ANTOLOGIA PALEONTOLOGICA
TOMO 2
ISMAEL FERRUSQUIA VILLAFRANCA

TOMO II

FERRUSQUIA V.I COMP.
ANTOLOGIA PALEONTOLOGICA

SOCIEDAD MEXICANA DE PALEONTOLOGIA, A. C.

ANTOLOGIA PALEONTOLOGICA - LECTURAS SELECTAS COMENTADAS SOBRE CONCEPTOS RECIENTES DE PALEOBIOLOGIA.

ISMAEL FERRRUSQUIA VILLAFRANCA, COMP.

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TOMO II

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PRESENTE.

Estimado Dr. Ferrusquía-Villafranca:

Me es grato saludarlo y hacer de su conocimiento, que el trabajo titulado:

"Antología Paleontológica-Lecturas Selectas Comentadas Sobre Conceptos Recientes de Paleobiología".

En fecha reciente se sometió a la consideración de la Sociedad Mexicana de Paleontología para su publicación, se ha recibido el dictamen aprobatorio del Comité Editorial, quien ha recomendado por el tamaño de la obra (702 cuartillas), se le presente como una "Publicación Especial", ya que no podría incluirse en la Revista; relacionado con lo anterior, cabe destacar que el costo de la publicación excede la capacidad económica actual de la SOMEXPAL, por lo que ya se busca la implementación de mecanismos de financiamiento adicional, que permita a la brevedad posible publicar su interesante trabajo, que estamos seguros será de gran utilidad en la docencia y en la investigación paleontológica y de disciplinas científicas afines.

Sin otro particular, al despedirme hago propicia la ocasión para expresarle mi consideración y aprecio.

Atentamente,

Biól. Beatriz Contreras y Montero
Presidenta

PROLOGO

La formación de recursos humanos de alto nivel, es la labor prioritaria de un país, ya que su riqueza y grandeza son en gran medida una función del número y calidad de gente preparada que posee.

En el caso de México esta actividad es todavía de mayor importancia, por la obligación que se tiene de superar el enorme rezago que muestra, con respecto a otros paises, en muchos de los campos de la cultura y la economía, así como la imperiosa necesidad de elevar en términos reales el nivel de vida de todos los mexicanos, apoyándose, claro está, en un desarrollo integral, armonioso y plenamente adecuado a la naturaleza del territorio nacional y a la idiosincracia de su población.

En este sentido resulta muy acertado el esfuerzo que realiza la UAM-Iztapalapa, para alentar a su personal académico a la preparación de textos y obras de índole diversa, que sean coadyugantes eficaces en la docencia a nivel profesional y de posgrado y que subsanen, aunque sea sólo en forma parcial, la necesidad que existe de estas obras en el país.

La presente **ANTOLOGIA PALEONTOLOGICA**, se inserta como una contribución en este noble esfuerzo universitario. El conjunto de trabajos comentados que la integran reflejan los avances recientes en torno al origen y evolución de los seres vivos y su diversificación cronoespacial que los llevó a ocupar todos los ámbitos disponibles integrando así el componente más dinámico del Sistema Tierra, la Biósfera.

La antología pretende ser un vehículo hacia una mejor comprensión de este sistema al que pertenecemos, lo cual sin duda, nos permitiría enfrentar el reto y responsabilidad de conservarlo. En ello va en juego no sólo la supervivencia del hombre como una bioespecie más, sino su misión de hacerlo de una nueva era y una nueva forma de vivir.

La preparación de la obra en si se inició en 1991, cuando el suscrito, investigador del Instituto de Geología, UNAM, y profesor del Departamento de Biología, División CBS, UAM-I, realizó una estancia sabática como docente en la Facultad de Ciencias Biológicas de la Universidad Autónoma del Estado de Morelos, con objeto de proporcionar apoyo al Area disciplinaria de Paleontología, y entre otras cosas, se le encomendó la responsabilidad de preparar una Antología Paleontológica que complementara en lo posible, la formación académica de los estudiantes, poniendo a su alcance, literatura científica especializada y relevante, organizada de manera temática y comentada, para facilitar su comprensión. Esta obra subsanaría parcialmente el gran vacío que al respecto acusa nuestro país, haciendo posible el acceso de material bibliográfico a usuarios potenciales, que difícilmente podrían estar en contacto con él.

La aceptación de tal responsabilidad se hizo de buen grado, ya que como paleóntologo profesional y docente en el área, se tenía plena conciencia de esta necesidad. La realización de la obra constituyó un reto y una experiencia enriquecedora. Pero también implicó un esfuerzo y un tiempo mucho mayores de los considerados, ya que se anlizaron unas 5000 referencias bibliográficas, consultándose casi 900 trabajos diversos, seleccionándose de manera preliminar unos 200 e incluyéndose finalmente sólo 60; aun así, la obra consta de 700 cuartillas. El trabajo académico principal se desarrolló en las bibliotecas de los Institutos de Geología (UNAM) y Mexicano del Petróleo, en México, así como en las del Department of Geological Sciences, The University of Texas-Austin, y el Natural History Museum, Los Angeles, California, en Estados Unidos. No sólo se examinó la literatura, sino que se duplicaron o adquirieron los trabajos más relevantes, muchos de ellos en ese país, por no estar disponibles en México. Posteriormente, la duplicación xerográfica definitiva, la redacción de la obra y la preparación de la bibliografía respectiva, se realizó en el Instituto de Geología.

Con la elaboración de la versión xerográfica de la obra, concluyó la responsabilidad del suscrito ante la Universidad Autónoma del Estado de Morelos, cuyas autoridades ante la la imposibilidad de publicarlo, dejaron ala autor en libertda de buscar los mecanismos para hacerlo, ya que a todas luces los resultados del esfuerzo realizado, merecían ser compartidos con la comunidad académica y quedar a disposición de los estudiantes y maestros en las áreas de Biología y de Geología. De la misma opinión fueron los colegas a quienes se les mostró el trabajo, incluídas las autoridades de la División de Ciencias Biológicas y de la salud, UAM-I, quienes recomendaron presentarla en el CONCURSO DE LA ELABORACION DE LIBROS DE TEXTO Y MATERIAL DIDACTICO DE APOYO A LA DOCENCIA que ofrece esta división cuya convocatoria se publicó el 22 de marzo de 1993.

La adecuación de la obra a los requisitos y lineamientos de la convocatoria, conllevó un esfuerzo adicional enorme consistente en su transcripción completa a un formato de de procesador de palabras. Al efecto el suscrito solicitó y recibió el entusiasta apoyo de sus alumnos de biogeografía, Trimestre 93I, quienes lo ejecutaron en las instalaciones de la UAM-I.

AGRADECIMIENTOS

Una obra como la presente, implica la colaboración y el apoyo de diversas instituciones y personas; a todas ellas el autor les queda muy reconocido. En la fase inicial, la Universidad Nacional Autónoma de México, al través de las instancias del caso -Instituto de Geología y H. Consejo Técnico de la Investigación Científica- autorizó la estancia sabática; la Facultad de Ciencias Biológicas y la Dirección de Investigación y Postgrado de la Universidad Autónoma del Estado de Morelos, amablemente extendieron la invitación para realizar la estancia, ejecutaron las gestiones académico-administrativas correspondientes, y durante ella, tuvieron con el suscrito únicamente amabilidades, brindándole todo su apoyo; por ello, este se encuentra muy agardecido, especialmente con los profesores Biól. Luciano Vargas Mendoza y M. en C. Gerado Avila García, Directores respectivos de esas instituciones. La subsecretaría de Educación Superior e Investigación Científica de la SEP, y el Consejo Nacional de Ciencia y Tecnología, proporcionaron el apoyo económico que posibilitó la estancia.

El trabajo académico conducente a la preparación de la presente Antología, se benefició ampliamente con las discusiones sostenidas con los Doctores James Sprinkle, Keith Young, Jhon A. Wilson y Ernst L. Lundelius, de la University of Texas-Austin; Edward C. Wilson y Craig C. Black, del Natural History Museum, Los Angeles; y Robert Douglas, de la University of Southern, California, quienes compartieron sus experiencias y conocimientos, así como permitieron el acceso a sus bibliotecas particulares, ofreciendo además valiosas sugerencias.

ADVERTENCIA

Aunque la presente Antología se encuentra terminada y se dispone de prototipos, su duplicación xerográfica preliminar multiple, y desde luego, su eventual publicación, requieren la consecución de los permisos pertinentes, que deberán otorgar en su caso, los tenedores de los derechos respectivos -copy right-. Por tanto, deberán realizarse las gestiones necesarias.

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AN ENIGMATIC CHORDATE FROM THE LOWER CARBONIFEROUS GRANTON 'SHRIMP-BED'OF THE EDINBURGH DISTRICT SCOTLAND

Briggs Derek E. G. & Clarckson, Euan N. K.

. 1987 04 15: An enigmatic chordate from the lower Carboniferous Granton 'shrimp- bed'of the Edinburgh district, Scotland. Lethaia, Vol. 20 pp. 107-115. Oslo. ISSN 0024-1164

A new soft-bodied chordate, Conopiscius clarki gen.et sp. now., whit V-shaped scale convering the trunk, and a pair of cone- shaped structures in the head, is described from the Lower Carboniferous of Granton, Edinburgh. It occurs in the shrimp-bed which, although dominated by eumalacostracan crustacean, has also yielded exceptinal preserved examples of ther taxa including the soft parts of conodonts. The new animal may represent a jawless craniate with affinites to Jamoytius. The parallels berween this and other faunas yielding similar chordates (e.g. Jamoytis) may be Taphonomic rather than environmental. Chordate, sofrparts, Conopiscius, Conodont, Lower Carboniferous.

D.E.G. Briggs, Department of geology, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ,England; E:N:K: Clakson, Grant Institute of Geology, University of Edinburgh, West Mains Road, Edinburgh, EH9 3JW, Scotland; 15th July, 1986.

The Diantian Granton shimp-bed is celebrate as the first locality to yield the soft parts of conodonts (Briggs et al. 1983; Aldridge et al. 1986). The fauna is dominated by the shrimp Wasterstonella, unique to this lacality, while the rest of the biota, restricted in diversity, is composed largely of other ligtly skeletized or soft bodied organims including additional crustaceans, wors (most notably polichaetes) and branching organims(? hydroids or algae) (Briggs & Clakson 1983). Rare fish and nautiloids are also present.

The original conodont animal specimen (Biggs et al 1983) preserved feactures which could be interpreted evidence of either chordate or chaetognath affinity. Until more specimen with preserved soft partswere discovered Biggs et al. (1983) preferred to assign the conodonts to a separate conodonta, thus empazising the uniques of conodont elements. Aldridge et al. (1986) have the conodonts as a separate gruop of jawaless craniates on the basis of the recentdicovery three further specimens with soft parts from the same 'shrimp-bed'as the first specimen. In this paper we described an additional soft.bodied chordate from the Granton locality.

CONOPISCUS CLARKI GEN. ET SP NOV.

Derivation of names.- Generic name alluding to the anterior cones and fish-like trunk. specific name after N.D.L. Clark, who discovered the first specimen of this taxon.

Types.- C. clarkin is the type and only kown species of Conopiscius. Only two specimen are Known, both held by the Royal Museum of Scotland, Edinburgh: holotype RSM GY 1986.25.5, part and incomplete counterpart; paratype RSM GY 1986. 25.6.

Diagnosis.- A small elongate craniate with a pair of juxtaposed cone-shaped structures in the head region, and V-shaped scale on the surface of the trunk.

DESCRIPTION

The specimen are preserved in a whistish mineral film (Fig.1), which is presumable the same as that in the associated crustaceand which analysis has shown to be fluorapatite. Neither the body outline, nor any trace of the gut, for example, are preserved, and the feactures which are evident presumably represent tissue that was strenghened in some way and therefore more resistant to decay. The morphology can be described under two headings, feactures of the trunk and those of the head.

Trunk.- An arry of closely spaced V-shaped bands, the apex of the Vs all oriented the same way (presumed pointing forwards). Is assumed to represent the trunk. The Vs from two series (FIgs.1,2): a line drawn through the apexes of those of one series runs parallel to that joining the apexes of other, In both spwcimwns the two series are offset, the Vs overlapping, but not superimposed.Althogh there no dicernible relief, each seriesappears to have lain at a different level; in RSM GY 1986, 25.5 spliting of the slab left the Vs of one series better preseved on the part, those of the other on the counterpart.

RSM GY 1986, 25.5 (Figs. 1B, 2A) preserves traces of abouth 26 Vs in a lengh of 31 mm RSM GY 1986 25.6 (FIgs. 1C, 2B) traces of 21 in 22 mm: the forter clearly represent a larger individual. In RSM GY 1986 25.5 the pexes of bbothseries of Vs are preserved lying off and to the same side of the axis of the trunk indicating that the Vs could not have been symmetrical about the mid-line in that view in life. This suggests that the specimes are flattened in a near lateral as opposed to near dorso-ventral orientation, as the latter would reveal the mid-line of bilateral symmetry. The two series of Vs probably correspond to the left and right sides of the trunk. The angle subtended by the Vs decreased posteioly from c. $55^{\circ\ 40}$ in RSM GY 1986, 25.5, and from c. $80^{\circ 70}$ in RSM GY 1986. 25.6. Is this strunk contrast real, or can difference in angle between the specimens be explained in terms of different orientation to bedding?

Briggs & Willams (1981) have show how different orientation to bedding can result, on flattening, in very different preserved configurations. There in no evidence that the V-shaped bands were mineralized; thus the major agent of flattening is likely to have been collapse (due to decay of softer tisue) rather than compactation and possible rotation. The apparentangle substented by the Vs vary with tilting of the long axis of the specimen to the beding, the degree og variation depending on how wide the trunk was in life. (A comparable example is provided by comparation of the intersommite bound aries in the abdomen of the burgess shale crustacen Canadaspis; Briggs 1978: 466.) Tilting downward anterioly woul decreased the angle sligthly initially; the degree of tilt in this direction requiere of the trunk. Any degree of tilting downward posteroly, on the other hand, would increasethe agle. Thus the contrast the anglesubstented by the Vs in the two specimens may be simply a reflection of different orientations to beding, rather thana real difference between individuals or parts of the trunk, for example. Curvature of the trunk could, in the same way, account for the decreased in the angle of successive Vs posterioly withing each specimen, and the similar gradation in both specimens may reflect a post-mortem curvature. Alternatively the reduction in agle along the length of the trunk may be an original feacture. Rotation of the specimen about the longitudinal axis (away from a prescisely lateral aspect) accounts for the offsenting of the Vs on either side of the of the trunk, which is somewhat greater in RSM GY 1986, 25.6, and also for any slight difference between theangles substented by the Vs in the opposing series.

The narrow strip of apatite which, define the Vs show some variation in which, but this may not be original. (The close spacing and consequent apparent narrowness of the arms of the Vs on one side of RSM GY 1986, 25.5, for example, is probably a fuction of orientation to beding). The leading edge appears slightly more pronouned than the trailing edge (fig. 1B, C), the latter sometimes fading into the matix but no evidence of structure is preserved. There is no evidence that the Vs articulated one another; they separeted by areas of which lack a convering of apatite. Similary there in no evidence of articultations or fractures along the length of individual Vs; they may have been flexible to some degree. the apex of the Vs is rouned rather than angular. In the anterior part of the trunk of RSM GY 1986, 25.6 the angle becomes larger and the VS are splayed corresponding wider. Here a sling indentation atthe apex of the V may correspond to the junction between the two arms (Figs. 1C, 2B). In this anterior part a series of leaf-like structures is evident along one margin (Fig 3), each structure pointing posterioly and corresponding in position more or less onewich the VS. these structures apper to be more heavily mineralized than The Vs perhaps reflecting a greater original thinkness. They may represent their distal terminations or they may be separete.

The nature of the V-shaped structures.- The V-shaped structures suggest two interpretation: they be either muscle blocks or external scales. In the case they would probably reflect the from and distribution of muscle block, but they would be superficial. The evidence suggests that are more likely to be scale. The incomplete nature of the specimens and lack of a body outline (fig 1) suggesst that only the more robust structure have been preserved. The way in which the Vs from twosuperimposed but offset series, one more strongly evident on the part, the other on the counterpart,suggest that they are external. It is not possible to determined wheter the were offset in life,like the alternating myotomess of amphioxus and myxinoids; in any case their relative positions have been affected by tiliting relativeto the bedding. The apex of the Vs is rounded and not angular as in the muscle blocks of fish (the muscle blocks of the lamprey are somewhat rounded due to the lack of a horizontal septum, but not curved to the extent of the Vs in Conopiscius). The preserved Vs are more heavily mineralized along the anterior margin than elsewhere. Ths may correspond with the thickened anterior margin of a scale, but more difficult to reconcile with an interpretation as the soft tissue of a muscle block. On the other hand, in places the arms of the Vs of RSM GY 1986, 25.5 preserve closely spaced fibre-like structures aligned parallel to the axis of the specimens. THese structure suggest trace of muscle fibres. They are most evident, however, where the apatite which delineates the Vs is thinor partially absent. Thus the may represent traces of muscle fibres on the inner surface or lying just beneath a scale. Scanning electron microscopy of a latex replica of the trunk revealed nofurter details of their structure.

Similar chevron-shaped structures have been observed in the Silurian agnatan Jamoytius (Ritchie 1968, 1984) and in Jamoytius-like vertebrates from the Lower Devonian of New York State (Janvier & Busch 1984). The structures in Jamoytius are offset on either side of the trunk (Rtchie 1968.Pl 6), as are those in Conospiscius.They wereoriginally interpreted as remains of myomeres (see discussion in Ritchie 1968:30) but were reinterpreted by Ritchie scale. Forey & Gardiner (1981) briefly reviewed Jamoytius, and readvocated a muscle block interpretation, but their views have been the subject of a recent rebuttal by Ritchie (1984). The structures in the Jamoytius-like vertebrate described by Javier& Busch (1984) are interpreted by them as scales. The majority conform to a V-shaped pattern; some however, are Z-shape with a possible articulation (Javier & Busch, 1984,fig.4). Sucha configuration might represent an obliquely flattened trunk, the so-called articulation corresponding to the junction between the scale on the righ and left side. True Z-shaped patterns,however, are known in some anaspids and cephalapids.

Head.- Both specimens preserved a pair of small curved cone- shaped structures which are assumed to belong to the head region (Fig.1A, 2B). They lie anterior to the V-shaped bands and arepreseerved in relief and apparently strengthened in some way, but there is no unequivocal evidence that they were originally mineralized. Each is just over 2 mm long, and about 1.5 mm broad ot the base. In RSM GY 1986, 25.6 they are clearly associated with the trunk, luing just anterior to the V-shaped band (Fig. 1C, 2B). In RSM GY 1986, 25.5, however, the cone-sphased structure lie some 15 mm anterior of the end the preserved trunk (i.e. about half its length distant), although they are still aproximately on line (Fig.1A). It is not clear whether this separation is due to disarticulation, or whether the cones are in situ and the intervening trunk is not preserved.

The cones of RSM GY1986, 25.6 are surrounded by a rather indistinct mass of minareal; their outlines is clearer in RSM GY 1986 25.5 (Fig.4A, C). in both cases a pair of curved cones is preserved, the convex side in juxtaposition, the concave side facing abaxially, the distal points directed more or less anteriorly. The proximal end of the cones is broad and base concave. The inner of the cones is gently convex; the outer is more strongly concave and show a pronounced change in direction into the elongate tip of the cone. RSM GY 1986, 25.5 preserved tenous evidence of a tiny denticle near the proximal extremity of the outer margin.

The distal extermited of the cones in RSM GY 1986 25.5 (fig. 4A,C) preserved that they were hollow structures. A small quantity of a were mineral infill is present near the distal extremity and similar material is scattered near the base of the cones. The main infill of the cone is an amorphus orange material. Part of the external surface of the cones is preserved, albeit diagenetically altered, in both specimes. It has a characteristic orange-brow colour, particulary when wet. In RSM GY 1986, 25.5 the surface appears to be wrinkled normal to the axis of the cone (FIg. 4A, C). In RSM GY 1986, 25.6 (FIg 4B) it looks similar to the duticle of the adjacent crustaceans. The board proximal part of the cone in both specimens show irregular ridges which are probably the result of the compaction of a holow structure.

It is difficult to discern any recognizable features in the mineralized area surrounding the cones in RSM GY 1986, 25.6 (FIG. 4B). A narrow unmineralized strip runs parallel to much of the concave outer margin of the right-hand cone. It is bouded by a distinct line which convergens with the distal tip of the cone and separates it from the mineralized are beyond. Such a lines is notevident adjacent to the left-hand cone. Other illdefined structures lying in the vicityin the cones in their specimen are more likely to represent fragments of crustaceans than part of the animal.

Scanning electron microscopy of latex replicas reveals the shape and convexity of the cones somewhat more clearly (Fig.4C,D) and in particular show the distal partof one of the cones of RSM GY 1986 25.5 in detail. There is some evidence of tuberculation near the expaneded bases of the cones and along the inner adge of the distal part.

AFFINITIES OF CONOPISCIUS

Clearly the small number of characters contrains a discussion of the relationhips of this organims.The V_shaped structures indicate a cephalochordate or craniate affinity. The absence of scale and of tooth-like conocal structures in the cephalochordates suggest that a craniate affinity is more likely. The V-shaped scale are likely to reflect the morphology of the underying myomeres. The scale were probably flexible; there is no evidence of fractiring or articulation.Nor is there evidence of the horizontal septumcharacteristic of gnathostomes. This indicates that the organims correspond to the 'agnathan'grade.Alternatively the specimens might represent a larva stage, the absence of other larva atributes such as external gills being a function of the preservation.

The silurian agnathan Jamoytis (Ritchie 1968,1984), from the Llandoverian Patrick Burn Formation of the Lesmahagow Inlier (Ritchie 1985), bears scale similar to those in the Edinburgh animal. It is considered to represent a sister-group of the petromizontidis (Janvier & LUnd 1983;Janvier & Busch 1984), although it lacks any tooth-like structure. This assignment is based mainly on the possible on the presence of an annular cartilage, and the nature of the branchial basket.Characteres such as these which. unlike the primitive V-shaped configuration of the scales, might be useful in determining affinity, are not preserved in Conopiscius. Neither are they present in the vertebrates from the Lower Devonian of New York which Janvier & Busch (1984) interpreted as Jamoytius-like. Than interpretation wasbased assentially on the nature and arrangement of the scale and their lack of mineralization. A possible head indicated on one specimen(Janvier & Busch 1984, Fig. 3A) but no detail is evident.Deep V-shaped unmineralized scale however are unknown in the other anapids (Moy-Thomas & Miles 1971) and this character suggest an affinity between Conopiscitius, Jamoytius and the from the Devonian of New York.

In the absence of evidence of the outline or structures within the head the position of the tooth-like structure preserved in Conopiscius cannot be determined.THey may lie near the anterior margin of the head, or more posterioly in a branchial region . Their morphology and arrangament, however, differ from normal teeth.

We are unaware of any closely analougus structures in living or fossil craniate, but one obvius place to seek comparision is among the small numberof other soft-bodied examples known from the fossil record.

The cones in Conopiscius show somw similarity to simple coniform euconodont elements, although they are differentiated by the apparent lack of mireralization, and by their morphology and preservation. Known apparatuses of coniform conodonts consist of more than a single pair of elements, the paired elements varying in morphology (Panderodus apparatuses, for example, consist of pairs; Smith et al. 1987). The cones in Conopiscius are also larger than most conodont elements. The conodonts have V-shaped myomeres but they lack scale, and there in no evidence of an affinity between them and Conopiscius . Alddridge et al. (1986) have interpreted the conodonts as a separate group of primitive jawless craniate, probably lying some where between the myxinoids and heterostracans.

The shape and hollow nature of the cones more closely resemble the horny cusps of myxinoids or petromyzontids than conodont elements, but their number (a single pair) and arrangement are not suggestive of a lingual apparatus. P: janvier (pers. comm.), however, points out than the transverse lingula lamina in the lamprey Geotria is similar-it becomes bidentate during the spawning run (HUbbs & Potter 1971). Conopiscius lacks any as those in the dantal apparatus of Geotria. The only known fossil myxinoid (Bardack 1985) has yet to be describet in detail, but although it has oral tentacles, it lacks any tooth-like structures. Neither of the two known specimen of fossil lamprey, Mayomyzon pieckoensis (Bardack & Zangerl 1968) from the Westphalian MAzon Creek fauna of Illions and Hardistiella montanensis (Janvier & Lund 1983) from the Namurian Bear Gulch Limestone of Montana, preserves an oral 'sucker.'A circular oral apparatus does occur in the Mazon Creek agnathan Pipscius zangerli (Bardack & Richardson 1977; Bardack 1979), but this stryeture consists of articulating plates rather than discrete cones .A second enigmatic softboided agnatha from the Mazon Creeck fauna, Gilpichthys greenei, displays a complexbuccopharygeal apparatus which consists of block-like muscle masses which are segamentally arranged. some 20 segments bear elongate frang-like teeth at least superficially similar to the cones in Conopiscius. Those at the anterior least,may have been everted to function (Bardack & Richardson 1977; Bardack 1979). The apparatus is much more complex than the simple pair of cones in the Edinburgh animal, and while it may be analougus,it provides no evidence of affinity.Pipscius and Gilpichthys are clarely agnatha, although the specimens may be juveniles(Bardack 1979 : 507). Janvier (1981, Fig.17) considers Gilpichthys to be related to the Myxinoidea.

Esconichthys apopyris Bardack, 1974 is the most abundant vertebrate in the Mazon Creek biota. Bardack (1979) concendes that it is not certain to which group of vertebrates is should berefered, but suggests than it may be a leval lungfish with a retared rate of ossification when comparated with living forms. Esconichthys bears two pairs of hard structures in the head region ,the anterior pair similar in outline to the cones in Conopiscius. Although the firts paired structure in Esconichthys is concave outwards, like than in Conopiscius , the of the pair are not preserved in juxtapotition and the outer, concave margin bears 20-25 fine needle-like projections.The position of the structure in Esconochthys led Brdack to conclude that they were unlikely to have fountioned in feeding either in association with the mouth or the gill arches. Their nature remains uncertain.

Most specimens of Esconichthys are flatted dorso-ventrally and preserved the hard structures flaking the axis of the head. Only laterally flattened specimens show clear evidence of myomeres. The hard structures are rarely evident in lateral aspect; there in equivocal evidence (Field Museum of Natural History PF 9761, for example) that they lie dorsalof the eyes. It is not Known whetre they would apper juxtaposed in laterally flattened specimens, but as they are clearly separate they are unlikely to adop the precise configuration seen in the specimens of Conopiscius. In adittion the presence of scale in Conopiscius renders any relationship between it and Esconichthys unlikely.

Shram (1979) described a pair of elements in the Lower carboniferous woerm Soris laboisus from the Bear Gulch Limestone of central Montana which are very similar in outline to the structures in Conopiscius. He considered the worm to be a polichaete, but it preserves insuficient characteres to allow in to be assigned to a family or order. Little detail of the jaw elements is preserved, but there is a slight indication that the convex margin of the cone might be serrate (Schram 1979). The elements are a little smaller than those in Conopiscius. Any similarity is undobtedly convergent. Similar structures werenoted in the content of one specimens of the conodont-eating animals from the same lacality (Conway Morris 1985).

Neiter the scale indication of the affiniti of Conopiscius does not represent a larve of the paleoniscid Rhandinichtys , the only fish so far from the associated fauna, and is unlikely to reoresent a larval gnathostome. It probably represenst a jawless craniate and the similarity of the scale to tose of Jamoytius suggests an affinity.

SEDIMENTARIA ENVIRONMENT

The is between (1) Conopiscius, (2) Jamoytius from the lower Silurian Lesmahagow inler, central Scotlan, and (3) the Jamoytius-like vertebrate of the Lower Devonian Manlius Formation of New York state prompont a comparasion between be associated boita and sedimentary seting of the three ocurrences, particulary in the ligh of that drawn between those of 2 and 3 by Janvier & Busch (1984).

(Busch (1983) and Janvier & Busch)1984) recorded the following taxa in associated with the Jamoytius-like vertebrate at locality 127 in the Manlius Formation: Ceratiocaris sp., Cystiods,crinoids, trilobites, ostracodes, brachiopods,bivalves, gastropods, trepostome bryozoans, favositid corals and tentaculitids. The Jaytius-like vertebrate are preserved in organic darkbrow to black shale occur as lenses in coarse-grained, cross-bedded, crinoidal calcarenites at the base of an upward shallowing unit (Punctuated Aggradational Cycle, Busch 1983). Janvier & BUsch interpreted the environment as shollow, nearshore, carbonate shelf-open water of normal or slightly higher salinity. The faunal list combines specimens from both shale and calcarenites; sahle from which the vertebrates were collected yield only rare crinoid columnals and brachiopod fragments (Busch,pers, comm). Busch (pers, comm.) envisages the shale as the siliciclastic mud filling of ripple troughs and other minor tophograpic depressions in the subtidal environment. The algal laminites, the predomonant lithology immediately above (Susch 1983, Fig 5, Janvier & Busch 1984, Fig.2) represent shallowing through to supratidal conditions. Janvier and Busch compared the occurrance in the Manlius Formation with that of Jamoytius in the Silurian near Lesmahagow, SCotland. the Jamoytius horizon in the Patrick Burm Formation (in the Lesmahagow inlier) yield a fauna wich is in some respects similar to that of the Manlius Formation in that it includes anaspids(i.e Jamoytius) and Ceraticaris. The more characteristically marine taxa (crinoids, trilobites,bryozoans, corals) which occur in the calcarenites associated with the shale in the ManliusFormation, however, are absent at Lesmahagow. It is possible, however, that the Manlius vertebrates were introduced with the silicilcastic muds which preserved them. The sedimentology at Lesmahagow has yet to be interpreted in detail. the fossils occur almost entirely in finely laminated grey-black carbonaceous silstones (Ritchie 1968: 24). Janvier & Busch (1984). conclude thatJamoytius and the associated fauna probably inhabited a shallow, somawhat restricted, near-shore environment, much the same as we have described for our association in the Lower Devonian of New York. The comparision is too general to allow any detailed conclusion to be drawn. Janvier & Busch consider that these two anaspid-phyllocarid associated probably lived in marine waters of near normal salinity, but were nevertheless tolerant of salinity fluctuations. The evidence for their degree of tolerance is circumstancial, however, based on the nature and diversity of the associated fauna.

The Granton shrimp-bed also yield a low diversity community dominated by arthropods, in this case the shrimp Waterstonella rather than a phyllocarid (Briggs & Clarkson 1983). Waterstonella, like the Phyllocarids, was apparently restricted in its distribution (it is unique to this locality). In this case however, the anaspid equivalent (Conospiscius) is much rare. The sedimentology insicates a shallow brackish lagoon which was subject to periods of emergence and occasional brief marine transgressions (Cater in press). Such a sea-level rise may have introduced Conopiscius, with subsequently perished as a result of abrup changes in oxyen levels (due to sting up of stagnat botton waters of algalblooms) with the fauna which became established.

All three ocurrences represent a nearshore subtidal to supratidal setting and are associated with organic rich laminated sediment. The condittions evidently inhibited decay, presumable due to a reduction in oxygen levels. The similarities may be merely a reflection of similar thaponomic circunstances leading to soft tissue preservation . the recent report of only one specimens of ?Jamoytius among the hundreds od fist collected fromthe lacutrine Middle Old Red Sandostone Achanarras fish bed (Trewin 1986:38), however, mayindicate a decreace from marginal marine to lacustrine environments. This suggestion can only be considered a tentative model for future testing, in view of the small number of known occurrence of Jamoytius and Jamoytius-like forms.

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Fig. 1 Conopiscius clarki. A. B. RSM GY 1986.25.5 part. A. Relarive of cones and trunk. *2.3 B. Trunk, * 3.6. C. RSM GY 1986.25.6 *3.6.

Fig. 2 Conopiscius clarki. Explanatory camera lucida drawings for comparison with Fig. 1. The two series of Vs are distinguished diagramatically - those on one side are shown as a solid line, those on the other stippled. The original thickness of the Vs is not depicted - their anterior margin, however, corresponds to the anterior edge of the line on the diagram. A. RSM GY 1986.25.5 part. B. RSM.1986.25.6.

Fig.3. Conopiscius clarki. RSM GY 1986.25.6 marginal structures. *14.2.

Fig. 4. Conopiscius clarki. anterior cones. A. C. RSM GY 1986.25.5. A in ordinary light. *27. C. Scanning electron mocrograph of latex replica. * 36.5. B. D. RSM GY 1986.25.6. B in ordinary light, showing an indistinet mineral mass surrounding the cones *25. D Scanning electron micrograph of latex replica, showing distal part of cone.92.

Figura 1.

Derek E. G. Briggs and Euan N. K. Clarkson

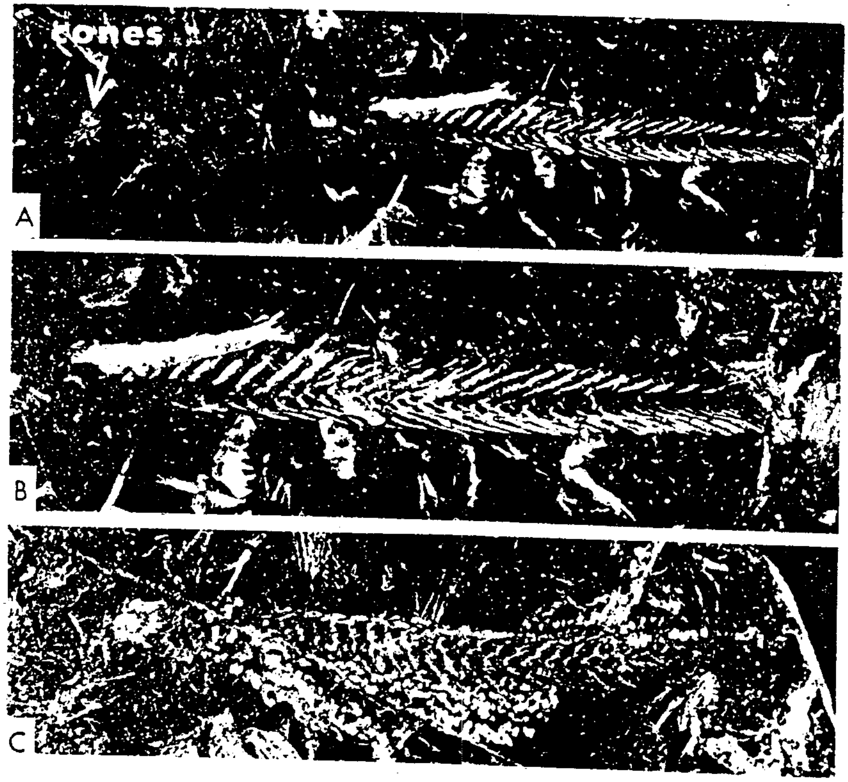


Figura 2. Derek E. G. Briggs and Euan N. K. Clarkson

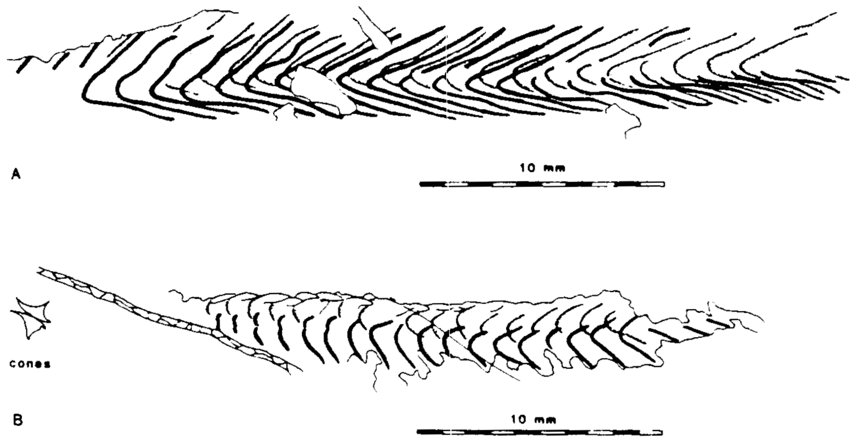
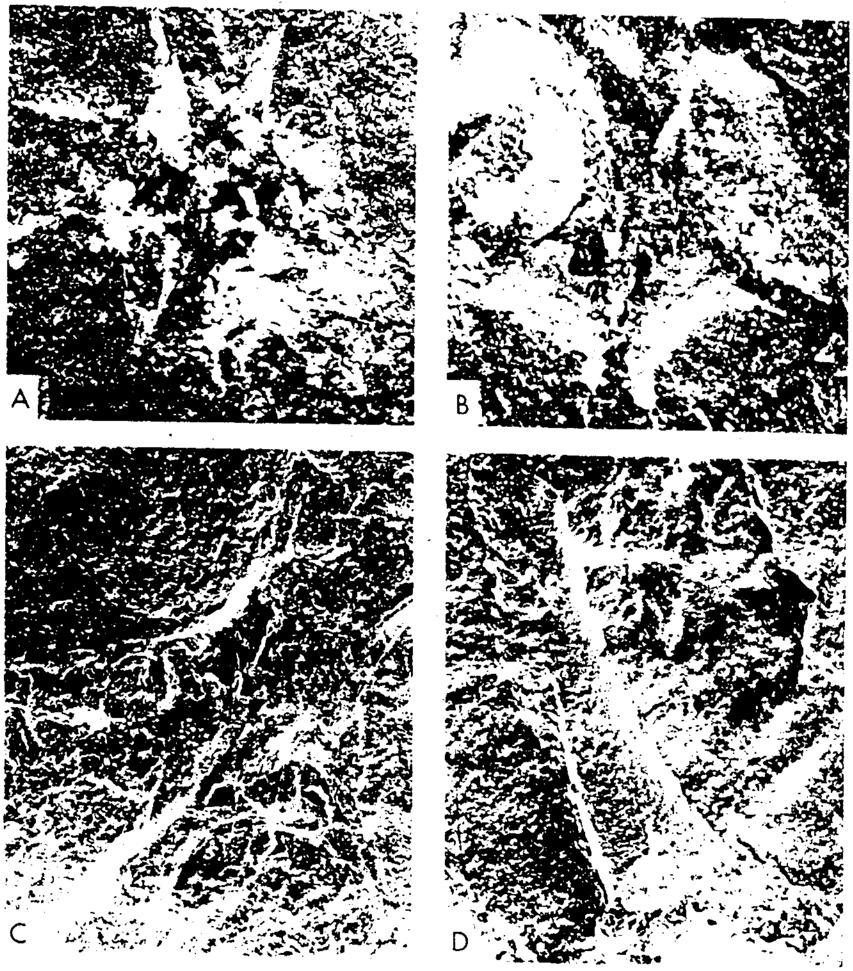


Figura 3. Derek E. G. Briggs and Euan N. K. Clarkson

Figura 4 Derek E. G. Briggs and Euan N. K. Clarkson



CAPITULO 5 FILTRADORES Y DETRITOFAGOS

5.1 Preambulo

En este capítulo se presenta información sobre organismos bentónicos , tanto de elementos epifáunicos como infáunicos , organizados en función de su modalidad ingestiva principal captar mediante mecanismos diversos de filtración, partículas alimenticias inertes o micropesas, que se encuentran suspendidas en el medio acuoso , por lo que a tales organismos se les designa indistintamente como filtradores o "suspensófagos", tal modalidad implica la existencia de corrientes que transporten alimento particularizado al organismo consumidor, por lo que tales mecanismos generalmente incluyen dispositivos generadores de corrientes y estucturas de retención o selección. La otra modalidad es la captación de partículas alimenticias o micropresas presentes en el sedimento del fondo marino , ingiriéndolo directamente y realizando la extracción del material alimentario en el interior del cuerpo del organismo consumidor - no fuera como en el caso anterior - concretamente en su tracto digestivo . El sedimento a ingerir puede ser simplemente "barrido" del fondo , y luego tragado , o puede ser "barrenado" activamente , cavando "galerías" y removiéndolo -bioturásndolo- extensamente . Dado que al sedimento tambíen se le designa material detrítico o simplemente detrito, a los organismos que lo consumen se les conoce como detritófagos .

Cada una de estas modalidades puede realizarse mediante estrategias de vida sumamente diversas , que a su vez implican disenos morfoestructurales particulares cuyo número puede ser en teoría muy grande, pero que se han realizado en la práctica en un número bastante menor, correspondiendo cada uno de los diseños básicos a un "plan" fundamental estructural ("grundplan") diferente , que ahora se reconoce como típico o característico de cada phylum. Tal diseño morfoestructural le permite a ese grupo de organismos explotar de manera peculiar al ambiente "apropiándose" de hecho de una zona adaptativa o de un segmento del hipervolumen ecológico. Tal apropiación sin embargo, no es permanente , tiene que ser mantenida activamente , quedando sujeta a las presiones de selección y a las contingencias del cambio ambiental - en gran parte dependiente de factores geológicos que evolucionan a su propio ritmo , y a cambios relacionados con la presencia y/o accíon de factores "extraordinarios" - periódicos o no , como el supuesto impacto de asteroides , o enfriamientos globales - que imponen modificaciones de gran enbergadura al ambiente , en tiempos geológicamente muy breves , y que presumiblemente afectan el curso de la evolución de estos grupos filogenwticos abriendo posibilidades -promoviendo así la diversificación - o reduciéndolas - a veces totalmente , ocasionando la extinción.

Ello se traduce en una serie sucesiva de cambios, verificables en el registro fósil más facilmente perceptibles cuando se estudian secuencias de registros - geológicos o paleontológicos , es decir estratigráficos líticos o de fósiles - y se les compara regional o globalmente. De ahí la nesecidad de documentar tan ampliamente como sea posible tales registros , de correlacionarlos y de interpretarlos , tareas que constituyen la base de la investigacipn en Ciencias de la Tierra , incluida la Paleobiología.

La tesis de la "permanencia" relativa de los "roles" ecológicos y la diversidad espaciotemporal de los "protagonistas" de este complejo drama geobiológico , expresada anteriormente y que sirve de encabezado a esta sección se ilustra en el presente capítulo, mediante la selección e inclusión de los siguientes trabajos:

Los dos primeros trabajos tratan sobre cuestiones teóricas introductorias al estudio de los metazoarios. En el primero, Jan Bergstrom diserta sobre el origen de los phyla animales y el reconocimiento de un nuevo phylum ancestral a muchos de ellos, el Procoelomata. Postula que los rasgos propios de los deuterostomados tienen carácter de "derivados" con respecto a los prosostomados, discute la significación del metamerismo y del surgimiento del celoma, y compara este modelo teprico con el registro precámbrico de metazoarios; concluyendo que los cambios de este diseno básico, expresados en el surgimiento de los varios phuyla deuterostomados, son de carácter macroevolutivo y tiene que ver con modalidades de locomoción y de alimentación - que son funciones vitales básicas -.

En el segundo artículo, B. Runnegar y Bengtson discuten la significación biológica evolutiva y filogenéica de la adquisición de un esqueleto mecánico mineralizado. Señalan que el material usado es diverso - principalmente calcáreo o silíceo - el proceso ocurre en grupos diferentes, en un lapso geológicamente breve - la transición Proterozoica-Cambrica - y concluyen que el proceso muy probablemente constituyé una respuesta a presiones de selección tal vez inducidas por depredadores. A su vez la biomineralizacipn esquelética, abrió amplias avenidas a la evolución, expresadas en la gran plasticidad que al disponer de un soporte mecánico, podían permitirse entonces los seres vivos.

La segunda parte del capítulo ests dedicada a los organismos filtradores, e incluye cinco trabajos, cuatro de ellos dedicados a otros tantos grupos taxonómicos: Francoise Debrenne, arqueocistidos; Paul Taylor y Gordon Curry, bryozoarios; A. Rowell, braquiopodos y Louis Lidjedhal, bivalvos. El otro trabajo, por David Bottjer y William Ausich, discute la ecoestratificacipn en filtradores, y constituye una excelente introduccipn al tema, por lo que se le ha puesto como la primera selección de esta parte.

La ultima parte se dedica a los detritófagos ilustrándose este "rol" ecológico con ejemplos de los grupos tratados en los trabajos de: Dieter Walossek y Klaus Muller, crustaceos cámbricos; Raimund Feist y Evan Clarkson, trilobites devónicos; Philip Signor, gasterópodos; y James Sprinkle, equinodermos. Este último también incluye a equinodermos no detritófagos, en esta panorámica del registro fósil del phylum en conjunto.

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5.6CONSIDERACIONES PALEOBIOLOGICAS

5.6 (A) The origin of animal phyla and the new phylum Procoelomata

JAN BERGSTROM

LETHAIA

Bergstrom,Jan 1989 07 15: The origin of animal phyla and the new phylum Procoelomata. Lethaia.Vol.22,pp.259-269.Oslo.ISSN 0024-1164.

A model of metazoan evolution presented previousli(Bergstrom 1986 in Zooloica Scripta 15) explains deuterostomian characters as derived from protostomian ones through loosenings of the constraints in the spiralian type of morphogenesis.This fits phylogenies derived from studies of molecular sequences.Themodel helps explain(1) the well-known mixture of proto and deuterostomian features in several groups; (2) the dificulties in making a phylogeny based on comparative anatomy, and (3) the fossil explosion in the Cambrian. Since protostomian features such as ciliated locomotory sole and a pelagic larva with ciliary bands are widely distributed in branches of the phylogenetic tree, they must have been present in the stem of the tree. Most probably the stem forms were pseudosegmented, which helps explain how segmentation, oligomery and non-segmentation could evolve repeatedly in derived groups. Origination of new phyla involved macroevolutionary changes primarily in the mode of feeding and locomotion. The stem phylum, from which most other phyla appear to have been derived directly, is here named the Procoelomata. Macheridian-type animals are referred to it.

The Ediacaran-type Precambrian fossils cannot be placed in the metazoan evolutionary tree. Biochemical evolution, Cambrian fossil explosion, Deuterostomia, eukaryote evolution, Machaeridia, macroevolution, Precrambrian fossils, Procoelomata, Protostomia. Jan Bergstrom, Geological survey of Sweden, Kiliansgatan 10, S-223 50 Lund, Sweden;present addres: Swedish Museum of Natural History, Palaeozoology, Box 50007, S-104 05 Stockholm, Sweden; 8th March, 1988. Sequences of nucleotide bases and amino (or nucleic) acids have been extensively mapped during the last 20 years and used for studies of molecular evolution.The maximum parsimony method selects the evolutionary tree which involves the lowest number of mutations in the particular type of molecule. Optimally, this tree should show the most likely path of real evolution. However, it should be stressed that not all sequences are equally reliable, and the reasons for this are not well understood. In simple nucleotide base sequences in particular, the most parsimonious trees often deviate strongly from what seems to be likely evolutionary pathways. A good example of such confusion is the 5S rRNA trees for Metazoa published by Hendriks et al.(1986), who also disscus the obvius problems with the material. The larger 16S rRNA and 18S rRNA appear more useful, particularly in combination with other criteria (Wolters and Erdmann 1986; Field et al. 1988). Whatever kind of sequence is used, it is necessary to exclude positions of high variability in the comparisons (e.g. Wolters and Erdmann 1986:156). In the case of cytochrome c we are in a position where some results can be evaluated. A comparison between evolutionary trees for the Vertebrata based on cytochrome c and on paeontology/comparative anatomy shows a virtual identity in all details (Bergstrom 1986, Fig.1), which is very good evidence of the potential usefulness of amino acid sequences. The metazoan phylogeny as represented by the evolution of cytochrome c (as summarized by Bergstrom 1986) and globin (Goodman et al. 1988) forms the main biochemical basis for the discussion below. It should be pointed out that Field et al.(1988) confirm the basal position of the platyhelminths and the closeness of arthropods and deuterostomes, but place the molluscs with the anellids. This seems to be a striking difference, but a phylogenetic analysis of the sequence data indicates that the resolving power is to small for mapping the branching pattern above the aschelmint level.

Anyway, all trees based on sequence analyses agree in deriving deuterostomes, as well as other animal groups with deuterostomian type characters, from protostomes. Althoug the phylogeny chosen here may not be correct, the conclutions on the anatomical evolution, the failure of comparative anatomy on the phylum level, and the Cambrian fossil explosion are not affected by even quite large rearrangements in the phylogenetic tree. Fig.1.Major shifts in the locomotory and feeding behaviour leading to the initiation of new phyla (cf.Fig.5). The starting-point was a slug-like Precambrian animal. A shared choice of behaviour led to parallel evolution in morphological and anatomical respects, as is best demonstrated by the sessile and filtering tentaculate groups. Most new phyla were "traped" in their new roles. The deuterostomia form a remarkable exception: the major shift led to such profound changes and simplifications that this group could form a secondary stem from which new phyla evolved, again through new major behavioural shifts (cf. Fig. 2).

PROTOSTOMIANS AND DEUTEROSTOMIANS

The split of triploblastic animals into protostomians and deuterostomians once represented a great step forwards in the understanding of animal organisation. The names refer to profoundly different modes of mouth development during ontogeny, but there are also a number of other characters typical of each of the two groups, which were supposed to form two main branches of the animal kingdom. This view has been generally accepted by zoologists for decades. However, as written in every textbook (e.g. Meglitsch 1972:671-672), proto- and deuterostomian characters are curiously mixed in several groups, a circumstance that casts serious doubt on the idea of two main branches. Moreover, no adults have fitted into the evolving stems, and in drawn representations of the phyletic tree the stem animals have commonly been represented only by larvae.This is cearly unsatisfactory, as adults must have lived and served as raw material for new phyla. In practice, understanding of the relationships between phyla and their origins has been at static level for many decades. The phyla were as separated from each other in the Cambrian as they are today. It is symptomatic of the situation that a book entitled The Origin of Major Invertebrate Groups (House 1979) hardly deals with the origin of phyla, except for a hypotetical discussion in one of the 18 chapters.

Origin of animal phyla.

Contrary to conventionally constructed evolutionary trees(e.g.Nielsen 1987), the shape of the tree used herein is entirely independent of judgments on morphological similarities, speculations on the reliability of various features, and hypoteses of morphological and anatomical evolutionary directions. Contrary to conventional methods, its is the tree that is the primary result, while conclusions on the bodily evolution come only afterwards. At the same time, the general character of the conclusions makes them fairly independent of the detailed shape of the tree. Studies of some organic molecule sequences indicate that the origin of the metazoans may be close to that of the flagellated protozoa(Lyddiatt et al.1978; Goodman et al.1975;Wolters and Erdmann 1986). Characteristic of the metazoans is of course that they are multicellular, and further that they have discrete organs.The first metazoans were most likely simple ciliated forms similar to the planula larvae of cnidarians. The cnidarians have a basically dipoblastic organisation, wich means that there are virtually no cells between ectoderm and endoderm. The planktic life which supposedly caused the origination of this phylum alsocaused the characteristic radial symmetry. In the sea, the important poving directions for animals with poor swimming ability is up and down, and therefore bilateral symmetry is less efficient than radial symmetry.

No change in this respect occurred with the development of sessile generations. Ctenophores are often compared with cnidarians. They may have a rudimentary third cell layer; in other words they may be triploblastic. They lack the cnidoblasts typical of cidarians, and they move by means of cilia rather than by muscles, as cnidarians do. An origin among flatworms has been suggested (e.g.Hadzi 1963) and is appaeling, although it is probably better to think of an origin from the general flatworm level than one among extant flatworm groups with all their specializations. If so, ctenophores presumably parallel cnidarians in having an origin associated with the adoption of a planktic life. This would explain the similarities between the two groups as well as the great differences. Progenitors of fltaworms (platyhelminths) selected the ocean floor as their habitat (Clark 1964 and in House 1979:67). For locomotion they used their ciliated ventral side. Egg cleavage adopted a determinate spiral pattern. A primary larva with ciliated bands in present in poycladid turbellarians. This combinations of characters is extremely significant. It is found in a number of phyla, although the originally adult character, the ciliated locomotory underside, is commonly preserved only as a larval feature(adults of turbellarian flatworms, nemertines, gastrotrichs, some rotiferans, the male of the echiurid Bonellia, some archiannelids, molluscs; larvae of endoprocts, spinculids, pogonophorans, phoronids, bryozoans and enteropneusts; Jagersten 1968; Kaestner 1969:275; Norrevang 1970;163; Salvini-Plawen 1972:315,333,336; Brasier in House 1979:126). It is notable that it is still present in adult Mollusca.

Biochemical evidence (summary in Bergstrom 1986; Goodman et al. 1988; Field et al. 1988) indicates that a number of phyla diverged from the main stem before the molluscs. Thus, the flatworm-molluscan or primitive spiralian characters mentioned above must have characterized much of the main stem(Fig. 1.5). some degree of organ repetition (pseudosegmentation) was presumably also developed rather than oligomery or true segmentation. For the first time this gives firm ground to the study of the origin of phyla: we ultimately realize that at least most protostomian phyla evolved directly from a basic stock of slug-like animals with spiral cleavage, a ciliated planktic larva, and a ciliated ventral side for locomotion on the sea floor.In such a model there obviously could not have been a successive development of characters from one phylum to the next.For instance, the biochemical evidence inicates that the segmented annelids and arthropods are apart on the phylogenetic tree (Lyddiatt et al. 1978;Goodman et al.1988), and by inference that the shared ancestors were slug-like animals without true segmentation but probably with pseudosegmentation. Virtually alone among tripoloblastic animals, platyhelmintes lack an anal opening (except in Haplopharynx; Gibson 1972:189).

The next step in the evolution consequently involved the acquisition of an anus. Such a structure is found among the nemerteans, derived from platyhelmintes and therefore not representing a separate branch from the main stem (e.g. Gibson 1972:187-189). The next animals to branch off from the main stem, according to the biochemical evidence, were a group including the nematodes. Opinions differ asto wheter the Aschelminthes are a natural group or not. I regard it as probable that they are, provided that the endoprocts are not enclosed(cf. Lang 1963). Such a group may contain the Rotatoria, Nematoda, Gastrotricha, Loriciferida, Nematomorpha, Kinorhyncha, Priapulida, and Acanthocephala. It is also possible that the Gnathostomulida, Tardigrada and Chaetognatha belong here. It is characteristic that this groups share the loss of the primitive pelagic larva, which indicates an early loss of the primitive pelago-benthic life cycle(cf. Jagersten 1968).The cycle could have been holobenthic, as adhesive feet, tubes or papillae are found in all typical aschelmints groups except for the parasitic ones, and also in chaetognaths (Spadella). Also the ciliated locomotory ventral side is lost throughout, except in the Gastrotrichia and some Rotatoria. In other groups, external cilia are lost completely. Well-known features which may be considered as synapomorphies include the presence of the adhesive organs just mentioned, a pseudocoel(body cavity supposedly derived fron the blastocoel and usually not lined whith epithelium), a cuticle which is often striated or annulated, and a cuticular lining of the proctodeaum. There also tends to be a special pharyngeal bulb, mouth stylets, and an almost disymmetric to radial cross section of the body.In all, this is a higly characteristic combination of features and not something that would be expected in a number of groups which are similar only due to convergent evolution. Sequence analyses indicate that the remaining phyla branched of at a higher level.

In comparision with aschelminths, the annelids have added a circulatory system(a blood-like fluid is actually found also in priapulid aschelminths; Mattisson and Fange 1973), which may be a synapomorphic character uniting the remainder of the animal phyla(although absent in the Sipunculida and Endoprocta and only vestigial in bryozoans; Carle and Ruppert 1983).

The most distinctive characteristics of the annelids are the segmentation and the well-developed coelom forming a hydrostatic skeleton. These features most probably evolved as the direct result of a shift of locomotory habits from ciliary gliding to peristaltic burrowing at the very origination of the phylum(Clark 1964). Echiurids and sipunculids are worm phyla without segmentation and with poor burrowing ability; they feed more or less with the aid of cilia. They may be closely related to annelids. If so, their lines probably diverged before the development of true segmentation. Another basic specialization from the primitive slug-like condition of the shared stem group is the acquisition of a sessile filtering mode of life.This could fairly easily have been the result of the paedomorphic retention of the mode of feeding found in the trocophora-type of larv, found for example in annelids, bryozoans, and molluscs.Of the filtering groups, the endoprocts are indeed little more than a trochophora set on a stalk (e.g. Meglitsch 1972:251).

Other filtering "tentaculated" phyla are the Bryozoa, Brachiopoda and Phoronida. As just mentioned, sipunculids and echiurids have a related mode of feeding. Pogonophorans parallel tentaculates and no doubt arose throug paedomorphosis, but their segmented tail indicates that they derived from annelids rather than from a stem phylum. All available sequence data indicate that the main arthaopod groups are interrelated, but it is no clear if they are the result of one or two divergences from the main stem(Lyddiatt et al.1978; Bergstrom 1986; Goodman et al. 1988; field et al. 1988). In the later case, they belong to two disctinct arthropoda phyla, the Uniramia and the Schizoramia, respectively (Manton 1973; Bergstrom 1976). The names reffer to the basic construction of the legs. The uniramians, including myriapods and insects, have unbranched legs. They pick or grasp their food below or in front of the mouth and chew it with whole-limb jaws. The schizoramians, including crustaceans and trilobitomorphs(and by shared ancestry the chelicerates) have branched legs, food collectingn behind the mouth, and gnathobases for chewing. Again the basis for the origination of this phyla must have been the aquisition of a new mode of locomotion associated with the development of limbs and segmentation. The ancestral uniramian was probably a benthic crawler without swimming ability, while the ancestral schizoramian is thought to— have been a swimming animal (Bergstrom 1981:11). As locomotion was on or above the sea rather than burrowing whitin it as the initial annelids, there was no extensive development of any coelom(except on the onychophorans, which may not belong here), and the skin rather than the coelomic fluid was used as a skeleton(again with the onycophorans forming the exception). As indicated above through the position of the tardigrades, an additional arthrpodization event appears to have occurred among the aschelminths. Anomalocaris of the Cambrian Burgess Shale may represent still another such event, possibly within the aschelminth frame. Thus again we are facing the possibility of parallel evolution of a particular type of organization perhaps several times. In a way it is easy to understand the origin of molluscs. They retain virtually all of the characteristics of the main evolutionary stem. This original character is so striking that molluscs are frequently compared with platyhelminths and sometimes even derived from "turbellariomorph" ancestors(Vagvolgyi 1967; Salvini-Plawen 1972:316-322, 1982; Clark inHouse 1979:67; Dzik 1987; disscusion and references in Wingstrand 1985:82).

Together with the wide distribution of primitive (spiralian) characters among other phyla, the position of the molluscs in a branch of the tree is firm evidence that the stem group must have retained the primitive features and most other phyla must have been derived directly from a stock with these primitive spiralian features. In effect, the molluscs therefore do not constitute still another revolutionary shift in feeding and locomotory pattern. Instead they form virtually the remains of the stem group. However, there are some features which may separate them as a distinct phylum, particularly the successive loss of pseudosegmentation and the development of a shell and perhaps a radula. It may be time to reinvestigate the systematic position of the aplacophorans. It could that they are not true molluscs but surviving members of the procoelomate stock. In this connection it is pertinent to note that locomotion trails made by a molluscan-type foot or sole are among the oldest trace fossils known (e.g. Brasier in House 1979:134-135 and Fig. 3). It remains to consider the deuterostomian phyla (Hemichordata, Echinodermata and Chordata). The origination of the deuterostomians is difficult to understand in detail, but their position within the protostomian evolutionary tree is acertained by different molecule sequence studies, although the position varies (Lyddiatt et al.1978; Hendricks et al. 1986; Bergstrom 1986; Goodman et al. 1988; Field et al. 1988). Salvini-Plawen (1972:354) saw no difficulties in deriving the hemichordate-echinoderm type of larva from a primitive trochophora of "Hüllglocken" type. Presumably the origination was associated with extreme paedomorphosis and simplification coupled with a complete loss of the developmental constraints of typical protostomians. The paedomorphic aspect including a filtering mode of life, which today is preserved only in some hemichordates and echinoderms (Fig.2). Again, therefore, we discern the rise of a tentaculated group, and again this development led to the development of a few coelomic compartment, as in bryozoans, brachiopods and phoronids (cf. Cclark 1964 and in House 1979). Then several steps were needed before the chordates evolved. The deuterostomian phyla therefore did not evolve directly from the stock of slug-like animals which gave rise to other phyla, but from something new and very different.

A place for problematic scaly fossils?.

Bengston and Conway Morris (1894) recently attempted to reconstruct the Cambrian Wiwaxia (Fig.3A-B) and Halkieria. The reconstruction shows a sug-like animal covered with variously sized and shaped hollow scales or elitra. The identification of a tooth aparatus is highly interesting; it is said to be reminiscent of a radula and therefore adds to the similarities with molluscs.The most recent attempt to summarize the knowledge on problematic scaly animals and to classify them was made by Dzik (1987), who considerably widened the concept of the class Machaeridia (Fig.3). The orders included were the Turrilepadida (with the Turrilepadidae, Plumulitidae and Lepidocoleidae), Tommotiida (Tommotiidae, Lapworthellidae, Tannuolinidae), Sachitida (Wiwaxiidae, Siphogonuchitidae), and Hercolepadida (Hercolepadidae). A feature shared by al this groups, as far as is known, is the prescence of hollow scales or elytra arranged in longitudinal rows and in a superficially segmental (pseudosegmental?) way on a bilaterally symetrical body. Dzyk reconstructs the problematic scaly animals with "a footlike crawling and digging organ" and concudes that this is incompatible with the body plan of the annelid phylum. Despite this his final concusion is that the scaly fossils could be annelids or molluscs, in the latter caes related to polyplacophorans and aplacophorans. The question is however, if they must belong to an extant phylum. Dzyk has difficulty in understanding the phylogenetic and systematic affiliation because he recognizes similarities in the one side (the sole or the foot) with platyhelminths and molluscs, which he accepts as closely interrelated following Salvini-Plawen (1982), on the other (the scales or elytra) with annelids, which he places on another evolutionary branch. The new model avoids these problems as the foot is recognized as part of the body plan which is synapomorphic for the Bilateria/Triploblastica as a whole and indeed found also as vestiges in the Annelida, particularly in the larvae (Jagersten 1968). Actually ,I think that Begston and Conway Morris (1984:327) are close to the solution when they say about Wiwaxia and Halkeria that "it seems conceivable that they were derived from a turbellarian-like worm in a maner reminiscent of the now widely accepted hypothesis of molluscs origins". There is reason to question also the systematic significance of the scales. Dzyk stresses the similarity with the elytra of annelids, but compares them also with the plates of polyplacophorans.This is perhaps also a case where the structure was already present in the common forebears ?. If so, it should be possible to find vestiges in other animal phyla, too. Looking around, there is a clear tendency among aschelminths to develop scales and spines, and these are commonly regularly arranged as in the scaly fossils. Such structures are found among the Rotatoria, Gastrotricha, Loriciferida and Kinorhyncha. They seem to consist of scleroproteins without mineralization. Another case is the lateral scales or shells of a bryozoan larva, the so-called cyphonautes larva. The shells form one pair, and in their distinctly triangular shape they are closely reminiscent of machaeridian scales. It is difficult to see any function of these shells, and Jagersten (1968) prophetically claimed that they were vestiges from sheled ancestors. It could be that they correspond to a frontal pair of scales in machaeridians like Plumulites, i.e.perhaps the first pair to be developed embryologically. It is most interesting to see that the machaeridian type of larva of Nematomenia banyulensis (Fig. 3c), an extant aplacophoran mollusc belonging to the Solenogastres. As argued by Salvini-Plawen (1972,1980) and Wingstrand (1985:59-61), the polyplacophoran shells could have been formed by fusion of such transvers rows. The other aplacophoran group, the Caudofoveata, is even less similar to ordinary molluscs and could easily be interpreted as a remnant of the Procoelomata.

The Procoelomata.

Procoelomata nov. phylum.

Diagnosis.- Stem group of metazoans, above the flatworm level, by inference with protostomian features such as ciliated ventral locomotory sole, anal opening, pseudosegmentation, spiral cleavage and trochophora larva. The delimitation against theMollusca is diffuse and unclaer since the originationof the molluscs was not associated with a macroevolutionary event; if a radula was developed in procoelomates, some or all aplacophorans may belong in the Procoelomata rather than in the Mollusca. Provisionally the following groups can be distinguished (machaeridians mainly according to Dzyk 1987): Machaeridia Withers 1926 (Class) Turrilepadida Pilsbry 1916 (Order): Plumulitidae, Turrilepadidae, Lepidocoleidae. Sachitida 1980: Siphogonuchitidae, Wiwaxiidae, Halkieriidae. Tommotiida Missarzhevsky 1970: Tommotiidae, Lapwortellidae, Tannuolinidae. Hercolepadida Dzyk 1987: Hercolepadidae Dzyk 1987?. Caudofoveata Boettger 1955 (Solenogastres Gegenbaur 1878 are closer to molluscs).

No place for Ediacaran forms.

In the last decades a large fauna has emerged from the uppermost Precambrian rocks. Surprisigly, however this fauna is very different from the succesive Cambrian faunas (Glaessner 1984; Fedonkin in Sokolov 1985). The distintive character is the strong dominance of forms which have been described as cnidarians. Out of some 75 genera (the dubious Petalonamae not counted), some 45 have been counted as cnidarians. Of the remaining genera, one could belong to the Porifera, one tube fossil to the Annelida, five tube fossils to the Pogonophora, and one body cast to the Echiurida. In addition, three forms have been referred to the Platyhelmintes, Dickinsonia and the sprigginids (Fig.4A) to the Anellida, Parvacorina (Fig.4C) and vendomiids (Fig. 4B) to the Arthropoda (but there are also other suggestions). How well founded are these affiliations?. The most critical view was offered by Seilacher (1984). He considers most of the suposed cnidarians to be either trace fossils or remains of unidentified benthic (rather than planktic) organisms. The various leaf-like organisms supposed to be pennatulids (FIG. 4D), chondrophores worms and arthropods, according to Seilacher, must have had a flexible outer surface consist of a resisting biomaterial, and they had a repetitive construction that supposedly provided rigidity and perhaps facilitated metabolic processes. None of them can be assigned to any extant phylum. Some vendomiids are poorly known. *Vendia sokolovi* (Fig. 4B) is a good exception (e.g. Glaessner 1979:A105). It has a discoidal shape with a large "head shield" and five chevron-shaped "segments". Glaessner (1979) placed it among the Arthropoda. There are some features, however, which are unusual for arthropods. First, the "segments" are not articulated but obviously only folds in an entire integument. Second, the two body halves are not symmetrical, actually the "segment" halves alternate in position. Third, the axis has a longitudinal median furrow. Each of these features taken a long would be a severe warning against an interpretation of this animal as a segmented worm or arthropod. Taken togheter they tell us one thing: Vendia is no arthropod and no annelid. Unfortunately it does not tell us what it is. Spriggina (Fig.

4A), placed among the Polychaeta by Glaessner (1979,1984), actually shares important features with Vendia. Thus, altough the "segment" number is up to 40, it is identical in displaying a pronounced asymetry both in the "head" and in the alternation of "segments", and the axis has a deep median furrow. It is not clear if the "segments" are really articulated. The asymmetry is not in accord with segment formation in animals. Spriggina may be closely related to Vendia. Then what are Spriggina and Vendia? Spriggina has some similarities with the Machaeridia. These similarities include the prescence of a median longitudinal furrow and the prescence on each side of two protruding elements forming half a "segment".

On the other side, the Machaeridia lack a head shield, and the scales do not form part of a continous integument as in Vendia. Spriggina and Vendia can also be compared to the Petalonamae: there is a general similarity for instance between the two and Charniodiscus, if the "head shield" of the former is compared with the disc of the latter. Could sprigginids and vendomiids be procoelomates, perhaps with some pseudosegmentation?. If so, they should have been strictly simmetric and had one soft side. Are they instead members of the Petalonamae and, if so, animals or plants?. Does Parvancorina belong in the same category?. Dickinsonia presents similar problems. It has been stated that this is closely related to the living polychaete Spinther, but from a theoretical point of view segmentation could have evolved in cylindrical, burrowing annelids long before specialized forms like Spinther could ocurr, and the problem is that there are virtually no signs of burrowing activity in any pre-Ediacaran rocks. Runnegar (1982) suggested an alternative evoloutionary model that fits better with *Dickinsonia* as an annelid. According to Runnegar, this form grow to a length of a metre which corresponds to more than a half metre in width although it was less than 3 mm thick.

Is this a reasonable construction for a worm, or is it perhaps a cnidarian as originally suggested by Sprigg (1947), or is it something quite different? Runeggar (1982) argues well for its state as an annelid. It has evidence of a complete gut whith anus. The gut is sometimes apparently filled with mud, indicating a benthic mode of life. The has up to some 60 segments and is distinctly symmetrical. The dorsal and ventral sides are virtually similar, without signs of polyps which would make it a hydrozoan. However, there are problems with Runeggar's determination. As indicated generally by Seilacher(1984), the integument must have been very durable. The segments are vremarkably short and curiously curved, and the thin, expanded body is virtually unique. These features are alien to annelids. The evidence from the Precambrian is obviously very scanty. I am strngly inclined to believe in Seilacher's characterization of the Ediacaran type fossils. Many of them appear to be burrows and imprints of cnidarians, while others are thin-bodied, tough-integumented, flexible organisms of unknown affinity. They cannot at present be placed in the phylogeny of animals.

The appearance of animal phyla and the Cambrian fossil explosion.

Using the molecular evolution as a clock, as has been done repeteadly, may appear to make it possible to tell roughly when the different metazoan phyla first made their appereances. However, this is a dangerous approach. First, it is now known that the speed of molecular evolution has not been the same all over. Second, the branching points in the molecular evolutionary tree tell us nothing about the anatomical evolution. A new phylum came into existence when a new basic animal type was first formed, not when evolutionary lines within the procoelomate morphological plexus split apart. At first sight vthis statement may seem difficult to accept, particularly if we want a "phylogenetic" or "vertical" classification. In such classifications a new group takes its origin at the point of branching. However, a phylum can only be defined and recognized from its characteristics, and the point where those features first occurred must be the point where the phylum came into existence. The branching points in the Precambrian stem in Fig. 5 are possible points of lineage splitting but not of anatomical divergence. The old slug type morphology probably lingered on in all lineages until changes in the oxygen pressure in the atmosphere made possible new histological and biochemical experiments with collagen and skeletons, which in turned opened the door to new constructions.

The parallel evolution of a number of lineages within a morphologically uniform basal procoelomate stock and the succesive parallel passage through a formative period of undefined extension can form a simple and straightforward explanation for the geologically sudden appereance of a large number of phyla with (and whithout) skeletons close to the Precambrian/Cambrian transition (Fig.5).

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Fig.1. Major shifts in the locomotory and feeding behaviour leading to the initiation of new phyla (cf. Fig.5). The starting-point was a slug-like Precambrian animal. A shared choice of behaviour led to parallel evolution in morphological and anatomical respects, as is best demonstrated by the sessile and filtering tentaculate groups. Most new phyla were "traped" in their new roles. The Deuterostomia form a remarkable exception: the major shift led to such profoun changes and simplifications that this group could form a secondary stem from which new phyla evolved, again through new major behavioural shifts (cf. Fig.2).

