

SCULPTURE AND MICROSTRUCTURE OF THE EXOSKELETON IN CHASMOPINID AND PHACOPID TRILOBITES

by LEIF STØRMER

ABSTRACT. This paper describes the detailed skeletal anatomy of chasmopinid trilobites from the Ordovician of the Oslo region, and *Phacops* from the Polish Devonian. Lamination of the cuticle is similar to that previously reported, and the outermost prismatic layer has been conclusively proved. Several types of tubercles or pustules on the surface of the exoskeleton have been identified, for which a classification is proposed. Canals through the exoskeleton range from about 1–40 μm in diameter. In *Chasmops* spp. apparently smooth tubercles have a thin central canal through the outer zone changing downwards into a wide canal. This smooth tubercle organ shows some resemblance with the sensory campanular organ (mechanoreceptor) in Recent arthropods. Sections of the big composite tubercles or pustules in *Phacops* have revealed two sets of ducts, partly with different directions: (1) numerous close-set fine (4 μm) canals in a fan-like arrangement, and (2) diffuse ramifying branches or tubes with distal bundles of tubules, the blunt terminals of which are inserted into the lower surface of the outer zone of the exoskeleton. This internal tubules organ might possibly, in general features, be analogous with the much smaller campanular organ in the halteres in Diptera. Just below the prismatic layer there are numerous small (10–20 μm) subsphaeric cavities apparently connected with the epidermis by a single thin (1.5–2.0 μm) perpendicular canal, which are termed Osmolska cavity organs.

There is a considerable variation in muscle-scar pattern. Some species have calluses on the inner surface corresponding to shallow pits on the outer surface. Similar pits and dark patches, and knobs or calluses on the inner surface of the exoskeleton, are scars or small apodemes of muscles leading from the dorsal exoskeleton to the presumed thin membrane representing the ventral body wall inside the marginal doublure.

THIS paper was planned to form a part of a monograph on the subfamily Chasmopinae of the Middle and Upper Ordovician of the Oslo Region. As the work proceeded, some of the characters which had to be studied in greater detail, for example in thin sections, were relevant to general problems of trilobite morphology and anatomy. These characters comprise the sculpture and microstructure of the exoskeleton, the relations between the hypostoma and cephalic appendages, and finally a possible distinction of exuviae and dead individuals based on the thickness of the exoskeleton.

MATERIAL AND METHODS

With few exceptions the specimens studied belong to the Middle Ordovician of the Oslo Region. In this area the Chasmopinae play an important role as guide fossils. In addition to the Norwegian material a few specimens from Estonia have been borrowed from the British Museum (Natural History) and from the Naturhistoriska Riksmuseet in Stockholm; the Polish *Phacops* specimens were presented by Dr. Osmolska.

The Norwegian specimens of the Chasmopinae are usually well preserved in limestones, either in massive beds or in nodules in shales. The relatively few specimens preserved in shale have provided good imprints of the surface sculpture. The limestone specimens are often considerably recrystallized preventing the preservation of the minute internal structures.

The preservation of the fine structural details varies in the material examined. In general it seems that specimens from Ringerike, Hadeland, and the Mjøsa areas are best for detailed studies. The good preservation of structural details is to a large extent dependent on the presence of fine-grained pyrite, as in well-preserved specimens of *Tretaspis* (Størmer 1930). The outer surface sculpture of the

Chasmopinae is mostly provided with various kinds of prominent tubercles or pustules. Since the inner surface is usually smooth, exoskeletons almost always split off along the inner surface leaving the outer surface unexposed. Most published illustrations of chasmopids are of internal moulds. The outer sculptured surface might occasionally be seen in weathered counterparts. The external surface in limestone specimens has to be studied in thin sections.

Most of the photographs of the surfaces of specimens or casts shown on the reproduced photographs were made from material covered with 'opaque' and ammonium chloride. All specimens and thin sections, with the exception of a few from British Museum (BM) and the Riksmuseum in Stockholm (RMS), belong to Paleontological Museum (PMO) of the University of Oslo.

LAMINATION OF EXOSKELETON

Microstructure of the trilobite exoskeleton has been much studied recently (Miller 1975; Osmolska 1975; Teigler and Towe 1975; Miller 1976, Dalingwater and Miller 1977). The recent results have been based mainly on Ordovician asaphids and Devonian phacopids. The structures studied mainly comprise the lamination of the exoskeleton, the surface sculpture, and the associating canals or ducts.

Among recent arthropods the cuticles of insects and decapod crustaceans are the best known. Although the arthropods have much in common, a complete conformity in structures is not present. According to current terminology the following units might be distinguished in the exoskeleton: (1) A very thin (around 4 μm) external epicuticle with very little or no chitin, (2) a thick procuticle, containing chitin, comprising: (2a) an outer hard and rigid exocuticle resulting from an impregnation by quinotanned proteins (in crustaceans and diplopods by calcareous substances), and (2b) an inner, more flexible, endocuticle. Dennell (1960, p. 456) divides the exoskeleton into an epicuticle and an endocuticle (which involves a different meaning of the latter term). The endocuticle comprises an outermost pigmented layer, a middle calcified layer, and lower uncalcified layer above the epidermis.

In trilobites the textural subdivisions of the exoskeleton has, among others, been described and discussed by Cayeux (1916), Størmer (1930), and more recently by Dalingwater (1973), Teigler and Towe (1975), and Dalingwater and Miller (1977). Teigler and Towe distinguished two layers in most of the species they examined. (1) a thin (20–30 μm) outer pigmented layer which might be prismatic in structure and is supposed to be composed of calcium phosphate, (2) a principal layer composed of calcium carbonate. In *Tretaspis* Størmer (1930, pl. 12, fig. 1) described a thin (20 μm) external pigment layer and a similar structure was noticed by Kielan (1954, p. 41). However, Miller (in Dalingwater 1973, p. 836) interpreted the pigment layer as a dense micritic envelope due to attack by foreign organisms. The variation in thickness might to some extent support this view, but the pigment layer seems to be confined to the outer surface only. Micritic envelopes would be expected to occur on both sides of fragments of the exoskeleton. In *Asaphus raniceps* Dalingwater and Miller (1977, p. 24, text-fig. 2) have been able to distinguish a principal layer comprising three laminate zones below a thin outermost layer. This outer layer would correspond to what has been described as the prismatic layer. The four units of the exoskeleton which we recognize are: (1) outer prismatic layer, (2) outer laminate zone, (3) central laminate zone, (4) inner laminate zone.

The thickness of the prismatic layer is not determined by the authors mentioned, but the outer laminate zone comprises up to one-fifth of the total thickness of the cuticle (less in the cephalon). The narrow laminar units of this zone are around 5 μm thick. The central and most prominent zone (50–70 μm) with 4–5 μm wide laminar units occupies around three-fifths of the total thickness. The zone grades into the relatively thin inner laminate zone, which has narrow laminar units similar to those in the outer zone, and is variable in thickness.

1. Prismatic layer

In most specimens examined this thin outermost layer is not preserved, but we can see this layer in *Phacops granulatus* and a few chasmopinids. One of the reasons for the lack of preservation of the prismatic layer is probably due to the perforation of the layer by Osmolska cavities just below the

prismatic layer. The prismatic layer and half of the layer with the cavities tends to break off at this level (text-fig. 6c). In a well-preserved specimen of *Toxochasmops* sp. from the Hamar District (Pl. 29, fig. 7a, b; text-fig. 9a-c) a thin (7–8 μm) layer outside the level with the Osmolska cavities, represents the prismatic layer. Traces of an outermost thin (5–6 μm) layer are seen in a thin section of *Chasmops* sp. nov. D (Pl. 29, fig. 2). The layer seems to be partly penetrated by the upper part of some of the Osmolska cavities.

In the *Phacops* specimens figured by Dalingwater (1973, pl. 109, fig. 2), Osmolska (1975, pl. 1, figs. 11–13), and Miller (1976, pl. 2, figs. 3, 4) the outer prismatic layer seems to have been completely worn off, possibly during the preparation of the specimens. The thin sections of *P. granulatus* shown here are better preserved and clearly show the prismatic layer (Pl. 30, figs. 3b–7; Pl. 31, figs. 1a–4; text-fig. 5a–e). The SEM photographs in particular show the outermost layer with the prisms (Pl. 34, figs. 1a, b, 7a, b). The thickness of the prismatic layer is about 8–10 μm , the exposed sides of the prisms about 2 μm . It is not possible to decide whether or not the layer is penetrated by minute canals ascending from below.

2. The outer laminate zone

In *Tretaspis* (Størmer 1930, pl. 12, fig. 1) this zone might be represented by a 20 μm -thick pigmented layer comprising about one-sixth to one-seventh of the total thickness of the exoskeleton. A relatively thin outer laminate zone seems also to be characteristic of the Chasmopinae. In a well-preserved large specimen of *Toxochasmops extensus extensus* (Pl. 25, fig. 1a, b), the outer laminate zone has a thickness of 30–40 μm representing about one-tenth of the exoskeleton. However, the lamination of the zone is not preserved and the boundary towards the central zone is not distinct. Fine lamellar units are only indicated in the tubercles (Pl. 25, figs. 3, 5a, b; Pl. 28, figs. 1, 2, 4a, b, 6), where they appear as sloping lamellae parallel to the outer surface of the lobes and cones. The distance between these laminae is only about 5 μm . The lamination of the tubercles might form a continuation of laminae of the remaining zone. In *C.* sp. nov. A (Pl. 25, fig. 5a, b; Pl. 28, figs. 4b, 5b) the lamination of the tubercles and their bases indicate that the outer laminate zone was relatively thicker than in *Toxochasmops*, comprising as much as almost half the thickness of the exoskeleton.

In *P. granulatus* zonation of the exoskeleton is normally not clear (Pl. 30, figs. 1a–2b; Pl. 31, fig. 3). The light zone above the tubules in the composite tubercles may belong to an outer (laminate) zone. In one of the SEM photographs (Pl. 34, fig. 3) an outer zone, 80 μm wide, is marked off from the rest of the exoskeleton. Traces of zigzag or parabolic structures are faintly indicated. In Recent decapod crustacea Mutvei (1974, fig. 1) has demonstrated vertical lamellae with a parabolic cross-section, connecting two horizontal lamellae of the exoskeleton. Towe (1978) notes the apparent lack of such structures in trilobites. Towe has suggested to me that the present structures are impressions of rhombohedral calcite crystals rather than primary parabolic structures.

3. The central laminate zone

The prominent laminar units of this zone are shown in the large specimen of *T. extensus extensus* (Pl. 25, fig. 1a, b, also Pl. 25, fig. 4). The laminar units consist of very thin (a few μm thick) laminae and much thicker (20–30 μm) interlaminae about seven in number. The outermost laminar unit is thinner than the rest and might represent a transition to the outer laminate zone. The central zone grades without any distinct boundary into the inner laminate zone. The thickness of the central zone in the specimens mentioned is about 220 μm which amounts to two-thirds the thickness of the exoskeleton. A thin section across the gena of the same subspecies (Pl. 25, fig. 2a, b) preserves the laminate structure in two small patches only. It is interesting that these patches occur just below small depressed smooth areas without tubercles or Osmolska cavities. The smooth depressed areas are evidently the genal muscle scars described below. It is possible that the absence of canals through these scars and the possible presence of some special organic compound in connection with the muscle fibrils (tonofibrils), might have caused the favourable preservation of the lamellar structure. The lamellar units tend to form dark and light bands (Pl. 25, fig. 2a) rather than thin laminae and

thick interlaminae as in Plate 25, fig. 1a. The structures resemble those described by Dalingwater and Miller (1977, text-fig. 2) in *A. raniceps* and in *Tretaspis seticornis* by Størmer (1930, pl. 12, fig. 1; text-fig. 41b). In the first species the number of laminar units is four to five, in the latter apparently seven.

4. The inner laminate zone

All three laminate zones are not preserved at the same time, usually only one zone is well preserved while the details of the other are evidently obliterated by recrystallization. A recrystallization of the inner zone is demonstrated in *Tretaspis* (Størmer 1930, pl. 12, fig. 4) and indicated in polarized light in *Chasmops* sp. nov. A (Pl. 25, fig. 5b). The lamination of the zone is demonstrated in *Toxochasmops extensus extensus* (Pl. 25, fig. 1a, b), in *T. extensus* subsp. nov. (Pl. 25, fig. 3) and in *C.* sp. nov. A (Pl. 25, fig. 5a, b). The lamellar units have a thickness of about 10 μm which is about half that of the central laminate zone. Around eight lamellar units seem to be present. The zone has a thickness of 90–110 μm in the *Toxochasmops* specimens and 90 μm in *Chasmops*, which comprises about one-third of the exoskeletal thickness. Since the inner part of the exoskeleton might be partly resorbed before molting, the thickness might be expected to vary.

In a thin section of *C. odini* from Estonia, a layering of the cephalic exoskeleton is indicated at the steep anterior border (Pl. 29, fig. 6). The laminar units are not very distinct and there seems to be a gradual transition between the central and inner (upper in section) more finely laminated zone. An outer zone is not marked off, but must have been thin. In the central zone the maximum thickness of the laminar units is 55 μm which is one-tenth the total thickness of the exoskeleton at this place. An inner zone separated from the central zone is faintly indicated in some of the SEM sections of *P. granulatus* (Pl. 34, figs. 4, 6).

Since Trinucleidae, Asaphidae, and Chasmopidae are not closely related a largely common type of structure of the exoskeleton in trilobites is suggested. As pointed out by Dalingwater and Miller (1977, p. 30, pl. 10, fig. 4) and by Størmer (1930, p. 99, text-fig. 41) the structures observed are similar to those of the exoskeleton in decapod crustaceans. However, the similarities do not need to imply any closer phylogenetic relationships.

EXPLANATION OF PLATE 25

- Figs. 1a, b, 2a, b. *Toxochasmops extensus extensus* (Boeck, 1838). 1a, perpendicular section of cephalic exoskeleton; 1b in crossed nicols. Lamination of thin outer laminate zone not preserved. 4b δ , E. Rauskjær, Asker, PMO 94416, $\times 100$. 2a, b, section across the gena near the eye. Dark colour due to tonofibrillae in exoskeleton below genal depressions. Tubercles of granule type and Osmolska cavities on outer surface between depressions. 4b δ , E. Rauskjær, Asker, PMO 94416, 2a $\times 50$, 2b $\times 100$.
- Fig. 3. *Chasmops* sp. nov. A. Perpendicular section of cephalic exoskeleton showing tubercles of granule type with 'christmas-tree' lamination and laminated inner zone. 4a, Vollen, Asker, PMO 94398, $\times 104$.
- Fig. 4. *Toxochasmops extensus* subsp. nov. Perpendicular section across lateral (?) border, either dorsal skeleton or doublure. Pyrite impregnation. Light narrow layer at inner border. 4b γ , Vestbråten, Røyse, Ringerike, PMO 69349, $\times 170$.
- Fig. 5a, b. *Chasmops* sp. nov. A. Perpendicular section of cone type of tubercle with 'christmas-tree' lamination. Central canal not in section; b, crossed nicols distinguishing dark inner laminate zone. 4a β , Vollen, Asker, PMO 94398, $\times 104$.

clz = central laminate zone, *gede* = genal depression, *gtu* = granule type of smooth tubercle, *ilz* = inner laminate zone, *Osc* = Osmolska cavity.



