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Kodymirus and the case for convergence of raptorial appendages in Cambrian arthropods

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Abstract Kodymirus vagans Chlupáč and Havlíček in Sb Geol Ved Paleontol 6:7-20, 1965 is redescribed as an aglaspidid-like arthropod bearing a single pair of enlarged raptorial appendages, which are shown to be the second cephalic appendage. A number of early Palaeozoic arthropods, recognized from predominantly Cambrian Konservat-Lagerstätten, are known to have borne single pairs of large raptorial appendages. They are well established for the iconic vet problematic anomalocarids, the common megacheirans, and the ubiquitous bivalved Isoxys. Further taxa, such as fuxianhuiids and Branchiocaris, have been reported to have single pairs of specialized cephalic appendages, i.e., appendages differentiated from a largely homonomous limbs series, members of which act in metachronal motion. The homology of these raptorial appendages across these Cambrian arthropods has often been assumed, despite differences in morphology. Thus, anomalocaridids, for instance, have long multiarticulate "frontal appendages" consisting of many articles bearing an armature of paired serial spines, while megacheirans and Isoxys have short "great appendages" consisting of few articles with well-developed endites or elongate fingers. Homology of these

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appendages would require them to belong to the same cephalic segment. We argue based on morphological evidence that, to the contrary, the raptorial appendages of some of these taxa can be shown to belong to different cephalic segments and are the result of convergence in life habits. *K. vagans* is yet another important example for this, representing an instance for this morphology from a marginal marine environment.

Keywords Cambrian · Arthropod · Raptorial appendages · Convergence · Bohemia · Paseky Shale

Introduction

The enigmatic arthropod Kodymirus vagans, from the early Cambrian (Series 2) Paseky Shale of the Barrandian area of central Bohemia (Czech Republic), was first described based on disarticulated head shields and trunk tergites (Chlupáč and Havlíček 1965), with subsequent collecting at the locality revealing articulated specimens and appendages. A more complete description by Chlupáč (1995) considered Kodymirus to be the earliest representative of Eurypterida, reconstructing the head as bearing six unusually large appendage pairs. Despite a lack of evidence, this interpretation has largely been accepted in the literature (Wills 2001; Park and Gierlowski-Kordesch 2007), although more recent work has referred Kodymirus to a group termed aglaspidid-like arthropods (Van Roy 2006; Ortega-Hernández et al. 2013), or even to the megacheirans (Lamsdell 2011). The original material has not been restudied since Chlupáč's (1995) redescription, in which a substantial part of the material was figured as interpretative line-drawings only. Our restudy of the material has revealed a number of discrepancies with the existing reconstruction, specifically regarding the "type B" and "type C" appendages (Chlupáč 1995) (Figs. 1 and 2). Fully articulated specimens of Kodymirus never have more than a single pair of raptorial appendages preserved, which is the modified second cephalic appendage,



Fig. 1 *Kodymirus vagans* raptorial appendages. **a** "Type A" trunk appendage (MR65828). **b** "Type B" raptorial appendage (MR65826). **c** "Type B" raptorial appendage (MR20489). **d** "Type C" raptorial appendage (MR65786)

corresponding to both types that grade into each other (Chlupáč himself frequently could not tell the two apart). The "type A" appendage (Chlupáč 1995) (Fig. 1) represents a biramous postantennular limb of the more or less homonomous series posterior to the second cephalic appendage. We present further support for *Kodymirus* belonging to Aglaspidida *sensu lato* Ortega-Hernández, Legg, & Braddy 2013.

Large, anteroventral, grasping appendages—the so-called great or frontal appendages—are recognized in a number of



Fig. 2 Kodymirus vagans, specimen revealing full complement of trunk tergites telescoped into the carapace displaying both "type C" raptorial appendages and "type A" trunk or cephalic endopods (MR30490). *cs* cephalic shield, *en* endopod, dt1-dt13 dorsal tergites 1–13, *ms* moveable spines, *ra* raptorial appendage, *te* telson

