THE CONODONT APPARATUS AS
A FOOD-GATHERING MECHANISM

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ABSTRACT. The possible functioning, rather than the zoological affinity, of the conodonts is discussed. Symmetry considerations, as well as arrangement of conodonts in apparatuses found on bedding planes, are best compatible with arrangement of the elements about the mouth. Homology between the elements indicates that certain conclusions may apply generally. Many kinds of element could scarcely have functioned if turned with denticles toward the inside, hence the hypothetical animal is figured with denticles toward the outside. The apparatus was covered by soft tissue that is likely to have belonged to a lophophore. This functioned in the same way throughout the post-larval life of the animal (isometric growth of elements indicated by germ denticles). The denticulate aspect of the animal would have had a deterrent effect on predators, and denticles broken on encounters with predators could be regenerated. Long sharp teeth and subapical barbs on certain teeth served as passive defence. When attacked the animal might have contracted within the expandable, spinose lophophore part. Conodont remains ingested by conodontochordates suggest the upper size limit of the conodont animals. They probably fed on microscopic particulate, as well as on dissolved, nutrients.

THE conodont animals had a skeleton that consisted of several kinds of individual conodonts. As the animals died, the skeleton usually fell apart. Conodont faunas therefore consist of mixed and sometimes incomplete assemblages of different-looking elements from which the skeletons, or apparatuses, have to be reconstructed. Fortunately, more or less complete apparatuses have been found in certain lithologies (Schmidt 1934; Scott 1934; Rhodes 1952; Schmidt and Müller 1964; Lange 1968; Mashkova 1972). Using these as a template it has been possible to reconstruct groupings of homologous apparatuses and follow their evolution in the Ordovician (Bergström and Sweet 1966; Schopf 1966; Webers 1966; Kohut 1969; Lindström 1971; Sweet and Bergström 1972), Silurian (Walliser 1964; Jeppsson 1969), Devonian (Klapper and Philip 1971), Carboniferous (von Bitter 1972), and Triassic (Sweet 1970). As one might expect, the establishment of skeletal evolution for whole apparatuses makes it easier to understand the evolution and suprageneric taxonomy of the conodonts (Lindström 1970).

Unfortunately, knowledge of conodont apparatuses has not solved the enigma of the zoological nature of the conodonts. One cannot even say that we know what function the conodonts had in the animal, and how they fulfilled this function. I have assumed that they served as part of a feeding apparatus. In the past they have been taken to be gastropod radular teeth (Loomis 1936), polychaete jaws (Zittel and Rohon 1886; Du Bois 1943; Rhodes 1954), fish teeth (Pander 1856; Ulrich and Bassler 1926), lophophore support (Lindström 1964, 1973), and jaws of chaetognath type (Rietschel 1973), although other authors have considered the conodonts as possible vertebrate parts without emphasizing their function as teeth (Schmidt 1934; Gross 1954; Schmidt and Müller 1964).

Inner structure, outer morphology, shape, symmetry, and homology must be the principal clues to the possible mode of life of the conodonts. The conodonts consist

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of calcium carbonate fluorapatite (Pietzner *et al.* 1968), but the chemistry apparently does not help much to explain their functioning and nature, so it will not be further discussed. Palaeoecological aspects are considered briefly, but they have not yet been found to be decisive.

STRUCTURE AND GROWTH

Complete conodont elements consist of conodont and basal filling. The basal filling may be funnel- or plate-shaped; it is inserted into a conical cavity at the widened base of the conodont. The conodont may consist of hyaline and white matter, but whereas the hyaline parts of well-preserved conodonts are amber coloured and translucent, the white matter is opaque to transmitted light. Some conodonts are entirely hyaline. Those with white matter may be referred to as albid (Lindström and Ziegler 1971). The white matter is concentrated in the denticles, particularly in the main denticle, or cusp, that is situated above the tip of the basal cavity.

Conodonts have growth lamellae, added in outwards sequence like the annual growth layers of wood, but in the white matter the lamellae are destroyed. This destruction occurred during growth, for the outermost, and hence youngest, layer is nearly always hyaline. The white matter may be recrystallized (Lindström and Ziegler 1971; Barnes *et al.* 1973, 1973*a*) and contains small vesicles that may be radially arranged, or irregular, thin canals (Lindström 1964; Pietzner *et al.* 1968; Lindström and Ziegler 1971; Müller 1972). Müller and Nogami (1971) consider the interlamellar spaces as a special kind of white matter. However, this is a different thing from white matter as originally defined (Lindström 1964). Rays of white matter may form a V-shaped pattern that opens toward the apex and transects the conodont lamellae (Lindström 1964; Müller 1972). The other configurations of white matter described by Müller and Nogami (1971) and Müller (1972) can be regarded as effects due to the plane of sectioning. There is much evidence that the conodonts fractured easily across the white matter even during the life of the animal. Indeed, the white matter, with frequent cross-cutting planes formed by recrystallization, as well as increased porosity, appears to be designed to somewhat weaken the conodont structure.

