

A NEW PELAGIC TRILOBITE FROM THE ORDOVICIAN OF SPITSBERGEN, IRELAND, AND UTAH

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ABSTRACT. *Opipeuter inconnivus* gen. et sp. nov. is described. It is included with *Cremastoglottos* Whittard in a new family, the Opipeuteridae, which is probably closest to the Remopleurididae. It is also possible that *Opipeuter* is related to the enigmatic trilobite *Bohemilla* Barrande. The functional morphology of *Opipeuter* indicates a pelagic mode of life.

STUDY of early Ordovician trilobites from the Valhallfonna Formation, Ny Friesland, Spitsbergen, and the Tourmakeady Limestone, Co. Galway, western Ireland, revealed some fragments of a trilobite which suggested that a new and peculiar species was common to both faunas. In 1971 the discovery of an almost complete dorsal exoskeleton in Spitsbergen enabled a definite association of the known fragmentary remains. Because of its particular interest this trilobite is described and discussed separately from the rest of the systematic work on the Spitsbergen and Irish faunas. Material of the new trilobite is deposited in three institutions: Paleontologisk Museum, Oslo (PMO NF), Sedgwick Museum, Cambridge (SMA), and the British Museum (Natural History) (BM It).

The stratigraphy of the Spitsbergen Ordovician has been described by Fortey and Bruton (1973) and the stratigraphical terminology given therein is used in the present account. The material from the Tourmakeady Limestone is from pink, brecciated limestones of Gardiner and Reynolds's (1909, pl. 4) locality 58. A discussion of the stratigraphy and correlation of the rocks of this area has been given by Dewey, Rickards, and Skevington (1970).

SYSTEMATIC DESCRIPTION

Superfamily REMOPLEURIDACEA Hawle and Corda, 1847

Family OPIPEUTERIDAE fam. nov.

Type genus. *Opipeuter* gen. nov.

Diagnosis. Remopleuridacea with greatly developed, convex eyes. Glabella with sub-triangular outline, tapering strongly forward, with one or two pairs of lateral glabellar furrows, and downturned glabellar tongue anteriorly. Fixed cheeks reduced or absent, posterior border modified to a spine extending backwards behind occipital ring in *Opipeuter*. Long narrow thorax (eleven segments) with convex axis and very short pleurae. Pygidium with entire margin, axis continued into a stout spine.

Genera included in family. *Opipeuter* gen. nov., *Cremastoglottos* Whittard 1961 (known from cranidia only).

OPIPEUTER gen. nov.

Type species. Opipeuter inconnivus sp. nov.

Derivation of name. Greek, 'one who stares'.

Diagnosis. Opipeuteridae with one pair of lateral glabellar furrows. Occipital furrow with a fairly straight, transverse course. Surface sculpture of fine raised lines arranged in polygons.

Opipeuter inconnivus sp. nov.

Plates 13, 14; text-figs. 1, 3a

Derivation of name. Latin, *inconnivus*, 'unsleeping'.

Diagnosis. As for genus.

Material. Holotype. Slightly damaged dorsal exoskeleton lacking free cheeks, from the Olenidsletta Member of the Valhallfonna Formation, occurring an estimated 60 m from the base of the Member on Olenidsletta north of Papegøyeneset, PMO NF 2062. Other Spitsbergen material includes one exfoliated cranidium with a few thoracic segments attached, SMA 84010, apart from which all other material consists of isolated cranidia, free cheeks, and pygidia. Material identified so far as belonging to this species includes:

Cranidia: PMO NF 700, 875, 2982–2984, 2986, 2989, 2995–2996, 2998; BM It 9799; SMA 84011.

Pygidia: PMO NF 2987, 2993–2994, 2990, 2997; SMA 84012.

Free cheeks: PMO NF 2980–2981, 2985, 2988.

The material from western Ireland consists of three cranidia: BM It 9795–9797, and one free cheek, BM It 9798.

Material from Utah consists of a single, well preserved free cheek, BM It 10279.

Stratigraphic occurrence. In Spitsbergen the species is confined to the Olenidsletta Member of the Valhallfonna Formation, the lowest occurrence being 9 m above the base of the Member, the highest 100 m from its base. Through most of this range it can be found with careful searching, but always as a rare element of the total fauna. The material from the Tourmakeady Limestone is from Locality 58 of Gardiner and Reynolds (1909).

The free cheek from Utah is from the upper part of the Fillmore Limestone, locality H of Hintze (1953).

EXPLANATION OF PLATE 13

Opipeuter inconnivus gen. et sp. nov., Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen.

Figs. 1, 10. Free cheek ($\times 11$) in dorsal, lateral views. 8 m from base of Olenidsletta Member. Note slender genal spine. PMO NF 2981.