taxa known from Lower Palaeozoic, predominantly Cambrian, Konservat Lagerstätten. Among these are the megacheirans, or short great appendage arthropods (Haug et al. 2012a, b), bivalved taxa such as Isoxys (Vannier et al. 2009; Stein et al. 2010; Fu et al. 2011) and Branchiocaris pretiosa (Budd 2008), the anomalocaridids (Daley et al. 2009; Daley and Budd 2010), and the more recently described Kiisortogia soperi (Stein 2010). These taxa are unlikely to represent a natural group and may even be polyphyletic (Edgecombe 2010; Kühl et al. 2009); however, homology of the great appendages is commonly assumed (Budd 2002; Legg et al. 2012). Arthropods with a frontal or great appendage have, in total or in part, been considered to resolve either as stem chelicerates or stem euarthropods, with the most recent analysis suggesting that the possession of a great appendage forms part of the euarthropod groundpattern (Legg et al. 2012). The segmental affinities of these appendages remain debated, but based on the underlying assumption of homology, a common segmental affinity for most, if not all, of them has been suggested (Budd 2002; Chen et al. 2004; Stein 2010; Legg et al. 2012). Here, we present evidence that the raptorial appendages of K. vagans, though reminiscent of the megacheiran great appendage, are the first postantennular appendage and, thus, belong to the tritocerebral segment. They are therefore not homologous to the megacheiran great appendage, which can be shown to belong to the deutocerebral antennular or cheliceral segment on positional grounds (Haug et al. 2012a, b; Stein 2010). Comparison of the various Cambrian frontal and great appendages suggests that enlarged raptorial appendages

have evolved multiple times convergently in Cambrian arthropods (Fu et al. 2011).

Material and methods

All examined specimens of *K. vagans* are deposited at the District Museum of Dr. B. Horák, Rokycany, Czech Republic (MR prefix). Specimens were photographed under polarized light with both parallel and crossed polarizers. Line drawings were prepared using Adobe Illustrator CS4 on a MacBook Pro running OS X.

The reconstruction was created with Cheetah3D 6.2 using a schematic line drawing of MR65789 as a blueprint for proportions. The phylogenetic analysis of 74 characters, scored for 55 taxa, is based on Stein et al. (2013), the matrix of which can be found in Online Resource 1. Coding, where different from Stein et al., is explained in Online Resource 2. The analysis was run in TNT (Goloboff et al. 2008) under equal weights and a heuristic search employing the ratchet and drift algorithms with 10,000 replicates.

Systematic palaeontology

Euarthopoda

Aglaspidida *sensu lato* Ortega-Hernández, Legg, & Braddy, 2013 *Kodymirus* Chlupáč and Havlíček, 1965

Revised diagnosis: Aglaspidid-like arthropod with 13 trunk segments and the first postantennular appendage greatly enlarged into a raptorial grasping limb.

Remarks: *Eolimulus alatus* (Moberg 1892), known from two carapaces from the Lower Cambrian of Sweden, was considered by Bergström (1968) to be the oldest representative of Xiphosura; however, the available specimens show some similarities with *Kodymirus*, namely, the form and position of the lateral eyes and the overall shape of the carapace. It is possible that *Eolimulus* too is an aglaspididlike arthropod, potentially with affinities to *Kodymirus*; however, without further material, it is impossible to make a firm assignment. Whatever its true affinities, *Eolimulus* cannot be allied to xiphosurans, lacking both a cardiac lobe and ophthalmic ridge. The structures identified as such by Bergström most likely arise from flattening of a more convex carapace, as in *Kodymirus*.

K. vagans Chlupáč and Havlíček, 1965

Synonymy: 1965 *K. vagans* n. sp., Chlupáč and Havlíček, p. 9–18, text-fig. 2, pls. 1–3, pl. 4, figs. 1–8, pl.5, figs. 1–8, pl. 6, figs 1–2, 4, 6–8

1979 K. vagans, Bergström, p. 37, fig. 1.17C

1989 K. vagans, Hesselbo, p. 641

1995 K. vagans, Chlupáč, p.10-16, figs. 4-7, pls. 1-6

2011 K. vagans, Lamsdell, p. 60

2013 *K. vagans*, Ortega-Hernández, Legg and Braddy, pp. 17–18, fig. 1b

Holotype: Ústřední ústav geologický (Geological Survey), Prague, Czech Republic; ÚÚG-ICh 454-1, 12 articulated trunk tergites and proximal portion of telson.

Paratype: Ústřední ústav geologický, Prague, Czech Republic; ÚÚG-ICh 454-2, seven articulated trunk tergites and proximal portion of telson.

Other material: Ústřední ústav geologický, Prague, Czech Republic; ÚÚG-ICh 442–444, ÚÚG-ICh 450, ÚÚG-ICh 452, ÚÚG-ICh 454-3–455, ÚÚG-ICh 457, ÚÚG-ICh 460, ÚÚG-ICh 463-464, ÚÚG-ICh 470, ÚÚG-ICh 473, ÚÚG-ICh 477, ÚÚG-ICh 479-480, ÚÚG-ICh 482–485, and District Museum of Dr. B. Horák, Rokycany, Czech Republic; MR20300, MR2483, MR20489–20490, MR20494, MR65758–65760, MR65762– 65766, MR65768, MR65778–65780, MR65782–65789, MR65791, MR65793–65799, MR65801–65807, MR65826, MR65828–65830, MR65835.

Horizon and locality: Paseky Shale, Czech Republic; Early Cambrian, stage 2.

Revised diagnosis: As for the genus.

