closely related naraoiids, helmetiids, tegopeltids and xandarellids to be homologous to the chelicerate chelicerae and megacheiran 'great appendages'. Although the proposals of Chen *et al.* (2004) and Scholtz & Edgecombe (2005) differ in their interpretation of the origins of these appendages, they both support a basal split between chelicerates and antennate arthropods. Neither of these schemes seems to leave a place for aglaspidids basal to Chelicerata. Instead, Aglaspidida would be located higher up in the tree and closer to the trilobites. In this respect, we note that in some analyses, *Emeraldella*, which as argued may be more aglaspidid-like than thought, appears at the base of the trilobite clade. A possible trilobite-aglaspidid relationship has been mentioned before (e.g. Briggs *et al.* 1979; Raasch 1939), and may be supported by their common possession of: (1) a mineralised cuticle; (2) a similar number of head appendages, the first antenniform; (3) all post-antennal appendages of similar, undifferentiated construction; (4) a hypostome in some aglaspidids. A mineralised (calcified) cuticle is generally considered a very strong trilobite apomorphy, but as pointed out above also evolved in parallel in crustaceans and diplopods. Walossek & Müller (1998) considered aglaspidids to possess only four pairs of cephalic appendages, a condition which they believed to represent the plesiomorphic state of the euarthropod head. The phylogenetic position of the marrellomorphs *Marrella splendens* Walcott, 1912 and *Mimetaster hexagonalis* Gürich, 1931, may prove problematic for this interpretation, the former having only two pairs of cephalic appendages, the latter only three pairs. Therefore, Cotton & Braddy (2004) considered the presence of four pairs of cephalic appendages rather representative of the plesiomorphic state of the euarthropod crown group. Still, the proposed very basal split between 'great appendage' arthropods, which include the extant chelicerates, and antennate arthropods, which include all other extant euarthropods (Chen *et al.* 2004; Scholtz & Edgecombe 2005), seems to draw the marrellomorphs firmly into the euarthropod crown. This apparently contradicts the idea of a plesiomorphic four-segmented euarthropod head, even if this plesiomorphy is restricted to the euarthropod crown as proposed by Cotton & Braddy (2004). In this respect, it is important to note that a possible third marrellomorph, *Vachonisia rogeri* Lehmann, 1955, which emerged as the most basal marrellomorph taxon in the analysis of Wills *et al.* (1995, 1998), indeed has four cephalic appendages (Stürmer & Bergström 1976). One can therefore argue that the lower number of cephalic appendages in *Marrella* and *Mimetaster* is secondarily derived, saving the idea of a plesiomorphic four-segmented euarthropod (crown?) head. Still, in this context, it is important to note that the marrellomorph affinity of *Vachonisia* is not entirely undisputed (e.g. Hou & Bergström 1997). So, if Walossek & Müller's (1998) proposal is accepted, the shared presence of four

appendage pairs in aglaspidids and trilobites would represent a plesiomorphic state, and thus be of limited use in uniting both groups. It must, however, be pointed out that Briggs *et al.* (1979) did not exclude the possibility that five pairs of cephalic appendages might be present in aglaspidids. Trilobites may have the same number of cephalic appendages, possibly linking both groups: Bergström & Brassel (1984) identified four post-antennal cephalic appendages in the Devonian trilobite *Rhenops* Richter & Richter, 1943, and Edgecombe & Ramsköld (1999) argued that a fifth pair of appendages situated below the border between the cephalon and the trunk in trilobites also belongs to the trilobite head. Hou & Bergström (1997) also supported the idea of the trilobite head carrying five appendage pairs. The apparent differences in construction between the appendages of trilobites and aglaspidids, and the supposed lack of exopods in the latter may be real, but may also be due partially to the very incomplete preservation of aglaspidid appendages. As a result of the uncertain status of *Kwanyinaspis*, the significance of the similarity of the exopods of this arthropod to those of trilobites is unclear. However, considering the absence of exoskeletal mineralisation and the probably plesiomorphic presence of ventral eyes (Edgecombe & Ramsköld 1999; Hou & Bergström 1997) in *Kwanyinaspis*, it seems likely that this arthropod occupies a position basal to both trilobites and aglaspidids. The lack of differentiation of the post-antennal appendages in aglaspidids and trilobites is likely plesiomorphic and hence of limited phylogenetic value. Walossek & Müller (1990) suggested that the possession of a hypostome might be a plesiomorphic character for stem arachnomorphs, whilst Cotton & Braddy (2004) argued that there was no reason to consider the labrum of crustaceans to be non-homologous with the hypostome-bearing structure of other arthropods. In this respect, it is important to note that the detailed homologies between the the trilobite hypostome and similar structures (sclerotised 'labrums') in other arthropods are unclear, as pointed out by Cotton & Braddy (2004). These authors therefore used a very broad definition of the term 'hypostome', embracing any sclerite representing a posteroventral extension of the pre-segmental acron, covering the mouth. The presence of a trilobite-like hypostome in some aglaspidids and aglaspidid-like arthropods opens up two possibilities. In the first case, a trilobite-like 'winged' hypostome represents a synapomorphy uniting aglaspidids and forms like *Kodymirus* and *Kockurus*, with the trilobites. This implies that the trilobite-like 'winged' hypostome was secondarily lost, being reduced to an unsclerotised labrum in most aglaspidids. In this respect it is important to note that the primary attached, or conterminant hypostomal condition of *Tremaglaspis*, the new Late Ordovician Moroccan aglaspidid, *Kodymirus* and *Kockurus*, is considered plesiomorphic in trilobites, characterising the primitive olenellids. Alternatively, the trilobite-like 'winged' hypostomes of *Tremaglaspis*, the new Late Ordovician Moroccan aglaspidid, *Kodymirus* and *Kockurus* may be homoplastic developments of a plesiomorphic, originally unsclerotised labrum, appearing in a number of derived aglaspidids and aglaspidid-like arthropods. This alternative seems more likely and is supported by the fact that both aglaspidids known to possess a trilobite-like 'winged' hypostome, *Tremaglaspis* and the new Late Ordovician Moroccan aglaspidid, with their Ordovician age, are amongst the youngest representatives of the clade and appear to be quite derived. The reasons for the convergent development of a trilobite-like 'winged' hypostome may be the adoption of new feeding strategies unknown in other, less derived aglaspidids.

It is clear that at present it is equally difficult to formulate robust synapomorphies that unite the Aglaspidida with either the Chelicerata or the Trilobita, but the recent findings of

Chen *et al.* (2004) and Scholtz & Edgecombe (2005) show that aglaspidids are likely to be considerably closer to trilobites than they are to chelicerates.

2. Materials and methods

The single specimen described in the present paper was collected during fieldwork in the Upper Ordovician sandstone deposits to the E of Erfoud, Morocco, in February 2000, and is housed in the collections of the National Museums of Scotland, Edinburgh, under accession number NMS G.2005.103.1. When first found, the specimen was cracked through the cephalon as a result of weathering. The two halves of the cephalon had slightly shifted position with respect to each other, and were re-cemented together by a calcrete infill. To restore the fossil to its original shape, and in order to reduce the width of the crack, the specimen was carefully taken apart. The calcrete was removed, the contact surfaces were cleaned and the specimen was re-glued, using cyanoacrylate glue. Preparation of the hard sandstone matrix was carried out using an electrical precision engraving tool with a tungsten carbide tip, and various hardened needles. A cast of the external mould of the doublure was obtained using Coltène-Whaledent AFFINIS lightbody, a fast-curing high-fidelity polyvinylsiloxane. Because of the coarse preservation and relatively large size of the specimen, use of a stereomicroscope in studying the fossil was considered impractical, and would not have resulted in the acquisition of additional details. Therefore, the specimen was drawn at a magnification of × 2·5 using a Jena *camera lucida*, which was custom-adapted for this task by the addition of a moveable specimen platform on which the fossil was placed in an upright position. Drawings of the left, right, front and upper sides of the fossil were prepared, with the main lighting consistently sourced from the NW, and slightly behind the specimen; the same applies for the reconstructions. Photographs of the dry, uncoated specimen were made under plain light using a Canon EOS 300D digital SLR with a Sigma EX 50 mm F 2.8 DG macro lens with the aperture value stopped down to f45 for maximal depth of field. The light sensitivity of the camera's CMOS was set to 100 ISO. The original images in Canon RAW format were processed using Bibble Lite 4.5. Unless noted otherwise, main lighting is from the NW.

2.1. Abbreviations

Abbreviations used in the figures are as follows: (a) raised axial region of tergite; (br) associated orthid brachiopod; (ce) cephalon; (d) doublure; (dep) depression on underside of tergite; (e) eye; (ex) structure viewed as external mould; (gl) glabella; (hyp) hypostome; (lmr) lateral marginal rim; (mb) median interocular bulge; (mn) median notch of doublure; (ms) associated machaeridian sclerite; (mu) depressions on cephalon, probable positions of muscle attachment; (pvp) postventral plates; (r) ridge on upperside of tergite; (t) tergite or tergite fragment; (tgd) transverse glabellar depression; (tsp) tailspine.

3. Geological setting and preservation

3.1. Upper Ordovician stratigraphy of the Erfoud area

The classical British terminology of Fortey *et al.* (1995, 2000) as usually applied to the subdivisions of the Ordovician in Morocco is still utilised here, but in this paper an effort is made to correllate this system to the newly established global subdivisions (Ogg 2004; Webby *et al.* 2004; Gradstein *et al.* 2005).

While they still need to be ratified, the new stage names recently proposed by Bergström *et al.* (2006) on the ISOS website are already used here. In the text, corresponding ages will be written as: Classical British Subdivision/International Subdivision. This discussion is summarised in Figure 1, which combines the correlation between the classical British units and the global stages with an overview of the lithostratigraphical subdivisions of the Moroccan Upper Ordovician in the Erfoud region.

