THE SCANDINAVIAN MIDDLE ORDOVICIAN TRINUCLEID TRILOBITES

by ALAN W. OWEN

ABSTRACT. Thirteen species of trinucleid are described from the lower Llanvirn to lower Caradoc platform successions of Norway and Sweden. Of these, five are established taxa, four are described under open nomenclature, and four are new: *Bergamia johanssoni* sp. nov., *Botrioides impostor* sp. nov., *B. simplex* sp. nov., and *B. margo* sp. nov. The genus *Botrioides* is stabilized by choosing a neotype for the type species '*Trinucleus*' *coscinorinus* Angelin and placing it in the synonymy of *B. bronnii* (Boeck). Two species groups are recognized within *Botrioides* centred on *B. bronnii* and *B. foveolatus* (Angelin). Trinucleids were largely restricted to the western, deepest water, parts of the platform. Although the oldest species, *Bergamia johanssoni* sp. nov., represents an early Llanvirn immigration of an Anglo-Welsh genus, the Baltic stocks were endemic until the mid-Llandeilo when *Botrioides* spread into the Gondwanan province and possibly *Reedolithus* extended into Scoto-Appalachian faunas. Middle and late Caradoc immigrations of *Broeggerolithus* and *Tretaspis* into Scandinavia were from the Anglo-Welsh basin and North America respectively.

NORWEGIAN trinucleids have long held an important place in studies of this stratigraphically important group especially since the work of Størmer in 1930. The Swedish species, however, have been largely neglected and the review of the family by Hughes *et al.* (1975) brought to light some fundamental problems involving the taxonomy and biogeographical affinity of the Scandinavian Trinucleidae. The present work follows studies of the Norwegian late Caradoc and Ashgill trinucleids (Owen 1980*a*, *b*, 1983) and involved an examination of all the available Llanvirn to lower Caradoc material from Scandinavia. It forms part of a revision of the whole trilobite fauna and stratigraphy of this part of the succession in Norway. The illustrated trinucleid specimens are housed in the Paleontologisk Museum, Oslo (PMO), Riksmuseum, Stockholm (RM), Paleontologiska Institutionen, Uppsala (UM), Sveriges Geologiska Undersökning (SGU), British Museum (Natural History) (BM), and the departments of Geology at the Universities of Lund (LO) and Copenhagen (MGUH).

SETTING

The Ordovician rocks of Scandinavia essentially belong to two distinct tectonic settings: the thick siliciclastic and volcanic sequences of the allochthonous Caledonides and the much thinner, carbonate-dominated autochthonous platform successions (see Bruton *et al.* 1985 for summary).

All but the lowest nappes of the Scandinavian Caledonides are far travelled and bear little or no sedimentological or provincial relations to the platform rocks and faunas. Diverse Arenig–Llanvirn faunas in the Trondheim Region in western Norway (text-fig. 1) show marked North American affinities and are interpreted as representing environments around oceanic islands far removed from their present position (Bruton and Harper 1985 and in press). Only in the upper Ordovician sequences of this part of Norway are there faunas similar to those of the Baltic platform. With the exception of the lowermost allochthon in Jämtland, Sweden, the only middle Ordovician trinucleids from the Caledonide belt are of uncertain provenance and comprise a cephalon of *Reedolithus* in a glacial erratic and a specimen of *Stapeleyella*? *forosi* (Størmer 1932; see also Hughes *et al.* 1975, pp. 559–560) found in a roofing slate. As the origins and ages of these specimens are unknown, neither can be used in models of faunal provincialism or migration.

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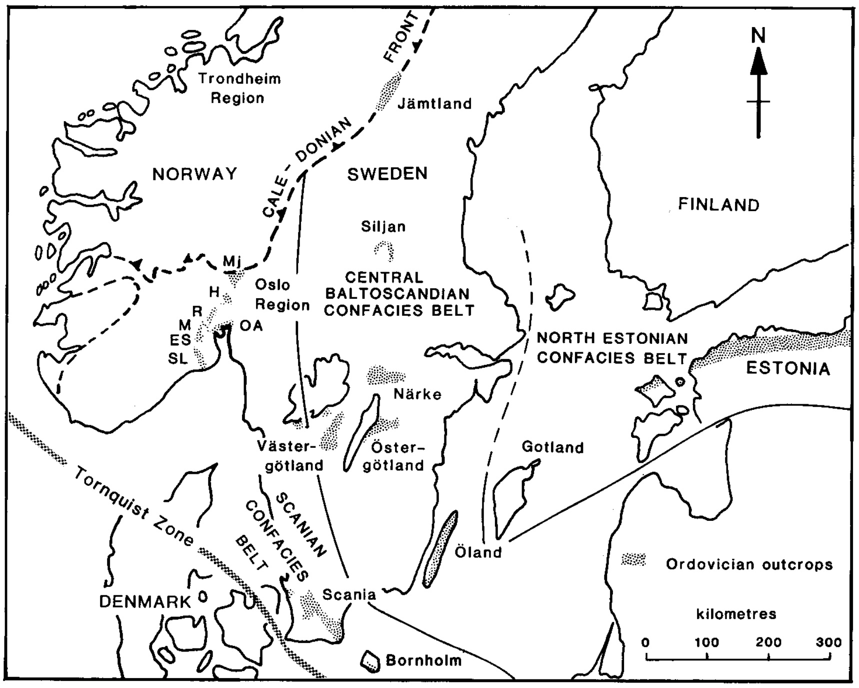
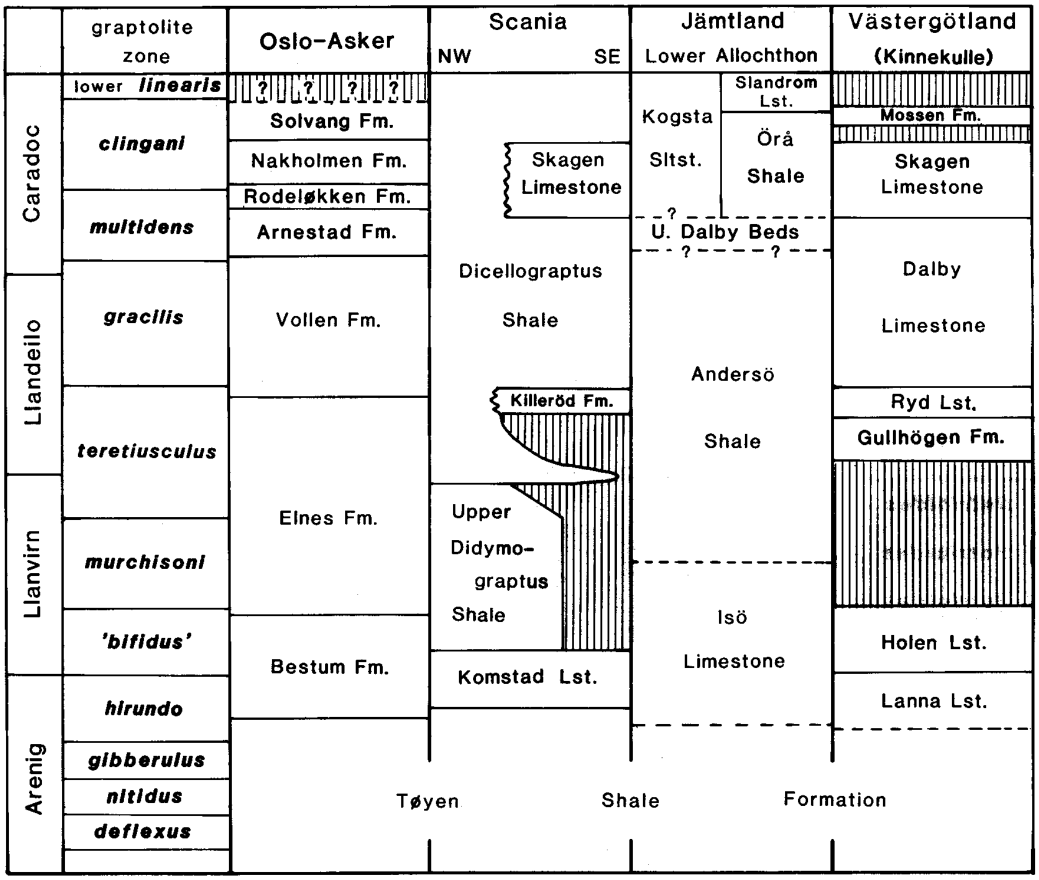


TEXT-FIG. 1. Map of Baltoscandia showing the Ordovician outliers and their position within the confacies belts defined by Jaanusson (1976). Districts of the Oslo Region, following Størmer (1953) are as follows: SL = Skien-Langesund, ES = Eiker-Sandsvaer, M = Modum, R = Ringerike, H = Hadeland, Mj = Mjøsa (Toten, Hamar-Nes, Ringsaker), OA = Oslo-Asker.

The platform successions are preserved in a series of outliers which Jaanusson (1976) interpreted as remnants of extensive areas of largely uniform, persistent, lithofacies and biofacies termed confacies belts (text-fig. 1) and showing an overall westward deepening. The successions of the Oslo Region do not fit readily into this scheme being tectonically more complex, thicker, and much more lithologically variable. Moreover, there is a general eastward deepening in the region. The stratigraphy of the Oslo Region has been undergoing revision in recent years with the long established but confused 'etasje' system being replaced by a modern lithostratigraphical terminology (e.g. Owen 1978, 1979). A full revision by the author and Norwegian based workers covering all the districts of the region is at an advanced state of preparation. The Arenig to Caradoc succession of the Oslo-Asker district is summarized in text-fig. 2 along with those of Scania, Jämtland, and Västergötland in Sweden.

Before the Caradoc the faunas of the Baltic platform were distinct not only from those of the North American and Celtic provinces but also from those of Gondwanaland, including the Anglo-Welsh area (Cocks and Fortey 1982; Dean 1985). This latter separation may have been the result of an oceanic barrier whose suture is now represented by the Tornquist zone (text-fig. 1). This was advocated by Cocks and Fortey (1982, p. 467), but in a review of the Tornquist zone, Pegrum (1984) considered it to have had a much longer history and to have acted primarily as a major transform lineament during the Caledonian Orogeny. The Baltic province (= Asaphid Province of Whittington) shared a few deep-water and rare pelagic trilobites



TEXT-FIG. 2. Correlation between the Arenig–Caradoc successions of Oslo-Asker, Scania, Jämtland, and Västergötland. Swedish units based on Bergström (1982), Jaanusson (1982*a*, *b*), and Jaanusson and Karis (1982). Many of the terms applied to the Oslo-Asker succession are new or recently introduced and replace an existing terminology as follows: Bestum Formation = 'Orthoceras Limestone' *sensu lato*, Elnes Formation = Upper Didymograptus Shale and Ogygiocaris Shale, Vollen Formation = Ampyx Limestone, Arnestad Formation = Lower Chasmops Shale, Rodeløkken Formation = Lower Chasmops Limestone, Nakholmen Formation = Upper Chasmops Shale, Solvang Formation = Upper Chasmops Limestone.

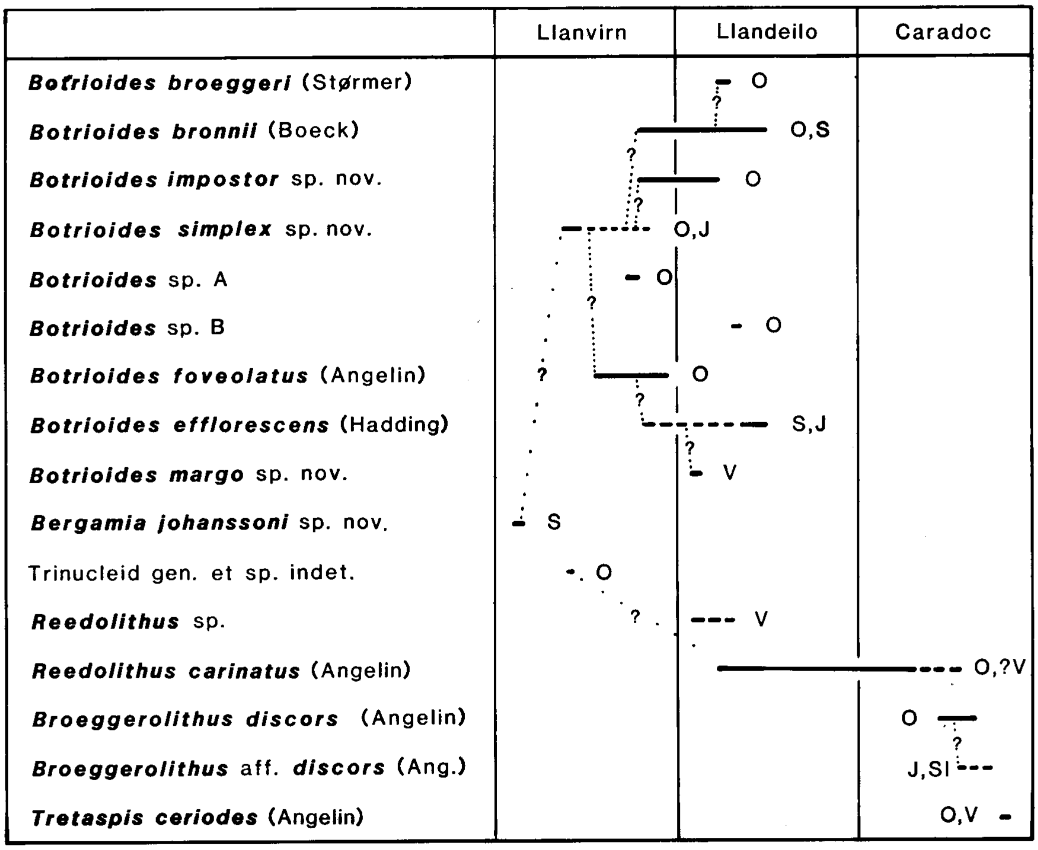
with other provinces but it was not until the Caradoc that significant mixing of shallower benthos took place.

