A new osteostracan fauna from the Devonian of the Welsh-Borderlands and observations on the taxonomy and growth of Osteostraci

Journal:	<i>Journal of Vertebrate Paleontology</i>
Manuscript ID:	Draft
Manuscript Type:	Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Keating, Joseph Sansom, Robert; University of Bath, Department of Biology and Biochemistry Purnell, Mark; University of Leicester, Department of Geology
Key Words:	Osteostraci, Taxonomy, Devonian, Growth

SCHOLARONE™
Manuscripts

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
50
51
52
53
54
55
56
57
58
59
60

A new osteostracan fauna from the Devonian of the Welsh-Borderlands and observations on
the taxonomy and growth of Osteostraci

JOSEPH N. KEATING,^{1,†} ROBERT S. SANSOM,^{*,1,2} and MARK A. PURNELL¹

¹Department of Geology, University of Leicester, Leicester, LE1 7RH, United Kingdom;
²Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath, BA2
7AY, United Kingdom, r.sansom@bath.ac.uk

[†]Current Address: 11 Park Way Close, Southwick, West Sussex, BN42 4LE, United
Kingdom, joe_keating@live.co.uk

RH: KEATING AND SANSOM—DEVONIAN OSTEOSTRACANS

*Corresponding author

1
2
3 ABSTRACT—The Osteostraci are a morphologically diverse group of jawless fishes
4 considered as sister-taxon to jawed vertebrates. Fossil Osteostraci therefore have wide
5 reaching ramifications for our understanding of the origin and evolution of gnathostomes.
6 Their utility in this context is currently impeded by rudimentary taxonomy of faunas from the
7 United Kingdom. Principal among these is a well-preserved, previously undescribed fauna
8 from the Early Devonian (Lochkovian) of Wayne Herbert Quarry, Herefordshire. Here we
9 provide a description of new osteostracan material from this fauna. Anatomical observations
10 of the character rich, taxonomically informative headshield, combined with quantitative
11 measurements, has permitted identification of 15 variable characters. From these, 7 discrete
12 morphogroups are recognised and used to establish the taxonomy of the material. This
13 includes two new species of Zenaspidae (*Zenaspis waynensis* and *Diademaspis janvieri*),
14 two new species of Cornuata incertae sedis (*Janaspis newtonensis* and *J. punctata*), two
15 indeterminate species and *Pattenaspis whitei* Stensiö, 1932, which is redescribed on the basis
16 of new material. Our analyses indicate that cornuate osteostracan species are likely over-split
17 due erection of new taxa based on poorly preserved type specimens, inadequate consideration
18 of taphonomic character loss, and over reliance on continuous rather than discrete characters.
19 Furthermore, patterns of dermoskeleton ornamentation and tessellation of *Diademaspis*
20 *janvieri* and Cornuata indet. gen. sp. B are used to infer mechanisms of dermoskeletal
21 growth. These new data allow incorporation of this fauna into scenarios of osteostracan
22 evolution, considerations of gnathostome origin and studies of global Lochkovian diversity.
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
50
51
52
53
54
55
56
57
58
59
60

INTRODUCTION

Much of the morphological gulf that separates extant jawless from jawed fish was once filled by the diverse jawless fishes now known only as fossils from Palaeozoic deposits from around the world. These fossil ‘ostracoderms’ are therefore of fundamental importance for helping us to reconstruct the origin and early evolution of gnathostomes- one of the most significant evolutionary events in vertebrate history. A group of central importance in this context is the Osteostraci. The Osteostraci are the sister group to all jawed vertebrates (Forey and Janvier 1993, Janvier 1996, Donoghue *et al.* 2000), and the two clades share a suite of characters including the presence of pectoral appendages and cellular bone (Sansom 2009a). Consequently, robust understanding of osteostracan palaeobiology is a prerequisite when considering the evolutionary transition through which jaws and other gnathostome characters developed. Detailed studies of the anatomy of the Osteostraci (Janvier 1981, 1985a) and phylogenetic analysis of intra-relationships of the group (Sansom 2008, 2009a, 2009b) allow reconstruction of scenarios of osteostracan and stem-gnathostome evolution. But further resolution of the phylogeny, palaeobiogeography and diversity of osteostracans is limited by the currently rudimentary taxonomic state of the British osteostracan faunas from the Welsh Borderlands. Many species erected during the 19th and early 20th century have been diagnosed with reference to character deficient holotype material while other subsequently discovered, well preserved, character-rich material, remains undescribed. Principal among these is the osteostracan fauna from the Lower Devonian of the Wayne Herbert Quarry, near Newton, Herefordshire, where vertebrates (also including acanthodians and heterostracans) have been preserved in fine detail (e.g. White, 1935; Miles, 1973; Dineley, 1999; Brazeau, 2009). Here we present a rigorous anatomical study of these well-preserved specimens, permitting robust taxonomic analysis and allowing us to determine the relevance of this fauna to our understanding of osteostracan evolution and Lochkovian global vertebrate diversity.

MATERIAL AND GEOLOGICAL SETTING

The specimens described here (listed in supplementary data) are housed at the Natural History Museum, London (NHM). They were recovered from a restricted lens of grey-green siltstone, 66m above the Bishop’s Frome Limestone member in the Ditton Group sediments at the Wayne Herbert Quarry (White, 1932, 1935; Allen & Tarlo, 1963; Dineley, 1999). The lens is within the *Rhinopteraspis crouchi* zone (White, 1935) consistent with a Lochkovian

age. The osteostracan bearing lens has also yielded the *Turinia pagei* thelodont assemblage, heterostracans including *Errivaspis waynensis* and ‘acanthodian’ grade vertebrates including *Ptomacanthus anglicus* (White, 1935a; Miles, 1973; White and Toombs, 1983; Blicek, 1984; Dineley, 1999). Sedimentological analysis (Allen and Tarlo, 1963) and isotopic data of vertebrate remains (Schmitz et al., 1991) indicate a fluvial, freshwater environment (see Dineley, 1999 for details). Prior to our study, the osteostracan material had been prepared using dilute HCl to remove the crushed bone which masked the fine detail of the specimens, leaving high fidelity impressions of internal and external surfaces (White, 1935a).

METHODS

In order to take full account of variation and to accurately describe the fauna without unnecessary taxonomic splitting, we have employed a step-wise approach involving 1) description of morphological variation (qualitative and quantitative) of specimens, 2) identification of distinct morphogroups, and 3) comparison of identified morphogroups with previously described fauna to establish taxonomy. For the first stage, the taxonomically informative headshield of each specimen was photographed and anatomical line drawings were produced (Macromedia Freehand) by combining tracing with observations under binocular microscope. Ten quantitative measurements (Fig. 1) were taken for each headshield (obtained from digital photographs using ImageJ image analysis software) and 15 qualitative anatomical characters were described for each (Supplementary data). Specimens sharing a common and unique suite of characters were then placed into distinct morphogroups (Appendix1). These morphogroups were subsequently compared with established species described from Great Britain, Podolia and Spitsbergen. New species are erected for morphogroups that are constrained by a number of discrete characters and found to differ from comparable taxa. Distinctive morphogroups identified from incomplete material however, are retained in open nomenclature following Bengtson (1988) and described appropriately. Synonymy lists are annotated following Matthews (1973).

SYSTEMATIC PALEONTOLOGY

Class OSTEOSTRACI Lankester, 1868

Subclass CORNUATA Janvier, 1981

Order ZENASPIDIDA Stensiö, 1958

Family ZENASPIDIDAE Stensiö, 1958
ZENASPIS Lankester, 1870

Type species—*Zenaspis salweyi* Egerton, 1857.

Emended diagnosis—Modified from Voichyshyn (2006, 2011): Zenaspididae with a midline headshield length of 80-130mm, equating to at least 60% of the maximum shield width. Hypophysial division of nasohypophysial opening is expanded relative to the nasal division. Orbital openings are small in proportion to the headshield and bear circumorbital raised rims. Median field is broad. Lateral fields broaden towards the posterior terminus and extend over 0-15% of the cornual processes. Abdominal division bears a dorsal median ridge. Tesseræ of the shield are strikingly small in proportion to the shield size and exhibit single broad central tubercles or granular ornamentation.

Species included—*Zenaspis metopias* Wängsjö, 1952; *Zenaspis podolica* Balabai, 1962; *Zenaspis major* Balabai, 1962; *Zenaspis dzieduszyckii* Voichyshyn, 2006; *Zenaspis kasmyri* Voichyshyn 2011. The new species described below, *Zenaspis waynensis* sp. nov. is provisionally assigned to this genus.

ZENASPIS WAYNENSIS sp. nov.
(Figs 2, 7)

Etymology—From Wayne-Herbert Quarry.

Diagnosis—Zenaspid with a midline headshield length approximately 92-95% of the maximum shield width measured just below the level of the pectoral sinuses. Median field short and broad, tapering anteriorly; orbits and median field enclosed within a raised rim; lateral fields narrow yet broad towards their posterior terminus, extending over approximately 15% of the cornual processes; robust cornua projecting posteriorly and constituting approximately 33% of maximum headshield length; pectoral sinuses narrow and deep; tesseræ ornamented with closely set minute tubercles producing a granular texture; ventral rim ornamented with elongate tubercles surrounded by pitted borders, increasing in size proximodistally and arranged in up to 10 rows slightly discordant with the margin of the headshield.

Material—NHM P24939-40 (holotype, fig. 2A,C), P23832-3 (fig. 2B) and P24945-6.

