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A three-dimensionally preserved fossil polychaete worm from the Silurian of Herefordshire, England

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Polychaete body fossils are rare, and are almost invariably compressed and too poorly preserved for meaningful comparison with extant forms. We here describe *Kenostrychus clementsi* gen. et sp. nov. from the Silurian Herefordshire Konservat-Lagerstätte of England, in which three-dimensional external morphology is preserved with a fidelity unprecedented among fossil polychaetes. The fossils, which are preserved in calcite, were serially ground and photographed at 30 μm intervals to produce computer-generated reconstructions of the original external surface. The new genus has a generalized polychaete morphology with large biramous parapodia, unspecialized anterior segments and a small prostomium with median and lateral antennae and ventral prostomial palps. Cirriform branchiae arise from the ventral surface of each notopodium, and may be homologous with the inter-ramal branchiae of the extant nephtyids. Through cladistic analysis, *Kenostrychus* is interpreted as a member of a stem group of either the Phyllodocida or the Aciculata (Phyllodocida + Eunicida). Direct comparison with other fossil forms is difficult, but hints that inter-ramal respiratory structures may be primitive within the Phyllodocida and/or the Aciculata.

Keywords: polychaete; exceptional preservation; Silurian; England; Konservat-Lagerstätte

1. INTRODUCTION

The polychaete annelids are a common and diverse group of marine animals, with over 80 Recent families (see Fauchald & Rouse 1997). As polychaetes are essentially soft-bodied, they are only rarely preserved as fossils, although scolecodonts, the fossilized jaw elements of euniceans, glycerids, goniadids and possibly nereidids (Bergman 1989), are well known. Body fossils of polychaetes are known from several Palaeozoic Konservat-Lagerstätten (e.g. the Burgess shale (Conway Morris 1979), Mazon Creek (Thompson 1979); see also Briggs & Kear 1993, table 1), but reconstruction of the morphology of these worms is hampered by the essentially two-dimensional nature of their preservation, making meaningful comparison with modern forms difficult. Only one three-dimensional (3D) polychaete specimen has been reported, an indifferently preserved possible spionid found within a boring of Devonian age from New York State (Cameron 1967). Furthermore, while several Cambrian and Upper Palaeozoic occurrences are known, only a single body fossil is known from the Ordovician (Pickerill & Forbes 1978) and none has hitherto been described from the Silurian. The material described below, from the Silurian Herefordshire Konservat-Lagerstätte (Briggs *et al.* 1996), is both 3D and rich in morphological information.

The phylogeny of the polychaetes is poorly understood, and while some of the Recent families form clear natural groupings (e.g. the 'scale-worms' and the euniceans), the inter-relationships of most have long been obscure. Many taxonomic and phylogenetic schemes have been proposed (for a review, see Fauchald & Rouse 1997), but none has gained wide acceptance; many authors have preferred not to use suprafamilial taxa (e.g. Day 1967; Dales 1977). The recent cladistic analyses of Rouse & Fauchald (1997) provide a coherent taxonomic scheme, adopted by Glasby *et al.* (2000) with minor modifications. None the less, this scheme is explicitly provisional. In view of these uncertainties, high-quality data from the fossil record are desirable.

At least three polychaete species were provisionally identified in the initial report on the Herefordshire fauna (Briggs *et al.* 1996), prior to the development of the grinding technique. However, further investigations have revealed the first species (Briggs *et al.* 1996, fig. 1*f*) to be a vermiform mollusc (Sutton *et al.* 2001*a*), and the second species (Briggs *et al.* 1996, fig. 1*g*) to be a sponge. The third species, described here, is the only polychaete currently known from the fauna.

2. PRESERVATION

The new polychaete worm, *Kenostrychus clementsi*, occurs as part of a 3D soft-bodied fauna of small marine invertebrates, first reported by Briggs *et al.* (1996). The fossils are preserved within carbonate concretions in a volcaniclastic deposit from the lower Silurian (Wenlock series) of Herefordshire, England. Specimens consist essentially of sparry calcite infills which, while preserving little or no internal morphology, reproduce the external surface of the animals with great fidelity. The taphonomic model (Orr *et al.* 2000*a*) for the co-occurring arthropod *Offacolus kingi* (Orr *et al.* 2000*b*) proposed that the sparry calcite precipitated into a void left after the decay of the animal. The polychaete fossils are assumed to have been

