THE TRILOBITE *TRETASPIS* FROM THE UPPER ORDOVICIAN OF THE OSLO REGION, NORWAY

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ABSTRACT. All known Norwegian species of *Tretaspis* are described. Six are established taxa: *T. ceriodes* (Angelin) *angelini* Størmer, *T. seticornis* (Hisinger), *T. anderssoni* Størmer, *T. hadelandica hadelandica* Størmer, *T. sortita* (Reed) *broeggeri* Størmer, and *T. kiaeri* Størmer. Three are new: *T. hisingeri*, *T. askerensis*, and *T. latilimbus* (Linnarsson) *norvegicus*. Most of these taxa have a broad range of variation encompassing two or more morphs. The relative proportions of these morphs are used to distinguish *T. latilimbus norvegicus* and *T. sortita broeggeri* from their nominate subspecies. The British form *T. convergens* Dean and its subspecies are reinterpreted as subspecies of *T. hadelandica*. Ingham's concept of species groups within *Tretaspis* is revised with the North American species and, provisionally, *T. kiaeri* and *T. calcaria* Dean being recognized as a distinct group centred on *T. sagenosus* Whittington. Neoteny is considered to have played a part in the evolution of *Tretaspis*.

SPECIES of the trinucleid *Tretaspis* have played an important part in the correlation of late Caradoc and Ashgill successions in Britain over the past two decades (Dean 1961, 1963; Ingham 1970; Price 1973, 1977; McNamara 1979). The classical studies by Størmer (1930, 1945) on the Scandinavian trinucleids include a number of species of *Tretaspis*, most of which are closely related to British forms. The present study is part of a broader project aimed at revising the late Caradoc and Ashgill stratigraphy and trilobite faunas of the Oslo Region. This area was divided into eleven districts by Størmer (1953, text-fig. 1) and *Tretaspis* is known from four of them (text-fig. 1). Of these, the upper Ordovician stratigraphy of two, Hadeland and Ringerike, has been revised by Owen (1978, 1979) and summaries of the successions in the other two, Oslo-Asker and Skien-Langesund, are given by Strand and Henningsmoen (1960, pl. 7). In the case of Oslo-Asker, the youngest Ordovician units were redescribed by Brenchley and Newall (1975). The present study includes an examination of all available museum material and samples of *Tretaspis* collected by the writer from 117 localities in Oslo-Asker, Hadeland, and Ringerike, now housed in the Paleontologisk Museum, Oslo (PMO) and the Hunterian Museum, Glasgow (HM).

TREATMENT OF DATA

The distribution of pits on the bilamellar fringe of trinucleids is one of the major taxonomic features of the group (Hughes, Ingham, and Addison, 1975, pp. 550–552) and the terminology applied herein is that advocated by Hughes *et al.* (1975, pp. 543–545, text-figs. 3, 4). Hughes (1970) demonstrated that although individual specimens of *Trinucleus fimbriatus* Murchison may show slight asymmetry in the development of fringe pits, there is no significant statistical difference between the left and right sides of the fringe when populations are considered. It has thus become standard practice to present data in terms of half-fringe pit counts and this is followed herein. Moreover, Hughes also demonstrated that the distribution and number of pits is independent of holaspid specimen size and this also is assumed for other trinucleids.

The number of arcs of pits and the number of pits in each arc has been used for defining species and subspecies in various trinucleids, not least *Tretaspis*. These features can be determined even in heavily distorted material and lend themselves to simple univariate techniques of display and analysis. Such an approach is adopted here and enables direct comparisons to be made with data presented in other studies. Moreover, few horizons in the Oslo Region have yielded more than a
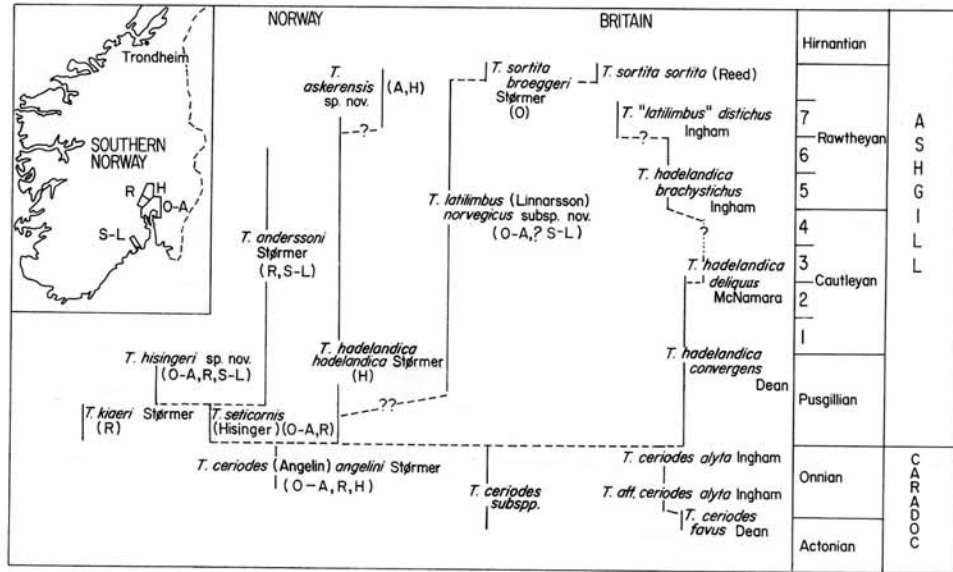
TEXT-FIG. 1. Stratigraphical ranges and suggested phylogeny of Norwegian and closely related British species of *Tretaspis* in terms of the standard British succession. The geographical distribution of Norwegian forms is given also: O-A = Oslo-Asker (Oslo is in the eastern part of this district), H = Hadeland, R = Ringerike, S-L = Skien-Langesund. The British species are revised to some extent herein.

dozen or so specimens and although many thousands of specimens have been examined, these comprise relatively few complete half-fringes, let alone entire fringes and thus most specimens have provided information on only a small proportion of the possible parameters. Univariate analysis therefore is preferred.

PROBLEMS OF POLYMORPHISM

Hughes *et al.* (1975, p. 590) noted that in many trinucleid stocks there is a progressive increase in the number of I arcs between I_1 and I_n. This is broadly the case in *Tretaspis* and in general terms the fringe criteria used in defining species and subspecies are, in decreasing order of importance: (1) the number of arcs present, (2) whether these arcs are complete anteriorly and/or posteriorly, (3) the range of variation in pit number per arc and along the posterior margin of the fringe. These features are closely related in most forms in that there is a threshold value (4-7 pits in Norwegian forms) for the number of pits present in the I arc adjacent to I_n before that arc can be complete anteriorly and a greater threshold (7-13 pits in Norwegian forms) before another incomplete arc can be developed between it and I_n. Other taxonomic fringe features are more dependent on preservation and include the extent of pits in adjacent arcs sharing sulci, the size of individual pits and the development of lists between arcs.

Many of the species and subspecies of *Tretaspis* described from Britain appear to have a fairly narrow range of variation with a purely typological concept based on characters 1 and 2 listed above being sufficiently diagnostic for both the taxon and all the individuals within it. In some cases this may be simply an artefact of small sample sizes. In contrast, Price (1977, pp. 764-772) found that some populations of *Tretaspis* from Wales have a range of variation in fringe characters which encompasses that seen in two named taxa which he considered to be end-member subspecies. Similarly, Lespérance and Bertrand (1976) distinguished a number of different morphotypes within

Cryptolithus although this needs reassessment in relation to the development of F pits on the posterior part of the fringe (Owen 1980).

Most of the Norwegian populations of *Tretaspis* have a broad range of variation, in some instances comprising morphotypes which correspond to the type specimens of described taxa. This presents great problems which, if taken to extremes could produce a taxonomy which is either very divisive and unweildy with each population sample comprising a number of formally named taxa or one which is grossly simplified to the extent of masking potentially useful affinities.

A fairly conservative approach is therefore adopted with different phenotypes within populations being recognized by the neutral term 'morphs' (Mayr 1969, p. 46). In the case of *T. ceriodes angelini* there is evidence for the progressive establishment of distinct phenotypes (see Hayami and Ozawa 1975 for a discussion of this process). In all the other Norwegian taxa only slight non-directional temporal and geographical changes in the relative proportions of constituent morphs are seen. To some extent the morphs are simply the product of variation exceeding the threshold values noted above. Thus, for example, it is not surprising that *T. ceriodes angelini* morph D (see below), which has arc I_4 developed, commonly has more pits in I_3 than does morph B. Moreover, I_3 is always continuous anteriorly in morph D but, by definition, is incomplete frontally in morph B. Nevertheless, the recognition of morphs is found to be very useful in describing variation and in making comparisons with named taxa from elsewhere which typologically resemble particular portions of the Norwegian range of variation.

The Norwegian species and subspecies therefore are defined in terms of recurrent associations of morphs (Table 1) and to some extent the relative percentages of these morphs. The boundaries between formally named taxa in some instances are ones of convenience, allowing for maximum stability of present usage within the new framework. Thus as Table 1 shows, the Norwegian taxa *T. latilimbus norvegicus* sp. nov. and *T. sortita broeggeri* are distinguished by the relative abundance of two morphs and the presence in the latter taxon of a third morph. This allows for formal expression of the greater similarity of *T. latilimbus norvegicus* to the Swedish *T. latilimbus latilimbus* (in which morph B is virtually absent) and of *T. sortita broeggeri* to the coeval *T. sortita sortita* from Scotland which is composed almost entirely of morph C.

Taxon	Morph %	Radii	E_2	I_2	I_3 % P.	I_3 %C. Post.	I_3 %C. Ant.	I_4 % P.	I_4 %C. Post.	I_4 %C. Ant.	I_5 % P.	I_5 %C. Post.	I_5 %C. Ant.
T. ceriodes angelini	A 34	I		C	96	8	48						
	B 13	I	C	C	90	0	0						
	C 26	I	C	C	100	18	100						
	D 27	I	C	C	100	66	100	100	0	14			
T. hisingeri sp. nov		2	Inc	Inc									
T. seticornis		2	Inc	C									
T. askerensis sp. nov		2	Inc	C	29	0	0						
T. anderssoni		2	Inc	C	100	0	0						
T. hadelandica hadelandica	A 37	2	Inc	C	100	0	61						
	B 56	2	Inc-C	C	100	100	23						
	C 7	2	Inc	C	100	67	100	100	0	0			
T. latilimbus norvegicus subsp. nov	A 59	2		C	100	100	100	100	10	29			
	B 41	2	Inc	C	100	100	100	100	0	17			
T. sortita broeggeri	A 5	2		C	100	100	100	100	0	0			
	B 58	2	Inc	C	100	100	100	100	0	75			
	C 37	2	Inc	C	100	100	100	100	0	93	100	0	0
T. kiaeri	A 65	2	C	C	100	100	100	100	3	100			
	B 35	2	C	C	100	100	100	100	9	100	100	0	22

TABLE 1. The basic fringe development in the Norwegian species and subspecies of *Tretaspis*. Where more than one morph is recognized, the pit distribution in each morph is given. Note that the range in pit number in each arc also serves to differentiate between the morphs and this is detailed in text-figs. 2–9. The shading marks the complete absence of an arc, Inc = incomplete, C = complete, P = present, Post. = posteriorly, Ant. = anteriorly

The revision of the Norwegian *Tretaspis* material has entailed a reassessment of some of the well-documented British forms. In addition, Dr. J. K. Ingham of Glasgow University has given me access to his data on some of the Swedish forms. Most of the numerous citations in the literature of Swedish and other European material are based on very limited collections, as is the North American *T. clarkei*. The polymorphic Norwegian material indicates that individual specimens with a particular fringe morphology could belong to one of a number of taxa. Large samples are required to determine the range of variation and presence of morphs before taxonomic assignment can be carried out with any confidence. Thus whilst the known material of *Tretaspis* from outside Norway and Britain is discussed, it would be premature to make more than general comments on its affinity.

SYSTEMATIC PALAEONTOLOGY

Family TRINUCLEIDAE Hawle and Corda, 1847
Subfamily TRINUCLEINAE Hawle and Corda, 1847
Genus TRETASPIS McCoy, 1849

Type species. Asaphus seticornis Hisinger, 1840, p. 3, pl. 37, fig. 2; from the Fjäcka Shale (early Ashgill), Dalarna, Sweden; by subsequent designation of Bassler (1915, p. 1285).

Discussion. Ingham (1970, pp. 41–45) divided *Tretaspis* into three species groups centred on *T. moeldenensis* Cave, *T. seticornis* (Hisinger), and '*T.*' *granulata* (Wahlenberg). Hughes *et al.* (1975, pp. 503–505) reassigned the species constituting the last-mentioned group to *Nankinolithus* Lu and slightly revised the other two groups.

The *T. seticornis* group was originally stated to be characterized by an incomplete or absent E_2, the I_1–E_{1-2} radii 'out of phase' with those containing the remaining I arcs, the number of pits in E_1 ranging from 16 to 23, rarely up to 27 (half-fringe), the thoracic rachial rings relatively broad (tr.) and bearing a median tubercle and the pygidium never having more than six pairs of apodemes. Populations described below as *T. hadelandica hadelandica* include specimens with E_2 complete and up to ten pairs of pygidial apodemes. Similarly, populations of *T. anderssoni* have seven pairs of apodemes. In all other respects these forms correspond to the *T. seticornis* group. *T. persulcatus* from the Upper Drummuck Group at Girvan, south-west Scotland, has a complete E_2 but otherwise corresponds to the *T. seticornis* group and was almost certainly derived from an unnamed form which has E_2 incomplete (see discussion of *T. hadelandica* below). Thus the extent of E_2 and the number of pygidial apodemes are not, *per se*, indicative of the *T. seticornis* group.

Ingham (1970, pp. 44–45) had difficulty in assigning *T. kiaeri* Størmer to his groups but Hughes *et al.* (1975, p. 563) assigned it to the *T. moeldenensis* group. *T. kiaeri* is redescribed here and has E_2 complete frontally, two sets of radii, up to $27\frac{1}{2}$ pits in E_1 and up to ten pairs of pygidial apodemes. It is therefore intermediate between the *T. seticornis* and the *T. moeldenensis* groups. *T. kiaeri* and its probable derivative *T. calcaria* Dean resemble a number of middle Ordovician species from North America: *T. canadensis* Staüble, *T. reticulata* Ruedemann, and *T. sagenosus* Whittington and broadly coeval allied species from Scotland and Ireland. (Hughes *et al.* 1975, pp. 564–565). These middle Ordovician forms are older than all other known species of *Tretaspis* and have a single set of radii, a large number of pit arcs and in most cases a high pit count in most arcs. They were assigned to the *T. moeldenensis* group by Hughes *et al.* (1975, pp. 563–564). Specimens from the low Carodoc of Belgium assigned to *Tretaspis* by Hughes *et al.* (1975, p. 564) belong to *Nankinolithus* (= *N.* sp. of Hughes *et al.* 1975, p. 559).