Description—The headshield of the holotype is 96mm long (to cornua tips) and 90mm wide while that of P23832/33 is a slightly larger and P24945/46 slightly smaller. The

1
2
3 prepineal division of the headshield of *Z. waynensis* is long, constituting approximately 49 –
4 51% of the midline headshield length, and broad anteriorly. Lateral fields (preserved only on
5 the holotype and P23832/33) are narrow, broadening posteriorly and extending only a short
6 distance over the cornual processes. The median field is conspicuously broad and short
7 (width 61 – 65% of its length), narrowing anteriorly towards the pineal plate. The
8 nasohypophysial opening lies within a narrow and elongate circumnasal depression. The
9 hypophysial division is larger than the nasal division. The orbital openings are circular and
10 fairly small in proportion to the headshield. Both orbits and median field are enclosed within
11 a raised rim. The pectoral sinuses are deep and narrow, bordered by a very robust posteriorly
12 projected cornual processes measuring 30 – 32mm in length. The abdominal division
13 constitutes approximately 14 - 21% of the shield length in midline and bears a low dorsal
14 median ridge. A large, dorsoventrally flattened portion of the body is preserved in the
15 holotype, consisting of 33 scale rows.
16
17

18 The headshield is composed of very small tesserae which are convex in profile and
19 exhibit a granular texture produced by minute and closely set tubercles. This granular texture
20 is also seen on the scale rows of the body. The ventral rim of the headshield is ornamented
21 with elongate tubercles which increase in size proximodistally, each encircled within a pitted
22 margin. These occur in rows which do not precisely follow the margin of the headshield,
23 rather diverging from it anteriorly. Similar ornamentation, comprising of elongate tubercles
24 surrounded by pitted margins, exists on the raised rim enclosing the orbits and median field.
25
26

27 **Remarks**—This species is in many respects comparable to species of the genus
28 *Zenaspis*: the headshield exhibits a broad anterior, an expanded hypophysial division, small
29 orbits, a broad median field, and poster widening of the lateral fields (the latter character is
30 diagnostic of the Zenaspididae (Janvier 1985a; Sansom 2009a). Another potentially
31 informative character shared between this species and all other *Zenaspis* species is that the
32 tesserae of the headshield are conspicuously small in proportion to the size of the shield
33 (Stensiö, 1932; Wängsjö, 1952; Janvier, 1985b; Voichyshyn, 2006). This condition appears
34 unique to the genus *Zenaspis* within the Osteostraci of Great Britain (Stensiö, 1932).
35
36

37 *Zenaspis waynensis* can be accommodated within Janvier's (1985b) diagnosis of
38 *Zenaspis* but differs from Voichyshyn's (2006, 2011) generic concept in its greater midline
39 headshield length/width ratio and different headshield tessera ornamentation. Shield
40 morphology is similar to the type species of the genus, *Zenaspis salweyi* Egerton, 1857. Its
41 size corresponds with the smaller specimens of *Z. salweyi*, and both demonstrate very small,
42 circular orbits and long cornual processes constituting around one third the maximum
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

headshield length. *Z. waynensis* differs from *Z. salweyi* however, in the general outline of the headshield, which is comparatively narrower and longer, with a relatively longer prepineal division. It can also be distinguished by its broad and robust cornual processes, its narrow pectoral sinuses and the shape of its median field. Furthermore the tesserae of *Z. salweyi* are ornamented by few large tubercles unlike the granular texture of *Z. waynensis*. The species compares less closely with *Z. metopias* Wängsjö, 1952 and *Z. dzieduszyckii* Voichyshyn, 2006 which exhibit broader and shorter headshields bearing short and thin cornua. The headshield of *Z. podolica* Balabai, 1962 is similar to *Z. waynensis* in being narrow with a fairly long prepineal section and robust cornual processes, but it differs in having broad pectoral sinuses (more akin to those of *Z. salweyi*) and ornamentation consisting of single large tubercles (Janvier 1985b). *Z. kasmyri* Voichyshyn, 2011 also exhibits a fairly narrow shield with narrow pectoral sinuses much as in *Z. waynensis*, but the former species is easily distinguished by its proportionally larger and much more robust cornual processes. *Z. kasmyri* also has a proportionally shorter pre-pineal division.

Comparisons with *Zenaspis major* Balabai, 1962 are limited by the poor preservation of the material referred to this species, but the shield outline is similar to that of *Z. waynensis*, particularly the cornual processes which are similar in their robustness and their proportions relative to the shield. *Z. major* is, however, much larger than *Z. waynensis*, and the extension of its lateral fields onto the cornual processes is less pronounced. *Z. waynensis* is clearly sufficiently distinct from all other cornuate Osteostraci to warrant erection of a new species, but because of the differences between this species and species assigned to the genus *Zenaspis*, the generic assignment remains open to debate. As we note below in discussion of *Cephalaspis*, a genus level review of cornuate Osteostraci is rather overdue. The disparities between *Z. waynensis* and *Zenaspis* species may be sufficient to merit erection of a new genus, but the broader taxonomic revisions required are beyond the scope of this study.

DIADEMASPIS Janvier, 1985a

Type species—*Diademaspis poplinae* Janvier 1985a

Emended diagnosis—Modified from Voichyshyn (2006, 2011): Zenaspididae attaining a midline headshield length of 90-250mm constituting over 90% of the maximum width. Expanded hypophysial division of nasohypophysial opening relative to the nasal division; pineal plate reduced or absent; small orbits with broad circumorbital raised rims; short and broad median fields; lateral fields narrow anteriorly, broadening significantly

towards their posterior terminus and extending slightly onto the cornual processes; abdominal division bears a dorsal median ridge; ornamentation of small tubercles surrounding 1 or more central large rounded tubercles.

Species included—*D. jarviki* Wängsjö, 1952; *D. species 1* – *D. species 4* of Janvier, 1985a; *D. stensioei* Afanassieva, 1989; *D. sp.* Voichyshyn 2006; *D. janvieri* sp. nov.

Remarks—The problematic species *D. ? mackenziensis* Adrain & Wilson, 1994, from the southern MacKenzie Mountains, N.W.T., Canada, differs from all other species assigned to *Diademaspis* in its small size, proportionally large orbits, shape of the dorsal field and style of ornamentation. Consequently we concur with Voichyshyn (2006, 2011) that no reason exists to allocate this species within the genus *Diademaspis*.

DIADEMASPIS JANVIERI sp. nov.

(Figs 3, 7)

Etymology—In honour of Dr Philippe Janvier.

Holotype—P24941/2 (Fig. 3C,D).

Diagnosis—*Diademaspis* with a prepineal length constituting approximately 50% of the shield length in midline. Diamond shaped expanded hypophysial division of nasohypophysial opening; wide median field (60% of length) with a linear posterior margin; lateral fields extend over less than 10% of the cornual processes; long cornual processes constituting approximately 37% of the maximum shield length; tesserae of exhibit 1-7 large tubercles forming a central island surrounded by 2-3 rows of smaller tubercles; ventral rim ornamented with irregular rows of elongate tubercles approximately following the shield margin.

Material—NHM P24941-2 (holotype, Fig. 3C,D), P16602-3 (Fig. 3B), P20004a-b, P20005a-b (Fig. 3A), P53026.

Description—All material attributed to this species is somewhat fragmentary in nature. Reconstructing the headshield indicates that the maximum length was likely to have exceeded 120mm (90-95mm in midline) with maximum width of 100-110mm just posterior to the level of the pectoral sinus. The prepineal division of the shield is long, constituting approximately 50% of the shield length. The lateral fields (73-80mm long) are narrow anteriorly, gradually broadening towards their posterior terminus. They attain a maximum width at the level with the pectoral sinus, extending slightly less than 10% over of the cornual processes. The median field is tapered anteriorly producing a tear drop shaped outline with a

linear posterior terminus; it attains a length around 23mm with a maximum width of approximately 12mm. The circumnasal depression is broad and shallow containing a nasohypophysial opening of which the diamond shaped hypophysial division is appreciably larger than the nasal division. The pineal plate is not directly observed in any specimen yet a weakly defined pineal depression can be seen in specimens P16603 and P24941. The orbits are fairly small in proportion to the shield size, and enclosed within broad circum-orbital raised rims. The pectoral sinuses are fairly broad and deep. The posteriorly projected cornual processes are robust and very long, measuring 45.5mm in the holotype, constituting 37% of its estimated maximum shield length. The exterior margins of the cornual processes curve posteriorly towards the midline. The abdominal division is fairly long, constituting approximately 20-27% of the shield length in midline. Specimen P20005a/b (Fig. 3A) exhibits a well preserved paddle shaped pectoral appendage measuring 36mm in length. Tesserae of the headshield are ornamented with 1 – 7 large central tubercles which are rounded anteriorly but become elongate posterolaterally, their axis of elongation following the margin of the shield. Each central ‘island’ of tubercles is surrounded by 2 – 3 rows of significantly smaller tubercles. The ventral rim is ornamented with up to 8 irregular rows of elongate tubercles broadly following the margin of the headshield. The pectoral appendages and scale rows of the body exhibit ornamentation of small closely set tubercles. These appear rounded on the pectoral appendages but are anteroposteriorly elongated on the scale rows.