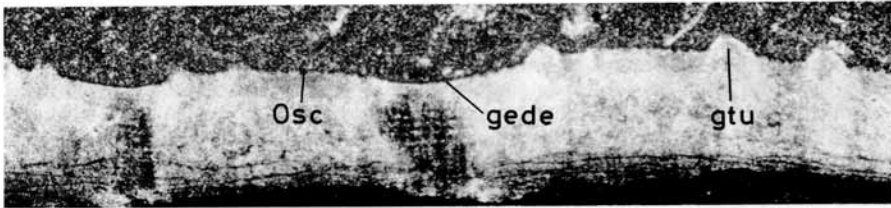
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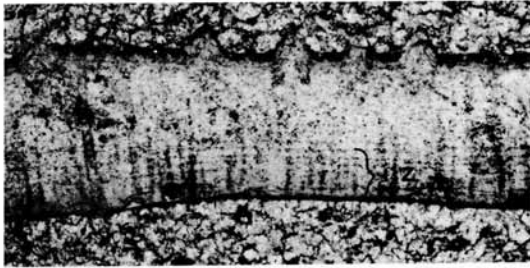
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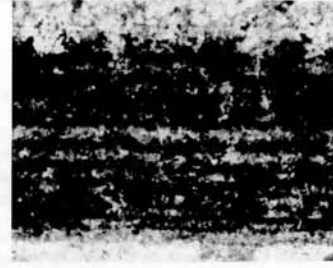
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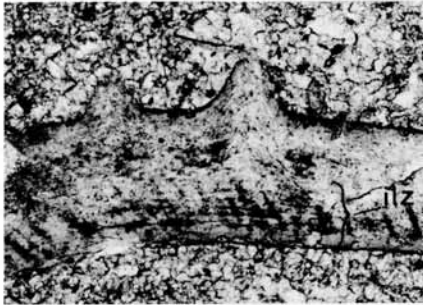
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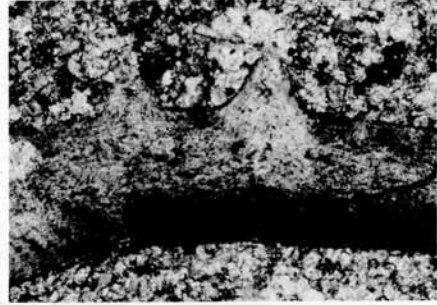
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4



5a



5b

STØRMER, trilobite microstructure

TUBERCLES AND ASSOCIATED INTERNAL STRUCTURES

In Recent arthropods the external solid surface is usually provided with various kinds of pustules, tubercles, scales, and spines as well as numerous perforations leading into canals through the exoskeleton. However, even in Recent forms the function of the various structures are little known (Grassé 1975).

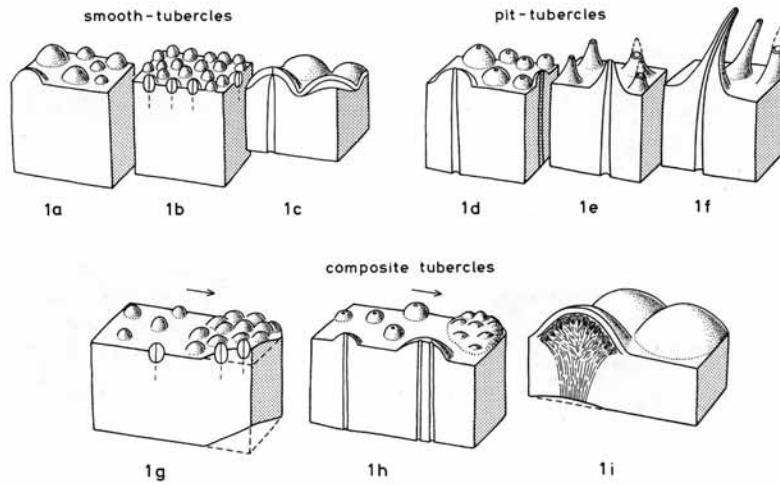
Terminology. Among the various types of sculptural elements, the tubercles or pustules are the most common in trilobites. Following the current practice the term tubercle is applied although the term pustule might seem more appropriate in several cases. Segury (1967) defines the term tubercle as a round lobe of variable size protruding from some part of the body or from an organ or from a duct. According to this definition the term tubercle comprises many different structures and functions. Kennaugh (1968) uses the term for several different structures, evidently with different functions, in three species of Ricinulei among Recent arachnids. In describing the sculpture or ornamentation in trilobites Harrington, Moore, and Stubblefield (1959) use the term tubercle in a broad morphological sense. Because of the particular internal structures of the large tubercles in species of *Phacops*, Miller (1976) suggests the term 'pseudotubercle' for this type of tubercle. I agree that this type of tubercle is unique, but since the morphology of the tubercles is so important in taxonomic descriptions of trilobites, I prefer to use the general term tubercle also for the special tubercles in *Phacops*.

The following morphological types of tubercles are distinguished here.

1. *Smooth tubercle.* Circular to subcircular discrete lobe without discernable apical pit or pits. Dimensions small to large.
 - Ordinary type (text-fig. 1a). Circular tubercle or lobe. Small to medium size.
 - Granule type (text-fig. 1b). Small circular hemispheric tubercle, convex at the top. Often appearing in great numbers forming a continuous granulate surface. Small size. Height 35-45 μm , width at base 70-80 μm .
 - Low convex type (text-fig. 1c). Circular convex, mostly low, tubercle. Medium to large size.
2. *Pitted tubercle.* Circular discrete lobe of various shape with apical pit. Small to medium size.
 - Ordinary type (text-fig. 1d). Lobe-shaped mostly hemispheric tubercle. Small to medium size.
 - Cone type (text-fig. 1e). High cone-shaped tubercle with upper part often broken off. Medium size.
 - Spine type (text-fig. 1f). Spine- or thorn-like tubercle. Small to large size.
3. *Composite tubercle.* Discrete or less discrete, mostly circular lobe or mound developing into flat pustule with steeper sides. Medium to very large size.
 - Fused smooth tubercle type (text-fig. 1g). Circular lobe composed of more or less fused smooth tubercles of granule type often appearing as a dome. Medium to large size.
 - Fused pit-tubercle type (text-fig. 1h). Circular lobe composed of more or less completely fused pit-tubercles of ordinary type. Small to medium size.
 - Phacopid type (text-fig. 1i). 'Pseudotubercle' of Miller (1976). Circular to subcircular lobe, convex or flattened with steeper borders. Indications of fine lateral apertures might be distinguished. Large to very large size.

On the *inner* surface of the cephalic exoskeleton tubercles in the shape of calluses or pads may be present, as described later. The terms and definitions mentioned above are based on the external morphology only. The internal structures present additional information on the various types of tubercles, which bear on their possible functions. Many transitional stages exist between the different types of tubercles, but the proposed classification should prove useful both to morphological and taxonomic studies.

Highly sculptured specimens with cone and spine tubercles have to be studied in thin section, but in some cases casts of counterparts demonstrate the sculpture (Pl. 27, fig. 6). Where the outer surface is covered by closely packed low tubercles the details can be exposed (Pl. 26, figs. 1a, b, 4a, b; Pl. 27, figs. 1-5; Pl. 32, figs. 4, 7, 9, 10; Pl. 33, figs. 1, 4). Whether or not the external surface of the exoskeleton is observed often depends on the degree of external spinosity.



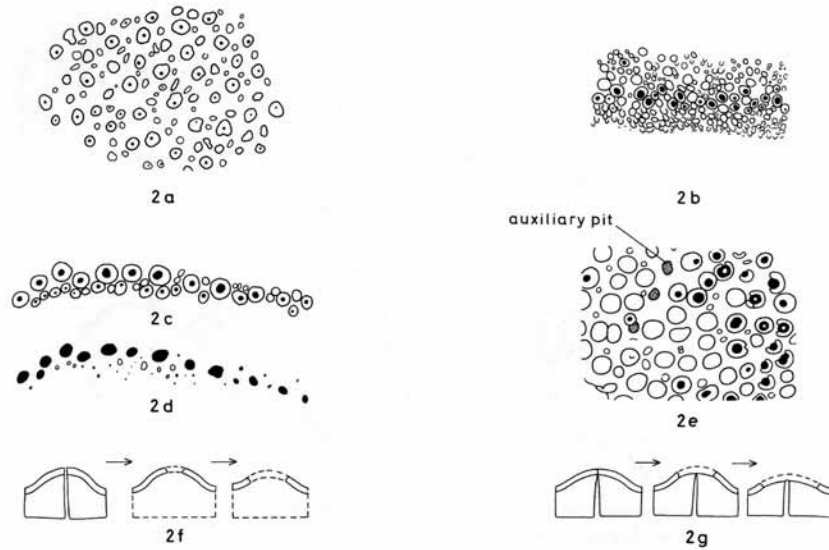
TEXT-FIG. 1. Diagrams of tubercles and spines on the cephalic exoskeleton: *a*, smooth tubercle of ordinary type; *b*, granule type with thin vertical canal preserved in upper onion-shaped portion only; *c*, low convex type, probably with a very thin central canal through upper layer and wide canal below; *d*, pitted tubercle of ordinary type with central canal, widening downwards; *e*, cone type, often with upper part broken off; *f*, spine type, often broken off; *g*, composite tubercle of fused smooth tubercle type. Arrow indicates transition from single to composite tubercle; *h*, fused pit-tubercle type. Arrow indicates transition from single to composite tubercles. *i*, Phacopid type.

Smooth tubercles

Granule type. These small tubercles have been studied in detail in *T. extensus extensus* and *T. extensus* subsp. nov. where they are very common. On exposed surfaces (Pl. 27, figs. 1, 2*a, b, 5*; Pl. 32, figs. 7, 9, 10) the tubercles appear as convex, more or less hemispherical nodes. This form is characteristic of the granules surrounding the lenses of schizochral eyes in many phacopid species. In thin sections (Pl. 25, figs. 2*a, 3*; Pl. 28, figs. 1, 2, 3) the upper part is convex, the lower part may form a part of a short cone (text-fig. 1*b*).

The height of the granule tubercle in *T. extensus extensus* and *T. extensus* subsp. nov. is around 35–45 μm . The tubercle is pierced by a central canal with a diameter around 2 μm (Pl. 28, figs. 1, 2). A cross-section of the duct is visible in one section (Pl. 28, fig. 3). A small opening at the summit is indicated only in thin section, hence its classification with the smooth group. Below the surface the granule tubercle is extended into an onion-shaped sac-like structure (Pl. 28, figs. 1, 2), distinguished in crossed polars (Pl. 28, fig. 2) by its lighter colour than the surrounding exoskeleton. The sack has radially sloping laminae forming in section a 'Christmas tree structure'. As noted above, the laminae might represent the outer laminate zone of the exoskeleton. The central canal does not continue further through the exoskeleton than the sac-like structure.

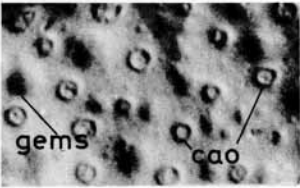
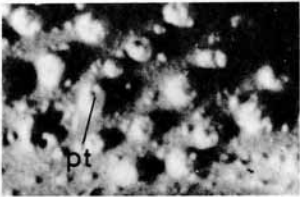
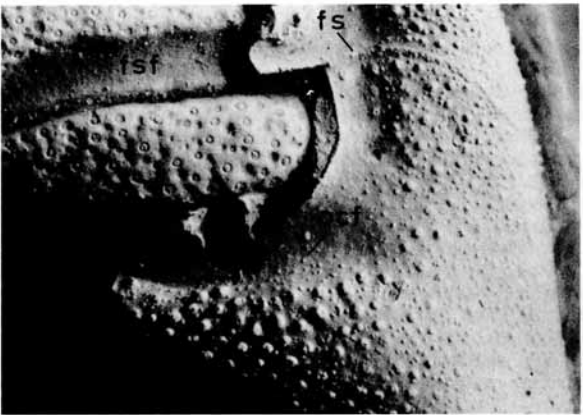
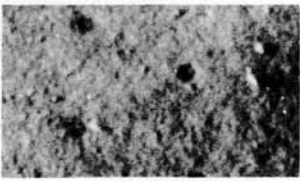
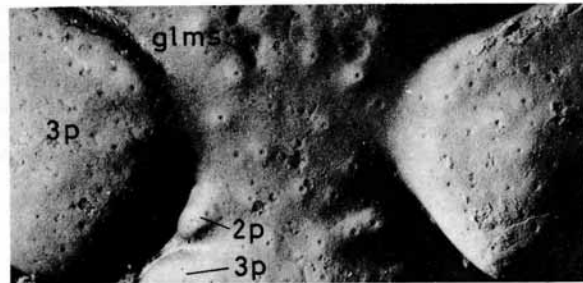
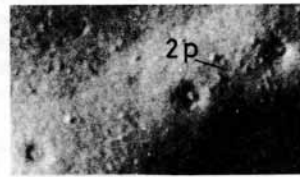
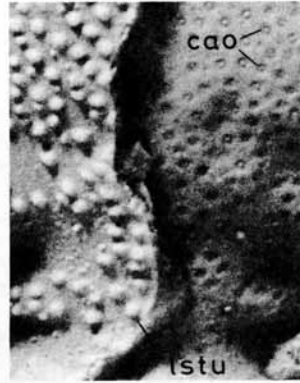
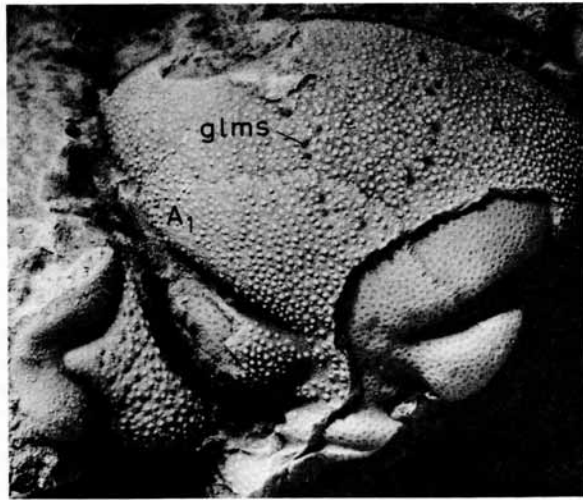
Low convex type. According to the present definition, this type occurs in *Chasmops* sp. nov. B (Pl. 26, fig. 1*a, b*; Pl. 32, fig. 4). The size of the relatively low tubercles varies with the size of the specimen, from about 130 μm to about 230 μm . In between these tubercles smaller ones of the granule type often occur. Some of the larger tubercles are partly abraded or worn off as shown also in text-fig. 2*e*. They vary from a convex surface or with a small opening at the summit, to one with a broad crater-like



TEXT-FIG. 2. Preservation of tubercles: *a*, Pitted tubercles of ordinary type, $\times 15$, from glabella of *Flexicalymene*; *b*, tubercles partly abraded at the apex, $\times 15$, from border of hypostoma of *Holia*; *c*, pit-tubercles, $\times 20$, from border of pygidium of *Flexicalymene*; *d*, large 'openings', $\times 20$, interior view of same silicified pygidium as in fig. 2*c*. The middle and inner zone were probably not silicified and therefore not preserved (Fig. 2*a*, *c*, *d* are based on Pl. 10, fig. 1; Pl. 9, figs. 15, 16 in Evitt and Whittington, 1953, fig. 2*b* on Pl. 21, fig. 5 in Whittington and Evitt, 1954); *e*, smooth tubercles of low convex type displaying various stages of abrasion, $\times 8.2$, from glabella of *Chasmops* (Pl. 32, fig. 4); *f*, diagram of presumed abrasion of pit-tubercles in *Flexicalymene*; *g*, the same in *Chasmops*.