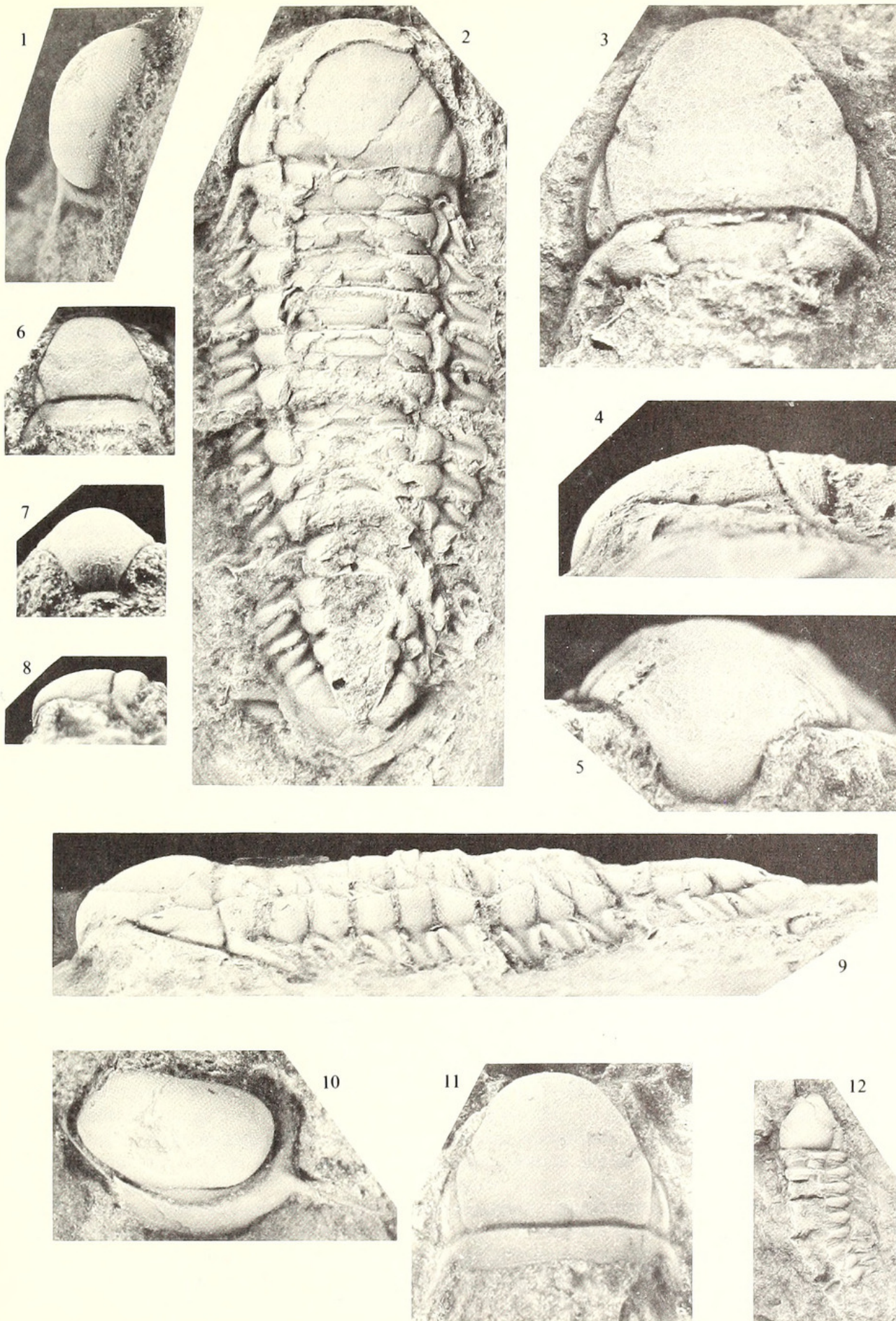
Figs. 2, 9. Holotype, dorsal exoskeleton lacking free cheeks ($\times 8$) in dorsal and left-lateral views. Olenidsletta, 60 m from base of Member. Axis of thorax and median part of cranidium are exfoliated, and the ninth thoracic segment is slightly displaced on the right-hand side. PMO NF 2062.

Figs. 3, 4, 5. Cranidium ($\times 13$), retaining exoskeleton except on mid part of occipital ring, dorsal, lateral, and anterior views. 60 m from base of Member. Note characteristic polygonal surface sculpture, palpebral lobe, and backward pointing border spine on left of specimen. PMO NF 875.

Figs. 6, 7, 8. Small cranidium ($\times 15$) in dorsal, anterior, and lateral views. Horizon as fig. 1. Note narrow, horizontal anterior border in fig. 7. PMO NF 2982.

Fig. 11. Cranidium ($\times 10$), retaining exoskeleton. 30 m from base of Member. SMA 84011.

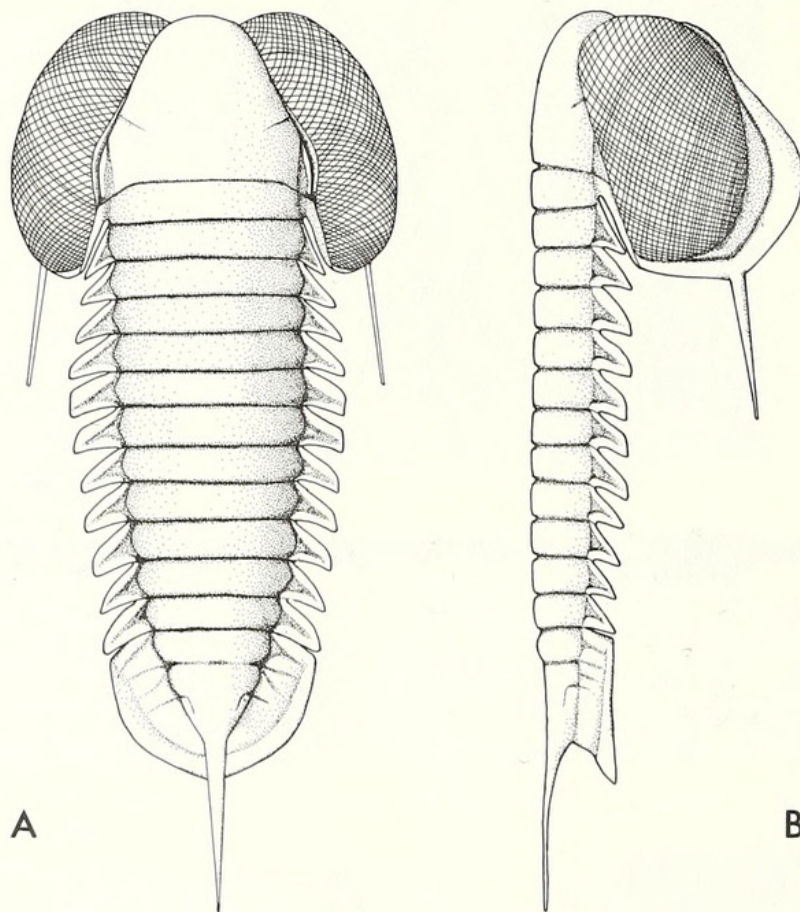
Fig. 12. Imperfectly preserved, flattened internal mould of cranidium and eight thoracic segments ($\times 2$). SMA 84010.



FORTEY, *Opipeuter*

Description. Exoskeleton fusiform, sagittal length (excluding pygidial spine) three times the transverse width across the mid part of the thorax.

Cranidium one-quarter the length of the exoskeleton, with triangular outline, transverse width across the base of the glabella equal to, or slightly exceeding sagittal length. The glabella occupies the major part of the cranidium, transversely convex, anteriorly sloping steeply downwards and slightly recurved into narrow glabellar tongue. Glabella expands in width very slightly in front of the occipital ring to a point at about half (sag.) its length, anteriorly tapering rapidly and uniformly to the anterior border, such that the transverse width at the anterior border is one-fifth the maximum width of the glabella. The one pair of lateral glabellar furrows meet the axial furrows just in front of the point of maximum width of the glabella, running inwards and backwards at an angle of between 40° and 60° to the sagittal line (angle measured from photographs of eight cranidia in dorsal view) and extending one-fifth across the glabella. The furrows are shallow on the dorsal surface of the cranidium, and on some specimens of internal moulds may not be clearly visible, particularly if some crushing has taken place. Occipital furrow narrow and deep, medially transverse, lateral extremities sloping backwards at a low angle. Occipital ring of uniform width (sag., exsag.), about one-fifth sagittal length of glabella, not clearly differentiated from the posterior border of the fixed cheek. Axial furrows shallow adjacent to the posterior part of the glabella in front of the occipital ring, deepening forwards.