Description: up to 80 mm long, showing granular cuticular ornament. Head shield wider than long, with raised (but ill-defined) axial region, and extended lateral folds (Figs. 3a and 4c). Axial region bearing axial node close to posterior margin. Head shield with subtriangular to rounded anterior projection, wider than axial region. Hypostome embraces anterior projection, carrying wide part of doublure (rostral plate) that extends laterally into indentations setting off the lateral folds from the anterior projection (Fig. 3b). Hypostome forms parabolic backward projection with concentrically defined median body and extends posteriorly for about half the length of head shield. Head shield with concentric doublure, comprising about 20 % of the width of head shield. Lateral eyes are sessile and incorporated into head shield anterolaterally to axial region (Fig. 4b). Visual surface of lateral eyes crescentic and buttressed by oval, almost reniform palpebral lobe.

Trunk consists of 13 tergites, extending laterally into falcate tergopleural spines, bearing an articulating ridge anteriorly that is longest axially and reduced on the tergopleurae (Figs. 3a, d and 4a). Each tergite carries an elongate axial node at posterior margin. A narrow concentric doublure is present on the lateral and posterior part of the tergopleurae. Tergal overlap is widest axially. Telson short styliform, about half the length of the trunk, with flat anterior portion and semicircular ventral recess (Fig. 3d).

Antennula is uniramous, short, and appears to consist of seven articles (Figs. 3a and 5a, b). No armature is preserved. First postantennular appendage is enlarged raptorial limb comprising eight articles, the first of which has a gnathobase and represents the basipod (Figs. 4c and 5c, d). Proximal articles



Fig. 3 *Kodymirus vagans*: a Carapace with antennula and raptorial appendage and six trunk tergites in series (MR65789). b Isolated hypostome (MR20300). c Specimen revealing cephalic limbs (MR65794). d Complete series of trunk tergites and telson

(MR65766). a2-a8 limb articles 2–8, an antennula, cs carapace shield, dt1-dt13 dorsal tergites 1–13, en endopod, hy hypostome, li limb insertion, mb median body, ms moveable spine, ra raptorial appendage, te telson, vr ventral recess of telson



Fig. 4 Kodymirus vagans. a Relatively complete specimen with carapace folded forward beneath the trunk (MR65795). b Carapace showing dorsal lateral eyes and first two trunk tergites (MR65762). c Disarticulated specimen showing series of basipod gnathobases

(MR65798). ba basipod, cs cephalic shield, dt1-dt13 dorsal tergites 1–13, gn gnathobase, le lateral eye, ms moveable spines, ra raptorial appendage, te telson



Fig. 5 *Kodymirus vagans*. a Interpretive drawing of specimen MR65789 in Fig. 3a. b Expanded view of cephalic region of MR65789. c Isolated raptorial appendage, showing basipod (MR65798). d Interpretive

drawing of MR65789. *a2–a8* limb articles 2–8, *an* antennula, *ba* basipod, *cs* carapace shield, *dt1* dorsal tergite 1, *gn* gnathobase, *hy* hypostome, *le* lateral eye, *li* limb insertion, *ms* moveable spine, *ra* raptorial appendage

are usually covered by the head shield, but there is no evidence of an exopod. Length of the first postantennular limb is equal to length of entire body (Fig. 4a). Articles two to five are robust, and three to five extend mediodistally into an endite carrying a single, massive spine equal in length to the remainder of the limb distal to the spine insertion. Articles six to eight are significantly more slender, the last forming a serrated hook. Articles six and seven carry a pair of small mediodistal spines and bear a distinct serration of finer spines alternating with more stout pegs along its ventral edge (Figs. 1b). Serration is also present in article five and, to a lesser extent, four. The insertion of this appendage can be traced to between the posterior margin of the lateral eyes and the posterolateral corners of the hypostome, posterior to the apparent insertion of the antennula (Figs. 3a and 5a, b). Posterior to the raptorial appendage two more limbs appear to insert beneath the head shield, as indicated by the preservation of the proximal insertions in MR65789 (Figs. 3a and 5a, b). The same specimen indicates that a single limb pair inserts at each subsequent trunk segment. These appendages are biramous with the median edge of the basipod forming a spinose gnathobase (Fig. 4c). The endopod consists of seven podomeres; the proximal four podomeres are enditic and the distal ones bear a serration of fine spines, similar to the raptorial appendage (Figs. 3c and 6a). In the foremost limbs, these endites also bear short, robust spines (Fig. 1a). The exopod is a flap fringed with short setae (Fig. 6a) that may be divided with a large distal lobe, although the state of preservation makes this unclear. The insertion of the exopod is unknown, but it appears to articulate with the lateral edge of the basipod and that of at least the first



Fig. 6 Kodymirus vagans trunk limbs (MR65829). a Anterior trunk limb with exopod and endopod. b Posterior trunk limb with endopod reduced in size in relation to exopod. dt dorsal tergites, en1-en7 endopod podomeres 1–7, ex exopod, ms moveable spines, se seta

proximal podomere of the endopod. Size and armature of the endopod decrease posteriorly; however, the exopod appears to retain its dimensions and so is comparatively larger than the endopods in the posterior limbs (Fig. 6b).

