THE TREMADOC TRILOBITE *PSEUDOKAINELLA IMPAR* (SALTER)

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ABSTRACT. Salter's species *Olenus impar*, 1866, from the Tremadoc of North Wales is referred to *Pseudokainella* and redescribed with the aid of new and better material. The record is the first for this genus in Europe. The species is compared with other records of the genus, and correlations with North and South America are discussed.

DURING current research into the trilobite faunas of the Tremadoc rocks of North Wales and Shropshire a number of specimens collected by the writer, and three others from the Geological Survey collections, have provided evidence of a new record for Europe.

A nearly complete, distorted specimen from Portmadoc (Geol. Soc. Coll. 6970) was described and figured by Salter (1866) under the name of *Olenus impar*, and it is interesting to note that he observed (1866, p. 303) a close resemblance of this species to '*Remopleurides*'. His illustration with respect to the specimen Geol. Soc. Coll. 6970 is reversed and evidently in part restored. Since then no further mention of the species has been made, even in the monographs of Lake (1906–46) and Henningsmoen (1957). The discovery of new and better material at Arenig substantiates my first suspicions arising from the study of the Geological Survey material that this is a member of the Remopleurididae, namely *Pseudokainella* Harrington, 1938.

Figured material is deposited at the Geological Survey Museum (GSM, Geol. Soc. Coll.) or at Birmingham University together with topotype material (BU).

SYSTEMATIC DESCRIPTION

Family REMOPLEURIDIDAE Hawle & Corda 1947

Remarks. The classification here adopted is that of the *Treatise on Invertebrate Paleontology Part O* (Moore 1959) except that the diagnosis of the Remopleurididae Hawle & Corda 1847 should be adapted to include the narrower thoracic doublure of *Pseudokainella*, where it extends only across the free pleural terminations. The term 'intergenal angle' used in this paper refers to the prominent angulation of the posterior cephalic margin, resulting in part from the rather forward position of the genal spines.

Subfamily RICHARDSONELLINAE Raymond 1924

Genus *Pseudokainella* Harrington 1938

Type species. Pseudokainella keideli Harrington 1938.

Remarks. A recent diagnosis of the genus has been given by Harrington and Leanza (1957). Kobayashi (1953) excludes this genus from the Richardsonellinae on the absence

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of an intergenal angle and includes it in his (new) subfamily Kainellinae. Subsequent work has however shown that this character can be present and even strongly developed, as in *P. keideli* and *P. impar*. Consequently his diagnosis of the Kainellinae, based partly on the presence of a nearly straight posterior cephalic margin (i.e. absence of intergenal angle), requires amendment. His subgenus *Parakainella* (1953, p. 43) is furthermore regarded as a subjective junior synonym for the reasons given by Harrington and Leanza (1957, p. 133).

Pseudokainella impar (Salter 1866)

Plate 75, figs. 1–8

1866 *Olenus impar* Salter, pp. 302–3, pl. 8, fig. 4.
1881 *Olenus impar* Salter, p. 496, pl. 8, fig. 4.

Holotype (by monotypy). Geol. Soc. Coll. 6970.

Other Material. GSM 70999, 71001; BU 398a and b, 399, 400.

Due to poor preservation of the holotype the following description is largely supplemented by BU 398. The material comprises one large complete specimen, one smaller disarticulated and nearly complete specimen, a number of small cranidia, and numerous isolated free cheeks and pygidia from the Arenig area; one complete specimen and two incomplete specimens (all distorted and one bearing a hypostome) from Portmadoc.

Diagnosis. A species of *Pseudokainella* with nearly parallel-sided glabella, two pairs of lateral glabellar furrows, prominent intergenal angles, and very long genal spines reaching beyond the posterior end of the pygidium; width of frontal area (tr.) about twice the posterior width (tr.) of the glabella; thorax with wide axis, and narrow doublure widening backwards; pygidium with four axial rings, margin bearing four pairs of evenly sized spines.