TEXT-FIG. 1. Reconstruction of *Opipeuter inconnivus* gen. et sp. nov. in dorsal (A) and lateral (B) views ($\times 5$).

Fixed cheeks reduced to narrow (trans.) triangular areas adjacent to the posterior, non-tapering part of the glabella, and continuing its downward slope. On larger cranidia this triangular area almost appears to be part of the glabella, as the occipital ring extends abaxially behind it, and particularly on internal moulds the axial furrows are not deeply defined. On the smallest cranidium the extra-glabellar origin of the area is more obvious (Pl. 14, fig. 3), and the triangular area is both distinct from the glabella

and lateral to the occipital ring. Along the lateral edge of the area there is a convex ridge. The posterior border is modified to form a flat, downward sloping spine which is directed backwards behind the posterior margin of the occipital ring at an angle of 20–30° to the sagittal line, reaching as far as the second thoracic segment. Palpebral lobe very narrow, almost horizontal, and lying at a level below that of the rest of the cranium. The greatest width (trans.) of the palpebral lobe is adjacent to the anterior part of the triangular area. Posteriorly it narrows gradually towards the posterior spine; anteriorly it becomes rapidly narrow in front of the outer end of the lateral glabellar furrow, anteriorly not continuing as a distinct lobe but rather as an extremely narrow V-shaped 'gutter' as far as the anterior border. The palpebral furrow is gently bowed outwards medially, quite deep, meeting the short posterior border furrow behind the ridge bordering the triangular fixigenal area. The cranium has a narrow (sag., trans.) horizontal anterior border, rim-like, and with a convex anterior margin. This border is extremely narrow (sag.) on large crania, and difficult to prepare (the palpebral lobes may present similar problems), but one small cranium (Pl. 13, fig. 7) shows it very well. The facial suture is considered to run from the tip of the posterolateral spine inwards and forwards in an almost straight line bounding the palpebral lobe and the anterior 'gutter' as far as the anterior border.

The dorsal surface of the glabella is covered with a very distinctive surface sculpture of fine raised lines which form a polygonal pattern. The polygons tend to become stretched out transversely on the sagittal region of the preoccipital glabella and on the occipital ring. This distinctive sculpture is present on even the smallest cranium. Internal moulds are smooth.

The free cheek consists largely of very large, subglobose eye with an elliptical outline. The eye has the greatest dorsoventral length of visual surface anteriorly. The lenses are hexagonal, arranged in files (vertically) of about forty lenses. The total number of lenses on the largest eye is estimated at 2000, on an eye half the length there are an estimated 1600 lenses, so that the number of lenses does not change greatly in late growth stages. The largest individual lenses occur on the front, and towards the top of the eye. At the base of the eye, and to the rear they are closely packed and small. The base of the eye is marked by a furrow which is deeper posteriorly, faint and diffuse anteriorly. The wide and flat border has an almost semi-circular posterior outline, anteriorly curving upwards, narrowing, and becoming horizontal, rim-like. There is a slender, backward-pointing genal spine, originating from the back end of the border at a point opposite the lower edge of the posterior part of the eye. Between the lower edge of the eye and the posterolateral part of the border there is a crescentic genal area, which is depressed below the level of the rest of the cheek. The border of the free cheek carries a surface sculpture of a few fine terrace lines, running sub-parallel to its outer margin.

Thorax of eleven segments, of subequal width (sag.) along its length. Axis extremely wide (trans.) relative to the pleurae, which even at their widest are less than one-quarter the axial width; axis highly convex transversely, parallel sided anteriorly, tapering gradually for the posterior four segments. Each axial ring is similar in form to the occipital ring, band-like, of constant width (sag., exsag.). Axial furrows shallow, bowed outwards adjacent to each axial ring. Pleurae of greatest transverse width on the fourth, fifth, and sixth thoracic segments. The pleurae of the first thoracic segment are extremely narrow (trans.), pointed, triangular, with convex bands at the anterior and posterior margins. Pleural furrow of the first thoracic pleura does not reach its tip. The anterior margin directed markedly backwards, thereby allowing for the backward passage of the posterior spines of the cranium. The pleurae of the second segment are of similar form to those of the first, but transversely wider. Posteriorly the pleurae become gradually subrectangular in outline and the pleural tips are truncate. Each pleura is crossed by a diagonal pleural furrow, which is fairly deep and reaches the tip of the pleura but is shallower abaxially. Adjacent to the axis the furrow is broad, almost equal in width (exsag.) to the adjacent axial ring. Within this broad part of the furrow there is a gently inflated triangular area adjacent to the axial furrow. The articulation between segments is sub-adjacent to the axis, and consists of a boss on the most anterior part of each thoracic segment which engages with an excavation on the posterior part of the preceding pleura. Thoracic pleurae are not in contact abaxially from the articulation—there is an open triangular area between them which gives a zigzag outline to the thorax. Articulating half-rings on the axis are wide (sag.), almost reaching as far as the front margin of the preceding axial rings.

