A new probable stem lineage crustacean with three-dimensionally preserved soft parts from the Herefordshire (Silurian) Lagerstätte, UK

Derek J. Siveter1,2,*, Mark D. Sutton3, Derek E. G. Briggs4 and David J. Siveter5

1Geological Collections, University Museum of Natural History, Oxford OX1 3PW, UK
2Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, UK
3Department of Earth Sciences and Engineering, Imperial College London, London SW7 2BP, UK
4Department of Geology & Geophysics, Yale University, PO Box 208109, New Haven, CT 06520-8109, USA
5Department of Geology, University of Leicester, Leicester LE1 7RH, UK

A new arthropod with three-dimensionally preserved soft parts, Tanazios dokeron, is described from the Wenlock Series (Silurian) of Herefordshire, England, UK. Serial grinding, digital photographic and computer rendering techniques yielded ‘virtual fossils’ in the round for study. The body tagmata of T. dokeron comprise a head shield and a long trunk. The head shield bears six pairs of horn-like spines and the head bears five pairs of appendages. The antennule, antenna and mandible are all uniramous, and the mandible includes a gnathobasic coxa. Appendages four and five are biramous and similar to those of the trunk: each comprises a limb base with an endite, an enditic membrane, and two epipodites, plus an endopod and exopod. The hypostome bears a large cone-like projection centrally, and there may be a short labrum. The trunk has some 64 segments and at least 60 appendage pairs. A very small telson has the anus sited ventrally in its posterior part and also bears a caudal furca. Comparative morphological and cladistic analyses of T. dokeron indicate a crustacean affinity, with a probable position in the eucrustacean stem group. As such the epipodites in T. dokeron are the first recorded in a eucrustacean stem taxon. The new species is interpreted as a benthic or nektobenthic scavenger.

Keywords: Arthropoda; Crustacea; exceptional preservation; Herefordshire Lagerstätte; Silurian; Wenlock Series

1. INTRODUCTION

The Herefordshire Lagerstätte from the Silurian Wenlock Series (approx. 425 Myr ago) of the Welsh Borderland (Briggs et al. 1996) represents one of only a few Lagerstätten known from the ca 70 Myr period between the Cambrian and the Devonian. This deposit has yielded radiolarians (Orr et al. 2002; Siveter et al. 2007a), a diversity of sponges; a polychaete worm (Sutton et al. 2001c); an aplacophoran-like mollusc (Siveter et al. 2001a, 2004); a platyceratid gastropod (Sutton et al. 2006); orthoconic nautiloids; several arthropods, including a pycnogonid (Siveter et al. 2004), a stem-group chelicerate (Orr et al. 2000b; Sutton et al. 2002), two myodocopid ostracodes (Siveter et al. 2003a, 2007b), a barnacle (Briggs et al. 2005) and a phyllocarid (Briggs et al. 2004); a brachiopod (Sutton et al. 2005b); several echinoderms, including an asteroid species (Sutton et al. 2005a); graptolites; and a number of organisms whose affinities remain enigmatic. The new species established here represents the fifth crustacean described from this Lagerstätte, the 78 known specimens comprising approximately 3% of the recorded fauna.

* Author and address for correspondence: Geological Collections, University Museum of Natural History, Oxford OX1 3PW, UK (derek.siveter@earth.ox.ac.uk).

2. MATERIAL AND METHODS

The fossils are preserved in three dimensions as calcitic void fills in early diagenetic carbonate concretions within volcaniclastic sediments (Orr et al. 2000a) and they retain fine morphological detail of external surfaces. Specimens were reconstructed through a combination of serial grinding, digital photography and computer rendering techniques, which produced three-dimensional ‘virtual fossils’ for study (Sutton et al. 2001a,b, 2002). Two specimens were reconstructed following serial grinding at 30 μm intervals: OUMNH C.29601 in entirety, OUMNH C.29602 anteriorly only. OUMNH C.29601 was cut prior to grinding with a 300 μm saw (twice anteriorly) and a 2 mm saw (posteriorly); these cuts are represented by gaps in the reconstruction. The virtual specimens were studied using interactive stereo-capable viewing software and hard-copy stereo-pair images.

