SOME PHACOPINA (TRILOBITA) FROM THE SILURIAN OF SCOTLAND

by E. N. K. CLARKSON, N. ELDREDGE, *and* J.-L. HENRY

ABSTRACT. *Acernaspis* (*Eskaspis*), a new subgenus, and *Podowrinella*, a new genus of Phacopina from Silurian inliers of the Midland Valley of Scotland, are here proposed. *A.* (*Eskaspis*) is restricted to the Telychian (upper Llandovery) and is referred to the subfamily Phacopinae. *A.* (*E.*) *sufferta* (Lamont) from the *M. crenulata* Zone of the Pentland Hills and *A.* (*E.*) *woodburnensis* from the upper *M. sedgwickii* Zone of Girvan are described. *Podowrinella*, which is found in the lower Wenlock of Girvan, and in the Telychian (upper Llandovery) of the Hagshaw and Pentland Hills, can probably be assigned to the Pterygometopidae, but possesses some character states normally considered representative of Phacopidae. Coaptative structures on the ventral doublures of *A.* (*Eskaspis*) and *Podowrinella* are described in detail, and information is given on the auxiliary impression system on the glabella of *A.* (*E.*) *sufferta*.

SILURIAN rocks in the Midland Valley of Scotland lie in a chain of inliers extending from Girvan to within a few kilometres of Edinburgh (text-fig. 1). At Girvan, in the Hagshaw Hills, and in the North Esk Inlier of the Pentland Hills, the Llandovery succession begins with turbidites or subturbidites, and passing upwards through shallow-water marine horizons (with shelly faunas well developed at certain horizons at Girvan and in the North Esk Inlier) the sequence changes to thin brackish or freshwater deposits and finally into redbeds, early in the Wenlock.

The large inlier of Lesmahagow, lying further to the north, has dominantly fresh or brackish water beds followed by redbeds.

In Telychian (upper Llandovery) mudstones and siltstones of the North Esk Inlier there occur abundant faunas, especially in the beds which have been referred to as the '*Plectodonta* mudstones' by Lamont (1947) and others.

Fossils were first discovered here in 1838 by Charles Maclaren of the Geological Survey, and Howell and Geikie listed them in 1861. The fine preservation and richness of the faunas led to much palaeontological activity in the next few decades, mainly by members of the Edinburgh Geological Society and associates (Haswell 1865; Henderson 1867; Brown and Henderson 1867; Henderson and Brown 1869; Etheridge 1874; Davidson 1874). But although extensive faunal lists were compiled, only Haswell (1865) and Davidson (1874) described any of the faunal elements. Haswell's descriptions and plates were very sketchy, but Davidson's monograph of the brachiopods was a valuable and enduring contribution to the palaeontology of the region.

The U.K. Geological Survey's faunal notes were updated by Peach and Horne (1899) and Mykura and Smith (1962), who described the area in detail.

Meanwhile, Lamont (1947, 1948, 1949, 1952) discussed the fauna at length primarily in a stratigraphical context, recognizing for the first time that the faunas were pre-Wenlock. New bivalves and chelicerates were later described (Lamont 1954, 1955). Though the starfish from well-known horizons in the Gutterford Burn were formally described by Spencer (1914–1940), most of the other elements in the

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rich and diverse fauna of the Pentland Hills remained imperfectly known or undescribed until very recently. Interest in the fauna has revived of late, however, and various elements have been revised or described for the first time by various authors. In recent works there have been described a new echinoid (Kier 1973), crinoids (Brower 1975), and the trilobite *Scotoharpes* (Norford 1973).

Tipper (1976) has remapped the region, revised the stratigraphy, erected new formation names, and distinguished three successive faunal assemblages from the upper Deerhope and lower Wether Law Linn Formation (Tipper 1975). In the present paper Tipper's formation names have been used throughout, replacing the older stratigraphical divisions (text-fig. 1).

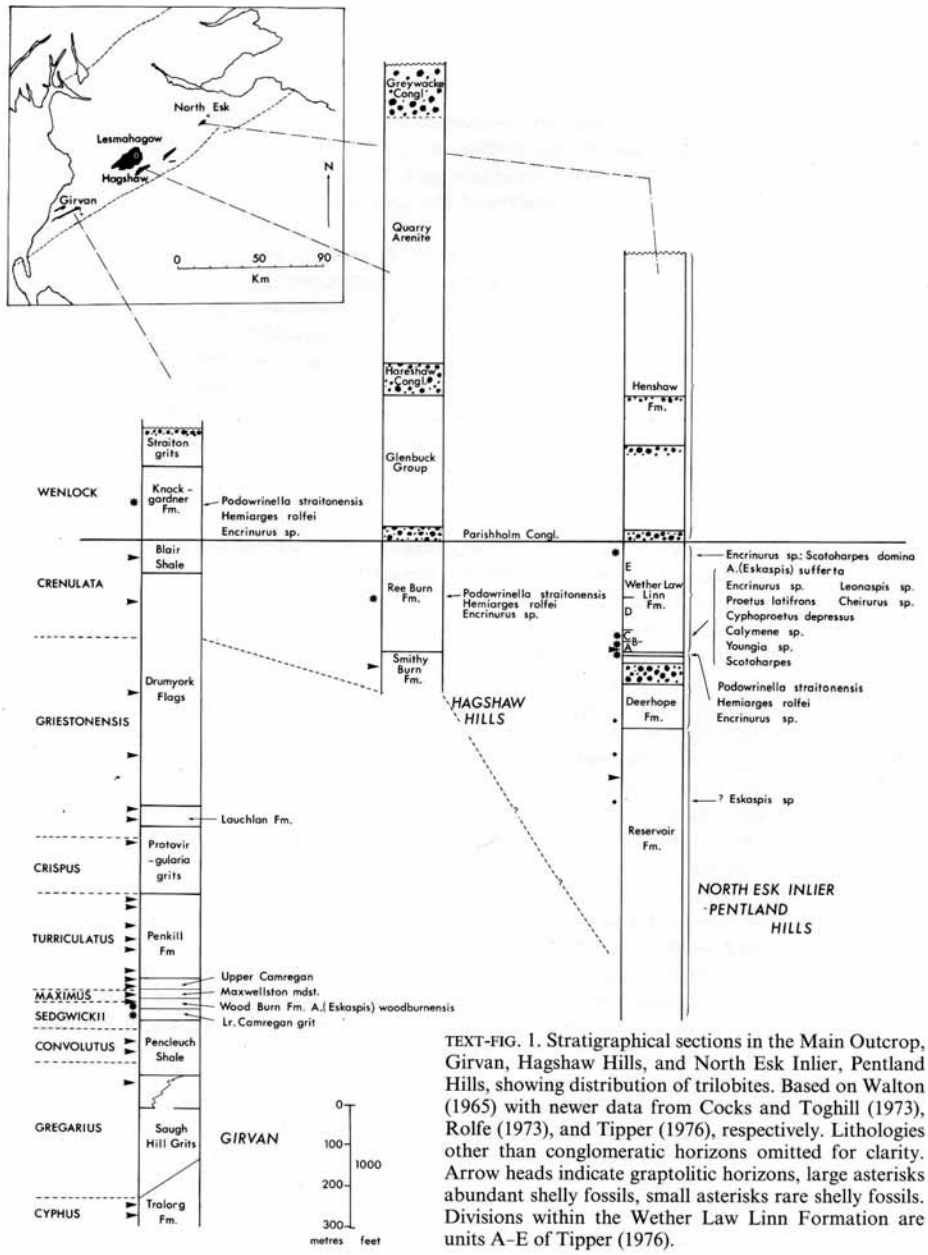
Trilobites, amongst many other fossils, especially brachiopods, are abundant at certain horizons within the upper Llandovery, and though the fauna is restricted to a comparatively few genera and species, individuals of these may be frequently encountered. In the Reservoir Formation these include occasional phacopids, probably *Acernaspis* (*Eskaspis*), n. sg. otarionids and odontopleurids, whereas *Podowrinella straitonensis*, *Encrinurus*, and *Hemiarges* together with less-common elements are present at the top of the Deerhope Formation. In the immediately overlying Wether Law Linn Formation (which includes the *Plectodonta* Mudstones), there is a rich fauna with *A.* (*E.*) *sufferta* (Lamont) (150 examples), *Encrinorus* sp. (*c.* 150 ex.), *Proetus latifrons* (M'Coy) (25 ex.), *Cyphoproetus depressus* (Barrande) (16 ex.), *Scotoharpes domina* (Lamont) (2 ex.), *Youngia* (6 ex.), *Calymene* sp. (6 ex.), *Cheirurus* sp. (1 ex.), and possibly other genera and species listed by Lamont (1948), though the validity of these has not yet been ascertained.

In the Wether Law Linn Formation the most abundant trilobites are found only at the base (in units A and C of Tipper) becoming less common towards the top of unit C of the succession. *Encrinurus* occurs quite abundantly, however, in the uppermost part of this formation, in unit E, in which the only other trilobite to have been collected is *Scotoharpes*. Tipper (1975) has shown that trilobites occur independently of the brachiopod communities which he described in this sequence.

In this paper the Phacopina of the Pentland Hills are described, these being *A.* (*E.*) *sufferta* (Lamont, 1947) and *Podowrinella straitonensis* (Lamont, 1965). *A.* (*E.*) *sufferta* is known from the Pentland Hills alone, but an earlier species, *A.* (*E.*) *woodburnensis*, n. sp. from the older Wood Burn Formation at Girvan can also be referred to that genus, and is the only other species known at present.