Some sixteen species of trinucleid, distributed amongst six or seven genera are known from the Llanvirn to Caradoc rocks of the platform and lowermost allochthon in Scandinavia (text-fig. 3). Llanvirn and Llandeilo species were largely restricted to the westernmost (i.e. deeper) parts of the area: Scania, the Oslo Region, and the lowermost allochthon in Jämtland. The short-lived appearance of trinucleids in the lower Llandeilo Gullhögen Formation in Västergötland in the Central Confacies Belt is related to a brief eastward transgression of the western facies (Jaanusson 1982*b*, p. 168). By the late Caradoc, however, trinucleids were more widespread, if rare, in the Central Confacies Belt.

EVOLUTION AND AFFINITIES

The oldest Scandinavian trinucleid is *Bergamia johanssoni* sp. nov. from the uppermost part of the Komstad Limestone and basal Upper Didymograptus Shale (low Llanvirn) in Scania. This constitutes the first undoubted record of a genus otherwise restricted to the Arenig to lower Llandeilo of the Anglo-Welsh area. Cocks and Fortey (1982, p. 470) noted that *Bergamia* was a component of a fairly deep-water biofacies and thus its extension to Baltica at a time of transgression (A. Nilssen, Copenhagen, pers. comm.) is consistent with the model proposed by Fortey (1984).

Bergamia may have given rise to *Botrioides* possibly by paedomorphosis, a heterochronic process which is well documented in many trilobite groups (McNamara 1983) including trinucleids (Owen 1980*a*). The oldest known species of *Botrioides* is *B. simplex* sp. nov. from the low-mid Llanvirn of the Oslo Region and like most other species, its small size and simple fringe shape and pitting suggest a paedomorphic origin. The lateral eye tubercles of *Botrioides* may have been derived from the eye ridges present in many juvenile trinucleines and even in the adults of *Bergamia johanssoni.*



TEXT-FIG. 3. The range and suggested phylogeny of trinucleid trilobites in the middle Ordovician of Norway and Sweden. Widely spaced dots indicate very tentative derivation of one species from another; closely spaced dots show more certain relationships. O = Oslo Region, S = Scania, V = Västergötland, Sl = Siljan, J = Jämtland. Species of *Broeggerolithus* and *Tretaspis* described by Owen (1980*a*, 1983); the remainder are treated herein.

Nine species of *Botrioides* are known from horizons in Scandinavia ranging up to the mid Llandeilo (text-fig. 3). Towards the end of its time range the genus crossed the Tornquist divide and extended into south-east Ireland and probably Cornwall and north-eastern Newfoundland. Most of the Scandinavian species along with those from outside the area have a narrow fringe with no more than two E arcs and two I arcs. *B. foveolatus* (Angelin), *B. efflorescens* (Hadding), and *B. margo* sp. nov., however, have up to five I arcs and up to four E arcs.

A trinucleid cephalon from the lower Elnes Formation (low-mid Llanvirn) in the Hadeland district of the Oslo Region is here considered under open nomenclature but may have important phylogenetic implications. Hughes *et al.* (1975, pp. 562-563) considered it close to the common ancestor of *Tretaspis* and *Botrioides* and ascribed it to the latter genus. However, it differs in several respects from that genus and also shares characters with *Reedolithus* which first appeared in the middle Llandeilo of Scandinavia and Canada. There is, however, a time gap between the Hadeland specimen and the first known appearance of *Reedolithus* and as is discussed below, there are doubts as to the age of *R. quebecensis* Staüble, the oldest Scoto-Appalachian species. Thus, the derivation of *Reedolithus* from the Hadeland form or even its origin within the Baltic province is only tentatively suggested here.

The appearance of *Broeggerolithus* in Scandinavia in the middle Caradoc represents the immigration of an essentially Anglo-Welsh genus late in its history. The Scandinavian material was described in an earlier study (Owen 1983) and although *Broeggerolithus* occurs in Jämtland, Siljan, and several districts of the Olso Region, it is only abundant in the deepest water facies of the latter region (Harper *et al.* 1985, pp. 298-299). As with *Bergamia* in the early Llanvirn, the appearance of *Broeggerolithus* in Scandinavia was probably associated with marine transgression but in addition, major interchanges of faunal elements between provinces were also taking place during the late Caradoc as the provincial barriers disappeared.

During the latest Caradoc, *Tretaspis* appeared in Scandinavia but had a long history in the North American province extending back to the early Caradoc and possibly the Llandeilo. The earliest species known of *Tretaspis* is *T. canadensis* Staüble which occurs with *R. quebecensis* Staüble in clasts in a mélange in the Citadel Formation in Quebec. As is discussed below under *R. carinatus* (Angelin), this part of the formation contains graptolites of the *Nemagraptus gracilis* Zone but the age of the mélange clasts is not known with certainty. *Tretaspis* occurs widely in the upper Caradoc and Ashgill of both Norway and Sweden and shares several species in common with the British Isles. In the deepest water facies in the Ashgill of Sweden the trinucleid *Nankinolithus* ('*Tretaspis granulatus*') is associated with *Tretaspis* such as in the fauna of the Ulunda Mudstone in Västergötland described by Bergström (1973). This fauna also includes rare cyclopygids and probably occupied a broadly similar niche to that of the *Opsimasaphus-Nankinolithus* Association of Price (1981) in the Ashgill of the Llŷn Peninsula in North Wales. *Cryptolithus* was a late immigrant from North America to the Oslo Region occurring in the upper Rawtheyan of Oslo in inner shelf regressive mudstones. This represents both migration consequent on the narrowing of the Iapetus Ocean and a change to a shallower water habitat. Poorly preserved specimens from the upper Ordovician of the Trondheim area may also belong in *Cryptolithus* (Størmer, 1932, pl. 28, figs. 2 and 3).

SYSTEMATIC PALAEONTOLOGY

The terminology used herein is that advocated by Hughes *et al.* (1975) and unless otherwise stated, pit counts refer to half-fringe values.

Family TRINUCLEIDAE Hawle and Corda, 1847
Subfamily TRINUCLEINAE Hawle and Corda, 1847
Genus BOTRIOIDES Stetson, 1927

Type species. *Trinucleus coscinorinus*, Angelin, 1854, p. 65, pl. 34, fig. 4, ?from the Lower Dicellograptus Shale of Scania, south-west Sweden (= *B. bronnii* (Boeck, 1838)); by original designation of Stetson (1927, p. 97).

Emended diagnosis. Fringe narrow, declined. Up to four I arcs and four E arcs present. Pits on upper lamella in deep radial sulci; on lower lamella absent or restricted to E arcs. Genal prolongation absent. Lateral eye tubercles present.

Discussion. Stetson (1927) established *Botrioides* to encompass a group of narrow-fringed Scandinavian trinucleines typified by *Trinucleus coscinorinus* Angelin, 1854. Although Størmer (1930, p. 13) considered that *Botrioides* could not be distinguished from *Trinucleus* Murchison, 1839, Hughes *et al.* (1975, p. 561) resurrected Stetson's genus in their revision of the Trinucleidae. However, as Angelin's original material of *T. coscinorinus* is lost, Hughes *et al.* preferred to refer to allied species as '*Botrioides*?'. This is clearly unsatisfactory as most of the species they included under this name form a close plexus which conforms in most of its diagnostic characters both to features of Angelin's illustration of *T. coscinorinus* and to Stetson's concept of *Botrioides*. In attempting to stabilize the genus, however, several taxonomic problems have to be resolved.

The type horizon and locality of *T. coscinorinus* was given by Angelin as being '*Regio C.*' at Fågelsång in Scania. This was accepted by Hadding (1913, p. 75) as being the 'Orthoceras Limestone' (= Komstad Limestone of modern usage) but Funquist (1919, pp. 35, 39) thought it more probable that the species was not from Fågelsång and was from a higher unit, the Lower Dicellograptus Shale. This view was adopted by subsequent workers. The only known trinucleid from the Komstad Limestone is the recently discovered material described below as *Bergamia johanssoni* sp. nov. which differs considerably from the accepted concept of *T. coscinorinus* in particular and *Botrioides* in general. Several workers described material as *T. coscinorinus* from the Lower Dicellograptus Shale in Scania including Funquist (1919) who included some Norwegian specimens amongst his illustrations. Størmer (1930, p. 19) considered *T. coscinorinus* a junior synonym of *T. bronnii* (Boeck, 1838): a view which was accepted by most subsequent workers in Sweden. As a result, stratigraphical terms used in Scania such as 'Coscinorinus limestone' were changed to (for example) 'Bronni limestone' (e.g. Hadding 1958, p. 217). The present study shows that the specimens which Størmer (1930) described as *T. bronnii* from Norway are not conspecific with the lectotype which he subsequently chose (on good grounds) for Boeck's species (1940). However, the lectotype morphology is the same as that of most of the cephala from Scania although preservation of the Swedish material is poor. Thus in order to stabilize *Botrioides*, a neotype for '*T.*' *coscinorinus* is here chosen from the Killeröd Formation (formerly included in the Lower Dicellograptus Shale) at Killeröd Quarry in Scania. The specimen is numbered LO 5717T and is illustrated on Plate II, fig. 5. This specimen falls well within the range of variation seen in *B. bronnii* as diagnosed herein and thus *B. coscinorinus* becomes its junior subjective synonym. The assignment to *Botrioides* of the other species described and discussed below now becomes unequivocal in terms of the reservations held by Hughes *et al.* (1975). All the named species which they provisionally assigned to *Botrioides* are here confirmed as belonging to that genus. Of the indeterminate materal which Hughes *et al.* listed, only the forms described originally by Dean (1971) and Sadler (1974) from the Llandeilo of northeastern Newfoundland and Cornwall respectively probably belong to *Botrioides*. The fragmentary material from the upper Arenig of northeastern Newfoundland described by Dean (1974; see also Neuman 1976 for age) is too incomplete for adequate determination but the presence of arc E_3 suggests it belongs elsewhere. The form which Hughes *et al.* (1975, pl. 4, figs. 48–51) listed as *Botrioides*? sp. from the Llanvirn of Hadeland, Norway is described below as trinucleid gen. et sp. indet.

Two species groups are here recognized within *Botrioides* (Table 1). One, centred on *B. bronnii* (Boeck) has a very narrow fringe comprising up to two I arcs and two E arcs. The radial sulci in which the fringe pits are dispersed are broad in proportion to their length and number between 12 and 17½ per half-fringe in the material available. Pygidia of the *B. bronnii* species group have only three to four axial rings. The second group, centred on *B. foveolatus* (Angelin), has up to five I arcs and up to four E arcs arranged in long, narrow sulci which are commonly more numerous (16½–22½ in the available specimens). Pygidia of the *B. foveolatus* group are more segmented, with seven to nine axial rings present. This latter group comprises *B. foveolatus*, *B. efflorescens* (Hadding), and *B. margo* sp. nov. and may ultimately prove worthy of separate generic status.

TABLE 1. Summary of fringe pit arcs and pygidial axis segmentation in the named Scandinavian species of *Botrioides*. C = complete arc, A = arc present anteriorly, L = arc present laterally, P = arc present posteriorly, al = arc present anterolaterally, × = arc absent. Number of sulci refer to half-fringe values on the upper lamella. Only *B. broeggeri* shows deep sulcation on the lower lamella where it is restricted to the E arcs.

	E_1	E_2	E_3	E_4	I_n	I_1	I_2	I_3	I_4	sulci	axial rings
B. bronnii species group											
B. bronnii (Boeck)	C	C	×	×	C	×-al	×	×	×	12½–16	4
B. impostor sp. nov.	C	×	×	×	C	al–C	×	×	×	13½–17½	3
B. broeggeri (Størmer)	C	A–C	×	×	C	×	×	×	×	12–15	—
B. simplex sp. nov.	C	×	×	×	C	×-P	×	×	×	14–16½	3–4
B. foveolatus species group											
B. foveolatus (Angelin)	C	×	×	×	C	C	C	C	×-L	17–22½	∼7
B. efflorescens (Hadding)	C	A	×	×	C	C	∼C	A+L	×	16½–21½	7-9
B. margo sp. nov.	C	C	A?+L	A?+L	C	C	C	—	—	22	—

Botrioides bronnii *Species Group*

Botrioides bronnii (Boeck, 1838)

Plate II, figs. 1–17

1838 *Trilobites Bronnii* Boeck, p. 144.
1854 *Trinucleus coscinorinus* Angelin, p. 65, pl. 34, fig. 4.
1854 *Trinucleus bucculentus* Angelin, p. 84, pl. 41, fig. 1.
?1857 *Trinucleus Bronnii*; Kjerulf, p. 94.
?1887 *Trinucleus bucculentus*; Ang.; Brøgger, p. 17.
non 1913 *Trinucleus coscino(r)rhinus* [*sic*] ANG; Hadding, pp. 74–75, pl. 7, figs. 18, 20 (= *B. efflorescens* (Hadding)), 19 (= *B. simplex* sp. nov.).
1919 *Trinucleus coscinorrhinus* [*sic*] ANG; Funquist, pp. 34–35, pl. 1, figs. 7–9, 11–22, *non* 10, 10*a* (= *B. impostor* sp. nov.).
1927 *Botrioides bucculentes* [*sic*] (Angelin); Stetson, pl. 1, fig. 11.
non 1927 *Botrioides coscinorrhinus* [*sic*] (Angelin); Stetson, pl. 1, fig. 12 (= *B. efflorescens* (Hadding)).
1930 *Trinucleus bucculentus* Ang.; Størmer, pp. 21–24, pl. 2, figs. 8–15; text-figs. 7–11, 16*e*.
1930 *Trinucleus bronni* (Sars and Boeck); Størmer, text-fig, 6; *non* pp. 19–21, pl. 2, figs. 1–7; text-figs. 5, 16*c*, 43 (= *B. impostor* sp. nov.).
non 1934 *Trinucleus bronni*; Størmer, p. 331 (= *B. impostor* sp. nov.)
1940 *Trinucleus bronni* (Sars and Boeck MS); Størmer, p. 147, pl. 1, fig. 18.
1940 *Trinucleus bronni* (Sars and Boeck MS); Grorud, p. 160, text-figs. 1, 2*e*, *f*.
1952 *Trinucleus bronni* Sars and Boeck; Nilsson (*pars*), pp. 684, 691–692 (some specimens *B. efflorescens* (Hadding)).
non 1953 *Trinucleus bronni*; Størmer, pp. 61, 83.
1958 *Tr. bronni*; Hadding, pp. 217–218.
1975 *Botrioides*? *bronnii* (Sars and Boeck *in* Boeck); Hughes *et al.*, p. 561 (*pars*), *non* pl. 4, fig. 44 (= *B. impostor* sp. nov.).
1975 *Botrioides*? *bucculentus* (Angelin); Hughes *et al.*, p. 562.
1982 *Botryoides coscinorhinus* [*sic*] (Angelin); Bergström (pars), p. 192 (some specimens *B. efflorescens* Hadding).
non 1984 *Botrioides*? *bucculentus* (Angelin); Wandås, pp. 234–235, pl.12G, J; pl. 13F (= *B. simplex* sp. nov.)