Because denticles contain a great deal of white matter, the denticles of early growth stages appear through a hyaline overgrowth. The occurrence of overgrown 'germ denticles' (Branson and Mehl 1933–1934) proves that conodont growth was centrifugal. However, it also demonstrates the strong tendency toward isometric growth, that is, retention of shape during successive growth stages. If the denticles had not become overgrown, the outer shape of the elements would have had to change. That this did not happen is important. A further point is provided by a group of compound conodonts occurring in Carboniferous and younger rocks. In these the main denticle, or cusp, has concentrated white matter in its initial stages. Later it becomes more hyaline so that one can see the shape of the initial cusp, which is reclined at an angle to the growth axis of the mature cusp. The initial cusp thus could have the same angle of recurvature as the fully-grown one.

When a conodont denticle broke off it was replaced by a new denticle growing from the stump. The latter, with a broken edge, may be seen in transmitted light, and this provided one of the first clues to the mode of growth of the conodonts (Hass

1941). It is far from rare; in some faunas it is even the rule (Miller 1969). What happened to the part that was broken off is uncertain, in most cases it probably left the conodont organism. Müller (1972) has suggested that it was resorbed. However, despite the claims of Müller and Nogami (1971) and Müller (1972), no convincing proof of resorption has been presented (the apparent disappearance of lamellae on certain conodont platforms can equally well be interpreted as due to extremely low rates of secretion, with thin to absent lamellae as a result). Thus the regenerated denticles are a further indication that conodonts grew outward. They must have been surrounded by soft secreting tissue, were subepidermal (Hass 1941), or perhaps mesodermal.

The conodont lamellae end at the base. Inside the basal cavity, and surrounding it on the lower face of the base, the edges of successive lamellae appear as concentric lines surrounding the oldest lamella, which is wrapped about the tip of the basal cavity. In most complete conodonts there is a basal filling that occupies the basal cavity. However, complete conodonts in this sense are relatively rare, since the basal filling very readily falls off. It is a relatively weak structure consisting of small, disorderly-arranged phosphate crystals (Pietzner et al. 1968; Lindström and Ziegler 1971). There is evidence that it consisted of pliable matter during the life of the animal and in early diagenesis (Lindström and Ziegler 1971). Its inner structure is concentrically lamellar like that of the conodont. Thus the whole conodont was surrounded by soft tissue and there is no evidence that this condition changed during the life of the animal. Since special modes of growth were devised in order to maintain the outer shape essentially unaltered during growth, the elements evidently had the same function all the time, whatever this function was.

Thus, conodonts cannot have had the biting, chewing, or rasping functions of polychaete jaws or radular teeth. Although the similarity between a conodont apparatus and the jaw apparatus of a polychaete may be striking, annelid jaws are epidermal structures formed to a certain size and functioning only as originally formed. Furthermore, they do not have any organ similar to the basal filling of conodonts.

SHAPE OF CONODONTS

The main groups of post-Cambrian conodonts can be derived from simple forms with a single, very long and very slender, more or less recurved denticle (that was apt to break). This is important to remember, because more evolved shapes might give the impression of possible functions which then turn out to be impossible to derive from any function that might be reasonably ascribed to the primitive conodonts. In the Distacodontacea the basic shape was retained. The recurvature of the cusp may be very strong, so strong in some species that the apex is directed at 180° opposite to the basal part. In many species there are longitudinal ridges that regularly face toward the concave side.

Very early in the Ordovician certain simple forms evolved into the two principal kinds of conodont element found in younger faunas, the platform type and the rami-form. In both kinds it is the basal part that was the most strongly modified, expanding into branches, lobes, and ledges that carry denticulate patterns on their upper faces.

In platform conodonts occurring in the Lower Ordovician there are three branches or processes, each with a row of denticles that begins at one of the edges of the cusp. In these forms the cusp is still very high, sharp, and slender. In more evolved conodont elements of platform type the cusp is relatively low, and the denticles of the anterior process are fused to form a blade. The posterior process may either form a continuation of the blade or expand into a platform with ridge and denticle patterns. The
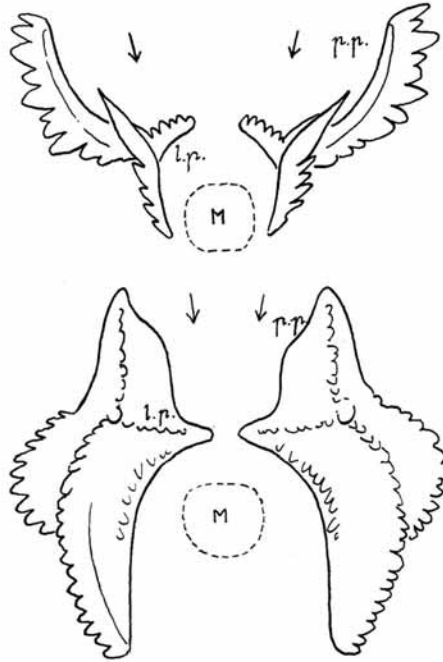
TEXT-FIG. 1. Hypothetical orientation of certain platform-type elements with respect to the mouth. Arrows—direction of main food current; p.p.—posterior process; l.p.—lateral process; M—mouth. The elements are seen in 'oral' view. *Top*: pair of prioniodiforms of *Oepikodus evae* (Lindström 1955). *Below*: platform elements of *Palmatolepis*.