P. straitonensis is known from the Ree Burn Formation in the Hagshaw Hills, from which it was first described from specimens collected by Rolfe, and also from the lower Wenlock Knockgardner Formation at Girvan. In the Pentland Hills it occurs in a coarse siltstone, whereas both in the Hagshaw Hills and at Knockgardner, specimens are found at the base of coarse turbidite flows where they occur with brachiopod faunas (Rolfe 1973; Cocks and Toghill 1973). In all these cases *Encrinurus* and *Hemiarges* occur in the same fauna, which, judging by its anomalous stratigraphic position (younger in the west), strongly indicates either a facies fauna (perhaps controlled in some way by the regressive sequence), or else inaccuracies in correlation.

The present work is the first of a series of papers in which the trilobite fauna of the Pentland Hills is described. The rest of the fauna will be described in later papers, some by other authors.



TEXT-FIG. 1. Stratigraphical sections in the Main Outcrop, Girvan, Hagshaw Hills, and North Esk Inlier, Pentland Hills, showing distribution of trilobites. Based on Walton (1965) with newer data from Cocks and Toghill (1973), Rolfe (1973), and Tipper (1976), respectively. Lithologies other than conglomeratic horizons omitted for clarity. Arrow heads indicate graptolitic horizons, large asterisks abundant shelly fossils, small asterisks rare shelly fossils. Divisions within the Wether Law Linn Formation are units A–E of Tipper (1976).

TAXONOMY

Nomenclature

Lamont (1965) described *Phacops straitonensis* from the Hagshaw Hills and Knockgardner. The discovery of this species in the Pentland Hills, and the collection of more material from all three localities gave the incentive for a more detailed study. No question arises over the validity of the specific name, though the holotype has been lost (Lamont, pers. comm.).

Podowrinella is here described as a new genus. It seemed to us initially that the poorly known, but suggestively named, genus *Pterygometopidella* Wedekind, 1912 (based on *Phacops quadrilineata* Angelin) might be available as a generic taxon for *P. straitonensis*. Wedekind (1912) described *Pterygometopidella* very inadequately from only two specimens collected from the c-marl (Silurian) of Gotland, and figured only one of them in a poor and tiny photograph which allowed few details to be seen but which seemed to indicate a close resemblance to *Eophacops musheni* (Salter). The two specimens, deposited in the collections of the Geologisch-Paläontologisches Institut der Universität Göttingen, are no longer in the Institute (Jahnke, pers. comm. 1974), and may have been destroyed. Struve (pers. comm. 1974) suggests that Wedekind may have erected the subgenus on an erroneously determined species and Schrank (1972) regards Wedekind's specimens of *P. quadrilineata* as incorrectly determined individuals of *E. musheni* (Salter), indicating that *Eophacops* is a junior synonym of *Pterygometopidella*.

Though the taxonomic problem of *Pterygometopidella* may not be entirely resolved, it is clear that this generic name is not available for *Phacops straitonensis*.

A. (*E.*) *sufferta*, on the other hand, was figured, though not described, by Lamont (1948) as *Eophacops sufferta*, in a paper in which many other trilobites from the Pentland Hills were also figured but for which no formal descriptions were given. There thus arises the question of the validity of the nomenclature, a matter which Norford (1973) has also referred to in dealing with *Scotoharpes*. *S. domina* Lamont was also figured in the same paper by Lamont (1948), and Whittington (1950) rejected the name as being invalid. Norford (p. 12), however, revived the name on the basis of Lamont's recognizable photograph and few words of description.

For the same reasons the specific name *sufferta* is here considered to be valid, since the photographs of Lamont's (1948, pl. 1, figs. 21, 22) which show a complete internal mould are clearly recognizable, and Lamont (pers. comm. 1974) has confirmed that the common phacopid trilobite at Wether Law Linn is, in fact his '*Eophacops*' *sufferta*, though the type, formerly in his possession, has now been lost. Though Lamont did not name the species in his 1947 paper on the stratigraphy and faunas of the region he states (p. 290) that 'a large *Eophacops* is very common at Wetherlaw Linn. It has more than 6 facets per radius in the eye, which rules out *E. elliptifrons* (Esmark). . . . The rather long pygidium with numerous axial segments, however, points to comparison with *E. elliptifrons* var *glaber* Marr & Nicholson . . .'. Lamont's notes which annotate the Grant Institute Library copy of Haswell's (1865) guide to the geology and faunas of the Pentland Hills refer to Haswell's figures (p. 6) of '*Phacops stokesii*' as '*E. sufferta*' and state, 'It should have shown 7–8 rings in the pygidial axis' and, 'Eye usually has 7 facets per column'.

There thus seems to be no question that the common and only species of phacopid trilobite from the Wether Law Linn Formation is what Lamont recognized as a new species and called *E. sufferta*, and it is here redescribed, under the generic name *Acernaspis* (*Eskaspis*).

SYSTEMATIC DESCRIPTIONS

Order PHACOPIDA Salter, 1864
Suborder PHACOPINA Struve, 1959
Superfamily PHACOPACEA Hawle and Corda, 1847
Family PHACOPIDAE Hawle and Corda, 1847
Subfamily PHACOPINAE Hawle and Corda, 1847
Genus ACERNASPIS Campbell, 1967
Subgenus ESKASPIS n. sg.

Type species. Eophacops sufferta Lamont, 1947. Upper Llandovery (Telychian). Wether Law Linn Formation, North Esk Inlier, Pentland Hills, Peeblesshire, Scotland.

Diagnosis. Relatively small Phacopinae. Cephalon roughly 1·8 times as wide as long; genae somewhat truncate postero-distally (in dorsal view) so that the cephalon is widest just anterior to the posterior branch of the facial suture. Anterior glabella lobe moderately inflated, rather flat on top and shelving more steeply anteriorly.

Axial furrows deeply emplaced. Glabellar furrows 3p and 2p lightly impressed; 3p in two distinct, unjoined parts with distal ramus straight, running at an exsagittal angle of 45°, not confluent with axial furrow; proximal ramus of 3p furrows convex anteriorly, inclined slightly antero-laterally. 2p furrows likewise convex and not confluent with axial furrows.

Glabellar furrows 1p confluent with axial furrow, concave anteriorly and not coalesced mesially, with stout apodemes developed in distal portion of 1p external surface. Intercalating ring thus confluent mesially with anterior glabellar lobe; intercalating ring depressed, with distal nodes. Occipital furrow deeply incised laterally. Occipital ring longest (sag.) at the midline, depressed laterally with nodes partially set off by exsag. furrows, not reaching height of anterior glabellar lobe in lateral view.

Posterior border furrow lightly impressed, becoming nearly obsolescent laterally but merging with lateral border furrow. Eyes large, nearly reaching, or some distance from, posterior border furrow, and, anteriorly, lateral border furrow, with eye socle developed only as small, depressed area beneath visual surface. Visual surface with sixteen to nineteen dorsoventral files of lenses, all protruding well beyond bounding sclera. Palpebral lobe flat, rather narrow, set off from palpebral area by faint palpebral furrow.

Anterior cephalic margin distinct laterally and smoothly continuous with anterior glabellar lobe, disappearing antero-medially. No anterior border furrow developed.

Anterior doublure fairly long (sag.), with inflated central lobe sometimes present. Vincular furrow present anteriorly only as paired subfrontal depressions meeting at midline, deeply impressed postero-laterally and bearing nine notches for pleural

tips. Anterior and posterior regions of vincular furrow unconnected, or connected by a faint furrow. Hypostoma unknown.

All parts of exoskeleton minutely granular; auxiliary impression system ovate, developed as depressions devoid of granules on anterior glabellar lobe, and as scars viscerally.

Thorax with distinct axial nodes set off by short non-communicating furrows inclined postero-proximally on both the anterior and posterior sides of axial ring. Pleural tips gently rounded. Pygidium with well-defined axial furrows, with about six axial rings and terminal piece. Axis rounded posteriorly, not meeting posterior margin of pygidium. Five pairs of pleurae present; pleural furrows becoming progressively fainter posteriorly; inter-pleural furrows present, but weakly impressed.

Remarks. Our diagnosis of *Acernaspis* (*Eskaspis*) includes character states inclusive of some other, particularly Silurian, Phacopinae. All characters included in the diagnosis do, in fact, vary in general amongst Phacopinae and are of potential value as diagnostic elements. Furthermore, inclusion of 'primitive' as opposed to strictly autapomorphous ('derived') characters, in a diagnosis, is of value in recognizing distinct genera, for only one or at most a few subordinate taxa in a defined group may in fact retain a particular primitive feature, hence its valid inclusion in a diagnosis. The minute granulation of *A.* (*Eskaspis*), for instance, is close to the primitive condition for all Phacopinae, yet is typical only of species of *A.* (*Eskaspis*) and *A.* (*Acernaspis*) among all known Phacopinae.

As written, the diagnosis of *A.* (*Eskaspis*) embraces some features of only three additional genera known to us: *Murphycops* Lespérance, *A.* (*Acernaspis*) Campbell, and in ventral morphology *Ananaspis* Campbell. We emphasize here the distinctly diagnostic traits of *Acernaspis* (*Eskaspis*) which serve to distinguish it from these other genera. *A.* (*Eskaspis*) shares with *Murphycops* some similarity in the coaptative device of the cephalic doublure, but otherwise differs from *Murphycops* in the cuticular granulation, development of auxiliary impression system, presence of a distinct palpebral furrow separating the palpebral lobe from the palpebral area, and the presence of nodes developed on the thoracic axial rings just proximal to the axial furrows.

A. (*Acernaspis*) and *A.* (*Eskaspis*) are dorsally very similar to one another, their over-all shape, degree of glabellar inflation, and auxiliary glabellar impressions, for instance are almost identical, and perhaps the only significant difference is the reduction of the anterior border in *A.* (*Eskaspis*), so that it is not visible in dorsal view. But we would here draw attention to the ventral morphology of the cephalon, as did Campbell (1967), and because of the coaptative enrolment mechanisms, to the pygidial doublure. Coaptative morphology has not yet been fully explored in Phacopina, but is clearly very important in taxonomy.