References to Swedish material cited, but not illustrated, by earlier workers were given by Funquist (1919, p. 35). Note that Angelin (1854) used the spelling *coscinorinus* in the text but *coscinorhinus* in the plate description of his work; hence the confusion of subsequent workers.

Lectotype. Selected by Størmer (1940, p. 147); the internal mould of a slightly crushed cephalon (PMO 61752) labelled 'Wraatz's Løkke', Oslo, horizon not known. Note that Størmer earlier (1930, p. 19) indicated that he had selected a lectotype from Boeck's 'cotypes' but he gave no further details at that time.

Material, localities, and horizons. In addition to four cephala/cranidia from the type locality, elements of the cephalon and one articulated thorax and pygidium are known from the upper part of the Elnes Formation (the 'Ogygiocaris Shales') elsewhere in Oslo-Asker. Specimens illustrated by Grorud (1940) from the lowest part of the overlying Vollen Formation ('Ampyx Limestone') at Tørtberg, Oslo also belong here, as does a cranidium from 1 m above the conglomerate at the base of this unit at Kulerud, Ringerike. The species occurs more commonly in the Lower Dicellograptus Shale (including the Killeröd Formation) in Scania, south-east Sweden.

Emended diagnosis. Pseudofrontal lobe subspherical, overhanging narrow fringe which comprises complete arcs. E_{1-2} and I_n. Arc I_1 may be present anterolaterally. Pits set in short sulci. Lateral eye tubercle very subdued, situated opposite L2 or posterior part of S2. External surface of pseudofrontal lobe in larger specimens bears concentric ridges superimposed on coarse reticulation. Median tubercle on thoracic axial rings. Pygidium transverse bearing up to four axial rings, four pleural ribs, and a broad border.

Description. Cephalon (excluding genal spines) semicircular in outline. Glabella weakly swollen posteriorly, very strongly so in front of S2. Occipital ring ridge-like, transversely directed except distally where it is deflected forwards slightly. Occipital furrow shallow but distinct mesially, deepening into occipital pit distally. Occiput short (sag., exsag.), very weakly swollen mesially, narrower (tr.) than occipital ring, and clearly defined from axial furrow. S1 deep, directed abaxially rearwards at about 75 % to the sagittal line. L2 triangular in outline, broadening abaxially, and poorly differentiated from axial furrow. S2 deep except distally where

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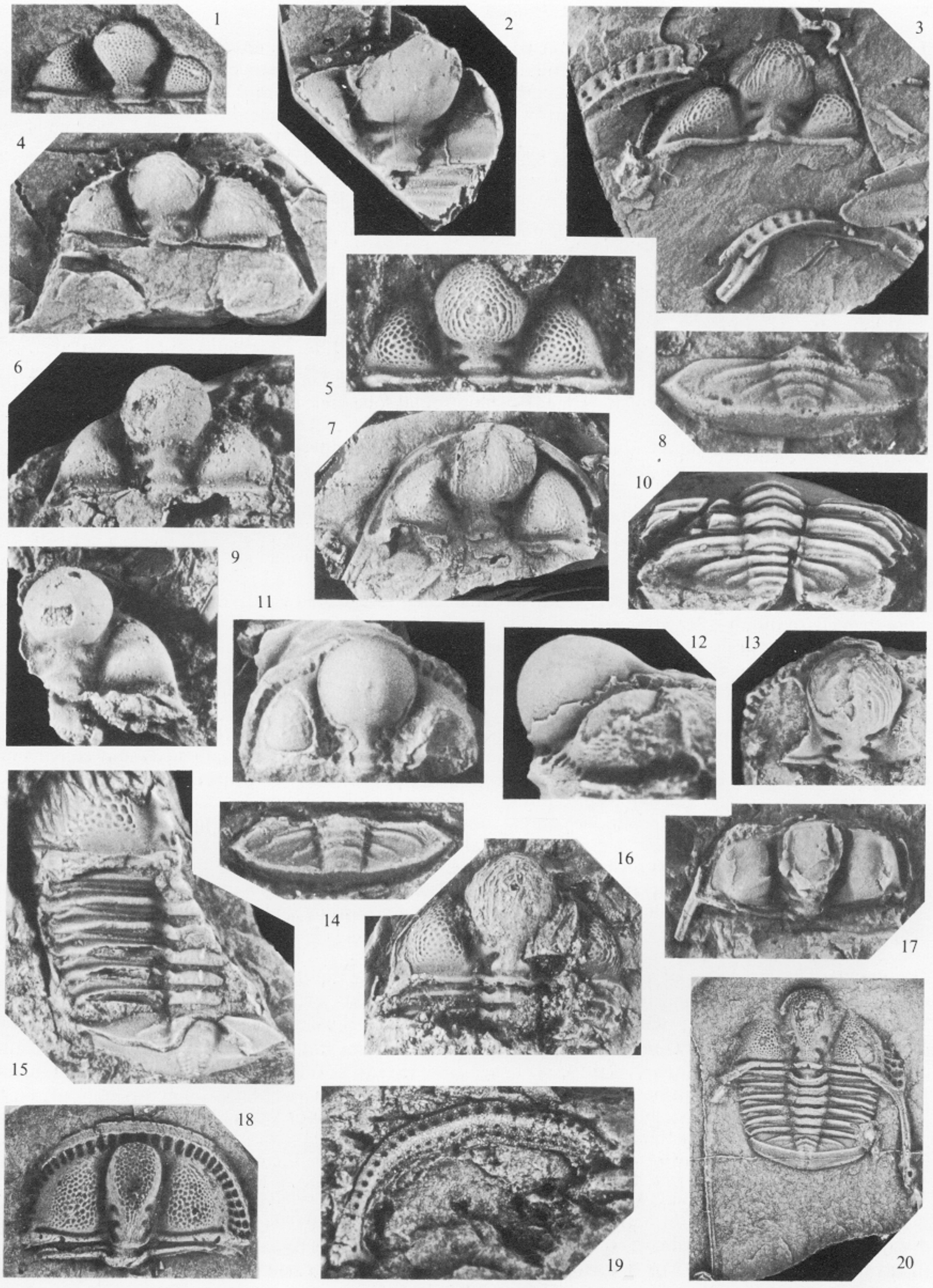
EXPLANATION OF PLATE 11

Figs. 1-17. *Botrioides bronnii* (Boeck). 1, Boeck 'cotype', PMO 113.224, dorsal view of latex cast of small cranidium, horizon unknown, Wraatz's Løkke, Oslo, ×5. 2, Boeck 'cotype', PMO 113.225, dorsal view of internal mould of cephalon and partial thorax, same locality as 1, ×4. 3, LO 2948*t*, latex cast showing dorsal view of cranidium and ventral views of two lower lamellae, probably Elnes Formation, Vestre Aker Church, Oslo, ×4; also figured by Funquist (1919, pl. 1, fig. 18). 4, lectotype, PMO 61752, dorsal view of internal mould of cephalon, same locality as 1, ×3; also figured by Størmer (1940, pl. 1, fig. 18). 5, LO 5717*t*, dorsal view of latex cast of cranidium, Killeröd Formation, Killeröd Quarry, Scania, ×5; here selected as neotype for '*Trinucleus*' *coscinorinus* Angelin. 6, LO 5718*t*, dorsal view of internal mould of cranidium, same locality and horizon as 5, ×4. 7, LO 5719*t*, dorsal view of latex cast of cephalon, Killeröd Formation, level k of Nilsson (1952), same locality as 5, ×3. 8, LO 5720*t*, dorsal view of latex cast of pygidium, same horizon and locality as 7, ×5. 9, LO 5721*t*, dorsal view of internal mould of cranidium, same horizon and locality as 5, ×4. 10, PMO H482, dorsal view of pygidium and posterior thorax, upper Elnes Formation, Engervik, Asker, ×4·5; also figured by Størmer (1930, pl. 2, figs. 14 and 15). 11 and 12, PMO H481, dorsal and lateral views of partially exfoliated cephalon, same horizon and locality as 10, ×3; also figured by Størmer (1930, pl. 2, fig. 13). 13, PMO H480, dorsal view of partially exfoliated cephalon, same horizon and locality as 10, ×3; also figured by Størmer (1930, pl. 2, figs. 8-10 as neotype of '*T.*' *bucculentus* Angelin). 14, LO 2946*t*, dorsal view of pygidium, Lower Dicellograptus Shale, Tommarp, Scania, ×4; also illustrated by Funquist (1919, pl. 1, fig. 16). 15, LO 2947*t*, dorsal view of partially exfoliated articulated individual, same horizon and locality as 14, ×4; specimen also figured by Funquist (1919, pl. 1, fig. 17). 16, LO 2950*t*, dorsal view of latex cast of cephalon and anterior thorax, same horizon and locality as 14, ×3; also figured by Funquist (1919, pl. 1, fig. 21). 17, LO 2937*t*, dorsal view of internal mould of crushed cephalon, same horizon and locality as 14, ×2; also figured by Funquist (1919, pl. 1, fig. 7).

Figs. 18-20. *B. impostor* sp. nov. 18, holotype, PMO HO566, dorsal view of latex cast of cranidium and first thoracic segment, upper Elnes Formation between Håkavik and Bjerkåsholmen, Asker, ×2·5; also figured by Størmer (1930, pl. 2, fig. 3) and Hughes *et al.* (1975, pl. 4, fig. 44). 19, paratype, PMO H401, ventral view of lower lamella, same horizon as 18, Gomnæs, Ringerike, ×4·5; also figured by Størmer (1930, pl. 2, fig. 5). 20, paratype, PMO HO574, dorsal view of latex cast of articulated individual, same horizon as 18, near Vollen, Asker, ×3; also figured by Størmer (1930, pl. 2, fig. 1).



OWEN, *Botrioides*

it shallows abruptly, oval in outline, and directed abaxially forwards at about 60° to the sagittal line. Pseudofrontal lobe subspherical, overhanging the fringe anteriorly, and bearing a median node a short distance behind its mid-point. In small specimens the pseudofrontal lobe is not as swollen and thus less well differentiated from the posterior part of the glabella. Axial furrow almost parallel to sagittal line, broad and shallow, bearing deep anterior fossula. Genal lobe quadrant-shaped, strongly convex (tr., exsag.) bearing a very subdued eye tubercle opposite L2 or the posterior part of S2, well away from the axial furrow. Small specimens also show a very weakly developed eye ridge directed towards the mid-part of the pseudofrontal lobe. Posterior border transversely directed; narrow (exsag.) proximally, broadening considerably distally. Posterior border furrow broad (exsag.) and shallow, transversely directed and bearing a deep posterior fossula distally.

Fringe narrow, bearing $12\frac{1}{2}$–16 sulci (n = 4) which contain arcs E_{1-2} and I_n over the whole fringe. A short I_1 arc is also developed anterolaterally in some specimens. Individual pits are difficult to discern on the upper lamella, especially the presence of two E arcs, but are clear on the lower lamella and in section (e.g. Størmer 1930, text-figs. 10 and 11). Posterior margin of upper lamella of fringe transversely directed or deflected very gently abaxially forwards. Lower lamella bears a distinct girder, a broad anterior band, and a genal spine of unknown length. Hypostoma not known.

External surface of glabella and genal lobe bears a fine reticulation. Larger specimens also show concentric ridges superimposed on the reticulation of the pseudofrontal lobe and the posterior part of the glabella is smooth. Internal mould smooth.

Thorax tapering very slightly rearwards. Each axial ring strongly convex (tr.) and bears a distinct, sagitally elongate median tubercle on its anterior two thirds. Posterior edge of ring transversely directed; anterior edge arched gently forwards mesially and curving abaxially forwards at about 60° to the sagittal line distally. Details of articulating half-ring not known. Axial furrow broad and shallow anteriorly, narrowing a little posteriorly. Thoracic segments transversely directed, each parallel-sided except over its distal 20 % where the anterior edge is deflected downwards slightly and abaxially rearwards through about 20°. The posterior edge is deflected a little more gently rearwards. Anterior band very narrow (exsag.) proximally, broadening a little over its outer 35 %. Pleural furrow very narrow proximally, broadening gently over its proximal half and more strongly so distally. Broad posterior band ridge-like, directed abaxially rearwards from just behind the anteromesial corner of the pleura to the posterolateral corner. The posterior face of this band bears a shallow but distinct furrow in front of the very narrow posterior border. External surface of posterior part of axial ring and the highest parts of the pleural bands bear a subdued, dense, granulation. Remaining areas smooth.

Pygidium smooth, transverse in outline having a sagittal length in dorsal view (including border) equal to about a third of the maximum width. Axis gently convex (tr.), tapering rearwards at about 30° and comprising an anterior articulating half-ring and four rings, the anterior one of which bears a subdued median tubercle. Ring furrows progressively less well defined posteriorly along the axis, bearing distinct apodemes distally. Up to six more pairs of apodemes are also seen on the subdued but distinct extension of the axis on to the border. Axial furrows narrow and shallow. Up to four pleural ribs present, dying out abaxially but only the anterior two are well developed. The first of these is directed abaxially rearwards at about 80° to the sagittal line, the second at about 60°. Anterolateral parts of pleural fields directed abaxially rearwards at 60° and declined steeply forwards. Posterior border broad, steeply declined but occupying up to 25 % of the sagittal length of the pygidium in dorsal view.