Pygidium (excluding articulating half-ring) three-quarters as long as wide, and about one-fifth total length of dorsal exoskeleton. The convex axis tapers gradually posteriorly (the axial furrows enclosing an angle between 35° and 45°) to 0.7 axial length of pygidium. Only the anterior axial ring is completely developed;

the ring furrow is much shallower medially. The second ring furrow is modified in a peculiar way: the outer parts, adjacent to the axial furrows, are deep and run more or less transversely up the side of the axis parallel to the deeper part of the anterior ring furrow; the inner parts curve sharply backwards parallel to the sagittal line, almost to the tip of the axis, so that the ring furrow is modified as a pair of hook-shaped furrows. The mid part of the axis posterior to the anterior ring furrow is transversely flat. The tip of the axis is prolonged into a subcircular postaxial spine of length slightly less than that of the pygidium; the spine continues in line with the tip of the axis, or is directed slightly upwards. Axial furrows shallow posteriorly, not defined around the tip of the axis. Pleural fields slope steeply away from the axis, both laterally and postaxially. Two pairs of pleural and two pairs of interpleural furrows, the posterior pleural and interpleural furrows fainter than the anterior, especially on internal moulds. The anterior interpleural furrows run almost to the margin of the pygidium, and with the well-defined anterior ring furrow on the axis, serve to separate the anterior segment from the rest of the pygidium, and give it a close resemblance to a free thoracic segment. The downward slope of the pleural fields stops abruptly at the horizontal posterior border, which has its greatest width posterolaterally, anteriorly tapering in width to the anterolateral corners of the cranidium where it is scarcely to be distinguished from the anterior parts of the first pygidial pleurae, posteriorly decreasing in width very slightly. The posterior margin of the border is convex in outline, broadly rounded about the sagittal line, coming to a rounded point medially. Pygidial doublure doubled back horizontally beneath posterior border, of similar width and outline, with surface sculpture of terrace lines subparallel to the posterior margin of the pygidium.

Ontogeny. The small cranidium (Pl. 14, fig. 3) (sagittal length 0.85 mm) is readily recognizable as that of *Opipeuter*. It differs from the adult in the broadly rounded anterior outline of the glabella, and in the narrow, deeply incised axial furrows which are parallel to the sagittal line. A free cheek which probably belonged to a comparably sized cranidium (Pl. 14, fig. 5) has the same general form as that of the adult, but differs in the following features: the border of the cheek is not clearly differentiated; the genal spine is stouter, more posteriorly positioned (only the base of the spine is present on the small cheek); eye lenses are only present dorsally (about 250 in number), the lower part of the visual surface being apparently smooth. The lenses are of equal size over the surface of the eye.

EXPLANATION OF PLATE 14

Opipeuter inconnivus gen. et. sp. nov., Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen.

Fig. 1. Pygidium ($\times 10$) in oblique lateral view, showing spine continuing backwards from tip of pygidial axis. About 80 m from base of Member. PMO NF 2987.

Figs. 2, 3. Very small cranidium in lateral ($\times 15$) and dorsal ($\times 30$) views, showing essentially similar form of cranidium to that of adult. 80 m from base of Member. PMO NF 2984.

Figs. 4, 6, 7. Free cheek in lateral, dorsal, and anterior views ($\times 20$). From the same bed as the free cheek of Pl. 13, fig. 1. PMO NF 2980.

Fig. 5. Lateral view of extremely small free cheek ($\times 37$) showing the small number of dorsally concentrated lenses on the eye. Base of genal spine on right. Same bed as the small cranidium in fig. 3. PMO NF 2985.

Figs. 8, 9, 10. Pygidium, preserved in full relief and retaining exoskeleton, in lateral, posterior, and dorsal views ($\times 14$). Posterior view shows the considerable transverse convexity. From a stream section on Olenidsletta about 80–85 m from the base of the Member. PMO NF 2990.

Opipeuter inconnivus gen. et sp. nov., Tourmakeady Limestone, Co. Galway, western Ireland.

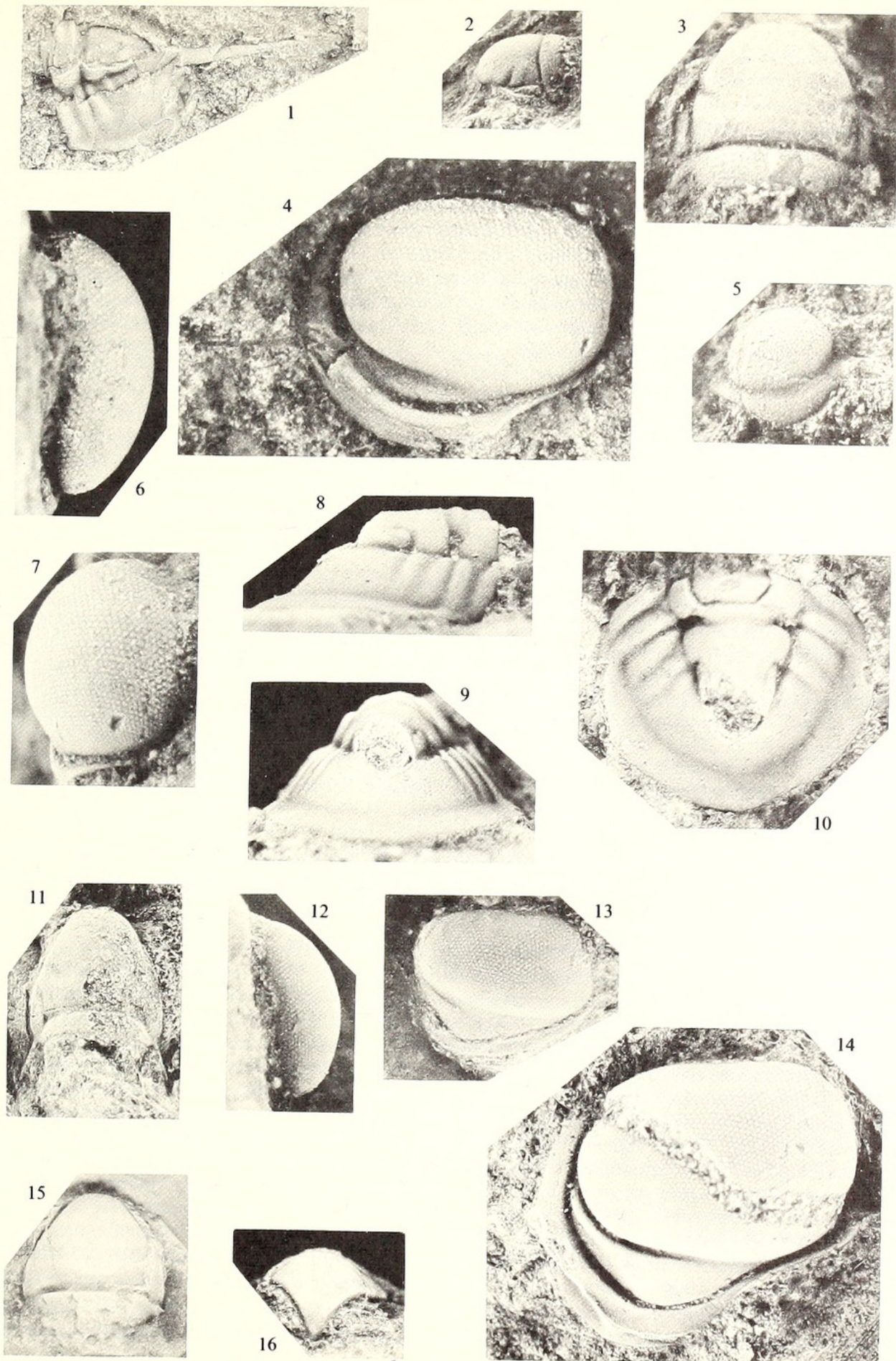
Fig. 11. Cranidium, dorsal view ($\times 6$), poorly preserved on right side. BM It 9795.