EXPLANATION OF PLATE 26

- Fig. 1*a*, *b*. *Chasmops* sp. nov. B. *a*, glabella with fixigena on left side. Sculptured outer surface with glabellar muscle scars (auxiliary pits) removed posterolaterally exposing impressions of canal openings on internal mould, $\times 9$; *b*, detail showing smooth tubercles of low convex type to the left and impressions of canal openings on the internal mould to the right, $\times 20$. 4*b* α (?) Tønnerud, Hadeland, PMO 57698.
- Figs. 2*a*, *b*, 3. *Toxochasmops extensus extensus* (Boeck, 1838). *a*, internal mould of median portion of glabella, cephalic length = 21 mm. In front impressions of a pair of calluses serving as muscule apodemes. Elsewhere impressions of canal openings, $\times 3$; *b*, details of impressions of canal openings, $\times 25$. 4*b* δ (16-10 mm below 4*c*), Ranskjær, Asker, PMO 94410, $\times 25$. 3, larger specimen from same locality (length of cephalon = 31 mm). Details of impressions of canal openings. PMO 94411, $\times 25$.
- Fig. 4*a*-*c*. *Chasmops* sp. nov. C. *a*, posterolateral angle of cephalon with facial suture in facial suture furrow. Upper left internal mould exposed. Outer surface, except in occipital and marginal furrows, provided with different sizes of pit-tubercles of ordinary type, $\times 9$; *b*, details of pit-tubercles (photographed upside down), $\times 25$; *c*, impressions of canal openings with dark genal muscle scars in between, $\times 25$. 4*b* α , Bratterud, Røyse, Ringerike, PMO 68615.
- A₁-A₂ = location of thin section Pl. 28, figs. 4, 5. *cao* = canal opening, *fs* = facial suture, *fsf* = facial suture furrow, *gems* = genal muscle scar, *gms* = glabellar muscle scar (auxiliary pit), *lp-3p* = lateral glabellar lobes, *ocf* = occipital furrow, *pt* = apical pit, *lstu* = smooth low convex tubercle.



STØRMER, trilobite sculpture

appearance. Crater-like forms are shown on Plate 32, figure 4. These different appearances are due to wear.

In the trilobites *Holia* and *Flexicalymene* Whittington and Evitt (1954, pl. 21, fig. 5) and Evitt and Whittington (1953, pl. 9, figs. 15, 16) found openings along the border of the cephalon and hypostoma which they interpreted as larger perforations surrounded by raised rims. The perforations were supposed to be the site of hairs of setae. Since 'craters' and tubercles without openings appear side by side, as in our Plate 32, figure 4, I interpret the American 'sockets' as due to abrasion. However, there is one difference. While in *Chasmops* sp. nov. B an outer thin layer is obviously abraded leaving smooth convex surface below, the wide openings in *Holia* pass right through the preserved exoskeleton and appear (text-fig. 2c, d) to be wider on the inner than on the outer surface. It seems possible that only the outer layer of the exoskeleton might have been silicified. The large inner opening would then correspond to the concave inside of the outer layer (text-fig. 2f).

In well-preserved specimens of *Chasmops* sp. nov. B showing the tuberculated outer surface and the internal mould side by side (Pl. 26, fig. 1a, b), there are impressions of prominent canals on the internal mould while the convex tubercles on the outside show no signs of canal openings. The wider canals belong to the deeper portion of the exoskeleton and become very narrow towards the outer surface. A thin section across the frontal lobe of the same specimen (Pl. 29, figs. 4, 5) clearly shows the prominent vertical canals with a diameter of around 24 μm through most of the thickness of the exoskeleton. One canal (fig. 5, left) seems to reach the outer surface. However, in another part of the section (fig. 4, right) the outermost short portion of the canals seems to be quite narrow, such as in the granule type of the smooth tubercle where the tiny apical aperture is not visible on exposed surfaces. The outer portion of the tubercle may have been subject to variable abrasion. The low convex tubercle of *C.* sp. nov. B has an apparently smooth surface, with a thin central canal running downwards through an outer layer which might correspond to the outer laminate zone. We do not know whether an outermost prismatic layer was penetrated by the fine canal. At the base of the presumed outer laminate zone the thin canal rapidly widens into a prominent canal running downwards through the central and inner laminate zones, flaring slightly at the inner surface. As shown below, the structures indicated in the reconstruction (text-fig. 1c) somewhat resemble certain campanular organs in Recent arthropods (text-fig. 7b).

EXPLANATION OF PLATE 27

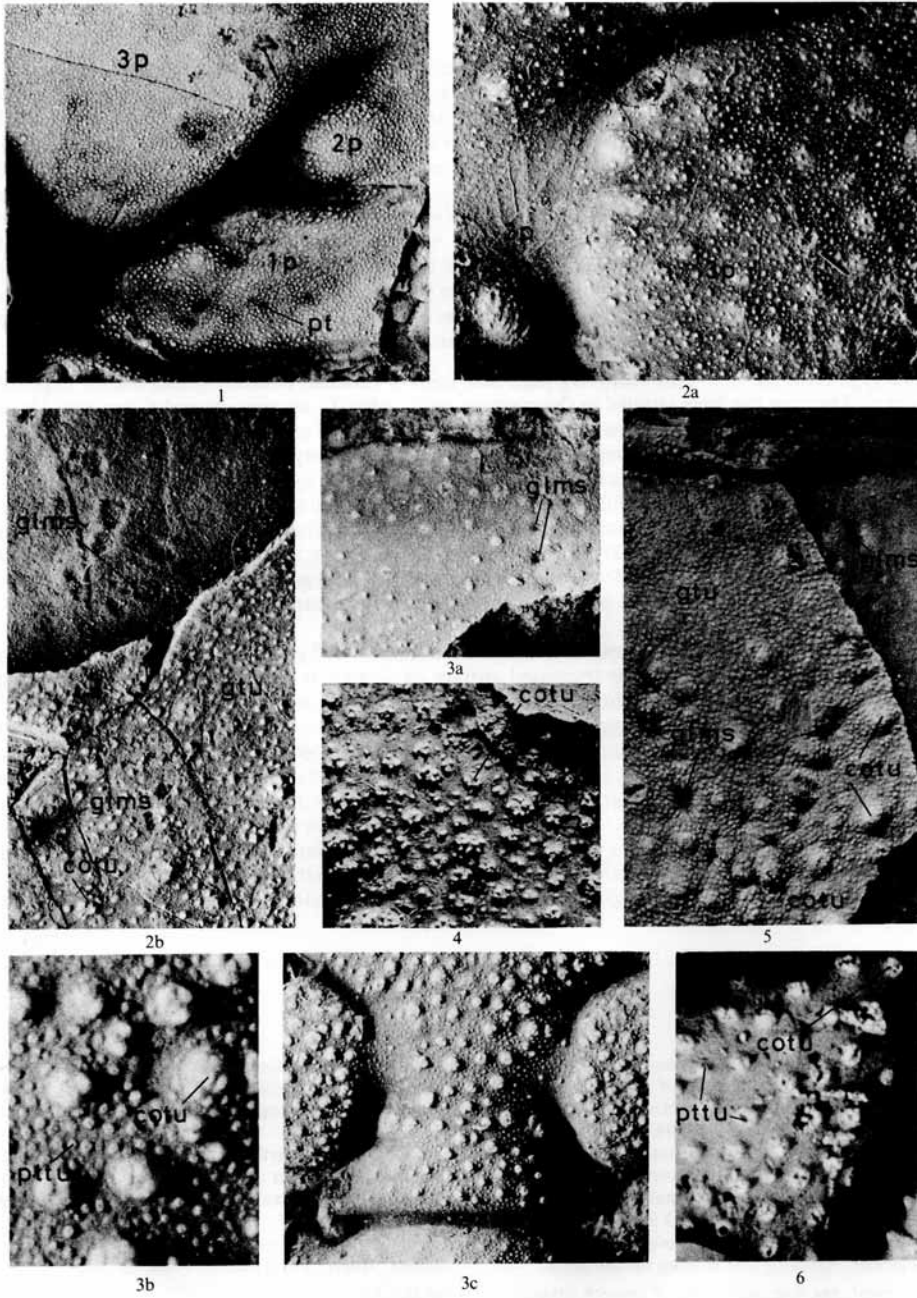
Fig. 1. *Toxochasmops extensus* subsp. nov. 4by, Vestbråten, Røyse, Ringerike, PMO 69345, $\times 9$. Posterior left portion of glabella, granulation consisting of close-set smooth tubercles of granule type. A few larger pits might be sockets of setae.

Figs. 2a, b, 5. *Toxochasmops extensus extensus* (Boeck, 1838). 2a, detail showing small glabellar lateral lobe 2p and parts of large lateral lobe 3p. Lobes covered with granule type of smooth tubercles which also cover the low less discrete composite tubercles; 2b, front, internal mould with imprints of calluses with muscle scars, further back, outer surface with corresponding muscle scars between granules and composite tubercles. 4b β - γ , Road section, Volla, Gran, Hadeland, PMO 68434, $\times 9$. 5, anterior median portion of glabella with row of pits representing muscle scars on the outer surface and pits on the internal moulds representing calluses on the inner surface. Granules and composite tubercles, 4b δ , PMO 105705, $\times 9$.

Figs. 3a-c, 4. *Toxochasmops* sp. nov. 3a, left anterior portion of glabella with two sizes of tubercles, some of the larger ones with one or two pits; 3b, posterior portion of glabella with discrete composite pit-tubercles surrounded by small ordinary pit-tubercles; 3c, details of small ordinary pit-tubercles between discrete composite pit-tubercles. 4by, PMO 20650, 3a, 3c $\times 9$, 3b $\times 29$. 4, less discrete composite tubercles with distinct elements, but without pits. 4by, Vestbråten, Røyse, Ringerike, PMO 68615, $\times 6$.

Fig. 6. *Chasmops* sp. nov. A. Cast of right glabellar lobe, with ordinary pit-tubercles (perhaps some broken tubercles of the cone type) and simple composite pit-tubercles. 4bz, Road to Tangen, Semsvann, Asker, PMO 94403, $\times 19$.

cotu = composite pit-tubercle, gtu = granule tubercle, glms = glabellar muscle scar or auxiliary pit, 2p, 3p = second and third lateral glabellar lobes, pt = pit, pttu = pit tubercle.



STØRMER, trilobite sculpture

Pitted tubercles

Ordinary type (text-fig. 1d). The ordinary type of the pitted tubercle is seen in *Chasmops* sp. nov. C (Pl. 26, fig. 4a, b), in *C.* sp. nov. A (Pl. 27, fig. 6), and in *Toxochasmops* (Pl. 27, fig. 3c). As in *Flexicalymene* (text-fig. 2a) the size of the ordinary pit-tubercle varies considerably. The internal mould of *Chasmops* shows the shape, size, and distribution of the inner openings of the canals (Pl. 32, fig. 6). Most of the circular openings have a diameter of 20 μm , but other sizes also occur in accordance with the size of the tubercles on the outer surface (Pl. 26, fig. 4a-c). Since the pit on the apex of the tubercle is much smaller than the inner opening, a widening of the canals is present in this type of tubercle. One section of a small tubercle of *C.* sp. nov. A (Pl. 28, fig. 5a, b) might represent two small pitted tubercles of the ordinary type with their thick internal canal. In the Devonian *Trimerocephalus caecus* the large tubercles have a prominent central canal reaching the surface (Osmolska 1975, pl. 1, figs. 2, 9; Pl. 31, figs. 6, 7). There are diverging fine canals around the central canal, features which might indicate a relationship with the composite tubercle in *Phacops*.

Cone type (text-fig. 1e). This relatively high and narrow tubercle is rarely preserved on exposed surfaces. The type has been studied in thin sections of *C. odini*, *C.* sp. nov. A, and *C.* sp. nov. D. In practically all sections of these three species the cones are truncated more or less at the same level. For this reason I was first inclined to regard the truncation as a primary feature with the apical 'crater' serving as a socket of a conspicuous seta. In *C.* sp. nov. A (Pl. 28, figs. 4a, b, 5a, b) the truncation is distinct, with a wide, partly pyrite filled, central canal opening at the top. However, in one case (Pl. 28, fig. 4a, b, right) a more complete cone is preserved. A similar condition is found in a young specimen probably of *C. odini* (Pl. 29, fig. 8). Here some of the cones have a smaller apical aperture which evidently is not due to rupture. Transitions between the cone type and the ordinary type of pit-tubercle can occur. The small tubercles with the powerful central canals shown on Plate 28, figure 6a, b are of this type.

In *C. odini* (Pl. 29, fig. 3) the truncate cone tubercle measures 70 μm in height and 120–125 μm in width. The diameter of the upper truncated surface or 'crater' is 6–7 μm . In *C.* sp. nov. A the corresponding dimensions of height and width are 45 μm and 95 μm , 70 μm and 100 μm , 90 μm and 100 μm , 80 μm and 90 μm (Pl. 28, figs. 4a–5b). In *C.* sp. nov. D the respective dimensions are 50 μm and 70 μm (Pl. 29, fig. 2). The secondary truncation at the summit represents a large aperture. This is demonstrated in one section of *C.* sp. nov. A (Pl. 28, fig. 4a, b, left) where the walls of the tubercle continue above the pyrite-filled central canal. A sac-like formation, light in crossed nicols, is present below the tubercle, and reaches about half the way down the section (Pl. 25, fig. 5a, b; Pl. 28, figs. 4b, 5b). Both the sac and the tubercle have indications of narrow lamellar layers forming a 'christmas tree structure'. The dimension of the laminated sac might indicate a relatively thick outer laminate zone. The large central canal penetrating the cone and the exoskeleton below is well shown in thin sections

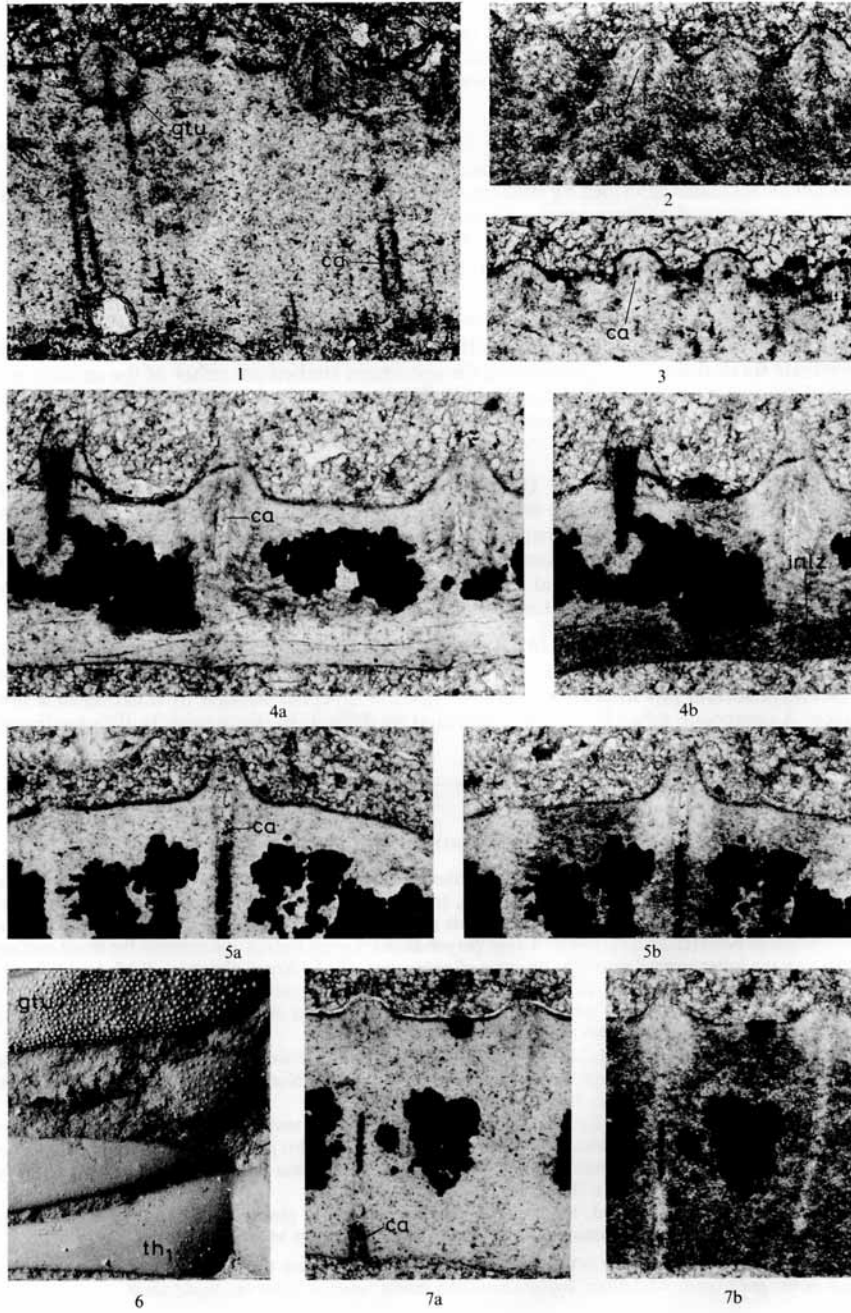
EXPLANATION OF PLATE 28

Figs. 1–3. *Toxochasmops extensus* subsp. nov. 1a, b, perpendicular; 1c, tangential sections of cephalic exoskeleton. Smooth tubercles of granule type. Tubercles pierced by fine central canal not continuing below onion-shaped body of tubercles. Wide canals evidently not opening through tubercles. 4b, Vestbråten, Røyse, Ringerike, PMO 68794, $\times 152$.