third, or lateral, process is reduced in many stocks but turns up again and again in the course of later evolution. This is the homeomorphy which is a recurrent feature of conodont evolution. The basic pattern appears in the Lower Ordovician and recurs until the Upper Triassic, and this indicates a strong correlation between shape and function.

The ramiform elements can have one to four denticle rows beginning at the base

of the cusp. In fully-evolved forms at least one denticle row continues as a long, slender process. The cusp is thin, high, and pointed, and several of the denticles may also be quite prominent. One process, most commonly the posterior one, is as a rule much longer than the cusp and other denticles. The denticles may rise thin and erect at 90° from this bar, or be reclined at various angles. In ramiforms with more than one prominent process, the arch formed by each pair of processes may be quite sharp, and the denticles of different processes point in different directions. The space between the processes may be occupied by the basal filling, when present. This applies to the earliest conodonts of platform type as well as for all ramiform ones.

One reason why the denticles are not always in one plane is that there may be more than two denticulate processes. These diverge at different angles from the base of the cusp. Even where there are only two processes, the denticle row of the anterior process may be directed toward one side at about right-angles to the posterior process, or the latter may form a crescent with the denticles inclined toward the convex side. A Lower Carboniferous element, *Hindeodella segaformis* Bischoff, 1957, has particularly long denticles interspersed between smaller ones at regular intervals along the bar. The long denticles are inclined to the left and the right in regular alternation. Not all denticles are situated on processes and platform lobes constructed about the basal part of the cusp. In a few Ordovician genera the apical part of the long, sharp cusp carries barb-like denticles, which are always inclined toward the base.

In the preceding section it was argued that because of their structure the conodont elements must have functioned as subepidermal organs throughout their growth. This excludes the possibility that they could have dealt mechanically with food particles. The shape of the elements strengthens this point. There are few, if any, conodonts that were ideally shaped for seizing and holding food. Teeth used for these purposes ideally taper rapidly from a broad base. The slender, recurved conodonts are the opposite to this ideal shape. Furthermore, as we have seen, their structural design allowed them to snap with some ease. Rietschel (1973) pointed to the similarity between certain simple conodonts and the pinching jaws of chaetognaths, and also showed how such elements might have functioned mechanically. However, the lever mechanism suggested by Rietschel would be practical only with some elements and not with more strongly recurved, homologous elements belonging to the same conodont genera. As Rietschel himself points out, it would be ineffective in the case of ramiform elements that are direct homologues of the simple conodonts. The presence of a basal filling modifies the shape and possible mechanical functioning of a conodont element. This is ignored by Rietschel's model. The very long and slender cusps were useful neither for seizing nor for holding food. If they had been used for such purposes the bases would have had to be very far apart, which would make the basal denticulation ineffective. Apical barbs, if penetrating into the food, would certainly have held it, but would also have prevented it from being passed on toward the pharynx. There is no way of orientating a great number of simple and ramiform elements so that they would efficiently seize, hold, or chew the food.

The shape of certain platform elements suggests that these might have been used in chewing or grinding food particles. Jeppsson (1971) has drawn a hypothetical section of an opposed pair of *Idiognathodus* platforms that match one another so as to leave very little room between. However, if such matches do occur, they are very

rare, and most platforms would not function well in grinding. This is certainly true for all of those forms in which the denticulated portions would have been kept apart by the long cusps, had they been arranged in opposed positions in the animal.

The persistency of conodont gross shape from the Lower Ordovician to the Upper Triassic suggests that shape and function were closely dependent on one another. The inner structure and growth show that conodont elements supported an organic tissue. It is plausible that the outer shapes of the conodont elements and the supported organ were interdependent (Lindström 1964, 1973). If this was the case, the structure supported by the conodont skeleton was frilled or tentaculate. The evolution of the conodonts indicates that it was advantageous that this structure had a great spread and surface. The functions that require great surface and spread are breathing, excretion, and the uptake of nutrients. It is only the gathering of particulate nutrients, which have to be forwarded to the pharynx, that poses specific requirements on the shape.

