

Original Article

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A new nektaspid euarthropod from the Lower Ordovician strata of Morocco

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Abstract

Nektaspids are Palaeozoic non-biomineralized euarthropods that were at the peak of their diversity during the Cambrian Period. Post-Cambrian nektaspids are a low-diversity group with only a few species described so far. Here we describe *Tariccoia tazagurtensis*, a new species of small-bodied nektaspid from the Lower Ordovician Fezouata Shale of Morocco. The new species differs from the type (and only other known) species from the Ordovician strata of Sardinia (Italy), *Tariccoia arrusensis*, in possessing more pointed genal angles, a cephalon with marginal rim, a pygidium with anterior margin curved forwards, a rounded posterior margin, and longer and more curved thoracic tergites. The two specimens of *T. tazagurtensis* sp. nov. show remains of digestive glands that are comparable to those seen in the Cambrian nektaspid *Naraoia*. The rare occurrence of *T. tazagurtensis* sp. nov. in the Fezouata Shale and the distribution of other liwiids suggest that these liwiids were originally minor members of open-marine communities during the Cambrian Period, and migrated into colder brackish or restricted seas during the Ordovician Period.

1. Introduction

Nektaspida Raymond, 1920 is a clade of artiopod euarthropods that were major constituents of Cambrian marine ecosystems, especially during Epoch 2 (Dzik & Lendzion, 1988; Hou & Bergström, 1997; Budd, 1999; Zhang *et al.* 2007; Paterson *et al.* 2010) and the Miaolingian Epoch (Whittington, 1977, 1985; Mayers *et al.* 2019). However, nektaspids are only rarely found in the younger strata of the Ordovician (Hammann *et al.* 1990; Fortey & Theron, 1994; Budil *et al.* 2003; Van Roy *et al.* 2010, 2015a; Van Roy, 2013) and Silurian (Caron *et al.* 2004) systems. Nektaspida is generally considered to contain three families – Naraoiidae, Liwiidae and Emucarididae (Paterson *et al.* 2010, 2012; Legg *et al.* 2013; Mayers *et al.* 2019) – and the genus *Buenaspis* (Lerosey-Aubril *et al.* 2017; Chen *et al.* 2019). In addition to these three families, recent phylogenetic analyses have suggested that Nektaspida may also include other artiopods not traditionally classified with this clade, such as *Petalopleura*, *Saperion*, *Tegopelte* (Mayers *et al.* 2019), *Phytophylaspis*, *Panlongia* (Legg *et al.* 2013; Hou *et al.* 2018) and *Campanamuta* (Legg *et al.* 2013). Consequently, they have been central to discussions of the first appearance and expanding diversity of euarthropods, and of animals more broadly, during the radiations of the Cambrian Period (Budd *et al.* 2001; Marshall, 2006; Daley *et al.* 2018). The possession of a non-biomineralized exoskeleton (Hammann *et al.* 1990; Edgecombe & Ramsköld, 1999), together with changes in their habitat preferences (e.g. Hammann *et al.* 1990), could explain such scarcity in the fossil record after the Miaolingian Epoch, after which time soft-tissue preservation declines in abundance and quality (Brasier *et al.* 2011; Gaines *et al.* 2012; Peters & Gaines, 2012; Daley *et al.* 2018). Consequently, the diversity of nektaspids in post-Cambrian ecosystems is low, but this seems likely to be a result of taphonomic bias, rather than representing a true evolutionary absence.

Similar bias occurs in our knowledge about the morphology and anatomy of nektaspid soft parts. The detailed information regarding morphology of the appendages, ventral sternites and digestive system is largely restricted to the Family Naraoiidae (Whittington, 1977; Chen *et al.* 1997; Vannier & Chen, 2002; Mayers *et al.* 2019; Zhai *et al.* 2019). In the family Emucarididae, only cephalic appendages have been described by Paterson *et al.* (2010). In Liwiidae, a pair of antennae were figured in *Liwia plana* (Lendzion, 1975) (see Dzik & Lendzion, 1988), but the data regarding post-antennal appendages are missing. This lack of morphological and anatomical information hinders our understanding of the phylogeny and ecology of the Nektaspida and the Artiopoda more broadly.

Here *Tariccoia tazagurtensis* sp. nov. is described from the Lower Ordovician (Tremadocian) Fezouata Shale Konservat-Lagerstätte of Morocco. This is the first species of Liwiidae (and of Nektaspida) to be described from the Lower Ordovician strata. *Tariccoia tazagurtensis* sp. nov.

shows strong similarity with *Tariccoia arrusensis* Hammann *et al.*, 1990 from the Upper Ordovician strata of Sardinia (Italy). The first description of the anterior digestive glands in Liwiidae is also presented, augmenting knowledge of soft parts in Nektaspida. Moreover, we evaluate palaeogeographic distribution patterns and habitat preferences in this euarthropod group.

2. Geological settings

The Fezouata Shale is a sequence of Lower Ordovician strata geographically belonging to the Anti-Atlas region of Morocco. North of Zagora, the Lower Ordovician strata are exposed in the Ternata plain, forming the Tremadocian – early Darriwilian Outer Feijas Shale Group (Choubert *et al.* 1947; Destombes *et al.* 1985). The Outer Feijas Shale Group unconformably overlies middle Cambrian sandstones of the Tabanite group and underlies the First Bani Group (Middle Ordovician; Destombes *et al.* 1985; Martin *et al.* 2015). The Outer Feijas Shale Group is subdivided into the Lower Fezouata Shale formation, the Upper Fezouata Shale formation, the Zini sandstone and quartzite formation, and the Tachilla Shale formation (Destombes *et al.* 1985).