Fig.2. Possible evolution of deuterostomes from a procoelomate stock. (1) Different biochemical evolutionary trees agree in placing molluscs or other protostomes close to the deuterostomes; (2) plesiomorphic protostomian characters are scattered aroun in the phyletic tree and must also have been present in the stem leading to the deuterostomes; (3) the adoption of small size and a filtering mode of life leads to extreme simplification in "protodeuterostomes" or "protohemichordates" (cf. endoprocts): creeping sole and ventral nerve cord deisappear and development from egg loses its strict protostomian-type control, enterocoel being one result; the course and function of larval cilial bands are modified; pharingeal slits and tentacles are new characteristics of the adult; (4) attachment with proboscis develops and results in assymetry and eventually in radial symmetry in echinoderms; in addition a mesodermal calcitic skeleton develops; (5) fusellar tube and posterior attachment develops in pterobranchs; (6) the extinct graptolites appear to have been close to pterobranchs, but with more advanced colony structure; (7) enteropneusts may have developed from pterobranchs through revertion to a free life, or directly from "protodeuterostomes"; (8) one line adopted swimming habits and direct development; the primary larva was thus lost, while new features include a muscular propulsive tail with endoskeleton (chorda) and incipient nervous segmentation; tentacles are incompatible with a swimming life and are lost, while the pharingeal slits are utilized for filtering; (9-12) urochordates kept the original chordate swiiming mode of life in one way or another; appendicularians (10) keep their tail, while thaliaceans (11) utilize the water current produced at the pharyngeal slits for propulsion; ascidians (12) have revrted to a sessile life as adults, but utilize the ancestral morphology in their "tadpole" secondary larva; (13) another lineage developed segmentation of thetail musculature; (14) acranians (cephalochordates) kept their filter feeding and prolonged the chorda to the anterior end; (15) craniotes (vertebrates) turned to a more active, non-filtering life, and developed segmentation of the chorda and a skeleton including cranium.

Fig.3 Reconstructions of some possible procoelomates. -B. Dorsal and saggital views of Wiwaxia corrugata (Matthew 1889). C. Lrva of extant solenogatrid mollusc Nematomenia banyulensis, reconstructed dorsal view and actual lateral view. D. Plumulites pieckorum Jell 1979, dorsal view. E. Tommotia sp. F. Turrilepas wrightiana (Koninck 1857), dorsal view. G. Aulakolepos sp., dorsal view. A-B, order Sachitida; D, F-G, order Turrilepadida; E, order Tommotida. Figs. A, D-G redrawn from Dzik (1986) without ornament but with direction of slope indicated; B new, C slightly redrawn from Wingstrand 1985, Fig. 21C-D.

Fig.4 Some Ediacaran type Precambrian fossils, drawn from casts and photographs for easy comparison. A. Spriggina floundersi. B. Vendia sokolovi. C.Parvancorina minchami. D. Charniodiscus arboreus. A-C are commonly thought to be articulates, possibly arthropods, because of the "segmentation" and "head". However, there is no indication that the "skin" was really articulated, the "segmentation" is alternating in B and diffuse in C, and the "head" is notably asymmetric in all three forms. Is the "head" a kind of basis or holdfast as in Petalonamae such as Charniodiscus?.

Fig.5. A direct descendent of most phyla from animals of a procoelomate morphology can help explain the Cambrian fossil explosion. Although lineages diverged earlier and the formation of new feeding and locomotion strategies occurred during an undefinied formative interval, the radia-

tion made possible by the aquisition of new strategies was a major and virtually simultaneous event probably made possible by new environmental conditions. The diagram gives a schematic view of the scenario. The list of phyla is not complete and not necessarily in natural order, and their radiation patterns are drawn in a uniform standard. The Deuterostomia form a whole new evolutionary tree comparable with although smaller than the Procoelomata and derived protostomian phyla. Procoelomates surviving into the Phanerozoic may include such forms as the Machaeridia.

phylum	major basic shift connected with origination of phyla	
	locomotory behaviour (old: creeping)	feeding behaviour (old: carnivorous swallowing)
PLATYHELMINTHES	(creeping)	(swallowing)
ASCHELMINTHES	semisessility	(swallowing)
ENDOPROCTA BRACHIOPODA BRYOZOA PHORONIDA DEUTEROSTOMIA	sessility	filtering
SIPUNCULIDA ECHIURIDA	hiding in burrows or crevasses	ciliary feeding and mud ingestion
ANNELIDA	perist. burrowing	(swallowing)
UNIRAMIA	walking	grasping limbs
SCHIZORAMIA	paddle-swimming	filtering limbs
MOLLUSCA	(creeping)	grazing

Fig. 1

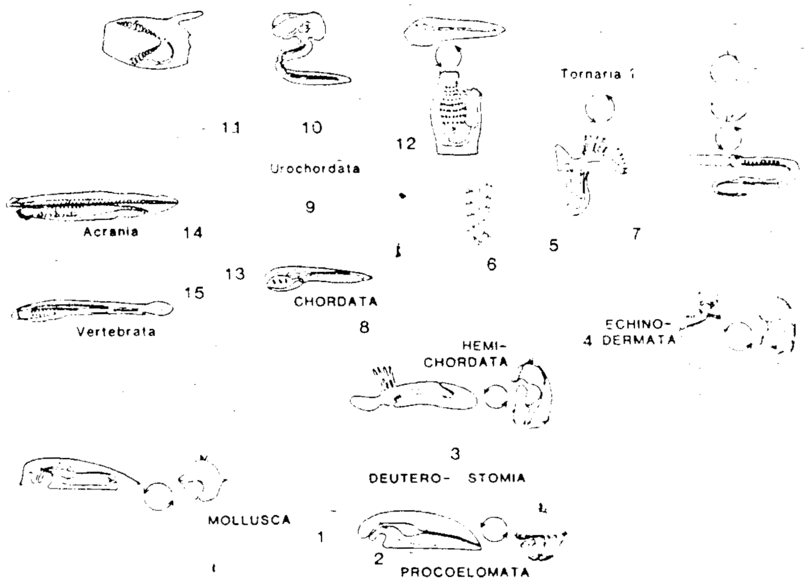

Fig. 2

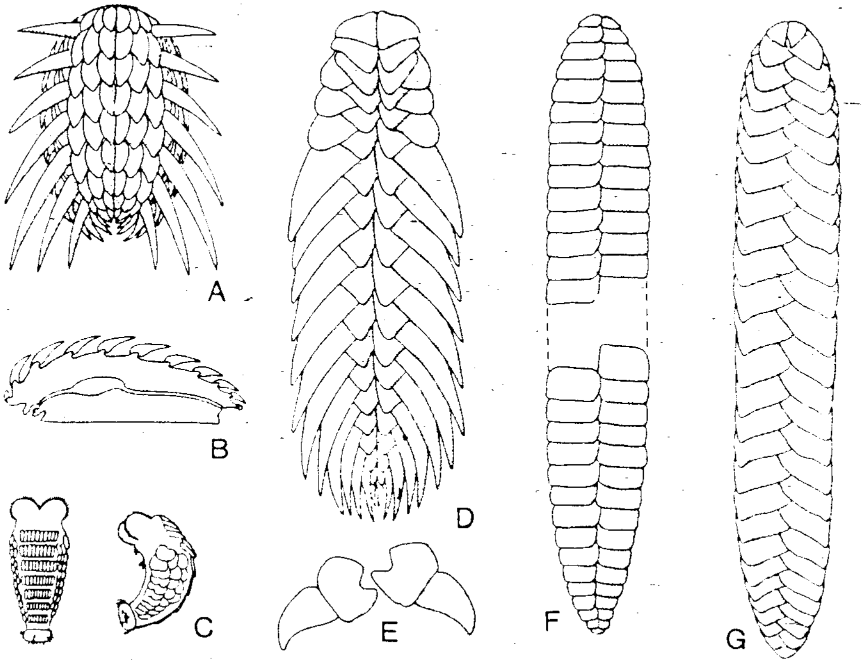

Fig. 3

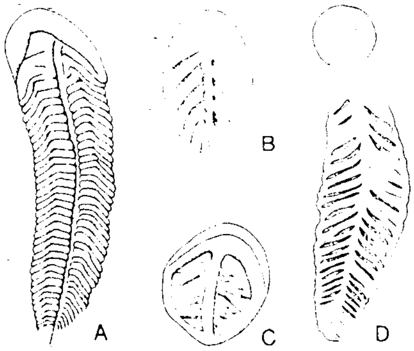

Fig. 4

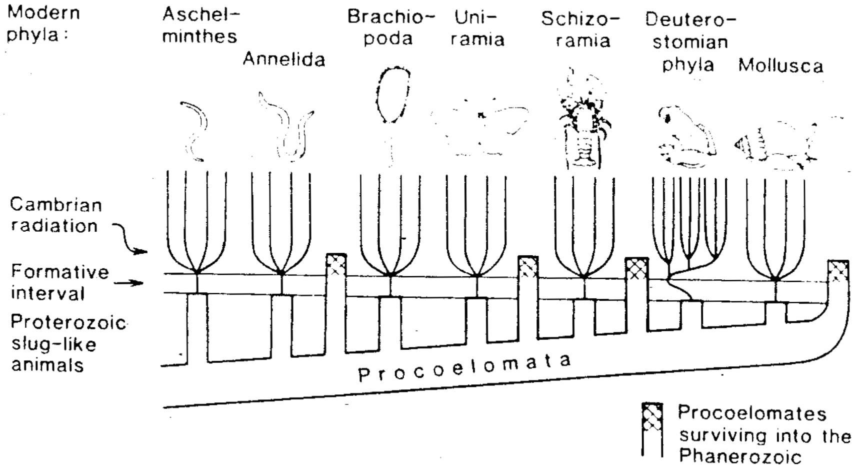
Modern phyla:
Aschelminthes
Annelida
Brachiopoda
Uniramia
Schizoramia
Deuterostomian phyla
Mollusca
Cambrian radiation
Formative interval
Proterozoic slug-like animals
Procoelomata
Procoelomates surviving into the Phanerozoic

Fig. 5

Origin of hard parts – Early skeletal fossils

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Introduction

Hard parts of organisms appearead almost instantaneously in the fossil record at the transition from the Proterozoic to the Phanerozoic. Biomineralization (Section 4.4) may have evolved close in time to that event. Earlier records of biogenic minerals are spurious and involve either very small, isolated cristals (magnetite of possible bacterial origin) or carbonate encrustation of cyanobacterial sheats that may have been induced indirectly by the photosynthetic activities of the organism. The earliest records of hard parts involve all major skeletal materials -calcite, magnesian calcite, aragonite apatite, and opal. (About 40 minerals are known to be formed by modern organisms (Lowenstam & Weiner 1983), but many of them are unstable under normal diagenetic conditions and they seldom form structures large or disctinct enough to be recognized in the fossil record.) All major types of skeletons are present -spicules, stiffened walls, shells sclerires and physiologically dynamic endoskeletons. The early Phanerozoic skeleton-forming biotas (Fig. 1) represent practically all major taxa of multicellular organisms known to produce mineralized skeletons today, some groups of biomineralizing protists, and a number of extinct groups of organisms, mostly metazoans (see also Section 5.2.5). The original mineralogy of the various groups of Late Precambrian and Cambrian fossils is not always well known . There are comparatively few studies on the diagenesis of early skeletal fossils. The composition of the skeletons in most groups is only known from their gross mineralogy in various types of rock, or inferentially through comparisons with known related taxa.

More detailed information has been derived from petrographic and geochemical studies of fossils and surrounding rocks (e.g James & Klappa 1983), and freom studies of replicated crystal morphologies (Runnegar 1985). This has been done in only a few cases, however, and further studies are needed.

Carbonate fossils.

Calcium carbonates mainly calcite, magnesian calcite, and aragonite, are the most common skeleton-forming minerals today, and appear to have been dominant already among the first skeletal fossils. Whereas aragonite is unstable in diagenesis and is rarely preserved in the fossil record, calcite and magnesian calcite may preserve their original crystallographic structure given favourable circumstances. The tubular fossil Cloudina (see also Sections 1.3, 5.2.5) is often considered to be the earliest known example of a mineralized skeleton, but its stratigraphic position is somewhat uncertain, and it is not clear that it significantly predates the earliest more diverse assemblage of skeletal fossils. The tubular skeleton of Cloudina consists of stacked imbricating calcareous half- rings, suggesting that it was constructed by a secreting gland of an animal that was able to twist around in its tube. The wall was probably part organic, stiffened by calcium carbonate impregnations. Other early carbonate tube-building animals include the anabaritids, first occurring in the c.550 Ma Nemakit-Daldyn assemblage (see Fig. 1). Anabaritids attained a wide distribution before their disappearance in the Atdabanian. They were triradially simetrical - an unusual feature suggesting a possible philogenetic relationship with tiradial metazoans of the Ediacaran fauna - and appear to have been less mobile in their tubes than Cloudina.The original mineralogy of the tubes is not known, but apparently ubiquitous recristallization suggest that they may have been formed of aragonite. The succeding Cambrian faunas contain more diverse types of tubular fossils. Some were cylindrical, resembling for example, protectivestructures built by certain modern annelids.

Others, in particular the widespread and diverse hyoliths (see also Section 5.2.5), had more obtuse tubes and were closed by opercula. They were bilaterally symmetrical annimals whit a U-shaped gut. The shell mineral was most probably aragonite, and a structure resembling molluscan crossed-lamellar fabric has been observed in younger Palaeozoic members of this group. Aragonitic shells are characteristic of early molluscs (Runnegard 1985) . The most primitive shell structure in Cambrian molluscs seems to have consisted of a single layer of sphrulitic aragonite prisms beneath an organic periostracum. This type of structure may grow in an inorganic manner, and the shape of the spherulitic 'prisms' is muoulded by surface forces rather than chemical bonds. These kinds of mineral deposits need to have been mediated by a protein substrate. Nacreous linings in prismatic shells had appeared by at least the Middle Cambrian and may have been present in Early Cambrian time. The fundamental differewnce between the aragonitic fibres of spherulitic 'prisms' and the flat aragonitic tablets of nacre lies in the difference in the habit of crystals; in nacre, growth on the (001) face is very slow, whereas in the fibres it is very fast. The result is a layered microstructure (nacre) which is much stronger than fibrous aragonite.

Most of the common molluscan ultrastructures had evolved by the Middle Cambrian.In addition to spherulitic primatic aragonite and nacre, these included tangentially arranged fibrous aragonite, crossed-lamellar aragonite, and foliated calcite. Varios solitary and colonial animals among the earliest skeletal biotasbuilt basal skeletons of calcium carbonate. Most of these are poorly known. The cup-shaped hydroconozoans and the probably colonial Bija and Labyrinthus may only questionably be referred to the cnidarians (Jell 1983). Others, such as Tabulaconus and Cothonion, have been studied in more detail and show certain similarities with corals, but their affinities nevertheless remain in doubt. Undoubted skeleton-forming cnidarians are not known until in rugose and tabulate coral skeletons were spherulitic tufts (trabeculae) formed by fibrous calcite. Modern scleractinian coral form similar structures of aragonite fibres. As with the spherulitic 'prisms' of mollusc shells, the process of formation appears to involve little matrix-mediated control of crystal shape. However, nucleation of the fibrous trabeculae may be under more direct biochemical control. The sponge-like archaeocyathans constructed a supporting skeleton typically shaped like a doublewalled perforated cup. They are preserved as microgranular calcite, interpreted as representing original magnesian calcite (James & Klappa 1983). Calcium carbonate (aragonite or calcite) skeletons are also formed by several groups of sponges ('sclerosponges' and 'sphinctozoans') from the Middle Cambrians until the Recent (Vacelet 1985). The more common type of sponge mineralization is, however, the spicular skeleton (see below). All the skeleton types described above exhibit incremental growth, which occurs by addition of material to earlier formed growth stages. This type of growth puts strong geometrical constraints on morphology. Ways of avoiding this problem are: (1) periodical moulting of exoskeleton,or (2) continuous construction and destruction of the mineral phase by intimately associated living tissue. Trilobites, common in Canbrian rocks from the Atdabanian (c. 540 Ma, Fig. 1), are an example of animals that periodically moulted their exoskeletons. These were of calcitic composition and often show well-preserved crystallographic fabrics in their mineralized cuticle. Other examples are the coeloscleritophorans, uniquely Cambrian organisms with a complex exoskeleton consisting of hollow carbonate sclerites with a basal opening. Their original mineralogy has not been definitely established, but the ubiquitous recrystallization and occasionally preserved fibrous structure suggest that they were aragonitic.

Echinoderms, first appearing in the Atdabanian and undergoing their fist substantive radiation in the Middle Cambrian, developed a calcium carbonate endoskeleton in which there was close interaction of mineral and living tissue.Modern echinoderms construct their skeletons of a meshwork (stereom) of almost pure magnesian calcite, in which each individual skeletal component is part of a large single crystal.

All fossil echinoderms, including the Cambrian ones, appear to have had an identical structure. Spicules -mineralized elements formed within living tissues -are widely distributed among Recent organisms. Spicules of magnesian calcite are characteristic of calcareos sponges and octocorals. In both groups the spicules are formed by epecialized clerocytes, sometimes originating intracellularly and later erupting from the cell membrane to be further enlarged by enveloping sclerocytes. Sponge spicules grow in crystallographic continuity, so that each spicule behaves optically as a sibgle crystal of calcite. By contrast, octocoral spicules typically are composed of smaller acicular crystals. As the echinoderm plates, sponge and octocoral spicules are made of magnesian calcite, it has been suggested that magnesium is used to shape the crystals by selectively poisoning appropiate parts of the lattice (O' Neill 1981). Calcitic sponge spicules have been found in the late Atdabanian (c. 535 Ma, Fig. 1.), and possible octocoral spicules also appear in beds of the same age.

Undoubted spicules of octocorals are kwon from the Silurian. The fossil sponge and octocoral spicules have the same crystallographic properties as their modern counterparts. Although fossil spicules of various origins are common, they are rarely dealt with in scientific literature because they tend to be disarticulated and therefore difficult to identify taxonomically. Some spicular skeletons may fuse to form frameworks, as in hexactinellids, 'lithistid' demosponges, and 'pharetronid' calcarerous sponges, or the axial skeletons of pennatulacean and a few alcyonarian octocorals. Such structures are rare in the early history of these groups. Fossils resembling calcified cyanobacteria became common in the Early Cambrian. One group of such organisms, the helically coiled filamentous Obruchevella, is present as uncalcified filaments in rocks ofVendian age, but is frecuently calcified after the beginning of the Cambrian.

Calcified cyanobacteria have their mucilagenous sheaths impregnated with crystals, perhaps as a by-product of the photosynthetic removal of CO2 from the water in wich they lived (Riding 1977). Fossils that may be true calcareous algae occur in the c. 550 Ma Nemakit-Daldyn beds of the northern Siberian Platform. More convincing examples are first known from the Middle Cambrian.

Phosphatic fossils.

As a skeleton-forming mineral, apatite occurs today only in inarticulated brachiopods and vertebrates.Some recent organisms are also known to produce amorphous calcium phosphate that may be crystalized later into apatite. Among the earliest skeletal organisms, however, calcium phosphate appears to have been more widespread. Tubular fossils of phosphatic composition are a common constituent of Cambrian faunas. Most of them are referred to as hyolithelminths. The fine structure of hyolitelminth tubes has not been sufficiently studied, but they appear to have grown incrementally by adition of lamellae. At last in some forms a systematic change in the orientation of fibrous elements in adjacent lamellâe occurs, producing a force-resistant structure similar to that of arthropods cuticles. The phosphatic tubes of the aiutiids had longitudinal septum-like structures on the inner surfaces. Conulariids had distinctly four-faceted cones built up of transverse phosphatic rods set in a fexible integument. Phosphatic shells wre also widespread. Inb additon to phosphatic inarticulated brachiopods, there are also a number of probematic phosphatic shells, such as Mobergella and related fossils, characterized by regularly placed paired muscle scars and a usualy flattened shape. The brachiopods include a number of phosphate - and carbonate-shelled clades, many of wich were short-lived. One characteristic and diverse Cambrian group is the tommotiids - multisclerite-bearing animals presumably covered with more or less twisted conical sclerites built up of phosphatic growth lamellae.they vary in skeletal organization from the irregularly shaped and frecuently fused sclerites of Eccentroheca to the highly organized scleritomes of Camenella and Tannuolina, in wich each of the two asymmetric sclerite types had its mirror-image counterpart. Examples of periodically moulted exoskeletons of calcium phosphated are rare, but the valves of the ostracode-like bradoriis are commonly preserved as phosphate. Although some of them appear to have been flexible, they were most probably impregnated to varying degrees with apatite crystallites. Like most arthropod skeletons, they did not grow by accretion, but were periodically shed. Whether or not the ecdysis involved resorption of mineral matter is not known, but resorption may explain the common occurrence of collapsed or bucked valves. The problematic fossil Microdictyon formed plate-like structures with a more or less regularly hexagonal network of holes and intervening nodes. They were constructed of two or three disctinct layers of aptite and show no evidence of incremental growth. Vertebrates , similar to echinoderms, have a plastic mode of skeleton formation as a result of a constant physiologial exchange between mineralized and cellular tissues. The phosphatic bone of vertebrates is intimately associated with fibrillar collagen, wich does not seem to be the case in the other phosphatic skeletons. Altough undoubted vertebrate remains are not known until the Ordovician, certain Cambrian phosphatic fossils show a fine structure suggesting association with fibrous organic matter that may be homologous with vertebrate collagen. The small buton-shaped sclerites of the utah-phosphans consists of a thin dense apatite layer covering a porous core; the latter has fine tubules or fibrils perpendicular to the lower surface. The 'buttons' are more or less densely set in an integument that is impregnated with smaller apatitic crystallites.

The tooth-shaped conodonts had a fibrous organic matrix in which the apatitic crystallites were embedded (Szaniawski 1987). In both these cases, a chordate affinity has been proposed using partly independent lines of evidence. Other suggested biomineralizing chordates (*Palaeobotryllus, Anatolepis*) are even more problematic in their interpretation. Therer are further examples of exclusively Cambrian fossils of phosphatic composition and unknown systematic affinity. Some of these are spine- or tooth-shaped objects, possibly reflecting the fact that apatite is a hard mineral suitable for the construction of wear-resistant structures.

Siliceous fossils.

Because of its non-crystalline, isotropic nature and intracellular method of formation, opal, (a minerai gel consisting of packed spheres of hidrated silica) has had limited potential as a skeletai material except in very small organisms. It is most widespread among protists. The only metazoans known to form it are hexactinellid sponges and demosponges, whch use it for spicule formation. Nost biogenic opal formed today is either dissolved in the water column before it is incorporated in the sediment or dissolved during early diagenesis, but under certain circumstances opaline skeletons may be preserved, usually as microcrystalline quartz or replacements by other minerals.

The distribution of opal among the earliest skeletal fossils differs significantly from that of calcium carbonates and phosphates.

Only four groups of silica-producing organisms are known from the time period under consideration (Fig. 1), hexactinellids, demosponges, radiolarians, and chrysophytes(?). All appeared during the Early Cambrian and all are still living. Whether this apparent immortality of opal-producing lineages is a chance effect due to the small number of clades involved, or whether it has a more profound meaning, the pattern differs considerably from that seen in the carbonate and phosphatic groups. In the latter two, the Cambrian radiation appears to have produced a large number of taxa of which only a few survived.

Early history of skeletal biomineralization.

Present knowledge of the fossils records confirms that mineralized skeletons of many different kinds and composition apperead very rapidlyin a number of clades at the beggining of the Phanerozoic. Analysis of the precise pattern is still difficult, because in many cases the original mineralogy is insufficiently known and the taxonomic understanding of the various enigmatic early skeletal fossils is incomplete (se also Section 5.2.5). It is therefore difficult to know how many clades developed the ability to form mineral skeletons at this time.It seems clear, however, that this ability evolved independently a number of times.

A current and widely held view is that those organisms that used phosphate rather than carbonatre or silica were the first to diversify. Phosphate has been stated to be the dominant or even exclusive mineral of the earliest skeletal faunas. A phosphate-carbonate transition is said to have ocurred within clades such as the Ostracoda, Brachiopoda, and Cnidaria, but also by the replacement through extintion of organisms with phosphatic skeletons by organisms with carbonate hard parts. Aragonitic materials are also postulated to have replaced calcitic ones thoughout the remainder of the Phanerozoic. Available data, including the pattern of distribution of clades of different biomineralizing habits through time (Fig. 1,2) and the phylogeny within these clades, do not appear to suport such views.

1. The relative amount of phosphate *versus* carbonate bound in biominerals in the Cambrian has been exagerated by sampling biases (most early skeletal fossils are of millmetre size, and chemical extraction of microfossils is more likely to destroy carbonates than phosphates) and unrecognized cases of secondary phosphatization (the Cambrian was a time of extensive deposition of phosphatic sediments).

2. Whereas phosphate skeletons were certainly more widely distributed among different clades in the Early Cambrian than they are today, the same may be said about carbonate ones. Among the clades shown in Fig.1, 42% of the carbonate skeletons survive until the present, as compared to 25% of the phosphatic ones (protoconodonts are regarded as chaetognaths whith mineralized grasping spines). Both categories include clades that are today very successful and diverse. Thus the restriction of phosphate minerals to two major clades today may simple be the result of the different evolutionary success of various early lineages. Nothing in the history of vertebrates suggests that their skeletal mineralogy puts them at an evolutionary disadvantage, and there is no reason to assume that the shell mineral was the particular factor that decided the survival of each of the early lineages.

3. The quoted examples of phylogenetic transition from phosphate to carbonate, or from aragonite to calcite, appear to be suspect. For example, a suggested evolutionary succesion from phosphate to carbonate hard parts within the cnidarians depens upon the dubious taxonomic decision to place the extincts conulariids within the Cnidaria. The proposed secondary origin of carbonate brachiopods from phosphate ones and the derivation of carbonate ostracodes from pre- existing phosphate forms have the merit of linking groups that clearly closed related, but the proposal of a mineralogical transition is neverthless weakly founded. In neither case has a strict phylogenetic analysis been able to demonstrate that the carbonate forms are in fact derived from the phosphate ones.

The Early Phanerozoic radiation cannot be seen just as a radiation of biomineralizing taxa. The trace fossil recods shows a similar rapid diversification of burrowing habits in non-biomineralizing organisms, and the appereance at the same time of resistant organic structures and agglutinating tubular fossils shows that the key event is not biomineralization as such (see also Section 1.5). To a certain extent, the appereance of mineralized skeletons may be seen as one of many aspects of the early radiation of multicellular organisms.

Nevertheless, the apparent absence of biominerals of the Ediacaran fauna and the nearly simultaneous 'skeletization' of cyanobacteria (notwithstanding reports of early sporadic cases of mineralized cyanobacterial sheaths), algae, heterotrophic portists (foraminiferans and radiolarians), and metazoans, seems to call for specific explanations. Attempts to explain the appereance of skeletons have often foundered on lack of universality. For example, models involving calcium availability or regulation do not explain the simultaneous appereance of opaline skeletons, and teh proposal that biomineralization began as a phosphate-excreting process at a time of high phosphate availability is not consistent with the pattern of appereance of various biominerals as discussed above. Models based on increasing PO2 may have more explanatory power, as an increasing availability of oxigen would have made it easier for organisms to form skeletals minerals and proteins, and made outer mineralized skeletons less of a respiratory disadventage. (Thereis a general but not perfect correlation between distribution of mineralized skeletons and oxigen levels in modern marine faunas).

A synecologically based explanation is that biomineralization in animals and plants primarily arose in response to selection pressures induced by grazers and predators. No evidence of grazers or predators is known from the Ediacaran fauna, whereas the first probable macrophagous predators (protoconodonts) appear with the first diverse skeletal biotas. Although the various types of skeletons in the early Phanerozoic biota often had complex functions, most of them would have had the advantage of at least passively deterring predators or grazers. Such an explanation stresses the view of the early evoution of skeletons as a complex event, integrated with other aspects of the rapid biotic diversification at this period. It is not in conflict with phisiologically and geochemically based models explaining how biomineralization became possible in the first place.

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Fig.1. Temporal ditribution of clades of biomineralizing and agglutinating organisms in the Late Precambrian to Late Ordovician, compiled from varioyus sources. Precambrian-Cambrian boundary (PreC-C) arbitrarily placed at the appereance of the Protohertzina-Anabarites assemblage and assigned an age of 550 Ma (see also Section 5.10.2). Clades defined as groups of taxa that appear to derive their biomineralizing habit from a common ancestor. (A few probably polyphyletic groups, such as "calcareous tubes", have been retained due to the poorly known phylogeny).

Fig.2. Cumulative courves of appereance of clades presumed to have independently evolved a biomineralizing habit. Based on the same data as Fig.1.

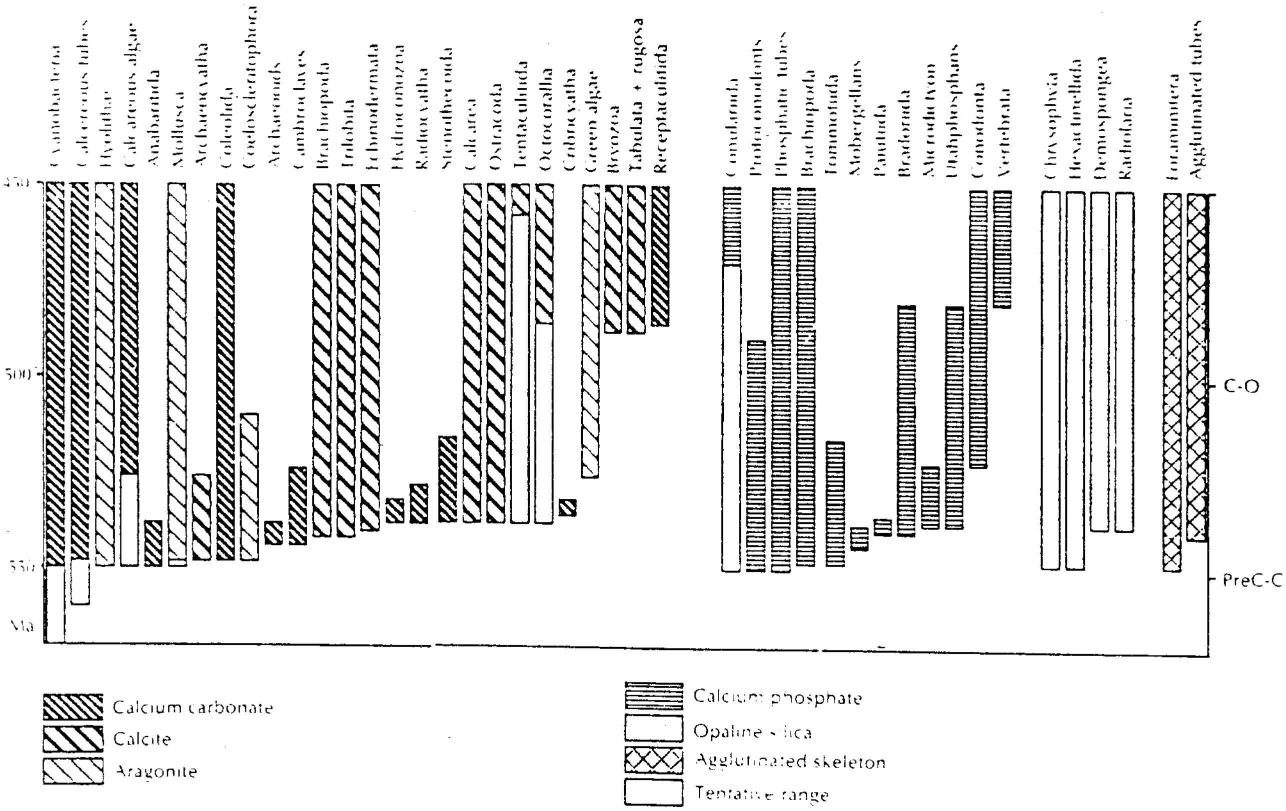
Cyanobacteria
Calcareous tubes
Hyolithae
Calcareous algae
Anabaritida
Mollusca
Archaeocyatha
Coleolida
Coeloscleritophora
Archaeooids
Cambroclaves
Brachiopoda
Trilobita
Echinodermata
Hydroconozoa
Radiocyatha
Stenothecoida
Calcarea
Ostracoda
Tentaculitida
Octocorallia
Cribricyatha
Green algae
Bryozoa
Tabulata + rugosa
Receptaculitida
Conulariida
Protoconodonts
Phosphatic tubes
Brachiopoda
Tommotiida
Mobergellans
Paiutiida
Bradoriida
Microdictyon
Utahphosphans
Conodonta
Vertebrata
Chrysophyta
Hexactinellida
Demospongea
Radiolaria
Foraminifera
Agglutinated tubes
450
500
550
Ma
C-O
PreC-C
Calcium carbonate
Calcite
Aragonite
Calcium phosphate
Opaline silica
Agglutinated skeleton
Tentative range

Fig. 1

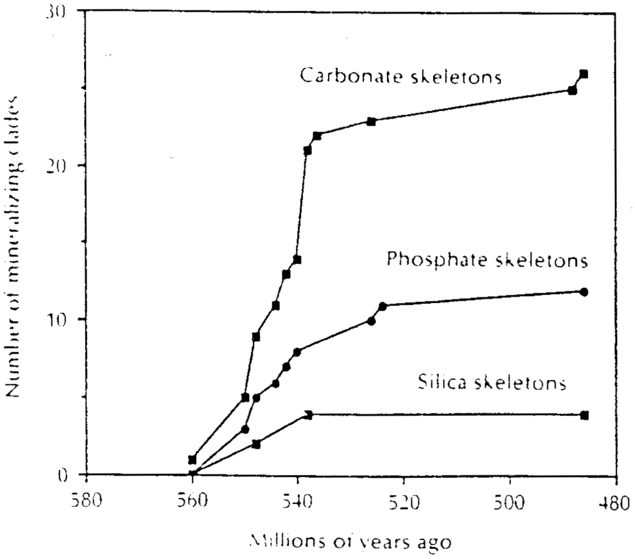
30
20
10
0
Number of mineralizing clades
Carbonate skeletons
Phosphate skeletons
Silica skeletons
580
560
540
520
500
480
Millions of years ago

Fig. 2

5.4 FILTRADORES

5.4(a)

Phanerozoic development of tiering in soft substrata suspension- feeding communities *

David J. Bottjer and William I. Ausich

Abstract.- Tiering is the vertical distribution of organisms within the benthic boundary layer. Primary tierers are suspension-feeding organisms with a body or burrow that intersects the seafloor. Secondary tierers are suspension-feeders that mantain positions above or below the sediment-water interface as either epizoans on primary tierers and plants or by living in the burrows of primary tierers. Different primary tierers from soft substrata, nonreef shallow subtidal shelf and epicontinental sea settings have had different tiering histories, resulting largely from contrasting constructional and phylogenetic constraints. Primary colonial tierers generally occupied lower epifaunal tiers during the Paleozoic and the Mesozoic, but since the Cretaceous they have been dominant in the highest tier (+ 20 to +50 cm).Primary echinoderm tierers have been almost exclusively epifaunal, and from the Paleozoic through the Jurassic they were present throughout the epifaunal tiered structure. Although primary byvalce tierers have been both epifaunal and infaunal, they have occupied only lower epifaunal tier, whereas they have adapted to all levels of the infaunal tiering structure, particularly from the late Paleozoic through the Recent. Brachiopods have lived primarily in tiers directly above or below the water-sediment interface and have not contributed significantly to tiering complexity.

Of the numerous physical and biotic processes and constraints that affect shallow marine benthos, a few have contributed more significantly to changes in tiering patterns.Trends for increasing body size could have accounted for most of the development of tiering complexity up to +50 cm and down to -12cm. Development of tiering above +50 could have been due to processes which would have yielded greater feeding capability, such as competitive interactions for a place from which to feed or adaptations to velocity gradients in the hydrodynamic boundary layer. The most significant process for development of infaunal tiering below -12 cm appears to have been as an adaptative response for predator avoidance.

Unlike infaunal tiering, which never declined after it developed, epifaunal tiering has undergone a general reduction twice. Reduction in epifaunal tiering at the end of the Paleozoic appears to have been the result of the mass extinction at this time, whereas long-term biotic processes seem to have been more important for the tiering decline at the end of the Mesozoic. Tiering structure through the Phanerozoic was thus produced through interaction of a number of physical and biotic factors, tempered by constructional and phylogenetic constraints of each primary tierer group.

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INTRODUCTION.

Benthic organisms live on, above, and below the seafloor. This space occupied by benthic organisms has been termed the "benthic boundary layer" (Rhoads and Boyer 1982). We have developed the tiering concept to describe the distribution of benthic organisms within this space (in ecological studies the term "stratification" is used, see Ausich and Bottjer {1983} for details of terminology).Studies of tiering have become more common in paleobilogy (i.e., Conway Morris 1979; Crame 1981; Palmer 1982; Bromley and Ekdale 1984, 1986; Anstey 1986; Savrda and Bottjer 1986; Wetzel and Aigner 1986). Our own research has been concernedwith tiering of suspension-feeding benthos. Life for a suspension feeder is "in most places... a marginal bussines, with the energy cost of processing water not far below the energy yield of the filtrate. Any device that increases the filtering rate without direct metabolic cost should therefore prove profitable"(Vogel 1978, p.133). The development of the tiering concept has been in

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* Publicado en Paleobiology, Vol. 12, Num. 4, 1986, p. 400-420.

part an attempt to better define the estructure of suspension-feeding communitiesso that the metabolic needs, ecologic constraints, and other limiting factors pertinent to individual suspension feedersmigth be better understood. it has also provided a means to trace patterns of ecological structure through the Phanerozoic which unlike other approaches (i.e., Bambach 1977, 1983; Thayer 1979,1983), can be formulated independently from enumerations of taxa.

Tiering is the vertical subdivision of space by the organisms within a community. However, in different settings the deposition of space and resources is quite different.Infaunal suspension feeders are predominantly sessile, and they are distributed through a medium from which they do not receive food . Infaunal suspension feeders all acquire food from the same basic position, the sediment-water interface, and the food is moving past them horizontally. Most epifaunal suspension feeders are also essentially sessile.However, they are distributed through the medium which carries their food, and that food is moving past them horizontally. For tiering in infaunal deposit-feeding communities, not treated here, deposit feeders are distributed throug the medium that contains their food. The distinction from suspension feeders is that deposit feeders are mobile, and their food is effectively stationary.

Our investigations have focused on suspension-feeding communities on soft substrata from nonreef, shallow subtidal shelf and conticontinental sea settings. In these settings we have outlined : (1) changes in tiering structure of suspension feeders in communities throughout the Phanerozoic (Ausich and Bottjer 1982); (2) the effect that tiering can have on microstratigraphic sampling metodology (Bottjer and Ausich 1982); (3) how tiering is related to diversity in both ecologic and evolutionary time scales (Ausich and Bottjer 1985a); and (4) the tiering history and the ecologic and evolutionary importance of tiering within echinoderms (Ausich and Bottjer 1985b). In this paper we focus on the following three questions: (1) what is the tiering history of different types of suspenssion feeding organisms; (2) what are the various constraints that could have led different organisms to occupy different tiering levels, within a single setting and among different settings; and (3) what can answers to questions 1 and 2 tell us about the factors that may have contributed to changes in tiering in suspension feeders in soft substrata from nonreef, shallow subtidal shelf and epicontinental sea settings throughout the Phanerozoic?.

Tiering History.

This tiering history is meant to display the potential characteristic maximum ammountof tiering present at any one time.Thus, the tiering history (Fig. 1)is not meant to show the history of the tallest and the deepest-burrowing suspension feeders, as a sort of Phanerozoic Guiness Book of World Records. A selection of important literature sources used to document the tiering history is Appendix A.

It is important to emphasize that the tiering history presented by Ausich and Bottjer (1982) was meant to show changes in only one broad environmental setting. In describing this setting (Ausich and Bottjer 1982), among other criteria, the environmental range was limited to shallow subtidal shelves and epicontinental seas. Ausich and Bottjer (1982) did not explicitly state the shallowest limit of this subtidal environment, but there are implicit limits related to the organisms which were studied. In soft substrata nonreef settings large epifaunal suspension-feeding organisms, such as crinoids with 1m long stems, have not occupied subtidal depths above normal wave base and normally had their shallowest distributional limits at most several meters below normal wave base. Although an absolute depth figure cannot be given, our definition of shallow, as used here , is several meters below normal wave base where normal surface current action and turbulence has little or no effect on the benthos.

The tiering history proposed by Ausich and Bottjer (1982) was presented with the knowledge that it would require modification as more communities and organisms were examined with this aspect of ecological structure in mind. Additional work on echinoderm tiering (Ausich and Bottjer 1985b, see subsequent section and Fig.3) has allowed a more detailed understanding of the history of the development of the intermediare eepifaunal tier. In the Ordovician the lower boundary of this tier changed from +10 to +15 cm, while in the Devonian it changed from +15 to +20 cm. The upper boundary of this tier was at +50 cm from the Ordovician to at least through the Missisipian, as well as during the Triassic and Jurassic.

Several workers have suggested that our interpretation of the infaunal history requires revision (Miller and Byers 1984; Pickerill 1984; Sheehan and Schiefelbein 1984). In summarizing the tiering history (Ausich and Bottjer 1982), we noted the presence of early Paleozoic burrows made by suspension-feeders which penetrated to depths greater than 6 cm below the sediment water interface. However, our interpretation of this evidence was that it was not characteristic for communities at that time. race fossil evidence presented by Miller and Byers (1984) has documented that the -6 to -12 cm tier originated in the Ordovician or perhaps some time in the Cambrian, and this has been added to the tiering history (Bottjer and Ausich 1985) (Fig. 1). In addition, a more detailed understanding of bivalve tiering indicates that bivalves began to occupy the upper portion of the -12 to -100 cm tier in the Missisipian (Fig. 4). Sheehan and Schiefelbein (1984) documented the presence of Ordovician Thalassinoides which they believed existed as open burrows to depths as great as 1 m below the sediment-water interface. Altough we do not doubt the results of Sheehan and Schiefelbein (1984), several questions remain before this infomation should be included in the tiering history. These are the following: (1) as is problematic with Mesozoic and Cenozoic Thalassinoides (e.g, MacGinitie 1934; Aller and Dodge 1974; Pryor 1975), were these Ordovician examples produced by suspension feeders or deposit-feeders;and (2) how common are these "deep" Thalassinoides in the Ordovician, so that it can be determined wheter they represent characteristic maximum tiering for this time? Continued study of early Paleozoic bioturbation (e.g., Droser and Bottjer 1985 a,b) will alow further refinement of our understanding of the initial development of infaunal tiering. In addition, future research should determine the relative abundance of Thalassinoides during the remainder of the Paleozoic (e.g., Bottjer et. al. 1984).

Component Taxa.

An understanding of several important characteristics of suspension feeders in the benthic boundary layer is necessary for interpreting the development of tiering. "Primary" tierers are defined here as suspension feeders which have a body or burrow that intersects the sea floor. "Secondary" tierers are suspension feeders that maintain a position above or below the sediment-water interface and that utilize a support structure or burrow of a primary tierer or a plant living in that environment. Wheter or not an organism is colonial or solitary also appears to be a determining factor in how that organism contributes to the tiering structure.

Primary Colonial Tierers.

The common colonial marine invertebrates of the Phanerozoic fossil record are epifaunal suspension feeders. No colonial suspension feeders occupy infaunal tiers, presumably due to functional and phylogenetic constraints on their various basic body plans. Colonial organisms generally feed and respire throughout the full height of the organism. Through astogeny, colonial organisms may progressively occupy more than one tier. Large colonial organisms can mantain the ability to feed and respire in all tiering levels that their colony intersects, but they can also restrict feeding and respiration to the tier or tiers at the uppermost portion of the colony. A tiering history of colonial suspension feeders, prepared from the evidence discussed in Ausich and Bottjer (1982) (Appendix A), is presented in Fig. 2. The 0 to +5cm tier was first occupued in the Cambrian by sponges as well as archaeocyatids (e.g. McKee and Gangloff [1969]; howeevr, archaeocyatids may not be metazoans {see Sepkoski 1979}). Bryozoans, corals, and graptolites appeared in this tier in the Ordovician. Further changes in the taxonomic composition of this tier included extinction of the archaeocyatids in the Middle Cambrian, extinction of the graptolites at the end of the Devonian, and the appereance og alcyonarians in the Triassic. The +5 to +10, +15, or +20cm tier has had the same history as the 0 to +5cm tier. Development of tall fenestrate bryozoans increased the height of this tier to at least +20cm by at least the Mississipian (Ausich 1980). During the Late Mississipian Archimedes may have locally extended above the +5 to +20cm tier (McKinney and Gault 1980). Sponges and alcyonarians became characteristic of th +20 to +50cm tier by at least the Cretaceous. In comparison to reefal settings, primary colonial tierers have played a relatively minor role in soft substrata, nonreef, shallow subtidal shelf, and epicontinental, sea settings.

Primary Solitary Tierers.

Primary solitary suspension feeders include organisms occupying both infaunal and epifaunal tiers. Solitary epifaunal suspension feeders feed and respire from a single tier level. These organisms either feed at the sediment-water interface or an attachment structure elevates the feeding structures into a tier above the seafloor. Through ontogeny, elevated solitary epifaunal suspension feeders feed and respire from progressively higher tiers. In contrast, solitary infaunal suspension feeders can occupy deeper tiers through ontogeny, although they always feed and respire from water that generally originates at the sediment-water interface--from the 0 to +5cm tier (Fig.1). Depending upon mobility, solitary infaunal suspension feeders can occupy different tier levels by occupying different parts of their burrows at different times.

In the environments considered, the only solitary macroinvertebrates that developed morphologies and behaviors so as to occupy deep infaunal tiers were crustaceans, bivalves, and various types of worms. Pelmatozoan echinoderms are the only primary solitary invertebrates to have developed structures that enabled them to occupy high epifaunal tiers. These differences in tiering abilities seem to result from differences in functional and phylogenetic constraints between each of these major groups. Such differences will be discussed for the following three examples, the echinoderms, the bivalves, and the brachipods.

Echinoderms.- Epifaunal suspension feedinghas been a very important habit among echinoderms. This Feeding mode was dominant among Paleozoic ehinoderms, a time during wich all echinoderms that were predominantly sessile were epifaunal suspension feeders (11 classes) (Ausich and Bottjer 1985b). Trophic plasticity has characterized post-Paleozoic echinoderms. The echinoderm classes that survived the terminal Paleozoic extintion are all still present and all include forms that are epifaunal suspension feeders. Of the 21 echinoderms classes generally recognized, only two, the Ophiocistoidea and Ctenocystoidea, are considered definitely not to have included suspension-feeding members (Sprinkle 1980).

Despite this propensity among echinoderms for suspension feeding, they have only occupied the epifaunal half of the potential tiering space. Echinoderms have evolved throughout the epifaunal suspension-feeding tiering structure and, indeed during the Paleozoic, are largely responsible for this structure. However, no true infaunal suspension feeding echinoderms are known. No other solitary suspension feeders have contributed significantly as primary tierers. The column of stalked echinoderms afforded them considerable morphological potential for developing throughout the epifaunal tiering structure, and stalked echinoderms were dominant as epifaunal tierers from the early Paleozoic through the middle Mesozoic.

Suspension-feeding mechanics have been studied in living crinoids and ophiuroids (Macurda and Meyer 1974; Warner 1977; La Barbera 1978; Meyer 1981). In all cases, these echinoderms are passive leeward suspension feders. By analogy to these living forms, most extinct echinoderms can be inferred to have also been passive leeward suspension feeders. Possible exceptions include echinoderms with low domal bodies (e.g., most edrioasteroids) which appear not to have been leeward feeders. Apparently echinoderms have always relied on ambient currents for feeding. This passive mode of suspension feding may have been a primary contributing factor to echinoderm succes as epifaunal tierers, as discussed below, but was probably also the factor that limited suspension-feeding types to the epifaunal habit. The tiering history of suspension-feeding echinoderms in Fig.3 was outlined by Ausich and Bottjer (1985b) and will be summarized here. Representatives of all suspension- feeding echinoderm classes exploited the 0 to Q5cm tier and many also occupied the +5 to +10, +15, or +20cm tier. Only three classes, Crinoidea, Blastoidea, and Diploporita, are thought to have commonly attained positions above +20 cm, and only crinoids reached heights above +50 cm. Present information indicates that Cambrian echinoderms were characteristically within +10 cn of the substratum. These included helicoplacoids, eocrinoids, edrioasteroids, crinoids, and possibly homoiostelans, homosteleans, stylophorans, and cyclocystoids (Fig.3). Sprinkle (1976) subdivided Cambrian suspension-feeding echinoderms into "low" and "high" levels, which correspond to our 0 to +5 and +5 to +10 cm Cambrian tierers, respectively.

To a large extent, the radiation of the "Paleozoic" fauna (Sepkoski 1981) was a radiation of echinoderm tiering. Echinoderms were a significant part of this event. Echinoderm class diversity increased from 6 to 18 from the Late Cambrian to the Middle Ordovician, and the number of echinoderm classes represented by predominantly suspension feeders increased from 3 to 10 during this same interval. By the Middle Ordovician, suspension-feeding echinoderms were distributed through the tiering structure as follows: 8 classes in the 0 to +5cm tier, 10 classes in the +5 to +10cm tier, 2classes in the +10 to +50cm tier(Fig.3) (Ausich and Bottjer 1985b). During the Middle Ordovician, crinoids became established as the highest potential tierers in soft- substrata, nonreef settings.

Maximum characteristic heights of crinoids increased to aproximately Q75cm in the Early Silurian (Eckert 1984) and to Q100 cm by the Middle Silurian (Watkins and Hurst 1977).Maximum epifaunal tier heights were attained approximately 80 ma after the Ordovician radiation began.Wachsmuth and Springer (1897, pp. 38-39) reported that they knew of no Paleozoic crinoid column greater than 100cm in length. Exceptions to this observations can undoubtedly be found, but the +100 cm height of crinoids is considered to have been the characteristic maximum height of benthic crinoids and of epifaunally tiered communities.

This +100cm level remained characteristic for crinoids in shallow subtidal settings until the end of the Jurassic, except for a temporary decrease in maximum levels that very likely ocurred during the terminal Paleozoic extinctions. Stalked echinoderms, other than crinoids, are not known to have lived above +50cm.

The +10 and +20 to +50cm tiers were occupied by crinoids, diploporites, and blastoids. Diploporites reached this tier by the Middle Ordovician and probably had representatives in this tier until they became extinct in the Devonian. Blastoids are thought to have begun ocupying the +10 to +50cm tier by at least the Silurian and continued there until the Late Permian when they became extinct.

Despite the progresive development of epifaunal tiering and tier subdivision after the Ordovician, class level diversity of predominantly suspension-feeding echinoderms declined from 10 in the Middle Ordovician to 6 in the Late Silurian, 4 in the Late Devonian, and 2 in the Late Pennsylvanian (Ausich and Bottjer 1985b,fig.3). The temporal trend in class level diversity is independent of that of generic level diversity, which stayed at essentiyally the same level through much of the Paleozoic (Ausich and Bottjer 1985b,fig.7). Thus, during the early and middle Paleozoic different echinoderm classes were apparently adapted to ocupy different levels within the tiering structure, but by the ealry Mississipian all tiers above +5cm that were occupied by predominantly suspension-feeding echinoderms were filled by crinoids and blastoids.

At the close of the Paleozoic, blastoids became extinct and crinoids nearly became extinct. Tiering heights and tiering complexity must have been reduced significantly, although the precise history of this change is not recorded. Among the suspension-feeding echinoderms that survived into the beginning of the Mesozoic are the Crinoidea, some holothurians, and some ophiuroids. Asteroids presumably developed the suspension-feeding habit in the Triassic.

Crinoids, ophiuroids, holothurians, and asteroids contributed to epifaunal suspension-feeding tiers during the Triassic and Jurassic. Crinoids, holothurians, and asteroids were primary tierers, and ophiuroids probably had members that were primary and secondary tierers, much like living ophiuroids. Characteristic maximum heights of +100cm were again attained by crinoids by the Triassic (Linck 1954). However , stalked crinoids have apparently not been a common component of shallow-water communities since the end of the Jurassic (Meyer and Macurda 1977). With stalked crinoids confined to oceanic depths, the remainingb echinoderms in shallow-water nonreef settings from the Cretaceous to the present included the holothurians, ophiuroids, and asteroids mentoioned above; echinoids adopted suspension feeding bduring the late Cenozoic (Stanton et al. 1979; De Ridder and Lawrence 1982).

Bivalves.- Active suspension feeding is the basic food-gathering method of the bivalves: only two orders (Nuculoida, Tellinacea in Veneroida) include deposit feeders. Indeed, Tevesz and McCall (1976) and Vogel and Gutman (1980) argued that bivalves arose as suspension-feeding molluscs. Among suspension-feeding bivalves, members of four orders have been epifaunal and members of 12 orders have been infaunal. These infaunal bivalves have been successful in occupying the full range of infaunal tiering space. This can be attributed to the evolutionary innovation of siphons in the middle Paleozoic (Stanley 1968, 1977), which has allowed bivalves to live at depths at least 1m below the seafloor in shallow settings. Suspension-feeding bivalves have not been as successful in ocupying epifaunal tiers because their attachment mechanisms -cementation or the byssus-have always served just to attach and not to elevate individuals above the substratum. Epifaunal bivalves have only been primary tierers in the lower epifaunal tiers.

The history of suspension-feeding bivalvesin tier subdivisions of Ausich and Bottjer (1982) is presented in Fig.4. Epifaunal suspension feeders are byssally attached, cemented, recliners, mud stickers or swimmers (Stanley 1970; Seilacher 1984), and thus as primary tierers have generally occupied the 0 to +5cm tier. The early occupants of this tier were members of the Pterioida in the Ordovician, followed by hippuritoids in the Silurian, arcoids in the Mississipian, and mytiloids in the Pennsylvanian. Since the Pennsylvanian mytiloids and in the Jurassic-Cretaceous hippuritoids grew large shells that enabled members of these orders to project into the +5 to +20cm tier without benefit of an attachment structure to elevate them above the substratum. Except for the Hippuritoida, which became extinctat the end of the Cretaceous, tiering structure for epifaunal suspension-feeding bivalves has not changed significantly since the Pennsylvanian.

The order Fordilloida includes the oldest bivalves, which occupied a life position in the 0 to -5cm tier. They were followed intothis tier by six additional orders in the Mississipian and one additional order in the Triassic. Of these, the Fordilloida did not last beyond the Cambrian, two orders that began in the Ordovician became extinct near the end of the Paleozoic (Actinodontoida-Permian, Praecardioida-Triassic), and the Unionoida occupied marine habitats only during the Triassic- Jurassic. The remaining nine orders that entered this tier in the Paleozoic are still present in this tier in recent seas.

Occupation of the -6 to -12cm tier by suspension-feeding bivalves occurred later than occupation of the 0 to -5cm tier. Pholadomyoids and veneroids became the first bivalve suspension feeders to inhabit this tier in the Devonian. This tier has been establishedby at least the Ordovician (Miller and Byers 1984; Bottjer and Ausich 1985). Mytiloids in the Mississipian and myoids and trigonoids in the Triassic also developed into the -6 to -12cm tier.

By the Mississipian the upper portion of the -12 to -100cm tier was occupied by pholadomyoids. Pholadomyoids were joined in this tier by the myoids and the veneroids in the Triassic, and members of all three orders have continued to inhabit this tier to the Recent.

Several generalizations on the infaunal tiering development of suspension-feeding bivalves can be made from this history. Although the movement into deeper tiers appears to be rapid in Fig.4, occupation of the -6 to -12cm tier occurred roughly 80ma after the main Ordovician radiation of shallow infaunal bivalves began, and burrowing into the -12 to -100cm tier ocurred roughly 80-100 ma after occupation of the -6 to -12cm tier. he number of orders which have been capable of living in deeper tiers in the Phanerozoic has been progressively fewer the deeper the tier -12 have lived in the 0 to -6cm tier, 5 in the -6 to -12 cm tier, and 3 in the -12 to -100cm tier. This trend appears to be directly related to the capability within each order for the development of long and large siphons. Life in the 0 to -6 cm tier has easily been managed by suspension-feeding bivalves with short siphons or not siphon at all. Occupation of the -6 to -12cm tier generally has been by bivalves with substantial siphons, but this level has also been possible for bivalves with short siphons but large bodies or by those with a mucus tube structure such as that used by lucinaceans. A suspension-feeding bivalve has generally only been capable of living in the -12 to -100cm tier if it has had substantial siphons. This pattern of progressive occupation of deeper tiers with little loss by extinction constrast with the pattern for epifaunal tiering of echinoderms, which shows relatively rapid occupation of higher tiers with subsequently much greater loss by extinction.

Brachiopods.- All brachiopods have been suspension feeders and have been free-living on the substratum by means of a pedicle or by cementation. Alexander (1977) outlined the modes of stabilization on the substratum developed by articulate brachiopods, which include: (1) anchorage by spines; (2) cementation(youthful stage only or throughout life); (3) unattached, commissure vertical (with umbonal weighting or interarea stabilization); (4) unattached, commisure horizontal (sessiloe and mobile?); and (5) with a functional pedicle (either as a tether or augmented by interarea stabilization). None of these modes of stabilization for articulate brachiopods, or for inarticulate brachiopods, has developed to the degree that individuals are projected to great heights above or below the seafloor. Primary brachiopod tierers have only occupied the levels directly above or below the substratum. Consequently, unlike the echinoderms with their column or the bivalves with their siphons, brachiopods have not figured prominently in the development of tiering complexity. For example, inarticulate lingulid brachiopods, to the extent to wich they have inhabited shallow subtidal shelf and epicontinental seas, which may have been minor (i.e., Sepkoski and Miller 1985), have inhabited the 0 to -6cm tier since the Ordovician (Rudwick 1970). Rudwick (1970) interpreted the morphology of many articulate strophomenid brachiopods to be indicative of a quasi- infaunal life habit, and thus they were inhabitants of the 0 to a -6 cm tier, from the Ordovician into the Jurassic. All other brachiopods, as primary tierers, have been inhabitants of the 0 to +5 cm tier since the Cambrian. Exceptions would include rare groups with very large body size so that they were positioned higher than + 5 cm.

Secondary tierers

Secondary tierers utilize the skeletons and burrows of primary tierersin order to mantain a life position above or below the substratum. In shallow-water nonreef environments epifaunal secondary tierers are epizoans and borers,and these have been studied extensively. The history of tiering for this organismshas not yet been determined, primarily because their original elevations above or below the seafloor generally cannot be determined from the fosil record. Ecological studies in other environmental settings indicate that as the complexity of the structure developed by primary tierersincreases the species richness of secondary tierers also increases (e.g.,phytophagous insects on plants,Lawton 1983). It seems likely that such a relationship may also exist in ecological time for benthic suspension-feeding communities in soft substrata. Thus, periods in the Phanerozoic of increased tiering height,depth, and complexity would be predicted to have had increased diversity of secondary tierers.

Secondary tierers generally differ from primary tierers in their relatively diminute size,common occupation of only one tier level during astogeny or ontogeny, and varying development of attachment structures as adults. They are probably parasitic on primary tierers, because they gain energetic efficiency by not developing their own burrows or epifaunal support structures, whereas primary tierers could lose energetic efficiency by having to support them as epizoans or to accommodate them in their burrows. Secondary tierers may be either solitary or colonial organisms. Altough the main purpose of this paper is to address the development of primary tiering structure, discussion of a few examples of adaptations of secondary tierers provides a useful contrast with those of primary tierers.

Colonial Organisms.-As for primary tierers, secondary colonial tierers never have occupied infaunal tiers. Epifaunal colonial tierers either encrust onto or bore into live or dead hard substrata.In Phanerozoic soft substrata environments colonial secondary tierers included boring and encrustig sponges, some corals and bryozoans. Cheilostome bryozoans are well adapted for and encrusting existence as secondary tierers. For example, the RecentMembranipora villosa develops a pattern of active and degenerate zooids which causes already filtered water to leave the surface of the colony as high-speed jets over the degenerate zooids(Cook 1977; Lidgard in Vogel 1981). This arrangement substantially reduces the possibility of zooids reprocessing water previously uesed by other zooids and is similar in effect to the systemof widely spaced osculae used by encrusting sponges. Trace fossils of boring briozoans and clionid sponges are among the most common of post-Paleozoic borings(Bromley 1970).

Echinoderms.-The considerable mobility of ophiuroids has offered them the hability to climb into the primary epifaunal tiering structure, thereby attaining much higher suspension-feeding levels than would other wise be possible. Crinoid juveniles may have commonly used adults for attachment(Brett 1978; Meyer and Ausich 1983).In this case the juveniles would hve been secondary tierers and the adults primary tierers.However, in general, echinoderms have played aminor role in Phanerozoic secondary tiering.

Bivalves.- In soft substrate environments, members of the pterioids, mytiloids, and arcoids have developed as epizoansecondary tierers. Pterioids have evolved as secondary tierers through cementation and byssal attachemen to primary tierers, but mytiloids and arcoids have used solely byssal attachment.In the post-Paleozoic, which has reduced primary epifaunal tiering height and complexity,byssate free-swinging bivalves, as well as other epizoans, attachd to algae and sea grasses and commonly formed and upper tier level(Rhoads et al. 1972;Brasier 1975). Bivalves have also adapted as infaunal secondary tierers. An example is the infaunal bivalve Cryptomya californica, which lives in the burrows of Callianassa californiensis along the west coast of North America(i.e., Peterson 1977). In addition, bivalves have participated as secondary tierers by development of boring habit. This has been particularly wel developed by members of the Pholadidae, Gastrochaenidae, and Mytilidae, whose activity is commonly expresed in the rock record by the ichnogenusGastrochaenolites(Kelly and Bromley 1984).

Brachiopods.- Despite the limits to the development of primary tiering imposed by brachipod attachment structures, brachiopods have developed a number of attachment modes that have allowed a secondary tierer life habit. For example, the Permian Linoproductus angustus developed spines which allowed it to attach to crinoid stems(Grant 1963) throughout ontogeny (cementation throughout life, sensu Alexander 1977). Other species of Linoproductus attached to crinoid stems as juveniles only and broke off later to live on the seafloor as primary tierers in the 0 to +5cm tier(Grant 1963) (cementation youthful stage only, sensu Alexander 1977). Brachiopods whit a functional pedicle probably also were successful as secondary tierers, although the relative importance of these brachiopods as secondary tierers cannot be assessed due to thaponomic information loss. The lack of a boring habit has also limited secondary tiering among brachiopods.

Factors Contributing to Changes in Tiering

Much previous work in ecology and paleoecology has operated under the assumption that a uniform set processes determined the behavior of all communities(Strong et al.1984a). However, recent research has increasingly used models in which different communities or different parts of communities respond to diferent processes (Ausich 1983;Strong et al.1984a). This latter approach is particularly important for and understanding of Phanerozoic tiering patterns, which include both infaunal and epifaunal habitats, and both primary and secondary tierers

We suggest that several different proceses and constraints were responsible for the development of Phanerozoic tiering patterns. No process or constraint or set of processes or constraints can be definitely demonstrated to be responsible for the development of tiering. Rather, the predicted biotic patterns of various processes and constraints must be compared to known ecologic and evolutionary patterns among suspension-feeders. Although correlation of patterns need not demand a causal link, correlation of predeicted and realized patterns warrants consideration. Our approach has been to consider all processes and constraints that display significant correlation of patterns.

Constructional and phylogenetic constraints on morphological pathwaqys for evolution , adaptive interactions whit the physical environment, as well as biotic interactions have led to changes in tiering , and these processes may have acted either independently or in conjuntion whit one another. In the following discussion several primary processes and constraints are offered as important factors that led to chnges in tiering. In our view the potential impactof each is significant enough that no listed processor constraint should be rejected, even thoug at certain times specific processes seem to have played a more significantrole. Furthermore, numerous processes have predicted patterns that are not similar to those in tiering history. Such processes are rejected and are not discussed further.

The role of biotic interactions in shaping faunal patterns, particularly competitive interactions, has been sharply debated during the past decade (i.e., Schoener 1982;strong et al. 1984b). Whereas competitive interactions were once thought to be major processes that influenced community structure in both ecologic and evolutionary time, now many consider competition to have only a minor role in communities. We adhere tomiddle ground by acknowledging that competition is a powerful processes in the natural world and that interspecific competition as well as other processes has played a significant role in developing faunal patterns.

Factors that have affected epifaunal tiering.- A broad variety of factors hva e affected the development of epifaunal tiering. In particular, phylogenetic constraints on the structural material available to each group of suspension feeders , and the biomechanical propeties of this structural material, strongly influencesc the height to which organisms can reach above the seafloor (Koehl 1984). In addition, studies in living suspension feedershave revelead the existence of three broad groups of suspension feeders. Passive suspension feeders are completely dependent upon ambient currents for supply of food and oxygen, whereas active suspension feeders pump water through their suspension-feeding structures (Jorgensen 1966; Vogel 1981). Between these two groups are organisms that have weak, active pumping but that also rely on ambient currents (Vogel 1978) (Table 1), which have been termend facultatively active suspension feeders by LaBarbera (1977,1984). These differences in mode of suspension feeding appear to directly affect the reaction of different suspension feeders to hydrodynamic boundary layer gradients. Foe example, Hughes (1975), in a study of secondary tierers living on the erect colonial hydroid Nemertesia antennina, found that most passive suspension feeders were attached to the top of the hydroid where ambient currents were greatest. Most active suspension feeders were attached relatively closer to the base of the hydroid within the lower part of the hydrodynamic boundary layer (Hughes 1975), thus creating a tiered structure of suspension-feeding types.

From these considerations an argument is made for the development of a tiered structure due to velocity gradients within the hydrodynamic boundary layer. The pattern of high-level passive suspension feeders and low-level active suspension feeders is based upon the metabolic need for increased feeding capability. Organisms that rely on ambient currents must feed from zones with higher velocity currents than active, pumping suspension feeders. Among living suspension feeders this predicted pattern is present in tthe example from Hughes (1975) cited above and in communities from relatively deep-water environments. In the deep sea, where flow is generally slower and the hydrodynamic boundary layer is generally thicker than in shallow shelf environments, individual organism heights as great as 1 m above the subtratum are common for many suspension feeders (Jumars and Gallagher 1982; Lipps and Hickman 1982). Similarly, for the Late Ordovoician of North America, Anstey (1986) has shown that offshore assemblages are differentiated from onshore assemblages by a much greater percentage of uppertier (+ 5 to + 10 cm) bryozoans. These taller bryozoans most likely reflect a adaptations toward greater feeding efficiency in these offshore environments (Anstey 1986), where the thickness of the hydrodynamic boundary layer would have been greater than in onshore environments.

The phyletic trend of larger body size can also place organisms at higher tier levels, but attainment of larger body size is quite different for colonial and solitary organisms. The clonal mode of colony growth allows easy construction of higher colonies for colonial organisms. For example, by adding a series of zooids to a vertically directed growth margin a fenestrate bryozoan could have easily constructed a zoarium that would be part of a higher tier. However, easy access for growth of primary tierers into significantly higher tiers has not been available to most solitary organisms. A solitary organism can only attain higher tier levels as a primary tierer by increasing individual size or by increasing the lenght of its attachment structure to the substratum. For either constructional or adaptational reasons, most solitary benthos have not attained high tier levels. A fairly restricted size range, that is within the lower tier levels, and relatively short attachment structures have rsetricted most solitary organisms to low tiers. For example, in brachiopods large sizeis more commonly thought to be correlated with adaptation to a veryhigh energy setting or with adaptation for the snowshoe effect (Thayer 1975). Long pedicles that would elevate brachiopods significantly of the bottom as primary tierers are not known from living brachiopods and have not been suggested for any fossil brachiopods.

Solitary stalked echinoderms are exceptions to this generalization because they had a means to position individuals into high tier levels. The column attachment structure of stalked echinoderms is constructed of individual plates added through ontogeny below the calyx. Taller individuals could have been developed by either recapitulation by acceleration or recapitulation by prolongation (*sensu* Gould 1977). The constructional argument for ease of height increase among echinoderms is also demonstrated by the tendency for height reduction displayed in these organisms. Stalked echinoderms display a repetead convergent evolution for adapting to varied levels in the tiered structure of communities, including column reduction or elimination for life on the substratum (Ettensohn 1984; Ausich and Bottjer 1985b). The evolutionary constructional pathway for increase in column height is also a pathway for height decrease.

At the seafloor, competition for food and space (Jackson 1983) can be intense. Potentially many organisms are competing for a supply of food that may be limited (Buss and Jackson 1981). In subtidal settings, this food is moving by in horizontally directed currents. From an organismal point of view, there is a single opportunity to capture a living food particleas it moves past along a more-or-less horizotal vector. Organisms that are able to reach to higher tier levels for feeding gain acces to food particles moving past the seafloor that are not available to their immediate neighbors. This offers high-level tierers a selective advantage in food competition. This food competition is competition for a place from which to feed which may have caused the development of a tiered structure (Ausich 1980).

These processes of adaptation to flow gradients in the hydrodynamic boundary layer, growth to a larger size, and competition for a space from which to feed are judged to be among the most important of processes that could have caused the development of an epifaunal tiered structure. In contrast, other important processes can cause the loss of a tiered epifaunal structure. Increased rates of predation by durophagous predators, which may cause elimination and even extinctionof epifaunal organisms (e.g., Vermeij 1977), could lead to a loss of epifaunal tiering structure. Similarly, increased rates of bioturbation by deposit feeders, which have been postulated to cause elimination of immobile suspension-feeders living on soft substrata (Thayer 1979, 1983), might also cause a reduction in epifaunal tiering structure. Periods of mass extinction which affected epifaunal organisms would also potentially cause the loss of epifaunal tiering structure.

Factors that have affected infaunal tiering.- Several physical constraints of the sediment-water interface have probably limited the maximum depth of infaunal tiering. These have included the usual depth below the sediment-water interface of the redox boundary in aerobic environments (i.e., Bromley and Ekdale 1984; Savrda and Bottjer 1986) and the increase of sediment stiffness with depth below the seafloor (i.e., Bokuniewics et al. 1975).

Just as levels of incrased durophagous predation may be a cause for reduction of epifaunal tiering, they are also thought to cause a greater level of infaunalization for benthic organisms (i.e., Stanley 1975; Vermeij 1977), and hence may have led to more complex infaunal tiering. Structuring of several Recent subtidal communities in tiers has also been attributed to space competition (Peterson 1977). However, Peterson (1979) indicated that this strategy to avoid interference competition in soft substrata by developing a tiered structure has been documented in only a few cases. This contrasts with hard substrata, where interference competition has been documented as a common process (Peterson 1979). Stanley (1975,1977) concluded that soft substrata suspension-feeding bivalves have rarely reached the densities necessary for competition and that predation is more important for these organisms. To better understand the role of infaunal space competition, further study of the relative importance of biotic processes is needed in tropical and subtropical infaunal communities.

Intertidal areas experience a pronounced rise and fall in the level of the water table through the tidal cycle. Stanley (1968, 1975) suggested that adaptations to deeper burrowing, and hence more complex tiering, may have first arisen in intertidal areas, as organisms tracked the daily movement of the water table in their burrows. this would have preadapted these infaunal burrowers to deep-burrowing in the subtidal environments treated in this study.

Although several processes such as adaptation to increased rates of predation and space competition are considered to have been significant in fostering the development of infaunal tiering, significant factors that might cause a loss of infaunal tiering, other than the reduction of levels of predation and competition, have never been postulated. Mass extinctions that significantly affect infaunal organisms are the most likely cause for reduction of infaunal tiering.

A causal history of tiering

The tiering history (Fig.1) has periods of change and periods of stasis. A preliminary assessment can be made of the several factors which most likely have led to variations in tiering at different times during the Phanerozoic. The tiering structure is a morphological as well as an ecological phenomenon. Thus, an assessment of rates of change of the tiering structure may allow an indirect "fingerprint" of the nature of the evolutionary dynamics which fostered the development of the tiering structure in the Phanerozoic.

Cambrian tiering.- Primitive suspension-feeding metazoans in soft substrata Cambrian environments developed communities with low tiering height, shallow tiering depths and minimal tiering complexity (Fig.1). Because of their constructional simplicity, in comparison with later Phanerozoic faunas, Valentine (1973) has referred to them as "grubby". Even consideration of the Burgess Shale fauna reveals relatively minor tiering complexity among Cambrian suspension-feeders (Conway and Morris 1979). As will be discussed in subsequent sections, much of the morphological complexity developed by suspension-feeding faunas after the Cambrian resulted from adptations to increased tiering.