The *T. seticornis* group as presently defined seems to be a natural grouping derived in the earliest Ashgill from *T. ceriodes* (Angelin), a member of the *T. moeldenensis* group. The removal of *T. kiaeri*, *T. calcaria*, and the middle Ordovician species listed above would leave the *T. moeldenensis* group as a close grouping within which phylogenetic relationships are fairly clear. The American province forms are poorly known but probably closely related and are here termed the *T. sagenosus* group. They almost certainly gave rise to *T. ceriodes*, the earliest known member of the revised *T. moeldenensis* group possibly by neoteny (giving a much simplified fringe morphology) and at a time of major

immigration into the Scandinavian area (Bruton and Owen 1979). *T. kiaeri* and *T. calcaria* have the typical large number of arcs and high pit counts of the *T. sagenosus* group and whilst having two sets of radii developed the possibility exists that they are more closely related to that group than to the other two groups and thus are provisionally included in it.

Tretaspis moeldenensis group

Tretaspis ceriodes (Angelin, 1854) *angelini* Størmer, 1930

Plate 89, figs. 1–12; text-fig. 2

1887 *Trinucleus*; Brøgger, p. 23.
1930 *Tretaspis cerioides* [*sic*] (Angelin); Størmer, pp. 44–48, pl. 9, figs. 1–4; text-fig. 21*b*.
1930 *Tretaspis cerioides* var. *angelini* Størmer, pp. 48–50, pl. 9, figs. 5–10.
1934 *Tretaspis cerioides*; Størmer, p. 331.
1945 *Tretaspis ceriodes* (Angelin); Størmer (*pars*), p. 402, pl. 1, fig. 6; *non* pp. 387, 404–405, pl. 1, fig. 7; pl. 4, fig. 16 (= *T. hadelandica hadelandica*).
1945 *Tretaspis ceriodes* var. *angelini* Størmer; Størmer, p. 402, pl. 1, fig. 5.
1945 *Tretaspis ceriodes* var. *donsi* Størmer, pp. 388, 402, 405, pl. 1, fig. 8.
1953 *Tretaspis ceriodes*; Størmer, pp. 68, 87, 94.
1953 *T. c. angelini*; Størmer, p. 68.
1973 *Tretaspis cerioides*; Lauritzen, p. 29.
1978 *Tretaspis ceriodes* (*sensu lato*) (Angelin); Owen, pp. 9, 14, 15.
1979 *Tretaspis ceriodes*; Owen, pp. 250, 251.
1979 *Tretaspis ceriodes* (Angelin) (*sensu lato*); Bruton and Owen, text-figs. 3–6.

Holotype. A cranidium (PMO H226) from 2 m below the top of the Upper Chasmops Limestone on Terneholmen, Asker.

Material, localities, and horizons. The subspecies has a short stratigraphical range and, although no complete specimens are known, a large number of disarticulated skeletal elements are known from the uppermost parts of the Upper Chasmops Limestone in Baerum and Asker in the western part of Oslo-Asker (see Bruton and Owen 1979 for detailed information), from 0·85–1·02 m above the base of the Lower Tretaspis Shale on Nakholmen, Oslo, from the uppermost parts of the Solvang Formation throughout Hadeland and at Norderhov in Ringerike, and from the lowest part of the Gagnum Shale Member of the Lunner Formation in the northern part of Hadeland.

Description. Sagittal length of glabella equal to 50–60% of width between posterior fossulae. Occipital ring arched gently upwards and rearwards and defined anteriorly by a shallow furrow which bears deep slot-like pits laterally. Occiput short (sag., exsag.), very weakly swollen. 1p furrows deep, transversely oval. 2p furrows large, deep, situated a very short distance in front of 1p furrows and diverging forwards at approximately 90°. Composite lateral glabellar lobes very narrow (tr.) adjacent to 2p furrows, anteriorly and posteriorly to which they are very weakly developed. 3p furrows developed as very shallow depressions on the pseudofrontal lobe directly in front of the mid-length of the glabella. Pseudofrontal lobe very strongly swollen, almost circular in dorsal view, occupying approximately 70% of the sagittal glabellar length. Median node situated on the highest part of the glabella at 60% of the sagittal glabellar length. Dorsal furrows broad (tr.) and shallow posteriorly, narrowing and deepening a little frontally, diverging forwards at approximately 30° to a level a short distance in front of the 2p furrows, anteriorly to which they are gently convex abaxially and bear deep fossulae frontally. Genal lobes quadrant-shaped, gently inclined from the dorsal furrows, more steeply declined towards the fringe. Lateral eye tubercles situated opposite or slightly in front of 2p furrows. Low but distinct eye ridges converge adaxially forwards at about 145° from the eyes to the outer parts of the dorsal furrows. Posterior border furrows deeply incised, transversely directed, bearing deep fossulae distally. Posterior borders ridge-like, transversely directed to behind posterior fossulae abaxially to which they are deflected steeply downwards and rearwards at approximately 60°. External surface of glabella and genal lobes bears a variable but usually strong reticulation which is coarsest around the glabellar node and lateral eye tubercles. On internal moulds the glabella is commonly smooth and the genal lobes bear a very subdued reticulation. Fringe flat-lying over the inner one or two I arcs anteriorly and anterolaterally, otherwise almost vertical.

All specimens have arcs E_1, I_1, I_2, and I_n complete but there is considerable variation in the development of arcs E_2, I_3, and I_4. On the basis of these arcs, four morphs are recognized (Table 1). Morph A lacks E_2 and I_4 and

has I_3 continuous in front of the glabella in 48% of 31 specimens where this could be determined and extending to the posterior margin in 8% of 24 specimens. I_3 is absent in 4% of 24 specimens. Morph B has a complete E_2, I_3 developed in 90% of 20 specimens but never continuous anteriorly or posteriorly and I_4 is absent. Morph C has a complete E_2, no I_4, and an I_3 arc which is always continuous anteriorly and extends to the posterior margin in 18% of 36 specimens. Morph D has E_2 complete, I_3 invariably complete anteriorly and complete posteriorly in 66% of 25 specimens and a short I_4 developed. The range of variation in arcs E_1, I_3, I_n, and the number of pits along the posterior margin of the fringe for *T. ceriodes angelini* as a whole and in the constituent morphs, is given on text-fig. 2 along with data on the development of I_4 in morph D. With the exception of the number of pits in I_3, these ranges are very similar for all the morphs although the mean values for morph A are lower than those of the other morphs. Arcs I_1, E_1, and E_2 (when present) commonly share sulci on the anterior and lateral parts of the fringe in most specimens. Although the extent of this feature was recorded wherever possible, there is often some difficulty in assessing the precise extent of the sulcation which may also be partially dependent on preservation and consequently this is not presented in histogram form. In a few specimens the sulcation does not extend laterally beyond the dorsal furrows and in a few it extends almost to the posterior margin. The mean extent is to about bR9 (fifty specimens, standard deviation 4) and there is no apparent difference between the morphs. Only one set of radii is developed. On external surfaces, lists are developed between all the I arcs. Genal spines parallel, length unknown.

Hypostoma and thorax not known.

Pygidium sub-semicircular in outline with sagittal length equal to approximately 35% of the anterior width. Rachis occupies 25% of the anterior width of the pygidium, tapers rearwards at about 30°, and is composed of an anterior articulating half-ring and five or six rings. Ring furrows progressively less well-defined rearwards along the rachis, bearing deep apodemal pits a short distance in from the weakly incised dorsal furrows. Pleural lobes flat-lying, bearing four pairs of very broad furrows which define three or four ribs which die out some distance from the weakly developed marginal rim. Pygidial border very steeply declined, broad, maintaining constant width. Antero-lateral corners of pygidium bear steeply declined facets which diverge abaxially backwards at about 120°.

Discussion. The absence of arc E_2 from morph A clearly distinguishes it from the other morphs where this arc is not only present, but complete. Morphs B, C, and D could be viewed as representing a single morphological type with a broad range of variation. However, three morphs are recognized because two, B and C, are similar to, or correspond to, the holotypes of named taxa, and there is also some evidence for a progressive development of levels of phenotype organization from morph A through B and C to D. In Hadeland, a sample of thirty-three specimens from an exposure of the Lieker Member of the Solvang Formation illustrated by Owen (1978, text-fig. 6) from a level near the first appearance of the species has the following morph composition: A88%, B6%, and C6%. Higher levels in the formation in the nearby stratotype section have yielded morph D, and ten specimens from broadly equivalent levels in the Gagnum Shale (including the holotype of *T. ceriodes donsi*) comprise B10%, C80%, and D10%. Similar results have been obtained from Oslo-Asker with early populations having morph A dominant over B and C; morph D being restricted to the later populations where A is rare or absent.

It can be argued, therefore, that morph A represents the primitive condition, the development of a complete E_2 arc in some members of the population giving morphs B and C and individuals of morph D type developed from morph C parents. It must be stressed, however, that the morphs are regarded as representing fairly broad portions of the range of variation in interbreeding populations.

Angelin's original material of *T. ceriodes* (1854, p. 65, pl. 34, fig. 2-2b) from the Upper Mossen Formation (late Caradoc) at Kinnekulle, Västergötland, Sweden, was reported by Størmer (1930, p. 45) to be lost and a neotype from the Solvang Formation in Ringerike was chosen. This neotype could not have any standing as it was not from the type locality and recently Angelin's probable syntypes have come to light in the collections of the Riksmuseum, Stockholm. A full examination of the E pit development can be made in only one of these and E_2 is not developed. Two specimens show the development of I_3 which in both cases is short (3-4 pits) and not present anteriorly. I_4 is absent. Thus these probable syntypes resemble *T. ceriodes angelini* morph A. Two other specimens in the Riksmuseum collections from the Upper Mossen Formation (locality not known) show an extensive I_3 development and while one lacks E_2, the other has it developed mesially but not beyond R4. This
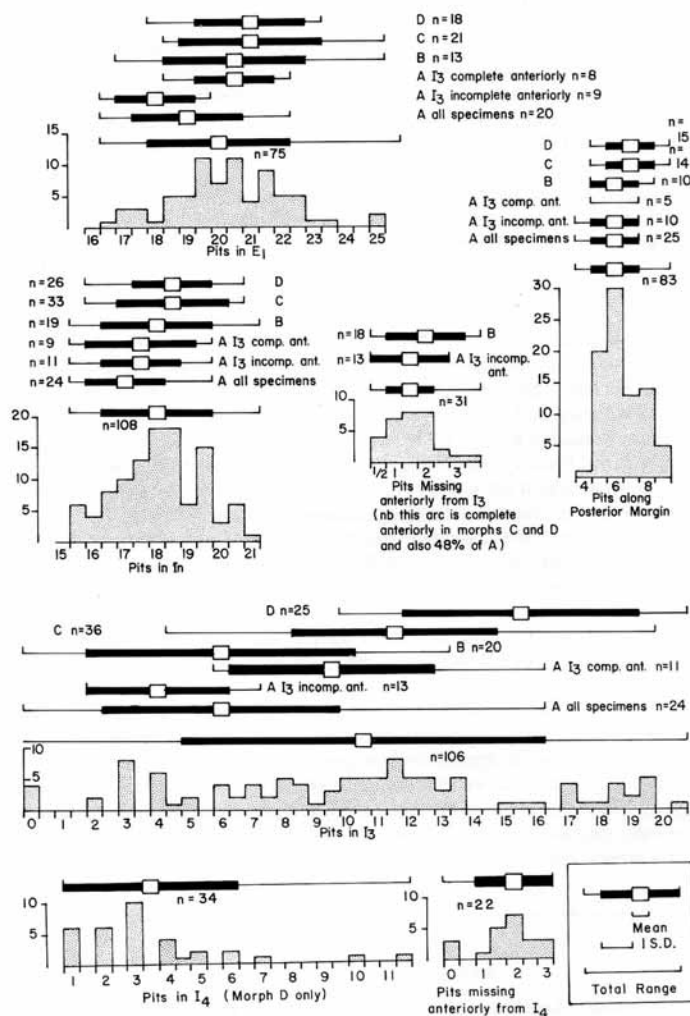
TEXT-FIG. 2. Histograms showing the range of variation in fringe characters of all available specimens of *Tretaspis ceriodes angelini* with a comparison of the range, mean, and one sample standard deviation on each side of the mean of the four morphs (A, B, C, and D) present in the subspecies. Morph A is also subdivided to compare these parameters in specimens with arc I₃ incomplete anteriorly (i.e. like morph B) with those in which this arc is complete anteriorly (i.e. like morphs C and D). It may prove useful to define separate morphs on this basis once more material is available. In all instances n = number of specimens in the sample.

condition is not known from any Norwegian specimen. Detailed comparisons of the Swedish and Norwegian forms must await the documentation of more material from Kinnekulle.

$T.$ *ceriodes alyta* Ingham, 1970, from the upper part of the Onnian Stage in northern England has arcs E_2 complete, I_4 absent, and I_3 extensive or complete posteriorly but incomplete anteriorly. It thus resembles $T.$ *ceriodes angelini* morph B, differing only in having a more extensive I_3 arc and the I_1-E_{1-2} sulci commonly extending almost to the genal angles. Examination of specimens from the Onnian Stage in the Cross Fell Inlier in northern England figured by Dean (1961, 1962) shows that Ingham was correct in suggesting that they belong to $T.$ *ceriodes alyta* (1970, p. 5). Some of the specimens of supposed Onnian age in Dean's collections in the Cross Fell Inlier (localities A12 and A15 of Dean, 1959, text-fig. 1) have a very large number of pits in I_n ($25\frac{1}{2}-28\frac{1}{2}$) and up to $9\frac{1}{2}$ pits in I_4 and most closely resemble $T.$ *moeldenensis* Cave, 1960 (see Price 1977, pp. 764–772 for a discussion of this species).

$T.$ *ceriodes favus* Dean, 1963, is a poorly known form based on specimens from the upper part of the Actonian Stage and the lowest beds of the Onnian Stage in the Onny River section and supposed Actonian strata near Cardington, Salop, England. The subspecies was diagnosed as having arc E_2 developed only laterally and I_3 complete anteriorly but not posteriorly. Whilst the latter is true for the holotype and other specimens from the Onny River, the material is too poorly preserved for the E pit development to be discerned fully although E_2 is certainly present. The I_3 development is closest to that seen in $T.$ *ceriodes angelini* morph C. All of the sixteen specimens from near Cardington in the British Museum (Natural History) (including Dean collection) and the Hunterian Museum (Owen and Ingham collection) in which the E arc development is clear, undoubtedly have E_2 complete. I_3 is incomplete anteriorly in this material (eleven specimens) and has 2–14 pits. Arcs I_1-E_{1-2} are sulcate over almost the whole fringe. The Cardington material therefore is similar to both $T.$ *ceriodes angelini* morph B and $T.$ *ceriodes alyta* and, as noted by Bruton and Owen (1979, p. 220), its association with *Onnia gracilis* may indicate an Onnian age for the strata here.

$T.$ *ceryx* Lamont, 1941, from the Raheen Shales (late Caradoc–early Ashgill) of Co. Waterford, Eire, differs from $T.$ *ceriodes angelini* morph C only in having very long, slot-like I_1-E_{1-2} sulci anteriorly and anterolaterally. The Irish form is probably best viewed as a geographical subspecies of $T.$ *ceriodes*.