In the Zagora area, the boundary between the Lower and the Upper Fezouata formation is unclear, with both formations grouped into a single, 850-m-thick unit called the ‘Fezouata Shale’ (Martin *et al.* 2016). The Fezouata Shale contains the only known Konservat-Lagerstätte from the Lower Ordovician strata, providing a critical link between the evolutionary events of the Cambrian Explosion and the Great Ordovician Biodiversification Event (Servais *et al.* 2010; Landing *et al.* 2018; Servais & Harper, 2018). The Fezouata Shale is renowned for its exceptional preservation of non-biomineralized body fossils and contains more than 160 different genera (Van Roy *et al.* 2010, 2015a, b; Saleh *et al.* 2020). The exceptional preservation occurs in two horizons (Martin *et al.* 2016; Lefebvre *et al.* 2018), the lower interval of which is about 70 m thick and situated 260–330 m above the Cambrian–Ordovician contact, and the second of which is about 50 m thick and 570–620 m above the Cambrian–Ordovician contact. With exceptional preservation, the lower interval is situated mostly within the *Araenograptus murray* Zone and lowermost parts of the *Hunnegraptus copiosus* Zone, which both correspond to a late Tremadocian age (Stage slice Tr3, see Gutiérrez-Marco & Martin, 2016; Lefebvre *et al.* 2018). This age is further corroborated by acritarchs and conodonts that also support a latest Tremadocian age for this level (Lehnert *et al.* 2016; Nowak *et al.* 2016). With exceptional preservation, the upper interval most likely belongs to the ?*Baltograptus jacksoni* Zone of Floian age (Lefebvre *et al.* 2018).

The Fezouata Shale is generally composed of argillites with blue-green to yellow-green sandy mudstone and siltstone interbeds (Destombes *et al.* 1985). It is interpreted to have been deposited around storm wave-base, in an open shallow-marine environment (Martin *et al.* 2015), ranging from proximal offshore to foreshore with a depth range of 50–150 m (Martin *et al.* 2015; Vaucher *et al.* 2016). The fluctuations of the water level are of low amplitude, but it is possible to recognize the deepest depositional environment in the middle of the Fezouata Shale (Martin *et al.* 2016).

3. Materials and methods

Two specimens assigned here to *Tariccoia tazagurtensis* sp. nov. were studied. Both specimens are covered by iron oxides and/or hydroxides and preserved as compressions in shales. To expose

the whole individual, the parts were mechanically prepared with a Micro-Jack 4 equipped with a 4/16” chisel. Photographs were taken with a digital camera Olympus E-PL8 with associated Olympus M.Zuiko 30 mm f/3.5 macro lens. The lens was equipped with a polarizing filter to reduce reflections, and a second polarizer on the light source created crossed polarization to increase contrast. All specimens were photographed with low-angle NW lighting, both dry and immersed in ethanol (to increase contrast between rock and specimen). The images were subsequently processed in Adobe Photoshop CC 19.0, to enrich brightness, contrast, shadows, highlights and saturation. Line drawings were made directly from photographs using Adobe Illustrator CC 22.0.1, like a digital camera lucida (Antcliffe & Brasier, 2011).

4. Systematic palaeontology

Order Nektaspida Raymond, 1920

Family Liwiidae Dzik & Lenzion, 1988

Emended diagnosis. Family of Nektaspida with the following combination of characters: three to four thoracic tergites that are narrower (tr) than the cephalic shield; first one or two thoracic tergites overlapped by cephalic shield; pygidium narrower than the cephalic shield, but of similar length to the cephalic shield.

Discussion. Liwiidae was originally proposed as a family, although not erected formally (Dzik & Lenzion, 1988). They used the presence of free thoracic tergites to distinguish it from Naraoiidae, which is characterized by the absence of articulating thoracic tergites. Fortey & Theron (1994) instead included the liwiid genera *Maritimella* Repina & Okuneva, 1969, *Liwia* Dzik & Lenzion, 1988, *Tariccoia* Hammann *et al.*, 1990 and *Soomaspis* Fortey & Theron, 1994 in the family Naraoiidae. They considered the presence of three or four free thoracic segments a plesiomorphic character of the group and not valid for designating a new family. Hou & Bergström (1997) formally elevated Liwiidae to family level, but without providing a diagnosis. They included the genera *Liwia*, *Tariccoia* and *Soomaspis* in the Liwiidae. Budd (1999) defined family Liwiidae by having more than one axial articulation and added the genus *Buenaspis* Budd, 1999. However, in recent phylogenetic analyses *Buenaspis* was always resolved either outside the Liwiidae, but inside Nektaspida (Legg *et al.* 2013; Lerosey-Aubril *et al.* 2017; Chen *et al.* 2019; Mayers *et al.* 2019), or even outside Nektaspida itself (Paterson *et al.* 2010, 2012). Recently, most analyses resolve Liwiidae as a monophyletic group that is sister to Naraoiidae (Paterson *et al.* 2010, 2012; Ortega-Hernández *et al.* 2013b; Lerosey-Aubril *et al.* 2017; Chen *et al.* 2019) or sister to Emucarididae (Legg *et al.* 2013; Hou *et al.* 2018). In the analysis of Mayers *et al.* (2019), liwiids were resolved within Naraoiidae, which led the authors to demote Liwiidae to the subfamily level and include it within the family Naraoiidae. We prefer to keep Liwiidae at the family level for two reasons: (1) the topology presented by Mayers *et al.* (2019) is the only analysis with Liwiidae resolved inside Naraoiidae in recent years; and (2) this topology also shows a low degree of nodal support in favour of the position of Liwiidae within Naraoiidae.

