SPECIES OF *TRETASPIS* (TRILOBITA) FROM THE ASHGILL SERIES IN WALES

by DAVID PRICE

ABSTRACT. Nine species of *Tretaspis* are recognized from various horizons of the Ashgill Series in Wales. *Tretaspis colliquia* Ingham is regarded as a sub-species of *T. moeldenensis* Cave. Four populations of *Tretaspis* are placed in *T. moeldenensis* (s.l.) and considered to occupy intermediate positions within the plexus connecting *T. moeldenensis colliquia* and *T. m. moeldenensis*; for the latter, large topotype samples also give increased knowledge of the fringe characters. *T.* cf. *radialis* Lamont occurs throughout the bulk of the Sholeshook Limestone Formation (south-west Dyfed) but is replaced in the topmost part by *T.* aff. *radialis*. The pygidium of an indeterminate species from the Birdshill Limestone at Llandeilo resembles that of *T. m. moeldenensis*. *T. hadelandica brachystichus* Ingham is described from the highest Sholeshook Limestone and succeeding Slade and Redhill Mudstone Formation, *T.* cf. *latilimbus distichus* Ingham from the high Ashgill of the south-west Berwyns and *T.* cf. *sortita* (Reed) from the topmost Ashgill of the Meifod area. An indeterminate form from the Slade and Redhill Mudstones and *T.* cf. *calcaria* Dean from the Rhiwlas Limestone are not yet placed within either of Ingham's two main species groups.

As with other trinucleid trilobites at lower levels in the Ordovician, species of the genus *Tretaspis* are of stratigraphical importance within the Ashgill Series in that, apart from their abundance and wide geographical distribution, some forms appear to exhibit progressive evolutionary changes. Good examples of this are seen in some of the species described by Ingham (1970, pp. 45–57) from the north of England. Although the phylogeny of *Tretaspis* is far from completely understood, some evolutionary relationships are known, and these can be used for correlation in different successions.

Terminology. The terminology and notation used in describing fringe characteristics largely follow those of Ingham (1970, pp. 40–41). Ingham has pointed out that in many species of *Tretaspis* new internal (I) arcs of pits are apparently inserted in evolution on the external side of the innermost arc already present. In many specimens this is strongly suggested by the disposition and small size of pits developed in this position (e.g. in the specimen illustrated here as Pl. 101, fig. 2). Accordingly the innermost pit-arc is regarded as complete and is unnumbered and referred to as the I_n arc. Hughes *et al.* (1975, p. 6) have found the concept of the I_n arc of wide application within family Trinucleidae and reveal that current work on silicified young stages of marrolithines shows I_n to be the first arc to develop on the immature fringe. Ingham (1970) is also followed in using an aR/bR notation to refer respectively to the radii containing the I_2–I_n pits and those with the I_1, E_1, and E_2 pits which in members of his *T. seticornis* species group (see below) are out of line, and in his use of the terms 'genal roll' and 'brim' solely for describing fringe shape. In addition, the term 'list' (Størmer 1930) is used for the concentric ridges sometimes developed between the inner pit-arcs on the upper lamella. The cephalic orientation adopted for descriptive purposes is that suggested by Hughes *et al.* (1975, pp. 546–547, fig. 7) with the anterior and posterior fossulae in the horizontal plane.

Repositories. The material upon which this paper is based is housed in the following museums, the prefixes for whose specimen numbers are indicated in brackets: British Museum (Natural History) (BM), Geology Museum, University of Birmingham (BU), Hunterian Museum, Glasgow (HM), Institute of Geological Sciences (GSM), National Museum of Wales (NMW), and the Sedgwick Museum, Cambridge (SM).

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SYSTEMATIC PALAEONTOLOGY

Family TRINUCLEIDAE Hawle and Corda, 1847
Subfamily TRINUCLEINAE Hawle and Corda, 1847
Genus TRETASPIS M'Coy, 1849

Type species. Subsequently designated by Bassler 1915, p. 1285; *Asaphus seticornis* Hisinger, 1840, p. 3, pl. 37, fig. 2; Fjacka Formation, Dalarna, Sweden.

Remarks. Ingham (1970, pp. 41–44) attempted a division of known species of *Tretaspis* into three species-groups typified respectively by *T. moeldenensis* Cave, 1960, *T. seticornis* (Hisinger), and '*T.*' *granulata* (Wahlenberg, 1818). '*T.*' *granulata* and allied forms such as '*T.*' *portrainensis* Lamont, 1941, have subsequently been removed from *Tretaspis* and placed in genus *Nankinolithus* Lu (Hughes *et al.* 1975). The genus *Tretaspis* is thus divided by the latter authors into two major groups of species.

As Ingham noted (1970, p. 41), the extent to which these groups form natural associations is not yet clear and there are difficulties in fitting a few forms (including two dealt with in this paper) into them. Accordingly the *T. moeldenensis* group and the *T. seticornis* group are adopted herein tentatively and with the reservation that the two forms referred to above (*T.* sp. indet. B and *T.* cf. *calcaria* Dean) are not placed in either group but are regarded as being, as yet, of uncertain affinity (see also p. 787 below).

THE *TRETASPIS MOELDENENSIS* GROUP

For the characteristics of the group see Ingham 1970, p. 43.

Tretaspis moeldenensis Cave, 1960 (sensu lato)

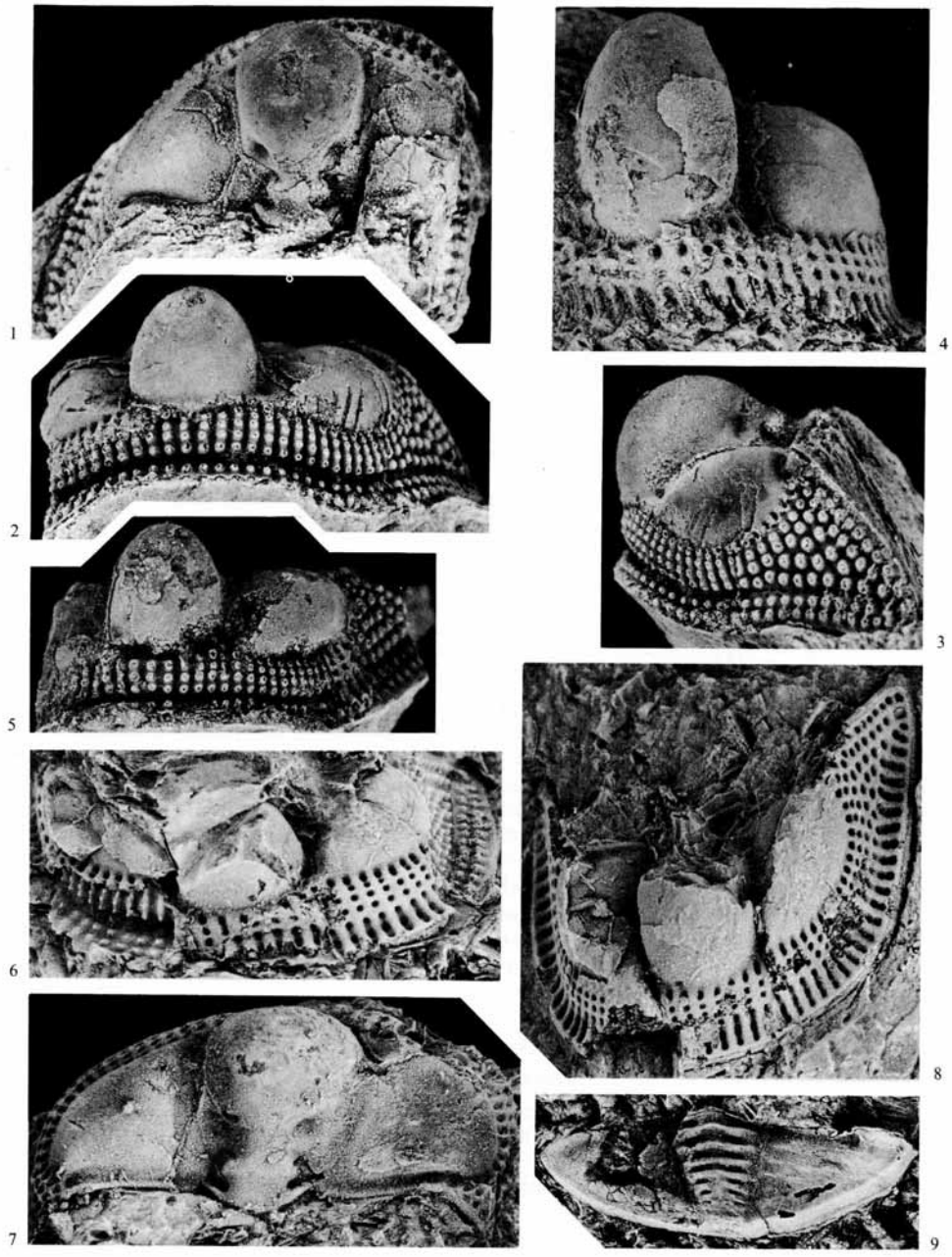
Plates 98 and 99; Plate 100, fig. 1; text-fig. 1

1909 *Trinucleus seticornis*, var. *bucklandi*, Barr.; Elles, faunal list, p. 182.
1909 *Trinucleus fimbriatus* Murch.; Strahan *et al.*, p. 56.
1921 *Trinucleus* cf. *nicholsoni* Reed; Wills and Smith, table, p. 187.
1921 *Trinucleus seticornis* Hisinger; Wills and Smith (*pars*), table, p. 187.
1921 *Trinucleus* sp.; Wills and Smith (*pars*), table, p. 187.
1927 *Trinucleus* cf. *nicholsoni* Reed; Wedd *et al.*, list, p. 40.
1927 *Trinucleus seticornis* (His.); Wedd *et al.* (*pars*), list, p. 40.
1927 *Trinucleus* sp.; Wedd *et al.* (*pars*), list, p. 40.
1928 *Trinucleus seticornis* group; King, lists, p. 698.

EXPLANATION OF PLATE 98

Figs. 1–5. *Tretaspis moeldenensis* Cave (s.l.), Population A, Bodeidda Mudstone Formation, Bodeidda, near Conway, ×6. 1–3, GSM RV 9144a, internal mould of cephalon, dorsal, anterior, and left-lateral views. 4, GSM RV 9141, partial internal mould of cephalon, anterior view. 5, GSM RV 9142, internal mould of cephalon, anterior view.

Figs. 6–9. *Tretaspis moeldenensis* Cave (s.l.), Population B, basal Tre-wylan Beds, Glan-yr-afon Farm, north of Llansantffraid-ym-Mechain. 6, Bu. 209, internal mould of cephalon, antero-dorsal view, ×4; original of Whittington 1938, pl. 38, fig. 2. 7, SM A94573a, internal mould of cephalon, dorsal view, ×5. 8, Bu. 208, internal mould of cephalon, oblique view, ×4; original of Whittington 1938, pl. 38, fig. 1. 9, SM A94592, internal mould of pygidium, dorsal view, ×5.



PRICE, *Tetraspis* from Wales

1929 *Trinucleus* sp.; Wedd *et al.* (*pars*), list, p. 61.
1938 *Tretaspis* cf. *kiaeri* Størmer; Whittington (*pars*), p. 445, pl. 38, figs. 1–3; *non* list, p. 452.
1960 *Tretaspis moeldenensis* Cave, pp. 334–337, pl. 10, figs. 1–7.
1961 *Tretaspis kiaeri* Størmer *radialis* Lamont; Dean (*pars*), pp. 122–125.
1962 *Tretaspis kiaeri* Størmer *radialis* Lamont; Dean, p. 86, pl. 9, figs. 2–4.
1970 *Tretaspis colliquia* Ingham, pp. 53–54, pl. 8, figs. 8–20; text-fig. 14*b*.
1970 *Tretaspis* cf. *moeldenensis* Cave; Ingham, pp. 54–55, pl. 8, figs. 21–26; pl. 9, figs. 1–7; text-figs. 14*c*, 19.
1973*a* *Tretaspis moeldenensis* Cave; Price, tables 3 and 4.
1973*b* *Tretaspis moeldenensis* Cave; Price, p. 540.
1974 *Tretaspis moeldenensis* Cave; Price, pp. 844–847, pl. 112, figs. 10–12; pl. 113, figs. 1–4; text-fig. 1.

Holotype. Figured by Cave 1960, pl. 10, figs. 1 and 3, SM A50668, from the basal Sholeshook Limestone Formation of Moldin (= 'Moelden'), near Llandowror, Dyfed, South Wales.