Discussion. The lectotype of *B. bronnii* selected by Størmer (1940) differs in several respects from the morphology of the specimens which he ascribed to the species in his major work on the Scandinavian trinucleids (1930) and which are described below as *B. impostor* sp. nov. Boeck's original description (1838; see also Størmer 1940, p. 147) was not accompanied by an illustration and could be applied equally well to either species bearing in mind the closeness of the two E arcs. None the less, there is no reason to doubt that the lectotype was chosen from Boeck's original material and is representative thereof. An unfortunate, but unavoidable, consequence of Størmer's concept of *B. bronnii* is that the strata in Norway which he and subsequent workers termed the '*bronni* beds' are not characterized by an abundance of that species but by *B. impostor* sp. nov.

B. bronnii is here considered to be the senior synonym of '*T.*' *bucculentus* (Angelin) which was based on Norwegian material. The neotype selection for *T. coscinorinus* Angelin made in the discussion of *Botrioides* (above) also places this species in the synonymy of *B. bronnii.* Angelin's illustration of *T. coscinorinus* does not show the marked anterior overhang of the glabella typical of *B. bronnii*, but his illustration may have been based on a crushed specimen in which this feature was not preserved. Such material is fairly common amongst samples from Scania and includes some of the specimens described by Funquist (1919). However, associated material and other morphological features show that they belong in *B. bronnii*. The neotype of '*T.*' *coscinorinus* comes from material which Nilsson (1952) ascribed to '*T.*' *bronnii*. Examination of this material shows that *B. bronnii* is present in his samples from horizons j, k, and l in the Killeröd Formation at Killeröd Quarry. The former two levels also contain *B. efflorescens* (Hadding) which is described below.

Botrioides impostor sp. nov.

Plate 11, figs. 18–20

?1857 *Trinucleus Bronnii*; Kjerulf, p. 94.
?1887 *Trinucleus bucculentus* Ang.; Brøgger, p. 17.
1930 *Trinucleus bronni* (Sars and Boeck); Størmer, pp. 19–21, pl. 2, figs. 1–7; text-figs. 5, 16*c*, 43; *non* 6 (= *B. bronnii* (Boeck)).
1934 *Trinucleus bronni*; Størmer, p. 331.
1953 *Trinucleus bronni*; Størmer, pp. 61, 83.
1975 *Botrioides*? *bronnii* (Sars and Boeck *in* Boeck); Hughes *et al.*, p. 561 (*pars*); pl. 4, fig. 44.

Holotype. The external mould of a cranidium and first thoracic segment (PMO HO566) from the upper Elnes Formation (the 'Ogygiocaris Shale') between Håkavik and Bjerkåsholmen, Asker.

Paratypes. The external mould of an articulated individual (lacking most of the fringe) (PMO HO574) from the uppermost Elnes Formation near Vollen, Asker and a lower lamella (PMO H401) from the upper Elnes Formation at Gomnæs, Ringerike.

Material, localities, and horizons. Disarticulated exoskeletal elements of this species are the most common fossils in the upper Elnes Formation especially in the uppermost, sandy, part of the formation throughout Oslo-Asker. The species occurs more rarely in the upper Elnes Formation of Ringerike. Fragmentary material in the Paleontologisk Museum, Oslo, from the Elnes Formation near Fure, Modum and the Kirkerud Group near Skiaker, Hadeland may also belong in this species.

Derivation of name. *Impostor*—a charlatan, referring to the incorrect belief of earlier workers that specimens of this species belonged in *B. bronnii*.

Diagnosis. Pseudofrontal lobe oval, only slightly overhanging narrow fringe which comprises complete arcs E_1, I_n, and in some specimens I_1. Pits set in short sulci except posteriorly. Very subdued lateral eye tubercle opposite L2. External surface of glabella reticulate. Median tubercle only on anterior thoracic axial ring. Transverse pygidium bearing three axial rings, two pleural ribs, and a broad border.

Description. Cephalon (excluding genal spines) approximately semicircular in outline. Glabella increasing in convexity (tr.) forwards towards the pseudofrontal lobe which has little independent convexity. Occipital ring and furrow, occiput, S1 and S2 similar to those of *B. bronnii*. Distal part of L2 joined to the pseudofrontal lobe as a very weakly developed composite lobe. Pseudofrontal lobe elongately oval and overhangs the fringe only very slightly. Axial furrow broad and shallow bearing deep fossula anteriorly. Quadrant-shaped genal lobe moderately convex (tr., exsag.) bearing subdued eye tubercle at its highest point, opposite L2.

Narrow fringe gently declined with a broad border. Arcs E_1 and I_n invariably complete, containing $13\frac{1}{2}$–$17\frac{1}{2}$ ($\bar{X} = 15\frac{1}{2}$, n = 11) pits in the half fringe. Arc I_1 may be complete or restricted to the anterolateral and lateral parts of the fringe. The holotype shows only three pits which may belong in this arc on the posterior part of the fringe. A few adventitious pits are included in the posterior few radii of the most specimens. Pits situated in deep sulci anteriorly on the upper lamella but this sulcation breaks down abaxially although radial alignment is maintained. Posterior margin of upper lamella of fringe directed very slightly rearwards. Lower lamella bears a genal spine directed parallel to the sagittal line and equal in length to at least two and a half times that of the sagittal cephalic length.

External surface of genal lobes, the pseudofrontal lobe, and the mesial part of the glabella behind S2 finely reticulate.

Hypostoma not known. Thorax essentially similar to that of *B. bronnii* except that the first axial ring is arched concave forward, there are no median tubercles and there is no surface granulation.

Pygidium transverse, sagittal length approximately one third of maximum width. Weakly convex axis tapers evenly rearwards at about 40° and is extended weakly on to the very broad border. Four axial rings present, only the anterior three of which are well developed. Axial furrow narrow and shallow. Two pleural ribs present, the first directed at about 80° to the sagittal line, the second at about 65°. Surface of pygidium smooth.

Discussion. As is noted in the discussion of *B. bronnii*, *B. impostor* sp. nov. is based on the material which Størmer (1930) described as '*T. bronni*' and which characterizes the so-called 'bronni beds' in Oslo-Asker. *B. impostor* differs from *B. bronnii* primarily in its much less swollen pseudofrontal lobe which lacks concentric ridges even in large specimens, in the absence of arc E_2, the common presence of an extensive I_1 arc, in the shape of the first axial ring of the thorax, the absence of median tubercles and granulation on the thoracic segments, and in having fewer axial rings (3, cf. 4) and pleural ribs (2, cf. 4) on the pygidium.

Botrioides broeggeri (Størmer, 1930)

Plate 12, figs. 1–6

1930 *Trinucleus hibernicus* REED var. *bröggeri* Størmer, pp. 24–27, pl. 3, figs. 1–14; text-figs. 12, 13, 16*d*.
1953 *Trinucleus hibernicus bröggeri*, Størmer, pp. 62, 84.
1953 *Trinucleus* cf. *hibernicus broggeri*; Størmer, pp. 72?, 73.
1953 *Trinucleus* aff. *hibernicus*; Størmer, p. 80 (*pars*).
1975 *B.? hibernicus broeggeri* (Størmer); Hughes *et al.*, p. 562.

Holotype. A cephalon (PMO H553) from the Vollen Formation ('Ampyx Limestone') at Gullerud near Norderhov, Ringerike.

Material, localities, and horizons. Elements of the cephalon occur abundantly in the Vollen Formation at Gullerud and are especially common in the conglomerate at the base of the formation. The thorax is not known and pygidia are rare. Cephalic elements also occur in the lowest part of the formation in Oslo-Asker and in the uppermost parts of the Elnes Formation in Eiker-Sandsvær and Skien-Langesund.

Emended diagnosis. Pseudofrontal lobe subcircular outline, weakly differentiated from rest of glabella, not overhanging fringe. Arcs E_1 and I_n complete, E_2 commonly incomplete posteriorly situated in sulci with E_1 on the lower lamella; ridges developed between these sulci. No other pit arcs developed. Marginal band of fringe very long mesially. Lateral eye tubercle prominent, situated opposite L2. External surface of genae and glabella coarsely reticulate.

Discussion. Størmer's detailed description of this species (1930) need not be repeated here other than to note the presence of a distinct composite lateral glabellar lobe and to describe the fringe pitting in more modern terms. The upper lamella shows 12–15 radial sulci ($\bar{X} = 14\frac{1}{2}$, n = 9) comprising arcs E_1 and I_n over the whole fringe and E_2 anteriorly at least, but this second E arc is commonly difficult to discern. On the lower lamella, however, arcs E_1 and E_2 are clearly seen to share oval sulci which become smaller abaxially and are separated by low but distinct ridges. E_2 is commonly incomplete posteriorly and comprises only $4\frac{1}{2}$ pits (half-fringe) in one specimen. No other arcs are developed and the 'zone of complication' is restricted to a single adventitious pit seen in a few specimens.

Størmer considered this form to be a subspecies of *B. hibernicus* (Reed, 1895) from the Tramore Limestone (Llandeilo–lowest Caradoc, see Carlisle 1979). Specimens of Reed's species illustrated by Hughes *et al.* (1975, pl. 4, figs. 45–47) and preliminary analysis of material in the Murphy Collection at the National Museum of Ireland show that the Irish species has a more spherical pseudofrontal lobe which overhangs the inner part of the fringe. The sulci on the upper lamella of the fringe are long and E_2 is distinct from E_1, these arcs do not share sulci anteriorly on the lower lamella and the lateral eye tubercle is much less prominent than in *B. broeggeri* which is thus given full specific status.

B. broeggeri differs from *B. bronnii* and *B. impostor* sp. nov. in the shape of the glabella, the distinct composite lateral lobe, the development of S3 on the side of the pseudofrontal lobe, the prominent lateral eye tubercle, and the marked abaxial tapering of the marginal band of the fringe. It is closest to *B. bronnii* in fringe composition but differs in consistently lacking I_1, in the E pit sulci on the lower lamella, and in commonly having arc E_2 incomplete posteriorly.

Størmer (1953, p. 80) recorded material as *T.* aff. *hibernicus* from the upper part of the Elnes Formation to the basal parts of the Fossum Formation between 46·6 and 63·0 m in the section at Flata, Eiker-Sandsvær. Examination of Størmer's material and collections made recently indicates that samples between 46·6 and 51·0 m belong in *B. broeggeri*, but specimens from 63·0 m differ significantly from this species and are described below as *B.* sp. B.

Botrioides simplex sp. nov.

Plate 12, figs. 7–11

1913 *Trinucleus coscino(r)rhinus* [*sic*] ANG.; Hadding (*pars*), pp. 74–75 ('Orthoceras Limestone' material only), pl. 7, figs. 19, *non* 18, 20 (= *B. efflorescens* (Hadding)).
?1963 *Trinucleus* sp.; Skjeseth, p. 63.
1982 *Botrioides*? *bucculentus*; Wandås, p. 138.
1984 *Botrioides*? *bucculentus* (Angelin); Wandås, pl. 12G, J; pl. 13F.

Holotype. A cranidium (PMO 83021) from the basal part of the Elnes Formation (7·75 m above base) at Furnes, Mjøsa.

Paratypes. Two articulated specimens (PMO 104064), possibly representing successive instars of the same animal, from 8·0 m above the base of the Elnes Formation at Vikersundbakken, Modum.

Material, localities, and horizons. Other complete and disarticulated specimens occur between 7·9 and 12·5 m above the base of the Elnes Formation at Vikersundbakken (see Wandås 1984) and a second cranidium is known from the type locality. Rare cephala and cranidia are also known from the upper part of the Isö Limestone (= 'Orthoceras Limestone') and possibly lower Andersö Shale in the Lower Allochthon in Jämtland.

Derivation of name. Simplex—simple, referring to the morphology of the fringe of this species.

Diagnosis. Pseudofrontal lobe subspherical, overhanging inner part of narrow fringe which comprises short sulci containing arcs E_1 and I_n. E_1 pits in lower lamella decrease in size abaxially. Ridges present between E pits on lower lamella. Composite lateral glabellar lobe distinct. Lateral eye tubercle well developed, located opposite S3.

Description. Sagittal length of cranidium equal to about 40 % of posterior width. Glabella similar to that of *B. bronnii* except that the pseudofrontal lobe overhangs the inner part of the fringe a little less, S2 is less extensive abaxially and thus there is a well-developed composite lateral glabellar lobe. There is also a shallow S3 discernible on the sides of the pseudofrontal lobe slightly behind level of median tubercle. Genal lobe quadrant-shaped, bearing distinct lateral eye tubercle opposite S3.

Fringe narrow, comprising pits of arcs E_1 and I_n set in 14–16½ (n = 3) sulci in a half-fringe. One specimen also shows three pits in the position of I_1 posteriorly. On lower lamella E_1 pits enlarged anteromesially where they are separated by distinct ridges when viewed in ventral view; E_1 size and distinctiveness of ridges decreases abaxially. Marginal band of lower lamella very broad mesially, tapering abaxially. Genal spine curving rearwards in a very broad arc from being directed abaxially proximally to gently adaxially distally, extending well beyond the level of the tip of the pygidium.

Internal mould of glabella smooth whilst gena bears a subdued but distinct reticulation. Details of external surface not known other than the reticulation on the occiput and posteromesial part of the genal lobe seen in the holotype.

Hypostoma not known. Thorax similar to that of *B. bronnii* except that there are no median tubercles on the axial rings. Transverse pygidium too poorly known other than to note the broad border and the presence of three or four rings on the axis and two pleural ribs.

Discussion. Although based on only a few rather poorly preserved specimens, *B. simplex* sp. nov. clearly differs significantly from the other narrow fringed species of *Botrioides*. The shape of the glabella is closest to that of *B. bronnii* but the pseudofrontal lobe is less spherical and overhangs the fringe less, S2 is less extensive abaxially, and thus there is a well-developed composite lateral glabellar lobe. The very simple fringe, comprising just E_1 and I_n is closest to that of those specimens of *B. impostor* which lack I_1 but the marked abaxial decrease in size of E_1 and the development of ridges on the lamella between these pits distinguish *B. simplex*. The ridges are only otherwise seen in *B. broeggeri*. The forwardly placed lateral eye tubercle distinguishes *B. simplex* from all these other species.