The Ordovician-Silurian change in epifaunal tiering could have resulted from growth to a larger size among individuals, adaptations to velocity gradients in the hydrodynamic boundary layer, competition for a place from which to feed, or some combination of this factors. The contribution of each of this factors can be evaluated with varying degrees of sucess.

If observations of pattern and process for adaptations to velocity gradients in the hydrodynamic boundary layer in ecologic time (i.e., Hughes 1975)can be extrapolated to evolutionary time, the predicted pattern would be for solitary passive suspension- feeders to have dominated among higher epifaunal tiers. This prediction is true, in part, for most of the Ordovician-Silurian increase in tiering height andcomplexity was brought about by stalked echinoderms that are passive, solitary suspension feeders (Fig.1,3). If, as they were inferred to be, the Cambrian ancestors of these Ordovician echinoderms were passive suspension feeders, then their contribution to the development of Ordovician-Silurian epifaunal tiering structure would have been caused by adaptations for increased feeding capability. A possible variation of this, however, is that stalked echinoderms evolved as passive suspension-feeders because (as already discussed) they could easily elevate their feeding structures to relatively high velocity regions of the hydrodynamic boundary layer.

Because other primary tierers that reached higher tier levels were colonial passive and facultatively active suspension feeders (Fig.2), other factors may have significantly contributed to this tiering change. However, the contribution of simple trends towards increase in size, as well as competition for a place from which to feed cannot be fully evaluated until more detailed studies (such as those of Ausich,1980, on Mississipian echinoderm tiering) are completed for this interval.

These changes in the benthos during the Ordovician to Silurian were stiking in terms of the changes in composition of communities and tiering height and complexity. The dramatic increase in echinoderm morphological complexity during this interval was described as a "constructional evolutionary event" by Derstler (1984).

Devonian through Pennsylvanian epifaunal tiering.- With the asumption that the absence of alcyonarians from the rock record is taphonomic, no major groups of Paleozoic tierers developed subsequent to the Ordovician. This was a period of relative stasis (Fig.1), so that adjustments of tiering positions and changes in relative abundance of existing primary tiering groups dominated.

For example, class diversity of principally suspension-feeding echinoderms decreased from a Middle Ordovician high of 10, to 4 in the Middle Devonian and 2 in the Pennsylvanian (Ausich and Bottjer, 1985b). The decrease by two of class diversity from the Middle Ordovician into the Silurian (Ausich and Bottjer, 1985b) may have been caused by processes operating during the Ashgillian mass extinction (Raup and Sepkoski 1982). Signor and Brett (1984) have documented that the Paleozoic increase in durophagous predation pressure began essentially in the Middle Devonian. This seem to have had little effect on the overall drop in class diversity of principally suspension-feeding echinoderms. Similarly, a causal connection between interspecific competition and the extinction of echinoderm classes cannot be efectively tested. However, it seems from the relatively stable pattern of echinoderm generic diversity during this time (Ausich and Bottjer 1985b) that surviving stalked echinoderms, especially crinoids, successfully competed for vacated niche space that resulted from these extinctions.

Paleozoic crinoids do display morphological adaptations for predator avoidance or for survival of predation attempts (Meyer and Ausich 1983; Signor and Brett 1984). However, these adaptations did not include any identifiable changes in the overall Paleozoic epifaunal tiering structure. Processes such as interspecific competition for different heights and for different food sizes within specific heights, as discussed by Ausich(1980) for Mississipian crinoids, were probably important, but more detailed information is needed to test this factor fully. Any possible changes in rates of bioturbation during this time (i.e., Thayer 1979,1983)had no discernible effect on the overall tiering structure.

Permian through Jurassic history of epifaunal tiering.- Details of the historical record of the Permian extinction of stalked echinoderms are very poorly known, because of a lack of an adequate number of well-preserved fossil localities through this interval. Consequently, details of changes in maximum tiering heights and of tiering complexity through the Permian-Triassic transition are not known. Although perhaps in part the result of taxonomic bias, a nearly complete distinction is present between Paleozoic and Triassic crinoids. No forms cross the boundary. Encrinus in a monogeneric family is present in the Triassic and is assigned to a subclass of otherwise Paleozoic crinoids; no Paleozoic forms are assigned to the post-Paleozoic subclass, the Articulata. Obviously, the near extinction of crinoids near the end of the Permian affected the tiering structure of epifaunal communities. We conclude that maximum tiering heights and heights of tier subdivision were reduced. Perhaps some of the intermediate tier subdivisions that we have included on Fig.1 may have been eliminated. No fossil evidence records these patterns; unfortunately, they must be inferred.

Fenestrate bryozoans are thought to be responsible for maintaining the +20cm tier in the late Paleozoic; however, in the latest Permian, they were undergoing a decrease in diversity that led to their eventual extinction in the Early Triassic (Ryland 1970). This diminished diversity leading to eventual extinction of fenestrates probably also indicates that this level declined, altough the actual tiering record of this has not been documented. Additionally, along with crinoids and fenestrate bryozoans, all other life was drastically reduced during the terminal Paleozoic extinction, with as many as 70%-90% of all species thought to have become extinct (Stanley 1985). Again tiering height and complexity of structure must have decreased as a consequence.

These inferred changes in tiering patternare thought to have been only changes in the degree of tiering, because by the middle Triassic tiering structure in epifaunal suspension-feeding communities had been basically restored to the Paleozoic pattern (Fig.1). Crinoidsestablished again a characteristic maximum tier level at approximately 100cm (Linck 1954). Important primary tierers in these restructured Mezosoic epifaunal communities included brachipods, bryozoans, bivalves, sponges, corals, and crinoids in the 0 to +5cm tier , sponges, bryozoans, corals, alcyonarians, and crinoids in the +5 to +20cm tier; crinoids, sponges, and alcyonarians in the +20 to +50cm tier; and crinoids in the +50 to +100cm tier.

Epifaunal suspension-feeding communities became less dominant i most soft substrata settings after the beggining of the Cretaceous (Jablonski and bottjer 1983; Jablonski et al. 1983). However, in such settings the same basic suite of Mesozoic suspension-feeders, minus crinoids, filled epifaunal tiers (Ausich and Bottjer 1982; see references in appendix A). Begginingin the Cretaceous, for the first time since the Cambrian, primary tierers above the lowest level were all colonial organisms. This pattern of change is consistent with the hypothesis that increased predation pressure caused a reduction in stalked crinoids (Meyer and Macurda 1977) and other epifauna during the late Mesozoic (Vermeij 1977), and with observations that colonial organisms are more able to survive predatory attacks than are solitary organisms (Jackson 1977). This reduction in epifaunal tiering height and complexity is also consistent with the hypothesis that increased amounts of bioturbation caused a reduction in epifauna during this time (Thayer 1979, 1983). However, before increases in bioturbation can be treated as a significant factor, more direct evidence documenting this process needs to be gathered from the stratigraphic record.

Ordovician through Permian increase in infaunal tiering depth and complexity.- Based on the trace fossil and body fossil record, infaunal tiering depth and complexity in the Paleozoic appears to have developed independently from the epifaunal tiering structure (Fig.1). The slower development of maximum infaunal tiering complexity, which may have taken twice as long as the development of epifaunal tiering complexity, may be an artifact because the record of Paleozoic infaunal tiering is incompletely known (i.e., see previous discussion on Thalassinoides). More likely, this difference is the result of different processes operating in epifaunal and infaunal settings and different constructional and phylogenetic constraints that influenced infauna and epifauna.

Much of the reason for development of the -6 to -12cm tier in the Ordovician may have been due to the tendency for infaunal suspension-feeders to grow larger and hence burrow deeper. This increase in tiering complexity may also have occurred owing to adaptations to competition for space. However, the contribution of each of these factors to the development of infaunal tiering in the Ordovician cannot presently be evaluated. Interestengly, as postulatedby Stanley(1968, 1975), a variety of trace fossil studies appear to indicate that deep-burrowing by suspension- feeders (i.e., see Skolithos in Hantzschel 1975) may have originated during the Cambrian in intertidal and nearshore environments.

The increase in Paleozoic predation documented by Signor and Brett (1984) at the beginning of the Devonian coincides with the time of bivalve ocupation of the -6 to -12cm tier (Fig.4).

Addition of the -12 to -100cm tier in the Carboniferous (Fig.1)may also have been the result of continually increasing Paleozoic predeation. Thus, much of the development of increased tiering depth and complexity, which by the late Paleozoic had reach the level present in modern seas, was most likely caused by increased levels of predation. Available evidence indicates that this level of infaunal tiering persisted through the Permian- Triassic mass extinction. In particular, the primary group of deep-burrowing bivalves, the anomalodesmatans, was not significantly affected by this event (Runegar 1974).

Mesozoic through Cenozoic infaunal tiering.- The patterns of post-Paleozoic infaunal tiering are similar to the patterns of post-Silurian paleozoic epifaunal tiering; relative stasis in tiering structure, with addition of a few new taxonomic groups of burrowers into deeper tiers.Thalassinoides burrows have been reported to be as deep as 2 (Bottjer 1985) to 3m (Kauffman and Pratt 1985) below upper Cretaceous discontinuity and disconformity surfaces. Whether they were created by suspension- feeders or not, their rarity precludes consideration of a characteristic tier below -100cm. The most prominent and well-documented groups of burrowers that entered deeper tiers were the myoid and veneroid bivalves (Fig.4) and the decapod crustacean creators of the trace fossil Ophiomorpha (Hantzschel 1975). The developmentof additional deep burrowers in the post-Paleozoic has also been attributed to a major trend of increased predation which began at this time, which Vermeij (1977) has termed the "Mesozoic Marine Revolution". Evidence presently available indicates that infaunal tiering structure was not significantly affected by any of the post-Paleozoic major mass extinctions documented by Raup and Sepkoski (1982).

Conclusions

We acknowledge that many factors have contributed to the developmentand change of tiering structure during the Phanerozoic, including undoubtedlyfactors not mentioned here. Among the processes and constraints postulated here, a factor or subset of factors can be postulated to have been more important than others in particular situations or at specific times in the tiering development. For example, trends within different organisms for growth to a larger body or colony size, which can be due to many processes, could very likely have accounted for most of the development of tiering complexity up to +50cm and down to -12cm. Large body size alone can be eliminated as a significant factor for the tiering complexity developed from +50 to +100cm and -12 to -100cm, because the morphologies and burrows of organisms in those tiers (crinoid bodies attached to long stalks, long siphons of bivalves, extensive burrow galleries of relatively small crustaceans, etc.) are undoubtedly not the result of optimized body size.

Stalked echinoderms were the only inhabitants of the +50 to +100 cm tier. Because the stem represents a significant investment of energy, the most plausible hypothesis for why echinoderms livedin this tier level is an adaptation toward greater feeding capability. From presently available evidence, however, it is imposible to distiguish wheter thsi increasein feeding capability was achieved through competitive interactions for a place from which to feed, adaptations to velocity gradients in the hydrodinamic boundary layer, or some combination of both. In contrast, occupation of the -12 to -100cm tier by infaunal suspension feeders did not increase feeding efficiency, because all infaunal suspension feeders acquiere food from water just above the water-sediment interface, and more energy is needed to pump water to greater depths. The most plausible hypothesis as to why infaunal suspension-feeders occupy the -12 to -100cm tier is an adaptive response to avoid predation.

Other factors can be hypothesized to have led to the reduction of height and complexity of epifaunal tiering. Infaunal tiering has never had a reduction in maximum depth or complexity. In particular, although extinctions have undoubtedly changed the types of organisms in different infaunal tier levels, infaunal tiering has never been affected in any significant way during periods of mass extinction. Epifaunal tiering, however, appears to have been significantly reduced by processes that led to the Late Permian mass extinction. The relatively slow elimination of stalked articulate crinoids from most shelf habitats during the Cretaceous indicates that the Cretaceous reduction in tiering was not due to mass extinction but to long -term biotic processes (Bottjer and Jablonski 1986). Additional studies are needed to test whether increases in rates of predation or amounts of bioturbation were the most significant of the long-term factors which caused reduction of epifaunal tiering in the Cretaceous.

Differences in rates of change of infaunal and epifaunal tiering may yield useful information on the nature of the infaunal and epifaunal adaptive zones at different times. Rates of change from three times, the Ordovician-Silurian increase in epifaunal tiering, the Paleozoic increase in infaunal tiering, and the Cretaceous reduction in epifaunal tiering, can be compared. Development of all epifaunal tiering above +5cm took aproximately 80 ma, whereas development of all infaunal tiering below -6cm took aproximately 180-200 ma. All other things being equal, this may indicate that during the Ordovician-Silurian the epifaunal adaptive zone had unchanging, relatively optimal conditions (when compared with later times) for occupation by suspension-feeders, whereas during the Paleozoic, conditions in the infaunal adaptive zone slowly became more optimal for inhabitation by suspension- feeders. This relatively slow increase in development of the infaunal adaptive zone may have been due to the slowly increasing significance of a biotic proceses- in this case most likely rates of predation. As has already been discussed, the slow reduction (one tier in approximately 80 ma) in epifaunal tiering during the Cretaceous was most likely due to the slow degradation of the epifaunal adaptive zone also by the action of biotic processes.

Alternatively, differences in rates of development of infaunal and epifaunal tiering could have resulted from differences in rates of evolution and the number of adaptive "steps" required to reach extreme tier levels. For example, as has already been discussed, crinoids only needed to make more parts (columnals) for a structure (the column) that already existed to rech higher tier levels, whereas bivalves neded an evolutionary innovation of a new structure (the siphon) to burrow to grater depths. This later alternative is more plausible given available evidence.

Detailed site-specific studies of tiering at different times and in different environments throughout the Phanerozoic are needed to further test and refine our understanding of the factors which led to the development and subsequent changes in tiering of soft substrata shallow subtidal shelf and epicontinental sea suspension feeders. One fundamental goal of future studies should be to further elucidate the nature of the evolutionary dynamics which have led to the development and subsequent changes of the tiering structure. Gould (1985) has defined evolutionary processes as occurring at three separate tiers (not the tiers discussed herein) of time: ecological moments, normal geological time (trends during milions of years), and periodic mass extinctions. This hierarchical approach may be a useful way to understand the development of tiering because the processes and constraints that we consider important for tiering have operated at all of these levels.

In the shallow subtidal environments considered in this study, suspension feeders are not the only macroinvertebrates present in a tiering structure. Relatively little is known of the Phanerozoic history of tiering of deposit feeders and carnivores. Current emphasis on the understanding of cross-cutting relationships among trace fossils, however (i.e., Bromley and Ekdale 1984,1986; Frey and Bromley 1985; Savrda and Bottjer 1986; Wetzel and Aigner 1986), may lead to a detailed history of deposit-feeder tiering during the Phanerozoic. Provision of such a history would alow an important comparision with the history history of tiering in suspension-feeders, not only to determine the different factors that have influenced tiering in each trophic group, but to evaluate the effect that each group has had upon the development of tiering in the other.

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Appendix A

Selection of key refferences (of approximately 1,200) that constitute the data base for the tiering history (Fig.1).

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Figure 1. Tiering in soft substrata suspension-feeding communities through the Phanerozoic. The heaviest lines represent the maximum level of tiering above or below the substratum at any time. Other lines represent levels of tier subdivision. Solid lines represent data, and dotted lines are inferred levels. Modified from Ausich and Bottjer (1982).

Figure 2. Tiering history of Phanerozoic colonial suspension feeders on soft substrata form nonreef, shallow subtidal and epicontinental sea settings. Vertical distribution shown here within each tier is arbitrary and only implies occupation in a tier for the time duration indicated.

Figure 3. Tiering of Phanerozoic suspension-feeding echinoderms on soft substrata from nonreef, shallow subtidal shelf, and epicontinental sea settings (modified from Ausich and Bottjer 1985b). Vertical distribution shown here within each tier is arbitrary and only implies occupation i a tier for the time duration indicated; highest tier is +50 to +100cm.

Figure 4. Tiering of Phanerozoic suspension-feeding bivalves on soft substrata from nonreef, shallow subtidal shelf and epicontinental sea settings (Actinodontia = Modiomorphoida). Compiled from data in Cox et al. (1969), Stanley (1968, 1970, 1975, 1977), Runnegar (1974), Pojeta (1978), and Sepkoski (1982). Vertical distribution shown here within each tier is arbitrary and only implies occupation in a tier for the time duration indicated.

Table 1. Suspension-feeding mode of selected invertebrates.

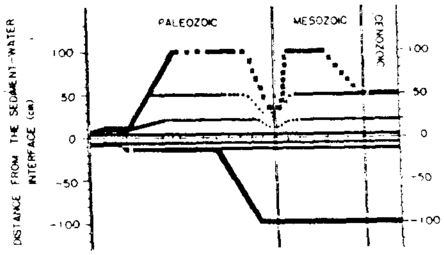
PALEOZOIC
MESOZOIC
CENOZOIC
DISTANCE FROM THE SEDIMENT-WATER INTERFACE (cm)
100
50
0
-50
-100
100
50
0
-50
-100

Fig. 1

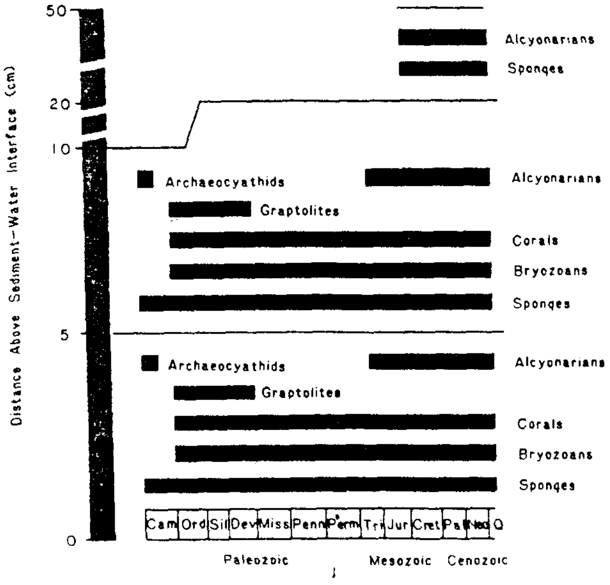
50
20
10
5
0
Distance Above Sediment-Water Interface (cm)
Alcyonarians
Sponges
Archaeocyathids
Graptolites
Alcyonarians
Corals
Bryozoans
Sponges
Archaeocyathids
Graptolites
Alcyonarians
Corals
Bryozoans
Sponges
Cam
Ord
Sil
Dev
Miss
Penn
Perm
Tri
Jur
Cret
Pal
Neo
Q
Paleozoic
Mesozoic
Cenozoic

Fig. 2

David J. Bottjer

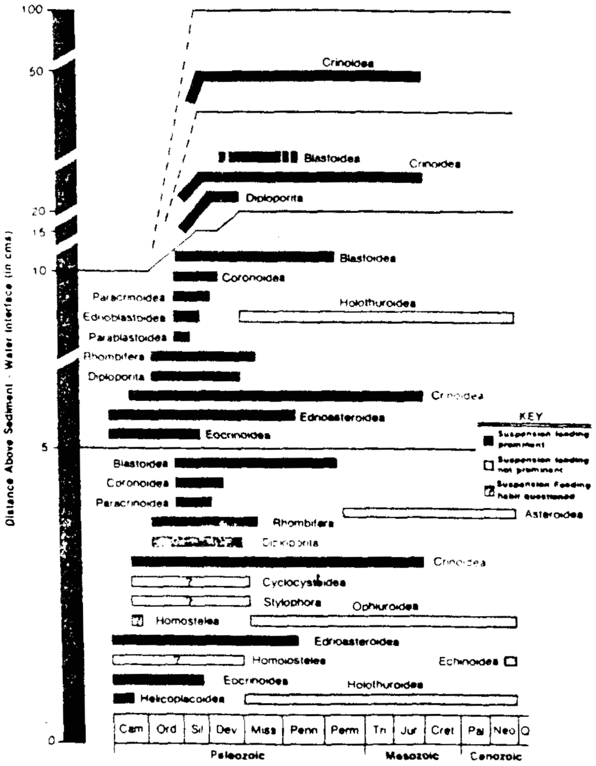

Fig. 3

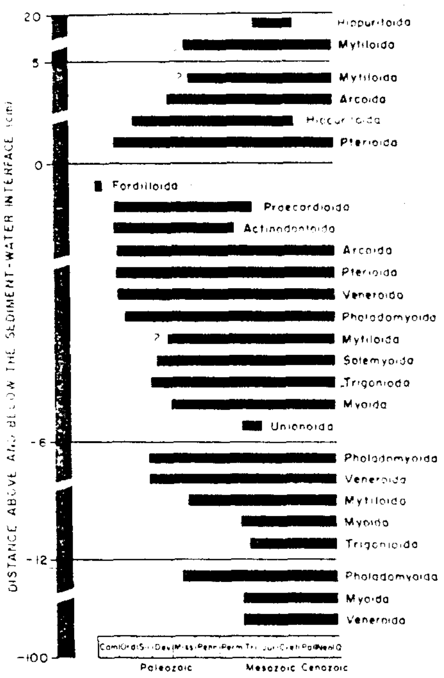

Fig. 4

Passive suspension feeders	Facultatively active suspension feeders	Active suspension feeders
Net-erecting trichopteran larvae[4]	Some sponges[1,4]	Most bivalves[4]
	Some brachiopods[4]	Ascidians[4]
Some barnacles[4]	Erect bryozoans[4]	Encrusting bryozoans[4]
Erect coelenterates[4,5]	One bivalve (*Placopecten*)[1]	Some sponges[4]
		Some gastropods[6]
Crinoids[5]	Some ascidians[2]	Some annelid worms[6]
		Most brachiopods[6]
Some ophiuroids[5]	Some barnacles[6]	Some ascidians[6]
Some holothurians[5]		
Some annelid worms[6]		
Hydroids[6]		
Gorgonians[6]		

[1] Hartnoll (1967), [2] Monniot (1967), [3] Vogel (1974), [4] Vogel (1981), [5] Warner (1977), [6] LaBarbera (1984)

Table. 1

In: RIGBY,J.K. & STEARN,C.W. ORGANIZERS. 1983. SPONGES AND SPONGIOMORPHS. NOTES FOR A SHORT COURSE: KNOXVILLE, TENN., UNIV. TENNESSEE DEPT. GEOL.SCI. STUDIES IN GEOLOGY 7, AND THE PALEONTOLOGICAL SOCIETY, P. 178-190.

Archaeocyathids: Morphology and Affinity

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INTRODUCTION

The Archaeocyatha were marine organisms developing mineral skeletons and using calcium carbonate for this purpose. Remains of their cups are found in carbonate shelfs and reef environments of the Early Cambrian seas. Few representatives of the family Archaeocyathidae are found through the Middle Cambrian to the Upper cambrian (Debrenne, Rozanov and Webers, in press).

MORPHOLOGY

General features of the skeleton

The basic skeleton of Archaeocyatha is relatively simple, composed of an individual "cup" comprising two coaxial, inverted, generally porous cones (the walls) which are connected by various, more or less radial and sometimes horizontal, elements (Fig.1). Exceptionally, the maximum diameter will reach 600mm and the maximum height 300mm - the minimum being 4mm for 10mm - but the average cups are about 10-25mm in diameter and 80mm in height.

The great majority of Archaeocyatha are solitary, slenderly conical, often ceratoid during the first stages of growth, becoming cylindrical in the adult stages (Fig.2a-b). Periodic bulging of the intervallum may affect the outer wall or both walls (Fig. 2c-d); longitudinal groves and fluting may occur (Fig. 2e-f). Large open cups are either expanding cones (Fig.2g) or even discoid and slightlyundulose (Fig. 2h). Some two-walled species without any intervallar structures have sub-sphaerical, bulbous shapes, free on the bottom (Fig.2i). Colonial forms do no exist, but are not very common. They present a small number of varieties: catenulate (Fig.2j) or dendroid (Fig.2k, k' (one- walled form)). Cups linked to one another by exothecal tissue analogous to coenenchyme may be regarded as massive colonies (Fig.21).

Ontogeny and development

The worlwide distribution of Archaeocyatha within the Lower Cambrian has suggested that they had planktonic larvae. Some small calcareous problematica have been considered by Vologdin (1932)as larval or young stages and by Zhuravleva (1981) as dispersion forms. There are no decisive arguments to prove any close relationship between those "Cribricyaths" and the Archaeocyatha.

"Ontogenic stages" of authors are in fact changes during the growth of the skeleton; they are studied by means of longitudinal axial sections and serial transverse ones. The observations have been well described by Zhuravleva (1960 and in Hill 1972). At the beggining there is a one-walled cup, with no pores, attached to the substratum by a solid sole. Two different ways are thus possible: 1) in Regulares the cup is rapidly perforated, radial rods appear (diameter 0.20mm) and then the inner wall. Septa and tubulae are present at a diameter of 0.40mm. Complexity of the outer wall is soon developed, and always before the inner wall. 2) in Irregulares the imperforate cup persists during a period variable in time, the inner cavity is filled by dissepiments and disoriented rods or small plates, sometimes up to 0.5mm diameter or more. Complexity of walls occurs late in developlment.

Outer wall (Fig.3)

In Regulares, the outer skeletal envelope shows a considerable variety of types. On the contrary, in Irregulares there is a gradation in complexity from species to species, so that the limits between types are difficult to draw. Outer wall pores may occupy a larger area than the skeleton, or smaller, nonporous walls may persist in adult stages. The pores are rounded, oval, polygonal, slit-like or irregular. The distributions in the apertures is in longitudinal rows, with pores of the neighbouring rows opposite or alternate.

Regular types of outer wall: 1) simple (Fig.3a); 2) simple tumuli (Fig.3b); 3)pore-tubes and bracts (Fig.3c-d); 4) multiperforate tumuli (Fig.3e); 5) with microporous sheath, independent from the primary wall (carcass) (Fig.3f); 6) independent microporous sheath on carcass with sigmoid tubes; 7) annuli or louvres (Fig.3g); 8) slit-like carcass with external fine grill of longitudinal plates (clthri) (Fig.3h); 9) microporous sheath atached to the carcass (Fig.3i).

Irregular types of outer wall: 1) rudimentary, formed by outer edges of intervallum structures; 2) simple pores in vertical rows; 3) peripherally arranged pores (Fig.3j); 4) pore-tubes; 5) porous carcass with pellis or microporous sheath (Fig.3k); 6a) porous carcass with beginning of subdivision of pores; 6b) with partial to complete subdivision of pores.

Intervallum (Fig.4)

The space between the two walls is called the intervallum. It is subdivided into loculi (Fig.1). The two walls are connected by various structures.

In Regulares: 1) horizontal rods arranged in vertical radialplanes analogous to septa, cross section of rods circular or vertically flattened; 2) horizontal porous tabulae without radial elements; 3) radial vertical planes, regularly perforated (Fig.4) more or less regularly (Fig.4a-b-c-d-e) progressively lacking porosity in evolution (Fig.4l). Septa are sometimes connected by sinapticulae (Fig.4f); 4) tabulae, porous, horizontal to arched partitions in association with septa. Repartition of tabulae is a diagnostic character. According to the shape of pores, several types are distinguished: a) simply porous (Fig.5g); b) with slit-like pores (Fig.5h); c) with pectinate partition (Fig.5i).

In Irregulares: 1) scattered, to three directional conected rods, with circular transverse section (dictyonal type, Fig.4k); 2) flattened amiboid plates, scattered or arranged in wavy vertical planes (taenioidal type, Fig.4j); 3) horizontal partitions: a) porous tabulae or pseudotabulae built on synapticulae, b) dissepiments (tabular structures may be associated with either rods or dyctional type or with pseudosepta); 4) hexagonal perforated tubes (syringocyathoidal type, Fig.4m-n).

Inner wall (Fig.5)

Regular types: 1) simple pores (Fig.5a); 2) simple pores covered with bracts or louvres (Fig.5b); 3) annuli (Fig.5c-d); 4) pore- tubes without lateral communication (Fig.5e); pore-tubes with lateral communications, straight or twisted (Fig.5f); 6) carcass and second microporous sheath (Fig.5g); 7) intervallum side with pore-tubes, central cavity side with various structures (Fig.5h); 8) intervallum side with annuli, central cavity side with various structures (Fig.5i).

Irregular types: 1) simple opening of the intervallar structures; 2) pore-tubesand bracts; 3) annuli; 4) pores or pore-tubes with partial to complete subdivision; 5) carcass and microporous sheath.

Central cavity

The central cavity is the space inside the inner wall There are generally no skeletal elements in it. They may occur in the lower part or periodically as "bridges" underlain by dissepimental tissues wich horizontally cross the entire organism. Endostrueture (see below) is generally developed when exostructuresand stereoplasma are present. Secondary thickening of the inner wall partially or totally occupies the whole inner space. The central cavity is absent in some Irregulares (*Agastrocyathus, Prismocyathus*) or when opposite parts of the intervallum in catenulate colonies are in contact. In discoidal forms (*Okulitchicyathus*, Fig.2h), the upper "inner" surface is difficult to interpret as a central cavity.

Exoskeleton structures

Archaeocyathan cups are often associated with skeletal constructions developed outside the outer wall (exostructures or outgrowths) or inside the inner wall (endostructures). The significance of these elements has always been controversial: symbionts or parasites for some authors, or production of the main cup of others. Exostructures, when present, induce the development of dissepiments and, very often, stereoplasma (i.e. thickening of the primary skeleton by means of succesive layers).

Dissepiments and stereoplasma have the same histological structures as the main skeleton, but with fine granules (see below p.181 and Fig.6b-c). Their development, when complete, closes the loculi; in that case, the living tissues are restricted to the upper part of the body, but this reduction is balanced by increasing the surface due to the outgrowth itself. Endostructure is present or not, and also may partly or totally close the central cavity.

Examination in ultra-thin section and scanning electron microscopy shows a continuation between the tissue of the main cup and the exo- and endostructures. The histological structures of the cup and the exoskeleton structures are identical; these results favour a productionof the cup rather than a parasitic origin.

Skeleton histology

Since 1910, Taylor has described the microscope texture of the skeleton as granules consisting of more or less spherical bodies from 0.03mm to 0.09mm. New techniques, using ultra-thin slides, 2-3um in thickness, with polished surfaces (Lafuste 1970-1974) and scanning electron microscopy give a more precise definition of the granules: the skeleton of Archaeocyatha is primarily made of globally polyhedral crystallites the surfaces of which are embossed by irregular cupules and bumps (Fig.6f). They may not be interpreted as sclerites or modified spicules, which are always independent elements, as the granules are perfectly geared and constitute a compact structure. Are these granules genuine or the result of some diagenetic process?. Tests have been made to verify this point in studying the microstucture: 1) on one genus (*Aldanocyathus*) of large geographic, stratigraphic, and ecologic distribution; 2)on different taxa of Archaeocyatha from the same assemblage; 3) on associated forms of the same assemblage. The results were conclusive: there is uniformity of microstructure among Archaeocyatha (Fig.6a-f). Other groups yield a different microstructure in the same assemblage (Fig.6h - *Renalcis,* Fig.6g- *Epiphyton*).

Nevertheless certain variations are observed. If there is no real difference between Regulares (*Aldanocyathus* - Fig.6d, *Ethmophyllum* - Fig.6a.) and Irregulares (*Archaeocyathus* - Fig.6b); in the latter the secretion is made in two stages, first the main skeleton, then dissepiments and stereoplasma, which are made of smaller granules (Fig.6c) Microstructures of endo- and exostructures have exactly the same pattern as the main skeleton. Forms with one wall (Monocyathida) (Fig.6e) have smaller and smoother granules than the two walled Archaeocyatha. Studies are in progress to find new trends in microstructures of Archaeocyatha.

SYSTEMATICS

It has been suggested that current classification of Archaeocyatha is a phyletic one, and that ontogenetic studies support this view. This assertion is based on Haeckel's rule of recapitulation of ontogenetic stages. Besides the classical criticisms expresed in this theory, one may remark that in the case of Archaeocyatha what is observed are steps in development of skeleton, with , as usual, cases of heterochrony, acceleration of growth pattern, etc.

The observation of different steps of growth, however, gives very useful indications on the hierarchy of characters in so far as it may be used for systematics. It must be always borne in mind that what are called genera, species and taxa, the real biological significance of which could not be comprehended. Having evaluated certain regularities in the evolution of Archaeocyatha, some authors have proposed to consider "territories" which have the same topographical situation within the skeleton as homological structures. The studies of homological changeability lead to the establishment of tables of repetitive homological series, which are considered as classificationm tables (Rozanov, 1974; Debrenne, 1974 and in press). It is posible to foresee new recombinations of characters and consequently new genera; it is true that all new taxa found since 1974 were easily put in the tables.

The proposed classification of Regulares is:

- suborders: constitution of the intervallum (empty, with radial bars, septa, septa and tabulae).
-superfamilies: types of outer wall (see p.179).
-families: types of inner wall (se p.180).

Attmpts of using a similar scheme for Irregulares have been made by Debrenne (1974) but have not been satisfactory because of the uncertainly of the limits between the porosity types of the walls, the gradations between rods, plates and pseudosepta, the different significance of the various tabular structures and dissepiments within the intervallum. The taxonomic range assigned on the basis of the homological series may be different in Regulares adn Irregulares. Research is in progress, but there are not yet any undeniable results for proposing a new classification.

AFFINITIES OF ARCHAEOCYATHA

The affinities of the group are still debated. The Archaeocyatha were classified among Porifera (Ziegler and Rietschel, 1970) or as an independentphylum close to the Porifera (Okulitch, 1955; Dbrenne, 1964; Hill, 1965-1972). Their affinities with Protista, Coelenterata or Algae are by no means fully apparent. It has even been proposed to put them in a special subdivision of organisms intermediate between Animals and Plants (Zhuravleva and Miagkova, 1972).

Archaeocyatha are organisms with a porous skeleton. By comparison with other porous groups, the pores may serve different functions: 1) filtration (type sponges); 2) apertures for pseudopodia (type Foraminifera); 3) apertures for gamete dispersion (type Algae). The differences in size of outer and inner wall pores and the presence of porous elements in the intervallum should have no significance in the last two cases. As for reproductive function, the number and the regular distribution of pores is not consistent with the hypotesis. Most of the authors consider teh Archeocyatha as filter-feeders. Controversial models have been proposed for the direction of the flow. For Zhuravleva and Elkina (1972) flow enters at the top of the central cavity, is directed downwards and, through the inner wall and intervallum, is ejected by the outer wall pores. Their argument is based upon the concavity of skeletal structures supossed to be pushed by the flow and consequently reflecting its direction. This is not verified by recent structures; for instance, inhalant pores are never in depressed areas as they should be according to Zhuravleva's assertion.

The other functional hypotesis is that flows enter through the outer wall pores and are exhaled upwards into the central cavity: it is a sponge model. Balsam and Vogel (1972) have tentatively tried to demonstrate that Archaeocyatha fed by passive flow through the outer wall going out at the top of the central cavity. Unfortunately the aluminium model tested does not correspond to any known Archaeocyatha: non porous septa and tabulae, wrong proportion of porous surface and solid skeleton. Besides, the minimum size of outer wall pores of real Archaeocyatha (20 um) is not consistent with a passive flow, which could not go through. If the direction of flow is most probably the one of Balsam and Vogel's model, it is necessary to conceive an additional pumping system, like sponges.

Therefore a sponge model is highly probable, with the same direction of flow and active pumping. As for the skeleton structure, the comparison between Archaeocyatha and modern sponges with calcified skeleton and no spicules (*Vaceletia*, "coralline sponges") is in favour of a close relationship between the two groups. According to new discoveries of Sphinctozoa in Australia and Archaeocyatha in Antartica within rocks of Upper Cambrian age the stratigraphical gap does not exist any more. The problem is now to decide whether Archaeocyatha must be included within the phylum Porifera, or is only close to it.

Explanations of figures

Fig.1 - Theoretical reconstruction of a composite Archaeocyatha (after Debrenne, 1964, mod.)

Fig.2 - External forms of Archaeocyatha (after Hill, 1965, mod.). a/cylindrical; b/ceratoid; c/periodic bulges of the outer wall; d/periodic bulging of both walls; e/vertical grooves; f/vertical fluting; g/expanding cone; h/discoid; i/ globular; j/catenulate colony; k/dendroid colony, double-walled cup; k'/dendroid colony, one-walled cup; l/colony with coenenchyme tissue (after Debrenne and James, 1981, mod.).

Fig.3 - Outer wall types (after Debrenne, 1964-1969, mod.). a/simple pores; b/simple tumuli; c-d/pore tubes and bracts; e/multiperforate tumuli; f/carcass and independent microporous sheath; g/annuli; h/clathri; i/carcass and non independent sheath; j/irregular simple pores; k/carcass irregular plus pellis (left) or microporous sheath (right).

Fig.4 - Intervallum types. a/simple regularly arranged pores; b/simple irregular pores; c/beggining of the oligomerisation of septa; d/non porous septa; e/type of irregular pores in pseudosepta, (a-e after Hill, 1972, mod.); f/synapticulae; g/normal porous tabulae; h/reticoscinus-type tabulae; i/pectinate tabulae; j/pseudosepta (taenioidal type); k/rods (dictyonal types), (f-k after Debrenne, 1964-1969); m/transverse section of hexagonal pore-tubes; n/longitudinal section of hexagonal pore- tubes, (m-n after Bedford in Hill,

1972, mod.); l/tridimensional recostruction of *Dailycyathus:* outer wall with bracts enterely covering the pores, inner wall with stirrup pores. Intervallum with imperforate septa and dissepiments.

Fig.5 - Inner wall types (after Debrenne, 1964-1969). a/simple pores; b/brcts; c-d/annuli; e/non communicating pore-tubes; f/laterally communicating pore-tubes; g/carcass plus microporous sheath; h/tubes plus annuli; i/annuli plus bracts.

Fig.6 - Skeleton histology. a/*Ethmophyllum;* b/main skeleton of *Archaeocyathus*; c/dissepiments and stereoplasma of *Archaeocyathus;* d/*Aldanocyathus;* e/*Archaeolynthus*; f/reconstruction of an elementary granule; g/*Epiphyton;* h/*Renalcis*.

Fig 1

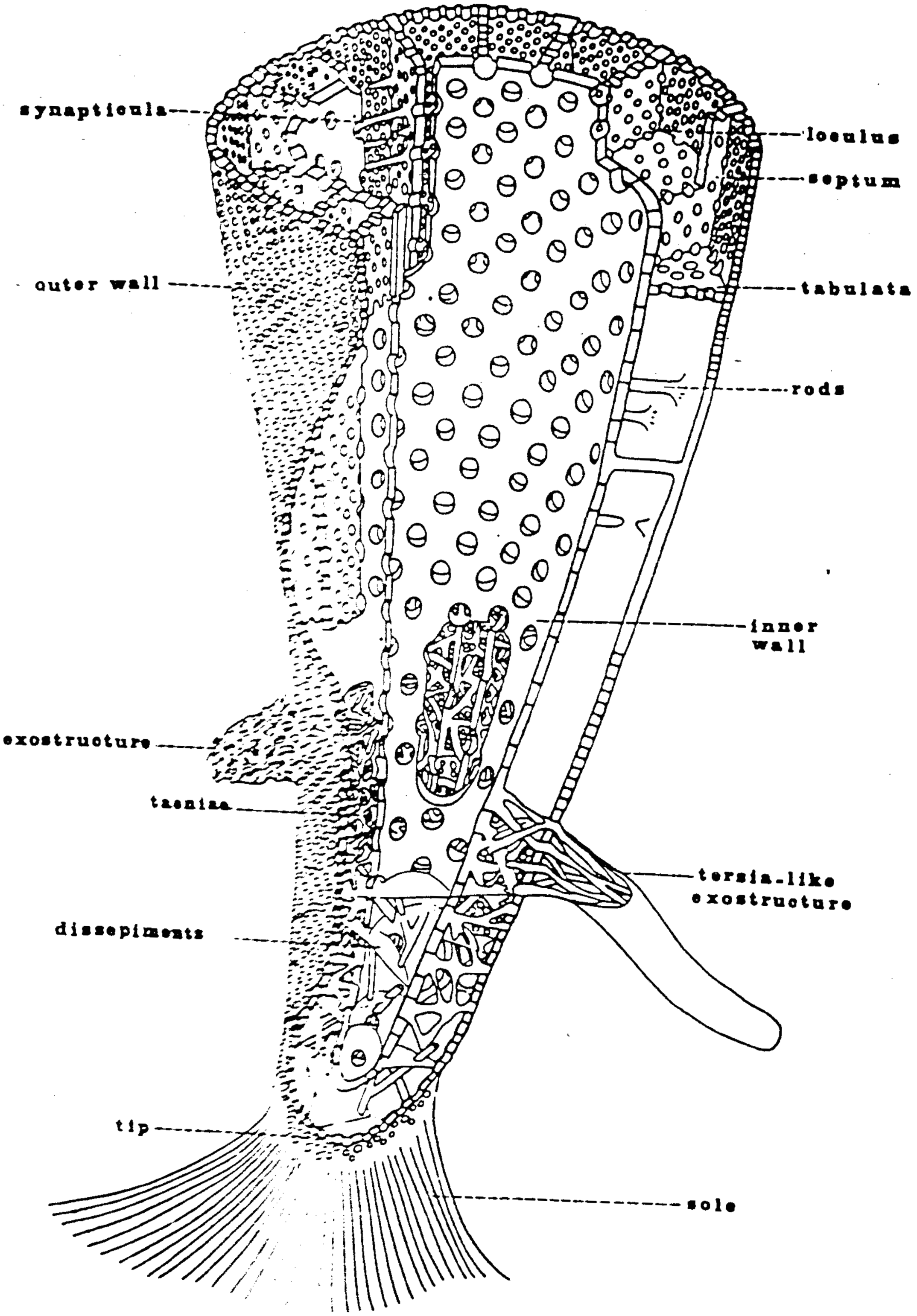

synapticula
loculus
septum
outer wall
tabulata
rods
inner wall
exostructure
taeniae
tersia-like exostructure
dissepiments
tip
sole

Fig 2

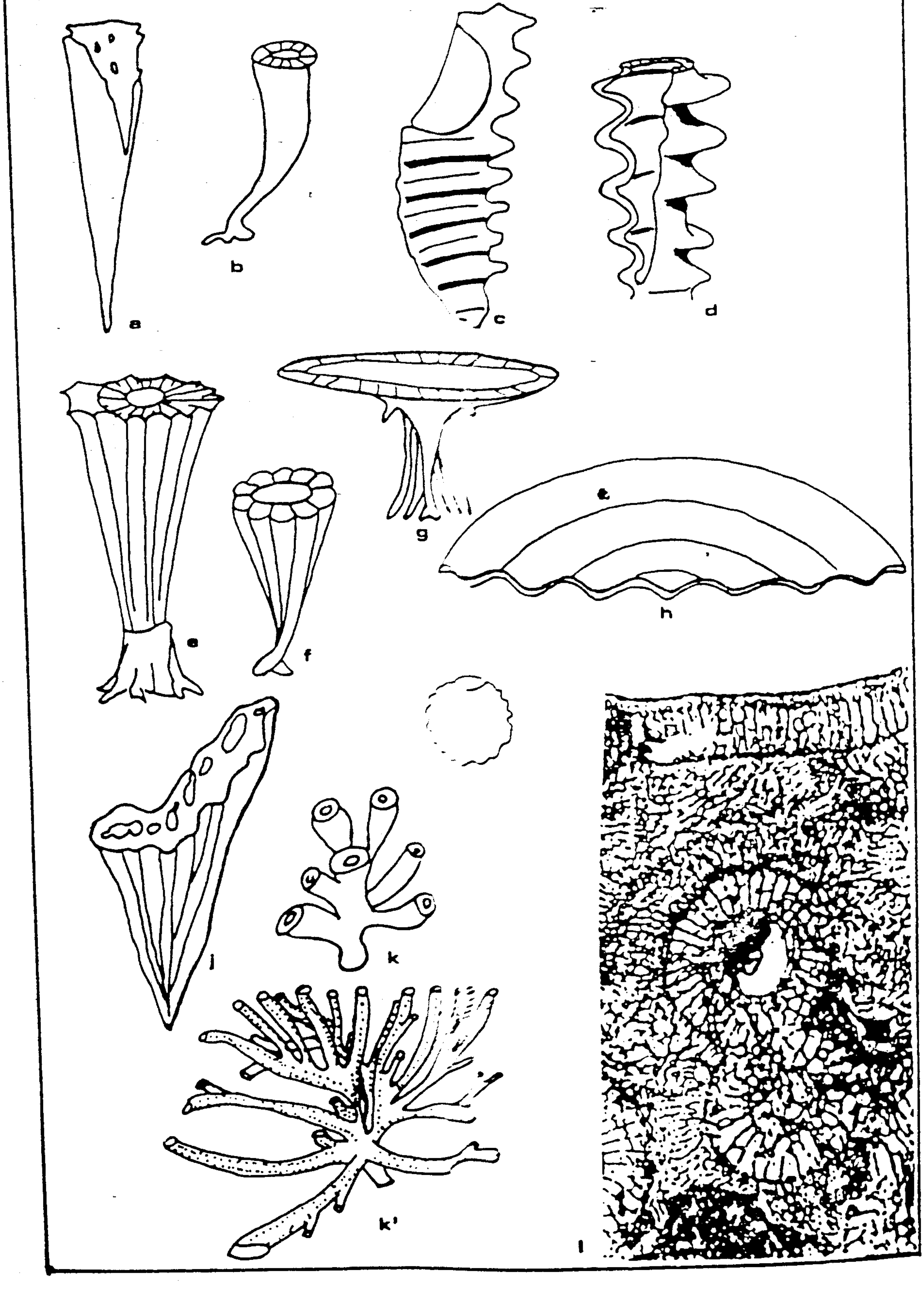


Fig 3

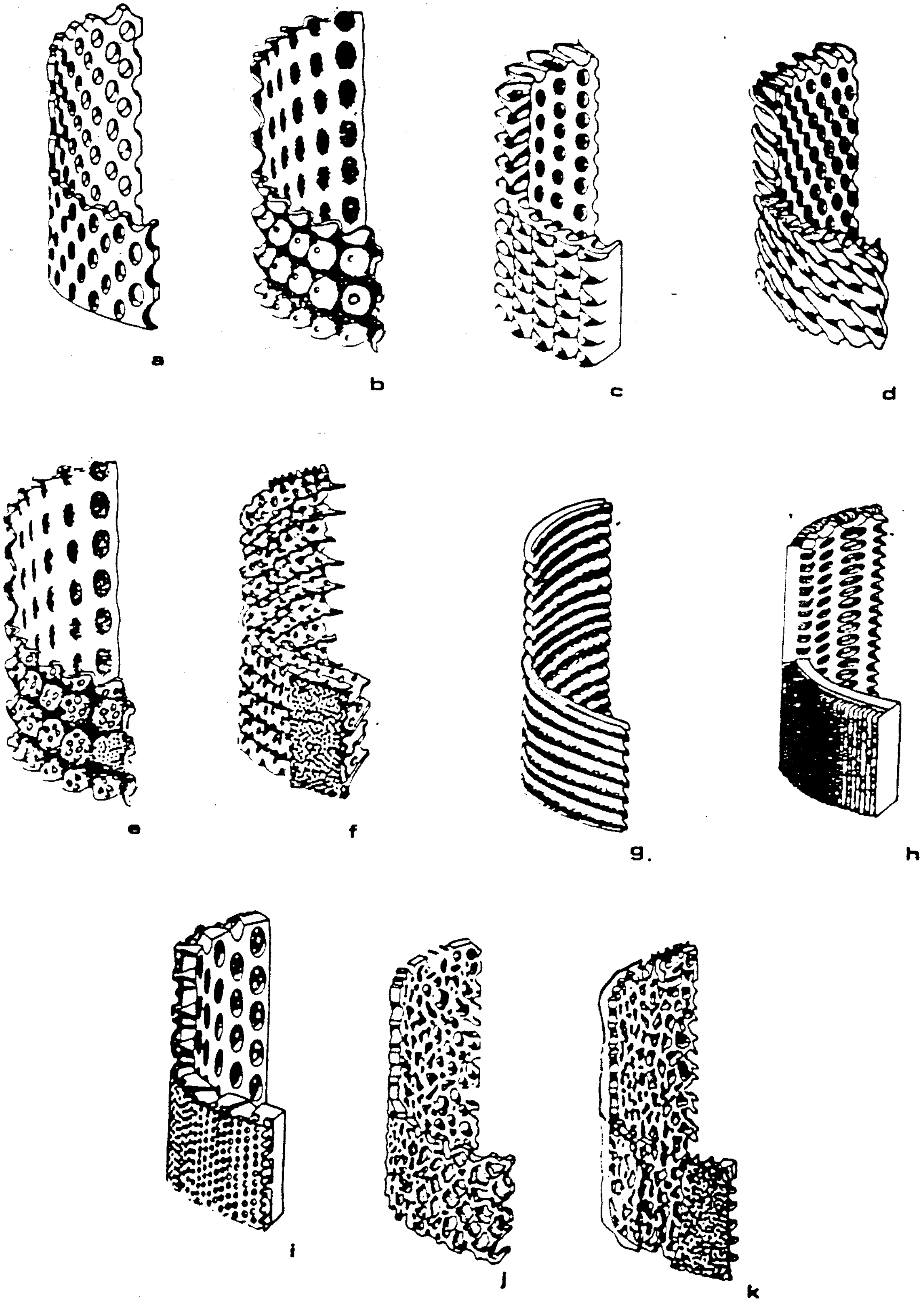


Fig 4

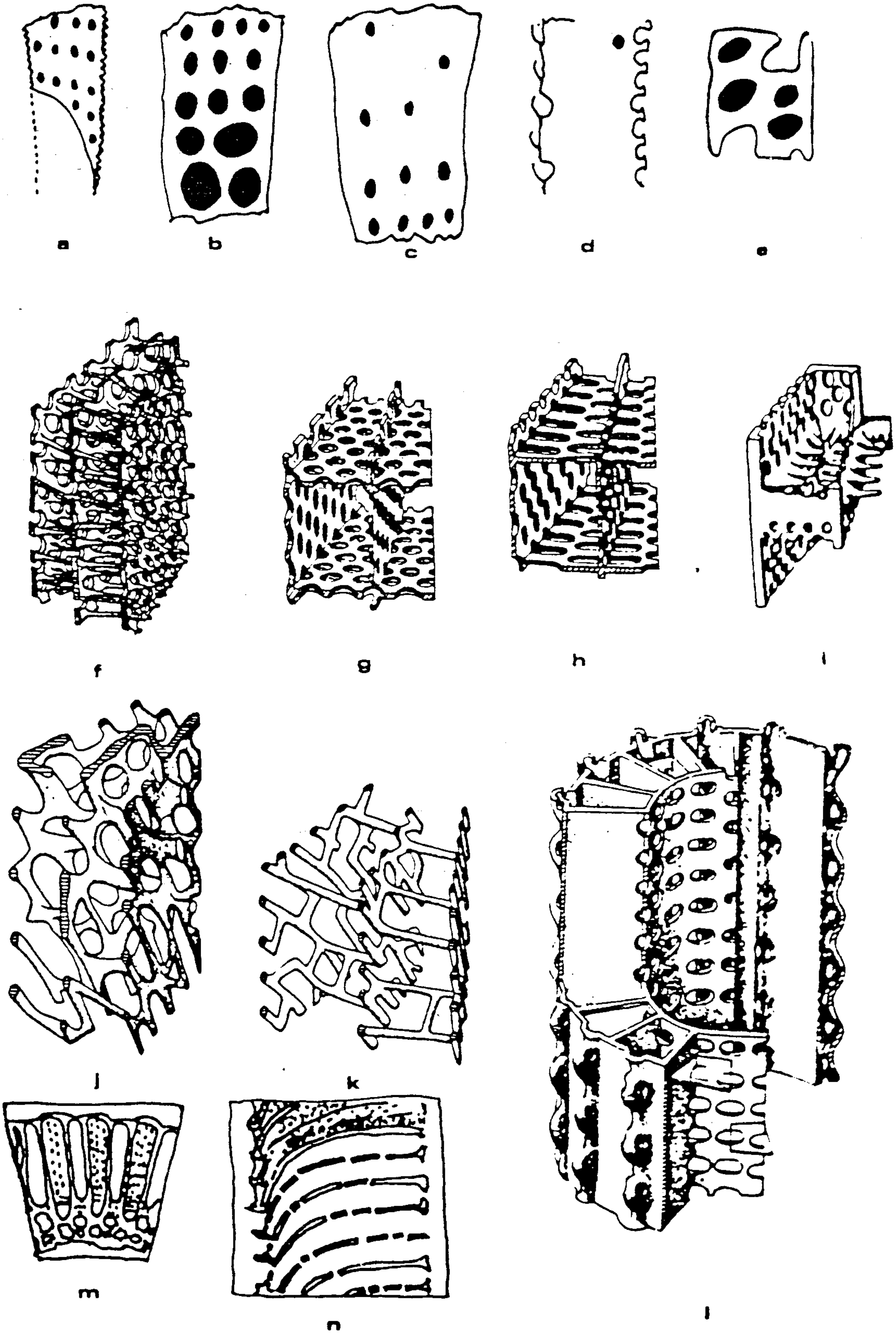


Fig 5

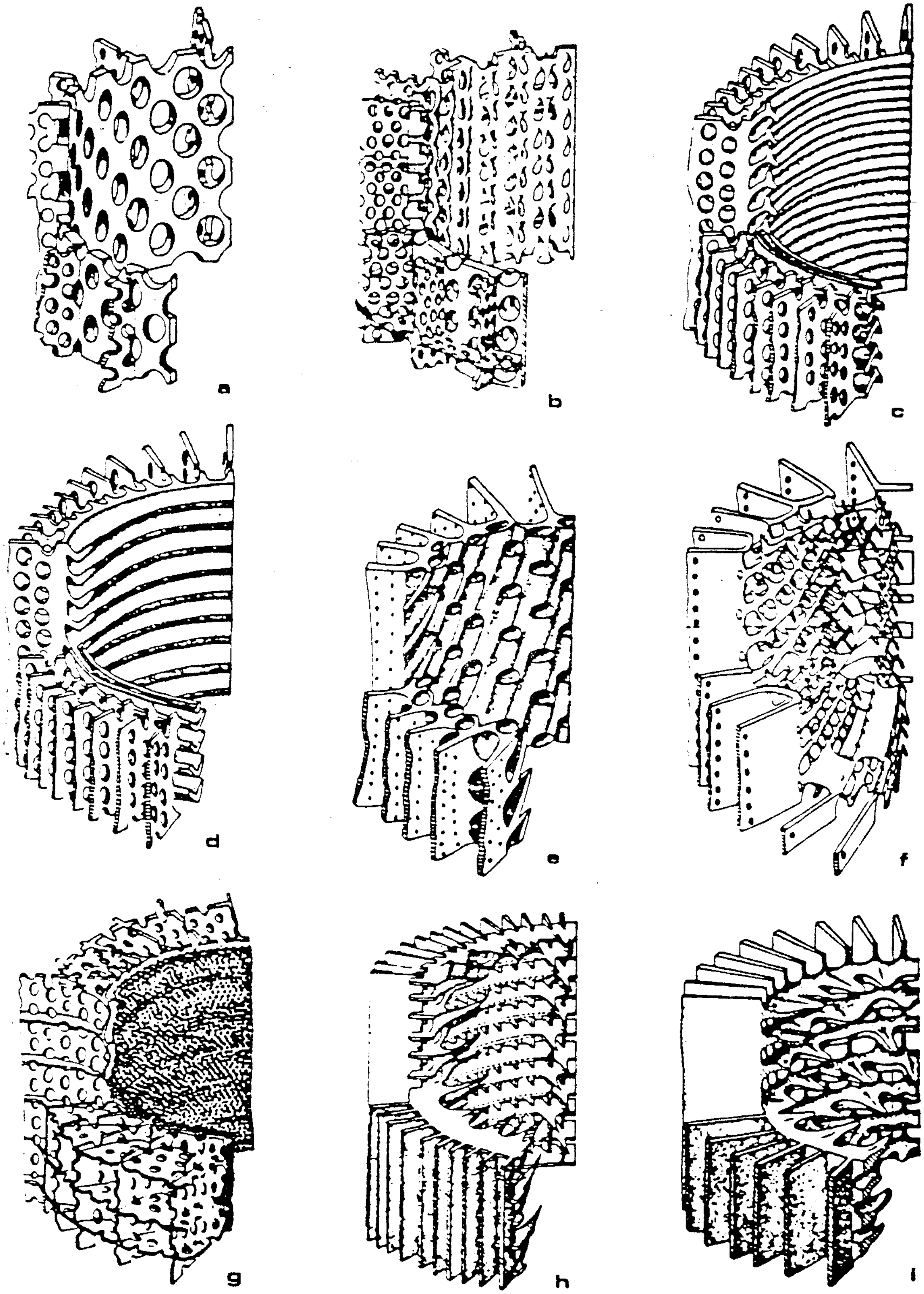
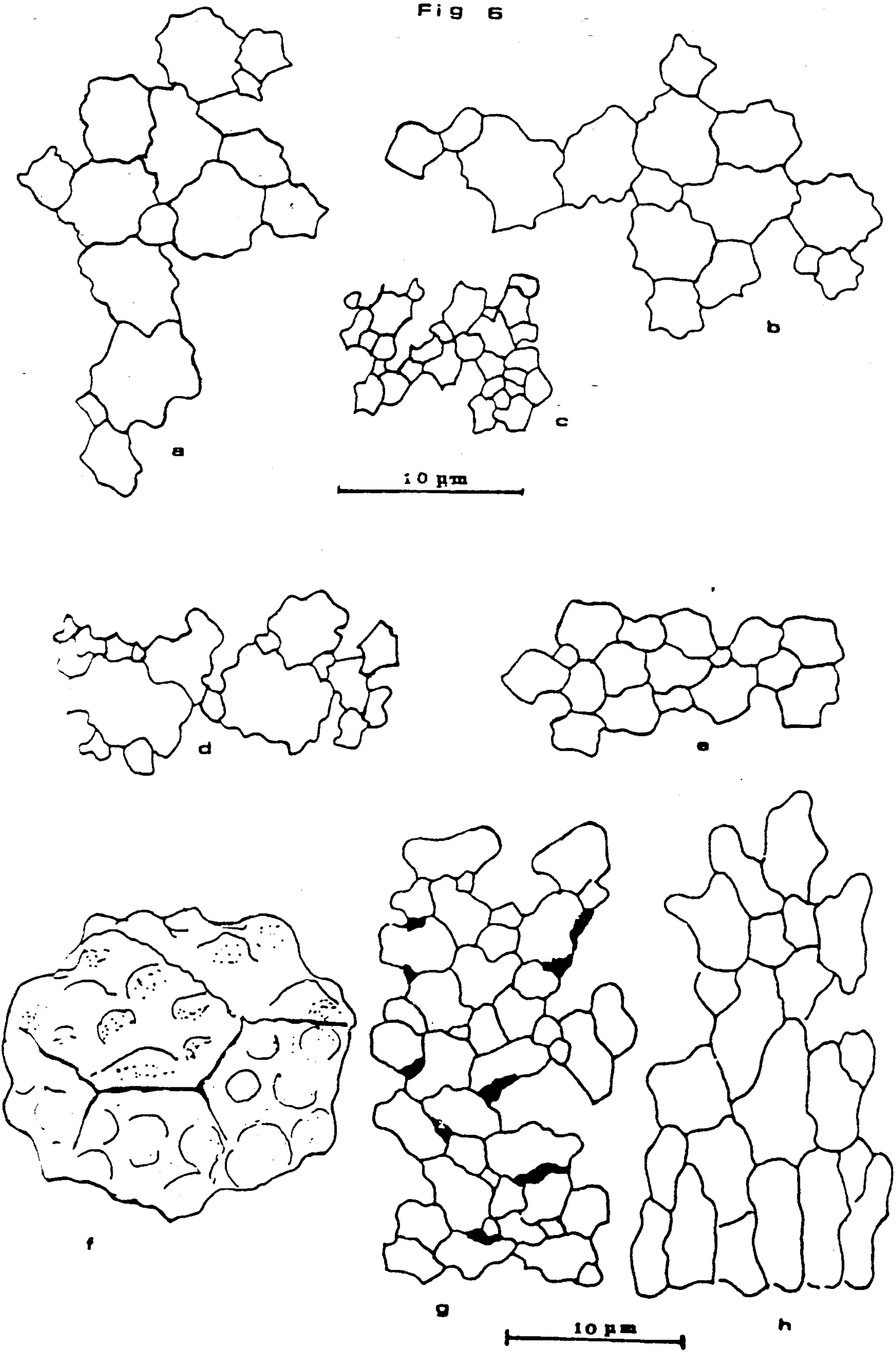


Fig 6



THE EARLIEST KNOWN FENESTRATE BRYOZOAN, WITH A SHORT REVIEW OF LOWER ORDOVICIAN BRYOZOA. *

by PAUL D. TAYLOR and GORDON B. CURRY

ABSTRACT. Silicified residues from the late Arenig Tourmakeady Limestone of County Mayo, Ireland, contain a new bryozoan,Alwinopora orodamnus gen. et sp. nov. Colonies have erected branches bearing two rows of alternating zooecial apertures on their frontal surface and barreb apertures on their reverse surface. Branches bifurcate irregularly, successive bifurcations tending to be approximately in the same plane. There is a strong gradient of branch thickening towards the colony base. Alwynopora is the earliest known bryozoan of the Order Fenestrata. The occurrence of bryozoans in the lower Ordovician is briefly reviewed; the thirty-eight taxa described have an extensive taxonomic distribution, are morphological diverse, and geographically widespread.

The Fenestrata are regarded as a disctinct order of stenoalemate bryozoans in the revised Treatise on invertebrate paleontology (Boardman et al. 1983), although some bryozoologists argue for their retention as a suborder of the Cryptostomata (Blake in Boardman et al. 1983). Most fenestrates are readily recognizable by their reticulate or pinnate collonies with zooecial apertures opening on one side of the branches only. Fenestrate bryozoans peaked in diversity during the late Palaeozoic when members of the families Fenestellidae and Acanthocladiidae dominated the majority of bryozoan faunas. However, the origins of the order may be traced back to the Ordovician. Hitherto the earliest described fenestrate bryozoan dates from the middle Ordovician. The purpose of this paper is to describe the first lower Ordovician fenestrate bryozoan, A. orodamnus gen. et sp. nov., from the Tourmakeady Limestone of western Irealand. In the absence of unequivocal Cambrian bryozoans, the earliest bryozoans are a modest number of taxa described from the lower Ordovician. The discovery of this new fenestrate bryozoan adds to the taxonomic distribution, morphological diversity, and geographical range of lower Ordovician bryozoans which are briefly reviewed. All described material bears British Museum (Natural History) (abbreviated BM (NH)) registration numbers.

GEOLOGICAL SETTING

The lower Ordovician Tourmakeady Limestone (Glensaul Group) of Co. Mayo, Ireland, is of considerable interest not only because of the abundance and diversity of the fossils it contains, but also because this fauna provides a link between contemporaneous American province faunas in Scotland, North America, and Spitsbergen. The stratigraphic setting of the Tourmakeady Limestone within the lower Ordovician inliers north of Lough Mask (text-fig.1) was first described by Gardiner and Reynolds (1910), although at that time the abundance of the indigenous shelly fossils was not appreciated, and the rich assemblages were not subjected to full taxonomic investigation. Gardiner and Reynolds did, however, recognize the stratrigraphic importance of the inliers, and their age determinations were based on lists of graptolitic and shelly faunas collected from various exposures within the Tourmakeady and Glensaul successions. The graptolite faunas have been reinvestigated (Dwey et al. 1970) following the discovery of some new localities. In addition, the rich brachiopod faunas have now been studied (Williams and Curry 1984), and descriptions of the associated trilobites are in preparation.

The great diversity and abundance of the Tourmakeady Limestone fauna was not fully appreciated until it was discovered that the indigenous fossils have been silicified. As a result, intensive collectingby Sir Alwyn Williams yielded over 2 tons of silicified limestone, which was subsequently etched to give over 10,000 silicified or chitino-phosphatic brachiopods and smaller numbers of silicified trilobites, gastropods, bryozoans, and crinoids. The Tourmakeady Limestone occurs as isolated blocks within well- bedded calcareous tuffs and grits, which togheter constitute the Shangort and Tourmakeady Beds of Gardiner and Reynolds (see text-fig.1). Non-silicified fossils, in particular brachiopods and trilobites, are also found at several localities within the tuff andc grit succession, and are conspecific and almost

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certainly contemporaneous with the silicified fossils in the limestone. However, the non-silicified fossils are generally in a poorer state of preservation, and indeed no well-preserved bryozoans have been recovered from the clastic sediments. The available material, therefore, consists entirely of silicified specimens recovered from etched residues.

Stratrigraphically the Tourmakeady Limestone and surrounding sediments occur above an uppermost lower Arenig graptolite assemblage ascribed to the Isograptus gibberulus Zone (Gardiner and are overlain by an upper Arenig assemblage of the Didymograptus hirundo Zone (Gardiner and Reynolds 1909,1910;Dewey et al. 1970).This is consistent with age determinations based on the shelly fossils from the Tourmakeady Limestone is thought to represent the disrupted remanants of an offshore carbonate buildup,perhaps deposited peripheral to submarine volcanic accumulations (Williams and Curry 1984). The indigenous fauna shows no sings of significant post-mortem transportation,and hence the majority of the benthic animals are assuned to have colonized a fine-grained calcareous mud substrate, subjeted to gentle water currents and low to moderate sediment accumulation rates. In keeping with this interpretation, many brachipods show morphological adaptation for a freelying mode of life(Williams and Curry 1984), while pedunculate forms can realistically be assumed to have developed modifications of pedicle form to achieve anchorage in fine-grained substrates (as happens in Recent forms, e.g. Curry 1981,1983).

SYSTEMATIC PALEONTOLOGY

Indeterminate ?bryozoan

Text-fig. 2A

Material. BM(NH) PD6230.

Description. A poorly preserved fragmentary fossil bearing contiguous, oval-shaped apertures about 0.40 x 0.25 mm in diameter.

Remarks. This may be a fragment of a briozoan colony, probably either a cystoporate or a trepostome.

Distribution. Tourmakeady Limestone (upper Arenig), Tourmakeady, Co. Mayo, Eire.

Order FENESTRATA Elias and Condra, 1957

?Family ENALLOPORIDAE Miller, 1889

Genus *ALWYNOPORA* gen. nov.

Type species. *A. orodamnus* sp. nov.

Derivation of name. After Sir Alwin Williams who collected the silicified limestone containing this new bryozoan.

Diagnosis. Fenestrata with branches bifurcating irregularly, usually in one plane, anastomosing occasionally, and becoming considerably thickened towards the colony base; two longitudinal rows of alternating zooecial apertures are borne on the frontal surface of each branch.

Alwinopora orodamnus sp. nov.

Text-figs. 2B-G, 3,4

Holotype. BM(NH) PD6231.

Paratypes. BM(NH) PD 6232-6272.

Occurrence. Tourmakeady Limestone (upper Arenig), Tourmakeady, Co. Mayo, Eire.

Derivation of name. Orodamnus, Greek meaning bough or branch.

Diagnosis. As for genus.

Description. Colonies have been recovered only as branch fragments which bifurcate unequally or, more rarely, dichotomously. Both bifurcation angle (mean = 50, range = 30- 135 from twenty-one determinations) and interval between bifurcations (mean = 1.73 mm, SD = 0.890mm, range = 0.40-4.05 mm from nineteen determinations) are very variable. Although anastomoses between branches may be observed, they are neither abundant nor regular. Branches are subcircular to ovoid in transverse section. Two rows of non-contiguous zooecial apertures open on one surface of the branch. Apertures on either side of this frontal surface alternate. Intraperturate spacing measured along the branch averages 0.54 mm (SD= 0.088mm, range= 0.45- 0.75mm, from twenty-five colonies). Branch width and depth are highly variable with the thickest branches over three times wider than the thinnest (mean width = 0.62mm, SD = 0.210mm, range = 0.32-1.08mm from twenty-five colonies). Some fragments show a proximal to distal gradient of decreasing branch width. Branches margins are gently sinuois in narrow branches, sinuosities corresponding to the positions of protuberant zooecial apertures, but straight-sided in thick branches. Striae or other branch ornamentation have not been observed. Possible colony bases are slight flat-bottomed expansions.

Zooecial apertures are circular to elliptical in shape and elonagted transversely, longitudinally, or obliquely. This apparently depends on preservational factors, several branches showing indications of compression and/or shear. A variably thick rim surrounds each aperture and measurements of apertural width variying between 0.08 and 0.22 mm are similarly dependent on state of preservation. Occlusion of apertures is a characteristic of some branches; this may be due to diaphragm formation or an artefact of silicification. Zooecial chambers are moderately long and have a length that slightly excceds external interapertural spacing. In shape they are essentially tubular, tapering towards the locus of budding on the midline near the reverse side of the branch. Zooecia were budded alternately left and right of the branch midline, paralleled the branch axis initially, and then turned outwards to meet the colony surface more or less at right angles. Diaphragms and other intrazooecial partitions have not been observed.

Affinities. Delicately brnched Ordovician bryozoans exists among three orders, Cyclostomata, Cryptostomata, and Fenestrata. All Ordovician cyclostomes are single-walled stenoalemates sensu Borg (1926). These include branching species of Clonopora Hall, 1883, Kukersella Toots, 1952, Mitoclema Ulrich, 1882, Mitoclemella Bassler, 1952, and Wolinella Dzik, 1981. Here the calcified zooid frontal wall that forms the branch surface is an exterior wall incapable of adding more calcite to its outer surface. Therefore proximally thickening branches of the kind found in A. orodamnus cannot be produced. However, criptostomes and fenestrates are double-walled stenoalemates with calcified zooid frontal walls that are interior walls and were capable of adding calcification to they other surfaces. A. orodamnus clearly belongs to one of this groups. Among Ordpvician genera, only arthrostylid cryptostomes (e.g. *Nematopora* Ulrich, 1888) and the fenestrate genus *Enallopora* d'Orbigny, 1849 closely resemble *A. orodamnus*. However, branches of arthrostylids tend to be straighter and do not develop the same amount of proximal thickening as *A. orodamnus*. Furthermore, *A. orodamnus* shows no indications of the uncalcified articulations found in most arthrostylids. The affinities of *Alwynopora* with the Order Fenestrata are indicated by a combination of three features: restriction of zooecial apertures to one side only of the branches, unjointed branches, and proximally thickened branches.

Enallopora, togheter with its subjective junior synonym *Protocrisina* Ulrich, 1889, has a branching pattern like that of *A. orodamnus* but the branches bear three or four rows of zooecial apertures, often with small 'accesory pores' between them. Elsewhere in the Order Fenestrata different generic names are accorded to taxa having two and more than two rows of zooecial apertures. These may reflect important differences in budding pattern. Therefore, disctintion between *Enallopora*, such as *E. ocilensis* (Wiman, 1902) from the Asghill of Sweden, exhibit proximal branch thickening of a similar magnitude to A. orodamnus (see Brood 1982, fig. 7A and F). Enallopora is unusual among fenestrates in lacking styles within the laminated skeleton (F.K. McKinney, pers. comm.). Unfortunately, unsilicified material of *Alwinopora* is not available for comparision of wall microstructure. Though *Enallopora* is usually assigned to the Family Fenestellidae King, 1850 (see Bassler 1953), the atypical microstructure may justify revival of the Family Enalloporidae Miller, 1889 to which Alwinopora is also tentatively assigned.

Discussion. The silicified preservation of *A. orodamnus* necessitates some interpretation as a preliminary to reconstruction of original skeletal morphology. In some specimens only the outer surfaces of the branches have been silicified so that acid treatment leaves specimens as hollow tubes lacking internal structure (text-fig. 5). Tavener-Smith (1973) reported similar preservation of Carboniferous fenestrates where silicification evidently progressed from the outside of the branches inward. In other specimens of *A. orodamnus*, however, silicification is more extensive and includes zooecial linings. The void between these linings and the outer branch surface represents unsilicified skeleton (text-fig. 5). These specimens are valuable in revealing details of internal structure including zooecial shape, dimensions, and budding pattern.