Genus *Tariccoia* Hammann *et al.*, 1990

Type species. *Tariccoia arrusensis* Hammann *et al.*, 1990; 100 m north of the mouth of the Roia Srappas into the Riu Is Arrus, c. 4 km SE of Fluminimaggiore (Sardinia, Italy); Riu is Arrus Member of the Monte Argentu Formation (Upper Ordovician, see Hammann & Leone, 1997).

Emended diagnosis. A genus of Liwiidae with the following combination of characters: cephalic shield sub-circular; four

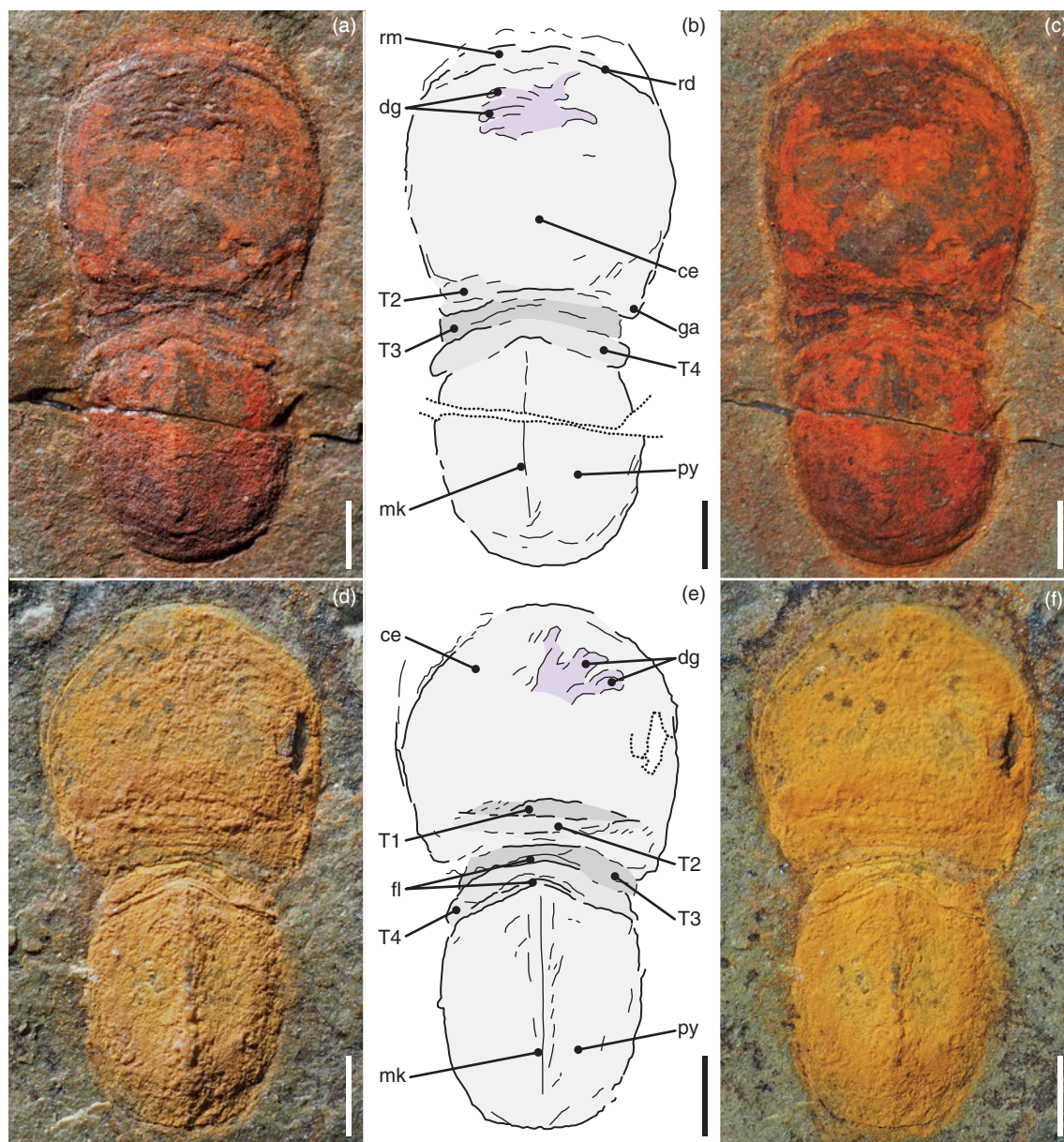


Fig. 1. (Colour online) *Tariccoia tazagurtensis* sp. nov., *Araneograptus murrayi* Zone (Tremadocian, Lower Ordovician), Fezouata Shale, near Beni Zouli (Morocco). MGL 102155a, holotype, (a) photographed dry, (b) interpretative drawing and (c) photographed under ethanol. MGL 103036a, (d) photographed dry, (e) interpretative drawing and (f) photographed under ethanol. ce, cephalic shield; dg, digestive glands; fl, flange; ga, genal angle; mk, median keel; py, pygidium; rd, marginal ridge; rm, marginal rim; T1–T4, thoracic tergite one to four. Scale bar is 1 mm.

thoracic tergites with rounded lateral extremes; first one or two thoracic tergites overlapped by posterior margin of cephalic shield; pygidium longer than wide, with a long median keel and smooth (non-spinose) margin.