Botrioides sp. A

Plate 12, figs. 13 and 14

Material, locality, and horizon. A cephalon and a pygidium from the middle part of the Elnes Formation (uppermost '$4a\alpha_2$' of earlier usage) road section at the ski jump at Slemmestad, Asker.

Description. Pseudofrontal lobe subspherical but not significantly wider than posterior part of glabella; only slightly overhanging fringe. Arcs E_1, I_1, and I_n complete, and comprise sixteen radii, I_2 developed laterally at least. Pits arranged in sulci except laterally where E_1 becomes discrete. Lateral eye tubercle prominent, situated far back on the genal lobe, opposite S1. Transverse pygidium with four axial rings, two pleural ribs, and a narrow border.

Discussion. The broad sulci containing only two complete I arcs and the segmentation of the pygidial axis suggest that this material belongs in the *B. bronnii* species group although the number of sulci is near the upper end of the range seen in the group and an albeit incomplete I_2 arc is present. The shape of the glabella and the large lateral eye tubercle suggest an affinity to *B. broeggeri*. Although that species has a very prominent lateral eye tubercle, that of *B.* sp. A is more posteriorly placed, the genal lobe is smooth and in addition to the E_1 development, the fringe comprises more I arcs (3, cf. 1), there are no E_2 pits and the number of radii and E and I arcs is closest to the condition in *B. impostor* although this species lacks I_2 pits and all the arcs or just I_n become discrete posteriorly.

EXPLANATION OF PLATE 12

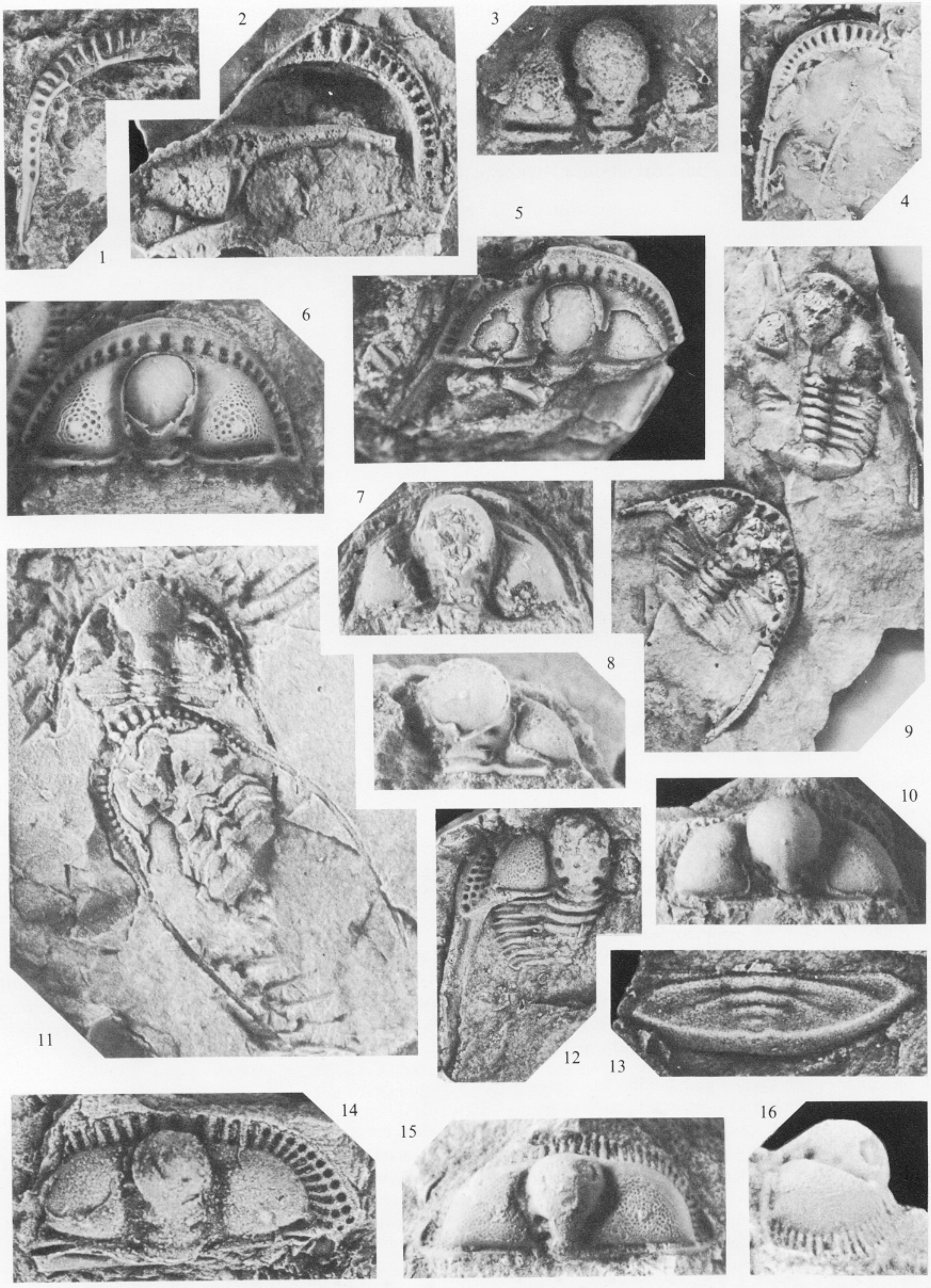
Figs. 1–6. ***Botrioides broeggeri*** (Størmer). 1, PMO H563, ventral view of lower lamella external to girder, Vollen Formation, Gullerud, Ringerike, ×4; also figured by Størmer (1930, pl. 3, fig. 10). 2, PMO 103.978, latex cast showing ventral view of lower lamella and dorsal view of cephalon, uppermost Elnes Formation 50·5 m above base of section, Flata, Eiker-Sandsvær, ×5. 3 and 4, PMO 66633, dorsal view of latex cast of cranidium and ventral view of latex cast of lower lamella, same locality as 2, 46·6 m above base of section, ×6, ×3. 5, holotype, PMO H553, dorsal view of partially exfoliated cephalon, same horizon and locality as 1, ×4; also figured by Størmer (1930, pl. 3, fig. 1). 6, PMO 81903, dorsal view of partially exfoliated cephalon, same horizon and locality as 1, ×6.

Figs. 7–11. ***B. simplex*** sp. nov. 7, LO 2541*t*, dorsal view of internal mould of cranidium, upper Isö Limestone, Andersön, Jämtland, ×4; also figured by Hadding (1913, pl. 7, fig. 19). 8, holotype, PMO 83021, dorsal view of partially exfoliated cranidium, 7·75 m above base of Elnes Formation Furnes, Mjøsa, ×4; also figured by Wandås (1984, pl. 12J). 9, PMO 104.055, dorsal view of latex cast of two articulated individuals, 7·9 m above base of Elnes Formation, Vikersundbakken, Modum, ×3; also figured by Wandås (1984, pl. 12G). 10, SGU Type 5064, dorsal view of internal mould of cranidium, probably lower Andersö Shale, Verkön, Jämtland, ×3. 11, Paratype, PMO 104.064, dorsal view of internal mould of two articulated specimens, possibly successive instars of the same animal which died during ecdysis, 8·0 m above base of Elnes Formation, same locality as 9, ×3; also figured by Wandås (1984, pl. 13F).

Fig. 12. ***B.*** sp. B, PMO 66650, dorsal view of latex cast of cephalon and anterior thorax, basal part of Fossum Formation, 63·0 m above base of section, Flata, Eiker-Sandsvær, ×3·5.

Figs. 13 and 14. ***B.*** sp. A. 13, PMO 81265, dorsal view of latex cast of pygidium, middle Elnes Formation, road section at ski jump, Slemmestad, Asker, ×9·5. 14, PMO 82168, dorsal view of partially exfoliated cephalon, same horizon and locality as 13, ×6.

Figs. 15 and 16. ***B. foveolatus*** (Angelin), neotype, RM Ar2310, dorsal and lateral views of cranidium, upper Elnes Formation, probably Oslo-Asker, ×6, ×7·5; also figured at Størmer (1930, pl. 1, figs. 4 and 5).



OWEN, *Botrioides*

Botrioides sp. B

Plate 12, fig. 12

1953 *Trinucleus* aff. *hibernicus*; Størmer, p. 80 (*pars*).

Material, locality, and horizon. A fringe fragment and a cephalon with five thoracic segments attached from the basal part of the Fossum Formation, 63 m above the base of the section at Flata, Eiker-Sandsvær.

Discussion. As noted in the discussion of *B. broeggeri*, *Botrioides* occurs at various levels in the section at Flata and whilst the specimens up to 51 m above the base of the section belong in Størmer's species, those from the 63 m level differ in several respects. The lateral eye tubercle is much less prominent, the reticulation on the gena is much finer, arcs I_1 and I_2 are present, and the sulcation on the upper lamella breaks down posteriorly. It is not known whether E_2 is developed. The shape of the glabella and genal lobe is very close to that of *B. hibernicus* but the subdued eye tubercle, fine reticulation, and fringe pitting are closest to the morphology of *B. impostor* sp. nov.

Botrioides foveolatus *Species Group*

Botrioides foveolatus (Angelin, 1854)

Plate 12, figs. 15 and 16; Plate 13, figs. 1-4

1854 *Trinucleus foveolatus* Angelin, p. 84, pl. 41, fig. 2.
1857 *Trinucleus foveolatus* Ang.; Kjerulf, p. 94.
1927 *Botrioides foveolatus* (Angelin); Stetson, pl. 1, fig. 10.
1930 *Trinucleus foveolatus* ANG.; Størmer, pp. 16-18, pl. 1, figs. 4-13; text-figs. 2*a-c* (*non* d = *B. efflorescens* (Hadding)), 3, 16*a*.
1930 *Trinucleus foveolatus* ANG. var. *intermedius* Størmer, pp. 18-19, pl. 1, figs. 1-3; text-figs. 4, 16*b*, 39.
1934 *Trinucleus foveolatus*; Størmer, p. 331.
1975 *B.? foveolatus* (Angelin); Hughes *et al.*, p. 562.
1975 *B.? foveolatus intermedius* (Størmer); Hughes *et al.*, p. 562.
non 1982*b* *Botryoides* [*sic*] *foveolatus*; Jaanusson, p. 168 (= *B. margo* sp. nov.).
1985 *Botrioides foveolatus* Angelin; Owen, table 1, text-fig. 5*h*.

Neotype. Selected by Størmer (1930, p. 16), a cranidium (RM Ar2310) from the upper part of the Elnes Formation, probably Oslo-Asker, Norway.

Material, localities, and horizons. Cephalic elements and pygidia occur in the middle part of the Elnes Formation ('4aα_2' and '4aα_3' of earlier usage) in Oslo-Asker. Cranidia are also known from this formation in Ringerike and the Mjøsa districts.

Emended diagnosis. Pear-shaped glabella evenly increasing in convexity to the mid-part of pseudofrontal lobe, overhanging fringe only very slightly. Arcs E_1, I_{1-3}, I_n situated in long sulci over whole fringe. I_4 present laterally in some specimens. Fringe narrows only slightly laterally. Small but distinct lateral eye tubercle just in front of level of S2. External surface of glabella and genae finely reticulate, fine concentric ridges also on mesial part of glabella. Pygidium with narrow border; about seven axial rings and five pleural ribs.

Description. Pear-shaped glabella increases evenly in width and convexity to the mid-part of the pseudofrontal lobe. Occipital ring and furrow arched very gently rearwards. Occiput weakly developed. S1 deep proximally, shallowing abaxially and directed rearwards at about 60° to the sagittal line. L1 short (tr.), extended as part of a very poorly swollen composite lobe directed abaxially forwards at about 30° to the sagittal line. S2 pit-like. S3 shallow depression at side of pseudofrontal lobe just behind the mid-line of the latter. Very weak median tubercle located at about same level as S3 and at the anterior end of a weak carina in many specimens. Genal lobe broader posteriorly than maximum exsagittal length; inner part rising gently from axial furrow, outer parts steeply declined. Lateral eye tubercle small but distinct, located just in front of level of S2.

Fringe steeply declined, narrowing very slightly laterally, comprising long sulci containing arcs E_1, I_{1-3}, and I_n. These arcs are complete, each containing 17-22½ pits in the half-fringe ($\bar{X}$ = 19½, n = 9). Arc I_4 is developed laterally in two of the five specimens where this can be determined confidently. Posterior margin of fringe directed very slightly abaxially forwards.

External surface of mesial part of glabella and inner part of genal lobe finely reticulate. This reticulation becomes more subdued away from the median and lateral eye tubercles and is associated with weak concentric ridges on the glabella. The surface sculpture is extremely subdued in the holotype and only specimen ascribed to *B. foveolatus intermedius* by Størmer (1930) and is no more than a fine pitting on the genal lobe and hence the eye tubercle appears more prominent. This sculptural difference is the only feature which distinguishes Størmer's specimen from other specimens of *B. foveolatus* and is here considered insufficient to warrant formal taxonomic status.

Hypostoma and thorax not known. Pygidium triangular in outline, sagittal length (including fairly narrow border) equal to about 35 % of maximum width. Axis tapers evenly rearwards at 25° and terminates on the inner part of the border. Seven axial rings present along with an anterior articulating half-ring and a short terminal piece which bears faint impressions of further apodemes. Axial furrow weakly raised. Five pleural ribs developed, the anterior three extending to edge of border.

