PAGEA STURROCKI GEN. ET SP. NOV., A NEW EURYPTERID FROM THE OLD RED SANDSTONE OF SCOTLAND

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ABSTRACT. Pagea sturrocki gen. et sp. nov., a new styloleonurid eurypterid from the Lower Old Red Sandstone of Angus, is described. The genus is characterized by the possession of eutoptus type prosomal appendages, but other features of the prosoma resemble those of Styloleonurus s. s. The affinities of the new genus are fully discussed and its anatomy compared with that of other styloleonid genera. Finer characters of the anatomy of the prosoma and prosomal appendages of Scottish type material of Styloleonurus s. s. and Cienopterus are described for the first time.

Among a collection of Old Red Sandstone fossils, generously presented to the Royal Scottish Museum by the Dundee Naturalists' Society, there is a magnificent styloleonid eurypterid, in a remarkably good state of preservation, which is the subject of the present paper. Unfortunately the circumstances under which this specimen was acquired by the Dundee Naturalists' Society are not known and so its provenance is incomplete. It is clear, however, that the large flagstone block, in which the specimen is preserved, was derived from the Lower Old Red Sandstone of Angus, and the lithology and mode of preservation would suggest that it comes from one of the quarries in the Carmyllie Group (Hickling 1908). Before reaching the museum the specimen had been rather ill-advisedly 'developed' as a result of which details of parts of the prosoma and prosomal appendages have been lost. It is probable that the left extremities of the body segments, together with most of the fifth and sixth prosomal appendages of the left side, were lost with the counterpart which has not been traced. With these exceptions, however, the specimen presents us with one of the most complete and one of the largest members of the Styloleonidae, and a notable addition to the fauna of the Scottish Old Red Sandstone.

Many years have passed since the classic descriptions of Scottish styloleonid material were made by David Page (1856 a, b, 1859), Henry Woodward (1864, 1865 a, b, 1866-78), and Malcolm Laurie (1892, 1893, 1899). Occasion is taken in the present paper, therefore, to redescribe and refigure certain details of the anatomy of Styloleonurus s. s. and Cienopterus made possible by a re-examination of the type material in the light of more recent work by European and American authors. This was a necessary study before affinities of the new genus could be properly determined.

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SYSTEMATIC DESCRIPTION

Genus Pagea nov.

Diagnosis. Large styloleonid eurypterid. Third and fourth prosomal appendages bearing a double row of numerous flat spines, fifth and sixth prosomal appendages simple, keeled, tapering; sixth appendage reaching as far as the pretelson. Shape of prosoma probably subrectangular, lateral eyes in the anterior half of the prosoma, subcentral.

Ventral marginal rim of prosomal doublure broad, crossed anterior to the lateral eyes by the epistomial sutures which converge posteriorly between the eyes; breadth of epistomial plate greater than its length, transverse line of doublure parallel with anterior margin of prosoma. Anterior margin of prosoma straight, uncrenulated. Metastoma narrow in relation to the width of the prosoma, its length being over twice its breadth, anterior notch fairly shallow. Abdomen slender with lateral epimera on the post-abdominal segments, axial furrows present on all abdominal segments. Telson long, styliform, keeled.

Genotype. Paeo sturrocki gen. et sp. nov.

Description of holotype. The prosoma. The specimen is seen in dorsal aspect but the dorsal surface of the prosoma is not preserved, the only dorsal character which can be seen being the mounds of the palpbral lobes of the lateral eyes. These are circular and have a subcentral position but are in the anterior half of the prosoma. Each eye is slightly nearer the median axis of the specimen than to the nearest portion of the lateral margin of the prosoma. It is probable that the axes of the lateral eyes are subparallel. The anterior part of the prosomal doublure is well preserved, although the lateral portions are not present. The almost straight, uncrenulated, anterior edge, passing gradually into curved antero-lateral angles, suggests that the shape of the prosoma was subrectangular. There is a broad marginal rim. The epistomial sutures (text-fig. 1) are well preserved and define a trapezoid epistomial plate in which the greatest lateral dimension is at the anterior margin and is approximately two and a half times the length of the plate measured along the median axis. The transverse line (tr.1) of the doublure is parallel with the anterior margin. A median keel (m.k.) is present. Antelateral sutures do not appear to be present. In order to establish the characters of the metastomal plate (mts.) part of the costa of the right sixth appendage, which obscured it, was

