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3 22 digestive glands that are comparable to those seen in the Cambrian **nektaspid** *Naraoia*. The rare
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5 23 occurrence of *T. tazagurtensis* sp. nov. in the Fezouata Shale and the distribution of other **liwiids**
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8 24 suggest that these **liwiids** were originally minor members of open marine communities in the
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10 25 Cambrian, and migrated into colder brackish or restricted seas in the Ordovician.
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13 26 **Keywords:** *Tariccoia*; Nektaspida; Euarthropoda; Ordovician; Morocco; Fezouata Shale
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19 28 1. Introduction

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22 29 Nektaspida Raymond, 1920 is a clade of artiopod euarthropods that were major constituents of
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24 30 Cambrian marine ecosystems, especially during Epoch 2 (Dzik and Lenzion 1988, Hou and
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26 31 Bergström 1997, Budd 1999, Zhang et al. 2007, Paterson et al. 2010) and the Miaolingian
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28 32 (Whittington 1977, 1985, Mayers et al. 2019). **Nektaspids, however, are only rarely found in the**
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31 33 **younger strata of the Ordovician (Hamman et al. 1990, Fortey and Theron 1994, Budil et al.**
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33 34 **2003, Van Roy et al. 2010, Van Roy 2013, Van Roy et al. 2015a) and Silurian (Caron et al.**
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35 35 **2004).** Nektaspida is generally considered to contain three families: Naraoiidae, Liwiidae and
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37 36 **Emucarididae** (Paterson et al. 2010, Paterson et al. 2012, Legg et al. 2013, Mayers et al. 2019),
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39 37 and the genus *Buenaspis* (Lerosey-Aubril et al. 2017, Chen et al. 2019). **In addition to these three**
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41 42 **families, recent phylogenetic analyses have suggested that Nektaspida may also include other**
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43 43 **artiopods not traditionally classified with this clade, such** as *Petalopleura*, *Saperion*, *Tegopelte*
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45 46 (Mayers et al. 2019), *Phytophylaspis*, *Panlongia*, (Legg et al. 2013, Hou et al. 2018) and
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48 49 *Campanamuta* (Legg et al. 2013). Consequently, they have been central to discussions of the
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50 50 first appearance and expanding diversity of **euarthropods**, and of animals more broadly, during
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52 51 the radiations of the Cambrian Period (Budd et al. 2001, Marshall 2006, Daley et al. 2018). The
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3 44 possession of a non-biomineralised exoskeleton (Hammann et al. 1990, Edgecombe and
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5 45 Ramsköld 1999), together with changes in their habitat preferences (e.g. Hammann et al. 1990),
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7 46 could explain such scarcity in the fossil record after the Miaolingian, after which time soft tissue
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9 47 preservation declines in abundance and quality (Brasier et al. 2011, Peters and Gaines 2012,
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11 48 Gaines et al. 2012, Daley et al. 2018). Consequently, the diversity of nektaspids in post-
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13 49 Cambrian ecosystems is low, but this seems likely to be a result of taphonomic bias, rather than
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15 50 representing a true evolutionary absence.

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20 51 Similar bias occurs in our knowledge about the morphology and anatomy of nektaspid soft-parts.
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22 52 The detailed information regarding morphology of the appendages, ventral sternites and
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24 53 digestive system is largely restricted to the Family Naraoiidae (Whittington 1977, Chen et al.
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26 54 1997, Vannier and Chen 2002, Mayers et al. 2019, Zhai et al. 2019). In the family Emucarididae
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28 55 only cephalic appendages have been described by Paterson et al. (2010b). In Liwiidae, a pair of
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30 56 antennae were figured in *Liwia plana* (Lendzion, 1975) (see Dzik and Lendzion 1988), but the
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32 57 data regarding post-antennal appendages are missing. This lack of morphological and anatomical
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34 58 information hinders our understanding of the phylogeny and ecology of the Nektaspida and the
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36 59 Artiopoda more broadly.

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41 60 Herein *Tariccoia tazagurtensis* sp. nov., is described from the Lower Ordovician (Tremadocian)
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43 61 Fezouata Shale Konservat-Lagerstätte of Morocco. This is the first species of Liwiidae (and of
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45 62 Nektaspida) to be described from the Lower Ordovician. *Tariccoia tazagurtensis* sp. nov. shows
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47 63 strong similarity with *Tariccoia arrusensis* Hammann et al., 1990 from the Middle or Upper
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49 64 Ordovician of Sardinia (Italy). The first description of the anterior digestive glands in Liwiidae,
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51 65 is also presented augmenting knowledge of soft parts in Nektaspida. Moreover,
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3 66 palaeogeographic distribution patterns and habitat preferences are evaluated in this euarthropod
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12 13 14 70 **2. Geological settings**

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17 71 The Fezouata Shale is a sequence of Lower Ordovician strata geographically belonging to the
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19 72 Anti-Atlas region of Morocco. North of Zagora, the Lower Ordovician is exposed in the Ternata
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21 73 plain, forming the Outer Feijas Shale Group, Tremadocian to early Darriwilian (Choubert et al.
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23 74 1947, Destombes et al. 1985). The Outer Feijas Shale Group unconformably overlies middle
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25 75 Cambrian sandstones of the Tabanite group and underlies the First Bani Group (Middle
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27 76 **Ordovician**; Destombes et al. 1985, Martin et al. 2015). The Outer Feijas Shale Group is
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29 77 subdivided into the Lower Fezouata Shale formation, the Upper Fezouata Shale formation, the
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31 78 Zini sandstone and quartzite formation and the Tachilla Shale formation (Destombes et al. 1985).