MORPHOLOGY

In addition to processes, denticles, and tubercles that can take the place of denticles, many conodont elements have thin, isolated ribs, or costae, along the sides of the main denticle. If the base is drawn out into processes, such costae continue along the processes as their denticulate edges. If the processes supported tentaculate frills, the costae are likely to have done so too. Many conodont elements are smooth, but some carry longitudinal striations on the denticles, and platform surfaces commonly have a network of thin ridges defining numerous polygonal pits. As the denticle bases are approached, the meshes are drawn out toward the denticle axes, and the ridges continue up the denticles as longitudinal striations. This pattern has a distinct polarity in the direction at right-angles to the platform and parallel to the denticles. To ascribe any function to the pattern of striation and reticulae, one has to consider that the earliest forms in which it appears (Arenigian species of *Prioniodus* and *Oepikodus*) had platform ledges that must have been far removed from one another owing to the size of the cusp and other denticles. I have suggested that the pattern served as attachment for muscles (Lindström 1973). These would have functioned as retractors of tentacles that were otherwise kept extended by turgor. It is improbable that these muscles moved the conodonts relative to one another since in that case the operating surface of the conodont elements would have been a closed system, one element facing another with only muscles between, and it would have been very difficult to imagine any shape-related function.

Symmetry. Most conodont elements are asymmetrical, as is apparent from the description of the platform elements. These may have three processes, one anterior, one posterior, and one lateral. In most cases there are right and left versions of such elements, and these are mirror images of one another. Thus it is generally assumed that most conodont animals were bilaterally symmetrical (Lindström 1964; Lane 1968). Certain elements, called trichonodelliform or hibbardelliform after the form genera *Trichonodella* and *Hibbardella*, are bilaterally symmetrical in themselves. They have two denticulate processes, one to each side, anteriorly and eventually a third process to the posterior. Such elements would have been situated in the

sagittal plane of the animal (Jeppsson 1971; Lindström 1964, 1973). This particular kind of conodont element is associated with others with identical morphology except that they show various degrees of asymmetry and reduction of processes. Such associations have been called symmetry transitions (Lindström 1964), and they provide a key to the composition and arrangement of conodont apparatuses.

Not all conodont apparatuses are bilaterally symmetrical. Asymmetry can appear in different manners in the platform component. In some cases only left- or right-sided elements are known (Lindström 1959; Lane 1968). For instance, only right-sided platforms of *Cavusgnathus s.s.* have so far been found. In others, the left element differs from its right counterpart by not being its mirror image (*Pseudopolygnathus primus* Group of Voges 1959, *Spathognathodus costatus* Group of Ziegler 1962, *Amorphognathus* Bergström, 1971). Such cases can be identified with relative ease when one of the alternative shapes is always left-sided and the other right-sided. However, it is possible that the distinguishing features may not be constantly tied to right or left. Then one will find specimens with two different sets of shape characteristics, left and right elements occurring with either set of features. This is normally interpreted as two different species, each of which had a bilaterally symmetrical apparatus. If the constant association of the two kinds of elements were established on a statistical basis, this might be erroneously inferred to be due to sexual dimorphism. Associations of this kind might, in the author's opinion, perhaps occur in American Carboniferous faunas (compare Merrill 1974).

Owing to the wide, in some cases global, distribution of conodont species in many kinds of marine sediments, including pelagic ones, conodonts are usually reconstructed as pelagic swimmers and the bilateral symmetry agrees with this. The absence of bilateral symmetry in some species has led to the suggestion that certain conodonts were floating, perhaps colonial forms (Lindström 1964). However, as remarked by Lane (1968), this latter interpretation is not compelling if the conodont apparatus was internal, for internal organs can be asymmetrical without affecting swimming capability. Now that there are reasons to believe that the conodont apparatus was external rather than internal, the question still remains whether conodonts must have been active swimmers. Urbanek (1966) demonstrated that lophophores of colonial organisms can show a marked asymmetry.

Apparatuses. In most conodont faunas of Silurian and younger age at least two kinds of complete apparatuses are represented. One of these consists of a pair of platform elements, a pair of platform-like (ozarkodiniform) elements, a pair of pick-like elements with straight and proclined, knife-like cusp (neoprioniodiform or synprioniodiform), and a number of very long and almost straight, bar-like elements with many very small denticles regularly alternating with fewer somewhat larger ones (hindeodelliform elements). The hindeodelliforms mostly show a well-developed symmetry transition at the anterior end (that end at which the initial denticle or cusp is situated). There may be further ramiform elements, a possible instance is the Silurian to Devonian *Ozarkodina*. According to Jeppsson (1969) this genus has trichonodelliform and plectospathodiform elements in addition to the hindeodelliform ones. However, a complete *Ozarkodina* apparatus found by Mashkova (1972) does not clearly show the latter kinds of element.