The Upper Ordovician of the area E of Erfoud (Fig. 2a, b) is dominated by the sandstone deposits of the Lower Ktaoua and Upper Tiouririne Formations (Destombes *et al.* 1985). In most areas where the Lower Ktaoua Formation outcrops, it consists of a succession of shale and sandstone deposits. However, in the Erfoud area it is characterised by virtually continuous coarse-clastic sedimentation, overlying the Middle–lower Upper Ordovician sandstones of the First Bani Group (Destombes *et al.* 1985). Near Erfoud, it can reach a thickness of ca. 300 m. The Lower Ktaoua Formation was originally believed to be restricted to the middle Caradoc/late Sandbyan to early Katyan (Late Ordovician). Destombes *et al.* (1985), basing their opinion on its macrofossil content, believed that the base of the formation belonged to the Soudleyan. Using chitinozoans, Elaouad-Debbaj (1986), revised this age attribution slightly downwards, placing the base of the Lower Fezouata Formation in the late Costonian–early Harnagian (early Caradoc/late Sandbyan, Late Ordovician). The top of the formation was considered by Destombes *et al.* (1985) to lie in the Longvillian (middle Caradoc/early Katyan, Late Ordovician). However, the work of Elaouad-Debbaj (1986) showed that the top of the terminal Agadir-Tissint Member of the Lower Ktaoua Formation is actually situated approximately halfway up the Pusgillian (Early Ashgill/middle Katyan, Late Ordovician). As a result, the Lower Ktaoua Formation ranges from the Costonian–Harnagian boundary (early Caradoc/late Sandbyan, Late Ordovician) to the Pusgillian (early Ashgill/middle Katyan). The overlying Upper Tiouririne Formation consists mainly of dark micaceous sandstones, which to the east of Erfoud can be locally replaced by bryozoan limestones, representing a lateral variation of this formation. When present, these limestones cut into the top of a conglomerate and rest onto it in angular discordance (Destombes *et al.* 1985). Locally, they can constitute the base of the formation. On the basis of macrofossil content, the Upper Tiouririne Formation was originally considered by Destombes *et al.* (1985) to have a late Caradoc/middle Katyan age (Late Ordovician). However, the work of Elaoud-Debbaj (1986) requires the lower boundary of the Upper Tiouririne Formation to be moved upwards, approximately halfway into the Pusgillian (Early Ashgill/middle Katyan, Late Ordovician). No micropalaeontological work was carried out on the sandstones of the Upper Tiouririne Formation itself, because this type of deposit is usually not conducive to the preservation of palynomorphs. In the Erfoud area, the overlying Upper Ktaoua Formation is not present. Working in other parts of Morocco, Destombes *et al.* (1985) dated the Upper Ktaoua Formation to the Ashgill (Late Ordovician), referring its upper part to the Rawtheyan (middle Ashgill/late Katyan, Late Ordovician). The chitinozoan work of Elaouad-Debbaj (1984) provisionally places the base of the Upper Ktaoua Formation in the late Pusgillian (early Ashgill/middle Katyan, Late Ordovician), while the top of the formation was dated to the middle of the Rawtheyan (middle Ashgill/late Katyan, Late Ordovician). This constrains the range of the subjacent Upper Tiouririne Formation to between the middle and the late Pusgillian (early Ashgill/middle Katyan, Late Ordovician). The Lower Second Bani Formation
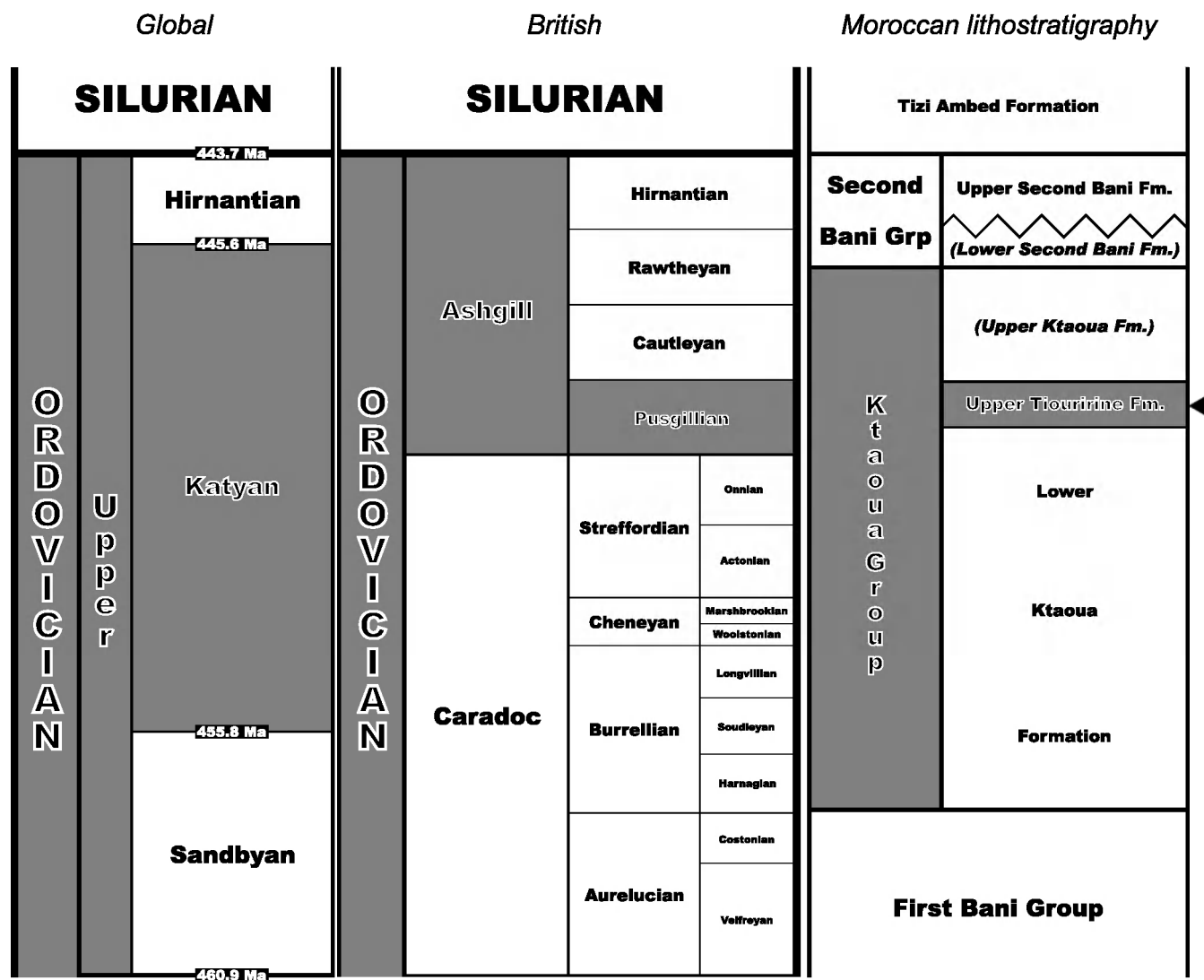
Global	British	Moroccan lithostratigraphy

SILURIAN | **SILURIAN** | Tizi Ambed Formation

Global	British			Moroccan lithostratigraphy	
SILURIAN 443.7 Ma	**SILURIAN**			Tizi Ambed Formation	
O R D O V I C I A N — Upper	**O R D O V I C I A N**				
Hirnantian (445.6 Ma)	Ashgill	Hirnantian		Second / Bani Grp	Upper Second Bani Fm.
		Rawtheyan			(Lower Second Bani Fm.)
Katyan		Cautleyan		K t a o u a G r o u p	(Upper Ktaoua Fm.)
		Pusgillian			Upper Tiouririne Fm. ◀
	Caradoc	Streffordian	Onnian		Lower
			Actonian		
		Cheneyan	Marshbrookian		Ktaoua
			Woolstonian		
		Burrellian	Longvillian		
455.8 Ma			Soudleyan		Formation
			Harnagian		
Sandbyan		Aurelucian	Costonian	First Bani Group	
460.9 Ma			Velfreyan		

Figure 1 Stratigraphical framework, showing the new global subdivisions of the Upper Ordovician on the left, their correlation to the classical British system as used in Morocco in the middle, and the lithostratigraphic divisions of the Moroccan Upper Ordovician on the right. Units relevant to the fossil site are indicated in grey and the approximate position of the fossil locality is arrowed. Lithological units not present in the Erfoud area are italicised and placed in brackets (compiled from Elaouad-Debbaj 1984, 1986; Destombes *et al.* 1985; Fortey *et al.* 1995, 2000; Ogg 2004; Webby *et al.* 2004; Gradstein *et al.* 2005; Bergström *et al.* 2006).

is, like the preceding Upper Ktaoua Formation, not present around Erfoud. The Moroccan Ordovician deposits terminate with the Upper Second Bani Formation of Hirnantian (Late Ordovician) age. If present near Erfoud, and in the greater Tafilalt region, it would be difficult to identify this formation; it is, however, possible that it is absent in the Tafilalt altogether (Destombes *et al.* 1985). Nevertheless, the geological map of the area (sheet nr 244 Tafilalt–Taouz, 1/200 000 scale), compiled in 1975 and printed in 1986 (Fetah *et al.* 1986), shows three tiny outcrops of the Upper Second Bani Formation directly to the east of Erfoud, although the legend of the map states this formation is only present in the west of the sheet.