Discussion

The Paseky Shale environment and mode of life of *Kodymirus vagans*

Arthropods with a frontal or great appendage occur in virtually all lower Palaeozoic Fossil-Lagerstätten (Daley et al. 2009; Liu et al. 2007; Kühl et al. 2009; Edgecombe et al. 2011; Briggs et al. 2008; Van Roy and Briggs 2011; Stein 2010) and appear to have played an important role in early



Fig. 7 Digital reconstruction of *Kodymirus vagans*: a dorsal view, b lateral view, and c anterior view

marine ecosystems; many are considered visual apex predators (Vannier et al. 2009; Paterson et al. 2011) (but see Daley and Bergström (2012)). Their distribution is restricted to marine shelf environments, potentially including the pelagic realm and deeper water environments, judging from distribution and depositional environments of the Lagerstätten from which they have been retrieved (Vannier and Chen 2000; Ivantsov et al. 2005). The Paseky Shale fauna is unusually depauperate and devoid of marine benthos, such as trilobites or brachiopods (Fatka et al. 2004), and inhabited shallow subtidal plains characterized by arkosic sandstones to fine shales (Fatka and Mergl 2009). Geochemical and sedimentological data have been interpreted as indicators of a brackish environment (Kukal 1995), while the microfossil assemblage is distinctly different to that of other assemblages from the region, having a much lower abundance of acritarchs (0-0.8 %), and a greater occurrence of filamentous microfossils (up to 65 %) (Fatka and Konzalová 1995). No similar assemblage is known from the Lower Cambrian or the Precambrian, and the uniqueness of the Paseky Shale microfossil community has also been attributed to the restricted marginal marine environment (Fatka and Konzalová 1995).



Fig. 8 Strict consensus of 273 MPTs derived from the matrix in the Online Resource 1. The composition of Artiopoda and Lamellipedia *sensu* Stein et al. (2013) are shown. *Names in bold* represent clades of higher taxa. The full consensus tree, including branch support values, is shown in Online Resource 4

A moderately diverse ichnofossil assemblage has also been reported from the Paseky Shale; however, trace fossils typically occurring in marine Cambrian sediments are completely absent (Mikuláš 1995), and the ichnoassemblage is quite distinct from any other known from the Cambrian. The majority of traces has been interpreted as being produced by Kodymirus moving close to the sediment surface and consists of parallel scratch marks of the Monomorphichnus type, produced by the elongate spines of the appendages (Mikuláš 1995); interestingly, there are never traces from more than one appendage pair. This indicates that Kodymirus was an active swimmer, as suggested by the posterior reduction in endopod size, while the exopods maintain a more or less constant dimension so they become comparatively larger compared to the endopod (Fig. 6). Furthermore, the endopods barely project from beneath the tergites (Fig. 7) and the extreme elongation of the second appendage means that Kodymirus would have been ungainly at best while walking on the substrate surface. The trace fossil evidence suggests that Kodymirus trailed the spines of the raptorial appendage in the substrate, possibly to sense for soft-bodied animals buried in the sediment that would then be grabbed by the raptorial appendages and brought up to the gnathobases for mastication. A purely sensory function of the appendages is highly unlikely. Given the interpretation of the depositional environment of the Paseky Shale as a brackish, possibly lagoonal environment, *Kodymirus* marks the earliest known occurrence of an active arthropod predator within the marginal marine realm.

Affinities of Kodymirus

K. vagans was originally interpreted by Chlupáč and Havlíček (1965) as being an aglaspidid due to the slight trilobation of the trunk tergites, marked pleural spines, lack of facets on the lateral eyes, absence of ocelli, simple telson spine, and cuticular sculpture, while noting that a number of features (the supposed tergite count of 12, the reniform lateral eyes, supposed possession of an epistoma, and supposed similarities in ventral carapace morphology) suggested eurypterid affinities. Bergström (1968, 1979) considered Kodymirus to be a true eurypterid, citing further the likelihood of a chitinous rather than phosphatic exoskeleton and the supposed occurrence of an anteromedian node between the lateral eyes, which was interpreted as an ocellar node. Therefore, when Chlupáč (1995) came to redescribe Kodymirus from newly discovered material, he did so within the framework of Kodvmirus being an early representative of Eurypterida. While noting that the cuticle was indeed phosphatic, and that the "epistoma" closely resembled the hypostome of trilobite-like arthropods, the newly discovered appendages were considered to resemble those of stylonurid or mixopterid eurypterids and Kodymirus was considered akin to the hypothetical "proto-stylonuroid" of Waterston (1979). This interpretation led to Kodymirus being reconstructed as bearing five pairs of long, spinous appendages in the head, with the first pair presumably being small (unobserved) chelicerae. This is despite no specimen preserving more than a single pair of enlarged appendages, and Chlupáč being unable to recognize any more than three different appendage morphologies.