Figs. 4, 5, 7. *Chasmops* sp. nov. A. 4a, b, exoskeleton of cephalon partly pyritized. Pit-tubercles of cone type broken off except to right; 4b, crossed nicols indicating dark inner (lamine) zone. 5a, b, broken cone tubercle and central canal. 7a, b, to show internal openings of central canal of tubercle. 4b, Østre brygge, Nesøya, Asker, PMO 94384, $\times 148$.

Fig. 6. *Toxochasmops extensus extensus* (Boeck, 1838). Posterior portion of gena and pleura of first thoracic segment. Granulation lacking on the latter. 4b, Raudskjær, Asker, PMO 94412, $\times 90$.

ca = canal, gtu = granule type of smooth tubercle, th = 1st thoracic segment.



STØRMER, trilobite sculpture

of *C. odini* (Pl. 29, fig. 3). The diameter of the canal within the tubercle is about 30 μm , and at the inner surface of the exoskeleton it flares to 75 μm . The inner openings are very distinct and narrowing upwards of the tunnel may be directly observed (Pl. 32, fig. 5; Pl. 33, fig. 3). In *C. sp. nov.* A the canals have similar dimensions.

Spine type (text-fig. 1f). Like the cone type, these thorn-like extensions would not be preserved on exposed surfaces. They are beautifully demonstrated, however, in silicified trilobites, e.g. in *Ceratocephala laciniata* described by Whittington and Evitt (1954, pl. 9, fig. 2). The spine tubercle is evidently rare among the Chasmopinae. Only in a thin section of *Chasmops sp. nov.* D a small spine tubercle occurs close to the eye (Pl. 29, fig. 1). The curved spine has a length of 60 μm and width at the base of 35 μm . A central canal is indicated.

Composite tubercles and internal tubular organ

These large, often discrete, pustules or mounds are probably formed by a fusion of separate tubercles. The separate small tubercles or elements in the specimens studied are either of the smooth granule type or of the ordinary type of pitted tubercles. Distinct composite tubercles have been figured by Dean (1961, pl. 52, fig. 6) in '*Chasmops*', and by Campbell (1977, pl. 7, fig. 2b) in *Paciphacops* (*Paciphacops*) *raymondi* (Delo).

Fused smooth tubercle type (text-fig. 1g). This type is well demonstrated in Norwegian species of *Toxochasmops* where the tubercular elements are of the granule type. In *Toxochasmops extensus* the development of a composite tubercle from single-granule tubercles is shown on Plate 32, figure 9. We notice all transitions from a single tubercle, through a few fused tubercles, to a great number of close-set tubercles mounted on a dome. The dome has a characteristic shallow depression on the inner surface of the exoskeleton.

The fused pitted tubercle type (text-fig. 1h). A cast of a weathered specimen of *C. sp. nov.* A (Pl. 27, fig. 7) shows numerous pit-tubercles, most of them of the ordinary type. Some of the lobe-shaped smaller tubercles have several pits indicating simple composite tubercles formed by a fusion of a few pit-tubercles. A composite tubercle of this type would be difficult to distinguish in thin section where

EXPLANATION OF PLATE 29

Figs. 1, 2. *Chasmops sp. nov.* D. 1, perpendicular section close to eye. Various tubercles and canals.

To the right small spine type of pit-tubercle. 2, truncated cone tubercle, Osmolska cavities, and narrow outermost and innermost layer. Cyclocrinus beds (4b γ), Furuberget, Hamar District, PMO 21999, $\times 116$.

Fig. 3. *Chasmops odini* (Eichwald, 1840). Large perpendicular canals flaring out towards the inner surface and opening on the outer surface through tubercles of cone type. C₂, Kukruse, Estonia. B.M. In 5147/5, $\times 107$.

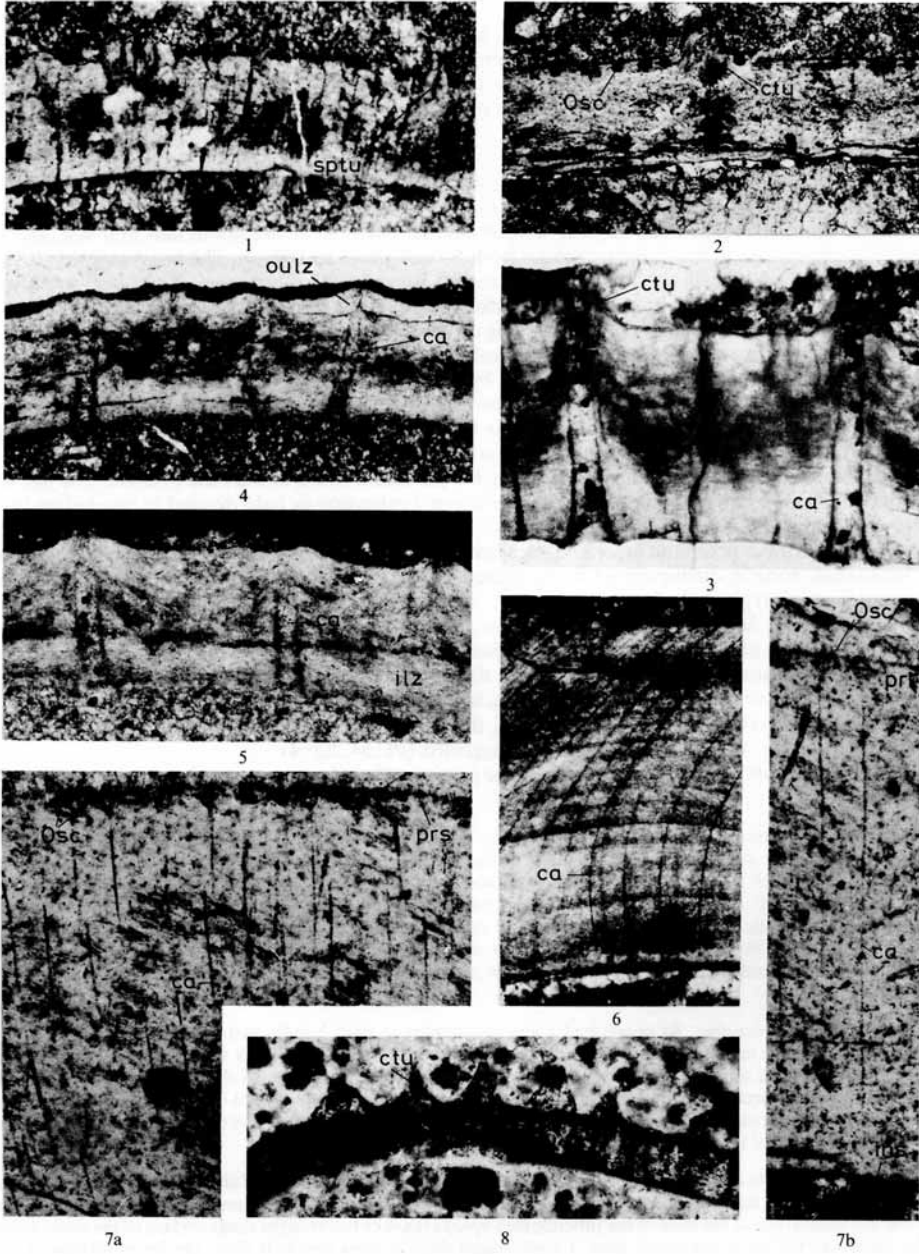
Figs. 4, 5. *Chasmops sp. nov.* B. Perpendicular sections through frontal lobe of glabella, A₁-A₂ in Pl. 26, fig. 1a. Outer laminate zone, which is mostly abraded, pierced by a very thin canal (fig. 4 right). 4b α (?), Tønnerud, Hadeland, PMO 57698, $\times 107$.

Fig. 6. *Chasmops odini* (Eichwald, 1840). Perpendicular section across the anterior doublure of cephalon. 8- μm -wide canals through the exoskeleton. In the section of the doublure the upper part represents the inside of the exoskeleton. C₂, Kukruse, Estonia. B.M. In 5147/5, $\times 107$.

Figs. 7a, b. '*Toxochasmops*' sp. Perpendicular sections through glabella showing traces of an outermost prismatic layer with Osmolska cavities just below. Each thin (1.5-2.0 μm) canal running upwards from the inner surface seems to be connected with one Osmolska cavity. Mjøsa limestone, 4b δ , Bergsvika, Helgøya, Hamar District, PMO 105704, $\times 183$.

Fig. 8. ?*Chasmops odini* (Eichwald, 1840). Perpendicular section of glabella of young specimen; unbroken pit-tubercles of cone type well-preserved. C₂, Kukruse, Estonia. B.M. In 5147/5, $\times 107$.

ctu = pit-tubercle of cone type, *ca* = canal, *sptu* = pit-tubercle of spine type, *ins* = inner surface, *ilz* = inner laminate zone, *prs* = prismatic layer, *osc* = Osmolska cavity, *oulz* = outer laminate zone.



STØRMER, trilobite cuticle microstructure

several canals rarely are sectioned in one plane. In *Toxochasmops* sp. nov. (Pl. 27, fig. 3a) the anterior portion of the glabella has separate pitted tubercles scattered on a finely granulated surface. Further back the surface is covered by clusters of tubercles forming composite tubercles (Pl. 27, fig. 3b, c). In another specimen (Pl. 27, fig. 4) the composite tubercles are less discrete but individual elements are clear.

Phacopid type (text-fig. 1i). Many authors have described the large globular tubercles on the glabella of various phacopid trilobites. In *Phacops rana africanus* Miller (1976) notices tubercles with diameters up to 2000 μm , while those described by Osmolska (1975) are about half that size, and in *Trimercephalus caecus* the diameter ranges from 500 μm down to 160 μm . The last dimension is less than the diameter of 250 μm found in the smooth tubercles of *C.* sp. nov. B. In well-preserved specimens of *Phacops* the surface of the tubercles appears to be smooth, but Campbell (1967, p. 27) found seven to eight small perforations in a ring on the flanks, and Miller (1976, p. 351) mentions the presence of pits with a diameter of 20 μm . Vertical thin sections of composite tubercles in *Phacops* and *Trimercephalus* have previously been figured by Dalingwater (1973), Osmolska (1975), and Miller (1976). The present specimens show several new structures in the outer portion of the exoskeleton. Plate 30, figures 1-8; Plate 31, figure 1a, b; text-figs. 3a-d, 5a-e, show the finer structures in normal and polarized light; SEM photographs are shown on Plate 34, figure 7a, b.

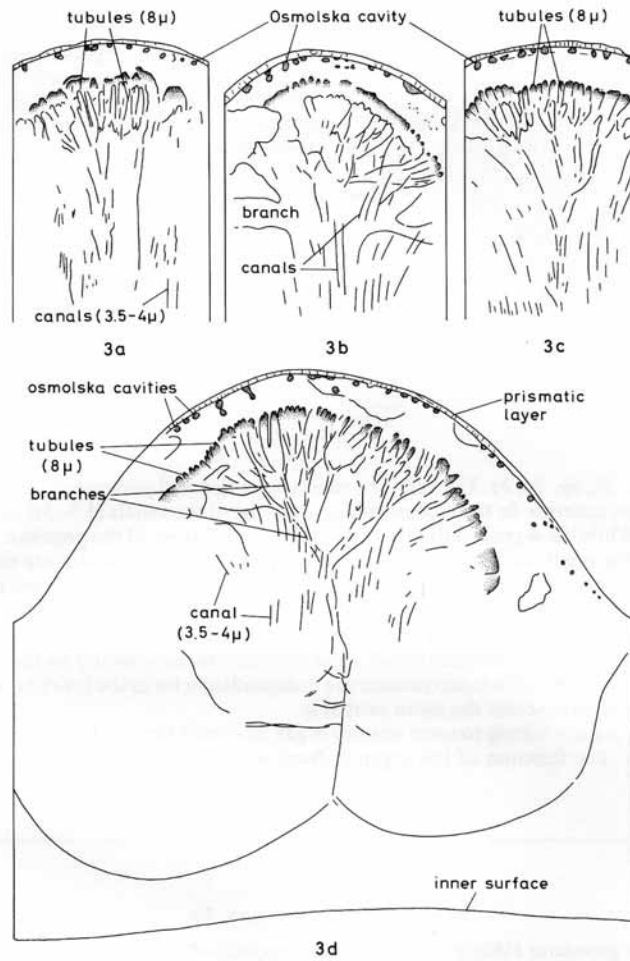
The convex tubercles have a height of about 300 μm and a width at the base of about 700 μm . In crossed nicols each tubercle has a light sac-like internal extension or halo divided in two halves by a dark vertical line (Pl. 30, figs. 1a-2b; text-fig. 4). In contrast to previously described specimens, ours show the outermost prismatic layer and the Osmolska cavities. Below the prismatic layer an outer, unlaminated, zone is distinguished by its lighter colour. The zone (including the layer with the Osmolska cavities) has a thickness of about 80-100 μm . The inner margin (Pl. 30, figs. 3a-7; Pl. 31, fig. 1a, b; text-fig. 3a-d) has numerous small notches or indentations with a diameter around 8 μm . The inner portion of the tubercle and the exoskeleton below are not divided into a central and inner zone. In crossed nicols (Pl. 30, figs. 1b, 2b) the darker inner portion below the 'light' sack or 'halo', might possibly have represented an inner zone, but since the darker colour also continues up to the outer surface between neighbouring tubercles, this seems less probable. In the SEM photographs, however, an inner, laminate zone is faintly suggested (Pl. 34, fig. 4).

In the tubercle and the exoskeleton below, the portion below the outer zone shows several different fine details:

Tubules with diameter about 8 μm . These cylindrical structures have blunt ends inserted into the notches at the inner surface of the outer zone. The direction of the straight tubules is normal to the surface. The closely packed tubules occur in vase-shaped bundles or 'bushes' which converge downwards into one unit or branch. The sections indicate that different bundles occur close behind each other so that the distal ends of the tubules cover more or less the whole internal surface of the outer zone. The dimensions of the bundles are largely the same which means that their bases are situated at about the same level. Assuming a fairly dense cover of tubules all over the outer surface of the inner portion of the tubercle, the number of tubules might have reached about 8000.