The other common type of apparatus consists chiefly of a symmetry transition of ramiform elements each of which carries several long denticles. This apparatus can be readily homologized with the first one. The place of the platform elements might be occupied by ramiform elements with similarities in plan to Ordovician prionio-diform elements (form genera *Metalonchodina*, *Enantiognathus*, etc.). In those cases
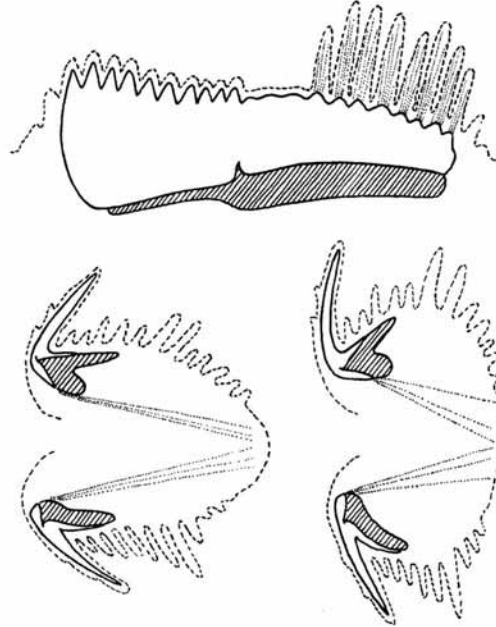
TEXT-FIG. 2. Hypothetical functioning of muscles in conodont animals, seen in longitudinal section. The posterior direction is to the right. The outer surface of soft tissue is shown by broken line. Muscles are stippled. The basal filling is indicated by diagonal line pattern. *Above*: platform element with long retractile tentacles. Specimen's muscle attachment is indicated by reticulate and pitted pattern on platform, strongly striate pattern on denticles. Muscles are likely to have been present on the blade (left) as well as on the platform; however, the former are likely to have been very short. *Below*: muscles attached to base of conodont serve to contract animal and erect the denticles in defence position.

in which the apparatuses are found with the elements obviously more or less *in situ*, the hindeodelliforms are aligned parallel to one another with the denticles pointing apparently in random directions (this includes the occasional specimen in which they all point in one direction). The neoprioniodiforms, as pointed out by Jeppsson (1971) are mostly outside of the sheaf of hindeodelliforms. The paired platforms, mostly lying together, can occupy almost any position relative to the ramiform elements,

and they may be turned toward or away from one another. They are as a rule anteriorly situated with respect to the similarly arranged ozarkodiniforms. (This circumstance was neglected in the reconstruction of Lindström 1973.)

Arrangement of the Conodont Elements. Fortunately enough data are available to put severe limitations on any reconstruction of the conodont apparatus. The homology of the initial portion of the elements, that part carrying the cusp, requires that all elements are turned with the posterior face of the cusp in the same direction. The hindeodelliforms must be parallel and close together as one group (if Jeppsson's reconstruction of *Ozarkodina* is correct, this genus must have had two batteries of hindeodelliforms as shown in the sketch by Lindström 1973). The bilaterally symmetrical ramiform must be at the mid-line. The platform elements must occupy neighbouring positions on each side of the mid-line. The same is true for the ozarkodiniforms, and is corroborated by the discovery of secondarily fused pairs of spathognathodiforms as well as similarly fused ozarkodiniforms (Rexroad and Nicoll 1964; Pollock 1969; and interpretations in Lindström 1973).

Reconstructions satisfying these data can be made according to two principles. Either the elements are arranged in groups after one another along the mid-line of the animal (Schmidt 1934; Rhodes 1952; Lindström 1964; Jeppsson 1971); or they encircled the mouth (or the pharynx if inside the mouth) (Lindström 1973), with the bilaterally symmetrical ramiform and the pairs of platforms and ozarkodiniforms at the sagittal plane but on opposite sides of the opening. In either case the platforms and ozarkodiniforms must be in a row, with the former in front of the latter ones. The second reconstruction was chosen because it allows the conodont elements to support a lophophore in close proximity to the mouth but situated outside of it. It also explains the disposition of the platforms and platform-like ozarkodiniforms at different orientations relative to the ramiform elements in apparatuses found on shale surfaces. According to this reconstruction the apices of the condont denticles are turned away from the mouth rather than toward its interior. There is probably no other direction in which they could effectively have been turned. A ramiform with a long sharp cusp could not have worked against soft tissue within the mouth. The long posterior bar would have prevented it from functioning as a mobile seizing organ projecting from the mouth. We have already seen that the conodont elements could not have worked against one another as seizing or masticating organs, and that they are more likely to have been the support for a spreading lophophore. As such, they would have been most efficiently deployed along a loop surrounding the mouth, with the denticulation pointing outward.