$T.$ *colliquia* Ingham, 1970, from the Pusgillian Stage in the Cautley district of northern England is probably a derivative of $T.$ *ceriodes alyta* and some specimens, like $T.$ *ceriodes angelini* morph D have a short I_4 developed. The English species is distinguished by its very large, deep, extensive I_1-E_{1-2} sulci and in having a very high E pit count (twenty-eight in the two specimens showing this feature).

Dr. J. K. Ingham of Glasgow University has informed me of an undescribed form of $T.$ *ceriodes* similar to $T.$ *ceriodes angelini* morph A from the Upper Whitehouse Group (late Caradoc–early Ashgill) at Girvan, south-west Scotland (Ingham 1978, pp. 170, 171).


EXPLANATION OF PLATE 89

Figs. 1–12. *Tretaspis ceriodes* (Angelin) *angelini* Størmer. 1, 3, 5, morph D, PMO100826, dorsal, anterior, and lateral views of internal mould of cranidium, 5·3–5·4 m below top of Solvang Formation, Norderhov, Ringerike, × 4. 2, 4, morph D, PMO101552, dorsal and anterolateral views of external surface of cephalon, approximately 1·7 m below top of Upper Chasmops Limestone, East Raudskjer, Asker, × 6. 6, holotype, morph C, PMO H226, oblique anterolateral view of partially exfoliated cranidium, 2 m below top of Upper Chasmops Limestone, Terneholmen, Asker, × 6½; also figured by Størmer (1930, pl. 9, fig. 5). 7, 10, morph A, PMO H593, posterolateral and frontal views of partially exfoliated cephalon, same horizon and locality as 6, × 5; also figured by Størmer (1930, pl. 9, fig. 10). 8, morph B, PMO H250, anterolateral view of partially exfoliated cephalon, same horizon and locality as 6, × 10. 9, PMO103952, dorsal view of pygidium, upper part of Solvang Formation, Lunner, Hadeland, × 4½. 11, morph C, PMO81100, anterolateral view of partially exfoliated small cranidium, same horizon and locality as 2, × 20. 12, morph A, PMO H495, anterolateral view of partially exfoliated cephalon, 0·85–1·02 m above base of Lower Tretaspis Shale, Nakholmen, Oslo, × 4.
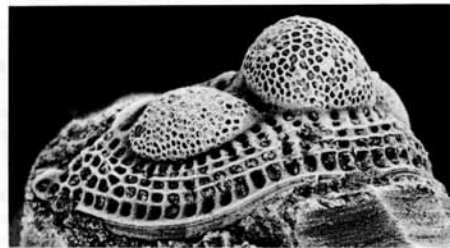
PLATE 89
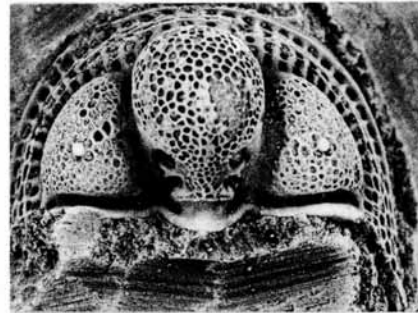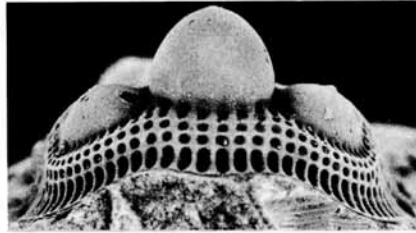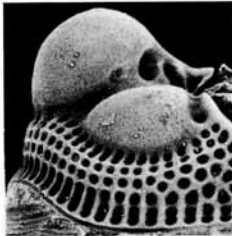
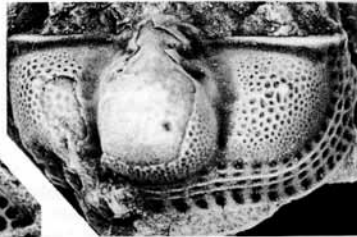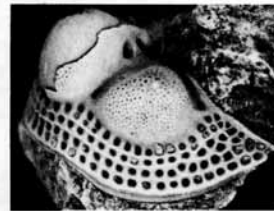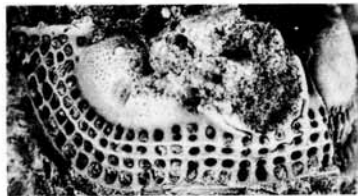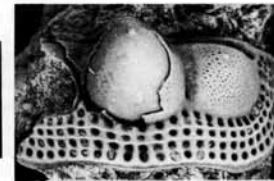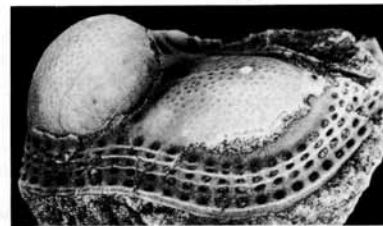

OWEN, trilobite *Tretaspis*

Tretaspis seticornis group

Tretaspis seticornis (Hisinger, 1840)

Plate 90, figs. 1–4

1840 *Asaphus seticornis* Hisinger, p. 3, pl. 37, fig. 2.
1840 *Asaphus cyllarus* Hisinger, p. 3, pl. 37, fig. 3.
?1845 *Trinucleus seticornis* (Hisinger); Lovén, p. 107, pl. 2, fig. 2.
?1854 *Trinucleus seticornis* (Hisinger); Angelin, p. 84, pl. 40, fig. 19.
?1869 *Trinucleus seticornis* (Hisinger); Linnarsson, p. 79.
1883 *Trinucleus seticornis* (Hisinger); Törnquist, p. 43.
?1884 *Trinucleus seticornis* (Hisinger); Törnquist, pp. 84–87.
?1887 *Trinucleus seticornis* (Hisinger); Brøgger, p. 24.
1930 *Tretaspis seticornis* (Hisinger); Størmer (*pars*), pp. 55–67, ?pl. 7; ?pl. 8; ?pl. 11, fig. 4; text-figs. 27, 28 (*pars*), ?29, 33*a*, 34*b* (*pars*), 34*c*, ?36, ?37*a, b*, ?42.
1934 *Tretaspis seticornis*; Størmer (*pars*), p. 330.
1936 *Tretaspis seticornis* (Hisinger); Asklund (*pars*), p. 4, pl. 1, figs. 1–3, ?5, ?6, *non* 4.
?1959 *Tretaspis seticornis* (Hisinger); Whittington *in* Moore, text-fig. 323.2.
1979 *Tretaspis seticornis seticornis* (Hisinger); Owen, pp. 250, 251, 252, text-fig. 6.
1979 *Tretaspis seticornis seticornis* (Hisinger); Bruton and Owen, text-fig. 6.

This synonymy only includes references to material which actually, or very probably, belongs to *T. seticornis*. A more complete list, comprising forty-seven entries, was given by the writer (1977, pp. 243–245) in an unpublished thesis and includes reidentifications wherever possible.

Material, localities, and horizons. Hisinger's syntypes of *Asaphus seticornis* from the Fjäcka Shale in well diggings at Furudal in Dalarna, Sweden, have not been identified unequivocally in the collections of the Riksmuseum, Stockholm, and as noted by Törnquist (1883, p. 43) may not have been collected *in situ.* The species, as here defined, is known from the lower part of the Fjäcka Shale (J. K. Ingham, pers. comm. 1976), the lower part of the Lower Tretaspis Shale at Ole Deviks Vei (lowest 5·86 m), Åstaddammen (lowest 4·65 m at least), S. Gråkommen and between Føssung and Høgstad in Oslo-Asker, and from the Høgberg Member of the Solvang Formation on Frognøya, Ringerike.

Description. Most of the available material is crushed to some extent. Glabella and genal lobes similar to those of *T. ceriodes angelini* except that the pseudofrontal lobe is more elongate. External surface of glabella and genal lobes smooth or bearing a faint reticulation. Internal moulds smooth. Steeply declined fringe bears complete arcs E_1, I_1, I_2, and I_n, and an incomplete E_2 arc. Arcs I_1–E_{1-2} are out of phase with radii comprising the other two I arcs. Pits in I_1 and E_1 share sulci anteriorly and anterolaterally. There is insufficient material to assess the range of variation in pit distribution. Only one Norwegian specimen is sufficiently well preserved for the number in E_1 to be determined (18), and whilst one specimen clearly lacks E_2, others show minimum values of 4, 7, 9 (3 specimens), and 10 pits. I_n is seen completely in 4 specimens where it comprises 15, 17½, 18, and 18½ pits and there are 6 (3 specimens) or 7 (3 specimens) pits along the posterior margin of the fringe. Lists are not developed. One specimen (pl. 90, fig. 4) does not conform to the typical *T. seticornis* development in having a stronger reticulation and in having pits developed in I_3 on the lateral parts of the fringe at aR6, 7, 9, 11–17. Such a development is most unusual for any species of *Tretaspis* and may reflect hybridization with *T. hadelandica hadelandica* which includes morphs with this arc complete posteriorly.

Hypostoma unknown.

Thorax barrel-shaped, comprising six segments of which the third and fourth are slightly broader (tr.) than the rest. Rachis occupies 30% of the width of each segment and is bounded laterally by very weakly incised dorsal furrows. Rachial rings strongly convex in transverse view and each bears a small median tubercle on its anterior edge and is separated from its articulating half-ring by a transversely directed furrow which bears deep apodemal pits laterally. Pleurae parallel-sided proximally, tapering slightly over the distal 25% where they are deflected gently downwards and rearwards. Pleural furrows shallow, each directed transversely and broadening (exsag.) from near the anteromesial corner of the pleura such that the posterior band tapers abaxially and the anterior band expands a little.

Pygidium broadly similar to that of *T. ceriodes angelini*. Rachis composed of six, possibly seven rings and the pleural lobes bear up to three poorly defined ribs.

Discussion. Hisinger (1840) described two species of *Tretaspis*, '*Asaphus*' *seticornis* and '*A*'. *cyllarus*, from the Fjäcka Shale. His illustrations of both show the development of four complete arcs of pits and there is a well-developed list between the inner and the outer pairs of arcs on his drawings of *T. seticornis*. Dr. J. K. Ingham informs me (pers. comm. 1976) that in the probable syntypes of both species and all other available specimens from the Fjäcka Shale at Furudal which have the fringe preserved, arcs E_1, I_1, I_2, and I_n are complete and a short E_2 is developed posteriorly. Thus it seems reasonable to assume that this is indeed the case with the syntypes and, in order to stabilize the species, it is advocated that this be assumed to be the case. Dr. Ingham has examined material from Dalarna described by Angelin (1854) as *T. seticornis* and considers that this identification probably is correct. Angelin's originals of *T. affinis* have a complete I_3 arc developed and thus are excluded from *T. seticornis*.

Størmer (1930) assigned a large number of specimens to *T. seticornis* from the Fjäcka Shale and various horizons in Norway. Many of these are reassigned herein to *T. anderssoni* Størmer and *T. hisingeri* sp. nov. It is clear that at least three forms are present in the Fjäcka Shale and so references to *T. seticornis* in this unit by Linnarsson (1869) and Törnquist (1884) are only tentatively included in the above synonymy. Further discussion of material previously assigned to *T. seticornis* is given below in the discussions of *T. anderssoni* and *T. hadelandica*.

Tretaspis anderssoni Størmer, 1945

Plate 90, figs. 5–10; text-fig. 3

?non1894 *Trinucleus seticornis* (Hisinger); Andersson, p. 532, figs. 1–5.
1930 *Tretaspis seticornis* (Hisinger); Størmer (*pars*), pl. 11, figs. 2, 5; pl. 12, figs. 1–5; pl. 13, figs. 1, 2, 5–7; ?pl. 14, figs. 4, 5; text-figs. 33*b*, *c* (*pars*), *d*, 37*c*.
?1936 *Tretaspis seticornis* (Hisinger); Asklund (*pars*), p. 4, pl. 1, fig. 4.
1945 *Tretaspis seticornis* (Hisinger) var. *anderssoni* Størmer, p. 401, pl. 1, fig. 2.
1959 *Tretaspis seticornis* (Hisinger); Harrington *in* Moore, text-figs. 52, 67.
non1965 *T. seticornis anderssoni* Størmer; Cave, p. 296 [? = *T. hadelandica brachystichus* Ingham].
1975 *Tretaspis seticornis anderssoni* Størmer; Hughes *et al.*, p. 563, pl. 4, figs. 52, 53.
1976 *Tretaspis seticornis* (Hisinger); Miller, text-fig. 2*h*.
1979 *Tretaspis seticornis anderssoni* Størmer; Owen p. 253 text-fig. 8.
?1979 [specimens resembling] *T. hadelandica* Størmer; Owen, p. 253.

Holotype. A cranidium (PMO65196) from the Frognøya Shale, on Frognøya, Ringerike.

Material, localities, and horizons. Specimens from low in the Frognøya Shale tentatively compared with *T. hadelandica* by Owen (1979) probably belong in *T. anderssoni* in which case cephala, cranidia, lower lamellae, and pygidia are known from throughout the type unit on Frognøya and from the overlying Sørbakken Limestone (except the lowest 9 m and the uppermost 17 m) on Frognøya and at Norderhov, Ringerike. Two poorly preserved cranidia from the Venstøp Shale in Skien-Langesund may belong here also.

Description. Cephalic proportions similar to those of *T. ceriodes angelini*. The fine structure of the median glabellar tubercle in *T. anderssoni* was described by Størmer (1930, p. 87, text-fig. 37*c*; pl. 11, fig. 5; pl. 13, figs. 5–7) who noted that it bears four small pits arranged as at the corners of a square and a slightly larger central pit which may bear a fine canal opening. Størmer (1930, pl. 12, fig. 3; pl. 13, figs. 1, 2) also illustrated a lenticular body within the exoskeleton of the lateral tubercles of this species. On the external surface of the glabella and genal lobes there is a weakly developed fine reticulation which is seen faintly on a few internal moulds.

Fringe narrow, very steeply declined except laterally where a narrow brim is developed. A gentle anterior arch is present. The details of fringe pitting are given on text-fig. 3. Two distinct sets of radii are present, arcs E_1, I_1, I_2, and I_n are complete and in all specimens a short E_2 arc is developed posteriorly and I_3 is developed anterolaterally but never complete mesially. Arcs I_1–E_{1-2} share sulci which extend to between bR5 and bR14. The limited evidence available suggests that there is no significant difference in pit development between early and late populations of *T. anderssoni*.

Hypostoma and thorax unknown.