Diffuse internal branches. As mentioned above the tubules in each bundle unite at the base of the bundle forming one branch or stem. This is indicated in the specimens figured, although the branches are somewhat diffuse. Each branch apparently belongs to a system of bifurcating branches, as shown in the reconstruction (text-fig. 4). The bifurcation is indicated in crossed nicols particularly in one section (Pl. 31, fig. 1b; text-fig. 3d). A vertical section through the flank of one tubercle (Pl. 30, fig. 6; text-fig. 3b) shows traces of a broad basal stem from which a pair of thick horizontal bifurcating branches extend.

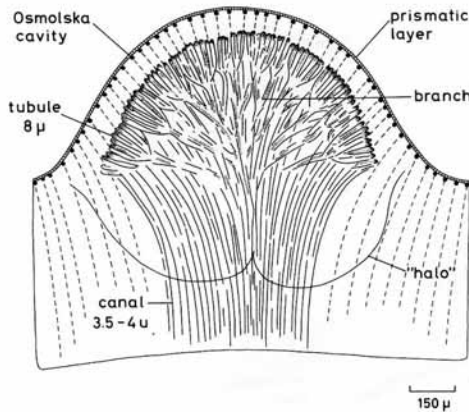
Distinct canals with a diameter of 3-4 μm . These densely packed canals are well shown in photographs taken by Osmolska (Pl. 31, fig. 5). Under high magnification each canal has a constant diameter. Below the tubercle the canals are vertical but at the base of the tubercle they spread fan-like towards the inner surface of the outer zone. The canals do not enter the outer zone. I have traced their courses upwards from the inner surface of the exoskeleton, but have not been able to trace their presence within the bundles of tubules. These canals have directions different from those of the branches described below. This is shown in the posterior portion of the



TEXT-FIG. 3. Perpendicular sections of composite tubercles in *Phacops granulatus* (Münster): *a* from Pl. 30, fig. 5, *b* from Pl. 30, fig. 6, *c* from Pl. 30, fig. 7, *d* from Pl. 30, fig. 3*a, b*; Pl. 31, fig. 1*a, b, b* with crossed nicols.

tubercles, where the canals are nearly vertical while the branches leading to the tubules are laterally directed (Pl. 30, figs. 1, 6; text-fig. 3*a, b*). Approaching the inner margin of the outer zone the tubules ($8\ \mu$) and the canals ($3\text{--}4\ \mu$) might have a common direction normal to the surface. The presence of the canals within the tubules have not been recognized.

Thus there are three different ducts penetrating the composite tubercle of the Phacopid type. In addition, a fourth type of duct or canal was evidently present leading to the Osmolska cavities, but except for certain very indistinct traces (Pl. 31, fig. 3) such canals have not been seen in the present material of *Phacops granulatus*. They appear to be present leading to the Osmolska cavities in



TEXT-FIG. 4. Reconstruction of composite tubercle in *Phacops granulatus* (Münster). The thin stippled canals from the Osmolska cavities are not demonstrated in the present specimens but suggested in *Toxochasmops* sp. (Pl. 29, fig. 7a, b).

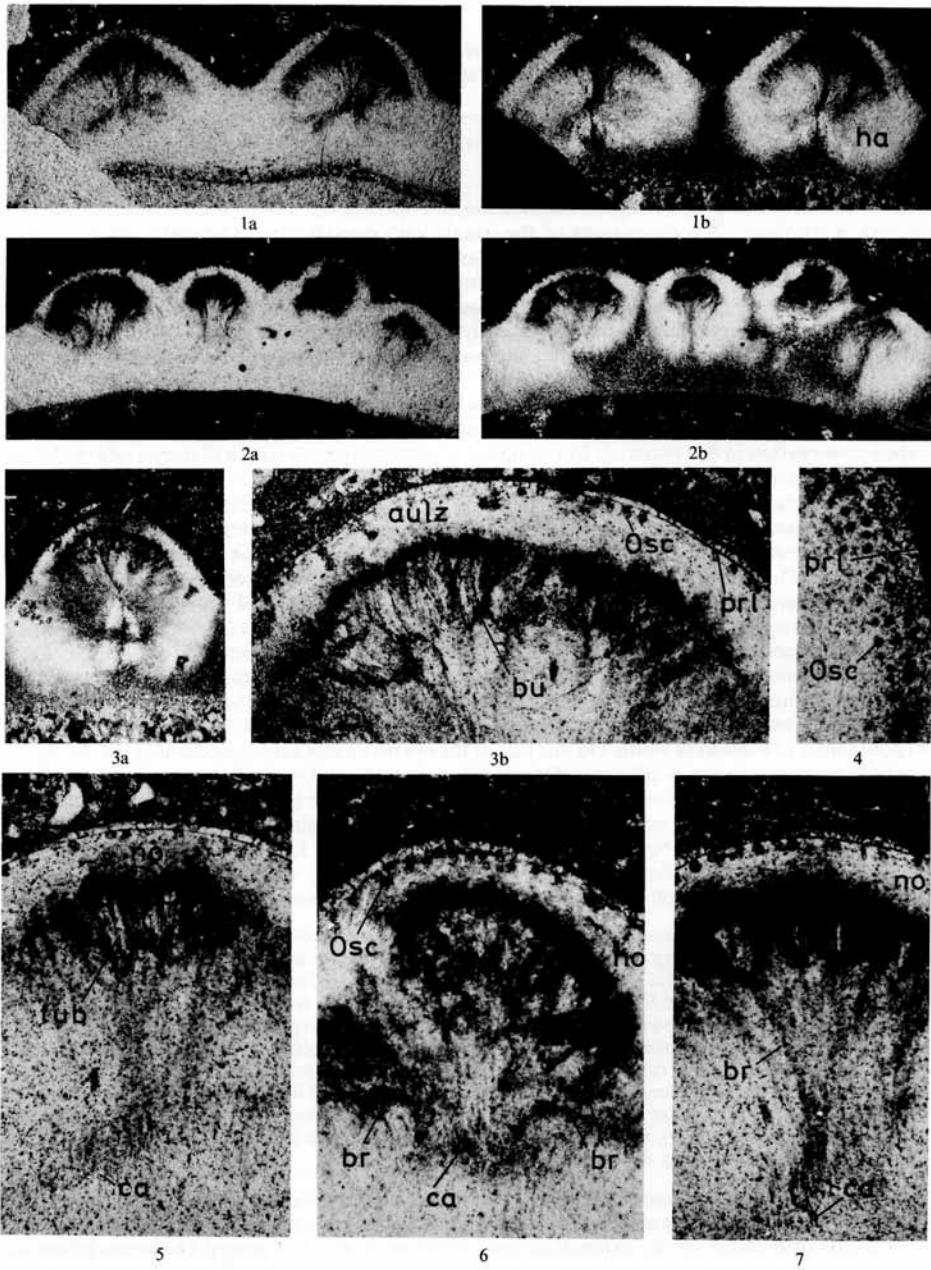
Toxochasmops (Pl. 29, fig. 7a, b). The very fine canals were not well preserved in the compact outer zone of the *Phacops* tubercle. In the reconstruction (text-fig. 4) the canals ($1.5-2.0\ \mu\text{m}$) are indicated by stippled lines. While the $4\text{-}\mu\text{m}$ canals distinctly cross the directions of the proximal portions of the diffuse branches, the relations between the $4\text{-}\mu\text{m}$ canals and the $8\text{-}\mu\text{m}$ tubules are not clear. In two cases the canals are seen to abut to the bundles of tubules. The canals have not been traced up to the lower boundary of the outer zone; this might, however, be due to lack of preservation. So either the $4\text{-}\mu\text{m}$ canals pass into the wider tubules of the bundles, the increasing width of the tubules being due to an internal branching of the canals into closely packed microtubules similar to the microtubules in Diptera (text-fig. 7f); or the canals and tubules run independently up to the lower border of the outer zone. The first alternative seems the more probable.

These unique structures belong to some sensory organ or organs for which the term *internal tubules organ* is suggested. The function of the organ is discussed below.

EXPLANATION OF PLATE 30

Figs. 1-7. *Phacops granulatus* (Münster, 1840). 1a, 2a, perpendicular sections of composite tubercles of phacopid type on the glabella, $\times 40$. 1b, 2b, the same in crossed nicols. 3a, b, tubercle in which the layer below the outer (laminar) zone is but slightly stained by iron oxide; 3a in crossed nicols indicates branching zone of tubules, $\times 40$; 3b, upper part of tubercle with prismatic layer above Osmolska cavities in the upper part of the outer (laminar) zone. At the base of the zone notches for the terminals of tubules ($8\ \mu\text{m}$) of the 'bush'-like bundles branching off at about the same level. Branches below the bundles faintly indicated below, $\times 100$. 4, tangential section of tubercle showing Osmolska cavities and prismatic layer, $\times 100$. 5, tubules ($8\ \mu\text{m}$) with finer canals ($4\ \mu\text{m}$) below bundles of tubules, $\times 100$. 6, perpendicular section through the flank of one tubercle. Traces of a diffuse broad stem with lateral branches. Fine canals crossing lateral branches, $\times 100$. 7, section showing prismatic layer with Osmolska cavities, and the notches with the inserted dark terminals of tubules branching off at about the same level. The common basic branches below the bundles are indicated as 'shadows', $\times 100$. Famennian of Poland.

br = branches below the bundles of tubules, bu = bundles of tubules, ca = canals ($4\ \mu\text{m}$), ha = 'halo', light base of tubercle, no = notches marking terminations of tubules, Osc = Osmolska cavity, outz = outer (laminar) zone, prl = prismatic layer, tub = tubule ($8\ \mu\text{m}$).



STÖRMER, *Phacops* tubercles

MICROSTRUCTURES NOT ASSOCIATED WITH LAMINATION
AND TUBERCLES

These structures comprise the vertical canals not connected with sculptural elements on the cuticular surfaces, and the small cavities just below the outer surface of the exoskeleton. Structures associated with muscle attachments are described below.

Canals. Vertical canals penetrating the exoskeleton and opening directly on the flat outer surface are common in trilobites. The dimensions of the canals vary considerably. Osmolska (1975, p. 202) noticed two size groups, one with a diameter of less than $2\mu\text{m}$ and another with a diameter of $10\text{--}30\mu\text{m}$. Miller (1976, p. 349) distinguished three groups with diameters of $5\text{--}10\mu\text{m}$, $15\text{--}20\mu\text{m}$ and $45\text{--}50\mu\text{m}$ respectively. However, Dalingwater and Miller (1977, p. 29) proved that the narrowest canals were about $1\mu\text{m}$ thick. Canals have recently been described by Campbell (1978). The present material comprises two main groups: fine, narrow canals up to $2\mu\text{m}$ wide, and larger canals with variable sizes.

The narrow canals have recently been studied by Dalingwater and Miller (1977) who thought they could be compared with the pore canals of Recent arthropod cuticles. The minute canals have usually escaped preservation in our material. But beautifully preserved canals with a diameter of $1.5\text{--}2.0\mu\text{m}$ are shown on *Toxochasmops* sp. from the Mjøsa Limestone (Pl. 29, fig. 7a, b; text-fig. 9a-c). Many of these are connected with the Osmolska cavities near the external surface. Similar narrow canals also occur in *Toxochasmops extensus extensus* (Pl. 32, fig. 2), and in *Chasmops* sp. nov. D (Pl. 29, fig. 1) which also shows larger canals. In *P. granulatus* the $4\mu\text{m}$ canals seem to occur in the exoskeleton between the large tubercles (Pl. 34, figs. 3, 5, 6, 8). They are usually $3\text{--}4\mu\text{m}$ wide, but in certain cases a corrosion or accretion of material seems to have taken place resulting in widths from $1.6\text{--}4.4\mu\text{m}$ (Pl. 34, figs. 4, 5, 6). Near the surface a peculiar radiation of a bundle of vertical canals is present (Pl. 34, fig. 6). The canals in *Phacops* are normally limited to the central zone and parts of the inner zone (Pl. 34, fig. 3).

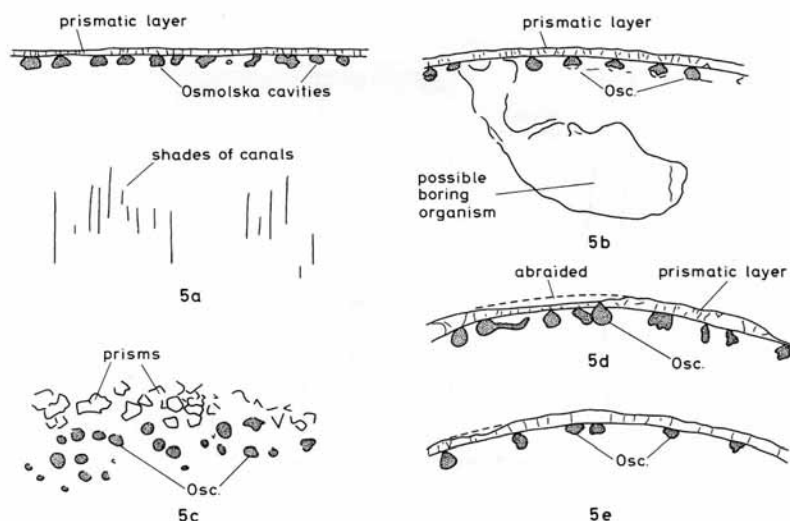
Wider canals occur in *C. odini*. In a section across the anterior doublure of the cephalon (Pl. 29, fig. 6) there are numerous curved canals, apparently with a diameter of about $8\mu\text{m}$. Larger canals opening directly on part of the upper surface are seen in *Chasmops* sp. nov. D, but thin sections near the eye show canals of a different width. On one side of the eye the canals vary considerably (Pl. 29, fig. 1), some of them connected with tubercles. On the other side (Pl. 32, figs. 1, 2) the canals have a fairly constant width of $10\text{--}20\mu\text{m}$. Some of the ducts are not perpendicular to the surface. These canals flare slightly on the inner surface, but not on the outer surface. Pits on the external surface representing openings of canals have been beautifully figured by Miller (1976, pl. 1, figs. 5, 6) in *P. rana*. Other pits have been demonstrated in *Tretaspis* by Størmer (1930, pl. 11, fig. 4a, b). In some of the *Phacops* specimens the pits measure $400\mu\text{m}$ across, and form bowls containing up to five pits at the bottom.

Miller (1975, figs. 2A, 3F, 4D) interprets certain lines crossing the exoskeleton in trilobites as canals. The lines run inwards from the base of scarps along terrace lines. Similar lines have been described in sections of *Tretaspis* (Størmer 1930, p. 105) and in other trilobites (Kielan 1954, text-fig. 34). I described these lines from the terrace lines on the trinucleid fringe and from the reticulate ridge-pattern on the frontal lobe of the glabella, as 'stay lines'. Osmolska (1975, p. 204) observed that if they were canals one would expect to observe corresponding rows of evenly spaced pits or canal openings on the outer surface. Scanning electron micrographs (Miller 1975, fig. 4A-C) do not show such rows of canal openings. The many pits along the border (fig. 4C) would have shown a mixture of canals of different dimensions and mutual distances. I am still inclined to interpret the 'canals' as sections of some kind of laminae or sheets. It seems possible that the laminae, which have no observable thickness (Størmer 1930, p. 103), might mark the boundary between fine lamellae from the laminate zones, meeting at a distinct angle along the ridges.

Subsurface cavities and the Osmolska cavities. With the term 'external pitting' Osmolska (1975, p. 203, pl. 1, figs. 7-18) described very small and relatively shallow pits occurring in great numbers and more or less evenly distributed on the external surface of the integument in several Devonian trilobites. These structures had been previously figured by Dalingwater (1973, pl. 105, figs. 2, 3), and form tiny cavities measuring $12\text{--}15\mu\text{m}$ in diameter and $10\text{--}18\mu\text{m}$ in depth. The size seems to be rather constant,

independent of the size of the individual. Miller (1976, p. 349, pl. 2, figs. 1, 6; text-fig. 2 α) interpreted the 'external pitting' as 'artifacts' produced by tangential sectioning of the 20- μ m-wide pits belonging to the 5-10- μ m-duct group. An external pitting similar to that of the Devonian phacopids also occurs in *Chasmops* sp. nov. A (Pl. 25, fig. 3), *C.* sp. nov. D (Pl. 29, fig. 2), and *T. extensus extensus* (Pl. 25, fig. 2a, b).