There remains the difficult question of which side was fore and which was aft on the conodont elements? Did the denticles curve backwards or forwards? The reconstruction of Lindström (1973) shows them to curve backward on the assumption that a basket formed by the posterior processes of certain platforms might have strained the food most efficiently with this orientation. At least one further argument speaks in favour of this orientation. If the concave side of the initial denticle, or cusp, was backward, the anterior part, carrying the cusp and the processes, including the one commonly referred to as posterior, would be close to the mouth. With the opposite orientation the growth of the long posterior process would push the cusp with its

plexus of processes and denticles a considerable distance away from the mouth. The orientation of the lateral processes would then have required that a sharp offset was present at the far end of the apparatus in order to leave the denticles free to carry tentacles. This offset must have moved away from the mouth during growth. Such an arrangement would be detrimental to efficiency because it separates the most strongly denticulated and spreading part of the apparatus from the mouth.

In the reconstruction by Lindström (1973) the planes of the hindeodelliform elements are radially arranged round the mouth. This interpretation is improbable in the case of ramiforms, including many hindeodelliforms, with symmetry transition. The symmetry transition involves a rotation of two anterior lateral processes with respect to the cusp and posterior process, so that in the end member of the series one process becomes anterior and one postero-lateral. If homology is to be preserved, with the posterior processes parallel and all denticulate edges near the surface, the anterior ends of elements belonging to a symmetry transition have to be arranged along an arch, with the planes of the posterior processes essentially parallel. This agrees with the observation that the denticles of hindeodelliform bars found parallel in bundles on shale surfaces can be randomly turned to one side or the other, as if they had leaned over at random from an original orientation normal to the plane of sedimentation.

CONODONTS AND THE CONODONTOCHORDATES

In 1969 William Melton discovered an animal with conodonts inside it in the Namurian Bear Gulch Limestone east of Lewistown, Montana. Four other specimens with identical shape and organization have since been discovered and described by Melton and Scott (1973) and Scott (1973), who referred the animals to the Conodonto-chordata, a new subphylum. The Bear Gulch Limestone is a fine-grained laminated limestone, apparently similar to the famous Upper Jurassic Solnhofen Limestone that has yielded numerous fossils with the flattened forms of soft parts preserved. The associated fauna is dominated by fish and shrimps. There are no burrowing forms except for a number of *Lingula* shells that might have been brought in from clastic nearshore sediments in the vicinity. Scott (1973) also reports two specimens of conodont apparatus that occur isolated from the conodontochordate animals. These apparatuses are of the same type as specimens previously found on shale surfaces. One of them appears to be double, since two pairs of platforms and more than one pair of neoprioniodiforms are visible. Scott interprets these specimens as fragments of the conodontochordate animal.

As orientated by Melton and Scott the animal is 60–70 mm long and 13–15 mm high, with the ends rounded, and the specimens apparently compressed from the sides. The anatomical features of the fossils are constant. There is a sac-like body to which the above measurements apply, although at one end the margin is poorly defined (this applies particularly for the side regarded as dorsal), and the details in this part of the animal might be somewhat arbitrary. At mid-length the fossil has an elliptical body of darker material, one-third as long as the surrounding sac, which Melton and Scott call the 'deltaenteron'. It is attached at one end, regarded as posterior to that margin of the surrounding sac that is regarded as dorsal. By this
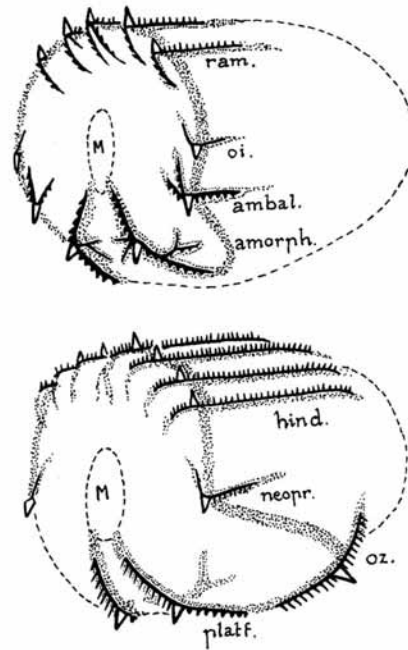
TEXT-FIG. 3. Hypothetical arrangement of conodont elements in prioniodontid (*above*) and polygnathid animal (*below*). M—mouth; ambal.—ambalodiform; amorph.—amorphognathiform; hind.—hindeodelliform; neopr.—neoprioniodiform; oi.—oistodiform; oz.—ozarkodiniform; platf.—platform; ram.—ramiform type of element. Lophophore and branches stippled. Conodont elements stylized, with cusp shown by empty triangle, and processes shown by denticulate lines.

orientation, there is ventrally to the deltaenteron a small, rounded, ferrugineous body called the 'ferrodiscus'. The so-called dorsal margin is simple, and the margin regarded as ventral is double and seems to consist of a narrow fold. Opposite to the attached end of the deltaenteron the margin is cut by a slit that was regarded as the anal pore. At the sharply defined end regarded as posterior, there is a grid-like structure in three of the specimens. Three new species were based on this material.

