The arthropod *Offacolus kingi* (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological reconstructions and phylogenetic affinities

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The small, non-biomineralized, three-dimensionally preserved arthropod *Offacolus kingi* Orr *et al.* from the Wenlock Series (Silurian) of Herefordshire, England, is re-evaluated, and the new family Offacolidae erected. This new study is based on specimens which have been serially ground, reconstructed by computer and rendered in the round as coloured models. *Offacolus* possesses a prosomal appendage array similar to that of *Limulus*, but also bears robust and setose exopods on appendages II–V which are unlike those found in any other arthropods. Opisthosomal appendages are similar in number and morphology to the book-gills of *Limulus*. Cladistic analysis places *Offacolus* basally within the Chelicerata, as a sister taxon to the eurypterids and extant chelicerates, but more derived than the Devonian *Weinbergina*.

Keywords: Chelicerata; *Offacolus*; Offacolidae; Silurian; England

1. INTRODUCTION

The Herefordshire Lagerstätte (Briggs *et al.* 1996) preserves a diverse fauna of small invertebrates from the Wenlock Series (*ca.* 425 Myr ago) of Herefordshire, England. The fossils preserve soft-tissue surfaces in spectacular three-dimensional (3D) detail, but this morphological information is very difficult to extract. Initial descriptive work was based on specimens exposed by fracturing the concretions in which they occur, supplemented by partial excavation. In this manner, Orr *et al.* (2000*b*) produced a description of the most abundant species in the Herefordshire macrofauna, the arthropod *Offacolus kingi*. That study determined the gross morphology of *Offacolus*, but many important details were not resolved. For this reason no formal investigation of relationships was attempted, although a chelicerate affinity was proposed. Subsequent investigations of Herefordshire fossils (Sutton *et al.* 2001*a,c*) have employed a 3D technique based on serial grinding and computerized reconstruction. In this paper, we apply an enhanced variant of this technique to *Offacolus* in order to illustrate and elucidate its morphology fully, and to allow an analysis of its affinities. There is currently no consensus on the phylogeny of the chelicerates and their relatives (see Dunlop & Selden (1997) and Weygoldt (1998) for discussion). An understanding of the morphology of *Offacolus* is important, as the addition of well preserved fossil forms can provide critical data that clarify relationships between other taxa,

and help to resolve phylogenetic patterns (e.g. Wills *et al.* 1995).

2. MATERIAL AND METHODS

The fossils of the Herefordshire Lagerstätte occur in concretions, preserved in 3D in sparry calcite, which precipitated in the void left after the decay of the animal (Orr *et al.* 2000*a*). Splitting the concretions yielded randomly oriented planar or sub-planar sections (e.g. figure 2*g*), which were then photographed under water using incident light and a digital camera mounted on a binocular microscope. Both part and counterpart of selected specimens were serially ground at 30 µm intervals, and photographed digitally to produce sets of 'slice images' (e.g. figure 2*h,i*). These datasets were used to generate 3D computerized reconstructions of the fossils (Sutton *et al.* 2001*b*), in which part and counterpart were reunited into a single model (the transverse cracks most noticeable in figures 1*d*, 2*c* mark joins between part and counterpart). Datasets underlying these models were edited to remove most extraneous material, and where possible to resolve fossil/matrix ambiguities. A refinement introduced with the present study generates false-coloured reconstructions (e.g. figure 1*a*), which greatly aid the illustration of morphology, particularly when rendered as stereo-pairs. During the editing stage, individual structures (e.g. appendages, tergites, etc.) were manually coded on each slice, enabling the computer to reconstruct each separately. The resulting surfaces were then placed together in their correct positions, separately coloured and rendered. The point at which the colour changes, where one structure meets another (e.g. an appendage and the body) is arbitrary, and it has not always been possible to maintain consistency (compare appendage VI*a*, figures 1*a*, 2*a*—the extension of body colour into the endopod in the latter is an

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Figure 1. (Caption on p. 1198.)

Figure 2. (Caption on p. 1198.)