Pygidium similar to that of *T. ceriodes angelini*. Six rachial ring furrows, each with deep apodemal pits laterally, are seen on the external surface of the rachis. On internal moulds, a seventh pair of apodemal pits lies directly in front of the pygidial border. Pleural lobes bear four weakly developed pairs of ribs, the posterior two barely discernible.
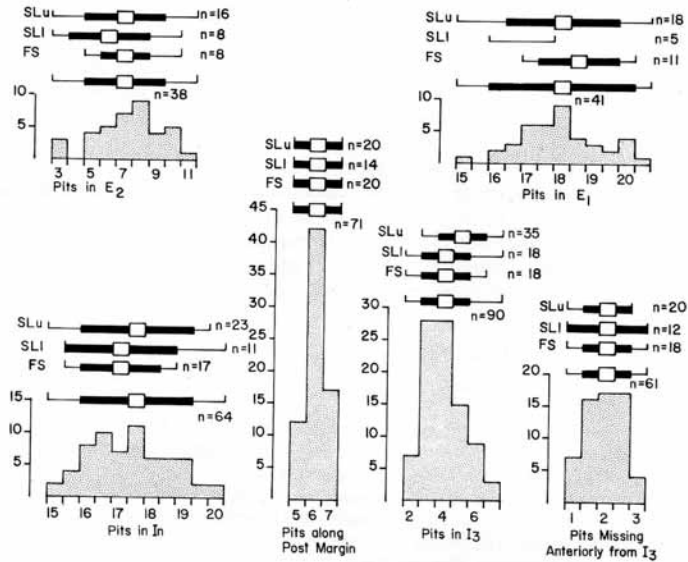
TEXT-FIG. 3. Histograms showing the range of variation in fringe features of all available specimens of *Tretaspis anderssoni* with a comparison of samples from the Frognøya Shale (FS), from 9-28 m above the base of the overlying Sørbakken Limestone (SLl) and from 17 m below the top of this unit (SLu).

EXPLANATION OF PLATE 90

Figs. 1-4. *Tretaspis seticornis* (Hisinger). 1, PMO103953, dorsal view of internal mould of almost complete specimen, 4·65 m above base of Lower Tretaspis Shale, Åstaddammen, Asker, ×2½. 2, PMO101553, ventral view of part of cranidium, Høgberg Member of the Solvang Formation, Frognøya, Ringerike, ×4. 3, PMO103954, dorsal view of cast of almost complete specimen, Lower Tretaspis Shale, Ole Deviks Vei, Oslo, ×3. 4, PMO103955, anterolateral view of cast of cranidium showing I_3 developed laterally, 1·65 m above base of Lower Tretaspis Shale, same locality as 1, ×4¾.

Figs. 5-10. *Tretaspis anderssoni* Størmer. 5, PMO103956, dorsal view of internal mould of pygidium, 17 m below top of Sørbakken Limestone, Frognøya, Ringerike, ×7½. 6, 8, 9, holotype, PMO65196, dorsal, anterior, and lateral views of internal mould of cephalon, Frognøya Shale, Frognøya, Ringerike, ×3; also figured by Størmer (1945, pl. 1, fig. 2) and Hughes *et al.* (1975, pl. 4, figs. 52, 53). 7, PMO H103, posterolateral view of cephalon, same horizon and locality as 6, ×2½; also figured by Størmer (1930, pl. 11, fig. 5). 10, PMO80670, frontal view of cast of cranidium, Venstøp Shale, Friefjord, Skien-Langesund, ×7½.

Figs. 11-14. *Tretaspis hisingeri* sp. nov. 11, PMO H71, frontal view of partially exfoliated cephalon, 3·0-4·5 m below top of Frognøya Shale, same locality as 6, ×3½. 12-14, PMO H75, dorsal, lateral, and frontal views of partially exfoliated cranidium, Frognøya Shale, same locality as 6, ×3, ×3½, ×3½; also figured by Størmer (1930, pl. 11, fig. 3; 1945, text-fig. 4).

PLATE 90
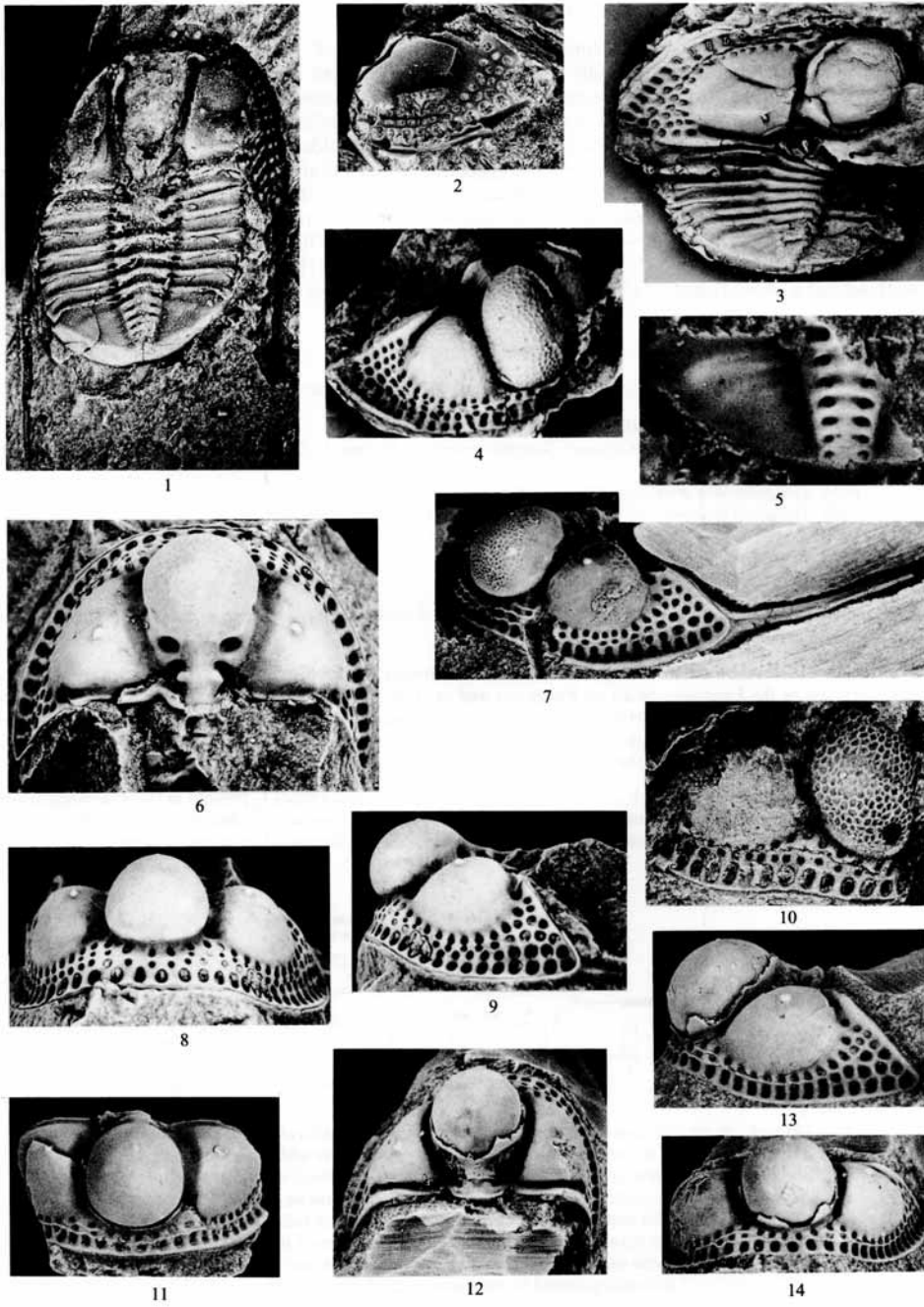
OWEN, trilobite *Tretaspis*

Discussion. T. anderssoni differs from its probable ancestor, *T. seticornis* in having a short I_3 developed in all specimens. A broadly similar fringe development is seen in a number of described taxa and their interrelationships are discussed below under *T. hadelandica.*

Størmer (1945, p. 401) considered that specimens figured by Andersson (1894) as *T. seticornis* from the Lower Johnstorp Formation (Pusgillian–?Cautleyan) of Hulderstad, Öland, Sweden, probably belong to *T. anderssoni.* Examination of these specimens reveals that they have pit counts at the upper end of, or even beyond, the range of variation seen in *T. anderssoni* from Norway. The counts in these Riksmuseum, Stockholm, specimens Ar21551 and Ar21553 respectively are as follows: E_1 22, 20; E_2 9 (?10), ?8; I_n *c.* $17\frac{1}{2}$, 18; I_3 5, 5. Without further specimens from Öland the affinities of this material must remain in doubt. Similarly, a specimen figured by Asklund (1936) from the Tretaspis Beds in Jemtland has a short I_3 but its affinities must await the description of further specimens.
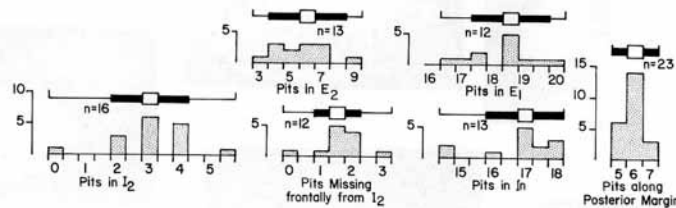
Tretaspis hisingeri sp. nov.

Plate 90, figs. 11–14; Plate 91, figs. 1–4; text-fig. 4

?1887   *Trinucleus seticornis* (Hisinger); Brøgger, p. 24.
  1930   *Tretaspis seticornis* (Hisinger); Størmer (*pars*), pl. 11, figs. 1, 3, 6, 7; text-figs. 33*c* (*pars*), ?37*a*, *b*, 40, 47.
  1934   *Tretaspis seticornis*; Størmer (*pars*), p. 330.
  1945   *Tretaspis seticornis* (Hisinger) forma typica; Størmer, p. 401, text-fig. 4.
  1970   *T.* sp. [?nov.]; Ingham, p. 41.
  1975   *T.* sp. ?nov.; Hughes *et al.*, p. 563.
  1979   *Tretaspis* sp. nov.; Owen, p. 253, text-fig. 8.

Holotype. An almost complete specimen (PMO H51) from 3·5–4·0 m below the top of the Frognøya Shale on Frognøya, Ringerike.

Material, localities, and horizons. The species has a limited stratigraphical distribution and is known from all but the lowest part of the Frognøya Shale on Frognøya and at Hole and Norderhov, and also between 9 and 14 m above the base of the overlying Sørbakken Limestone on Frognøya, Ringerike. The species is also known from the upper part of the Lower Tretaspis Shale at Ole Deviks Vei and on Bygdøy and Lindøya in Oslo, the Tretaspis Limestone at Nesbru, Asker, and the Venstøp Shale in Skien-Langesund.

Diagnosis. Very narrow fringe has E_1, I_1, and I_n complete, E_2 short and a short I_2 present in the vast majority of specimens but rarely continuous anteriorly, and in some instances asymmetrically distributed about the sagittal line. Two distinct sets of radii mesially and where I_2 is developed but laterally I_n is in phase with I_1–E_{1-2}.

TEXT-FIG. 4. Histograms showing the range of variation in all available specimens of *Tretaspis hisingeri* sp. nov. In the case of I_2, only specimens which are symmetrical about the sagittal line or which have only one side of the fringe visible are included. An additional five specimens are asymmetrical, and inclusion of the right or left counts with the data shown here does not change the mean value although the left counts increase the standard deviation to $1\frac{1}{2}$. The number of pits missing from I_2 anteriorly from these specimens is the same for both right and left sides, and thus are incorporated in the histogram of this feature.

Description. The glabella and genal lobes of *T. hisingeri* differ from those of *T. ceriodes angelini* only in having the median node situated a little further forward, the lateral eye tubercles a little closer to the glabella, and in most of the larger holaspids lacking any reticulation on the external surface of the exoskeleton. A specimen of meraspis degree 4, however, has a very strong reticulation on both glabella and genae (pl. 91, fig. 4). Similar reduction in the extent and intensity of reticulation with growth in trinucleids is well documented (Čech 1975). Genal spines extending well beyond the pygidium. The fringe is very narrow with only E_1, I_1, and I_n complete. A short E_2 is developed posteriorly and nearly all specimens have a few pits in I_2 which is rarely continuous frontally (one specimen out of twelve). In some of the specimens where the development of I_2 can be seen on both sides of the glabella there are up to two pits less on one side than on the other. In an extreme case the arc is absent on the left side but contains two pits on the right (Pl. 90, fig. 11). The range of variation in fringe features is illustrated on text-fig. 4. Arcs I_n, I_1, E_1, and (where present) E_2 are arranged in a single set of radii laterally but I_1 and E_1 are out of phase with I_n mesially and with the inner two I arcs where I_2 is developed.

Hypostoma unknown.

Thorax of holaspis similar to that of *T. seticornis*. That of the meraspis degree 4 noted above has a narrower rachis which occupies 25% (cf. 30%) of the segment width.

Holaspid pygidium known only from the holotype in which it is incomplete. Rachis bears at least 6 pairs of apodemal pits. Meraspis degree 4 pygidium sub-semicircular in outline with a rachis of approximately 5 rings of which only the anterior 2 are distinct.

Discussion. The short I_2 development distinguishes *T. hisingeri* from all other named species. *T. hisingeri* succeeds *T. seticornis* without overlap and probably was derived from it by neoteny. A very similar form in which I_2 is incomplete but more extensive than in *T. hisingeri* occurs in the Fjäcka Shale in Sweden, and it too succeeds *T. seticornis* (J. K. Ingham, pers. comm. 1976).
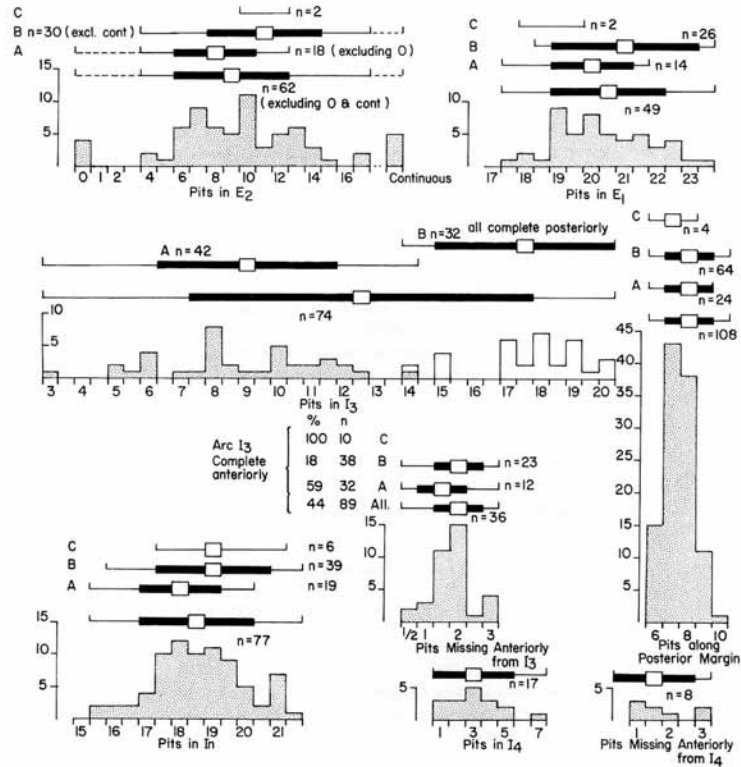
Tretaspis hadelandica hadelandica Størmer, 1945

Plate 91, figs. 5–14; Plate 92, figs. 1, 2; text-fig. 5

1923 *Trinucleus* sp.; Holtedahl *in* Holtedahl and Schetelig, p. 22.
1945 *Tretaspis seticornis*; Størmer, p. 384.
1945 *Tretaspis seticornis* var. *hadelandica* Størmer, pp. 384, 388, 406–407, pl. 1, figs. 3, 4.
1945 *Tretaspis ceriodes* (Angelin); Størmer, pp. 387, 404–405, pl. 4, fig. 16.
1945 *Tretaspis kiaeri* Størmer; Størmer, pp. 387, 406, pl. 1, fig. 11.
1970 *Tretaspis hadelandica hadelandica* Størmer; Ingham, text-fig. 17.
1973 *Tretaspis seticornis*; Lauritzen, p. 29.
1978 *Tretaspis hadelandica hadelandica* Størmer; Owen, pp. 11, 13, 14, 17.