The high degree of variability in branch thickness between specimens of *A. orodamnus* also warrants comment. Variation is continuous and there is no indication that more than one species is present at Tourmakeady. Thin and thick branches have the same alternating biseaial arrangement of apertures with equivalent interapertural spacing. A gentle but disctinct distal taper in some branch lengths (e.g. text-fig. 3c) is evidence that branch thickness is age-related. Young branches are narrow and have thin walls and sinuous margins (e.g. text-fig. 2c). During growth addition og calcification to the outher surfaces of branches resulted in substantial branch thickening and loss of sinuosity (text-fig. 4). This was accompanied by lengthening of zooecial chambers, divergence of aperturesfrom the branch midline, and by the formation of diaphragms over zooecial apertures (assuming aperture occlusion is not a preservational artefact).

An important consequence of branch thickening was the reduction and eventual elimination of the spaces between adjacent branches (e.g. text-fig. 4). As fenestrate bryozoans are thought to have generated feeding currents that drew water towards the frontal surface of branches and expelled filtered water through the spaces between branches and towards their reverse surface (Cowen and Rider 1972; Taylor 1979), occlusion of the spaces betwenn branches during colony growth may have impaired feeding. However, basal regions of briozoan colonies (e.g. adeoniform cheilostomes, see Cheetham and Thomsen 1981) may be occupied by zooids which have lost their feeding function. The same is likely for *A. orodamnus* colonies, especially if zooecial apertures in basal branches were closed by diaphragms. Basal branches of A. orodamnus may have fulfilled a supportive function. For this role the kind of thick calcification present in many colonies would have been advantageous in resisting bending stresses imposed by water movement around the colony (cf. adeoniform cheilostomes, see Cheetham and Thomsen 1981).

LOWER ORDOVICIAN BRYOZOA

Discovery of the first fenestrate bryozoan in the lower Ordovician prompts a brief review of worldwide records of lower Ordovician Bryozoa. As yet there are no unequivocal bryozoans of pre-Arenig age (Taylor 1984), but by the late early Ordovician a moderately diverse bryozoan fauna had become established. Table 1 summarizes the bryozoan taxa recorded from the lower Ordovician with their stratigraphical occurrence and provenance. This table is the basis for the following commentson taxonomic distribution, morphological diversity, and palaeogeographical distribution. The lower-middle Ordovician boundary is here placed at the top of the Arenig Series in Britain Williams et al. 1972), very approximately equivalent to the top of the Volknov Stage (B2) in Estonia, and the top of the Valhallen Stage in North America (Fortey 1980).

Taxonomic distribution

A striking feature of the thirty-eight species recorded from the lower Ordovician is their wide taxonomic distribution (Table 1). All five orders of stenoalemate bryozoans recognized in the revisedbryozoan Treatise (Boardman et al. 1983) are represented. Given the uncertainties in correlation within the lower Ordovician, one may conclude that stratigraphical evidence on the relative time of appereance of the ordersis never likely to be of value in resolving phylogenetic relationshipsat ordinal level. A smaller proportion of taxa have lower Ordovician representatives at successively lower taxonomic levels. Three of twelve (25%) cystoporate families (Utgaard in Boardman et al. 1983) are known from the lower Ordovician, eight of nineteen (42%) trepostome families (Astrova 1978, with the addition of the Dianulitidae), and two of thirteen (15%) cryptostome families (Karklins in Boardman et al . 1983; Blake in Boardman et al. 1983); lack up-to-date information on fenestrate and cyclostome classification precludes their analysis. At the genus level the lower Ordovician has only four of ninety (4%) cystoporate genera, eleven of eighty-seven (13%) trepostome genera, and three of eighty (4%) cryptostome genera. Such early diversification at high taxonomic levels is also a feature of many phyla other than the Bryozoa. However, unlike some phyla (notably the Echinodermata, see Paul 1979) many of the higher taxa established during early bryozoan evolution were of long duration. All five stenoalemate orders persisted thoughout the Paleozoic at least.

Another aspect of the data (Table 1) si the considerable contribution of trepostomes to the early diversification of the Bryozoa. This early trepostome dominance was eroded somewhat during the middle Ordovician when other orders, especially the Cryptostomata (e.g. Ross1964), became more important. However, palaeogeographical distribution may be a major factor in this apparent evolutionary pattern. Most lower Ordovician bryozoans come from the trepostome-dominated region of Estonia Whereas younger faunas are known also from regions of markedly different faunal composition, e.g. the middle to upper Ordovician of the Siberian Platform where trepostomes are scarce and ptilodictyine cryptostomes dominate (Nekhoroshev 1961).

Morphological diversity

Lawood and Taylor (1979) have already emphasized the wide variety of colony-forms present in bryozoans of the Ordovician as a whole and their possible ecological significance. Many of these colony-forms were established during early Ordovician times. Dome-shaped colonies (e.g. Revalotrypa gibbosa) are particularly prevalent but also present in the lower Ordovician are cylindrical branched colonies of several types (e.g.Wolinella baltica, A. orodamnus, Dittopora annulata), frondose colonies(e.g. Trepocryptopora dichotomata), and laminate colonies (e.g. Ceramopora? unapensis). Subdivision of colonies into subcolonies (cormidia) is known from lower Ordovician bryozoans, notably Dianulites hexaporites and the dianulitid described by McLeod (1978). Other morphological characters (many used taxonomically) include laminar and granular wall structures, acanthostyles, interzooidal communication pores, diaphragms, hemiphragms, interzooidal vesicles, lunaria, calcified exterior walls, and various types of zooidal polymorph. Ananalysis of the distribution of these and other characterswould clearly be of value in resolving phylogenetic relationships. Lower Ordovician representatives of each stenoalemate order may be expected to posses a high proportion of morphological characters in primitive states. This could assist the disctinction between primitive and advanced character states which is important in reconstructing phylogeny within each stenoalemate order.

Paleogeographical distribution

Lower Ordovician bryozoans are known from three main paleogeographical regions: the Baltic Plate (Estonia and Novaya Zemlya), the North American Plate (Tourmakeady and localities in the U.S.A.), and the Yangtze Plate (Liamgshan). During Arenig times the Baltic Plate is likely to have been temperate (Cocks and Fortey 1982), the North American Plate tropical (Scotese et al. 1979), and the Yangtze Plate tropical or subtropical (R.A.Fortey, pers. comm. 1983). These three plates were widely separated, demonstrating the wide distribution of bryozoans in the early Ordovician. This substantial geological spread in conjunction with the taxonomic variety of Arenig bryozoanspoints to a considerable pre-Arenig history that is as yet unknown and may be crucial to the testing of various models (e.g. Larwood and Taylor 1979; Taylor 1981) of early bryozoan diversification.

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TEXT-FIG. [illegible] [illegible] Geological map of the Glensaurus [illegible] in Co. Ma[illegible] [illegible]ire, showing the [illegible]mestone lo[illegible].

TEXT-FIG. [illegible] [illegible] Bryozoa[illegible] from the Tour[illegible]one. A. inde[illegible]nate ?bryozoan, [illegible]. x17. B-G [illegible]nopora orodam[illegible] [illegible]teral view [illegible] [illegible]pressed branch [illegible]ce lowerm[illegible] BM(NH)PD6235, [illegible]ng fragme[illegible] BM(NH)PD6241, [illegible] with encr[illegible]n at distal end, [illegible]1, x27;E, [illegible] surface of [illegible]pertures, [illegible]H)PD6265, x10; [illegible]face of [illegible] slightly com[illegible] BM(NH[illegible], F x25, G x56. [illegible]on microg[illegible] A,B gold-coated [illegible] secondar[illegible] [illegible]rons: C-G, un[illegible]ens usi[illegible] [illegible]- scattered

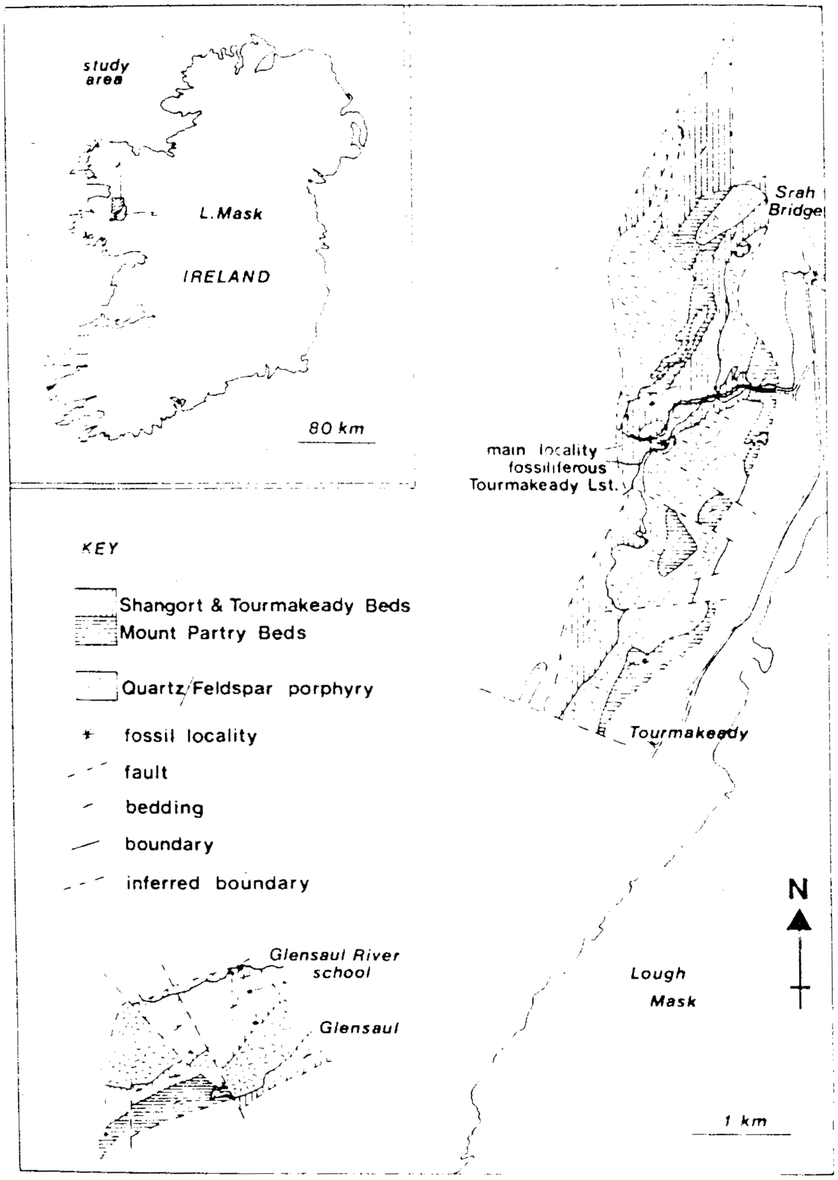
TEXT-FIG. [illegible] [illegible] Outline sha[illegible] [illegible]ome branching [illegible]ynopora o[illegible]nus sp. nov. Ar[illegible] growth dir[illegible] – indicates a [illegible]ng towar[illegible] [illegible] observer. a, [illegible]63; b, P[illegible] cPD6266; d, [illegible]251; f, PD[illegible]

TEXT-FIG. [illegible] [illegible] Alwinopor[illegible] [illegible]amnus sp. nov.m [illegible]ranches wi[illegible] [illegible]cation of inter[illegible] [illegible]M(NH)PD[illegible] [illegible]aning electron [illegible]f reverse [illegible] of uncoated [illegible] back-scatte[illegible] [illegible]trons. A, close[illegible]hes with ba[illegible] [illegible]s removed and [illegible] distal parts [illegible] [illegible]al linings, x14; [illegible]th basal [illegible] [illegible]ract (left) and [illegible], detail o[illegible] [illegible]cation of distal [illegible]cial lining[illegible] D, complete [illegible] zooecial li[illegible] [illegible]owing zooecia [illegible] budding loc[illegible] [illegible] centre of the [illegible]

TEXT-FIG. [illegible] [illegible]. Interpreta[illegible] [illegible]ilicification in [illegible] orodamnu[illegible] [illegible]v. shown in [illegible]tion. Calcifi[illegible] [illegible] are stippled, [illegible] are black. S[illegible]on occurs as a [illegible] the outer su[illegible] [illegible]ers of skeleton and sometimes (upper sequence) the lining of the zooecial chambers.

TEXT-FIG. 6. Dagrammatic reconstruction of morphology in a distal branch (young) and a proximal branch (old) of Alwinopora orodamnus sp. nov. Calcified wall is evenly stippled in the tangential and transverse sections.

TABLE 1. Records of bryozoans from the lower Ordovician.


study area
L. Mask
IRELAND
80 km
KEY
Shangort & Tourmakeady Beds
Mount Partry Beds
Quartz/Feldspar porphyry
fossil locality
fault
bedding
boundary
inferred boundary
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main locality fossiliferous Tourmakeady Lst.
Tourmakeady
N
Lough Mask
1 km

Fig. 1

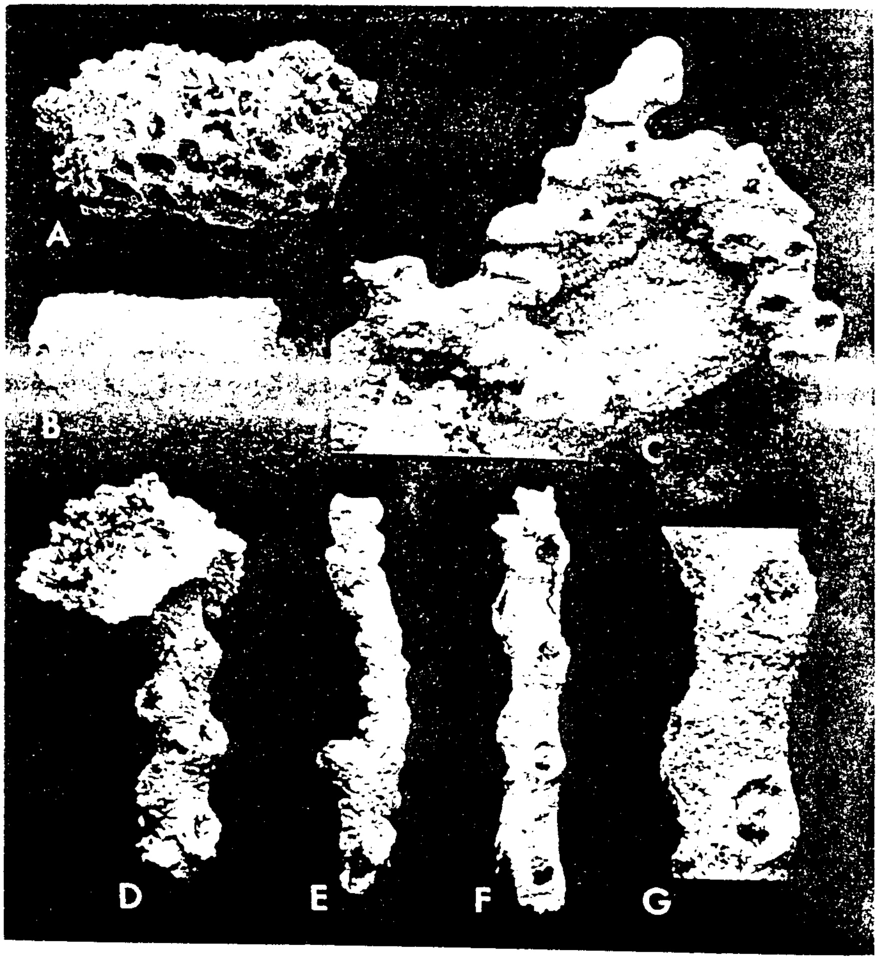

Fig. 2

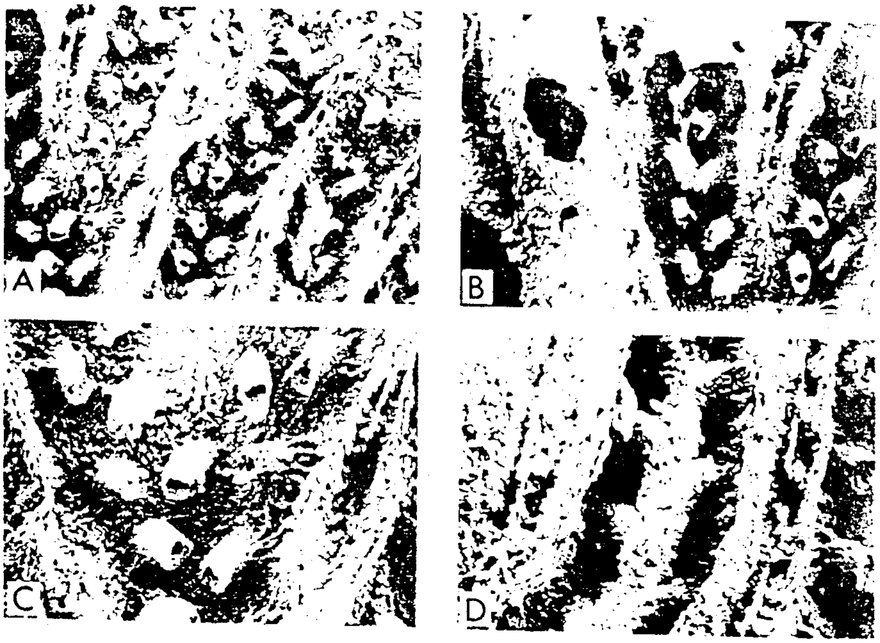

Fig. 3

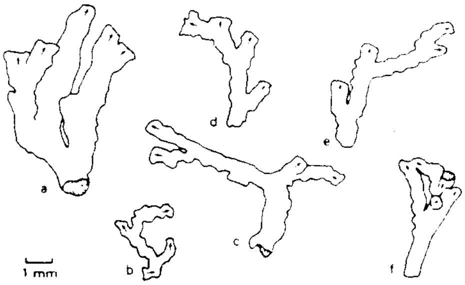

Fig. 4

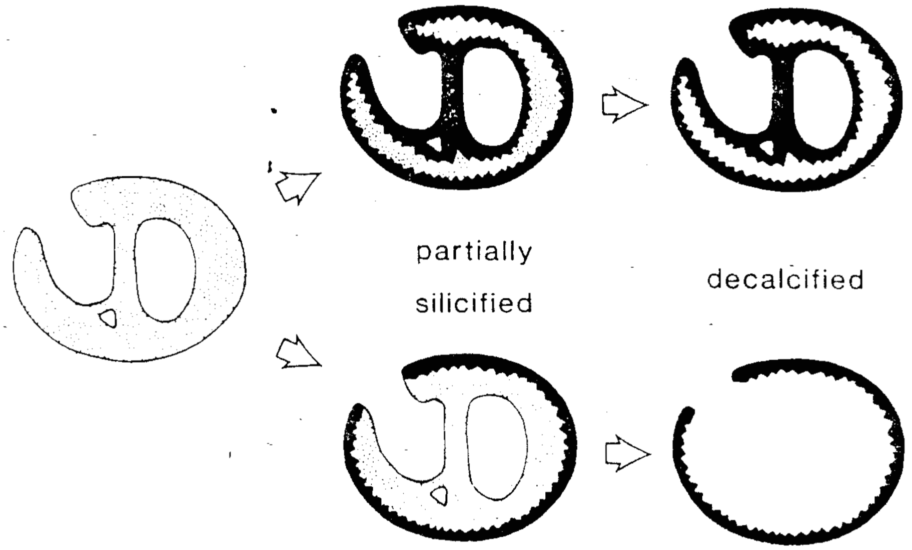
partially
silicified
decalcified

Fig. 5

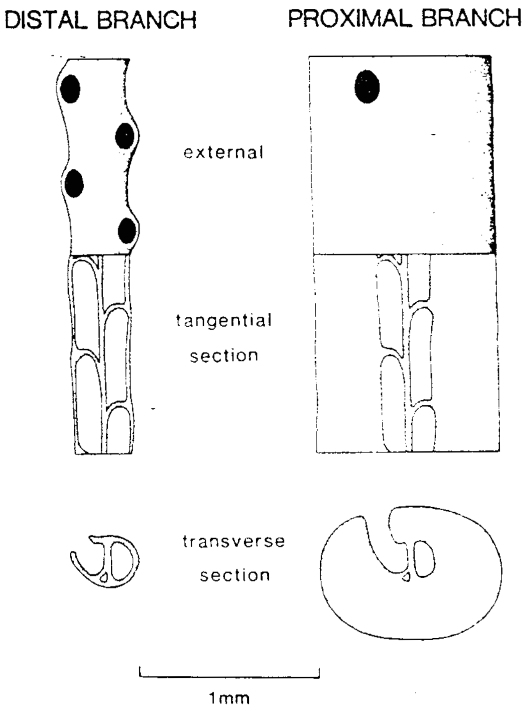
DISTAL BRANCH
PROXIMAL BRANCH
external
tangential section
transverse section
1mm

Fig. 6

Paul D. Taylor and Gordon B. Curry

TABLE 1. Records of bryozoans from the lower Ordovician

Taxon	Stratigraphy	Locality	Reference
ORDER CYCLOSTOMATA			
Family Corynotrypidae			
Wolinella baltica Dzik	M. Volkhov Stage	Estonia; Poland	Dzik 1981
ORDER CYSTOPORATA			
Family Ceramoporidae			
Ceramopora? unapensis Ross	Kindblade Fm	Oklahoma	Ross 1966
Family Anolotichiidae			
Lamtshinopora hirsuta Astrova		Vaigach Is., U.S.S.R.	Astrova 1965; Utgaard in Boardman *et al.* 1983
Profistulipora arctica Astrova		Novaya Zemlya, U.S.S.R.	Astrova 1965; Utgaard in Boardman *et al.* 1983
Profistulipora retrusa Astrova		Novaya Zemlya, U.S.S.R.	Astrova 1965, Utgaard in Boardman *et al.* 1983
Family Xenotrypidae			
Xenotrypa primaeva (Bassler)	Volkhov Stage	Estonia	Bassler 1911, Utgaard in Boardman *et al.* 1983
ORDER TREPOSTOMATA			
Family Esthonioporidae			
Esthoniopora communis Bassler	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Esthoniopora lessnikovae (Modz.)	Volkhov Stage	Estonia	Modzalevskaya 1953, Mannil 1959
Esthoniopora curvata Bassler	Volkhov Stage	Estonia	Mannil 1959
Family Orbiporidae			
Orbipora solida Bassler	Volkhov Stage	Estonia	Modzalevskaya 1959
Orbipora acanthopora Bassler	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Dittoporidae			
Dittopora clavaeformis Dybowski	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Dittopora annulata (Eichwald)	Volkhov Stage	Estonia	Bassler 1911; Modzalevskaya 1953
Dittopora ramosa Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Dittopora sokolovi Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Hemiphragma rotundatum Bassler	Volkhov Stage	Estonia	Modzelevskaya 1953
Family Halloporidae			
Diplotrypa petropolitana Nicholson	Volkhov Stage	Estonia	Bassler 1911
Diplotrypa bicornis (Eichwald)	Volkhov Stage	Estonia	Bassler 1911
Family Trematoporidae			
Revalotrypa gibbosa (Bassler)	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Nicholsonella huoi Yang	U. lower Ord.	Liangshan, China	Yang 1957
Nicholsonella papillaris Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Nicholsonella rotundicellularis Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Nicholsonella arborea Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Amplexoporidae			
Anaphragma vetustum Bassler	Volkhov Stage	Estonia	Modzalevskaya 1953
Monotrypa helenae Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Atactotoechidae			
Orbignyella antiqua Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Dianulitidae			
Dianulites fastigiatus Eichwald	Volkhov Stage	Estonia	Bassler 1911
Dianulites petropolitana Dybowski	Volkhov Stage	Estonia	Bassler 1911, Modzalevskaya 1953
Dianulites glauconiticus Mannil	Volkhov Stage	Estonia	Mannil 1959
Dianulites janischewskyi Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Dianulites hexaporites (Pander)	Volkhov Stage	Estonia	Modzalevskaya 1953
Dianulites multimesoporicus Modz.	Volkhov Stage	Estonia	Modzelevskaya 1953
'Dianulitid'	Cassinian	Arkansas, Missouri	McLeod 1978
ORDER CRYPTOSTOMATA			
Family Arthrostylidae			
Arthroclema cf. *armatum* Ulrich	Volkhov Stage	Estonia	Bassler 1911, Mannil 1959
Family Stictoporellidae			
Stictoporellina gracilis (Eichwald)	Volkhov Stage	Estonia	Bassler 1911, Mannil 1959
Family incertae sedis			
Trepocryptopora dichotomata Yang	U. lower Ord.	Liangshan, China	Yang 1957, Karklins in Boardman *et al.* 1983
Trepocryptopora flabelata Yang	U. lower Ord.	Liangshan, China	Yang 1957
ORDER FENESTRATA			
? Family Enalloporidae			
Alwynopora orodamnus sp. nov	U. Arenig	Tourmakeady, Eire	this paper

Table. 1

In: DUTRO,J.T.,Jr. & BOARDMAN,R.S., ORGANISERS. 1981. LOPHOPHORATES, NOTES FOR A SHORT COURSE: KNOXVILLE, TENN., UNIV. TENNESSEE DEPT. GEOL. SCI. STUDIES IN GEOLOGY 5, AND THE PALEONTOLOGICAL SOCIETY, P. 97-109.

5.4(d) The Origin of the Brachiopods

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INTRODUCTION

Brachiopods are characterized by being solitary, bivalved, bilaterally symmetrical coelomates. A ciliated, filament-bearing lophophore occupies much of the mantle cavity of all living representatives and functions as the principal food-gathering and respiratory organ of the animal. The coelom is divided into two principal spaces. The largest one is the posteriorly located metacoel that forms the body cavity and encloses most of the organs. The smaller mesocoel is the coelomic space inside the lophophore.

Brachiopods are one of the few groups that have a fossil record spanning the entire Phanerozoic. Although they have been reported from Precambrian rockssuch records have not been sustained (Rowell, 1971). The occurrences are either of objects that are of Precambrian age but are not brachiopods, or they are brachiopods but are not of Precambrian age. The oldest undoubted brachiopods occur in the lower Tommotian Stage of Siberia (Pelman, 1977), commonly regarded as basal Lower Cambrian. Fortunately for paleontologists brachiopods are still extant. Without knowledge of the lophophore and distribution of coelomic spaces, neither of which are preserved fossil, we might be hard-presed to sugest any other group of organisms as possible ancestors or close relatives.

The traditional view of brachiopods is that they constitute a monophyletic clade (Williams and Rowell, 1965b, Williams and Hurst, 1977) whose closest relatives are other lophophorates, the phoronid worms and bryozoans (Hyman, 1959). It is commonly accepted that these lophophorates radiated from a trimerous, tubicolous coelomate ancestor (Clark, 1979), which is usually regarded as being a phoronod-like organism. The implication is that brachiopods share a common genealogycal history such that they most recent common ancestor was itself a brachiopod (Fig.1).

There is an alternative view of early phylogeny of brachiopods. Cowen and Valentine (in Valentine, 1973b) accepted that they arose from infaunal phoronid-like ancestors, but contended that the various early brachiopod lineages developed separately and independently from different groups of phoronid-like forms. With this interpretation brachiopods are regarded as a grade of organization and any formal taxon that unites them, but excludes their ancestors, must logically be considered as blatantly polyphyletic (Fig.2). The corollary, as Cowen and Valentine recognized, is that the several monophyletic taxa would be needed to classify the organisms that presently are termed brachiopods. Wrights (1979a) recent views on the Lower Paleozoic brachiopod radiation are similar in some respects to those of Cowen and Valentine. Wright (1979a, p.236) concluded that the brachiopods were not a monophyletic clade and that they may have originatedfrom as many as seven different brachioporate stocks. The later were described (Wright, 1979a, p.238) as, "... infaunal lophophorate stocks with the potential to develop into epifaunal brachiopods." They were shown (Wrght, 1979a, fig.1) as infaunal wormlike creatures with lophophores projecting freely from their tubes.

These two views of the origin of the brachiopods, whether they arose monophyletically or polyphyletically, are mutually exclusive and obviously both cannot be correct. I shall argue, however, that the differences are not major as they might seem at first glance. Paradoxically, there is no significant dispute over the empirical paleontological evidence; the digreement is confined to its interpretation. I should like to review this evidence in so far as it is known.

Probably nobody would claim that knowledge of Cambrian brachiopods is anywhere near complete. Almost every study of a new area, particularly if it is based on material etched free from limestone, reveals new taxa. Our understanding of Early Cambrian brachiopods particularly weak.

They have been described in some detail only from two areas of the world, teh western United States Rowell, 1977) and Siberia (pelman, 1977), but less complete information fron other continents is consistent with teh stratigraphic ranges of the principal orders show in Figure 3. It should be noted, however, that brachiopods from what we are here regarding as earliest Early Cambrian, (the Tommotian Stage), have been adequately investigated only in Siberia. In many areas of the world rocks of this age are poorly fossiliferous and so far have not yielded brachiopods. Otehr regions are thought to have brachiopods of this age, but they have yet to be studied.

PRINCIPAL FEATURES AND STRATIGRAPHIC DISTRIBUTION OF CAMBRIAN ORDERS

Figure 3 shows the stratigraphic distribution of the Cambrian orders that bare commonly recognized. The ordinal classification differs somewhat from that advocated by Wright (1979a) who restricted the Acrotretida to include only teh Acrocretidae and Curticiidae (see Rowell, 1965), and erected a new order, the Discinida, to include *Acrothele* and the inferred descendant Discinacea. Wright (1979a) also removed the Craniacea from the Acrotretida and elevated them to ordinal status as the Craniida. He believed that both Discinida and Craniida were independently derived from brachioporate ancestors (Wright, 1979a. fig.1). I have elsewhere briefly discussed this mdifference in taxonomic treatment (Rowell, 1981), but for the present it is sufficient to note that if the Discinida are accepted as a taxon then Figure 3 requires an additional bar to mrepresent them ranging upward from the middle Lower Cambrian. The Craniida are unknown in the Cambrian. The oldest brachiopod genus is *Aldanotreta* Pelman (1977) from the basal zone of the Tommotian of Siberia., The genus is not well known but seemingly is a paterinide. The order is well-represented higher in the Cambrian by Phosphatic-shelled forms with relatively straight posterior margins and posterior sections of both valves bisected by triangular openings. Although paterinides are commonly regarded as inarticulate brachiopods many authors (e.g., Williams and Rowell, 1965b; Rowell 1980) have had reservations about their taxonomic position. Unlike "typical" inarticulates their principal shell musculature is medianly located and scars radiate outwards from the beak (Fig.4). The calcareous-shelled Kutorginida (Rowell, 1965) are an enigmatic order because their musculature also is medially located and they seemingly have a supra-apical pedicle foramen togheter with straight posterior margins to their valves. They are variously regarded as inarticulates, articulates, or placed in unknown taxonomic position. As with the paterinides no articulatory mechanism has ever been found between the valves. Bearing the Kutorginida and Paterinida nin mind Wrights (1979a, p.236) comment that, "... there are several stocks whose placement withineither the articulates or inarticulates is controlled more by the bilief that they must belong to one class or the other, rather than on evidence of undoubted affinity based on shell morpholpgy" is understable. The paterinides range into the Middle Ordovician, but the Kutorginida have a more limited stratigraphical distribution (Fig.3).

The Obolellida are another relatively small order of calcareous- shelled brachiopods with a limited stratigraphic range (Rowell, 1962). They are relatively cosmopolitan and individuals are commonly numerous in the middle and upper part of the Lower Cambrian. In many respects they resemble obolid lingulides and indeed are often misidentified as obolids. Their musculature, like that of the lingulides and acrotretides, is not medially located in the body cavity, but id peripheral, close to the body walls.

The Lingulida (Fig.5) and Acrotretida (Fig.6) are the two principal inarticulate orders having about 60 and 130 genera respectively. Both are presently first recorded in Middle Cambrian rocks and both range throughout the Phanerozoic. They are predominantly phosphatic-shelled forms, entirely so in the Cambrian. Their musculature is peripherally placed in the body cavity and is relatively complex. Between two and four pairs of oblique muscles occur in addition to the principal adductor muscles. In living species the valves are opened hydraulically. Some of the oblique muscles are inserted at one end into the body wall and muscular contraction compresses the coelomic fluid in the body cavity causing increased separation of the two valves (Gutmann and others,).

The remaining two orders of Cambrian brachiopods are both articualates, the Orthida and the Pentamerida. The oldest described articulate brachiopod is a poorly preserved orthide occurring with *Fallotaspis longa* in California (Rowell, 1977). The associated trilobite fauna suggests a middle Early Cambrian age for this taxon . In upper Lower Cambrian rocks a variety of orthide genera are known but undoubted pentamerides have not been recorded from beds older than the Middle Cambrian. Although at least 35 genera of articulates are known from Cambrian rocks they typically form a small proportion of the brachiopod fauna, which was dominated by representatives of the other orders, particularly acrotretides. The ecological preferences of Cambrian articulates are still not well understood but they have a very patchy stratigraphic distribution. They tend to be relatively abundant at a few horizons and localities but more typically they are absent. There are more differences of opinion about the details of the subsequent Paleozoic phylogenetic history of articulate brachiopods. Wright (1979b), for example, considered that the Spiriferidina arose directly from an othide stock, whereas Williams and Hurst (1977) postulated an origin from the Athyridina. It is universally accepted, however, that the genealogy of all articulate brachiopods may be traced back to an orthide lineage. The problem at hand is the relationship of the Orthida to other non-articulate Cambrian brachiopod orders, and the relationship between these other orders.

SUMMARY OF PRIOR ARGUMENTS FOR ORIGIN OF BRACHIOPODS

One of the advantages of a plausible, but nontheless relatively radical hypothesis is that it encourages examination of its claims and also provokes reexamination of the basis for the ortodox position. Ideally both hypothesis should allow tests whose outcome maypotentially falsify the hypothesis.

When examined, neither the arguments that have been used in advocating a polyphyletic history, not those advanced for a monphyletic origin appear very strong. In essence they collapse to differing statements about the significance of similarities between early representatives of the various brachiopods lineages. Those who support a polyphyletic origin draw attention to the differences between the various inarticulate stocks and the Articulata and infer that they are too large to have arisen by divergence from a common ancestral brachiopod lineage. Valentine, for example, noted, "It has long been suspected that the Articulata and Inarticulata might not be conphyletic, for they have very disctinctive larval lives and several basic and consistent anatomical differences." He then argued that an adaptive of their origin, "... suggests strongly that each arose from a phoronid-like infaunal worm, but along separate adaptive pathways...." (Valentine, 1973b, p.100). He elaborated on this adaptive model subsequently (Valentine,1975) and developed an elegant 'scenario' for the origin of brachiopod.like organisms. The usefulness of functional-adaptive analysis in recostructing phylogeny is debatable. Bock (1981) has argued that it plays an essential role in testing phylogenetic hypothesis. Cracraft (1981, p.35) has concluded that, "... a convincing case has not been presented that functional data are a necessary component of phylogenetic analysis." I tend to agree with Fisher (1981) that in some circumstances a functional analysis may help in the construction of a phylogenetic tree by suggesting that some character changes are not independent of others. Furthermore, adaptive considerations may suggest the direction of character change, but some functional analyses do not pose very robusts tests for a hypothesis. In the present case, relatively trivial modifications in Valentines (1975) adaptive model would allow it to be consistent with a monophyletic origin for brachiopods. This is not to denigrate adaptive models in general nor Valentines in particular. They have obvious heuristic value and provoke questions. My objection is that highly generalized models are commonly not good tests of a specific hypothesis of a historical set of events. Indeed they may be little more than "... stories of might have happened." (Cracraft, 1981, p.29).

Proponents of a monophyletic origin of the brachiopods, including myself, may have been less than convincing in arguing their case. It appears to have been tacitly assumed that the observed resemblances between the principal brachiopod lineages were clear indications of the monophyletic nature of the stock. Alternatives were commonly not disscused. Thus Williams and Rowell (1965b, p.167) speaking of the Orthida and inarticulate orders noted, "... it is known whether they were all independently derived from a remote common ancestor or whether there is a fundamental regularity in the succession of their appereance with one order arising from another." Likewise Williams and Hursts, 1977, p.88) reconstruction of a prototypic brachiopod is based on an amalgam of the features shared in common by early brachiopods.

Although I still consider that brachiopods are monophyletic I recognize that the arguments that have been used to support the position might not convince the skeptic. In tying to decide between a monophyletic or polyphyletic origin it is not enough to point to differences or stress similarities. The differences may have arisen as consequence of later evolutionary divergence. Williams and Rowell (1965b, p.195) argued that many of thefeatures that differentiate articulates from inarticulates did not appear with the origin of the orthides. They suggested, for example, that mantle reversal did not occur until the evolution of the rhynchonellides, although it is characteristic of all living articulates. However, similarities alone add also an inadequate basis for postulating a monophyletic origin. The important question is how did the similarities arise? Answeing this question, of course, is part of the basic approach of cladistic analysis.

CLADISM AND THE ORIGIN OF BRACHIOPODS

General comments.-- Cladistic analysis has one of its objectives understanding genealogical relatioships. Cladistic techniques were initially developed by neontologists concerned with phylogenetic relationships among forms with a poor fossil record (Hennig, 1966). There is neither the space, nor is it perhaps appropiate, to attempt to explain the details of cladistic methodology. Excellent summaries (Eldredge, 1979) or more comprehensive accounts (Eldregde and Cracraft, 1980) are available written by those with considerable understanding of the nature of the paleontological record.

In general, cladistic techniques and philosophy have not been well received by paleontologists. Campbell (1975, p.87) observed, "A spectre is haunting palaeontology-- the spectre of cladism." Boucot (1979, p.199) has commented that cladistics, "... is nothing more or less than old-fashioned taxonomic classification so ,plastered over with jargon as to be unrecognizable to the casual reader." These rather strong reactions are perhaps not typical of the responses of paleontologists as a body, but none- the-less remains a conflict between stratophenetic philosophy (Gingerich, 1979), which in its various guises has been the basis of methods employed in most paleontological investigations, and cladistic theory. The differences of opinion regarding the merits of these two approaches are greatest when trying to reconstruct phylogenetic trees as opposed to cladograms (see Bretsky, 1979; Eldredge, 1979; Wiley, 1979).

The stratophenetic approach is not applicable in trying to address the problem of the origin of brachiopods. With present knowledge of the stratrigraphic record of brachiopods there are wide morphological gaps between the various orders and we cannot trace one evolving into manother. This may be a deficiency that future collecting will remedy; but it may be, as Wright (1979a) has mantained, that the first appereance of the various lineages marks the time at which they developed the ability to secrete mineralized skeletons, not the time at which the lineages arose. They may have had a significant prior evolutionary history as small forms whose mantles secreted only organic material.

Cladistic techniques are helpful in trying to resolve the pattern of evolution in the circumstances that we face. Indeed, I would argue that in this situation they are the only techniques available to us. As Eldredge (1979, p.167) has stressed perhaps the major contribution of the cladistic scholl has been the clear recognition that when the effects of resemblance due to convergence are removed two types of evolutionary similarity are possible. At any given level of analysis, the resemblance between two taxa may be due to "... shared evolutionary novelties inherited from an immediate common ancestor and thus not be found in any other taxon..."-(Eldredge, 1979, p.167). Such similarities are termed synapomrphs and they are in contrast to the other forms of similarity, simplesiomorphs, which are relatively primitive similarities inherited from some more remote common ancestor that may also be found in other descendant taxa. Only synapomorphs, shared evolutionary novelties, provide information on the close phylogenetic relationship between two taxa. Their presence effectively labels members of the new lineage.

Thus, to addres the question of the origin of the brachiopods, ,it is necessary to analyze the similarities shared by brachiopods and to evaluate which, if any, of them are, 'evolutionary novelties' relative to other lophophorates. If brachiopods are monophyletic they should share one or more 'evolutionary novelties' that unite the group. If, on the other hand, they arose polyphyletically, then all similarities should be either false similarities and the results of convergence, or symplesiomorphic, inhrited from some more distant ancestor that was not itself a brachiopod.

Synapomorphs of brachiopods.-- One of the strengths of cladistic methodology is that may one use both living and fossil forms to recognize 'shared evolutionary novelties'. Thus the distribution of synapomorphs in living brachiopods potentially may provide information on the earliest evolutionary history of the group.

Figure 7 is a cladogram for the major superfamilies of living brachiopods. In both diagrams the phoronids are shown as the nearestknown relatives. The brachiopods and phoronids togheter with the bryozoashare many synapomorphs that unite them as lophophorates. The principal 'evolutionary novelties' at this level include a mesosomal lophophore, which bears hollow ciliated filaments, and is partially completely separated from a non segmented metacoel.

At this point we need not be particularly concerned with the synapomorphs shown by broken lines in Figures 7 and 8. It is worth noting, however, than if those Figure 8 are correct then the Paterinida, Kutorginida, ,and Orthida (togheter with the remainder of the Articulata) are the sister group of the Lingulida, Obolellida, and Acrotretida. In turn the Lingulida and Obolellida are the sister group of the Acrotretida. Each of these three major branches has a lineage that is represented today by living brachiopods. Consequently it follows that any 'evolutionary novelty' present in all recent brachiopods logically has to have been an 'evolutionary novelty' common to all brachiopods.

We need to direct attention to the seven numbered solid lines of Figures 7 and 8. These are shown as synapomorphs, 'derived evolutionary novelties', present in their original or yet more derived states in all brachiopods. If even one of them is correctly identified as a synapomorph it would follow that brachiopods are monophyletic. Two questions need to be asked of these postulated 'derived evolutionary novelties'. Are they true similarities and not merely the result of convergence or parallelism? Secondly, if they are homologous features are they indeed synapomorphs and not merely symplesiomorphs?.

If phoronid and brachiopod lophophores are compared there are obvious differences. The structural features of brachiopod lophophores, however, are almost identical and there can be little question that the similarities are true homologies. Figure 9 is a diagramatic view into both phoronid and brachiopod lophophores, the dots represent the location of filaments. In phoronids the adult lophophore is typically spirally coiled and bears a single palisade of filaments on both sides of the axis (Hyman, 1959; Emig, 1977). In contrast, all brachiopods fundamentally have only a single palisade of two filaments about the lophophore axis. Figure 10 shows segments of the two lophophore types and illustrates additional persistent differences. All brachiopods have two coelomic spaces in the lophophore, phoronids have only one. All brachiopods have a brachial lip bounding the food groove, in phoronids the opposing palisade of filaments is in this position. Virtually all brachiopods have the adult filaments of the palisade arranged in a double row alternating in position, in phoronids they are invariably in a single row. A fifth similarity, common to all brachiopods and unknown in phoronids, is the possession of mantle canals. These are fingerlike extensions of the body cavity into the mantles found in all living brachiopods and commonly reflected in the shell of fossil forms.

Two features are shown as potential synapomorphs uniting all brachiopod lineages in Figure 8. One would have to concede that perhaps one of these may have arisen by convergence and is not a true similarity. Although it is an empirical observation that brachiopod valves always are secreted by mantles that are dorsal and ventral, and never left and right, it is possible that this orientation could have arisen independently in different stocks being controlled by the orientation of the lophophore. The detailed morphological resemblance of the second potential synapomorph, the developlment of slender, bristlelike sensory setae along the margin of both mantles, suggests that this is true similarity, not the consequence of parallelism or covergence. These setae rarely occur fossil because of their delicacy, but are known in living representatives of each of the tree major branches of brachiopods and occur also in Cambrian Paterinida from the Burgess Shale (Walcott, 1912).

Given that there are six, possibly seven, similarities shared by all brachiopods, tehnext question is are they indeed 'derived evolutionary novelties?' The cladograms of Figures 7 and 8 although they show the nested distribution of various similarities among brachiopods do not show the direction of the ancestral-descendent relationships between brachiopods and phoronids. This information of course, is crucial to deciding whether the shared similaritis of brachiopods are 'derived evolutionary novelties' or symplesomorphic.

The conventional view is that phoronid-like organisms gave rise to brachiopods. the general aspects of Valentine's (1975) adaptive model of change from an infaunal to epifaunal existence make sense only with this ancestral-descendant relationship. Although no paleontological range data or meaningful outgroup comparison Eldredge and Cracraft, 1980) are available to verify this hypotesis, it is supported by limited ontogenetic information among the features that have been discussed. In most living brachiopods the early stages of lophophore development resembled those of phoronids in having only a single row of filaments. The double row of filaments characteristic of most adult brachiopods appears later in development thus supporting the view that phoronid condition is primitive.

CONCLUSIONS

If phoronids-like animals gave rise to the brachiopods then the six or seven similarities common to all brachiopods are 'derived evolutionary novelties' and the brachiopods are monophyletic. To refute this statement it would be necessary to hsow that one or more brachiopod orders is phylogenetically more closely related to some other group of organisms than it is to the remaining brachiopods.

I know of no evidence consistent with the hypothesis that brachiopods arose polyphyletically from a phoronid-like ancestral stock. Before attempting to demonstrate that this was the case it would be necessary to show that all seven features that have been regarded as synapomorphs were merely the results of convergence or parallelism. The near identity of these features in different brachiopod lineages suggests that this is unlikely.

Valentine's (1975) model of the adaptive radiation of brachiopods suffers little damage by the assertion that the group is monophyletic. It is necessary to modify the model only to the extent that the synapomorphic features of the group were acquired prior to the radiation of the organisms that we presently recognize as brachiopods. Indeed, there may be an adaptive explanation for the development of these features. A brachiopod lophophore is seemingly mechanically better organized for pumping, filtration and separation of inhalent and exhalent currents in a partially enclosed space than is the phoronid type, which functions in an open environment.

Wright (1979a) may well be correct in this view that it is possible, even probable, that some brachiopod lineages differentiated prior to the acquisition of a mineralized shell. If so, development of a mineralized shell is an example of convergence within the group. Terms like monophyly and polyphyly, however, are determinated by group relationships, not by level of development of one or more characters (Patterson, 1978). Consequently, Wright's (1979a) views and my own may be reconciled only by regarding shell-less forms that possessed any of the features that are synapomorphic for brachiopods as brachiopods, not brachioporates nor phoronid-like worms.

ACKNOWLEDGEMENTS

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FIG. 1- Diagrammatic representation of a monophyletic orgin of the brachiopods from a phoronid-like ancestor. Heavy bars depict relative stratigraphic ranges of the principal orders. The six bars on the right of the diagram together are the Articulata.

FIG. 2- Diagrammatic representation of a polyphyletic origin of the brachipods from several phoronid-like ancestors. With this interpretation the brachiopods represent a grade of organization. Stratigraphic ranges of principal brachiopod orders shown as in Fig. 1.

FIG. 3.- Stratigraphic ranges of brachiopod orders in the Cambrian.

FIG. 4.- Paterinida. **A**. Oblique posterior view of a young complete shell showing delthyrium and notothyrium. **B**. Internal view of ventral valve of Dictyonina showing musculature radiating from the beak.

FIG. 5.- Lingulida. Internal views of the valves of Lingulella. **A**. Ventral. **B**. Dorsal.

FIG. 6.- Acrotretida. Internal views of the valves of the acrotretid Hadrotreta. **A**. Dorsal. **B**.Ventral.

FIG. 7.- Cladogram showing relationships between major taxa of extant brachiopods. Synapomorphies, uniquely derived evolutionary novelties, shown by bars connecting taxa are: (1) Filaments in a single palisade about lophophore axis. (2) Double row of filaments on adult lophophore. (3) Brachial lip bounding food griive. (4) Two mesocoelic cavities in lophophore. (5) Mantle canals. (6) Hydraulic mechanism for opening valves. (7) Prescence of larval shell. (8) Diductor muscles and hinge mechanism. (9) Posterior fusion of mantles. (10) Fibrous secondary shell. (11) Pedicle as larval rudiment.(12) Mantle reversal on settlement. (13) No larval shell. (14) Closely comparable oblique internal and oblique lateral muscle paths. (15) Holoperipheral growth in both valves. (16) Pesence of loop.

FIG. 8.- Cladogram showing relationships between principal taxa of Cambrian brachiopods. Synapomorphies, uniquely derived evolutionary novelties, shown by bars connecting taxa are: (1) Development of ventral and dorsal mantles. (2) Development of setae at mantle margin. (3) Peripheral location of shell muscles in body cavity. (4) Medially located muscle scars. (5) Straight posterior margin of shell. (6) Open delthyrium, may be partially closed apically. (7) Pseudodeltidium. (8) Apical foramen. (9) Large anterior adductors. (10) Marginal beak in both valves.

FIG. 9.- Distribution of lophophore filaments, comparison between brachiopods and phoronids. Base of filaments shown diagrammatically by dots. In brachiopods filaments arranged in a single palisade subparallel with lophophore axis. In phoronids filaments arranged in double palisade subparallel with lophophore axis.

FIG. 10.- Comparison of lophophore structure of brachiopods and phoronids shown diagrammatically as a small segment cut from lophophore.

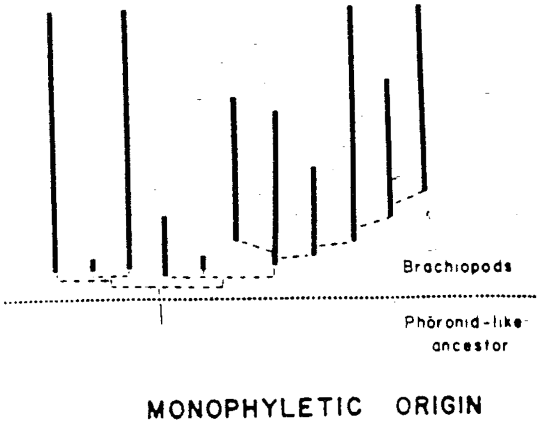


Fig. 1

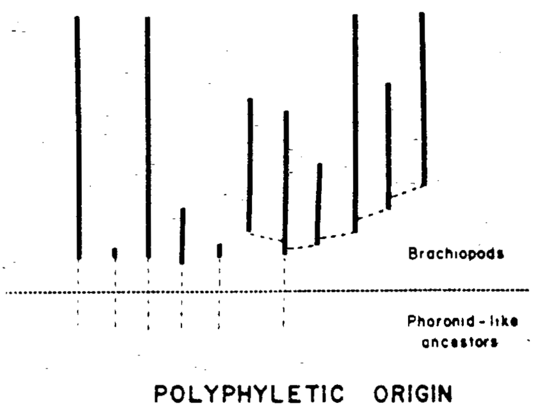


Fig. 2

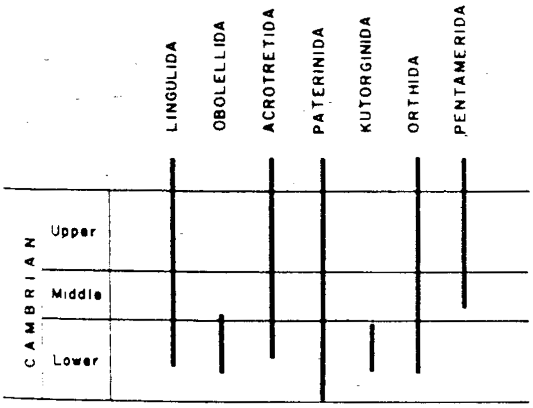


Fig. 3

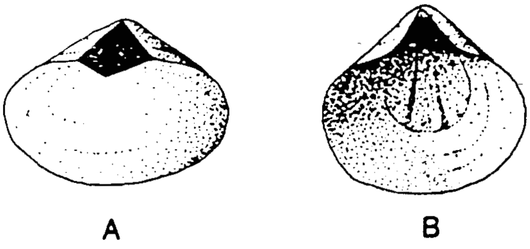


Fig. 4

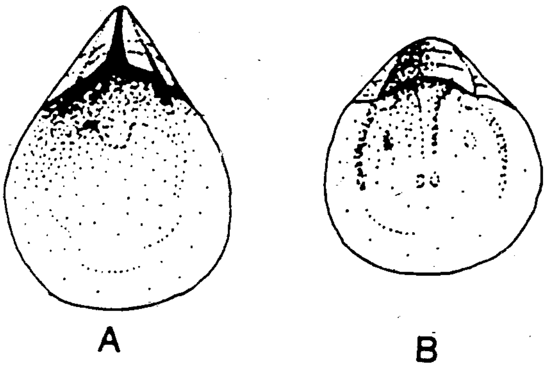


Fig. 5

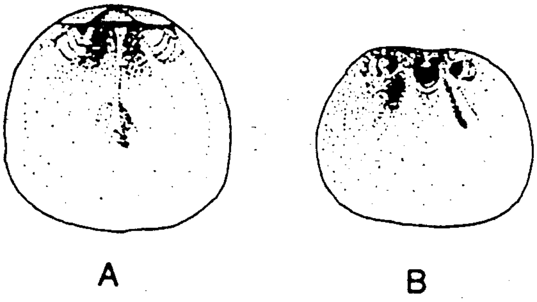


Fig. 6

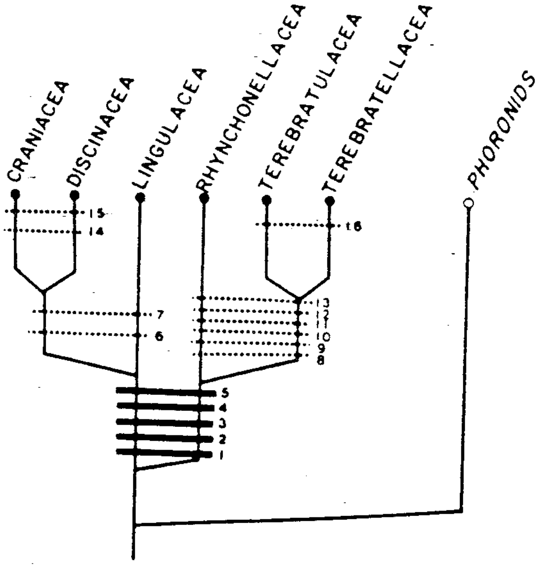


Fig. 7

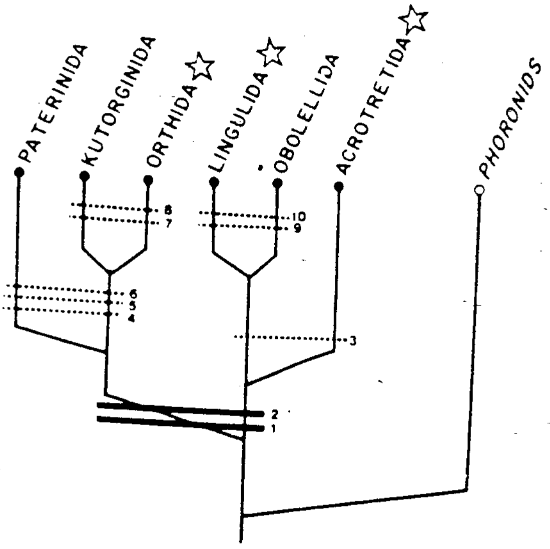
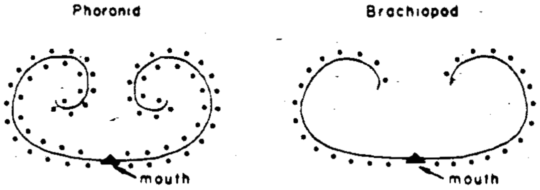
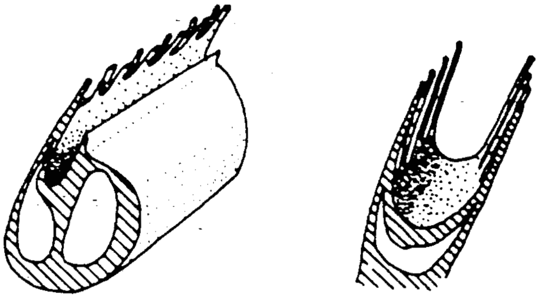


Fig. 8



DISTRIBUTION OF FILAMENTS

Fig. 9



LOPHOPHORE STRUCTURE

Fig. 10

5.4(e) Ecological aspects of a silicified bivalve fauna from the Silurian of Gotland

Louis Liljedahl

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The silicified Wenlockian (Silurian) bivalve fauna from Möllbos, Gotland, is part of life assemblage. The vast number of shells show unusual phenomena, e.g. shell repair, pearl and tumour formation, etc. A number of shells contain epibionts and bored, round holes. Presumptive predators of the bivalve community are discussed. Size-frequency distribution of the two most abundant species possibly reflects age classes. The fauna, comprising eleven species, is dominated by deposit-feeders (90%). They exhibit niche diversification, including at least three different feeding levels within the sediment. Bivalves, palaeoecology, population analysis, trophic structure, periodic growth features, bore holes, shell repair, pearl formation, malformation, epibionts, predation, Silurian, Gotland, Sweden.

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The bivalve shell reflects the anatomy, and hence the life habit of the living animal. Shell that are exceptionally well preserved may even indicate soft-part morphology and are therefore well suited for palaeoecological interpretation. Silicified fossils are generally superior in quality to other fossils material and have many advantages. For example, specimens can be studied both externally and internally and the acid extraction method (see next-section) makes it possible to obtain material useful for statistical studies.

Laufeld & Jeppsson (1976) were the first to use methodical investigations on silicified fossils from Gotland. Their prediction that the internal structures could be studied, and that the reconstruction of ontogenetic growth series etc. could be made, has been borne out. This paper on the ecology of the bivalves from Möllbos 1, Gotland, is based on previously described material (Liljedahl 1983, 1984), and the work is part of a large-scale project (PSSFG, Project Silicified Silurian Fossils from Gotland) initiated by Lennart Jeppsson, encompassing a number of localities. apart from Möllbos 1 (Jeppsson 1983:121).

The Late Wenlockian Halla Beds at Möllbos abond in silicified fossils (Liljedahl 1983). The excellent state of preservation made possible the reconstruction of soft-part anatomy of some bivalve species, which in turn gave clues to their functional morphology and life habit (Liljedahl 1984, 1985): The high quality and unusual abundance of the specimens makes this one of the best known Silurian bivalve faunas.

Material and Methods.

The abundant fossil material from Möllbos 1 (for location see Laufeld 1974b: locality description Lijedahl 1983) was obtained by etching samples in 10% acetic acid (the matrix is unaffected by silicification; cf. Laufeld & Jeppsson 1976:31; for details of sampling levels, etc. see Liljedahl 1984). From 511 kg limestone dissolved, 11 species comprosing 3, 421 bivalve shells were recorded. The state of preservation of the bivalves is good to fairly good.

A fragment with the umbonal part preserved was counted as one valve, even though this was the only part of it left. Fragments lacking the umbonal part werenot included (roughly 50% of the material). Articulated valves need not necessarily be represented by complete valves, even though most of the articulated specimens are intact (cf., however, Janeia silurica in the next section).

The specimens were coated with ammonium chloride before being photographed. Scanning electron micrographs were taken with a Leitz electron scanning microspore and the specimens were coated with gold/palladium. The material is now deposited, together with appurtenant data, in the Type Colection of the Geological Survey of Sweden, Museum Departament, Box 670. S751 28 Uppsala, Sweden. For lithological descriptions and lists of fauna see Hede (1927:35. 1960:67), M 81962:53). Fáhraeus (1969:9), Laufeld (1974a:29. 1974b:102) Liiljedahl (1983:7-8) and Jeppson (1983).

Fragmentation.

Fragmentation is usually caused by physical factors. Since the Möllbos fauna contains well-preserved specimens, abrasion caused by wave action, transportation and the like must be ruled out (see section Life or death assemblages).

However the post mortem history of skells may include fragmentation caused by biological processes such as attacks by predators, scavengers and endolithic organisms (Dodd & Stanton 1981:305-306; see section Possible predators of the bivalves of Möllbos).

The degree of fragmentation of the Möllbos material is variable, the debris comprising both pre- and post-silicification fragments (cf. Boyd & Newell [illegible]; see Fig.1A, B, C, herein).

The two most abundant infaunal species, *Nuculodonta gotlandica* (18% articulated valves of [illegible]) and *Nucoloidea lens* (32% articulated valves [illegible]) are less fragmented than Janeia silurica for example, (see discussion below) possibly because their shells are thicker and the space between the articulated valves was filled with sediment after death. The valves probably opened when the strong ligament pulled them apart during the constant activity of abundant deposit-feeders. Consequently, compaction could not break the sediment-filled valves (cf. Shinn et al. 1976).

Most of the almost 600 valves of Janeia silurica are fragmentary. However, a considerable part (32[illegible] of these shells are articulated. The mantle is assumed to have had fussed ventral margins (Liljedahl 1985) which would prevent sediment from entering the mantle cavity for some time after death. Thus most of the high degree of fragmentation in this thin-shelled species may be due to compaction. The great number of articulated valves of this species support the assumption that it was a deep burrower that did not undergo reworking (Liljedahl 1984, 1985; see also Population analysis).

The thin-shelled infaunal species Palaeostraba ba[illegible] is represented by 25 valves, only a few of which are complete, two being articulated. There are [illegible] valves of the infaunal Caesariella lindensis, three of which are complete and well- preserved though none are articulated. The only find of Gen. [illegible] indet., also infaunal, comprises two articulated valves, one of which has a damaged umbo.

The shell of the semi-infaunal Freja fecunda is fairly thin. Of 164 valves, 12 are articulated juveniles while only a few are complete adult valves. Of 138 specimens, two complete, articulated juvenile valves of the semi.infaunal Molinicola gotlandicawere observed and of the 42 valves of the semi-infaunal Goniophora onix none were articulated. The four valves of the epifaunal *Mytilarca? sp.* are fragmentary or much worn. The only valve of *Maminka sp.*, which is thik-shelled, is complete and well preserved.

Environmental influnce reflected in sheell morphology

Growth lines and growth stops.- Under normal conditions bivalve shells grow by daily addition of thin layers of calcium carbonate and organic matter (Clarke 1968; House & Farrow 1968; Panella & MacClintock 9168). Growth is influenced by various environmental and ontogenetic factors such as periodical physical events, e.g. diurnal, tidal and seasonal changes and spawning periods, which are recorded by the bivalve shell in a characteristic growth increment pattern. Non-periodic incidents, such as storms, changes in salinity, etc. also leave their markin the individual growth record (Craig & Oertel 1966:323).

Winter rings reflecting periods of retarded growth are more pronounced in medium- to high-latitude shallow-water areas, while in tropical regions the difference between summer and winter growth is difficult to discern (Rhoads & Panella 1970:145, 153). In tropical and subtropical areas the breeding period patterns of bivalves are the most striking, since here the winter growth pattern is less obvious than in temperate regions (Panella & MacClintock 1968:72). Several preservational aspects of Paleozoic bivalves make the interpretation of growth increment patterns somewhat speculative. Although lacking microscopic growth structures such as dily increment layers, the original shell texture of the silicified material from Möllbos having been lost, external concentric growth lines are visible on several specimens (Fig.1D).

In addition, conspicuous growth stops alternating with thin growth lines (Fig. 1E) were observed on about a dozen valves of Nuculodonta gotlandica and Nuculoidea lens. In valves less than 5mm in length such growth stops are rare. Large valves may contain up to four conspicuous stops, growth stops as well as growth lines being less pronounced in the older parts of the shell as a result of abrasion.

If the grwoth lines, on the average ocurring in series of about twelve, interrupted by growth stops, represent a monthly inhibition of growth, then the periodical larger stops are an indication of an annual period of slow or inhibited growth. The number of growth lines proximal to the first stop in some valves exceeds twelve. Thus a first-year growth stop either became eroded or did not form. A few valves show about 20 growth lines in some of the intervals between growth stops, possibly indicating continuous growth. Other specimens have fewer than 12 lines between the stops, some of which have probably been caused by non-periodical events. Thus, the age of the animals is difficult to estabish. The largest specimens of Nuculoidea lens (more than 14mm) died at about 7 years of age (cf. maximum age of different specie of *Recent Nucula.* 12-20 years. In Allen 1954:471). Since the bivalves of Möllbos lived in tropical waters, the growth stops probably indicate annual spawning periods.

Malformation.-Longer periods of inhibition of growth may indicate a patological state (Boshoff 1968:202), as is possibly the case in one articulated specimen of *Nuculodonta gotlandica* (Fig. 2B). After a stop in growth, subsequent growth wasprobably slow, since the shape of the valves has become modified. Alternatively, the malformation could be the result of predation (Jeffrey Levinton, pers. comm.)

Shell repair.- An example to the repair of the mantle edge reflected in markings on the shell is seen in a specimen of Nuculodonta gotlandica (Fig.2A). Damage to the margin, probably caused by a predator, resulted in a discontinuity in the concentric growth line sculpture. However, the mantle gradually recovered, producing an almost normal ventral edge before the death of the animal.

Pearl formation.- Bivalves are known to repair their shell by means of exccessive accretion (Boshoff 1968:208). The blister pearl phenomenon in bivalves is caused by an irritation of the outer epithelium of the mantle caused by the larvae of a parasite, boring animals or foreing bodies within the shell (e.g. Jameson 1912; Boetgger1954; Bohsoff1968). The blister pearl of inorganic origin is characterized by a total overgrowth of the extraneous matter and by being incorporated in the shell (see e.g. Newell 1969:177).

Blister pearls occur in the silicified material. The infaunal *Nuculodonta gotlandica* contains a pearl immediately dorsal to the anterior pedal protractor muscle scar (Fig. 3B; see also section Boreholes). These bivalve pearls are, to the best of my knowledge, the oldest known (prior to this, the oldest known being of Ludlovian (Silurian) age, see Kriz 1979:40).

Tumour formation, evidence of commensalism?.- 'Raised blisters' found in fossil shells are believed to be caused by parasites and commensals. The Middle Devonian putative parasite Diorygma atrypophilia bored into the valves of the brachiopod Atrypa zonata, on the inside of which a tube was formed by the simultaneous growth of the brachiopod shell and parasite (Biernat 1961; MacKinnon & Biernat 1970).

Another Middle Devonian tube-dweller, Burrinjuckia spiriferidophilia did not penetrate tha brachiopod which it inhabited but entered at the commisural line, and its tube was built up of shell material by the brachiopod itself. The tube is in the middle of the brachial valve between the spires where the inhalant current entered. This position, in combination with a number of other factors, supports the theory that the organism was a commensal filter feeder (Chatterton 1975).

In one right valve of Nuculodonta gotlandica there is an abnormality in the posterior part (Fig.3A, C). A tube-like excrescence, 0.8mm long and 0.5mm wide, is situated immediately ventrally to the posterior adductor muscle scar. The tube extends laterally along the ventral limitation of this scar and the distal end is 1mm from the posterior margin of the shell. There is a gradual transition from the proximal part of the protuberance to the shell. On the outside of the shell there is a conspicuous growth stop ring corresponding in comarginal posotion to the tube. The base of the protuberance is slightly wider than the rest of it, the distal half not being attached to the shell. The distal end is rounded, partially broken and exhibits a jagged opening.

The tube resembles *B. spiriferidophilia* in that is attached at is base only. The mantle epithelium may have secreted shell material around the (parasitic or commensal) organism for protection, causing the bivalve shell to cease growing for some time and thereby giving rise to the conspicuous growth stop ring on the shell exterior. Since the tube is close to the posterior adductor muscle scar in the vicinity of the anus, and opens posteriorly, this suggests the possible commensal affinity (coprophagy?) of its inhabitant (cf. living polychaete Polydora which lives incorporated into the shell of bivalves, discussed by Bromley 1970:5

Bore holes.- Two shells of *Molinicola gotlandica* are bored. The holes are circular, 200 to 300 m in diameter, long, cylindrical and perpendicular to the shell surface (Fig. 2E). One of the valves has 10 bore holes, five of which have left conspicuous traces of defence by the bivalve as excess accretion of shell material (blister pearls). At the position of four of these, the additional shell 'layers' have partially been worn off after death, so the holse are now visible also from the inside (Fig.2C, D). Three holes shown no sign of repair. The second valve exposed to borers has two holes penetrating the shell and these show no overgrowth by shell material. All bore holes found are situated in the anterior part of the shells.

Drilled round holes are not common in Paleozoic shells, and since the hole is never preserved with its maker, the nature of its origin can only be hypothetical. Quite a few gastropod groups contain borers, none of which, however, are known to have existed in the Early Paleozoic. In fact the oldest bore holes assigned to gastropods are from the Late Mesozoic (Bromley 1981. [illegible] . Bromley (1981:59, pi, 3:4) reported a round, somewhat bevelled hole, 500 m in diameter, in a gatropod shell made by the cephalopod *Octopus vulgaris*. Thyeoctopus usually penetrates the bivalve shell mechanically in the vccinity of one of the adductor muscles (Bromley 1981:5 This is also the location of the roun holes in the studied bivalve material from Möllbos. The preserved cephalopod fauna from this locality is dominated by oncocerids (oldest known octopods being of Mesozoic ages, see Moore, Lalicker& Fischer 1952:343). Their aperture was too small to allow the protrusion of a sufficiently large jaw apparatus for bivalve predation (Sven Stridsberg pers. comm.; see also Stridsberg 1981; 270, Fig 1A,B).

Bore holes produced by extant nematodes are much smaller vthamn those in the present material (ca. 10m in diameter, Silter 1971:20). The extant marine boring sponge Cliona produces a gallery of chamberlets (Boekschoten 1966:350) which differs considerably from the present simple cylindrical holes.

Bore holes of a different kind were observed in one specimen of *Nuculodonta gotlandica* (Fig. 1B). The two holes are preserved as thin-walled parallel tubes with a diameter of 150 and 300 m, respectively, which run parallel to the shell wall and close to the xeternal surface. The bivalve specimen is broken and therefore does not reveal the continuation of the holes.

Numerous holes or groups of holes do not suggest predation (Richrd Bromley pers. comm.). Instead, a slow-boring sedentary organosm might prompt its host to repair the damage (Fig.2C,D). With our present knowledge the origin of the holes in the Möllbos material cannot be determinated.

Epibionts.- Epibionts on empty shells, for example, tube-forming worms, corals, bryozoans, etc. are extremely common in prsent day seas, and fosiil evidence of epibionts is abundant (see e.g. Voight 1965).

About a dozen specimens of the semi-infaunal Molinicola gotlandica and Goniophora onix show evidence of encrustation by epibionts; for exmple tabulate and rugose corals, ?bryozoans, serpulids and other tube-forming worms (Fig.4A, B, C, E.). Holdfasts have also been found (Fig.4d). The epibionts are seen attached to both the inside and the outside of the shells, indicating that these were empty at the time of colonization (see Stel & deCoo 1977 on alveolids, auloporids and bryozoans on Pteronitella retroflexa in the Hamra oncolite, Gotland). Similarly, many of the macrogastropods from Möllbos are infested with epibionts. In spite of the fact that the infaunbal species make up almost 90% of the total number of the shells at Möllbos, only one specimen, a nuculoid, has a worm-tube inside the shell (Fig.4B).

Possible predators of the bivalves of Möllbos.- Recent bivalves are the prey of several carnivorous groups. The bivalves are crushed by crustaceans, fish and birds, drilled by octopods and gastropods and swallowed by asteroids, gastropods, sea-anemones, fish another vertebrates (Carter 1968; Vermeij 1978, etc.). However, predation is extremely difficult to detect, many attacks, succesful and unsuccesful, being undetectable in both extantand fossil material. Part of the fragmentation of the Möllbos material, though, was probably caused by predators like trilobites and eurypterids.

Other presumptive predators of bivalves at Möllbos were fish, cephalopods and asterozoans. Gastropods must be ruled out, since no carnivorous form has been found among the 20 species at this locality (Peter Mleson pers. comm.). The fish fauna at Möllbos has not yet been thoroughly investigated. Only one spevies (agnathan) has been discovered (Doris Fredholm pers. comm.). Agnathans probably fed on organic mud, bottom detritus and plankton or small nectic invertebrates (Tiiu Märss pers. comm.). Another fish goup, teh acanthodians (probably predators), had already in the Silurian well-developed jaws with large tteeth (cf. Devonian acanthodians in Obruchev 1964:175-195). They were rare in the Wenlockian (Tiiu Märss pers. comm.) and have not yet been found at Möllbos (Doris Fredholm pers. comm.).