Figs. 12, 13. Free cheek in dorsal, lateral views from same block as cranidium in fig. 11 ($\times 14$). BM It 9798.

Opipeuter sp., upper part of Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen.

Fig. 14. Free cheek ($\times 12$) in lateral view, showing extra-marginal flange on posterior part of border. 96 m from base of Member. PMO NF 52.

Figs. 15, 16. Internal mould of cranidium ($\times 6$) in dorsal, anterior views. Note long and narrow glabellar tongue. 102 m from base of Member. PMO NF 2991.



Changes which occur during the ontogeny of the cephalon thus include a gradual relative increase in the length of the glabella associated with a more hyperbolic anterior outline, a shallowing and inward migration of the posterior part of the axial furrows, and an increase in number of lenses on the eye and their ventral migration, together with a differentiation in lens size such that the larger lenses are anteriorly and dorsally positioned. The glabellar tongue of the small cranidium does not curve downwards anteriorly to the same degree as on larger cranidia.

Variation. The material from Spitsbergen compares closely with that from the Tourmakeady Limestone, although a pygidium has not yet been found from western Ireland. The free cheek from the Fillmore Limestone is similar to that illustrated on Plate 13, fig. 1 from the Valhallfonna Formation.

Variation among specimens of *O. inconnivus* from Spitsbergen seems to be confined to relatively small differences in the anterior outline and relative length of the glabella, some specimens being relatively shorter and slightly more truncate anteriorly than others (Pl. 13, figs. 2, 11). The border of the free cheek is narrower on some specimens than others (compare Pl. 13, fig. 10; Pl. 14, fig. 4). One cranidium and one free cheek occurring stratigraphically above all material of *O. inconnivus* from the Valhallfonna Formation is believed to represent the only material of a second species of *Opipeuter*. The cranidium (Pl. 14, figs. 15, 16) has a glabella that tapers more rapidly than that of *O. inconnivus*, a narrower, longer glabellar tongue, and apparently also posterolateral cranidial spines that are directed backwards almost parallel to the sagittal line. The free cheek (Pl. 14, fig. 14) possesses a flange running alongside the border of the cheek at its widest part, which is not seen on cheeks of *O. inconnivus*. Although this material indicates the presence of a second species of *Opipeuter* the single cranidium and free cheek are not considered sufficient to formally name it as such.

Age. The Spitsbergen and western Ireland material is of Arenig age. The earliest occurrence of the species in the Valhallfonna Formation is with an assemblage of graptolites of early Arenig (late *fruticosus* Zone) age (Fortey and Bruton 1973), while the latest occurrence of the species is just below a graptolite assemblage of the *Isograptus* Zone in North American terms, an assemblage which may be correlated with the Zone of *Didymograptus hirundo* of the British sequence. The species in Spitsbergen thus ranges through the pre-*hirundo* Arenig (probably *deflexus* to *gibberulus* Zones of the British Arenig). The Tourmakeady Limestone locality is well dated in terms of graptolite assemblages occurring above and below (Dewey, Rickards, and Skevington 1970, p. 29) as 'late *Isograptus gibberulus* Zone or early *Didymograptus hirundo* Zone in age' (Skevington 1971, p. 80). If the former of these alternatives proves to be the case, this correlates exactly with the upper part of the range of *Opipeuter* in Spitsbergen. The free cheek from the Fillmore Limestone of Utah occurs with the Zone I fauna of Hintze (1953).

Affinities. A trilobite as unusual as *Opipeuter* poses particular problems in assessing its relationships. The various families which have been considered are briefly discussed below.

Remopleurididae. It is believed that *Opipeuter* is most closely related to the remopleuridids, particularly to *Remopleurides* and allied genera (subfamily Remopleuridinae). The glabella of these remopleuridids occupies the entire distance between the palpebral lobes, and in *Remopleurides*, *Remopleuridiella*, *Robergiella*, and *Remopleurella* is produced anteriorly downwards into a narrow glabellar tongue similar to that of *Opipeuter*. The postocular fixed cheeks of such Remopleurididae are reduced to spines, although transversely directed rather than posteriorly directed as in *Opipeuter*. The narrow, transversely horizontal anterior border of the cranidium of *Opipeuter* is closely similar to the cranidial border on such remopleuridids as *Robergiella sagittalis* (Whittington 1959, pl. 6, figs. 20, 21) and *Remopleuridiella caudalimbata* Ross 1951 (see Hintze 1953, pl. 5, figs. 10a-c). Such a border is not to be found among species of the other families (below). Palpebral rims of remopleuridids are characteristically broader (trans.) than those of *Opipeuter*, but narrow anteriorly into grooves with a V-shaped cross section adjacent to the glabellar tongue in just the same way as those of *Opipeuter*. Like *Remopleurides*, *Opipeuter* has eleven thoracic segments, the axis being transversely wide compared with the pleurae and the articulation close to the axial furrows. In its major morphological features *Opipeuter* thus seems to be more closely comparable with the Remopleurididae than any other trilobite family. But there are a number of important features which distinguish *Opipeuter* from the Remopleurididae. In *Opipeuter*:

- (i) The occipital ring is transversely very wide, and the cranidium tapers anteriorly from it. Remopleurididae

have the glabella expanding forward to a point at about the mid length of the palpebral lobes. The facial suture is similarly bowed outwards medially in remopleuridids, rather than running almost uniformly inwards-forwards as in *Opipeuter*.

(ii) The greatly developed eyes are inflated, subglobose. Among Remopleurididae the form of the eye is characteristic and quite different: it forms a flat, near vertical band-like surface of nearly uniform height along its length (see for example Whittington 1959, pl. 19, fig. 11; Shaw 1968, pl. 2, fig. 29).