EXPLANATION OF PLATE 20

Figs. 1–2. Paeo sturrocki gen. et sp. nov. 1, The holotype (R.S.M. 1956.14.11), Lower Old Red Sandstone, Angus, Scotland, × $\frac{1}{2}$, the fifth prosomal appendage having been removed to reveal the fourth appendage. 2, The right prosomal appendages of the same, × $\frac{1}{2}$, showing the fifth appendage in position.

Fig. 3. Ctenopterus elegans (Laurie). The holotype (R.S.M. 1897.32.66), Gala-Tarannon, Gutterford Burn, Pendand Hills, Midlothian, × $\frac{1}{2}$, left side of prosoma showing metastoma and prosomal doublure.
removed. The metastoma is coffin-shaped, being broadest one-quarter of its length from the anterior. The angles are rounded, and there is a shallow anterior notch. The length of the metastoma is more than twice its greatest breadth. The anterior part bears a sub-squamate pattern and a median keel extends over the central half of the plate.

*The proximal appendages.* The fourth, fifth, and sixth appendages of the right side are preserved in their entirety. The fifth appendage is crossed over the fourth and part of the
former was temporarily removed to exhibit the complete fourth appendage at a lower level in the matrix. The coxa of the third and part of the coxa of the second appendages of the right side are also seen. There has been some displacement between the coxae of the fourth and fifth appendages. On the left side four joints of the fourth appendage are present but parts of two joints only of the fifth and sixth appendages are seen. The fifth prosonal appendage is 1.7 times the length of the fourth, and the sixth is 1.3 times the length of the fifth. The fourth appendage has six joints as well as the coxa, the proximal five of which bear spines. The spines on the second, third, and fourth joints are borne in two rows of four spines, the length of the spines increasing towards the distal end of each joint. The longest spines of each joint increase in length from second to third and from third to fourth joint. The spines are flattened and striated. The penultimate joint bears fewer spines than the joints proximal to it and the ultimate joint of the fourth appendage appears to take the form of a spine of similar type to those borne on the other joints. The fifth prosonal appendage is composed of eight joints due to the presence of a double trochanter. This appendage does not bear spines but is keeled and tapers distally. The sixth appendage is similar to the fifth, being free of spines, keeled, and tapering distally. It is unusual, however, in being composed of nine joints, there being a double trochanter and an extra joint between the trochanter and the pre-femur. The sixth appendage reaches posteriorly to the level of the pretelson.

The abdomen. The posterior five pre-abdominal tergites are seen in dorsal view, the first two not having been preserved. In the case of four of the tergites the doublures are well seen. The right lateral margins of the posterior three tergites are the only ones preserved, all the other margins having been lost through breakage. Such evidence as is provided by the margins present, however, would suggest that the posterior part of the pre-abdomen gradually tapers posteriorly. The segments are relatively narrow compared to their length. The posterior pre-abdominal segment appears to be longer than the others, and its post-lateral angles are produced into an acute form if not quite an epimer. The pre-abdominal segments bear distinct axial furrows dividing the tergites into axial and pleural portions. The axial furrows are placed slightly closer together as tergite succeeds tergite posteriorly. The reconstruction (text-fig. 2a) shows a simple axial portion of the pre-abdomen. It is possible, however, that the axis may have been formed of two lobes divided by a median furrow and that none of the left pleural parts of the tergites remain on the holotype. If this were the case, the reconstructed width of the pre-abdominal tergites would be increased by approximately one-third over that shown in the text-figure. Ventral structures of the abdomen are not seen, thus the nature of the operculum and median abdominal appendage remains unknown.