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33 79 In the Zagora area, the boundary between the Lower and the Upper Fezouata formation is
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35 80 unclear, with both formations grouped into a single, 850 m thick unit called the “Fezouata Shale”
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37 81 (Martin et al. 2016). The **Fezouata Shale contains** the only **known** Konservat-Lagerstätte from
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39 82 the Lower **Ordovician** providing a critical link between the evolutionary events of the Cambrian
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41 83 Explosion and the Great Ordovician Biodiversification Event (Servais et al. 2010, Landing et al.
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43 84 2018, Servais and Harper 2018). The Fezouata **Shale** is renowned for its exceptional preservation
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45 85 of **non-biomineralised body fossils** and contains more than 160 different genera (Van Roy et al.
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47 86 2010, Van Roy et al. 2015b, Van Roy et al. 2015a, Saleh et al. 2019). The exceptional
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49 87 preservation occurs in two horizons (Martin et al. 2016, Lefebvre et al. 2018), the lower interval
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3 88 of which is about 70 m thick and situated 260–330 m above the Cambrian-Ordovician contact,
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5 89 and the second of which is about 50 m thick and 570–620 m above the Cambrian-Ordovician
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8 90 contact. The lower interval with exceptional preservation is situated mostly within the
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10 91 *Araenograptus murray* Zone and lowermost parts of the *Hunnegraptus copiosus* Zone, which
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12 92 both correspond to **the** late Tremadocian (Stage slice Tr**3**, see Gutiérrez-Marco and Martin 2016,
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14 93 Lefebvre et al. 2018). This age is further corroborated by acritarchs and conodonts that also
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16 94 support **a** latest Tremadocian age for this level (Lehnert et al. 2016, Nowak et al. 2016). The
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18 95 upper interval with exceptional preservation most likely belongs to the *?Baltograptus jacksoni*
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20 96 Zone, which is of Floian age (Lefebvre et al. 2018).

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24 97 The Fezouata Shale is generally composed of **argillites** with blue-green to yellow green sandy
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26 98 mudstone and siltstones **interbeds** (Destombes et al. 1985). It is interpreted to have been
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28 99 deposited around storm wave-base, in an open shallow marine environment (Martin et al. 2015),
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30 100 ranging from proximal offshore to foreshore with a depth range from 50 to 150 m (Martin et al.
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32 101 2015, Vaucher et al. 2016). The fluctuations of the water level are of low amplitude, but it is
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34 102 possible to recognize the deepest depositional environment in the middle of the Fezouata Shale
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36 103 (Martin et al. 2016).

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47 106 Two specimens assigned here to *Tariccoia tazagurtensis* sp. nov. were studied. Both specimens
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49 107 are covered by iron oxides and/or hydroxides and preserved as compressions in shales. To
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51 108 expose the whole individual, the parts were mechanically prepared with a Micro-Jack 4 equipped
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53 109 with 4/16" chisel. Photographs were taken with a digital camera Olympus E-PL8 with associated
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3 110 Olympus M.Zuiko 30 mm f/3,5 macro lens. The lens was equipped with a polarizing filter to
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5 111 reduce reflections, and a second polarizer on the light source created crossed polarization to
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7 112 increase contrast. All specimens were photographed with low angle NW lighting, both dry and
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9 113 immersed in ethanol (to increase contrast between rock and specimen). The images were
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11 114 subsequently processed in Adobe Photoshop CC 19.0, to enrich brightness, contrast, shadows,
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13 115 highlights and saturation. Line drawings were made directly from photographs using Adobe
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15 116 Illustrator CC 22.0.1., like a digital *camera lucida* (Antcliffe and Brasier 2011).
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26 119 4. Systematic palaeontology

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29 120 Order Nektaspida Raymond, 1920

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31 121 Family Liwiidae Dzik & Lenzion, 1988

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37 123 *Emended diagnosis.* Family of Nektaspida with the following combination of characters: three to
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39 124 four thoracic tergites that are narrower (tr.) than the cephalic shield; first **one or** two thoracic
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41 125 tergites overlapped by cephalic shield; **pygidium** narrower than the cephalic shield, but of similar
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43 126 length to the cephalic shield.
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50 128 *Discussion.* Liwiidae was originally proposed as a family, although not erected formally (Dzik
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52 129 and Lenzion 1988). They used the presence of free thoracic tergites to distinguish it from
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54 130 **Naraoiidae**, which is characterized by the absence of **articulating thoracic** tergites. Fortey and
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3 131 Theron (1994) instead included the liwiid genera *Maritimella* Repina & Okuneva, 1969, *Liwia*
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5 132 Dzik & Lenzion, 1988, *Tariccoia* Hammann et al., 1990, and *Soomaspis* Fortey & Theron, 1994
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8 133 in the family Naraoidae. They considered the presence of three or four free thoracic segments a
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10 134 plesiomorphic character of the group and not valid for designating a new family. Hou and
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12 135 Bergström (1997) formally elevated Liwiidae to family level, but without providing a diagnosis.
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14 136 They included the genera *Liwia*, *Tariccoia* and *Soomaspis* in the Liwiidae. Budd (1999) defined
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16 137 family Liwiidae by having more than one axial articulation and added the genus *Buenaspis*
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18 138 Budd, 1999. However, in recent phylogenetic analyses *Buenaspis* was always resolved either
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20 139 outside the Liwiidae, but inside Nektaspida (Legg et al. 2013, Lerosey-Aubril et al. 2017,
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22 140 Mayers et al. 2019, Chen et al. 2019), or even outside Nektaspida itself (Paterson et al. 2010,
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24 141 Paterson et al. 2012). Recently, most analyses resolve Liwiidae as a monophyletic group that is
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26 142 sister to **Naraoidae** (Paterson et al. 2010, Paterson et al. 2012, Ortega-Hernández et al. 2013a,
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28 143 Lerosey-Aubril et al. 2017, Chen et al. 2019) or sister to **Emucarididae** (Legg et al. 2013, Hou et
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30 144 al. 2018). In the analysis of Mayers et al. (2019) liwiids were resolved within Naraoidae, which
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32 145 led the authors to **demote** Liwiidae to the subfamily level and include it within the family
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34 146 Naraoidae. **We prefer to keep Liwiidae at the family level for two reasons: 1) the topology**
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36 147 **presented by Mayers et al. (2019) is the only analysis with Liwiidae resolved inside Naraoidae**
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38 148 **in recent years; and 2) this topology also shows a low degree of nodal support in favour of the**
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40 149 **position of Liwiidae within Naraoidae.**
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51 151 Genus *Tariccoia* Hammann, Laske and Pillola 1990
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3 153 *Type species. Tariccoia arrusensis* Hammann et al., 1990; 100 m N of the mouth of the Roia

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5 154 Srappas into the Riu Is Arrus, ca. 4 km SE of Fluminimaggiore (Sardinia, Italy); Riu is Arrus

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8 155 Member of the Monte Argentu Formation (Upper Ordovician, see Hammann and Leone 1997).