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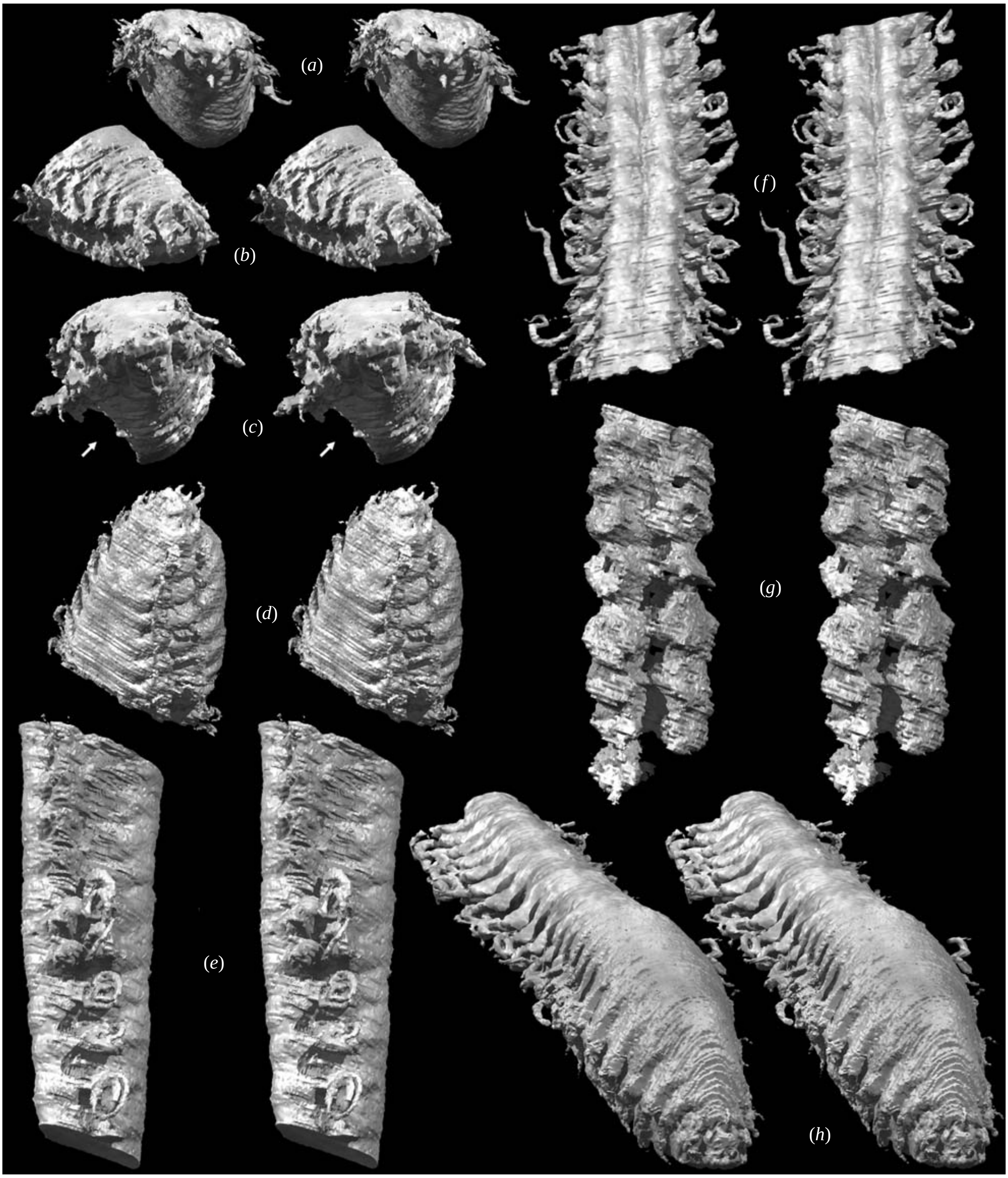

Figure 1. Stereo-pairs of reconstructed specimens of *Kenostrychus clementsi*. Note that the orientation of the reconstructions is not consistent, as we prefer to maintain a constant lighting direction. (*a*) OUM C.29543, anterior fragment, anterior view (ventral surface uppermost), with the possible mouth indicated by the arrow, × 12. (*b*,*c*) OUM C.29544, (*b*) anterior fragment, oblique lateral view (dorsal surface uppermost), × 12; (*c*) anterior fragment, anterior view (ventral surface uppermost), with collapse structure indicated by the arrow, × 15. (*d*–*h*) OUM C.29545, (*d*) anterior fragment, ventrolateral view, × 12; (*e*) trunk fragment (edited by selective deletion of rami and associated structures to show four neuropodia, three notopodia and part of a fourth, and two unedited parapodia), lateral view (anterior surface uppermost, ventral surface to the left), × 16; (*f*) trunk fragment, ventral view (posterior surface uppermost), × 10; (*g*) halo surrounding parapodia of the trunk fragment, lateral view (anterior surface uppermost, ventral surface to the left), × 16; (*h*) composite reconstruction of anterior and trunk fragments, oblique anterodorsal view, × 12.