Figure 1. (See p. 1196.) *Offacolus kingi* Orr *et al.* (2000b); stereo-pairs of computer reconstructions of OUM C.29557. Ilen–Vlen, Ilex–Vlex, VII, prosomal appendages (ex, exopod, en, endopod); TI–III, FI–III, mesosomal tergites/appendages; C, carapace; Mt, metasoma. Colours (except c): body/exoskeleton, orange and brown; chelicerae, white; Ilex–Vlex, green; Vlex, white; Ilen–Vlen, blue; VII, green; FI–III, red. (a) Ventral view, $\times 15$. (b) Antero-ventral view, $\times 15$. (c) Oblique antero-ventral view, body/III (reconstructed as one object) and chelicerae, $\times 15$. (d) Dorsal view, $\times 15$ (see also figure 3a). (e) Oblique dorso-lateral view of Ilen–Vlen and VII, $\times 23$ (see also figure 4a). (f) Oblique lateral view of carapace and body anterior, appendages removed, $\times 21$ (see also figure 3b). (g) Oblique antero-ventral view, appendages removed (attachment points labelled), tail spine truncated, $\times 15$.

Figure 2. (See p. 1197.) *Offacolus kingi* Orr *et al.* (2000b); labels as in figure 1. (a–f) Stereo-pairs of computer reconstructions. (a–c) OUM C.29558, colours as in figure 1. (a) Ventral view, $\times 17$ (lack of basal continuity of appendage colour is an artefact (see § 2)). (b) Oblique ventro-lateral view (lacking anterior), appendages except VI removed, some lateral exoskeleton removed, VI coxa/Vlen/body reconstructed as one object, $\times 17$. (c) Oblique lateral view, $\times 17$. (d) OUM C.29559, ventro-lateral view of single-object reconstruction, $\times 17$. (e) OUM C.29557, dorsal view of IIIex, $\times 18$ (see also figure 4a). (f) OUM C.29559, oblique postero-lateral view (anterior left, dorsal up) of VII, FI (orange) with subsidiary flaps (white, blue, red and bronze), $\times 20$. (g–i) Photographs of 2D sections. (g) OUM C.29560, sub-sagittal section, $\times 15$. (h–i) OUM C.29559. (h) Sub-exsagittal section (near midline), $\times 9$. (i) Sub-exsagittal section (more abaxial than (h)), $\times 9$. (j) OUM C.29558, transverse section through mesosoma (VII, trailing setae of appendage VII), $\times 18$.

artefact). This method also introduces a slight gap where two objects join (e.g. appendage bases, figure 2a). Where necessary these gaps have been eliminated by reconstructing both objects together, and rendering them in one colour (figures 1c, 2b).

Specimens of *Offacolus* are housed in the University Museum of Natural History, Oxford (OUM) and the Department of Geology, University of Leicester (LEIUG).

3. SYSTEMATIC PALAEONTOLOGY

Subphylum: Chelicerata Heymons 1901. Family: Offacolidae fam. nov.

Diagnosis. As for genus and species.

Offacolus kingi Orr *et al.* 2000b.

1996 new arthropod; Briggs, Siveter & Siveter, pp. 248, 249, fig. 1a–c,e.

2000a, unnamed arthropod; Orr, Briggs, Siveter & Siveter, pp. 173–186, figs 1a,b, 2–9.

*2000b *Offacolus kingi*; Orr, Siveter, Briggs & Siveter, pp. 1497–1504, figs 1–4.

Amended diagnosis. Chelicerate ca. 2 mm in width with parallel sided carapace; opisthosoma divided into mesosoma with three free segments, metasoma of five fused segments, basally articulated terminal spine with distal articulation and bifurcation. Seven pairs of prosomal appendages: pair I (chelicerae) uniramous; II–VI biramous with endopod gracile and chelate, exopod robust and setose except in VI, where it is tendril-like; VII uniramous,

Figure 3. *Offacolus kingi* Orr *et al.* (2000b); interpretations of external features, based on computer reconstructions of OUM C.29556. (a) Dorsal view based on figure 1d, $\times 17$. (b) Oblique lateral view of carapace and anterior of body with all appendages removed, based on figure 1f, $\times 20$.

flap-like, posteriorly directed. Opisthosomal appendages recurved and flap-like: each segment of mesosoma with single pair giving rise to three or four subsidiary nested flaps; three pairs lacking subsidiary flaps arising from anterior of metasoma.