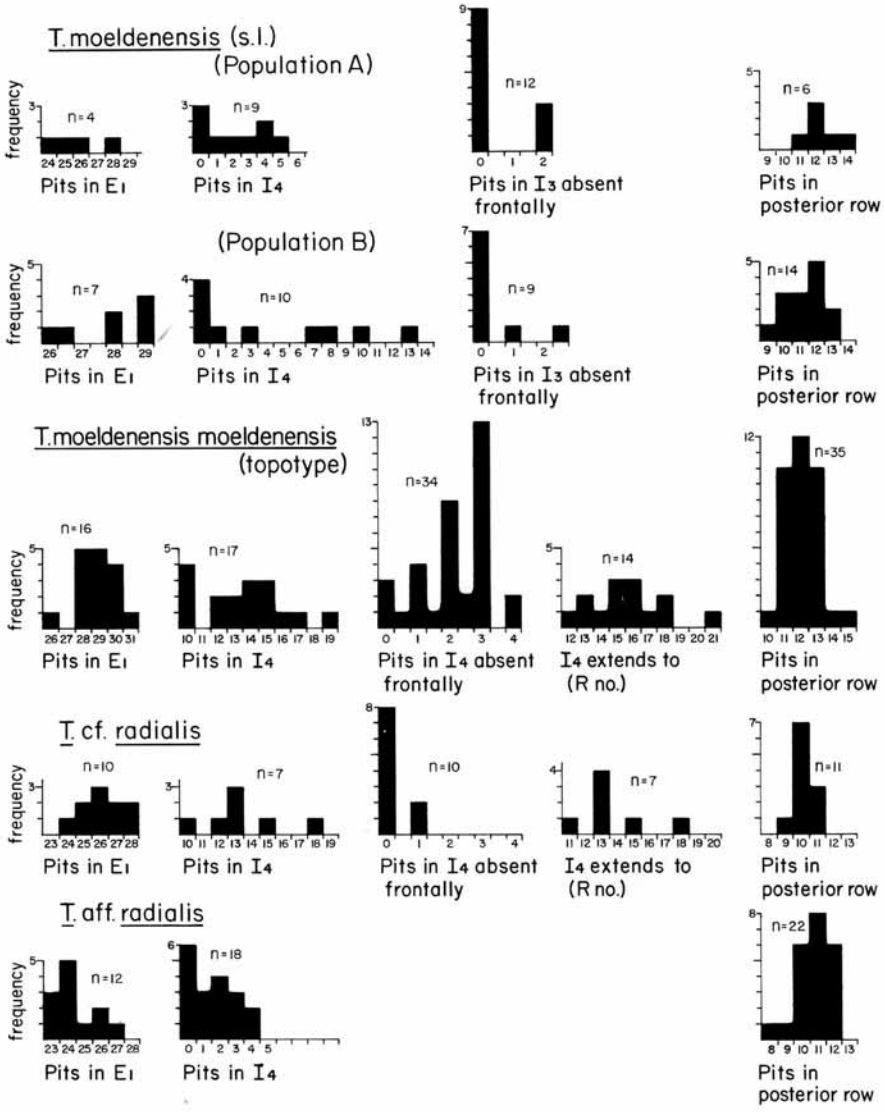
Remarks. Ingham (1970, p. 55) has referred to an evolving *T. colliquia–T. moeldenensis* plexus. In Wales there appear to be at least three or four populations which fall within this plexus and whose members in general show characters intermediate between those of *T. colliquia* and *T. moeldenensis*. In terms of fringe-characters, particularly the development of the I_4 pit-arc, each of these populations shows much variation. This variation can be such (in Population B of text-fig. 1 for instance) that the fringe-characters of some members of a single population fall within the range of *T. colliquia*, the fringe-characters of other members within the range of *T. moeldenensis*, and those of yet other members fall between, outside the known range of either form. For this reason, *T. colliquia* and *T. moeldenensis* are no longer regarded as specifically distinct and *T. colliquia* is treated here as a sub-species of *T. moeldenensis* (s.l.). The name *T. m. colliquia* is considered applicable to populations with a similar range of fringe variation to that of the sample described by Ingham (1970, see synonomy) while the name *T. m. moeldenensis* is similarly applied to populations falling within the range of fringe variation of topotype material of that form (here described). Populations where the variation ranges outside that of either of these end-members might be compared with one or other of them by the use of such designations as 'cf.' and 'aff.'. The large range of variation already referred to within some of these populations, however, renders such terms difficult of application. Partly for this reason and partly because of the small sample sizes and consequent limited knowledge of the range of variation of some of the populations involved (and of the described material of *T. m. colliquia*), such a course is not adopted and the populations described here are referred to as populations of *T. moeldenensis* (s.l.). This solution is also felt to be more appropriate in reflecting the probable existence of a continuum between *T. m. colliquia* and *T. m. moeldenensis*.

Population A

Plate 98, figs. 1–5; text-fig. 1

Material, horizon, and locality. Twenty specimens, in the collection of the Geological Survey, from the Bodeidda Mudstone Formation; quarry 14 m west of Bodeidda, about 2·5 km south-west of Conway, Gwynedd, North Wales.

Description. Cephalon approximately semicircular in dorsal view; exact proportions masked by distortion. Pseudofrontal glabella lobe occupying almost two-thirds of total glabellar length (sag.), sub-circular in



TEXT-FIG. 1. Histograms of selected fringe characters in species of *Tretaspis* of the *T. moeldenensis* group. n is the sample number for each character shown. All histograms show half-fringe data. *T. moeldenensis* (s.l.): Population A from Bodeidda Mudstone Formation, Bodeidda, near Conway, Population B from basal Tre-wylan Beds, near Llansantffraid-ym-Mechain, Powys. *T. moeldenensis moeldenensis* from basal Sholeshook Limestone Formation, Moldin, near Llandowror, Dyfed. *T.* cf. *radialis* from Sholeshook Limestone Formation of Haverfordwest and Llandowror, Dyfed. *T.* aff. *radialis* from topmost Sholeshook Limestone and Slade and Redhill Mudstone Formation of Haverfordwest area.

dorsal view, strongly domed, particularly transversely, but never sub-spherical so that the outline in anterior view remains parabolic (Pl. 98, figs. 2, 4–5); bearing small, apically situated median tubercle; barely overhanging the fringe anteriorly. Occipital ring narrow and strongly convex (sag. and exsag.), orientated postero-dorsally; curving forwards abaxially. Occipital furrow broad and shallow mesially, abaxially containing deep ovoid apodemal pits. 1p lateral glabellar lobes short (tr.), gently convex, abaxially rounded. 1p lateral furrows in form of strongly oblique shallow slots, diverging posteriorly and almost reaching the occipital apodemes. 2p lobes only gently convex (exsag.), set transversely, narrowest adaxially, broadening outwards and coalescing anteriorly, around the 2p furrows, with the pseudofrontal lobe. 2p furrows in form of large, shallow ovoid depressions of rather indistinct outline. 3p furrows present as faint but definite depressions on sides of pseudofrontal lobe. Axial furrows broad (tr.), particularly posteriorly; anteriorly containing small, deep fossulae. Genal lobes sub-quadrant shaped, moderately convex, and dropping steeply antero-laterally but not overhanging fringe; bearing lateral tubercles, rather larger than the median tubercle, on about the level of the anterior edges of the 2p lateral furrows; dropping steeply to broad (exsag.) posterior border furrows which abaxially contain large posterior fossulae. External moulds show surface of glabella and genal lobes to be smooth. Fringe moderately broad, comprising steeply inclined, convex genal roll and well-developed, gently concave brim; internal moulds show a deep, rather narrow girder. Outer 3 pit-arcs, E_{1-2}, I_1, arranged frontally and antero-laterally in deep radial sulci which persist on one specimen to about R19, on another to R24. The number of pits in E_1 ranges from 24 to 28 (half-fringe, see text-fig. 1); pits of E_2 are usually absent from the posterior row and sometimes from the posterior-most 2 rows. The number of pit-arcs developed internally to the 3 outer arcs and their degree of completeness is very variable. In addition to I_n, all specimens have a complete I_2 arc. Nine specimens show a complete I_3 arc but on 3 others I_3 pits are absent frontally from R1 and R2 (e.g. Pl. 98, figs. 4, 5). These 3 specimens do not show an I_4 pit-arc but on the 9 where I_3 is complete, a short I_4 arc, normally with between 1 and 5 pits, is developed in front of the axial furrows. One specimen, however (GSM RV9133), shows at least 10 I_4 pits. In no specimen is the I_4 arc complete frontally, pits generally being developed from R3 or R4 outwards. Pits of the I_n arc are frequently large. All pits are arranged in strict radial alignment until the genal prolongations are reached, where the alignment breaks down due to the intercalation of extra pits between the I_1 and I_2 arcs; the fringe, thus expanded, may have from 11 to 14 pits in the posterior row. No lists have been observed on the fringe upper lamella. On the lower lamella, pits of the internal arcs are arranged, except on the genal prolongations, in strong radial sulci (Pl. 98, fig. 3).

Thorax and pygidium unknown.

Population B

Plate 98, figs. 6–9; text-fig. 1

Material, horizon, and locality. Useful material comprises about twenty-eight specimens from the basal Tre-wylan Beds exposed around a small waterfall in the dingle 370 m north-west of Glan-yr-afon Farm, about 4 km north of Llansantffraid-ym-Mechain, Powys, Mid-Wales. This is Locality 42 of Whittington 1938 and Locality 3 of Wedd *et al.* 1929 (list, p. 62).

Description. The general form and proportions of the cephalon are very similar to those described for specimens in Population A; however, no specimen so far seen definitely shows the presence of 3p lateral glabellar furrows. Again, the genal lobes, though dropping steeply antero-laterally, do not generally overhang the fringe. Both these and the pseudofrontal lobe are smooth. The fringe itself has a well-developed brim, particularly laterally and antero-laterally. Pit-arcs E_2, E_1, and I_1 are contained in deep radial sulci which persist laterally to R23 or R24. E_1 contains from 26 to 29 pits; E_2 pits are absent from the posterior row or posterior 2 rows. All specimens have a complete I_2 arc. Of 9 specimens which show clearly the distribution of pits anteriorly, 7 have the I_3 arc complete, the others have respectively 1 and $2\frac{1}{2}$ pits of I_3 missing. I_4 is very variably developed. Apart from the definite numbers shown in the histogram (text-fig. 1), this arc in other specimens contains respectively 1 or 2, at least 3, at least 4, at least 11, and at least 13 pits. Only in one specimen is the I_4 arc complete frontally, pits of I_4 usually being developed from R3, R4, R5, or R6 outwards. One specimen, however, appears to show a single pit of I_4 at about R10. Pits of I_n are frequently rather larger than those of the other arcs. The posterior row contains between 9 and 13 pits. Lists do not appear to be developed. The girder is broad and deep with weak, closely spaced terrace lines.

Pygidium (Pl. 98, fig. 9) sub-triangular in outline, broad (tr.), the sagittal length only about one-third

of the maximum width; postero-lateral margins moderately convex; bluntly rounded posteriorly. Maximum pygidial width about four and a half times anterior width of axis. Latter tapers posteriorly at about 25° and is gently convex (tr.). Ring furrows shallow, gently arched forward, each containing a pair of deep apodemal pits a short distance from the axial furrows; axis bears eight such pairs of pits in all, the posterior-most pair usually only weakly developed. Pleural lobes flat, with up to four faintly defined pleural ribs. There is no submarginal rim.

Population C

Plate 99, figs. 1–5

Material, horizon, and locality. Twenty-four specimens in the collection of the Geological Survey, from the basal Ty'n-y-twmpath Beds of the Northern Berwyns; Locality 47 of Wedd *et al.*, 1927 (p. 41), in the headwaters of the Nant-y-Lladron, about 5 km south-south-east of Corwen. Most of this material is distorted and/or fragmentary and the comments below are effectively based on less than half of it.

Description. Cephalon similar in over-all morphology to that described for specimens of Population A, with the surfaces of the pseudofrontal and genal lobes smooth and with the latter, although steep antero-laterally (Pl. 99, fig. 1), not overhanging the fringe. No 3p lateral glabellar furrows have been seen in the present material. Fringe with well-developed brim. E_2, E_1, and I_1 pits arranged in deep radial sulci except on posterior parts of prolongations. I_2 and I_3 arcs complete frontally on all available material. The I_4 arc is variably developed. On 2 specimens (Pl. 99, figs. 1, 3) it is definitely not developed and on a third it appears to be absent also. On 3 other specimens I_4 is developed though the number of pits is difficult to estimate. On the original of Plate 99, fig. 5 at least 3 and possibly 5 pits are present, on the original of Plate 99, fig. 4, 2 pits are clearly present opposite the axial furrow and up to 7 further pits may be present sharing sulci with pits of I_n; a third specimen shows at least 2 and possibly 3 or 4 I_4 pits. The pits of the I_n arc tend to be large (Pl. 99, figs. 1, 3, 4). The number of pits in the E_1 arc is difficult to count accurately due to fringe distortion but estimates on 4 specimens are as follows: 27 or 28, about 29, 28 or 29, about 28. There are 11 pits in the posterior row (3 specimens). Two pygidia are far too distorted for their proportions to be of any use. One of them (GSM LW836) shows at least 7 pairs of apodemes.

Discussion. The material of *T. m. colliquia* described by Ingham (1970, pp. 53–54, pl. 8, figs. 8–20; text-fig. 14*b*) from the lower part of the Pusgillian Stage of the Cautley Mudstones shows less variation in fringe characters than the forms described here. Even so, the variation does encompass a frontally incomplete I_3 pit-arc and up to two or three pits in the I_4 arc. Population A is thus relatively close to *T. m. colliquia* while Population B of the Welsh material differs more markedly in the relatively more frequently and more extensively developed I_4 arc. In this respect it is nearer to *T. m. moeldenensis* in which, however, the I_3 arc is invariably complete and in which no specimen has yet been seen with less than ten pits in the I_4 arc (text-fig. 1). All the Welsh material differs from *T. m. colliquia* in apparently lacking the faint pseudofrontal lobe reticulation seen in the latter and in that the genae do not definitely overhang the fringe. Pygidia, though relatively poorly known, differ too in that none shows definitely more than eight pairs of apodemal pits on the axis.

Another small sample of a form belonging within *T. moeldenensis* (s.l.) comes from the basal Ashgill Mudstones of the stream section south of the old quarry at Pen-y-garnedd, about 20 km north-west of Welshpool, Powys (Locality 1 of Wedd *et al.* 1929, list, p. 61). Of 8 specimens known, only 3 are complete enough and well-enough preserved to yield useful data. SM A42898 has 29 or 30 pits in the E_1 arc, 6 pit-arcs (E_{1-2}, I_{1-3}, I_n) anteriorly from R1 to R4 and has the I_4 arc developed from R5 to at least R13 (i.e. at least 9 pits are present); a specimen on the same block (SM A94999) shows at least 8 I_4 pits. The third specimen, however, GSM WK 389, shows no sign

of the I_4 arc even in the axial furrow region, although I_3 is complete. Again the variation is considerable though still well within the range seen, for instance, in Population B described above. Clearly a larger sample is needed before the relationships of this form can be properly assessed.

Tretaspis moeldenensis moeldenensis Cave, 1960

Plate 99, figs. 6–9, ?10; ?Plate 100, fig. 1; text-fig. 1

1909 *Trinucleus fimbriatus* Murch.; Strahan *et al.*, p. 56.
?1921 *Trinucleus* sp.; Wills and Smith (*pars*), table, p. 187.
?1927 *Trinucleus* sp.; Wedd *et al.* (*pars*), list, p. 40.
?1928 *Trinucleus seticornis* group; King, lists, p. 698.
1960 *Tretaspis moeldenensis* Cave, pp. 334–337, pl. 10, figs. 1–7.
1973*a* *Tretaspis moeldenensis* Cave; Price, tables 3 and 4.
1974 *Tretaspis moeldenensis* Cave; Price, pp. 844–847, pl. 112, figs. 10–12; pl. 113, figs. 1–4; text-fig. 1.