Botrioides efflorescens (Hadding, 1913)

Plate 13, figs. 5–13

1913 *Trinucleus coscino(r)rhinus* ANG; Hadding, pp. 74–75, pl. 7, figs. 18, 20, *non* 19 (= *B. simplex* sp. nov.).
1913 *Trinucleus efflorescens* Hadding, p. 75, pl. 7, fig. 21*a–c*.
1927 *Trinucleus efflorescens* (Hadding) [*sic*], Stetson, pl. 1, fig. 4.
1927 *Botrioides coscinorrhinus* [*sic*] (Angelin); Stetson, pl. 1, fig. 12.
1930 *Trinucleus foveolatus* ANG., Størmer, p. 18 (*pars* Jämtland material only), text-fig. 2*d*.
1952 *Trinucleus bronni* SARS and BOECK; Nilsson (*pars*), pp. 684, 691–692 (layers, f, j (*pars*), and k (*pars*)).
1982 *Botryoides* [*sic*] *bronni* (Sars); Karis, p. 58.
1982 *Botryoides efflozescens* [*sic*] (Hadding); Karis, p. 58.
1982 *Botryoides* [*sic*] *coscinorhinus* (Angelin); Bergström, p. 190 (*pars*—material recorded by Nilsson 1952).

Holotype. By monotypy, an external mould of a cranidium (LO 2543T) from the Andersö Shale at Andersön, Jämtland.

Material, localities, and horizons. Cephalic elements and rare pygidia are known from the type unit and locality and from the Killeröd Formation in Killeröd Quarry, Scania.

Emended diagnosis. Pear-shaped glabella with moderately swollen pseudofrontal lobe overhanging fringe very slightly. Arcs E_1, I_1, and I_n complete, E_2 and I_2 present anteriorly and, in the case of I_2 laterally, I_3 present anterolaterally. Fringe narrows markedly posteriorly. Small but distinct lateral eye tubercle opposite antereomesial edge of L2. External surface of gena smooth. Pygidium with narrow border, seven to nine rings and up to three, weak, pleural ribs.

Discussion. B. efflorescens was placed in the synonymy of *B. foveolatus* by Størmer (1930, p. 3) and the two are clearly closer to each other than to other species of *Botrioides*. There is an overall similarity in the shape of the glabella and genae, the number of radii in the fringe ($16\frac{1}{2}$–$21\frac{1}{2}$ in *B. efflorescens* (n = 3)), and the presence of arcs I_2 and I_3. Features which distinguish the cephalon of *B. efflorescens* from *B. foveolatus* include the more rounded anterior part of the glabella, the slightly more posteriorly situated lateral eye tubercle, the presence of E_2 pits (although these are small and difficult to discern on the dorsal surface), and the absence of I_2 and I_3 pits posteriorly thus producing a markedly tapered fringe. The narrow pygidial border of *B. efflorescens* also allies it to *B. foveolatus*, but the sparser and more subdued ribbing of pleural area serves to distinguish the Swedish species.

Botrioides margo sp. nov.

Plate 13, figs. 23–25; Plate 14, figs. 1 and 2

1982*b* *Botryoides* [*sic*] *foveolatus*; Jaanusson, p. 168.

Holotype. A cranidium (RM Ar52033) from the lowest 10 cm of the Gullhögen Formation, at Hällekisbrottet, Kinnekulle, Västergötland, Sweden.

Paratypes. Six cephala/cranidia/lower lamellae from the type formation at the type locality and at Gullhögen Quarry, Västergötland (all specimens UM).

Derivation of name. *Margo*—brim, referring to the presence of such a feature on the outer part of the fringe of this species.

Diagnosis. Fringe broad, declined with a distinct brim. E_{1-4} developed anterolaterally but only E_1 extending to posterior margin, at least three I arcs present anterolaterally to posteriorly. Pits on upper lamella in very narrow sulci. Sulci on lower lamella restricted to very shallow depressions linking E pits in ventral view. Lateral eye tubercle distinct.

Description. Glabella increasing evenly in convexity forwards to the swollen pseudofrontal lobe which overhangs most of the mesial fringe. L1 small, marked anteriorly by short (tr.), transversely directed S1. Adaxial swollen part of L2 almost square in outline; outer part confluent with pseudofrontal lobe as a very narrow (tr.) composite lobe outside the pit-like S2. Pseudofrontal lobe subcircular in outline, bearing a prominent median node a short distance behind its longitudinal mid-point. Axial furrow broad (tr.) and shallow, directed abaxially forwards at about 25° to the sagittal line to opposite S2 in front of which it curves gently adaxially towards the anterior fossula. Genal lobe quadrant-shaped except anteromesially where it is gently indented, gently inclined from axial furrow, more steeply so from posterior border furrow, steeply declined towards fringe. Lateral eye tubercle situated at highest point of genal lobe, opposite and slightly in front of S2. One internal mould (Pl. 14, fig. 1) shows a weak eye ridge directed adaxially forwards from the eye tubercle. This specimen also shows five subparallel ridges directed rearwards from the abaxial side of the tubercle towards

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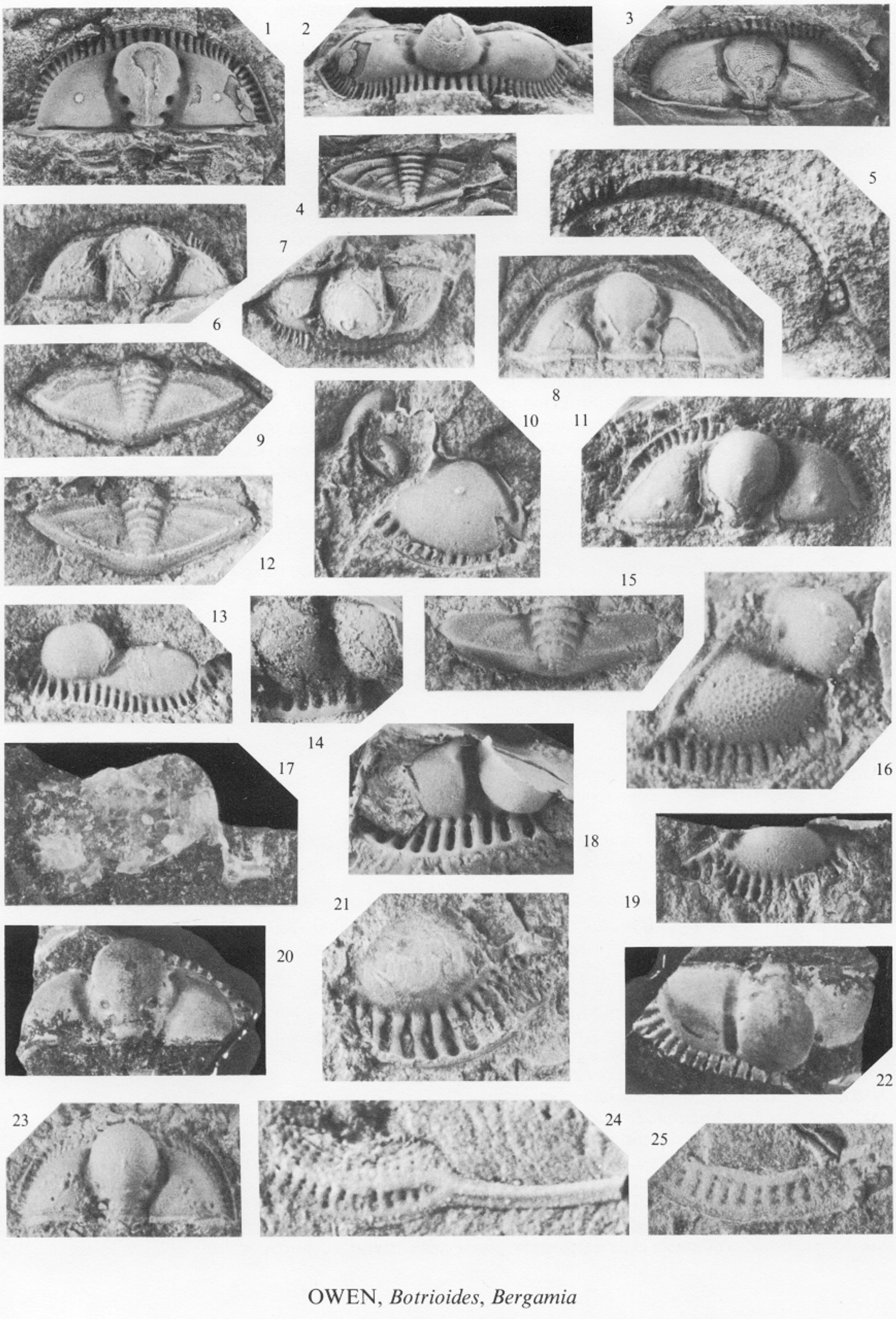
EXPLANATION OF PLATE 13

Figs. 1-4. ***Botrioides foveolatus*** (Angelin). 1 and 2, PMO H391, dorsal and frontal views of cranidium, upper Elnes Formation, promontary south of Engervik, Asker, ×2·5; also figured by Størmer (1930, pl. 1, figs. 1-3) as holotype of '*Trinucleus*' *foveolatus intermedius*. 3, PMO HO538, dorsal view of latex cast of cranidium, same horizon as 1, Huk, Bygdøy, Oslo, ×4: also figured by Størmer (1930, pl. 1, fig. 8). 4, PMO HO538, dorsal view of pygidium, on same block as 3, ×4·5.

Figs. 5-13. ***B. efflorescens*** (Hadding). 5, LO 5723*t*, oblique ventral view of lower lamella, Andersö Shale, Andersön, Jämtland. 6 and 7, holotype, LO 2543*T*, dorsal and oblique frontal views of latex cast of cephalon lacking upper lamella of fringe frontally, same horizon and locality as 5, ×4; also figured by Hadding (1913, pl. 7, fig. 21). 8, LO 2540*t*, dorsal view of partially exfoliated cranidium, same horizon and locality as 5, ×5; also figured by Hadding (1913, pl. 7, fig. 18). 9, LO 2542*t*, dorsal view of internal mould of pygidium, same horizon and locality as 5, ×5; also figured by Hadding (1913, pl. 7, fig. 20). 10, SGU Type 5065, oblique posterolateral view of partially exfoliated cranidium, same horizon and locality as 5, ×4. 11, SGU Type 5066, dorsal view of partially exfoliated cranidium, same horizon and locality as 5, ×2. 12, LO 5722*t*, dorsal view of pygidium, Killeröd Formation, level k of Nilsson (1952), Killeröd Quarry, Scania, ×5. 13, SGU Type 5067, anterolateral view of latex cast of cranidium, same horizon and locality as 5, ×5.

Figs. 14-22. ***Bergamia johanssoni*** sp. nov. 14, RM Ar53002, anterolateral view of latex cast of etched cranidium showing reticulation on glabella, uppermost part of Komstad Limestone, Fågelsång, Scania, ×5. 15, RM Ar53003, dorsal view of pygidium, same horizon and locality as 14, ×7. 16, RM Ar53004, oblique posterolateral view of juvenile cranidium, same horizon and locality as 14, ×10. 17, RM Ar53005, approximately sagittal section through cephalon, same horizon and locality as 14, ×5·5. 18, RM Ar53006, oblique anterolateral view of latex cast of cranidium, same horizon and locality as 14, ×4. 19, RM Ar53007, lateral view of latex cast of cranidium, same horizon and locality as 14, ×4·5. 20 and 22, holotype, RM Ar53001, dorsal and oblique frontal views of unwhitened cranidium, same horizon and locality as 14, ×3. 21, MGUH 16872, anterolateral view of gena and fringe, 30 cm above base of Upper Didymograptus Shale, same locality as 14, ×5.

Figs. 23-25. ***Botrioides margo*** sp. nov. 23, holotype, RM Ar52033, dorsal view of cranidium, lowest 10 cm of Gullhögen Formation, Hällekisbrottet, Kinnekulle, Västergötland, ×4. 24, UM Vg983/1, ventral view of lower lamella, lower part of Gullhögen Formation, Gullhögen, Västergötland, ×12. 25, UM Vg981, ventral view of part of lower lamella external to girder, same horizon and locality as 24, ×9.



OWEN, *Botrioides*, *Bergamia*

the posterior border furrow. The holotype shows a single, weak ridge extending from the eye tubercle to the posterior border furrow on the left genal lobe which is partially exfoliated. External surface of glabella bears a fine, weak reticulation on which is superimposed a series of subdued concentric ridges on the pseudofrontal lobe. External surface of genal lobe smooth or weakly reticulate. Internal mould of glabella and genal lobe smooth or finely pitted.

Inner part of fringe steeply declined, outer parts flattening out to form a distinct brim and bounded by a broad marginal band. On upper lamella, pits arranged in very narrow radial sulci (twenty-two sulci in the half fringe of two specimens). The width of these sulci increases slightly distally and in this broader part up to four pit arcs can be discerned anterolaterally, otherwise individual pit arcs cannot be determined. Fragments of lower lamellae show that at least three discrete I arcs are present laterally and up to four E arcs, arranged in very shallow sucli in ventral view, are developed anterolaterally although this number of E arcs clearly decreases both adaxially and abaxially. Only one E arc is present over the posterior few radii. There is no zone of complication or genal prolongation. The girder is prominent and the lower lamella is extended as a spine of unknown length, approximately parallel to the sagittal line.

Hypostoma, thorax, and pygidium not known.

Discussion. The narrowness of the sulci, the extensive E arc development causing a distinct brim on uncompressed cephala, and the anterior overhang of the glabella serve to distinguish *B. margo* sp. nov. from *B. foveolatus* and *B. efflorescens*. The presence of more than two E arcs in a trinucleine is otherwise recorded in *Stapeleyella* Whittard, 1955 and *Decordinaspis* Harper and Romano, 1967 (see Hughes *et al.* 1975, pp. 559, 566). Dean (1974, pp. 5–6) also noted a short E_3 arc in specimens which he termed *Bergamia*? sp. but which Hughes *et al.* (1975) reassigned to *Botrioides*. Both *Stapeleyella* and *Decordinaspis* have four E arcs but the pit development of both E and I arcs is much more complex than the simple radial sulci of *B. margo*. Dean's material from the upper Arenig of north-east Newfoundland is too incomplete for adequate generic assignment although unlike species of *Botrioides*, the sulcation breaks down for the inner I arcs posteriorly.

Genus BERGAMIA Whittard, 1955

Type species. Bergamia rhodesi Whittard, 1955, pp. 32–35, pl. 3, figs. 8–13, from the uppermost part of the Mytton Flags (*D. hirundo* Zone), Bergam Quarry, Shelve, England; by original designation of Whittard (1955, p. 31).