The ventral cephalic morphology of *A.* (*Acernaspis*), here represented by the Idwian *A.* (*A.*) *elliptifrons* (Esmark) from Girvan, Ayrshire, Scotland, is substantially different from that of *A.* (*Eskaspis*) *sufferta*. There are some variations within *A.* (*Acernaspis*) judging by the photographs of the doublures of various species given by Campbell (1967), Männil (1970*a*, *b*), and Sherwin (1972), but nowhere is there the

kind of conformation illustrated by *A.* (*E.*) *sufferta*. Both *elliptifrons* and *sufferta* have nine vincular notches, the last one being indistinct in *elliptifrons* (text-fig. 3*a–c*). In *elliptifrons* the vincular notches are narrow and all about the same width forming a more or less parallel-sided row deeply indenting the flat surface of the doublure and subparallel with its edges. The notches are all centrally excavated to about the same depth and are joined by shallower passages. The anterior notch runs into a deep vincular furrow behind which the doublure forms a pronounced flat shelf. *Sufferta*, on the other hand, has a much wider series of obliquely set vincular notches, becoming broader and deeper posteriorly and evidently adapted for receiving a flattened pleural end rather than a more pointed tip. The two ridges separated by the vincular notches are oblique to one another when seen in lateral view, and the outer one is indented by continuations of vincular notches. *A.* (*E.*) *sufferta*, the type species, has no trace of a vincular furrow, but has a pair of shallow subfrontal depressions meeting on the midline. *A.* (*E.*) *woodburnensis* has these subfrontal depressions as well, but also has a shallow vincular furrow joining each of them to the vincular notches. It is not a deeply incised furrow like that of *elliptifrons*, however, but a lightly impressed indentation. The vincular morphology of *woodburnensis* is in many ways intermediate between that of *elliptifrons* and that of *sufferta*, being anteriorly more similar to the former, and posteriorly resembling the latter; the three are illustrated here as a morphological series (text-fig. 3). In many ways, however, there is a fair resemblance between the vincular morphology of *woodburnensis*, to that of *Ananaspis* species (Campbell 1967, pl. 14, figs. 9, 13–15), though the presence of the subfrontal depressions links it with *Acernaspis* (*Eskaspis*) to which it is, with slight reservations, assigned here.

A. (*Eskaspis*) seems to have been a localized late Llandovery derivative of the *A.* (*Acernaspis*) stock, retaining most of its plesiomorphic (primitive) features of dorsal cephalic morphology, but having more advanced ventral morphology. This in *woodburnensis* is rather like that of the 'derived' genus *Ananaspis*, which it does not closely resemble in dorsal morphology, though it also has features pointing towards the more extreme, and indeed unique construction of the doublure of *Acernaspis* (*E.*) *sufferta*, which seems to have been a terminal endpoint.

Acernaspis (*Eskaspis*) *sufferta* (Lamont, 1947)

Plate 18, figs. 1–9; Plate 19, figs. 1–7, 10; text-figs. 2*a*, *f*, 3*a*, *b*, 4*a*, *c*

1861 *Phacops Stokesii* M.-Edw.; Howell and Geikie, p. 134.
1865 *Phacops Stokesii* Haswell, p. 37, pl. 4, figs. 6, 7.
1867 *Phacops Stokesii* Henderson, pp. 22–23.
1869 *Phacops Stokesii* Brown and Henderson, p. 31.
1899 *Phacops Stokesii* (M.-Edw.); Peach and Horne, p. 597.
1947*a* *Eophacops* cf. *elliptifrons* var. *glaber*. Marr and Nicholson; Lamont, p. 290.
1947*b* *Eophacops sufferta* n. sp. Lamont, p. 6, pl. 1, figs. 21, 22.
1962 *Phacops* aff. *stokesii* (Milne-Edwards); Mykura and Smith, p. 138.
1975 *Acernaspis* sp. Tipper, p. 297.

Material. Neotype, IGS 1034. Pl. 18, fig. 1, is here selected since Lamont's holotype is lost.

Other figured material. Gr. I. 40282, Pl. 18, fig. 2; Gr. I. 40279, Pl. 18, figs. 3, 7; IGS 5783, Pl. 18, fig. 4; Gr. I. 40269, Pl. 18, fig. 5; Gr. I. 40270, Pl. 18, fig. 6; Gr. I. 40262, Pl. 18, fig. 8; Gr. I. 40281, Pl. 18, fig. 9;

Gr. I. 40257, Pl. 19, fig. 1; Gr. I. 40243, Pl. 19, fig. 2; Gr. I. 40281, Pl. 19, fig. 3; Gr. I. 40260, Pl. 19, fig. 4; Gr. I. 40280, Pl. 19, fig. 5; Gr. I. 44093, Pl. 19, fig. 6; Gr. I. 40261, Pl. 19, fig. 7; Gr. I. 40275, Pl. 19, fig. 8; Gr. I. 44094, Pl. 19, fig. 10.

Additional material examined. Approximately 150 specimens from the Wether Law Linn Formation (Tipper's units A and C) from the Deerhope Burn and Wether Law Linn localities from the collections of the Grant Institute (Gr. I.) (mainly Tipper and Clarkson Collections), the Royal Scottish Museum (RSM), and the Institute of Geological Sciences (IGS) of Edinburgh.

Distribution. This species is confined to the lower Wether Law Linn Formation in the North Esk Inlier, Pentland Hills. It occurs quite abundantly and in good preservation as internal and external moulds at all levels, and complete specimens are not infrequently found. Fragmentary specimens recently discovered by S. Wood in the Reservoir Formation may belong to this species.

Diagnosis. A species of *Eskaspis* lacking connection between the subfrontal depressions of the anterior region of the doublure and the posterior, notched portion of the vincular furrow. Eyes large, with nineteen files (rarely eighteen in adults) with a general lens formula of 565 787 877 765 543 2 and about 116 lenses in all. Smaller specimens (approximately half adult size), with eighteen files of no more than six lenses. Lowermost lenses very small, elliptical in some specimens.

Dimensions. Holotype: total length (sag.) 20·0 mm, cephalic length (sag.) 5·7 mm, width 13·0 mm. Range in cephalic length 2·2–9·0 mm, width 5·0–17·5 mm.

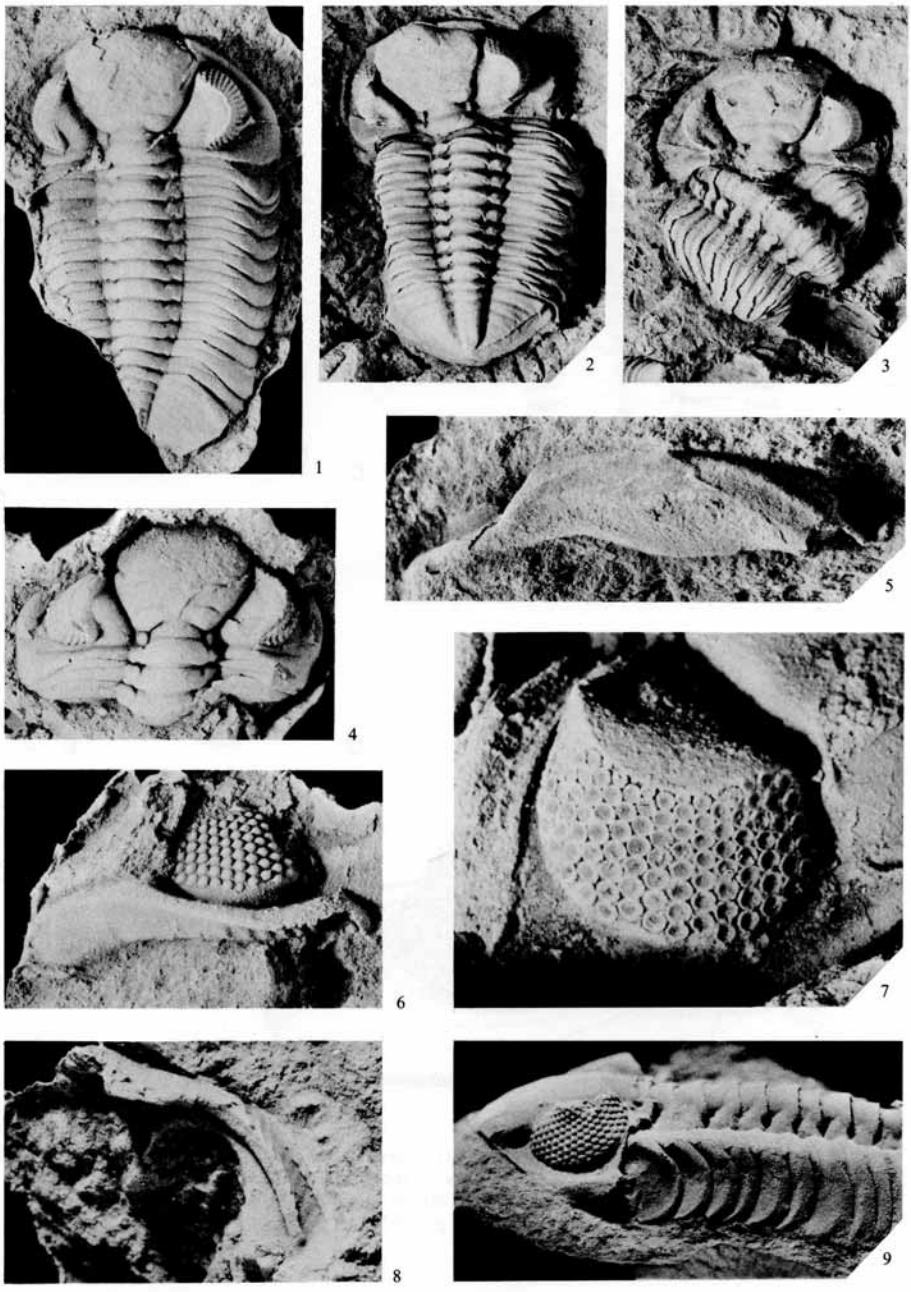
Description. Cephalon relatively broad, width/length ratio being approximately 2:1, and with an almost rounded (subangular) anterior margin (text-fig. 2*a*). Glabella half the cephalic width at its widest, broadly heptagonal, expanding anteriorly, widest in front of eyes where it is about as broad as its length. Glabellar crown (in profile) slightly higher than palpebral lobes (text-fig. 2*d*). In lateral profile the glabella is rather flattened on top, but slopes with increasing steepness to meet the anterior margin at about 80° with no real preglabellar furrow or preglabellar field, so that the glabella is directly in contact with the cephalic doublure. Axial furrows moderately deeply impressed, running forwards from lobe 1p at about 45° to an exsagittal line and changing direction where the palpebral furrow contacts glabellar lobe 3p, thence diverging from the exsagittal line only by some 10°, its course being indented slightly by the anterior edge of the eye. Axial nodes small, usually round but sometimes elongate.