The most common foodof living asterozoans comprises molluscs, especially bivalves, and these echinoderms were also important early bivalve predators (Carter 1968:43,62). No asterozoan remains have been recognized with certainty in the Möllbos material (thebivalves alone having been exhaustively investigated), but asterozoans are prone to desintegrate rapidly after death and the individual elements are therefore not often recognized. Asterozoans have been found on Gotland in strata both older and younger than those of Möllbos (Regnéll 1960:174). Thus, the posibilities that they were present at this locality and were possible predators of bivalves cannot be excluded.

The cephalopods as possible predators, by means of drilling, have been discussed above. The most common cephalopod method of opening bivalve shells, however, is to pull the valves apart by means of their suckers (Carter 1968:41), which leaves the empty shell undamaged and hence leaves no clue in the fossil record.

Population analysis

Life- or death assemblages.- In palaeoecology it is important to decide the character of the fossil accumulation, i.e. whether it is a life assemblage (preserved in situ; see Craig & Hallam 1963:732) or a death assemblage (transported). There is evidence that the Möllbos bivalve fauna was preserved in situ. Firstly, the matrix is extremely fine-grained and secondly, the greatest part of the shell edbris is identifiable, the number of articulated and well-preserved shells being high. Furthermore, the number of right and left valves is almost equal and, finally, no size-sorting has occurred (Fig.5).

Size-frequency distribution of articulated versus disarticulated valves of *Nuculodonta goylandica* and *Nuculoidea lens,* respectively, of the largest sample (G77-28LJ) can be see in Fig.5. The two diagrams based on disarticulated and articulated specimens correspond fairly well in the two species. The first peaks in the diagrams of articulated valves of both species, however, have no corresponding peak in the diagram of disarticulated valves. This may perhaps be because of a more likely fragmentation of smaller, disarticulated shells, while, when rapidly buried, the articulated valves were not affected. In general, the size-frequency from Möllbos is similar between articulated and disarticulated valves.

In most samples from Möllbos, about 30% of all measurable valves of the deeper burrowing *Nuculoidea lens* and *Janeia silurica* are articulated, while the corresponding figure for the shallow burrower *Nuculodonta gotlandica* is only 20%. This constant relation between articulated and disarticulated valves throughout the section may be due to the fact that the shallow burrowing species are more affected by bioturbation and predation than the deep burrowing ones.

Craig & Hallam (1963:743) argued that polymodal peaks in size- frequency distributions of fossil associationsof species are not a result of sorting but reflect events during the life of the population. Recruitment, growth rate , mortality rate and seasonal differences in the growth rate influence size-frequency distribution patternsof living and dead populations (Craig & Oertel 1966:315). Also spawning periods can be recognized on those individuals surviving these severe periods (cf. section on growth stops above).

Thesize.distribution of the populations of *Nuculodonta gotlandica* and *Nuculoidea lens* at Möllbos is sightly negatively skewed (Fig.5), which may reflect a low juvenile mortality and decreasing growth-rate, with the result that the older age classes merge (cf. Craig & Oertel 1966:349).

Although it is extremely difficult to estabñish the ecological status of fossil species based on their abundance (Johnson 1965:85), the size-frequency distributions of Nuculodonta gotlandica and Nuculoidea lens, supported by preliminary results on growth-ring studies, may indicate seasonal mortality (e.g. spawning periods). Thus, the bivalve accumulations of Möllbos most probably represent life assemblages (cf. Craig & Hallam 1963:743).

Diversity and provenance of the species.- The number of species at Möllbos per sample ranges from 4 to 9 (Fig.6). The bivalve fauna is strongly dominated by three infaunal species, two of which (the non-siphonate nuculoids Nuculodonta gotlandica and Nuculoidea lens constitute more than 70% of all valves recorded. In some samples thesetwo species make up more than 90% of all valves and in 13 of the 25 samples they are ranked first and second in thisd order. Nuculodonta gotlandica isd first in 19, second in 4 and third in 2 samples while Nuculoidea lens is first in 6, second in 14 and third in 5 samples. The third most common species, Janeia silurica, is first in 2, second in 7 and third in 16 samples (in some samples two species can be ranked equal).

Although ocurring in small numbers, the remaining species are, just as the three most abundant ones, considered to have been living at thesite of burial (see section Life- or death assemblages), with the possible exception of *Mytilarca*? sp. This species was epibyssate. This does not, however, necessarily indicate transport, since non-preservable algae or the like might have constituted a suitable substrate for attachment on a muddy bottom.

Trophic structure

A deposit-feeder-dominated community.- Several students have recorded a strong positive correlation between clay-rich sediment and an abundance of deposit-feeders (e.g. Sanders 1958, 1960). The unstable physical character of a sediment of high silt-clay particle content subjected to biogenic reworking by deposit- feeders also causes the clogging of the food-gathering and respiratory organs of suspension-feeding organisms (Rhoads & Young 1970:171; Levinton & Bambach 1975:108). Disturbance of the substrate may also prevent juveniles of suspension-feeders from securing a stable life position (Levinton 1977:218). Exclusion of many suspension-feeders from this habitat thus further emphasizes the dominance of deposit-feeders.

The bivalve fauna of Möllbos is an excellent example of such a community, since it is numerically dominated by deposit-feeders, on an average comprising 90% of teh total population. The semi-infaunal suspension-feeders constitute 10% and the epifaunal suspension-feeders only 0.03 %.

Usually, competitive exclusion by exploitation does not occur in suspension-feeding bivalve populations (Levinton 1972), and evidently different suspension-feeding species at Möllbos did not compete for the same niche, unlike the deposit-feeding species (see below), Since the maximum abundance of suspension-feeders occurs in well-sorted sandy sediments (Sanders 1958; Levinton 1972), the extremely muddy habitat of Möllbos favoured deposit- feeders, whose activity affected the size of the suspension-feeding population.

Autecology and niche diversification.- The autecology of the bivalves of Möllbos has been discussed by Liljedahl (1984, 1985). Only the bivalves have been investigated at this locality and thus a synecological synthesis must wait till the hole fauna is treated.

Nuculodonta gotlandica (comprising 44% of all bivalves at Möllbos) was non-siphonate, moderately slow-burrowing deposit- feeder living slightly below the surface of the sediment (Fig.7; see also Liljedahl 1983, 1984). *Nuculoidea lens*

(27%), also a non-siphonate deposit-feeder, was a moderately rapid, active burrower and fed at a somewhat deeper level than the former (Fig.7; see Liljedahl 1983, 1984). *Paleostraba baltica* (0.7%) was a rapidly burrowing deposit-feeder which had siphons for respiration, and occurred at a rather shallow feeding depth (Fig.7; see Liljedahl 1984). A second siphonate nuculoid is *Caesariella lindensis* (0.4%). This was a slow burrowing deposit-feeder with a life position immediately or somewhat below the sediment surface (Fig.7; see Liljedahl 1984). The deepest position in the sediment was occupied by *Jaeia silurica* (18%). This was an active, relatively rapid, deeply burrowing deposit-feeder, possibly (in analogy with its descendant, the living Solemya) living in symbiosis with chemoautotrophic bacteria (cf. Cavnaugh et al. 1981) in a feeding niche of its own, which was perhaps sulphur-rich and therefore lethal to mother species (see Liljedahl 1985). Janeia silurica and Nculoidea lens show the largest number of articulated valves, indicating a deeper life position in the sediment in relation to the remaining infaunal dwellers.

Consequently thier remains were not affected by even intensive bioturbation (see under Fragmentation).

Deposit-feeders are suitable for the study of interspecific competition and niche diversification (Levinton 1977:192). Although feeding-depth below the sediment surface is age- dependent in some species, specific feeding levels in the sediment might develop due to differences in feeding efficiency or feeding speed of trhe species. Levinton & Bambach (1975:108) record how *Yoldia limatula* feeds faster than *Nucula proxima*, resulting in avoidance and niche stratification.

The co-existence of the non-siphonate deposit-feeders Nuculodonta gotlandica, Nuculoidea lens and *Janeia silurica* indicates niche diversification with feeding depths in order of increasing depth.

Out of statistically reliable samples, 9 contain *N.lens* and *J. silurica* in fairlyequal numbers (less than 10% percent difference) uggesting yhat they inhabited different feeding levels (compare the co-existence, at different feeding levels, of *Nucula* proxima and *Solemya velum* where the former is attracted to the burrowing openings of the latter, in Levinton 1977:208, 209, Fig.13). Since *J. silurica* is most probably the direct ancestor of *Solemya* (see Liljedahl 1984) and Nculoidea lens is possibly a forerunner of the extant *Nucula*, the co-ocurrence of the two Silurian bivalves perhaps indicates a relationship which has now lasted for more than 400 million years.

The great numerical dominance of *Nuculodonta gotlandica*, *Nuculoidea lens* and *Janeia silurica* may reflect exploitation ninteractions in which the siphonate deposit-feeders Paleostraba baltica and *Caesariella lindensis* were almost completely crowded out owing to the disturbance of the substrate by non-siphonate deposit-feeders, as described above. In statistically reliable nsamples, *Nuculodonta gotlandice* dominates markedly the asmples lacking *Paleostraba baltica* and *Caesarella lindensis*, while *Nuculoidea lens* ans *Janeiasilurica* togheter dominate the samples containing *Paleostraba baltica* and *Caesariella lindensis*. Thus, the last two co-existed with *Nuculoidea lens* and *Janeia silurica* and probably inhabited a different level from them, i.e. they most probably shared the shalowest level in the sediment with *Nuculodonta gotlandica*. As was expected, in sample G79-79LJ containing the largest number of *Paleostraba baltica* and *Caesarella lindensis*, the number of *Nuculodonta gotlandica* is the lowest in all statistically reliable samples and only half of that of *Nuculoidea lens* and *Janeia silurica* taken together. The morphology of *Paleostraba baltica* further indicates a fast- burrowing life habit (Liljedahl 1984), typical of deep-burrowing species. The siphons may have enabled this species tomigrate dowm to the feeding depth of *Nuculoidea lens*, but this assumption is not supported by statistical data.

Conclusions

The bivalves of Möllbos are well-preserved, represented by a large number of articulated specimens, and have not been subjected to size-sorting. Thus, the faunais preserved in situ. It is also concluded that (almost) all taxa were contemporaneous. Co-occurrence of species suggests co-existence either at different feeding levelsor in a patchy distribution. The fine- grained limestone, in Wenlockian times a muddy, soft-bottom environment dominated by deposit-feeders, would appear to have contained abundant micro-organisms. In this habitat siphonate deposit-feeders and suspension-feeders were almost totally outnumbered by non-siphonate deposit-feeders.

Shells of semi-infaunal and epifaunal species were much more heavily fragmented and worn than those of infaunal ones. A large porportion of the epibionts settled on empty shells (many are found on the inside). Thus, the lack of epibionts on empty shells of infaunal species indicates that the se were only rarely exposed even post mortem. Bore holes are found in shells of only one semi-infaunal species. Some of the borings were made pre mortem, the bivalve having formed extraneous shell material ('blister pearls') as protection, while other holes were either lethal or made pot mortem. Due to their protected life position in the sediment, the shells of infaunal species are articulated to a high deegre and usually less fragmentary than nthose of semi.infaunal and epifaunal species.

The degree of wear and fragmentation andthe distribution of epibionts, borings, pearls, etc. are distinctly dissimilar between the different species. The taxa considered to be semi.infaunal (based on morphological reasons, in Liljedahl 1983, 1984) were much more strongly affected by environmental influences than the numerically dominant infaunal ones. Thus, the ecological assumptions agree with and support the conclusions reached through morphological studies.

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Fig. 1. A., Nuculoid, pre-silicified fragment (see text, Fragmentation). SGU Type 3943, x6.4, sample G78-2ll. B., Nuculodonta gotlandica, post-silicified fragment showing two borings parallel to the shell surface (at arrows), SGU Type 3944, x19, G79-99LJ. C. Pre-silicified fragment showing three layers (original shell structures?). SGU Type 3945, x2.6, sample G79- 99LJ. D. Nuculoidea lens, left valve with growth lines (see sections Growth lines and growth stops). SGU Type 901, x3.9, sample G77-28LJ. E. Nuculodonta gotlandica, right valve with conspicuous growth-stops and thin growth lines in between .SGU Type 999, x4.3, sample G78-1LL. (A,B,C are scanning electron micrographs, D,E photographs.)

Fig. 2. A. Nuculodonta gotlandica, external view of right valve showing old deformed shell margin caused by damage to mantle which recovered and evntually produced a normal shell margin. SGU Type 1884, x4.8, sample G78-2LL. B. Nuculodonta got.alandica, external view of aberrant shell form resulting from growth inhibition followed by slow growth, SGU Type 1206, 1207, x4.6, sample G79-90LJ. C. Molinicola gotlandica, internal lateral view of left valve demonstrating shell repair at bore holes (see detail at arrow in D), SGU Type 3949, x2, sample G79-86LJ. D. Detail of C.x 14.7. E.Molinicola gotlandica, external view of anterior part of left valve with five round bore holes, same as in C, x7.3.

Fig. 3. A Nuculodonta gotlandica, internal antero-lateral view. C. Detail of A. lateral view, x21.

Fig. 4. A. Molinicola gotlandica, internal view of right valve containing worm-tubes, SGU Type 3685, x1.8, sample G79-83LJ. B. Nuculodonta gotlandica, postero-lateral view of interior of a left valve showing a worm-tube, SGU Type 1165, x5.8, sample G69- 3LL. C. Goniophora onyx, intenal view of right valve attached rugose coral and tabulate coral, SGU Type 3946, sample G79-90LJ. D. Molinicola gotlandica, internal view of ventral margin with holdfast, SGU Type 3947, x5.2, sample G77-38LJ. E. Molinicola gotlandica, internal view eexhibiting serpulid tubes, SGU Type 3948, x4.8, sample G79-99LJ. (All specimen are coated with ammonium chloride before being photographed.)

Fig. 5. Size-frequency of single and articulated valves of sample G77-28LJ. A. Nuculoidea lens. B. Nuculodonta gotlandica.

Fig. 7. Suggested life positions of the bivalves of Mölbos. Three feeding lavels (a, b, c) are distinguished within the sediment (for discussion see section Trophic sructure). Drawings based on specimens described and illustrated in Liljedahl 1984. (Sizes of the shells are not relative to one another and are not drawn to scale).

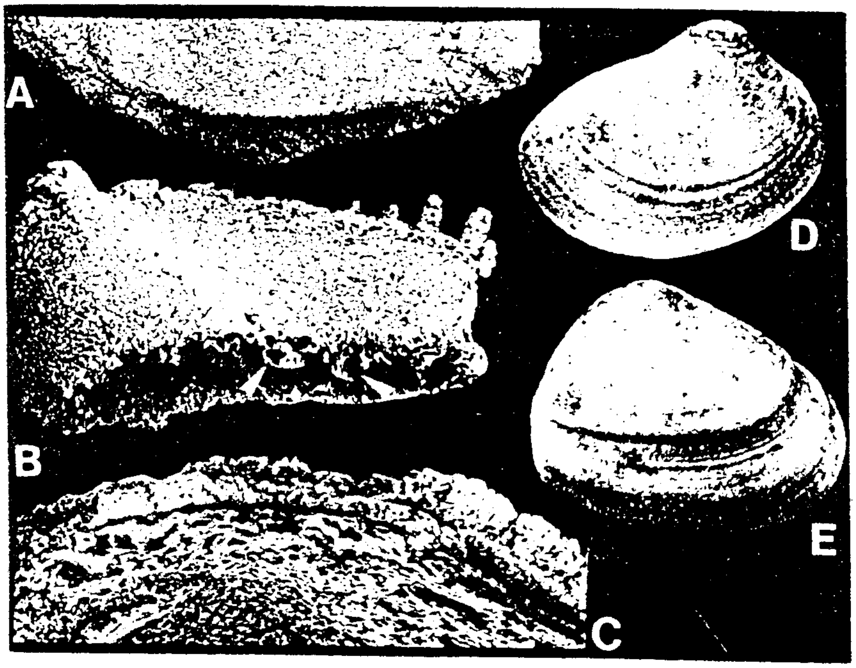

Fig. 1

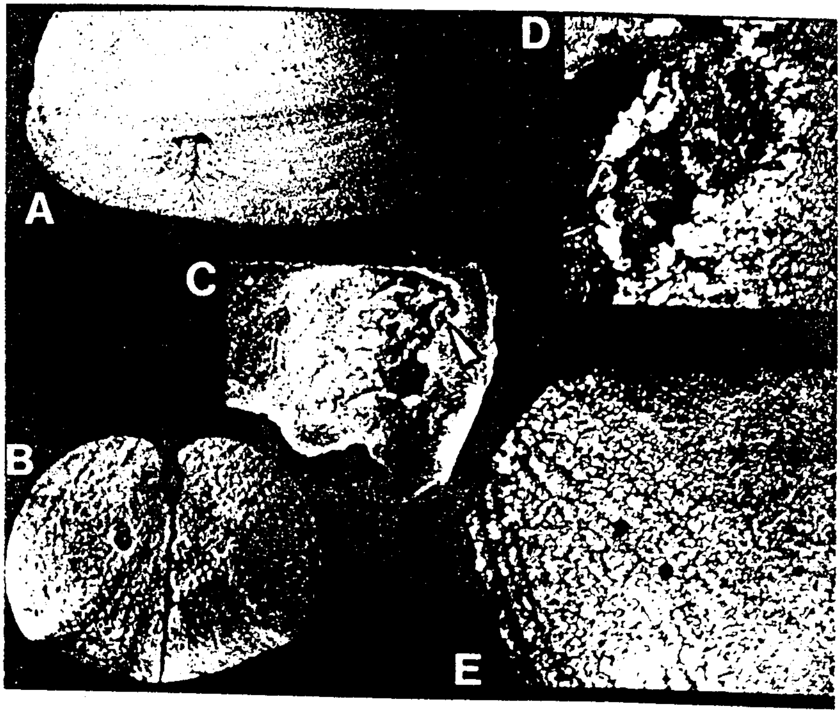

Fig. 2

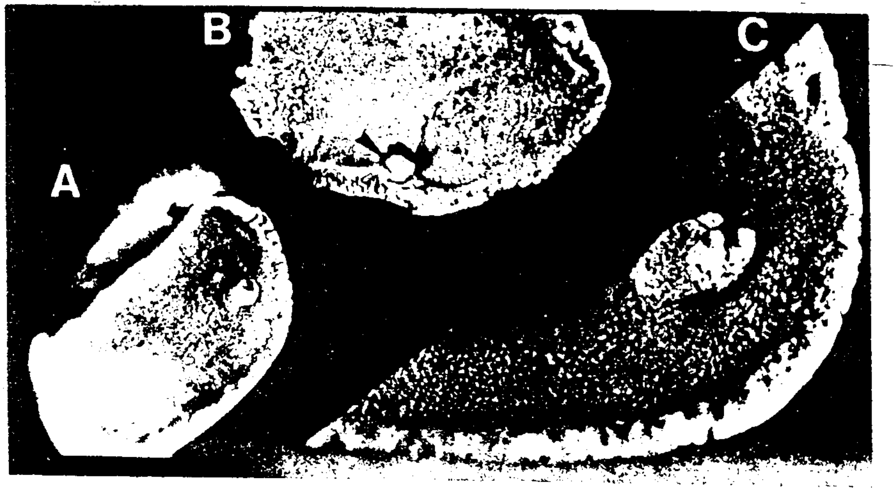

Fig. 3

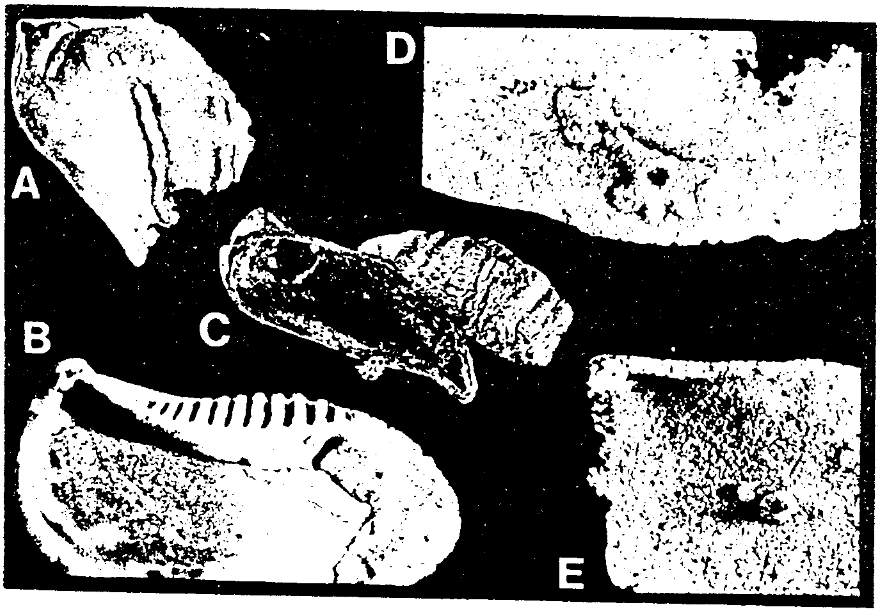

Fig. 4

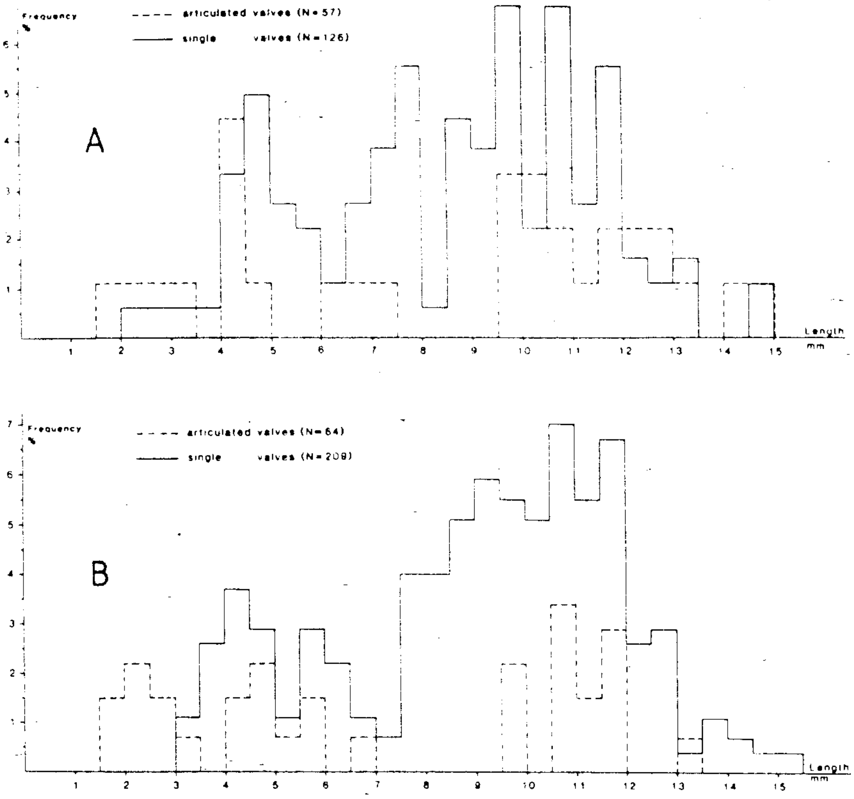
Frequency
%
---- articulated valves (N=57)
—— single valves (N=126)
A
1
2
3
4
5
6
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Length
mm
Frequency
%
---- articulated valves (N=64)
—— single valves (N=208)
B
1
2
3
4
5
6
7
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Length
mm

Fig. 5

Sample	Number of valves (N)	Sample weight (kg)	N/kg	No. of species	Nuculodonta gotlandica	Nuculoides lens	indeterminable juvenile nuculoids	Janeia silurica	Freia fecunda	Molinicola gotlandica	Goniophora onyx	Palaeostraba baltica	Caesariella lindensis	Mytilarca sp.	Maminka sp.	gen. et sp. indet.
G77-28LJ	716	78	9.2	9	291 (58) 40.6	192 (62) 26.8	14 (12) 2.0	156 (56) 21.8	26 (4) 3.6	17 2.4	11 1.5	4 0.6	3 0.4			2 (2) 0.3
G78-2LL	161	17	9.5	8	72 (14) 44.7	28 (4) 17.4		29 (16) 18.0	13 8.1	9 5.6	3 1.9	5 3.1	2 1.2			
G78-78LJ	187	24	7.8	8	90 (8) 48.1	35 (10) 18.7	2 (2) 1.1	42 (12) 22.5	10 5.4	2 1.1	3 1.6	1 0.5	2 1.1			
G78-99LJ	103	15	6.9	8	41 (12) 39.8	22 (6) 21.4	2 (2) 1.9	23 (2) 22.3	6 5.8	6 5.8	1 1.0	1 1.0				
G78-84LJ	228	38	6	8	103 (14) 45.2	64 (28) 28.1	12 (2) 5.3	34 14.9	4 1.8	8 3.5	1 0.4	1 0.4		1 0.4		
G78-90LJ	194	18	9.6	8	113 (22) 58.3	36 (16) 18.6	10 (10) 5.7	16 (4) 8.3	9 4.6	3 1.6	5 2.6	1 0.5		1 0.5		
G78-95LJ	256	32	8	8	96 (16) 37.5	79 (20) 30.1	6 (6) 2.3	43 (8) 16.8	15 5.9	13 5.1	1 0.4	2 0.8	1 0.4	1 0.4		
G78-92LJ	71	16	4.4	7	24 (2) 33.8	21 (8) 29.6	4 (4) 5.6	13 (6) 18.3	4 5.6	2 2.8	1 1.4	2 2.8				
G78-12LL	39	5	7.8	7	16 41.0	8 20.5		9 (4) 23.1	1 2.6	1 2.6	3 7.7	1 2.6				
G78-82LJ	83	18	4.6	7	33 (10) 39.8	24 (16) 28.9	2 (2) 2.4	15 (2) 18.1	4 4.8	2 2.4	1 1.2	2 2.4				
G77-29LJ	74	29	2.6	7	42 (4) 56.8	15 (8) 20.3		8 (6) 10.8	5 6.8	1 1.4	2 2.7				1 1.4	
G78-79LJ	119	30	3.9	7	30 (6) 25.2	33 (10) 27.7	2 (2) 1.7	22 (12) 18.5	9 (2) 7.6	16 13.5		4 (2) 3.4	3 2.5			
G78-83LJ	332	54	6.1	7	118 (22) 35.5	100 (36) 30.1	23 (22) 6.7	54 (26) 16.3	13 (6) 3.9	22 (2) 6.6		1 0.3	1 0.3			
G78-1LL	171	17	10.1	6	105 (22) 87.8	27 (8) 15.8		27 (12) 15.8	5 2.9	5 2.9	2 1.2					
G78-86LJ	61	25	2.4	6	8 13.1	29 (16) 47.5	2 (2) 3.3	10 (2) 16.4	5 8.2	6 9.8	1 1.6					
G79-2LL	28	8	3.5	6	9 32.1	10 (6) 35.7	2 (2) 7.1	1 3.6	4 14.3	1 3.6	1 3.6					
G78-8LL	96	13	7.4	6	35 (2) 36.5	28 (4) 29.2		21 (2) 21.9	8 8.3	3 3.1	1 1.0					
G79-115LJ	168	13	12.9	6	96 (16) 57.1	26 (16) 15.5	12 (12) 7.1	22 (6) 13.1	4 2.4	7 4.2	1 0.6					
G79-3LL	143	14	10.2	5	66 (18) 46.2	50 (14) 34.9	4 (4) 2.8	13 9.1	7 4.9	3 2.1						
G78-80LJ	41	18	2.3	5	6 14.6	14 (2) 34.2		14 (10) 34.2	5 12.2	2 4.9						
G78-93LJ	26	13	2.0	5	3 (2) 11.5	10 (2) 38.5		3 11.5	4 15.4	6 23.1						
G78-98LJ	56	7	8	5	24 (6) 42.9	15 (2) 26.8	4 (4) 7.1	9 16	3 5.4		1 1.8					
G78-108LJ	12	1.4	8.6	5	3 16.8	4 (2) 33.3	2 (2) 16.7	1 8.3		1 8.3	1 8.3					
G78-109LJ	26	3.4	7.6	5	8 (2) 30.1	5 19.2	2 (2) 0.8	8 30.1		1 3.9	2 7.0					
G78-9LL	30	5	6	4	13 (2) 43.3	10 (2) 33.3	2 (2) 6.7	4 (2) 13.3		1 3.3						
Σ	3421	511.8	6.7	11	1445 (258) 42.2	885 (288) 25.9	107 (94) 3.1	597 (190) 17.5	164 (12) 4.8	138 (2) 4.1	42 1.2	25 (2) 0.7	12 0.4	3 0.1	1 0.03	2 (2) 0.06

Fig. 6

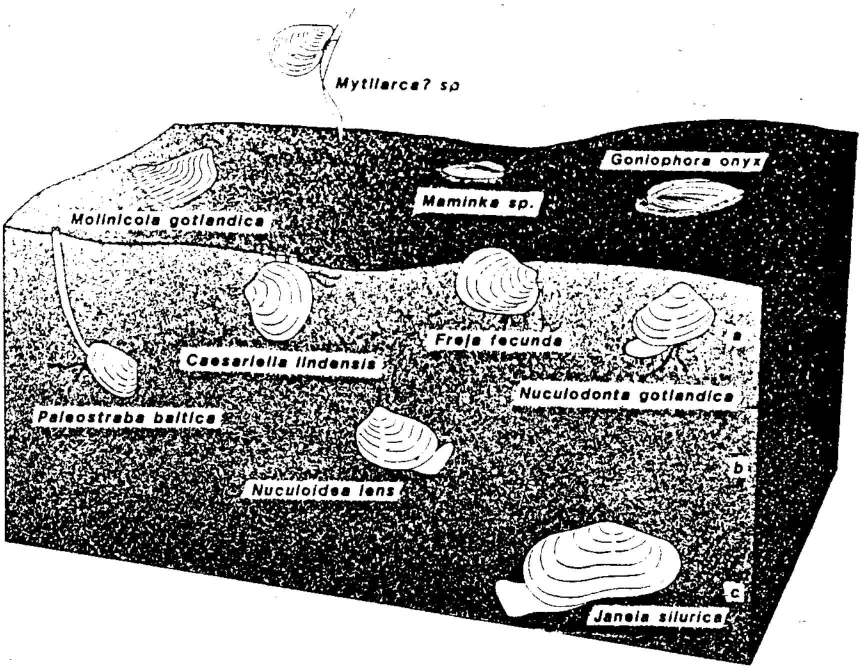
Mytilarca? sp
Goniophora onyx
Maminka sp.
Molinicola gotlandica
Freja fecunda
Caesariella lindensis
a
Nuculodonta gotlandica
Paleostraba baltica
b
Nuculoidea lens
c
Janeia silurica

Fig. 1

5.5 DETRITOFAGOS

5.5 (a)

Upper Cambrian stem-lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus*

DIETER WALOSEK AND KLAUS J, MÜLLER

Walossek, D. & Müller,K.J. 1990 10 15: Upper Cambrian stem- lineage crustaceans and their bearing upon the monophyletic origin of the Crustacea and the position of Agnostus. Lethaia. Vol. 23. pp. 409-427. Oslo. ISSN 0024-1164.

Three new arthropods in uncompressed condition have been discovered in Upper Cambrian limestone nodules (Orsten) of Västergötland, Sweden. Together with Martinssonia elongata Muller & Walossek, 1986, they are recognized as descendants of early offshots from the stem-lineage of Crustacea. Their morphology provides new insights into the evolutionary path and progressive development of groun plan characteristics along the stem-lineages and gives further support for the monophyletic origin of Crustacea s. str., which embraces all taxa with extant derivates. Structures of the ventral morphology shared between these stem-lineage crustaceans and*Agnostus* lead to the consideration of alternatives for the currently assumed position of agnostids. Crustacea, ,ontogeny, phosphatization, phylogeny, stem-lineage, Sweden, 3D-preservation, Trilobita,Dieter Walossek and Klaus J. Müller, Institut für Paläontologie, Rheinische Friedrich-Wilhelms-Universität. Nußalle 8, D-5300 Bonn 1, Deutschland; 19th september, 1989.

In 1975 secondarily phosphatized soft parts of small arthropods in three-dimensional preservation were discovered in Upper Cambrian limestone nodules from Sweden (Müller 1979). Since then, further fieldwork and extensive processing has broughtto ligth a rich fauna mainly of minute crustaceans and crustacean-like arthropods, also including larval stages (Müller 1979, 1982, 1983;Müller & Walossek 1985a, b, 1986a, b, 1988a, b; Walossek & Müller 1989).

Among them, Martinssonia elongata Müller & Walossek, 1986, with five known instars in a size range from 0.3 to 1.2 mm, superficially resembles a erustacean. In particular the trunk of the segmented stages with its bifurcate end (Figs. 5C1, 6) resembles that of zoëa larvae of modern shrimps. Closer examination, however, revelead significant differences from any known crustacean. This is evident in the design of the limbs (serial homology of postantennular head appendages) and in the anterior head region, lacking a distinctive labrum, an atrium oris and a sternum with paraghnaths and setation.

Another unexpected find was the ventral body bmorphology of Agnostus pisiformis (Wahlenberg, 1821), which has been described from eight succesive instars up to the first 'juvenile' stage (holaspis) of about 0.8-0.9 mm in shield lenght (Müller & Walossek 1987). This tiny arthropod had lived enclosed within the valvate head and tail shields of about equal size and design. The considerable structural differences to other trilobites did not, however, permit any improvementin understanding of the phyletic relationships of Agnostus and the agnostidsz. This was not least due to difficulties in evaluating the character statesof this species with regard to the paucity of comparable data.

Recently, three new arthropods have been discovered in the 'Orsten' material. Two of them are agin represented by different developmental stages. Besides their peculiar design and distinctive morphology, they exhibit a number of characters in commonwith Martinssonia. Although clearly set apart from other coexisting forms recognized as crustaceans (Müller 1979, 1982, 1983), which in part have been assigned to particular subtaxa (Müller & Walossek 1985a, 1988b), they seem to be more closelyallied to Crustacea than to any other arthropod group. If these forms are assignable to Crustacea, one should expect at least one of the apomorphicchracters of this taxon. Or they should show a structure that even in a modified state turns up as a typical crustacean feature and thus can be recognized as apomorphy for thge whole group.

The attempt to treat these fossils systematically, however, soon revelead considerable inadequacies ibin the current characterization of Crustacea. It is, thus, the intention of this article to stimulate discussion about the phylogeny of Cruatacea by proposing a new characterization of this taxon which can also be applied to the fossils in question. Furthermore, a number of structural similarities of the three new forms with Martinssonia and Agnostus throws new light on the systematic status of the group to which the latter form is allied.

Definition of Crustacea

Evaluations in the relationships of fossils with a particular taxon would be facilitated if clear concepts of the phylogenetic relationships of this taxon are already on hand. Taking the Crustacea, not only are the relationships between the different subtaxa still far from being well understood, but also the relationships of the whole group are not, in our view, unequivocal. Its monophyletic origin is generally accepted, but current characterizations show cosiderable deficiencies. For example, certain features may occur elsewhere and, thus are not apomorphic to Crustacea. Other features are apomorphies of a particular subtaxa but not of Crustacea as a whole, such as the 'two pairs of sensorial antennae' ('Diantennata', see Kaestner 1967:879) which characterize only Malacostraca. With regard to this feature, the 'Treatise' even leaves the reader with the choice between two,one and no antenna at all. The plesiomorphic status, on the other hand, is retained for example in Cephalocarida, where the uniramous 1st antenna, made of several articles, is included in the locomotory apparatus (Sanders 1963a). The advanced state of the birramous malacostracan 1st antenna can be deduced from the morphogenesis of this appendage: the second ramus appears rather late during onotgeny, and prior to this the design og the 1st. antenna is just as in other crustaceans.

[illegible] is another feature that, in the strict sense, can be applied to eumalacostracan crustaceans only. Again, the 'two pairs of maxillae' (see Moore & McCkormick 1969 in the 'Treatise') have also been discredited by the discovery of extant Cephalocarida with their unspecialized, limb-like 2nd maxilla (Sanders 1963a, b). Recently Müller & Walossek (1988b) added to this the information that also early in maxillopodan evolution the 2nd maxilla was still a functional and morphological trunk limb. Expresions like 'many', 'most', or 'often' variously used in characterizations are unsatisfactory since they do not addres the status of the character.

Lauterbach (particularly 1986) has discussed various 'groun plan characters' of Crustacea. They cannot be repeated here at lenght. His hypothetical approach, however, is considered as insufficient for several reasons. A number of his assumptions are either not in accord with the evidence [e.g. segmental organs are not restricted to the segments of 2nd antenna and 2nd maxilla in Crustacea: see Benesch (1969) for Anostraca and Schram & Lewis (1989) for Remipedia] or are based on an implausible functional concept [e.g. the assumptions of Luterbach that fltration was the primary feeding mode of Crustacea based on *Cephalocarida*, which in fact are not filter feeders (see Sanders 1963a, b).

What is more, the status of various characters has not been worked out clearly since the author, at that time, did not consider the stem-lineage of Crustacea. This led him to misidentify various characters of crown group crustaceans as plesiomorphies rather than as sypomorphies. According to the stem-lineage concept (see Ax 1985) characters of a monophyletic unit have progressively accumulated along its stem-lineage. Beyond the level of the 'last common ancestor'of the crown group, the monophylum in the strict sense , the number of these characters decreases down the stem-lineage towards the stem species of the whole monophylum, which represents the incipient step in the new direction (a step not likely to be recognized and a form unlikely to be found in the fossil record). On the other hand, new features may appear early in the evolution of a monophylum but transform or are even lost later [see also Willmann (1989), particularly his Fig.3].

In this way it is necessary to know also about the stem-lineage members of a monophylum, and in particular about those characters taht are not kept in the ground pattern of the crown group. Apomorphic features, occurring in stem-lineage members of a monophylum, may thus look plesiomorphic when compared with the crown group members or may even lost in their primordial quality along the stem-lineage.

Following Dahl (1956), one of the major evolutionary forces of Crustacea is seen in the development of new locomotory and feeding strategies, probably closely linked with a more free- swimming mode of life. Taking this into account, it becomes that various atrutures of the locomotory and feeding apparatus are not only common to all extant subtaxa of Crustacea but are unknown from other arthropod groups This complex of structures is suggested as characteristic of the crown group crustaceans, the Crustacea s. str., and serving as evidence for the recognition of their monophyletic origin [for the sake of clearness, the prefix 'Pan-' is added to Crustacea when we refer to Cruatacea including its stem.lineage (as proposed by Lauterbach 1989)]

Among this complex, major synapomorphic characters of Crustacea s. str., are recognized in:

- the possession of a bipartite feeding apparatus, which includes a naupliar apparatus (1st antennae, biramous 2nd antennae and mandibles) and a postmandibular ste of limbs including the 1st maxilla modified to interact between the naupliar set and the subsequent series of limbs;

-the mouth region including the fleshy labrum, which forms the cover of the atrium oris and with setulate, brush-like sides, and a sternum with humped paragnaths originating from the mandibular sternite;

-the specialization of the posterior set of limbs for swimming and suspension feeding (no filtration), which, as in the 2nd antenna and mandible, is achieved by exopod movements;

-the telson with terminal anus and a pair of articulate, paddle.shaped furcal rami serving as steering devices in swimming;

-the ontogeny starting with a nauplius as the most oligomeric type of a feeding larva, with only three pairs of appendages; and

-the retention of the functionality of the naupliar limbs at least until the apparatus is definitely developed after a number of moults.

The stem-lineage forms

The groupof arthropods presented here does not comply either with current descriptions of Crustacea or with the characterization of Crustacea s. str., given above, which excludes them at least from membership in the crown group. Yet, they and Martinssonia have characters in common with the crustaceans but which are not developed in this fashion in any other arthropod group. One feature is the 1st antenna ('antennule'), which is not a sensorial, multi-segmented tentacle, as for example in trilobites, 'trilobitoids' or tracheates, but is mainly adapted to locomotion and feeding. Sensorial devices are present basically only at its tip.

Another character is a separated, spine-bearing, enditic outgrowth at the proximo-medial edge of the limb base of postantennular appendages. It is termed 'proximal endite' in the following text. Both features are basically present in all Crustacea s. str., or at least show up during their ontogeny. Accodingly, they permit the recognition of all four forms as members of the Crustacea in the broad sense, but in a position prior to the crown group level, the Crustacea s. str., as characterized above.

The distinctive morphology of the four species under discussion suggests that they do not form a natural unit, but descended from different stem-lineage members. We are aware that systemetizing these species and solving of the relationships between them remains preliminary until further evidence from more stem-lineage crustaceans is available. Yet, we attempt to evaluate whether and how the new forms contribute to the presumed progressive acquisition and modification of crustacean ground plan characters.

Eye structures.- External eye structures are present in Cambropachycope, Goticaris and Henningsmoenia. In the former twothe large frontal bulges with faceted anterior surfaces are interpreted as a single sessile compound eyes (Figs. 1A, C, 3A, B, 5A1, B1). In Henningsmoenia the lateral eyesare stalked (Figs. 4B, 5D1, 2). Since they develop fron simple blisters, their morphology may have been adapted to extend beyond the bowl-shaped dorsal shield. According to this interpretation, these eyes indicate that in terms of evolution stalked eyes represent the apomorphic state (see also Bowman 1984) and it is likely that they have developed independently several times among arthropods. As a further consequence, the stalked eyes of eumalacostracan and anacostracan crustaceans, for example, may have developed by convergence from simple sessile compound eyes. External eyes are missing in Martinssonia and Agnostus. At least the latter form may have had light sensitive structures. Müller &

Walossek (1987) assumed that the pair of soft areas on the hypostome may represent the median pair of cups of the frontal eye complex.

Head.- The heads of Cambropachycope and Goticaris comprise only four limb-bearing segments, which is the same number as in Agnostus, Henningsmoenia and Martinssonia have five head appendages. In the later, the deep tarnsverse incision of the head shield behind the fourth limb-bearing head segment (arrow in Fig.5D1) may be simply functional (Müller & Walossek 1986a). Alternatively, this may be interpreted as incomplete inclusion of the fifth segment.

It is noteworthy that no trilobite has been recorded with more than four head appendages [Müller & Walossek (1987): in contrast to our view, Schram (1986) regards the trilobitan antenna as the equivalent of the crustacean 2nd antenna], with the exception of a Lower Devonian trilobite with five head appendages(Bergström & Brassel 1984). This occurrence in a late member of this group may be explained as an advanced state: similar inclusion of further trunk segments into the head had occurred in the various members of Crustacea s. str. in the course of parallel evolution.

A head with four limb-bearing segments has also been found in an Upper Cambrian chelicerate larva (Müller & Walossek 1986a, 1988a); the same tagma can be seen in the larvae of pantopods ('protonymphs') as well as in various Euchelicerata (antennular segment reduced!). Within Crustacea s. str., the head comprises five limb-bearing segments. The 2nd maxilla, the fifth head appendage, however, is a morphological and functional trunk limb in Recent Cephalocarida (Sanders 1963), in the Upper Cambrian maxillopod Breocaris admirabilis Müller, 1983 (Müller & Walossek 1988b), and probably also in the Lower Devonian anostracan branchiopod Lepidocaris rhyniensis Scourfield, 1926 (cf. Schram 1986: 335-343).

Likewise, the morphogenesis of this limb variously coincides closely with the postcephalic limbs in other crustacean taxa. Hence, a head with four specialized postantennular appendages is not a character of the ground plan of Crustacea s. str. (see also Lauterbach 1986, 1988). On the dorsal side of the head, however, tagmosis had already progressed to the inclusion of the fifth limb-bering segment in the ground plan of Crustacea s. str. Accordingly, a clear distiction must be made between inclusion of further segments into the head and the modification of limb morphology, which apparently was delayed.

With regard to this, Cambropachycope and Goticaris would exhibit the more primordial condition in having only three postantennular head appendages, while a further limb id added to the head in Henningsmoenia and Martinssonia (but see below) In the light of the above observations, this character of the former two taxa would even reflect the condition of the common ancestor of Pan-Crustacea and Arachnata (sesu Lauterbach 1986, 1988; [illegible] Pan- Chelicerata after Lauterbach 1989, [illegible] Trilobitomorpha after Bergström 1980).

Labrum and hypostome.- The labrum, as developed in crustaceans, is a complex organ with sensorial and glandular functions which forms the roofing of the atrium oris, It is a common character of virtually all members of Crustacea s.str. (synapomorphic), but is missing in all other arthropodan taxa (although the term has variously been applied to superficially similr features of the forehead region). Herein, a clear distnction is made between labrum and hypostome, which, in turn, is a skeletal element of the forehead (cf. Müller & Walossek 1987). These two structures are not considered as homologous. The Upper Cambrian taxa Skara, Bredocaris, Rehbachiella, [illegible] Müller 1983, see also Müller & Walossek 1985a., 1988b), and the phosphatocopine ostracodes (Müller 1979, 1982) possess a labrum. This is one of the criteria for their inclusion into the Crustacea s. str.

The four stem-lineage crustaceans as well as Agnostus lack a labrum as characterized above. In Cambropachycope and Goticaris the Y-shaped mouth opens directly on the ventral surface in front of the second pair of appendages (Figs. 5A1, [illegible]). In Henningsmoenia the mouth is also Y-shaped but is located at the rear of a bulging frontal structure (Fig. 5D1, 2), in a strikingly similar manner as seen in Agnostus (Fig. 5E1). We regard the structure of Henningsmoenia as basically corresponding with the hypostome of Agnostus and, as a further consequence, with the more strongly sclerotized hypostome of trilobites. In both species the mouth is raised from the ventral surface, and neither of the two possesses a labrum and an atrium oris. Again, in all these forms, rigid grinding structures are missing on the limbs close to the mouth, suggesting that nutrients wererather sucked in or swallowed [cf. Müller & Wallosek (1987) for Agnostus].

The position of the mouth has not been clarified for trilobites. It has been assumed to be located either at the rear of the hypostome (e.g. Jaekel 1901; Clarkson 1986, his Fig. 11.5b), or as a funnel-shaped opening below the hypostome, according to Cisnes (1975, 1981) reconstructions. In Martinssonia the forehead of the segmented stages is also somewhat ventrocaudallyprojecting but is less sclerotized than in Henningsmoenia or even Agnostus (Fig. 5C1). A labrum is clearly missing, but the position of the transvesely slit-shaped mouth at the proximal rear of this less-defined hypostome might indicate an incipient step towards the development of an atrium oris. With the regard to Crustacea s. str., the stem-lineage crustaceans are thus interpreted as having retained the plesiomorphic state by possesing merely the hypostome. In consequence, Henningsmoenia would reflect the lowest evolutionary level, while Martinssonia would be relatively closer to the ground plan of Crustacea s. str. he status of ambropachycopidae remains unclear in this respect.

In our opinion, the crustacean labrum must have developed after the branching-off of the last of the stem-lineage group of forms and, moreover, its development was closely correlated with the progressive appereance of the other new feeding structures (e.g. sternum, paragnaths, setation). This does not imply that the primordial hypostome has been lost entirely in the Crustacea s. str. It may still be retained in the anterior part of the crustacean forehead in front of the true labrum (e.g. in endoskeletal elements as attachment devices of the 1st antennae).

Larvae.- Henningsmoenia and Martinssonia have similar egg-to spindle-shaped early larval stages, recognizable in particular in their gross design and appendage morphology (Figs. 5C2, 3, 5D3). Their principal differences are in the development of the hypostome and mouth, which are present from the first stage in Henningsmoenia, while in Martinssonia these structures do not appear before the third instar. The first two stages of Martinssonia lack mouth and anus and were clearly non-feeding. In both forms the larvae have locomotory 1st antennae and three more pairs of functional and birramous appendages. This is one more pair of functional limbs than in the orthonauplius, which represents the basic larval type of Crustacea s. str., as characterized herein. The youngest stage of Goticaris is much larger than the larvae of the other stem-lineage forms but has the same number of appendages(Fig. 3A).

Proximal endite.- With regard to head segmentation, Martinssonia and Henningsmoenia seem to be the more advanced forms, while in the design of the limbs there is another order which seems to give more value to the observations on the hypostome. Cambropachycope, Goticaris, and Martinssonia, are multi- segmented, equipped with thin median setae and probably adapted for swimming.

Henningsmoenia and Agnostus, on the other hand, share a robust subrectangular limb base. This bse is medially drawn out into a vertically oriented blade-like endite (whole-limb base endite) with a marginal fringe of spines (Figs. 4C, D, 5D4-6, 4E3-5) similar to that of the trilobitan postantennular limbs. Remarkably, in both Henningsmoenia and Agnostus the proximal articles of the twi rami of the limbs behind the third one another (arrows in Figs. 4D, 5D6, 5E5). Furthermore, both have a similar type of peculiar soft setae at the outer proximal edge of the limbs. Similar structures are unknown from other arthropods. he exopods of the limbs subsequent to the third are paddle-shaped in Henningsmoenia. The ontogeny shows, however, that the undivided paddle originates from a segmented stage in the first instar.

The limb base of stem-lineage crustaceans and Agnostus is uniform (widely stippled in Fig.5) and, as in trilobites, etc., carries the two rami. This seems to contrast with the morphology of the 2nd antennae and the mandibles of Crustacea s. str. In these the limb base, the protopod, is subdivided into a coxa and a basipod, which carries the two rami. Th postmandibular limbs are much more diverse; the subdivision of their protopods ranges from being very distinctive to completely absent.

Proximal to the limb baseHenningsmoenia, Cambropachycope, Goticaris, and Martinssonia possesses a separate endite (Figs. 5A2, 3, 5B2, 3, 5C4-6, 5D3, 4). This feature stes these forms apart from Agnostus, which clearly lacks such an endite (Fig. 5E3-5). A comparable structure isalso unknown from trilobites, other arachnatans, or the tracheates/unirramians, while a similar proximal enditeis developed in the postmandibular limbs of virtually all Crustacea s. str. at least in essence. This distinction from the more distal enditic lobes on the protopod is variously enhanced by terms such as arthrite, median, or basal endite, gnathite or gnathobase in crustacean literature.

Prior to the concept of a stem-lineage for crustaceans, Sanders (1963) proposed an elegant and convincing explanation for the protopodal portions. Recognizing the striking similarity in the morphogenesis of the 1st maxilla and the larval mandible of Cephalocarida see also Sanders & Hessler 1963, their Figs 4, 5), he homologized the distinctively defined coxa and basipod of the 2nd antenna and mandible with corresponding subdivisions of the maxillary protopod. Following this, and by considering also the morphogenesis of the 1st maxilla, we believe that the comparatively samll poximal endite of stem-lineage crustaceans as well as the phyllopodial type of limbs of various Crustacea s. str., can also be homologized with the coxal portion of the protopods of the 1st maxilla and the two postantennular naupliar limbs.

In consequence, this endite once developed must have been modified considerably according to functional needs. This obviously affected the nauplir limbs and the posterior limb set in different directions and at different times. In the naupliar limb set, the endite enlarged greatly to form distinctive coxa below the original limb base. Furthermore, its spine-bearing median surface grew out in the mandible to form the blade-like grinding plate or gnathobase, obliquely angled against the coxal body.

In addition to this new structure, the ancestral base carrying the two rami is retained along the stem-lineage of Pan-Crustacea and in the basipod in the Crustacea s. str., particularly in the naupliar limbs. Hence, the proximal endite is recognized as an autapomorphy of Pan-Crustacea, being synapomorphic to the four stem-lineage forms under discussion and the Crustacea s. str. In its primordial shape, the large limb base with a small proximal endite is clearly recognizable in the postmandibular limbs of the various Crustacea s. str., along the series of their morphogenesis. On the other hand, enhancement of the proximal endite may also occur in postmandibular limbs (e.g. in the 1st maxilla of Cephalocarida or in thoracopods of Eumalacostraca) as well as reduction (e.g. on the proximal limb portion of copepodan thoracopods only a seta hints of this element).

Trunk end.- In all stem-lineage forms, the trunk terminates in a single caudal spine, at least in their larval stages. Only in the segmented stages of Martinnsonia is the atil bifurcate, carrying short spines around its terminal margin (Figs. 5C1, 6). The plesiomorphic status of Henningsmoenia, Cambropachycope, and Goticaris is clear, while it remains unclear to us whther the tail of Martinnsonia can be regarded as an incipient step towards th typical telson with articulate furcal rami, as is suggested to characterize the ground plan level of Crustacea s. str.

Again, all stem-lineage crustaceans have a papilla-like anus ventrally at the base of the caudal spine (or on the last trunk segment; e.g. Fig.3D for Goticaris and Fig.6 for Martinnsonia). In Agnostus, the weakly defined ventral trunk body is completely covered by a shield and fades without any distinctive caudal end prior to the anus at about two-thirds of the shield lenght. By contrast, in the Crustacea s. str. the anus is basically located at the truncate rear of the cylindrical telson, flanked by the furcal rami.

Conclusions

In early stages of our work, Martinnsonia was set apart from all other Upper Cambrian arthropods because of its unique mixture of crustacean and non-crustaceancharacters. The findings presented here show that there are more forms in the Orsten naterial that share in this pattern. Yet, they are probably not members of a monophyletic unit but represent distinctive taxa with their own autapomorphies.

Cambropachycope and *Goticaris* are likely to be closed allied to one another. They are linked at least by their supposedly single compound eye, which is separated from the head by a constriction where the 1st antennae insert the mouth, which opens freely on the ventral side in front of the 2nd appendages, and the uniramous paddle shape of the trunk limbs. In the light of this likely sinapomorphies they are considered to comprise a natural unit, for which the name Cambropachycopidae is proposed. In this context, it is not important whether they are in a sister group relationship or just members of a larger monophyletic entity.

The proposed systematic status of the new forms and *Martinnsonia* is included in the simplified phylogram of Fig.7. Relationships within the Arachnata, as the possible outgroup of Pan-Crustacea, and within the rtilobites are not discussed here, not least because the phylogeny of the latter is in a state of flux (cf. Fortey & Whitington 1989; Hahn 1989; Lauterbach 1989; Fortey 1990). Our scheme deviates from Lauterbachs and similar ones only in that Mandibulata as the sister taxon of Arachnata is replaced by Pan-Crustacea. Postulated sister group relationships of Tracheata or Uniramia with Crustacea (sensu Lauterbach 1986, 1988) are not unchallenged. Again, the stem- lineage crustaceans presented here throw more doubt on this assignment than support. This issue is left open for future discussion here.

In the scheme, the characters locomotory and feeding 1st antenna and prximal enditeappear as earliest recognized features of the stem-lineage of Pan-Crustacea (combined as character 1 in Fig.7). Since it is unlikely that one of the new forms under discussion represents the stem species, other apomorphic features may well have developed earlier. Again, it is suggested that the whole complex locomotory and feeding apparatus is characterized of the last common ancestor of the , i.e. is a complex feature of its ground plan (combined as character 4). It includes the fleshy labrum with setulate sides, the sternum with paragnaths, the subdivided limb bases in accord with new tasks for the different parts and the development of lobate endites on the protopods of feeding limbs, and new types of setation, including setules, on different parts involved in feeding. Possibly also the 1st maxilla was already modified to interact between the two apparatuses.

Together , the four forms are considered to represent descendants of early offshots from the stem-lineage of Pan-Crustacea (their position not directly on the stem-lineage is apparent by their specific autapomorphies). Most of the characters of Crustacea s. str. were not even initiated save for the proximal endite and the modified 1st antenna as earliest prerequisites of new feeding and locomotory strategies. Accordingly, the mode of locomotion and feeding of these forms was also most likely to have been a more primordial one.

A division into a naupliar feeding and locomotory apparatus is not recognizable in any of the four. Their ontogeny, as far as is known, suggests a regular and progressive addition of further segments and limbs without significant changes or differentiation from the beggining. In the light of these finds, it is also apparent that, in contrast to Lauterbach (1986, 1988), a further synapomorphy of Crustacea s. str. must be seen in the ontogeny starting with a true naupliys (orthonauplius). This larval type with its characteristic labrum and two pairs of specialized, functional postantennular limbs is common to all known crown group crustaceans, including representatives from mthe Upper Cambrian (e.g. Müller & Walossek 1988b). Such a specialized oligometric hatching stage is not present in the stem-lineage forms. Their earliest stagea have one more pair of functionsal limbs (FIGs. 4A, 5C2, 3, 5D3).

Moreover, development of this new larval type cannot have preceded the enhancement of the proximal endites in the 2nd antenna and mandible to form tha disntinctive coxae (particularly in the mandible). This is also true for the definition of the labrum, sternum and otehr feeding structures in the mouth area. Primordial types of nauplii of Crustacea s. str. are swimming and feeding, as can be recognized in the five metanauplii of Upper Cambrian Bredocaris [Müller & Walossek (1986b); for the intimate connection between thw two mechanisms see Gauld (1959), in contrast to Lauterbach, e.g. (1988)]. on the other hand, the distinctiveness of the eye structures is seemingly of little help for positioning the stem.-lineage forms.

Among the stem-lineage crustaceans discussed here, a definite elaboration ot their phyletic relationships remains difficult. Henningsmoenia might be in the most basic position. This assumption refers to the appendage morphology. Apart from the posetion of proximal endites on the postantennular limbs, they are still very similar to a trilobitoid limb type, such as Agnostus (Fig.5E3.5). The position of the mouth at the posterior end of the bulging hypostome, remarkably similar to Agnostus (see below), may also reflect an ancestral design.

Uncertaintities remain with respect to the specializations of the two limbs behind the 1st antennae - as recognizable in Agnostus, while in Martinssonia the second to sixt limbs are serial. Considering the position of these limbsd and their exopods with few cylindrical articles and rigid spine-like setae, it might simply be a convergent attempt at the formation of mouth parts. Similarity to the nauplius design would, thus, be only superficial.

A more advanced level might have been achiaved by the Cambropachycope, in part with regard to their limb morphology. Their subtriangular base with major enditic spine is essentially as in Martinssonia and is apparently much closer to the design of basipods from crown group crustaceans (character 2 in Fig.7). Again, their multisegmented exopods are clearly natatory, as can be derived from their finer median setae (Figs. 5A2, B2, 3). Martinssonia seems to be the most advanced of the four stem- lineage forms. This may be derived at least from the shape of the mouth (initiated formation of an atrium oris) and the modified hypostome, possibly also by the shape of the caudal end (character 3 in Fig.7).

Such possitioning must, however, remain tentative. For example, the status of the number of limb-bearing head segments, being four in Cambropachycopidae but five in Henningsmoenia and Martinssonia, cannot be satiafactorily explained as yet. The inclusion of a fifth limb-bearing head segment might have occurred after the branching of Cambropachycopidae, but convergence might be an alternative explanation for the situation in Henningsmoenia. Knowledge of further stem-lineage crustaceans is thus required.

Nevertheless, these Orsten fossils, with their exceptional preservation, in our view may well be of considerable use for the evaluation of the status of characters and decisions about the homology of shared similarities. According to the concept presented here, the stem-lineage members of a particular monphylum may still exhibit only some or few of the characters of the crown group. Again as is demonstrated by the proximal endite, apomorphic features may also start in a more primordial design and be differentially modified subsequently.

A character wothwhile considering in further analyses of the phylogenyof Crustacea may be the segmentation of the endopods. In trilobites and Agnostus there are seven articles, while there are five or less in the stem-lineage crustaceans, and six in the extant Cephalocarida (Sanders 1963).

As a consequence of our interpretations, the trilobitoid limb base, as occurring in trilobites and other trilobitomorphs (sensu Bergström 1980), would not be homologous to the crustacean coxa but to iys basipod, which basically retains the shape and the habit to carry the two rami. Hence, any attempt to evaluate possible relationships between Tracheata\Uniramia and Crustacea has now to prove whether the tracheate mandible originated from the proximal endite , which transforms into the coxa in Crustacea, or from the trilobitoid limb base . In any case, it is clear to us that a head tagma including five limb-bearing segments does not represent the plesiomorphic character status in Pan.Crustacea, nor in its possible sister taxon.

The position of *Agnostus*

Agnostids arecgenerally understood as diminutive and specialized trilobites (e.g. Harrington 1959). More recent attempts to reconstruct the phylogeny of Trilobita place the group in somewhat different positions: Lauterbach (1980, 1983) considers them as a sister taxon of other polymeroids within Eutrilobita and after the branching point of redlichiids, which is about the same position as in Fortey &Whittington (1989); Hanh (1989) also places agnostids within Eutrilobita but beyond redlidchiids, as does Fortey 1990).

The present paper does not seek to discuss these approaches and their major conceptual differences (inclusion of taxa, particularly the positioning of olenellids, and acceptance of characters) in detail. With regard to agnostids, it is, however, noteworthy that all placements hitherto rest on two closely linked hypotheses, namely that the morphology of agnostids results from secondary reduction, and that they are closely related to the eodiscids, enclosed as the monophylum Agnostida (= Miomera).

These relationships are, in our view, not unequivocal. Even if acceptedm the possibility that different groups of agnostids arose from eodiscid ancestors (see Fortey 1990) would imply that the later are paraphyletic and the former polyphyletic (in his diagram Fortey, however, treats both as sister groups). Uniting the two groups severely affects the polarity state of agnostid features. The position of eidiscids closer with th Eutrilobita (Trilobita s. str. after Lauterbach 1989) seems to be substantiated by the prescence of synapomorphies such as dorsal eyes, dorsal facial sutures, and the ontogeny starting with a calcified protaspis (Zhang 1989). Since agnostids lack this and other features, they should have lost aal these features by reduction. The difficulties of lumping two groups of uncertain affinities with one anoyither are particularly apparent in Hahns (1989) classification, in which tha agnostid hypostome is used to characterize the whole Agnostida, although the eodiscid hypostome is clearly different and much as in other trilobites (see also Shergold 1988).

With the description of the evntral morphilogy of Agnostus pisiformis things have not become easier, since it idis very distinctive from that of trilobites (Müller & Walosek 1987), Prior to the discovery of the stem-lineage crustaceans, the apparent differences could well be explained as adaptations to life in a box., and of little systematic value (see also Fortey 1990) since autapomorphies do not count for the systematic status of a group. On the other hand it was this difference that led Shergold (1988) in his review of the Agnostus paper of Müller & Walossek (1987) to claim, he would have thought that a statement foreshadowing a classification of Agnostida (with or without eodiscids) somewhere between Crustacea and Trilobita would be more appropiate in view of the interpretations presented.

Müller & Walossek (1987) have discussed the possible derivation of the bulging agnostid hypostome, which is free from the anterior margin of the head shield, from the more primordial types of eodiscids and trilobites. Now, in the light of the remarkable similarities with the free and bulging hypostome of *Henningsmoenia*, also bearing a membranous field on its surface and the mouth exposed at its rear (ig.5D1, 2), it may alternatively be that the hypostome of *Agnostus* (Fgi. 5E1) developed from some kind of primordial type of hypostome. The only demands are that it aws not attached to the anterior margin of the shield originally and that it was less sclerotized than in the trilobite condition.

Such a reversal of view of characters can be applied to other structures as well. For example, the design of the postantennular appendages of Agnostus is no closer to trilobites than to any otherearly arachnats (Fig.5E5). In other words, itsupports affinities neither to the Eutrilobita nor to the Trilobita in the broad sense (sensu Lauterbach 1980; = Pan-Trilobita *sensu* Luterbach 1989). According to Bergström (1980 and pers. comm.), the trilobites and trilobitomorphs basically have exopods with lamellate spine. Agnostus clearly has no such lamellae but slender spines or spine-like setae with circular cross section (Müller & Walossek 1987, particularly their Pl. 26:4, 5). Again, the distal end of a trilobite endopod bears a claw, while Agnostus has slender spines covered with tiny bristles. It may well not be that the robust claw spines preceded the slender ones of Agnostus but the other way round.

The presence of dorsal facial sutures has been regarded as an autapomorphy of all Trilobita (Ax 1985).This contrasts whit Fortey & Whittington (1989), Fortey (1990) and Hahn (1989) who all include the olenellids with the trilobites. These lack dorsal facial sutures. So does Agnostus, and there is no evidence from the ventral morphology that it was developed originally and reduced subsequently (see also Müller & Walossek 1987). similarly, oelenellids and agnostids lack a protaspis larval stage, present in eodiscids and other trilobites. Its abscence in agnostids may thus be interpreted as reflecting the primary condition rather than asecondary loss just after trilobites had invented such a stage on their stem-lineage. Further features, such as head including four limb-bearing segments, trilobed dorsal design, and presence of a hypostome - whether lightly sclerotized or not - are not unique to trilobites but occur also in other arthropods, in part also in the stem-lineage crustaceans. Such likely symplesiomorphic characters can also give little support for closer affinities of agnostids with trilobites.

Müller & Walossek (1987) remarked that the anterior head portion with its paired frontal organ in front of the hypostome, the feeding 1st antennae (Fig. 5E2) and two more specialized appendages around the hypostome (Fig.5E3, 4) serving as major locomotory aqids looks crustacean-like (Fig. 5E1). The similarities between Agnostus and Henningsmoenia in their blade- like limb base with spinose inner edge , do not count as ondicators of relationships, since they are likely to be symplesiomorphic. Two more features shared between Agnostus and Henningsmoenia are, however, unique and noteworthy: the fusion of the proximal parts of the two rami only in the fourth and subsequent limbs, and the soft setae on the outer edges of the limbs (arrows in Figs.5D6, 4E5; sos for soft setae).

With this and the new classificatory schemes in mind, more alternatives for placing Agnostus than have to hitherto been considered are avilable (marked by arrows with ? in Fig. 7): a position within Eutrilobita, above the redlichiid level (sensu Lauterbach 1980); a psoition on the stem-lineage of Pan-Trilobita (depending on the position of olenelloids, as arrowed with ?); a position on the stem-lineage of Arachnata prior to the branching of trilobites, i.e. with considerable morphological similarities to the early stem-lineage derivates of the sister taxon; a position prior to the branching of Arachnata and Pan.Crustacea (stem-lineage of Euarthropoda); a position on the base of the stem-lineage of Pan-Crustacea, prior to the development of the separate proximal endite.

The last possibility could, at least, explain the non-sensorial but feeding 1st antenna of Agnostus and the features in common with Henningsmoenia. It is not possible at present to promote one or other alternative due to the paucity of information on the ventral body morphology of other early arthropods, particularly the eodiscids.

However, as stated above, even the trilobited exoskeletal morphology and abscence of the proximal endite could not definitely rule out a possible basic position of Agnostus on the stem.lineage of Pan-Crustacea.

The systematic status of agnostids remains problematical, but we think that more evidence is now available particularly against a position of this group as the sister group of other polymeroid trilobites within the Eutrilobita (sensu Lauterbach 1980, 1983). To retain a clearer view on characters, one should at ñeast refrain from lumping agnostids together until their affinities can be based on synapomorphies other than reductive features. Exoskeletal similarities of agnostids and eodiscids could well be due to convergent adaptation to a similar natant life strategy.

The alternatives presented for a position for Agnostus and its remarkable similarities with the stem-lineage crustaceans throw, in our view, new light on a common ancestry of chelicerates, trilobites, and trilobitoid forms on the one side (= Arachnata after Lauterbach 1980; = Pan-Chelicerata after Lauterbach 1989; = Trilobitomorpha after Bergström 1980) and the crustaceans on the otherm as has been postulated particularly by Hessler & Newman (1975).

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Systematic palaeontology

The order of the daignoses reflects the supposed derivation of the forms from the stem-lineage of Crustacea (seeFig.7). More detailed analysis based on additional material, including further developmental stages, will be published elsewhere (Müller & Walossek in preparation).

Henningsmoenia n.gen.

Derivation of name.- In honour of G. Henningsmoen, Oslo.

Type species .- Henningsmoenia scutula n. sp.

Diagnosis.- As for the type species.

Henningsmoenia scutula n. sp.

Derivation of name.-After the bowl-shaped shield.

Material.- Holotype UB 102, illustrated in Fig. 4b, c, additionally UB 101, representing the first larval stage (Fig.4A) and UB 103, a trunk fragment of an advanced stage (Fig. 4D).

Type locality and stratum.- Gum at the Kinnekulle (r 03525 h 89250); Västergötland, Sweden; zone 1 (Agnostus pisiformis) of Upper Cambrian Alum Shales.

Diagnosis.- large, bowl-shaped shield, which covers the complete head and anterior or firat trunk segment; shield with broad duplicature around anterior and lateral sides; posterior of shield truncate, providing a gap for the segmented trunk; lateral eye composed of ovoid lobes nesting on a rod-shaped peduncle which inserts at anterior edge of the elongate hypostome; the latter is free from the anterior margin, oval in the outline and raised from the ventral surface; its distal surface bears an oval softer area, encircled by a faint ring wall; the Y-shaped mouth is located within soft area at the posterior edge of the hypostome. Five pairs of head appendages. First antennae uniramous, rod- shaped and composed of few tubular articles. Subsequent appendages biramous. Exopods of second and third limbs annulated and carrying rigid spine-like setae medially, exopods of posterior limbs paddle-shaped and with rigid spine-like setae along their distal margin. Limb base of all postantennular limbs robust, flattened in anteroposterior direction, and blade-like extended medially. Inner edge armed with short stout spines, similar spines occur also on the separate proximal endite (Figs. 4C, D, 5D4-6).

Trunk comprises four segments which progressively decrease in size. Anterior three segments with gently convex tergites, each overlapping the subsequent one. Ventral surface of the segments concave and pliable around the insertions of the appendages. Last trunk segment conically tapering, slightly dorsoventrally compresed, and with few marginal spines at bluntly rounded end. Papilla-like anus anteroventrally on this segment, enclosed within finely folded area.

Remarks.- This form is known from at least eight successive instars. The earliest larva is about 0.2mm long and egg-shaped (Figs. 4A, 5D3); it has 1st antennae and three more pairs of supposedly functional limbs. Its Y-shaped mouth is located at the rear of a bulging, ventrocaudally projecting forehead structure, which is regarded as homologous to the rtilobitanhypostome. The shield appears after a few stages and enlarges progressively during ontogeny. Below its truncate posterior margin the trunk projects ventrocaudally. After a number of instars two blisters appear anterior to the hypostome at the inner margin of the duplicature, which eventually become stalked; they are regarded as lateral eyes (Figs. 4B, 5D1, 2). The body of the largest growth stage at hand was presumably slightly longer than 1mm. In particular the bowl shape of the shield and the appendage morphology point to a benthic mode of life for this form.

Cambropachycope n. gen.

Type species.- Cambropachycope clarksoni n. sp.

Derivation of name.- After the large unilobed facette eye and its age.

Diagnosis.- As for the type species.

Pachycope clarksoni n.sp.

Derivation of name.- In honour of E.N.K. Clarkson, Edinburgh.

Material.- Holotype UB96, illustrated in Fig. 1A,B, Additionally UB97, representing an isolated eye (Fig. 1C).

Type locality and stratum.- Gum at the Kinnekulle (r 03525 h 89250); Västergötland, Sweden; zone 1 (Agnostus pisiformis) of Upper Cambrian Alum Shales.

Diagnosis.- Body spindle-shaped, unsegmented in the head region and with about four distinct segments in the trunk (Fig. 1A). Forehead bulging, supposedly representing a uniform compund eye (Fig. 1C). Shape of eye structure sub.oval, higher than long, dorsocaudally tapering into a conical extension, and with an anteriorly pointing process ventrally. Anterior surface faceted (100 facets). Forehead separated from head by narrow constriction, where the first pair of appendages insert.