The lack of more than a single pair of enlarged spinous appendages led Lamsdell (2011) to suggest that *Kodymirus* may represent a megacheiran, interpreting the "epistoma" as a hypostome and drawing similarities between the apparent six articles of the *Kodymirus* appendages and the four armature-bearing articles and bipartite peduncle of the great appendages of *Leanchoilia* and *Yohoia*. Van Roy (2006) meanwhile rejected eurypterid affinities for *Kodymirus* based on the lack of any convincing metastoma, genital operculum, or genital appendage despite the discovery of large amounts of material, instead considering it to be an aglaspidid-like arthropod. Ortega-Hernández et al. (2013) retrieved *Kodymirus* as a component of the aglaspidid sister group through phylogenetic analysis; however, all of the appendage characters were coded as unknown in their matrix. **Table 1**Table showing thelocation of enlarged, raptorial(great) appendages in arthropods

		Protocerebrum 0	Deutocerebrum I	Tritocerebrum II
Lobopodians				
	Kerygmachela		0	
Radiodonta				
	Anomalocaridida		0	
Stem-Euarthropods				
	Fuxianhuia			•
"Bivalved arthropods"				
	Branchiocaris			•
	Isoxys		0	
Short great appendage arthropods				
	Megacheira		•	
Aglaspidid-like arthropods				
	Kodymirus			•
Arachnida				
	Scorpiones		•	•
	Pedipalpi		•	•
	Pseudoscorpiones		•	•
Eurypterida				
	Mixopteroidea		•	•
Arthropoda incertae sedis				
	Kiisortoqia		•	
	Captopodus			0

A number of groups possessing raptorial appendages on post-cerebral somites (such as stomatopods and thylacocephalans) are not shown. Solid circles indicate the presence of enlarged raptorial appendages, hollow circles indicate the presence of enlarged raptorial appendages where the segmental affiliations are uncertain, and small solid circles indicate the presence of chelicerae. Fuxianhuia possesses specialized non-raptorial appendages on the tritocerebral segment. Arachnids have developed raptorial tritocerebral appendages independently a number of times, including in Scorpiones, Pedipalpi, Pseudoscorpiones, and laniatorid harvestmen

For all the discussion surrounding the affinities of Kodymirus, the only authors to have physically studied the material until now were Chlupáč and Havlíček (1965) and Chlupáč (1995). Almost two decades on, restudy of the material allows for a reinterpretation of the morphology of Kodymirus based on comparison with new arthropod discoveries and an analysis of the material without relying on Chlupáč's interpretive drawings, which in some instances were influenced by his interpretation of Kodymirus as a eurypterid. Perhaps, the most critical example of this is the "coxa" (which would be equivalent to the basipod of non-chelicerate arthropods) figured only as a drawing by Chlupáč (1995, fig. 6.2). This structure is in fact an exopod, as indicated both by its oval shape and the fringe of short setae it bears along with its position dorsal to the endopod (Fig. 6a). The actual basipods are much smaller, having a somewhat rounded, clearly gnathobasic, ventral edge (Fig. 4c), and strongly resemble the basipods of lamellipedians such as Emeraldella (Stein and Selden 2012, fig. 5). There are also a number of limbs preserved associated with more complete specimens that Chlupáč did not describe; these are mostly smaller endopods originating from either the trunk (Fig. 6b) or head (Figs. 2 and 3c) regions that equate to the "type A" appendages; however, one specimen (Figs. 3a and 5a, b) preserves a short, antenniform cephalic appendage that inserts alongside the hypostome in the position for the deuterocerebral antennula. In form, it closely resembles the antennula of Habelia (Whittington 1981, figs. 78-80), while the proximal articles and position of their insertion correspond closely to the preserved portions of the antennula in Aglaspis (Hesselbo 1992, fig. 5.3). The "epistoma" of Chlupáč is here considered a true hypostome, in part due to the large number of isolated disarticulate specimens and because of the close similarities in morphology to the hypostomes of Aglaspis (Hesselbo 1992, fig. 5.3) and Emeraldella (Stein and Selden 2012, fig. 4c). Kodymirus differs from Aglaspis, however, in the number of thoracic tergites; aglaspidids are generally considered to possess eleven trunk tergites, although this can vary (Van Roy 2006), while Kodymirus was described as possessing 12 (Chlupáč 1995). At least one specimen, however, shows that the trunk is comprised of 13 tergites as derived from a simple count of the number of pleura (Fig. 3d). This number of trunk tergites is, however, known in several megacheirans (Chen et al. 2004; Haug et al. 2012b). Nonetheless, tergite count is a problematic character to rely on for assessing arthropod relationships, as a number of arthropods sequentially increase the number of trunk tergites through ontogeny, and this form of growth probably represents the plesiomorphic condition for Euarthropoda (Lamsdell and Selden 2013).