Description. Dorsal exoskeleton oval in outline. The cephalon is sub-semielliptical, slightly more than twice as wide as long, gently convex transversally and less so sagittally. The glabella is raised above the level of the librigenae, is gently convex, longer than wide, tapers very slightly forwards, and is very gently curved in front with rounded antero-lateral corners; it is expanded slightly opposite distal ends of posterior glabellar furrows and at occipital ring; well-defined by axial furrows which are accentuated by distortion in GSM 70999, 71001. Two pairs of lateral glabellar furrows are discontinuous across the glabella and are more or less isolated from the axial furrows by slight swellings (distortion may give the impression that they are confluent across the glabella). Anterior (2p) furrows short, faint, directed backwards and inwards in a slightly forward convex curve. Posterior (1p) furrows longer, very slightly sinuate especially in young cranidia, directed backwards at a greater angle and stronger than 2p, being deepest at their mid-length, and commence opposite mid-points of palpebral lobes. Occipital furrow wide (sag. and exsag.), relatively shallow, bending forwards at the middle and more strongly forward-outward abaxially, descending to meet the axial furrows just behind the posterior ends of the palpebral lobes; occipital ring prominent, wider than the rest of the glabella, turning forwards abaxially and well-defined laterally by an outward curve of the axial furrows.

Fixigenae much reduced; palpebral areas very narrow (tr.), elongate-crescentic; posterior areas extremely narrow, blade-like, extending out to a distance about equal to two-thirds the width of the occipital ring; anterior areas expanded, triangular, somewhat inflated. Preglabellar area rather narrow, nearly flat, set below the level of the glabella and lateral extensions of anterior fixigenal areas; it is bounded anteriorly by the wider (sag. and exsag.), gently convex, forward-curved anterior border which narrows abaxially, and by the anterior border furrow which carries a row of small pits. Palpebral lobes moderately large, narrow, crescentic, raised well above level of cheeks abaxially; situated slightly behind the mid-line (tr.) of the glabella and closer to it in front than behind; they extend from opposite outer ends of 2p furrows to just in front of occipital furrow. Palpebral furrows prominent but fairly shallow; visual surfaces of eyes not preserved. Librigenae are gently convex with moderately wide lateral borders which extend into strong spines without angular deviation from the general curvature of the cephalic border; genal spines reach back beyond the posterior margin of the pygidium in a gentle outwards curve; the lateral border furrows are wide and shallow. The posterior cephalic border, at first directed slightly backwards, widens rapidly and then turns sharply forwards through about 80° to form a prominent intergenal angle, finally becoming narrower towards the genal angles. The intergenal angles encroach strongly across the first and part of the second thoracic segments. The posterior border furrow is flat and wide, commencing opposite the middle of the occipital ring; it more or less follows the curve of the posterior border but bends through only 45°; its confluence with the lateral border furrow is usually obtuse (but see below). Inner spine angle (see Henningsmoen 1957, p. 13) acute, about 45°.

Sutural pattern kainelliform. Anterior sections of facial suture are short and strongly divergent forwards with an angle of 145° between them; after turning abruptly around the anterior border they become marginal and meet axially, continuing across the doublure as a median suture. The anterior sections reach the axial furrow immediately in front of the palpebral lobes. The posterior sections, which do not quite reach the axial furrow, turn sharply backwards and outwards behind the palpebral lobes and curve gently back to cut the posterior border of the cephalon just inside the intergenal angle.

The hypostome, previously unrecorded, shows a typical Apatokephalid form, though it is rather elongated by distortion. The general outline is ovate (probably originally more or less oval) with length greater than breadth; the frontal margin is well rounded and probably has a narrow, flat anterior border. A slight posterior increase in breadth

EXPLANATION OF PLATE 75

Figs. 1–8. *Pseudokainella impar* (Salter). 1, Holotype, Geol. Soc. Coll. 6970, ×2½; Tremadoc (? Portmadoc Flags), Pen-y-clogwyn, Portmadoc, Caernarvonshire. G.R.56553830. Figured and partly restored by Salter. 2, Hypostome, excavated and enlarged from fig. 3, GSM 71001, ×4; Tremadoc Slates, Portmadoc. 3, Cranidium, hypostome, and part of thorax, GSM 71001, ×2½; Locality as for fig. 2. 4, Attached librigena showing genal caeca and reticulate ornament, BU 399, ×2½; Upper Tremadoc, *Shumardia* Beds, Ceunant-y-garreg-ddu, Arenig. G.R.82153603. 5, Small uncrushed cranidium showing anterior border pits, BU 400, ×4; Upper Tremadoc, *Shumardia* Beds, stream section near Amnodd Bwll, Arenig. G.R.80753690. 6, Damaged cranidium and part of thorax (note effect of deformation on glabellar furrows), GSM 70999, ×2½; locality as for fig. 2. 7, 8, Internal mould (BU 398a) and latex cast of counterpart (BU 398b) respectively, both ×1½; Upper Tremadoc, *Shumardia* Beds, locality as for fig. 5.