Conodonts were found in the deltaenteron of four of the specimens, but for the specimen in which no conodonts were found it was stated (Scott 1973) that the mould of the deltaenteron had fallen out. The conodonts are mostly disordered and do not occur in any particular area within the deltaenteron, and they may be more scattered than in other natural assemblages, including those from the Bear Gulch. Their sizes differ greatly; the hindeodelliforms found in one specimen are about 0·5 mm long, those found in another specimen about 1·5 mm. Only one deltaenteron (that of *Scottognathus elisabethae*) contains the remains of a nearly complete apparatus;

however, in this case the platform set occurs twice. In the other specimens several important constituents of a conodont apparatus are missing. For these several reasons I regard the conodontochordates as conodont eaters, rather than conodont animals. Even if this is the case, the discovery made by Melton is very important because it associates the conodonts with another animal. If the conodonts were eaten by conodontochordates, this gives us an idea of the maximum size of the conodont animal. Even an animal that carried 1·5 mm long hindeodelliforms was small enough to pass into the deltaenteron that in its present state of preservation is about 20 mm long. This probably means that the conodont animal was, at the most, five or six times as long as the hindeodelliform bars. With this limitation on size, the animal is more likely to have been oblong or even barrel-shaped rather than long and worm-shaped.

## CONODONT ELEMENTS AS PASSIVE PROTECTION

How could the conodont denticles have been broken and regenerated in the living animal? Since the environment of most conodonts appears to have been free of purely mechanical clashes against hard objects—high-energy shore deposits with conodonts are rare—it is likely that breakage was usually the consequence of contacts with predators, which implies that the conodont apparatus served as a defence mechanism. In particular the function for defence of the very long and sharp denticles with barbs near the apex (referred to in a previous section) appears obvious. According to a well-known synecological rule, the defence must have been displayed to be effective. This means once more that the outer shape suggested the presence of the denticulation. The denticles must have been directed outwards. If attacked, the animal might have been able to contract within the denticulated zone surrounding the mouth; this zone could be radially expanded because the conodont elements were not fused with one another.

If the conodont animals were oblong rather than elongated in their outer shape and carried singly arranged or aligned denticles as their most obvious ornamentation, their aspect might, at least from some directions, have so much resembled certain palaeocope ostracodes that representatives of the two groups may have mimicked one another. The habitats of conodonts and palaeocope ostracodes are known to have overlapped to a great extent, and their stratigraphic ranges are very similar. Any criticism that this theory is extremely speculative is endorsed with conviction, however the idea of a defensive mimicry between the Palaeocopa and the Conodonta might perhaps be worth recording for future scrutiny.

PALAEOECOLOGY

Conodonts occur in many different kinds of marine sedimentary rock, but not all conodonts occur in all lithologies. In particular several authors have remarked on differences in conodont faunas between shallow-water and pelagic facies. To explain such differences Seddon and Sweet (1971) compared the conodonts with the chaetognaths, proposing similarities between the two groups, and suggesting that conodonts, like chaetognaths, were depth stratified. Accordingly the inhabitants of deeper water could not reach the shallow zones. Species living near the surface would occur near shore as well as in the uppermost part of the oceanic water column and would thus

have a wider distribution than deep-water forms. This agrees with some but not all experience (Barnes *et al.* 1973a; Druce 1973). There is, however, general agreement that the conodonts would have belonged to widely distributed, plankton-feeding communities.
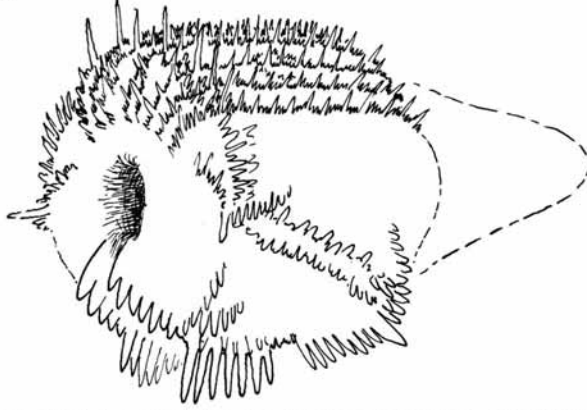
TEXT-FIG. 4. Hypothetical reconstruction of conodont animal of the Superfamily Polygnathacea, with emphasis on the aspect of the lophophore. Length (sa.) of lophophore about 3–6 mm.