3. SYSTEMATIC PALAEONTOLOGY

Phylum: Arthropoda
Subphylum: Crustacea
Genus: Tanazios gen. nov.

Derivation of name: Greek, tanazos (long) + zoon (animal) + pelagios (of the sea)

Diagnosis: Tagmata comprise a head shield and trunk. Head shield comprises axial and fringe areas, the latter bearing six pairs of horn-like spines. Head bears five pairs of
Figure 1. (Caption opposite.)
appendages: tiny antennule, an antenna about five times longer and mandible, all uniramous, the mandible including a basis and a large coxa with a well-developed gnathobase; appendages four and five biramous, structurally the same as the trunk appendages. Hypostome with large, central cone-like projection. Trunk elongate, length-to-width ratio 4.5 : 1, comprising approximately 64 segments, each with one appendage pair except possibly segments 61–64. Trunk appendages each comprise limb base with an endite, enditic membrane and two epipodites, plus a slender endopod and exopod. Telson small, bearing two long caudal rami. Anus ventral near posterior of telson.

Species: Tanazios dokeron sp. nov

Derivation of name: Greek, dodeka (twelve) + kerouchos (horned) + epikranon (helmet).

Diagnosis: as for the genus (monotypic).

Holotype: OUMNH C.29601 (figures 1, 2c–q.s and 3a–d,e and f(par)), an almost complete specimen; median length 29.7 mm; maximum width (at between 0.4 and 0.6 times the overall length) 6.6 mm.

Other material: OUMNH C.29602 (figures 2a,b,r and 3e and f(par)) and 76 other specimens. Datasets and specimens are housed in the Oxford University Museum of Natural History (OUMNH).

(a) Head shield

The head shield (figures 1a,g,j, 2a,b,r and 3a,c) is subsemicircular in dorsal outline, the length approximately 0.75 times the width and 0.1 the total median length of the body, and divided into a fringe and an axial region. The lateral margins converge gradually anteriorly and then more abruptly to a transversely short anterior margin; posterolaterally they define a narrow, high projection with a gently rounded posterior margin. The posterior margin is subtransverse. In lateral outline, the head shield is wedge shaped, and in frontal view its anterior margin forms an inverted ‘v’, curving gently downwards and outwards (figure 2a). The anterolateral part of the fringe region bears an array of six pairs of variably sized, dorsally projecting, horn-like spines, including one pair on the anterior margin and the largest pair posterolateral of these.

The axial region is semi-ovoid in dorsal outline, defined anteriorly by a sagittally wide furrow which becomes narrower laterally, is convex transversely and sagittally and 2.3 times as wide as long, and divided by a narrow median furrow that extends weakly beyond it, just posterior to the largest spines. Lateral to the posterolateral margin of the axial region, there is a narrow ledge that pinches out anteriorly and continues posteriorly as the inner pleural region of the trunk. Posteriorly in the axial region, a shallow transverse furrow defines the anterior margin of a segment similar in length to those of the trunk (seen especially on the left side; figures 1g,j and 3a,c).

Laterally on the fringe region, there are traces of the posterior margins of possibly up to three pleurai; the most posterior of these is very weakly indicated and question-able, the two more anterior margins coincide with the two smallest spines. Eyes are absent.

(b) Head

The antennule lies beneath the largest spine, just lateral of the anterolateral margin of the hypostome (figures 1d,e,h,k, 2b, and 3c,f); it is uniramous and very short (individual podomeres are unresolved). The antenna (figures 1d,e,h,k, 2a,b,g and 3c,f), which inserts immediately posterolaterally of the antennule, is about five times longer, uniramous, subcircular in cross-section proximally, more ovoid distally, and includes three sections recognized by two angular changes in direction that are taken to represent podomere boundaries (the proximal section probably comprising two subequally long podomeres, the boundary between them recognized by slight marginal indentations in each ramus).

A pair of short, widely diverging seta-like structures are present distally on the antenna of the holotype but they are absent on OUMNH C.29602 (figure 2a,b,r) and may be preservational artefacts. The mandible is separable from the antenna by much of the length of the hypostome, alongside the posterior part of which there is a ventralateral bulge that lies beneath the third largest dorsal spine (figures 1j,k and 2a). The nature of this bulge is uncertain; it seems unlikely to represent an eye, as it is almost completely surrounded by the head shield and appendages.