All glabellar furrows faintly impressed and approximately equidistant from one another. 1p is the deepest; it is discontinuous and anteromedially directed at 45°.

EXPLANATION OF PLATE 18

Figs. 1–9. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Wether Law Linn Formation (Telychian), North Esk Inlier, Pentland Hills. 1, neotype. Wether Law Linn (WL), IGS 1035,* ×3·5. 2, complete specimen. Deerhope Burn (DB), Gr. I. 40282,† ×2·3. 3, almost complete, somewhat disarticulated specimen (DB), Gr. I. 40279,† ×2·5. 4, partially enrolled specimen (WL), IGS 5783,* ×3·5. 5, anterior doublure, showing subfrontal depressions, antero-ventral view (WL), Gr. I. 40269,* ×4·5. 6, eye and vincular notches, ventro-lateral view, Gr. I. 40270,* ×5. 7, right eye, Gr. I. 40279,† ×10. 8, doublure (cf. text-fig. 3) (DB), Gr. I. 40262,* ×5. 9, almost complete specimen in lateral view (DB), Gr. I. 40281,† ×4.

* Latex replica of external mould. † Internal mould.



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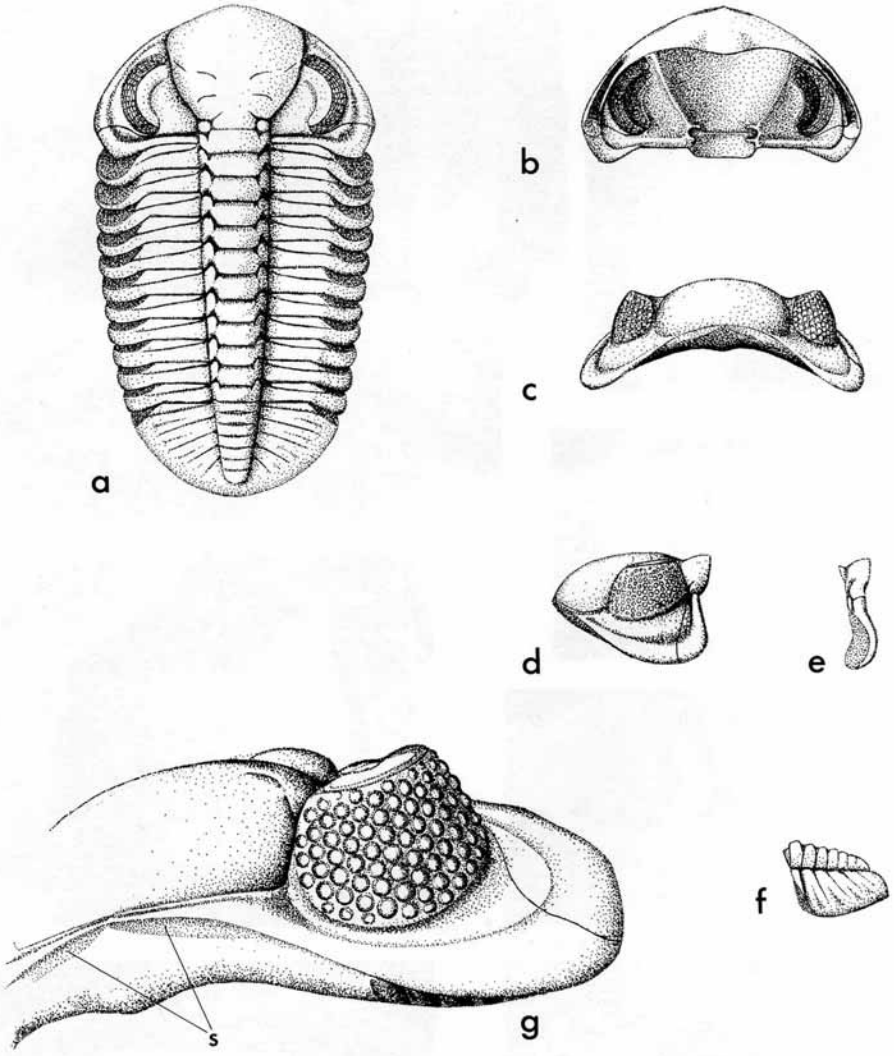


TEXT-FIG. 2. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Reconstructions of *a*, whole animal in dorsal view. *b–d*, cephalon in ventral, frontal, and lateral view. *e*, thoracic segment showing facet in lateral view. *f*, pygidium in lateral view. *g*, cephalon in oblique lateral view, showing subfrontal depressions (s). *a–f*, ×3·5; *g*, ×8·5.

Furrow 2p nearly transverse with the outer tip recurved; 3p in two distinct unjoined parts, inner part directed slightly forwards, outer part at 45° and not reaching the axial furrow. Intercalating ring not sharply demarcated anteromedially, but confluent with composite glabellar lobes. Anterior lobe half the total length of the glabella. Auxiliary glabellar impressions form a circular pattern, some are quite deeply impressed (text-fig. 5) (cf. *Acernaspis* figured by Eldredge 1971, text-fig. 2J).

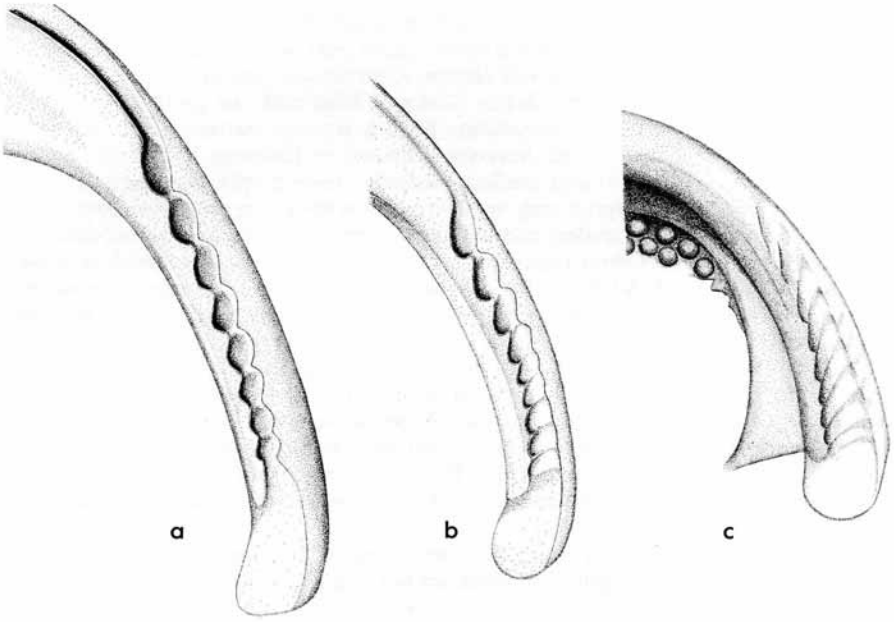
Occipital furrow straight and shallow medially, more deeply impressed laterally, at the apodemal pit, occipital ring very large (as wide as the posterior part of the glabella including lateral nodes) and with prominent lateral lobes directed forwards and outwards at 45°. Genal region with a definite lateral border which is widest postero-laterally, and delimited by a broad, shallow, lateral border furrow, less distinct below the eye, but becoming more incised anteriorly and nearly reaching the glabella. Posterior border furrow straight and deeply incised. Genal angles truncated, projecting somewhat posteriorly and subangular.

Palpebral lobes large, slightly inflated, and with a faint external rim extending from furrow 3p to the occipital furrow. Palpebral furrow usually distinct though may be rather vaguely defined in the central part. Palpebral area quite broad, triangular, mainly flat or slightly inflated. Eyes very large, nearly half the total height of the cephalon, the posterior edge slightly further from the midline than the anterior (Pl. 18, fig. 7; text-fig. 1*g*).

Lenses projecting beyond the sclera, not sunken, arranged in nineteen dorsoventral files (commonly eighteen in juveniles but rarely in adults) with a general lens formula:

567 787 877 765 543 2. Maximum per file eight. Total 116.