Remarks—This species can be confidently assigned to the genus *Diademaspis* because it exhibits a suite of characters diagnostic for this genus (Janvier, 1985a; Voichyshyn, 2006.). It shares with *Diademaspis jarvicki* Wängsjö, 1952 long cornual processes constituting over a third of the maximum shield length, a short and broad median field and lateral fields that broaden posteriorly, extending only slightly onto the cornual processes. *D. jarvicki* is, however, distinct from *D. janvieri* in the outline of its headshield (which is significantly broader), the shape of its median field (which is approximately rectangular and does not taper anteriorly), and the condition of its tesserae (which are smaller in proportion to the size of the shield and ornamented with tubercles which do not form central islands) (Janvier, 1985a). The occurrence of central ‘islands’ of large rounded tubercles is a character *D. janvieri* shares with *D. poplinae* Janvier 1985a, as well as *Diademaspis* sp. 1 and sp. 2 of Janvier (1985a). *D. poplinae* differs from *D. janvieri* by its comparatively broader shield with proportionally shorter cornual processes, lateral fields which are broader anteriorly and a median field that is roughly rectangular in shape. Comparison with *D. stensioei* Afanassieva, 1989 is difficult due to the incomplete and

compressed nature of the latter material. It appears distinct from *Diademaspis janvieri*, however, in that its pre-pineal division is proportionately shorter. The fragmentary shield of *Diademaspis* sp. 1 greatly exceeds the size range of *D. janvieri* and bears proportionally smaller cornual processes (Wängsjö, 1952; Janvier, 1985a). *Diademaspis* sp. 2 can be easily distinguished by the conspicuous grooves of its lateral line system which are bounded by 3-4 rows of tubercles (Janvier, 1985a). The fragmentary shield of *Diademaspis* sp. 3 exhibits a median field which is tapered anteriorly much as in *D. janvieri*, yet differs in its bilobate posterior terminus (Janvier, 1985a). The incomplete *Diademaspis* sp. described by Voichyshyn (2006) exhibits a similar tapered median field with a bilobate posterior terminus, thus distinguishing it from *D. janvieri*. *Diademaspis* sp. 4 differs in its shield outline and ornamentation (Janvier, 1985a). *D. janvieri* can clearly be distinguished from all species previously attributed to *Diademaspis*, thus meriting erection of a new species. *Diademaspis* is previously known from Spitsbergen (Wängsjö, 1952) and Podolia (Janvier, 1985a, 1985b; Voichyshyn, 2006, 2011), this is therefore a new record of this genus in Great Britain.

Order INCERTAE SEDIS

JANASPIS gen. nov.

Type species—*Janaspis pagei* Lankester, 1870.

Etymology—After Janus, the Roman god of transitions (a reference to the currently transitional state of osteostracan taxonomy) who also gives his name to the month of January, and subsequently, Dr. P. Janvier.

Diagnosis—Cornuate osteostracan of small size (maximum headshield length or width 60mm) with rounded headshield of approximately equal width and length; maximum headshield width at tips of cornua; median dorsal spinal process; stout cornua of medium length which can possess posteriorly directed spiny tubercles on medial margin; Posterior half of lateral field adjacent to headshield lateral margin, extending onto cornual process whilst anterior half of lateral field extends more medially, leaving a gap between lateral margin of field and lateral margin of headshield.

Species included—*Janaspis pagei* Lankester, 1870; *J. newtonensis* sp. nov., *J. punctata* sp. nov. and potentially “*Cephalaspis*” *powrei* Lankester 1870, and “*Cephalaspis*” *watsoni* Stensiö, 1932.

Remarks—“*Cephalaspis*” *pagei* has been recognised as distinct from the genus *Cephalaspis* for some time (Janvier, 1985a: p.134). Description here of new material from the

Wayne Herbert Quarry here reveals similarities between “*C.*” *pagei* and two new species, especially that of the lateral field shape. These similarities warrant the erection of a new genus, *Janaspis*. “*Cephalaspis*” *powriei* Lankester, 1870, has been considered as close to *Janaspis pagei* (Stensiö, 1932; Janvier, 1985a) but “*C.*” *powriei* has shorter, wider, cornua and it is not clear if it possesses the lateral field shape characteristic of *Janaspis*. Furthermore, “*Cephalaspis*” *watsoni* Stensiö, 1932 exhibits some general similarities with the species of *Janaspis* but has more distinct curvature of the cornual processes. The precise species composition and morphological variation of the proposed genus will therefore require further examination.

JANASPIS NEWTONENSIS sp. nov.
(Fig. 4A,B)

Etymology—For the village of Newton, Herefordshire

Diagnosis—Cornuate osteostracan with a midline headshield length approximately 82-87% of the maximum shield width, measured at the tips of the cornual processes. Orbits bear circum-orbital raised rims; long and thin median field (width 36% of length) with parallel straight margins; lateral fields taper anteriorly and extend over approximately 26% of the cornual processes; robust cornual processes constituting approximately 34% of the maximum headshield length; long abdominal division tapering posteriorly, terminating slightly before the tips of the cornual process; prominent dorsal median spine; granular texture on tesserae of headshield with single broad flat tubercle in centre; ornamentation of ventral rim comprising up to 13 distinct parallel rows of tiny pits.

Material—The holotype only, P17488-9 (Fig. 4A,B).

Description—The headshield of the holotype is 53mm long (to cornua tips, 50mm in midline) and 55mm wide although the left portion of the shield is slightly laterally compressed meaning the maximum width of the shield may have been greater. The shield is broadly triangular in shape, narrowing conspicuously towards rostral margin. The prepineal distance is 21mm (42% of the midline headshield length). The lateral fields (36mm long) are fairly narrow anteriorly, broadening gradually towards the posterior and extending only a short distance onto the cornual processes, terminating with slightly pointed margins. The median field is broad and fairly long (4mm x 12mm respectively); its margins are broadly straight and parallel to the effect that the width of the median field remains consistent throughout its entire length. The nasohypophysial opening is fairly diminutive and lies within

1
2
3 a shallowly depressed and weakly defined circumnasal depression. The hypophysial division
4 is diamond shaped and larger than the nasal division. The orbital openings are fairly large and
5 possess thin circumorbital raised rims. A short and narrow pineal plate exists between the
6 orbits. The pectoral sinuses are fairly broad and deep. The robust cornual processes are 18mm
7 long and directed posterolaterally. The abdominal division, measured from the level of the
8 pectoral sinus, is 17mm constituting approximately 33% of the headshield midline length.
9 The tesserae of the headshield grade into the scale rows of the body, with the effect that the
10 posterior margin of the abdominal division is difficult to discern accurately. The abdominal
11 division bears a prominent dorsal median spine, however its shape and dimensions cannot be
12 accurately determined (the specimen is too fragile to permit a plaster moulding). The pectoral
13 appendages have patchy preservation; the right appendage being the most complete. Its
14 length is estimated to be 18.5mm. The pectoral appendage exhibits a paddle-like morphology
15 which is regarded as a generalised character of cornuate Osteostraci (Coates, 2003; Janvier et
16 al., 2004; Sansom et al., 2008; Sansom 2009a).

17
18 The headshield shield is composed of fairly small tesserae, each ornamented with a
19 single broad low relief central tubercle. This is overprinted by minute and closely set
20 tubercles, producing a granular external texture. The ventral rim of the headshield, preserved
21 as an external mould on the counterpart (p17489). It is ornamented with conspicuous parallel
22 rows of tubercles which follow the margin of the shield. The rim is broadest at the rostral
23 margin, where up to 13 rows of pits are discernable. The pectoral appendage is formed of
24 tesserae much smaller than those of the headshield. The ornamentation comprises closely set
25 tubercles, similar to those of the headshield tesserae, yet lacking broad central tubercles. The
26 scale rows of the body are ornamented with a similar granular texture.

27
28 **Remarks**—The species compares most strikingly with *Janaspis pagei* Lankester,
29 1870. The shield falls within the size range of this species, as identified by Stensiö (1932) and
30 shares a similar shield profile, with maximum width occurring towards the tips of
31 posterolaterally projected cornual processes, narrowing significantly towards the rostral
32 margin. The shape of the lateral fields and nasohypophysial opening, as well as the presence
33 of a dorsal median spine, are all consistent with Stensiö's (1932) redescription of the species.
34 *Janaspis newtonensis* differs however in the shape of its median field, which is broader,
35 shorter and does not narrow anteriorly. Furthermore, its ornament differs from the condition
36 observed in *J. pagei* i.e. small, rather widely spaced and well developed tubercles
37 surrounding 1-2 larger central tubercles. It also lacks posteriorly projected spiny tubercles on
38 the interior margin of the cornual processes. This character, however, could well reflect
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

differences in preservation or preparation (i.e. splitting through different rock layers). Because of this difficulty, absence/presence of tubercles on the interior margins of the cornual processes cannot confidently be used to distinguish between species. The ventral rim of *J. newtonensis* is ornamented similarly to that of *C. cradleyensis* Stensiö, 1932 (White and Toombs, 1983), but its shield morphology is quite different. *J. newtonensis* is distinguished from *C. cradleyensis* by the ornamentation of its dorsal headshield tesserae, as well as its relatively broader shield, shorter prepineal division, and shorter cornual processes. The headshield of *J. newtonensis* therefore differs significantly from previously described cornuate Osteostraci to merit the erection of a new species, which falls within the variation of the newly identified genus *Janaspis*.

JANASPIS PUNCTATA sp. nov.
(Figs 5A-F, 7)

Etymology—Latin; meaning ‘dotted’, in reference to the ornamentation of the headshield.

Diagnosis—Cornuate osteostracan with a midline headshield length approximately 70-76% of maximum width which occurs approximately mid length of the cornual processes. Median field narrow anteriorly, broadening posteriorly with maximum width approximately 40% of length; thin circumorbital raised rims ornamented with up to 3 rows of minute tubercles; broad lateral fields extending over 20% of the cornual processes; cornual processes constituting approximately 32-40% of the maximum shield length; tesserae of the headshield exhibit granular texture of minute, closely set tubercles which overprints 7-10 large obtuse and evenly spaced tubercles; ventral rim demonstrates up to 13 irregular rows of pits which approximately follow the margin of the shield.

Material—NHM P24920-1 (holotype, fig. 5B), P16604-5, P16606-7 (Fig. 5C), P16608, P20004a (Fig. 5A), P20004c, P24920/21 (Fig. 5E,F), P24926-7, P24924-5 (Fig. 5B), P24929-30, P24935-6 (Fig. 5D), P53027a-b.