Remarks. The diagnosis of *Tariccoia* provided by Hammann *et al.* (1990) is now regarded as the diagnosis of the type species *Tariccoia arrusensis* Hammann *et al.*, 1990.

Discussion. *Liwia* differs from *Tariccoia* in its pointed tips of the thoracic tergites and sub-trapezoidal pygidium with well-defined axial part and with marginal spines. *Soomaspis* differs from *Tariccoia* by having only three thoracic tergites with articulating half-rings, an axial part defined on the trunk and a sub-circular pygidium showing five pleural furrows.

Tariccoia tazagurtensis sp. nov.

Figures 1–3

Zoobank no. [urn:lsid:zoobank.org:act:E5DAD3BB-FD01-4F6B-8272-06583783276B](https://doi.org/10.26434/chemrxiv-2020-06583)

Material, locality, horizon. Holotype (Fig. 1a–c): MGL 102155a (part) and MGL 102155b (counterpart). Other material: MGL 103036a (part) and MGL 103036b (counterpart). Both specimens come from an outcrop located in the Ternata plain, c. 18 km NW of the city of Zagora (Morocco) and c. 6 km NNE of the village of Beni Zouli. The outcrop falls within the lower exceptional preservation interval of the Fezouata Shale (*Araneograptus murrayi* Zone, Tremadocian, Lower Ordovician). Material is stored in the collections of the Cantonal Museum of Geology (Lausanne, Switzerland). Exact locality data curated with the specimens.

Etymology. In Tamazight language, Tazagurt (ⵜⴰⴳⴰⵖⴰⵔⵜ) in Neo-Tifinagh script) is a name for the city of Zagora near which

the material was discovered. Tamazight is a language of the Amazigh people, an ethnic group that is indigenous to North Africa and who have a large population in the Anti-Atlas region of Morocco.

Diagnosis. A small (up to 8 mm long) species of *Tariccoia* having the following unique combination of characters: cephalon with pointed genal angles and marginal rim, pygidium with anterior margin curved forwards, a rounded posterior margin and a medial keel that does not reach posterior pygidial border.

Description. The total exoskeletal length is 6.68 mm in specimen MGL 103036a and 7.24 mm in specimen MGL 102155a. Cephalic shield is sub-circular in outline and its sagittal length ranges between 3.04 mm in MGL 103036a and 3.39 mm in MGL 102155a, and transverse width between 3.47 mm in MGL 103036a and 3.79 mm in MGL 102155a. The anterior and lateral margins of the cephalic shield ('ce' in Fig. 1b, e) are rounded, and the posterior cephalic margin is anteriorly curved. The cephalic shield reaches its maximum width near the mid-length. A distinct anterior marginal cephalic rim ('rm' in Fig. 1b) is delineated by a sharp ridge ('rd' in Fig. 1b). The length of the cephalic rim extends to about one-fifth of the cephalic shield, being longest (sag) in the medial part. The postero-lateral edges of the cephalic shield form distinct, pointed genal angles ('ga' in Fig. 1b) with rounded tips. The dorsal surface of the cephalic shield is without trilobation, facial sutures or visual organs. The holotype MGL 102155a (Fig. 1a–c) shows raised finger-like structures ('dg' in Fig. 1b, see also Fig. 2a) that are connected medially and located in the anterior half of the cephalic shield. In specimen MGL 103036a (Fig. 1d, e), the surface of the cephalic shield preserves distinct, radially arranged, wrinkles ('dg' in Fig. 1e, see also Fig. 2b).

The thorax is comparatively narrow (tr), being approximately 70–80% of the width of cephalic shield. It is composed of four thoracic tergites, but the anterior two (1st and 2nd) tergites ('T1' and 'T2' in Fig. 1b, e) are overlapped by the posterior portion of the cephalic shield ('ce' in Fig. 1b, e), and consequently are not easily discernible in the holotype, but are clearly visible in MGL 103036a. The two posterior (3rd and 4th) thoracic tergites ('T3' and 'T4' in Fig. 1b, e) are completely exposed (Fig. 1a–f). In dorsal view all thoracic tergites are curved backwards and slightly downwards abaxially. The thoracic tergites become slightly wider (tr) and more curved posteriorly, so the 4th tergite is the widest and is in its medial part strongly deflected forwards. The first tergite seems to taper abaxially. No distinct axial lobe is visible in any of the tergites. The lateral extremes of each tergite end in rounded tips. No articulating facets or articulating half-rings are present in the thoracic tergites. The tergites seem to be articulated with each other by a narrow flange ('fl' in Fig. 1e) that is visible and runs along the anterior margin of the 3rd and 4th tergites (Fig. 1d–f), but is probably also present in the 1st and 2nd.

Pygidium ('py' in Fig. 1b, e) is sub-oval in outline, elongated and measures 3.08 mm (MGL 103036a) and 3.18 mm (MGL 102155a) in sagittal length and 2.52 mm (MGL 103036a) and 3.04 mm (MGL 102155a) in transverse width. Consequently, the pygidium is approximately 25% narrower than the cephalic shield, and is just slightly wider than the thorax. The anterior margin of the pygidium is curved forwards, exactly matching the posterior margin of the last thoracic tergite. A narrow flange ('fl' in Fig. 1e) runs along the anterior margin of the pygidium. The posterior margin of the pygidium is rounded. The central part of the pygidium is slightly inflated and slopes down abaxially and posteriorly. In its medial part, the pygidium carries a pronounced median keel ('mk' in



Fig. 2. (Colour online) *Tariccoia tazagurtensis* sp. nov., *Araneograptus murrayi* Zone (Tremadocian, Lower Ordovician), Fezouata Shale, near Beni Zouli (Morocco); close-up of the anterior part of the cephalic shield of the holotype (a) MGL 102155a and (b) MGL 103036a. (a) Arrows pointing to proximal parts of digestive glands and (b) to bifurcation of digestive glands. Scale bar is 1 mm.