All five postabdominal segments are preserved, but the margins of the fifth only are complete. The right margins of the third and fourth are present but other margins are lost due to breakage. From the evidence of the third and fourth postabdominal segments it is clear that the first four segments of the postabdomen bore small epimerae. Like the pre-abdominal segments they are narrow in comparison with their length. The pretelson is remarkably specialized. It is between three and four times the length of the other postabdominal segments and has a barrel-shaped outline, the lateral margins being regularly curved and the greatest width of the segment being midway along its length. Posteriorly the curves of the margins converge without interruption to form the
outer margins of the broad epimeral angles. As with the pre-abdominal tergites, the postabdominal segments bear axial furrows which, on the first four segments, converge slightly posteriorly, from segment to segment. On the pretelson, however, the axial portion is waisted and the pleural parts barrel-shaped, the axial furrows curving regularly in the opposite sense to the margins of the segment. The entire abdomen is ornamented with a fine granulation.

The telson is long and styliform. The axial ridge is continued on the telson, the furrows being straight and converging posteriorly to meet at the posterior tip of the telson. The ridge has more the nature of a keel in its posterior third.

Measurements of the holotype. Probable length of prosoma 120 mm., probable breadth of prosoma 120 mm. Length of metastoma 62 mm., maximum breadth of metastoma 31 mm. Distance from anterior margin to lateral eyes 43 mm., distance between lateral eyes 33 mm. Greatest distance between epistomal sutures 70 mm.

Measurements of fourth prosomal appendage: trochanter 22 mm.; femur 32 mm.; patella 32 mm.; tibia 22 mm.; tarsus 20 mm.; pretarsus 20 mm.

Measurements of fifth prosomal appendage: trochanter 1, 23 mm.; trochanter 2, 11 mm.; prefemur 32 mm.; femur 53 mm.; patella 51 mm.; tibia 37 mm.; tarsus 25 mm.; pretarsus 25 mm.

Measurements of sixth prosomal appendage: trochanter 1, 17 mm.; trochanter 2, 15 mm.; prefemur 1, 17 mm.; femur 2, 41 mm.; femur 27 mm.; patella 48 mm.; tibia 57 mm.; tarsus 42 mm.; pretarsus 25 mm.

Measurements of the pre-abdomen: 7th and 8th segments not known. 9th, length 25 mm.; 10th, length 25 mm.; 11th, length 29 mm., restored maximum breadth based on measurement of complete right side of tergite 84 mm.; 12th, length 27 mm., restored maximum breadth 80 mm.; 13th, length 39 mm., restored maximum breadth 66 mm.

Measurements of the postabdomen: 14th, length 24 mm.; 15th, length 25 mm.; 16th, length 27 mm., restored maximum breadth 60 mm.; 17th, length 22 mm., restored maximum breadth 56 mm. Length of pretelson 47 mm., maximum breadth 65 mm. Length of telson 141 mm.

The restoration (text-fig. 2a and b) follows directly from the observed characters of the holotype (text-fig. 1) except for the form of the prosoma, the nature of the chelicerae, and the third prosomal appendage. Because of the similarity of the observed anterior portion of the prosoma to that of Styloponus powriei Page, and because the form of the prosoma in S. powriei appears to agree with that suggested by the ventral configuration of P. sturrocki, a prosomal outline closely approximating to that of the Scottish Lower Old Red Sandstone form S. powriei has been adopted in the restoration. The third prosomal appendage has been drawn like the observed fourth appendage since the three posterior walking legs of the new eurypterid closely resemble those of Ctenopterus, a genus to which it appears to be related, and it is assumed that, as in Ctenopterus, the third and fourth prosomal appendages would be similarly spinose. The chelicerae (text-fig. 2b) have been reconstructed as fairly broad, a character which appears to be common to stylophonid eurypterids and described in such forms as Ctenopterus excelsior (Hall) (in Hall and Clarke 1888) and Brachyopterus pentagonalis (Stormer) (in Stormer 1934).

AFFINITIES

The morphological features of Pugea sturrocki make it clear that the new Scottish eurypterid is a member of the Family Stylophonidae of Diener 1924 as emended by Stormer (1931, p. 413). It shows a curious mixture of characters usually associated with the genera Styloponus s.s. and Ctenopterus in addition to which there are features, such
TEXT-FIG. 2. Pagea xitrooki gen. et sp. nov., diagrammatic reconstructions. A, Dorsal view, × ¼, B, Ventral view of the prosoma and proximal portions of the prosomal appendages, × ½.
as the marked trilobation of the abdomen and the extraordinary enlargement of the pretelson which are specializations not seen to the same degree in either of these genera.