(iii) The modified posterior border spines of the cranidium extend backwards behind the occipital ring, this being possible because of the extreme narrowness (trans.) of the first thoracic pleurae. No such structure is to be found among the remopleuridids.

(iv) The pygidial margin is entire. In *Remopleurides* and allied genera a spinose margin to the pygidium is the rule. The postaxial pygidial spine of *Opipeuter* has no parallel among mature remopleuridid pygidia, although long axial spines are present on some small transitory pygidia of *Remopleurides*.

(v) The defining characters of *Opipeuter* are present even on small cranidia less than 1 mm long which do not resemble remopleuridid cranidia of the same size.

(vi) The lateral parts of the thoracic pleurae are not in contact with one another.

These differences are considered of such importance that *Opipeuter* is here assigned to a new family.

The genus *Cremastoglottos* Whittard 1961, which is known only from four compressed cranidia from the early Llanvirn Hope Shales of Shropshire, England, and one probable fragmentary cranidium from the Caradocian of Bohemia (Marek 1966b), possesses a number of features which suggest that it should be included in the same family as *Opipeuter*. In the type and only species, *Cremastoglottos occipitalis* (Whittard 1940) (see Whittard 1961, p. 187, pl. 25, figs. 1-5) the general cranidial outline is similar to that of *Opipeuter inconivus*, being triangular, anteriorly tapering, and produced into a narrow downward-deflected glabellar tongue. A narrow palpebral rim runs along the edge of the cranidium as in *Opipeuter*, and the occipital ring is transversely very wide. The main differences between *Cremastoglottos* and *Opipeuter* are that the former genus has two pairs of deeply incised glabellar furrows which do not reach the axial furrows, and possesses a curiously undulating occipital furrow quite distinct from the nearly straight transverse occipital furrow of *Opipeuter*. It is of interest to note that Whittard originally (1940, p. 136) assigned *Cremastoglottos occipitalis* to the Cyclopygidae, but later (Whittard 1961, p. 187) to the Remopleurididae.

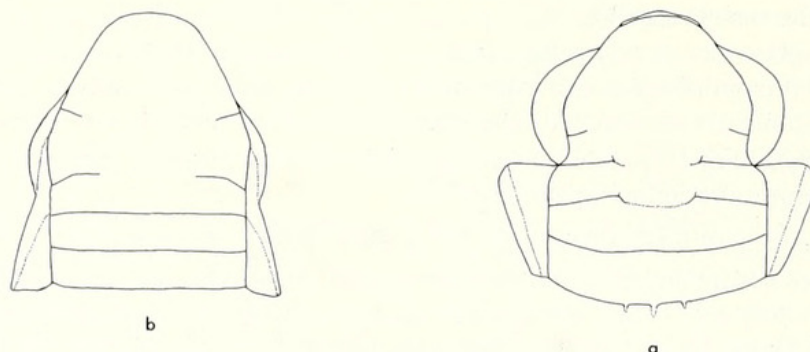
Telephinidae. A number of similarities may be noted between *Telephina* species and *Opipeuter*. The glabellar outline in dorsal aspect of small specimens of *Opipeuter* may be compared with such species as *T. bipunctata* (Ulrich 1930, pl. 5, fig. 1); the occipital ring is well developed in all telephinids. The posterior part of the fixed cheek may be modified as a short spine, as in *T. americana* (Billings 1865) (see Whittington 1965, pl. 37, figs. 9, 18), a structure comparable with the modified posterior border of *Opipeuter*. The thorax of *Telephina*, which is completely known only in *T. spinifera* (Ulrich) (see Fischer 1946) with nine segments, has a broad convex axis with narrow, rather blunt-tipped pleurae, each segment being similar in these respects to those of *Opipeuter*. Pygidia of some species of *Telephina* are not greatly different from that of *Opipeuter*. For example the pygidium of *Telephina* (*Telephops*) *bicornis* (Ulrich 1930, pl. 4, figs. 12, 13) has a similar outline to that of *Opipeuter*, is similarly transversely convex, with a prominent axis with two axial rings and a rim-like posterior border.

In spite of these similarities *Opipeuter* is not thought to be related to the Telephinidae. The critical differences are considered to be: (i) There is no glabellar tongue developed on *Telephina* species. (ii) The structure of the anterior cranidial border is quite different in *Opipeuter* and telephinids. In the latter the border is a steeply arched convex rim which may be reduced to a pair of spines in some species; this is quite different from the narrow, horizontal rim of *Opipeuter*. (iii) All the telephinids have well-developed triangular fixed cheeks with broad palpebral rims, which give the inner (sutural) margin of the eye a curved outline. In addition the postaxial spine on the pygidium of *Opipeuter* does not seem to be found among telephinids, nor do they have such a broad border to the free cheeks.

Following Nikolaisen (1963, p. 563) it is believed that certain genera of the Komaspidae, such as *Carrickia*, *Carolinites*, and *Goniophrys*, are closely related to *Telephina*; the differences considered of importance between telephinids and *Opipeuter* apply equally to this group of komaspids, except that their facial sutures do not have the strongly curved outline of *Telephina*.

Cyclopygidae. The eleven thoracic segments of *Opipeuter*, the wide border of the free cheek, and the convex pygidium with its relatively long axis produced posteriorly into a spine serve to exclude the genus from the

Cyclopygidae. The cranium of *Opipeuter*, however, shows a number of similarities with cyclopygids, which are believed to be due to homeomorphy. The generally tapering glabella, which occupies almost the entire cranium, the downward deflected anterior glabellar tongue and the narrow, gutter-like palpebral rims can be matched with such cyclopygids as *Novakella bergeroni* (Kloucek 1916) (see Marek 1961, pl. 4, figs. 10–15; text-fig. 19). This species also possesses triangular fixigenal areas adjacent to the basal part of the glabella, which increases its resemblance to *Opipeuter*, although, like most cyclopygids, it lacks an occipital ring. An occipital ring and well-defined glabellar furrows are, however, present on the distinctive cyclopygid *Ellipsotaphrus* (Whittard 1961, pl. 23, figs. 3, 4).