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14 157 *Emended diagnosis.* A genus of Liwiidae with the following combination of characters: cephalic

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16 158 shield sub-circular; four thoracic tergites with rounded lateral extremes; first one or two thoracic

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18 159 tergites overlapped by posterior margin of cephalic shield; pygidium longer than wide, with a

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20 160 long median keel and smooth (non-spinose) margin.

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26 162 *Remarks.* The diagnosis of *Tariccoia* provided by Hammann et al. (1990) is now regarded as the

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28 163 diagnosis of the type species *Tariccoia arrusensis* Hammann et al., 1990.

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34 165 *Discussion.* *Liwia* differs from *Tariccoia* in its pointed tips of the thoracic tergites and sub-

35
36 166 trapezoidal pygidium with well-defined axial part and with marginal spines. *Soomaspis* differs

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38 167 from *Tariccoia* by having only three thoracic tergites with articulating half-rings, an axial part

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40 168 defined on the trunk, and by a sub-circular pygidium showing five pleural furrows.

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48 170 *Tariccoia tazagurtensis* sp. nov.

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50 171 Figs 1–3

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3 173 *Zoobank no.* Will be added.
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9 175 *Material, locality, horizon.* Holotype (Fig. 1a-c): MGL 102155a (part) and MGL 102155b
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11 176 (counterpart). Other material: MGL 103036a (part) and MGL 103036b (counterpart). Both
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13 177 specimens come from an outcrop located in the Ternata plain, ca. 18 km NW of the city of
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15 178 Zagora (Morocco) and ca. 6 km NNE of the village of Beni Zouli. The outcrop falls within the
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17 179 lower exceptional preservation interval of the Fezouata Shale (*Araneograptus murrayi* Zone,
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19 180 Tremadocian, Lower Ordovician). Material is stored in the collections of the Cantonal Museum
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21 181 of Geology (Lausanne, Switzerland). Exact locality data curated with the specimens.
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29 183 *Etymology.* In Tamazight language, Tazagurt (ⵜⴰⴳⴰⵖⴰⵔⵜ in Neo-Tifinagh script) is a name for
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31 184 the city of Zagora near which the material was discovered. Tamazight is a language of the
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33 185 Amazigh people, an ethnic group that is indigenous to north Africa and have large population in
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35 186 the Anti-Atlas region of Morocco.
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42 188 *Diagnosis.* A small (up to 8 mm long) species of *Tariccoia* having the following unique
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44 189 combination of characters: cephalon with pointed genal angles and marginal rim; pygidium with
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46 190 anterior margin curved forwards, a rounded posterior margin, and a medial keel that does not
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48 191 reach posterior pygidial border.
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3 193 *Description.* The total exoskeletal length is 6.68 mm in specimen MGL 103036a and 7.24 mm in
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5 194 specimen MGL 102155a. Cephalic shield is **sub-circular** in outline and its sagittal length ranges
6
7 195 between 3.04 mm in MGL 103036a and 3.39 mm in MGL 102155a, and transverse width
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9 196 between 3.47 mm in MGL 103036a and 3.79 mm in MGL 102155a. The anterior and lateral
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11 197 margins of the cephalic shield ('ce' in Fig. 1b, e) are rounded, and the posterior cephalic margin
12
13 198 is **anteriorly curved**. The cephalic shield reaches its maximum width near the mid-length. A
14
15 199 distinct anterior marginal cephalic rim ('rm' in Fig. 1b) is delineated by a sharp ridge ('rd' in
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17 200 Fig. 1b). The length of the cephalic rim extends to about one fifth the cephalic shield, being
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19 201 longest (sag.) in the medial part. The postero-lateral edges of the cephalic shield form distinct,
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21 202 pointed genal angles ('ga' in Fig. 1b) with rounded tips. **The dorsal surface of the cephalic shield**
22
23 203 **is without trilobation, facial sutures or visual organs. The holotype MGL 102155a (Fig. 1a–c)**
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25 204 **shows raised finger-like structures ('dg' in Fig. 1b, see also Fig. 2a) that are connected medially**
26
27 205 **and located in the anterior half of the cephalic shield. In specimen MGL 103036a (Fig. 1d–e), the**
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29 206 **surface of the cephalic shield preserves distinct, radially arranged, wrinkles ('dg' in Fig. 1e, see**
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31 207 **also Fig. 2b).**
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33 208 The **thorax** is comparatively narrow (tr.), being approximately 70–80% of the width of cephalic
34
35 209 shield. It is composed of four thoracic tergites, but the anterior two (1st and 2nd) tergites ('T1'
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37 210 and 'T2' in Fig. 1b, e) are overlapped by the posterior **portion** of the cephalic shield ('ce' in Fig.
38
39 211 1b, e), and consequently are not easily discernible **in the holotype**, but are clearly visible in MGL
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41 212 103036a. The two posterior (3rd and 4th) thoracic tergites ('T3' and 'T4' in Fig. 1b, e) are
42
43 213 completely exposed (Fig. 1a–f). In dorsal view all thoracic tergites are curved backward and
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45 214 slightly downwards abaxially. The thoracic tergites become slightly wider (tr.) and more curved
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47 215 posteriorly, so the 4th tergite is the widest and is in its medial part strongly deflected forward.
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3 216 The first tergite seems to taper abaxially. No distinct axial lobe is visible in any of the tergites.
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5 217 The lateral extremes of each tergite end in rounded tips. No articulating facets or articulating
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7 218 half-rings are present in the thoracic tergites. The tergites seem to be articulated with each other
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9 219 by a narrow flange ('fl' in Fig. 1e) that is visible and runs along the anterior margin of the 3rd
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11 220 and 4th tergites (Fig. 1d–f), but is probably also present in the 1st and 2nd.