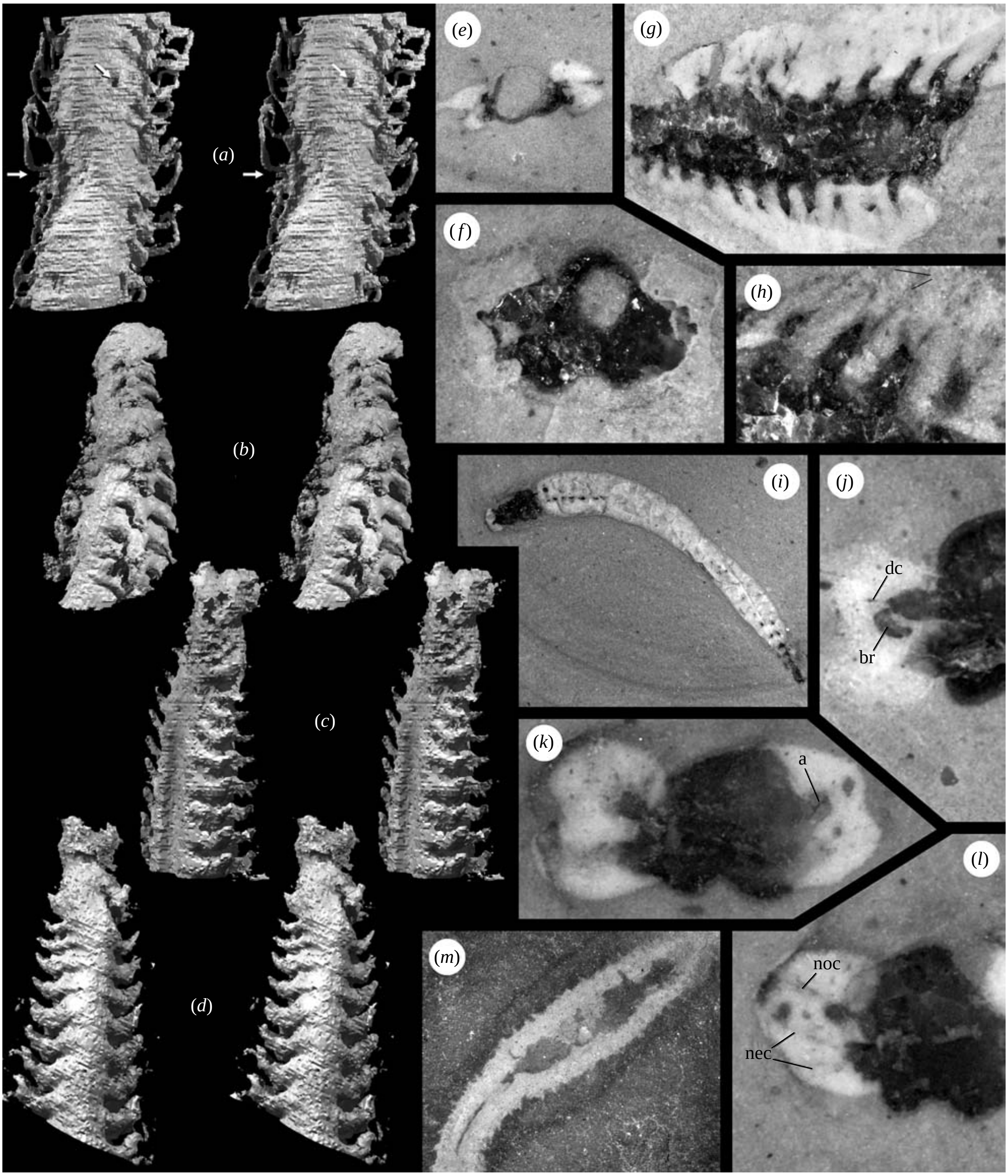

Figure 2. (*a–l*) *Kenostrychus clementsi*; (*a–d*) are stereo-pairs of reconstructed specimens. (*a*) OUM C.29546, trunk fragment, dorsal view, with decay structures indicated by arrows, ×12. (*b*) OUM C.29544, posterior fragment, dorsolateral view, ×12. (*c*,*d*) OUM C.29543, posterior fragment, (*c*) ventrolateral view, ×12; (*d*) dorsal view, ×12. (*e*) OUM C.29545, serial grinding image of sub-transverse section, with expanded sediment fill, ×12. (*f*) OUM C.29548a, transverse section, with infilled gut, ×20. (*g*) Holotype, OUM C.29525a (part), sub-horizontal section, ×12. (*h*) Holotype, OUM C.29525b (counterpart), detail of neuropodia and neurochaetae (nec), photographed through a blue filter, ×24. (*i*) OUM C.29549b, exsagittal section through parapodia and haloes (except at the extreme left, where the section is sub-transverse through the body), ×2.5. (*j*) OUM C.29545, part of serial grinding image, transverse section, showing junction of branchia (br) with notopodia and dorsal cirrus (dc) near attachment point, ×20. (*k*,*l*) OUM C.29546, serial grinding images, (*k*) sub-transverse section showing acicula (*a*) within notopodia, ×20; (*l*) part of sub-transverse section showing notochaetae (noc) and neurochaetae (nec), ×20. (*m*) *Didonotogaster cordylina* Thompson, 1979, Mazon Creek Essex Fauna, Carboniferous, Illinois, Field Museum of Natural History PE.46141a, anterior with swollen gut, ×3.

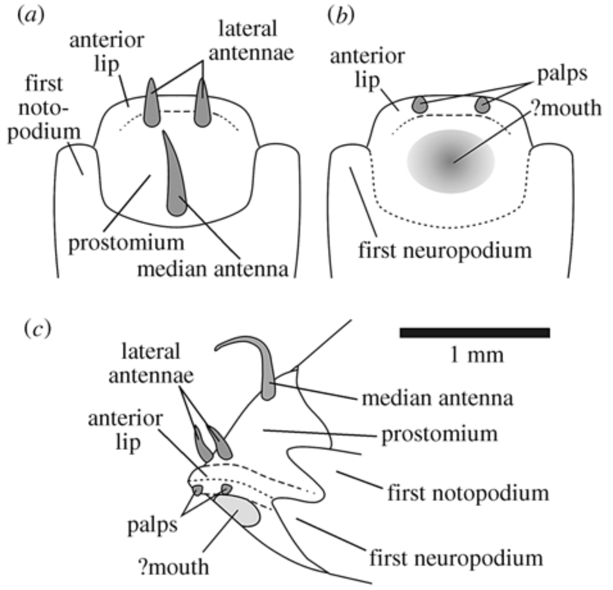

Figure 3. Reconstructions of the anterior region of *Kenostrychus clementsi*; (*a*) dorsal view, (*b*) ventral view and (*c*) sub-lateral view.