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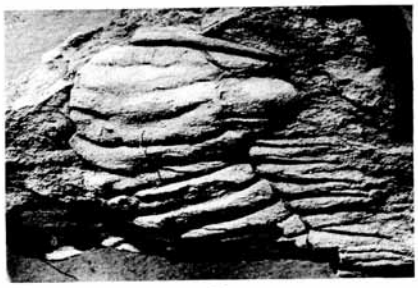

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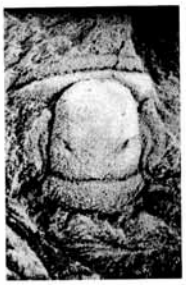

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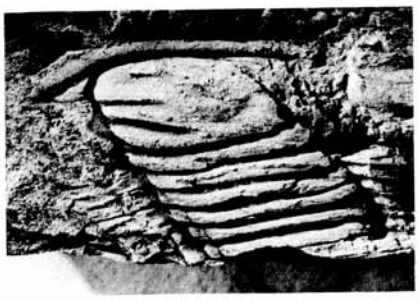

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WHITWORTH, Tremadoc trilobite *Pseudokainella*

coincides with a widening of the lateral border. Anterior wings if present are not preserved. The middle body is strongly convex, reaching a maximum in front of centre; it is oval and bounded laterally by a deep border furrow which continues around the posterior margin. Maculae appear to be absent, and a posterior body is not defined (except by a lowering of convexity which may be due to crushing). The lateral border furrow becomes deep postero-laterally where the border is slightly expanded and upward-turned. The posterior furrow is much narrower and shallower, defining a rounded margin to the posterior lobe and a gently convex posterior border.

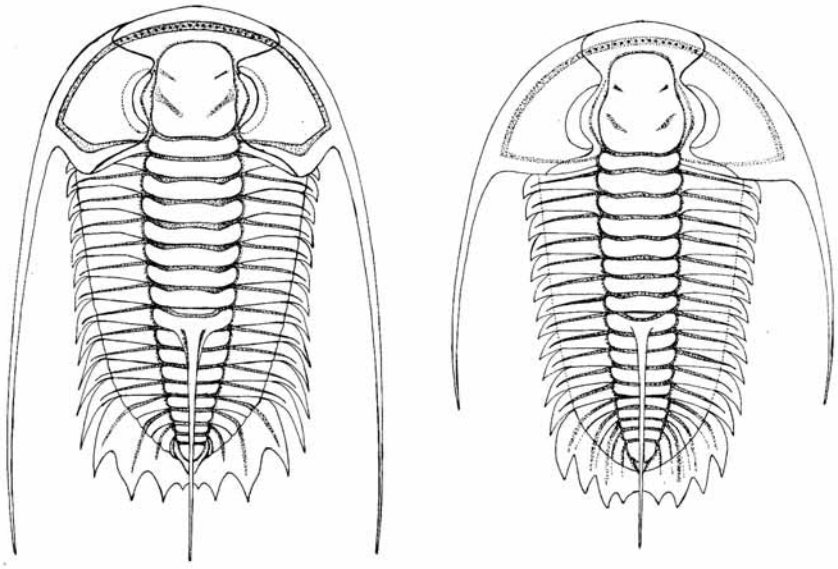
The cephalic doublure and dorsal surface of the cephalic border are ornamented with some 9 or 10 well-spaced terrace lines, and the glabella, librigenae, and anterior areas of the fixigenae have a close-set reticulate ornament.

The specimen from Ceunant-y-garreg-ddu (BU 399) shows two features not seen on the other material. The first is the angle of intersection of the lateral border- and posterior border-furrows which, normally rather obtuse, is here acute and directed strongly backwards and outwards in a point. The second is the presence of a strong caecal ridge on the librigena; this commences opposite the mid-point of the palpebral lobe and crosses the librigena obliquely backwards and outwards at an angle of 40° with the axial normal; at a position level with the posterior end of the palpebral lobe it turns abruptly outwards and runs directly towards the genal angle, dying out before reaching the same. These features could prove to be of varietal significance, but further material is required before more definite conclusions can be reached.