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15 221 **Pygidium** ('py' in Fig. 1b, e) is sub-oval in outline, elongated and measures 3.08 mm (MGL
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17 222 103036a) and 3.18 mm (MGL 102155a) in sagittal length and 2.52 mm (MGL 103036a) and
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19 223 3.04 mm (MGL 102155a) in transverse width. Consequently, the pygidium is approximately 25%
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21 224 narrower than the cephalic shield, and is just slightly wider than the thorax. The anterior margin
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23 225 of the pygidium is curved forward, exactly matching the posterior margin of the last thoracic
24
25 226 tergite. A narrow flange ('fl' in Fig. 1e) runs along the anterior margin of the pygidium. The
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27 227 posterior margin of the pygidium is rounded. The central part of the pygidium is slightly inflated
28
29 228 and slopes down abaxially and posteriorly. In its medial part, the pygidium carries a pronounced
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31 229 median keel ('mk' in Fig. 1b, e), that is nearly as long as the entire pygidium but does not reach
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33 230 its posterior margin.
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42 232 *Discussion.* *Tariccoia tazagurtensis* sp. nov. resembles *Tariccoia arrusensis* from the Ordovician
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44 233 of Sardinia (Hammann et al. 1990, Hammann and Leone 1997), in overall morphology of both
45
46 234 the cephalon and pygidium and in possessing four thoracic tergites with rounded lateral
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48 235 extremes. The differences between these two species are (see also Fig. 3a, b for comparison): 1)
49
50 236 more pointed genal angles in *T. tazagurtensis* sp. nov.; 2) the cephalon with marginal rim in *T.*
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52 237 *tazagurtensis* sp. nov.; 3) the pygidium in *T. tazagurtensis* sp. nov. has anterior margin curved
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54 238 forwards and rounded posterior margin, while in *T. arrusensis* the anterior pygidial margin is
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3 239 nearly straight and the posterior margin is pointed; 4) the thoracic tergites are proportionally
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5 240 longer (sag.) and more curved in *T. tazagurtensis* sp. nov.; 5) the median keel in *T. tazagurtensis*
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7 241 sp. nov. never reaches the posterior pygidial margin, but it does in *T. arrusensis*; and 6) the
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9 242 pygidium of *T. tazagurtensis* sp. nov. lacks the sharp lateral edges forming a ventral ridge seen in
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12 243 *T. arrusensis* (sensu Hammann et al. 1990, text-fig. 4).

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15 244 The sharp ridge that separates the marginal rim of the cephalon is one of the characters that
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17 245 distinguishes *T. tazagurtensis* sp. nov. from *T. arrusensis*. This structure is only preserved well
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19 246 in the holotype (MGL 102155, Fig. 1a, b). For this reason, it is not easy to interpret it
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21 247 unambiguously. This structure could also be interpreted as an imprint of the cephalic doublure or
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23 248 compaction related deformation of the cephalic margin.

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27 249 The exact number of thoracic tergites in *T. tazagurtensis* sp. nov. is not easy to determine,
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29 250 because the anterior ones are overlapped by the cephalic shield. Such an overlap in *Tariccoia*,
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31 251 *Liwia* and *Soomaspis* was recognised by Edgecombe and Ramsköld (1999, character 9) and used
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33 252 as one of the synapomorphies of Liwiinae (= Liwiidae in this paper). Contrary to Edgecombe and
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35 253 Ramsköld (1999), we suggest that in *Tariccoia* the cephalic shield overlap the first and also the
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37 254 second (at least partially) thoracic tergite. In all articulated specimens of *T. arrusensis* usually
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39 255 two or at most three thoracic tergites are exposed, while specimens lacking the cephalic shield
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41 256 always show four (Hammann et al. 1990, pl. 1–3; Hammann and Leone 1997, pl. 1, fig. 1–3). In
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43 257 some articulated specimens, however, the anterior one or two tergites are imprinted onto the
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45 258 posterior portion of the cephalic shield (Hammann et al. 1990, pl. 1, fig. 1, 2, 5). Similar
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47 259 exoskeletal configuration was likely present also in *T. tazagurtensis* sp. nov. Specimen MGL
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49 260 103036a (Fig. 1d–f) shows clearly two posterior tergites, and traces of two more under the
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51 261 posterior part of the cephalic shield. Although, the slightly different shape of the 1st thoracic
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3 262 tergite (Fig. 1d) in *T. tazagurtensis* sp. nov. resembles an articulating half-ring, the interpretation
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5 263 of it as a thoracic tergite is favoured for two main reasons. Firstly, it is too wide to be an
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8 264 articulating half-ring, and secondly, it is quite similar to the shape of first thoracic tergite in *T.*
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10 265 *arrusensis* (cf. Hammann et al. 1990, pl. 2, fig. 2a–b).

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13 266 The articulation of individual thoracic tergites and of the pygidium was apparently facilitated by
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15 267 a structure morphologically similar to a flange as is known in the pleural parts of numerous,
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18 268 especially basal, trilobites (Whittington 1989, Geyer 1996, Ortega-Hernández et al. 2013b,
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20 269 Esteve et al. 2013, Laibl et al. 2016). Such an articulation can be regarded as functionally simple,
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22 270 as no other articulation structures are present (e.g. articulating half-rings, fulcrum, or articulating
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25 271 facet, cf. for example with Bruton and Haas 1997). With such a simple articulation, it seems
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27 272 unlikely that *T. tazagurtensis* sp. nov. was able to enroll, as the flange does not allow for rotation
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29 273 movement of arched structures, such as the thoracic tergites of *T. tazagurtensis* sp. nov.