The mandible is uniramous and comprises a presumed coxa (cf. figure 2h and, for e.g. Boxshall 2004, fig. 9f), basipod and endopod (figures 1d,e,h,k and 2b). The coxa is massive, subrectangular (the long axis transverse) and strongly gnathobasic. The gnathobase is distinguished from the coxa by a dorsal notch and raised sharply into an incisor-like process; its medial face is essentially planar and only slightly dentate. The basipod is subrectangular in cross-section, wide proximally, narrowing distally and curving medially. The first section (comprising one podomere) of the endopod is slightly longer than the basipod and subovoid in cross-section; the second (one podomere) is
Figure 2. (Caption opposite.)

approximately 0.25 times as long; the third (probably at least five short podomeres) is slightly longer than the first two combined and tapers to a finger-like distal extremity.

The fourth appendage comprises a limb base with an endite, enditic membrane and probably two epipodites, plus an endopod and exopod (figure 2f). The limb base viewed posteriorly is subrectangular in outline (long axis transverse) and bears a large, swollen, subtriangular area dorsomedially and a smaller one dorsolaterally (presumed muscle insertion sites). A dorsomedially to ventrolaterally elongate, flange-like endite projects posteroventrally from the limb base; dorsally it is separated from the base by a notch and here its medial face is slightly faceted and aligned in the same plane as those of the mandibular gnathobase and the conjoined limb base endite and enditic membrane of each trunk appendage. The limb base bears an epipodite dorsally, and probably another more ventrally. Running from the medial side of the endopod at about mid-length to the posteromedian margin of the limb base, there is a fine membrane, details of which are obscure, but homologues on the fifth and the trunk appendages are clearer. The endopod is long, arises from near the anterior endite, enditic membrane and probably two epipodites, posterodorsal and posterolateral stereo-pairs, ×13, ×20. The endopod is incomplete distally. (q–o) Head region and most anterior part of trunk, with and without short gut section, ventral stereo-pairs, ×14. (m,n,g) Gut section, dorsal, ventral and lateral stereo-pairs, ×24. (s) Transverse section through the trunk in the region of the base of second trunk appendage, ×12.

Figure 2. (Opposite.) Tanazios dokeron. (a,b,r) Partially reconstructed specimen, OUMNH C.29602; (c–q,g) holotype, almost complete specimen, OUMNH C.29601. (a–r) ‘Virtual’ reconstructions; (s) holotype specimen in rock. (a,b,r) Anterior part of head region, anterior and ventral stereo-pairs, lateral view, all ×15. (c–e) Posterior part of trunk, the telson, and anterior part of caudal furca, dorsal, posteroventral and ventral stereo-pairs, ×18, ×13, ×18. (f) Posterior part of trunk, the telson and caudal furca, posteroventral view, ×10. (g) Antennae, anteroventral stereo-pair, ×13. Dotted lines here and on (h–j) indicate discrete sections of the appendage defined by presumed podomere boundaries; some sections probably equate to one podomere, others to more than one (see description). (h) Mandibles, posteroventral stereo-pair, ×13. (i,j) Third and fourth appendage pairs, posterodorsal stereo-pair, ×13. (k,q) Seventh trunk appendage pair, posterodorsal and posterolateral stereo-pairs, ×13, ×20.

The endopod is incomplete distally. (l,p) Head region and most anterior part of trunk, with and without short gut section, ventral stereo-pairs, ×14. (m,n,g) Gut section, dorsal, ventral and lateral stereo-pairs, ×24. (s) Transverse section through the trunk in the region of the base of second trunk appendage, ×12.