Thorax of 12 segments. Axis wider than the pleurae for the first 8 segments, then becomes increasingly narrower than the pleurae; it is moderately convex and raised well above the pleural regions. The first axial segment is slightly wider (tr.) than the occipital ring, and the second slightly wider again, thereafter each becoming successively smaller. Axial rings are straight medially but bend forwards abaxially and form vaguely defined marginal lobes; ring furrows are wide axially where they bend forwards, but laterally they become narrower and deeper as they curve forwards to meet the axial furrows. Articulating half-rings are well developed. Axial furrows are strong and slightly outwards curved around the abaxial ends of each axial ring. 8th segment bears a broadly based median spine which extends well beyond the posterior margin of the pygidium; it appears to have a double base—the main ridge, developing from the anterior part of the axial ring, is supported by a broader triangular base which originates from the posterior part of the ring and extends back as far as the 10th segment before the two parts merge into a single spine. Pleural regions are nearly flat and of constant width (tr.); weak proximal fulcra can be made out in each of the first few anterior segments only. Each pleura is crossed by a prominent oblique pleural furrow, commencing in confluence with the axial furrow in a shallow axial socket at the anterior margin of the pleura, and reaching the inner edge of the doublure in the posterior half of the segment.

The original convexity of the exoskeleton seems to have been rather low and the shell material thin. As a result a thin layer of deposit lying between the dorsal exoskeleton and the doublure remains attached to the external mould, and the pleural furrows have been impressed through it on to the doublure. This layer is present on both thorax and pygidium and is too thin and firmly attached to allow removal without damaging the underlying surface. This is why the impression of the doublure is seen on the external mould.

The pleural furrows can therefore be seen to continue into the pleural terminations in each segment. Each furrow approaches the posterior pleural border and dies out before reaching the acute, backward-pointed spinose termination. These pleural terminations become progressively longer and more spinose posteriorly, an appearance which is somewhat exaggerated by a corresponding increase in the width of the doublure with its ornament of step-like terrace lines. Each axial ring bears a reticulate ornament of Bertillon pattern as on the glabella; the wider posterior band of each pleura also has a weak reticulate ornament.



TEXT-FIG. 1. Comparative diagrams of two species of *Pseudokainella*. (*a*) *P. impar* (Salter) from BU 398. (*b*) *P. lata* (Kobayashi) after Harrington and Leanza 1957. Both ×1·4.

Pygidium sub-elliptical and twice as wide as long. Axis is convex and raised above the level of the pleural regions; it tapers gradually backwards and bears four segments plus a rounded sub-triangular terminal piece, the latter being prolonged at a lower level into a weak, flattened post-axial ridge which dies out shortly behind the anterior edge of the pygidial doublure; the abaxial terminations of the first and second rings are feebly lobate. Axial and ring furrows are straight and become weaker posteriorly. Pleural regions, unlike those of the thorax, are somewhat inflated and the pleural terminations are turned slightly upwards. Three well marked pairs of pleurae and a fourth less prominent pair close to the terminal axial segment are seen. Interpleural furrows are weaker than the oblique pleural furrows, but both curve backwards and are directed backwards at increasing angles until the fourth pair lie nearly parallel to the axis. The first two pleural furrows

extend into the marginal spines, the third is considerably shorter, and the fourth does not extend beyond the inner limit of the doublure. The pygidial margin is extended into four pairs of lateral spines which correspond with the continuations of the pleurae; they are short and triangular with wide bases, and each pair, except for the innermost which are small and tooth-like, becomes only gradually smaller adaxially. Doublure wide, reaching over half-way in towards the axis, and ornamented with terrace lines which converge and become closely crowded behind the axis.

Measurements (in mm.) of BU 398

Width of cephalon (at occipital ring)	32·0
Length of cephalon	*c.* 17·0
Width of cranidium (at eyes)	12·8
Width of glabella (at eyes)	9·0
Length of glabella (exc. occipital ring)	10·3
Width of occipital ring	9·3
Length of occipital ring (sag.)	2·8
Length of palpebral lobe	5·0
Length of thorax	*c.* 25·0
Width of thorax (anterior)	26·0
Width of thoracic axis (anterior)	10·3
Width of pygidium (anterior)	19·3
Length of pygidium (excluding spines)	8·7
Width of pygidial axis (anterior)	5·5
Length of pygidial axis	6·5

The holotype is considerably less than half the overall size of BU 398 and is too distorted to obtain reliable measurements from.

Localities. Tremadoc Slates, Portmadoc, and Pen-y-clogwyn (no other information known); *Shumardia* Beds, north bank of stream 150–60 paces upstream from east end of wall by forestry road and 200 yards NW. of Amnodd Bwll farm, G.R.80753690; *Shumardia* Beds, south bank of Ceunant-y-garreg-ddu gorge about 30 yards upstream from stone wall at bottom and 1 mile SE. of Amnodd Bwll, G.R.82153603.