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

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

280 The holotype of *T. tazagurtensis* sp. nov. shows finger-like structures connected medially under
281 the anterior half of the cephalic shield (Fig. 2a). We interpret these structures as the proximal
282 parts of a pair of well-developed ramified digestive glands connected to an anterior part of the
283 digestive tract. Both their preservation and morphology strongly resemble such structures as seen

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3 284 in *Naraoia spinosa* Zhang and Hou, 1985 from Chengjiang (cf. Vannier and Chen 2002, fig. 2A,
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5 285 B, Zhang et al. 2007, fig. 28, 29). The distal ramification of the digestive glands is not preserved
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7 286 in the holotype, but the other specimen (MGL 103036a) shows numerous wrinkles, some of
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9 287 which seem to bifurcate distally (Fig. 2b). These are likely not compression-related wrinkles,
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11 288 which are usually concentric (cf. Hammann et al. 1990, Budd 1999, Caron et al. 2004) or
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13 289 randomly orientated (Peng et al. 2012), as opposed to radial in MGL 103036a. These structures
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15 290 therefore likely represent the distal parts of the ramified digestive glands. Digestive structures are
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17 291 known from *Megistaspis (Ekeraspis) hammondi* Corbacho & Vela, 2010 and other trilobites
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19 292 from the Fezouata Shale (Gutiérrez-Marco et al. 2017; Van Roy et al. 2015a), showing that
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21 293 preservation of gut features is possible at this locality. Preservation of internal soft tissues in
22
23 294 general is relatively rare in the Fezouata Shale compared to other BSTs such as the Burgess and
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25 295 the Chengjiang Biota, and is usually only found in the presence of a mineralized or sclerotized
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27 296 external cuticle (Saleh et al. 2020), as is the case with trilobites and *T. tazagurtensis* respectively.
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33 297 Within Nektaspida the digestive system is known only in *Naraoiidae* and up to now, two
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35 298 different morphotypes have been recognized (Vannier and Chen 2002) – one with a long,
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37 299 extensively ramified anterior pair of digestive glands, present in species of *Naraoia* Walcott,
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39 300 1912 and in *Misszhouia canadensis* Mayers et al., 2019 (see Vannier and Chen 2002, Mayers et
40
41 301 al. 2019) and one with only short digestive glands present in *Misszhouia longicaudata* Zhang and
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43 302 Hou, 1985 (Vannier and Chen 2002). Given that the digestive system of *T. tazagurtensis* sp. nov.
44
45 303 resembles the ramified pattern seen in *Naraoia* and *M. canadensis*, we suggest that these
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47 304 morphologies are homologous. Indeed, the majority of phylogenies would suggest a single origin
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49 305 for the well-developed ramified digestive glands in both naraooids and liwiids (e.g. Paterson et al.
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51 306 2010, Ortega-Hernández et al. 2013a, Lerosey-Aubril et al. 2017, Mayers et al. 2019).

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309 6. Distribution and habitat preferences in **liwiids**

310 The distribution of liwiids shows a different pattern than that of other **nektaspids** (Fig. 4).
311 **Naraoiids** have a comparatively wide distribution, being known from low latitudes of
312 Laurentia/Laurussia (Whittington 1977, Robison 1984, Caron et al. 2004, Schwimmer and
313 Montante 2007, Mayers et al. 2019, Lerosey-Aubril et al. 2020), South China (Hou and
314 Bergström 1997, Chen et al. 1997, Zhang et al. 2007, Peng et al. 2012, Fu et al. 2019) and
315 possibly also from high latitudes **on** the West Gondwana margin (Budil et al. 2003). Emucaridids
316 are **restricted** to low latitude areas of East Gondwana (Paterson et al. 2010) and South China
317 (Zhang et al. 2012). **According to the results of Mayers et al. (2019) putative nektaspids**
318 **including petalopleurans indicate a broader distribution, equatorial in Laurentia (Whittington**
319 **1985, Budd 1999, 2011), South China (Hou and Bergström 1997) and Siberia (Ivantsov 1999),**
320 **with the exception of *Xandarella mauretanic* Ortega-Hernández et al., 2017 from West**
321 **Gondwana (Ortega-Hernández et al. 2017).**

322 In the Cambrian, the only liwiids (**sensu stricto, i.e. without genus *Buenaspis***) so far described
323 are *Liwia convexa* (Lendzion, 1975) and *Liwia plana* (**see** Lendzion 1975, Dzik and Lendzion
324 1988), both known from boreholes in NE Poland (Baltica, Fig. 4). An **Atdabanian** age for the
325 *Liwia* bearing beds has been inferred (Dzik and Lendzion 1988), which roughly corresponds to
326 the provisional Cambrian Stage 3 within the **early** Cambrian subdivision (Zhang et al. 2017),
327 making this older than the more famous and fossiliferous Early Cambrian Konservat-
328 Lagerstätten: the Sirius Passet and Chengjiang biotas (Zhang et al. 2001, Harper et al. 2019).

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3 329 After this early first appearance, liwiids are completely absent from the renowned low latitude
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5 330 Konservat-Lagerstätten of the rest of the Cambrian, including Sirius Passet (Harper et al. 2019),
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7 331 the Chengjiang Biota (Hou and Bergström 1997, Zhao et al. 2009), Emu Bay Shale (Paterson et
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9 332 al. 2016), Burgess Shale (Dunne et al. 2008, Caron and Jackson 2008) and Weeks Formation
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11 333 (Lerosey-Aubril et al. 2018). This suggests that during the Cambrian, liwiids were either
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13 334 extremely rare, formed **restricted** populations, and/or preferred specific environmental conditions
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15 335 **that were not conducive for exceptional preservation.**

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20 336 Previously published Ordovician liwiids are only known from localities **that represent atypical**
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22 337 marine conditions, where nektaspids **are not commonly found**. *Soomaspis splendida* **Fortey &**
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24 338 **Theron, 1994** is known only from the Soom Shale Member of the Cedaberg Formation, South
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26 339 Africa (Fortey and Theron 1994; Fig. 4), where the depositional environment is interpreted to be
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28 340 brackish-to-marine setting, close to a retreating and downwasting ice front (Theron et al. 1990,
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30 341 Aldridge et al. 1994). *Tariccoia arrusensis* occurs abundantly in **the Riu Is Arrus Member of the**
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32 342 **Monte Argentu Formation** of SW Sardinia (Hammann et al. 1990; **Hammann and Leone 1997**)
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34 343 that is considered to be largely deposited in terrestrial and **marginal marine** environments
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36 344 (Oggiano et al. 1986, Hammann et al. 1990). Sedimentological, biostratigraphical and
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38 345 palaeontological data suggest that *T. arrusensis* inhabited a restricted marine oxygen deficient
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40 346 (sheltered bay, lagoon) environment, populated mainly by this species and macroscopic algae
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42 347 (Hammann et al. 1990; **Hammann and Leone 1997**).