Figure 3. Tanazios dokeron. Interpretations of morphology, based on computer reconstructions of OUM C.29601 (holotype) and OUM C.29602. (a,c) Head shield and anterior four trunk segments, dorsal and anterolateral views, ×8. (b) Seventh trunk appendage, posterodorsal view, ×15. The endopod is incomplete distally. (d) Telson and part of caudal furca, posteroventral view, ×32. (e,f) Hypostome and surrounding area, lateral and ventral views, ×18. Diagonal hatches on b and d–f indicate sliced surfaces.

one-third, the hypostome descends ventrally and inwards steeply, and very steeply, from the lateral and posterior margins, respectively. The lateral margin is slightly convex medially and impinged on by the lateral bulge of the head. The presumed posterior margin is weakly convex posteriorly, posterior to which there is a short lip-like feature that may represent a labrum. Dorsal to the hypostome and labrum there is a short, sediment-filled gut section that is constricted where they meet (figure 2l–n,p). Immediately posterior to the constriction, this infill shows a pair of short ventrolateral projections, and dorsally it is roof-like; anterior to it the ventral surface is subplanar, and the dorsal surface irregular. The constriction is interpreted as the mouth, the sediment posterior to it as possibly infilling an atrium.
ors, and that anterior to it as infilling the beginning of the 
oesophagus; whether the other more minor structures 
reflect biological or diagenetic features is uncertain.

(c) Trunk
The trunk of the holotype is made up of approximately 64 
segments inclusive of a tiny terminal axial piece, plus a 
telson and caudal furca (figure 1a–c). One anterior 
segment and five posterior segments are inferred to have 
been present in the two gaps that represent saw cuts. 
Segments are mostly similar in size; the anterior 
approximately 10 become progressively smaller anteriorly 
and the posterior approximately 20 smaller posteriorly, the 
last few segments becoming tiny. All trunk segments bear a 
single pair of biramous appendages with the possible 
exception of the last four (? perhaps too small to be 
preserved). A narrow deep food groove runs the length of 
the trunk, broadening somewhat posteriorly.

The axis is at least 0.8 times the width of the trunk 
across the inner pleural regions. A narrow median furrow 
continues from the head shield onto the first three 
segments. The axis is mostly roof-like in transverse profile, 
sides sloping uniformly and progressively more steeply 
up to at least trunk segment 37. Approximately between 
segments 44 and 55, the central part of the axis descends 
very steeply laterally and the outer part more gently. 
Posterior to segment 55, the steeper central axial part 
progressively takes up the whole of the axial width. In 
lateral view, the anterior segments have a posteriorly 
directed, saw-toothed dorsal outline; from about segment 
22, the apex of each is transformed into a mediad spine 
except for the two segments immediately anterior to 
the terminal piece (figure 2c), which each bear a small 
median node.

The pleural region comprises a very narrow inner ledge 
and, except for the first segment, descending pleural facets 
(figure 1j). The first segment lacks a pleura, which may 
have been incorporated into the posterolateral part of the 
head shield. The second pleura is reduced in size relative 
to more posterior pleurae. The pleural facets have a 
subrounded-to-pointed distal margin, a slightly thickened 
posterior margin and they show slight (15–20%) overlap. 
In lateral view, the anterior facets swing forwards, the mid-
trunk ones point downwards and the posterior ones swing 
progressively backwards; these attitudes may in part be 
controlled by the dorsal (concave) curvature of the trunk. 
The last three or four trunk segments either lack pleuraea 
or they are too small to be preserved or resolved. 
Immediately posteroventral of the posterior axial margin of 
many segments, there is a subparallel line that may represent 
the posterior margin of an articulating half-ring (figure 1g). 

The trunk appendages vary in size proportional to their 
respective segments. The structure of each appendage is the 
same and is like that of head appendages four and five, 
although the smaller posterior ones are less well resolved. 
The seventh trunk appendage (individually rendered; 
figures 1h, 2k,q and 3b) shows that the limb base is convex 
 anteriorly in lateral view, and subrectangular in outline (long 
axis dorsoventral) and weakly divided into dorsal and ventral 
parts along the line of curvature in posterior view. The limb 
base has a large, swollen (presumed muscle attachment) 
area dorsomedially and a smaller one dorsolaterally, and a 
well-developed dorsomedially to ventrolaterally elongate, 
posteroventrolaterally directed, flange-like endite. The more dorsal 
of the two large, blade-like epipodites is the smaller. Both are 
variously disposed backwards and outwards and are 
apparently articulated basally.