Fig. 9 "Great appendage" arthropods. a *Branchiocaris pretiosa* (Resser 1929) showing both the antennula and the raptorial "great appendage" first postantennular limb (USNM 189028). b *Isoxys volucris* Williams, Siveter, & Peel, 1996, ventral view revealing the raptorial antennula (MGUH 29012). c *Kiisortoqia soperi* Stein, 2010, view of enlarged "great appendage" antennula (MGUH 28948). d *Anomalocaris canadensis* Whiteaves, 1892, specimen showing robust raptorial great appendages flanking the oral cone (GSC 7555). It is debated whether

these appendages are protocerebral or deutocerebral (Budd 2002; Chen et al. 2004). Image courtesy of Allison Daley. e *Leanchoilia superlata* Walcott, 1912, specimen showing the "short great appendage" antennula (ROM 61882). Image courtesy of Joachim Haug. *an* antennula, *cs* carapace shield, *db* doublure, *ds* dorsal shield, *dss* dorsal spine, *ex* exopod, *fs* fixed spine, *ga* great appendage, *hi* hinge, *le* lateral eye, *lf* lateral flap, *mf* median fixed "finger," *ms* moveable spine, *oc* oral cone, *pa1–pa3* postantennular limbs 1–3, *te* telson, *tl* trunk limb



Fig. 10 Schematic diagram of raptorial appendages in relation to head segmentation: a *Onychodictyon ferox*, after Ou et al. (2012); b *Kerygmachela kierkegaardi*; c *Fuxianhuia protensa*; d megacheirans; e trilobites; f *Kodymirus vagans*. Colored structures: *dark gray oval*

mouth, *light gray* segments and tergal formations belonging to the head, *magenta* appendage of deutocerebral segment, *cyan* appendage of tritocerebral segment. Note that the dorsal position of lateral eyes may not be homologous between trilobites and *Kodymirus*

Chlupáč (1995) reconstructed *Kodymirus* as possessing five pairs of postoral cephalic appendages, based on no evidence other than that is the number that eurypterids have. The bestpreserved specimen, however, shows the limb insertions flanking the axial region of both the head and trunk (Figs. 3a and 5a, b) along with the orientation and extent of the gnathobases. This specimen reveals that *Kodymirus* possesses only three pairs of postoral cephalic appendages, the first of which are the enlarged raptorial appendages most commonly encountered in the material. In this manner, the cephalic region of *Kodymirus* comprises the typical "euarthropod head" (see Chen 2009).

Despite the possession of enlarged raptorial appendages, *Kodymirus* cannot be allied to either anomalocaridids or megacheirans, given that the raptorial appendage is evidently postantennular and therefore not homologous to the frontal or great appendages of anomalocaridids or megacheirans, which are likely proto- or deutocerebral (Budd 2002; Stein 2010; Chen et al. 2004; Haug et al. 2012b; Richter et al. 2013). Endopods comprising seven segments are shared with the trilobite-like arthropods, while megacheirans have an endopod of at least nine podomeres. A recent redescription of the megacheiran *Leanchoilia superlata* suggested seven podomeres in the

endopods of that taxon (Haug et al. 2012a), but an appendage figured by Bruton and Whittington (1983, fig. 105) clearly demonstrates the presence of at least eight, not including the basipod. The appendage morphology of Kodymirus shows further similarities with that of artiopods; in both, the basipod carries a single endite forming a gnathobase as opposed to a series of multiple spinous endites (Liu et al. 2007), and the four proximal endopod podomeres are massive and carry each a single endite with multiple spines (Fig. 6a) while podomeres five through seven are considerably more slender and nonenditic (Stein and Selden 2012). The distal podomere, being a serrated hook, rather than a distal claw or prong as in, e.g., trilobites, is similar to Sidneyia inexpectans (Stein 2013), as is the presence of paired mediodistal spines on podomeres five and six. It is noteworthy that the endopods of Kodymirus do not closely resemble those of the aglaspidids Aglaspis (Hesselbo 1992, fig. 5.3) and Flobertia (Hesselbo 1992, figs. 20, 21, 27) which appear to be short, lacking armature and composed of relatively few podomeres. Nor do the exopods of Kodymirus, with their fringe of short setae, resemble the lamellate exopods of the aglaspidid-like strabopid Khankaspis (Repina and Okuneva 1969, pl. 14, figs. 3-5). Neither Aglaspis nor Flobertia

shows any evidence of exopods; however, it is unclear whether this is a genuine absence or a preservational one.