3.2. Stratigraphical assignment and age of the specimen

The fossil was discovered at a sandstone outcrop approximately 11 km to the east of the town of Erfoud, in southeastern Morocco (Fig. 2a, b). Although the site is undoubtedly of Late Ordovician age, a more precise stratigraphical assignment is difficult. When plotted on the geological map (sheet nr 244 Tafilalt–Taouz, 1/200 000 scale), the outcrop falls into an area denoted as belonging either to the Lower Ktaoua or Upper Tiouririne Formations, which the map fails to differentiate near Erfoud, indicating only a lithological difference between

sandstones and bryozoan limestones (Fig. 2b). The latter obviously belong to the Upper Tiouririne Formation, but no distinction is made on the map between the sandstones of the Lower Ktaoua and Upper Tiouririne Formations. Using chitinozoans from a thin, shaly intercalation, Samuelsson *et al.* (2001) dated the site to the Rawtheyan (middle Ashgill/late Katyan, Late Ordovician), erroneously placing it in the Upper Ktaoua Formation, which is actually not present in the area. The microfossil assemblage recovered is indicative of a largely Ashgill age, but the detailed attribution of the sample to the Rawtheyan by Samuelsson *et al.* (2001) actually hinges on poorly preserved chitinozoan specimens referred with some doubt to *Ancyrochitina ?merga* (Jenkins 1970). Therefore, a precise attribution of the chitinozoan sample to the Rawtheyan is overly ambitious, but a general Ashgill age can be retained. A more precise age and stratigraphical attribution for the site can be obtained by examining trace fossils and mineralogical evidence. At the locality, large, cord-like trace fossils are present. Nils Spjeldnaes (pers. comm. 2001) noted that this type of trace fossil occurs in the area E of Erfoud from 30 m to 0·3 m below the contact between sandstones and the bryozoan limestones belonging to the Upper Tiouririne Formation. In their description of *Rosfacrinus robustus*, Le Menn &
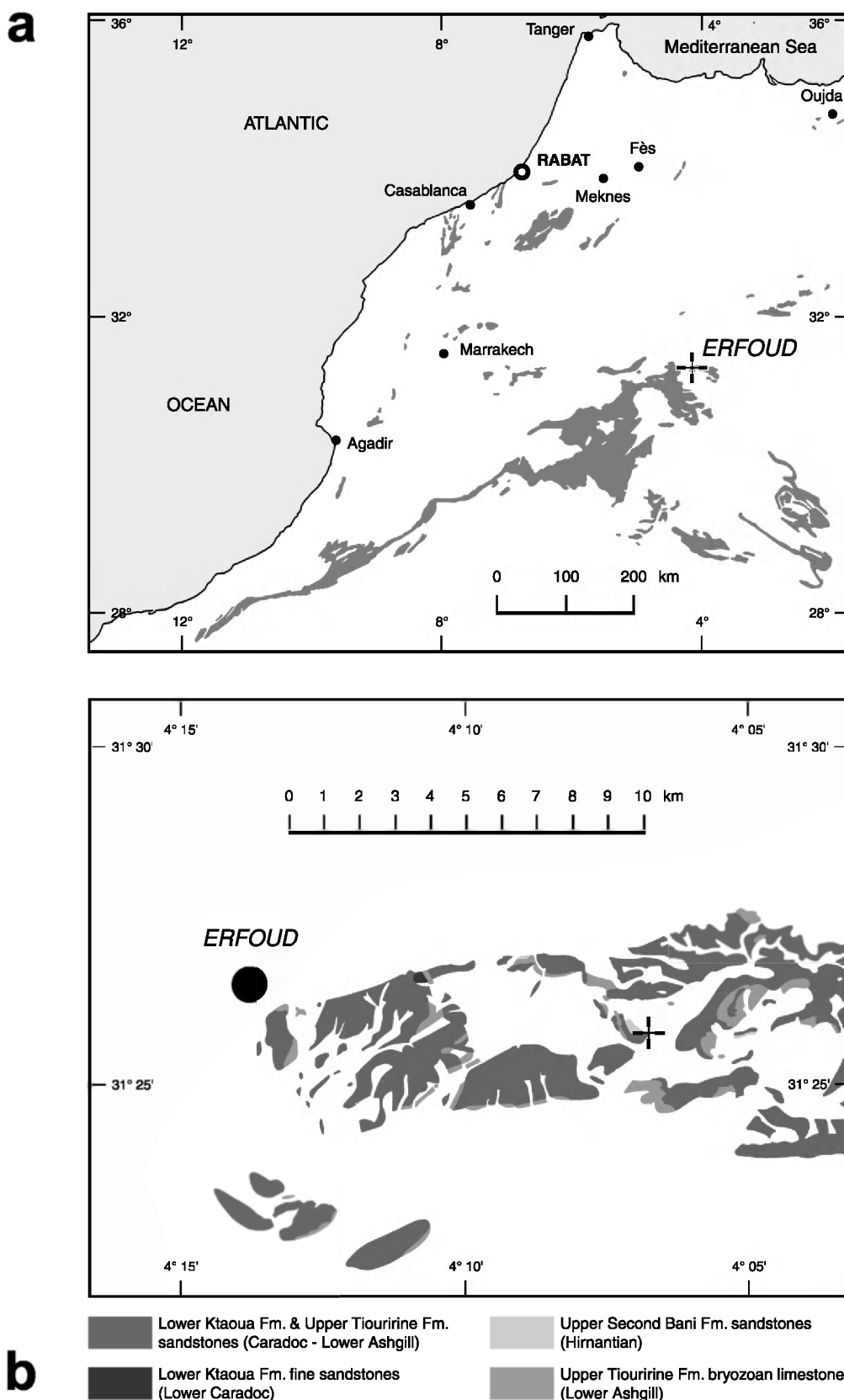
a

b

Figure 2 Geographical location of Ordovician surface outcrops in Morocco: (a) overview map (adapted from Destombes *et al.* 1985); (b) map showing the geographic location of Ordovician surface outcrops east of Erfoud, according to the geological map of the area (sheet nr 244 Tafilalt–Taouz, 1/200 000 scale). Cross-hairs indicate the position of the site where the aglaspidid was found.