Sections from some excellently preserved specimens of *P. granulatus* show details which necessitate a new concept of the 'external pitting'. As described above, the exoskeleton of the cephalon has an outermost prismatic layer about 10 μ m thick (Pl. 30, figs. 3b, 5-7; Pl. 31, fig. 1a, b; text-figs. 3, 5, 6).



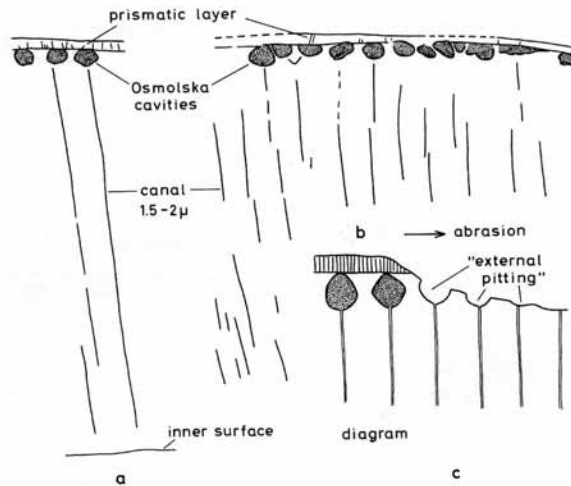
TEXT-FIG. 5. *Phacops granulatus* (Münster) from the Devonian of Poland. Prismatic layer with Osmolska cavity organs below: a, b, d, e, perpendicular sections of the glabella; c, tangential section. (a from Pl. 31, fig. 3; b from Pl. 31, fig. 3; c from Pl. 30, fig. 4; d from Pl. 30, fig. 7; e from Pl. 30, fig. 5).

The layer is partly worn off in some specimens, but not as much as in those figured by Dalingwater (1973, pl. 109, figs. 2, 3), Osmolska (1975, pl. 1, figs. 2-9, 11-20, reproduced on Pl. 31, fig. 5), and Miller (1976, pl. 2, figs. 1, 3, 4, 6). The present *Phacops* material shows that the external 'pits' are parts of cavities occurring distinctly below the prismatic layer. A small portion of the cavities may exceptionally invade the lowermost part of the prismatic layer (text-fig. 5d). Because of the numerous vertical lines forming the walls of the prisms (Pl. 34, figs. 1, 2) it is difficult to decide whether the cavities communicate with the outer surface. In vertical sections the cavities vary considerably from circular, flask- or pear-shaped to triangular (Pl. 31, fig. 4). In the last case the lowermost portion of the cavities evidently have not been filled with a fine brownish material, assumed to be iron oxide. The cavities extend downwards in the upper (laminar) zone to a level about 15-20 μ m below the prismatic layer. In a few specimens this lower level or boundary is suggested by a faint line parallel to the surface (Pl. 30, fig. 7; Pl. 31, fig. 4). In tangential sections the cavities have a more or less circular outline with a diameter corresponding to the width in vertical sections (Pl. 30, fig. 4; text-fig. 5c). I propose the term *Osmolska cavities* for these structures.

SEM photographs do not pick out the colour contrast of the thin sections so that the Osmolska cavities are poorly displayed (Pl. 34, figs. 1, 2, 4, 7a, b). However, the position below the prismatic layer is evident. The width of the cavities varies from 10 to 20 μ m.

In the cephalon of *Phacops* the distribution of the Osmolska cavities on the large tubercles is fairly regular as shown in the sections, limited areas without cavities might occur (Pl. 30, fig. 3b; text-fig. 3d). According to Osmolska (1975, p. 205) the cavities also occur on the doublure in *P. granulatus*. In sections of *Phacops* from areas without tubercles, Osmolska cavities may be very numerous (Pl. 31, fig. 3; text-fig. 5a). Closely packed cavities facilitate the breaking off of the prismatic layer in these specimens.

Structure apparently identical to the Osmolska cavities occur in three different Norwegian Chasmopinae a hundred million years older than the Fammenian occurrences in Poland. The



TEXT-FIG. 6. *Toxochasmops* sp. from the Ordovician of the Hamar District. Prismatic layer with Osmolska cavity organs below: a, b, perpendicular sections showing the thin (1.5–2.0 μm) vertical canals probably connected with the Osmolska cavities above (Pl. 29, fig. 7a, b); c, reconstruction indicating several successive stages in the abrasion of the outermost part of the exoskeleton. The prismatic layer is removed, an 'external pitting' is formed, and finally, to the right, the outer surface appears as smooth.

Norwegian occurrences are sporadic, which may be due to imperfect preservation. When the cavities are absent so also is the prismatic layer. The absence of Osmolska cavities in most specimens might therefore be due to abrasion of the outermost cuticular layers of the exoskeleton (text-fig. 6c). In *Chasmops* sp. nov. A the pit-like structures are shown in the left part of the section. In *C.* sp. nov. D the round cavities are distinct (Pl. 29, fig. 2) and traces of a prismatic layer are visible to the right. Osmolska cavities are preserved in some thin sections of *T. extensus extensus* (Pl. 25, fig. 2a, b) and *Toxochasmops* sp. (Pl. 29, fig. 7a, b; text-fig. 6a, b). In the first species the cavities occur as pits between the granule tubercles and are lacking on the depressed surfaces interpreted as areas of genal muscle scars, in the second both cavities and traces of the prismatic layer are preserved. The cavities have a somewhat irregular outline, but the size is constant. Of particular interest is the presence of well-preserved thin (1.5–2.0 μm) vertical canals below the cavities. Some of the canals penetrating the exoskeleton seem to be directly connected with the Osmolska cavities near the external surface (Pl. 29, fig. 7b; text-fig. 6a, b).

The Osmolska cavities are either caused by boring organisms, or they are primary components of the exoskeleton. In favour of the first alternative is the fairly uniform size in various species and in young and adult specimens. Certain other structures in *P. granulatus* might indicate cavities formed by boring organisms, such as big sack-like structures of irregular outline (Pl. 31, figs. 2, 4). Teigler and Towe (1975, p. 139) have demonstrated the presence of a phosphatic layer near the surface of the exoskeleton in *Calymene*. If the Osmolska cavities were boring algae they might have preferred to live in a phosphatic layer near the surface. In *Phacops* there is apparently no phosphatic layer, because polished cuticular sections do not stain with MoO_2 and NH_3 . In favour of the second alternative is lack of Osmolska cavities on the lower surface of the exoskeleton, their occurrence at a constant level below the outer surface and in distantly related trilobites from the Ordovician and the Devonian. Most important, however, is the presence of fine vertical canals evidently connecting the cavities with the epidermis below the cuticle. The arguments for their primary nature are more compelling, and the cavity probably housed a special organ.

POSSIBLE FUNCTIONS OF STRUCTURES DESCRIBED

The functions have to be deduced from a comparison with Recent arthropods, with the caution that similar structures, such as the composite eyes in crustaceans and insects, might develop independently in different groups. Analogous structures, however, might be an important key to the understanding of the functions of the organs in the fossil forms.

Pore canals, canals of sensory setae and of tegumental glands

The fine canals with a diameter below 1–2 μm have been interpreted by various authors as pore canals. The present material does not add new information of these tiny structures. It is probable that most of the finer and thicker canals through the exoskeleton in trilobites contained extensions of nerve cells in the epidermis. It is assumed that these extensions were connected with one or more hairs or sensory setae (sensillae) on the outer surface. (Dalingwater 1973, p. 837; Miller 1976, p. 345). The openings on the apex of the tubercles support this assumption. The actual movable setae, which easily break off, have never been observed in trilobites. Whittington and Evitt (1954, fig. 1) show the setae or hairs in their reconstruction of *Ceratocephala laciniata*. In the present material the pitted tubercles of various kinds probably carried setae on the apex. The thickness of the central canal and especially the apical aperture indicate the dimensions of the setae. Typical sockets with distinct surrounding ring or ridges like those in eurypterids and scorpions (Størmer 1963, text-fig. 45; pl. 12, fig. 1) have apparently not been observed in trilobites, and the only comparable structures are probably due to abrasion of tubercles (text-fig. 2).

The hair-like extensions and narrow spines occurring in *Triarthrus*, *Olenoides*, and *Ceraurus* (Raymond 1920; Størmer 1933; Whittington 1975) were probably fixed, not sensory extensions of the cuticle (macrotrichs of Weber 1954, p. 44). Probably the majority of cuticular setae in trilobites served as mechanoreceptors. In cases where the canals open into a large bowl-shaped pit on the surface, the setae would have had a considerable movability (not unlike the trichobotriae in Recent arachnids). In other cases a large bowl could have had a bundle of several setae. Major canals opening directly on a smooth surface might (Osmolska 1975, p. 202) have served as ducts for tegumental glands.

Smooth tubercle organ

The *campaniform organ* in Recent Crustacea and Hexapoda is compared with the smooth tubercle of *Chasmops*. In decapod crustaceans the organ (text-fig. 7a) consists of a canal around 8 μm wide penetrating the calcified exoskeleton and covered at the surface by a chitinous, relatively flexible, cap (Shelton and Laverack 1968). Inside the canal, extensions of two sensory neurones are united into a peg which touches the inside of the cap. Pressures on the cap are transferred to the epidermal neurones. In insects various developments of campaniform organs occur. One type (text-fig. 7b) resembles that of the crustaceans. A dome-shaped cuticular membrane has a peg underneath.

The low convex tubercle of the trilobites studied, has no discernable pit on the apex of the outer layer or 'cap'. Just below this layer, a wide vertical canal occurs which continues downwards to the lower surface of the exoskeleton (text-fig. 1c). The 'cap' and the canal, which narrows abruptly towards the 'cap', recall the structures of the campaniform organ in the Hexapoda. In that case the extensions of the neurones in the wide canal would have been united into a peg leading up to a 'cap' representing the outer zone of the exoskeleton. However, in contrast to the typical campaniform organ the smooth tubercle organ might have had a very thin canal penetrating the outer cap or layer.

Internal tubules organ

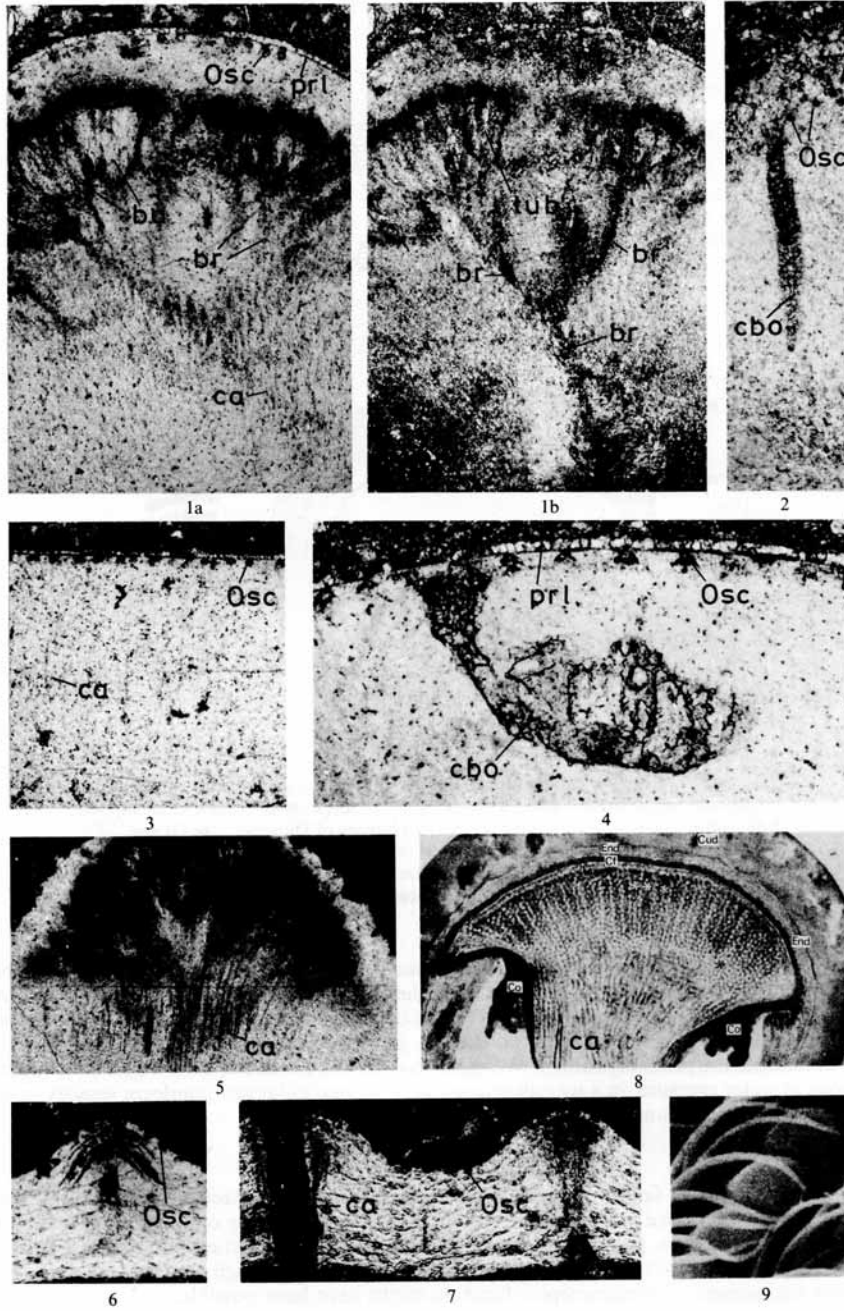
The composite tubercle of the phacopid type evidently had a special function. Miller (1976) points out the importance of the composite tubercle ('pseudotubercle') in *Phacops* as a sensory organ, and suggests that the tubercle served as some kind of a chemoreceptor. A special type of campaniform organ in Recent Hexapoda shows some similarity to the trilobite structures. In Diptera the halteres, which are modified second pairs of wings, have complex sensory organs serving as mechanoreceptors (Smith 1969; Grassé 1975). The very minute organs appear as convex papillae surrounded by a few hairs (Pl. 31, fig. 9). Perpendicular sections of a papilla (Pl. 31, fig. 8; text-fig. 7d-f) show: (1) a relatively thick and solid outer cap, (2) a thin and soft endocuticle with (3) a 'plasma membrane' (below a thin and dark inner thin cap) into which (4) numerous radially disposed narrow bundles of densely packed microtubules (0.01 μm) are inserted, (5) a reticulum of dark-walled lacunae occupying most of the prominent fan-like median portion, (6) discrete tubules with a diameter (0.02 μm), less than half that of the bundles, fill the space below the fan. In Diptera all the tubules and micro-tubules of one papilla belong to one epidermal cell only (Grassé 1975).