Description—The headshield ranges from 44-54mm long (to level of cornua tips, 37-42mm midline headshield length only) with maximum width of 54-57mm in the region of the cornua. The prepineal division is rather short, constituting approximately 42-45% of the shield length in midline. The lateral fields are broad (27-34mm) and extend over the cornual processes. The median field (13-15mm long, 5-6mm maximum width) is narrow anteriorly. The median field of P24920/21 is bottle-shaped and preserves the external openings of the

endolymphatic ducts at the postero-lateral margins. The nasohypophysial is within a narrow and shallowly circumnasal depression which exhibits a pointed anterior margin. The hypophysial division appears to be expanded relative to the nasal division. The orbital openings are fairly large relative to the headshield and are enclosed within narrow circumorbital raised rims (Fig. 5D). They are connected via a thin and short pineal plate. The slender cornual processes project posteriorly and attain a length of 14-23mm, constituting 32-40% of the maximum shield length. The abdominal division (9-11mm long) constitutes roughly 25% of the shield length in midline and does not appear to bear a dorsal median ridge. NHM P16606 preserves as an external mould the right pectoral appendage which is incomplete and composed of discrete rows of very small tesserae. Impressions of the ventral surface of the shield, preserved in specimens P20004a (i) and P24935, suggest at least 8 external branchial openings were present. Specimen P24924/25 (i) (Fig. 5B) exhibits an almost complete articulated body, compressed laterally, bearing a single posterior dorsal fin posterior of approximately 20 scale rows.

The headshield ornamentation is preserved on all specimens and consists of evenly spaced, large obtuse tubercles which themselves are overprinted by minute and closely set tubercles which produce a granular texture. The tesserae of the shield can only be discriminated in the lateral and median fields of specimen P24921. They are small in proportion to the shield size and each ornamented with 7-10 obtuse tubercles. The ventral rim is ornamented with up to 13 irregular rows of small pits which approximately follow the margin of the headshield. The circumorbital raised rims of specimen P24920 are ornamented with up to 3 rows of minute tubercles. The tubercles of the body scales are closely set and elongated anteroposteriorly.

Remarks—The species also compares closely with *Janaspis pagei* Lankester, 1870. Again, the headshields fall within the known size range of this species (Stensiö, 1932) and shares characters including large orbital openings in proportion to the headshield size, a median field which is narrow anteriorly, lateral fields that are broad and extend considerably over the cornual processes and a similar style of ornamentation consisting of minute tubercles producing a granular texture which overprints a single obtuse central tubercle (rather than several evenly spaced obtuse tubercles). *Janaspis pagei* can be distinguished from the morphogroup described here, however, by its proportionally shorter cornual processes, which bear conspicuous spiny tubercles on their interior margins, and by its prominent dorsal median spine. Perhaps a closer comparison can be drawn with '*Cephalaspis*' *watsoni* Stensiö, 1932 which possesses broad lateral fields that extend considerably over long cornual

processes, a median field that is bottle-shaped and a style of ornamentation identical to that of the Wayne Herbert specimens. ‘C’. *watsoni* may be distinguished, however, by its more strongly medially curved cornual processes and by the dorsal median ridge of its abdominal division. It is possible that discovery of more material will reveal that ‘C’. *watsoni* and *Janaspis punctata* are part of a single, variable species, but this is currently speculative. The lack of a dorsal median ridge may be a taphonomic artefact as all specimens exhibit compression to some degree. Furthermore, ‘C’. *watsoni* exhibits variability with regards to the curvature of the cornual processes (NHM P16157 has incomplete cornua but they are nevertheless weakly curved in comparison to the holotype). Given the data presently available however, it is preferable to acknowledge *Janaspis punctata* as a new species.

PATTENASPIS Stensio 1958

Type species—*Pattenaspis acuminata* Wängsjö, 1952.

Emended diagnosis—Modified from Stensjö (1958), Janvier (1985a) and Voichyshyn (2011): Small to medium sized cornuate osteostracan with long, fine, medially curved cornua; narrow headshield with accentuated rostral point and short abdominal division with low dorsal ridge; narrow lateral fields; well developed pineal plate; oval shaped oralobranchial fenestra.

Species included—*P. acuminata* Wängsjö, 1952; *P. artensis* Blieck and Janvier, 1989; *P. bardenheuri* Friman, 1986; *P. divaricata* Wängsjö, 1952; *P. deltoides* Wängsjö, 1952; *P. eukeraspidoides* Stensjö, 1927; *P. eurhynchus* Wängsjö, 1952; *P. foeyni* Wängsjö, 1952; *P. heintzi* Stensjö, 1927; *P. oreas* Wängsjö, 1952; *P. pygmaea* Wängsjö, 1952; *P. rogalai* Balabai, 1962; *P. watneliei* Stensjö, 1927; *P. woschmidtii* Friman, 1986.

Remarks—*Pattenaspis* was initially erected by Stensjö (1958) although under fairly loose criteria describing principally ventral or internal features which make it difficult to make meaningful comparisons with other species. Although initially described by Stensjö (1958) as “<*Cephalaspis*> species du type *whitei*” we follow Janvier (1985) in considering *P. acuminata* as type species.

PATTENASPIS WHITEI Stensjö, 1932

(Figs 4C-E, 7)

[?P] *Cephalaspis lyelli* Woodward, 1891: 179-181

[?P] *Cephalaspis salweyi* Woodward, 1891: 181-182

[?] *Cephalaspis* sp. Patten, 1903: 844, pl. 1, fig. 4

[v] *Cephalaspis whitei* Stensiö, 1932: 93-96, figs. 9, 3B, 30, Pl. 18; figs. 3-6, Pl. 19; figs. 1-2, Pl. 20; fig. 3, Pl. 21, Pl. 27; fig. 5, Pl. 32; fig. 6, Pl. 61, 62.

[vP] *Cephalaspis jacki* White, 1932.

Emended diagnosis—Cornuate osteostracan with a midline headshield length approximately 67-78% of the maximum shield width. Prepineal division approximately 47-48% of midline shield length; narrow circum-orbital raised rims; median field long and broad with an elongate octagonal outline, width 40-59% of length; lateral fields fairly broad, extending over 25-28% of the cornual processes, terminating with pointed posterior margins; cornual processes long (approximately 37-41% of maximum headshield length) with spiny tubercles on interior margin; abdominal division fairly short with low dorsal median ridge; tesserae of the headshield ornamented with approximately 7-10 large rounded tubercles which are evenly spaced and surround a similar sized or slightly larger central tubercle.

Material— P16310 (Fig. 4E) and P19198/9 (Fig. 4C,D), in addition to the holotype (NHM P5048) and 20 other specimens attributed to the species by Stensiö (1932).

Description—Of the two Wayne Herbert specimens, one has a larger headshield (NHM P16310, 99mm long, 96mm maximum width, 74mm midline headshield length) and other smaller (P19198-9, 76mm long, 87mm wide, 58mm midline headshield length). The pineal plate is short, well defined and enlarged medially. The prepineal division of both shields constitutes approximately 48% of the midline headshield length. The orbital openings are roughly circular and enclosed within thin circumorbital raised rims (Fig. 4). The nasohypophysial opening is anteroposteriorly elongate and exhibits a slightly expanded hypophysial division relative to the nasal division. In specimen P16310 the nasohypophysial opening is found within a shallow circumnasal depression. The median field is approximately octagonal, tapering anteriorly at the level of the posterior margin of the circumorbital raised rims. The lateral fields measure 50-61mm, extend over 25-28% of the cornual processes and terminate posteriorly with pointed margins. The cornual processes measure 28-41mm, constituting approximately 37-41% of maximum shield length. They are medially curved, with the effect that the maximum headshield width occurs at a level approximately mid-length of the cornual processes. The abdominal division is short, constituting approximately 19-22% of the midline shield length, and bears a low dorsal median ridge. The abdominal division of p19198-9 is fairly broad where as that of P16310 appears to taper posteriorly,

producing extremely broad pectoral sinuses. The nature of the shields preservation makes it difficult to discern whether the specimen is in fact missing the lateral margins of its abdominal division. P16310 preserves ornament of the headshield tesserae comprising 7-10 large rounded and evenly spaced tubercles surrounding a slightly enlarged central tubercle. The ornamentation of the ventral rim is unknown in the Wayne Herbert specimens.

Remarks—The species is distinguished from other Wayne Herbert species by the shape of its lateral and median fields, the presence of a low median ridge, and by its ornament. One specimen attributed to this species (p16310) was described by White (1932) as *Cephalaspsis jacki*. White distinguishes the species from *Zenaspis salweyi* Egerton, 1857 by its longer and more slender cornual processes, its wider and shallower pectoral sinuses and its less developed dorsal median ridge. *C. jacki* most closely resembles *Cephalaspis whitei* Stensiö 1932, published marginally before. The Wayne Herbert specimens fall within the size range of ‘C’. *whitei* identified by Stensiö (1932) (midline headshield length 45-70mm), although P16310 slightly exceeds the size of the largest ascribed specimen. Both specimens from Wayne Herbert differ from the holotype, however, which exhibits a median field which extends onto the abdominal division, as well as elongate tubercles on the interior margins of the cornual processes. Stensiö (1932) regarded the later character as diagnostic for the species. Examination of the attributed material, however, reveals that the posterior extent of the median field is variable rather than a discrete character which could be used to distinguish between species. Furthermore the absence of tubercles on the interior margins of the cornual processes could easily reflect differences in preservation or preparation (see above). The Wayne Herbert specimens are attributed to *Pattenaspis whitei* (which takes priority over *C. jacki* White 1932) on the basis of their shield breadth, fairly long prepineal division, long, medially curved cornual processes, and characteristic median and lateral field shape as well as ornamentation of the headshield tesserae (preserved in P16310) which is indistinguishable from that of the holotype. *P. whitei* compares closely with ‘C’. *fletti* Stensiö, 1932; both species share a similar headshield outline as well as broad lateral fields with pointed posterior margins that extend considerably onto long, medially curved cornual processes bearing spiny tubercles on their interior margins. ‘C’. *fletti* is distinguished from *P. whitei* however by its shorter prepineal division, its narrower lens shaped median field and its ornamentation consisting of large obtuse tubercles restricted to the lateral and rostral margins of the shield (Stensiö, 1932). *P. whitei* also compares closely with ‘C’. *whitbachensis* Stensiö, 1932 which differs from ‘C’. *fletti* only in the lack of tubercular ornamentation. It is speculated here that ‘C’. *whitbachensis* and ‘C’. *fletti* are synonymous and that the lack of ornamentation may be

the result of taphonomic differences rather than taxonomic disparity. The disparity between 'C'. *fletti* and 'C'. *whitei* is considered taxonomically significant at the species level in the current study, yet could potentially be eroded if subject to a more complete revision of all material attributed to these species. Furthermore, additional study of 'C'. *fletti* and 'C'. *whitbachensis* will be necessary to assess whether they are appropriate for inclusion in *Pattenaspis*.