Holotype. As under *T. moeldenensis* (s.l.) above.

Horizons and localities. Apart from its presence in a thin basal horizon of the Sholeshook Limestone Formation of South Wales (Localities 17, 24a, and 25 of Price 1973*a*), the subspecies is here tentatively recognized from (locally) basal or near-basal Ashgill strata at two localities in the Berwyn Hills.

Discussion. Topotype material of *T. m. moeldenensis* has already been redescribed in detail (Price 1974, see synonomy), though fringe characters were dealt with at that time on the basis of rather small samples (Price 1974, text-fig. 1). However, to allow clear distinctions to be made between *T. m. moeldenensis* and other closely related forms, it was considered desirable to work with much larger samples and extensive re-collecting of topotype material was undertaken. This has resulted in a much-increased knowledge of fringe characters as shown by the histograms in text-fig. 1. (The I_3 arc, where seen frontally, is invariably complete.)

Larger samples of topotype pygidia show that larger and better preserved specimens occasionally bear nine pairs of apodemes on the axis, though the last pair is usually very faint (Pl. 99, fig. 9). Eight is the much more usual number (Pl. 99, fig. 6) and even then the posterior-most pair is often faint.

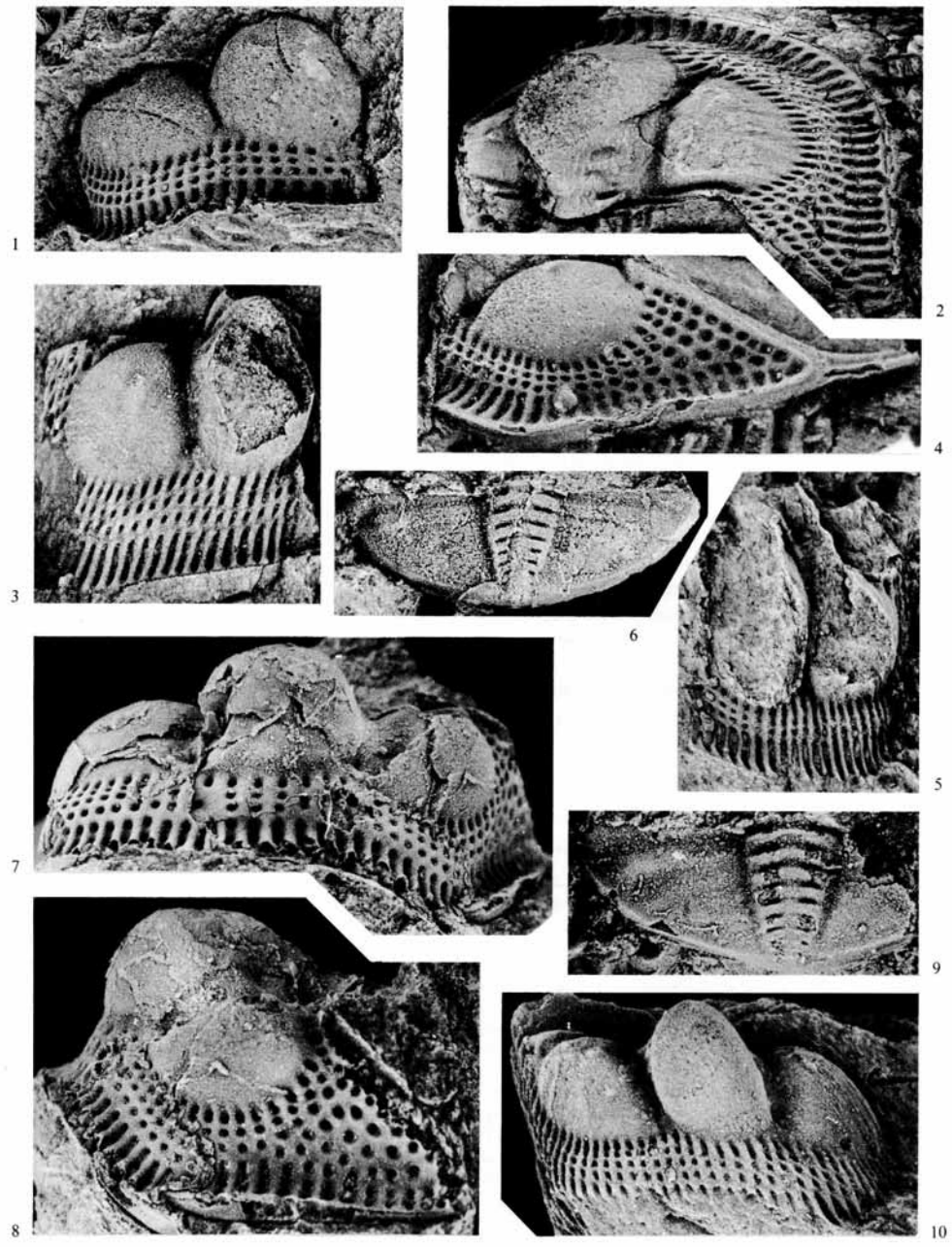
A small sample of *Tretaspis* from a locality (Locality 36 of Wedd *et al.* 1927, p. 41)

EXPLANATION OF PLATE 99

Figs. 1–5. *Tretaspis moeldenensis* Cave (s.l.), Population C, basal Ty'n-y-twmpath Beds, headwaters of Nant-y-Lladron, south of Corwen. 1, GSM JM 3908, cast from partial external mould of cephalon, anterior view, ×6. 2, GSM JM 3905, incomplete internal mould of cephalon, dorsal view, ×4. 3, GSM LW 832, partial internal mould of cephalon, anterior view, ×6. 4, GSM LW 844, cast from partial external mould of cephalon, left-lateral view, ×5. 5, GSM LW 835, partial internal mould of cephalon, antero-dorsal view, ×6.

Figs. 6–9. *Tretaspis moeldenensis moeldenensis* Cave, basal Sholeshook Limestone Formation, Moldin, near Llandowror. 6, SM A77741, internal mould of pygidium, dorsal view, ×5. 7, 8, SM A94951a, internal mould of cephalon, anterior and left-lateral views, ×5. 9, SM A77734, incomplete internal mould of pygidium, dorsal view, ×6.

Fig. 10. ?*Tretaspis moeldenensis moeldenensis* Cave, GSM LW 1289, internal mould of cephalon, low Ty'n-y-twmpath Beds, headwaters of Nant-y-Lladron, south of Corwen, anterior view, ×6.



PRICE, *Tetraspis* from Wales

in the Ty'n-y-twmpath Beds of the Northern Berwyns, close to and stratigraphically perhaps 40 m above that from which Population C of *T. moeldenensis* (s.l.) was collected, appears to belong with *T. m. moeldenensis*. External moulds show the cephalon to be non-reticulate. Three specimens show, in addition to a complete I_3 pit-arc, at least 14 (Pl. 99, fig. 10), at least 10 (Pl. 100, fig. 1) and 9 or 10 (GSM LW 1297) pits in I_4. In the original of Plate 99, fig. 10, I_4 pits are absent for $1\frac{1}{2}$ rows frontally; the position in the original of Plate 100, fig. 1 is not clear. In the 3 specimens referred to, the I_4 pits, apart from being more extensively developed than in specimens of the slightly older Population C of *T. moeldenensis* (s.l.), are larger and more clearly separated from the I_n pits, not closely associated with them as they are when developed in specimens of the latter form and the I_n pits themselves are not noticeably large. A fourth specimen (GSM LW 1310) is a distorted pygidium which appears to show at least 8 pairs of apodemal pits.

A form first recorded by King (1928, p. 681) from the basal Ashgill Mudstones near Glyn Cottage at the head of Cwm Nant-y-meichiaid, 3 km north-west of Meifod, may also belong here. Material collected by the author (SM A94800–94811, A94826–94830, and 94832) is of a non-reticulate form with 26 or 27 pits in E_1 (one specimen in each case). Seven specimens showing the appropriate regions of the fringe have a complete I_3 pit-arc and an extensive I_4 arc developed. On one specimen I_4 is incomplete frontally for 2 radii and on 4 others for an indeterminate but small number. In the first specimen I_4 extends from R3 to R14 (i.e. 11 pits), in 2 others to around R16. Two further specimens show respectively 11 and at least 10 pits in I_4 and a fringe fragment shows part only of an I_4 arc with 7 pits. The posterior row shows 10, 11, 12 (1 specimen each), or (in 3 specimens) 13 pits. An incomplete pygidium shows 7 or 8 pairs of apodemes on the axis.

For other material not described here but regarded as belonging within *T. moeldenensis* (s.l.) (see synonomy of that form), there is insufficient fringe data, particularly in relation to the extent of the I_4 pit-arc, to establish its relationship with *T. m. moeldenensis*.

Tretaspis cf. *radialis* Lamont, 1941

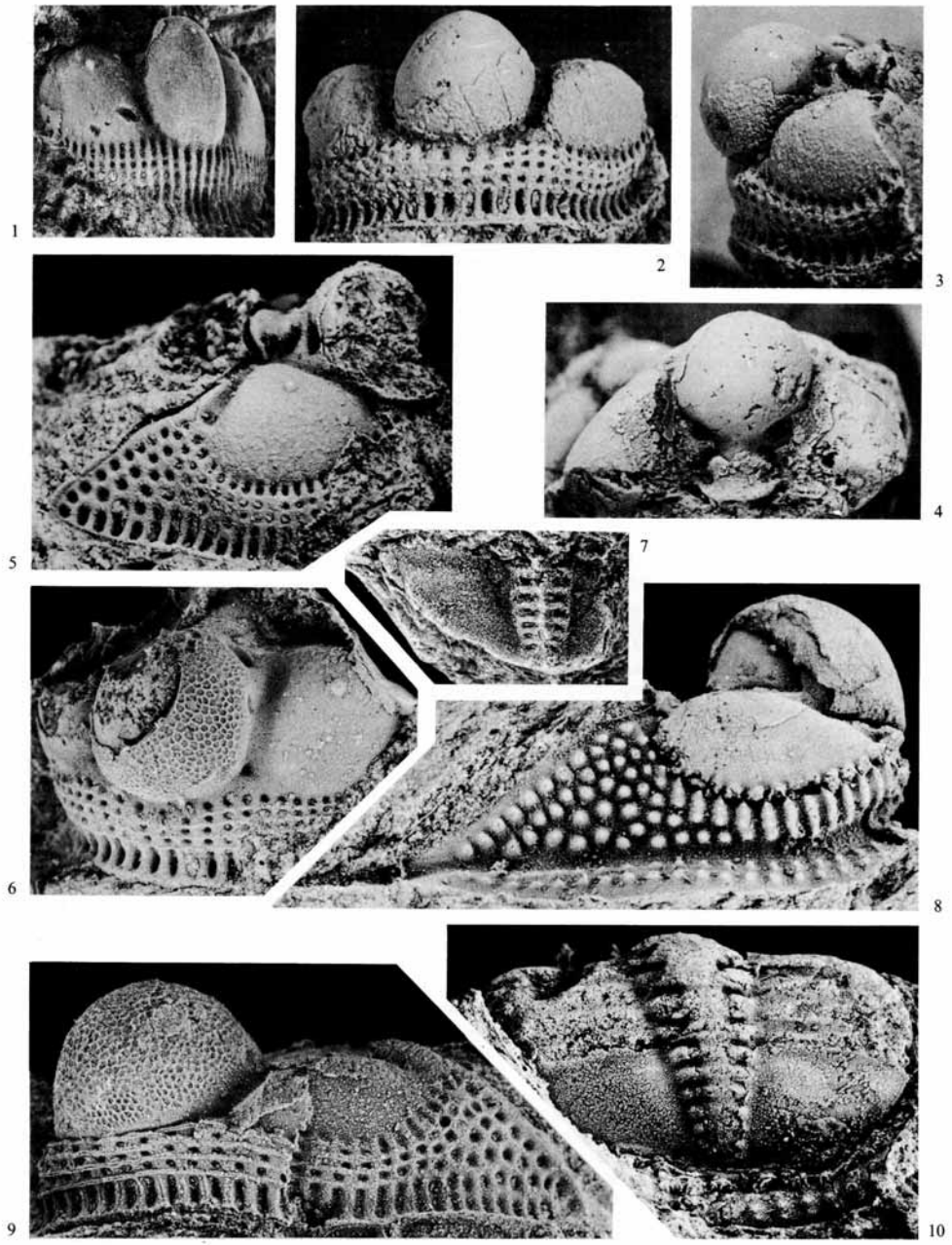
Plate 100, figs. 2–10; text-fig. 1

1909 *Trinucleus* sp.; Strahan *et al.*, table, p. 58.
1912 *Trinucleus seticornis* (Hisinger); Reed, p. 391, pl. 19, fig. 5, 5*a*.

EXPLANATION OF PLATE 100

Fig. 1. ?*Tretaspis moeldenensis moeldenensis* Cave, GSM LW 1311, internal mould of cephalon, low Ty'n-y-twmpath Beds, headwaters of Nant-y-Lladron, south of Corwen, antero-lateral view, ×6.

Figs. 2–10. *Tretaspis* cf. *radialis* Lamont, Sholeshook Limestone Formation of Sholeshook and Prendergast, Haverfordwest, ×5. 2–4, BM It. 9200, internal mould of cephalon partially retaining exoskeleton, topmost Locality 8d, anterior, left-lateral, and dorsal views. 5, BM It. 9259, incomplete internal mould of cephalon, topmost Locality 8d, right-lateral view, ×5. 6, BM It. 9252, cast from incomplete external mould of cephalon, topmost Locality 8d, oblique view. 7, SM A85138, incomplete internal mould of pygidium, Locality 9h, dorsal view. 8, 9, SM A77523a, b, internal mould and cast from external mould of cephalon, Locality 9e, right-lateral and left antero-lateral views. 10, SM A31529, internal mould of pygidium and posterior part of thorax of enrolled specimen, Sholeshook, dorsal view of pygidium. Locality numbers are those of Price 1973*a*.