Spjeldnaes (1996) accepted that these sandstones, containing the cord-like trace fossils, also belong to the Upper Tiouririne Formation. The medium to dark grey colour and the micaceous content of the sandstones at the site are also consistent with the assumption that the locality would belong to the Upper Tiouririne Formation, as mentioned previously. Combining the available evidence, it seems justified to attribute the fossil site to the Upper Tiouririne Formation, which, as per Elaouad-Debbaj (1984, 1986), has a middle to late Pusgillian (early Ashgill/middle Katyan, Late Ordovician) age (Fig. 1).
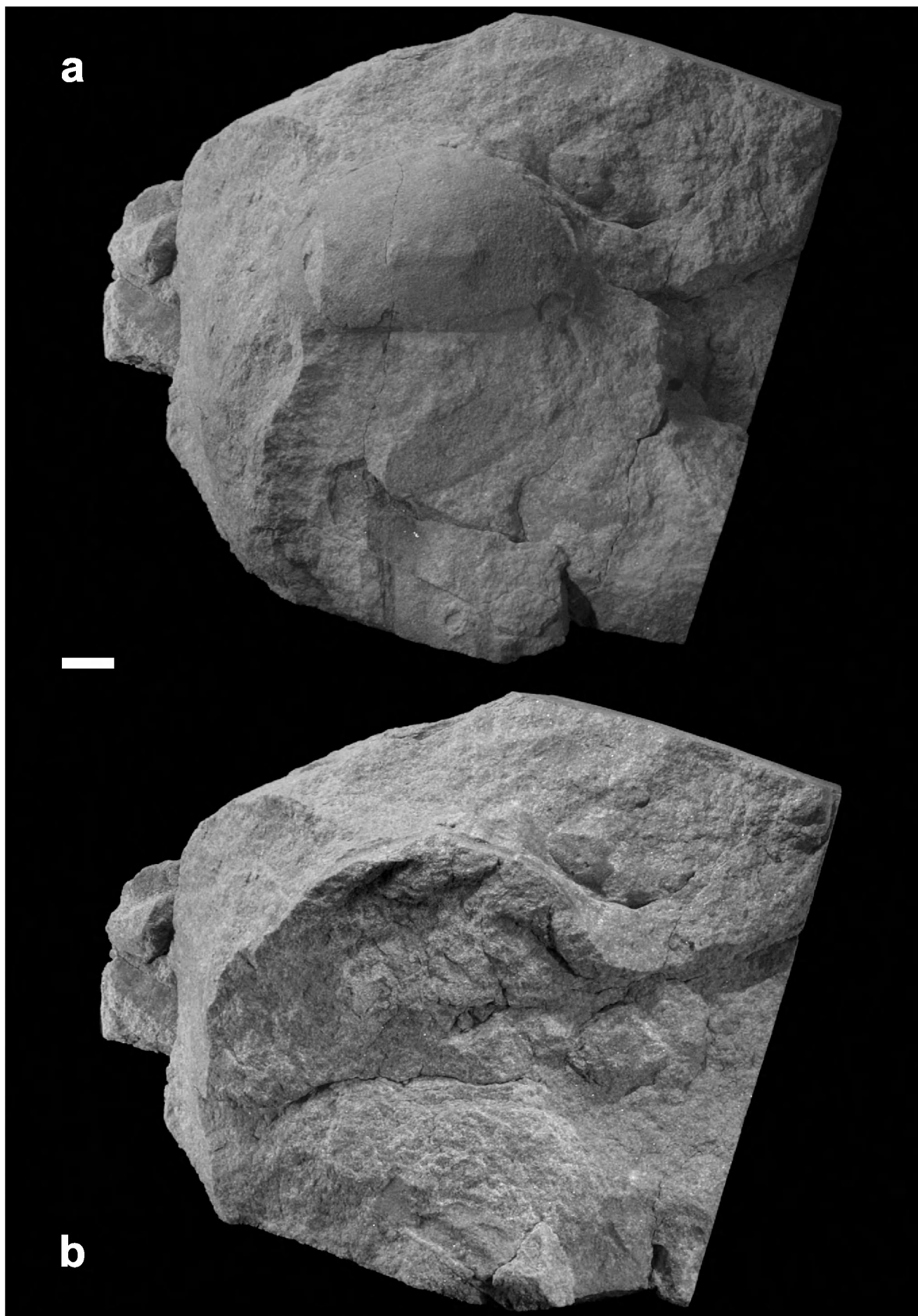
Figure 3 Single specimen NMS G.2005.103.1 of *Chlupacaris dubia* gen et sp. nov., Pusgillian, Ashgill/Katyan, Upper Ordovician, Upper Tiouririne Formation, ca. 11 km E of Erfoud, southeastern Morocco: (a) top view with all three levels present; (b) top view of same specimen, upper level removed. Scale bar=10 mm.
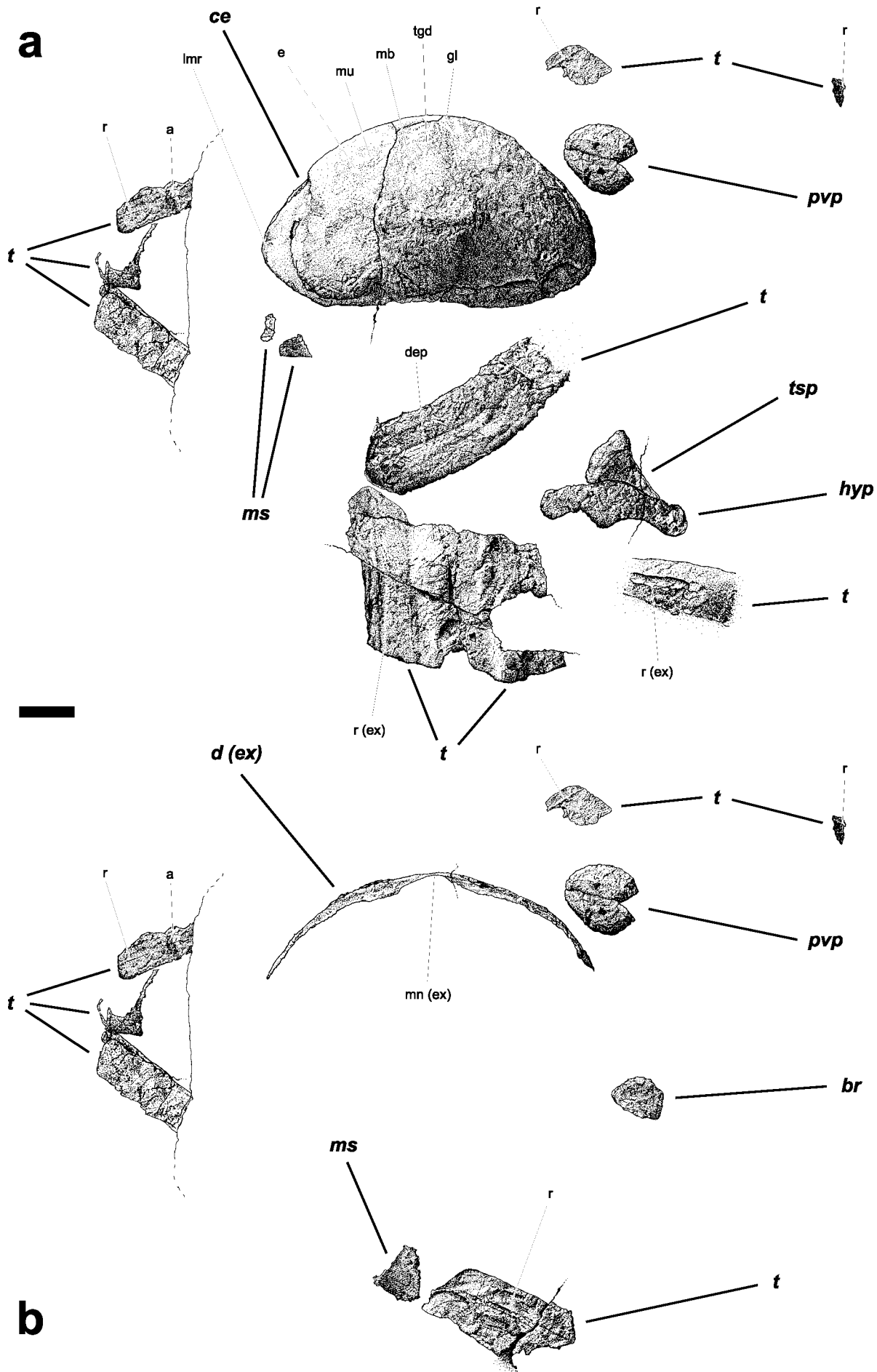
Figure 4 *Camera lucida* drawings of the single known specimen: (a) top view, all levels present; (b) top view, upper level removed. Scale bar=10 mm. Abbreviations defined in the text (section 2.1).
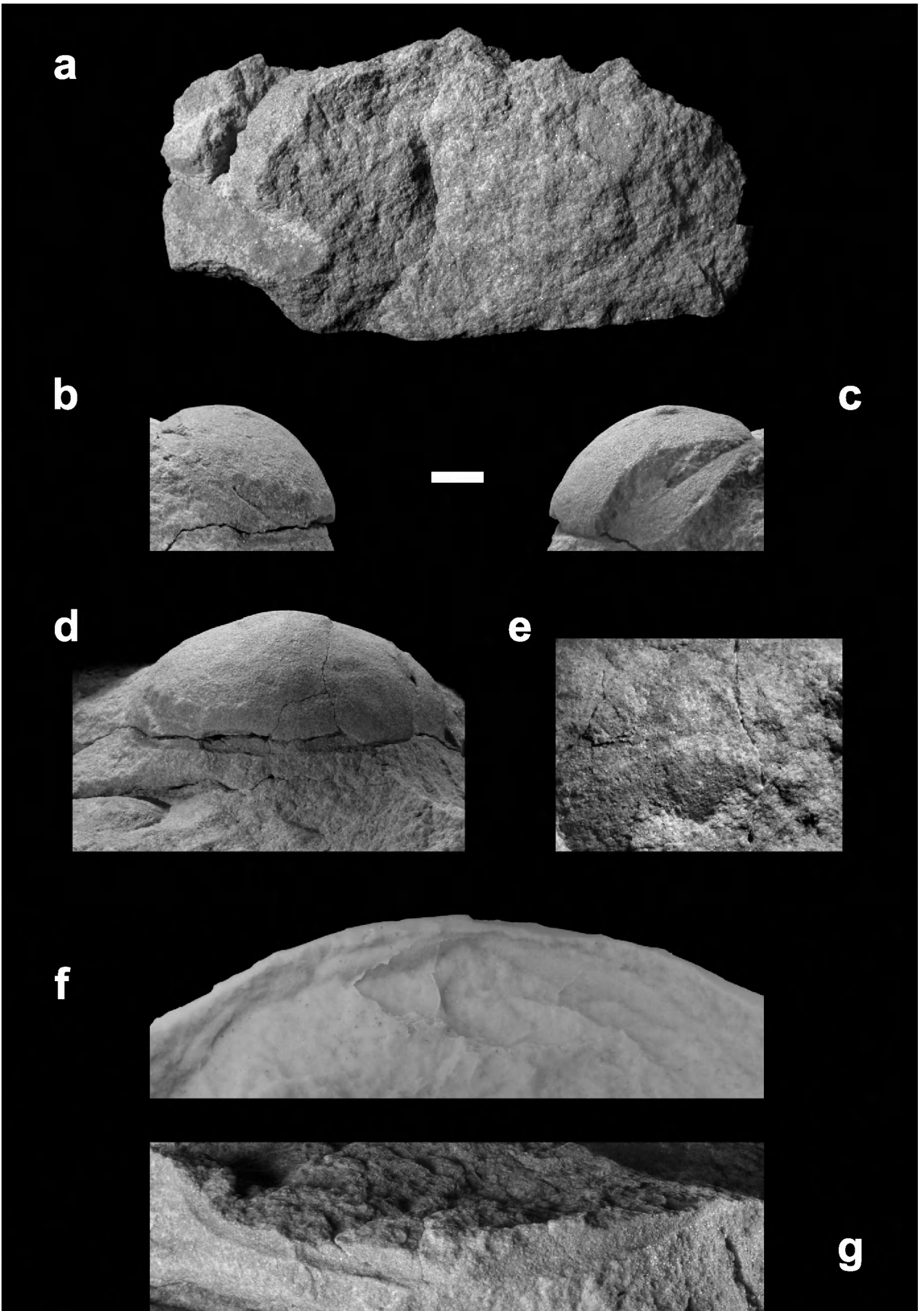
3.3. Co-occurring fauna and depositional environment

The fossil comes from a 30–50 cm thick, massive, medium grained sandstone layer, forming the highest exposed level at the site. The upper surface of the sandstone layer often exhibits well developed wave-ripples, and exhibits mud cracks in various places. A level of fine sandstones about 10 m below the aglaspidid occurrence has yielded several specimens of asaphid, dalmanitid and odontopleurid trilobites, together with crinoids and ophiuroids. The fauna at the level from which the aglaspidid was collected is, however, much less diverse. It is entirely dominated by soft-bodied eldonioids, which are an intriguing group of problematic Palaeozoic discoidal organisms with possible affinities to the echinoderms (Friend 1995; Friend *et al.* 2002) or the lophophorates (Chen *et al.* 1995; Dzik *et al.* 1997). The Moroccan fossils, which were mistakenly placed in the Cambrian genus *Eldonia* Walcott, 1911, by Alessandrello & Bracchi (2003), locally occur in high densities at this, and a number of other sites in the area. Some of the eldonioids show evidence of shrinkage. Other fossils at the site are much rarer and include: a problematic, soft-bodied discoidal organism resembling the Cambrian '*Ediacaria*' *booleyi* Crimes, Insole & Williams, 1995 from Ireland (MacGabhann *et al.* in press); large conulariids; orthid brachiopods; trinucleid trilobite fragments; plumulitid machaeridian sclerites; and crinoid columnar fragments. Various trace fossils, probably produced by vermiform organisms, are also present at the site. From this evidence, it appears that the massive sandstones preserving these fossils were deposited in a very shallow, highly energetic and well aerated open marine environment. The presence of mud cracks in the sediment, and desiccation wrinkles in the eldonioids, points to episodes of sub-aerial exposure, emphasising the extremely shallow, possibly inter-tidal nature of the sediments. It is likely that some of the fossils preserved at this level, such as the trinucleids, are not *in situ*, but were washed in from deeper water. The marginal nature of this environment could explain the relatively low diversity of the fauna, dominated by eldonioids. The preservation of soft-tissues in these shallow marine sandstones is puzzling, and together with the massive, structureless nature of the level preserving them, points to episodes of very rapid, possibly storm-influenced, burial.

