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

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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 (Sutton 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 echiinoderms, 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.

2. MATERIAL AND METHODS
The fossils are preserved in three dimensions as calcitic void fills in early diagenetic carbonate concretions within volcanioclastic 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, tanaos (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

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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, dokera (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,i,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,i and 3a,c). Laterally on the fringe region, there are traces of the posterior margins of possibly up to three pleura; 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 3e,f); it is uniramous and very short (individual podomeres are unresolved). The antenna (figures 1d,e,h,k, 2a,b,g and 3e,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 but they are absent on OUMNH C.29602 (figure 2a,b,r) and may be preservational artefacts. The mandible is separated 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 1f,j,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 2b 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 posteromedially 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 proximally as it trends ventroposteriorly, and becomes more finger-like distally; it appears to consist of three sections, the two most proximal (each one podomere?) of subequal length and the other most distal (in which podomeres cannot be distinguished) about twice as long as each of these. The exopod originates posterolaterally on the limb base, is ribbon-like, has a similar disposition to the endopod and probably also comprises three sections (thus at least three podomeres), and although imperfectly preserved distally, it is shorter.

The fifth appendage (figure 2j) is similar to the fourth but slightly larger; the enditic membrane projects more dorsally above the endite; and both ventral and dorsal epipodites are clearly present.

The hypostome (e.g. sensu Waloszek 2003) is subrectangular in overall outline, approximately 1.4 times as long as wide, and extends from just anterior of the antennules to the mandibular gnathobases (figures 1d, f, j, k, 2a, b, l, o and 3e, f). Its anterior margin is poorly resolved but appears to be transversely directed and to bear four small spines. Anterolaterally there is a relatively small, laterally projecting, wing-like process. In its anterior quarter, the hypostome projects ventrally and steeply backwards and inwards from the anterior and lateral margins, respectively, to a break in slope on which, bilaterally, there is a short spine. Posteriorly from here, the central body extends more ventrally to a cone-like central projection that extends posteriorly to approximately 0.6 of the hypostomal length. In its posterior...
oris, 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.

**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, its 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 medial 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 pleurae 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–j).

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, 2h, 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, posteromedially 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 enditic 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 medial 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 ventroposteriorly, narrowing only slightly as it does so, and ends in a short, broadly pointed termination. Exopod podomere boundaries cannot be determined.

**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 2e–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 *Tunazios*—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 *Ercia minuscule* from the Lower Cambrian of Chengjiang (*Chen et al. 2001*). However, this type of morphology is probably plesiomorphic (cf. the ‘urcrustacean’ proposed by *Hessler & Newman 1975*), and moreover all of these taxa differ in detail. *Tunazios* also shows resemblance in overall body form to the Hunsrück Slate (Devonian) monotypic arthropods *Eschenbachiellus,*
Cambronatus and particularly Wingerthesilicus (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 Wingerthesilicus have been allied tentatively (Haas et al. 2003) with the monotypic Hunsrück Slate genus Devonohexapodus, as hexapods within Atelocerata (myriapods + hexapods), but the hexapod affinities of Devonohexapodus 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 remipede, 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 Labphorpa; 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 Henningsmoenicaris, 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 phasphatic, 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 factaging on the dorsomedial 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) Labphorpa, or with the stem-lineage derivative forms Cambropachycope, Goticaris, Cambrocaris, Martinsonia, Henningsmoenicaris and Oelandocaris, outside the labrophoran clade. Relationships among the stem-lineage derivatives remain unresolved apart from the sister group relationship of Cambropachycope and Goticaris (Cambropachycopeidae), 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 derived 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 Offalcoolus, the polychaete Kenostrychus and the vermiform mollusc Acaenoplax), while natatory forms (the ostracodes Colymbosothion and Nymphatellina, and the phyllocardin 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 transpor- tation of food along the endite-flanked food groove (the plesiomorphic state for eurypods; 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 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.

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REFERENCES


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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.