Holotype. An incomplete cranidium (PMO65187) probably from the Gagnum Limestone Formation south of Gagnum, Hadeland.

Material, localities, and horizons. A few complete specimens and a large number of disarticulated skeletal elements occur abundantly in the Gagnum Shale (except the lowest part in northern Hadeland) and Lunner Kirke members of the Lunner Formation, the shales of this formation around Lunner, and in the Gagnum Limestone and Kjørrven formations. The species is rare in the Grina Shale Member of the Lunner Formation. Fragmentary museum material from Nittedal (precise horizon unclear), between Oslo and Hadeland, may belong here also.

Description. Proportions of glabella and genal lobes very similar to those of *T. ceriodes angelini*. Specimens from the Gagnum Shale have a well-developed reticulation on the external surface and commonly on the internal mould, but most specimens from other units have only a subdued reticulation or are smooth. Fringe steeply declined with a slight brim developed laterally. Genal spines long, diverging rearwards very slightly. All specimens have two distinct sets of radii, and arcs E_1, I_1, I_2, and I_n are complete. Three morphs are recognized on the development of E_2, I_3, and I_4 (Table 1) and the distribution of pits in each arc is shown on text-fig. 5. Arc I_4 is absent from morphs A and B which respectively have I_3 incomplete and complete posteriorly. These morphs occur in all samples, whereas morph C, which has a short I_4 developed, is known only from a few populations from the lower part of the Gagnum Shale Member, the upper part of the Lunner Formation around Lunner, and from the Gagnum Limestone. In one specimen (Pl. 92, figs. 1, 2) I_3 is complete on the right side of the cranidium but not on the left, an asymmetry which encompasses both morph A and morph B. Samples are not large enough

TEXT-FIG. 5. Histograms showing the range of variation in fringe features of all available specimens of *Tretaspis hadelandica hadelandica* with a comparison of the range, mean, and sample standard deviation of the three morphs (A, B, and C) present in the subspecies.

to enable detailed unit by unit comparison of the variation in each morph but no obvious stratigraphical changes are apparent.

Hypostoma unknown. Thorax like that of *T. seticornis*.

Pygidium sub-semicircular in outline. Rachis crossed by 5–7 furrows each bearing apodemal pits laterally. On the ventral surface of the pygidium there are up to ten pairs of apodemes, the posterior three of which are situated on the steeply declined pygidial border. Pleural lobes bear three low ribs.

Discussion. When present, morph C occurs with morphs A and B which are always found together. Their great similarity in pit distribution in arcs E_1, I_n, and along the posterior margin argues strongly for these morphs being no more than broad phenotypes from the same gene pool. Their relative abundance, however, may be ecologically controlled. Table 2 gives the relative percentages of morphs present in the stratigraphical units in which they occur in measurable abundance.

3×2 and 2×2 contingency tests were carried out on the specimen numbers used to calculate these percentages. The latter test was used where morph C was absent from both samples under examination, or where expected frequencies of morph C were less than 5; Yates's Correction was applied in both instances. These tests show that the Gagnum Shale abundances are significantly different from all but those of the Kjørrven Formation at the 0·1% level. The Kjørrven Formation

TABLE 2. Percentages of each morph present in collections of *T. hadelandica hadelandica* from stratigraphical units in Hadeland

Morph	Gagnum Shale Member	Lunner Kirke Member	Lunner Formation above Lunner Kirke Member	Gagnum Limestone	Kjørrven Formation
A	55	17	18	13	47
B	31	83	75	77	53
C	14	0	7	10	0
Number of specimens	106	35	44	39	19

abundances differ from those of the Gagnum Shale near the 50% level which is not significant, and from those of the other three units at the 5% level which is considered significant. No significant differences are present between the remaining three units where, in fact, there is a high degree of correlation. The similarity between the Gagnum Shale and Kjørrven Formation abundances is the product of high proportions of morph A in these units. It may be noteworthy that both units have a much higher trilobite diversity (measured by the total number of known taxa) than the others, but speculation on the reasons for this similarity in morph composition would be very unreliable in view of the small sample size from the Kjørrven Formation.

T. hadelandica brachystichus Ingham, 1970, was based on samples from the Rawtheyan Stage (Ashgill Zones 5 and 6) in the Cautley area of northern England which have I_3 incomplete anteriorly and posteriorly. Ingham also tentatively included fragments from the mid-Cautleyan Stage (Zone 3) in this subspecies and suggested that specimens from the Gagnum Shale assigned to *T. ceriodes* by Størmer may belong to the north of England form. These Gagnum Shale specimens are assigned to *T. hadelandica hadelandica* morph A herein. Ingham's material and specimens assigned to *T. hadelandica brachystichus* by Price (1973, 1977) and Cocks and Price (1975) from the uppermost part of the Sholeshook Limestone and lower part of the Slade and Redhill Mudstone (mid-Ashgill) in south Wales, have a range of variation which overlaps that seen in the Norwegian morph A (text-fig. 6). In the case of arcs E_2 and E_1 and the number of pits along the posterior margin, the range and, in the E arcs, the mean is higher than that of the Norwegian morph. The variation in number of pits in I_3, however, overlaps at the lower end of that seen in *T. hadelandica hadelandica* morph A and is closer to that of *T. anderssoni* which, in all these characters, has a range of variation which overlaps only at its upper end with that of *T. hadelandica hadelandica* morph A (text-fig. 6).

T. convergens Dean, 1961, was described originally from Pusgillian strata in the Cross Fell Inlier in northern England and subsequently by Ingham (1970) from Pusgillian and lower Cautleyan (Ashgill Zone 1) strata at Cautley and by McNamara (1979) from mid-Cautleyan (Zone 2 and lowest part of Zone 3) strata in the English Lake District. As noted by McNamara (1979, p. 62), the limited evidence available suggests that there is a progressive reduction in I pits with the Cross Fell specimens having a short (up to ten pits) I_4 arc, some specimens lacking this arc in the Cautley material, and in all the Lake District specimens this arc is not developed. This trend is continued in Ashgill Zone 3 in the Lake District with *T. convergens deliquus* McNamara, 1979; I_3 becoming incomplete anteriorly and then laterally. The earliest examples with *T. convergens deliquus* morphology occur with specimens with I_3 complete anteriorly (K. J. McNamara, pers. comm. 1979).

As text-fig. 6 shows, the over-all pit distribution and the broad range of variation seen in the subspecies of *T. convergens* is very similar to that of *T. hadelandica hadelandica* and consequently the English forms are regarded as subspecies of *T. hadelandica*. It seems reasonable to suggest that Ingham's indeterminate specimens from Zone 3 are, in fact, *T. hadelandica deliquus* and that the progressive decrease in pit number in I_3 documented by McNamara continued, giving rise to *T. hadelandica brachystichus*. Moreover, if the Zone 3 material from Cautley is indeed *T. hadelandica deliquus*, the restriction of *T. hadelandica brachystichus* to Zones 5 and 6 (i.e. lower Rawtheyan) in northern England would add weight to Ingham's suggestion (1977, p. 118) that the uppermost part of the Sholeshook Limestone is early Rawtheyan in age. *T. convergens* has been recorded from lower

Ashgill strata at Girvan, south-west Scotland (Ingham 1970, p. 46), but the affinities of this material are not known.

The succession of subspecies of *T. hadelandica* in northern England seems to represent a single local stock and the above revision is based on this. An alternative, but more contrived hypothesis would be the ecological replacement of *T. hadelandica hadelandica* morphs. Thus the Norwegian morph C resembles early *T. hadelandica convergens*, morph B resembles late *T. hadelandica convergens*, and early *T. hadelandica deliquus* and morph A resembles *T. hadelandica brachystichus*.

As far as morph A is concerned, the absence of E_2 in some specimens, the high percentage of individuals in which I_3 is continuous frontally, and the fairly limited overlap in number of pits in I_3 serves to distinguish it from *T. hadelandica brachystichus*. Chi-squared tests show that the ranges in I_3 pits and pits missing anteriorly from this arc are distinct at the 0·1% level, even when Ingham's samples from Zones 5 and 6 are considered together. There is only a limited amount of information on *T. hadelandica convergens* and *T. hadelandica hadelandica* morph C from the Gagnum Shale but this suggests that the English form commonly has more pits in E_1 ($19\frac{1}{2}$–$22\frac{1}{2}$ cf. 18–$19\frac{1}{2}$) and along the posterior margin (7–12 cf. 6–7), but fewer in E_2 (6–11 cf. 10–13) and in all cases I_3 is complete whereas it is incomplete posteriorly in 33% (of nine specimens) of the Norwegian morph C. The English form is also distinguished by its more swollen pseudofrontal lobe. Although later
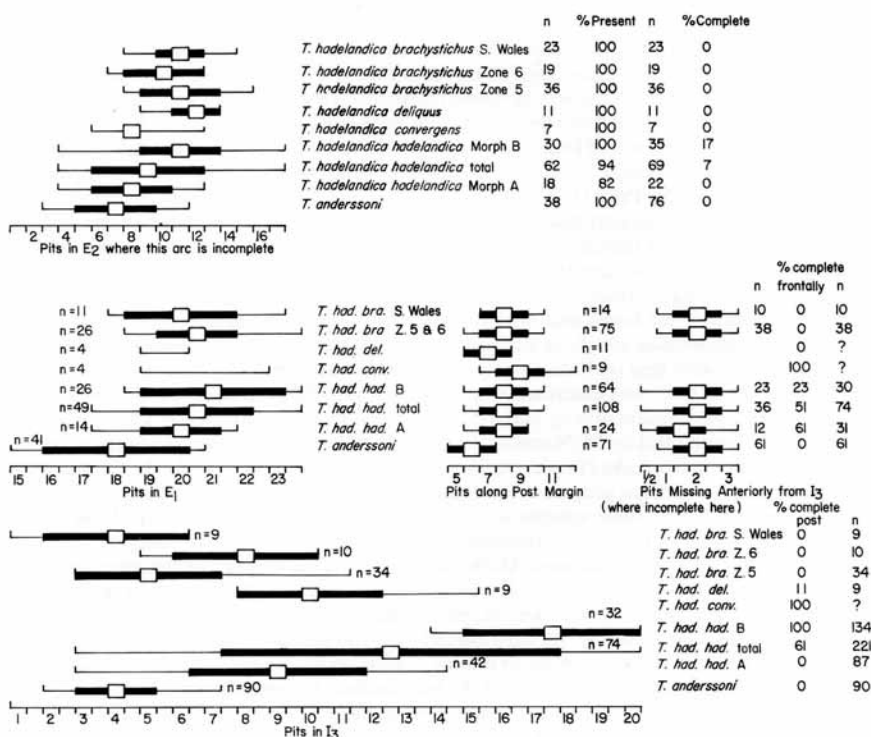
TEXT-FIG. 6. Range, mean, and sample standard deviation of selected fringe characters of members of the *Tretaspis seticornis* group in which I_3 is incomplete in at least some individuals. Data for *T. hadelandica convergens*, *T. h. deliquus*, and *T. h. brachystichus* based on histograms given by Ingham (1970), McNamara (1979), and Price (1977).

populations of *T. hadelandica convergens* and early *T. hadelandica deliquus* lack I_4, they differ from *T. hadelandica hadelandica* morph B in always having I_3 complete frontally. It seems most likely, therefore, that *T. hadelandica hadelandica* with its broad range of variation (morphs A, B, and C) and the British series of subspecies with, at any one level, a much narrower range of variation were at most connected by a series of clines throughout much of the Ashgill.

T. clarkei Cooper (*in* Schuchert and Cooper, 1930) from Ashgill units in Quebec, Canada, has two distinct sets of radii and thus belongs to the *T. seticornis* group and is not a synonym of *T. ceriodes* (cf. Whittington 1941, p. 29; Lespérance 1968, p. 813; Bolton 1970, pp. 35–36). The holotype from the Whitehead Formation and specimens figured by Bolton (1970, pl. 6, figs. 12, 15, 17, 19) from the Vauréal Formation have I_3 incomplete posteriorly at least. Of the three specimens from the Whitehead Formation in the Hunterian Museum, two (HM A4319; 4320) have eight pits in I_3 which is incomplete anteriorly. A third specimen (HM A4321) has twelve pits in I_3 which is complete anteriorly and three pits in I_4. It is not known whether the specimens are from the same horizon but all fringe features fall within the range seen in *T. hadelandica*. Detailed sampling of *T. clarkei* populations is needed before its affinities can be fully determined.

As is noted in the discussion of *T. seticornis*, specimens of *Tretaspis* with arc I_3 developed are known from the Fjäcka Shale in Sweden. In addition to Angelin's material of *T. affinis*, which has this arc complete, other specimens in the Riksmuseum, Stockholm, have I_3 incomplete but, in some cases, extensive (J. K. Ingham, pers. comm. 1976). Dr. Ingham has also examined a specimen from the Slandrom Limestone (probably early Pusgillian) in the Siljan district (Jaanusson and Martna 1948, p. 187) which has a short I_3 and a coarsely reticulate glabella and genal lobes. Dr. P. J. Brenchley of Liverpool University has sent me a specimen resembling *T. hadelandica hadelandica* morph B from the flank facies of the Boda Limestone (Ashgill) in the Siljan district and this is the only specimen of *Tretaspis* known from these beds, and the genus is not known from the Boda Limestone itself. The Swedish species of *Tretaspis* are being revised by Dr. Ingham who has taken well-localized samples from the Fjäcka Shale.