In some specimens the lowermost lenses are very small and elliptical. Eye socle very reduced. Facial suture apparently functional in holaspids, the anterior branch cutting antero-lateral corners of the anterior face of the glabella, meeting at a distinct point on the midline. Posterior branch directed at first anteriorly, then curving outwards and backwards again to reach the border opposite the posterior edge of the eye. The suture appears again on the postero-lateral part of the doublure making a posteriorly convex, symmetrical U-shaped lobe behind the course of the dorsal part of the suture (text-fig. 3). Cephalic doublure nearly a third the length of the glabella sagittally its rear margin convex posteriorly, the central part convex downwards. Vincular furrow marked anteriorly only as a pair of elongate, contiguous, and shallow subfrontal depressions on either side of the midline (text-fig. 1*b*, *g* (marked 's')). Where the depressions meet, there is a tiny forwardly projecting point. Subfrontal depressions separated from the notched lateral vincular furrow which extends from below the anterior edge of the eye to nearly below its posterior edge. The inner lamella of the lateral doublure is less steeply inclined in lateral aspect than the outer lamella which forms the postero-lateral margin of the cephalon. Posteriorly, the inner lamella ends abruptly below the dorsal facial suture in front of the U-shaped lobe; the outer lamella extends further back (text-fig. 3). The most anterior notches are less deeply impressed than those which lie posteriorly; nine notches are evident in all, and are arranged radially from a point posterior to the U-shaped lobe defined by the doublural suture. The doublure turns abruptly at the



TEXT-FIG. 3. The lateral part of the ventral doublure, showing vincular structures and coaptative morphology in *Acernaspis* (*Acernaspis*) and *A.* (*Eskaspis*). *a*, *A.* (*Acernaspis*) *elliptifrons* (Esmark), from the Newlands Formation (Idwian), Girvan, Ayrshire. BM It 9121. *b*, *A.* (*Eskaspis*) *woodburnensis* n. sp. from Wood Burn Formation (lowermost Telychian), Lauchlan Burn, Girvan, Ayrshire. IGS 5777. *c*, *A.* (*Eskaspis*) *sufferta* (Lamont), Wether Law Linn Formation (upper Telychian), Pentland Hills, near Edinburgh. Gr. I. 40262 (see Pl. 18, fig. 8), all $\times 14$. All these illustrations are camera-lucida drawings made from latex replicas of external moulds.

genal angle and tails off to terminate just behind the posterior edge of the eye. Occipital and 1p apodemes distinct on ventral surface of the cephalon.

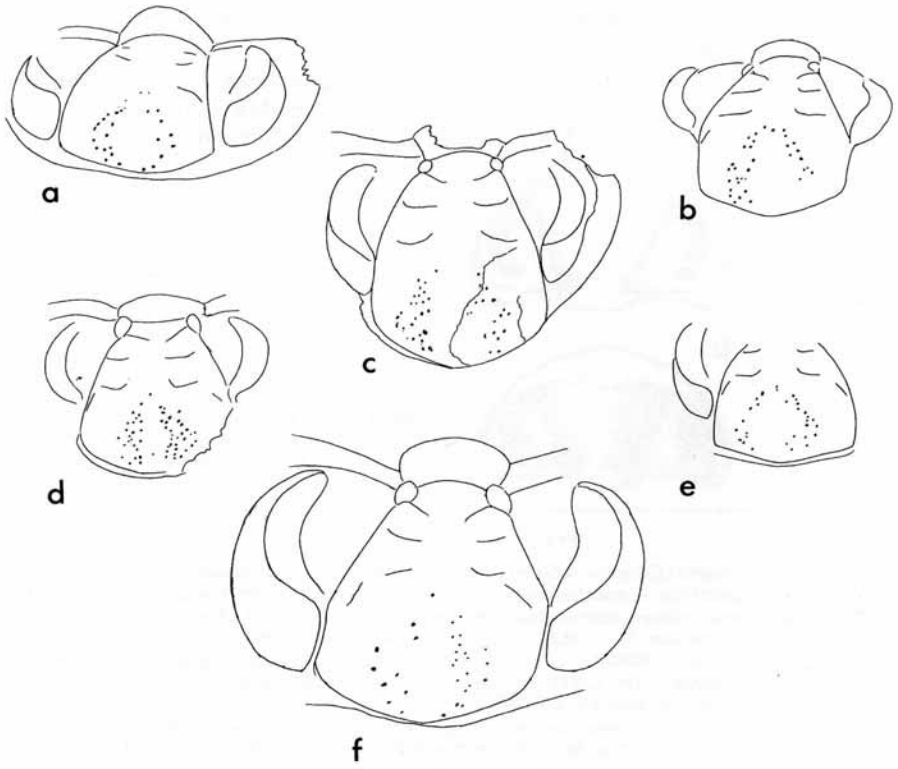
Thorax of eleven segments tapering backwards slightly, having quite strongly arched rings. Axis is quarter the total width. Each axial ring is indented anteriorly by deep paired incisions, which together with shallower posterior incisions placed closer to the axial furrows delimit chevron-shaped axial lobes, set further forward than the axial part of the ring but are not swollen as nodes (text-fig. 2*a*, *e*). Posterior border of each axial ring high and sharp. A distinct furrow divides the articulating half-ring from the axial ring.

Pleural regions flat but strongly bent down distally. Pleural furrows straight or slightly curving, narrow, of moderate depth, and extend as far as the articulating facets. Facets very pronounced anteriorly while the pleural ribs are very narrow and curved, but diminishing in size and curvature posteriorly. The rear edge of the flat top of each pleuron has a narrow flange articulating with a corresponding anterior groove on the next segment.

Pygidium with rounded or almost imperceptibly pointed margin with nine to ten rings diminishing in size posteriorly (text-fig. 2*a*, *f*). The last two axial rings are indistinct, the first three or four have a pseudo-articulating half-ring. There are four or five pleural furrows whose obliquity increases backwards, the first being quite deep, the others increasingly shallow, interpleural furrows weakly impressed, and disjunct. All pleural and interpleural furrows fade out some distance before the pygidial margin, leaving a broad smooth border zone.

Pygidial doublure broad, with two lateral parts forming a small notch in the sagittal line and shaped to fit the two vincular depressions on the cephalon.

All parts of the exoskeleton are covered with dense microgranular sculpture except for the subocular groove which is smooth. On the doublure, glabella, and axial rings and pleural ribs this sculpture is especially dense, though it is sparser on the flat tops of the pleurae.



TEXT-FIG. 4. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Camera-lucida drawings showing auxiliary impression patterns on the anterior glabellar lobe. All ×5. *a*, Gr. I. 40271; *b*, Gr. I. 40263; *c*, Gr. I. 40281; *d*, Gr. I. 40265; *e*, Gr. I. 40264; *f*, Gr. I. 40257.

Acernaspis (*Eskaspis*) *woodburnensis*, n. sp.

Plate 19, figs. 9, 11–13; text-fig. 5*a*, *b*

1899 *Phacops stokesi* (M.-Edw.). Peach and Horne, p. 538.
1906 *Phacops elegans* Sars and Boeck. Reed, p. 155.

Locus typicus. Lauchlan Burn (Bargany Pond Burn, Girvan, Ayrshire).

Stratum typicum (Wood Burn Formation, lowermost Telychian) (Cocks and Toghill 1973, p. 225)

Diagnosis. Axial furrows straight, diverging forwards to a point in front of the eye. Eyes fairly large, not particularly high, posterior edge more distant than the anterior edge from the sagittal line. Lenses distributed in sixteen files as follows:

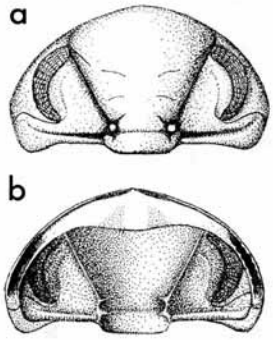
566 677 776 766 534 3. Maximum per file seven. Total 90.

Posterior section of doublure has ?nine vincular notches on each side connected by a shallow vincular furrow to the subfrontal depressions.

Types. Holotype IGS 5777. Paratypes IGS 5778–5779, 5780–5781 (parts and counterparts).

Other material. Ten specimens in IGS collections.

Remarks. A. (*E.*) *woodburnensis* is the oldest member of this subgenus known at present but is stratigraphically younger than the middle Llandovery *A.* (*A.*) *elliptifrons* of the Newlands Formation. It is particularly interesting that here a