Material. Holotype, OUM C.29501a,b (Orr *et al.* 2000b, fig. 2a,b). 285 other specimens, four of which have

been ground away and reconstructed in 3D (three figured here, OUM C.29557–9). Other figured specimens: OUM C.29500–1, LEIUG 116110 (Briggs *et al.* 1996); OUM C.29507–10 (Orr *et al.* 2000a); OUM C.29506, 29515–24 (Orr *et al.* 2000b); OUM C.29560 (this paper).

(a) *Dorsal exoskeleton*

(i) *Carapace*

High and parallel sided with wide anterior and ventral gapes (figures 1a,b,d,f,g, 2a,c), and a mean maximum width of 2.21 mm (range 2.0–2.4 mm, s.d. = 0.1 mm, $n = 24$). Maximum height averages 1.51 mm (s.d. = 0.9 mm, $n = 3$) and median length along the dorsal surface averages 2.08 mm (s.d. = 0.18 mm, $n = 3$). In transverse section the carapace is sub-semicircular with its widest point slightly dorsal of the ventral gape, and is similar in size and shape along its length, except near the anterior. The ventral margin is slightly convex in lateral view, curving dorsally into the anterior margin (figure 1f), at which point the margin is turned inwards to very slightly constrict the gape (figure 1b). The posterior margin is transverse in dorsal view (figure 1d) and laterally extends into a short and stout postero-ventral spine (figures 1d,f, 2c, 3b). The anterior margin is weakly convex in dorsal view and is sculpted into one axial and three paired lateral spines (figures 1c,d,f,g, 2c, 3a,b), which diminish in size laterally and project between the exopods of appendages II–V (see below). The spines are sub-triangular in form and are initially directed adaxially but curve abaxially distally. The more median of these, at least, possess small subsidiary sub-triangular spines near each base (see especially figures 1d, 3a). The carapace thins slightly between the marginal spines, forming internal shallow grooves which accommodate the prosomal exopods (figure 1f,g). The corresponding external thinning noted by Orr *et al.* (2000b, p. 1498) occurs only at the extreme anterior, although the anterior extension of the ‘outer sunken region’ (see below) lies approximately above the groove of the exopod of appendage II.

The external surface of the carapace bears several structures of weak relief (figures 1d,f, 2c, 3). A wide low ridge extends along most of the axis of the carapace, dying out posteriorly in a shallow sub-semicircular depression which occupies the posterior third of the carapace. This median sunken region is delineated laterally by a broad break in slope termed the shoulder. The median ridge is flanked by a weaker depression, the outer sunken region, which is narrow anteriorly but expands abruptly posteriorly. A third weakly expressed break in slope, the lateral shoulder, runs sub-parallel to the postero-ventral margin. No external sculpture is visible.

(ii) *Mesosoma*

Three similar tergites are present (figures 1d,g, 2c, 3a), decreasing in size from anterior to posterior and also decreasing slightly in height-to-width ratio. In transverse section each tergite is sub-semicircular. The external surface is divided by a shoulder into a shallow median sunken region apparently continuous with that of the carapace, and a near-vertical sub-planar lateral facet (figures 1d, 3a). In dorsal view, the lateral margins are straight, and the posterior margin is slightly concave within the median sunken region, and curves postero-ventrally into a short

stout spine (figures 1d, 2c). The ventral margin is weakly convex in lateral view, curving strongly anteriorly into the dorsal margin (figures 1g, 2b). Each tergite is overlapped by the preceding one (tergite I is overlapped by the carapace), and the length of tergite exposed depends on the flexure of the opisthosoma. In OUM C.29558, tergite II is angled ventrally with respect to tergite I (figure 2c). The antero-median region of tergite II thus exposed is an articulating shelf (‘half-ring’), divided from the rest of the tergite by a transverse furrow steeper anteriorly than posteriorly. This morphology is assumed to be present in all tergites. No external sculpture is present.