There is a great deal of other material of the *T. seticornis* group with an incomplete I_3 and in need of modern study. This includes specimens from Ashgill units in Poland ascribed to *T. seticornis* by Kielan (1957, 1960) and Tomczyk (1962), and material from the Kràlův Dvůr Formation (mid-Ashgill) in Bohemia examined by the writer in the collections of the British Museum (Natural History). Specimens from this latter unit were referred to *T. seticornis* by Havlíček and Vaněk (1966) and Přibyl and Vaněk (1969). Ingham (1970, pp. 41, 49) noted that specimens which Lamont (1935, 1941) assigned to *T. seticornis* from the Lower Drummuck Group (Cautleyan) at Girvan has a short I_3 and was termed *T.* sp. by Hughes *et al.* (1975, p. 563). Price (1977, p. 786) noted a similarity between an unnamed form from low in the Slade and Redhill Mudstones and this species. Dr. Ingham informs me (pers. comm. 1976) that *T. seticornis* of Portlock (1843) and Fearnsides, Elles, and Smith (1907) from the Killey Bridge Beds (low Cautleyan) in Pomeroy, Ireland, may well prove synonymous with the broadly coeval Lower Drummuck Group form as both have a short I_3, a very extensive E_2, and large lateral eye tubercles quite close to the glabella. Moreover, *T.* sp. probably gave rise to *T. persulcatus* (Reed, 1935) from the Upper Drummuck Group (late Rawtheyan) in which E_2 is complete and the girder is indistinct posteriorly where an external pseudogirder is developed between E_1 and E_2 (see Ingham, 1970, p. 44).

Schmidt (1894) assigned specimens to *T. seticornis* from the Lykholm Group (late Caradoc to Ashgill) in Estonia, and Jaanussòn (1956, pp. 379, 383) listed the species from the lower part of the group, the Nabala Formation (late Caradoc). It is not known whether the material referred to by Jaanusson is from the same beds as Schmidt's specimens, one of which (1894, pl. 5, fig. 22) is illustrated as having I_3 complete posteriorly, but it is not clear whether two sets of radii are developed. Assuming that existing correlations are correct, the Estonian specimens listed by Jaanusson would prove the oldest record of the *T. seticornis* group should they prove correctly ascribed to it.

Tretaspis latilimbus (Linnarsson, 1869) *norvegicus* subsp. nov.

Plate 92, figs. 3–7; text-fig. 7

1887 *Trinucleus seticornis* (Hisinger) (?) var.; Brøgger, p. 26.
1887 *Trinucleus* conf. *seticornis*; Brøgger, p. 29.
1887 *Trinucleus*; Brøgger, p. 30.
1887 *Trinucleus Wahlenbergi*; Brøgger, p. 31.
?1887 *Trinucleus Wahlenbergi* Rouault; Brøgger, p. 32.
1897 *Trinucleus Wahlenbergi* Rouault; Kiaer, p. 33 [Upper Isotelus Limestone, ?'5a'].
1930 *Tretaspis latilimbus* (Linnarsson); Størmer (*pars*), pp. 67–69 [Tretaspis Limestone specimens only], pl. 11, figs. 8, ?9, 10, 11; text-figs. 33*f*, ?*g*, *non e* [= *T. anderssoni*], *non* 34*d* [= *T. latilimbus latilimbus*].
1934 *Tretaspis latilimbus*; Størmer, p. 330.
1945 *Tretaspis latilimbus* (Linnarsson); Størmer, p. 403, pl. 1, fig. 9.

Holotype. A cephalon (PMO11751) from the Tretaspis Limestone on Lindøya, Oslo.

Material, localities, and horizons. A great deal of very fragmentary material and rarer more complete specimens occur at various levels in Oslo-Asker: Tretaspis Limestone on Langåra, Lindøya, Ostøya, and Treneholmen; Upper Tretaspis Shale on Hovedøya and Nakholmen; Upper Isotelus Limestone on Hovedøya, Langøyene, Lindøya, and Skjaerholmen; all but the upper few metres of the Husbergøya Shale Formation on Hovedøya and possibly Husbergøya, Rambergøya, and Langøyene. A specimen in limestone (?Herøya Limestone) from the Skien–Langesund district probably belongs here also.

Diagnosis. Arcs E_1, I_{1-3}, and I_n complete. I_4 short to complete, E_2 present in 41% of thirty-four specimens. Reticulation on external surface of glabella and genae subdued.

Description. Proportions of glabella and genal lobes similar to those of *T. ceriodes angelini*. There is a fine, subdued reticulation on the external surface of the mesial part of the glabella and the adaxial parts of the genal lobes, but they are smooth on internal moulds. Arcs E_1, I_{1-3}, and I_n are complete, and I_4 is developed in all specimens, most having $3-11\frac{1}{2}$ pits (twenty-four specimens) in this arc but one extreme specimen from the Tretaspis Limestone has this arc complete. Two morphs (A and B) are defined on the absence or presence

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EXPLANATION OF PLATE 91

Figs. 1–4. *Tretaspis hisingeri* sp. nov. 1, 2, holotype, PMO H51, dorsal and lateral views of partially exfoliated almost complete specimen, 3·5–4·0 m below top of Frognøya Shale, Frognøya, Ringerike, × 2¾, × 2; also figured by Størmer (1930, text-fig. 47). 2, PMO80613, frontal view of partially exfoliated cranidium, Frognøya Shale, Ringsåsen, Norderhov, Ringerike, × 2. 4, PMO103957, dorsal view of cast of complete meraspis degree 4, 7·91–7·94 m above base of Lower Tretaspis Shale, Ole Deviks Vei, Oslo, × 12½.

Figs. 5–14. *Tretaspis hadelandica hadelandica* Størmer. 5, 8, 11, holotype, morph B, PMO65187, dorsal, frontal, and lateral views of partially exfoliated cephalon, probably from the Gagnum Limestone Formation, south of Gagnum, Hadeland, × 2; also figured by Størmer (1945, pl. 1, fig. 4). 6, morph B, PMO98489, dorsal view of lower lamella external to girder showing E_2 complete frontally, upper part of Lunner Formation, Kjevlingen, Hadeland, × 3½. 7, morph C, PMO103958, anterolateral view of partially exfoliated cranidium, Gagnum Limestone Formation, 500 m south-east of Lunner Bakken, Hadeland, × 4½. 9, morph A, PMO99537, oblique anterolateral view of cast of cranidium, 7·1–7·2 m below top of Gagnum Shale Member of the Lunner Formation, 75 m south of Roko, Hadeland, × 5. 10, PMO103959, dorsal view of unwhitened pygidium, lower part of Lunner Formation, 400 m east-south-east of Lunner Kirke, Hadeland, × 8. 12, PMO101483, dorsal view of internal mould of pygidium, Gagnum Limestone Formation, Ballangrud, Hadeland, × 4. 13, PMO103960, dorsal view of unwhitened thorax and pygidium, lower part of Lunner Formation, Haga, Hadeland, × 4. 14, morph A, PMO65193, dorsal view of partially exfoliated almost complete specimen, Gagnum Shale Member of the Lunner Formation, Gagnum, Hadeland, × 3½; also figured by Størmer (1945, pl. 4, fig. 16).
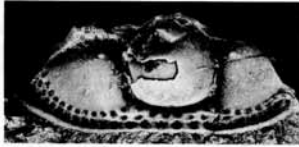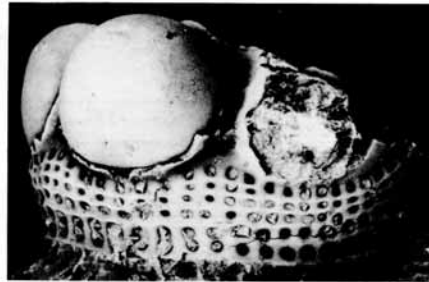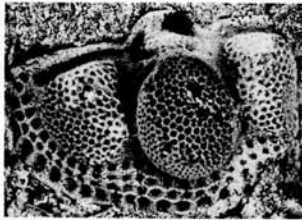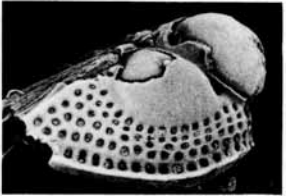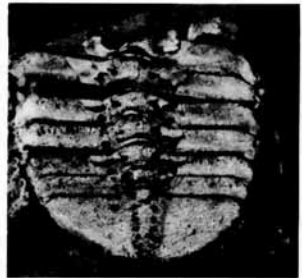
PLATE 91

OWEN, trilobite *Tretaspis*

respectively of E_2 which occurs in 41% of the thirty-four specimens in which this feature could be determined (Table 1). As in all species of *Tretaspis* the most posterior one or two E_1 pits always lack equivalent E_2 pits. The range of variation in fringe pitting is illustrated on text-fig. 7. Arcs I_1, E_1, and, where present, E_2 are out of phase with the remaining I arcs and share sulci which extend to the anterolateral part of the fringe or even to the zone of complication. The available samples are too small to detect differences from rock unit to rock unit and both morphs are known from all but the lower part of the Husbergøya Formation. Personally collected material from the Upper Tretaspis Shale shows both morphs in the same bed.

Hypostoma unknown. Thorax similar to that of *T. seticornis*.

Pygidium only known with certainty from a few fragments. The one figured by Størmer (1930, pl. 11, fig. 9) may belong here or to *T. sortita broeggeri* (see below) as the precise horizon in the Husbergøya Formation is not known. This specimen has ten pairs of apodemal pits, the posterior three lying on the pygidial border.
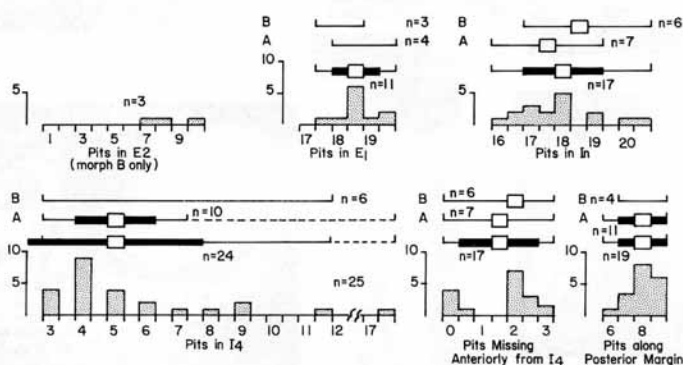
TEXT-FIG. 7. Histograms showing range of variation in fringe features of all available specimens of *Tretaspis latilimbus norvegicus* with a comparison, where possible, of the range, mean, and sample standard deviation of the two morphs (A and B) present in the subspecies. In many instances the samples are too small for reliable standard deviations or even means to be calculated.

Discussion. Ingham (1970, p. 50, text-fig. 18*a*, *b*) chose a lectotype from Linnarsson's original material of *T. latilimbus* from the Upper Johnstorp Formation (Rawtheyan) of Västergötland, Sweden, and he figured a number of topotypes (1970, text-fig. 18*c-f*). Dr. Ingham has allowed me to collate some of his data on topotype material of the Swedish form in the collections of the Riksmuseum, Stockholm. All these specimens have an incomplete I_4 arc (2-11 pits in forty-two specimens) which is not continuous mesially. Where the E arc development is sufficiently well preserved, only one specimen out of thirty-five is seen to have pits in E_2 and thus the vast majority correspond to the development seen in *T. latilimbus norvegicus* morph A. The range of variation seen in the pit distribution of other arcs is similar to that of the Norwegian material and it is most likely that the Swedish form is simply a geographical subspecies of *T. latilimbus norvegicus* in which morph B has been virtually excluded. Fragments of *Tretaspis* from the Ulunda Formation (Rawtheyan) in Västergötland have a pit development similar to that of *T. latilimbus norvegicus* morph B (J. K. Ingham, pers. comm. 1976).

T. 'latilimbus' distichus Ingham (1970, p. 50, pl. 7, figs. 8-16, text-figs. 14*g*, 16) was based on material from the Rawtheyan Stage (Ashgill Zone 7) in the Cautley district of northern England and is characterized by the presence of a short I_4 and seven to ten pits in E_2. It thus resembles *T. latilimbus norvegicus* morph B and might be regarded as being a subspecies which developed in the same way as *T. latilimbus latilimbus*. However, Ingham (1970, p. 50) suggested that *T. 'latilimbus' distichus* may

have been derived from *T. hadelandica brachystichus* with the completion of I_3 and the development of a short I_4. Indeed, one specimen of the latter was noted by Ingham to have a pit in I_4. When the ranges in variation in E_2 and I_3 in *T. hadelandica brachystichus* are considered for Zones 5 and 6 separately (text-fig. 6; Ingham 1970, text-fig. 16) there is a suggestion of a trend towards the condition seen in *T. 'latilimbus' distichus*. Moreover, McNamara (1979, p. 63) has noted the occurrence of specimens which he terms *T. aff. latilimbus distichus* from the White Limestone (top of Zone 6) in the Lake District which he considers to be intermediate between *T. hadelandica brachystichus* and *T. 'latilimbus' distichus*. Dr. McNamara informs me (pers. comm. 1979) that the White Limestone form has I_3 complete posteriorly and in some specimens there is a single pit in I_4. Thus it seems likely that the Zone 7 form is not directly related to *T. latilimbus* and ultimately may best be considered a stratigraphical subspecies of *T. hadelandica*.

The origins of *T. latilimbus* are not clear but *T. hadelandica hadelandica* seems to be the most likely ancestor.

Tretaspis sortita (Reed, 1935) *broeggeri* Størmer, 1945

Plate 92, figs. 8–11, 13, 14; text-fig. 8

?1887   *Trinucleus Wahlenbergi* Rouault; Brøgger, p. 32.
?1897   *Trinucleus Wahlenbergi* Rouault; Kiaer, pp. 32 (*pars*, '4dδ' specimens only), 73.
  1945   *Tretaspis latilimba* (Linnarsson) var. *brøggeri* Størmer, p. 403, pl. 1, fig. 10.
  1979   *Tretaspis sortita* (Reed) *broeggeri* Størmer; Owen, p. 257.

Holotype. An incomplete cephalon (PMO11957) from the upper part of the Husbergøya Shale Formation on Skjaerholmen, Oslo.

Material, localities, and horizons. Cephala, cranidia, and rare thoracic segments are known from the upper few metres of the Husbergøya Formation in Oslo, on the islands of Skjaerholmen, Husbergøya (upper 2 m), Hovedøya (upper 2·5 m), South Langøyene (upper 5 m), Lindøya, and Gressholmen.

Description. Glabella and genal lobes similar to those of *T. ceriodes angelini* but bear a variably developed, subdued, fine reticulation on the external surface (on the genal lobes this is restricted to the posterior parts) and are smooth on internal moulds. Fringe steeply declined with a well-developed anterior arch and a distinct brim laterally. Arcs E_1, I_{1-3}, and I_n are complete, I_4 is incomplete, and three morphs are recognized on the basis of the E_2 and I_5 development (Table 1) thus: morph A lacks E_2 and I_5, morph B lacks I_5 but has a short E_2, morph C has both E_2 and I_5 present but incomplete. The range of variation in pit development is shown on text-fig. 8. There are too few specimens to give meaningful comparisons of some of the parameters in the three morphs separately, and in some instances morphs A and B are considered together on text-fig. 8. Arc E_2 is irregularly developed in a few specimens (e.g. Pl. 92, figs. 8, 10) but in most cases where it is present it is restricted to the posterior part of the fringe. In all morphs, arcs I_1–E_1 share sulci to bR2–8 (mean bR5, sample standard deviation 1, eighteen specimens) and distinct lists are developed between most arcs over the whole fringe except E_1–I_1, where they share sulci and between E_1 and E_2 and also I_5 and I_n. Two sets of radii are developed.