The raptorial appendage of Kodymirus corresponds in its gross morphology to the biramous appendages of its trunk, except for the massive enlargement, elongate spines on articles three to five, and likely absence of an exopod. This is in stark contrast to the megacheiran great appendages, which are of drastically disparate morphology from the subsequent limbs. The dorsal lateral eyes and telson shape indicate an assignment within Artiopoda or Lamellipedia to Aglaspidida sensu lato, with which it was resolved in an analysis by Ortega-Hernández et al. (2013). This is corroborated by our analysis (Fig. 8) where K. vagans is resolved as the sister taxon to Aglaspidida, represented by Aglaspis spinifer and Flobertia kochi. The clade K. vagans+Aglaspidida resolves in a large polytomy of basal Lamellipedia including, among others, taxa often referred to the "xenopods" or considered closely related (see Stein 2013 for discussion), the Marrellamorphs, and the unnamed clade NN1 of Stein et al. (2013).

Convergent evolution of raptorial appendages

This evidence suggests that single enlarged raptorial appendages evolved multiple times in Cambrian arthropods. The unjointed frontal appendages of the lobopods Megadictyon cf. haikouensis, Jianshanopodia decora, and Siberion lenaicus and the lobopod-like Kerygmachela kierkegaardi and Pambdelurion whittingtoni have commonly been considered to be protocerebral, homologous with the onychophoran antenna. Either loss or complex transformation of this appendage along the euarthropod stem-lineage into the labrum has been invoked (e.g., Budd 2002; Scholtz and Edgecombe 2005, 2006; Eriksson et al. 2010). More recently, homology of the onychophoran antenna with the frontal filaments known from many crustaceans has been suggested (Scholtz and Edgecombe 2006; Frase and Richter 2013). Richter et al. (2013) argued on morphological and positional grounds that the "rostral spines" of K. kierkegaardi are more likely candidates for protocerebral appendages and that the frontal appendage is probably deutocerebral. More data from the other taxa will be required to support or reject that hypothesis. The segmental homology of the articulated, pivot-jointed frontal appendage of anomalocaridids remains a matter of debate, with either protocerebral or deutocerebral position being discussed (e.g., Budd 2002; Chen et al. 2004; Daley et al. 2009; Stein 2010). This hinges to some extent on the question of homology between the anomalocaridid frontal appendage with the long great appendage of K. soperi, which is equally debated (Stein 2010; Edgecombe and Legg 2013). The great appendage of Kiisortogia is argued to be deutocerebral, as is the short great appendage or multichela of megacheirans (e.g., Haug et al. 2012a, b). In both cases, the great appendage is the most anterior cephalic appendage, followed by three biramous appendages (Stein 2010; Haug et al. 2012a, b). Direct evidence for a preoral position of the great appendage comes from the problematic Parapeytoia yunnanensis (Hou et al. 1995), which has been discussed as either a possible anomalocaridid or megacheiran (Stein 2010). Haug et al. (2012b) present evidence for the great appendages of Leanchoilia illecebrosa inserting lateral to a hypostomal sclerite, as do the antennulae of, e.g., trilobites or derivatives of the crustacean stem-lineage (Cisne 1975; Stein et al. 2008), suggesting that they share the same segmental affinity. A new specimen of K. soperi (MGUH 30485) preserves fragments of the hypostomal sclerite (Online Resource 3a), laterally to which the proximal portions of the great appendages insert, indicating a similar configuration there. The presence of small, antenniform appendages anterior to the great appendage has been reported in the megacheirans Fortiforceps (Hou and Bergström 1997) and Kootenichela (Legg 2013), but evidence remains inconclusive. The alleged appendage in Kootenichela is in fact a strip of cuticle dorsal to the eyes that requires a high degree of interpretation; it could equally represent an anterior projection of the head shield as in Leanchoilia (Haug et al. 2012a), part of the eye peduncle, or simply cuticle that has been taphonomically displaced. The problematic taxon Worthenella was also interpreted as a megacheiran with antenniform anterior appendages (Legg 2013); however, the appendage is identical to short, rod-like structures representing unidentified organic remains common on Burgess Shale specimens (see Briggs and Collins 1988, pl. 71, fig. 1; Holmer and Caron 2006, fig. 5b; Budd 2008, pl. 1, fig. 1; Haug et al. 2011, figs. 1, 3F; Conway Morris and Caron 2012, fig. 9J) and surround the anterior portion of the Worthenella specimen (Legg 2013, fig. 5.2). The antenniform anterior appendage therefore likely represents a taphonomic artifact, while the ostensible great appendage is itself spurious at best. The supposed antenniform appendages in Fortiforceps, meanwhile, were discounted by Chen et al. (2004); however Liu et al. (2007) state that new material clearly shows a structure in front of the great appendages but that further work is needed before interpretation is possible. If corroborated, those reportedly gracile, small appendages could be homologous to the protocerebral frontal filaments. Megacheirans have been discussed as either derivative of the euarthropod stem lineage (Budd 2002; Daley et al. 2009; Legg et al. 2012) or of the chelicerate stem lineage (Chen et al. 2004; Haug et al. 2012a; Stein et al. 2013). For the latter interpretation, the stem pycnogonid Cambropycnogon klausmuelleri (Waloszek and Dunlop 2002) is important, a crown group chelicerate that has small, potentially appendicular structures apically and anterior to the chelicerae. These were initially interpreted as the vestigial deutocerebral antennae, under the now falsified traditional hypothesis of tritocerebral chelicerae. If they represent frontal filaments, their presence in a basal crown group chelicerate together with their presence in many Crustacea may be taken as an argument for "primary antennae" (cf Scholtz