(iii) *Metasoma*

This tagma consists of probably five segments fused into a tapering unit averaging 1.2 mm long (s.d. = 0.14 mm, $n = 3$) in the plane of the ‘flange’ (see below). It forms a sub-triangular structure in dorsal view, converging posteriorly at an angle of *ca.* 80° (figures 1d, 2a, 3a). The anteriormost tergite is similar to those of the mesosoma, and is overlapped by mesosoma tergite III (figures 1d, 3a). Its posterior margin is indistinct medially, but is normally defined laterally by a furrow (figure 1d). The tergite is slightly swollen medially, particularly posteriorly, but is not developed into a discrete node. The posterior margins of the succeeding tergites are indistinct. In transverse section the tergites are sub-semicircular, with a lateral concave curvature forming a weak marginal ‘flange’. The flange corresponds in position and form to the ‘shoulder’ in preceding tergites. In lateral view, the dorsal surface of the tagma curves evenly to the posterior margin (figure 2c) and bears three postero-dorsally directed nodes that arise from the posterior of tergites II–IV of this tagma. The nodes are inconsistently preserved, but that on tergite III of OUM C.29558 (figure 2c) is relatively spine-like. The posterior termination of the metasoma is marked by an expanded ‘bulb’, from which the tail spine emerges (figures 1a,d,g, 2a–d, 3a), and which probably represents a fifth segment.

(b) *Body and ventral exoskeleton*

(i) *Prosoma*

Distinction between the body and bases of appendages under the carapace is difficult (much of what appears to be anterior ‘body’ structure in figure 1g is almost certainly appendage), but body margins are more clearly recognized medially. An anterior bulge with parallel sub-planar lateral margins protrudes between the endopods of appendage II. This bulge extends to approximately the plane of the prosomal ventral margin as a slightly elongate dome (figures 1a,c,g, 2d). Immediately posterior to this structure there is a depression, forming an oral cavity surrounded by the coxae of appendages II–VII.

(ii) *Opisthosoma*

The mesosoma body region is not as deep (does not extend as far ventrally) as that beneath the carapace; these regions are connected by a smooth slope (figure 2b). The structures visible immediately posterior to the base of appendage VII in figure 1a,g are not part of the body (see below). The sternites of the mesosoma are, in transverse section, weakly convex medially and weakly concave laterally; the body between tergite and sternite occupies

approximately half the height of the tergite (figures 1*g*, 2*b*, *j*). The contact between sternite and tergite is at or near the external shoulder (the flange in the metasoma). The first sternite of the metasoma is of similar form, but the more posterior segments increasingly lose the lateral concave region, until the ventral surface is essentially convex, interrupted only by the terminal bulb (see above).

(c) Tail spine

The tail spine, known completely in only two specimens, is 2.5 mm long in OUM C.29557 (figures 1*a*, *b*, *d*, 3*a*) and 2.6 mm in OUM C.29560 (figure 2*g*) (the spines of OUM C.29558, figure 2*a*, *c*, and OUM C.29559, figure 2*d*, are incomplete). The surface appears irregular. A single articulation is present at ca. 80% along its length: the proximal section does not taper, is weakly compressed dorso-ventrally, and has a weak ventral furrow (figure 1*b*); the distal section consists of two sub-parallel tapering spines. The basal articulation allowed at least 180° of dorso-ventral movement (compare figure 2*c*, *d*), and 60° of lateral movement (figure 1*a*, *b*, *d*). The mobility of the distal articulation is less well known, but OUM C.29557 displays a 50° ventral deflection (figure 1*a*, *b*, *d*).

(d) Prosomal appendages

Seven pairs (I–VII anterior to posterior) arise radially from the prosoma. Proximal details are difficult to resolve as the bases of appendages II–VI are often preserved as a single mass, undifferentiated from the body (e.g. figure 1*g*).