preserved in a broadly analogous manner, although more signs of decay are evident. Matrix is occasionally preserved inside specimens, and in some cases may represent a sediment-filled gut (e.g. figure 2*f*). However, one such fill, when traced by serial grinding (see § 3), was found to expand down the length of the worm until the rest of the body, including the parapodia, became indistinct and vanished (figure 2*e* is from this sequence). We interpret this fill as the result of partial decomposition of the specimen prior to burial, with associated infiltration of sediment, and hence assume that, while it may follow the path of the gut, it does not provide reliable information on gut size, morphology or *in vivo* contents. We avoid drawing any conclusions from other such 'gut fills', pending further investigation.

Briggs & Kear (1993) described the stages of decay of the Recent polychaete *Nereis*, providing a basis for assessing the duration of decay prior to the formation of the preserved external surface in the Herefordshire fossils. Features such as the small dorsal hole in figure 2*a* (upper arrows) and the broad partial-collapse structures in figures 1*c* (arrows) and 2*a* (lower arrows) are consistent with the early decay structures observed by these authors. Their studies also showed that, under all experimental conditions, polychaete carcasses collapsed to an essentially two-dimensional state within six days. Assuming that decay processes in *Kenostrychus* were similar to those in *Nereis*, the 3D state of the fossils implies that less than six days elapsed between death and 'freezing' of the sediment.

The vast majority of *Kenostrychus* specimens display 'haloes' of lighter (or occasionally darker) coloured matrix abutting the fossil laterally (figure 2*e*–*l*). These haloes are semi-continuous along the length of the fossil, and are developed most consistently around the parapodia, and in particular their distal portions. Although the process by which they formed is not understood in detail, it is clear from their position, size and shape that they are associated with the chaetae. They have therefore been used to provide evidence for the details of chaetal arrangement.

3. MATERIAL AND METHODS

Splitting the concretions yielded randomly orientated planar or sub-planar sections through the worms, which were then photographed under water using incident light and colour film (or a digital camera). Selected specimens were cut into sections 5–10 mm in length, which were serially ground at 30 μm intervals and digitally photographed to produce sets of 'slice images'. These datasets were aligned and used to generate 3D computerized reconstructions of the fossils. The datasets underlying these reconstructions have been edited to remove most of the extraneous material and, where possible, to resolve fossil–matrix ambiguities. This method is described in detail by Sutton *et al.* (2001*b*). Specimens and datasets are housed in the University Museum of Natural History, Oxford (OUM).

4. SYSTEMATIC PALAEONTOLOGY

Kenostrychus clementsi gen. et sp. nov.

1996 third polychaete species; Briggs, Siveter & Siveter.

2000*a* unnamed polychaete worm; Orr, Briggs, Siveter & Siveter, fig. 2*d*.

2001*b* unnamed polychaete annelid; Sutton, Briggs, Siveter & Siveter, fig. 12.

(i) *Derivation of names*

The generic name is derived from the Greek *keneon* (flank) and *bostrychos* (a curl or lock of hair), alluding to the lateral coiled branchiae; gender, masculine. The specific name is after Dr Roy Clements, Geological Curator, University of Leicester, who drew our attention to the potential significance of the Herefordshire material.

(ii) *Diagnosis of genus (monotypic)*

The body is *ca.* 15–20 mm long; the trunk consists of approximately 40–45 segments; the anterior and posterior few segments are smaller in diameter. The parapodia are all well developed and biramous; each notopodium bears cirriform inter-ramal branchiae, attached immediately beneath the distal point, and a dorsal cirrus, attached at or immediately dorsal to this point; each neuropodium bears a ventral cirrus. Both rami bear fine hair-like chaetae. The anterior trunk segments lack tentacular cirri or other modifications. The prostomium is small and rounded and bears a single short median antenna and two lateral antennae. The palps are greatly reduced, prostomial and ventrally placed. The peristomium is reduced or absent.

(iii) *Material*

The holotype is OUM C.29525 (figure 2*g*,*h*). About 80 other specimens are known. Five specimens (OUM C.29543–7) have been serially ground in nine individual fragments, eight of which (four anterior terminations, two posterior terminations and two mid-trunk sections) have been reconstructed in three dimensions. Other figured specimens are OUM C.29511 (Orr *et al.* 2000*a*) and OUM C.29548–9 (this paper).

(a) *Size and overall form*

The total length and number of segments are not obtainable directly from any single specimen. The average segment frequency varies between approximately 2.1 and 2.6 segments per mm in reconstructed fragments, and is fairly constant along the body, although it may be higher at the extreme anterior and posterior ends. The largest specimen (OUM C.29549, figure 2*i*) is at least 16 mm long and, as exposed, lacks an anterior termination. It is therefore estimated that a typical body length is 15–20 mm, suggesting that a full segment count is probably between 40 and 45. The trunk height and width in transverse section are typically similar (except near the posterior, see §4c), and are in the range of 1–2 mm. However, the shape and size of the transverse sections are variable both between specimens and along individual specimens. This variation apparently relates primarily to the relative contraction and extension of the trunk.