Affinities with Ctenopterus Clarke and Ruedemann 1912. The prosomal appendages of Pagea starrocki are similar to those of Ctenopterus in having a double row of flat spines on the fourth, and presumably the third, appendages while the fifth and sixth are long, keeled, and without spines. The best-known species of Ctenopterus is the genotype C. cestrotus (Clarke) from the Shawangunk Grit, Middle Silurian, of Otisville, New York State. The joints of the third and fourth appendage of this species bear between six and nine pairs of spines which are of approximately equal length. Clarke was able to develop the underside of one of the two known specimens of C. excelsior (Hall) from the Catskill Group, to reveal the cheleeca and second appendage of the prosoma which bore paired spines, but, as noted by Clarke and Ruedemann (1912, p. 292), in Beecher's famous restoration of this gigantic eurypterid (1900, pl. 1), as in their own restoration of it (1912, p. 47), the paired spines shown on the third and fourth appendages were restored after C. cestrotus and have never been seen in C. excelsior. It is in the Scottish species C. elegans (Laurie) from the Gala-Tarannan Beds of the Pentland Hills, however, that the appendages of P. starrocki can be most closely matched. Although the increase in the size of the spines distally on each joint, shown by Pagea, is not so well seen in C. elegans, the spines on the distal joints of the third and fourth appendages of that species certainly do show an increase in size as in Pagea. The spines are also similarly striated.

While the appendages of P. starrocki are similar to those of Ctenopterus, the prosomal characters differ. In Pagea the axes of the lateral eyes appear to be almost parallel, in contrast to the axes in Ctenopterus which converge anteriorly. The shape of the prosoma in Ctenopterus, where it is known, as in C. cestrotus, C. elegans, and C. excelsior, narrows anteriorly, the greatest width being in the posterior half. Unlike the strongly curved anterior margin of Ctenopterus, Pagea has an almost straight anterior margin. In dealing with the restoration of Pagea, reasons have been given for supposing that the shape of the prosoma was probably similar to that of S. powiei. Although likely, however, this cannot be proved until more specimens come to hand, but a comparison of the prosomal doublure in Pagea and Ctenopterus reveals a distinction. Clarke and Ruedemann (1912, p. 289) state that the prosomal doublure (= ventral marginal rim, see Stormer 1934, p. 22) of C. cestrotus is broad and thick and widest along the frontal margin where it exhibits a deep concentric furrow. An unsatisfactory picture is given (pl. 49, fig. 2) in illustration of this description. In the original illustration of C. excelsior (Hall 1888, pl. 26) one of the epistomal sutures is indicated. Otherwise the nature of the ctenopterid doublure appears to be unknown. Re-examination of the type material of C. elegans (Laurie), a species which Clarke and Ruedemann regarded as typical of their genus Ctenopterus, has provided further evidence of the ventral structures of the prosoma of that genus.

Laurie's description of Ctenopterus elegans (1899, p. 580) was based on five specimens which he regarded with certainty as belonging to this species. Of these, two appear to be the right and left sides of the same specimen and are now mounted together (R.S.M. 1897.32.66) and were figured by Laurie as figures 13 and 19. A third (R.S.M. 1897.32.190) was figured (fig. 14) and shows the dorsal aspect of the anterior part of the prosoma and clearly demonstrates the convergence of the margins of the prosoma towards the anterior.
The other two specimens used by Laurie, but not figured by him, are R.S.M. 1897.32.67 and 1897.32.66A. Re-examination of the figured specimens has made possible a restoration of the prosoma in ventral and dorsal aspect (text-fig. 3a and b). In the restoration the shape of the prosoma has been taken from 1897.32.66, the largest specimen, in which the outline is preserved on the left half where the margin is complete except for a portion at the median part of the anterior. This part was restored from 1897.32.190 in which the anterior is complete. The dorsal structures are drawn from 1897.32.190, but