(i) Appendage I (cheliceræ)

Uniramous, ca. 1.5 mm long, with the base situated antero-medially (figure 1*b*, *c*). In cross-section it is sub-circular proximally but highly laterally compressed distally. It projects anteriorly, curving ventrally and then posteriorly, terminating near the ventral bulge of the anterior body (see above). Podomeres are difficult to discern, although a threefold division, into short proximal, long medial and short flared distal units, may be present (figure 1*c*). The third of these units terminates in a short chela (figures 1*a*, *c*, 2*a*).

(ii) Appendages II–V

Biramous, with each limb-stem (termed a coxa) dorso-ventrally elongate, and successively anteriorly (II) to laterally (V) positioned around the prosoma. The attachment points of the coxae to the prosoma have not been resolved, and hence the most basal regions of these appendages have not been identified. The position of the boundaries between coxa and rami are poorly constrained (figure 4*c*), and the possibility that the coxa contains multiple podomeres cannot be excluded. Endopods are attached ventrally and exopods dorsally (figures 1*c*, *g*, 2*h*, 4*c*).

The endopods of appendages II–V are sub-equal in size, each ca. 2–2.5 mm in extended length, and form a fan-like arrangement extending laterally and anteriorly from the oral cavity (figure 1*a*, *e*). Their bases (together with those of the endopod of VI and the base of VII) project ventrally of the prosoma, and nest together around the oral cavity (figures 1*a*, 2*d*). The cross-section of each ramus varies somewhat proximally to distally, but is always sub-circular or sub-elliptical (weakly compressed laterally). Each

Figure 4. *Offacolus kingi* Orr *et al.* (2000*b*); (*a*, *b*) interpretations of prosomal appendages, based on computer reconstructions of OUM C.29556. (*a*) Oblique dorso-lateral view of right-hand rami of endopods of appendages II–VI, based on part of figure 1*e*, $\times 32$. (*b*) Dorsal view of exopods of appendage III based on figure 2*e*, $\times 26$; dashed line in P6 is break of slope. (*c*) Idealized reconstruction showing part of dorsal carapace (sagittal section) and prosomal appendage II (exsagittal section) exopod, endopod and 'coxa'; anterior to left, ca. $\times 15$. Question marks indicate uncertainties in position of boundaries. Note that the attachment point of coxa/prosoma is unresolved, and that the 'coxa' has not been unambiguously shown to be a single unit.

ramus generally appears sinuous, but six post-coxal podomeres have been identified (P1–P6; figures 1*e*, 4*a*). P1 is normally sub-horizontal (figure 1*c* shows it best), and directed sub-anteriorly in anterior appendages to sub-laterally or even postero-laterally in posterior appendages

(figures 1*a*, 2*a*). In horizontal section it is sub-triangular with a sharp medially-directed vertex (see Orr *et al.* 2000*b*, fig. 2*i*, *j*). Its junction with the coxa is obscure. P2 is directed antero-dorsally in all appendages. P3–P4 direct the ramus anteriorly and then ventrally, although one example is preserved directed sub-dorsally (OUM C.29557; figures 1*a*, *b*, *d*, *e*, 4*a*). Divergent spines arise distally on P4, the most prominent on the dorsal surface (see figure 1*a*, right hand endopods of II and III). P5 terminates in a chela, one element of which is always sub-parallel to the surface of P5 proximal to it. The other element is preserved at varying angles to P5, and is therefore assumed to represent a mobile sixth podomere P6 (see figure 4*a*).

The exopods of appendages II–V are sub-equal in size, each *ca.* 1.5 mm in extended length (excluding terminal setae). The diameter of each is consistently greater than that of the corresponding endopod. These rami form a dorsal and lateral fan-set emerging from the anterior gape of the carapace. They separate dorsally and laterally from the basal appendage mass, close to the carapace (figure 1*c*, *g*). The rami are in similar positions in all specimens, and show little variation in angle between podomeres. Six podomeres are identified (P1–P6; figures 2*e*, 4*b*). P1, which appears to attach basally to the coxa, is sub-circular to sub-elliptical (compressed ad/abaxially) in cross-section and is directed essentially anteriorly. P2 is sub-triangular, with acute vertices directed adaxially, and is directed anteriorly and adaxially. P3 is sub-circular in cross-section, and is directed anteriorly. No variation in angle has been observed between P2 and P3, which may instead represent a single long and curved unit. P4 and P5 are shorter, increasingly sub-circular in cross-section, and direct the ramus increasingly abaxially. The adaxial surface of P5 distally bears two long divergent spines that in most cases are parallel with the surface, flanked by two less clearly defined and shorter divergent spines. A similar pair of spines is present on the adaxial surface of P4: these are shorter, less robust, and lack flanking spines. P6 is directed abaxially with respect to P5, and terminates in a brush-like splay of long setae. The setae of adjacent rami overlap or abut (figures 1*b*, *d*, 2*c*), and are assumed to have worked as a functional unit, although there is a consistent median gap between the appendage II exopods.