3.4. Preservation

Most of the disarticulated remains of the specimen are preserved as internal moulds in the sandstone, with some tergite fragments represented by external moulds. Fragments of other, originally calcified, organisms directly associated with the specimen have largely undergone decalcification. Some of the original calcium carbonate was apparently partially converted into a patchily distributed, reddish mineral of possible iron carbonatic composition. Preservation of the arthropod specimen appears to be broadly similar to that of the associated fossils, indicating its cuticle was most likely also calcified. Because the specimen is almost completely disarticulated, it probably represents either a fresh exuvium, or an individual that died shortly before burial. Total disarticulation was probably caused by water currents in the high energy environment and the actions of scavengers and bioturbators. However, since all sclerites and sclerite fragments are still in close

association, the specimen must have been buried very shortly after the onset of disarticulation. Otherwise the remains would have quickly become broken up and spread out over a large area. Synsedimentary movements in the water-saturated sands after burial may also have contributed to the disarticulation of the fossil.

4. Systematic description

Phylum Arthropoda von Siebold, 1848
Order Aglaspidida *s.s.* Raasch, 1939

Emended diagnosis. Small to medium-sized arthropods having a mineralised cuticle. With the possible exception of a hypostomal suture, cephalon totally devoid of visible ecdysial sutures. Four, or possibly five, cephalic appendage pairs present. First appendage pair antenniform, all postantennal appendages of similar, undifferentiated construction. Appendages lacking below undifferentiated terminal three or four trunk tergites. All trunk tergites free, with pleurae, and carrying a pair of anterior tergal processes. Postventral plates located beneath posterior tergites and base of tailspine (emended from Hou & Bergström 1997).

Included taxa. *Aglaspella granulifera, Aglaspis barrandei, Aglaspis spinifer, Aglaspoides sculptilis, Chlupacaris dubia* gen. et sp. nov., *Chraspedops modesta, Cyclopites vulgaris, Flobertia kochi, Glyptarthrus vulpes, Glyptarthrus simplex, Tremaglaspis unite, Uarthrus instabilis.*

Genus Chlupacaris gen. nov.

Diagnosis. As for species.
Type and only species. *Chlupacaris dubia* gen. et sp. nov.
Derivation of name. Conflation of *Chlupac*, in honour of the late Dr Ivo Chlupáč, foremost specialist on the arthropods and geology of the Palaeozoic of Bohemia, and *caris*, from Latin, meaning 'crab, shrimp', and indicating the arthropod affinity of the fossil. Gender feminine.

Chlupacaris dubia gen. et sp. nov.
(Figs 3–8)

· *2001* 'possible aglaspidid' Samuelsson, Van Roy & Vecoli, p. 365, 367.

Diagnosis. Medium-sized aglaspidids with a highly convex cephalon and moderately convex trunk. Cephalon approximately twice as wide as long, with a broadly rounded anterior margin, rounded genal angles and a faint glabellar area. Ovolunate eyes located subcentrally on cephalon, connected by slightly raised, broad ridge, medially widening to an interocular bulge. Anterior cephalic doublure divided by deep median notch. Probably conterminant hypostome with central ovoid body and large lateral wings present. Tergites slightly curved, with weakly expressed pleural spines, and arranged subparallel to each other. Axial region slightly raised and poorly delimited. Tailspine short. Complete postventral plates subcircular and pointed posteriorly.
Derivation of name. From Latin, *dubius, -a, -um,* meaning 'doubtful'.
Holotype. NMS G.2005.103.1, kept in the collections of the National Museums of Scotland, Edinburgh, U.K.

Figure 5 Single specimen NMS G.2005.103.1 of *Chlupacaris dubia* gen et sp. nov., Pusgillian, Ashgill/Katyan, Upper Ordovician, Upper Tiouririne Formation, ca. 11 km E of Erfoud, southeastern Morocco: (a) top view of third, lowermost level; (b) right-lateral view of cephalon; (c) left-lateral view of cephalon; (d) anterior view of cephalon, with sideview of postventral plate; (e) hypostome and tailspine, upper level, lighting from the upper right; (f) silicone cast of external mould of inclined anterior cephalic doublure; (g) frontal view of external mould of cephalic doublure. Scale bar in (a)–(d): 10 mm; in (e)–(g) 5 mm.
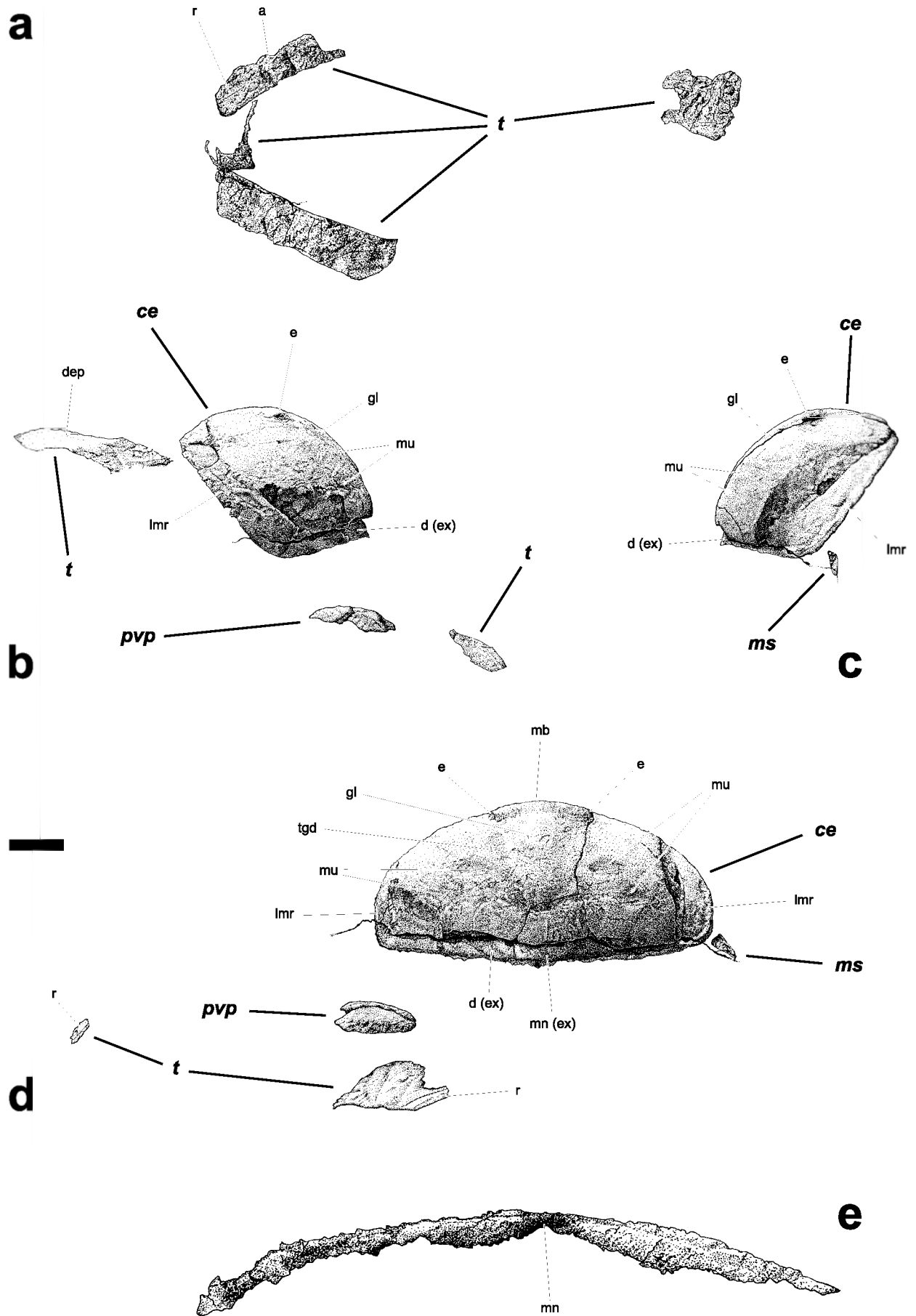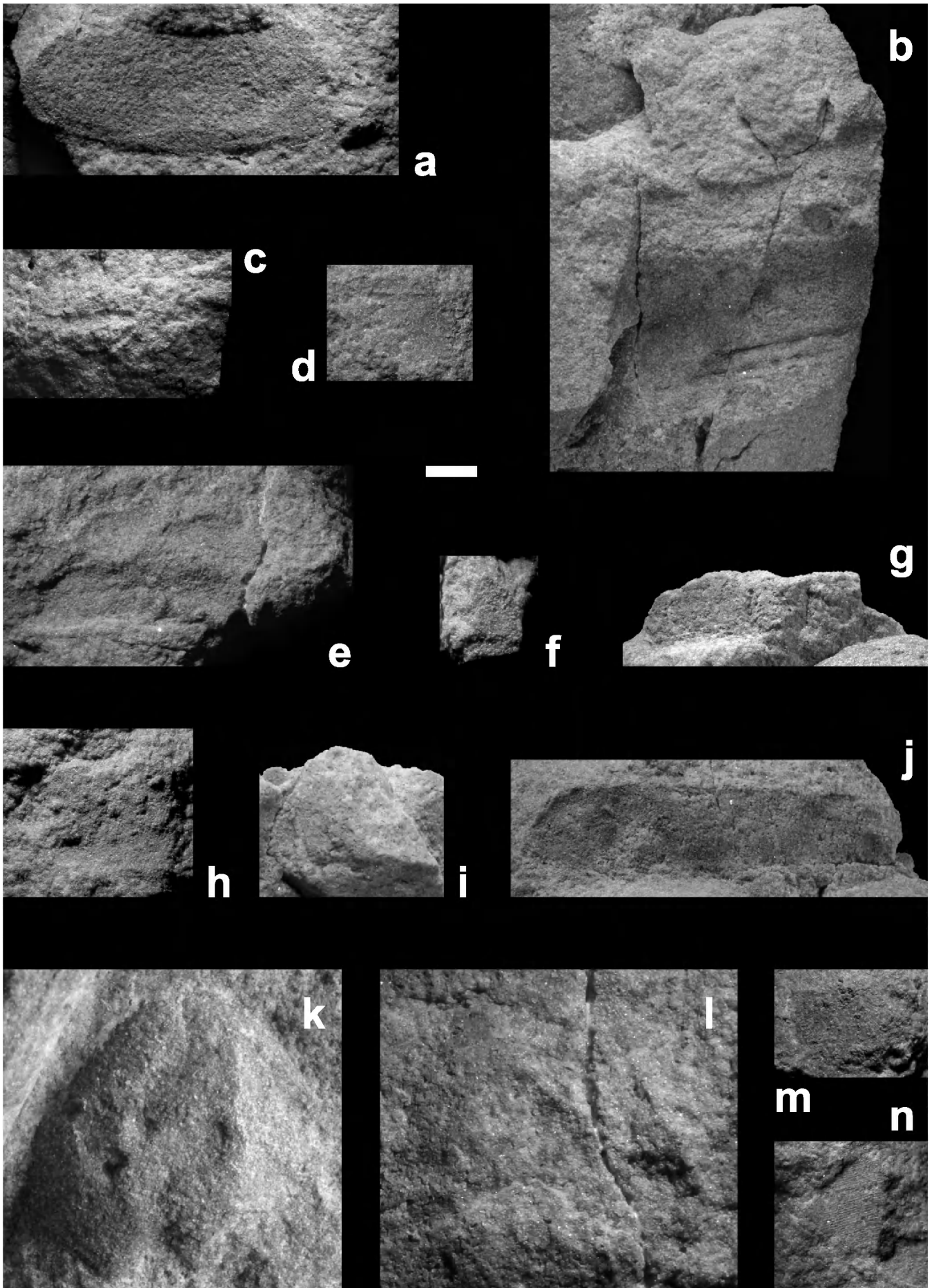
Figure 6 Interpreted *camera lucida* drawings: (a) lower, third level of specimen, top view; (b) right side; (c) left side; (d) anterior view; (e) drawing of silicone cast of doublure. Scale bar in (a) – (d)=10 mm, in (e) 5 mm. Abbreviations defined in the text (see section 2.1).