(b) *Anterior structures*

The prostomium is typically 0.5 mm in width and slightly more in sagittal length; it forms a dome-like structure (figures 1*b*,*c*, *h* and 3) with a marked anterior lip, giving it a sub-acuminate profile in lateral view. Its junction with the first trunk segment is clearly delineated dorsally and laterally (figure 1*b*, *h*). The dorsal surface of the prostomium is evenly convex in sagittal and transverse sections, and bears three tapering projections (figure 1*a*–*d*,*h*), which are apparently circular in cross section. These are interpreted as a single median and two lateral antennae. The median antenna attaches 0.1–0.2 mm from the posterior of the prostomium, is 0.5–0.6 mm long, somewhat less than 0.1 mm in diameter proximally and tapers distally. This antenna was clearly flexible, being sharply flexed anteriorly in both specimens where it is fully preserved (near its base in figure 1*b*,*c*; near its midpoint in figure 1*d*,*h*). The lateral antennae, which attach 0.1–0.2 mm from the anterior margin of the prostomium and are spaced 0.2–0.25 mm apart, are short and stubby, as wide as the median appendage proximally but only 0.15–0.2 mm long. They project approximately anterodorsally in all cases, and are not observed to flex strongly. A pair of very short and poorly resolved projections of the anteroventral prostomium, arising from the ventral side of the anterior lip (figure 1*b*,*c*), are interpreted as greatly reduced ventral palps. The ventral surface of the prostomium is sub-planar, sloping ventrally backwards at a steeper angle than the surface of the immediately adjacent trunk; the junction between the trunk and the prostomium on this surface is marked by a weak break of slope rather than a discrete boundary (figure 1*d*). On one specimen an indistinct hollow, which may represent a mouth, is evident on the ventral surface of the prostomium (figure 1*a*, arrow). No peristomium, nuchal organs or eyes were observed: these structures are either reduced and obscure or absent (eyes might also be subdermal).

(c) *Trunk*

Ventrally, two evenly convex lateral surfaces, separated by a distinct median groove (e.g. figure 2*f*,*k*), extend along most of the trunk, becoming shallower towards both terminations and never extending to either terminal segment. The groove depth is variable, and while it can be up to 20% of the trunk height, it is typically about 10%. Annulation is weakly expressed on the ventral surface (figure 1*f*) and very indistinctly so on the smooth and evenly convex dorsal surface (figure 1*h*).

In one specimen (figure 1*h*) the anterior region of the trunk is swollen substantially relative to the region behind it, the widest point being at about the tenth segment. The extent to which this is a reflection of the contractile nature of the trunk rather than a character of the species is not clear. However, all the anterior fragments examined taper anteriorly in a similar manner. In dorsal and ventral views, the trunk tapers increasingly rapidly from the tenth to the first (anteriormost) segment; the latter is approximately half the width of the former. In lateral profile, the dorsal margin of the anterior trunk behind the fifth segment is nearly parallel with a horizontal plane through all the neuropodia or notopodia ('parapodial plane'), but it curves ventrally between the fourth and fifth segments into a sub-linear slope at nearly 45° to the parapodial plane. The corresponding ventral surface is sub-parallel to the parapodial plane behind a point at about the third segment, anterior to which it curves weakly dorsally to join the ventral surface of the prostomium; this junction is sometimes marked by a break of slope.

Posteriorly, the trunk tapers weakly, in dorsal and ventral views, towards the posterior over at least eight segments. In lateral view, the dorsal surface slopes gently ventrally over a similar distance. In one specimen this slope levels off about six segments from the pygidium (figure 2*b*), in another it continues sub-linearly to the posterior (figure 2*d*). In both specimens the parapodia of the posteriormost segments are mid-lateral in position.

(d) *Parapodia and chaetae*

All trunk segments bear well-developed and similar biramous parapodia (see, for example, figures 1*e*,*f*,*h*, 2*c*,*k* and 4). Except posteriorly, these are positioned nearer to the ventral than to the dorsal margin (the notopodium is typically attached near to the mid-height). The notopodia and neuropodia are large and sub-equal in size: their proximal to distal length is up to 0.5 mm. Both parapodial rami are broadly sub-conical in form, though relatively short anteroposteriorly (figure 1*e*). They are often recurved in dorsal and ventral views, and were clearly flexible to some degree during life. The parapodia of the anteriormost few segments are consistently directed anteriorly (figure 1*b*,*d*,*h*), but those of the remaining segments could apparently be directed anteriorly or posteriorly (figures 1*f* and 2*b*,*c*).