Remarks. Pseudokainella impar seems to be closest to the Argentinian species *P. lata* (Kobayashi 1935) in general outline and in the characters of thorax and pygidium. It differs however in having a less constricted anterior lobe to the glabella, more strongly divergent anterior sections to the facial suture, smaller palpebral lobes which do not extend so far backwards, a weaker occipital furrow, wider posterior border furrows, and a strong intergenal angle. The thoracic axis is also wider and the reticulate ornament generally stronger. *P. keideli* Harrington 1938 is much smaller and shorter over-all. Its cephalon has larger palpebral lobes, narrower anterior glabellar lobe, shorter posterior sections to the facial suture, and more divergent genal spines. Its pygidium is shorter and has a macropleural first segment. *P. pustulosa* Harrington & Leanza 1957 is intermediate between *keideli* and *lata* and has a strong pustulose ornament.

Of the other recorded occurrences referred to this genus, *P. armatus* Hintze 1953 was believed by Ross (1957) to belong to an unnamed and 'undescribed, more primitive genus', and was later redescribed by Lochman (1964) as *Praepatokephalus armatus*. Sando's (1958) two specimens from the Stonehenge Limestone of Pennsylvania, which he tentatively compares with *P. armatus*, are, therefore, not to be included in the genus; indeed, the glabellar shape and furrows are much more reminiscent of *Apatokephalus*

s.l. than of *Pseudokainella*. Kobayashi (1960) illustrates and describes a ?new species (*sic*), but I prefer not to include this at present in *Pseudokainella* on the grounds of insufficient and fragmentary material, especially as he himself expresses doubt as to its correct assignment. *P? macarenae* (Harrington and Kay 1951) has a rather long preglabellar field bearing radiating ridges suggestive of *Kainella*, but otherwise it closely resembles *P. lata*; it has recently been placed in the new subfamily Artokephalinae by Chugaeva (1964).

Until now *Pseudokainella* has been recorded only from Argentina, Korea, Columbia, and recently North America (R. J. Ross Jr., personal communication), and the present record lends credence to the idea that it may well be, like its close relative *Kainella*, considerably more widespread than at present believed. Its presence strengthens the relationship between the *Kainella*/*Ceratopyge* faunas of South America and the *Pharostomina* fauna of Balto-Scandia (Whittington 1966). The genus occurs largely in the Lower Tremadoc of Argentina but only in the Upper Tremadoc of North Wales. This seems to indicate a temporary influx into the Welsh area late in Tremadocian times after a northward migration from South America. This migration could well have been along the North American–Balto-Scandian–Russian zone, since it is now known to occur in North America (see below). Such a migration route may perhaps be indicative of an early development of the dispersal directions indicated by Whittington (1966, text-fig. 2) for the Arenig-Llandeilo period.

R. J. Ross Jr. (personal communication) informs me that a species of *Pseudokainella* is now known to occur in Clear Creek Canyon, Monitor Range, Nevada (Lowell 1965) in association with *Hypermecaspis* and *Parabolinella*, an assemblage very reminiscent of that in both Argentina and Britain (the British species *Parabolinella rugosa* Crosfield & Skeat is thought to be a *Hypermecaspis*, see Harrington and Leanza 1957 and Henningsmoen 1957). Precise correlation of the American assemblage is not yet settled, although it 'seems to correlate with the lowest *Hystricurus–Symphysurina* assemblage further east', i.e. Utah (Ross, personal communication). Since the underlying *Saukia* Zone of North America, usually placed in the late Upper Cambrian, now seems for certain to correlate with the lower part of the Mexican Tiñu Formation (Lower Tremadocian) of Robison and Pantoja-Alor 1968, the *Symphysurina* Zone might be considered as Upper Tremadocian in age. As such it would correlate well with the British Upper Tremadocian, and if Ross's correlations are verified the mutual presence of *Pseudokainella* would support this. That the Mexican and British Tremadoc are closely equivalent can be readily seen from the presence in both areas of species of *Geragnostus*, *Asaphellus*, *Angelina*, *Bienvillia*, *Parabolinella*, *Leptoplastides*, *Peltocare*, and *Shumardia*. In addition to the presence of *Hypermecaspis* in Nevada, affinities between North America and Britain are further strengthened by the mutual association of species of *Shumardia*, *Beltella*, and *Apatokephalus*. These last all occur in the Goodwin Limestone, Pogonip Formation of Nevada (Merriam 1963, Nolan and others, 1956) and some occur in the middle part of the Garden City Formation, Utah (Ross 1951). Both may therefore be considered as equivalent to some part of the Tremadocian (the Garden City Formation in part only).

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