PRICE, *Tetraspis* from Wales

1914 *Trinucleus seticornis*, Hisinger; Reed, pl. 28, fig. 5, 5*a*.
1914 *Trinucleus seticornis* (His.); Strahan *et al.* (*pars*), table, p. 64.
1914 *Trinucleus seticornis*? (His.); Strahan *et al.*, table, p. 64.
1938 *Tretaspis* cf. *kiaeri* Størmer; Whittington, list, p. 452.
1945 *Tretaspis ceriodes* var. *sortita*; Lamont, p. 123.
1966 *Tretaspis* aff. *kiaeri* Størmer radialis Lamont; Ingham, pp. 467, 470, 471, 486, 499–501.
1966 *Tretaspis kiaeri* Størmer; Whittington (*pars*), p. 91.
1968 *Tretaspis kiaeri* Størmer; Whittington (*pars*), pl. 29, figs. 1, 2, 4 only.
1970 *Tretaspis* cf. *radialis* Lamont; Ingham (*pars*), pp. 55–57, pl. 9, figs. 8–16, 20; text-figs. 14*d*, 19; *non* pl. 9, figs. 17–19.
1973*a* *Tretaspis* cf. *radialis* Lamont; Price (*pars*), pp. 229, 234, 236, 238–239, 242; tables 1–5.
1973*b* *Tretaspis* cf. *radialis* Lamont; Price, pp. 538–540.
1974 *Tretaspis* cf. *radialis*; Price (*pars*), p. 847.

Lectotype. Subsequently selected by Dean 1961, p. 124, SM A16202, original of Lamont 1941, text-fig. 5, p. 497; from the Portrane Limestone, Portrane, Co. Dublin.

Material, horizons, and localities. This description is based on some forty-five specimens from the Sholeshook Limestone Formation of South Wales. In the type development at Sholeshook and Prendergast (Haverfordwest, Dyfed) the species is common throughout all but the topmost four metres of the formation, the highest occurrence being in topmost Locality 8d of Price 1973*a*. Around Llandowror it appears to range through most of the formation but is absent from the basal Moldin horizon (Localities 17, 24a, 25) and is not known with certainty above Locality 18a. One other occurrence, in Mid-Wales, is noted in the discussion.

Description. Cephalon sub-semicircular in dorsal view. Pseudofrontal lobe of glabella occupying two-thirds of sagittal length; sub-spherical in form, standing high above level of genal lobes and overhanging fringe in lateral view (Pl. 100, fig. 3); strongly reticulated and apically bearing a small median tubercle. Occipital ring narrow and strongly convex (sag. and exsag.), orientated postero-dorsally, abaxially curving forwards. Occipital furrow broad (sag. and exsag.) and shallow mesially, abaxially containing deep, ovoid apodemal pits. 1p lateral glabellar lobes short (tr.), convex, abaxially rounded. 1p lateral furrows in form of deep, strongly oblique apodemal slots, converging anteriorly at 120–130°. 2p lateral lobes only gently convex (exsag.), set transversely, narrowest (exsag.) adaxially, broadening outwards and merging anteriorly with the pseudofrontal lobe around the 2p lateral furrows (Pl. 100, figs. 4–6). Latter in form of large, deep, ovoid pits, diverging anteriorly at about 140°. On well-preserved specimens the 3p lateral furrows are clearly visible as shallow, elongate-ovoid pits on the sides of the pseudofrontal lobe, slightly behind its mid-length (Pl. 100, fig. 6). Axial furrows broad (tr.) posteriorly, narrowing forwards and constricted slightly on about level of 3p lateral furrows at the adaxial ends of faintly developed eye-ridges; at anterior ends containing deep, round anterior fossulae of about the same size as the pits of the I_n arc of the fringe. Genal lobes sub-quadrant shaped; convex (tr. and exsag.), bearing prominent lateral tubercles at the level of the anterior margins of the 2p lateral furrows; variably reticulated, sometimes strongly, sometimes not at all. Where reticulation is absent, the faint eye-ridge referred to above may be seen on the external surface running obliquely forwards from the lateral tubercles to the level of the 3p furrows (Pl. 100, fig. 6). Genal lobes drop steeply to broad (exsag.), adaxially shallow posterior border furrows. Posterior borders narrow (exsag.) and gently convex (exsag.) adaxially, broadening outwards. Fringe with steeply inclined, convex genal roll; brim narrow anteriorly but broadening laterally. Internal moulds show a broad, deep girder with fine, closely spaced terrace lines (Pl. 100, fig. 8). Arrangement of pits similar to that in *T. moeldenensis* (s.l.), the strict radial alignment only breaking down on the genal prolongations. There are 6 completely developed pit-arcs, E_{1-2}, I_{1-3}, I_n, and a variably developed I_4 arc. In 8 out of 10 specimens showing the pit arrangement frontally, the I_4 arc is complete in front of the glabella, while in both of those remaining I_4 pits are absent from R1 (text-fig. 1). The number of pits in I_4 ranges from 10 to 18 (half-fringe), the pits merging with those of the I_n arc between R12 and R19. The E_1 arc has from 24 to 28 pits in the half-fringe. Pits of E_2 are absent from the posterior-most row and occasionally from the posterior-most 2 rows; the posterior row contains from 9 to 11 pits. As in *T. moeldenensis*, the sulci containing E_2, E_1, and I_1 pits anteriorly and antero-laterally on the upper lamella tend to contain only the E_1 and E_2 pits on the genal prolongations (Pl. 100, fig. 9), where the sulci containing the I_{1-n} pits on the lower lamella also break down (Pl. 100, fig. 8).

Well-developed lists separate the pits of the I' arcs anteriorly on the upper lamella (Pl. 100, figs. 6, 9; see also Whittington 1968, pl. 29, fig. 1) and may persist laterally to around R14 or R15.

Thorax poorly known but apparently similar to that described below for *T.* aff. *radialis*. Pygidium (Pl. 100, figs. 7, 10) similar in over-all form to those described for Population B of *T. moeldenensis* (s.l.) though with axis relatively slightly broader (tr.), occupying about one-quarter of total width anteriorly, tapering posteriorly at about 25° and bearing, in well-preserved specimens, seven pairs of apodemal pits, though frequently only six are visible in poorer specimens. Pleural lobes on available material poorly preserved.

Discussion. This form is synonymous with *T.* cf. *radialis* described by Ingham (1970) from the Cautleyan and low Rawtheyan Stages of the Cautley Mudstone Formation. Ingham concluded (1970, pp. 56–57) that this form is more likely than *T. m. moeldenensis* and related forms to be identical with *T. radialis* Lamont from the Portrane Limestone. Whether or not this is the case (and the issue is now further complicated by the presence of a third related species in the Welsh faunas—*T.* aff. *radialis*, see below), separation of the form from *T. m. moeldenensis* is justified on the basis of several morphological differences. Apart from the pit-count differences in the fringe (text-fig. 1) which mainly relate to the number of pits in E_1 and in the posterior row, the distinction is based on the degree of inflation of the pseudofrontal glabellar lobe, the presence or absence of reticulation, the presence or absence of 3p lateral furrows and of well-developed lists, the degree to which the brim is developed anteriorly, and the number of pairs of apodemal pits on the pygidial axis.

T. cf. *radialis* has also been collected by the author (Price 1973*b*, p. 539) (specimens SM A94697, A94701, 94704, 94712, and 94718) from a quarry at Ty-isaf-mawr near Llantsantffraid-ym-Mechain in the Berwyns, a locality which Whittington (1938, his Locality 53) included in the '*Diacalymene marginata* Zone' of the Lower Tre-wylan Beds.

Tretaspis aff. *radialis* Lamont, 1941

Plate 101, figs. 1–7; text-fig. 1

1914 *Trinucleus seticornis* (*His.*); Strahan *et al.* (*pars*), tables, pp. 64, 75.
1914 *Trinucleus seticornis* (*His.*), var. *bucklandi* (Barr.); Strahan *et al.*, table, p. 75.
1914 *Trinucleus* sp.; Strahan *et al.*, table, p. 75.
1923 *Trinucleus* sp.; King (*pars*), list, p. 495.
?1970 *Tretaspis* cf. *radialis* Lamont; Ingham (*pars*), pl. 9, figs. 17–19 only.
1973*a* *Tretaspis* cf. *radialis* Lamont; Price (*pars*), pp. 229, 238–239, 242; tables 1, 2, 5.
1974 *Tretaspis* cf. *radialis*; Price (*pars*), p. 847.

Material, horizons, and localities. This form replaces *T.* cf. *radialis* in the topmost four metres of the Sholeshook Limestone Formation of Prendergast Place (Localities 8c, 8b of Price 1973*a*) and continues into the overlying Slade and Redhill Mudstone Formation (Locality 8a). It is the only species of *Tretaspis* known from the exposures in the latter formation at Redhill Quarry (Locality 7 of Price 1973*a*). Material from these sources totals thirty-nine specimens (of which twenty-four are from the topmost Sholeshook Limestone). A further occurrence at Aber-marchnant in the south-west Berwyns is noted in the discussion.

Description. In over-all cephalic morphology this form does not differ appreciably from *T.* cf. *radialis*, except in the extent of surface reticulation. On the pseudofrontal glabellar lobe, reticulation is subdued and appears to be confined to the post-apical region (just visible, for instance, on Pl. 101, fig. 7); the genal lobes on all known specimens are smooth. The main difference between the two forms is in the development of the I_4 pit-arc of the fringe. Of 18 specimens of *T.* aff. *radialis* showing the frontal area of the fringe, one-third had no I_4 pits at all and the remaining 12 had short I_4 arcs of between 1 and 4 pits (text-fig. 1).

When present, this short I_4 arc is developed between R2 and R6 with at least 1 and possibly as many as 5 pits absent frontally (half-fringe). There may also be a tendency for the E_1 arc in *T.* aff. *radialis* to contain slightly fewer pits than that in *T.* cf. *radialis* (text-fig. 1). Otherwise the arrangement of pits is similar in both forms, with the I_3 arc invariably complete.

Thorax (Pl. 101, fig. 3), known from single, poorly preserved specimen, of six segments. Axis occupies about one-third of total width (tr.) anteriorly, gradually tapering posteriorly, only gently convex (tr.). Axial rings separated by broad (sag. and exsag.) articulating furrows containing deep, ovoid apodemal pits a short distance from the axial furrows. Axial furrows rather shallow. Pleurae broad (exsag.), flat, apparently horizontal for most of length (tr.). Pygidium similar in over-all form to those described previously with axis occupying slightly over one-quarter of total width (tr.) anteriorly, tapering back at 25–30° and bearing six or seven pairs of apodemal pits. Pleural lobes on available material again poorly preserved.

Discussion. T. aff. *radialis* is readily distinguished from both *T.* cf. *radialis* and *T. m. moeldenensis* by virtue of its very short or absent I_4 pit-arc. In this respect, however, the fringe is very similar to that of *T. m. colliquia.* This last form does show some fringe differences such as the anteriorly well-developed brim, the occasionally incomplete I_3 arc, and the large I_n pits. There are differences, too, in the degree of inflation of the pseudofrontal glabellar lobe, the degree to which the genal lobes overhang the fringe and in pygidial characters, particularly the relatively broader and more rapidly tapering pygidial axis of *T.* aff. *radialis* with its fewer pairs of apodemal pits. So far as the Welsh populations of *T. moeldenensis* (s.l.) described herein are concerned, these show much greater variation in the development of the I_4 arc in addition to most of the differences listed above.

Lamont (1941, p. 456) originally described *T. kiaeri radialis* on the basis of two fragments from the Portrane Limestone of Co. Dublin, Eire. Of these, the lectotype, SM A16202, has at least twelve pits clearly visible in the I_4 arc and the remaining syntype, SM A16203, appears to have had an extensive I_4 arc as well. The form described above is not, therefore, thought likely to prove identical with *T. radialis.* Nevertheless, redescription of the latter form from topotype material and clarification of the status of related forms is clearly urgent.