There is an endite membrane comprising three 
separately attached flap-like elements two of which (at 
least) are united. The first element is attached to the limb 
base where the base is met by the median margin of the 
endopod; it is horizontally disposed and medially turns 
upwards into a curtain-like section that becomes partially 
confluent with the endite, which in some appendages is 
seen to project dorsomedially through it. The second 
originates on the endopod proximally, at the bottom of its 
downward curve and at its mid-width; it extends medially, 
then folds dorsally and extends laterally before folding 
dorsally again to become confluent with the first element. 
The third element connects to the endopod just distal of 
where the ventroposterior curve of the endopod levels out, 
and at its mid-width, distal to which it is raised slightly off 
the endopod, though otherwise its form is unresolved. 

The seventh trunk endopod curves ventroposteriorly 
proximally where it is broad, flat and ribbon-like; distally it 
becomes very much narrower, more subovoid in cross-
section and trends posteromedially, but is here incomplete 
(when entire, the trunk endopods extend much more distally 
in finger-like form (figure 1b), as in head appendages four 
and five). If the distal two flaps are proxies for podomere 
boundaries, at least three podomeres are present. The 
exopod is shorter than the endopod and slightly less broad 
than it is proximally where (as with head appendages four 
and five) they touch, though it is unknown whether their 
margins here are fused; it is ribbon-like, curves ventropos-
teriorly, narrowing only slightly as it does so, and ends in a 
short, broadly pointed termination. Exopod podomere 
boundaries cannot be determined.

(d) Telson and caudal furca
Behind the terminal axial piece, there is a small telson that 
bulges laterally and is extended posteriorly into a short, 
median, triangular flap beneath which is a similar ventral 
flap (figures 2c–f and 3d). Two incomplete ovoid (long 
axis horizontal) rami, with a preserved length 0.08 times 
the body length, project from the posterolateral margins of 
the telson to form a caudal furca; proximally they are 
subparallel, distally they deflect weakly outwards (figure 1a–c), 
and they lack evidence of podomeres. A small orifice sited 
ventrally in the posterior part of the telson is interpreted as the 
anus; it is flanked by a pair of short, posteroventrally directed subconical projections.

4. DISCUSSION
(a) Affinities
The gross morphology of Tanazios—a long, narrow body 
with only two tagmata, and a trunk with numerous segments 
each bearing a pair of homonomous biramous appendages— 
resembles that of extant and fossil remipedes (Schram et al. 
1986; Emerson & Schram 1991), and also the purported 
stem crustacean Ercaia minuscula from the Lower Cambrian 
of Chengjiang (Chen et al. 2001). However, this type of 
morphology is probably plesiomorphic (cf. the ‘urcrustae-
can’ proposed by Hessler & Newman 1975), and moreover 
all of these taxa differ in detail. Tanazios also shows 
resemblance in overall body form to the Hunsrück Slate 
(Devonian) monotypic arthropods Eschenbachiellus,
Cambronatus and particularly Wingertshelicus (Briggs & Bartels 2001; Moore et al. in press), which were described as ‘crustaceanomorphs’. However, Boxshall (2004) regarded the crustacean affinities of Cambronatus as equivocal, and Cambronatus and Wingertshelicus have been allied tentatively (Haas et al. 2003) with the monotypic Hunsrück Slate genus Devonoxenopodus, as hexapods within Atelocerata (myriapods + hexapods), but the hexapod affinities of Devonoxenopodus have been disputed (Regier et al. 2004; Willman 2005). The body of Tanazios is generally myriapod-like, and if the long, apodous area of the head between the mandible and the preceding appendage were to represent the intercalary segment of that group, a stem mandibulate assignment for it could be entertained. Under this scenario, the two rami recognized herein as the antennule and antenna would then represent an antennule that comprised two branches, one or both of which is a flagellum (Boxshall 2004). However, while these two rami are proximally close, they show no sign of joining, a common origin, or being branches of the same appendage, and neither ramus seems particularly flagellum like.