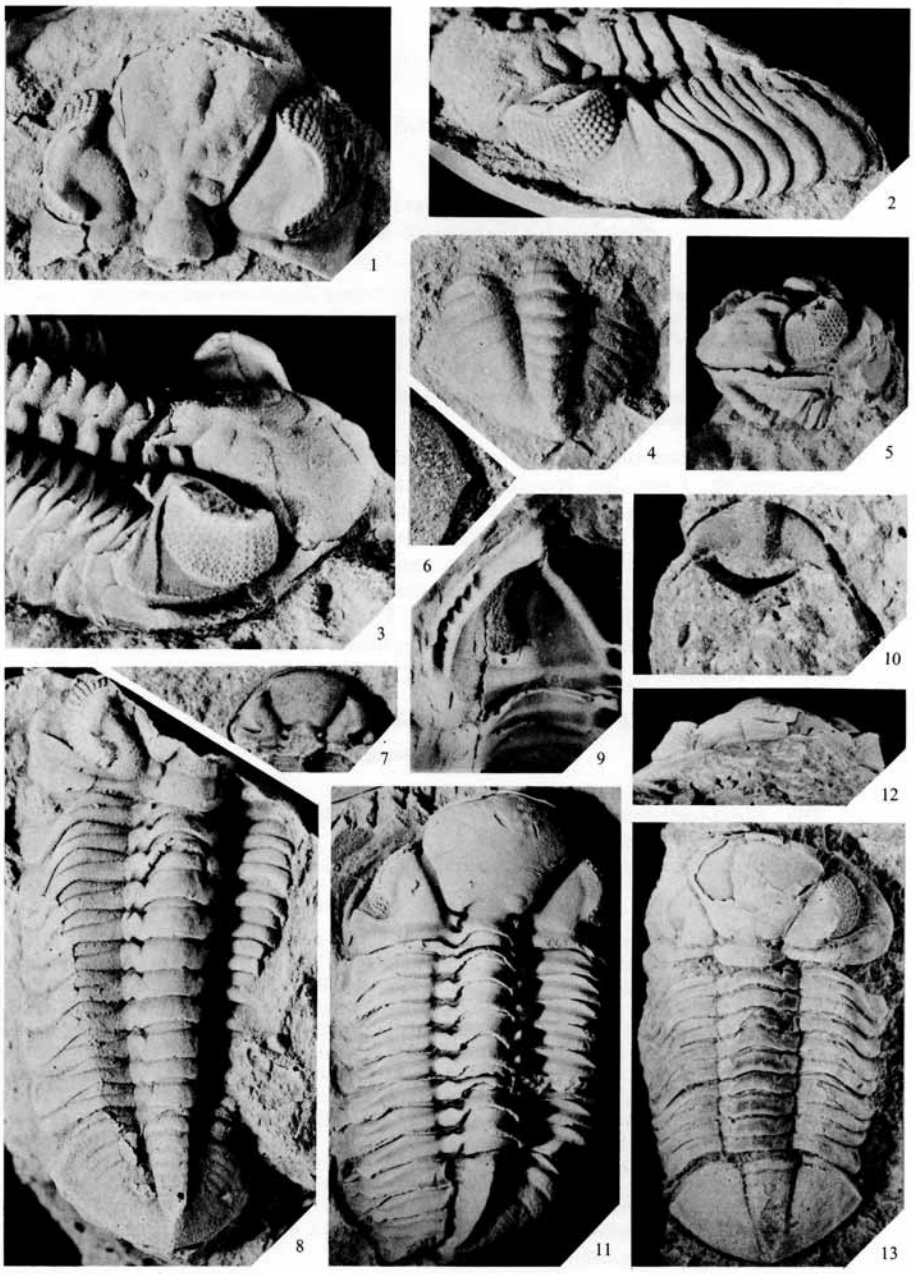
TEXT-FIG. 5. *Acernaspis* (*Eskaspis*) *woodburnensis*, n. sp. *a*, *b*, cephalon reconstructed in dorsal and ventral view, ×2·25.

EXPLANATION OF PLATE 19

Figs. 1–7, 10. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Wether Law Linn Formation (Telychian), North Esk Inlier, Pentland Hills. 1, cephalon with auxiliary impression patterns, Gr. I. 40257,* ×3·5. 2, cephalon and part thorax, oblique anterolateral view, Gr. I. 40243,* ×3·75. 3, almost complete specimen, oblique antero-lateral view, Gr. I. 40281,† ×5·25. 4, pygidium, Gr. I. 40260,* ×6. 5, almost complete enrolled specimen, Gr. I. 40280,† ×2·75. 6, genal point, visible only on internal mould, Gr. I. 44093,† ×15. 7, small cephalon, Gr. I. 40261,† ×4. 8, almost complete specimen, Gr. I. 40275,* ×3·75. 10, doublure of small specimen, Gr. I. 44094,† ×5·5.

Figs. 9, 11–13. *A.* (*Eskaspis*) *woodburnensis*, n. sp. Wood Burn Formation (lowermost Telychian). 'Bargany Pond Burn' = Lauchlan Burn, Maxwellton Hill, Girvan. 9, ventral view of holotype cephalon showing doublure with shallow furrow connecting vincular notches to subfrontal depressions, IGS 5777, ×3·5. 11, holotype, IGS 5777,† ×2·5. 12, 13, anterior and dorsal views of complete specimen retaining its cuticle though altered and exfoliated in places, IGS 5780, ×2.

* Latex replica of external mould. † Internal mould.



CLARKSON, ELDREDGE and HENRY, *Acernaspis*

shallow vincular furrow is present, though absent in the otherwise quite similar *A. (E.) sufferta*.

Dimensions. Holotype: total length (sag.) 28·0 mm, cephalic length (sag.) 10·0 mm, width 18·5 mm. Range in cephalic length 9·5–11·0 mm, width 17·0–20·0 mm.

Superfamily DALMANITACEA Vogdes, 1890
Family PTERYGOMETOPIDAE Reed, 1905
Genus PODOWRINELLA gen. nov.

Type species. *Podowrinella straitonensis* (Lamont, 1965) by original designation and monotypy, from the Knockgardner Formation (?Wenlock) of the Blair-Straiton district near Girvan, Ayrshire, and the Ree Burn Formation (?Telychian, upper Llandovery), Hagshaw Hills, and the Deerhope Formation (Telychian), North Esk Inlier, Pentland Hills.

Etymology. From the Podowrin Burn in the Hagshaw Hills where the Ree Burn Formation outcrops and where fossils are common in the turbidites.

Diagnosis. Small Phacopina combining features of both phacopid and pterygometopid organization. Cephalon roughly triangular but with truncated genal angles. Glabella pear-shaped with furrow 1p connected to 3p as in Pterygometopidae but 3p in two distinct parts as in Phacopidae, and confluent with axial furrows. Eyes with about eighteen files with up to seven lenses each, about 100 lenses altogether. Cephalic doublure traversed by deep, broad coaptative grooves, continuous laterally, becoming dorso-medial just before they meet. Thorax with axial nodes and strongly downturned outer parts of the pleurae. Pygidium somewhat triangular with a rounded or occasionally slightly pointed margin.

Podowrinella straitonensis (Lamont, 1965)

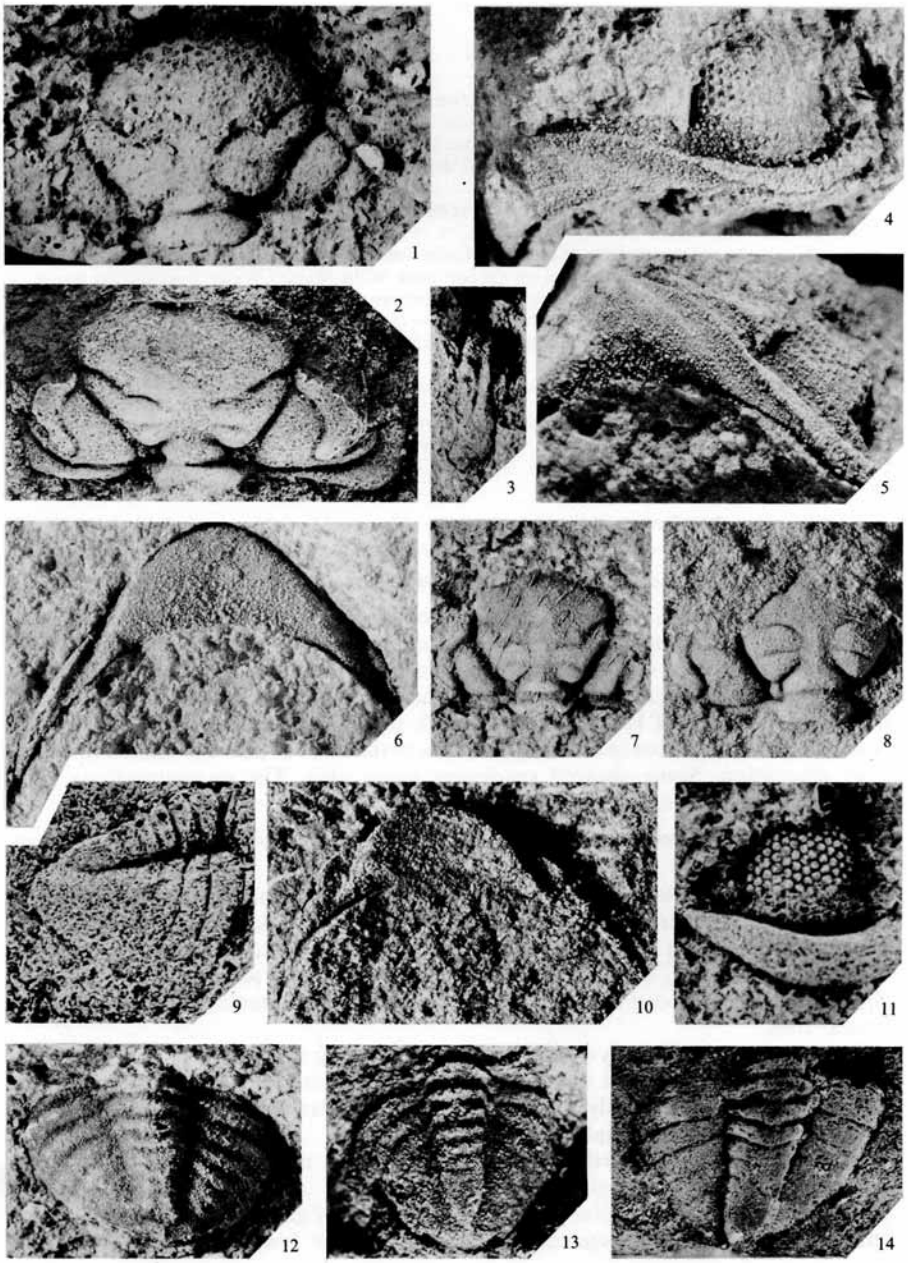
Plate 20, figs. 1–14; text-fig. 6*a–h*

1962 *Phacops* sp. nov. Rolfe, p. 252.
1965 *Phacops straitonensis* sp. nov. Lamont, p. 39, pl. V, fig. 5.
1973 *Phacops straitonensis*. Rolfe, p. 109.