and Edgecombe 2005) in the ground pattern of Euarthropoda, which got reduced in some of the in-group taxa.

Further large raptorial appendages have been demonstrated for Isoxys (García-Bellido et al. 2009; Vannier et al. 2009; Stein et al. 2010; Fu et al. 2011) and have been reasonably argued to represent a deutocerebral appendage by Fu et al. (2011). An important specimen is the small individual of Isoxys auritus figured by Vannier et al. (2009, fig. 3i, j) that shows a long great appendage similar to that of Kiisortogia. Isoxys volucris has some seven articles with biserially arranged spines of similar morphology like Kiisortogia, which, as in the latter, arise from the article's point of maximum width, pointing away at a moderate angle. I. acutangulus has a short great appendage consisting of two peduncle and four spine bearing articles with spines inserting on well developed endites (García-Bellido et al. 2009). Isoxys may represent the interesting case of an independent shortening of a deutocererbal long great appendage convergently to the megacheirans.

Recently, the long debated presence of large specialized cephalic appendages in fuxianhuiids, derivatives of the early euarthropod stem lineage, has been corroborated (Yang et al. 2013). They are short, consisting of only three podomeres without armature, the second forming a geniculation. Their morphology differs markedly from the subchelate multichela of megacheirans, the latter being anteriorly oriented and consisting of a bipartite peduncle and four articles, each extending into a finger forming the multichela with an elbow joint developed between the second peduncle article and the first finger bearing article. The specialized differentiated appendages of fuxianhuids further insert at the posterolateral corners of the hypostome, in postoral position, in contrast to the clearly preoral multichela. The fuxianhuiid appendages are therefore not homologous to the megacheiran multichela and could represent a synapomorphy supporting a monophyletic Fuxianhuiida Bousefield, 1995. The raptorial appendages of Branchiocaris also clearly insert posteriorly to the short antenniform anteriormost appendage and are likely tritocerebral. The appendage shows some superficial similarity to that of the fuxianhuids. Branchiocaris is poorly understood; it has been suggested to belong to a grade of bivalved arthropods that comprise part of the euarthropod stem lineage (Legg et al. 2012). Homology of the Branchiocaris appendage with the specialized (sensu Yang et al. 2013) appendages of fuxianhuiids is unclear, but given that it is stratigraphically relatively younger than the Chinese species, it could represent a derived fuxianhuiid.

Conclusions

Great appendages have evolved at least once on the deutocerebral segment, possibly with a long great appendage

being independently shortened multiple times, and potentially multiple times on the tritocerebral segment (Table 1, Figs. 9 and 10). The tritocerebral raptorial appendages of Branchiocaris and Kodymirus are also likely to be independently derived; those of Branchiocaris consist of a long peduncle of five or six articles and a distal claw, while those of Kodymirus are more readily compared to the "multichela" (Haug et al. 2012a) of megacheirans. The specialized appendage pair of fuxianhuiids is apparently an independent, early specialization of the tritocerebral limb. A number of chelicerates have also enlarged their second cephalic appendage into a raptorial limb (Table 1), including multiple times independently within arachnids, and it appears that there may be an underlying predisposition towards secondary differentiation of this structure. Further support for this comes from the apparently independent reduction of the tritocerebral limbs in hexapods and myriapods so that both possess a limbless intercalary segment (Scholtz and Edgecombe 2006). Given that enlarged raptorial appendages have likely evolved multiple times on both the deutocerebral and tritocerebral segments of Cambrian arthropods (Fig. 10), great care should be taken when proposing homology statements for the various great appendages, and the hypothesis that the possession of a great appendage comprises part of the euarthropod ground pattern should be reevaluated.

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