Each notopodium bears a long tapering tentacle-like structure (figure 1*f*,*h*), which is up to 1.7 mm long and *ca.* 0.1 mm in diameter at its widest point, arising from the ventral side of the notopodium, immediately beneath its distal termination (figures 1*e* and 2*j*). At the point of attachment to the notopodium the structure normally appears constricted (figure 2*j*). The structure, which is interpreted as a cirriform branchia, is typically coiled but is preserved in a variety of contorted states. At, or immediately dorsal to, the point at which the branchia is attached to the notopodium, a sub-linear structure arises, which extends laterally to dorsolaterally for up to 0.4 mm (figures 1*e* and 2*j*). Approximately halfway along the ventral surface of each neuropodium there is an apparently fairly rigid linear structure up to 0.6 mm long (figure 1*e*), which is typically held at a low angle to the margin of the parapodium. The size, position and consistent form of these structures strongly suggest that they represent a dorsal and a ventral cirrus, respectively. The presence of a dorsal cirrus on all notopodia cannot be confirmed, but both the branchiae and the ventral cirrus are present on parapodia of all segments; the branchiae become noticeably shorter on notopodia near the anterior end. Several slice images of one notopodium (e.g. figure 2*k*) confirm the presence of an acicula, a linear structure, internal to the parapodium and approximately parallel to its axis, which arises near the junction of the parapodium with the body wall and appears to extend to the distal tip, immediately dorsal to the attachment point of the branchia.

Both neurochaetae and notochaetae are preserved impersistently as fine curvilinear structures, little more than 10 μm in diameter at their thickest points (figure 2*h*). They are not preserved with sufficient fidelity to reveal whether they are simple or compound, or to feature as individual structures in 3D reconstructions. Chaetae are typically evident in sections as impersistent dark 'sweeps' of material emerging from the parapodia and extending laterally for *ca.* 1 mm (figure 2*l*). Their detailed disposition is difficult to determine, but a reconstruction (figure 1*g*) of the light-coloured halo that surrounds the parapodia of one specimen (see § 2), supplemented by study of serial slice images, has enabled a reconstruction of their general pattern. Notochaetae arise from the dorsal surface of each notopodium, and the halo (figure 1*g*) suggests that they comprise a broad but homogenous array directed primarily anterolaterally to dorsolaterally (not posterolaterally). Neurochaetae, in both horizontal and exsagittal sections, often appear to be represented by discrete fascicles, and arise from all distal surfaces of the neuropodium (figure 2*h*,*l*). The halo reconstruction (figure 1*g*) suggests that distally these chaetae form an indistinct arc arrayed around the distal tip of the neuropodium. The arc occupies slightly more than 180°, and its central point, which is often a concavity, is posterodorsally placed. Thus, it appears that at least the most prominent neurochaetae arise in two discrete or semi-discrete fascicles, one positioned anterodorsally and the other posteroventrally (figure 4). These chaetae arise at a low angle to the parapodium, and to some degree overlap distally.

Indirect evidence from haloes in serial slice images suggests that chaetae are of a similar length in most segments, but are shorter near the anterior and posterior terminations.

(e) *Pygidium*

The pygidium is poorly preserved in all the specimens examined, and the posterior boundary of the fossil is often far from clear (for example, in figure 2*c*,*d* the bifurcate structure at the posterior is calcite that precipitated externally to the animal, and the position of the true posterior termination is uncertain). It appears to be a rounded structure, slightly expanded relative to the posteriormost trunk segments (figure 2*b*–*d*). The presence or absence of pygidial cirri cannot be determined.

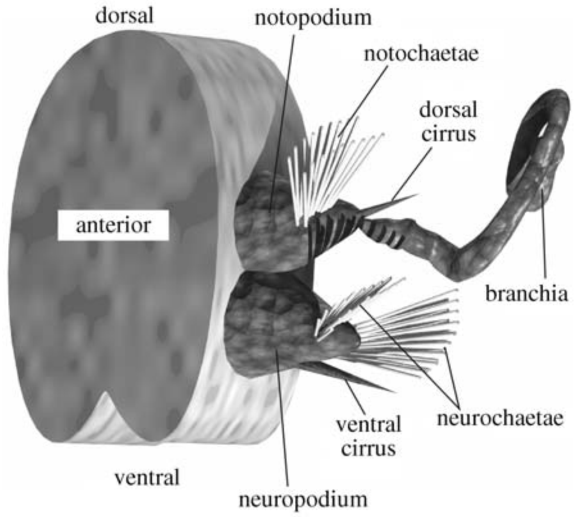

Figure 4. Reconstruction of parapodial structures from a trunk metamer of *Kenostrychus clementsi*. Only distal chaetae are shown on parapodia for clarity.

5. AFFINITIES

(a) *Affinities with extant polychaetes*

The familial descriptions of Fauchald & Rouse (1997), together with the accompanying cladistic analyses of Rouse & Fauchald (1997), represent the most comprehensive and rigorous taxonomic and phylogenetic synthesis available of Recent polychaetes. The coding scheme and the phylogenetic conclusions of this work have not been accepted uncritically. Other authors (e.g. Westheide 1997; Budd & Jensen 2000) support an alternative model of annelid phylogeny in which the clitellates are derived rather than primitive (and hence the polychaetes are paraphyletic). However, the dataset of Rouse & Fauchald (1997) provides the only available cladistic framework within which *Kenostrychus* can be analysed, and hence we have followed the work of these authors herein. Their favoured 'A/Pwr' analysis was re-run using their original procedure and data matrix, to which *Kenostrychus* was added (table 1). The only other modification to the matrix was the removal of the Euarthropoda and Onychophora, in response to recent molecular, morphological and palaeontological studies that cast doubt on the close relationship of these taxa to the polychaetes (e.g. Aguinaldo *et al.* 1997; Schmidt-Rhaesa *et al.* 1998; Budd 1999). The resulting tree, together with the classification of Rouse & Fauchald (1997), is shown in figure 5.