EXPLANATION OF PLATE 20

Podowrinella straitonensis (Lamont). 1, neotype cranidium, figured by Lamont (1965, pl. V, fig. 5), almost undistorted. Ree Burn Formation, Hagshaw Hills (Rolfe's loc. 31), BU 1900,* ×6. 2, cranidium in W-mode deformation. Top of Deerhope Formation, Deerhope Burn, North Esk Inlier, Pentland Hills (locality B), Gr. I. 40340,* ×5·5. 3, thoracic segment in lateral view. Pentland Hills (loc. B), Gr. I. 40348,† ×3·5. 4, 5, anterolateral and ventrolateral view of detached librigena showing vincular furrows and eye, small quarry in the Ree Burn Formation, nearly opposite junction of Shiel Burn with Monk's Water, Hagshaw Hills (loc. A), RSM 1975-43-2,† ×6·5. 6, ventral surface showing vincular furrows, RSM 1975-43-3,† ×6. 7, undistorted cranidium. Knockgardner Formation, Knockgardner, IGS M 13219,† ×3·5. 8, cranidium. Pentland Hills (loc. B), Gr. I. 40310,* ×5·55. 9, lateral view of compressed pygidium. Pentland Hills (loc. B), Gr. I. 40345,* ×7·5. 10, ventral surface W-mode deformation). Pentland Hills (loc. B), Gr. I. 40358,† ×6. 11, left eye and subjacent librigena. Hagshaw Hills (loc. A), RSM 1975-43-4,* ×7·5. 12, pygidium. Hagshaw Hills (loc. A), RSM 1975-43-5, ×5·5. 13, pygidium (L-mode deformation). Pentland Hills (loc. B), Gr. I. 40349,* ×5. 14, pygidium showing accessory half-ring on segment 1. Pentland Hills (loc. B), Gr. I. 40307,* ×6·5.

* Latex replica of external mould. † Internal mould.



CLARKSON, ELDREDGE and HENRY, *Podowrinella*

Material

(*a*) Hagshaw Hills.

(1) Twenty-five specimens from the Rolfe Collection, University of Birmingham, including BU 1900a, b figured by Lamont (1965, pl. V, fig. 5), which is herein designated as neotype, since the unfigured holotype from Knockgardner is now lost (Lamont pers. comm.).

Neotype. BU 1900a, b (from Rolfe's locality 31/48 in unpublished thesis; University of Birmingham 1960).

Other material. Thirty other specimens in the collection of the Department of Geological Sciences, University of Birmingham.

(2) One hundred specimens from the Ritchie Collection, Royal Scottish Museum, collected from a small quarry in the Ree Burn Formation on the east bank of the Monk's Water, opposite the mouth of the Shiel Burn, Hagshaw Hills. These include the paratypes RSM 1975-43-1, RSM 1975-43-2 (Pl. 20, figs. 4, 5), RSM 1975-43-3 (Pl. 20, fig. 6), RSM 1975-43-4 (Pl. 20, fig. 11), RSM 1975-43-5 (Pl. 20, fig. 12).

Also twenty-five RSM specimens from the foot of the Podowrin Burn, east of Monk's Water, Hagshaw Hills.

In addition, fifty-five other specimens from the same localities in the Grant Institute Collections (Gr. I.).

(*b*) North Esk Inlier. Specimens from Tipper and Clarkson Collections. Top of Deerhope Formation, Deerhope Burn. Paratypes Gr. I. 40340, Pl. 20, fig. 2; Gr. I. 40348, Pl. 20, fig. 3; Gr. I. 40310, Pl. 20, fig. 8; Gr. I. 40348, Pl. 20, fig. 9; Gr. I. 40358, Pl. 20, fig. 10; Gr. I. 40349, Pl. 20, fig. 13; Gr. I. 40307, Pl. 20, fig. 14.

(*c*) Knockgardner. Blair-Straiton Inlier, east of Girvan. Maconochie Collection. IGS M 13219 (Pl. 20, fig. 7) and twenty-five other IGS specimens. Also thirty specimens in Grant Institute of Geology.

Range. Telychian (North Esk, Hagshaws)—?lower Wenlock (Knockgardner).

Remarks. The material available from Knockgardner and the Hagshaw Hills is all preserved as disarticulated fragments collected from the base of turbidite flows. Specimens are found in all orientations and most individuals have suffered some distortion. The notable variation in width and length between specimens resembling the L and W forms of Henningsmoen (1960, p. 207) and Sadler (1974, pp. 81, 85) is attributed to stress due to crushing pressure of the mass of unconsolidated turbidite after deposition. Some sheared specimens occur also. The reconstructions were made from the less distorted specimens.

Dimensions. Holotype: cephalic length (sag.) 5 mm, width 10 mm. Range in cephalic length 4–6 mm, width 8–12 mm.

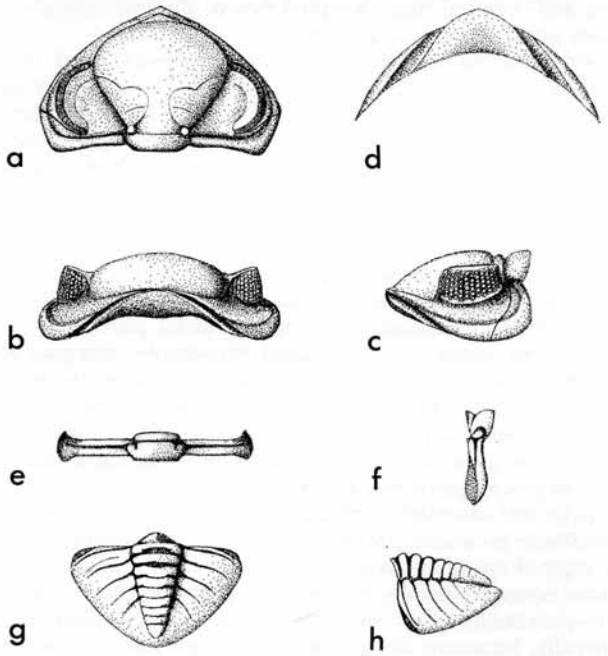
Description. Small Phacopidae with roughly triangular cephalic outline (in dorsal view), modified by truncated genal angles. Cephalon widest at distal librigenal/fixigenal junction. In lateral view (text-fig. 6*c*) (in standard orientation), glabella depressed anteriorly, sloping regularly postero-dorsally, with central region of glabella extending above level of palpebral lobes. Large anterior arch developed in frontal view.

Axial furrows moderately deeply implaced, diverging at an angle of approximately 65° then abruptly reflected directly in front of the anterior edge of the palpebral lobe, and curving smoothly around anterior glabellar lobe, becoming confluent with anterior and lateral cephalic border furrows.

Glabella pear-shaped, with anterior, 3p, 2p, and medial portion of 1p lobes united to form composite glabellar lobe (text-fig. 6*a*). Anterior glabellar lobe sub-ovate, continuous with medial portion of remainder of glabella. Anterior margin of anterior glabellar lobe rounded, bounded by furrow bearing anterior ramus of

facial suture antero-laterally. Facial suture continuous with anterior border furrow medially; anterior border, border furrow, and facial suture thus meeting in a distinct point medially, delimiting a small, triangular pre-glabellar field proximal to facial suture. Anterior border thin, though distinct in front of this field; concentric with facial suture, but disappearing marginally.

Glabellar furrow 3p in two parts, with sharp bend between distal and proximal branches; branches generally connected at bend by shallow furrow, occasionally



TEXT-FIG. 6. *Podowrinella straitonensis* (Lamont). *a–c*, reconstructions of cephalon in *a*, dorsal, *b*, frontal, *c*, lateral aspects. *d*, cephalic doublure in ventral view. *e*, *f*, thoracic segment in dorsal and lateral view. *g*, *h*, pygidium in dorsal and lateral view. All ×4.

wholly disconnected on internal and external moulds. Distal branch of 3p furrow deepest proximally, confluent with axial furrow just opposite anterior margin of visual surface, slightly convex anteriorly, running at an angle of approximately 55° from the midline. Proximal branch of 3p furrow comma-shaped, with proximal terminus slightly posterior to distal terminus. Proximal terminus continuous with a broad, shallow, variably developed longitudinal glabellar furrow running posteriorly and communicating smoothly with 1p glabellar furrows. Glabellar furrow 2p short, comma-shaped (convex anteriorly) with distal and proximal tips in transverse line, and not communicating with axial furrow distally, but confluent with

longitudinal glabellar furrow medially. Glabellar furrow 1p deeply incised distally. confluent with axial furrow, and recurved antero-proximally. Glabellar furrow 1p apparently continuous medially as broad, shallow furrow, delineating an intercalating ring.

Glabellar lobe 3p hypertrophic distally; ratio of glabellar lobe lengths along axial furrow roughly: 4·7:2:1 for 3p:2p; 1p. 2p lobe small, ovate, 1p lobe longest medially, reduced to nodes distally, and depressed below concordant surface of anterior glabellar region and occipital ring. Occipital furrow shallow, straight; occipital ring of approximately equal length (sag.) throughout.

Posterior border furrow shallow, communicating with axial furrow, running nearly transversely, distally becoming more shallow and recurved antero-distally, confluent with lateral border furrow of librigena. Posterior border distinct, roughly transverse proximally, becoming thickened distally near genal margin, thereby causing slight deflection to posterior margin of cephalon. Posterior border sharply reflected antero-distally, forming a bluntly pointed genal angle of approximately 100°. Lateral cephalic border reflexed antero-proximally at point where crossed by posterior ramus of facial suture. Lateral border continuous with anterior border; anterior border becoming progressively thinner approaching midline.