Fig. 1b, e) that is nearly as long as the entire pygidium but does not reach its posterior margin.

Discussion. *Tariccoia tazagurtensis* sp. nov. resembles *Tariccoia arrusensis* from the Ordovician strata of Sardinia (Hammann *et al.* 1990; Hammann & Leone, 1997) in overall morphology of both the cephalon and pygidium, and in possessing four thoracic tergites with rounded lateral extremes. The differences between these two species are (see also Fig. 3a, b for comparison): (1) more pointed genal angles in *T. tazagurtensis* sp. nov.; (2) the cephalon with marginal rim in *T. tazagurtensis* sp. nov.; (3) the pygidium in *T. tazagurtensis* sp. nov. has anterior margin curved forwards and rounded posterior margin, while in *T. arrusensis* the anterior pygidial margin is nearly straight and the posterior margin is pointed; (4) the thoracic tergites are proportionally longer (sag.) and more curved in *T. tazagurtensis* sp. nov.; (5) the median keel in *T. tazagurtensis* sp. nov. does not reach the posterior pygidial margin, but does in *T. arrusensis*; and (6) the pygidium of *T. tazagurtensis* sp. nov. lacks the sharp lateral edges forming a ventral ridge seen in *T. arrusensis* (*sensu* Hammann *et al.* 1990, text-fig. 4).

The sharp ridge that separates the marginal rim of the cephalon is one of the characters that distinguishes *T. tazagurtensis* sp. nov.

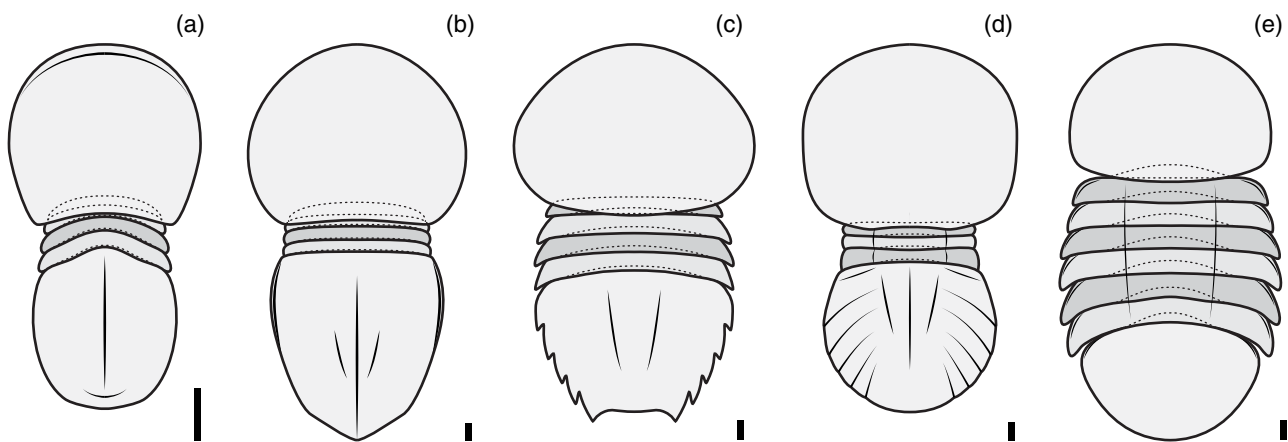


Fig. 3. Reconstruction of members of the family Liwiidae Dzik & Lendzion, 1988 and the genus *Buenaspis* Budd, 1999: (a) *Tariccoia tazagurtensis* sp. nov., Fezouata Shale, Morocco; (b) *Tariccoia arrusensis* Hammann *et al.*, 1990, Riu is Arrus Member of the Monte Argentu Formation, Sardinia; (c) *Liwia plana* (Lendzion, 1975), Zawiszyń Formation, Poland; (d) *Soomaspis splendida* Fortey & Theron, 1994, Soom Shale, South Africa; (e) *Buenaspis fortleyi* Budd, 1999, Buen Formation, Greenland. Dotted lines represent underlying structures of the dorsal exoskeleton. Scale bar is 1 mm. Reconstruction of *T. arrusensis*, *L. plana*, *S. splendida* and *B. fortleyi* based on Hammann *et al.* (1990), personal observation, Fortey & Theron (1994) and Budd (1999), respectively.

from *T. arrusensis*. This structure is only preserved well in the holotype (MGL 102155, Fig. 1a, b). For this reason, it is not easy to interpret it unambiguously. This structure could also be interpreted as an imprint of the cephalic doublure or compaction-related deformation of the cephalic margin.