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48 348 *Tariccoia tazagurtensis* sp. nov. is the only Ordovician liwiid described from **a** typical open
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50 349 marine **deposits**. Unlike the abundant *T. arrusensis* **of the Monte Argentu Formation**, *T.*
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52 350 *tazagurtensis* sp. nov. is a very rare faunal component of the Fezouata Shale community. This
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54 351 species is not even locally abundant as shown by its general absence from most of the excavated

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3 352 sites and from both the proximal and distal parts of the Fezouata Shale, despite extensive
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5 353 collecting in these areas. **Moreover**, the available specimens of *T. tazagurtensis* sp. nov. are
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8 354 complete and articulated. Considering their non-biomineralized exoskeleton and the presence of
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10 355 digestive glands, these specimens likely represent carcasses. Interpretations of the
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12 356 palaeoenvironmental settings of the Fezouata Shale (Martin et al. 2016) suggest that these fossils
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14 357 experienced little or no transport before deposition. Therefore, it seems that *T. tazagurtensis* sp.
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16
17 358 nov. was living in the environment in which it was found.

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20 359 From a palaeogeographic point of view, all Ordovician liwiids were restricted to cold-water
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22 360 settings (Fig. 4). Both *T. tazagurtensis* sp. nov. and *T. arrusensis* are known from very high
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24 361 latitudes **on** the West Gondwana margin (cf. Scotese 2004, Torsvik and Cocks 2013a, 2013b),
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26 362 close to the South Pole. **Soomaspis** *splendida* comes from an area that was located at around
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28 363 30°S in **the** Late Ordovician (Torsvik and Cocks 2013a, 2013b), apparently in cold water very
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31 364 close to a retreating ice shield (Aldridge et al. 1994). Liwiids might thus have preferred cold
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33 365 water conditions (at least during Ordovician), in contrast to **naraoiids**, emucaridids and other
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36 366 **nektaspids**.

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39 367 The stratigraphic distribution of liwiids suggest that they were originally components of open
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41 368 marine communities (*Liwia*, *T. tazagurtensis* sp. nov.), but were apparently rare. By the Middle
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43 369 and Upper Ordovician, some of their members had migrated to brackish marine environments (*S.*
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45 370 *splendida*) or to restricted areas where they formed locally abundant populations (*T. arrusensis*).

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55 373 **7. Summary**

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3 374 1. A new species of a small nektaspid euarthropod – *Tariccoia tazagurtensis* sp. nov. – is
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5 375 described from the Lower Ordovician (Tremadocian) Fezouata Shale Konservat-
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7 376 Lagerstätte of Morocco. This species is characterized by a sub-circular cephalon with
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10 377 pointed genal angles and with a marginal rim; a thorax consisting of four tergites, the 1st
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12 378 and 2nd of which are overlapped by the cephalic shield; and by a pygidium with its
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14 379 anterior margin curved forwards, a rounded posterior margin, and a long medial keel that
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16 380 does not reach the posterior pygidial border.
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20 381 2. *Tariccoia tazagurtensis* sp. nov. preserves remains of the anterior part of the digestive
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22 382 tract, which is comparable to the ramified digestive glands seen in species of *Naraoia* and
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24 383 *Misszhouia canadiensis*. This is the first description of the digestive system in Liwiidae.
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27 384 3. From the distribution and abundance data of Liwiidae, it is likely that members of this
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29 385 group preferred cold-water settings, in contrast to other nektaspids, and were members of
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31 386 open marine communities during their early evolutionary history, but later migrated to
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33 387 brackish or restricted environments.
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44 391 related to digestive system in euarthropods and to *Tariccoia arrusensis*, respectively. The
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401 **Conflict of interest.** None.

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9 **Figures**

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12 609 Figure 1. *Tariccoia tazagurtensis* sp. nov., *Araneograptus murrayi* Zone (Tremadocian, Lower
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14 610 Ordovician), Fezouata Shale, near Beni Zouli (Morocco). MGL 102155a, holotype,
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16 611 photographed dry (a), interpretative drawing (b), photographed under ethanol (c). MGL 103036a,
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18 612 photographed dry (d), interpretative drawing (e), photographed under ethanol (f). Abbreviations:
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21 613 ce, cephalic shield; dg, digestive glands; fl, flange; ga, genal angle; mk, median keel; py,
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23 614 pygidium; rd, marginal ridge; rm, marginal rim; T1-T4, thoracic tergite one to four. Scale bar is 1
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26 615 mm.

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32 617 Figure 2. *Tariccoia tazagurtensis* sp. nov., *Araneograptus murrayi* Zone (Tremadocian, Lower
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34 618 Ordovician), Fezouata Shale, near Beni Zouli (Morocco); close-up of the anterior part of the
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36 619 cephalic shield of the holotype, MGL 102155a (a) and of MGL 103036a (b). Arrows pointing to
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38 620 proximal parts of digestive glands (a), and to bifurcation of digestive glands (b). Scale bar is 1
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41 621 mm.