Head region includes four pairs of appendages: uniramous, rod- shaped 1st antennae and three pairs of biramous limbs (Fig.5A2,3). Mouth opening Y-shaped, located on the ventral surface in front of the second pair of limbs. Head covered by a shield with weakly defined margins. Trunk segments with weakly defined tergites, last segment tapering conically, bearing the anus on its ventral side. Anterior two segments carrying uniramous, paddle-shaped limbs. First one is almost one third as long as the whole body and is composed of a soft shaft and three articles which form the distal paddle (Fig. 1A). Outer edge of paddle almost straight, inner edge broadly rounded. Second limb similar in outline, but considerably smaller, and made only of two articles (Fig. 1B).

Remarks.- The holotype is fairly complete, though laterally compressed. It gives a good idea of the shape. The total lenght of the animal is about 1.5mm long. The head appendages are known only in part, except for the third one, which is preserved with its complete limb base and endopod (Fig. 1A).

Goticaris n. gen.

Type species.- *Goticaris longispinosa* n. sp.

Derivation of name.- Gotes = tribe which lived in Southern Sweden during the Dark Ages.

Diagnosis.- As for the type species.

Goticaris longispinosa n. sp.

Derivation of name.- After the long caudal spine.

Material.- Holotype UB99, illustrated in Fig. 2A,B; additionally UB98 (Fig. 3A,B) which represents an early instar and UB100 (Fig. 3C,D), a trunk fragment of the largest growth stage known, with four trunk limbs.

Type locality and stratum.- Gum at the Kinnekulle (r 03525 h 89250); Västergötland, Sweden; zone 1 (Agnostus pisiformis) of Upper Cambrian Alum Shales.

Diagnosis.- Body completely unsegmented and barrel-shaped (Fig. 5B1). Forehead bulging, longer than high, broadly rounded anteriorly, tapering conically dorsocaudally and with a hook-like process anteroventrally (arrows in Fig. 3A, B,; 5B1). Anterior surface with 20-30 facets (Fig.3B). This structure is regarded as a uniform compound eye. Forehead set off from head by narrow constiction, where a pair of spherical blisters is positioned dorsal to the insertions of the first pair of appendages (Figs. 2, 3A, B, 5B1).

Head without a shield. Mouth located directly on ventral surface, in front of the second pair of limbs. Four head appendages: uniramous, rod.shaped 1st antennae and three more pairs of biramous limbs. Head and trunk not separated from one another, but boundary recognizable by the grap between last head limb and anterior trunk limb. Four pairs of large uniramous and paddle-shaped trunk limbs in the largest growth stage known (Fig. 3C). Limbs inserted on the ventral surface and with pliable joint areas. Trunk continues into a long caudal spine behind the last pair of limbs. Anus papilla.like, being surrounded by a circular pliable membranous field, located ventrally, slightly anterior to the transition from trunk into the caudal spine (Fig. 3D).

Remarks.-More than ten specimens are available, which represent various stages. They can be ditinguished from one another by their progressive increase in body size, from approximately 0.3 to 1.5mm, and the number of trunk limbs. Of the illustrated specimens, UB98 represents an early larva with only the four head appendages (Fig.3A). Holotype UB99 is a slightly older instar, showing the first trunk limb as a uniramous paddle (Fig.2A, B); the forehead is not preserved. UB100 is a trunk fragment of the largest stage known so far; of the four pairs of trunk limbs two are partly preserved. These fragments widen distally and bear few spinules medially (Fig. 3C), being considerably longer than the height of thebody (one is illustrated in the reconstruction of Fig. 5B1).

The bulging forehead is very similar to Cambropachycope, but can be differentiated by its shape which is elongated in lenght rather than in height (arrows in Figs. 3A, B; 5B1). In Goticaris, a pair of blisters is positioned at the constriction, which has not been found in Cambropachycope. The different number of facets, however, may be of little value for distinguishing the two forms since material of Goticaris with the complete head is known only from early developmental stages.

Table 1. Lists of symbols.

Table 2. Selection of characters used for comparison between stem-lineage crustaceans, Crustacea s. str., Agnostus and non- agnostid trilobites.

Fig. 1. Cambropachycope clarcksoni n. gen. et n. sp., Upper Cambrian of Västergötland, Sweden, Agnostus pisiformis Zone (total lenght of specimen approx. 1.5mm; for abbreviations in this and thew following figures see also Table 1). A. Lateral view of our most complete specimen holotype UB96; forehead (f) somewhat twisted, probably representing a single compound eye (ce?); 1st antennae (ant) behind constriction between forehead and rest of head which bears three more limbs (app 2-4); first trunk limb large and paddle.- shaped (app 5). B. Same specimen as in 1, view of psterior end of trunk from opposite side; left set of limbs broken off prmitting a view of the large fifth limb and the smaller sixth one (esp = caudal spine). C. Lateral view of isolated forehead structure (UB97) with facets at anterior edge; structure seemingly torn off from the body; on lower left spine on ventral side.

Fig. 2. Goticaris longispinosa n. gen. et n. sp., Upper Cambrian of Västergötland, Sweden, Agnostus pisiformis Zone. A. Lateral view of holotype, UB99, missing the bulging of the forehead structure; note the gap between the last head and the first trunk limbs; caudal spine broken off distally. B. Ventral view of same specimen; ventral surface collapsed between limbs and in anal region.

Fig. 3. Goticaris longispinosa n. gen. et n. sp., Upper Cambrian of Västergötland, Sweden, Agnostus pisiformis Zone. A. UB98, young individual attached to a piece of coarse phosphatic matter (bl = blister at constriction between presumed compound eye and rest of head; facets faintly visible but much fewer in number than in Cambropachycope (arrow points to spine ventral to facets; compare with Fig.1C). C. UB100, trunk fragment of largest instar known; two limbs of the right set are partly preserved, the others are ssemingly torn off, leaving holes in the body wall (an = anus). D. Same specimen; close-up of membranous, papilla-like anal opening; caudal spien broken off (hole on right side).

Fig. 4. Henningsmoenia scutula n. gen. et n. sp., Upper Cambrian of Västergötland, Sweden, Agnostus pisiformis Zone. A. UB101, earliest larval stage in lateral view (hyp = hypostome; other abbreviations as in preceding figures). B. Anterior view of holotype, UB102, representing a late developmental stage, with large shiel (sh) and stalked eyes (ce); exopods of 2nd and 3rd limbs segmented, while that of the subsequent limb is an undivided paddle (ex app4; st = eye stalk). C. Same specimen; view into median foot path, postantennular limbs preserved with their proximal parts (en = insrtion of endopod, ex = insertion of exopod; hyp = hypostome). D. UB103, close-up of trunk limb of advanced instar, with trilobitoid limb base but separate proximal endite (end); arrow points to connection between proximal articles of inner and outer rami (en, cx).

Fig. 5. Reconstructions of Upper Cambrian stem-lineage crustaceans and their appendages, compared with Agnostus pisiformis. Appendages and setation omitted in part, unknown parts with dashed lines; sizes not scaled; limb bases enhanced by filling with widely spaced dots, proximal endites more densely dotted (abbreviations as in preceding figures, see also Table 1; cl = club-shaped outgrowth on endopods of Agnostus; i = incipient; j = joint; m = mouth; plt = pleotelson-shaped last tail segment of Martinssonia; sos = soft setae of (Henningsmoenia and Agnostus). A. Cambropachycope clarksoni n. gen. et n. sp., 1 gross morphology (arrow points to spine on ventral side of forehead), 2 second appendage, 3 third one. C. Martinssonia elongata Müller & Walossek, 1986, 1 gross morphology, arrow points to incision between fourth and fifth limb-bearing head segments, 2 first larva, 3 third larva, 4 second limb, representative of postantennular head limbs which are similarly designed (modified from Müller & Walossek 1986a). D. Henningsmoenia scutula n. gen. et n. sp., 1 ventral

view, membranous area on hypostome encircled by dashed line, 2 partial saggital section of a late stage, 3 first larva from ventral, 4 second limb, 5 third one, 6 fourth one (arrows points to fusion between rami). E. Agnostus pisiformis (Wahlenberg, 1821), 1 partial saggital section, boundary between head (C) and trunk (T) demarcated by a dashed line, 2 1st antenna, 3 second limb, endopod reduced (arrow), 4 third limb, 5 fourth one, also representative for trunk limbs (arrow as in Fig. D6; modified from Müller & Walossekj 1987).

Fig. 6. Lateral view of almost complete, new specimen of Martinssonia elongata Müller & Walossek, 1986 (UB104, Upper Cambrian of Västergötland, Sweden, Agnostus pisiformis Zone) in the typical mode of preservation of this animal (abbreviations as in preceding figures, see also Table 1; arrow points to joint between fourth and fifth limb-bearing head segments).

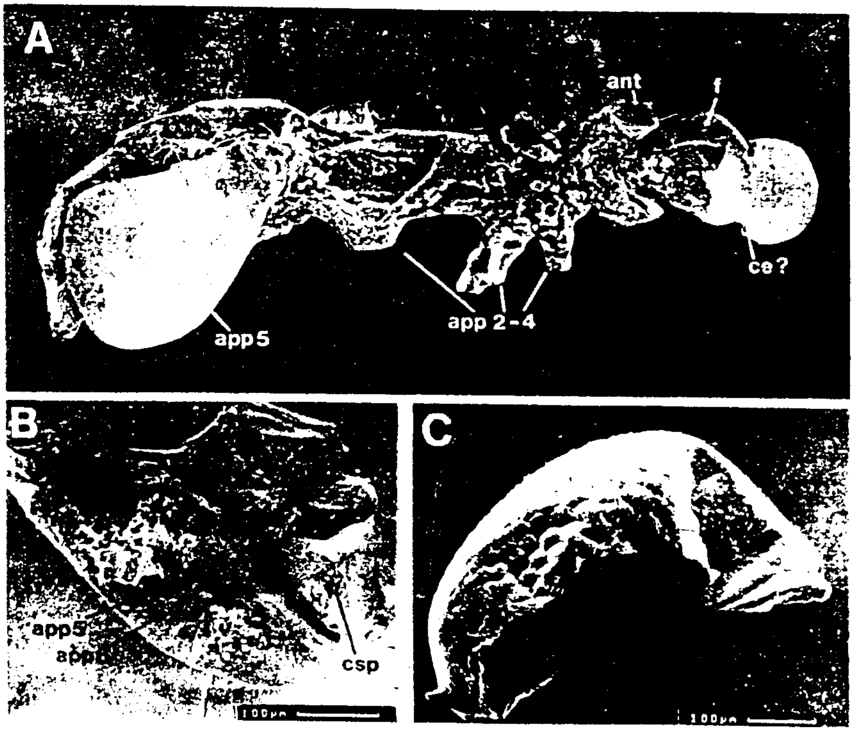
Fig. 7. Presumed phyletic relationships of Henningsmoenia scutula n. gen. et n. sp., Cambropachycope clarksoni n. gen. et n. sp., Goticaris longispinosa n. gen. et n. sp., and Martinssonia elongata on the stem-lineage of Crustacea, including alternatives for the relationships of Agnostus pisiformis (for explanation see text). Dots mark the position of the last common ancestor of suggested monophyletiv units; parentheses frame the stem-lineages of Arachnata and Pan-Crustacea.

an	– anus
ant	– first antenna, antennula
app	– appendage
bl	– blister at constriction of forehead in *Goticaris*
C	– cephalon
ce	– compound eye (with question mark in *Cambropachycope* and *Goticaris*)
cl	– club-shaped outgrowths of posterior limbs of *Agnostus*
csp	– caudal spine
en	– endopod
end	– separate endite medioproximally on limb base
ex	– exopod
f	– forehead
hyp	– hypostome
i	– incipient
m	– mouth
plt	– pleotelson-like tail of *Martinssonia*
sh	– shield
sos	– soft setae of limbs of *Henningsmoenia* and *Agnostus*
st	– eye stalk of *Henningsmoenia*
T	– trunk
UB	– repository number at Institut für Paläontologie, Universität Bonn

Table 1

	1st larva	Labrum	Hypostome	Mouth	1st antenna (uniramous)	Appendages	Proximal endite	Trunk end
Martinssonia	4 functional limbs, non-feeding	No	Yes small	Exposed slit at rear of hypostome. Y-shaped appears by the 3rd instar	Few segments, for feeding and locomotion	5 head appendages, 2 on the segmented trunk, 2nd–6th limbs of same design, all with subtriangular basis and proximal endite, endopod 5-segmented, exopod multisegmented, natatory, spines on limb basis, no setae 7th limb, uniramous (rudimentary?)	Yes on all postantennular limbs	Elongate, bifurcate terminally, spinose margin, ventral anus papilliform
Cambropachycope	?	No	No	Opening trees anterior to 2nd appendages, Y-shaped	Few rod-shaped segments, distal part unknown	4 head appendages, limb basis, proximal endite and rami as in *Martinssonia*, trunk limbs as uniramous paddles, probably 2 only	Yes on all three postantennular head limbs	Conical, ventral side soft, ventral anus papilliform
Goticaris	4 functional limbs	No	No	as in *Cambropachycope*		4 head appendages similar to *Cambropachycope*, 4 uniramous leaf-shaped trunk limbs, distal parts unknown	Yes as in *Cambropachycope*	Long spine, ventral anus papilliform
Henningsmoenia	4 functional limbs	No	Yes	Exposed at rear of hypostome Y-shaped in all stages	[illegible]	5 head appendages, 2nd and 3rd with exopod made of few segments, subsequent limbs with paddle-shaped exopods, limb basis blade-like drawn out medially and spinose, rami partly fused proximally, at least the 3rd limb with soft setae at outer edge	Yes on all postantennular limbs	Conical, slightly flattened, ventral side soft, ventral anus papilliform
Agnostus	4 in the head, 3–4 on trunk, 1 functional	No	Yes	Exposed at rear of hypostome	[illegible]	4 head appendages in all stages, 2nd and 3rd with large exopod for locomotion, 4th head limb and 5 trunk of same design, with large endopod	No	Trunk fading into soft ventral side of large shield, ventral anus
Trilobita	4?, protaspis	No	Yes	At rear of hypostome (or below?	[illegible]	4 head appendages, probably all postantennular limbs similar in design, endopods 7-segmented	No	Pygidium, position of anus unknown
Crustacea s. str.	3 functional limbs, nauplius	Yes	No	Recessed within atrium oris, overhung by labrum as glandular and sensorial organ	[illegible]	5 head appendages, 2nd and 3rd similar, subsequent limbs basically similar to each other, 1st maxilla modified to interact between naupliar and posterior sets of limbs	Yes modified to a coxa in 2nd and 3rd limbs, basically small in posterior 1	Cylindrical telson with terminal anus and articulate furcal rami

Table 2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ant
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Fig. 1

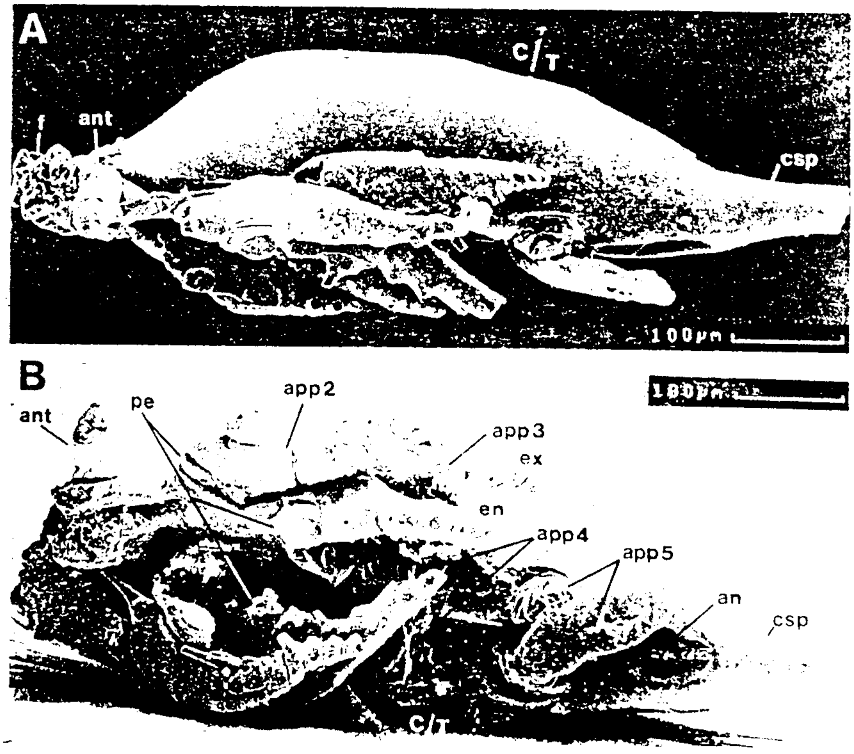
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Fig. 2

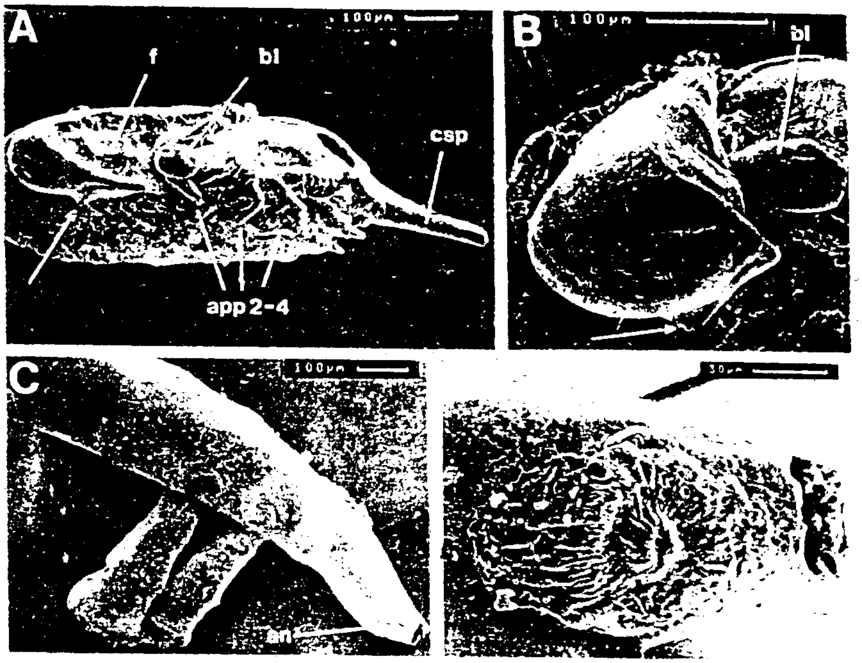
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Fig. 3

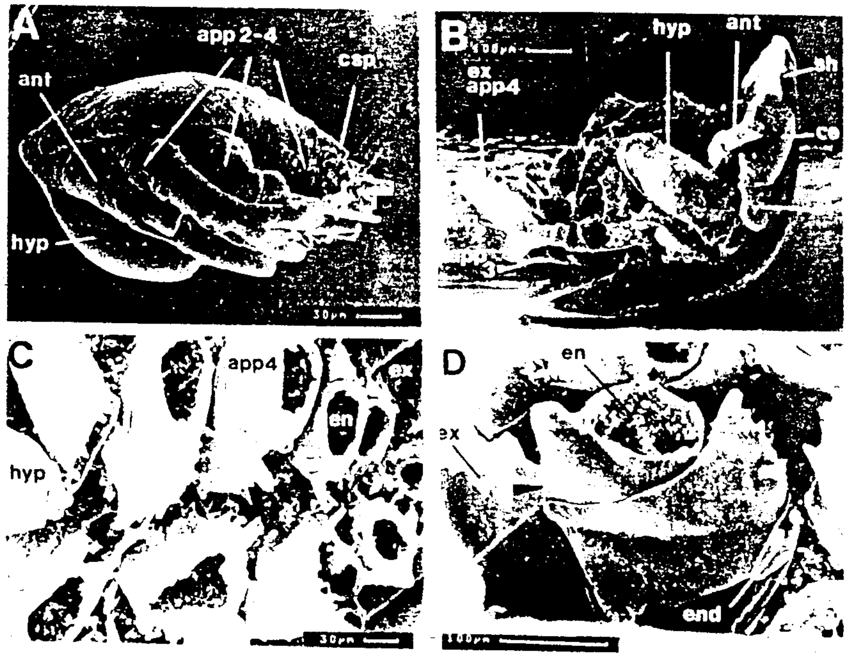
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Fig. 4

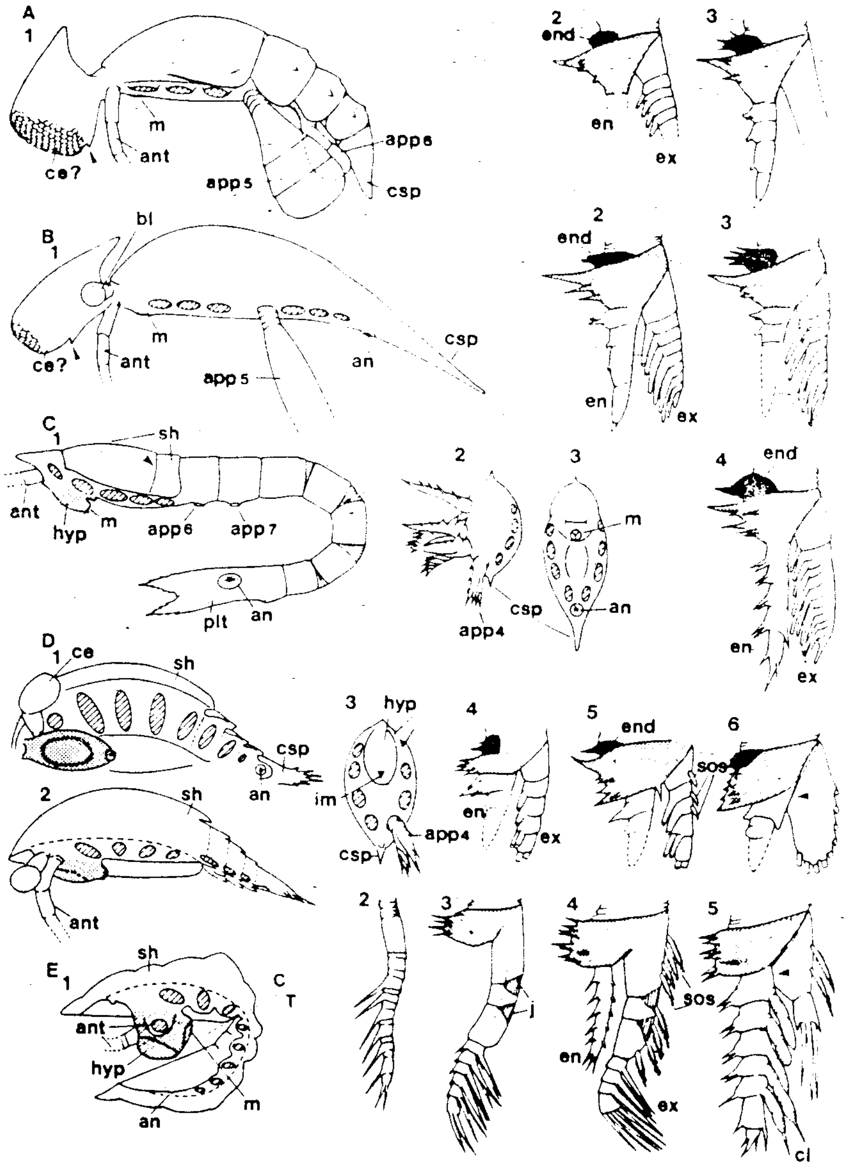
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Fig. 5

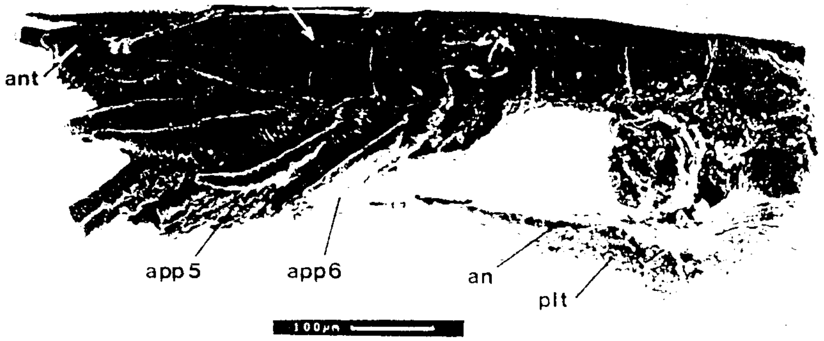
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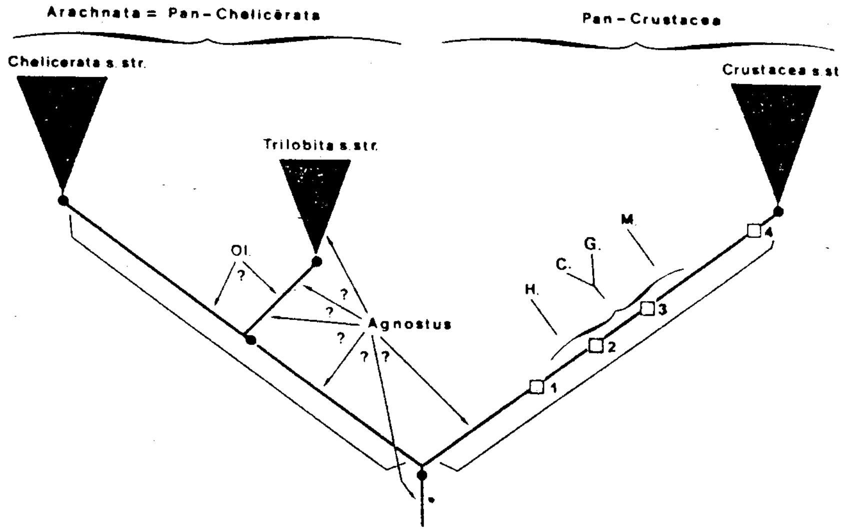
Fig. 6


Arachnata = Pan-Chelicerata
Pan-Crustacea
Chelicerata s. str.
Trilobita s. str.
Crustacea s. str.
Ol.
?
?
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Agnostus
H.
C.
G.
M.
1
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4
*

Fig. 7

5.5 (b)

ENVIRONMENTALLY CONTROLLED PHYLETIC EVOLUTION, BLINDNESS AND EXTINCTION IN LATE DEVONIAN TROPIDOCORYPHINE TRILOBITES

RAIMUND FEIST AND EUAN N.K. CLARKSON

LETHAIA

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The Middle ad Upper Devonian carbonate succession of the Montagne Noire, Southern France has been precisely zoned by an un broken sequence of conodont zones. Strratrigraphic control is excellent, and has allowed evolutionary changes in tropidocoryphine trilobites, which occur throughout the succession, to be directly established. The tropidocoryphines had been a stable group for some 40 million years, however, they underwent rapid evolution and exhibit some striking transformations of the cephalon and the regression and virtual disapearance of the eye within a relatively short space of time. They also show a marked diminution in size, and lose their original relief so that the glabella becomes virtually flush with the surface. There are two separate lineages, both of wich show eye-reduction and subsequence blindness. In the earlier lineage Tropidocoryphe(Longicoryphe)-ErbenocorYph e, the main features of the ancestral roostock are conserved and the stable, strongly divergent anterior sutural pattern of the cephaion rfemains the same. The eye, however, became reduced to a sliughtly convex surface lacking lenses, only indiostinctly defined. Erbenicorphe is confined to well-oxygenated facies, and probably lived as a shallow burrower within the sediment; it became extinct in the early Frasnian. The second lineage T.LKongicoryphe- Poterocoryphe-Pteroparia shows a remarkable backward migration of the suture, which progressively swings posteriorly in successive species spaning four Frasnian conodont zones8about three million years duration9. At the same time the eye progressively degenerates so that the last forms are blind. Sutural migration and eye reduction are n ot genetically linked, however; the unusual form of the cephalon and suure probably resulted from an adaptation to the euxinic enviroment inb which Pterocoryphe originated. The loss of the eye resulted from the adoption of an endobenthic habit in Pteroparia which descended from the ancestral Pterocoryphe but which had migrated to an oxygenated facies. Eye-reduction is therefore parallel in the two linerages, but superimposed upon a different original cephalic configuration. The last Pteroparia became extinct when the late Frasnian fauna became overwhelmed by the first pulse of the Kellwasser Event (probably an anoxic overturn).The evolving characters, through virtually all observed steps, show progressive unidirectional change without sudden breaks or saltations . Such unidirectional evolution is an adaptive response to constant long-lasting enviromental influences.Evolution, Devonian trilobites, France,gradualism, eye reduction.

Raimund Feist, Institut des Sciences de l'Evolution, U.A. 327du C.N.R.S., Univesité de Montpellier, France; Euan N.K. Clarkson, Gran Institute of Geology, University of Edinburgh, EH93JW, Scotland: 23rd August, 1988.

Few examples of continuous evolutionary trends in trilobites have hitherto been reported. In Upper Devonian Tropidocoryphinae, however, there is unequivocal evidence of eye-reduction leading to blindness, which is followed by the extinction of the group. These events are directly related to environmental change. Such evolutionary changes can only be determined if, as in this case, there is precise stratigraphical control. In recent years much attention has been given to modes of evolution (puntuated versus gradual) and to what extent evolutionary changes are related to environmental influences. We report hare on patterns of unidirectional but enviromentally related evolutionary change in the Middle and early Late Devonian, prior to the first pulse of the 'Kellwasser Event': a world-wide catastrophic mass extinction around the Frasnian-Famennian boundary (McLaren 1970, 1982).

Our investigations have centred mainly in the Montagne Noire of southern France. In this region the Middle and Upper Devonian sequence is one of the most complete in the world. It shows an unbroken record of conodont zones,on the basis of which the stratotype of the series boundary has been selected (Klapper et al. 1987): the entire carbonate succession shows a complete sequence of conodont zones and subzones from the Middle Givetian to the topmost Frasnian (Feist & Klapper 1985). Tropidocoryphine trilobites occur as disarticulated exuviae throughout the sequence and becacause of the excellent stratigraphic documentation, all observed evolutionary steps can be precisely dated (Fig. 1). Such evolutionary modifications essentially concern the cephalon, for the thoracic parts and especially the pygidium seem to remain without fundamental change. If and when complete carapaces are discovered, this last point may need to be reconsidered.

On the basis of earlier wors (R.& E. Richter 1919; Feist 1976) as well as current observations, we have been able to establish that the last Tropidocoryphe, which had been a stable group for some fifty million years, exhibit in their last seven million years some striking transformations of the cephalon and the regression and the virtual disappearance of the eye within a relatively short space of time. In the trilobites compound eyes are primary structures, appearing in the earliest genera and present in most species until the extinction of the group in the late Permian 350 million years later (Clarkson 1979). There are, however, many instances of secundary blindness, primarily in long-lived major taxa (Agnostida, Trinucleida), but also in some representatives of groups in which the eyes are normally well developed. Secondary blindness is especially common in Upper Devonian Proetida and Phacopida, as has long been Known (R. & E: Richter 1926). Examples hitherto recorded from the Rhenish slate mountains, however, showing lateral migration of the facial suture accompaying eye degeneration and finally blindness were based upon morphological series only, since at that time the stratigraphy was but poorly known. In the Montagne Noire, on the other hand, conodont based stratigraphy has been clearly defined (in different facies)(Feist 1985). This allows ancestor specimens studied have been collected in place from stratigraphically defined horizpons in exclusively limestone sequences), with particular reference to contemporaneous enviromental influences.

EVOLUTION WITHIN THE LAST TROPIDOCORYPHINAE

Earlier history of the subfamily. -The early Tropidocoryphinae which originated from Proetidellinae such as Decoroproetus in mid-Silurian times (Pribyl & Vanek 1987) constitute a typical element of the Variscan realm of Central and Western Europe and North Africa, and also of the Canadian Arctic and Australia in the Lower and Middle Devonian (Erben 1966a: Snajdr 1980; Wright & Chatterton 1988). According to Lütke (1980), representatives of Tropidocoryphe as T. aff undulans (Fig. 31-K) are characterized by a cephalon with strongly divergent anterior branches of the facial suture and a generally extended preglabellar field, often showing tropidia and Y-shaped radial swellings ('genal caeca', Fig. 6). They have a medium to large- sized pygidium with typically predominant anterior bands of pleural segments. The taxa are characterized by high kidney- shaped eyes with more than 1000 lenses and always well developed, adjoined to a long sigmoidal outwardly curved palpebral lobe. The cephalon is also characterized by stable divergent anterior branches of the facial suture, a large concave preglabellar field and a continuous, pronounced tropidia. The main root stock of Tropidocoryphe split into two lineages in early Devonian (Pragian) time; the main tropodicoryphe lineage and a descendant branch leading, with a rapid shift of characters to Astycoryphe (Feist 1976). Astycoryphe, clearly distinguished by its broader glaella, smaller preglabella field and less divergent anterior branches of the suture survived with little change in morphology and habitat until the end of the Middle Devonian (Fig. 2). The last representatives have recently been discovered by us in the Upper Givettian reefal limestones of Torquay (Devonshire) (Fig. 3L-N). In contrast to the highly conservative Astycoryphe, the main Tropodicoryphe lineage gave rise by the end of the Eifelian to T. (Longycoryphe). The cephalon of this subgenus shows a slight reduction of the formerly large palpebral lobe and in the height of the eye. On the other hand there is a marked diminution of the treopidia, which becomes tiny and interrupted adaxially in representatives at the end of the Givetian. It is from this taxon that the final tropidocoryphine lineages arose.The T. (Longicoryphe)- Erbenicoryphe lineage.- T. (Longicoryphe) contitutes a heterogeneous group in which two tendencies are to be observed. The first one conserves the essential features of the main rootstock, i.e. large preglabellar field, concave anteriorly with upwardly turned frontal border and consistently straight divergent anterior branches of the facial suture. In species mof this kind, such as T.(Longicoryphe) circumincisa, the reduction of the tropidia and the palpebral lobe previously mentioned are very evident by the end of the Givetian. In addition, the length of the glabella increases at the expenses of the preglabella field, which in turn shows a forward migration and increased development of the vaulted posterior portion at the expenses of the concave anterior region. The latter shows, moreover, a tendency to split into two concave zones separeted by a shallow ridge parallet to the anterolateral border. The newly acquired feature which distinguishes T: (Longicoryphe) from the nominate subgenus, i.e. the enrolled anterior border, is retained to the same degree in all representatives from the oldest to the youngest.

From such trilobites arose, in lowermost Franian, the new genus Erbenicoryohe (see Taxonomic addendum) in which the palpebral region underwent some major transformations. The palpebral lobe dissapeared completely after the suture between the turning points gamma and epsilon (cf. Fig. 9) straightened out, and the eye lobe became reduced to a slightly convex surface lacking lenses, separeted from the genal field only by an indistinct furrow. The individual vaulting of the glabella is more subdued than in the latest ancestral form and no trace of the tropidia remains. On the other hand, shape and subdivision of the preglabella and genal fields are closely comparable. Erbenicoryphe is so far represented by two species (only the type-species is figured here) confined to the Montagne Noire and apparently restricted to the Lower asymmetricus Zone, giving rise as far as is known to no further descendants. Thusm, the main lineage T.(Tropodicoryphe)- T(Longicoryphe)-Erbenicoryphe seems to have become extinct at this level:The T.(Longicoryphe)-Pterocoryphe-Pteroparia lineage. -The second tendency which is evident within the Longicoryphe (s.1.) group essentially affects the anterior part of the cephalon: the large preglabellar field inflates losing its concavity, the anterior border enrolls further to form a prominent cylindrical rim and the angle of the suture increases thought the sutures still remain straght. There is in consequence a much broader (tr.) preglabellar field in representatives of this group than in any tropidocoryphine of the T. (Longicoryphe)-Erbenicoryphe lineage; this group might be considered as ancestral to the Pterocoryphe-Pteroparia lineage.

The most spectacular feature of Pterocoryphe is trhe progressive backward migration of the anterior branches of the suture exaggerating the tendency we have already noted in T. (Longicoryphe). The preglabellar field, though similar to that of Pt. (Longicoryphe).bissousensis n. sp. (see Taxonomic addendum) is devoid of the tropidia; some specimens, however, show an indistinct crest, restricted to the central part, which nmay be a tropidial relic (Feist, 1976). As in bissousensis no prefrontal groove is evident. A pair of Y-shaped genal caeca are weakly developed (Fig. 6B). The beta turning points are situated laterally opposite each other in the early form of Pterocoryphe (Lower asymmetricus Zone) and in a slightly more lateral posterior position the late form (Middle asymmetricus Zone). The palpebral though it is less prominent and with a smaller visual surface.

The backward migration of the anterior suture reaches an extreme in Pteroparia, where the beta turning points subtend an aangle of about 270. This configuration of a retrograded suture is unique within the Proetida. In the early forem of pteroparia (Upper asymmetricus Zone), Pteroparia oculata n. sp. (see Taxonomic adendum), the degree of backward migration of the suture between turning points gamma and delta after complete reduction of the T. (Longicoryphe)-Erbenicoryphe lineage the anterior border furrow. This feature is the most evident in the early form of Pteroparia. As in Erbenicoryphe the prominence of the glabella tends to diminish within Ptroparia. In the early form the anterolateral border has a rather similar shape to that ofPterocoryphe, but this resemblance diminishes in late forms such as P. coumiacensis, in which the border is much flatter and the border furrow is pitted (Fig. 6C;Feist 1976).Pteriparia, in common with all tropidocoryphines studied retains the Y shaped genal caeca on the preglabellar field which may be diagnostic of the whole subfamily. The avolutionary pattern within the genus Ptewroparia shows once more a gradual reduction of the eye very similar to that already noted in the older Erbinicoryphe, i.e. in situ flattening and dissapareance of the eye lobe, leaving a smooth area indistinctly separated from the genal fields by a werak plataform furrow. Within the genus the younger 'blind' forms show slightly larger and appreciably flatter fixed cheeks than the early form. The unusual configuration of the anterior branches of the facial suture, however, stabilizes early and thereafter shows little change. The last 'blind' forms of the Pterocoryphe-Pteroparia lineage occur at the top the Lower gigas Zone and no representatives of the Tropidocoryphinae are reported thereafter.

INTERPRETATION OF LIFE HABIT AND MODE OF ADAPTATION

The older tropidocoryphines form a component part of the trilobite assemblages adapted to perireefal, high-energy and shallow-water subtidal enviroments of offshore submarine platforms (Chlupác 1983). All the representatives of this facies have large eyes with many lenses and well developed tropidia. They are believed to have been good swimmers, as indicated by the shape of their flattened, largely extended body (R.& E.Richter 1919, 1926; Chlupác 1983). Although the nature and function of the tropidia are unknown they migth possibly be interpreted as a gas-field tubelike float; if so, they could have aided a nektobenthic life habit.

The first major transformation can be observed where the tropidocoryphines, represented by T:(Longicoryphe) migrated into the deeper-water open marine 'pelagic' facies (i.e. carbonate mud accumulating at depth as a slow fallout of small pelagic organisms) which developed contemporaneously with neritic reef complexes during the Givetian and progressively became the dominant enviroment of the Variscan realm during the Late Devonian. Whereas many of the trilobite groups formely associated with tropidocoryphines (lichids, cheirurids, most of the protids and odontopleurids) did not adapt to the changing condictions and became extinct by the end of the Middle Devonian. Whereas many of the tropidocoryphines not only survived as part of the deep water benthic faunal community, but by changing their life habits underwent a major radiation. Two sedimentary milieus can be distinguished within the deepwater 'pelagic' limestone facies; oxygenated and euxinic, and the tropidocoryphines became adapted to them in different ways.

First in the oxygenated milieu a diminution in size of the trilobites is very noticeable. The exoskeleton becomes more regularly vaulted than before, but the glabella loses its high relief and becomes virtually flush with the general curvature of the cephalon (Fig. 8). All prominent surface sculpture tends to disappear, and in particular the eyes, which formerly protruded, flatten out and lose their convexity: progressive reduction of the eye eventually leads to blindness (Fig. 5C). The latter feature has been interpreted as an adaptation to an endobenthic life (Clarkson 1967). The sediments in which these trilobites occur are normally bioturbated and lack an epifauna such as corals or brachiopods, indications not inconsistent with endobenthy. This is particularly the case in Erbenicoryphe, which is found in red bioturbated calcareous mudstones rich in styliolines and cephalopods deposited on submarine local rises and slopes which characterize the local paleographic condictions in the Lower Frasnian of the Montagne Noire (Tucker 1974: Feist & Klapper 1985: Wendt & Aigner 1985).

Whereas the 'pelagic' limestone facies was generally well oxygenated, there developed an oxygen-deficient milieu in basinal enviroments of very low energy alongside rises. These black 'euxinic' limestones are found from Lower asymmetricus times onward (Fig.2), and it is in this milieu that Pterocoryphe lived. This sapropelic facies with its oxigen-deficient conditions inevitably excludes an endobenthic life. In Pterocoryphe the anterior part of the sutures, the cephalon is vaulted and the cephalic borders with their prominent terrace lines have become enrolled (Fig. 7B). Such a combination of extended fringe and vaulted cephalon, evident in Harpes and other trilobites, was suggested by Richter (1920) as an adaptation which stabilized the trilobite when resting upon the sea floor, and like a snowshoe prevented it from sinking into the anoxic mud. Harpids, incidentally, are common in reefs and Bergstrom (1973) considered that their morphology may have aided them in clinging to reef surfaces. Althougt the migration of the anoxic mud. Harpids, incidentally, are common. The presence of such a functional visual system, together with adaptations which prevented the trilobites when resting upon a life habit is not. Such a life habit is not fundamentally different from that of ancestral tropidocoriphines by contrast with that of contemporaneous representatives of the T.(Longicoryphe)-Erbenicoryphe group) lineage which, as we have seen, changed their mode of the suture was essentially constant: it remained exactly as in of the anterior suture in Pterocoryphe, which liberated it form. The striking evolutionary step. This was entirely contigent upon adaptation to the oxygen-deficient enviroment and retained this unusual sutural pettern.

The genus *Pteroparia* is not separated from Pterocoryphe on account of its somewhat more backwardly bant anterior suture but because the paalpebral region is straightened and the eye is subsequently reduced. These evolutionary changes took place in the oxigenated from Pterocoryphe and therefore has its origin in the euxinic environment, migrated into the euxinic enviroment, migrated into the well-oxygenated 'Schwellen-facies' where it is widespread, occurring not only in the Montagne Noire, but also in the Renish slate mountains and in the Harz Mountains where it has been know for a long time (Richter 1913; R.&.E. Richter 1926). The mode of eye-reduction follows that described by Erben (1961) as the Piriproteus mode; the straightening of the facial suture and subsequent enlargement of the fixigena (tr.) between turning points gamma and delta, epsilon being straightened out. This indicates that eye-reduction is linked to reduction of the palpebral lobe. The migration of the anterior suture in Pterocoryphe-Pteroparia stabilized before the eyes became reduced.Sutural migration and eye-reduction must therefore be independent rather than linked as formerly thought (R. &. E. Richter 1926). The migration of the suture seems rather to have been initiated by the inflation of the cephalon and downward bending of the lateral borders compined with the enrrollet of the enrrollet of the peripheral cephalic border. Since both the environment and the mode of eye-reduction are exactly the same in both lineages, we interpret evolutionary changes affecting the eyes as the result of endobenthy. In the final stages of both lineges the eye lenses are lost, and since all that remains of the eye is a smooth plataform all these trilobites must be considered as blind. The link between enviroment and unidirectional evolutionary changes is apparent. There is no evidence as to why the Erbenicoryphe group became extinct. We can only speculate that the lack of broadening of the cranidium, otherwisw a feature of the successful contemporaneous genus Pterocoryphe, may have imposed a limitation on their further development. On the other hand it is possible that descendants of these forms may yet be discovered. These is better evidence to explain the extinction of the Pterocoryphe-Pteroparia lineage. The last representatives os Pteroparia, adapted to an endobenthic life in an oxigenated enviroment, became 'traped' when a catastrophic anoxic event interrupted the milieu of oxygenated 'pelagic' sedimentation within the Variscan realm This major event, which evidently consisted of a sapropelic upwelling de oxigenating the sea waters (Buggisch 1972;McGhee 1982), has been called the 'Kellawasser Event' (House 1985) after is type locality in the Harz Mountains. It produced a first pulse at the end of the Lower gigas Zone and major pulse resulting in a mass extinction at the Frasnian/Femennian boundary (McLaren 1970,1982).The last surving tropidocoryphine, the highly specialized-Pteroparia coumiacensis became extinct at the first pulse of this global catastrophe.

GRADUAL OR PUNCTUATIONAL EVOLUTION?

Since the publication of Eldredge & Gould's article(1972) and Stanley's Macroevolution (1979), the concept of punctuated qequilibria has become pervasive in palentology. Punctuational change and subsequent stasis have become accepted as a dominant mode of species-to-species transition in marine invertebrates as well as the norm for major evolutionary bursts. Ar first sight the chart (Fig.2) which shows the different stages of progressive evolution apperars to be consistent with the allopatric model,whit punctuationally separated taxa - another example of punctuated equilibria. The evolving characters through all the observed steps, however, belong to the same complex of transformation which (with the possible excetion of the T. (Longticoryphe) bissousensis-Pterocoryphe transition) ilustrate prograssive unidirectional change and not sudden breaks or saltations (Fig.9). We consider that within the deep-water environment of 'pelagic' carbonate mud, species transition in the gradualistic mode can be observed. This is particulary clear in the Pterocoryphe-Pteroparia lineage, even though there is a change of facies from euxinic to oxigenated. Although we have used established taxonomic categories the actual differences between the genera Pterocoryphe and Pteroparia are really very small; though the different modes os life indicated by the sedimentary enviroment testify to some ecological plasticity. According to their respective diagn oses (Feist 1976; R. &. E. Reichter 1919) the morphological differences are first the slightly more backwardly and downwardly bent lateral glabellar field and secondly the lack of a functional visual surface in the latter (which as shown here for the first time is a relict of a demonstrably functional visual surface in the early form of Pteroparia). It is hard to distinguish the early form os Pteroparia from the late form of Pterocoryphe and hace it is probable that the transition between the two is really at the species-to-species level. We expect that this will be proved by further discoveries of other intermediate morphotypes between both the early and late forms of Pterocoryphe and between the latter and Pteroparia. Application of the conventional Linnean concept of binominal taxonomy will then be more and more arbitrary if it is based on the dominant gradualistic evolving characters alone. As it is not likely, however, that all characters evolve contemporaneously and whith the same speed, subdivisions into taxonomic units might still be possible. In our case *Pteroparia* is clearly distinguished as an independent genus, not upon the degree of suture divergence but upon the obsolescence of the palpebral lobes. A derivation of *Pteroparia* from Erbenicoryphe is excluded by the fact that early Pteroparia still possesses eyes whereas the older Erbenicoryphe is blind.

We see evidence of species-to-species transformation within the Pterocoryphe-*Pteroparia* lineage and also in the transition from T. (Longicoryphe) to Erbenicoryphe. It is not certain, however the origin of the early Pterocoryphe from such a form as T. (Longicoryphe) bissousensis was sudden or gradual. The latter already shows a backward swing of the anterior suture and there may have been a range of intermediates between this and Pterocoryphe. Any such forms, as yet undiscovered, would be expected to have a more divergent suture and a loss of tropidia (as for example is seen in the fragmentary cranidium of T. (Longicoryphe)? sp., Fig.3E). Equally,Pterocoryphe may have by saltation and in the lack of asvailable evidence no further comments can be made at present. The stippled line on the chart (Fig.2) indicates our view of the relationships of the taxa and the links between the (very short) periods of statasis. The changing proportions of the cephalon are readily ilustrated by the method of transformation grids os Cartesian coordinates (D'Arcy Thompson 1971)(Fig. 9). The cephalon of the ancestral Tropidocoryphe has here been drawn within an undeformed squared network. In stratigraphically successive species of the T. (LOngicoryphe)-Pteroparioa lineage, grids have been drawn so that each coordinate passes through points on the cephalon corresponding to those of Tropidocoryphe. These diagrams show first that almost all the changes can be accounted for by a simple change in relative proportions -the anterolateral expansion of the cephalon, and secondly that these changes are progressive and unidirectional. The populations we have studied here are very small, but this is to be expected. For as demonstrated, for example, by Erben (12966) with reference to the origin of the earliest ammonoids from Lobobactrites in the earliest ammonoids from Lobactrites in the Hunsruck shale early memebers of an ultimately successful group, in a phyletic lineage, may develop in and remain confined to geographically restricted areas, in small populations, and are therefore only rarely found. The short lived Pterocoryphe has only rarely found in a single locality (Serre, Montagne Noire), whereas Pteroparia is widespread and is known on both sides of the Variscan belt. Gradual evolution is more normal in pelagic enviroments due to their comparative homogeneity and stability through space and time (Fortey 1985; Sheldon 1987). We consider that the appareance of discrete and distinctly separated taxa in sediments of pelagic origin may often be an artifact resulting from scarcity of material. The Ordovician trilobites studied by Sheldon (1987) show a comparable situation; he found it difficult to place his closely sampled intermediates into established taxa based upon type-locality colecting alone. Since the neritic realm is more influenced by inconstancy of facies and by rapid changes of sedimentary enviroment it is here that allopatric speciation is likely to be the norm.

CONCLUSIONS

Summarizing all observations we state that the evolution of the Tropidicoryphinea is characterized during its first 45 million years by stasis with punctuated equilibria in aan unstable, rapidly changing enviroment. Thereafter, in a short period of five million years we observe an acceleration of evolutionary activity with unidirectional transformations under permanent control of stable enviroment of deep-weater pelagic carbonate mud. Within this period, in particular, the gradualistic transition between the genera Pterocoryphe and Pteroparia is accomplished within a time span of about three million years which comprise four standard conodont zones [= 9 zones after Klapper (1987)]. This is the so far finest stratigraphical resolution of any know trilobite-bearing sequence. As our example demonstrates, unidirectional evolution is an adaptive response to the permanent influence of long-lasting constant envirómental conditions. This is particulary evident in a case of parallel development in two independent lineages controlled by the same enviromental conditions. Inversaly, in different even though contemporaneous facies, there are different processes of unidirectional transformations. All unidirectional evolution leads to specialization fatally diminishing the capacity for further adaptation. The Kellwasser event affected the last representative of a formerly successful subfamily. Declined and extinction is, as demonstrated, the result of the unidirectional evolutionary process.

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TAXONOMIC ADDENDUM

Only diagnoses and short discussions of the new taxa are presented; detailed descriptions based upon both specimens figured in this article and additional material will be published elsewhere (Feist, in prep.). Type material material is held by the Service des colletions. Universite des Sciences & Techniques du Languedoc (Montpellier).

ERBENICORYPHE PARVULA gen. et sp. nov.

Derivation of name: - Generic name after Professor H.K. Erben, author of classic paperts on Tropidocoryphines and eye-reduction in Proetids; species name: parvulus = tiny.

Material. - Tgree cranidia (USTM 2, holotype, Fig. 3B; USTM 1, Fig 3D) from red calcilutites,Coumiac Formation, Pic de Bissous, section VSE bed 48 (Feist & Klapper 1985), Lower asymmetrycus Zone (Lower Frasnian).

Diagnosis.-Tropidocoryphine with triangular, laterally non- constricted smooth glabella, straightened palpebral sutures, flattened eyelobes lacking lenses; antero-lateral border with narrow upturned rim: short preglabellar field without tropidia.

Discussion. -The short-lived new taxon seems to be restricted to the oxygenated facies developed in the nappe area of the Montagne Noire. Besides the particular course os faciual sutures which still closely resembles that of the older tropidocoryphines, there are strinking similarities with reporesentatives of the younger Pteroparia: shape and vault of cranidium, elevated abaxial portions of pygidial anterior pleural segments.

PTEROPARIA OCULATA sp. nov.

Derivation of name.- Oculatus = having eyes.

Material.- Seven cranidia (USTM 16, holotype, Fig. 4E; USTM 29- 34), 1 librigena (USTM 15, Figs. 4D,5B), 1 pygidium (USTM 17, Fig. 4F) from pink calcilutites, Coumiac Formation, Pic de Bissous, section VSE bed 100 (Feist & Klapper 1985), Upper asymmetricus to triangularis Zone (Middle Frasnian).

Diagnosis.- Petroparia with individualized eye lobes and visual surfaces displaying lenses. Antero-laterai border with rather broad cylindrical rim. Border furrow split into two parallel furrows. Anteriorly broadly rounded subtriangular glabella. Sharp elevation of distal anterio bands of second pygidial segment.

Discussion.- The new species is so far the oldest representastive of the genus and is the only one which exhibits functional eyes.

PTEROCORYPHE PROGEDIENS sp. nov.

Derivation of name.- Progrediens = progressive, designating the postero-lateral migration of the facial sutures.

Material.- Six cranidia (USTM 19, holotype, Fig.. 4H; USTM 26, Fig.6B; USTM 35-38), 1** librigena (USTM 18, Fig. 4G), 1 pygidium (USTM 20, Fig 41) from dark grey calcilutites. La Serre Formation, section La Serre A bed 43 (Feist & Klapper 1985). Middleto Upper asymmetricus Zone (Lower Frasnian).

Diagnosis.- Species of Pterocoryphe characterized by the lack of tropidia or equivalent, the postero-lateral extensuion ofd the preglabellar field, the beta turning points of the facial suture subtending more than 180,their transversal projection crossing the glabella behind its frontal third of sagital length.

Discussion.- Due to the postero-lateral extension of the preglabellar field the new species is intermediate between the type-species of Pterocoryphe and attribution to one or the other genus is difficult based on this character alone. The possession of well-developed palpebral lobes and kidney-shaped eyes, however, integrates the new taxon into Pterocoryphe. In the slightly older type-species languedociana the angle between beta turning points never exceeds

180 and the projection beta-beta does not cross the glabella behind its anterior third.

TROPIDOCORYPHE (*LONGICORYPHE*) *BISSOUSENSIS* sp. nov.

Derivation of name.- Bissousensis = from Pic de Bissous, north of Cabrieres, type-locality of the new series.

Material.- Two cranidia (USTM 24, holotype,Fig.4N,6A; USTM39), 1 librigena (USTM 23 Fig.4M). 1 pygidium (USTM 25, Fig.40) from light grey calcilutites, Coumiac Formation, Pic de Bissous, section VSE bed 3 (Feist & Klapper 1985), hermanni-cristatusPY Zone (Upper Givetian).

Diagnosis.- Species of the subgenus Longicoryphe characterized by a highly vaulted preglabellar field borded by prominent cylindrical rim asnd strongly divergent anterior sutures. Pygidial axis long and slender, extending near to the posterior border furrow.,

Discussion.- The degree of divergence of anterior sutures in this distinct species is the most advanced and the strongly vauted preglabellar field with its strong cylindrical border is rather atypical recalling characteristic features os Pterocoryphe.

Fig. 1. Location map synthetic columnar sections of the Devonian. Montagne Noire,southern France. Tropidocoryphine distribution in the oxigenated carbonate facies of the nappe sequence (left) and on the right, the Cabrieres kippen domian with reducing environments during the Frasnian.

Fig. 2. Range chart of Late Tropidocoryphinae according to the standaard conodont zonation and to the dominant environments developed in the Motagne Noire during the Late Middle and early Upper Devonian.

Fig. 3. Middle Devonian and early Frasnian Tropidocoryphinae. [Deposition of figured material: USTM = Universite des Sciences et Techniques de Montpellier: IT = British Museum ((Natural Hystory), London].

Fig. 4. Characteristic species of the Longicoryphe-Pteroparia lineage. Late Givetian to Late Frasnian (Deposition of figured material: USTM = Universite des Sciences et Techniques de Montpellier: FSL = Faculte des Sciences, Universite de Lyon).

Fig. 5. Eye-development in late Tropidocoryphinae.

Fig. 6. Characteristic patterns of the preglabellar field in late Tropidocoryphines.

Fig. 7. Comparison of the cephalic vault (lateral view).

Fig. 8. Comparison of the cephalic vaulting ((lateral view).

Fig. 9. Morphogical change in the late last Tropidocoryphinae shown by transformation grids.

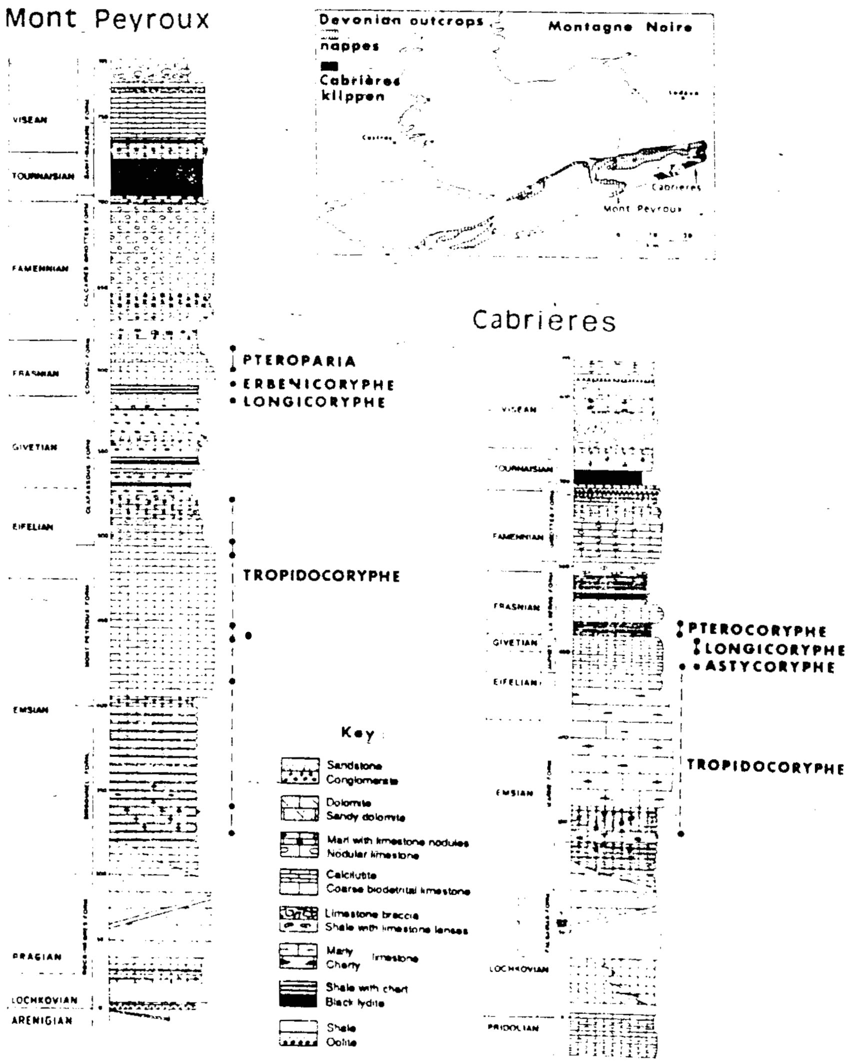

Mont Peyroux
VISEAN
TOURNAISIAN
FAMENNIAN
FRASNIAN
GIVETIAN
EIFELIAN
EMSIAN
PRAGIAN
LOCHKOVIAN
ARENIGIAN
PTEROPARIA
ERBENICORYPHE
LONGICORYPHE
TROPIDOCORYPHE
Devonian outcrops
nappes
Cabrières klippen
Montagne Noire
Castres
Lodève
Cabrières
Mont Peyroux
Cabrières
VISEAN
TOURNAISIAN
FAMENNIAN
FRASNIAN
GIVETIAN
EIFELIAN
EMSIAN
LOCHKOVIAN
PRIDOLIAN
PTEROCORYPHE
LONGICORYPHE
ASTYCORYPHE
TROPIDOCORYPHE
Key
Sandstone
Conglomerate
Dolomite
Sandy dolomite
Marl with limestone nodules
Nodular limestone
Calcilutite
Coarse biodetrital limestone
Limestone breccia
Shale with limestone lenses
Marly limestone
Cherty
Shale with chert
Black lydite
Shale
Oolite

Fig. 1

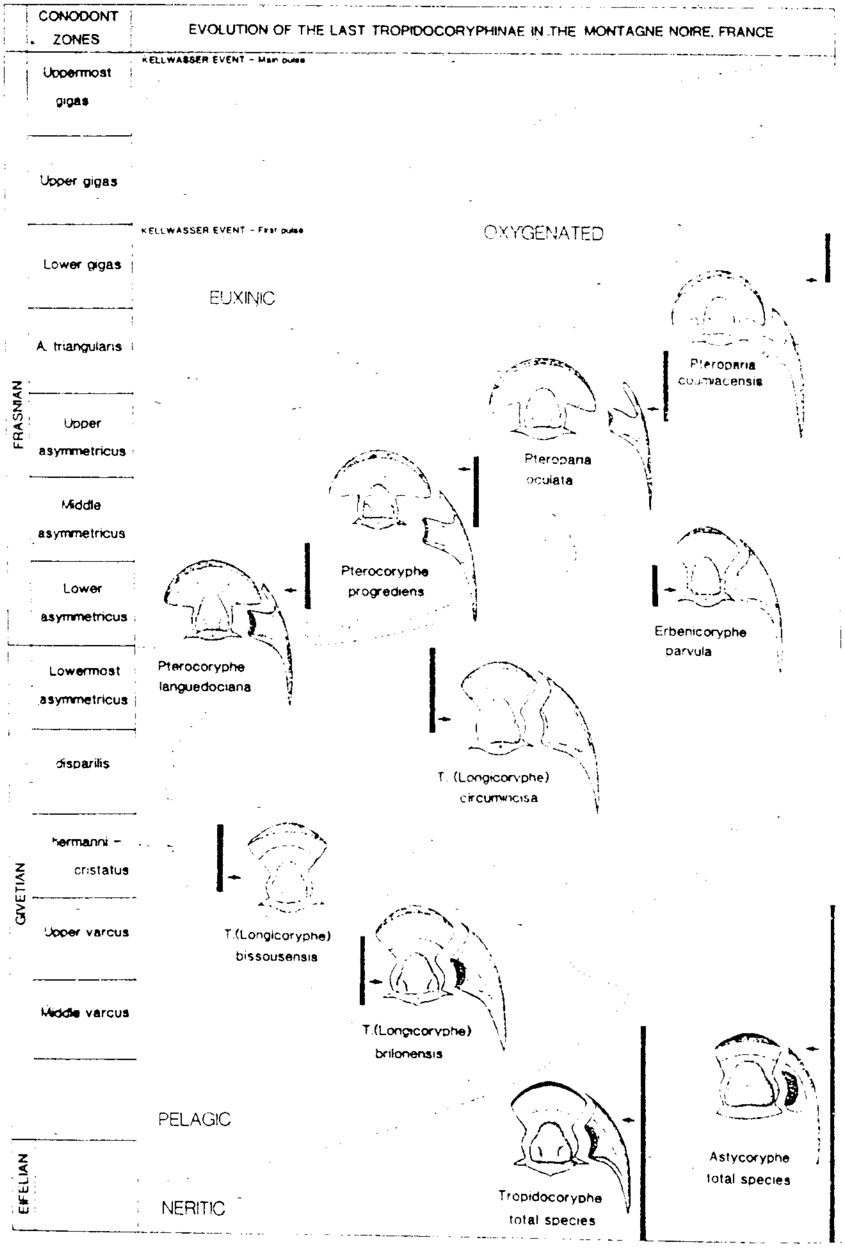

CONODONT ZONES
EVOLUTION OF THE LAST TROPIDOCORYPHINAE IN THE MONTAGNE NOIRE, FRANCE
KELLWASSER EVENT - Main pulse
Uppermost gigas
Upper gigas
KELLWASSER EVENT - First pulse
OXYGENATED
Lower gigas
EUXINIC
A. triangularis
FRASNIAN
Upper asymmetricus
Middle asymmetricus
Lower asymmetricus
Lowermost asymmetricus
disparilis
hermanni - cristatus
GIVETIAN
Upper varcus
Middle varcus
PELAGIC
EIFELIAN
NERITIC
Pteroparia coumiacensis
Pteroparia oculata
Pterocoryphe progrediens
Erbenicoryphe parvula
Pterocoryphe languedociana
T. (Longicoryphe) circumincisa
T.(Longicoryphe) bissousensis
T.(Longicoryphe) brilonensis
Tropidocoryphe total species
Astycoryphe total species

Fig. 2

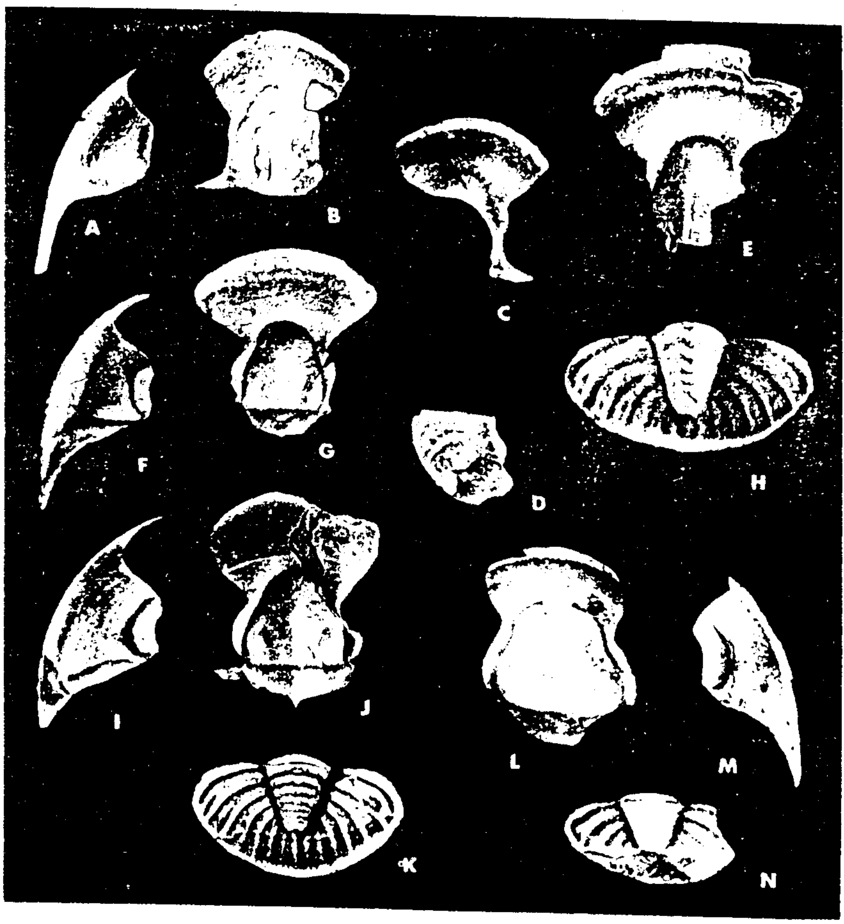
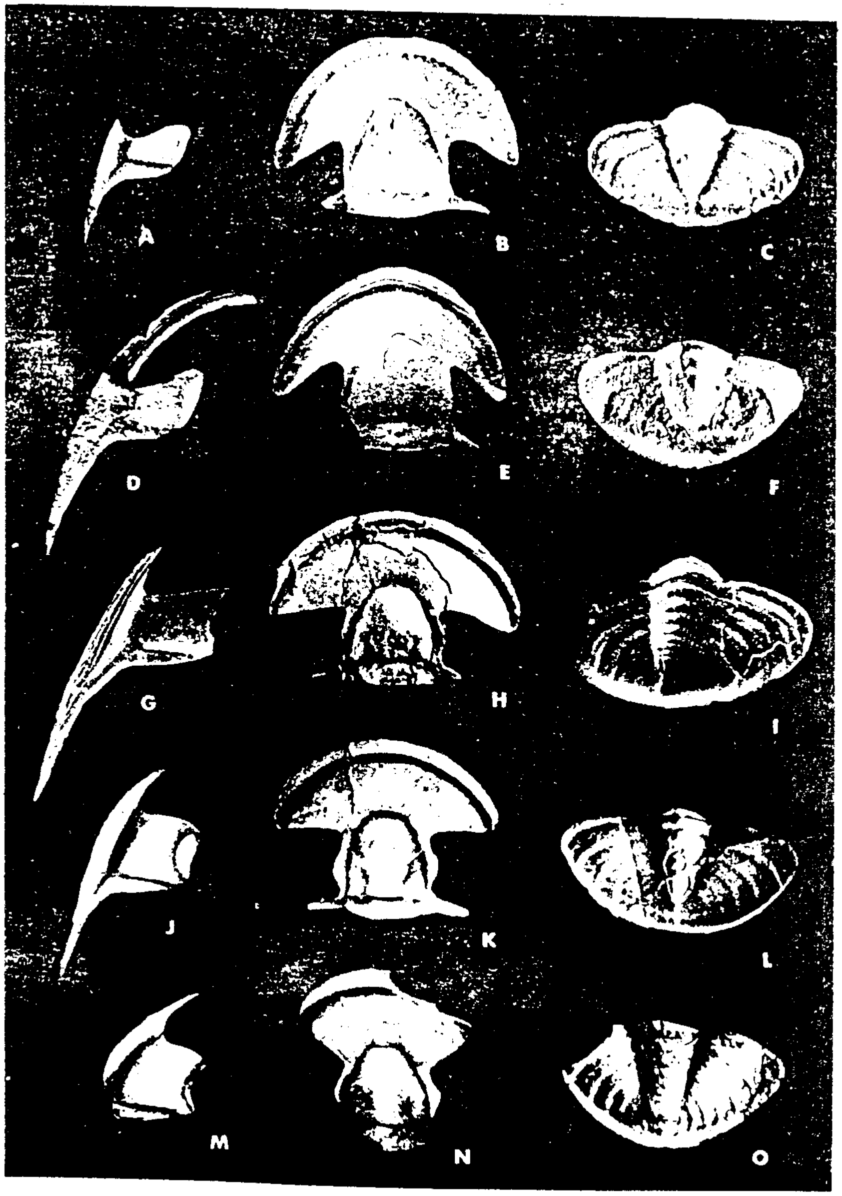


Fig. 3



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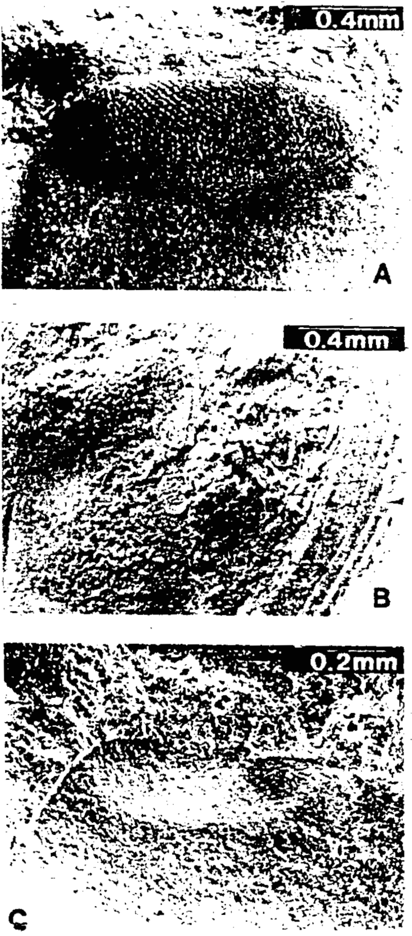


Fig. 5

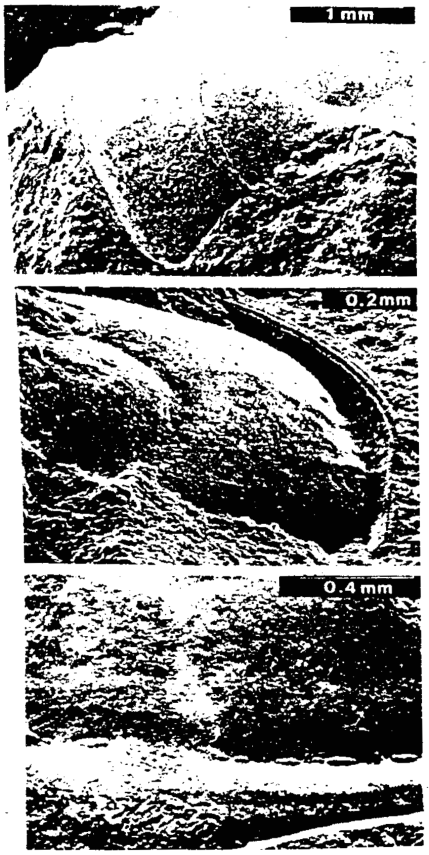
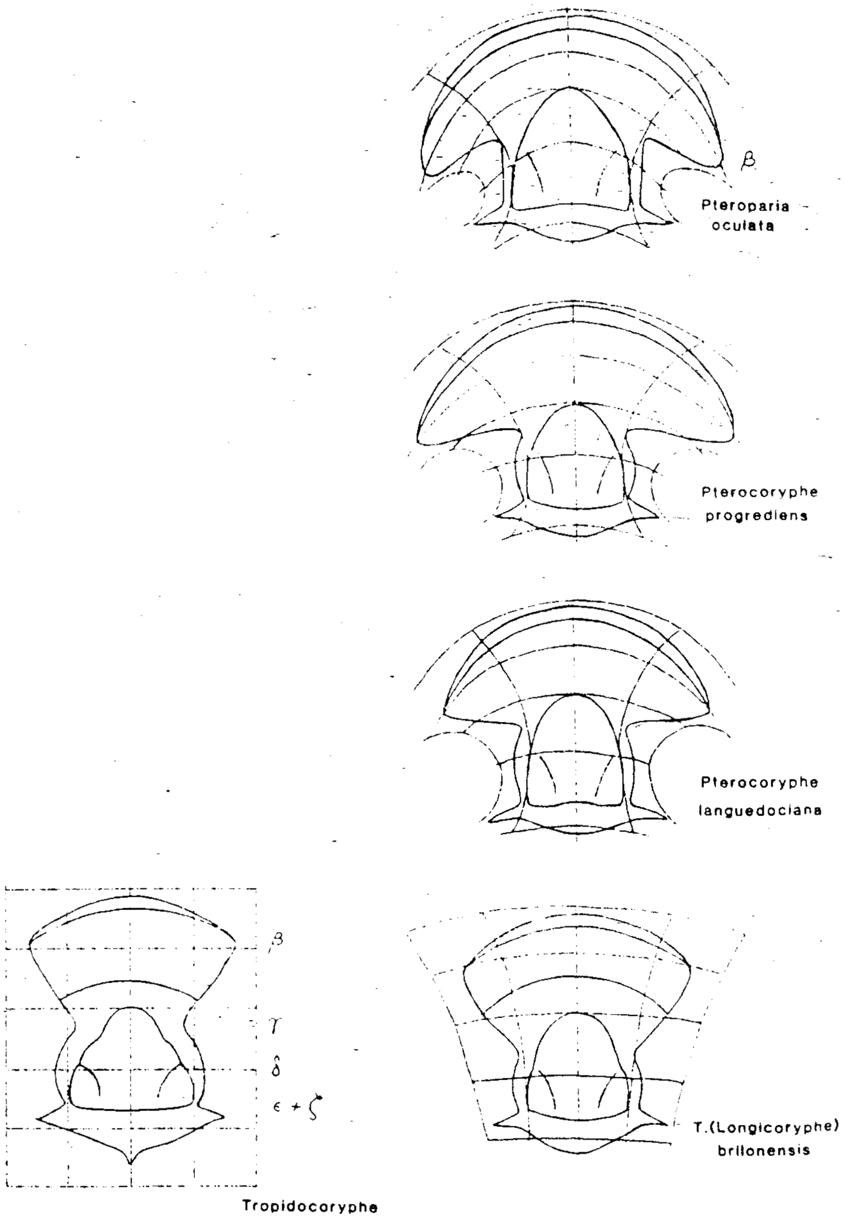


Fig. 6

Fig. 7

Fig. 8


β
Pteroparia oculata
Pterocoryphe progrediens
Pterocoryphe languedociana
β
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ε + ζ
Tropidocoryphe
T.(Longicoryphe) brilonensis

Fig. 9

In: BOTTUER, D.J., HICKMAN, C.S. & WARD, P.D. ORGANIZERS, 1985 MOLLUSKS, NOTES FOR A SHORT COURSE: KNOXVILLE, TENN., UNIV. TENNESSEE DEPT. SCI. STUDIES IN GEOLOGY 13, AND THE PALEONTOLOGICAL SOCIETY, P. 157-173.