Bergamia johanssoni sp. nov.

Plate 13, figs. 14–22

Holotype. A cranidium (part and counterpart) (Rm Ar53001) from the uppermost part of the Komstad Limestone at Fågelsång, Scania, south-west Sweden.

Paratypes. Seven cranidia/cephala and one pygidium from the type horizon and locality. One cephalon from a thin limestone bed in the basal part of the Upper Didymograptus Shale, 30 cm above the Komstad Limestone at the type locality.

Derivation of name. After Mr J. V. Johansson of Sköllersta who collected most of the material.

Diagnosis. Swollen pseudofrontal lobe partially overhanging fringe. Internal mould of gena smooth. Short eye ridges present. Arcs E_1, E_2, I_1, and I_n complete, I_2 and I_3 extensive but incomplete anteriorly.

Description. Cranidium sub-semicircular in outline. Occipital ring not known. Occipital furrow broad (sag., exsag.) and shallow; transversely directed. S1 deep, oval in outline, directed abaxially rearwards at about 45° to sagittal line. S2 directed abaxially forward at about 60°, in which direction it deepens before shallowing abruptly such that a narrow (tr.) composite glabellar lobe is developed. L1 expands (exsag.) abaxially and is connected to the pseudofrontal lobe by the composite lobe. S3 developed as shallow indentation in the pseudofrontal lobe at the axial furrow. In transverse profile the preoccipital part of the glabella rises evenly to the highest part of the swollen pseudofrontal lobe where the glabellar node is developed, approximately level with S3. In front of this the glabellar profile is markedly convex forwards and the glabella overhangs the cephalic fringe slightly. In dorsal view the pseudofrontal lobe is almost circular in outline with a maximum width only slightly less than the sagittal length. In a juvenile specimen (Pl. 13, fig. 16) the pseudofrontal lobe is more oval in outline. Axial furrow broad (tr.) and shallow posteriorly, directed forwards at about 20° in which direction it narrows, deepens, and bears a deep anterior fossula a short distance in from the fringe. Quadrant-shaped genal lobe bears a subdued eye ridge near its inner edges. This ridge is directed abaxially rearwards from the dorsal furrow at S3 at about 80°. On internal moulds the glabella and genal lobes of large specimens are smooth. The preservation of these specimens in pure limestone is such that the calcareous exoskeleton remains with the counterpart to the internal mould. Careful etching of a specimen with 10 % HCl revealed a fine reticulation on the external surface but this was largely seen as colour mottling and because of the close compositional similarity between skeleton and matrix further etching failed to produce a true external mould. A latex cast of the resulting mould shows a faint reticulation on the glabella (Pl. 13, fig. 14). The juvenile cranidium shows reticulation even on the internal mould (Pl. 13, fig. 16). Posterior border furrow shallow, broadening (exsag.) abaxially where it bears a deep fossula. Ridge-like posterior border transversely directed over most of its length, deflected very gently rearwards distally.

Cephalic fringe broadens abaxially; steeply and fairly evenly declined mesially. Less steeply declined laterally where the outer parts flatten out as a distinct brim. The juvenile specimen shows this brim much less well pronounced. No complete fringes are available but the pit distribution is constant between the various incomplete fringes. Arcs E_1, E_2, I_1, and I_n complete with E_2 and I_1 becoming progressively more distinct abaxially from E_1 and I_n respectively. Approximately fifteen pits are present in the half fringe of I_n. I_2 missing only one pit mesially in the holotype, I_3 beginning at R_6. Both arcs continuous posteriorly. Pits arranged in sulci at about 90° to the inner edge of the fringe except posteriorly on the distinct, short, genal prolongation. The sulci here are arranged at an acute angle to the first set and are thus at a high angle to the posterior border rather than parallel to it. Lower lamella bears a robust genal spine of unknown length set at a slight angle to the sagittal line. Remaining details of lower lamella not known.

Hypostoma and thorax not known. Pygidium transverse, sagittal length (including border) equal to about 35 % of the maximum width. Convex (tr.) axis occupies 20 % of the anterior width of the pygidium, tapering rearwards at 35°. Three distinct and two more subdued rings present in front of the border. Axis continues on to posterior border where it is very gently swollen and bears a further six weak rings. Pleural field bears two gentle ribs extending and dying out rearwards from the first and second axial rings at angles to the sagittal line of 80° and 60° respectively. Articulating facet short (tr.) and directed rearwards at 60° to the sagittal line. Inner edge of border marked by a narrow ridge anterolaterally; this ridge dying out towards the axis. Border steeply declined, becoming broader adaxially and changing from concave outwards to convex outwards towards the axis; thus the mesial part is swollen. Internal mould of pygidium smooth.

Discussion. As noted above in the discussion of *Botrioides*, Angelin's original material of the type species of that genus, *Trinucleus coscinorinus*, was thought to be from the Komstad Limestone at Fågelsång. The present material differs from the specimen illustrated by Angelin primarily in having a much broader fringe and a well-developed genal prolongation. The latter feature, along with the absence of lateral eye tubercles, distinguishes the Komstad Limestone specimens from species ascribed to *Botrioides*. Thus on both morphological and pragmatic grounds the present material is not considered conspecific with '*T.*' *coscinorinus*. The neotype selected above for Angelin's species is from a higher horizon in Scania but is more in keeping with Angelin's illustration and the accepted concept of *Botrioides*.

The presence of pit arc E_2 and the short simple pygidium exclude the Komstad Limestone material from *Trinucleus* Murchison, 1839 and indicate that it belongs in *Bergamia*. Hughes *et al.* (1975, p. 556) also gave the absence of eye ridges as a diagnostic feature of *Bergamia* although they did figure a specimen of *B. prima* (Elles, 1940) on which they drew attention to the presence of short, faint ridges (1975, pl. 2, fig. 25). *B. johanssoni* sp. nov. has these ridges more pronounced, resembling the condition in juvenile specimens of *Trinucleus* (e.g. Hughes *et al.* 1975, p. 556) and even in adults of *T. bicallis* Rushton & Hughes, 1981.

Unlike *B. johanssoni*, most other described species of *Bergamia* have a narrow fringe with, in addition to E_1 and E_2, no more than two I arcs, I_1 and I_n; the latter being incomplete frontally or laterally. E_2 is also incomplete in some species. *B. whittardi* Hughes, 1971 has an anterior and anterolateral pit development similar to that of *B. johanssoni*, but E_2 is restricted to the anterior part of the fringe and a fifth I arc (I_4) is developed laterally. Hughes's species, from the lower

Llandeilo of central Wales, also has more numerous pit radii, a larger genal prolongation with a more complex pit distribution, and a more elongate pygidium.

B. johanssoni shows some resemblance to '*T.*' *sedgwicki* Salter, a species from the middle Arenig of south Wales which Whittard (1955) and subsequent workers tentatively placed in *Bergamia*. Drs R. A. Fortey and R. M. Owens, however, propose to include Salter's species along with a new middle Arenig species in a new genus in their forthcoming revision of the Arenig of south Wales. Dr Owens informs me (pers. comm. 1985) that the new genus is distinguished from *Bergamia* (including *B. johanssoni*) in having inter-radii developed in the I pit series, no deep sulci, and a narrower pygidial axis and border.

The overall cephalic morphology and fringe pit distribution of *B. johanssoni* is similar in many respects to some of the younger Ordovician trinucleines, especially the late Caradoc *Tretaspis ceriodes* (Angelin) (see Owen 1980*a*) which was also an immigrant to Scandinavia, at a time of probable regression, and which also occurs in limestone units. The two forms are, however, homeomorphs and are not directly related. The absence of lateral eye tubercles, the strong brim on the fringe, the absence of fringe lists, and the pitting on the genal prolongation all serve to distinguish *B. johanssoni* from the much later form.

Subfamily REEDOLITHINAE Hughes, Ingham, and Addison, 1975
Genus REEDOLITHUS Bancroft, 1929

Type species. Trinucleus subradiatus Reed, 1903, pp. 12-14, pl. 2, figs. 1-6; from the Balclatchie Group (lower Caradoc) near Girvan, south-west Scotland; by original designation of Bancroft (1929, p. 77).

Reedolithus carinatus (Angelin, 1854)

Plate 14, figs. 4-10, 13-16; text-fig. 4

1854 *Trinucleus carinatus* Angelin, p. 65, pl. 34, fig. 3, 3*a*.

EXPLANATION OF PLATE 14

Figs. 1 and 2. *Botrioides margo* sp. nov. 1, UM Vg982, dorsal view of partially exfoliated cephalon, lower part of Gullhögen Formation, Gullhögen, Västergötland, ×4·5. 2, UM Vg983/2, oblique posterolateral view of internal mould of cranidium, same horizon and locality as 1, ×8·5.

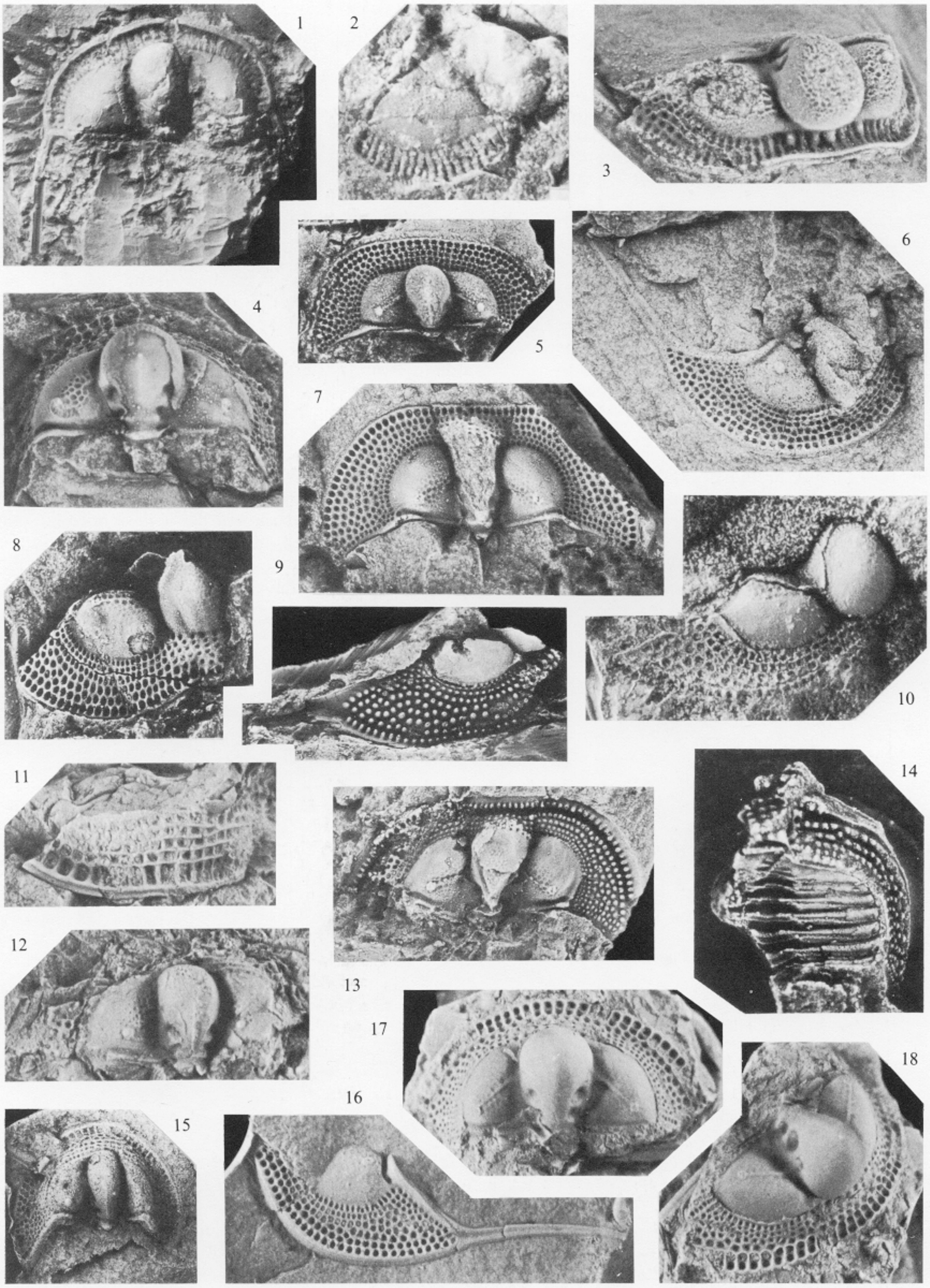
Fig. 3. Trinucleid gen et sp. indet. PMO 87252, anterolateral view of cephalon, about 16 m above base of Elnes Formation, Hovodden, Hadeland, ×7; also figured by Hughes *et al.* (1975, pl. 4, figs. 48-51) and Wandås (1984, pl. 12H, K, L).

Figs. 4-10, 13-16. *Reedolithus carinatus* (Angelin). 4, neotype, PMO H460, dorsal view of partially exfoliated cranidium, Vollen Formation, Gomnæs, Ringerike, ×4·5; also figured by Størmer (1930, pl. 4, figs. 10 and 11). 5, PMO H441, dorsal view of cranidium, same horizon as 4, ×5·5; also figured by Størmer (1930, pl. 4, figs. 5-7). 6, PMO 69176, dorsal view of latex cast of cephalon, lower Fossum Formation, borehole at Saltboden, Frierfjord, Skien-Langesund, ×4. 7, PMO 81684, dorsal view of internal mould of cranidium, Arnestad Formation, Bjørnsviken, Gyssestad, Asker, ×6·5. 8, PMO 81682, oblique anterolateral view of internal mould of cranidium, same horizon and locality as 7, ×6·5. 9, PMO 81772, lateral view of cephalon showing lower lamella of fringe, same horizon and locality as 7, ×3. 10, RM Ar49461, posterolateral view of latex cast of cranidium, labelled Skagen Limestone, Västergötland, ×5. 13, PMO 81688, dorsal view of cephalon showing lower lamella of fringe, same horizon and locality as 7, ×5. 14, PMO H449, dorsal view of lower lamella of fringe and impression of thorax and pygidium, same horizon and locality as 4, ×5·5. 15, PMO 69549, dorsal view of deformed cranidium, 1 m below top of Arnestad Formation, Lindøya, Oslo, ×2·5. 16, PMO 31264, lateral view of latex cast of cephalon, erratic block, Skattvold, Trøndelag, ×4·5.