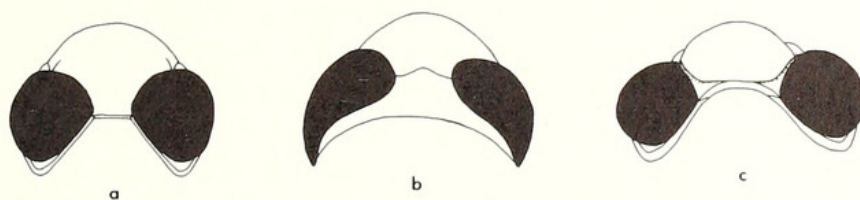
TEXT-FIG. 2. *a*, outline reconstruction of the cranium of *Bohemilla* sp. from the Llanvirn of the Great Paxton Borehole. Based on specimens in the Institute of Geological Sciences, London, especially By 8561, By 8529; *b*, hypothetical cranium derived from *Opipeuter* by incorporation of two thoracic segments posteriorly (see text). Both approx. $\times 5$.

Hypothetical relationship to Bohemilla. The bizarre arthropod *Bohemilla* Barrande 1872 (type species *B. stupenda* Barrande 1872) was excluded from the Trilobita by Whittard (1952, p. 320) and this interpretation was followed in the *Treatise*. The genus is known from occurrences ranging from Llanvirn to Ashgill in age. I have been able to examine some slightly crushed but otherwise well-preserved material (text-fig. 2a) of a *Bohemilla* species of Llanvirn age from the Great Paxton borehole, Huntingdon, England.

It is suggested that *Bohemilla* may be related to the Opipeuteridae, and hence, more distantly, to the Remopleurididae, and that its peculiar features may be explained without having to remove it to some non-trilobite group. From a study of the type and other species of *Bohemilla* Marek (1966a, p. 146) also concluded that the genus was related to the Remopleuridacea. The *Bohemilla* cranium has the fixed cheeks reduced to backward tapering bands adjacent to the posterior part of the glabella. The glabella is parallel sided posteriorly, tapering forwards anteriorly. The two posterior glabellar furrows pass transversely completely across the glabella, the posterior of which may be regarded as the occipital furrow; the anterior two pairs are shorter, transverse. There is a narrow, horizontal anterior rim in front of the relatively narrow anterior 'tongue' of the glabella. That part of the cranium lying in front of the anterior transverse glabellar furrow is similar to that of *Opipeuter*, notably in the tapering glabella, the position and length of the anterior glabellar furrow, and the narrow anterior cranial rim. It is possible that *Bohemilla* could have been derived from an *Opipeuter*-like ancestor by incorporation of two thoracic segments into the cephalon. The backward directed posterior border spines of *Opipeuter* already effectively include the first thoracic segment within the area of the cephalon. Ankylosis of the spine with the pleural remnant and loss of articulation would then completely incorporate the segment within the cephalon. Like the axis of the thorax, the glabella thus formed would be parallel sided. Such a method of cephalic segmental accretion would be unique among trilobites, as so far known, but may not be so improbable given an ancestor like *Opipeuter*. Thoracic segments associated with *Bohemilla* from the Great Paxton borehole have very narrow triangular pleurae similar to those of the anterior thoracic segment of *Opipeuter* (see also Marek 1966a, figs. 2, 4). I would prefer to regard the Bohemillidae as a family within the Remopleuridacea, rather than as a monogeneric superfamily as considered by Marek (1966a). Note that the band-like palpebral rims of *Bohemilla* are more like those of remopleuridids than those of *Opipeuter*. Text-fig. 2b is an attempt to model a *Bohemilla*-like cranium from *Opipeuter* by incorporation of two thoracic segments.

Functional morphology. Discussion of the functional morphology of *Opipeuter* is based on the reconstruction of the whole dorsal exoskeleton (text-fig. 1). The free cheek is believed to hang below the level of the rest of the dorsal exoskeleton. Only with the cheek in this position do the sutures on the cranidium and the inner margin of the eye correspond exactly, the result being that the border of the cheek slopes steeply downwards below the surface of the eye. The convex visual surface then commands a very wide field of view. There are lenses directed forwards, backwards, laterally, upwards, and even downwards. Backward vision is made possible by the narrowness (trans.) of the thoracic pleurae, downward vision is possible because of the steep slope of the cheek, and especially anteriorly where the border narrows greatly. Probably the only area not visible to the trilobite was directly below the exoskeleton. If the size of the lenses is a measure of their visual efficiency the concentration of large lenses anteriorly and dorsally may indicate that upward (assuming the trilobite swam with the exoskeleton uppermost) and anterior vision were of principal importance to the animal. This all round vision may be contrasted with that of *Remopleurides* with its narrow strip-like eyes, with the lenses in near-vertical files commanding predominantly lateral field of view.

In anterior view (text-fig. 3a) the front margin of the cephalon is deeply arched. Similarly, anteriorly arched profiles are to be found among the Cyclopygidae and *Carolinites* species (text-figs. 3b, 3c), which, as has been discussed above, are similar



TEXT-FIG. 3. Outline reconstructions to show similarity of anterior cephalic profiles of *Opipeuter*, *Priscyclopyge*, and *Carolinites*. Visual surfaces black. a, *Opipeuter inconnivus* gen. et sp. nov. (about $\times 4$); b, *Priscyclopyge binodosa* (Salter), after Marek (1961, text-fig. 8) ($\times 2$); c, *Carolinites sibiricus* Chugaeva, based on new material of this species from the upper part of the Valhallfonna Formation, Ny Friesland, Spitsbergen ($\times 4$).

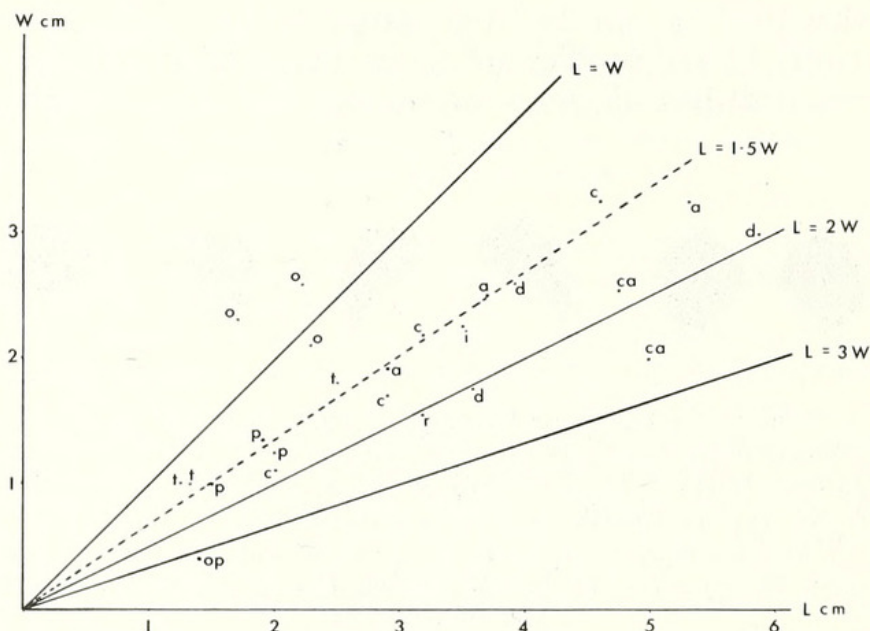
in many ways to *Opipeuter* and are regarded as homeomorphic. The vaulted anterior profile, together with the cheeks which project well below the thorax with the 'cutting' edge of the border facing downwards indicate that the trilobite was not adapted to rest on the sediment surface. This is in contrast to the profile of, for example, asaphids such as *Ogygiocaris* which are dorsoventrally flattened, and in which a ventral platform formed by the broad cephalic doublure lies on a level with the tips of the thoracic pleurae and the outer-part of the doublure of the pygidium; the anterior arch of the cephalon is reduced or absent. Such a morphology distributes the weight of the animal over a wide surface area, and the broad ventral doublure is suitable for resting on soft mud.