Additional specimens. None

Type locality. Site located ca. 11 km east of Erfoud, south-eastern Morocco (Fig. 2b), and belonging to the Upper Tiouririne Formation. Exact coordinates of the site are available from the author.

Age. Based on Elaouad-Debbaj (1984, 1986) it follows that the Upper Tiouririne Formation, from which the specimen was collected, ranges from the middle to the uppermost Pusgillian (early Ashgill/middle Katyan, Late Ordovician).

Description of NMS G.2005.103.1. Specimen almost completely disarticulated, with fragments exposed on three levels (Figs 3a, b, 4a, b, 5a, 6a) within matrix. Separation between upper and lower levels ca. 65 mm. Middle level exposed in front of cephalon without need for removing upper level.

Cephalon cracked from anterior to posterior, slightly to left of midline. Part of anterior cephalic margin missing over 2–4 mm. On right side, near anterior margin, surface of cephalon damaged over area of ca. 0·75 cm². Deformation limited, left lateral side of cephalon pushed slightly downward, posterior edge also slightly crushed in places. Cephalon width=61 mm, length=33 mm, height=28 mm. Anterior margin broadly rounded in top view (Figs 3a, 4a), exhibiting subtle compound curvature with central median third of margin curving slightly stronger than anterolateral margins. Specimen lacking genal spines, having blunt genal angles. Posterior margin almost straight, centrally curving upward and forward, forming shallow indentation with width=15 mm. Lateral outline of cephalon resembling quarter circle, with faint bulge starting about 5 mm above anterior margin (Figs 5b, c, 6b, c). In anterior view (Figs 5d, 6d), upper outline of cephalon gently curved over most of its length, but curvature becoming stronger laterally with sides of cephalon sloping almost vertically. Pair of eyes located subcentrally on cephalon, length=ca. 5 mm. Eyes set 18 mm apart and connected by faint, centrally raised, axially-widening ridge. Inconspicuous glabella extending behind and in front of eyes, tapering rearward, disappearing shortly before meeting posterior cephalic margin and extending forward to ca. 9 mm from anterior margin. Glabella surrounded anteriorly by shallow depression and divided by faint transverse depression 5 mm from tip. Pair of faint, 6–7 mm long, elongated depressions flanking glabella on same level as division. Second pair of more or less circular depressions, diameter=3–4 mm, situated below depressions, at same height as tip of glabella. Below glabella, lower 5 mm of middle third of anterior margin bulging slightly forward. Lateral margins of cephalon with more or less flattened marginal rims. Raised line running parallel to posterior cephalic margin visible to left of weak axial indentation. Ventrally, anterior doublure largely missing, but preserved on left side. External mould of doublure located on middle level (Figs 3b, 4b, 5f, g, 6e), showing doublure to be oriented at angle of ca. 60°–70° to the horizontal, and subdivided by deep, 5–7 mm wide, median notch.

Five fragmentary tergites visible behind cephalon, on upper level (Figs 3a, 4a). Well-preserved fragment of tergite viewed from underside (Fig. 7a) lying closest to cephalon, length=12·5 mm, preserved width=ca. 30 mm. Fragment weakly curved in both horizontal and vertical planes. Margin

farthest away from cephalon thinnest. Median depression running along entire preserved width of tergite. Approximately 2 mm behind and parallel to linear depression, other faint depression observable along two-thirds of preserved width. Behind this tergite fragment lay the weathered partial remains of two other articulated tergites (Fig. 7b), preserved as external moulds of the upper side. Fragments deformed by local small-scale fracture. Length of tergites difficult to measure, but estimated to be between 13 mm and 15 mm. Preserved width=ca. 30 mm. Transverse linear impression running approximately along middle of preserved width evident on both external moulds. Other linear depression surrounded by faint remains of tergite fragment lying to right of these fragments (Fig. 7c). Preservation too poor for any useful measurements. Two small tergite fragments lying on middle level (Figs 3b, 4b), in front of cephalon and to right of it (Fig. 7d, f), both carrying distinct, sharp ridge. Removal of upper level revealing complete pleura near the edge of matrix, ca. 70 mm behind external mould of the doublure (Fig. 7e). Length=11 mm, greatest preserved width=ca. 33 mm. Pleura slightly curving in vertical plane, anterior and posterior margins almost straight; posterior margin most strongly curved near distal tip of the pleura, where it meets moderately curving lateral pleural margin. Narrow transverse ridge running along entire width of pleura, recurving near lateral pleural margin. Faint furrow possibly present behind ridge, but due to some minor deformation difficult to resolve unequivocally. Faint, depressed line ca. 2 mm behind raised ridge, running parallel to it for most of preserved width of pleura. Lowermost third level (Figs 5a, 6a) showing complete tergite together with fragments of three other tergites. Complete tergite flattened, showing deformation in central area and near lateral margins (Fig. 7j), length=8.5 mm, width=35 mm. Anterior and posterior margins straight, running parallel to each other. Posterior margin with faint indentation medially, curving slightly distally, where meeting lateral pleural margins. Lateral margins curving gently backward. Tergite fragment with moderate vertical curvature, most pronounced near lateral margins, embedded at angle of ca. 45° in front of complete tergite (Fig. 7i). Situated in front of this fragment is other tergite, approximately two-thirds complete (Fig.7g), posterior margin mostly broken away. Length=ca. 6·5 mm, total preserved width=ca. 27 mm. Anterior margin straight. Partly-preserved right lateral margin curving backward. Axial region 5 mm wide, raised. Faint median transverse ridge present. Other tergite fragment to right of this cluster of three tergites (Fig. 7h).

Tailspine and hypostome (Fig. 5e) situated on top level, behind cephalon, to right of well preserved tergite fragment, lying in close proximity to each other. Crack running through both sclerites. Tailspine (Figs 5e, 7l) having wide base and showing thickened marginal rim, total length=16 mm. Blunt anterior of tailspine carrying a pair of short, stout, antero-laterally directed processes.

Hypostome situated directly behind tailspine, partially overlapping it (Fig. 5e). Anterior of oval central body of hypostome removed but outline compacted onto tailspine. Anterior of hypostome central body pointed, posterior rounded. Length of central area=ca. 13 mm. Central body

Figure 7 Single specimen NMS G.2005.103.1 of *Chlupacaris dubia* gen et sp. nov., Pusgillian, Ashgill/Katyan, Upper Ordovician, Upper Tiouririne Formation, ca. 11 km E of Erfoud, southeastern Morocco: (a)–(j) tergite and tergite fragments. Especially noteworthy are: (b) weathered external mould of two partial tergites in articulation; (e) pleural fragment, showing limited curvature of pleurae; (g) tergite fragment, showing slightly raised axis; and (j) virtually complete tergite, showing straight outline and limited curvature; (k) postventral plate, lighting from the right; (l) tailspine, lighting from the upper right, with base of tailspine situated on the left; (m) orthid brachiopod and (n) machaeridian sclerite associated with *Chlupacaris*. (a)–(c) and (l) upper level, (d)–(f), (k), (m) and (n) middle level, (g)–(j) lower level. Scale bar in (a)–(j), (m) and (n) 5 mm; in (k) and (l) 2·5 mm.

carrying pair of postero-laterally directed 'wings', total width of plate including 'wings'=ca. 24 mm.

Postventral plates situated immediately in front and to the right of cephalon, on middle level (Fig. 7k). Length=14 mm, maximum width =12·5 mm, greatest height=ca. 2·5 mm. Plates having moderate convexity, greatest at rear, joined along almost straight inner margin, outer margin semicircular, becoming pointed at rear.

Remarks. In general outline, *Chlupacaris* most strongly resembles the Late Cambrian aglaspidid *Flobertia kochi* from Wisconsin. Although differing considerably in overall outline, the presence of a trilobite-like 'winged' hypostome is shared by both *Chlupacaris* and *Tremaglaspis unite* from the Tremadoc/ Tremadocian (Early Ordovician) of Wales. In addition, the Early Cambrian aglaspidid-like arthropods *Kodymirus vagans* and *Kockurus grandis* from Bohemia have hypostomes that are extremely similar to that of *Chlupacaris*.