The exact number of thoracic tergites in *T. tazagurtensis* sp. nov. is not easy to determine, because the anterior thoracic tergites are overlapped by the cephalic shield. Such an overlap in *Tariccoia*, *Liwia* and *Soomaspis* was recognized by Edgecombe & Ramsköld (1999, character 9) and used as one of the synapomorphies of Liwiinae (= Liwiidae in this paper). Contrary to Edgecombe & Ramsköld (1999), we suggest that in *Tariccoia* the cephalic shield overlaps the first and also the second (at least partially) thoracic tergite. Usually two or at most three thoracic tergites are exposed in all articulated specimens of *T. arrusensis*, while specimens lacking the cephalic shield always show four (Hammann *et al.* 1990, pl. 1–3; Hammann & Leone, 1997, pl. 1, figs 1–3). In some articulated specimens, however, the anterior one or two tergites are imprinted onto the posterior portion of the cephalic shield (Hammann *et al.* 1990, pl. 1, figs 1, 2, 5). Similar exoskeletal configuration was likely present also in *T. tazagurtensis* sp. nov. Specimen MGL 103036a (Fig. 1d–f) clearly shows two posterior tergites, and traces of two more under the posterior part of the cephalic shield. Although the slightly different shape of the 1st thoracic tergite (Fig. 1d) in *T. tazagurtensis* sp. nov. resembles an articulating half-ring, the interpretation of it as a thoracic tergite is favoured for two main reasons. First, it is too wide to be an articulating half-ring, and second, it is quite similar to the shape of first thoracic tergite in *T. arrusensis* (cf. Hammann *et al.* 1990, pl. 2, fig. 2a, b).

The articulation of individual thoracic tergites and of the pygidium was apparently facilitated by a structure morphologically similar to a flange as is known in the pleural parts of numerous, especially basal, trilobites (Whittington, 1989; Geyer, 1996; Esteve *et al.* 2013; Ortega-Hernández *et al.* 2013a; Laibl *et al.* 2016). Such an articulation can be regarded as functionally simple, as no other articulation structures are present (e.g. articulating half-rings, fulcrum or articulating facet; cf. Bruton & Haas, 1997). With such a simple articulation, it seems unlikely that *T. tazagurtensis* sp. nov. was able to enrol, as the flange does not allow for rotation movement of arched structures, such as the thoracic tergites of *T. tazagurtensis* sp. nov.

5. Digestive system in *Tariccoia tazagurtensis* sp. nov.

There is currently little understanding of the soft anatomy in the Liwiidae. So far, only a pair of antennae were described for *Liwia plana* (Dzik & Lendzion 1988), and no other information of the postantennal appendages, the digestive system or the nervous system has been reported.

The holotype of *T. tazagurtensis* sp. nov. shows finger-like structures connected medially under the anterior half of the cephalic shield (Fig. 2a). We interpret these structures as the proximal parts of a pair of well-developed ramified digestive glands connected to an anterior part of the digestive tract. Both their preservation and morphology strongly resemble such structures as seen in *Naraoia spinosa* Zhang & Hou, 1985 from Chengjiang (cf. Vannier & Chen, 2002, fig. 2A, B; Zhang *et al.* 2007, figs 28, 29). The distal ramification of the digestive glands is not preserved in the holotype, but the other specimen (MGL 103036a) shows numerous wrinkles, some of which seem to bifurcate distally (Fig. 2b). These are likely not compression-related wrinkles, which are usually concentric (cf. Hammann *et al.* 1990; Budd, 1999; Caron *et al.* 2004) or randomly orientated (Peng *et al.* 2012), as opposed to radial in MGL 103036a. These structures therefore likely represent the distal parts of the ramified digestive glands. Digestive structures are known from *Megistaspis (Ekeraspis) hammondi* Corbacho & Vela, 2010 and other trilobites from the Fezouata Shale (Van Roy *et al.* 2015a; Gutiérrez-Marco *et al.* 2017), showing that preservation of gut features is possible at this locality. Preservation of internal soft tissues in general is relatively rare in the Fezouata Shale compared with other Burgess Shale-type preservations such as the Burgess and the Chengjiang Biota, and is usually only found in the presence of a mineralized or sclerotized external cuticle (Saleh *et al.* 2020), as is the case with trilobites and *T. tazagurtensis*, respectively.

Within Nektaspida the digestive system is known only in Naraoiidae and, until now, two different morphotypes have been recognized (Vannier & Chen, 2002): one with a long, extensively ramified anterior pair of digestive glands, present in species of *Naraoia* Walcott, 1912 and in *Misszhouia canadensis* Mayers *et al.*, 2019 (see Vannier & Chen, 2002; Mayers *et al.* 2019), and one with only short digestive glands, present in *Misszhouia longicaudata* Zhang & Hou, 1985 (Vannier & Chen, 2002). Given that