CORNUATA gen. indet. sp. A

(Figs 6A,C, 7)

Material—P19229 (Fig. 6A,C)

Description—The headshield of this specimen attains a maximum length of 58mm with a maximum width exceeding 60mm. The midline headshield length likely exceeded 53mm. The prepineal division measures 26mm therefore constituting >49% of midline headshield length. The shield is narrow towards the rostral margin. The lateral fields are short and broad throughout their entire length, attaining a length of approximately 41mm and terminating slightly before the level of the pectoral sinuses. The median field is fairly long and broad with approximately parallel straight lateral margins; its width constituting roughly 48% of its length. The pineal plate is short and very narrow. The hypophysial division of the nasohypophysial opening is expanded relative to the nasal division. It lies within a narrow and shallowly depressed circumnasal depression. The orbital openings are fairly large in proportion to the shield size, oval shaped and lack circumorbital raised rims. The pectoral sinuses are narrow, bordering a broad and short abdominal division exceeding 23% of the shields length in midline. The posteriorly projected cornual processes are extremely short and gracile, their length constituting 22% of the maximum headshield length. Only the basal laminar layer of tissue is preserved therefore shield ornament cannot be observed.

Remarks—The headshield of this morphogroup is remarkable in its shape and proportions which are without close comparison. Exceptionally short cornual processes are known in a number of taxa; notably *Diademaspis poplinae* Janvier, 1985a, '*Cephalaspis*' *lornensis* Traquair, 1898 and *C. cradleyensis* Stensiö, 1932. The specimen described here has lateral fields which are limited in the degree to which they extend over the cornual processes, a characteristic it shares with *D. poplinae*. *D. poplinae* is, however, much larger with fundamentally different shield morphology. 'C'. *lornensis* offers perhaps the closest comparison to the specimen. Both share fairly large orbital openings in proportion to shield size, a roughly similar shaped median field, a broad abdominal division, narrow pectoral

sinuses and lateral fields that do not extend onto the cornual processes. ‘*C*’. *lornensis* differs from the specimen, however, in its short and broad prepinial division and its more robust cornual processes. With *C. cradleyensis*, this specimen shares fairly large orbital openings in proportion to shield size, a prepineal division constituting around 50% of the midline shield length and a broad abdominal division with adjacent narrow pectoral sinuses. However the shield of *C. cradleyensis* remains broad anteriorly and exhibits a narrow lens shaped median field and the lateral fields that extend well onto the cornual processes. The specimen thus likely represents a new species characterised by its short and thin cornual processes, narrow rostrum and limited posterior extent of its lateral fields. Unfortunately the current material is incomplete to the extent that the morphology of the abdominal division, as well as the nature of shields ornamentation, is completely unknown. Accordingly the specimen is retained in open nomenclature.

CORNUATA gen. indet. sp. B
(Figs 6B,D, 7)

Material—P24922/3 (Fig. 6B,D)

Description—The headshield of this single specimen attains a maximum length of approximately 43mm with a maximum width, measured slightly above the tips of the cornual processes, approximately 54mm. The shield measures an estimated 39mm in midline headshield length. The shield is fairly broad, particularly towards the anterior where the shield rapidly narrows to produce a blunt rostral margin. The prepineal division constitutes approximately 49% of the shield length in midline. No trace of the lateral fields can be seen, however it is unclear whether the shield originally lacked lateral fields or, perhaps more likely, they have not been preserved. The median field is poorly preserved and its posterior extent is unknown. The nasohypophysial opening cannot be observed although a shallow, short and narrow circumnasal depression exists directly above the thin and poorly preserved pineal plate. The orbital openings are roughly circular and lack circumorbital raised rims. The pectoral sinuses are broad and deep. The abdominal division constitutes approximately 30% of the midline shield length and does not appear to bear a dorsal median ridge. The cornual processes are extremely robust and project posterolaterally, slightly curving medially at their tips. They constitute roughly 32% of the shields maximum length. Posterior to the headshield, the articulated body is preserved, with up to 15 scale rows observed. It is twisted laterally and compressed into a single plane with the effect that venterolateral scales are observed on the left margin, while dorsal median ridge scales occur close to the right margin. Tesserae of the

shield are well preserved. Their size is variable with small units occurring posteromedially and extremely large units occurring towards the rostral and lateral margins of the shield. They are ornamented with minute and closely set tubercles which exhibit a random distribution producing a granular texture within the centre of each unit, yet are differentiated into discrete rows towards the margins of the tesserae. The largest tesserae exhibit up to 30 rows of tubercles. The ventral rim appears to be similarly ornamented. The scales of the body are ornamented with minute rows of closely set tubercles.

Remarks—The single specimen of this morphogroup bears some resemblance to that of *Cephalaspis lankesteri* Stensiö, 1932; both share long and robust cornual processes and broad pectoral sinuses. In addition, Stensiö's (1932) shield reconstruction shares a similar outline to that of the specimen i.e. pronounced anterior-lateral corners of the headshield margin. However, *C. lankesteri* may be distinguished by its narrower rostral margin, the presence of a dorsal median ridge and the lack of tubercular ornamentation producing a smooth dorsal shield surface. Specimen P24922-3 can be distinguished from other cornuate Osteostraci by its broad prepineal division with a blunt rostral margin and by the presence of large tesserae ornamented with rings of minute closely set tubercles. The extent of the median field cannot be determined accurately at present and the morphology of the lateral fields is completely unknown. Consequently the specimen is retained in open nomenclature.

THE STATE OF OSTEOSTRACAN TAXONOMY

Application of this morphogroup approach to the taxonomy of the Wayne Herbert fauna and subsequent comparison with previously described species of Osteostraci highlights important difficulties with the current state of osteostracan taxonomy at both species and genus level. Difficulties with genus level taxonomy need consideration from a historic perspective. The first osteostracan taxon to be erected was *Cephalaspis lyelli* Agassiz 1835 which designates a single part and counterpart (NHM 20087/P3233). Unfortunately over 100 years passed before a detailed description of this specimen was published (White, 1958) and in the intervening time period many generalised cornuate Osteostraci were assigned to the genus *Cephalaspis* despite possessing characters which distinguish them from this genus (Janvier and Newman, 2004). Janvier and Newman (2004) suggest that *C. lyelli* can be distinguished from most other generalised forms by its long prepineal division, narrow median field and approximately parabolic anterior shield margin. Only 3 species (*C. producta* Wängsjö, 1952, *C. Cradleyensis* Stensiö, 1932 and *C. sollasi* Stensiö, 1932) demonstrate

comparable morphology, thus are regarded as more closely related to *C. lyelli* than to any other osteostracan (Janvier 1985a, 1985b, Janvier unpublished data). The genus name *Cephalaspis* may therefore be retained for these species. A number of generalised forms assigned to *Cephalaspis* have since been recognised as distinct genera (e.g. Denison, 1951; Jarvik, 1954; Stensiö, 1958; Janvier 1976, 1985a, 1985b) however many species remain assigned to *Cephalaspis* that exhibit none of the derived characters which distinguish this genus. Clarity is therefore needed regarding these many species of ‘*Cephalaspis*’ to provide a better taxonomic framework and context for investigations of diversity and phylogeny (Sansom 2009a). Unfortunately a genus level taxonomic revision of cornuate Osteostraci is beyond the scope of this study. Of the morphogroups identified in the Wayne Herbert fauna, two have been assigned to *Janaspis* gen. nov., one to *Pattenaspis* and two have been described as *Cornuata* gen. indet. This reflects current taxonomic limitations and it is anticipated that these species will be attributed to different or new genera once the taxonomy of *Cephalaspis* is revised.

Regarding species level taxonomy of Osteostraci, it is apparent that there may have been a historic tendency for ‘over-splitting’ of species. Three main causes are suggested. Firstly, species have been erected on the basis of fragmentary material which is character deficient and thus cannot be meaningfully compared with previously erected taxa. *Cephalaspis sollasi* Stensiö 1932, for example, was erected on the basis of one incomplete specimen which is identifiable as *Cephalaspis* but lacks any diagnostic features that could be used to reliably distinguish it from *C. lyelli* (for which the cephalic shield ornamentation is also unknown). Secondly, taphonomy of specimens has been inadequately considered. The presence and number of tubercles on the interior margins of the cornual processes has been used as key diagnostic feature (Stensiö 1932), but for species for which only a few specimens are known, it is not possible to discern if tubercles are absent due to poor preservation rather than original condition. Thirdly, an over reliance on continuous rather than discrete characters within species diagnoses can lead to ambiguity. Whilst continuous characters, such as cornual process size, orbit size or median field size, may be taxonomically informative and have been used to differentiate some species (e.g. *Zenaspis dzieduszyckii* Voichyshyn, 2006), these may easily represent end members of a spectrum of morphological variation exacerbated by missing intermediates (Sansom 2007). We therefore suggest that continuous characters are supported by discrete characters.