(iii) Appendage VI

Biramous, with coxa and endopod similar to those of appendages II–V (figure 1*e*). The coxa is positioned posteriorly and slightly laterally to that of appendage V (figure 1*g*). The tendril-like exopod is attached to the dorso-lateral tip of the coxa (figure 2*b*), in a position serially homologous to the exopods of II–V. The structure is sub-circular in cross-section, *ca.* 0.1 mm in diameter and 2 mm in length. It appears to have been flexible, and is preserved coiled in a vertical plane in all specimens examined (e.g. figures 1*a*, 2*b*). In OUM C.29557 one exopod of VI protrudes into the opisthosoma where it is preserved between flaps of the opisthosomal appendages (not figured).

(iv) Appendage VII

Uniramous, arising ventro-laterally from the prosoma at the posterior of the oral cavity and from near the midline

Figure 5. Fifty per cent majority rule consensus tree of 32 386 equally parsimonious trees (470 steps) produced by cladistic analysis. Database is that of Wills *et al.* (1998) with *Offacolus* added and *Agnostus* coded as '2' for character 34 (see table 1). Details of clades other than the Arachnomorpha (*sensu* Wills *et al.* (1998)) are not shown. Figures below nodes indicate the percentage of fundamentals in which the grouping occurs—these are 100% where no figure appears. Analysis performed using PAUP v. 3.1.1 (Swofford 1993), using 10 random addition replicates from a seed value of 1, followed by TBR branch-swapping heuristic searches using DELTRAN optimization. Analysis was halted when the maximum number of trees supported by the software was reached after three replicates.

(figures 1*a*, 2*a*). The ramus flares posteriorly and laterally from an initially ventrally directed proximal podomere to form a large flap-like structure (figures 1*a*, *e*, 2*a*) which extends ventrally of the opisthosomal appendages. In all specimens examined, this flap lies close to the plane of the ventral gape of the opisthosoma (figure 2*c*, *j*). It averages 0.6 mm long at the longest point (near the lateral margin) and 0.75 mm wide, and median separation averages 0.35 mm. Its posterior and lateral margin bears approximately 14 stout and radially to posteriorly directed setae, the longest of which are up to 0.3 mm in length and on the posterior margin. OUM C.29557 (figure 1*a*, *g*) has poorly preserved sub-symmetrical lobe-like structures arising from near the base of appendage VII and directed posteriorly. These projections are absent from other specimens examined, and are thus likely to be external diagenetic calcite rather than fossil. The possibility that they are biological structures cannot however be ruled out.

(e) Opisthosomal appendages

Each sternite of the mesosoma bears a similar pair of appendages (FI–FIII), apparently attached in a lateral position, towards the anterior of each sternite (figure 1*g*). Each ramus flares out rapidly into a wide flap-like struc-

Table 1. Coding of *Offacolus* according to the scheme of Wills *et al.* (1995, 1998). Note that a new state ‘2’ representing ‘robust and multi-segmented’ is introduced for character 34 (‘Form of outer rami of appendages of second post-acronal somite’). This character state is also applied to the genus *Agnostus*.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
1	0	0	1	0	0	1	1	1	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	0	?	?	0	7	0	c	1	1	2	0	1	0	0	0	0	g	1	1	1	1	0	0	0	
49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
?	?	?	?	1	0	0	1	0	0	0	0	0	0	0	0	0	?	1	0	0	0	?	?	0	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	