A further sample of 12 specimens of *T.* aff. *radialis* comes from the (locally) basal Ashgill strata of Aber-marchnant in the south-west Berwyns (locality α1 of King,

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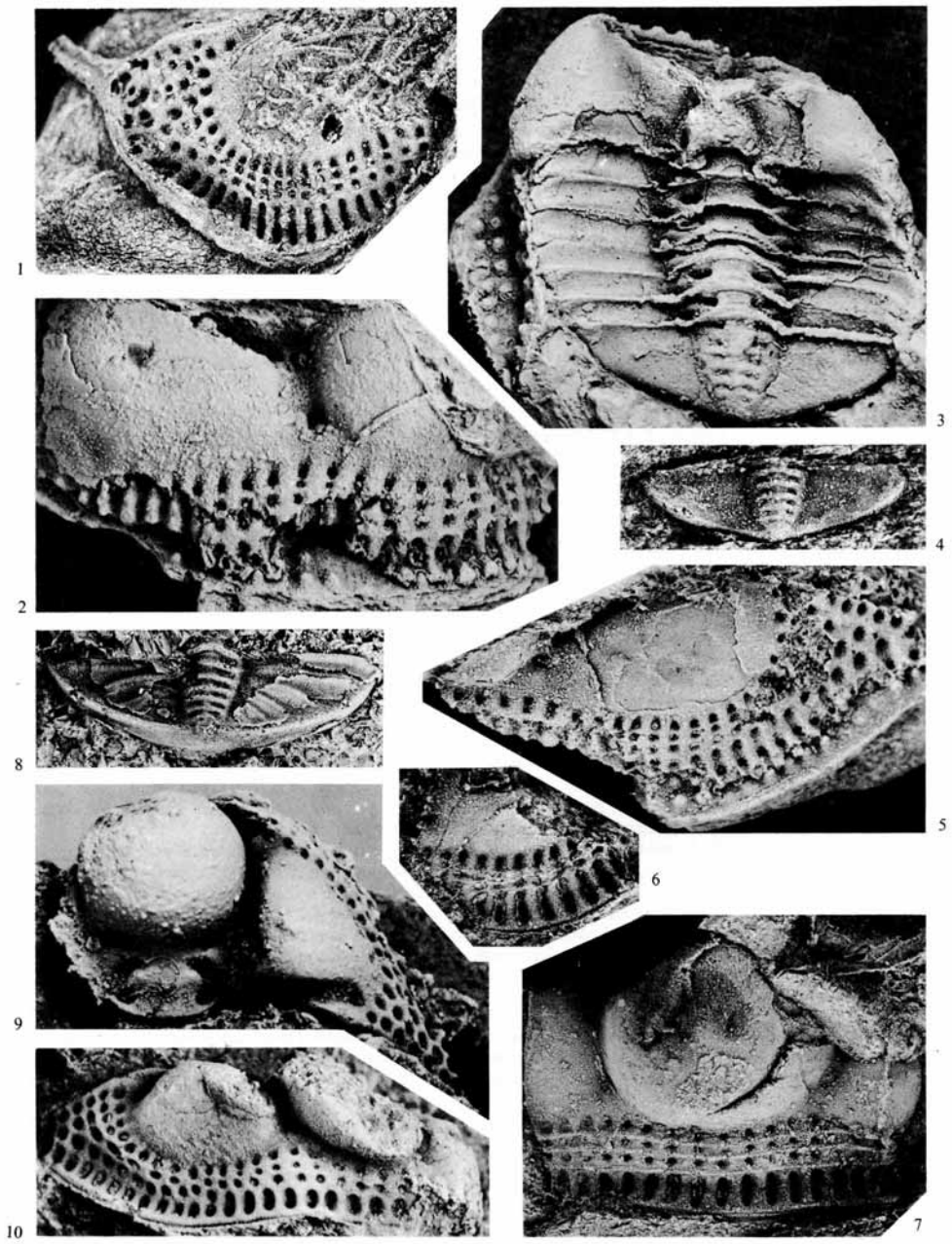
EXPLANATION OF PLATE 101

Figs. 1–7. *Tretaspis* aff. *radialis* Lamont. 1, SM A94505, cast from partial external mould of cephalon, basal Ashgill Mudstones, Aber-marchnant, south-west Berwyns, oblique view, ×5. 2, BM It. 9203, partial internal mould of cephalon, basal Slade and Redhill Mudstones of Prendergast Place, Haverfordwest, oblique view, ×5. 3, SM A77860a, internal mould of articulated exoskeleton, basal Slade and Redhill Mudstones of Prendergast Place, dorsal view, ×4. 4, SM A31597, internal mould of pygidium, high Sholeshook Limestone of Prendergast Place, dorsal view, ×6. 5, SM A56043, partial internal mould of cephalon, topmost Sholeshook Limestone of Prendergast Place, oblique view, ×5. 6, SM A94507a, partial internal mould of cephalon, horizon, and locality as for fig. 1, oblique view, ×6. 7, SM A94998, cast from partial external mould of cephalon, horizon and locality as for fig. 5, anterior view, ×5.

Fig. 8. *Tretaspis* sp. indet. A, BM It. 8953, cast from external mould of pygidium, Birdshill Limestone, Birdshill Farm, near Llandeilo, dorsal view, ×6.

Figs. 9, 10. *Tretaspis hadelandica* Størmer, *brachystichus* Ingham. 9, BM It. 9275, incomplete internal mould of cephalon. Sholeshook Limestone horizon at Robeston Wathen (Locality 10a of Price 1973*a*), dorsal view, ×6. 10, SM A77794, incomplete internal mould of cephalon, horizon and locality as for fig. 9, antero-lateral view, ×6.



PRICE, *Tetraspis* from Wales

1923). One specimen has 23 pits in E_1. The number of pits in the posterior row is 11 in 2 specimens and 12 in a third though the original of Plate 101, fig. 1 shows only 6! The number of pits in I_4 varies from 0 (1 specimen) through 1 and 2 (1 specimen in each case, in the latter the original of Pl. 101, fig. 1) to 4 or 5 (original of Pl. 101, fig. 6). Two external moulds show subdued reticulation on the posterior part of the pseudofrontal glabellar lobe. In all other general features the material resembles *T.* cf. *radialis*. What makes its identity with *T.* aff. *radialis* of further interest is its occurrence at Aber-marchnant together with *T. hadelandica* Størmer *brachystichus* Ingham and *Kloucekia robertsi* (Reed), a situation exactly paralleled with *T.* aff. *radialis* in the high Sholeshook Limestone (see Price 1973*a*, p. 229 and table 2).

Ingham (1970, pl. 9, figs. 17–19) has figured, among forms which he refers to *T.* cf. *radialis*, a specimen from Zone 5 of the Rawtheyan Stage in the Westerdale Inlier which appears to have only four pits in the I_4 arc and which on the cast from the external mould does not appear to be obviously reticulated. It is conceivable that this and other forms referred to *T.* cf. *radialis* in the topmost part of its range might belong with the forms described here as *T.* aff. *radialis*. Ingham (1970, p. 56) notes an association with *T. hadelandica brachystichus* and it is from Zone 5 also that *Kloucekia* cf. *robertsi* is recorded (Ingham 1966, table 2).

Tretaspis sp. indet. A

Plate 101, fig. 8

1973*a* *Tretaspis* of *T. moeldenensis* group; Price, list, p. 244.

Material, horizon, and locality. Eight specimens from the Birdshill Limestone of the old quarry 180 m north-west of Birdshill Farm, 2·5 km west-north-west of Llandeilo, Dyfed. These specimens (BM It. 8946–8948, 8950–8954) comprise 4 fragments of fringe and 2 internal moulds and 2 external moulds of pygidia.

Description. The fringe fragments show that the pits are arranged in strict radial alignment and with the following arcs developed in all 4: E_{1-2}, I_{1-3}, I_n. One fragment appears to show 1 or 2 pits of an I_4 arc. On the upper lamella the E_2, E_1, and I_1 pits are contained in radial sulci and all the internal arcs are arranged in such sulci on the lower lamella. The E_2 pit is absent from the posterior row.

Pygidium (Pl. 101, fig. 8) sub-triangular in outline, broad (tr.), maximum width three times sagittal length. Postero-lateral margins convex, posterior bluntly rounded; these margins strongly bevelled from a distinct sub-marginal rim. Axis narrow, occupying about one-fifth of maximum width (tr.) anteriorly and tapering back at about 25°; moderately convex (tr.). Ring furrows shallow mesially, gently arched forward, each containing a pair of prominent apodemal slots abaxially. Eight such pairs of slots are visible, the posteriormost markedly fainter than the rest. Axial furrows shallow. Pleural lobes nearly flat, horizontal, crossed by four distinct, broad pleural ribs and a faint fifth; ribs separated by shallow pleural furrows and each with faint interpleural furrows.

Discussion. The sparsity and fragmentary nature of the available material precludes detailed comparison with other forms. A close similarity may be noted, however, between the pygidia described above and topotype pygidia of *T. m. moeldenensis* (Pl. 99, figs. 6, 9).

THE *TRINUCLEUS SETICORNIS* GROUP

For the characteristics of the group see Ingham 1970, p. 41.

Tretaspis hadelandica Størmer, 1945, *brachystichus* Ingham, 1970

Plate 101, figs. 9, 10; Plate 102, figs. 1–5; text-fig. 2

1885 *Trinucleus seticornis*, His.; Marr and Roberts (*pars*), p. 480 (centre).
1914 *Trinucleus seticornis* (His.); Strahan *et al.* (*pars*), tables, pp. 64, 75.
1914 *Trinucleus seticornis* (His.), var. *bucklandi* (Barr.); Strahan *et al.* (*pars*), tables, pp. 64, 75.
1914 *Trinucleus seticornis* (His.), var.; Strahan *et al.*, table, p. 75.
1923 *Trinucleus* sp.; King (*pars*), list, p. 495.
1938 *Tretaspis ceriodes* (Angelin); Whittington, list, p. 452.
1938 *Tretaspis* sp.; Whittington (*pars*), list, p. 452 (bottom).
1965 *Tretaspis seticornis anderssoni* Størmer; Cave, p. 296.
1970 *Tretaspis hadelandica* Størmer *brachystichus* Ingham, pp. 46–49, pl. 6, figs. 13–19; pl. 7, figs. 1–7; text-figs. 14*f*, 16.
1973*a* *Tretaspis* cf. *hadelandica* Størmer *brachystichus* Ingham; Price, pp. 229, 233–234, 237, 239; tables 1–3, 5.
1975 *Tretaspis* cf. *hadelandica* Størmer *brachystichus* Ingham; Cocks and Price, pp. 705–706, pl. 81, figs. 8, 9.

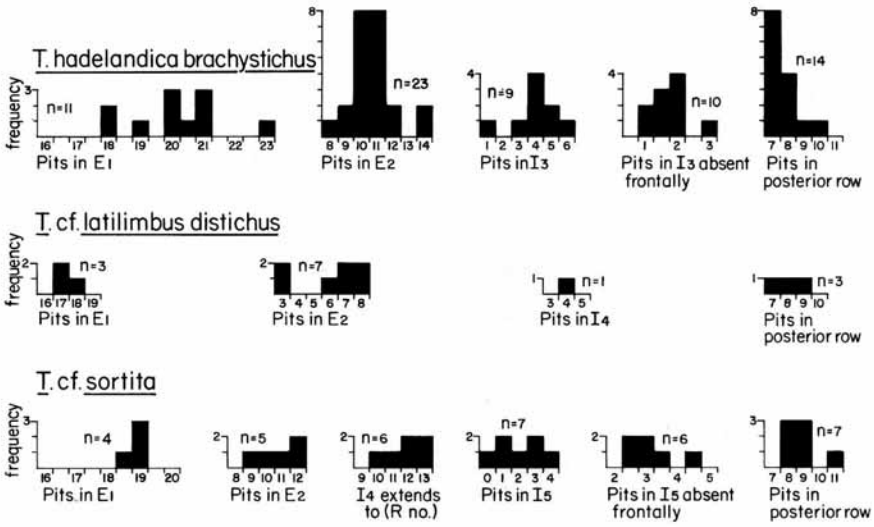
Holotype of subspecies. Figured Ingham 1970, pl. 6, fig. 15, HUD 4.10, an enrolled specimen from the Rawtheyan Stage, Zone 5, of the Cautley Mudstone Formation.

Material, horizons, and localities. The following description is based on samples totalling thirty-five specimens from the high Sholeshook Limestone and basal Slade and Redhill Mudstone Formations of the areas around Haverfordwest, Robeston Wathen, and Llandowror, Dyfed (Localities 8a, 8b, 9d, 10a, 15, and 22 of Price 1973) and a further sample of fourteen specimens from the high Slade and Redhill Mudstone Formation of Haverfordwest (Locality I of Cocks and Price 1975). When histograms of fringe data are plotted separately for these two sets of specimens there are no appreciable differences. They are therefore treated together in the histograms on text-fig. 2 and in the description. Occurrences in the Ashgill Series of the Berwyn Hills and of the Lleyn Peninsula are noted in the discussion.

Description. Cephalon approximately semicircular in dorsal view. Pseudofrontal lobe of glabella subspherical in form, standing high above level of genal lobes, occupying almost two-thirds of total glabellar length (sag.), and apically bearing a small median tubercle. Occipital ring narrow and strongly convex (sag. and exsag.), strongly arched (tr.), and orientated postero-dorsally. Occipital furrow broad (sag. and exsag.) and shallow mesially, abaxially containing deep, ovoid apodemal pits. 1p lateral glabellar lobes short (tr.), convex, abaxially rounded. 1p lateral furrows deep, slot-like, converging anteriorly at 140–150°. 2p lobes gently convex (exsag.), set transversely, narrowest (exsag.) adaxially, broadening outwards. 2p lateral furrows in form of large, ovoid pits, diverging anteriorly at 150–160°. Well-preserved ex ernal moulds show the presence of a faintly developed pair of depressions on the sides of the pseudofrontal lobe representing the 3p lateral furrows. Axial furrows broad (tr.) posteriorly, less so anteriorly where they contain deep anterior fossulae of about the same size as the pits of the I_n arc of the fringe. Genal lobes sub-quadrant shaped, steeply declined antero-laterally, not overhanging fringe; bearing prominent lateral tubercles on the level of the anterior margins of the 2p lateral furrows. In all external moulds so far examined, the surface of the glabella has been coarsely reticulated. In all but two of these external moulds the entire surface of the genal lobes has also been coarsely reticulated (Pl. 102, fig. 4; Cocks and Price 1975, pl. 81, fig. 9). Specimens GSM Pg. 216 and Pg. 226, however, both from the high Sholeshook Limestone of Prendergast Place, Haverfordwest (Locality 8b, Price 1973) and similar in all other respects, including glabellar reticulation, show completely smooth genal lobe surfaces. The genal lobes drop steeply to broad, deep posterior border furrows which contain large posterior fossulae abaxially. Posterior borders narrow (exsag.) abaxially, broadening outwards. Fringe with anteriorly steep, gently convex genal roll; a gently curled brim is developed laterally. Genal prolongations rather short (Pl. 101 fig. 10), produced into stout

genal spines which project beyond the posterior margin of the pygidium (Pl. 102, fig. 2). Genal spines with narrow dorsal groove and a strong ventral ridge which is continuous with the prominent girder; the latter carries a few faint, widely spaced terrace lines. The half-fringe contains from 18 to 23 pits in the E_1 arc (text-fig. 2). Anteriorly these pits are contained in sulci with pits of the I_1 arc but beyond about R7 the 2 arcs become separate (Pl. 101, fig. 10). The E_2 arc is only developed postero-laterally where from 8 to 14 pits share sulci on the upper lamella with pits of the E_1 arc. E_2 pits are absent from the posterior row which contains from 7 to 10 pits, most usually 7 or 8. Pits in the arcs I_2 to I_n are developed in separate aR radii which are out of line with the bR radii containing the E_{1-2} and I_1 pits (Pl. 101, fig. 10; Pl. 102, figs. 4, 5). In front of the axial furrows pits of arcs I_2, I_3, and I_n are developed but the I_3 arc merges with the I_n arc both laterally and in front of the glabella. The number of pits in this short I_3 arc is usually between 3 and 6 in the available material though one specimen (GSM Pg. 226) shows only a single pit; from 1 to 3 pits (half-f inge) are absent in front of the glabella. Lists may be developed on the upper lamella of the fringe separating the I_1 and I_2 arcs up to about aR6 and the I_2/I_3 and I_3/I_n arcs over the region in which I_3 is developed. On the lower lamella pits of the I_2–I_n arcs lie in deep radial sulci forward of the genal prolongations. One of the fringes examined shows a slight irregularity antero-laterally where, in aR10, a single pit of the I_2 arc is absent and appears to have merged with the rather large I_n pit in the same radius (Pl. 101, fig. 10).