5. Interpretation and reconstruction

Although the specimen is disarticulated, individual parts are preserved well enough to allow the exoskeleton to be pieced together. A reconstruction of the dorsal aspect of the animal is given in Figure 8a, while Figure 8b shows a left lateral view and Figure 8c represents the frontal aspect of the arthropod. The entire exoskeleton appears to have been smooth, lacking any sculpture in the form of pustules or pits, but this may be an artefact, caused by the coarse sediment in which the fossil is preserved. Anyhow, if any ornament was present in life, it must have been quite inconspicuous. As reported earlier, the preservation of the specimen is comparable to that of other, originally calcified fossils associated with it (Fig. 7m, n), indicating the exoskeleton was mineralised, probably having been calcified.

5.1. Cephalon

Because of the limited deformation of the specimen, the reconstructed general shape of the cephalon does not differ significantly from the description above. The subtle compound curvature of the anterior cephalic margin, as seen in top view, and the slight anterior bulge visible in lateral view correspond to the forward bulging of the median part of the lower 5 mm of the anterior margin. The ovolunate eyes obviously had greater relief in life, being somewhat crushed on the specimen, and were most probably compound. The function of the median bulge between both eyes is unclear; it may have carried a pair of median ocelli. Median eyes are usually regarded as typical for chelicerates, but are also known from other arthropods, such as the marrellomorph *Mimetaster hexagonalis* (Stürmer & Bergström 1976). Raw (1957) suggested that median eyes might have been present in the aglaspidid *Chraspedops modesta*. The marginal cephalic rims of *Chlupacaris* are apparently only limited to the lateral margins of the cephalon, and do not seem to continue over the anterior or posterior margins. They may represent structural reinforcements (Raasch 1939; Hesselbo 1992). The faint depressions flanking the glabella probably indicate sites of muscle attachment. The sclerotised, winged hypostome described above covered a backward-facing mouth. It resembles the hypostome of trilobites in overall shape, but lacks any dividing furrows or border (Fig. 8e, g). Because the specimen is disarticulated, the mode of attachment and orientation of this hypostome cannot be observed directly. The arrangement of the doublure (Fig. 8d, e), however, sheds light on these questions. The median notch of the doublure clearly accommodated the central anterior extension of the plate, as shown in Figure 8e. This close association between the

hypostome and the doublure suggests that the hypostome probably was attached to the inner margin of the doublure, representing the conterminant hypostomal condition, as defined by Fortey & Chatterton (1988) for trilobites. The subvertical orientation of the anterior cephalic doublure further indicates the hypostome must have been oriented at a similar upturned angle. The elongated depressions flanking the glabella dorsally coincide with the position of the 'wings' of the ventral hypostome, and may be associated with musculature connecting to this structure, to the mouth or to the anterior part of the gut. The gentle bulging of the lower central part of the cephalon, resulting in the subtle compound curvature of the anterior cephalic margin, also coincides with this hypostome. The faint, discontinuous line flanking the median upward and inward curve of the central part of the posterior cephalic margin may indicate the presence of a narrow posterior doublure. With the probable exception of a hypostomal suture, no other visible ecdysial sutures appear to have been present on the cephalon; it probably split open along its entire anterior margin during ecdysis, as is the case in modern-day horseshoe crabs.

5.2. Trunk
From a number of observations, the shape and arrangement of the trunk tergites can be deduced: (1) the largely straight posterior cephalic margin only allows for a faint curvature of the first trunk tergite; (2) the larger fragments of the anterior tergites on the upper and middle levels show only very limited curvature; (3) the two most complete posterior tergites exposed on the lower level also clearly exhibit nearly straight anterior and posterior margins. From this, it follows that all the trunk tergites had a similar, largely straight shape, being differentiated only by a gradual reduction in size posteriorly and that all tergites must have been arranged subparallel to each other. In the vertical plane, the pleurae had only a moderate curvature, as shown by the tergites preserved on the middle and lower levels. Hence, since the sides of the cephalon slope almost vertically in their lower half, the first tergite can have extended only about halfway down the sides of the cephalon, conferring to its gently curving upper part, as visible in the lateral reconstruction (Fig. 8b). As a result, the trunk was much less convex than the cephalon. The complete tergites of the lower level show there was a faintly raised, poorly delimited axial region. In the case of the partial tergite that is embedded at an angle, the raised axial region may have become somewhat accentuated by lateral compression. Further evidence for this axial region is presented by the indention and upward curve of the median posterior margin of the cephalon, which served to accomodate the faint axis when the body was flexed upward. A depression on the underside corresponds to the pronounced transverse ridge running dorsally across each tergite. It represents an articulating ridge as seen in other aglaspidids. Behind this ridge is a faint depression, which is at its widest and most pronounced near the lateral margins of the pleurae. The function of the articulating ridge is not entirely clear, but in aglaspidids it probably served to limit movement of the tergites (Hesselbo 1992). In order for this articulating ridge to have been effective, an overlap of at least one third of the length of each tergite is needed in *Chlupacaris*. This large overlap and the corresponding large articulating flange allowed great flexibility of the body. Nevertheless, enrolment was probably impossible for *Chlupacaris*. Because the only available specimen is disarticulated, the total number of tergites cannot be established with certainty. In all, there are eleven tergites or tergite fragments present in the specimen, but the possibility that some fragments actually belong to the same tergite cannot be excluded. However, the size of the base of the tailspine
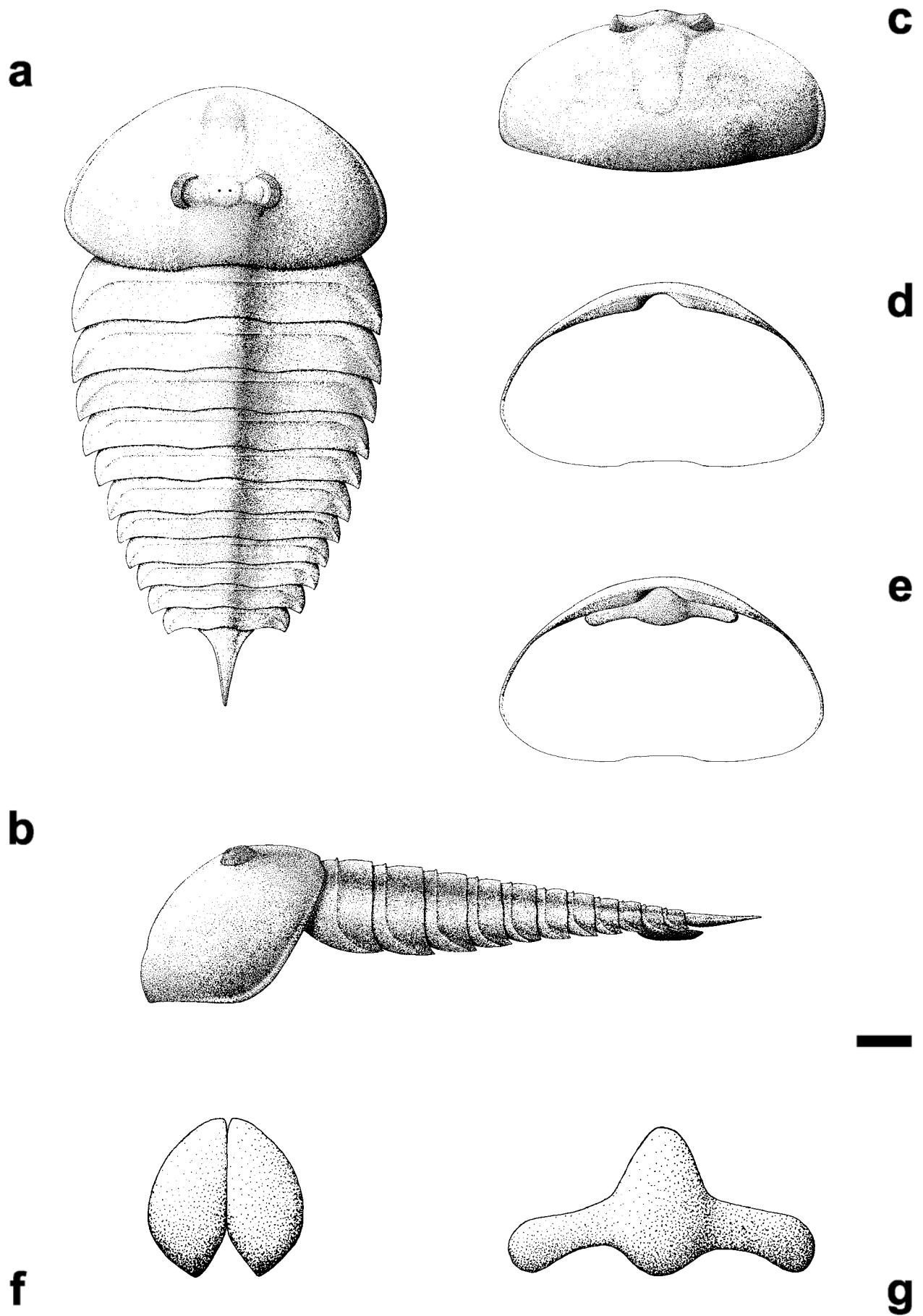
Figure 8 Reconstructions of *Chlupacaris dubia* gen et sp. nov.: (a) dorsal; (b) lateral. Note that the lateral aspect of the tailspine is uncertain and may have been thicker; (c) anterior view; (d) ventral view of anterior cephalic doublure with median notch; (e) ventral view of anterior cephalic doublure with inclined hypostome in place; (f) postventral plates; (g) hypostome. Scale bar in (a)–(e)=10 mm; in (f) and (g) 5 mm.

makes the presence of less than ten tergites unlikely, whilst at the same time leaving space for no more than twelve tergites with pleurae at most, as can be seen from the dorsal reconstruction (Fig. 8a). It follows that most probably the trunk of *Chlupacaris* comprised between ten and twelve tergites with pleurae. It cannot be excluded that behind the last tergite with pleurae a number of (semi)cylindrical sclerites preceded the tailspine, as is the case for example in *Emeraldella*, but this seems unlikely. The reconstructions (Fig. 8) chose to depict the animal with an eleven-segmented trunk.