Lateral border of librigena steeply inclined, capped by sharp ridge; lateral border furrow broad, smoothly confluent with concave distal portion of librigena (text-fig. 6*c*). Librigena becoming steeply inclined proximally, merging with eye socle (not distinctly defined because of lack of ornamental features due to poor preservation). Visual surface nearly vertical, with eighteen d-v files with up to seven lenses per file, about 100 lenses in all. Eye moderately long, not reaching posterior border furrow. Palpebral lobe quite narrow, inflated above palpebral area and set off from it by a sharply implaced palpebral furrow. Palpebral area relatively flat, sloping postero-proximally and smoothly confluent with fixigenal area posterior to eye.

Cephalic doublure produced anteriorly into flat trapezoidal spatulate process, inclined at an angle of approximately 25° (in lateral view) and visible in frontal view. Spatulate process bounded distally by deep, broad grooves traversing doublure, and inclined antero-proximally at an exsagittal angle of approximately 35°. Grooves continuous laterally, becoming dorsal where converging at midline (text-fig. 6*b*, *d*). Anterior-most medial portion of cephalon a thin ridge where anterior border, vincular groove, and spatulate process coterminate. Cephalic doublure developed as thin ridge postero-distally to vincular grooves; inner wall nearly vertical. Hypostoma unknown.

Auxiliary impression pattern and details of cephalic ornament unknown; cephalon apparently smooth (based on study of external moulds).

Thorax incompletely known; most of the thoracic segments examined (probably the anterior ones) with the axis one-quarter the width of the whole, axial nodes set off by short, deep anterior furrows (text-fig. 6*e*, *f*). Pleural furrows relatively shallow, of moderate depth, and straight. Inner part of pleura flat, outer third sharply turned down; pleural tips pointed. Pleural facets present but not very distinct.

Pygidium (text-fig. 6*g*, *h*) equilaterally triangular with, however, its posterior apex truncated, having approximately eight axial rings and terminal piece; two or more accessory half-rings present. Axis not reaching posterior pygidial margin, acutely

rounded posteriorly. At least four pairs of pleurae present; inter-pleural furrows obscure. Pleural furrows becoming fainter posteriorly, and nowhere reaching pygidial border. Most specimens have a rounded pygidium, but in some examples the posterior border is slightly pointed, especially in those from the Pentland Hills.

Remarks. This genus cannot be readily confused with any other taxon known to us. To clarify its diagnosis and to aid in recognition of related forms we briefly discuss which features are peculiar to the taxon alone, and which are 'phacopid-like' and 'pterygometopid-like'.

There is no question that *Podowrinella* is, in the great majority of its features, pterygometopid in aspect. In fact, *Podowrinella* is very similar indeed to the Ordovician pterygometopids *Calyptaulax* and *Eomonarachus*, in particular to those species of *Calyptaulax* from Europe which, as Shaw (1974, p. 42) has noted, have a 'noticeable bend' along glabellar furrow 3p. Pterygometopid-like features of *Podowrinella* include over-all conformation of cephalon; possession of a distinct lateral and anterior border (reduced anteriorly in *Podowrinella*); glabellar segmentation, generally, including size and shape of glabellar lobes and presence of longitudinal glabellar furrows; narrow palpebral lobes; anterior branch of facial suture meeting in a distinct point; presence of a spatulate medial projection of the cephalic doublure; and a somewhat triangular pygidium, pointed in some examples.

Podowrinella is phacopid-like in the following features: presence of a 3p glabellar furrow divided into two parts, discontinuous in some specimens of *P. straitonensis*, with the proximal moiety nearly transversely oriented (the distal ramus remains pterygometopid-like in conformation); a smoothly rounded anterior glabellar margin; truncated genal angles, without genal spines; nearly complete loss of interpleural furrows, and sharp reduction in the number of pleural furrows, on the pygidium. We hasten to add that some species of *Calyptaulax*, particularly *C. callicephala*, are very much like *Podowrinella* in having a smoothly rounded anterior glabellar margin and truncated genal angles; supposed 'phacopid-like' characters. Finally, *Podowrinella* appears to be rather unique in the coaptative doublure morphology, though some pterygometopid species, again, particularly *C. callicephala*, are somewhat similar in possessing a vincular furrow traversing the doublure and converging antero-dorsally at the midline.

Though we have been unable to reach a final agreement on the taxonomic position of *Podowrinella*, the unusual combination of characters which it displays does reinforce Eldredge's (1971) suggestions as to a close relationship between Phacopidae and Pterygometopidae. There are some interesting resemblances between *A.* (*Eskaspis*) and *Podowrinella*, in terms of glabellar furrowing, eye size and position, and genal angles. Sometimes specimens of *A.* (*E.*) *sufferta* show traces of extended glabellar furrows, so that 1p and 3p are faintly connected (e.g. the slightly crushed specimen in Pl. 19, fig. 1). There seem to be possible grounds for restructuring the current classification of Phacopina and the curious morphology of *Podowrinella* could be critical.

Coaptative structures in A. (Acernaspis), A. (Eskaspis), *and* Podowrinella: *some remarks*

Within trilobites of the Phacopina and other suborders there have been described a substantial array of structures on the ventral doublure of the cephalon which interlock during enrolment with mirror-image structures on the thorax and the pygidium. Examples have been figured by Campbell (1967), and others have been discussed in detail by Henry and Nion (1970), Clarkson and Henry (1973), and Henry and Clarkson (1975). These have arisen independently in a number of trilobite groups and have been defined (Hupé 1953; Clarkson and Henry 1973) as coaptative mechanisms. They have, in our estimation, much potential value in taxonomy, as well as their intrinsic interest from the functional and evolutionary point of view, but before this can be effectively realized, it is essential to illustrate and document the various types present in different trilobite groups.

This study gives information of the nature of coaptative mechanisms of *A.* (*Acernaspis*), *A.* (*Eskaspis*), and *Podowrinella.* In *A.* (*Eskaspis*) (text-fig. 3*c*) there are nine vincular notches on each side which receive the tips of the thoracic pleurae. Though no complete enrolled specimens have been found which might enable further details of the mechanism to be elucidated, it appears that these notches are for the reception of the last nine pleural tips; the first two pleurae are shorter and have wider facets. During enrolment, they probably locked in against the end of the inner ridge of the doublure (text-fig. 3) close together with the tip of the third pleuron. The more posterior pleurae were fitted into depressions which became progressively more spaced out towards the anterior of the doublure, whilst becoming less deeply impressed. By contrast with *A.* (*Acernaspis*) which has a well-marked semicircular vincular furrow connecting the two lateral sets of vincular notches (text-fig. 3*a*), *A.* (*E.*) *woodburnensis* has only a very shallow furrow, connecting with the two subfrontal depressions, whilst *A.* (*E.*) *sufferta* only has the two depressions, and no furrow at all. In both species of *A.* (*Eskaspis*) two slightly swollen areas on the pygidial doublure fit into the subfrontal depressions; otherwise the pygidium comes to rest freely against the flat (or only slightly indented in the case of *A.* (*E.*) *woodburnensis* surface of the anterior part of the cephalic doublure. This difference between the coaptative morphology of the doublure of *A.* (*Acernaspis*) and *A.* (*Eskaspis*) is coupled with the fact that in the former subgenus the surfaces of the parallel vincular ridges lie in the same plane, whereas in the latter they are somewhat oblique to one another, so that the inner ridge as seen in lateral profile having the higher angle to the horizontal; there are other differences also as previously mentioned (p. 125). It is not certain whether the morphological sequence illustrated in text-fig. 3, and previously referred to is a true evolutionary sequence. Had the specimens all been collected from a single vertical section it would be almost unequivocal. Even so, the morphology, confined distribution, and stratigraphically sequential changes suggest a definitive evolution towards the grade of organization in *A.* (*E.*) *sufferta* within a fairly localized area.

Podowrinella has no separate notches for the reception of individual pleural tips, but only a pair of elongated furrows, deepening posteriorly and becoming slightly twisted in the process. With this type of structure the pleural tips come to rest in the groove, as does the doublure of the pygidium, and presumably the triangular point

at the extreme anterior of the cephalon forms a seal with the similarly angular sagittal edge of the said pygidial doublure. Such coaptative morphology resembles that of some Pterygometopidae though in a more extreme form.

The range in morphology of coaptative structures amongst Phacopina is considerable; compare, for example, the ventral morphology of the doublure in *Kloucekia*, *Morgatia*, and *Crozonaspis* species (Henry and Nion 1970; Clarkson and Henry 1973), with that of the trilobites discussed in this paper. The value of these in taxonomy is probably very great, but there is, as present, a need for detailed study covering a wider spectrum than is presently known, and only then will their actual value be able to be established.

Acknowledgements. We thank Dr. John Tipper who collected many of the specimens, discussed many points with us, and read critically the final manuscript. Dr. Charles Waterston and Mr. William Baird of the Royal Scottish Museum (RSM), Edinburgh, loaned specimens and discussed localities, as did Peter Brand of the Institute of Geological Sciences, Edinburgh (IGS), who first drew the specimens of *A.* (*E.*) *woodburnensis* to our attention. Dr. Isles Strachan, University of Birmingham (BU) loaned specimens from the Rolfe Collection. Mr. B. Johnstone prepared most of text-fig. 1.

Finally, Dr. Archie Lamont of Carlops, Peeblesshire, who encouraged us to work on these trilobites, corresponded with us throughout, and helped with many queries.

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E. N. K. CLARKSON

Grant Institute of Geology
West Mains Road
Edinburgh EH9 3JW

N. ELDREDGE

Department of Invertebrate Paleontology
American Museum of Natural History
Central Park West
New York, NY 10024, U.S.A.

J.-L. HENRY

Institut de Géologie
Université de Rennes
Avenue du Général-Leclerc
35031 Rennes-Cedex, France

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