TEXT-FIG. 3. Ctenopterus elegant (Laurie), diagrammatic reconstructions based on the holotype (R.S.M. 1897.32.66), also R.S.M. 1897.32.190, both from the Gala-Tarannon of the Grattenford Barn, Pentland Hills, Midlothian. A, Ventral view of the prosoma and prosomal appendages of the right side, showing form of the prosomal doublure and metastoma, ×4. B, Dorsal view of the prosoma, ×4. r.f. = rostral field, tr.l. = transverse line, e.p.s. = epistomial suture, l.s. = lateral shield of doublure, mts. = metastoma, m.o. = median ocella, l.e. = lateral eye.

the position of the lateral eyes is also seen in 1897.32.66 from which the ventral structures were drawn. The prosomal doublure is well shown in 1897.32.66 in which part of the left half of the epistoma, the left epistomial suture and the left lateral shield are preserved. The doublure is deep anteriorly, restoration indicating that the epistoma, at its greatest width, is approximately twice as broad as it is long, measured in the median line. The greatest width of the plate lies approximately at the mid point. The epistoma is crossed by an arcuate transverse line defining a rather large rostral field. The absence of the median part of the anterior of the specimen makes it impossible to say whether or not a median keel is present. A crenulated border is present which is deepest anteriorly and
narrates laterally. The lateral shields of the doublure are narrow, the inner margins

tending to follow the outline of the prosoma, but converging towards it posteriorly.
No antelateral suture is indicated.

The characters of the prosomal doublure as shown by C. elegans differ markedly
from those of Pagea sturrocki. The difference in the outline of the prosoma is reflected
in a different shape of cepstral plate which in Pagea is relatively broader than in
Ctenopterus with the maximum width at the anterior margin of the plate instead of at
the mid point. The transverse line in Pagea is simple instead of arcuate as in Ctenopterus
elegans and the rostral field much less large.

From the left side of R.S.M. 1897.32.66 it is clear that the metastoma of Ctenopterus
is broad in relation to its length and also in relation to the width of the prosoma. The
plate is subrectangular in shape, the length being only about one and a half times the

greatest breadth. There is a shallow anterior furrow which is ornamented at the margin
by small crenulations. The antero-lateral areas of the plate are ornamented with pustules
of various sizes. At the posterior and postero-lateral parts of the plate there is an area
of centrally directed anastomosing ridges, the ridges terminating at the margins of the
plate, and anteriorly along a curved line extending from the margins of the plate about
the middle of its length posteriorly to cross the median axis one-fifth of the length of the
plate from the posterior margin. The indentation of the margin at the left postero-lateral
angle shown by Laurie (1899, fig. 13) does not exist and was due to the matrix hiding
the form of the plate at this point. Development of the plate reveals the shape as that
shown in text-fig. 3a.

The form of the metastoma in Ctenopterus elegans is therefore quite distinct from that
of Pagea in shape, in the greater relative breadth, and in the high degree of ornamentation.

Affinities with Stylonurus Page 1856. It is unfortunate that the only specimen of the
genotype Stylonurus powiei Page (R.S.M. 1891.92.101) shows only the fifth and sixth
prosomal appendages, the anterior appendages not having been preserved. The dis-
cov ery of Pagea gives rise to an interesting speculation with regard to this specimen
since it now appears quite possible that had the third and fourth appendages been pre-
served they need not have been simple as in S. logani, but could have been spinose as in
Pagea since other characters of the body, such as the shape of the prosoma and the
slight trilobation of the abdomen, are similar to the new genus.