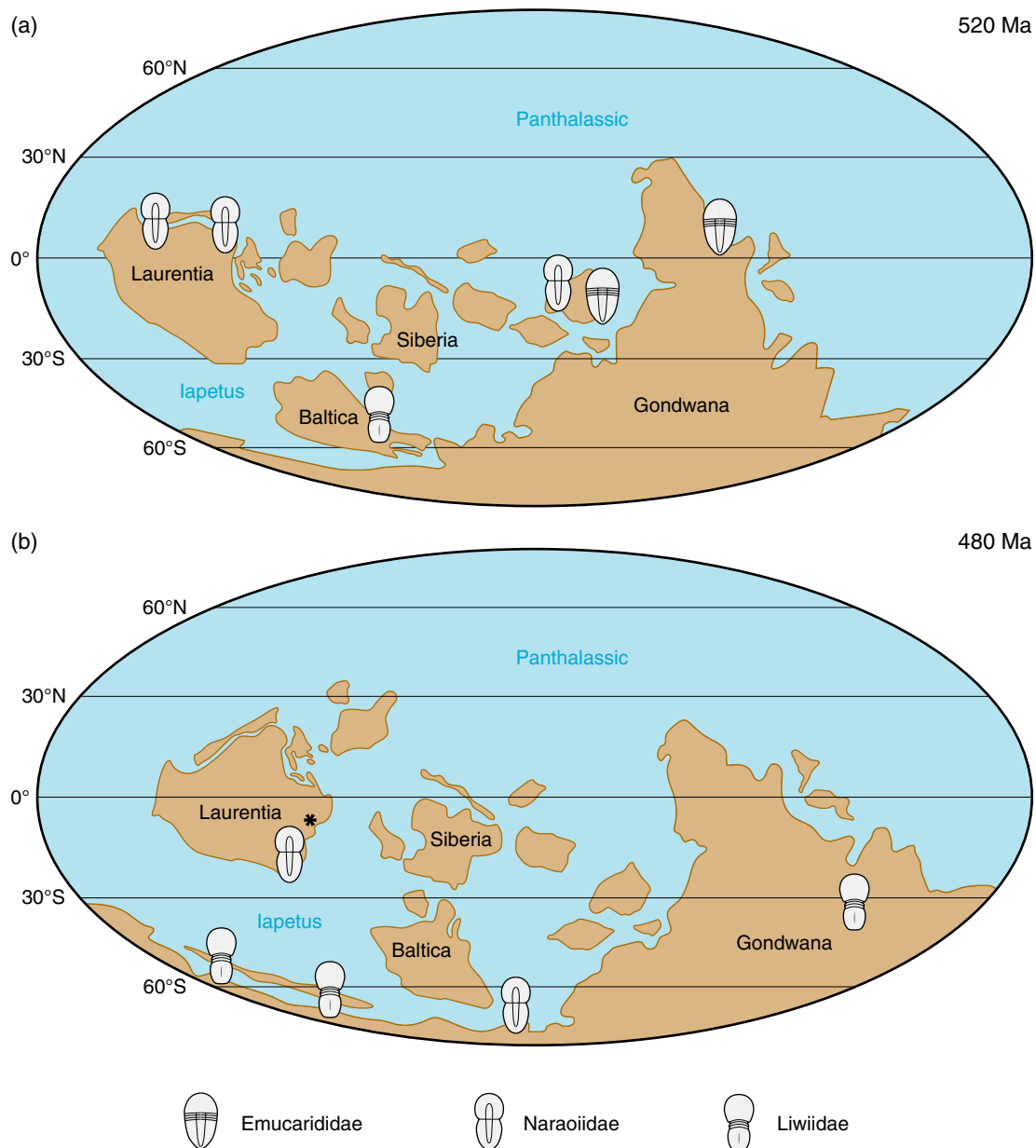


Fig. 4. (Colour online) Palaeogeographical distribution of nektaspids during the (a) Cambrian, (b) Ordovician and Silurian periods. Map reconstruction for (a) early Cambrian (520 Ma) and (b) Early Ordovician, Tremadocian (480 Ma) time. Redrawn, adapted and simplified from Torsvik & Cocks (2013a, figs 2.7, 2.11). The Silurian species *Naraoia bertensis* Caron *et al.* 2004 is marked by asterisk. Distribution data based on Whittington (1977), Robison (1984), Dzik & Lenzion (1988), Hammann *et al.* (1990), Fortey & Theron (1994), Hou & Bergström (1997), Chen *et al.* (1997), Budd (1999), Budil *et al.* (2003), Caron *et al.* (2004), Schwimmer & Montante (2007), Zhang *et al.* (2007), Paterson *et al.* (2010), Peng *et al.* (2012), Zhang *et al.* (2012), Fu *et al.* (2019), Mayers *et al.* (2019) and Lerosey-Aubril *et al.* (2020).

the digestive system of *T. tazagurtensis* sp. nov. resembles the ramified pattern seen in *Naraoia* and *M. canadensis*, we suggest that these morphologies are homologous. Indeed, the majority of phylogenies would suggest a single origin for the well-developed ramified digestive glands in both naraoids and liwiids (e.g. Paterson *et al.* 2010; Ortega-Hernández *et al.* 2013b; Lerosey-Aubril *et al.* 2017; Mayers *et al.* 2019).

6. Distribution and habitat preferences in liwiids

The distribution of liwiids shows a different pattern from that of other nektaspids (Fig. 4). Naraoiids have a comparatively wide distribution, being known from low latitudes of Laurentia/Laurussia

(Whittington, 1977; Robison, 1984; Caron *et al.* 2004; Schwimmer & Montante, 2007; Mayers *et al.* 2019; Lerosey-Aubril *et al.* 2020), South China (Chen *et al.* 1997; Hou & Bergström, 1997; Zhang *et al.* 2007; Peng *et al.* 2012; Fu *et al.* 2019) and possibly also from high latitudes on the West Gondwana margin (Budil *et al.* 2003). Emucaridids are restricted to low-latitude areas of East Gondwana (Paterson *et al.* 2010) and South China (Zhang *et al.* 2012). According to the results of Mayers *et al.* (2019), putative nektaspids including petalopleurans indicate a broader distribution, equatorial in Laurentia (Whittington, 1985; Budd 1999, 2011), South China (Hou & Bergström, 1997) and Siberia (Ivantsov, 1999), with the exception of *Xandarella mauretana* Ortega-Hernández *et al.*, 2017 from West Gondwana (Ortega-Hernández *et al.* 2017).