The morphology and arrangement of the head appendages in Tanazios, together with the morphology of the trunk appendages, indicate that its affinities lie with the crustaceans. This is supported by our cladistic analysis of the morphological character matrix of Wills et al. (1998), to which we added Tanazios. Although the phylogenetic conclusions of Wills et al. (1998) have been superseded by more recent molecular and total evidence approaches (e.g. Giribet et al. 2001, 2005; Regier et al. 2005; Mallatt & Giribet 2006), and by re-evaluation of the position of Trilobita (Scholtz & Edgecombe 2005), it remains the most recently published morphological database that accommodates both palaeontological and neontological characters, and hence still provides a basis for the placement of fossils within the major arthropod groups. Having determined a crustacean affinity for Tanazios, we analysed its placement within the more comprehensive morphological database of fossil and living crustaceans provided by Wills (1998), which includes nearly three times as many relevant taxa. Tanazios falls in a basal position, more derived only than the Cambrian Odanina. (Note, however, that recent molecular phylogenies suggest that remipedes, used as outgroup by Wills (1998), are not basal crustaceans.)

We then considered the placement of Tanazios within the crustacean stem group using the phylogenetic scheme put forward by Waloszek and co-authors (Walossek & Müller 1990, 1998; Walossek & Szaniawski 1991; Walossek 1999; Waloszek 2003). The presence in Tanazios of a short antennule with few podomeres identifies it as a total group (stem plus crown) crustacean. Special distal setae used for locomotion and feeding on the antennule, a moveable proximal endite and exopodal setae directed towards the endopod in the postantennular limbs, are apparently lacking in Tanazios, and other autapomorphies of the total group crustaceans concerning endopod and exopod podomere numbers cannot be determined. The presence of a mandible with coxa, five limb-bearing head segments, and a labrum and atrium oris, suggest a placement for Tanazios within the labrophoran clade (Phosphatocopina + Eucrustacea; Siveter et al. 2003b). However, in Tanazios, the morphology of the basal part of the antenna appears simple, presumably reflecting an undifferentiated limb base, and thus it seems to lack a coxa (sensu Waloszek), the presence of which is an autapomorphy of Labphorora; the possible small labrum and atrium oris might simply represent a posterior extension of the hypostome and associated gut; furthermore, a head with five limbs is known from less derived, labrophoran stem lineage derivatives such as Hemingsoemoenarcis, Oelandocaris and, though possibly not fully so, Martinsonia. Other labrophoran autapomorphies (Siveter et al. 2003b; Waloszek 2003) are indeterminate in Tanazios (fusion of antennal to maxillulary sternites into a single sternum), or are apparently absent (paragath outgrowths on the mandibular sternites/ part of the sternum, and fine hairs on the sides of the labrum). Key phosphatocopine autapomorphies, such as a phospathic, bivalved head shield enclosing the body and reduction of trunk segments to less than six, are also absent. The final autapomorphy listed for Phosphatocopina, an antennule much reduced in size and numbers of podomeres and setae, can mostly be confirmed in Tanazios. Tanazios lacks key eucrustacean autapomorphies, such as modification of the fourth head appendage into a specialized mouthpart and the presence of a terminally positioned anus. There is slight facting on the dorsomeral part of the endite of the fourth, and to a lesser extent fifth, appendage of Tanazios (see description), but these limbs are essentially like those of the trunk (even in Cephalocarida, which is often referred to as showing the least serial specialization of limbs among Eucrustacea, the fourth (adult) limb is more differentiated from the fifth and the trunk limbs; see Hessler 1969). A caudal furca, articulated and leaf shaped with marginal setation, may be an autapomorphy of Eucrustacea, but possible furcae have also been identified in Phosphatocopina, so potentially moving this character down to this level (Maas et al. 2003; Waloszek 2003).

Thus, Tanazios appears to fall within the eucrustacean stem lineage in the scheme of Waloszek and co-authors, either basally within (a redefined) Labphorora, or with the stem-lineage derivative forms Cambropachycope, Goticaris, Cambrocaris, Martinsonia, Hemingsoemoenarcis and Oelandocaris, outside the labrophoran clade. Relationships among the stem-lineage derivatives remain unresolved apart from the sister group relationship of Cambropachycope and Goticaris (Cambropachycopidae), and most recently Oelandocaris has been considered the most basal of them (Stein et al. 2005). Tanazios differs from these other taxa in possessing a mandible with a coxa, and on the evidence of this character, it would be considered the most basal of them (see Walossek & Müller 1990; Waloszek 2003; Stein et al. 2005; though see also Walossek & Szaniawski 1991 for a report of a coxa in Cambrocaris). The uniramous mandible and antenna of Tanazios, both presumably representing the derived condition, are also unique among these genera, and the overall form of its post-mandibular appendages is distinct, in particular the slender, apparently setae-less exopod and epipodite-bearing limb base.