In this analysis, *Kenostrychus* resolves basally as a sister taxon of the Phyllodocida. This position is only weakly supported, and unweighted analyses place it as a sister taxon of the Eunicida. For consistency with Rouse & Fauchald (1997), we present the former position, although a more conservative view might be to treat the Phyllodocida–Eunicida–*Kenostrychus* split as a polychotomy. In either case, *Kenostrychus* is clearly a primitive aciculate polychaete. The relatively large number of undetermined characters may contribute to the basal placement within the clade, but characters relating to the generalized prostomial morphology and the lack of differentiation of the anterior segments are clearly plesiomorphic. Characters

Table 1. Coding of *Kenostrychus* according to the absence-or-presence scheme of Rouse & Fauchald (1997). We were able to determine 58 out of the 124 characters; those not determined (coded as '?') are not listed.

state	character
1	1 prostomium clearly demarked by a distinct groove
0	2 prostomium fused to the peristomium, but distinct
0	3 prostomium fused to the peristomium, and limited
0	4 prostomium on peristomium, frontal edge fused
0	5 peristomium forms a distinct ring
0	6 peristomium forms two distinct rings
0	7 peristomium elongate
0	8 peristomium forms rings and a collar
1	9 peristomium limited to lips only
1	10 prostomial antennae
1	11 median prostomial antenna
1	12 pair of prostomial antennae
1	13 palps
0	16 peristomial grooved palps
0	17 prostomial paired palps
0	18 prostomial multiple palps
0	19 prostomial palps form a crown
0	20 peristomial paired palps
0	21 peristomial palps multiple
1	22 prostomial (sensory) palps
1	23 prostomial (sensory) palps ventral
0	24 prostomial (sensory) palps ventrolateral
1	30 segmentation
0	31 first segment indistinct
1	32 first segment similar to those following
0	33 first segment surrounds head
0	34 first segment fused to head
0	35 first segment dorsolateral around head
0	36 first segment elongate
1	37 first segment appendages same as following
0	38 first segment appendages and chaetae absent
0	39 first segment tentacular cirri only
0	40 first segment with notopodia only
0	41 first segment with neuropodia only
0	42 first segment with arthropod appendages
0	43 tentacular cirri
1	44 parapodia
1	45 parapodia with similar rami
0	46 parapodia with projecting neuropodia
0	47 parapodia in part with tori
0	48 parapodia in part notopodial ridges
0	49 parapodia spiomorph
1	50 dorsal cirri
1	51 dorsal cirri cirriform
0	52 dorsal cirri include elytra
0	53 dorsal cirri foliaceous
0	54 dorsal cirri limited
1	55 ventral cirri
1	56 parapodial branchiae
0	57 dorsal simple branchiae
0	58 dorsal flattened branchiae
0	59 dorsal branchiae in a few anterior chaetigers
0	61 dorsal cirrus organs
0	63 epidermal papillae
1	105 chaetae
1	108 aciculae
0	118 spines in one anterior chaetiger
0	119 spines generally

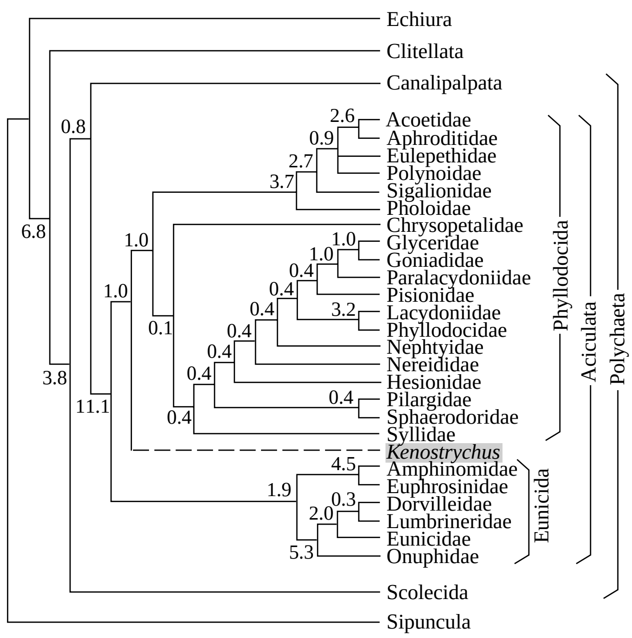

Figure 5. Phylogeny and classification of the Polychaeta. Strict consensus of the three most-parsimonious trees computed using PAUP 3.1.1 (Swofford 1993) after successive weighting of the 'A/Pr' dataset of Rouse & Fauchald (1997), with *Kenostrychus* added (see table 1) and Euarthropoda and Onychophora removed (see § 5a). Values to the left of each node represent rescaled branch support values (Bremer 1988, 1994), computed using AUTODECAY 3.0.3 (Eriksson & Wikström 1996). Taxonomic scheme after Rouse & Fauchald (1997, fig. 73).

such as the presence of aciculae, dorsal cirri, ventral cirri and a pair of prostomial antennae strongly support the placement of *Kenostrychus* within the Aciculata. It should be noted that several clades within the Aciculata are less strongly supported in our analysis than in that of Rouse & Fauchald (1997, fig. 59), most notably the Phyllodocida itself (branch support value of 1.0 rather than 7.3). However, the Aciculata remains strongly supported (branch support value of 11.1), and the Eunicida reasonably so (branch support value of 1.9 rather than 2.8).