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47 623 Figure 3. Reconstruction of members of the family Liwiidae Dzik & Lenzion, 1988 and the
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49 624 genus *Buenaspis* Budd, 1999: (a) *Tariccoia tazagurtensis* sp. nov., Fezouata Shale, Morocco; (b)
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51 625 *Tariccoia arrusensis* Hammann et al., 1990, Riu is Arrus Member of the Monte Argentu
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53 626 Formation, Sardinia; (c) *Livia plana* (Lenzion, 1975), Zawiszyn Formation, Poland; (d)
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56 627 *Soomaspis splendida* Fortey & Theron, 1994, Soom Shale, South Africa; (e) *Buenaspis fortleyi*

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3 628 Budd, 1999, Buen Formation, Greenland. Dotted lines represent underlying structures of the
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5 629 dorsal exoskeleton. Scale bar is 1 mm. Reconstruction of *T. arrusensis*, *L. plana*, *S. splendida*
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8 630 and *B. fortey* based on Hammann et al. (1990), personal observation, Fortey and Theron (1994),
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10 631 and Budd (1999), respectively.
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16 633 Figure 4. Paleogeographical distribution of nektaspids during the Cambrian (a), Ordovician and
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18 634 Silurian (b) periods. Map reconstruction for the early Cambrian (520 Ma) (a) and Early
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20 635 Ordovician, Tremadocian (480 Ma) (b); redrawn, adapted and simplified from Torsvik & Cocks
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22 636 (2013a, fig. 2.7 and fig. 2.11). The Silurian species *Naraoia bertensis* Caron et al. 2004, is
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24 637 marked by asterisk. Distribution data based on Whittington 1977, Robison 1984, Dzik and
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26 638 Lendzion 1988, Hammann et al. 1990, Fortey and Theron 1994, Hou and Bergström 1997, Chen
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28 639 et al. 1997, Budd 1999, Budil et al. 2003, Caron et al. 2004, Schwimmer and Montante 2007,
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30 640 Zhang et al. 2007, Paterson et al. 2010, Peng et al. 2012, Zhang et al. 2012, Fu et al. 2019,
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32 641 Mayers et al. 2019, Lerosey-Aubril et al. 2020.
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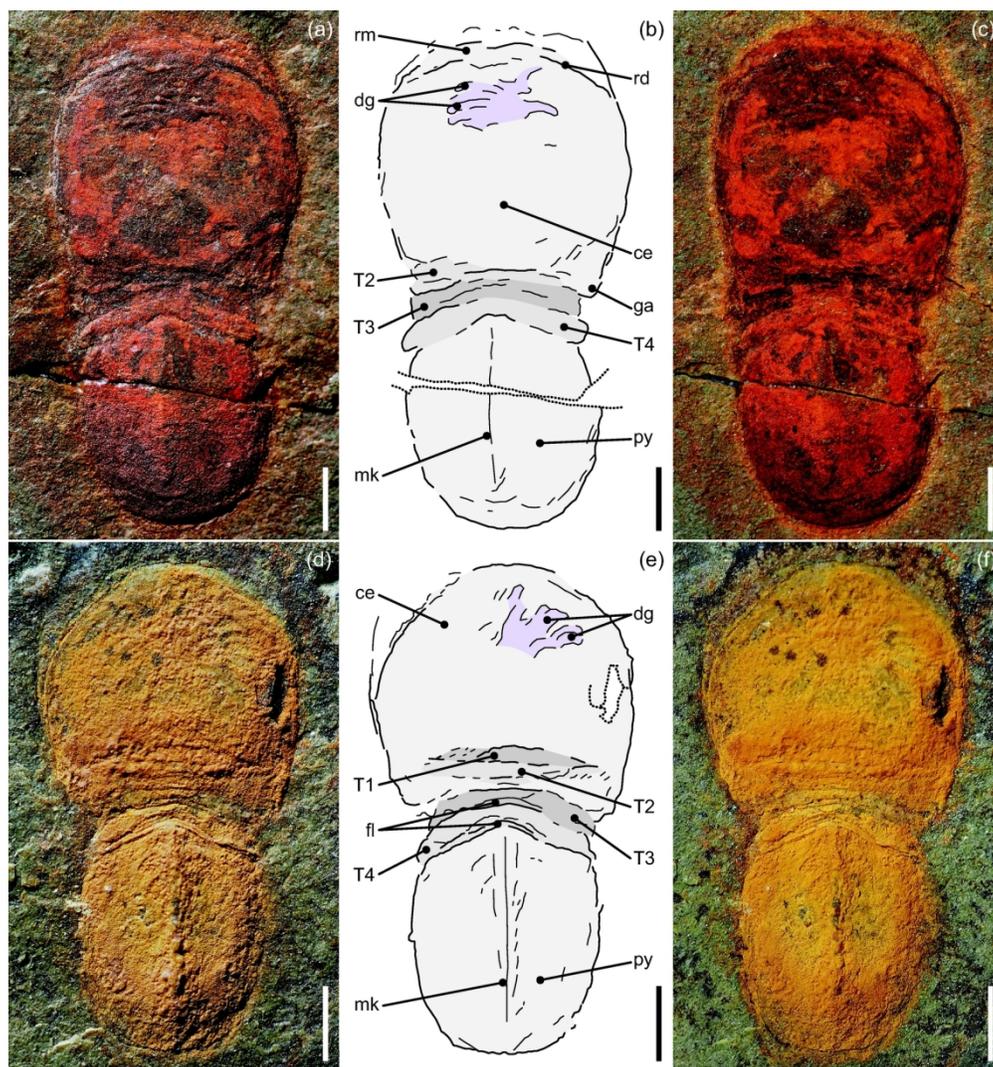


Figure 1. *Tariccoia tazagurtensis* sp. nov., *Araneograptus murrayi* Zone (Tremadocian, Lower Ordovician), Fezouata Shale, near Beni Zouli (Morocco). MGL 102155a, holotype, photographed dry (a), interpretative drawing (b), photographed under ethanol (c). MGL 103036a, photographed dry (d), interpretative drawing (e), photographed under ethanol (f). Abbreviations: 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.

168x180mm (300 x 300 DPI)



Figure 2. *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, MGL 102155a (a) and of MGL 103036a (b). Arrows pointing to proximal parts of digestive glands (a), and to bifurcation of digestive glands (b). Scale bar is 1 mm.