Thorax, known only from single internal mould (Pl. 102, fig. 2), of six segments. Axis occupies about one-third of total width (tr.) anteriorly. Axial rings moderately convex (tr.), slightly arched forward mesially, separated by bro: d (sag. and exsag.) articulating furrows which contain deep, ovoid apodemal pits a short distance from the axial furrows. The elongated median tubercle near the anterior margin referred to by Ingham (1970, p. 48) and the associated row of small, sub-circular projections are not seen in this specimen. Axial furrows shallow. Pleurae directed transversely, straight, and horizontally for most



TEXT-FIG. 2. Histograms of selected fringe characters in species of *Tretaspis* of the *T. seticornis* group. n is the sample number for each character shown. All histograms show half-fringe data. *T. hadelandica brachystichus* from highest Sholeshook Limestone Formation and Slade and Redhill Mudstone Formation of Haverfordwest, Robeston Wathen, and Llandowror areas, Dyfed. *T.* cf. *latilimbus distichus* from '*Calymene quadrata* Mudstones' of south-west Berwyns. *T.* cf. *sortita* from highest Ashgill strata of Craigwen Quarry, near Meifod, Powys.

of length (tr.), deflected ventrally and slightly posteriorly at distal extremities. Broad (exsag.) pleural furrows are directed obliquely along each pleura.

Pygidium sub-triangular in form, about three times as broad (tr.) as long (sag.). Postero-lateral margins moderately convex, strongly bevelled, and covered in fine, sub-parallel terrace lines (Pl. 102, fig. 3). A strong sub-marginal rim is developed. Axis rather over one-quarter the maximum pygidial width anteriorly; crossed by six shallow, forwardly arched furrows, the posterior-most of which is extremely faint and each of which contains a pair of deep apodemal slots a short distance in from the axial furrows. Axial furrows shallow, converging posteriorly at about 35°. Pleural lobes horizontal; crossed by four pairs of divergent pleural furrows. Up to two pairs of very faint, narrow interpleural furrows are sometimes visible.

Discussion. The form described above is very similar in both over-all morphology and fringe characters to that described by Ingham (1970, see synonomy) as *T. hadelandica brachystichus* subsp. nov. from the Rawtheyan and ?Cautleyan Stages of the Cautley Mudstone Formation and the two are regarded here as synonymous. The only major difference is in the degree of genal lobe reticulation which in mature individuals of the North of England populations affects only the posterior parts of the lobes. In view of the two Welsh specimens mentioned above with completely smooth genal lobes and in view of the great variability of reticulation in the other Welsh samples discussed below, it is thought that this difference may be of purely local (adaptive) significance.

Twelve specimens from the Crugan Mudstones of the Lleyn Peninsula (BM It. 9350–9353, 9355–9358, 9360–9362, and 9419) from an exposure at Berllan Cottage, 1·8 km north of Llanbedrog, also belong with this form (see Pl. 102, fig. 5) as do small samples from the following horizons and localities within the Ashgill Series of the southern Berwyn Hills: Locality 54 of Whittington 1938, an exposure by the side of a track 450 m north of the crossroads at Cefn-y-blodwel, 1·5 km north-north-west of Llanyblodwell, Powys and within Whittington's '*Diacalymene drummuckensis* Zone' of the Lower Tre-wylan Beds; Locality 61 of the same author which lies just below the basal Llandovery near Gelli Farm, 1·75 km south-east of Llansantffraid-ym-Mechain; and Locality α1 of King 1923, in (locally) basal Ashgill strata 140 m north-east of Aber-marchnant Farm, 2 km east of Llanwddyn. The fringe characters of all these samples fall within the range given for the South Welsh forms. In spite of this, there is extreme variation in the degree of surface reticulation. External moulds from the Berllan Cottage material show no sign of either glabellar or genal lobe reticulation while reticulation on the specimens from Whittington's Locality 54 is so coarse on both the glabella and genal lobes as to be clearly visible on the internal moulds.

Ingham (1970, p. 49) has distinguished *T. hadelandica brachystichus* from *T. h. hadelandica*, *T. seticornis seticornis*, and other related Scandinavian forms.

Tretaspis cf. *latilimbus* (Linnarsson, 1869) *distichus* Ingham, 1970

Plate 102, figs. 6–11; ?Plate 103, fig. 8; text-fig. 2

1923 *Trinucleus* cf. *bucklandi* Barrande; King, list, p. 497 (bottom).
?1923 *Trinucleus bucklandi* Barrande; King, list, p. 498.

Holotype of subspecies. Figured Ingham 1970, pl. 7, fig. 15, HUD 4.25, partial cephalon from the Rawtheyan Stage, Zone 7 of the Cautley Mudstone Formation.

Material, horizon, and locality. The description below is based on sixteen specimens (NMW 74.6G.1–15, 72.18G.133) from Locality λ8 of King 1923, fig. 3, in the higher part of his '*Calymene quadrata* Mudstones'

at Craig-Fawr, 3 km south-east of Hirnant in the south-west Berwyns. A further single specimen (SM A39862) from King's Locality δ6 near by may also belong here.

Description. Cephalon similar in over-all form and proportions to that of *T. h. brachystichus*. Pseudofrontal lobe of glabella sub-spherical in form with depressions representing the 3p lateral furrows clearly developed along its sides about midway between the anterior margins of the 2p furrows and the anterior fossulae. Neither the pseudofrontal glabella lobe nor the genal lobes overhang the fringe. Glabellar and genal surfaces strongly reticulated. The reticulation, clearly visible on internal moulds (Pl. 102, figs. 9, 11), is particularly coarse on the inner posterior parts of the genal lobes (Pl. 102, fig. 6); it is terminated posteriorly on the occiput at a transverse ridge joining the posterior parts of the 1p lateral lobes. Fringe anteriorly steep and only gently convex; the narrow, slightly curled brim is developed only laterally (Pl. 102, fig. 8). Pit-arcs E_1, I_{1-3}, and I_n are developed both frontally and laterally with either 17 or 18 pits in E_1. Though pits of arcs I_3 and I_n appear to merge laterally on 1 or 2 specimens at around aR12 (Pl. 102, fig. 7), they remain separate on others. On the upper lamella E_1 and I_1 pits share sulci frontally up to about aR6 but form discrete arcs laterally. E_2 pits are only developed laterally from bR10 or 11 where on the upper lamella they share sulci with the E_1 pits. Usually E_2 pits are absent from the posterior row so that between 6 and 8 pits are present in the half-fringe. On 2 specimens, however, E_2 pits are absent from the posterior-most 3 rows; these 2 specimens are responsible for the 2 lowest counts on the histogram in text-fig. 2. A short I_4 arc is developed in front of the axial furrow. The number of pits can only be counted in 1 specimen where 4 are present from aR5 to aR8 (Pl. 102, fig. 8). This same specimen has lists developed separating each of the internal pit-arcs. The number of pits in the posterior row is 7, 8, or 9 (1 specimen in each case).

Thorax incompletely known. Axis moderately convex (tr.), occupying about one-third thoracic width anteriorly. Axial rings with broad (sag. and exsag.) ring furrows which contain deep, ovoid apodemal pits abaxially—at a distance of about their own length (tr.) inside the axial furrow. Pleurae flat and horizontal for most of length (tr.), deflected ventrally and slightly posteriorly near distal tips. Pleural furrows commencing at inner anterior corners and running obliquely outwards and posteriorly, broadening rapidly and separating narrow (exsag.) transverse anterior bands from adaxially broad (exsag.) triangular posterior bands which narrow towards the fulcrum and have a prominent, slightly raised, oblique anterior margin.

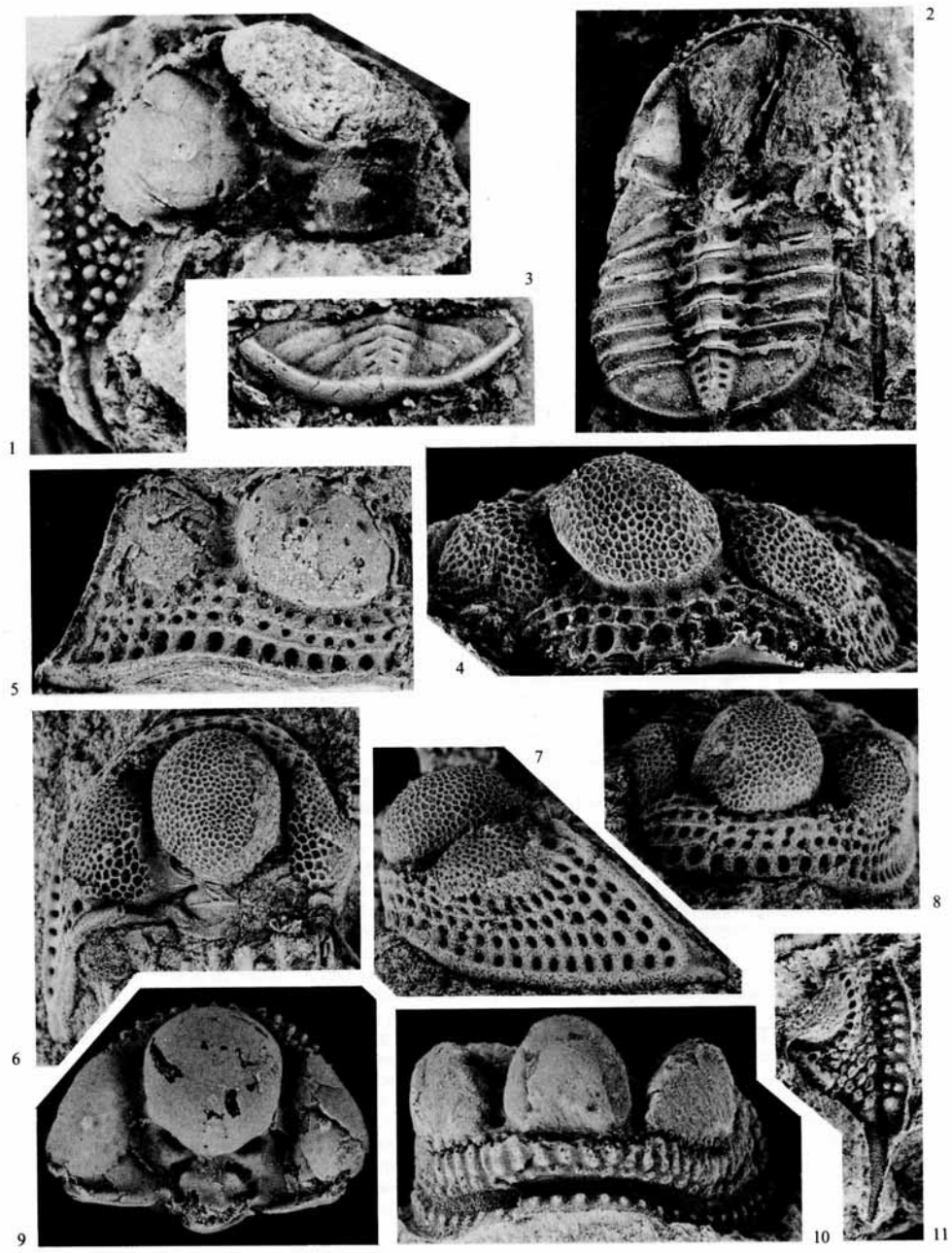
Pygidium sub-triangular in form, about three times as wide (tr.) as long (sag.). Axis occupies about one-third of total width anteriorly and tapers back at 30–35°; on available material bears six apodemes. Axial furrows broad (tr.) and shallow. Pleural lobes not well-preserved; bearing perhaps four pleural ribs. There is a well-developed marginal rim.

Discussion. Although detailed comparison is hindered by the rather small amount of material, giving very low sample numbers on the histograms in text-fig. 2, the form described above does seem close to *T. latilimbus distichus* as described by Ingham (1970, p. 50, pl. 7, figs. 8–16; text-figs. 14*g*, 16) from the Rawtheyan Stage, Zone 7 of the Cautley Mudstones. The stratigraphically older form *T. convergens* Dean

EXPLANATION OF PLATE 102

Figs. 1–5. *Tretaspis hadelandica* Størmer, *brachystichus* Ingham. 1, BM It. 9272, incomplete internal mould of cephalon, Sholeshook Limestone horizon at Robeston Wathen (Locality 10a of Price 1973), dorsal view, ×6. 2, SM A77802a, internal mould of articulated exoskeleton, horizon and locality as for fig. 1, dorsal view, ×4. 3, SM A77811b, cast from external mould of pygidium, horizon and locality as for fig. 1, dorsal view, ×6. 4, SM A77581b, cast from external mould of cephalon, horizon and locality as for fig. 1, anterior view, ×6. 5, BM It. 9352, cast from partial external mould of cephalon, Crugan Mudstone Formation, Berllan Cottage, north of Llanbedrog, anterior view, ×6.

Figs. 6–11. *Tretaspis* cf. *latilimbus* (Linnarsson) *distichus* Ingham, '*Calymene quadrata* Mudstones', Locality λ8 of King 1923, south-west Berwyns. 6–9, NMW.74.6G.1b, a, cast from external mould of cephalon in dorsal, left-lateral, and anterior views and internal mould in dorsal view, all ×5. 10, NMW. 74.6G.13, internal mould of cephalon, anterior view, ×5. 11, NMW.72.18G.133, partial internal mould of cephalon, dorso-lateral view, ×4.