ture, strongly recurved and *ca.* 1–1.5 mm in extended length (figures 1*a*, 2*a,d,f,h,i*), which barely projects below the opisthosomal tergites. The ramus is thickened proximally (figure 2*d,i*) and bears short closely spaced setae(?) distally (figure 2*j*). A number of nested ‘subsidiary flaps’ (figure 2*d,f,i*) are attached to the ventral surface of the thickened proximal region of each ramus (figure 2*i*). These structures lack a thickened base, and are smaller and less strongly recurved than the main ramus (figure 2*i*). The more anterior subsidiary flaps of each ramus are successively longer and more laterally positioned (figure 2*f*). FI and FII possess four subsidiary flaps; only three have been observed in FIII. Three rami similar to FI–III occur beneath the anterior of the metasoma (figures 1*a*, 2*a,d,i*), and decrease successively in size posteriorly (the third is vestigial). These rami lack subsidiary flaps, and appear to attach to the antero-lateral regions of metasoma sternites I–III.

(f) Discussion

Our description largely expands on rather than contradicts that of Orr *et al.* (2000*b*), but several critical differences exist, especially with regard to the appendages. Orr *et al.* (2000*b*) considered all the prosomal appendages to arise ventrally, from around the oral cavity. The new evidence indicates that the ‘robust rami’ (exopods of II–V) arise dorsally rather than ventrally. We now consider the ventrally placed ‘bilobed termini’ of the previous authors to be artefacts, variously of preservation, of photography (foreign particles in the water layer), or of sectioning near to the junction between the coxa and endopod podomere P1. Orr *et al.* (2000*b*) considered appendage II to be uniramous and the four pairs of ‘robust rami’ to correspond to ‘gracile rami’ IIIa–VIa (endopods of III–VI). Here we show that they belong to II–V, thus our IIen (endopods of appendage II) and IIex–Vex (exopods of appendages II–V) are equivalent to II and IIIb–VIb respectively of Orr *et al.* (2000*b*). The tendril-like exopod of VI was not observed previously. The new evidence, contrary to Orr *et al.* (2000*b*), indicates that only a single appendage pair occurs beneath each tergite, and that each opisthosomal tergite corresponds to a single segment. Structures interpreted by Orr *et al.* (2000*b*, p. 1503) as ‘sections through the near-vertical lateral margins of each tergite’ and ‘setae extending postero-ventrally from the posterior face of each ramus’ are here interpreted as primary rami and subsidiary flaps respectively. Orr *et al.* (2000*b*) reported that the anterior four tergites of the metasoma bore medial nodes, but the new material shows the anteriormost of these to lack a discrete node, bearing only a poorly defined median swelling.

Increased confidence in the chelicerate affinities of *Offacolus* (see below) allows us to identify many structures with those of chelicerates. Several of these homologies are

assumed in our description: the appendage I rami of Orr *et al.* (2000*b*) are chelicerae; the ‘cephalic shield’ is a carapace (prosomal exoskeleton); and the ‘thorax’ and ‘posterior tagma’ are the mesosoma and metasoma of an opisthosoma. Other possible homologies include the identification of the ventral bulge of the antero-median body as a labrum, the median carapace ridge as a cardiac ridge, and the median sunken area of the carapace as a cardiac area. A further possibility is that the outer sunken region is homologous with the inter-ophthalmic region of the Xiphosurida, and that its margin is thus an ophthalmic ridge. We also suggest that the lateral shoulder of *Offacolus* may be at least analogous to the cheek ridge of the Carboniferous xiphosurid *Xaniopyramis* (Siveter & Selden 1987).