80x128mm (300 x 300 DPI)

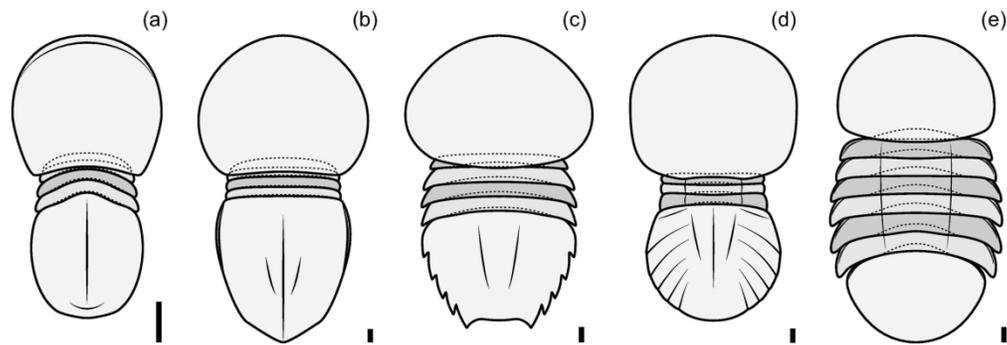
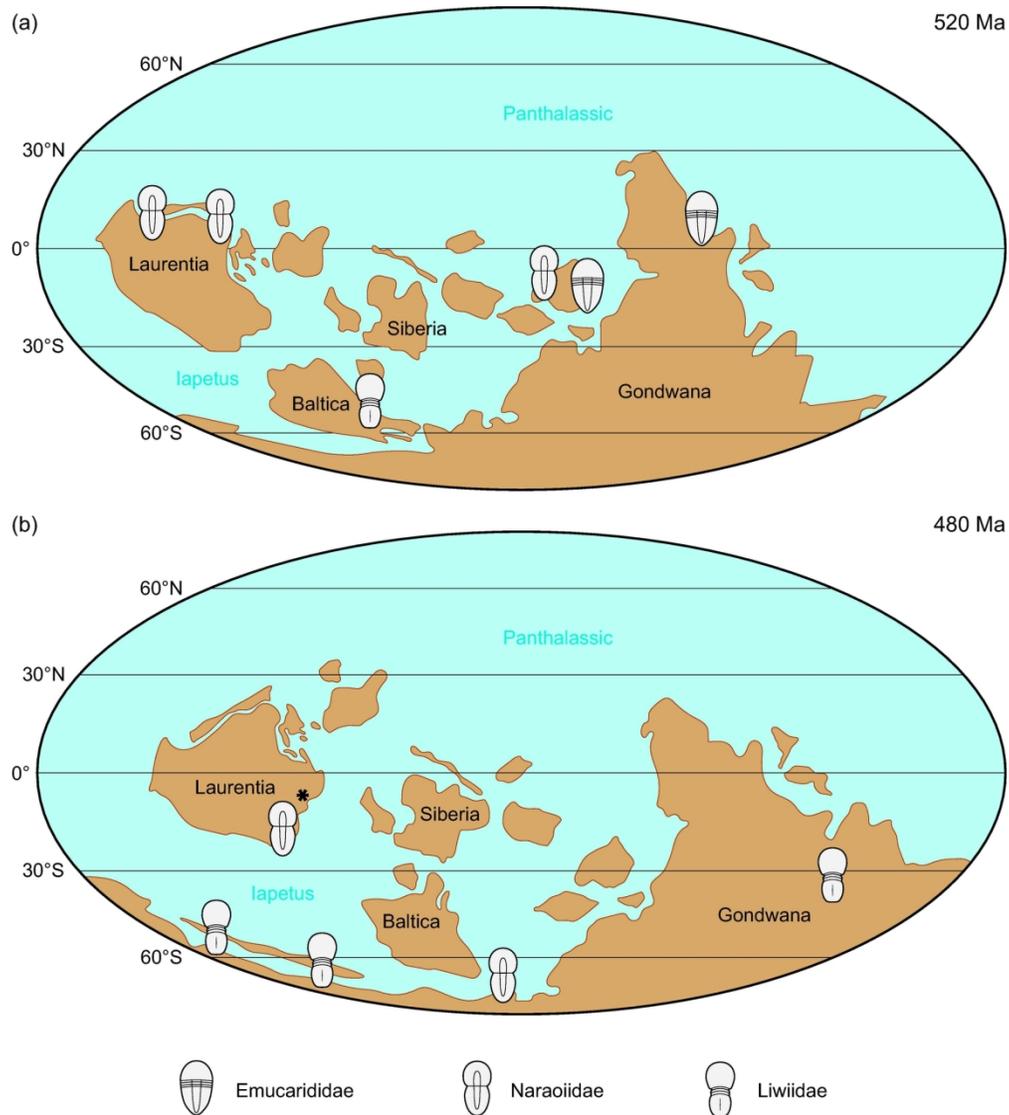


Figure 3. Reconstruction of members of the family Liwiidae Dzik & Lenzion, 1988 and the genus *Buenaspis* Budd, 1999: (a) *Tariccoia tazagurtensis* sp. nov., Fezouata Shale, Morocco; (b) *Tariccoia arrusensis* Hammann et al., 1990, Riu is Arrus Member of the Monte Argentu Formation, Sardinia; (c) *Liwia plana* (Lenzion, 1975), Zawiszyn Formation, Poland; (d) *Soomaspis splendida* Fortey & Theron, 1994, Soom Shale, South Africa; (e) *Buenaspis forteyi* 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. forteyi* based on Hammann et al. (1990), personal observation, Fortey and Theron (1994), and Budd (1999), respectively.

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Figure 4. Paleogeographical distribution of nektaspids during the Cambrian (a), Ordovician and Silurian (b) periods. Map reconstruction for the early Cambrian (520 Ma) (a) and Early Ordovician, Tremadocian (480 Ma) (b); redrawn, adapted and simplified from Torsvik & Cocks (2013a, fig. 2.7 and fig. 2.11). The Silurian species *Naraia bertensis* Caron et al. 2004, is marked by asterisk. Distribution data based on Whittington 1977, Robison 1984, Dzik and Lenzion 1988, Hammann et al. 1990, Fortey and Theron 1994, Hou and Bergström 1997, Chen et al. 1997, Budd 1999, Budil et al. 2003, Caron et al. 2004, Schwimmer and 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, Lerosey-Aubril et al. 2020.

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163x182mm (300 x 300 DPI)