PRICE, *Tetraspis* from Wales

(1961, p. 127, pl. 9, figs. 1–6; see also Ingham 1970, pp. 45–46, pl. 6, figs. 1–12; text-figs. 14*e*, 15) is similar in many respects to the Welsh material but differs in having a greater number of pits in E_1, in having E_1 and I_1 more extensively sulcate frontally and in its characteristic swollen genal lobes.

Another specimen which may belong here comes from King's Locality δ6 (1923, fig. 4) about 1 km south-west of Craig Fawr and from stratigraphically slightly higher than the other material. This specimen (Pl. 103, fig. 8) is similar in most features but differs in showing 12 pits in the E_2 arc and 7 pairs of apodemal pits on the pygidial axis. There are 10 pits in the posterior row. It may be noted that the number of apodemal pits on the pygidial axis in this specimen exceeds the maximum of 6 stated by Ingham (1970, p. 41) to be characteristic for the *T. seticornis* group.

Tretaspis cf. *sortita* (Reed, 1935)

Plate 103, figs. 1–7; text-fig. 2

1928 *Trinucleus seticornis* Hisinger; King (*pars*), list, p. 699 (top).
?1968 *Tretaspis kiaeri*?; Whittington, p. 92, list, p. 123, pl. 29, figs. 3, 5.

Type material. A lectotype has yet to be selected from the syntypes figured by Reed (1935, pl. 1, figs. 4–10) from the Starfish Bed of the Upper Drummuck Group, Girvan, Scotland.

Material, horizon, and locality. Fifteen specimens from the highest Ashgill Mudstones of Craig-wen Quarry, 120 m west of Craig-wen-fach Farm, 7 km south-west of Meifod (Locality 59 of King 1928). The specimens are all from phosphatic nodules and so retain the original convexity and many have the exoskeleton preserved.

Description. Cephalon sub-semicircular in dorsal outline. Pseudofrontal lobe occupying three-fifths of glabellar length (sag.); sub-circular in dorsal view, strongly convex (tr. and sag.) but not overhanging fringe anteriorly; apically bearing small median tubercle. Occipital ring convex (tr.), orientated slightly dorsally and strongly posteriorly so that the mesial section is broad (sag. and exsag.) in dorsal view, rather flat and not sharply separated from the occipital furrow, the posterior margin convex. Occipital furrow broad and shallow, transverse, abaxially containing deep, ovoid apodemal slots. 1p lateral glabellar lobes short (tr.), convex, strongly rounded abaxially. 1p and 2p lateral furrows deep and prominent, the former slot-like, diverging posteriorly at about 95°, the latter large ovoid pits diverging anteriorly at 110–120°. Between them the 2p lateral lobes broaden (exsag.) abaxially. There may be very faint traces of the 3p lateral furrows on some specimens but they are never clearly developed. Glabella separated from genal lobes by broad (tr.) axial furrows which in dorsal view are slightly divergent anteriorly and abaxially convex. Anterior fossulae small, rather far back from I_n arc of fringe. Genal lobes sub-quadrant shaped, convex (tr. and exsag.) but not overhanging fringe; bearing prominent lateral tubercles on the level of the anterior margins of the 2p lateral furrows; dropping steeply posteriorly to broad (exsag.), transverse posterior border furrows which abaxially contain large posterior fossulae. Posterior borders narrow (exsag.) over transverse adaxial section, broadening rapidly towards the posterior fossulae where they are deflected posteriorly. External moulds and specimens retaining the exoskeleton show the pseudofrontal lobe of the glabella to be finely reticulated in a manner very similar to that seen in a specimen of *T. l. latilimbus* figured by Ingham (1970, text-fig. 18*f*). This reticulation is terminated posteriorly in a narrow (sag. and exsag.), anteriorly convex ridge joining the posterior parts of the 1p lateral glabellar furrows. The genal lobes are smooth. The posterior margins of the posterior borders bear fine, sub-parallel terrace lines. Fringe anteriorly comprises steep, gently convex genal roll; the narrow (tr.), very slightly curled brim is developed only laterally. Anteriorly 6 pit-arcs are present in the fringe: E_1, I_{1-4}, and I_n. The pits of E_1 and I_1, which are out of line with the I_2–I_n pits, in 1 or 2 specimens share short radial sulci but in most remain clearly separate (Pl. 103, figs. 1, 6). Available material shows 18½ or 19 pits in E_1. E_2 is only developed laterally from between bR7 and bR10 outwards and is absent from the posterior row so that between 9 and 12 pits are present. Arcs E_1, I_{1-3}, and I_n are complete. Arc I_4 merges with I_n laterally between aR11 and aR14. In all but 1 of 7 specimens

showing the appropriate region of the fringe, a short I_5 arc is developed of between 1 and 4 pits, extending between aR3 and aR6 and absent frontally for between $2\frac{1}{2}$ and $4\frac{1}{2}$ radii. There are between 8 and 11 pits in the posterior row. On the upper lamella of the fringe lists may be developed between the internal pit-arcs and, laterally, between I_1 and E_1. Internal moulds show that on the lower lamella the I_2–I_n pits are associated in radial sulci which, as in other forms, break down on the genal prolongations. Girder broad, deep anteriorly but shallow laterally, ornamented with moderately strong, widely spaced sub-parallel terrace lines.

Thorax of six segments. Axis occupying slightly less than one-third total width (tr.) anteriorly; only moderately convex (tr.). Axial rings strongly convex (sag. and exsag.) mesially, becoming flatter and broadening (exsag.) outwards to form sub-quadrilateral axial lobes; separated by broad (sag. and exsag.) ring furrows from lower, less strongly convex half-rings. Axial furrows shallow. Pleurae straight and flat for almost three-quarters of length (tr.) then deflected ventrally and strongly posteriorly with strongly truncated, rounded antero-lateral corners. Pleural furrows commencing at inner anterior corners where they are narrow and broadening rapidly as they run outwards and back separating narrow anterior pleural bands from broader posterior bands. Anterior margins of latter raised and forming prominent oblique ridges.

Pygidium slightly less than three times as wide (tr.) as long (sag.), with convex postero-lateral margins and strongly bevelled from a narrow sub-marginal rim. Axis occupying rather over one-quarter of total width (tr.) anteriorly, tapering back at about 35° and bearing six pairs of slot-like apodemal pits within the mesially shallow ring-furrows. Pleural lobes almost flat and horizontal, crossed on available material by at least two poorly defined ribs. Bevelled margin ornamented with fine, closely spaced, sub-parallel terrace lines.

Discussion. In terms of fringe characters the form described above relates to *T. sortita* (Reed) as briefly characterized by Ingham (1970, p. 50, pl. 8, fig. 1). The specimen illustrated by Ingham has four pits in I_5 and as far as can be judged the numbers of pits in other arcs are similar to those for the Welsh material. Dr. Ingham too comments (pers. comm.) that the fringe characters of the Welsh specimens appear to fall within the range of variation of *T. sortita* from the Upper Drummuck Group and that there is a close similarity in general morphology. More detailed comparison is precluded until *T. sortita* itself is redescribed.

Ingham has also noted (1970, p. 43) the occurrence of a form apparently similar to *T. sortita* in the Ddolhir Beds of the Cynwydd area of the Northern Berwyns in Wales. A specimen figured by Whittington (1968, pl. 29, figs. 3, 5) as *T. kiaeri*? has 19 pits in E_1, a laterally incomplete I_4 arc, 2 or 3 pits in I_5, 13 pits in E_2, and 9 in the posterior row. Five other specimens from the same general area (BM I 1308) are poorly preserved but give the following pit-counts: 18, $19\frac{1}{2}$ (1 specimen in each case), or 20 (2 specimens) pits in E_1, 7, 12, or 14 pits in E_2 (1 specimen in each case) and, in 1 specimen, 4 or 5 pits in I_5. As will be seen from the specimen figured by Whittington, the over-all morphology is very similar to that of the Meifod specimens described here. Close comparison, however, must await better-preserved material. The Cynwydd area specimens in the BM collections are poorly localized (see Whittington 1968, p. 123) and their position within the Ddolhir Beds uncertain.

TRETASPIS OF UNCERTAIN AFFINITY

Tretaspis sp. indet. B

Plate 103, fig. 14

1909 *Trinucleus seticornis* (His.); Strahan *et al.*, faunal list, p. 59.

Material, horizon, and locality. GSM Pr. 161, 162, counterpart moulds of almost complete articulated exoskeleton; Pr. 130, poorly preserved internal mould of incomplete exoskeleton, both from a low horizon

in the Slade and Redhill Mudstone Formation at Lower Cresswell Farm, about 3·75 km south-east of Llandowror, Dyfed. Three other specimens from the same locality, a poor pygidium (Pr. 170) and two fringe fragments (Pr. 163, 165), probably also belong with this species.

Description. Cephalon approximately semicircular in outline with a sub-spherical pseudofrontal glabellar lobe and strongly convex (tr. and exsag.) genal lobes, sub-quadrant shaped and not overhanging the fringe. Both glabella and genal lobes are coarsely reticulated and this reticulation is strong enough to be discernible, faintly, even on internal moulds. The available fringes are incomplete and poorly preserved so that the over-all pit distribution is not clear. The half-fringe has about twenty-one pits in the E_1 arc. An E_2 arc is developed and the pits in this are clearly separate from the E_1 pits except in the anterior-most radius (R1) where they become conjunct. Pits of the I_1 arc are radially in line with the two E pits and these three pits are contained together in radial sulci on the upper lamella. On the lower lamella the pits of the remaining internal arcs are associated in radial sulci and these are seen to be out of line with the radii containing the E_2, E_1, and I_1 pits. The number of internal arcs in addition to the I_2 arc is uncertain but in front of the axial furrows there appear to be at least two more (I_3, I_n, ?). There are at least seven pits in the posterior row. The girder is broad and deep frontally, shallower laterally. The genal prolongations are relatively short and there are long, slender genal spines with dorsal grooves.

Thorax of six segments. Axis broad (tr.), gently convex, with broad (sag. and exsag.), mesially shallow articulating furrows containing deep, ovoid apodemal slots abaxially. Pleurae broad (exsag.), horizontal for most of length, deflected ventrally and slightly posterior at distal extremities.

Pygidium about two and a half times as broad (tr.) as long (sag.), with strongly rounded postero-lateral margins. Axis occupies about one-quarter of total width (tr.) anteriorly and tapers back at about 25°. Mesially shallow ring furrows contain deep apodemal slots near the abaxial ends; six such pairs of slots are clearly visible and a seventh may be faintly developed. Axial furrows shallow. Pleurae flat, crossed by four oblique, abaxially broadening, faintly defined ribs. A sub-marginal rim is developed and the posterior margin is strongly bevelled.

Discussion. Whilst the out-of-line arrangement of the E_{1-2}, I_1, and the I_2–I_n pits in aR and bR radii in this species is characteristic of the *T. seticornis* species group of Ingham (1970, p. 41), the significance of the virtually complete E_2 arc is uncertain. Species within the *T. seticornis* group are characterized by an E_2 arc which is only developed laterally while the known species in which the E_2 arc is continuous frontally have been placed (with the exception of *T. persulcatus* Reed, 1935) in the *T. moeldenensis* group (Hughes *et al.* 1975, pp. 563–564). The typical form of the E_2 arc in the species described here can only be ascertained when more material is available. While such information as this and the number and degree of completeness of the inner I arcs is lacking, comparisons are difficult.

Dr. Ingham (pers. comm.) has, however, drawn attention to the similarity of the form described here to a form, as yet unnamed, from the Lower Drummuck group of the Girvan area. This latter species, which appears to be a precursor of *T. persulcatus* Reed, is characterized by an E_2 pit-arc which is incomplete frontally and also lacks the external pseudogirder which is developed in *T. persulcatus* itself (Hughes, *et al.* 1975, p. 564).

Tretaspis cf. *calcaria* Dean, 1971

Plate 103, figs. 9–13

1966 *Tretaspis kiaeri* Størmer; Whittington (*pars*), pl. 28, figs. 1, 6–14; *non* pl. 29.

Holotype. Figured by Dean 1971, pl. 4, fig. 1, BM It. 8135, a cephalon from the Chair of Kildare Limestone of Eastern Ireland.

Remarks. Neither *T. kiaeri* nor the allied *T. calcaria* fit readily into one or other of

Ingham's two species groups. Whilst the fringe is made up of aR and bR radii out of line, the E_2 pit-arc is continuous frontally and, moreover, the arrangement of pits is very similar to that seen in such forms as *T. moeldenensis* and *T.* cf. *radialis* belonging to the *T. moeldenensis* species group. It is possible to emphasize these similarities and to consider, as Dean has done (1971, p. 16), that the affinities of *T. kiaeri* and *T. calcaria* are with these members of the *T. moeldenensis* group and that the significance of the out-of-line arrangement of pits in aR and bR radii is not, in this case, very great. On the other hand, the development of the E_2 arc in members of the *T. seticornis* group is very variable. It is tempting, to the present author at least, to consider the form described above as *Tretaspis* sp. indet. B as a member of the *T. seticornis* group in which E_2 has become almost complete frontally. It is then possible to regard *T. kiaeri* and allied forms more reasonably as members of the *T. seticornis* group in which E_2 is frontally complete.

Material, horizon, and localities. Available material totals some twenty-nine specimens in various collections (BM, BU, NMW, and SM). Most of these are distorted and/or fragmentary and sample numbers for pit-counts are extremely small. The material is from various localities in the Rhiwlas Limestone (Rawtheyan) of the Bala area, North Wales.

Description. Whittington's recent treatment (1966, see synonomy) of this form renders extensive illustration unnecessary.