THE PLAN OF THE CONODONT LOPHOPHORE

The recurrence of branching according to a limited set of plans, in conodont elements of all stratigraphic ages, suggests that the lophophore consisted of tentaculate frills that branched according to a certain pattern. The idea underlying this interpretation is that the conodont soft tissue was to a variable extent supported by conodont elements, and that the soft structure retained a similar plan even where it was not supported by conodont elements. Evolution in different conodont stocks included differing degrees of support of the lophophore by skeletal matter. Conodont elements preferentially grew from the junctions between branches of the lophophore, and some junctions might have lacked the corresponding conodont elements in certain species, genera, or families. In such cases the skeletal apparatus was incomplete, compared with taxa in which all loci of potential skeleton formation were occupied by conodont elements. Apparatuses with presumably only one pair, or a few pairs, of elements are known from all the major groups of conodonts (Sweet 1970; Sweet and Bergström 1972).

Of all kinds of elements the platforms have the strongest tendency to branch and form accessory denticles. This is particularly evident in the Ordovician *Amorphognathus*, the Silurian *Kockelella*, the Devonian *Pedavis* and *Ancyrodella*, and the Carboniferous *Staurognathus*. Accessory denticle rows, probably corresponding with tentaculate frills, are arranged parallel to the main denticle row, as in the rostrum of *Siphonodella* and several other polygnathids, including species of *Palmatolepis*; or repeatedly at right angles to it, as on *Polygnathus linguiformis* and many gnathodids. The tentacles of these forms might, as suggested by the micromorphology, have been

provided with retractor muscles. It is suggested that these elements were close to the mouth and thus formed the terminus of the lophophore loop.

The relative position of the platform elements and the platform-like ozarkodini-forms is not without problems. Silurian clusters (Rexroad and Nicoll 1964; Pollock 1969) contain fused ozarkodiniforms as well as fused spatognathodiforms, so that neither type of element could have flanked the other laterally. However, well-preserved assemblages may be found on shale surfaces with the posterior processes of spathognathodiforms or other elements of platform type overlapping on the anterior process of ozarkodiniforms, although admittedly this could be due to tele-scoping by contraction of the animal. However, in the Ordovician homologues of ozarkodiniforms and platforms, referred to respectively as ambalodiforms and amorphognathiforms, the ambalodiforms are so strongly arched that it is almost impossible to figure them as aligned behind the amorphognathiforms without much of the denticulation being deeply hidden in soft tissue. This problem could perhaps be solved by assuming that the amorphognathiforms were flanked by ambalodiforms (that are intermediate in shape between the amorphognathiforms and the ramiforms making up the rest of the apparatus) and that in the course of evolution the platforms migrated forwards so as to allow the evolved homologues of the ambalodiforms, i.e. the ozarkodiniforms, to align along the food groove at the mid-line. This is sug-gested by the illustrated reconstruction.

It remains to be seen how the platform elements of each pair might have been arranged relative to one another. Possible arrangements of *Oepikodus evae* (text-fig. 1) illustrate this problem. If the arguments presented above are correct, the cusps could not have been opposed, nor were their points turned in opposite direc-tions, nor were the anterior parts of the elements facing one another. *Oepikodus evae*, like several other elements with the same function, has a terminal twist (Lindström 1973) of the posterior process. If food passed forwards between the elements, the con-cave side of the twist would have collected the food current, provided that the concave sides were turned toward one another. But the concave side faces in the direction of the lateral process that is customarily referred to as outer; hence in this case there would be a discrepancy between the (arbitrary) terminology and the actual orientation of the elements. The suggested orientation could mean that the concave side of the blade of palmatolepids faces toward the mouth, which appears to be a reasonable interpretation.

If we assume that the platform elements supported that part of the lophophore which was the least suited for defensive display, their position might have been ventral. In a preceding section it was argued that the main ramiform elements were concentrated on the opposite side of the animal, so that by this orientation they were dorsal. To judge from the disposition of processes in the ramiform elements, the lophophore loop in this sector had several parallel branches in the posterior direction as well as a variable number of shorter branches in the direction of the mouth.

FEEDING AND LIVING HABITS OF THE CONODONTS

The conodont animal thus sketched was not necessarily very mobile. It might even have been a passive floater, relying on its battery of unpalatable denticles for its pro-

tection. Some conodont animals might have formed colonies. Dispersion took place by ocean currents. This might be a reason why the conodont fauna can differ so strongly between pelagic geosynclinal regions and shelf environments, for example in the Ordovician of North America (Barnes, Rexroad and Miller 1973; Bergström 1973). The food gathered by conodonts might have been both microscopic particulate matter and dissolved material. If this is true we might expect the conodonts to occur most plentifully in areas where such nutrients are abundant, as for instance in environments characterized by upwelling deeper ocean water. Such environments may occur on the margins of oceanic troughs or along submarine rises. The occurrence of conodonts in certain fossil sediments (black muds and trough-rise limestone facies) appears to agree with this prediction.

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