Kenostrychus is unusual in possessing cirriform branchiae arising from the ventral surface of the notopodia. These invite comparison with the inter-ramal branchiae (or inter-ramal cirri) of the nephtyids, that are attached in a similar position and are associated with similarly positioned dorsal cirri (Rainer 1984). No other Recent polychaete family possesses inter-ramal respiratory structures, and homology between nephtyid and *Kenostrychus* branchiae, while not assumed in our cladistic analysis, might have implications for the phylogenetic positions of both fossil and Recent forms (see § 5b). Note that the parapodia and chaetae (and to a lesser extent the pygidium) of *Kenostrychus* are also closely comparable with those of the nephtyids, but the genus is excluded from this family by the presence of a median antenna and relatively unmodified anteriormost segments.

Jaw elements have not been found in association with *Kenostrychus*; while this might be an artefact of preservation, there is no good reason to suppose that they would not have survived the fossilization process. While most aciculate taxa (including the nephtyids) possess jaws, character states at the phylogenetic position inferred for *Kenostrychus* make no predictions about the presence or absence of jaw structures, and hence we tentatively infer that the genus did not possess them.

(b) *Affinities with fossil polychaetes*

Comparison of *Kenostrychus* with other fossils is hampered by the lack of contemporaneous polychaete body fossils, by the relatively poor preservation of other Palaeozoic material and by differential taphonomic filtering of characters. The Carboniferous polychaetes of Mazon Creek, USA (Thompson 1979), for instance, preserve features such as chaetae, jaws and gut relatively well, and, by virtue of the large number of specimens, enable the presence or absence of an eversible pharynx to be deduced with more confidence. All details of external morphology, however, are preserved very poorly. The material described herein preserves a very different set of characters, dominated by details of external morphology, and so only limited comparisons can be made.

Thompson (1979) placed most Mazon Creek polychaetes within Recent families, and, while other authors (e.g. Fauchald & Rouse 1997, p. 122) have questioned these assignments, some of the Mazon Creek taxa are clearly closely related to Recent families on the basis of jaw structures. As reconstructed, none is closely comparable with *Kenostrychus*. The putative nephtyid *Astreptoscolex* Thompson, 1979, is similar in gross form to *Kenostrychus* and is reconstructed with inter-ramal branchiae, although these are not cirriform but bear multiple filaments (Thompson 1979, fig. 6). *Astreptoscolex*, however, possesses nephtyid-like jaws, and it therefore seems likely that it is closer to extant nephtyids than to *Kenostrychus*. A second putative nephtyid genus, *Didontogaster* Thompson, 1979, is reconstructed (Thompson 1979, fig. 7) with an inflated anterior similar to that shown in figure 1*h*. However, it shares few other characters with *Kenostrychus*, and indeed shares few characters with the nephtyids. A re-examination of some of Thompson's material by one of us (M.D.S.) suggests that the inflated anterior is not common to all specimens and is a reflection of a somewhat engorged gut in the eversible region (i.e. anterior to the jaws in the retracted position, see figure 2*m*). This, in turn, suggests that the anterior inflation observed in *Kenostrychus* may indicate the presence of an eversible pharynx, although, as discussed in § 5a, we suggest that this structure, if present, was probably unarmed.

None of the Middle Cambrian polychaetes from the Burgess shale, Canada, (Conway Morris 1979; see also Butterfield 1990) is close to *Kenostrychus* in both prostomial and parapodial morphology. The reconstruction of *Canadia* Walcott, 1911, by Conway Morris (1979, p. 247) shows similarities in its inter-ramal branchiae, which are attached either to the ventral surface of the notopodium or to the inter-ramal body wall, although these branchiae are multidigitate rather than cirriform. *Canadia* was interpreted as a relatively primitive member of the Phyllodocida by Butterfield (1990), who suggested that the genus (together with *Wiwaxia*) was allied to the chrysopetalids. Fauchald & Rouse (1997, p. 121) also treated *Canadia* as a member of the Phyllodocida (*sensu* Fauchald 1977, broadly equivalent to the Phyllodocida of Rouse & Fauchald 1997).

Conway Morris & Peel (1995) suggested that the respiratory structures of *Canadia* might be plesiomorphic homologues of the ctenidia of molluscs. Although this homology cannot be tested with existing fossil material, the repeated occurrence of inter-ramal respiratory structures in *Astreptoscolex*, *Canadia* and *Kenostrychus*, three morphologically disparate Palaeozoic polychaetes, all of which appear to belong within the Phyllodocida, is striking. If these structures are homologous with each other, the implication would seem to be that inter-ramal respiratory structures are indeed primitive in the Phyllodocida (and maybe the Aciculata). A further implication, if these structures are also homologues of the branchiae of the nephtyids, is that this family retains aspects of plesiomorphic morphology, and may, thus, be more primitive than previously suspected.

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