Tanazios is the first of the five crustaceans described from the Herefordshire Lagerstätte that does not appear to belong to the crown group. The recognition of epipodites in a probable eucrustacean stem-group form is noteworthy; these structures are otherwise known only from undoubted eucrustaceans, the Herefordshire Lagerstätte Colymbosathon, Cinerocaris and Nymphatellina representing the earliest examples. Given the mounting evidence of a close hexapod–crustacean relationship (e.g. Giribet et al. 2005;
Regier et al. (2005), this provides evidence that ‘structural progenitors’ of insect wings (Averof & Cohen 1997) may have existed in the earliest crustaceans (Boxshall 2004).

(b) Mode of life
The Herefordshire Lagerstätte was deposited in an outer shelf muddy bottom setting within the Anglo-Welsh Basin under maximum water depths of approximately 200 m (Briggs et al. 1996). Tanazios does not have a typical arthropod ‘walking’ leg. However, its apparent blindness is more consistent with living on or near the bottom than primarily in the water column; other co-occurring, presumed benthic taxa were blind (e.g. the chelicerate Ofaccomys, the polychaete Kenostrychus and the vermiform mollusc Acaenoplax), while natatory forms (the ostracodes Colymbosathon and Nymphatella, and the phyllocarid Cinerocaris) possessed eyes. The numerous trunk appendages of Tanazios would probably have enabled active swimming, the caudal furca functioning as a stabilizer. The epipodia, by analogy with living crustaceans, would have served in respiration, either directly or to ventilate other respiratory parts—perhaps the exopods, the body wall or maybe even the enditic membranes. Anterior transporation of food along the endite-flanked food groove (the plesiomorphic state for euarthropods; Hessler & Newman 1975; Waloszek 2003) must have occurred, and the enditic membranes may have helped contain it in this channel. The similarity of the fourth and fifth head appendages to those of the trunk implies similarity of function. The tiny antennule is not of typical sensorial form, at least not mechanosensory, and it seems unsuited either for locomotion or food collection (Waloszek 2003; Boxshall 2004). Dorsoventral flexure of the trunk was probably possible to some degree: witness the overlap of pleural facets and the possible articulating half-rings. The horn-like dorsal spines may have been defensive.

Tanazios was blind and therefore probably not a predator, yet it had a substantial mandibular gnathobase; this suggests that it fed on detritus. Tanazios is thus interpreted as a benthic or nektobenthic scavenger.

The Leverhulme Trust (F/08581/E) and English Nature are thanked for their financial support, K. Saunders for technical assistance, G. Boxshall for discussion, and R. Fenn, T. Hall and J. Sinclair for their general assistance.

REFERENCES


NOTICE OF CORRECTION

Figures 1 and 2, and the legend of figure 3 are now presented in the correct form. 8 August 2007
Errata


Soft tissue and cellular preservation in vertebrate skeletal elements from the Cretaceous to the present

Mary Higby Schweitzer, Jennifer L. Wittmeyer and John R. Horner

The funding acknowledgement in the acknowledgement section was incorrect, and should read as follows:

Funding for this work was provided by National Science Foundation (EAR-0541744), Discovery Channel and North Carolina State University.


Fidelity and over-wintering of sea turtles

Annette C. Broderick, Michael S. Coyne, Wayne J. Fuller, Fiona Glen and Brendan J. Godley

The scale bar in figure 2b was incorrect, and should read as follows:

5 km.


A new probable stem lineage crustacean with three-dimensionally preserved soft parts from the Herefordshire (Silurian) Lagerstätte, UK

Derek J. Siveter, Mark D. Sutton, Derek E. G. Briggs and David J. Siveter

Figures 1 and 2 were incorrectly sized and the magnifications in the legend of figure 3 were incorrectly stated.

The online version of the article has now been corrected.