Figs. 11 and 12. *Reedolithus* sp. 11, UM Vg986, anterior view of fringe, Gullhögen Formation, near Viske-Kleva crossroads, Mösseberg, Västergötland, ×3·5. 12, UM Vg987, dorsal view of internal mould of cranidium, same horizon and locality as 11, ×4.

Figs. 17 and 18. *Reedolithus quebecensis* Staüble. BM It7360, dorsal and oblique posterolateral view of partially exfoliated cranidium, Citadel Formation, Quebec City, Canada, ×4.

PLATE 14



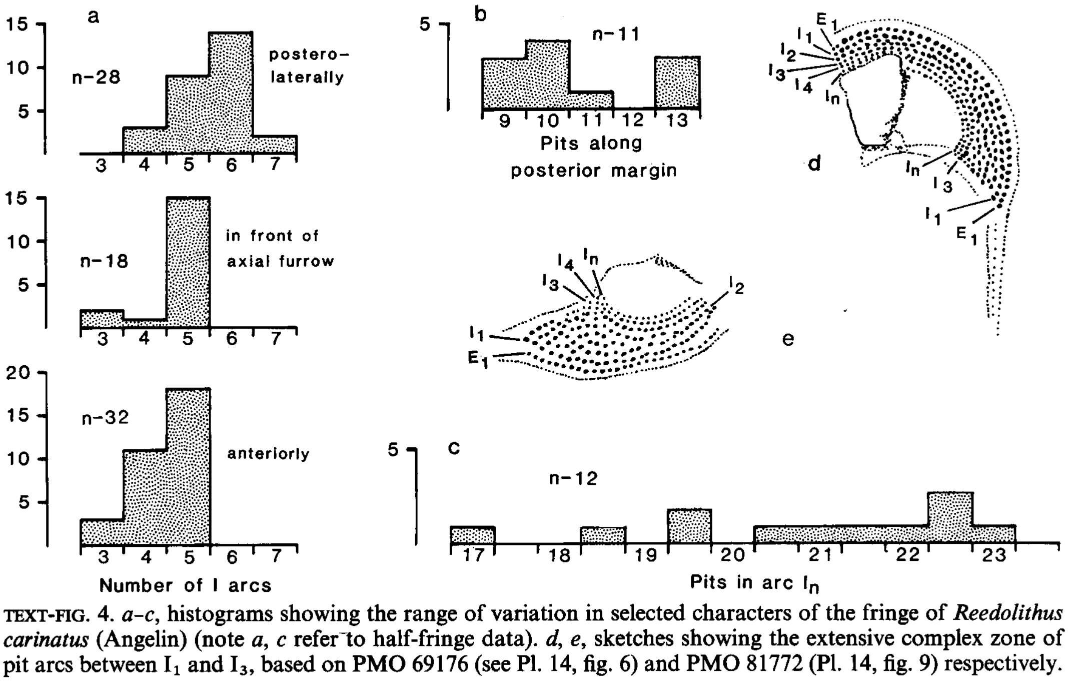
OWEN, *Botrioides*, *Reedolithus*, trinucleid indet.

1930 *Reedolithus carinatus* (ANG.); Størmer, pp. 30-39, pl. 4, figs. 1-13; pl. 5, figs. 1-18; text-figs. 17-20.
1934 *Reedolithus carinatus*; Størmer, p. 331.
1940 *Reedolithus carinatus* (Ang.): Grorud, pp. 159-160, text-fig. 2*a*.
?1948 *Reedolithus carinatus* (Ang.); Thorslund *in* Wærn *et al.*, pp. 344, 347.
1953 *Reedolithus carinatus*, Størmer, pp. 62, 73, 81, 83, 84.
?1982*b* *Reedolithus carinatus*; Jaanusson, p. 168.

Neotype. A cranidium (PMO H460) from the Vollen Formation ('Ampyx Limestone') at Gomnæs, Ringerike; selected by Størmer (1930, p. 31), but see discussion below.

Material, localities, and horizons. Cephala, cranidia, and lower lamellae occur throughout the Vollen Formation and Arnestad Formation ('Lower Chasmops Shale') of Oslo-Asker and in the former unit in Ringerike where incomplete thoraxes and pygidia are known also. The species is known also from broadly comparable levels in Skien-Langesund and Eiker-Sandsvær. A cephalon from a glacial erratic of unknown provenance at Skattvold, Trøndelag, is included here as is a cranidium from Västergötland which is labelled 'Skagen Limestone' but may be from a lower horizon (see discussion below).

Description. The morphology and ontogeny of this upper Llandeilo-lower Caradoc species were described in detail by Størmer (1930) on the basis of Vollen Formation specimens. The species is also recorded here from the overlying Arnestad Formation but no redescription is necessary other than a reassessment of the fringe pitting in more modern terms. Pits progressively decreasing in size from arcs E_1 to I_n, most discrete although pits in E_1 and I_1 share shallow sulci in a few specimens. A first internal pseudogirder is developed laterally (e.g. Størmer 1930, pl. 5, fig. 18). Most specimens show a general radial alignment of pits anteriorly and anterolaterally but this breaks down posteriorly. As text-fig. 4*a* shows, arcs E_1, I_{1-2}, and I_n invariably developed mesially where up to two more I arcs may also be present. By the anterior end of the axial furrow



TEXT-FIG. 4. *a-c*, histograms showing the range of variation in selected characters of the fringe of *Reedolithus carinatus* (Angelin) (note *a*, *c* refer to half-fringe data). *d*, *e*, sketches showing the extensive complex zone of pit arcs between I_1 and I_3, based on PMO 69176 (see Pl. 14, fig. 6) and PMO 81772 (Pl. 14, fig. 9) respectively.

most specimens have arcs E_1, I_{1-4}, I_n developed. The insertion of incomplete I arcs on the anterior and anterolateral parts of the fringe conforms to the 'normal' trinucleid pattern outlined by Hughes *et al.* (1975, p. 544), i.e. immediately outside arc I_n. Thus the arc numbering given above corresponds to that applied to homologous structures in other trinucleids. Posterolaterally, however, the course of I_2 commonly becomes difficult to define unequivocally and up to three short arcs are developed between I_1 and I_3 (text-fig. 4*d*, *e*). This area may be viewed as an extended zone of complication but in contrast to other trinucleids, in *R. carinatus* it includes distinct arcs and very few adventitious pits. Thus the posterolateral fringe in *R. carinatus* contains up to seven I arcs (text-fig. 4*a*) and where E_1 can also be counted it is seen to contain a few more pits than I_n. Nine to thirteen pits are present along the posterior margin of the fringe, excluding the posterior fossula (text-fig. 4*b*).

Discussion. Although the neotype of *R. carinatus* was selected, without discussion, by Størmer from Norway, Angelin's original material was from loose blocks in Västergötland, Sweden. Angelin's illustration (1854, pl. 34, fig. 3, 3*a*) is of a cranidium with a swollen, carinate, glabella, an occipital spine base, genal nodes close to the posterior border, a distinct genal prolongation, and a broad fringe with large, discrete pits. Thus the concept of *R. carinatus* based on Norwegian material does not differ from that exemplified by Angelin's missing specimen. The only specimen from Västergötland seen by the writer which can be placed unequivocally in Angelin's species is a cranidium (Pl. 14, fig. 10) collected by Jarvik in 1938. The horizon given on the specimen label is the Skagen Limestone which in its present definition is low-mid Caradoc (Jaanusson 1982*a*, fig. 4) but its looser usage in the past may have included lower horizons. Specimens of *Reedolithus* collected by Jaanusson from the Gullhögen Formation (Llandeilo) in Västergötland are too fragmentary for detailed determination and are illustrated here under open nomenclature (Pl. 14, figs. 11 and 12), although of the named species, they are closest to *R. carinatus.*

R. carinatus differs from the type species *R. subradiatus* (Reed, 1903; see also Hughes *et al.* 1975, pl. 5, figs. 64–69) primarily in its more transverse cephalic outline, posteriorly placed genal nodes, and larger I_2–I_n pit size. In *R. subradiatus* pits in arcs E_1 and I_1 are considerable larger than those of the remaining I arcs especially laterally, and are separated from them by a list on the upper lamella and a well-developed first internal pseudogirder on the lateral and posterior parts of the lower lamella. Only I_2 laterally approaches the size of the two arcs outside it. Examination of Reed's syntypes in the British Museum (Natural History) shows that there are five to seven I arcs in front of the axial furrow (cf. 3–5 in *R. carinatus*). This increases to eight laterally before the extensive zone of complication in which the regular pit arrangement between arcs I_3 and the innermost three I arcs breaks down completely. *R. carinatus* and *R. subradiatus* have an overlapping stratigraphical range: Llandeilo-lowest Caradoc for the former and lower Caradoc (see Tripp 1980, table 1) for the latter.

The only other species undoubtedly ascribed to *Reedolithus* is *R. quebecensis* Staüble, 1952 (Pl. 14, figs. 17 and 18) from the Citadel Formation (= Quebec City Formation, see Globensky and Riva 1982, pp. C39–49) of Quebec, Canada. This species is from limestone blocks in mélange horizons in the lower part of the formation which also contains graptolites of the *Nemagraptus gracilis* Zone (Riva 1972; Globensky and Riva 1982). The age of the blocks is not clear but as earlier assessments of their shelly fauna suggested levels *above* the *N. gracilis* Zone (e.g. Osborne 1956; Globensky and Riva 1982) they are unlikely to be significantly older than that zone. Its distinction from *R. carinatus* was discussed fully by Staüble (1953, pp. 114–117). Suffice it to note here that examination of Staüble's illustrations and a topotype sample in the British Museum (Natural History) shows that the fringe of *R. quebecensis* has a distinct brim, pits in arcs E_1 and I_1 are enlarged compared to those in the other I arcs (although the contrast is not as marked as in *R. subradiatus*), and share shallow sulci. Four or five I arcs are present anteriorly ($n = 7$) and in front of the axial furrow ($n = 9$), five to seven laterally ($n = 7$). A zone of complication between arcs I_2 and the innermost three I arcs is developed posterolaterally and although pitting in this area is commonly very irregular, a few specimens (e.g. Staüble 1953, fig. 3) show the development of short arcs. Its fringe characters are thus intermediate between those of *R. carinatus* and *R. subradiatus* but on balance they are closer to the former.

Trinucleid gen. et sp. indet.

Plate 14, fig. 3

1975 *Botrioides*? sp.; Hughes *et al.*, pp. 563–564, figs. 48–51.
1984 *Botrioides* sp.; Wandås, pp. 234–235, pl. 12H, K, L.

Material, locality, and horizon. A cephalon (PMO 87252) from about 16 m above the base of the Elnes Formation (Kirkerud Group) at Hovodden, Hadeland.

Description. Maximum width of pear-shaped glabella equal to about 75 % of sagittal length. Preoccipital part of glabella increases markedly and evenly in convexity forwards to the strongly swollen pseudofrontal lobe which overhangs the fringe and axial furrow. Weakly swollen ala directed abaxially forward at 30° situated opposite weakly inflated occiput. S1 and S2 deep. Composite lateral lobe swelling and broadening forwards. S3 is a very gently depressed smooth area a short distance in front of S2. Genal lobe quadrant-shaped; bearing a large lateral eye tubercle opposite S2, well away from the glabella. External surface of glabella bearing a coarse reticulation mesially. This becomes finer and dies out abaxially. Genal lobe bears a similar reticulation around the eye tubercle and this reticulation also dies out towards the outer parts of the lobe except for a broad (exsag.) strip which extends to the axial furrow opposite, and for a short distance in front of S3.

Fringe narrow mesially, broadening abaxially, steeply declined with a narrow brim marginally. Anterior arch and genal prolongation distinct. Approximately 19 pits in I_n and about 22 in E_1. Mesially E_1 and 2–3 I arcs are represented in sulci although there is some irregularity both in the radial disposition of the sulci and in one sulcus bifurcating distally. This latter feature may reflect a repaired injury (see Owen 1985 for other examples). Beyond the axial furrow, individual pits become clearly distinguishable and additional arcs appear such that by R12 there are 5 I arcs and 2 E arcs with sulci restricted to a very shallow depression containing E_1 and E_2. Weak lists are present between I_2–I_3 and I_3–I_4 here and these persist posteriorly where a sixth I arc appears along with an I_1–I_2 list. A few adventitious pits are also present posteriorly and about 9 pits are present along the posterior margin of the fringe. Marginal band broad. Long genal spine parallel to sagittal line.

Discussion. Although the glabella and genal lobes of this specimen suggest an affinity to trinucleines such as *Botrioides* the fringe shows few characters in common with the genus, points of difference being the anterior arch, the irregularity of the sulci anteriorly, the absence of major sulci and breakdown of regular radii laterally and posteriorly, the probable restriction of E_2 to the posterior part of the fringe, and the development of an appreciable genal prolongation.

Hughes *et al.* (1975) considered the Hadeland specimen to be close to the common ancestor of *Botrioides* and *Tretaspis*. They noted that the anterior part of the fringe has sulci incorporating pits of each arc, as in *Botrioides*, and the outermost arc is probably E_1 whereas posteriorly the sulcation is restricted to E_1 and a short E_2 arc, as in many species of *Tretaspis*. Equally, however, the lateral and posterior fringe morphology (with the exception of the probable E_2 pits) and the overall shape of the glabella and genal lobes are close to the morphology of *R. carinatus*. The possibility that the Hadeland cephalon is a reedolithine may be even more likely in view of the palaeogeographical difficulties of the earliest *Tretaspis* species being found in Scoto-Appalachian faunas in the early Caradoc and not appearing in Baltica until late in the Caradoc (Hughes *et al.* 1975, p. 585). In contrast, *Reedolithus* appears virtually simultaneously in both Scoto-Appalachian and Baltic faunas during the Llandeilo.

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