5.5(c) GASTROPOD EVOLUTIONARY HISTORY

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INTRODUCCION

If taxonomic richness or ecological diversity defines evolutionary success, then the gastropods must be placed among the most successful clades of all time. Today, the gastropods are the most speciose class of fossilizable marine invertebrates. They have a rich fossil record extending nearly to the base of the Phanerozoic, documenting an almost uninterrupted taxonomic and ecological diversification (Figure 1). Yet the snails have been often overlooked as a focus of evolutionary or paleoecological study. Classic evolutionary studies os gastropods, for axample Fisher et al.'s (1964) study of Athleta or Gould's (1969) work on Poecilozonites, indicate no inherent deficiencies in the taxon and suggest a simple lack of attention. The purpose of this paper is to summarize4 some of the major features of the history of grastopods, and to reiterate some long-standing questions about the evolution and relationships of ancient snails. The goal is not only to provide a useful guide for non-speciallists facing the prospect of lecturing on the beasts, but also to direct prospective students to problems perhaps worthy of their future research effort. There is certain diversity of opinion regarding most major aspects of gastropod evolutionary history. I have attempted to outline the opposing views in each debate rather than emphasizing any one opinion, providing the diverging views seem reasonable.

WHAT IS, AND IS NOT, A SNAIL?

Gastropods share as a cammon heritage a developmental and post- larvalmorphogical-characteristic that is uniquenamong animals. All gastropods undergo torsion during their ontogeny,wherein thje viscera and shell orthe bilaterally symmetrical veliger larva rotate 180 degrees counter-clockwise relative on the foot and head, bringing the mantle cavity to a position above the head. The nervous system istwisted into a figure eigth and the gut nerve cords are looped. In the best know study of torsion (Crofts, 1937, 1955), torsion was found to occur in two phases first 90 degrees is accomplished by sudden contraction of the better developed left larval retractor muscle, while the remaining 90 degrees occurs more slowly through differential growth. This pattern of torsion is known to vary throughout the class (Underwood, 1972). In cladistic terms, torsion is the shared derived character (synapomorphy) that defines the Class Gastropoda. Many gastropods, especially some opisthobranchs, have secondarily achieved a high degree of bilateral not always in the adult morphology, of gastropods.

WHY TORSION?

One of the fundamental questions regarding the evolutionary history of the Gastropoda is the origin and function of torsion. A number of perceptive and defensible hypotheses, not all mutually exclusive, have been proposed, but the debate continues uncheckied. No ocurrent theory successfully addresses the origin and inmediate selective value of torsion (versus current adaptation), the reason for the consistent direction of torsion, and the relationshipo of torsion to the overall evolutionary diversification of the gastropods, Regardless of the specific mechanism, many hypotheses suggest a rapid origin for torsion. Torsion has been presented as one of the best examples of sudden, extreme morphochange (e.g. Stanley, 1979).

There is fairly universal agreement that the Gastropoda are derived from an ancestor with bilateral symmetry, a single dorsal valve, and a broad foot modifed for creeping: in short, a monoplacophoran. While some authors have postulated the derivation of the Gastropoda from a tergomyan (limpet-like) monoplacophoran with multiple paired muscles (e.g., Garstang, 1929; Ghiselin, 1966), other current theories derive gastropods from a cycloman (coiled) form with only a single pair of retractor muscles (e.g., Pojeta and Runnegar, 1976; Peel, 1980). The individual hypotheses are too numereous to explore in detail, so a brief summary of selected hypotheses, strengths and weaknesses, and appropriate references are inclued here:

The Larval Retraction Hypothesis (Garstang,1929): This hypothesis suggests that torsion resulted from a single mutation affecting the relative timing of retractor muscle development in a pelagic veliger. Contraction of the unequally developed muscles caused torsion. The putative benefit to the larva was the ability to retract the head and velum into the shell before the foot, thus protecting these presumably vulnerable areas. Garstang also supposed shifting of the mantle cavity would provide space where the head and velum might be retracted. In this view, the torted condition is imposed on the adult and is maintained by selective advantages accruing to the juvenile. This hypothesis is perhaps the most widely accepted, and is widely cited in texts on invertebrates zoology (e.g., Barnes, 1980). However, Thompson (1967)found the veliger foot to be equally susceptible tyo demage by predators and noted that the position of the mantle cavity seems to have little realations to efficiency of retraction in juveniles.

The Larval Settling Hypothesis (Ghiselin, 1966): This hypothesis suggests torsion aroese gradually and was immediately advantageous to planktonic juveniles during settling. The exogastric (coiled forwad over the head, rather than to the rear as in an endogastric shell) shell was envisioned as detrimental to locomotion and shell balancing by the newly settled snail. Other advantages, such as suggested by Garstang (1929) would also accrue as secondary effects. Against this hypothesis is the fact that the advantages, while plausible, are not supported (or contradicted) by observation or experimental results.

Underwood (1972) has observed that newly settled, post-torsional larvae of Gibbula cineraria were unable to crawl four days after torsion. Clearly, torsion did not solve the problem of post-settling locomotion!

The Veliger Swimming Hypothesis (Underwood, 1972): Underwood observed that torsion by contraction of asymmetric larval retractors does not occur in species lacking a planktonic stage. In these forms, the entire torsion process is accomplished through differential growth. He also observed that the second phase of torsion in gastropods with plancktonic larvae often does not occur until aft6er settling. He then hypothesized that the initial phase of torsion , through muscular contraction, benefited juveniles by adjusting the posotion of the shell relative to the velum to a more hydromechanically effiecient arrangement. Torsion through differential growth in juveniles or adults was interpreted as an adaptation for the adults, perhaps by moving inhalant currents to the front of the animal. The advantages of torsion for adultsor juveniles to be demonstrated.

The Well-Adapted Adult (Morton,1958): Morton argued that torsion would never survive solely as a larval adaptation. He observed that torsion rotates the mantle cavity and associated organs to the front of the animal. In more advanced prosobranchs, the siphon allows the snail selectively to sample water in the direction of locomotion. Inhalant water currents will be drawn from undisturbed areas, rather than from behind the animal. These potential advantages for adult snails might be correct, but they do not provide a mechanism for torsion itself. Furthermore, these advanteges seem to apply more to relatively derived mesogastropods and neogastropods than to archaegastropods, where torsion originated.

The Opercular Imperative (Stanley, 1982): Stanley argued that no present hypothesis for the adaptive significance of torsion explained the tremendous success of torted molluscs, while allowing for the protracted persistence of cycloman monoplacophorans into the Early Triasic. He observed that an untorted, multispiral mollusc woulkd not withdraw the foot last, as do gastropods, hence the operculum could not be located on the dorsal surface of the foot. Nor is there any at their position for the operculum in cyclomyan Monoplacophora. He suggested that

Torsion allowed for the eventual evolution of the operculum. The operculum provides protection once the snail has retracted, a feature that would become increasingly advantageous as the intensity of predation on the marine benthos increased through the Phanerozoic. This hypothesis seems plausible but, like Morton's (1958), does not account for the origin of torsion.

The Helicospiral Hypothesis (Pojeta and Runnegar, 1976). Most biologists dealing with the torsion problem have accepted earlier paleontologist's hypothesis that the planispiral bellerophonts [illegible] (e.g., Knight, 1974). Pojeta and Runnegar [illegible], in the absence of convincing [illegible] the bellerophontids' affinities, and [illegible] Wenz (1938), concluded the bel[illegible] were cvyclomyan Monoplacophora [illegible] of torsion coincided with evolution [illegible] shell and visceral mass necessary [illegible] shell during locomotion (also see [illegible] 1981). This hypothesis unifies and ex[illegible] important questions, shell position is [illegible] produce the full rotation of the vis[illegible] necessary for torsion.

[illegible] of hypothesis is by no means com[illegible] have the individual hypotheses been [illegible] appropriately thorough discussion. More [illegible] discussions of hypotheses prior to 1945 [illegible] Yonge (1947), and an excellent recent [illegible] provided by Lever (1979).

[illegible] THE GASTROPODA

[illegible] torsion defines the Gastropoda, it [illegible] simple task to identify the earliest [illegible] torted molluscs in the fossil record [illegible] even to distinguish their sister group. [illegible] is only to recognize where the tran[illegible] Monoplacophora to Gastropoda oc[illegible] Unfortunately, recognizing torsion in [illegible] is an uncertain proposition; criteria [illegible] torsion, prposed by various authors [illegible] 1947, 1952; Linsley, 1977; harper and [illegible] are not universally accepted among [illegible] These criteria include the presence of [illegible] muscle scars (Rollins and Batten, [illegible] anteriorly-directed angulations or [illegible] on the aperture (Linsley, 1977) and well developed parietal deposits (Harper and Rollins, 1982).

The earliest conispiral, calcitic shells are the Early Cambrian genera Aldanella and Pelagiella and their close relatives. Aldanella and other aldanellids first apperar in pre-trilobite shelly faunas at a variety of localities around the world and persist through the Early Cambrian. These fossils have variously been interpreted as gastropods (Missarzhevsky, 1969; Runnegar 1981b, Pojeta, 1980), paragastropods (Linsley and Kier, 1984), or worms (Yochelson, 1978). *Aldanella* is small and rarely well preserved. Insufficient evidence is available to resolve the debate, so *Aldanella* and its allies can be assigned only provisionally to the Gastropoda.

The Pelagielidae also occur in the Early Cambrian and persist through the Middle Cambrian. These small fossils are generally accepted as molluscs (Pojeta and Runnegar, 1976; Linsley and Kier, 1984; Yochelson, 1978; Runnegar, 1981b, but their position among the gastropods is doubtful (Yochelson, 1978; Linsley and Kier, 1984). Linsley and Kier (1984) conclude *Pelagiella* is a paragastropod and Yochelson suggests the Pelagiella are a separate class. Pojeta (1980) documents unequal and sligthly offset muscle scars in *Pelagiella alantoides* and concludes the genus was partially torted. Runnegar (1981b) also described the specimen and interpreted it as partially torted monoplacophoran, the possible ancestor of *Aldanella* and other early gastropods.

Another group of early molluscs commonly interpreted as gastropods are the planispiral Bellerophontina. The systematic position of the bellerophonts has been a source of considerable debate over the past decade (e.g., Runnegar and Jell, 1976; Pojeta and Runnegar, 1976; Linsley, 1977; Yochelson, 1978; Peel, 1980; Runnegar, 1981b), with much of the debate centering around the significance of single or multiple symmetrically paired muscle scars found in some bellerophont species. Bellerophonts traditionally have been included in the Gastropoda (e.g., Yochelson, 1967) on the basis of their multispiraled shell and the sinus or the slit characteristic of the Sinuitidae or Bellerophontidae, respectively. At least nine genera have been shown to have multiple paired muscle scars, including members of the Cyrtolitidae, Bellerophontidae, Multifariidae, and Sinuitidae (Table 1). Given the widespread distribution of paired, symmetrical muscle scars in the order, and apparent lack of other shared derived characters to unite the Bellerophontina with the gastropods, Runnegar and Jell (1976) and Pojeta and Runnegar (1976) concluded bellerophonts were untorted and assigned the Bellerophontina to the Monoplacophora.

Knight ((1947, 1952) interpreted bellerophonts with a single pair of muscle scars as gastropods. Presuming that such early "gastropods" would not have evolved the asymmetrically retractor muscles characteristic of younger, conispiral snails. Therefore, Knight accepted his discovery of a single pair of muscle scars in *Bellerophon* and *Sinuites* as confirming their assignement to the Gastropoda.

Peel (1980) observed that bellerophonts with increasingly tighter coiling have fewer pairs of muscle scars (Fig.2). As coiling increases, and rate of whorl expansion decrease. Peel interpreted this trend as reflecting a shift from limpet-like forms that "clamp" to the substrate to snail-like retractile forms. He also pointed out that torsion would be more simple, in a mechanical sense, if it occurred in a deep- retracting monoplacophoran with only a single pair of muscle scars. From this viewpoint, the single pairs of muscle scars observed by knight (1974) are entirely compatible with a monoplacophoran assignment. At the least, paired muscle scars should be interpreted as shared primitive characters insufficient for a definitive assignment. Lacking other criteria indicative of torsion, Bellerophon and Siniutes should remain in the Monoplacophora.

Linsley (1977) suggested an alternative view of bellerophont affinities based on his functional analyses of aperture shape. He noted thast angulations on the apertures of modern gastropods usually suggest the presence of an inhalant or exhalant current at that site, and that inhalant currents are directed as anteriorly as possible. From this observation, he adduced that forms with lateral angulations, such as Cyrtolites, were probably monoplacophora with a posterior mantla cavity and lateral inhalant currents. He interpreted as gastropods those forms with reentrants adjacent to the medial slit (e.g.., Knightites). Berg-Madsen and Peel (1978) proposed a similar interpretation of Protowenella flemingi. Linsley (1977) and Berg-Madsen and Peel (1978) concluded that the Bellerophontina is probably an assortment of monoplacophorans and gastropods.

Harper and Rollins (1982 hold that muscle scars cannot be accepted as reliable evidence for bilateral symmetry because secondary symmetryy in many archaegastropod limpets also produces symmetrical muscle patterns. They argue that none of thev previously proposed criteria provide adequate distinction betweengastropods and monoplacophorans.Instead, they suggest parietal deposits are a valid discriminator;gastropods could have a parietal inductura but monoplacophorans would not. They noted that no extant monoplacophorans have parietal inductura but monoplacophorans would not. The functional significance of parietal deposits, if any, is unknow, so speculation concerning the position of these secondary deposits seems premature.Since modern gastropods, such as Nassarius and Strombus, commonly have thick parietal deposits located over the head of the animal, it is difficult to understand why monoplacophorans could not also have a parietal inductura. he muscle scars of bellerophonts a[ppear homologous with those of the cap-shaped, or tergomyan, monoplacophorans, an argument supported by a fairly continous morphogical series from the tergomyan Propilina the more elevated Cyrtonella to the cycloman Sylvestrophaera (Peel,1980). Harper and Rolins deny the apparent homology and refer to all muscle scars as analogous.

A more divergent view is presented by Yochelson (1978,1984), who continues to montain the gastropod affinities of the Bellerophontacea (butnot the Helcionellacea!) less "... a few coiled putative monoplacophoirans that should be removed" (1984, p. 267). Yochelson, as did Knight(1952), considered the slit characteristic of bellerophontacea phorans that should be classified within that superfamily.

Linsley and Kier (1984) have removed several early taxa from the Gastropoda. They erected a new class of molluscs, the Paragastropoda, to include conispiral but heterostrophic (apparently left-coiled or sinistral but actually dextral with the apex projecting in the opposite direction from "normal" shells), untorted molluscs. Included in this new class are the Onychochilidae (Upper Cambrian to Lower Devonian).Linsley and Kier (1984) also include the Aldanellidae and Pelagiellidae in the Paragastropoda. Linsley (1977) recognized that onychochilids, macluritids and their close relatives were distinctly peculiar in their aperture shaphe and coiling geometry, and Linsley and Kier interpreted these peculiarities to imply they were untorted. The gastropoda was erected as a polyphyletic taxon (Linsley and Kier, 1984 p. 247-248) and does not represent a clade. Certainly the morphogical diversity within the Monoplacophora, including the Gastropoda. It is too early to determine how the Paragastropoda will be received.

The earliest undisputed gastropods, therefore, are the Lte Cambrian pleurotomariaceans such as Sinuopea. These conispiral, slit shells that their affinities are not doubted. How much appeared will remain uncertain pending resolution of the various de bates regarding the affinities of earlier forms.

GENERAL EVOLUTIONARY TRENDS AMONG THE GASTROPODA

Generalizations in any diverse taxon are difficult to make: exceptions in individual component clades overwhelm overall trends. But three paterns; in addition to the general diversification already noted, stand out starkly in the geologic history gastropods. These are tendency toward loss one of the pairedinternal and mantle cavity organs, and a bimodal distribution of shell geometries.

Paired Organs: A persistent trend among the prosobranch gastropods is a loss internally, paired mantle cavity and osphradium and ventricle. The right nephridium persists but functions only as a portion of the genital duct.

Paralleling the reduction in organs in the mantle cavity is a tendency toward simplification of gill structuyre and patterns of water nflow. The primnitive is bipectinate, and one gill is located on each side of the mantle cavity. In extant pleurotomariaceans,the inhalant water streams enter the mantle cavity on each side of the medial slit, pass over the gills and exit through the slit.More derived gastropods have anterior end pass over gill and then exit near the posterior end of the mantle cavity.

The functional basis of these trends is not well understood. Presumablyt, some hydrodynamic advantage is gained throug simplification of the mantle cavity, but thios has not been demonstrated. This hypothesis has recently been tested by Gilinsky substrates(1985), who found no difference in the abilities of forms with monopectinate or bipectinate bills to respire in turbid water. The reason for the shift from a bipectinate to a monopectinate condition is unknown.

Predator Deterrence: The diversity of shell-breaking, or durophagous, predators has increased through the phanerozoic ((Vermeij, 1977,1978, 1983; Signor and Breet, 1984). Probable early Paleozoic predators include nautiloids and phyllocarid arthropods, joined durophagous predators, including shell-crusing teleosts, rays, stomatopod crustaceans and others, appeared in the Mesozoic (Vermeij,1977).

Several evolutionary trends amongst marine gastropods appear to corresaponds to the increasing intensity of durophagy through time.Vermeij (1975, 1977) has argued these geometries are more susceptible to attack by durophagous predators than other forms. Shells with narrow apertures ((e.g., Conus) became more common throgh the Mesozoic and Cenozoic.

Well-developed sculpture is much more common among geologica;lly younger gastropods (Vermeij, 1977,1978).They make the prey relatively larger, reducing the amount of return relative to prey size. And these sculptures teand to distribute applied stresses across the shell, increasing the force necessary to demolish the shell. Parallel increasses, though less accentuated, in the frequencies of sculpture can also be seen in Paleozoic Bellerophontina, Nautiloudea, Brachiopoda and Crinoidea (Signorand Brett, 1984).

Variations from the primitive pattern of continuous, indeterminate growth may also be related to the overall trend tpward an increasse in predation survery, it appears that determinate growth was much less common in the Paleozoic. In a similar fashion, discontinouos growth allows construction of predation-resistant features not atherwise possible (linsley and Javidpour, 1980), such as the apines of murex shells or heavy varices of the Cymatiidae.

The Bimodal Distribution of Shell Form: Cain (1977) observed a surprising bimodal distribution of apical angles among both aquatic and terrestrial gastropods. Shells tend either to be high-spired or low-spired, with relatively few falling between. A. Seilacher (pers. comm., 1979) has pointed out to me that the distribution may only reflect two stable shell positions, sitting on the base or on the side. The functional basis of this pattern remains to be explored.

EVOLUTIONARY TRENDS AMONG THE MAJOR GASTROPOD TAXA

Archaeogastropods: At the family level, archaeogastropods attained their highest diversity of 34 families in the Middle Devonian (Fig.3), although a Late Triassic peak was nearly as high. Since the early Mesozoic the number of families has declined stesdily to the present twenty-odd femilies.

Neograstropods and masograstropods in many exhibit surprising convergence in shell form. Earlier workers (e.g., Cox, 1960) interpreted these similarities in shell form as reflecting common heritage, and this no doubt influenced Cox's earlier decision to erect the Caenogastropoda. The similarities are now recognized as convergences and, as such are some of the best examples of convergent evolution within the marine realm.

Opisthobranchs: For the most part, the opisthobranchs play a minor role in the fossil record of the Gastropoda. But three superfamilies have, at times, been quite important.

The Nerineace were uniformly high-spired, some exceedingly so, and all were characterized by internal shell sculpture. The sculpture consistend of internal spiral folds, similar to columellar folds, but not restricted to the columella. These folds greatly reduced the internal volume of the shell. The function of these folds in uncertain; one suggestion is that they prevented predatory crustaceans from inserting their mandibles or chelae into the she to begin the shell-breaking process (Signor and Kat, 1984). Nerineaceans were especially abundant in shallow, tropical carbonate environments throughout the Tethys region (Wieczorek, 1979).

Pulmonates: The pulmonates play no role among fossil marine assemblages but do have a long fossil record in terrestrial and marginal marine sediments (Solem and Yochelson, 1979). The Stylommatophora appear first, in the Early Pennsylvanian. Solem and Yochelson (1979) document a surprisingly diverse pulmonate fauna in the Pennsylvanian, including representatives of four different families. The supposedly less derived Basommatophora first occurs in the Jurassic (Solem and Yochelson, 1979).

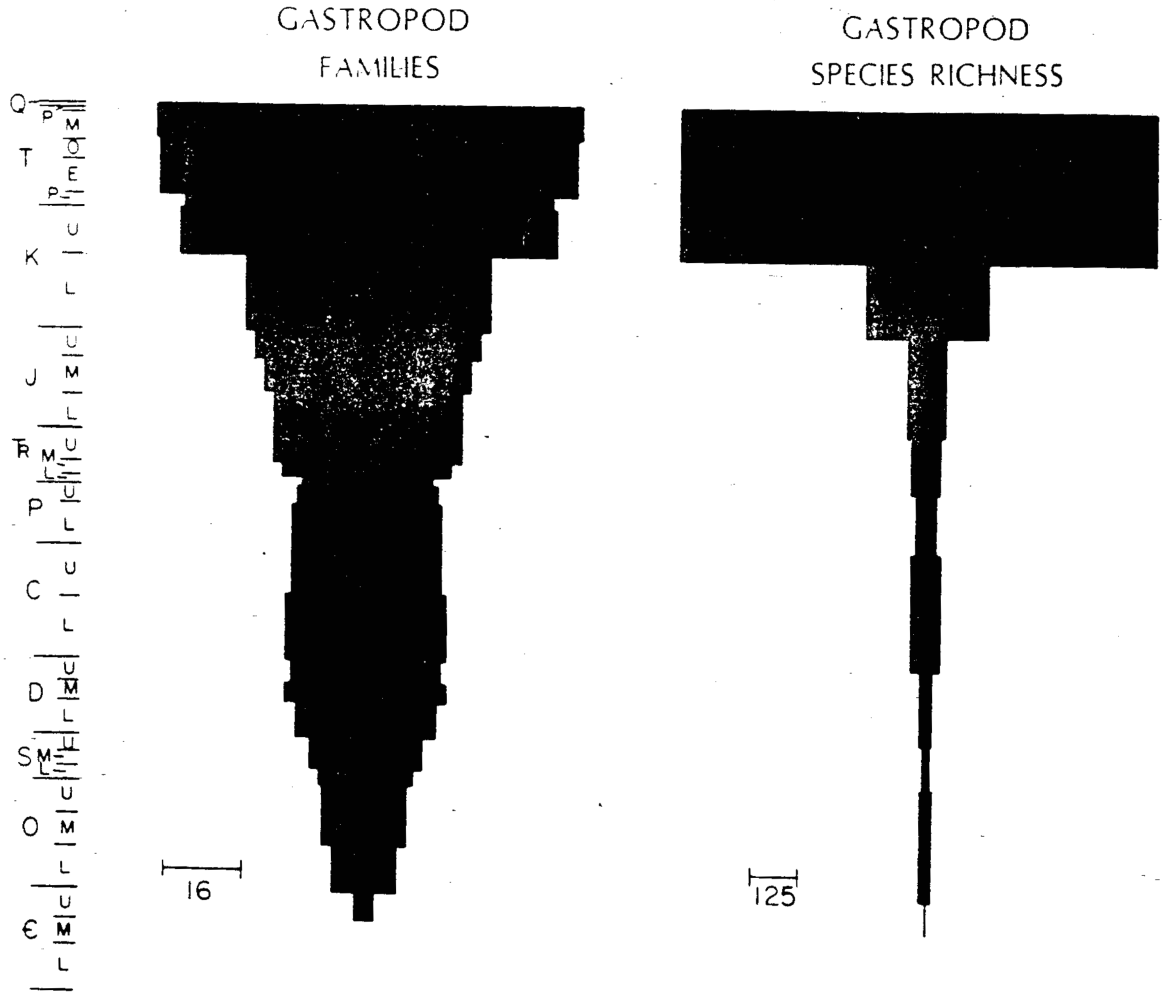
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Fig. 1

BELLEROPHONTACEAN GENERA WITH SYMMETRICALLY PAIRED MUSCLE SCARS

FAMILY	GENUS	REFERENCE
Cyrtolitidae	*Cyclocyrtonella*	Horný,1962,-1963
	Cyrtolites	Horný,1965a,b
	Cyrtonella	Wenz,1940; Rollins,1969
	Yochelsonellis	Horný,1962,1963; Rollins,1969
Bellerophontidae	*Bellerophon*	Knight,1947; Peel,1972
	?*Bucania*	Runnegar,1981b
	Megalomphala	Peel,1976
	Salpingostoma	Peel,1972
	Tremanotus	Peel,1972
Multifariidae	*Multifariites*	Bjaljj,1973
Sinuitidae	*Sinuites*	Knight,1947; Runnegar,1981b
	Sinuitopsis	Rollins and Batten,1968
	Sylvestrosphaera	Peel,1980

Table. 1

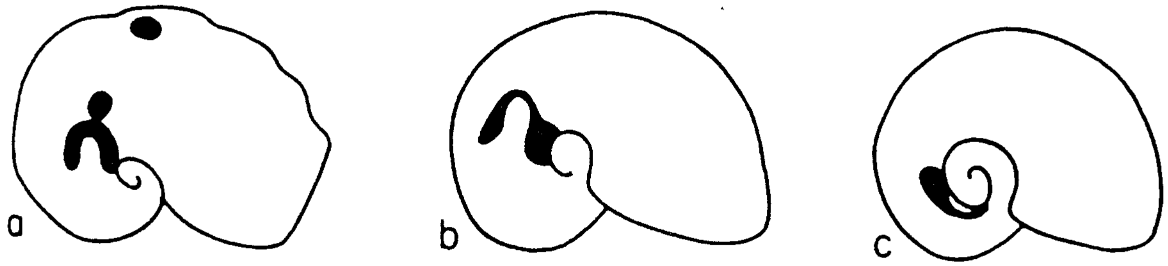

Fig. 2

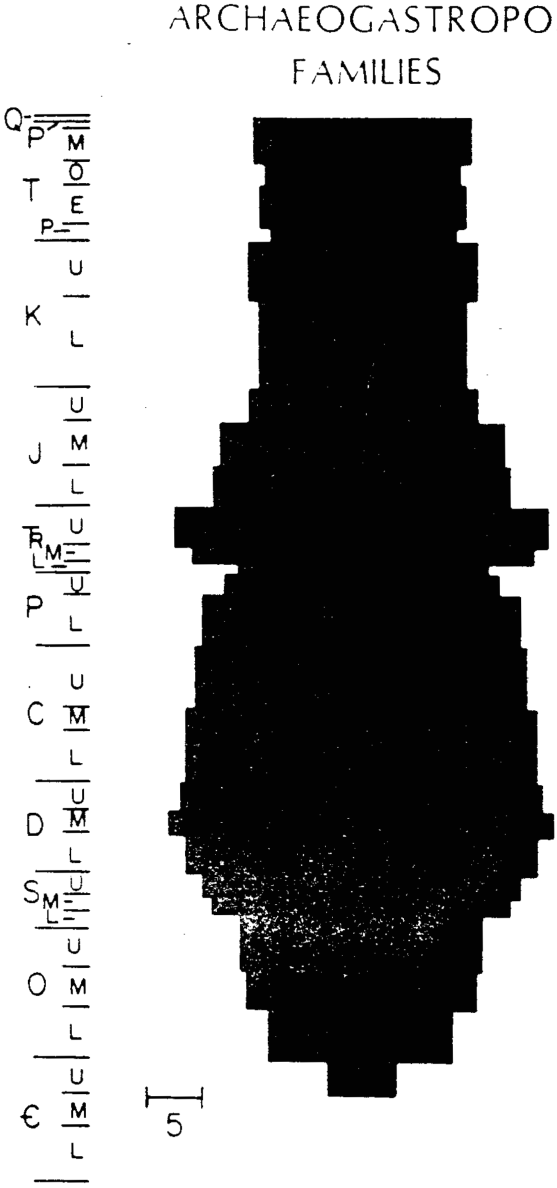
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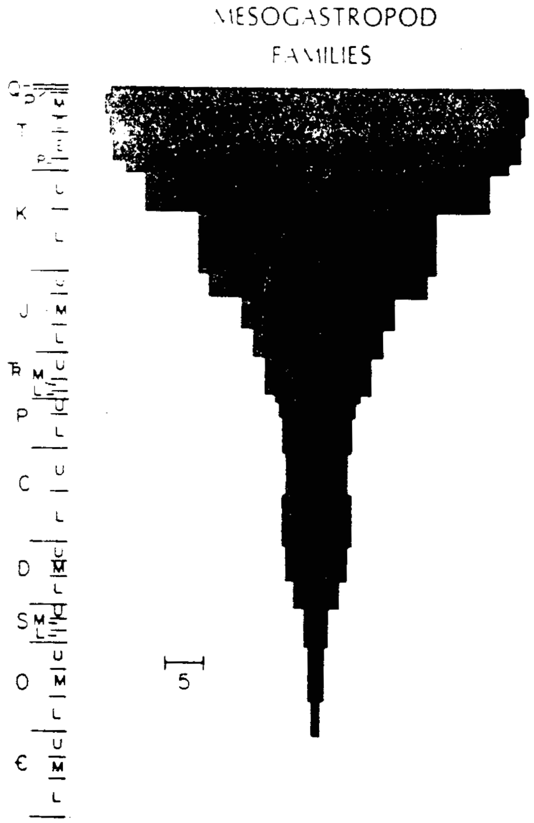
Fig. 3



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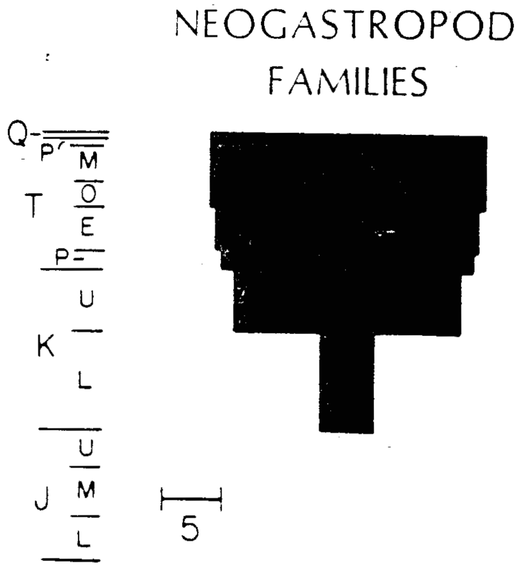

Fig. 5

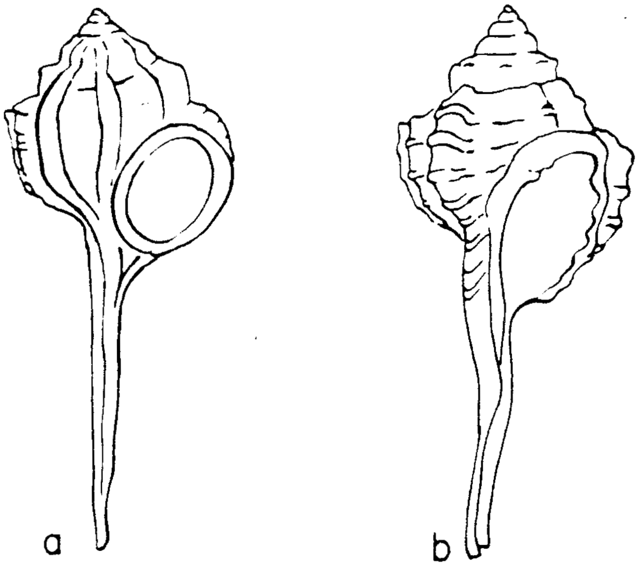

Fig. 6

In: BROADHEAD.T.W. &. WATERS. J.A., COEDITORES. 1980.ECHINODERMS. NOTES FOR A SHORT COURSE: KNOXVILLE. TENN., UNIV. TENNESSE DEPT. GEOL. SCI. STUDIES IN GEOLOGY 3, AND THE PALEONTOLOGICAL SOCIETY. P, 15-26.

5.5(d) AN OVERVIEW OF THE FOSSIL RECORD

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INTRODUCTION

Echinoderms are a moderately successfull phylum today with five classes and about 6,000 living species. They are found in all marine enviroments from achinoderms have a stable calcite skeleton made up of many distinctively shaped plates, spines,stem and arm segments, and other parts, echinoderms have the potential to produce a long and segments, and other parts, echibnoderms have the potential to produce a long and rich fossil record, and we find this to be true. Although our knowledge of this record is far fom complete, some past echinoderm faunas may have approached present-day echinoderm communities in number of coexisting genera and species. Also, many classes os achinoderms are known only from the fossil record-, and as many as 12-13 classes may have accurred together at some times in the past. Although they have a wide ecologic range today, most fossil eechinoderms are found in rocks representing shallow-water, subtidal, marine environments, either past continental shalves or epicontinental seas.

CLASSIFICATION

At present, fossil and living echinoderms are assigned to five subphyla and 20 classes (table 1) and total more than 3500 genera. The fossil record of echinoderms goes back at least to the Earlyy Cambrian and perhaps into the latest Precambrian (fig. 1). All of the living classes are longranging and have a fair to very rich fossil record; four extend back to the Early or Middle Ordovician and one may extend back to the Middle Cambrian. Several other now-extinct clesses were present and fairly diverse throughout much of the Paleozoic (Table 1 and Figure 1). In contrast, some Early Paleozoic echinoderm classes were very short-lived, known from only one or a few faunal zones, had low diversity (two classes have only a single described genus and one or two species), and may not have been verywidespread or abundant. Even though they were not very "successful" in terms of persistence through time or amount of diversity they had, these groups developed such unusual mophology that it would be diffficult to lomp them with members of ther classes. Although some authors have objected to having 20 classes of echinoderms (Beerbower, 1968; Breimer and Ubaghs, 1974), in my opinion most of these are probably valid (Sprinkle, 1976a).

TWO-STAGE INITIAL RADIATION

The initial explosive radiation of echinoderms from the Early Cambrian up into the Middle Ordovician (see Figure 1). This radiaton may have begun in the latest Precambrian, but only a few rare matazoan fossils are known from this interval. By the Middle Ordovician, this radiation had produced all 20 echinoderm classes known from the fossil record; however, the occurrence of holothurians based on microscopic sclerites in the Middle Ordovician has been questioned (Frizzell and Exlinc,1966,p.U658) and possible blastoid specimen have only recently been described (Broadhead, 1980). Most of the classes appeared suddenly from unknown ancestors, perhaps implying that they either may have been softor else showed very rapid evolution from some differently-appearing ancestral group (see Sprinkle, 1980).

Three echinoderm classes appeared in the Early Cambrian, six more in the Middle Cambrian, giving a total of eight living at that time, and possibly one more in the Late Cambrian out of a total of four (Figure 1). Several of these Cambrian classes (helicoplacoids, homosteleans, ctenocystoids) were very short- lived and rap;idly became extinct, and several others (crinoids, cyclocystoids) represent isolated occurrrences of groups that only later became more important. Members of these Cambrian classes have primitive morphology with numerous thecal plates, poorly developed pentameral symmetry, short and rather simple feeding appendages, and, in early medium-level suspension feeders, either a primitive attachment structure called a holdfast or short stem (Sprinkle, 1976b). Genera tend to be short-lived and have a limited geographic range, and Cambrian faunas usually have only 1-2 echinoderm genera occurribng together in any one unit. No echinoderm class became dominant in the Cambrian, and indeed the largest echinoderm class in this period (eocrinoids) has only about 32% of known Cambrian echinoderms. This pattern contrasts greatly with arthropods. where trilobites, with their huge diversity, represent over 90% of all known Cambrian arthropod genera.

This diversifications of echinoderms continued in the Early and Middle Ordovician with the appearance of many new echinoderm classes and several new ways of life and "designs". Five new echinoderm classes appeared in the Early Ordovician, giving a total of 10 classes living at that time (Figure 1). Five additional new echinoderm classes appeared in the Middle Ordovician giving a total of 17 classes, the highest number of echinoderm classes ever living at one time. Individual echinoderm faunas also became much more diverse at the generic and specific levels than in the Cambrian; many Middle Ordovician units have between 5-50 echinoderm genera ocurring together (for example, see Kolata, 1975, text-fig. 4; Sprinkle and Longman, 1977). These echinoderms were more advanced and specialized than their ancestors or relatives in the Cambrian. Calyes had fewer plates with better organized pentameral symmetry, longer and more elaborate feeding appendages, specialized respiratory structures in some groups, and a long stem in many suspension feeders. The first echinoderm herbivores and carnivores appeared during the Ordovician, along with many more medium to high-level suspension feeding groups. Until the Middle Ordovician, no single class of echinoderms had dominated the record although stemmed suspension feeders had become the largest general way of life (Figure 1, left). By the Middle Ordovician, crinoids had risen to become the dominant class of echinoderms, a position that they easily maintained throughout the rest of the Paleozoic.

MIDDLE TO LATE PALEOZOIC STABILITY

The interval from the Middle Ordovician to the end of the Permian is characterized by a gradual decrease in the number of echinoderm classes (Figure 3), a gradual expansion of diversity within the remaining classes, and development of adaptations for special ways of life, new environments, and batter protection from predators. Diversity at the generic and specific levels peaked in the Middle Ordovician, Early Devonian, and the Middle Mississippian (Figure 4), followed by a moderate decline through the rest of the Paleozoic until a major extinction ocurred at the Permo-Triassic boundary. Crinoids strongly dominated this Middle and Late Paleozoic record (Figures 1 and 4), much of the time exceeding the generic diversity of all other echinoderm classes combined. However, other classes such as blastoids and echinoids also showed the same general pattern of increasing and decreasing generic diversity (see Figure 1), although at a much lower level. As the generic diversity of echinoderms and other metazoans increased, archaic and inefficient echinoderm classes gradually dropped out of the record, so that the number of echinoderm classes dropped from 17 in the Middle Ordovician, to 14 in the Middle Silurian, to 11 in the Middle Devonian, to seven in the Middle Mississippian, and finally to six in the Late Pennsylvanian and Permian (see Figure 3). This "weeding-out" process probably resulted from such things as severe competition in certain ways of life, increased predation on echinoderms by groups such as cephalopods, fish, and crustaceans, perhaps lower primary productivity in the oceans (Tappan, 1971), evolution of actively burrowing deposit feeders that disturbed the sediment for attached epifaunal suspension feeders (trayer, 1979), and favoring of specialized over generalized forms in a nearly saturated marine ecosystem (Valentine, 1969).

During this time various groups of echinoderms developed new adaptations for living in special enviroments. Some groups became adapted to living under rough-water conditions, such as crinoids associated with reefs or banks (Lane, 1971) or edrioasteroids and rhombiferans living on current-swept hardgrounds or nearshore areas (Koch and Strimple, 1968; Sprinkle and Bell, 1978). These forms developed new adaptations for living in special environments. Some groups became adapted to living under rough- water condictions, such as crinoids associated with reefs or banks (Lane, 1971) or edrioas asteroids and rhombiferans living , cooler temperatures, less food and oxygen in the water column, soft muddy substratres, and periodic slumps or mud slides of the soft sediment. A few Early Permian crinoids and Blastoids are found associated with glacial deposits in Australia, implying that they lived in cold-water marine environments in high temperate latitudes 1980,p. 15-16; Breimer and Macurda, 1972, p. 300-301).

MESOZOIC TO RECENT REEXPANSION

All of the surviving classes of echinoderms slowly recovered in the Early Mesozoic from the severe Permo-Triassic-extinction, but crinoids never recovered the dominant position they had held in the Mesozoic and Cenozoic (Figures 1 and 4). Late Paleozoic regular echinoids with near-perfect pentameral symmetry had gradually reduced the number of plate columns in their test, made the test rigid instead of flexible, and increased the size of the protective spines (Keir, 1965). Echinoids with this advanced desing then barely made it through the Permo-Triassic ectiction while many of their competitors (and perhaps predators) did not. Surviving echinoids had a distinct advantage in these partly open environments, and they soon began to expand their diversity and morphologic range. By the JUrassic, several new type of epifaunal regular echinoids had evolved, and the first heart-shaped or irregular echinoids had appeared. These forms became mobile, infaunal detritus feeders, an entirely new way of life for echinoids, and many morphologic features were altered because of this change in enviroments. All of these various types of echinoids underwent a major radiation during the Cretaceous and especially the Early Tertiary (Fig. 4), producing a dominant class in echinoderms (like crinoids had been in the Paleozoic). Echinoids have decreased somewhat today compared to their generic diversity in the Early Tertiary, but still represent a major group (Fig. 1).

Asteroids, ophiuroids, holothurians, and even crinoids have only a moderate amount of fossil diversity in the Mesozic and Cenozoic, but today asteroids and ophiuroids are the largest groups of living echinoderms, common in both shallow and deep- water enviroments, and holothurians and crinoids are moderately large and diverse groups aldso. Most holothurians have tiny ossicles, fall apart easily. These factors affecting preservation probably explain why the present -day generic diversity of these groups is so much larger than their fossil record in the Mesozoic and Cenozoic. Also, ophiuroids, holothurians, and crinoids are quite diverse today in the deep sea, an environment representing only a small percentage of fossil occurrences. Based on the present-day diversity of these groups and knowledge about these preservational biases, the true Mesozoic and Cenoizoic diversity of these echinoderm groups is probably several times larger then indicated, but still smaller than that for the echinoids.

Fig. 1. Evolutionary history of echinoderm classes based on their Known Phanerozoic fossil record. Stratigrasphic range indicated by vertical scale; generic diversity indicated by orizontal width of band (see scale at right).

Fig. 2. Major ways of life shown by different groups of echinoderms.

Fig. 3. Number of preserved echinoderm genera at different times during the Late Precambrian and Phanerozoic. White - total diversity for all classes; note three peaks in Paleozoic, drop- off at Permo-Triassic boundary, higt levels in Cretaceous and Cenozoic, and much higher diversity in well known extant echinoderms.

Table 1. The author's preferred classifications of echinoderms down to the class level, with author of group, date established,stratigraphic range, nad number of genera . + indicates class or subphylum is extinct.

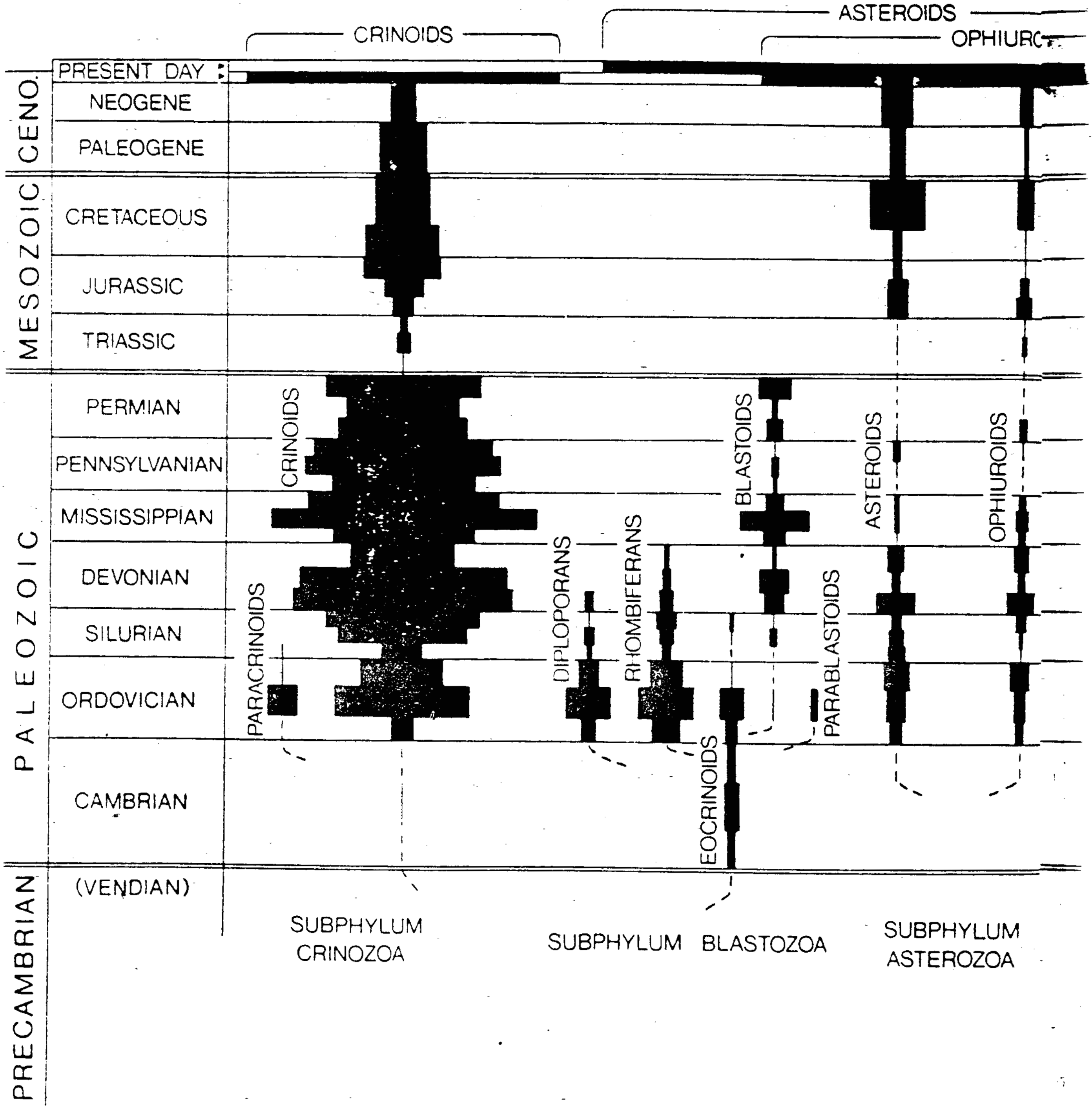

CRINOIDS
ASTEROIDS
OPHIURO
PRESENT DAY
CENO.
NEOGENE
PALEOGENE
MESOZOIC
CRETACEOUS
JURASSIC
TRIASSIC
PALEOZOIC
PERMIAN
PENNSYLVANIAN
MISSISSIPPIAN
DEVONIAN
SILURIAN
ORDOVICIAN
CAMBRIAN
PRECAMBRIAN
(VENDIAN)
CRINOIDS
PARACRINOIDS
DIPLOPORANS
RHOMBIFERANS
EOCRINOIDS
BLASTOIDS
PARABLASTOIDS
ASTEROIDS
OPHIUROIDS
SUBPHYLUM CRINOZOA
SUBPHYLUM BLASTOZOA
SUBPHYLUM ASTEROZOA

Fig. 1

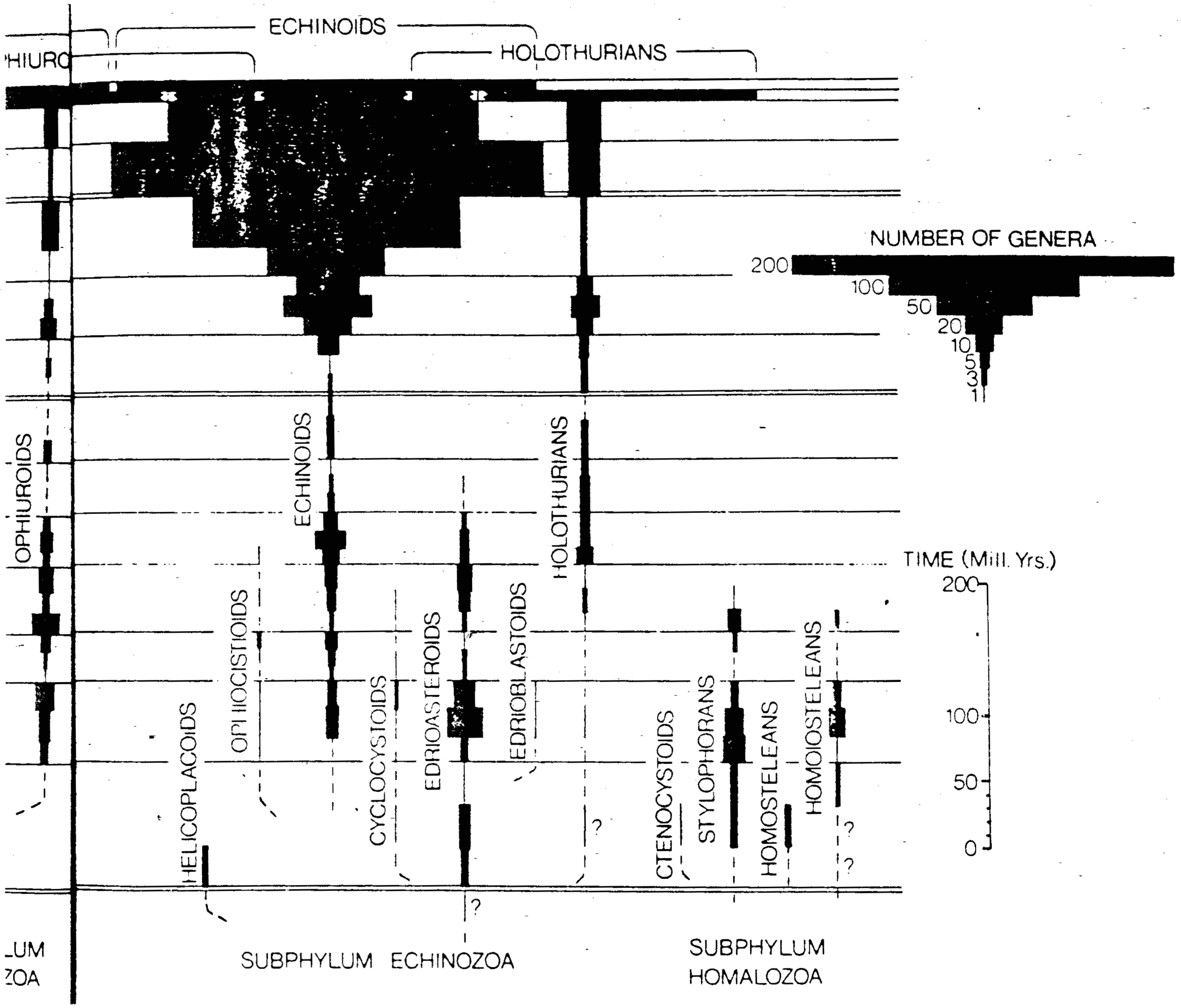
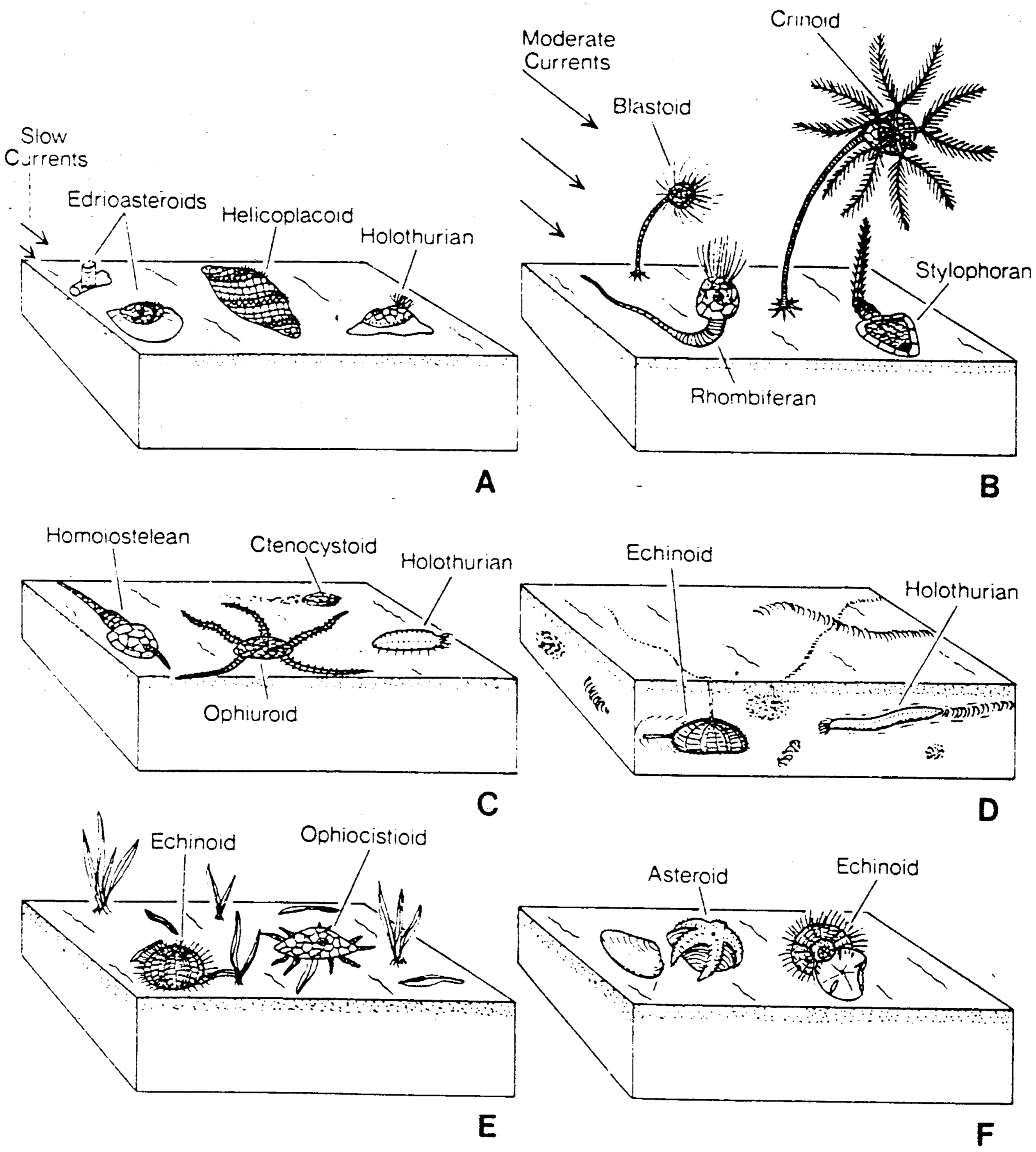
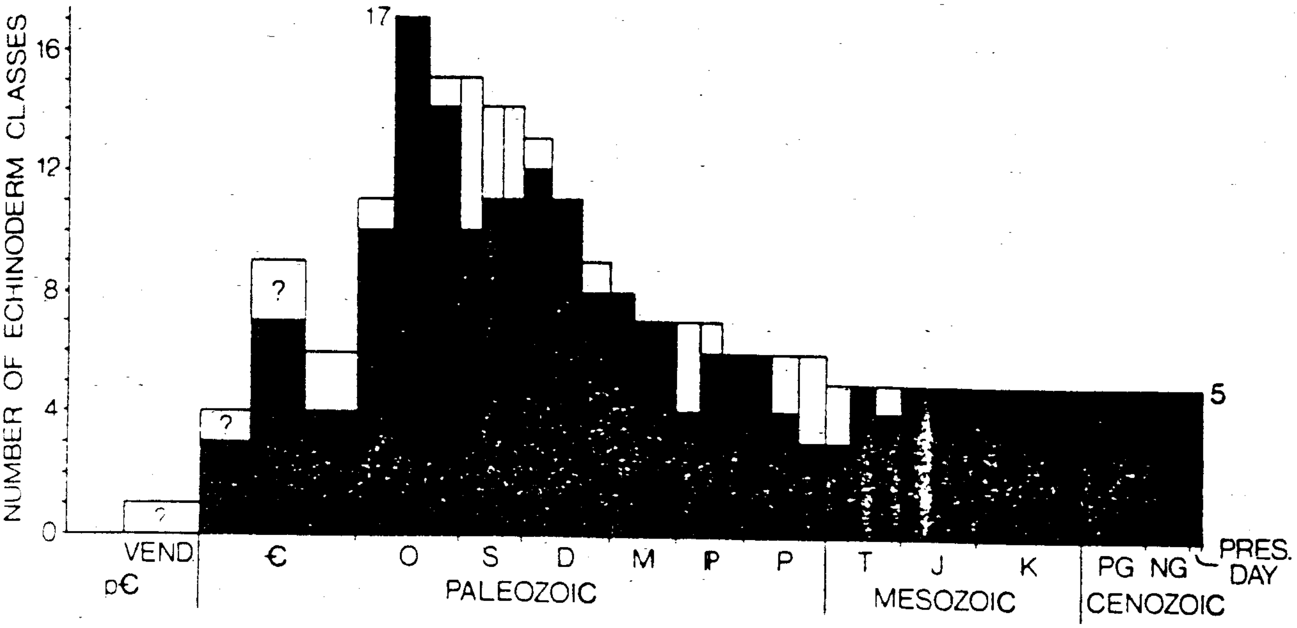

ECHINOIDS
HOLOTHURIANS
'HIURC
NUMBER OF GENERA
200
100
50
20
10
5
3
1
OPHIUROIDS
ECHINOIDS
HOLOTHURIANS
TIME (Mill. Yrs.)
200
100
50
0
OPHIOCISTIOIDS
HELICOPLACOIDS
CYCLOCYSTOIDS
EDRIOASTEROIDS
EDRIOBLASTOIDS
CTENOCYSTOIDS
STYLOPHORANS
HOMOSTELEANS
HOMOIOSTELEANS
?
?
?
?
-LUM
ZOA
SUBPHYLUM ECHINOZOA
SUBPHYLUM
HOMALOZOA

Fig. 1 (cont.)



NUMBER OF ECHINODERM GENERA

Fig. 2


NUMBER OF ECHINODERM CLASSES
0
4
8
12
16
17
5
?
?
?
?
VEND.
p€
€
O
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PALEOZOIC
T
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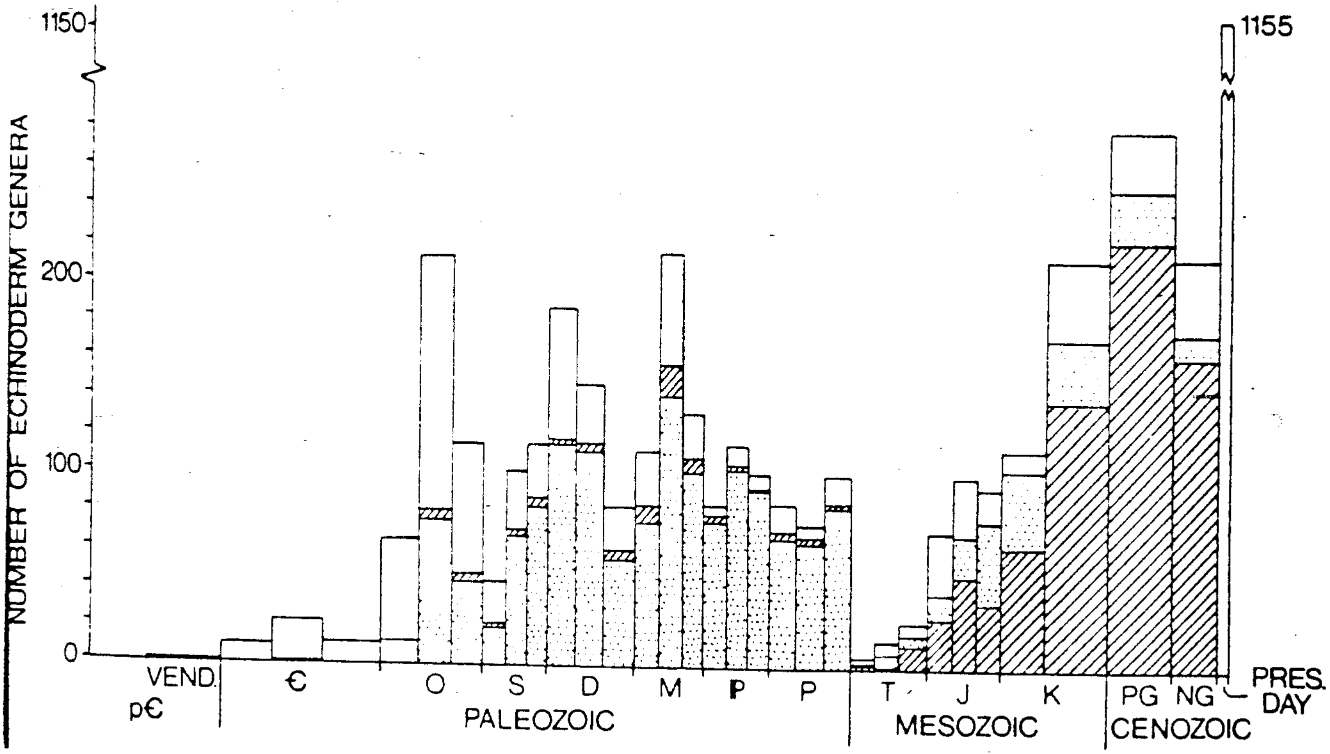
K
MESOZOIC
PG
NG
CENOZOIC
PRES. DAY

Fig. 3


NUMBER OF ECHINODERM GENERA
0
100
200
1150
1155
VEND.
p€
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O
S
D
M
ℙ
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PALEOZOIC
T
J
K
MESOZOIC
PG
NG
CENOZOIC
PRES. DAY

Fig. 4

- Phylum Echinodermata de Bruguière, 1791
  - Subphylum Crinozoa Matsumoto, 1929
    - Class Crinoidea Miller, 1821, M.Camb., E.Ord.-Holocene, ∿1005 Genera
    - Class Paracrinoidea† Regnéll, 1945, M.Ord.-E.Sil., 16-17 Genera
  - Subphylum Blastozoa† Sprinkle, 1973
    - Class Eocrinoidea† Jaekel, 1918, E.Camb.-L.Sil., 32-33 Genera
    - Class Rhombifera† Zittel, 1879, E.Ord.-L.Dev., ∿60 Genera
    - Class Diploporita† Müller, 1854, E.Ord.-E.Dev., ∿42 Genera
    - Class Parablastoidea† Hudson, 1907, M.Ord., 3 Genera
    - Class Blastoidea† Say, 1825, M.Ord.?, M.Sil.-L.Perm., ∿95 Genera
  - Subphylum Asterozoa Zittel, 1895
    - Class Asteroidea de Blainville, 1830, E.Ord.-Holocene, ∿430 Genera
    - Class Ophiuroidea Gray, 1840, E.Ord.-Holocene, ∿340 Genera
  - Subphylum Echinozoa Zittel, 1895
    - Class Edrioasteroidea† Billings, 1858, E.Camb.-M.Penn., ∿35 Genera
    - Class Edrioblastoidea† Fay, 1962, M.-L.Ord., 1 Genus
    - Class Cyclocystoidea† Miller and Gurley, 1895, M.Camb.-M.Dev., 2 Genera
    - Class Helicoplacoidea† Durham and Caster, 1963, E.Camb., 3 Genera
    - Class Ophiocistioidea† Sollas, 1899, E.Ord.-E.Miss., 6 Genera
    - Class Echinoidea, Leske, 1778, M.Ord.-Holocene, ∿785 Genera
    - Class Holothuroidea de Blainville, 1834, M.Ord.?-Holocene, ∿200 Genera
  - Subphylum Homalozoa† Whitehouse, 1941
    - Class Stylophora† Gill and Caster, 1960, M.Camb.-M.Dev., ∿32 Genera
    - Class Homoiostelea† Gill and Caster, 1960, L.Camb.-E.Dev., 12-13 Genera
    - Class Homostelea† Gill and Caster, 1960, M.Camb., 3^+ Genera
    - Class Ctenocystoidea† Robison and Sprinkle, 1969, M.Camb., 1 Genus

Table. 1

CAPITULO 6

DEPREDADORES Y ARRECIFES

6.1 PREAMBULO

Este capítulo está dedicado a los organismos cuya vida depende de tomar la de otros seres aún vivos, utilizándolos directamente como alimento. Esta modalidad ha sido ampliamente realizada por los metazoarios, y de hecho su surgimiento tuvo consecuencias biologicas importantísimas, ejerciendo continuamente una presion de selección, que ha influido poderosamente en la morfoestructuración y funcionamiento tanto de depredadores como de presas, manteniendo a ambos en un equilibrio dinamico, a veces harto precario. Las posibilidades de realizacion de esta modalidad son muy diversas, y han estado abiertas a variados disenos morfoesatructurales, que sin embargo deben de satisfacer ciertas necesidades funcionales básicas: Movilidad superior a la de la presunta presa; alternativamente a realizar ataques emboscados o sorpresivos a presas "desprevenidas:" mecanismos de captura y sujeción, mecanismos de trituracion o despedazamiento; el mantenimiento de una densidad de poblacion muy inferior a la de las presuntas presas, etc. Tales rasgos son reconocibles en mayor o menor grado en todo el espectro de depredadores, independientemente de su posición taxonómica, o de edad geológica, lo cual constituye una prueba de gran peso en favor de la tesis explicitada en el título de esta sección. El capítulo se ha subdividido en tres apartados, uno dedicado a los depredadores sésiles, otro a los invertebrados como depredadores móviles y una más a los vertebrados, en su calidad de depredadores móviles por antonomasia. En la selección realizada, se trató de mostrar una parte significativa de este espectro "depredacional" tanto en lo taxonómico como en lo geocronológico. En la primera parte, se incluyen dos trabajos: En el primero, Bjorn Neuman discute algunos aspectos de las estrategias de vida de los corales rugosos paleozoicos, que como se sabe son formas solitarias; reconoce cinco modalidades estratégias -anfitópicas, liberosésiles, fijosesiles y vagiles- que son parcialmente reproducidas por corales solitarios modernos. En la segunda, Colin Stearn muestra que tanto los constructores de arrecifes paleozoicos como los modernos, tienen formsas de crecimiento que responden a profundidad y turbulencia, asi como a la compleja interaccion de numerosos mbientales. En la porcion dedicada a los invertebrados depredadores, se incluyen 3 artículos. En el primer, Curt Teichert discute los principales rasgos de la evolucion de los cefalopodos, y muestra qque ésta puede entenderse en función a diferentes intentos de resolver el problema dse la flotabilidad, a su vez directamente reloacionado con la movilidad. En el último, Frederick Schram discute la filogenia de los crustáceos, grupo que incluye también numerosos depredadores y que tiene gran diversidad; este autor desarrolla la idea de que los crustáceos derivan de un tipo funcional que usaba las extyremidades cefálicas como únicas involucradas en la captura y/o traslado del alimento a la boca.

En el siguiente trabajo, Michael Taylor ofrece una nueva interpretación sobre la morfología funcional de uno de los grupos de reptiles más enfáticamente adaptados al dominio marino, el de los ictiosaurios. En el último, Larry Barnes discutre el origen y evolución de los cetáceos, que junto con algunos condrictios -tiburones- y osteictios, constituyen el grupo dominante de vertebrados marinos desde el Cenozoico Temprano.

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6.3 DEPREDADORES SESILES

6.3 (a)

Some aspects of life strategies of Early Palaeozoic rugose corals.

Björn E.E. Neuman

LETHAIA

Neuman, Bjorn E.E. 1988 04 15: Some aspects of life strategies of early paleozoic rugose corals Lethaia, vol 21, pp. 97-114 Oslo ISSN 0024-1164.