A potential solution to the problems of taxonomic ambiguity is provided by the ornamentation of the dermoskeleton of the cephalic shield. We have documented

considerable variability in ornament, and differences in ornamentation of the headshield tesserae, ventral rim, and circumorbital raised rims might prove to be taxonomically useful characters.

GROWTH OF OSTEOSTRACI

Osteostraci possess complex dermoskeletal tissues comprising a composite of cellular and acellular bone like to that of jawed vertebrates, particularly placoderms (Donoghue and Sansom 2002; Donoghue et al., 2006). It has been assumed that ossification of the osteostracan dermoskeleton began only once an individual attained adult size, and that development of the dermal armour effectively inhibited further growth (Stensio, 1927, 1932; Denison 1952; Janvier, 1996). This differs from the condition recognized in primitive gnathostomes which typically demonstrate indeterminate growth (Hawthorn et al., 2008; Cloutier, 2010). Given the phylogenetic position of the Osteostraci as the sister group to all jawed vertebrates (Forey and Janvier, 1993; Janvier 1996; Donoghue et al., 2000) it follows that recognising patterns of dermoskeletal growth within the Osteostraci is informative regarding the pleisiomorphic state of jawed vertebrate dermoskeletal development.

Until recently, evidence of osteostracan growth has been limited to recognition of incompletely mineralised dermoskeletal units (Dineley and Loeffler, 1976; Janvier, 1985a; Belles-Isles, 1989), deposition and resorption of dentine and bone (Denison, 1952) and intraspecific headshield size variation (White and Toombs, 1983; Janvier, 1985a; Janvier and Arsenault, 1996; Sansom, 2007; see also Hawthorn et al., 2008). Such observations are of limited use when considering patterns of ossification through ontogeny. A recent study by Hawthorn et al. (2008) was able to address this issue, however, through identification of the ontogenetic sequence of the Lochkovian cornuate osteostracan *Superciliaspis gabrielsei* Dineley and Loeffler, 1976. Hawthorn et al., were able to provide a comprehensive model for growth of the tessellate osteostracan dermoskeleton, adapted from Halstead Tarlo's (1967) model of dermoskeleton growth in tessellate heterostracans. They suggest that each tessera grew individually by means of marginal addition of skeletal tissue. Ossification is suggested to have initiated by development of a 'primordial' central tubercle with an internally open pulp cavity. This was followed by marginal ossification of tuberculated rings of bone and finally through addition of untuberculated rings (Fig. 8). Furthermore they observe tesserae at different developmental stages present within individual shields suggesting the headshield grew through a combination of addition of new tesserae as well as centrifugal addition of tissue to existing tesserae. Postcranially, the squamation pattern of adult specimens,

comprising large rectangular scales, is suggested to have formed as a result of fusion of smaller scales. The model presented by Hawthorn et al. (2008) differs from that of Halstead Tarlo (1967) which suggests the tessellate dermoskeleton of some heterostracans is a product of individual centrifugally growing units abutting together as the headshield becomes fully encased in bone, thereby inhibiting further growth. In contrast Hawthorn et al. (2008) recognise ‘adolescent’ specimens which demonstrate a fully ossified dermal skeleton composed of incompletely developed tesserae implying is that *Superciliaspis gabrielsei* was capable of indeterminate growth. *Superciliaspis gabrielsei*, however, is a fairly derived osteostracan with unusual dermoskeletal histology (Dinely and Loeffler, 1976; Hawthorn et al., 2008; Sansom 2009a). It thus remains unclear whether this model of dermoskeletal growth reflects the plesiomorphic condition of tessellate growth within the Osteostraci.

Two species of Osteostraci from Wayne Herbert (*Diademaspis janvieri* and *Cornuata* gen. indet. sp. B) demonstrate dermoskeletal growth patterns which support the model of centrifugal growth proposed by Hawthorn et al. (2008). The growth pattern of *Cornuata* gen. indet. sp. B is most comparable to that of *Superciliaspis gabrielsei*. The shield of the single specimen attributed to the species exhibits tesserae of varying size; the largest of which are ornamented with up to 30 concentric rings of tubercles surrounding undifferentiated central tubercles, while the smallest tesserae are entirely undifferentiated, lacking tubercle rings. It suggests that ossification began with the development of ‘primordial’ small tesserae with undifferentiated tubercles which subsequently grew by means of marginal addition of tuberculated rings of bone (see fig. 8). Presently it cannot be determined whether these undifferentiated units developed by means of centrifugal or synchronous ossification, yet the strong polygonal pattern of the tubercle rings indicates that tesserae were already abutting during marginal ossification (Halstead Tarlo 1967, Halstead 1973), thus supporting the hypothesis that osteostracans were capable of indeterminate growth. The smallest and least well ossified of the *Superciliaspis gabrielsei* specimens, interpreted as most juvenile, already exhibit a well ossified cephalic brim (Hawthorn et al., 2008), indicating ossification may have initiated marginally. A similar conclusion may be drawn from the size distribution of tesserae observed in *Cornuata* gen. indet. sp. B, wherein the largest units, exhibiting the most tubercle rings, occur at the margins of the shield with smaller units comprising fewer tubercle rings occurring towards the shield’s centre.

The complex and variable dermoskeletal ornamentation of *Diademaspis janvieri* is more difficult to interpret in terms of growth patterning. Ostensibly, each tessera comprises central large tubercles surrounded by up to 3 rows of minute tubercles; a pattern indicative of

centrifugal growth by means of marginal addition of tuberculated 'rings'. However, close inspection of the high fidelity dermoskeletal impressions of specimens P20005a and P24942 reveals surprising variation in the number of central tubercles, as well as the number of 'rings' of minute tubercles, occurring within tesserae. The simplest tessera comprises a single central tubercle surrounded by 2 'rings' of minute tubercles however, up to 7 large tubercles may form a central 'island' enclosed within several 'rings' of tuberculated bone. Following the models presented by Halstead Tarlo (1967) and Hawthorn et al., (2008) the large central tubercle may be regarded as primordial discrete ossification centres which formed within the skin of the 'naked' animal, however in contrast to previous models these seem to have frequently fused together producing 'islands' of large tubercles before subsequent centrifugal addition of tuberculated 'rings' of bone. Several tesserae forming part of the shield of specimen P20005a are observed to share the exterior most 1-2 tuberculated 'rings' while possessing separate interior most 'rings'. This pattern may have arisen as a result of fusion between two independent tesserae into a single larger plate. One means of attaining such fusion would be a reduction or ceasing of ossification at the abutting margins, allowing the formation of continuous rings of tuberculated bone to envelope adjacent tesserae (Fig. 8). The tuberculated 'rings' demonstrate a polygonal pattern, much as in *Superciliaspis gabrielsei* (Adrain and Wilson, 1994; Hawthorn et al., 2008) indicating that the headshield tesserae of *Diademaspis janvieri* were capable of indeterminate growth following abutting of the tesserae. *D. janvieri* demonstrates a more complex growth pattern than has been previously described and provides evidence for superficial fusion of independent centrifugally growing tesserae within the Osteostraci.

CONCLUSIONS

The generalised cornuate osteostracan morphology presents a challenge to taxonomists. There are few discrete characters which can be used to differentiate species and this has led to a historic tendency to instead establish species based on character deficient, poorly preserved and/or fragmentary material with inadequate consideration of taphonomic character loss and an over reliance on continuous rather than discrete characters. The osteostracan fauna of Wayne Herbert quarry, however, has been subject to a step-wise quantitative and qualitative analysis of morphology, permitting recognition of 7 morphogroups. After comparison with existing descriptions, it has been possible to recognise two new species of Zenaspididae (*Zenaspis wayenensis* and *Diademaspis janvieri*) as well as

two new species of Cornuata incertae sedis (*Janaspis newtonensis* and *Janaspis punctata*). This approach has ensured that species identification accurately reflects intra- and inter-taxon variation within the fauna. The high fidelity preservation of osteostracan material from Wayne Herbert also reveals ornamentation patterns which provide support for models of indeterminate growth within the Osteostraci. These new taxonomic results and anatomical data enable a better understanding of the diversity and development of the Osteostraci and will help to elucidate the evolutionary diversification of this intriguing group.

ACKNOWLEDGEMENTS

Firstly, the authors are indebted to E. White who originally collected and prepared the material and was intending to describe it before his passing. P. Forey (formally NHM) is thanked for initially making the authors (R. Sansom) aware of the material and its context. Z. Johanson (NHM) is thanked for enabling access and loan of the material and D. Unwin (Leicester) for providing transport.

LITERATURE CITED

Adrain, J. M. and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. *Journal of Vertebrate Paleontology* 14:301-319.

Affanassieva, O. B. 1989. [New cephalaspids (agnatha) from the Lower Devonian of Podolia]. *Palaeontologičeskij žurnal* 3:51-59. [Russian]

Agassiz, J. L. R. 1835. *Reserches sur les Poissons Fossiles*. 2. Contenant l’histoire de l’ordre des Ganoïdes. Neuchâtel 85-300pp.

Allen, J. R. L. and L. B.H. Tarlo. 1963. The Downtonian and Dittonian facies of the Welsh Borderland. *Geological Magazine* 100,129-155.

Balabai, P. P. 1962. [The fauna of the cephalaspids of Podolian plate]. *Naukovi zapysky Naukovo-pryodo-znavčogomuzeâ AN URSR* 10:3-8. [Ukranian]

Belles-Isles, M. 1989. *Yvonaspis*, nouveau genre d’Osteostraci (Vertebrata, Agnatha) du Dévonien (Emsien-Eifélien) des Grès de Gaspé (Québec, Canada). *Canadian Journal of Earth Sciences* 26:2396–2401.

Bengtson, P. 1988. Open nomenclature. *Palaeontology* 31:223–227.