The endopods of *Offacolus* are closely comparable to the walking legs of the extant xiphosurid *Limulus* in terms of morphology and position of origin, and are assumed to be homologous. Endopod podomeres PI–P6 of *Offacolus* can be identified with the trochanter, femur, patella, tibia, and tarsus and pretarsus of *Limulus*. The chelicerae, labrum and anterior of the body of *Offacolus* are also similar to those of the extant genus. Both *Limulus* and *Offacolus* possess five post-chelicerate walking legs in the prosoma, although II and VI are somewhat modified in the former. Both genera also possess a posteromedially placed flap-like seventh prosomal appendage, and hence we assume that the chilaria of *Limulus* are reduced homologues of appendage VII of *Offacolus*. Appendage VI is biramous in *Limulus*, the coxa bearing a lateral spatulate ‘flabellum’ (e.g. Ruppert & Barnes 1994, fig. 13–3). The tendril-like exopod of VI in *Offacolus* may be the homologue of this structure. The prosomal appendages of the well-preserved Devonian xiphosuran *Weinbergina* (Stürmer & Bergström 1981) are somewhat less like those of *Offacolus*. *Weinbergina* also has *Limulus*-like chelicerae, but possesses six pairs of similar non-chelate walking legs, the posteriormost of which are presumably homologous to the chilaria of *Limulus* and appendage VII of *Offacolus*. It does not possess a flabellum.

Limulus, *Weinbergina* and *Offacolus* all possess six pairs of lamellate appendages in the opisthosoma. Those of *Limulus* also bear subsidiary flaps (forming a ‘book-gill’ apparatus), although these are far more numerous than in *Offacolus*. The flattened opisthosomal limbs in *Limulus*, however, are sub-planar rather than recurved, and the anteriormost is modified into an operculum. The opisthosomal appendages of *Limulus* also bear reduced endopods, which have not been identified in *Offacolus*. The book-gills of *Weinbergina* are poorly known, but are sub-planar and bear a large number of ‘gill lamellae’ (Stürmer & Bergström 1981), and hence appear to be closer to those of *Limulus* than *Offacolus*.

Many characters of *Offacolus* serve to distinguish it from

all other chelicerates, and to justify the erection of a new family. These include the form of the anterior margin (with anterior gape and distinctively arranged spines), the presence of an articulation in the tail spine, the low segment count and pattern of tagmosis in the opisthosoma, and especially the biramous nature of the prosomal appendages II–V. The exopods of II–V in *Offacolus* have no clear homologue in *Limulus*, *Weinbergina*, or any related arthropod. Biramous anterior appendages are known from arachnomorph taxa, for example the Cambrian *Sanctacaris* (Briggs & Collins 1988), but their exopods are almost always filamentous or antenniform (Wills *et al.* 1998); robust multi-segmented exopods are unusual (present for example in *Agnostus*, see Müller & Walossek (1987)), and unlikely to be plesiomorphic. Thus although the presence of these exopods in *Offacolus* may be a primitive character, their form is likely to be derived.

4. PHYLOGENY

A suite of characters clearly identifies *Offacolus* as a chelicerate (*sensu* Dunlop & Selden 1997; Wills *et al.* 1998), especially the chelicerae, the prosoma and opisthosoma (the latter divided into a mesosoma and metasoma), and the number of appendages in the prosoma. Several phylogenetic and taxonomic schemes have been used for the chelicerates, and a number of cladistic studies have been published in recent years (Dunlop & Selden 1997; Wills *et al.* 1998; Wheeler & Hayashi 1998). In order to analyse the position of *Offacolus*, we have made use of the database of Wills *et al.* (1995, 1998), which is based on a large number of characters and includes both fossil and extant taxa. While the conclusions of Wills *et al.* (1995, 1998) are at odds with recent analyses of molecular data (Giribet *et al.* 2001; Hwang *et al.* 2001), this database remains the best available cladistic framework for the analysis of fossil taxa. Table 1 shows our codings for *Offacolus* under this scheme, and figure 5 summarizes the results of this analysis, which are essentially identical to those of Wills *et al.* (1998, fig. 2.1). *Offacolus* groups with the chelicerates, emerging as more derived than *Weinbergina* (and hence within the Chelicerata, albeit not within the crown-group), and representing a sister taxon to the eurypterids and the extant chelicerates. This phylogeny suggests that all higher taxa within which *Offacolus* could be accommodated (e.g. the Xiphosura, Synziphosurida or the unnamed taxon of Anderson & Selden (1997)) are paraphyletic, and hence we do not assign the family Offacolidae to any taxa below the rank of Chelicerata.

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