Hypostoma not known. Thorax and pygidium known only from a few poorly preserved fragments.

Discussion. The holotype of *T. sortita broeggeri* has eleven pits in E_2 and one in I_5, and thus is of morph C type. Morphs A and B are indistinguishable from the two morphs constituting *T. latilimbus norvegicus* although their relative abundances are very different with E_2 being developed much more commonly in *T. sortita broeggeri*. Størmer's subspecies probably was derived from *T. latilimbus norvegicus* with the development of I_5 in some individuals and replaces the earlier form quite abruptly in the Husbergøya Formation, although it is not possible to assign unequivocally isolated specimens of morphs A and B to either form.

T. sortita sortita (Reed, 1935, pp. 3–6, pl. 1, figs. 4–10; see also Begg 1944, pp. 114, 115, pl. 5, figs. 2–7) was based on material from the Upper Drummuck Group (late Rawtheyan) at Girvan, south-west Scotland. A complete topotype specimen was figured by Ingham (1970, pl. 8, fig. 1) who noted (1970, p. 50) that the Scottish form has an incomplete E_2, an extensive but incomplete I_4, and a few pits in I_5. Dr. Ingham has informed me (pers. comm. 1976) that the vast majority of specimens from
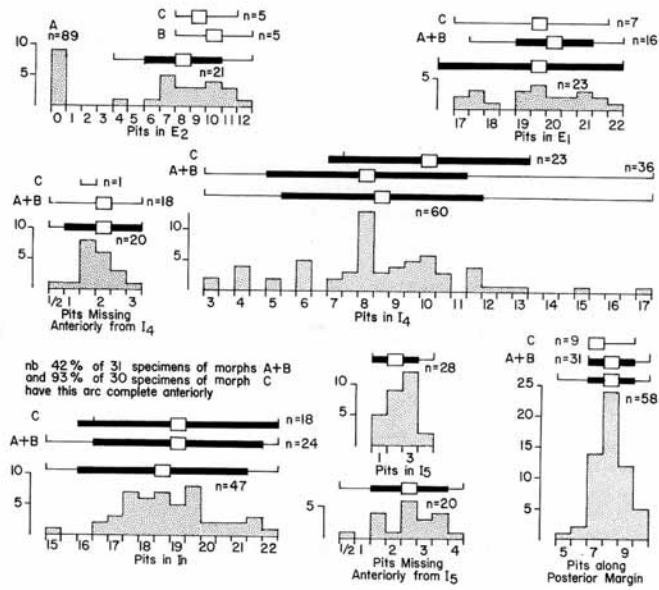
TEXT-FIG. 8. Histograms showing the range of variation in fringe features of all available specimens of *Tretaspis sortita broeggeri* with a comparison of the range, mean, and sample standard deviation of the three morphs (A, B, and C) present in the subspecies. Owing to the limited amount of data for morphs A and B, these are considered together in most instances.

EXPLANATION OF PLATE 92

Figs. 1, 2. *Tretaspis hadelandica hadelandica* Størmer. PMO103961, right and left lateral views of internal mould of cranidium showing asymmetrical I_3 development, lower part of Gagnum Shale Member of the Lunner Formation, 200 m north of Åslund, Hadeland, ×8.

Figs. 3–7. *Tretaspis latilimbus* (Linnarsson) *norvegicus* subsp. nov. 3, holotype, ?morph A, PMO11751, antero-lateral view of incomplete cephalon, Tretaspis Limestone, Lindøya, Oslo, ×4; also figured by Størmer (1945, pl. 1, fig. 9). 4, morph B, PMO101551, anterolateral view of partially exfoliated cranidium, same horizon as 3, west Rambergøya, Oslo, ×3. 5, morph A, PMO80518, oblique anterolateral view of internal mould of cephalon, Husbergøya Shale Formation, North Langøyene, Oslo, ×3. 6, morph A, PMO103962, dorsal view of internal mould of cephalon and part of thorax, Upper Tretaspis Shale, north Hovedøya, Oslo. 7, morph B, PMO80573, oblique posterolateral view of cephalon, same horizon as 3, Ostøya, Baerum, ×3.

Figs. 8–11, 13, 14. *Tretaspis sortita* (Reed) *broeggeri* Størmer. 8, morph B, PMO31010, anterolateral view of internal mould of incomplete cephalon showing irregular E_2 development, upper part of Husbergøya Shale Formation, South Langøyene, Oslo, ×2½. 9, holotype, morph C, PMO11957, lateral view of internal mould of incomplete cephalon, same horizon as 8, Skjaerholmen, Oslo, ×4½; also figured by Størmer (1945, pl. 1, fig. 10). 10, PMO100720, ventral view of cast of lower lamella, pygidium, and thorax, top of Husbergøya Shale Formation, Rambergøya, Oslo, ×2½. 11, 14, morph C, PMO103963, frontal and anterolateral views of cast of cephalon, same horizon as 8, Hovedøya, Oslo, ×3. 13, morph C, PMO103964, posterior view of cast of crushed cephalon and incomplete thorax, note weak reticulation on posteromesial parts of genal lobe, upper 2 m of Husbergøya Shale Formation, Husbergøya, Oslo, ×4.

Figs. 12, 15. *Tretaspis askerensis* sp. nov. 12, PMO64649, frontal view of cast of crushed cranidium, middle part of Grina Shale Member of the Lunner Formation, Grina, Hadeland, ×4; also figured by Størmer (1945, pl. 1, fig. 1). 15, PMO6376, posterolateral view of cast of incomplete cephalon, from either the lower part of the Langåra Limestone-Shale Formation or the Husbergøya Shale Formation, Hvalstad, Asker, ×6.

PLATE 92
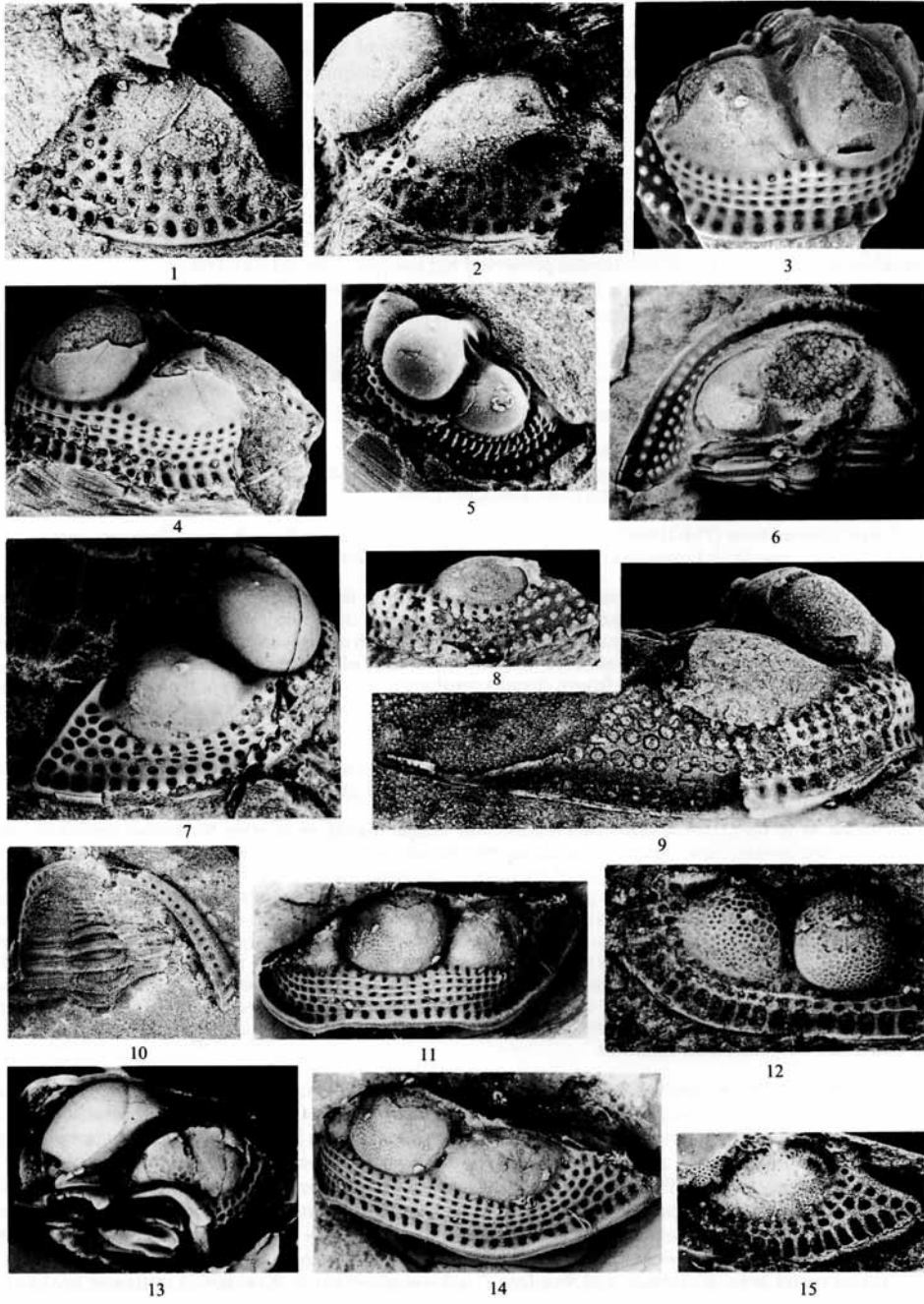
OWEN, trilobite *Tretaspis*

Girvan are of this type and are very similar, if not identical, to the Norwegian morph C. Thus *T. sortita broeggeri* differs from the Scottish form only in the proportions of constituent morphs.

Price (1977, pp. 784–785, pl. 103, figs. 1–7; text-fig. 2) assigned material to *T. sortita* from late Ashgill mudstones in the Meiford area and commented on other Welsh material probably belonging to this species. The specimens which he described have E_2 developed and only one out of seven lacks pits in I_5. Unlike both the Norwegian and Scottish forms, the genal lobes are completely smooth, arcs I_1–E_1 share short sulci in only a few specimens and lists are less well developed.

Dr. Ingham informs me (pers. comm. 1976) that one specimen of *Tretaspis* from the type unit and locality of *T. latilimbus latilimbus*, the Upper Johnstorp Formation in Västergötland, has a short I_5 developed (four pits). The E pits are not preserved but the specimen may well be of *T. sortita* type and further, well-localized, collections may enable greater correlation between the Swedish, Norwegian, and British upper Ashgill sequences.

Tretaspis askerensis sp. nov.

Plate 92, figs. 12, 15; Plate 93, figs. 1–5.

1902 *Trinucleus Wahlenbergi* Rouault; Kiaer, p. 78.
1945 *Tretaspis seticornis* (Hisinger) forma typica; Størmer, p. 406, pl. 1, fig. 6.
1978 *Tretaspis* aff. *seticornis seticornis* (Hisinger); Owen, p. 15.

Holotype. A cranidium (PMO100657) from either the Husbergøya Shale Formation or the lower part of the Langåra Limestone-Shale Formation (i.e. '5a' of Brenchley and Newall 1975) Holmenskjaeret, Holmen, Asker.

Material, localities, and horizons. Four incomplete cranidia from the type horizon and locality, a cephalon probably from '5a' at Øvre Nes badestrand, a cranidium possibly from this unit at Hvalstad, three cranidial fragments from 2–3 m above the base of the Husbergøya Formation on Brønnøya and 1–4 m above the base of this unit on Langåra, all Asker. Two cranidia from the lowest 13 m of the Husbergøya Formation on Kalvøya, Baerum. Three fragmentary cranidia from a channel conglomerate in the upper part of the Langåra Formation on Ostøya, Baerum (indicating transport from the west), and one external mould of a cephalon from the Grina Shale Member of the Lunner Formation at Grina Hadeland.

Diagnosis. Pseudofrontal lobe strongly swollen, almost circular in dorsal view. Arcs E_1, I_1, I_2, and I_n complete. A short I_3 is present in a few specimens. I_1–E_1 sulci deep. E_2 short or absent.

Description. Most specimens of this form are noticeably smaller than those of other Norwegian species but the material is too incomplete to quantify this adequately. Pseudofrontal lobe strongly swollen, almost circular in dorsal view but otherwise the proportions of the glabella and genae very similar to those of *T. ceriodes angelini*. The external surface of the glabella and genae bears a well-developed reticulation which is very fine except on the posteromesial parts of the genal lobes where it is coarser. Some internal moulds fairly strongly reticulate. Fringe steeply declined. Arcs E_1, I_1, I_2, and I_n complete. E_2 developed in two specimens (of four) where it comprises up to six pits. I_3 present in two specimens (of seven) where it contains two or three pits, beginning at about aR3. There are eight pits along the posterior margin of the fringe in three specimens. There are nineteen pits in I_n in one topotype specimen and the Grina Shale cephalon and $16\frac{1}{2}$ in a specimen from Kalvøya. Arcs E_1 and I_1 share deep sulci over all but the posterior part of the fringe and are out of phase with the remaining I arcs.

Remainder of exoskeleton unknown.

Discussion. The fringe development of *T. askerensis* resembles that of *T. seticornis* and the Grina Shale specimen was assigned to this species by Størmer (1945) and Owen (1978). *T. askerensis* differs in its deep I_1–E_1 sulci, in having I_3 developed in a few specimens, in having eight (cf. six or seven) pits along the posterior margin, and the number of pits in I_n extends beyond the maximum recorded for *T. seticornis*. Clearly the very limited number of specimens of both species makes objective comparison very difficult. The more circular outline of the pseudofrontal lobe and much stronger reticulation also distinguish the younger species although the latter character may have little taxonomic value (see Price 1977, p. 781). *T. seticornis* has a very short stratigraphical range, being restricted to low Pusgillian strata in both Norway and Sweden. *T. askerensis* occurs in Rawtheyan units and probably

was derived from, for example, *T. hadelandica hadelandica* or *T. latilimbus norvegicus*. The relatively small size, well-developed reticulation (see Størmer 1930, p. 65) and simple fringe morphology suggest a neotenous origin for the species.

<p style="text-align:center">*Tretaspis sagenosus* group?</p>

<p style="text-align:center">Tretaspis kiaeri Størmer, 1930</p>

<p style="text-align:center">Plate 93, figs. 6–15; text-fig. 9</p>

1921 *Trinucleus*; Kiaer, p. 500.
1930 *Tretaspis kiaeri* Størmer, pp. 50–55, pl. 10, figs. 1–6; pl. 11, fig. 12; pl. 13, fig. 13; pl. 14, figs. 1–3; text-figs. 21c, 23–26, 38.
1945 *Tretaspis kiaeri* Størmer; Størmer (*pars*), p. 403, pl. 1, fig. 12; *non* pp. 387, 406, pl. 1, fig. 11 [= *T. hadelandica hadelandica*].
1953 *Tretaspis kiaeri*; Størmer, p. 87.
1959 *Tretaspis kiaeri* Størmer; Harrington *in* Moore, text-fig. 70c.
*non*1966 *Tretaspis kiaeri* Størmer; Whittington, pp. 90–92, pl. 28, figs. 1, 6–12, 14.
*non*1968 *Tretaspis kiaeri* Størmer; Whittington, p. 93, pl. 29, figs. 1, 2, 4.
1975 *T. kiaeri* Størmer; Hughes *et al.*, p. 563.
*non*1975 *T.* aff. *kiaeri*; Hughes *et al.*, p. 563.
1979 *Tretaspis kiaeri* Størmer; Owen, pp. 250, 251, 252, text-fig. 6.
1979 *Tretaspis kiaeri* Størmer; Bruton and Owen, text-fig. 6.