- 1
2
3 Blicek, A. R. M. 1984. Les Hétérostracés ptéraspidiformes, Agnathes du Silurien-Dévonien
4 du continent Nord-Atlantique et des blocs avoisinants. Cahiers de Paléontologie, Centre
5 National de la Recherche Scientifique, Paris, 199 pp.
6
7
8 Blicek, A. R. M., and Janvier, P. 1989. Vertébrés agnathes du Dévonien Inférieur de
9 l'Artois(Pas-de-Calais, France): Implication biostratigraphiques. Annales de
10 Paléontologie 75:125-167.
11
12
13 Brazeau, M. D. 2009. The braincase and jaws of a Devonian 'acanthodian' and modern
14 gnathostome origins. Nature 457:305-308.
15
16
17 Cloutier, R. 2010. The fossil record of fish ontogenies: Insights into developmental patterns
18 and processes. Seminars in Cell & Developmental Biology 21:400-413.
19
20 Coates, M. I. 2003. The evolution of paired fins. Biomedical and Life Sciences 122:266-287.
21
22 Denison, R. H. 1951. Evolution and classification of the Osteostraci. Fieldiana: Geology
23 11:156-196.
24
25 Denison, R. H. 1952. Early Devonian Fishes from Utah. Part 1. Osteostraci. Fieldiana:
26 Geology 11:265-287.
27
28 Dineley, D. L. 1999. Late Silurian fossil fish sites of the Welsh Borders; pp. 63-106 in D. L.
29 Dineley and S. J. Metcalf (eds), Fossil Fishes of Great Britain. Joint Nature
30 Conservation Committee, Peterborough, UK.
31
32
33 Dineley, D. L., and J. Loeffler. 1976. Ostracoderm faunas of the Delorme and associated
34 Siluro-Devonian Formations, North West Territories, Canada. Palaeontological
35 Association Special Papers in Palaeontology 18:1-214.
36
37
38 Donoghue, P. C. J., P. L. Forey, and R. J. Aldridge 2000. Conodont affinity and chordate
39 phylogeny. Biological Reviews 75:191
40
41 Donoghue, P. C. J. and I. J. Sansom. 2002. Origin and early evolution of vertebrate
42 skeletonization. Microscopy Research Techniques 59:352-372.
43
44
45 Donoghue, P. C. J., I. J. Sansom and J. P. Downs. 2006. Early evolution of vertebrate skeletal
46 tissues and cellular interactions, and the canalization of skeletal development. Journal
47 of Experimental Zoology Part B: Molecular and Developmental Evolution 306:1-
48 17.
49
50
51 Egerton, P. M. G. 1857. Palichthyologic notes. No. 9. On some fish-remains from the
52 neighbourhood of Ludlow. Quarterly Journal of the Geological Society of London
53 13:282-289.
54
55
56 Forey, P. L., and P. Janvier. 1993. Agnathans and the origins of jawed vertebrates. Nature
57 361:129-134.
58
59
60

- 1
2
3 Friman, L., and P. Janvier. 1986. The Osteostraci (Vertebrate, Agnatha) from the Lower
4 Devonian of the Rhenish Slate Mountains, with special reference to their anatomy and
5 phylogenetic position
6
7
8 Halstead, L. B. 1973. The heterostracan fishes. Biological Reviews of the Cambridge
9 Philosophical Society 48:279-332.
10
11 Halstead Tarlo, L. B. 1967. Agnatha, 629–636 pp. in Harland, W. B., C. H. Holland, M. R.
12 House, N. F. Hughes, A. B. Reynolds, M. J. S. Rudwick, G. E. Satterthwaite, L. B. H.
13 Tarlo, E. C. Willey (eds). The Fossil Record. London Geological Society, London.
14
15 Hawthorn, J. R., M. V. H. Wilson and A. B. Falkenberg. 2008. Development of the
16 dermoskeleton in *Superciliaspis gabrielsei* (Agnatha: Osteostraci). Journal of
17 Vertebrate Paleontology, 28:951-960.
18
19 Janvier, P. 1976. *Hildenaspis digitalis* nov. gen., nov. sp.(Agnatha, Cephalaspidomorpha),
20 Cephalaspide nouveau du Devonien inferieur d'Allemagne. Geobios 9:223-225.
21
22 Janvier, P. 1981. The phylogeny of the Craniata, with particular reference to the significance
23 of fossil “agnathans”. Journal of Vertebrate Paleontology 1:121-159.
24
25 Janvier, P. 1985a. Les Céphalaspides du Spitsberg. Cahiers de Paléontologie, Section
26 Verébrés, Éditions du Centre National de la Recherche Scientifique, Paris, 183-195pp.
27
28 Janvier, P. 1985b. Preliminary description of Lower Devonian Osteostraci from Podolia
29 (Ukrainian S.S.R.). Bulletin of the British Museum (Natural History), Geology 38:309-
30 334.
31
32 Janvier, P. 1996. Early Vertebrates. Oxford University Press, Oxford, 408pp.
33
34 Janvier, P., and M. Arsenault. 1996. Osteostraci; 123-133pp in Schultze, H. P. and R.
35 Cloutier (eds.), Devonian Fishes and Plants of Miguasha, Quebec, Canada, Friedrich
36 Pfeil, Munich.
37
38 Janvier, P. and M. J. Newman. 2004. On *Cephalaspis magnifica* Traquair, 1893, from the
39 Middle Devonian of Scotland, and the relationships of the last osteostracans.
40 Transactions of the Royal Society of Edinburgh: Earth sciences. 95:511-525
41
42 Janvier, P., M. Arsenault and S. Desbiens. 2004. Calcified cartilage in the paired fins of the
43 osteostracan *Escuminaspis laticeps* (Traquair 1880), from the Late Devonian of
44 Miguasha (Québec, Canada), with a consideration of the early evolution of the pectoral
45 fin endoskeleton in vertebrates. Journal of Vertebrate Paleontology 24:773-779.
46
47
48 Jarvik, E. 1954. On the visceral skeleton in *Eusthenopteron* with discussion of the
49 parasphenoid and palatoquadrate in fishes. – Kungliga Svenska
50 Vetenskapsakademiens Handlingar, Fjärde Serien 5:1-104.
51
52
53
54
55
56
57
58
59
60

- Lankester, E. R. 1870. A monograph of fishes of the Old Red Sandstone of Britain. Part I. The Cephalaspidae. The Palaeontographical Society, London, 62pp.
- Matthews, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, 16:335-380.
- Miles, R. S. 1973. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. *Bulletin of the British Museum (Natural History), Geology*, 24:113–213.
- Patten, W. 1903. On the structure of the Pteraspidae and Cephalaspidae. *The American Naturalist* 37:827-865.
- Sansom, R. 2007. A review of the problematic osteostracan genus *Auchenaspis* and its role in Thyestidian evolution. *Palaeontology* 50:1001-1011.
- Sansom, R. S. 2008. The origin and early evolution of the Osteostraci (Vertebrata): a phylogeny for the thyestiids. *Journal of Systematic Palaeontology* 6:317–332.
- Sansom, R. S. 2009a. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). *Journal of Systematic Palaeontology* 7:95–115.
- Sansom, R. S. 2009b. Endemicity and palaeobiogeography of the Osteostraci and Galeaspida: A Test of scenarios of gnathostome evolution. *Palaeontology* 52:1257-1273.
- Sansom, R. S., S. A. Rodygin, and P. C. J. Donoghue. 2008. The anatomy, affinity and phylogenetic significance of *Ilemoraspis kirkinskayae* (Osteostraci) from the Devonian of Siberia. *Journal of Vertebrate Paleontology* 28:613-625.
- Stensiö, E. A. 1927. The Downtonian and Devonian vertebrates of Spitsbergen. 1. Family Cephalaspidae. *Skrifter om Svalbard og Ishavet* 12:1-391.
- Stensiö, E. A. 1932. The Cephalaspids of Great Britain. *British Museum (Natural History)*, London, 220pp.
- Stensiö, E. A. 1958. Les cyclostomes fossiles ou ostracodermes; pp 173–425 in Grassé, P. P. (ed.), *Traité de Zoologie*, Paris.
- Schmitz, B., G. Åberg, L. Werdelin, P. Forey and S. E. Bendix-Almgren. $^{87}\text{Sr}/^{86}\text{Sr}$, Na, F, Sr, and La in skeletal fish debris as a measure of the paleosalinity of fossil-fish habitats. *Geological Society of America Bulletin* 103:789-794.
- Traquair, R. H. 1898. Report on fossil fishes. Summary of progress of the Geological Survey of the United Kingdom, *Memoirs*, 1897:72–76.
- Voichyshyn, V. 2006. New osteostracans from the Lower Devonian terrigenous deposits of Podolia, Ukraine. *Palaeontologica Polonica* 51:131-142.

Voichyshyn, V. 2011. The Early Devonian armoured agnathans of Podolia, Ukraine. *Palaeontologia Polonica* 66:1-211.

Wängsjö, G. 1952. The Downtonian and Devonian Vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen Cephalaspids. Results of Th.Vogt's Expedition 1928 and the English-Norwegian-Swedish Expedition 1939. *Norsk Polarinstitutts Skrifter* 97:1-611.

White, E. I. 1932. Note on new discoveries of Lower Old Red Sandstone vertebrates in Herefordshire. *Transactions of the Woolhope Naturalists' Field Club* 179-191pp.

White, E. I. 1935. The Ostracoderm *Pteraspis* Kner and the relationships of the agnathous vertebrates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 225:381-457.

White, E. I. 1958. On *Cephalaspis lyelli* Agassiz. *Palaeontology* 1:99-105.

White, E. I. and H. A. Toombs. 1983. The Cephalaspids from the Dittonian section at Cwm Mill, near Abergavenny, Gwent. *Bulletin of the British Museum, Natural History. Geology* 37:149-171.