Where the prosomal appendages of Stylonurus species are better known, as in S.
dolichopterides Stormer (1934, p. 103), S. macrophtalmus Laurie (1899, p. 579), and
S. ornatus Laurie (Lamont 1955, p. 211), it is clear that they form a graded series increas-
ing in length posteriorly, the first three pairs of walking legs bearing spines and the last
two being free of spines. Since the publication of Woodward’s reconstruction of S.
logani (1866-78, text-fig. 131) there has been some doubt as to whether the appendages
of this species conform to the general stylurid pattern, and later authors such as
Clarke and Rudefelmann (1912, pp. 278-84) have made it clear that they regarded Wood-
ward’s reconstruction, with the subequal third and fourth appendages and the much
longer but subequal fifth and sixth appendages, as being in error. Since S. logani was
one of the forms which was illustrated by Page in his first figures of the genus (1859,
p. 181, fig. 1) the present opportunity is taken to correct Woodward’s reconstruction
and confirm that the appendages of this species do conform to the general stylourid pattern.

*Stylonurus logani* is known from the holotype only of which the part in the Geological Survey Museum (GSM. 87357) and the counterpart in the Royal Scottish Museum (1891.92.33). Although the Survey specimen was figured by Woodward in his monograph (1866-78, pl. xxiv, fig. 1) it was the counterpart that he figured in his original description (1864, pl. x, fig. 1) and this specimen bears more evidence of the prosomal appendages, which in most cases have become detached from the body, than does the Survey specimen. A re-examination of the counterpart has made possible the reconstruction in dorsal aspect reproduced in text-fig. 4. This was done by making careful drawings of the legs as they appear on the specimen (text-fig. 4, III–VI) and reassembling them with the prosoma in restoration in dorsal aspect. The visual areas of the palpebral lobes of the lateral eyes are also seen clearly in this specimen and have been drawn in the reconstruction.

There is no serious exception to the generally accepted pattern of the prosomal appendages of *Stylonurus s.s.*, but it is clear also that the appendages of *Paxea*, with their many pairs of flat spines on the joints of the third and fourth appendages, are

**TEXT-FIG. 4. Stylonurus logani** Woodward, diagrammatic reconstruction of the holotype, based on the counterpart (R.S.M. 1891.92.33), dorsal view of prosoma and prosomal appendages, × 1, with drawings of the prosomal appendages as they appear on the counterpart, × 1 1/2 approx.
quite distinct from this pattern. When other prosomal characters are considered, however, a considerable degree of conformity may be noted.

The shape of the Pagea prosoma, with its almost straight anterior margin, suggests a similarity with that of Styloanus s.s. as seen in the genotype. The parallel axes of the lateral eyes which are probable in Pagea are also typical of Styloanus. Similarities are also apparent in the doublure. Størmer has described the epistomal sutures in his species S. ruedenmanni and S. dolichopteroides (1934, pp. 100 and 102). In the former the sutures cross the border at points anterior to the lateral eyes and converge posteriorly between the eyes, and in the latter they are indicated by faint crossing lines in front of each lateral eye. These features accord completely with structures seen in Pagea in which, as in the Norwegian species, the greatest width of the epistoma is at its anterior margin. The proportions of the metastoma of Pagea, and its size in relation to the length and width of the prosoma, are very close to those in Styloanus, as for example in S. ornatus Laurie (1892, pl. 1, fig. 7) and S. macrophilabbus Laurie (1899, pl. 1, fig. 4). In both these species, however, the metastoma bears a much deeper anterior notch than in Pagea.

The long, keeled styliform telson of Pagea resembles that of S. ornatus Laurie although it does not exhibit the specialization noted by Lamont (1955, p. 209) in that species. It is interesting to note also that in S. ornatus there is a distinct lengthening of the pretelson, although not to the extreme degree as in P. starrocki.

**Conclusion.** In prosomal characters such as the outline of the prosoma, the position and axes of the lateral eyes, the structure of the prosomal doublure, and the proportions of the metastoma, Pagea resembles Styloanus s.s. and differs from Ctenopterus. In the nature of the prosomal appendages, however, Pagea resembles Ctenopterus and differs from Styloanus. In the author’s opinion Pagea is more closely related to Styloanus than to Ctenopterus since the presence or absence of spines on the anterior walking legs would appear to be a more flexible taxonomic character than the prosomal characters.

**REFERENCES**


—1899. On a Silurian scorpion and some additional Eurypterid remains from the Pentland Hills. Ibid. 39, 575–90.


—1859. Ibid., 2nd edition.


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