From the Cambrian strata, the only liwiids (*sensu stricto*, i.e. without genus *Buenaspis*) so far described are *Liwia convexa* (Lendzion, 1975) and *Liwia plana* (see Lendzion, 1975; Dzik & Lendzion, 1988), both known from boreholes in NE Poland (Baltica, Fig. 4). An Atdabanian age for the *Liwia*-bearing beds has been inferred (Dzik & Lendzion, 1988), which roughly corresponds to the provisional Cambrian Stage 3 within the early Cambrian subdivision (Zhang *et al.* 2017), making this older than the more famous and fossiliferous Early Cambrian Konservat-Lagerstätten: the Sirius Passet and Chengjiang biotas (Zhang *et al.* 2001; Harper *et al.* 2019). After this early first appearance, liwiids are completely absent from the renowned low-latitude Konservat-Lagerstätten of the rest of the Cambrian strata, including Sirius Passet (Harper *et al.* 2019), the Chengjiang Biota (Hou & Bergström, 1997; Zhao *et al.* 2009), Emu Bay Shale (Paterson *et al.* 2016), Burgess Shale (Dunne *et al.* 2008; Caron & Jackson, 2008) and Weeks Formation (Lerosey-Aubril *et al.* 2018). This suggests that, during the Cambrian Period, liwiids were either extremely rare, formed restricted populations and/or preferred specific environmental conditions that were not conducive for exceptional preservation.

Previously published Ordovician liwiids are only known from localities that represent atypical marine conditions, where nektaspids are not commonly found. *Soomaspis splendida* Fortey & Theron, 1994 is known only from the Soom Shale Member of the Cedaberg Formation, South Africa (Fortey & Theron, 1994; Fig. 4), where the depositional environment is interpreted to be brackish-to-marine setting, close to a retreating and down-wasting ice front (Theron *et al.* 1990; Aldridge *et al.* 1994). *Tariccoia arrusensis* occurs abundantly in the Riu Is Arrus Member of the Monte Argentu Formation of SW Sardinia (Hammann *et al.* 1990; Hammann & Leone, 1997) that is considered to be largely deposited in terrestrial and marginal marine environments (Oggiano *et al.* 1986; Hammann *et al.* 1990). Sedimentological, biostratigraphical and palaeontological data suggest that *T. arrusensis* inhabited a restricted marine oxygen-deficient (sheltered bay, lagoon) environment, populated mainly by this species and macroscopic algae (Hammann *et al.* 1990; Hammann & Leone, 1997).

Tariccoia tazagurtensis sp. nov. is the only Ordovician liwiid described from a typical open-marine deposits. Unlike the abundant *T. arrusensis* of the Monte Argentu Formation, *T. tazagurtensis* sp. nov. is a very rare faunal component of the Fezouata Shale community. This species is not even locally abundant as shown by its general absence from most of the excavated sites and from both the proximal and distal parts of the Fezouata Shale, despite extensive collecting in these areas. Moreover, the available specimens of *T. tazagurtensis* sp. nov. are complete and articulated. Considering their non-biomineralized exoskeleton and the presence of digestive glands, these specimens likely represent carcasses. Interpretations of the palaeoenvironmental settings of the Fezouata Shale (Martin *et al.* 2016) suggest that these fossils experienced little or no transport before deposition. It therefore seems that *T. tazagurtensis* sp. nov. was living in the environment in which it was found.

From a palaeogeographic point of view, all Ordovician liwiids were restricted to cold-water settings (Fig. 4). Both *T. tazagurtensis* sp. nov. and *T. arrusensis* are known from very high latitudes on the West Gondwana margin (cf. Scotese, 2004; Torsvik & Cocks, 2013a, b), close to the South Pole. *Soomaspis splendida* comes from an area that was located at around 30° S during Late Ordovician time (Torsvik & Cocks, 2013a, b), apparently in cold water very close to a retreating ice shield (Aldridge *et al.* 1994). Liwiids

may therefore have preferred cold-water conditions (at least during the Ordovician Period), in contrast to naraoids, emucaridids and other nektaspids.

The stratigraphic distribution of liwiids suggest that they were originally components of open-marine communities (*Liwia*, *T. tazagurtensis* sp. nov.), but were apparently rare. By Middle and Late Ordovician time, some of their members had migrated to brackish-marine environments (*S. splendida*) or to restricted areas where they formed locally abundant populations (*T. arrusensis*).

7. Summary

1. A new species of a small nektaspid euarthropod – *Tariccoia tazagurtensis* sp. nov. – is described from the Lower Ordovician (Tremadocian) Fezouata Shale Konservat-Lagerstätte of Morocco. This species is characterized by a sub-circular cephalon with pointed genal angles and with a marginal rim; a thorax consisting of four tergites, the 1st and 2nd of which are overlapped by the cephalic shield; and by a pygidium with its anterior margin curved forwards, a rounded posterior margin and a long medial keel that does not reach the posterior pygidial border.
2. *Tariccoia tazagurtensis* sp. nov. preserves remains of the anterior part of the digestive tract, which is comparable to the ramified digestive glands seen in species of *Naraoia* and *Misszhouia canadiensis*. This is the first description of the digestive system in Liwiidae.
3. From the distribution and abundance data of Liwiidae, it is likely that members of this group preferred cold-water settings in contrast to other nektaspids, and were members of open-marine communities during their early evolutionary history, but later migrated to brackish or restricted environments.

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Conflict of interest. None.

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