The all-round vision of the eyes, taken together with the distinctive profile of the cephalic region, suggests that *Opipeuter* was a free-swimming species. In particular,

the downward vision of the eyes would scarcely be pertinent to a benthonic animal. The other features of the exoskeleton are consistent with the same interpretation:

(i) The exoskeleton is, for a trilobite, extraordinarily long and narrow, and laterally compressed. Text-fig. 4 shows the dorsal exoskeletal length (excluding caudal spines) compared with transverse thoracic width at the mid point of the thorax of several Ordovician species in the British Museum (Natural History). Uncrushed specimens from different families within the major groups shown were chosen to give a wide taxonomic spectrum. Most show a length of about one and a half to two times the thoracic width; *Trinucleina* tend to be more ovate. No specimen was found which approached the relative length of *Opipeuter*, three times as long as wide. Such an elongate form is almost invariable among recent actively swimming Crustacea.

(ii) A very convex thoracic axis, as Richter (1919, p. 229) observed, probably allows for greater room for muscles necessary for vigorous swimming. The exoskeleton is relatively thick, which may be necessary for the support of powerful musculature. The very broad (sag.) articulating half-rings no doubt lent the thorax a great deal of flexibility in the vertical plane.



TEXT-FIG. 4. Graph of sagittal length (L) (excluding caudal spines) plotted against thoracic width (W) at the mid point of the thorax for a number of perfectly preserved complete trilobites (Ordovician) in the collections of the British Museum (Natural History). *o*—Odontopleurids, *p*—Proetacea, *a*—Asaphina, *t*—Trinucleina, *c*—Cheirurina, *d*—Dalmanitacea, *r*—Remopleuracea, *ca*—Calymenacea, *i*—*Iliaenus*, *Op*—*Opipeuter*.

(iii) The transverse abbreviation of the thoracic pleurae enables a reduction in the total weight of the exoskeleton, and the pleural remnants may also have acted as stabilizing 'fins' along the edge of the thorax. *Opipeuter* exhibits the opposite tendency to the Odontopleuridae, in which the wide thoracic pleurae are greatly extended laterally by their continuation into one or more long and often slender spines such that the transverse thoracic width of the odontopleurid may exceed the sagittal length

(text-fig. 4). Both Richter (1919) and Raymond (1920) considered that these spines may have functioned as frictional brakes to prevent sinking and that the odontopleurids were planktonic. Functional studies (Seilacher 1959; Clarkson 1969) have indicated that the odontopleurids were more probably benthonic. Even if the planktonic view is correct it is clear that the odontopleurid mode of life must have been very different from that of *Opipeuter*, for spines which inhibited sinking would also have opposed active swimming.

(iv) The functional significance of the gaps between thoracic pleurae is not obvious, although three suggestions may be made. The gaps may have been necessary to permit enrolment of the long, narrow thorax, or they may have served simply to further reduce the bulk of the exoskeleton, or they may have permitted a small amount of lateral 'wriggling' movement in the thorax. Possibly all three factors may have acted in combination.

The depth at which the actively swimming *Opipeuter* may have lived is subject only to indirect evidence. Large eyes alone do not necessarily indicate life in the surface waters, for, as Clarkson (1967, p. 371) points out, recent arthropod species with enlarged eyes may be found at considerable depths in the sea. It is of interest to note that among recent marine arthropods the development of exceptionally large eyes is a frequent concomitant to the adoption of a pelagic (whether epi- or bathypelagic) or planktonic mode of life. Among the Amphipoda, for example, the single group Hyperiidea is almost entirely planktonic, and compared with other amphipods the eyes are very large and convex, occupying almost all the available genal region. The same relative expansion of visual area applies to the Isopoda, in such genera as *Eurydice* and *Aega* which spend at least part of their lives actively swimming and may constitute part of the plankton. These latter genera also have an elongate body form and transversely narrow, small, downward-sloping epimera, a gross form not unlike that of *Opipeuter*. Both pelagic isopods and the amphipods are of similar size to *Opipeuter*.

Indirect evidence on the life habits of *Opipeuter* comes also from the lithology of the limestones in which *O. inconnivus* is found, and from the fauna associated with it. In Spitsbergen the species occurs with olenid trilobites and graptolites in dark, laminated bituminous limestones in the lower part of the Valhallfonna Formation, but also with a completely different assemblage of trilobites dominated by asaphids, nileids, and raphiophorids, often in greyish, crystalline limestones, for the upper part of its range. In western Ireland the species occurs in pure, white or pink sparites with a third assemblage of trilobites dominated by *Iliaenus* and Cheiruridae, and associated with abundant articulate brachiopods, algal structures, and bryozoans suggestive of shallow water (possibly even 'reef') conditions. This independence of associated fauna and lithology is what might be expected of a pelagic animal, and the occurrence of *Opipeuter* with a shallow water assemblage further indicates that the species was capable of living in near-surface waters. This does not preclude the possibility that it was equally adapted to life in deeper waters.

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Note added in press. Dr. T. Tjernvik has recently shown me a pygidium of an *Opipeuter* species from the early Arenig (*dalecarlicus* zone) of Sweden. The pygidium was found in a boulder in glacial clay near Orebro, Narke, derived from a source outcrop in the region of the South Bothnian Bay.



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