Holotype. An almost complete internal mould of a cephalon (PMO H197) from the Høgberg Member of the Solvang Formation, Frognøya, Ringerike.

Material, locality, and horizon. The species is known only from the type horizon and locality from which many hundreds of disarticulated skeletal elements are known.

Description. Proportions of glabella and genal lobes similar to those of *T. ceriodes angelini* except that the glabella is a little more inflated and overhangs the fringe a little. Reticulation variable. On the glabella it is coarsest around the median node and extends to a transverse line at the maximum width (tr.) of the occiput. The reticulation of the genal lobes is finer and more subdued than that of the mesial part of the glabella and becomes finer abaxially. On some internal moulds there is a faint reticulation on the genal lobes and, less commonly, the glabella. Fringe steeply declined laterally, less so across I_n mesially, in front of which it is vertical. Arcs E_{1-2}, I_{1-3}, and I_n complete mesially and posteriorly. I_4 is continuous mesially but extends to the posterior margin in only 5% of sixty-one specimens. Two morphs are defined on the absence (A) or presence (B) of I_5 which occurs in 35% of eighty-one specimens and extends mesially in 22% of the twenty-three specimens in which its frontal extent can be determined (Table 1). The range of variation in selected fringe characters is shown on text-fig. 9. Two sets of radii are developed and pits in the outer set, I_1, E_{1-2}, share sulci to the posterior part of the fringe in some specimens but in a few this sulcation is less extensive and I_1 becomes discrete as far forwards as bR5. Very fine lists are developed between all I arcs except I_4 and I_5.

Hypostoma unknown. Thorax similar to that of *T. seticornis*, although it is not known whether or not median tubercles are present. The pygidial rachis commonly has up to six transversely directed furrows bearing deep apodemal pits distally. These furrows are progressively less well incised rearwards along the rachis and on well-preserved specimens (Pl. 93, fig. 9; Størmer 1930, pl. 10, fig. 4) a further three to five pairs of apodemal markings are seen, the posterior two or three pairs being situated on the anterior part of the border. Three pairs of weakly developed pleural ribs present.

Discussion. Whittington (1966, 1968) ascribed specimens from the Ashgill of Wales to *T. kiaeri*. One of these (1966, pl. 28, fig. 13) was referred to *Nankinolithus* Lu by Hughes *et al.* (1975, p. 559). The remainder comprise at least three distinct forms of *Tretaspis* and have been reassessed by Price (1977, pp. 786–787) who considered specimens from the Rhiwlas Limestone (probably Rawtheyan) figured by Whittington (1968, pl. 28, figs. 12, 16) to be similar to *T. calcaria* Dean, 1971, a form described originally from the Chair of Kildare Limestone (probably Rawtheyan) in Eire. *T. calcaria* is almost certainly related to *T. kiaeri* but differs in having I_4 always complete posteriorly, I_5 more extensive, and all complete arcs have a higher pit count (e.g. 30–31 cf. $20\frac{1}{2}$–$27\frac{1}{2}$ in E_1). As noted by Price, the

poorly preserved Rhiwlas Limestone material is difficult to compare with Dean's species but differences in fringe pitting seem slight.

Other British and Irish forms previously assigned to *T. kiaeri* have been reassessed by Ingham (1970, pp. 44–57) and Price (1974, pp. 844–847; 1977, pp. 766–778). Most are clearly members of the *T. moeldenensis* group and thus are distinguished from *T. kiaeri* primarily in having complete radial alignment of the fringe pits. A few are *T. seticornis* group members and have E_2 incomplete mesially.

## EVOLUTION OF THE *TRETASPIS SETICORNIS* GROUP

The study of populations of *Tretaspis* from Norway indicates that the phylogenetic relationships are more complex than was thought previously and that a purely typological approach to their taxonomy is not possible. Nevertheless, the broad evolutionary history of the *T. seticornis* group is becoming clear (text-fig. 1).
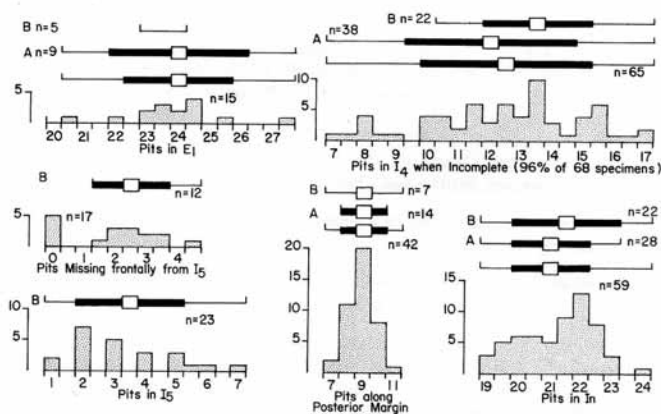
TEXT-FIG. 9. Histograms showing the range of variation in fringe features seen in all available specimens of *Tretaspis kiaeri* with a comparison of the range, mean, and sample standard deviation of the two morphs (A and B) present in the species.

EXPLANATION OF PLATE 93

Figs. 1–5. *Tretaspis askerensis* sp. nov. 1–3, holotype, PMO100657, dorsal, lateral, and anterolateral views of partially exfoliated cranidium, Husbergøya Shale Formation, or lower part of Langåra Limestone-Shale Formation, Holmenskjaeret, Holmen, Asker, × 7. 4, PMO80463, anterolateral view of partially exfoliated cranidium, same horizon and locality as 1–3, × 10. 5, PMO100878, cast of flattened incomplete cephalon, probably from the type unit, Øvre Nes badestrand, Nesbru, Asker, × 6.

Figs. 6–15. *Tretaspis kiaeri* Størmer, Høgberg Member of the Solvang Formation, Frognøya, Ringerike. 6, 10, holotype, morph B, PMO H197, dorsal and frontal views of internal mould of cephalon, × 3½; also figured by Størmer (1930, pl. 10, fig. 1). 7, morph B, PMO H338, lateral view of internal mould of cephalon, × 3; also figured by Størmer (1930, pl. 10, fig. 3). 8, PMO103965, dorsal view of cast of pygidium and incomplete thorax, × 4½. 9, PMO103966, dorsal view of internal mould of pygidium, × 4½. 11, morph A, PMO103967, anterolateral view of internal mould of incomplete cephalon, × 2. 12, morph A, PMO H208, posterolateral view of incomplete partially exfoliated cranidium showing pitting along the marginal band, × 4; also figured by Størmer (1930, pl. 11, fig. 12). 13, PMO103968, slightly oblique dorsal view of cast of glabella and left genal lobe, note glabellar reticulation, × 4½. 14, morph B, PMO103969, dorsal view of internal mould of cephalon and part of thorax, same specimen as 8, × 4. 15, morph B, PMO354, oblique anterolateral view of cephalon, × 3; also figured by Størmer (1945, pl. 1, fig. 12).

PLATE 93
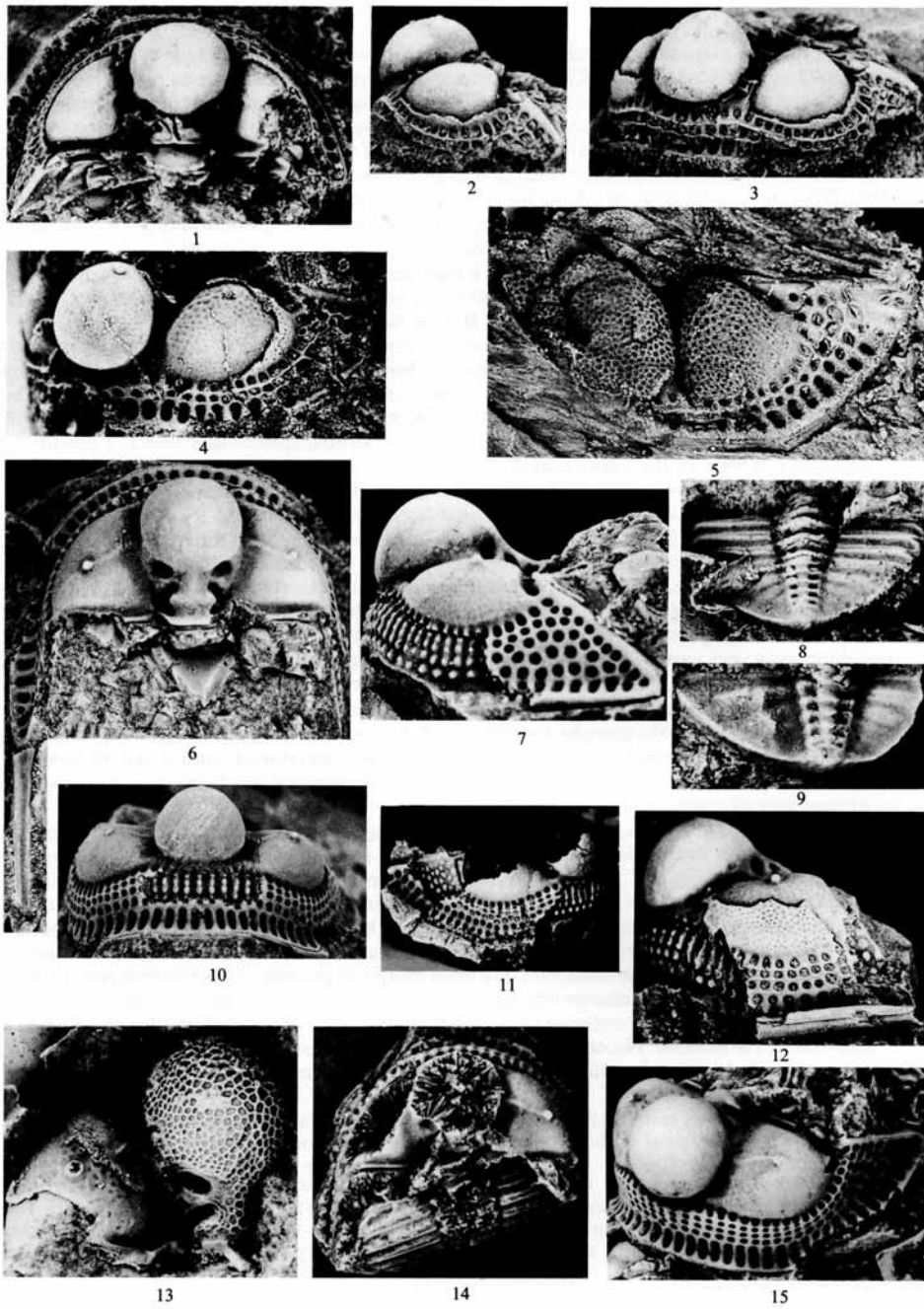
OWEN, trilobite *Tretaspis*

The earliest known species of *Tretaspis* from the Anglo-Welsh and Scandinavian areas is *T. ceriodes* which is restricted to latest Caradoc units in all these areas. The species is polymorphic in Norway and almost certainly gave rise to the *T. seticornis* group, the replacement of the former by the latter being geologically instantaneous and an excellent tool in recognizing the Caradoc-Ashgill boundary (Owen 1979, p. 251). The earliest representatives of this group are distinct in different areas with *T. hadelandica* in England and Hadeland and *T. seticornis* in Oslo-Asker, Ringerike, and Sweden. This rapid speciation involved the development of two sets of pit radii and, with the exception of some members of early *T. hadelandica* populations, the restriction of E_2 to the lateral parts of the fringe. The polymorphic nature of the ancestral *T. ceriodes* populations accounts for all other fringe features of the early *T. seticornis* group forms. Local populations of *T. hadelandica* became isolated very early on, giving rise to what are interpreted as geographical subspecies. The *T. moeldenensis* group persisted into the Ashgill in Britain but not in Scandinavia.

In Britain, *T. hadelandica* is now interpreted as ranging from earliest Pusgillian to mid/late Rawtheyan with a series of stratigraphical subspecies showing a progressive simplification of fringe characters (*T. h. convergens—T. h. deliquus—T. h. brachystichus*) followed by a slight reversal of this trend within *T. h. brachystichus* which may have been continued with the development of *T. 'latilimbus' distichus*. This reinterpretation strengthens the stratigraphical usefulness of the British forms especially in view of the long-ranging homeomorphs present in Norway. The origins of the Irish and Scottish *T.* sp. from which *T. persulcatus* were descended are unclear.

In Hadeland, *T. hadelandica hadelandica* persisted from early Pusgillian to Rawtheyan times, and although there are differences in the percentages of constituent morphs in different units, these are considered to reflect ecological rather than temporal controls. *T. hadelandica* may have given rise to a homeomorph of *T. seticornis*, *T. askerensis* which occurs in Hadeland and Asker.

In Oslo-Asker, Ringerike, and Sweden, *T. seticornis* has a short stratigraphical range and gave rise to another short ranging form, *T. hisingeri*. In Ringerike, *T. seticornis* also gave rise to *T. anderssoni*, a form which has a very narrow range of variation throughout its range from mid-Pusgillian to early Rawtheyan. In Oslo-Asker, *T. hisingeri* is replaced by *T. latilimbus norvegicus*, a polymorphic form of uncertain origin which extends well into the Rawtheyan and which almost certainly gave rise to *T. sortita broeggeri*. One of the morphs constituting *T. latilimbus norvegicus* is by far the dominant form in the nominate subspecies which is a Swedish taxon developed during the Rawtheyan. Populations of *T. sortita sortita* from the late Rawtheyan of Scotland differ from *T. sortita broeggeri* in the proportions of constituent morphs.

There is still very little information on bed-by-bed changes in populations of *Tretaspis*, and the Norwegian material is not sufficiently abundant for such a study. There is a suggestion that the development of phenotypes in *T. ceriodes angelini* is to some extent progressive but as far as morphs B, C, and D are concerned this represents no more than an increase in the upper limit of the range of variation. Many forms have long stratigraphical ranges within which there is no directional change. The only likely example of evolutionary trends are the zigzag evolution seen in the British *T. hadelandica* subspecies and the introduction of a third morph to produce *T. sortita broeggeri* from *T. latilimbus norvegicus*. The latter change was fairly abrupt as was the development of the *T. seticornis* group itself. There is insufficient evidence to say whether or not the changes in the British subspecies of *T. hadelandica* are gradual. Neoteny is thought to have produced two species, *T. hisingeri* and *T. askerensis* and probably also *T. ceriodes* from the *T. sagenosus* group.

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