A comparison between the haltere-papilla and the phacopid composite tubercle shows the following resemblances and differences. In both cases the convex sensory tubercle or papilla has a relatively thick solid outer cap or zone, a dark endocuticle in the Diptera might possibly be compared with the dark-stained layers below the outer zone in *Phacops*. As in trilobites, the inner and basal portion of the papilla has numerous closely packed fine canals vertical at the base and spreading fan-like in the upper part. In both groups the terminals of tubules or bundles of microtubules, are inserted at the base of the external cap (into the soft 'plasma membrane' in Diptera). In the Diptera the tubules (with the microtubules inside) have a diameter about twice that of the canals below the fan-like portion of the organ. Also in *Phacops*, the tubules probably have about twice the width of the canals below the fan. On the other hand, the diameter of the tubercle is almost eighty times that of the papilla. The

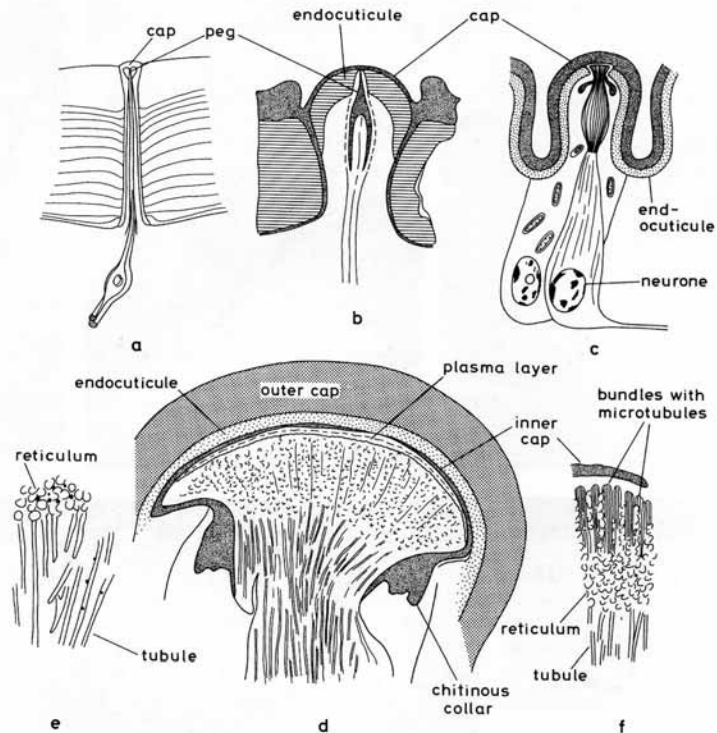
EXPLANATION OF PLATE 31

Figs. 1-5. *Phacops granulatus* (Münster, 1840). 1a, b, median portion of composite tubercle of phacopid type; 1a showing 'bush-like' bundles of tubules (8 μm) and canals (4 μm) at deeper levels; 1b, crossed nicols, the basal branching below the bundles is indicated. One diffuse stem runs down to the base of the exoskeleton, $\times 100$. 2, oblique, nearly tangential section showing possible cavity of boring organism, $\times 100$. 3, exoskeleton with prismatic layer and Osmolska cavities. Thin perpendicular canals are indicated, $\times 100$. 4, details of prismatic layer and Osmolska cavities, large sac-like body possibly due to a boring organism, $\times 200$. 5, 4- μm canals of tubercle of which portion below the outer zone is strongly stained, $\times 65$ (after Osmolska 1975). Figs. 6, 7. *Trimerocephalus caecus* (Gürich, 1840), Famennian Limestone, Poland. 6, tubercle with distinct layering and Osmolska cavities, $\times 95$ (after Osmolska 1975). 7, perpendicular section of two pit-tubercles. Because of the indications of fine canals beside the central one this pit-tubercle might be related to the composite tubercle in *Phacops*. Osmolska cavities also present between the tubercles (after Osmolska 1975). Figs. 8, 9. Sensory papillae (tubercles) of campaniform organ on halteres in Diptera. 8, perpendicular section of papilla with structures compared with those in *Phacops*, $\times c. 15\,000$. 9, papillae (tubercles) with setae in between, $\times 2000$ (after Smith 1969).

hbt = basal branch below bundles of tubules, *bu* = bundle of tubules, *cho* = possible cavity of boring organism, *ca* = canal, *Osc* = Osmolska cavity, *prl* = prismatic layer, *tub* = tubule.



STØRMER, trilobite tubercle structure



TEXT-FIG. 7. Sensory campaniform organs in Recent arthropods: *a*, decapod crustacean (after Shelton and Laverack 1968); *b*, more simple organ in Hexapoda (after Grassé, 1975); *c*, composite organ in a haltere of Diptera (after Grassé, 1975 from Snodgrass); *d*, perpendicular section of papilla of a campaniform organ in a haltere of Diptera, corresponds to upper part of fig. 7*c*; *e*, detail of tubules; *f*, details of tubules with reticulum and microtubules (after Smith 1969).

papilla lacks the outermost prismatic layer and Osmolska cavity organ, and there is no trace of the branches with the distal bundles of tubules as in the tubercle of *Phacops*. The preservation of the trilobite tubules does not show microtubules within them. The position of the sensory tubercles and papillae is obviously also very different in the two groups.

The similarities are probably enough to suggest that the tubules in trilobites might have registered variations in water pressure, in a way analogous with the particular campaniform sensory organ in insects which records changes in air pressure.

Osmolska cavity organ

I have not been able to find any description of a similar organ in Recent arthropods. If the big tubercles in *Phacops* served as a mechanoreceptor, the Osmolska cavity organ possibly had another function. It has not been possible to decide whether or not the cavities, situated just below the prismatic layer, had access to the surrounding water environment through one or several fine ducts. If an access was present, a chemoreceptor function might have been possible.

MUSCLE INSERTION AREAS

In *Chasmops* and Phacopidae smooth, outer exoskeletal surfaces are confined to particular areas: the axial and pleural furrows of thorax and pygidium, and the furrows of the cephalon. The smooth areas usually correspond to processes on the inner surface which served as apodemes for muscle attachment. Eldredge distinguishes four main types of areas of muscle attachment: (1) exoskeletal invaginations, (2) calluses or pads, (3) dark markings, and (4) pits or scars. Below it is shown that absence of canals through the exoskeleton is also characteristic of areas of muscle attachments or muscle scars. The familiar major invaginations serving as apodemes on the inner surface are not described here; we describe muscle attachments on and within the exoskeleton of the glabella and genae in the Chasmopinae.

Glabellar muscle scars (auxiliary pits)

Barrande observed what he called 'impressions auxiliaires' on the frontal lobe of the glabella in phacopids. Born (1919) described these structures in *Chasmops odini*, and more recently Eldredge (1971) has reviewed the previous literature. He figured auxiliary impressions in many different genera of the Phacopidae. In the Chasmopinae a typical 'necklace' arrangement of the muscle scars occurs.

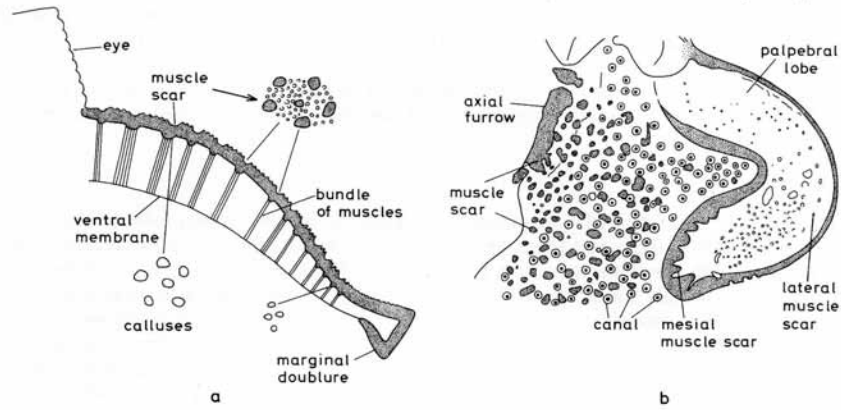
In specimens of *T. extensus extensus* and *T. extensus* subsp. nov. both the scars on the outer (Pl. 27, figs. 2*b*, 5; Pl. 32, figs. 7, 10) and inner (Pl. 27, fig. 3; Pl. 32, fig. 8) surface of the exoskeleton can be seen. On the outer surface each scar forms a small depressed smooth area or shallow pit surrounded by small smooth tubercles of the granule type. The granules are to some extent radially arranged round the depressed area. In *Toxochasmops* sp. nov. the anterior pairs of scars form small pits (Pl. 27, fig. 3*a*). The area varies in outline from circular to oblong. On the inner surface the areas of muscle attachment appear as low, flat calluses or pads. The two scars in the preglabellar furrow are more prominent than those behind. The shape and distribution of individual scars are highly variable. A triangle of three major scars may occur behind the single row of scars (Pl. 26, fig. 2*a*; Pl. 32, fig. 8). *C. odini* (Pl. 32, fig. 5) shows a V-shaped row of dark calluses or pads on the inside of the exoskeleton. One extra callus or muscle scar occurs in the middle and in the left row, one callus is double. The dark colour of the calluses is characteristic of muscle scars in well-preserved trilobites. The figured specimen also shows the openings of major canals connected with pit-tubercles, probably of the cone type, on the outer surface of the exoskeleton. None of the calluses or pads are penetrated by a canal, a condition which confirms their function as muscle scars. A canal containing an extension of a cell in the epidermis would hardly occur among muscle fibrils attached to the muscle scars or apodemes. The same lack of canals is noticed on the internal mould of *Chasmops* sp. nov. C (Pl. 32, fig. 6; text-fig. 7). In *Chasmops* sp. nov. B (Pl. 26, fig. 1*a*; Pl. 32, fig. 4) the muscle scars appear on the dorsal surface as deeper pits rather than shallow depressions. In the preglabellar furrow two small pits are seen between the larger ones.

The functions of the muscle scars related to the anterior portion of the digestive tract seems reasonable. The prominent scars in the preglabellar furrow and the three markings behind the 'necklace' might have served other purposes. Campbell (1977, fig. 26*b, c*) interprets muscle scars on the anterior portion of the frontal glabellar lobe as belonging to muscles leading to a presumed anterior ventral cephalic bar.

Genal muscle scars

Within the order Phacopida the surface of the cheeks is provided with both tubercles and pits. This kind of sculpture differs in related species (*Placoparia*, Henry and Clarkson 1975, text-fig. 3). In *C. odini* the granulated outer surface has certain pits and smooth depressed circular areas (Pl. 33, fig. 4) resembling the glabellar muscle scars in *T. extensus extensus* (Pl. 32, figs. 7, 10). On the inside of the exoskeleton in *C. odini* numerous dark calluses or pads occur, diminishing in size towards the marginal rims above the doublure, where they are absent (Pl. 32, fig. 11; text-fig. 8*b*). Adaxial to the palpebral lobe the inner surface of the genal exoskeleton shows numerous dark markings between

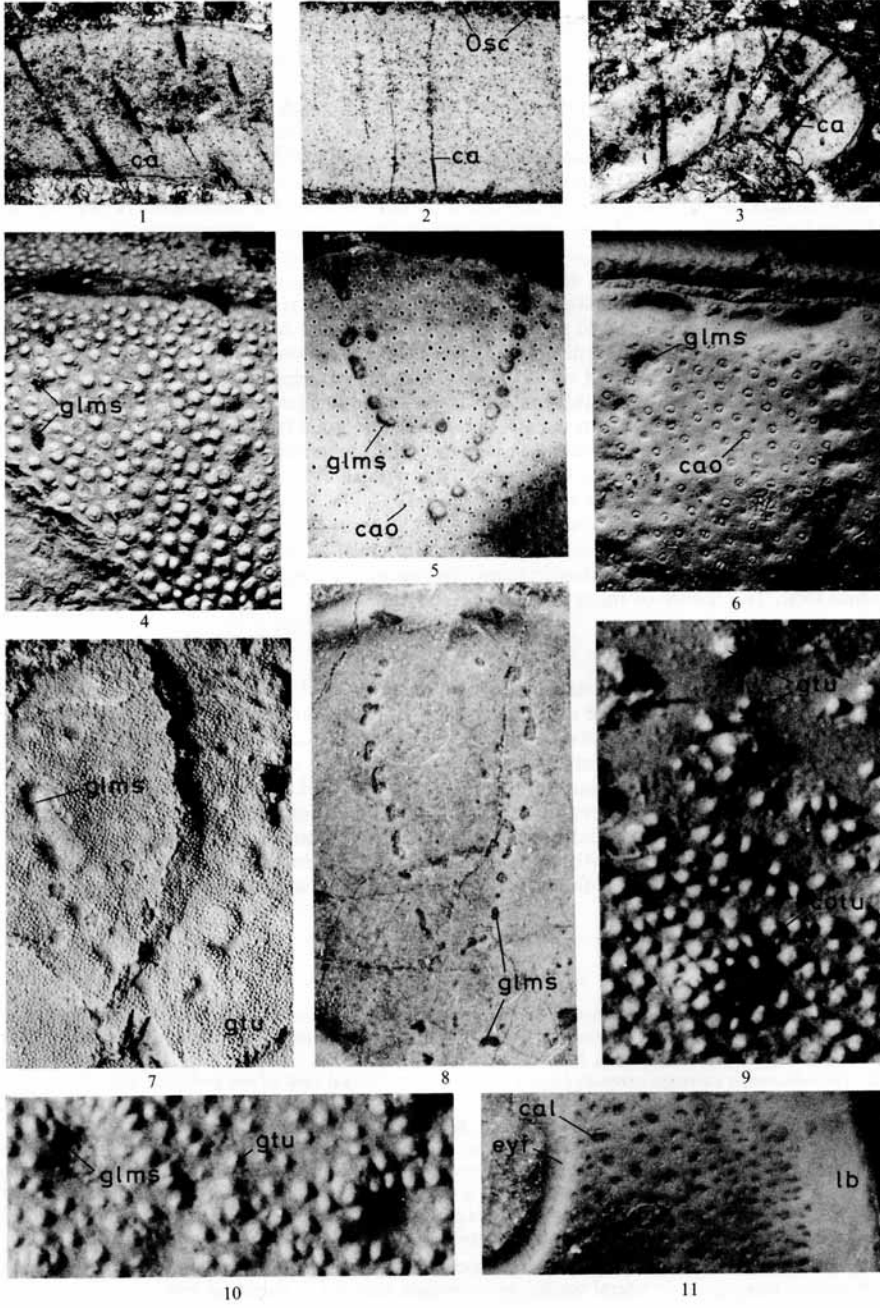
openings of major canals identical to those on the inner surface of the glabella (Pl. 33, fig. 3; text-fig. 8b). The dark colour of the markings suggests the presence of small muscle scars. This interpretation is confirmed by the fact that the scars are not penetrated by the canals. Other Baltic species with their white exoskeletons, e.g. *Ceraurus aculeatus* (Öpik 1937, pl. 18) also have small dark scars partly mounted on calluses, on the inside of the genae. They also alternate with pits representing



TEXT-FIG. 8. Probable genal muscle scars in *Chasmops odini* (Eichwald): a, diagrammatic section of lateral portion of gena with details of outer and inner surfaces of exoskeleton; b, inside of exoskeleton of portion of gena and palpebral lobe showing canals and muscle scars.