Woodward, H. 1881. Note on the fine headshield of *Zenaspis* (*Cephalaspis*) *salweyi*, Egerton sp. = *Cephalaspis asterolepis* (Harley). *Geological Magazine* 8:193-194.

FIGURE 1. Dimensions of an osteostracan headshield that were collected in order to quantitatively characterize specimens. [planned for column width]

FIGURE 2. *Zenaspis waynensis* sp. nov. **A.** NHM P24940; **B.** P23832; **C.** Interpretation of P24940. To scale (20mm) except **C.** **Abbreviations**—**cp**, cornual process; **cr** circumorbital raised rim; **hd** hypophysial division of nasohypophysial opening; **lf**, lateral field; **mf**, median field; **mr**, median ridge; **nd**, nasal division of nasohypophysial opening; **o**, orbit; **pf**, paired pectoral fin; **pp**, pineal plate; **t**, tessera. [planned for page width]

FIGURE 3. *Diademaspis janvieri* sp. nov. **A.** NHM P20005; **B.** P16602; **C.** P24941; **D.** Interpretation of P24941. To scale (20mm) except **D.** **Abbreviations**—as for figure 2. [planned for two thirds page width]

FIGURE 4. *Janaspis newtonensis* sp. nov. and *Pattenaspis whitei*. **A.** *J. newtonensis* NHM P17488; **B.** Interpretation of P17488; **C.** *P. whitei*, interpretation of P19198; **D.** *P. whitei*

P19198; **E.** *P. whitei* P16310. To scale (20mm) except B, C. **Abbreviations**—as for figure 2.
[planned for page width]

FIGURE 5. *Janaspis punctata* sp. nov. **A.** NHM P20004; **B.** P24924; **C.** P16606; **D.** P24935; **E.** P24920; **F** Interpretation of . To scale (20mm) except F. **Abbreviations**—as for figure 2.
[planned for page width]

FIGURE 6. Cornuata gen. indet. sp. A and sp. B. **A.** sp. A NHM P19299; **B.** sp. B. P24922; **C.** Interpretation of P19299; **D.** Interpretation of PP24922. To scale (20mm) except C, D. **Abbreviations**—as for figure 2. [planned for two thirds page width]

FIGURE 7. Reconstructions of the headshields of the Wayne Herbert osteostracan fauna. To scale (20mm). [planned for page width]

FIGURE 8. Growth stages of headshield tesserae of three osteostracan species: **A.** *Superciliaspis gabrielsei* reproduced from Hawthorn et al. (2008), with ossification of primordial tubercle followed by rings of tubercles and bones around; **B.** Cornuata gen. indet. sp. B, from simplest discernable unit of a tesserae plate with undifferentiated tubercles, followed by centrifugal addition of up to 30 tuberculated ‘rings’ of bone; **C.** *Diademaspis janvieri* sp. nov. from simplest discernable unit of individual large tubercles followed by fusion of up to 7 central tubercles surrounded by rings and then either individual tesserae fusing together by addition of tuberculated rings of bone enclosing the two separate units or growing as individual abutting units via marginal addition of tuberculated ‘rings’. [planned for two thirds page width]

FIGURE 9. Reconstruction of *Diademaspis janvieri* sp. nov. [planned for column width]

Dimensions of an osteostracan headshield that were collected in order to quantitatively characterize specimens.
90x54mm (300 x 300 DPI)

Zenaspis waynensis sp. nov. A. NHM P24940; B. P23832; C. Interpretation of P24940. To scale (20mm) except C. Abbreviations—cp, cornual process; cr circumorbital raised rim; hd hypophysial division of nasohypophysial opening; lf, lateral field; mf, median field; mr, median ridge; nd, nasal division of nasohypophysial opening; o, orbit; pf, paired pectoral fin; pp, pineal plate; t, tessera.
182x124mm (300 x 300 DPI)

Diademaspis janvieri sp. nov. A. NHM P20005; B. P16602; C. P24941; D. Interpretation of P24941. To scale (20mm) except D. Abbreviations—as for figure 2. 120x127mm (300 x 300 DPI)

Janaspis newtonensis sp. nov. and Pattenaspis whitei. A. J. newtonensis NHM P17488; B. Interpretation of P17488; C. P. whitei, interpretation of P19198; D. P. whitei P19198; E. P. whitei P16310. To scale (20mm) except B, C. Abbreviations—as for figure 2.
182x136mm (300 x 300 DPI)

Cornuata gen. indet. sp. A and sp. B. A. sp. A NHM P19299; B. sp. B. P24922; C. Interpretation of P19299; D. Interpretation of PP24922. To scale (20mm) except C, D. 122x107mm (300 x 300 DPI)

Reconstructions of the headshields of the Wayne Herbert osteostracan fauna. To scale (20mm).
182x178mm (300 x 300 DPI)

Growth stages of headshield tesserae of three osteostracan species: A. *Superciliaspis gabrielsei* reproduced from Hawthorn et al. (2008), with ossification of primordial tubercle followed by rings of tubercles and bones around; B. *Cornuata* gen. indet. sp. B, from simplest discernible unit of a tesserae plate with undifferentiated tubercles, followed by centrifugal addition of up to 30 tuberculated 'rings' of bone; C. *Diademaspis janvieri* sp. nov. from simplest discernible unit of individual large tubercles followed by fusion of up to 7 central tubercles surrounded by rings and then either individual tesserae fusing together by addition of tuberculated rings of bone enclosing the two separate units or growing as individual abutting units via marginal addition of tuberculated 'rings'.

122x110mm (300 x 300 DPI)

Reconstruction of *Diademaspis janvieri* sp. nov.
90x99mm (300 x 300 DPI)

APPENDIX 1. Character suites defining morphogroups of the Wayne Herbert osteostracan fauna.

	Morphogroup and subsequent taxonomic assignment						
	A	B	C	D	E	F	G
	<i>Zenaspis</i>	<i>Diademaspis</i>	<i>Janaspis</i>	<i>Janaspis</i>	<i>Pattenaspis</i>	Cornuata	Cornuata
	<i>waynensis</i>	<i>janvieri</i> sp.	<i>newtonensis</i>	<i>punctata</i> gen.	<i>whitei</i>	gen. indet.	gen. indet.
	sp. nov.	nov.	gen. et sp.	et sp. nov.		sp. A	sp. B
			nov.				
Shield midline length/max width	92-95%	96-100%	82-87%	70-76%	67-78%	>88%	72%
Pre pineal length	49 – 51%	50%	42%	42-45%	47-48%	>49%	49%
Circumorbital raised rims	Narrow	Thick	Narrow	Narrow	Narrow	Absent	Absent
Hypophysial expansion	Present	Pronounced	Present	Present	Present	Present	Present
Median field W/L	59%	58%	36%	37-45%	40-59%	48%	?
Median field shape	Short and broad, tapering anteriorly	Short and broad, tapering anteriorly for much if its length	Elongate with linear straight margins	Narrow anteriorly broadening posteriorly	Long and broad with an octagonal outline	Long and broad with parallel lateral margins and tapered posterior	?
Lateral field shape	Narrow, broadening posteriorly	Narrow, broadening posteriorly	Fairly broad, anterior half of field tapers anteriorly	Broad, with slightly tapered anterior terminus	Fairly broad with pointed posterior margins	Broad and short	?
Lateral Field extent over cornual processes	15%	10%	26%	18-22%	25-28%	0%	?
Cornual process length/max shield length	33%	37%	34%	32-40%	37-41%	22%	32%
Cornual process shape	Robust and posteriorly projected,	Robust and posteriorly projected,	Posterolaterally projected. Maximum	Posterolaterally projected and curving	Posterolaterally projected and curving	Gracile and short	Extremely robust, projecting

		max. width	curving	width at tips	medially.	medially.		posterolateral
		just below	medially.	of cornual	Max length	Max length		ly and
		level of the	Max. width	processes.	measure mid	measure mid		slightly
		pectoral	just below		length of the	length of the		curving
		sinuses	level of the		cornual	cornual		medially at
			pectoral		processes.	processes.		their tips
			sinuses					
	Pectoral sinus	Narrow and	Fairly	Broad and	Broad and	Broad and	Broad and	Very broad
		deep	narrow and	deep	deep	deep	shallow	and deep
			deep					
	Dorsal median	Low	Low	Prominent	?	Low	?	?
	ridge			dorsal				
				median spine				
	Ornamentation	Closely set	Each tessera	Tesserae	Tesserae of	Tesserae	?	Tesserae
	of shield	minute	exhibits 1-7	exhibit a	the	display 7-10		display up to
	tesserae	tubercles	large	broad, low	headshield	large		30 rows of
		with granular	tubercles	relief raised	covered by	rounded		tubercles
		texture.	forming a	centre	minute,	tubercles		surrounding
			central island	overprinted	closely set	surround a		a granular
			surrounded	by minute	tubercles	similar sized		centre
			by 2-3 rows	tubercles.	which	- slightly		
			of smaller		overprint 7-	larger central		
			tubercles		10 large	tubercle		
					obtuse and			
					evenly			
					spaced			
					tubercles			
	Ornamentation	Elongate	Irregular	Up to 13	Up to 13	?	?	Ornamentati
	of ventral rim	tubercles	rows of	distinct	irregular			on similar to
		surrounded	elongate	parallel rows	rows of pits			the dorsal
		by pitted	tubercles	of tiny pits	which			shield.
		borders,	approximatel		approximatel			
		increasing in	y following		y follow the			
		size	the shield		margin of the			
		proximodista	margin		shield			
		lly and						
		arranged in						
		up to 10						
		rows, slightly						
		discordant						
		with the						
		margin of the						

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
50
51
52
53
54
55
56
57
58
59
60

headshield

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
50
51
52
53
54
55
56
57
58
59
60