The broad tailspine was rather short with thickened lateral margins. The anterolateral protrusions at its base represent points for muscle attachment. One side of the tailspine was flat, as seen in the specimen. The other side, and hence the cross-section of the tailspine, is unknown. The cross-section may have been flattened or relatively high, and may have been triangular, as is the case in extant horseshoe crabs. In addition to the large overlap between tergites, the short tailspine suggests a marked dorso-ventral flexibility, as the animal clearly did not rely on this structure to right itself. Dorso-ventral flexibility may have been comparable to that of synziphosurines, and was probably greater than that of many long-tailed aglaspidids such as *Aglaspis* and *Glyptarthrus*.

Paired postventral plates were located (Fig. 8f) below the last two tergites and the base of the tailspine.

5.3. Mode of life
The specimen may not be preserved in its living environment but may have been washed in from deeper water, as is probably the case for the trinucleid fragments from the same horizon. Because nothing is known about the appendages of *Chlupacaris*, its mode of life is uncertain. Its general shape indicates a benthic arthropod and its smooth exoskeleton suggests it was able to burrow through the substrate, with the high-set eyes protruding above the sediment. The conterminant, upward-directed hypostome, together with the highly convex cephalon and much less vaulted trunk, may indicate a filter feeder, as has been suggested for trilobites of similar gross morphology (Fortey & Owens 1999). Trilobites using a cephalic filter-feeding chamber often have elaborate genal spines, but some of the supposed filter-feeders like *Illaenus* lack these structures. Therefore, the lack of genal spines in *Chlupacaris* does not necessarily exclude a filter-feeding mode of life. In this scenario, the appendages would stir up sediment in the cavity formed by the strongly convex cephalon and the upturned hypostome, with the less convex trunk being kept suspended. *Chlupacaris* may also have lived with its cephalon lying horizontal on the sea floor and with the trunk burrowed at an angle in the sediment, as postulated for the trilobites *Bumastus* (Bergström 1973) and *Stenopilus* (Stitt 1976). The forward-sloping arrangement of the rear cephalic margin in lateral view of *Chlupacaris* lends some support to this notion, but it should be noted that no proof exists for this mode of life in either *Bumastus* or *Stenopilus* (Whittington 1997). A filter-feeding strategy for at least some aglaspidids may be supported by the rusophyciform trace fossil *Raaschichnus gundersoni* Hesselbo, 1988. Schmalfuss (1981) formulated a hypothesis in which rusophyciform trilobite burrows are interpreted as filter-feeding chambers. Although probably not generally applicable (Fortey 1985; Seilacher 1985), this theory may hold true for a number of rusophyciform traces. Little is known about the mode of life of other aglaspidids, but they are usually considered to have been generalist predators or scavengers (Hesselbo 1992). A predatory mode of life is often considered primitive (e.g. Fortey & Owens 1999). Since *Chlupacaris* is one of the youngest aglaspidids known, a more derived filter-feeding life-style for this arthropod is conceivable.

6. Morphological comparison of *Chlupacaris* with other aglaspidids and aglaspidid-like arthropods

Based on the new provisional set of aglaspidid characters proposed in section 1.3, the demonstrable presence of characters 1 (mineralised exoskeleton), 2 (lack of visible ecdysial sutures other than hypostomal suture), 6 (possession of postventral plates) and 8 (trunk terminating in a tailspine) in *Chlupacaris* favours placement in the Aglaspidida *s.s.*

Of all aglaspidids *s.s.* and aglaspidid-like arthropods from the Cambrian of North America discussed by Raasch (1939) and Hesselbo (1989, 1992), *Chlupacaris* most strongly resembles the genera *Tuboculops*, *Flobertia*, *Setaspis* and *Cyclopites* in that they all lack genal spines and exhibit rounded genal angles. *Tuboculops* and *Setaspis* are known only from isolated cephala and these differ mainly from the cephalon of *Chlupacaris* in the anterior placement of the eyes. *Cyclopites* was probably more laterally flattened and had an anteriorly located bilobed eye-node, which differs strongly from the median eyes seen in *Chlupacaris*. The new fossil most strongly resembles *Flobertia*. Only the anterior tergites of *Flobertia* are known but these seem to be similar to the tergites as reconstructed for *Chlupacaris*, being only moderately curved and lacking pleural spines. The cephalon of *Flobertia* differs in having smaller and slightly more anteriorly located eyes. The small, poorly preserved aglaspidid-like arthropod *Quasimodaspis brentsae* from the Upper Cambrian of Nevada (Waggoner 2003) resembles *Chlupacaris* in lacking genal spines and apparently having a rather short tailspine. It differs from *Chlupacaris* by its sharper genal angles, its short pleural spines, its tergites becoming progressively more recurved towards the rear and its pitted surface texture. Jago & Baillie (1992) reported a small Late Cambrian aglaspidid-like arthropod from Tasmania. Only one poorly preserved specimen is figured, which seems to resemble *Chlupacaris* in the lack of genal and pleural spines and the parallel arrangement of the trunk tergites. Differences concern the more anteriorly placed eyes, the possibly sharper genal angles and the possession of a long tailspine. It should be noted that this arthropod seems to have had twelve trunk tergites.

The presence of a hypostome separates *Chlupacaris* from all aglaspidids *s.s.* and aglaspidid-like arthropods discussed above. Both Briggs *et al.* (1979) and Hesselbo (1992) reported the presence of a labrum in *Aglaspis spinifer*, but this structure is clearly different from the plate in *Chlupacaris*. However, Fortey & Rushton (2003) recently described the highly atypical aglaspidid *Tremaglaspis unite* from the Tremadoc/ Tremadocian (Early Ordovician) of Wales as possessing a large, well developed hypostome. *Tremaglaspis* has a long, spatulate cephalon without eyes and an elongated body with a broad axis and short pleurae. As in *Chlupacaris*, the tailspine is short and the exoskeleton is devoid of ornamentation. The paired postventral plates, which Fortey & Rushton (2003) consider to be most likely fused along the midline, are quite similar in shape to those of *Chlupacaris*, having a pointed posterior cleft but being slightly more elongated. At first sight, the hypostome of *Tremaglaspis* is rather different from that of *Chlupacaris*. However, the central body of both plates is similar, the main difference lying in the very small wings in *Tremaglaspis* as compared to the strongly developed lateral wings in *Chlupacaris*. The central body of the hypostome of *Tremaglaspis* is also proportionately larger than that of *Chlupacaris*. The greater overall size of the hypostome of *Tremaglaspis* may indicate it handled larger food items than *Chlupacaris* with its supposed filter feeding mode of life. Notwithstanding their differences, the presence of a hypostome

in both *Tremaglaspis* and *Chlupacaris* may point to a sistergroup relationship between these arthropods.

Two other arthropods exhibiting a 'winged' hypostome closely associated with the doublure and very similar to that of *Chlupacaris* are the problematic arthropods *Kodymirus vagans* (Chlupáč & Havlíček 1965; Chlupáč 1995) and *Kockurus grandis* (Chlupáč 1995) from the Lower Cambrian of the Czech Republic. Both Czech arthropods differ from *Chlupacaris* in the shape of the cephalon, presence of pleural and dorsal spines and a longer tailspine. Nevertheless, the 'winged' hypostome of *Kodymirus* is highly similar to that of *Chlupacaris*, the only notable difference being the lack of a pointed median protrusion in the former. In *Kockurus* too, the hypostome is very similar to that of *Chlupacaris*, differences being the lack of a pointed median protrusion, and the more strongly recurving wings. Although a convergent origin for the hypostomes of *Kodymirus* and *Kockurus* on the one hand and *Tremaglaspis* and *Chlupacaris* on the other currently cannot be excluded, their great similarity may indicate a closer relationship between these arthropods than generally realised.

Another problematic arthropod from the Czech Republic showing some resemblance to *Chlupacaris* is the Late Ordovician *Zonoscutum solum* (Chlupáč 1999a, b). *Zonoscutum* is only known from a single cephalon. It shows a convexity comparable to that of *Chlupacaris* and has a similar lateral and frontal outline. *Zonoscutum* differs in having a procurved posterior cephalic margin, pointed genal angles, more anteriorly positioned eyes, which are also smaller, and the presence of three pairs of faint furrows flanking the vague glabellar area behind the eyes. Chlupáč (1999a) considered that the exoskeleton of *Zonoscutum* was mineralised.

Other genera showing some similarity to *Chlupacaris* are *Paleomerus* from the Lower Cambrian of Sweden (Størmer 1956; Bergström 1971; Tetlie & Moore 2004) and Poland (Orłowski 1983) and *Strabops* from the Upper Cambrian of North America (Beecher 1901; Clarke & Ruedemann 1912; Raasch 1939). Their general outline is aglaspidid-like and they most probably had a mineralised exoskeleton. *Paleomerus* was originally considered to differ from *Strabops* in having an additional twelfth triangular tergite in front of the tailspine, but Tetlie & Moore (2004) have shown this is not the case, making both genera virtually indistinguishable, a fact commented on earlier by Dunlop & Selden (1998). Both genera resemble *Chlupacaris* in having a short, broad triangular tailspine. The tailspines of *Paleomerus* and *Strabops* are, however, much more massive than that of *Chlupacaris*. Other differences include the shorter, less convex cephalon with its recurving rear margin, the widely spaced anterior position of the eyes and the complete lack of any kind of trilobation of the exoskeleton. The Chinese *Parapaleomerus sinensis* Hou, Bergström, Wang, Feng & Chen 1999, from the Lower Cambrian of Chengjiang is broadly similar to *Paleomerus* and *Strabops*, but it is distinguished from the latter by its lack of eyes and by having only ten tergites anterior to the tailspine.

Chlupacaris does not seem to particularly resemble any of the problematic Ordovician arthropods described by Černyšev (1945, 1953) or Andreeva (1957), but the Russian material is very incomplete and was rather poorly described and figured by the original authors.

7. Acknowledgements

8. References

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