EXPLANATION OF PLATE 32

- Figs. 1, 2. *Chasmops* sp. nov. D. Exoskeleton (close to eye) devoid of tubercles but pierced by major canals. Cyclocrinus beds, 4by, Furuberget, Hamar District, PMO 21999, $\times 112$.
- Fig. 3. *Toxochasmops extensus* (Boeck, 1838). Perpendicular section through glabella. Osmolska cavities and fine canals. 4b δ , Rauskjær, Asker, PMO 94401, $\times 100$.
- Fig. 4. *Chasmops* sp. nov. B. Glabellar muscle scars between smooth tubercles of convex type on anterior portion of frontal lobe of glabella. To the right upper layer of tubercles partly abraded. 4b β , Ostøya, Asker, PMO 20396, $\times 8.2$.
- Fig. 5. *Chasmops odini* (Eichwald, 1840). Inner surface of exoskeleton of frontal lobe with glabellar muscle scars appearing as a somewhat asymmetric row of calluses. Calluses devoid of canal openings. C₂, Kukruse, Estonia, RMS Ar. 46034, $\times 8.2$.
- Fig. 6. *Chasmops* sp. nov. C. Anteromedian portion of glabella of internal mould. Glabellar muscle scars devoid of canal openings. In pre-glabellar furrow, larger pits with smaller pits between. 4bz, Bratterrud, Røyse, Ringerike, PMO 69395, $\times 8.2$.
- Fig. 7. *Toxochasmops extensus* subsp. nov. Glabellar muscle scars on the outer surface of the exoskeleton appearing as shallow depressions devoid of the surrounding smooth tubercles of granule type. 4by, Vestbråten, Røyse, Ringerike, PMO 69345, $\times 12$.
- Figs. 8-10. *Toxochasmops extensus extensus* (Boeck, 1838). 8, inner surface of anteromedian portion of the glabellar exoskeleton. Narrow 'necklace' with three extra muscle scars behind. Two larger muscle scars in pre-glabellar furrow. 4b δ , Gåsøy, Bærum, PMO 63592, $\times 9$. 9, details of anterior portion of glabella demonstrating an increasing density of smooth tubercles of the granule type resulting in the formation of a composite tubercle, PMO 94412, $\times 28$. 10, two auxiliary pits surrounded by granule tubercles partly radially arranged, $\times 28$, as Fig. 9, Rauskjær, Asker.
- Fig. 11. *Chasmops odini* (Eichwald, 1840). Lateral portion of gena with calluses forming muscle scars decreasing in size towards the lateral border. C₂, Kukruse, Estonia, RMS Ar. 46033, $\times 9$.
- ca = canal, cal = callus or pad, cao = canal opening or its impression, eyf = eye furrow, Osc = Osmolska cavities.



STØRMER, Chasmopinid cuticle structure

canal openings. We have made similar observations on *Chasmops* sp. nov. D (Pl. 33, fig. 1) and *Toxochasmops extensus* (Pl. 33, fig. 2). In another specimen (Pl. 32, fig. 8) the adaxial portion of the gena has dark markings like those in *C. odini*.

A thin section across the gena close to the eye of a specimen of *T. extensus extensus* shows interesting details of the shallow depressions on the external surface (Pl. 25, fig. 2a, b). The smooth surface of the depressions are surrounded by a surface provided with tubercles of the granule type and with the lower part of Osmolska cavities. The prismatic layer is evidently abraded. Of particular interest is the dark colour of the exoskeleton below the depressions. The dark colour, evidently due to fine-grained pyrite, might have been caused by decomposition of organic matter in the exoskeleton. In Recent arthropods the muscles are attached by tonofibrils, and Weber (1954, p. 57, figs. 23, 31) notes that the new cuticle formed after moulting might develop so rapidly that the tonofibrillar attachment can remain as a visible cone ('Faserkegel') within the exoskeleton. The dark colour in the specimen figured (Pl. 25, fig. 2a, b) might be interpreted as due to a decomposition of tonofibrillar substance formed during the growth of the exoskeleton after moulting.

Thus chasmopids probably had many narrow bundles of genal muscles with a dorso-ventral vertical direction. These were probably attached either to the genal caeca or to the ventral integument of the gena, which needed support by numerous bundles of muscles (text-fig. 8a). This was not the case with the thick and solid marginal doublure where there are no signs of muscle insertion. If the muscles reached the ventral cuticle they had to pass strongly ramified caeca, probably of the kind known in *Elyx* and *Ptychoparia* (Harrington 1959, fig. 73).

Additional muscle scars are indicated by a darker colour in *C. odini* (Pl. 33, fig. 3). The palpebral lobe has a row of small scars near the lateral border. Similar structures have been figured by Clarkson (1975, pl. 6, fig. 8) in *Reedops*. Muscle scars also occur on the median (adaxial) margin of the palpebral lobe. The nature of these scars are unknown.

SUMMARY

The trilobite exoskeleton includes an outer, prismatic layer, and inner laminate layers with varied development. The external surface of the exoskeleton has a characteristic sculpture—tubercles of various kinds. Three main groups of tubercles are recognized: smooth tubercles, pitted tubercles, and composite tubercles. In the small granule type of smooth tubercles a central canal is observed as a very thin duct in the upper part of the exoskeleton. The medium-sized, low, convex smooth tubercle has (below the outer zone) a wide, perpendicular canal which might continue upwards through the outer zone as a very thin duct or canal. This kind of tubercle can be compared with the sensory campaniform organs in Recent arthropods. Wide openings in tubercles are interpreted as due to abrasion. Pitted tubercles have a distinct central canal with an apical aperture.

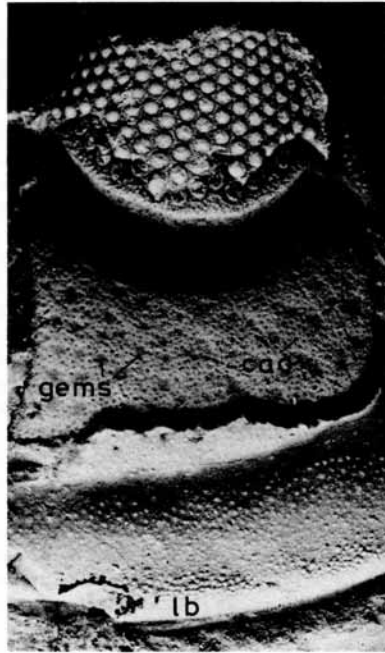
EXPLANATION OF PLATE 33

Fig. 1. *Chasmops* sp. nov. D. Lateral view of eye with internal mould of librigena and outer surface of lateral border. On the internal mould genal muscle scars and numerous impressions of canal openings. Cyclocrinus beds (4bγ) Røykenvik, Hadeland, PMO 34109, ×11.

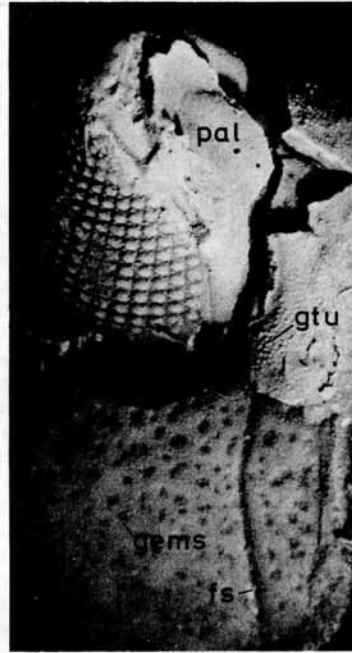
Fig. 2. *Toxochasmops extensus extensus* (Boeck, 1838). Dorsolateral view of eye and gena with crossing facial suture. Outer surface with granule tubercles, internal mould with genal muscle scars forming pits corresponding to calluses on inner surface. 4bδ, Bjerkøy, Asker, PMO 94322, ×11.

Figs. 3, 4. *Chasmops odini* (Eichwald, 1840). 3, inner surface of gena with palpebral lobe and part of glabella. Dark circular canal openings surrounded by narrow light rims. Dark spots, not penetrated by canals represent genal muscle scars. Special muscle scars also on palpebral lobe. C₂, Kukruse, Kiviõti, Estonia. B.M. In 51475, ×12.9. 4, details of outer surface of gena near occipital furrow. Circular muscle scars forming smooth depressions between close-set small tubercles, some with central pits. B.M. In 51475, ×40.

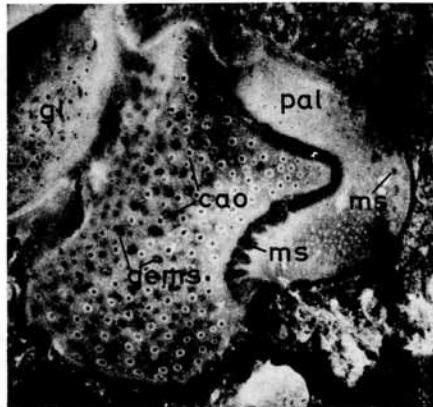
cao = canal opening or its impression, fs = facial suture, gl = glabella, gems = genal muscle scar, gtu = granule type of smooth tubercle, lb = lateral border, ms = muscle scar, pal = palpebral lobe.



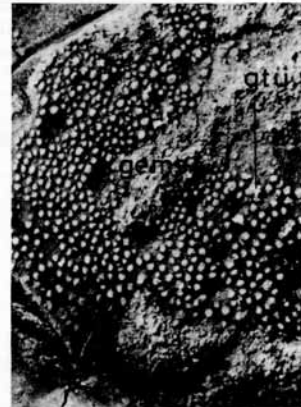
1



2



3



4

STØRMER, Chasmopinid cuticle structure

Three types of composite tubercles occur, two formed by fusion of small smooth tubercles or pitted tubercles respectively, and the complex type occurring in Devonian Phacopidae. The phacopid convex composite tubercle has a thin (8–10 μm thick) outermost prismatic layer, a thin (10–20 μm) layer with small (15–20 μm wide) Osmolska cavities forming the upper part of a thicker (80 μm) unlaminate light outer zone. This zone apparently has close-set basal notches into which about 8- μm -wide tubules, ascending from the central zone, are inserted (text-fig. 4). In the dark-stained outer part of the central zone the tubules are arranged in bush-like bundles branching off more or less at a common level from diffuse bifurcating branches. Apparently independent of these structures the whole interior of the tubercle is filled by densely packed 3–4 μm canals, vertical in the lower part and spreading fan-like upwards towards the outer light zone. The canals partly cross the diffuse branches, it is uncertain, however, whether the canals are connected with the tubules in the bush-like bundles. *Phacops* tubercles have several features in common with the much smaller campaniform organ in the halteres of Recent Diptera, an organ serving as a mechanoreceptor.

Apparent external pitting of the exoskeleton is shown to be due to abrasion of small round cavities occurring in considerable numbers in a layer just below the rarely preserved prismatic layer. The cavities, the Osmolska cavities, occur both in Devonian *Phacops* and in Ordovician Chasmopinae. In the latter very thin (1.5–2.0 μm) vertical canals seem to be connected with the cavities.

Canals not associated with tubercles on the surface are of several kinds. Thin canals with a diameter up to 2 μm might correspond to pore canals. Certain vertical lines seen in section crossing the exoskeleton are interpreted as subvertical laminae rather than true canals.

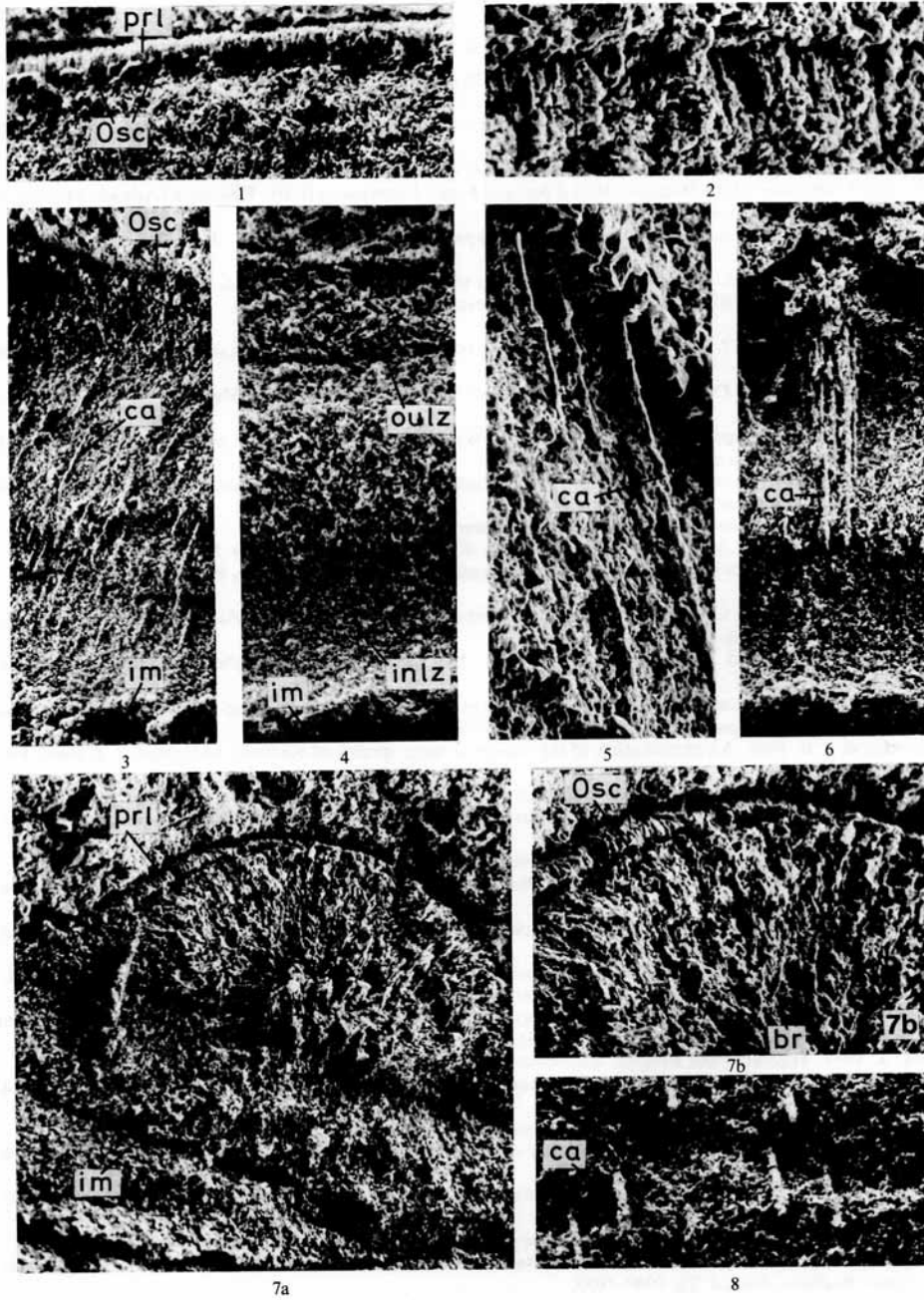
Glabellar muscle scars are not penetrated by canals, and the same is the case with the numerous small markings on the outer and inner surface of the exoskeleton of the genae in well-preserved specimens. These structures are interpreted as due to narrow bundles of muscle supporting the thin ventral integument inside the marginal doublure. Necklace-like muscle scars on the glabella of chasmopids were mostly related to muscles attached to the anterior part of the intestinal tract.

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EXPLANATION OF PLATE 34

Figs. 1–8. *Phacops granulatus* (Münster, 1840), Devonian Famennian Limestone of Poland. 1, prismatic layer at the surface with traces of Osmolska cavities below, $\times 300$. 2, prismatic layer, $\times 1000$. 3, section through the exoskeleton with Osmolska cavities and canals. An outer zone is faintly indicated, $\times 150$. 4, section through the exoskeleton with Osmolska cavities below a prismatic layer. An outer (laminar) zone with traces of parabolic structures either primary, or due to imprints of rhombic calcite crystals, $\times 200$. 5, details of corroded perpendicular canals, $\times 500$. 6, small cone-shaped protuberance (tubercle?) within which a star-like radiating arrangement of canals is suggested. From this 'star' a bundle of perpendicular canals extend downward as far as to the inner zone, $\times 150$. 7a, b, composite tubercle near the eye. Prismatic layer preserved to the left, abraded to the right. Osmolska cavities present below the prismatic layer. Tubules and canals not distinguished but a possible branching zone of the former is suggested, a, $\times 150$, b, $\times 300$. 8, parts of perpendicular canals with a diameter of 4 μm , $\times 400$.

br = diverging branches (?), ca = canal, im = inner margin, ilz = inner laminar zone, osc = Osmolska cavity, oulz = outer laminar zone, prl = prismatic layer.



STØRMER, *Phacops* cuticle structure

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Professor Størmer died not long after submitting this paper. The manuscript has been shortened by the editors

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