Pseudofrontal lobe of glabella strongly inflated, sub-parabolic in anterior view, standing high above level of genae; in lateral view dropping very steeply anteriorly. Neither pseudofrontal lobe nor genal lobes overhang fringe. Surface of both genal lobes and glabella as far back as 1p latera lobes finely reticulated (Pl. 103, fig. 12). Genal roll steep and gently convex anteriorly, brim rather narrow (sag. and exsag.), only becoming well-developed laterally. In front of the axial furrows the 8 pit-arcs E_{1-2}, I_{1-5}, and I_n are developed. I_5 is absent for $1\frac{1}{2}$ (1 specimen), 2 (2 specimens), or 3 radii (1 specimen) frontally but is developed from aR2–4 to approximately aR18 (estimate on 1 specimen). In all specimens examined the I_5 and I_n pits do not share radial sulci but are clearly separate over the region in which the former arc is developed (Pl. 103, figs. 9, 11). Arcs I_2–I_4 and I_n are complete laterally. On the upper lamella pits of the E_{1-2} and I_1 arcs are contained in bR radii which are out of line with the I_2–I_n pits in the aR radii. I_1 is contained in radial sulci with E_1 and E_2 to around bR15 or 16 outwards from which the sulci contain the E pits only except in the posterior row where there is a single E_1 pit. This posterior row contains 11 (1 specimen) or 12 pits (3 specimens). The number of pits in E_1 varies from ?26 to 28 or 29 (1 specimen in each case). On available internal moulds the girder is ornamented with only very weakly developed sub-parallel terracelines.

Pygidium sub-triangular, with postero-lateral margins strongly convex; rather over two and a half times as wide (tr.) as long (sag.). Axis occupies rather over one-quarter of total width (tr.) anteriorly, is moderately convex (tr.), and tapers back at about 30° bearing seven pairs of apodemal pits. Pleurae crossed by at least three faint ribs. There is a low sub-marginal rim.

Discussion. Though the fragmentary and distorted nature of much of the Rhiwlas material renders comparison difficult, there appears to be close similarity in many features to the specimens of *T. calcaria* described by Dean (1971, pp. 12–16, pl. 4, figs. 1–8, 10, 11; pl. 5, fig. 6) from the Chair of Kildare Limestone. One difference is that in the Rhiwlas specimens I_5 is developed as a clearly separate arc whereas in the Chair of Kildare specimens I_5 and I_n pits are closely associated in short sulci. I_5 may be slightly more extensive laterally in the Welsh material. Otherwise differences in pit distribution between the two forms are slight, the Irish material possibly having a slightly higher peripheral pit-count. Irish material also appears to lack the well-developed lists seen in the Welsh specimens.

T. kiaeri Størmer (1930, p. 50, pl. 10, figs. 1–6; pl. 11, fig. 12; pl. 13, fig. 3; pl. 14, figs. 1–3; text-figs. 22–26; 1945, pp. 403, 406, pl. 1, figs. 11, 12) from the highest beds of the Upper Chasmops Limestone (in the lithological sense—the '4bδ2 sub-zone' of Størmer 1945) on Frognø, Ringerike, and the lower part of the Gagnum Shale of Hadeland, differs from both the type material of *T. calcaria* and the Welsh specimens described above in the respects noted by Dean (1971, p. 14).

LIST OF OCCURRENCES

Tretaspis moeldenensis Cave (s.l.). Bodeidda Mudstone Formation; quarry 14 m west of Bodeidda, 2½ km south-west of Conway, Gwynedd (Population A). Basal Tre-wylan Beds exposed around waterfa l in dingle 370 m north-west of Glan-yr-afon Farm, 4 km north of Llansantffraid-ym-Mechain, Powys (= Locality 42 of Whittington, 1938 = Locality 3 of Wedd *et al.* 1929, list, p. 62) (Population B). Basal Ty'n-y-twmpath Beds in headwaters of Nant-y-Lladron, 5 km south-south-east of Corwen, Clwyd (= Locality 47 of Wedd *et al.* 1927, p. 41) (Population C). Basal Ashgill Mudstones in stream section south of quarry at Pen-y-garnedd, 20 km north-west of Welshpool, Powys (= Locality 1 of Wedd *et al.* 1929, p. 61).

Tretaspis moeldenensis moeldenensis Cave. Thin, basal horizon of Sholeshook Limestone Formation around Llandowror, 3 km south-west of St. Clears, Dyfed (Localities 17, 24a, and 25 of Price 1973*a*, last = type locality).

?*Tretaspis moeldenensis moeldenensis*. About 40 m above base of Ty'n-y-twmpath Beds in headwaters of Nant-y-Lladron, 5 km south-east of Corwen, Clwyd (= Locality 36 of Wedd *et al.* 1927, p. 41). Basal Ashgill Mudstones, stream section in Cwm Nant-y-meichiaid at Glyn Cottage, 3 km north-west of Meifod, Powys (= Locality 29 of King, 1928).

Tretaspis cf. *radialis* Lamont—Ranges throughout all but topmost 4 m of Sholeshook Limestone Formation of Sholeshook and Prendergast, Haverfordwest, Dyfed, while around Llandowror it is absent from the base of the formation (Localities 17, 24a, 25) and not known with certainty above Locality 18a of Price, 1973*a*, Lower Tre-wylan Beds; quarry at Ty-isaf-mawr, 1·75 km north-east of Llansantffraid-ym-Mechain, Powys (= Locality 53 of Whittington, 1938).

Tretaspis aff. *radialis* Lamont. Topmost 4 m of Sholeshook Limestone Formation and overlying Slade and Redhill Mudstone Formation at Prendergast Place, Haverfordwest, Dyfed (Localities 8c–8a of Price 1973) and latter formation at Redhill Quarry, 2·5 km north-west of Haverfordwest (Locality 7). Basal Ashgill

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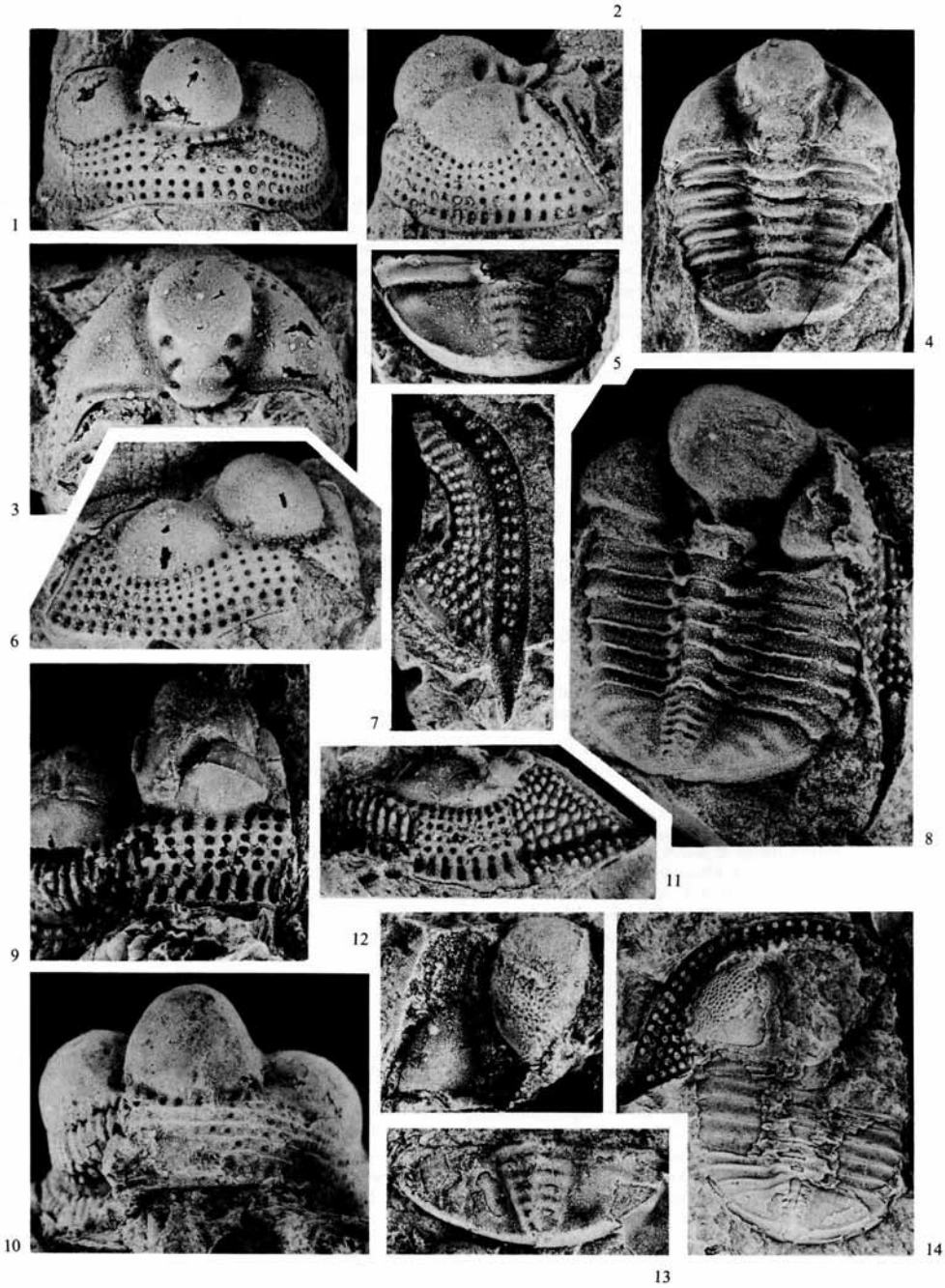
EXPLANATION OF PLATE 103

Figs. 1–7. *Tretaspis* cf. *sortita* (Reed), topmost Ashgill of Craig-wen Quarry, south-west of Meifod. 1–3, SM A14390, internal mould of undistorted cephalon, anterior, left-lateral, and dorsal views, ×6. 4, SM A14389, internal mould of articulated exoskeleton, dorsal view, ×4. 5, SM A14395a, pygidium and posterior part of thorax, part of enrolled specimen retaining exoskeleton, pygidium in dorsal view, ×5. 6, SM A14393a, internal mould of cephalon, antero-lateral view, ×6. 7, SM A14392, internal mould of right genal area of fringe, dorso-lateral view, ×5.

Fig. 8. ?*Tretaspis* cf. *latilimbus* (Linnarsson) *distichus* Ingham, SM A39889a, internal mould of articulated exoskeleton, Locality δ6 of King 1923, head of first tributary on south side of Marchnant valley, south-west Berwyns, dorsal view, ×4.

Figs. 9–13. *Tretaspis* cf. *calcaria* Dean, Rhiwlas Limestone, Bala area. 9, SM A41329, partial internal mould of cephalon, anterior view, ×5. 10, NMW.27.110.G541, cephalon partially retaining exoskeleton, anterior view, ×4. 11, NMW.56.316.G9, partial internal mould of cephalon, antero-lateral view, ×6. 12, SM A41330, partial cephalon partly retaining reticulated exoskeleton, dorsal view, ×5. 13, SM A85521, internal mould of pygidium, dorsal view, ×5.

Fig. 14. *Tretaspis* sp. indet. B, GSM Pr. 162, articulated specimen partly retaining exoskeleton, Slade and Redhill Mudstone Formation, Lower Cresswell Farm, south-east of Llandowror, dorsal view, ×4.



PRICE, *Tetraspis* from Wales

Mudstones, stream section east-north-east of Aber-marchnant Farm, 2 km east of south end of Lake Vyrnwy, Powys (Locality α1 of King 1923).

Tretaspis sp. indet. A. Birdshill Limestone; old quarry 180 m north-west of Birdshill Farm, 2·5 km north-west of Llandeilo, Dyfed.

Tretaspis hadelandica Størmer, *brachystichus* Ingham. Highest Sholeshook Limestone Formation and base of succeeding Slade and Redhill Mudstone Formation at Sholeshook and Prendergast, Haverfordwest, and around Llandowror (Localities 8a, 8b, 9d, 15, and 22 of Price 1973*a*); Sholeshook Limestone horizon at Robeston Wathen (Locality 10a); high Slade and Redhill Mudstones on west bank of Western Cleddau, Haverfordwest (Locality I of Cocks and Price 1975). Crugan Mudstone Formation; exposure at Berllan Cottage, 1·8 km north of Llanbedrog, Lleyn Peninsula. Lower Tre-wylan Beds; exposure by track 450 m north of crossroads at Cefn-y-blodwell, 1·5 km north-north-west of Llanyblodwell, Powys (= Locality 54 of Whittington 1938). Upper Tre-wylan Beds; exposure 45 m north-north-west of Gelli Farm, 1·75 km south-east of Llansantffraid-ym-Mechain, Powys (= Locality 61 of Whittington 1938). Basal Ashgill Mudstones, stream section east-north-east of Aber-marchnant Farm, 2 km east of south end of Lake Vyrnwy, Powys (Locality α1 of King 1923).

Tretaspis cf. *latilimbus* (Linnarsson) *distichus* Ingham. Higher part of '*Calymene quadrata* Mudstones' on Craig-Fawr, 3 km south-east of Hirnant, Powys (= Locality λ8 of King 1923, fig. 3).

?*Tretaspis* cf. *latilimbus* (Linnarsson) *distichus* Ingham. '*Trinucleus bucklandi* Mudstone' of King 1923, exposed near head of first tributary on south side of Marchnant valley, 2·6 km south-south-east of Hirnant, Powys (= Locality δ6 of King 1923, fig. 4).

Tretaspis cf. *sortita* (Reed). From phosphatic nodules in mudstones immediately beneath the Craig-wen Sandstone in Craig-wen Quarry, 120 m west of Craig-wen-fach Farm, 7 km south-west of Meifod, Powys (= Locality 59 of King 1928).

?*Tretaspis* cf. *sortita* (Reed). Ddolhir Beds of area around Cynwydd, 3·5 km south-west of Corwen, Clwyd (exact horizons and localities uncertain).

Tretaspis sp. indet. B. Low horizon in Slade and Redhill Mudstone Formation; exposure at Lower Cresswell Farm, about 3·75 km south-east of Llandowror, Dyfed.

Tretaspis cf. *calcaria* Dean. Rhiwlas Limestone Member of Moelfryn Mudstone Formation; various localities around Bala, Gwynedd (for details see Whittington 1966, p. 90).

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