Comparatively little is published about the palaeobiology and life strategies of Ordovician and Silurian rugose corals from Balto-Scandia. MOst modern scleractinian corals are hard-bottom dwellers and the type of substratum on which the planula larvae can settle must be hard and clean. Rugose corals with an attachment disc or scar with or whithout talons attached in their early growth stages on hard bottom or on skeletal fragments which acted as hard-botton patches on soft botton, but are seldom found still anchored to the substratum. After further growth, either the particle used as the attachment substrate cannot carry the weight of the individual any more or the attachment becomes troo weak to provide the necesdsary suport for the increased weight. The coral falls over, normally onto a soft sediment. If the coralwas adapted for a life lying on its side on a soft botton, it assumed a recumbent mode of life,. Inspired by Jaanusson (1979)and the papers on the ecology of corals by Elias (1984) and brachiopods by Bassett (1983). I started an examination of some unusually well preserved material of number of well-represented species of solitary rugose corals from the Silurian of Goland. The possible life strategies of each species, besed on detailed observations of the external and internal structures of numereous conspecific corallites, are discussed below. The various categories of life strategies for the rugose corals studied for this paper are summarized in Fig. 15..

DESCRIPTION OF THE MATERIAL

RHABDOCYCLUS OCKSARVENSIS n. sp.
Figs. 7F-K and 8A-G

Holotype.- RM CN59*******126a. figured in Fig. 8A

Type stratum and locality.- Hemse beds. Hemse Marl; Likmide 1 (ditchat Oeksarve farm, 1.9 km NV of hemse perish, Gotland.

Diagnosis.- Small, low and broadly patellate Rhabdocyclus species with an almost straightn or weakly conical apex; corallite in early neanic stage sharply bent at rigth angles towards the apex.

Taxonomic remarks.- In connection* with a description of other species of Rahabdocyclus from Gotland, R. ocksarvensis will be described in detail. The general morphology is clearly seen in Fig.8A, showing small preadult specimens. The most* important morphological features are presented below under description of growth.

DESCRIPTION OF GROWTH

Even in this well-preserved topotypic sample, the species is seldom found with a complete apex. The larvae mus have been able to attach themselves to horizontally vertically and obliquely oriented surfaces, as indicated by the great variability in the direction of growth of the apex.

Specimens with a concave cardinal side and a prolonged fastening disc on that side were probably attached to oblique surfaces and had to reorient themselves in order to attain the best direction for further growth. In a recumbent position the corallites were always oriented with the cardinal side downwards and continued to grow obliquely apwards. If this orientation was disrupted then the upwards growth was readjusted. The event of readjustement is marked as oblique lines of rejuvenescence. A very high percentage of the large specimens had succeeded in resting with the convex cardinal side downwards throughout life. Some large specimens, however, had failed to adopt the normal position. They initially reclined on one of their alar sides but managed subsequently to adjust the direction of growth such that it continued upwards. The change of growth direction of growth such that it continued upwards. The change of growth direction is indicated by a very marked zone of rejuvenescen, the cardinal side becoming twisted during further growth into the correct growth position . This has been observed in a very limited number of spencimens of the sample, but a few have reoriented the growth direction three to four times. Reorientation of growyth direction can occasionally be observed in fairly small specimens. This species is clearly ambitopic with as fixosessile early stage, later becoming recumbent.

LACCOPHYLLUM LINDSTROEMI (Weyer,1978)

Taxonomic remarks.- This species was described and illustrated in great detail by Weyer(1978). His description was based on only three specimens derived from an unknow locality on Glotand. For the present paper large collection from the Slite Beds of the locality Svarvare (see Laufeld 1974:132) was examined. Numereous serial sections have shown faily large variation in development of the morphogical structures, including growth stages identical or similar to Sutherlandinia gotlandica Weyer, 1978 and Sutherlandinia erratica Weyer, 1978. S.gotlandica seems to be a clear synonymy with S. erratica cannot at present be proved with equal certainty. A more detailed description of the syringaxonids from Gotland is under preparation.

Description of growth.- Laccophyllum lindstroemi has a small, 10 to16mm high, normally erect corallite with a flat attachament disc on the cardinal side. The disc can become rather large and reache 1/4 of the total height of the corallite and have irregular peripheral flanges but no talons (see Fig. 11G-Land 12A, D). In most specimens the outermost tip of the apex is broken. Where best preserved, it seems to be conical and have a flattened cardinal side (basal disc). The almost complety flat attachment disc (see Fig.11 and 12)indicates that the corallite was fastened to a flat substrate, such as a skeletal fragment. Some specimens have rather peculiar, small scar-like fastening structures. Orientation in a preferred life position is proved by the fact that the apex is fairly often sharply bent towards one of the alar sides (Fig. 12C). In addition, all specimens which were obviosly fixed to an almost horizontal surface have almost the same apical angle, indicating a simliar orientation in life. Other specimens were obviously fixed to vertical or obliquely oriented skeletal fragments (Fig. 11k) with basal discs oriented more in the medial plane. In a few cases this species is found actually anchored to a skeletasl fragment. Fih. 12B shows one these specimens with a well-preserved apex.

DISCUSSION

The material examined indicates that in the Silurian of Gotland solitary rugose corals were mostly soft substrate dwellers resting free on the level sea floor. In these forms the corallite was initially attached to some hard or firm grain but subsequently became detached from it and then conducted a recumbent n-mode of life. In many species the asttachment area is very small or not recognizable at all, indicating that the particle which sized sedimentary grain. Thus the coral could settle down directly on a soft bottom even if there were no patches of bionegic hard bottom. In spite of the ainitial stage os-f attacment such forms can preferably be classifield as liberosessile. None of the recumbent species examined for this paper had an attachement area of a size which would suggest that they were attached to apatch of hard bottom, that is to say, to a particle of the size of at least gravel pebble (2mm or larger). Therefore none of this group can be classified confidently as ambitopic. Examination of other species of solitary rugose corals from Glotand also indicates that strictly ambitopic forms obviously were rare, that is forms which were attached to hard bottom during early growth stages but werecapable. These various life strategies are discussed in some detail below.

ORIENTATION

Even if rugose corals are seldom found in situ, some specimens clearly indicate a preferred orientation of the calice upwards with the rim parallel or subparallel to the horizontal plane. If the orientation of most attachment structures indicates fastening of the corallite to almost structures indicates fastening of the corallite and somewhat lower on the cardinal side. ZThis is most evident in forms with attachment discs, with or without talons. Ketophyllid and solitary kodonophyllid corals seem to have the level of the calice oriented horizontally. The growth pattern of species of Dokophyllum from Gotland normally shows a very regular straight upwards growth, resulting in a turbinate shape. Some specimens of ketophyllid corals which have fallen over and continued to grow, show a very sharp angle between the former and later growth directions. This is illustrated here by specimen of *Dokophyllum bullatum* from the Slite Beds, from the locality Lerbeget, Stora Karlso, Gotland (Fig. 14A). This specvimens does not show any reorientation of the4 cardinasl side in conection with the alteration of the direction of growth. In contrast, this is observed in fallen specimens of *Phaulactis angelini* (Fig. 10H in this paper). Some of the species examined above clearly show that the apex is curved in the alar plane. The reason for this is probably to oriented the calice towards the main direction of currents and food intake. Olsson (1985) demonstrated in specimens of *Stauria favosa* that the cardinal septa of most corallites are consistently oriented in almost the same direction McAuley & Mattison (1987) recently oriented in almost the same direction.The problems concerning directional orientations of solitary rugose corals based on Upper Ordovician material from North America.

CONCLUSIONS

Careful observations of external morphogical features of well- preserved corallites of different rugose taxa provide valuable information on life strategies and other palaecological aspects. The different categories of life strategies among rugose corals and their relation to the substrate are summarized in Fig. 15. In well-preserved specimens of liberosessile forms an examination of the orientation of the growth-lines reveals changing from early juvenile attachjed to a subsequent recumbent mode of life. In fixosessile forms the growth direction changes comparatively slowly, attached as they were throughout life by well developed attachment discs or scars with or without talons. Both straight and curved corallites are ammon in this group. Rhizosessile forms have secondary rhizoid (= root-like) holddfasts. The rizoid holdfasts of Dokophyllum species must have been rounded, tentacle-like processes emamating from the polyp which secreted non-tabuled tubes of calcite. These processes must have been either cut or withdrawn rather quickly after the tube-like skeleton was formed. Tabuled skeletons of the holdfasts of operculate corals, such as *Rhizophyllum* and *Goniophyllum*, are normally connected via tube-channels with the calice. Vagile forms could possibly be represented by small discoid corals such as *Palaecyclus*. Although rugose corals are seldom found in situ they sometimes show a preferred life orientation. As several authors have reported, most solitary corals have the cardinal septum on the most convex side of the corallite, and this is normally placed downwards both in recumbent forms, as well in most fixosessile forms.

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Fig. 1. Holophragma calceoloides (Lindstrom,1886). Reconstruction of life strategies and habits.

Fig. 2. Holophragma calceoloides (LIndstrom, 1866).

Fig. 3. Rhegmanphyllum conulus (Lindstrom, 1868).

Fig. 4. Rhegmaphyllum conulus (LIndstrom, 1868).

Fig. 5. Palaeocyclus porpita (Linne,1767). A-G Reconstructions of life strategies and habits.

Fig. 6. Palaeocyclus porpita (linne,1767).

Fig. 7. Rhabdocyclus ocksarvensis n. sp. A-E Reconstruction of life strategies and habits.

Fig. 8. Rhabdocyclus ocksarvensis n. sp.

Fig. 9. Phaulactis angelini (Wedekind. 1927). A-F The normal life strategies and life habits.

Fig. 10. Phaulactis angelini (Wedekind, 1927). A-B, Transverse sections showing the internal morphology.

Fig. 11. Laccophyllum lindstroemi Weyer, 1978. Recontruction of life strategies and habits.

Fig. 12. Laccophyllum lindstroemi Weyer 1978. The specimen was originally attached to a vertical skeletal grain, indicated by the almost vertical attachment disc oriented to the right in the picture.

FIG. 13. Dokophyllum. Reconstruction of life strategies and habits of this typical rhizosessile genus.

Fig. 14. Dokophyllum annulanum (Wedekind, 1927). Specimen whith has fallen aver and continued upward growth.

Fig. 15. Summary of categories of life strategies of rugose corals distinguished in this paper.

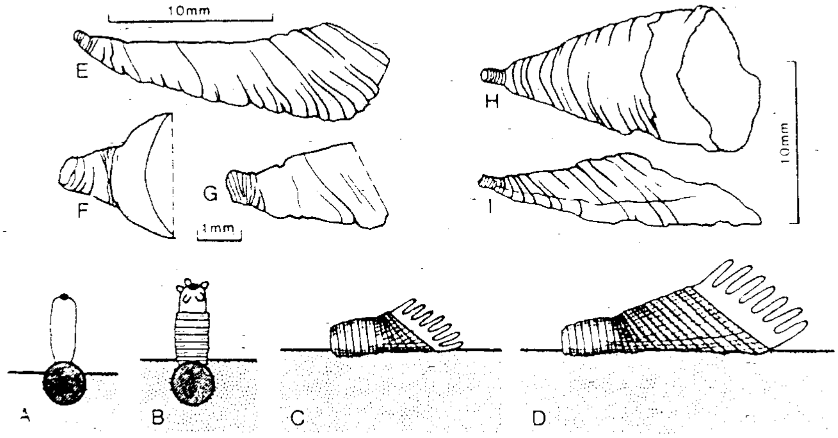
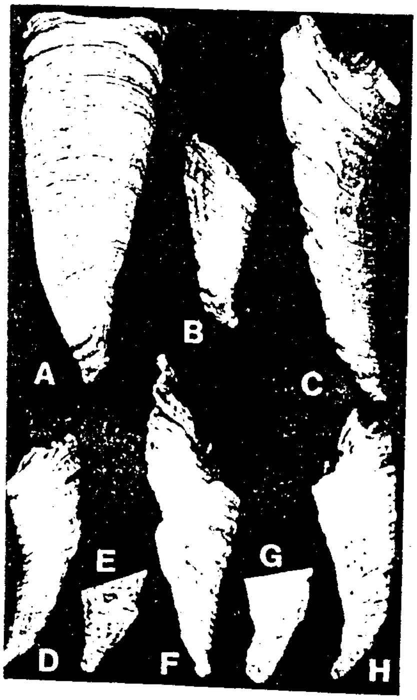


Fig. 1



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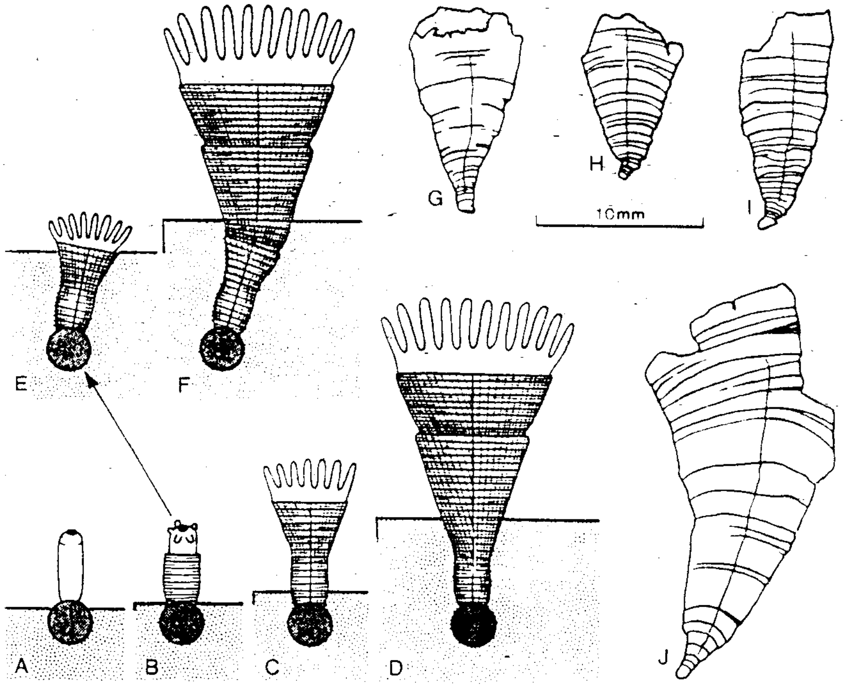

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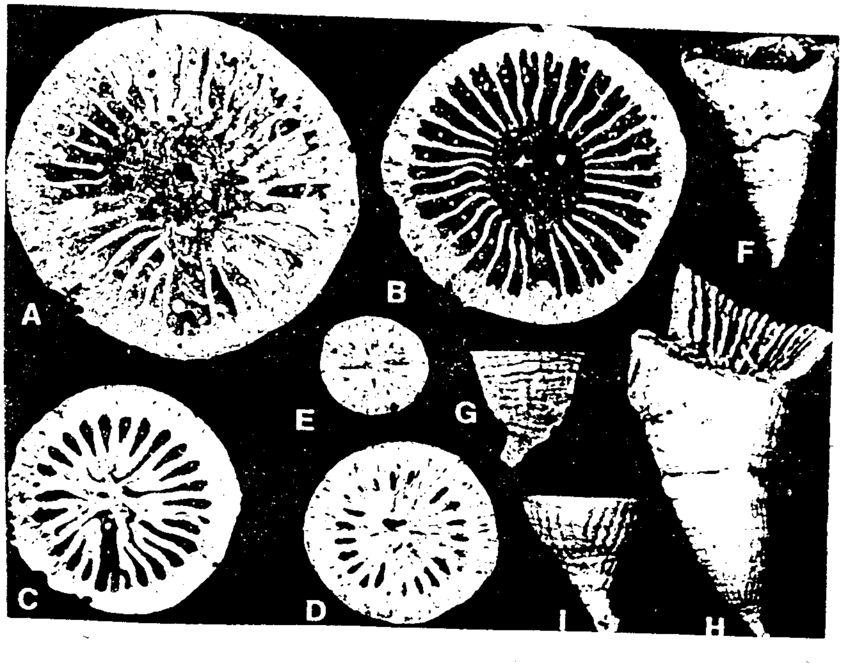

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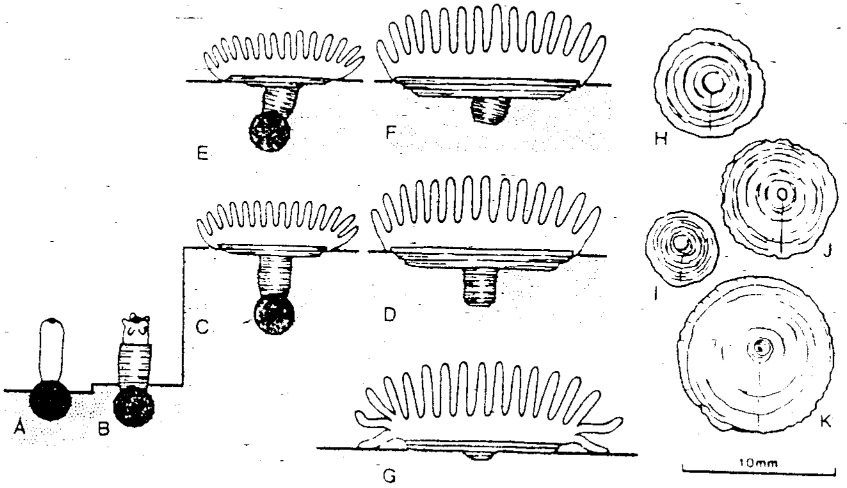

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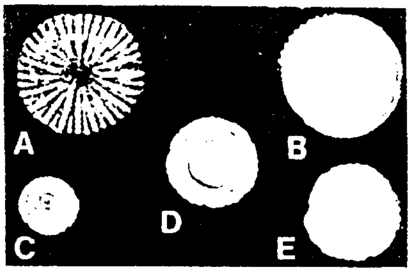

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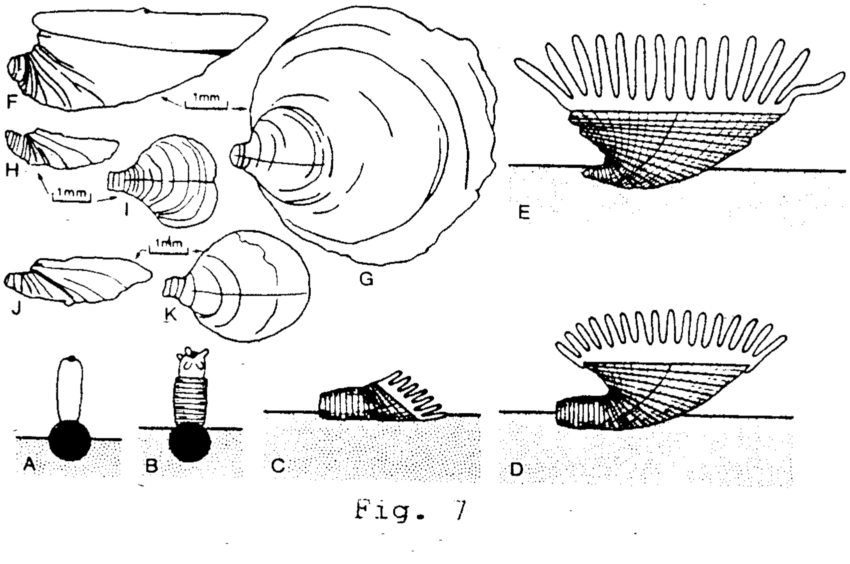

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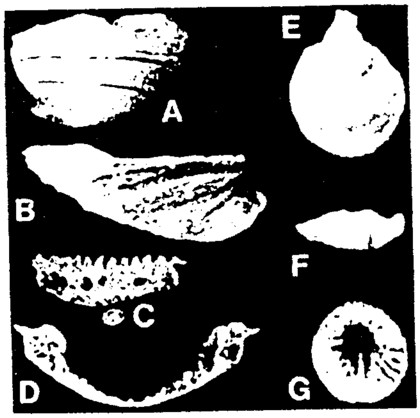


Fig. 8

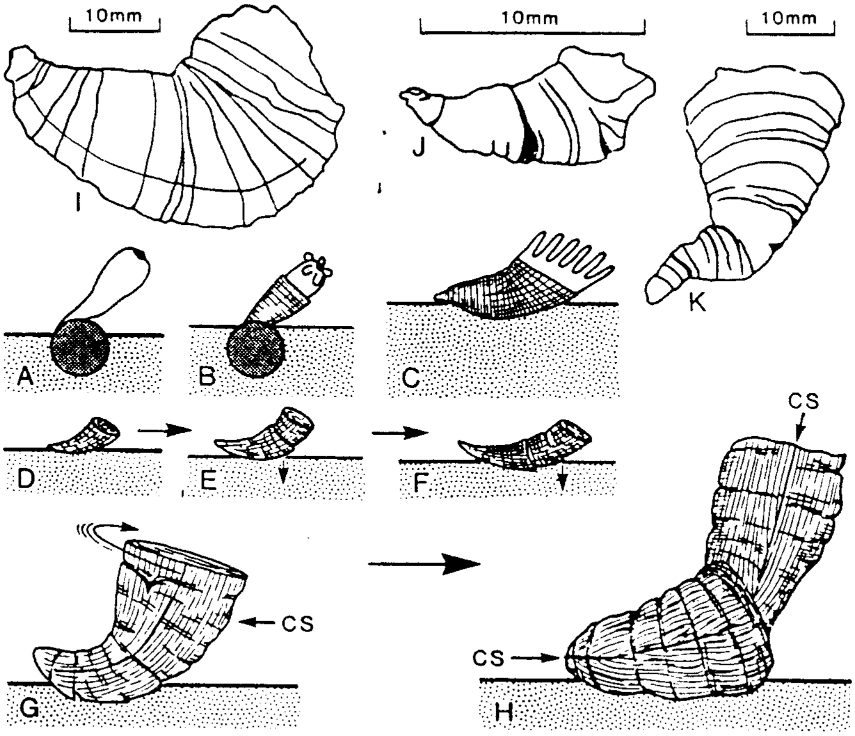
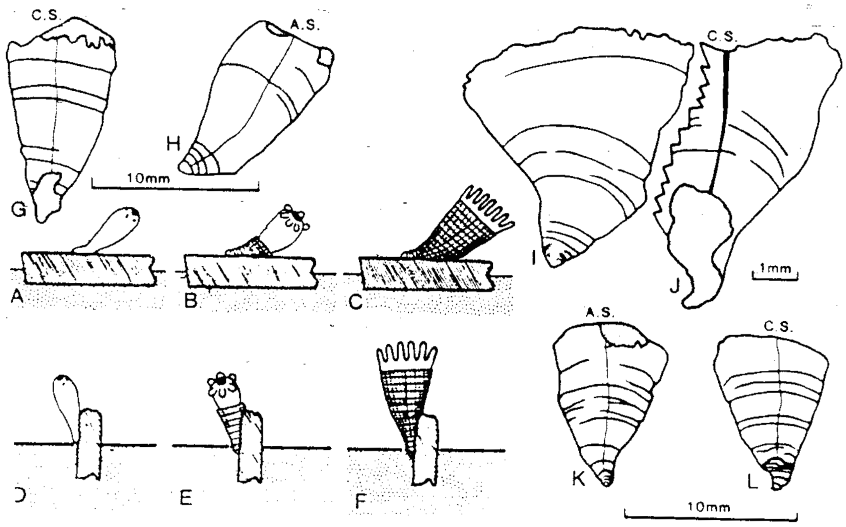


Fig. 9

Fig. 10



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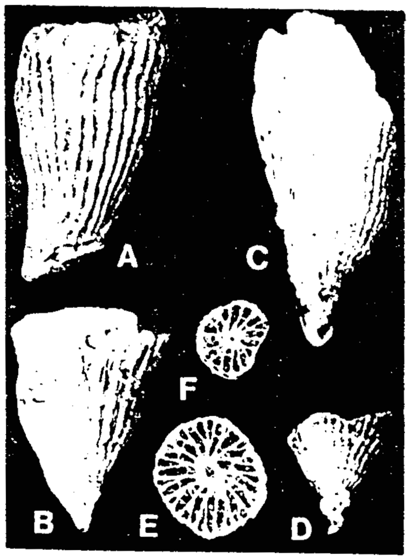

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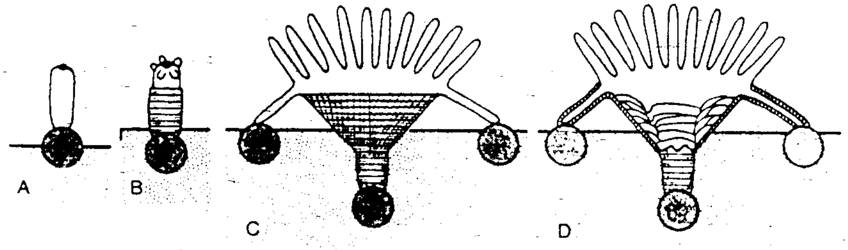


Fig. 13

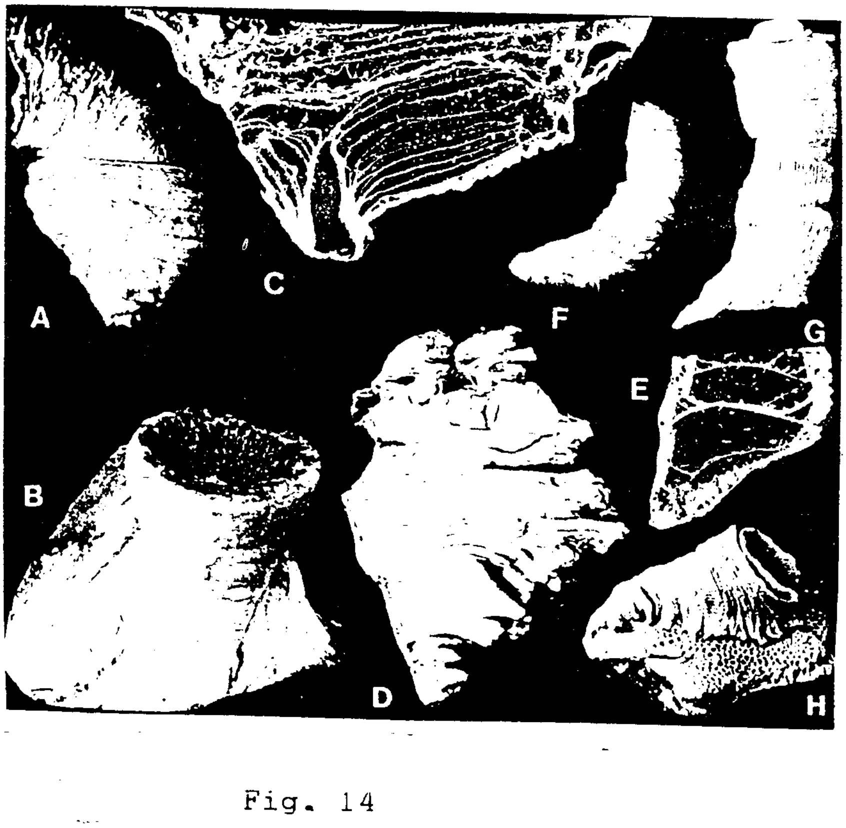
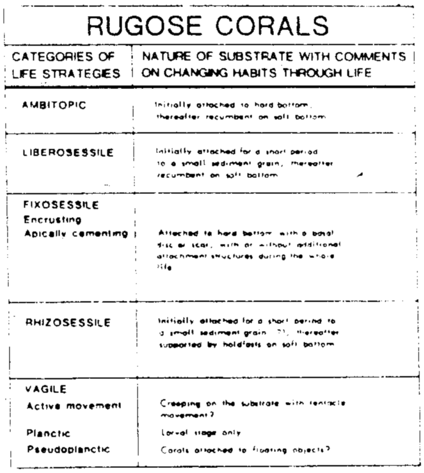


Fig. 14

Bjorn E.E. Neuman



RUGOSE CORALS

CATEGORIES OF LIFE STRATEGIES	NATURE OF SUBSTRATE WITH COMMENTS ON CHANGING HABITS THROUGH LIFE
AMBITOPIC	Initially attached to hard bottom, thereafter recumbent on soft bottom
LIBEROSESSILE	Initially attached for a short period to a small sediment grain, thereafter recumbent on soft bottom
FIXOSESSILE Encrusting Apically cementing	Attached to hard bottom with a basal disc or scar, with or without additional attachment structures during the whole life
RHIZOSESSILE	Initially attached for a short period to a small sediment grain (?), thereafter supported by holdfasts on soft bottom
VAGILE	
Active movement	Creeping on the substrate with tentacle movement?
Planctic	Larval stage only
Pseudoplanctic	Corals attached to floating objects?

Fig. 15

6.3 (b)

Paleobiology, 8(3), 1982, pp 228-241

THE SHAPES OF PALEOZOIC AND MODERN REEF-BUILDERS: A CRITICAL REVIEW.

COLIN W. STEARN

INTRODUCTION

Within the last 20 years the distribution of shapes of Paleozoic stromatoporoids and corals has been the su7bject of many studies. The basic assumption of these studies is that the distribution of shapes of extinct reef-builders can provide a key to the interpretation of the anciet enviroment in which these animals lived. Bed to bed gradients within the stratigraphic succession have been atributed to allogenic and autogenic succession(Walker and Alberstadt 1975). An assumption of these studies is that the enviroment of deposition is an important control of the shape of reef-forming organisms and that genetic factors may determine the internal structure but have less influence on the growth form. Either implicitly or explicitly reference is made in of these studies to the zonation of growth forms that occurs on modern reefs. The basis of the paleoecological deductions are generally uniformitarian; that is, paleoecologists reason that because certain growh forms in modern reefs are controlled by gradients in such environmental parameters as radiance flux, food.I summarize studies of shape distribution of stromatoporoids in Paleozoic reefs and assess the validity of their paleoeclogical conclusions in the light of modern studies.

SPECIES ZONATION

Coral reefs exhibit a zonation of taxa that is parallel to shorelines and is apparently controlled by enviromental gradients which are normal to the seaward slope. WELLS(1954) and Stoddard(1969) review early papers on species zonation. The species zonation of coral reffs is poorly defined; that is, each ecologic zone contains a large number in cammon with adjacent zones, probably because corals are tolerant range of microenvironments.

SHAPE ZONATION

Few surveys have been published in which the zopnation of a reef is formulatedon the basis of shape alone, but some quantitative species surveys allow variations in shape across a reef to be plotted if assumptions are made that the species grow in forms that are typical.

Barnes et al.(1967) divide the corals of Aldabra into seven shape classes and distinguish six shape zones which are summarized in Fig.3. They suggest that the major controls on shape zonation are ligth intensity and surfaction. The shape zonation that James and Ginsburg (1979) suggest applied to their owen investigations in Belize and to others' work in the Indian and Pacific oceans is replotted in Fig. 3. These figures show that zones have been defined on the bisis of growth form encompass a variety of shapes and are recognized on the basis of changes in propotion of the shapes present. Most shape zones are inhabited by a complete range of forms. Even observation underwater shwos ,that each zone of a reef contains corals of many different shapes.

The variety of shape zonations shown by figs. 1 to 3 and the papers reviewed above indicate that localities that differ in their exposure to waves or in underwater topography hav3e different patterns of shape zonation. Geister(1977) ascribes the zonation of growth forms may differ between biogeographic provinces. There is some evidence (fig.1-3) that inshore zones of Caribbean reefs are typically occupied by corals of domal form and that in Indo-Pacific reefs this zone is occupied by branching corals (James and Ginsburg 1979). Growth forms, like that of Acropora palmata that are typical of the breakers zone in Caribbean reefs, are not found in Indo Pacific reefs, are not found on modern reefs, there is some evidence that an onshore to offshore succewssionfromthickbranched, to domal, to fine branched and tabular is cammon.

CONTROLS OF GROWTH FORMS

For 150 yr marine zoologists have struggled to define the controls on growth habit of reef builders. Because many species of corals are defined by fgrowth form, discrimination of valid species requieres a definition of these controls. There is no argument that the growth pattern is a product of the interaction of genetic factors (that is, a typical growth program inherent in the portance of these two influences.

DISCUSSION

Variation in a single environmerntal factor or a simple combination of them cannot account for the distribution of shapes on cannot account for the distribution of shapes on a reef. Nor is shape zonation on a modern coral reef caused by a simple vegetative response to environmental parameters. The basic growth pattern of a coral species is genetically dictated. Plasticity of form is however common in reef corals aqnd may be one of the reasons for their success (Foster 1980), but extent of plasticity varies greatly from species to sopecies.

ENVIRONMENTAL SIGNIFICANCE OF STROMATOPOROID SHAPES

The evidence for assinig atromatoporoids of difrent growth patterns to different environments on ancient reefs is varied. Some writers have assigned shapes to environments without offering particular evidence for the association(St. Jean 1971; Tsien 1974; Abboot 1976).

CONCLUSIONS

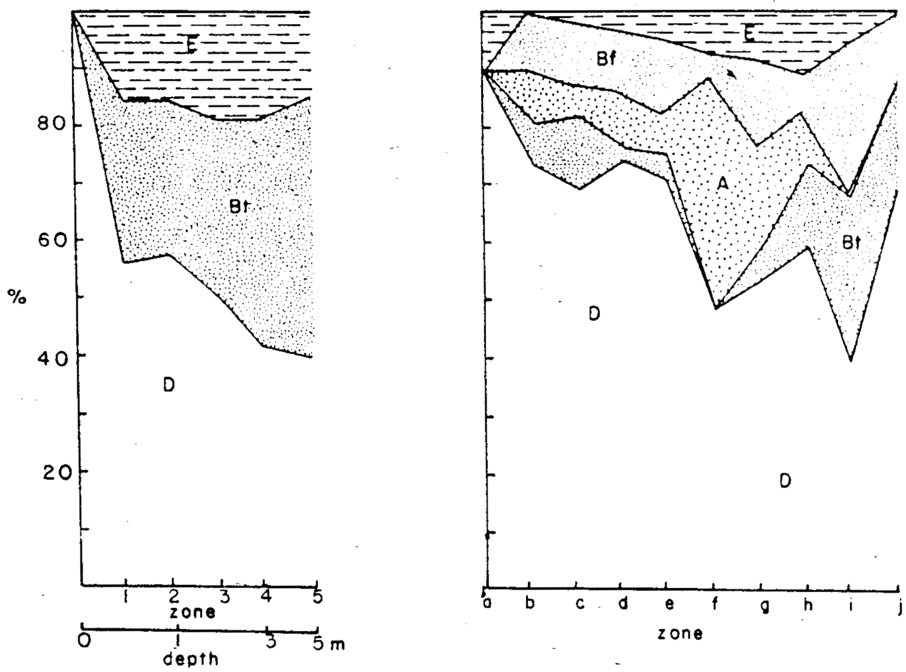
The aim of paleoecologists is to reconstrucpast environments on the basis of skeletons of animals and plants that were adapted to them.Paleoecologistshave been tempted to interpret skeletal features as vegetative responses to interpret sketal in particular seem to have followed the extreme view of the t the turn of the century ecologist in concluding that the various zones of the reef should be populated by distinctive growth-forms whose occurrence is controlled by one or a few, environmental parameters.

Fig. 1. Zonation in the shapes of corals on two Caribbean reefs. The porcentage of cover by each shape is plotted against the zones of the reef from shoreward (left) to seaward (right). To aid comparison between diagrams, the same patterns are used for the shape groups in each.

Fig. 2. Zonation in the shapes of corals al Piscadera Bay, Curacao (from data in Bak 1977). Percentage of cover by each shape is plotted agains stations on a line survey; depths have been estimated from the bathymetric profile in Bak's diagram.

Fig. 3. Zonation in the shapes of corals at Aldabra and Belize. Porcentage of cover by each shape is plotted against depth inb meters. The shape classes are those recorded by the describers of these reefs. right- Belize Barrier reef (replotted from James and Ginsburg 1979).

Colin W. Stearn



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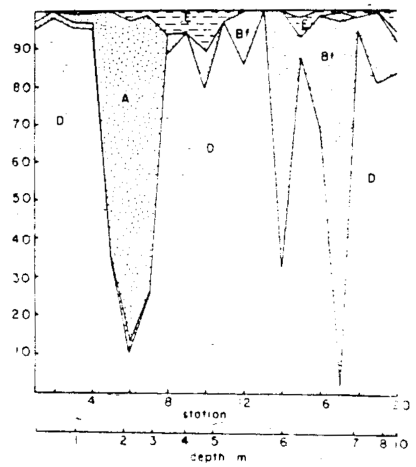
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Fig. 2

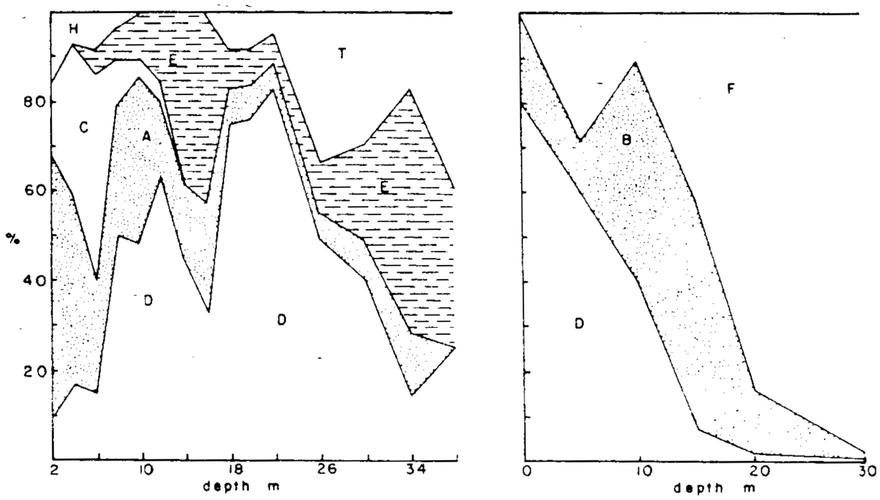
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Fig. 3

6.4 DEPREDADORES MOVILES: INVERTEBRADOS

In C.Teichert & E. Yochelson, Edits., ESSAYS IN PALEONTOLOGY & STRATIGRAPHY, R.C. MOORE COMMEMORATATIVE VOLUME: Univ. Kansas, Dpt. Geol., Spec. Publ. 2, pp 162-210; Univ. Kansas Press, Lawrence, Kan. & Londres, Ingl.

6.4 (a) Major Features of Cephalopod Evolution

Curt Teichert, 1967.

INTRODUCTION

During the past decade more progress has been made toward an understanding of the major features of the Cephalopoda and of their relations than during any similar period before. In this interval appeared all but one of the volumes of the Treatise on Invertebrate Paleontologii dealing with cephalopods; significant new belemnite faunas of Paleozoic age were described; the origin of the ammonoids was document , and probably also for *Nautilus*; and many other advances were made.

This paper attempts to present the major structural innovations in their shell morphology. This means that emphasis is on discussion of evolution of characters generally regarded as indicating ordinal taxonomic rank. Evolution of characters generally, will not satisfaty every cdephalopod worker, By and large, however, it is believed that the plotted data conveny a generally accurate picture of morphologic diversification and evolutionary rates within individual orders. These features would have marited more detailed interpretative discussion which had to be omitted because of space limitations.

Cephalopod Evolution

make it possible for paleontologists to travel, with no loss of time.to museums and collecting localities in far distant places in order to study and compare with ease types of genera and species astablished by many authors of many periods, who formerly worked with little mutual contact in geographically separated areas. The result will be a consolidation of the taxonomic structure of the Cephalopoda as well as other groups, that could not be achieved by piecemeal work on a parochial basis. Several such worldwide studies are now under way. But these should not deter us from occasional stocktaking.

THE OLDEST CEPHALOPODS

The origin of the cephalopods, like that of other mollusks, is shrouded in the darkness of the Precambrian Era. For Volborthella this was stated long ago (Teichert, 1929). More recentlo, Balashov (in Ruzhentsev et al., 1962) established the genus Vologdinella (family Vologdinellidae). While interpretation of Lower and Middle Cambrian shells as cephalopods is controversial, no controversy exists in regard to a small group of fossils which occur close to the top of the Cambrian System and whose affinities are conceded by every paleontologist.

The only additional specimen of this genus was obtaind from Liao-tung, Manchuria, across the Yellow Sea from Shantung (Kobayashi, 1953). Fourteen years later Korder (1949) reported finding two specimens of late Cambrian.

Further, Flower (1964) reported interesting new discoveries of Upper Cambrian cephalopods in the Llano Uplift of Texas. Onesingle specimen was considered to be a new species of Plectronoceras; four additional fragmentarty specimens ofPalaeoceras were described; another species of the same genus was described from four small fragments; and a new genus, Balkoceras was established on four small fragments of exogastric shells. For the same genus was corresponds biostratigraphically to the ighest of 17 Cambrian time had passed before cephalopods made their first appearance.

This is the earliest, and simplest, device developed by cephalopod evolution unfolds, it will bee seen that most of its major features can b e understood as attempts to cope with the problem of buoyancy in a great of ways.

EARLY ORDOVICIAN ERUPTION

The Ordovician was a time of tremendous proliferation of cephalopods, accomplished in three major steps:(1)at the beginning of the Ordovician, (2) in the middle of the Early Ordovician, and (3) at the Beginning of the Middle Ordovician. Although cephalopods do not count among the most abundant fossils in rocks of Early Ordovician age, ample and diversified faunas have been described from North and South America, nothern Europe, Siberia, China, and Australia. They are represented by thousands of specimens in collections the world over. In the Treatise on Invertebrate Paleontology (Teichert et al., 1964) authors whose assigments included Early Ordovician cephalopods recognized about 125 genera in that epooch. Before accepting this figure one must realize that the state of preservation of many Early Ordovician . It is difficulted to conceive of the Troedssonnellidae as an ancestral or archaic group of the Orthocerida, and their stratigraphic occurence suggests that they are more probably a branch of the Early Ordovician endocerid radiation.

CEPHALOPOD EVOLUTION

(2) A second important development in the middle and late Early Ordovician (Middle and Late Canadian) was the appearance of a group of coiled shells, presently placed in the order Tarphycerida (((Fig. 4, c,d,). Their origin in the ellesmerocerid family Basslerocerettidae with which they are connected through a morphologically intermediate genus, Aphetoceras, of the family Estonioceratidae, is reasonably well established (Flower,1955). Four families made almost simultaneous appearances, but only two survived the Early Ordovician Epoch. In retrospect we find that by the end of the Early Ordovician cepohalopods had multipied in numbers, diversified in morphoilogical types, and expanded their area of distribution. Cephalopods are reasonably common fossils in rocks of late Canadian age. Coied age. Coiled shells had developed ((Tarphycerida), as well as larger straight shells with diversified endosipuhncular structures (Endoceratoidea), and, in all, four orders with about 20 families were represented. In addition, the first orthocerids and actinocerids might have appeared before the end of Early Ordovician time, but if they were insignificant. Also, by the end of early Ordovician time cephalopods had spread far beyond the realms to which they were restricteds in the late Cambrian and earliest Ordvician into seas covering what is now Austraklia, Tasmania, and sohth America.

MIDDLE AND LATE ORDOVICIAN ACME

The Middle and Late Ordician was the time of greatest differentiation in basic morphologic patterns in the history cephalopod evolution. The four orders that were present in the Late Canadian continued into the Middle Ordovician. In addition, five new orders and one new suborder appeared: Actinocerida, Orthocerida, Ascocerida, Oncocerida, Discosorida, and Barrandeocerina. The origins of the. (1) Endosiphuncular calcareous (aragonitic) deposits were secreted by members of the order Actinocerida, and by some Orthocerida and Discosorida They were most complex in the Actinocerida, where their shape was conditioned by a system of vascular canals thaat was not filled with calcareous deposit (Fig. 5) Mutvei (1964) has recently denied the existence of such canals, but I believe that the features named "dorsoventral grooves" by him, which are seen on the surfaces of the "calcareous discs", of which the endosiphuncular filling is composed, are in fact the sities of canals (see Mutvei, 19964, pl.16, figs.1-10. pl. 24, Fig.2).

They are characteristic of virtually all Actinocerida, all Orthocerida, Oncocerida, and Barrandeocerina, which differ from typical tarphycerids only having thin connecting rings.

(2) The shell features of Middle Ordovician forms. Veritable giants having shells up to 30 feet long developed among the Endocerida, but long orthoconic shells are also typical of theorthocerida and the Actinocerida. In the Orthocerida the outer side of the shell wall acquired ornamentations of various kinds: transverse and longitudinal striae, grooves, and ridges, superimposed on smoot or on annulate shells. In the Oncocerida and Discosorida generally unornamented straight or cyrtoconic brevicones and short cirtocones were developed in a great variety of shapes. Body chambers with anteriorly converging sides and contracted apertures developed among actinocerids, oncocerids, and

discosorids. Among coiled forms the first torticone, of cameral deposists, and of the process of shell truncation, the latter as yet poorly understood from the biological point of view. Some details of evolutionary patterns of the new features introduced in Middle Ordovician time are discussed in the following section.

POST-MIDDLE ORDOVICIAN PATTERNS

UNSUCCESSFUL GROUPS

Ten orders and suborders of cephalopods existed in the Middle Ordovician, exhibiting the greatest display of diversified structural patterns in the history of the class. One order, the Intejocerida, became extinct at the end of the Middle Ordovician; another one, Tarphycerina, survived into the Silurian with only one genus each, both know from only a few specimens, and each from one locality only. But But whereas the endocerid line vanished with itslast representative, the tarphycerid line carried on through the Barrandeocerina until well into Devonian Time. Its shells were modified in various ways, forming torticones . Little need be said about the small order Ascoceridaa, whose main features have already been discussed. The3re is a gap in the geologic record of that group, becauser no Early Silurian representatives are known. In the Middle and Late Silurian odd specializations, like lacunose septa and complex septal formations in the body chamber, develop. The order died out at the end of the Silurian and left no descendan ts. It is apparently unrelated to the two orthocerid families in which deciduos shells developed: The Middle Silurian Sphooceratide and the Pennsylvanian Brachycycloceratidae.The cause of the extinction of Actinocerida may have been that their solutions to the hydrostatic problem in the long run proved unsuccessful in competition with the Nautilida that arose early in the Devonian, and they were finally swept aside by the multitude of ammonoids that burst upon the scene in the Late Devonian.

SUCCESSFUL LINES

Among the Clydonautilaceae it was the family Liroceratidae that survived into the Triassic, giving rise in that period three new short-lived families. The most important survivor was the family Grypoceratidae of the Trigonocerataceae, becausen it gave rise, in the Triassic, to the family Sryringnautilidae, from which in turn the single genus Cenoceras evolved in late Triassic times, the only one of some 30 Late Triassic nautilid genera to survive into the Jurassic Period, ancestor of all later Mesozoic and Cenozoic nautilids. One family of Ceratitida, the Otoceratidae, crossed the Permian-Triassic boundary; however, this was a specialized branch, possesing carinate venters and prominent umbilical shoulders. It did not survive after the Early Triassic. Another family, the Araxoceratidae (Ruzhentsev, 1962, and earlier papers) with complex sutures and specialized shells had existed in the late Permian. The main flow of ammonoid evolution was along the line leading from simple Upper Permian Xenodiscidae to Lower Triassic Ophiceratidae. The only significant difference beetwen these two families is addition of a third external lateral lobe in the Ophiceratidae to the two possessed by the Xenodiscidae (Fig. 16), although this picture may be oversimplified (W.M Furnisch, written communication).

The degree of morphological diversification of the Ceratitida is ilustrated by the fact that approximately 400 genera have been described from Triassic rocks. That is, about 25 porcent of all know ammonoid genera are crowded into about 10 porcent of the time span during which ammonoids existed. Cerphalopods, including the Nautilida, were obviously highly successful in ocupying ecologic niches left vacant after the mass extinctions of marine invertebrate life at and around the Permian-Traissic boundary. Fast evolutionary rates make Traissic ammonoids some of the best index fossils in the geologic record. Kummel (in Arkell et al., 1957, p.124) recognized 30 ammonoid zones into which ~~the~~ Triassic system can be divided. Thus the time equivalent of a Triassic ammonoid zone averages about 800,000 to 850,00 years, a figure close to the ultimate power of resolution provived by the paleontological method of correlation (Teichert,1958).

POST-TRIASSIC DEVELOPMENTS

In the following outline of phylogenetic ralationships of Jurassic and Cretaceous ammonoids I am largely following Schindewolf, who based his conclusions essentially on comparative studies of the ontogenetic development of sutures (Schindewolf, 1961,1962,1963, and earlier papers). Space does not permit an evaluation of relative merits of morphologic criteria used by authors in attempts to delineate relationships in the great complex of post-Triassic ammonoids. However, the premise regarded as valid here is that methods of investigation which lead to simpler and more elegant interpretations of relationships beetwen natural things are to be considered superior to methods that have opposite results. Comparative studies of the ontogenetic development of the sutures of many Jurassic and Cretaceous ammonoids by Schindewolf have led to a simpler, hence more satisfying pincture of evolution of at least some of the post-Triassic ammonoids. The position of the Phylloceratina and Lytoceratina as conservative stocks is confirmed, and likewise the relationships of the heteromorphs to the Lytoceratina come up from the Trassic, but the former are shown to be a sterile line, whereas the latter gave rise, at the very beginning of the Jurassic, to the earliest psiloceratids, the first of the Ammonitina from which all later Jurassic ammonitina are derived.

According to Arkell (in Arkell et al.,1957) a total of 19 ammonoid genera occurs in rocks of earliest Jurassic (Lower Hettangian) age. All are know from Europe, and handful also from other parst of the world, notably Nevada, Peru,Tibet, and Indonesia. Three genera belong to the family Psiloceratidae, which includes earliest representatives of the Ammonitida. Phyllocerids and lytocerids originated in the Triassic; the psilocerids are the first of many offshoots from the lytocerid stock.

COLEOIDEA

All living cephalopods with the exception of the genus Nautilus, belong to the subclass Coleoidea, also called Dibranchiata. The latter name refers to the fact that these animals posses two gills as distinct from Nautilus, wich has four. This distinction was long given much weight in cephalopod classification when grouped in one subclass Tetrabranchiata. However, it is now believed that the Coleoidea were derived from dibranchiate, rather than tertrabranchiate, aancestors (Sweet, Teichert, and Kummel in Teichert et al.,1964).

The coleoids developed a variety of anszwers to the buoyancy problem. We do not know for certain whether the earliest coleoids were ectocochlian or endocochlian. Presumably the transitiuon fro m the first to the second condition was accomplished somewhere between the bactritid an the "eobelemnitid" stage. Even the large rostra of belemnites were small in comparison to the size of entire belemnite the amount of liquid contained in their cuttlebone(Denton,1964).

RESPONSES TO THE BUOYANCY PROBLEM

Most major features in ceohalopod evolution that have been discussed may be interpreted as responses to the need fgor buoyancy control which was a major problem ectocochlian shells. Devonan (1964) has written of the "evolution of buoyancy", and in the present paper this matter has been treated in somewhat graeter detail. The chambered shell of a cephalopod must be in close approximation to hydrostatic equilibrium, because if it was not, the animal could not have moved actively. To achieve buoyancy control, weight must be either added or pods by development of a considerable variety of devices. The problem of buoyancy control, especially in the many groups having coiled shells, has always been pussling to paleontologists, but is now more easily understood, since Bidder (1962) reported presence of liquid in camarae of Nautilus. To my knowledge the possibility that liquid (water) may enter camarae to reduced buoyancy of cephalopod shells was first suggested by Hermann Schmidt (1930), but his idea received little attention.

The predominantly orthoconic Orthocerida, togeter with their direct ancestors, the Ellesmerocerida, and their inmediate offshoot, the Ascocerida, are removed from the subclass Nautiloidea, which includes predominantly breviconic, cyrtoconic forms. The Orthoceratoidea form a genetically well-defined sand interrelated group that I regard as the central cephalopod stock from which all other cephalopods were derived.

In the restricted subclass Nautiloidea, the Oncocerida and the Tarphycerida had independent origins in the ellesmerocerid family Bassleroceratidae; and the Nautilida in the Oncocerida. The Discosorida, which are believed to stem from the ellesmerocerid Plectronoceratidae, asre only provisionally retained in this subclass. The Bactritoidea given the rank osf subclass because of their fundamental importance as rooststock of the subclasses Ammonoidea, but they should not included in the Ammonoidea. Troughout this paper emphasis has been on discussion of these features at the expense of discussion of generic and family evolution, which have received much attention in paleontological literature and which can to some extent be gleaned from the chart (Fig.20).

CRISES IN CEPHALOPOD EVOLUTION

There has been much discussion concerning wholesale extinctions of major fossil groups at certain stratigraphic, chiefly Era, boundaries, and the extinction of the Ammonoidea at the end of the Cretaceous period is oner of the best-document and most- discussed examples. It is frecuently overlooked that during their evolutionary history the cephalopods passed through several severe crises during which their survival depended on that of a single genus or a single evolutionary line. For example, the entire history of the order Goniatitida henged on the survival of the single genus Tornoceras, whichn originated in the Middle Devonian and existed through the Frasnian as sole survivor of the order. No genus of ammonoids crossed the TriassiJurassic boundary and only continuation of two teneous lines in the phyllocerids and lytocerids made possible the enormous Jurassic-Cretaceous explosions. The near-extinction of the ammnoids at the end of the Paleozoic is more common knowledge. If the Xenodiscidae had become extinct at the end of the Permian, the Mesozoic seas would have been without ammonoid life. The nautiloids and their ancestors also went through periods of crisis. The evolutiuon of the earliest nautiloids, presumably from oncocerids, must have run along a very tenuous line whose rupture would have resulted in extinction of that stock during the Carbonifereous. At the end of the Trissic all nautiloids became extinct except one genus,Cenoceras. No particular crises mark the history of the Ellesmerocerida, Actinocerida, Endocerida, and Orthocerida. They just faded away.

ACKNOWLEDGMENTS

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Fig. 1. Upper Cambrian Ellesmerocerida.Texas, X2.2.

Fig. 2. Early Ordovician Ellesmerocerida.

Fig. 3. Middle Ordovician to Silurian orthocerid.

Fig. 4. Early Ordovician endocerid. (After Treatice, Part k.).

Fig. 5. Ordovician and Silurian Actinocerida. Norte America.

Fig. 6. Advanced discosorid and tarphycerid.

Fig. 7. Diverse types of oncocerids from the Devonian of Europe. Cythoceratites, dorsal.

Fig. 8. Early nautiloid, Ptenoceras alatum (Barrande). LowerDevonian, Czechoslovakia.

Fig. 9. Diverse types of Devonian nautiloids. Ptyssoceras, Europe.

Fig. 10. The oldest nautilid, Cenoceras trechmanni (Kummel). Upper Trassic (Carnian), New Zeland.

Fig. 11. Initial parts of conchs of bactritids and earlies ammonoids.

Fig. 12. Evolution of earliest ammonoids from bactritids. Cyrtobactrites.

Fig. 13. Common Upper Devonian cephalopods.

Fig. 14. Comparison of prolecanitid and goniatitid suture. (After Schinedewolf, 1954).

Fig. 15. Ontogenetic development of goniatitid and prolecanitid sutures. Sporadoceras, Upper Devonian, Germany. (After Schindewolf, 1954).

Fig. 16. Xenodicid and ophiceratid. Xenaspis, Upper Permian, widespread.

Fig. 17. Early stages of sutures of phyllocerid, Iytocerid, and psiloceratid.

Fig. 18. Early phillocerid, Iytocerid, Rhacophyllites, Upper Triassic. (Norian)

Fig. 19. Main features of evolution of Coleoidea. (Freely adapted from various sources. Not to scale).

Fig. 20. The families of the Cephalopoda shown in their Known or assumed relationships. Each line represents a family. Numbering is by orders as folous (Orders arranged alphabetically).

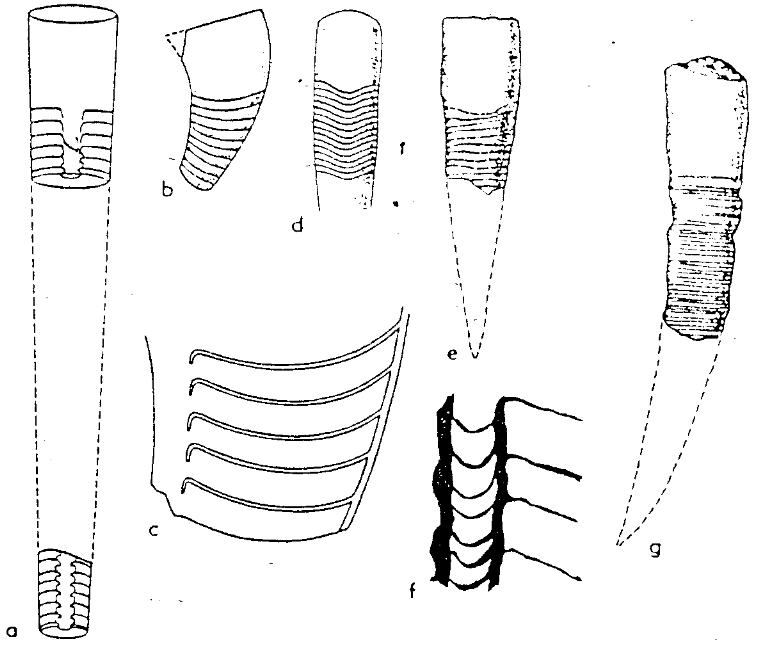
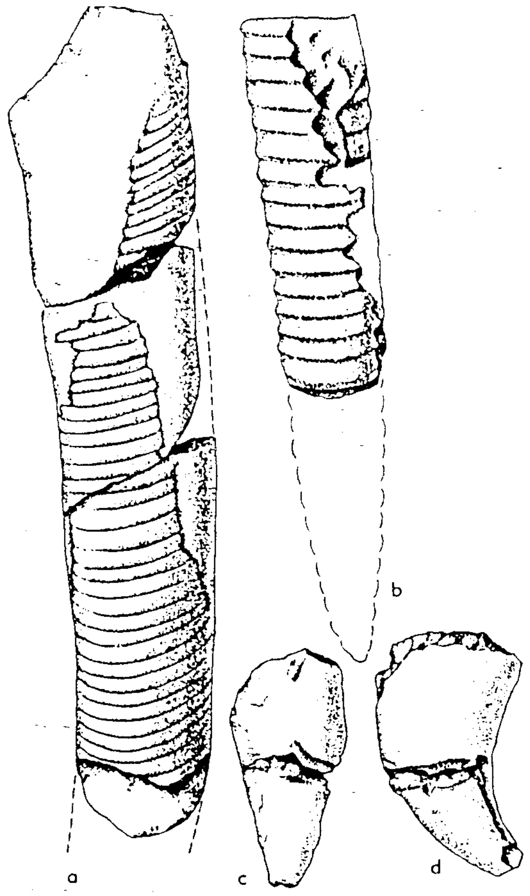


Fig. 1



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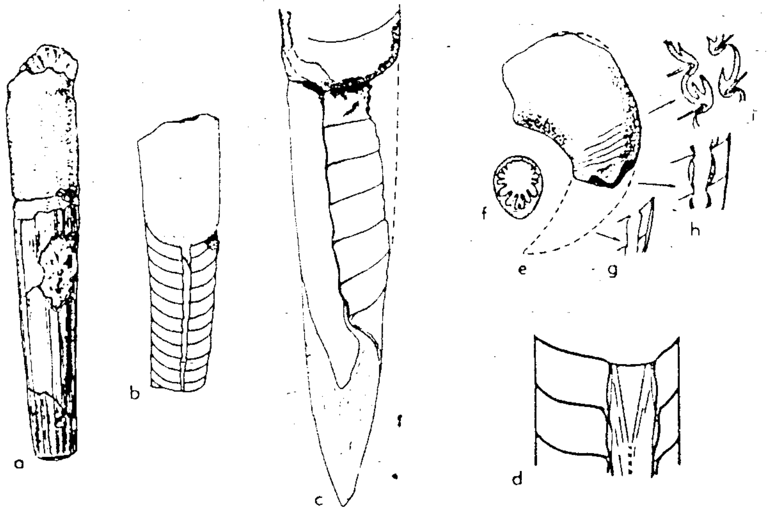

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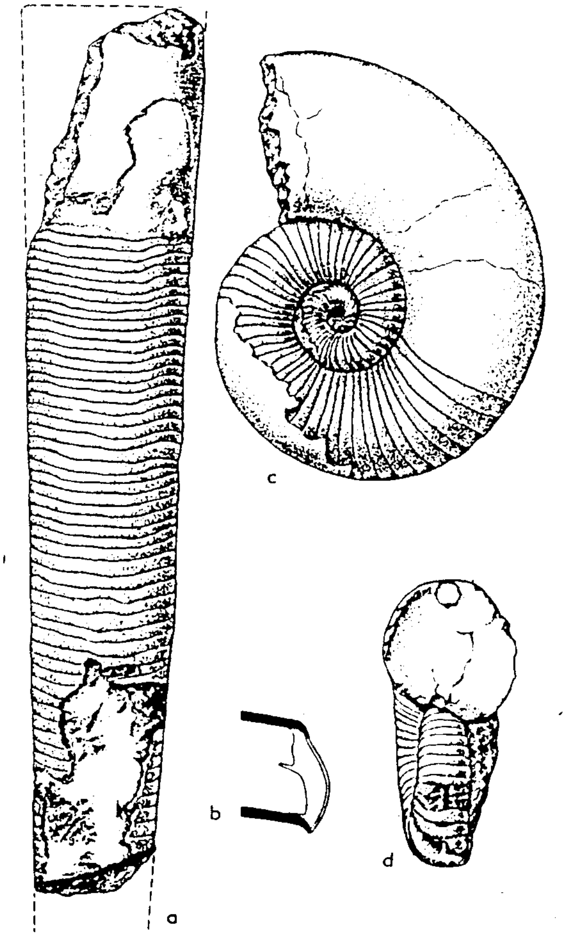

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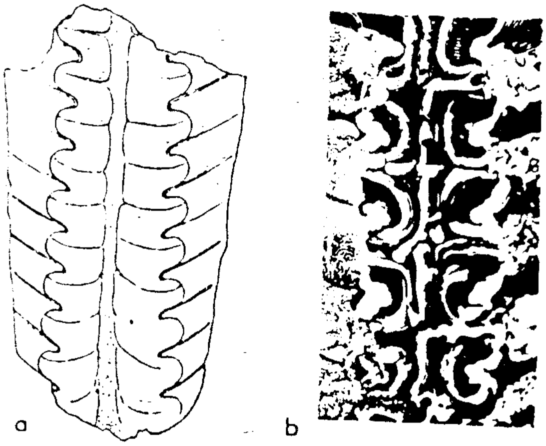

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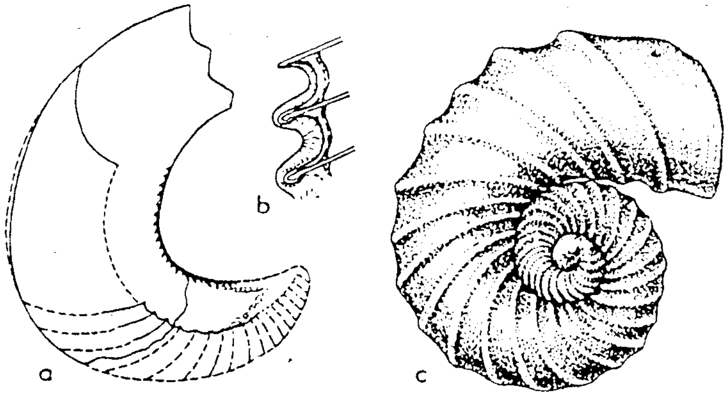

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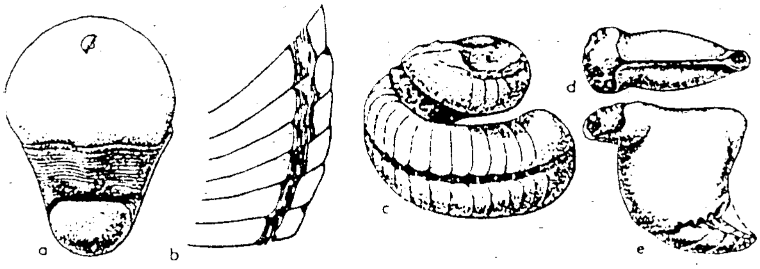

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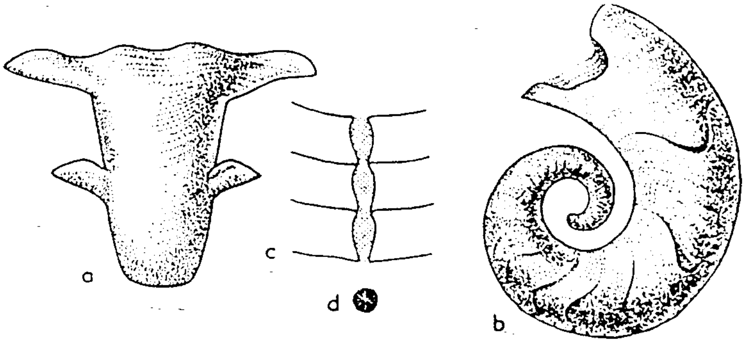

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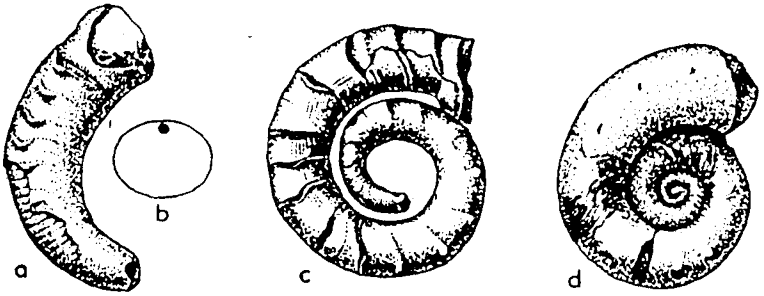

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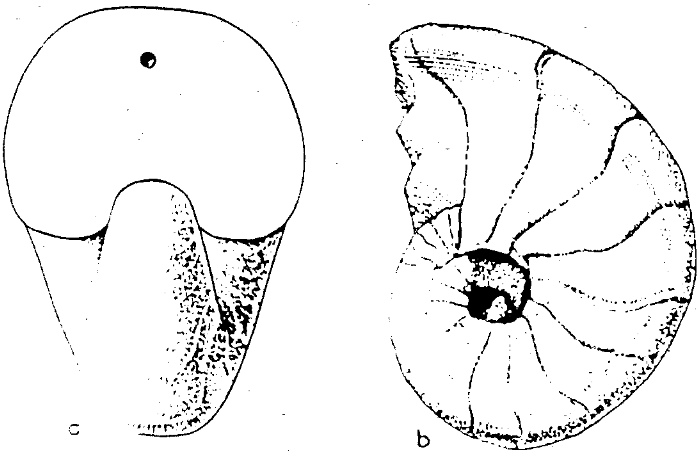
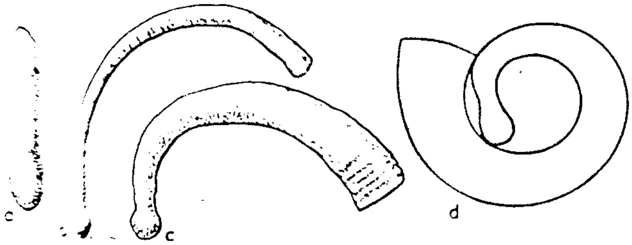


Fig. 10



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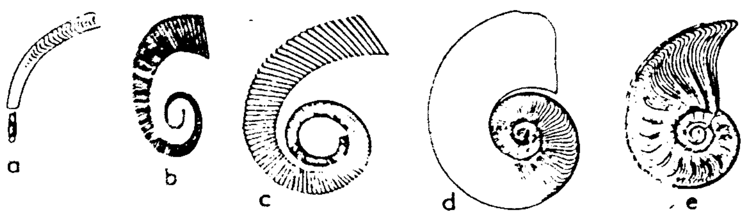

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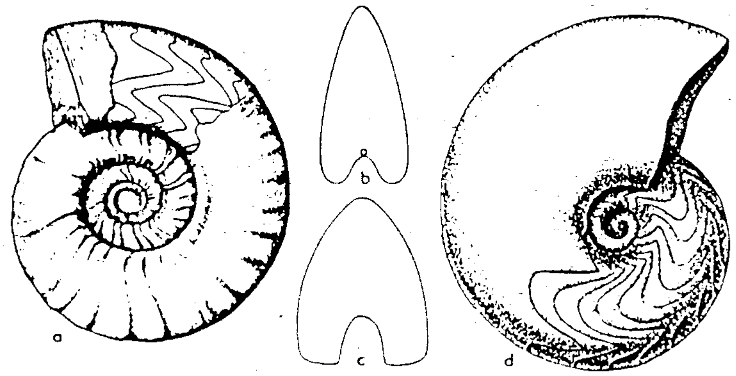

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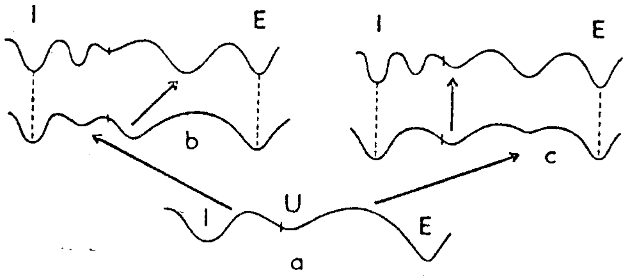

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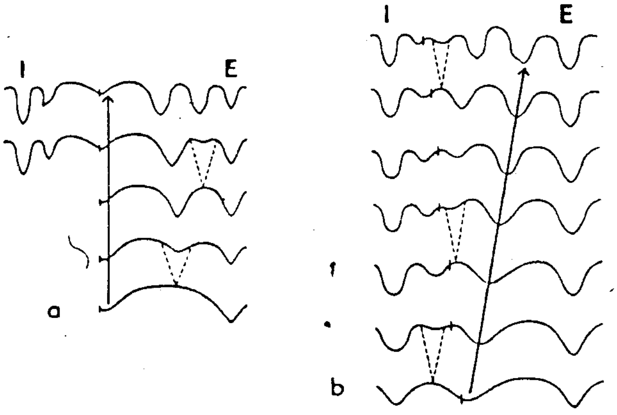

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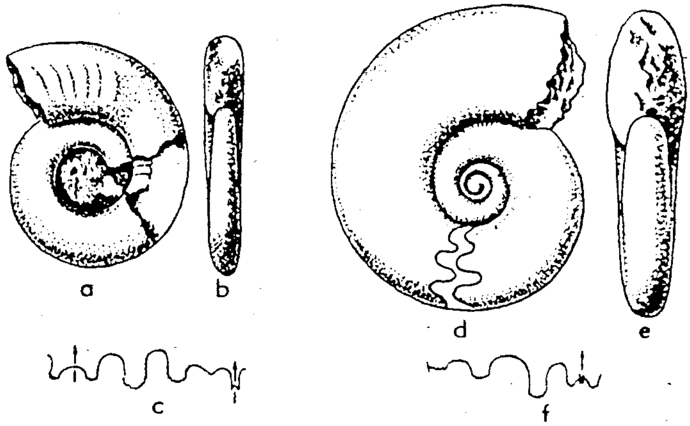

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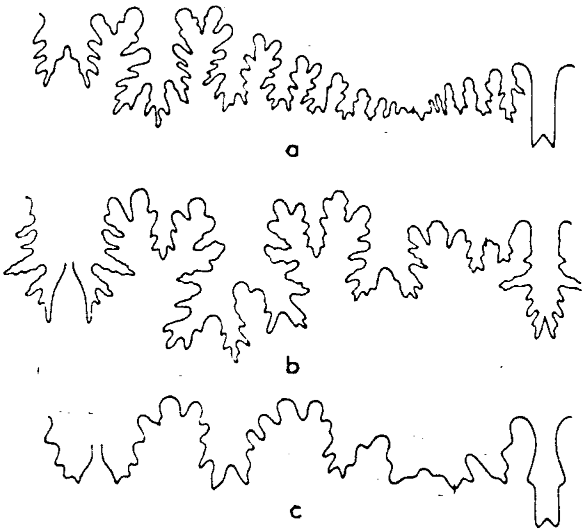

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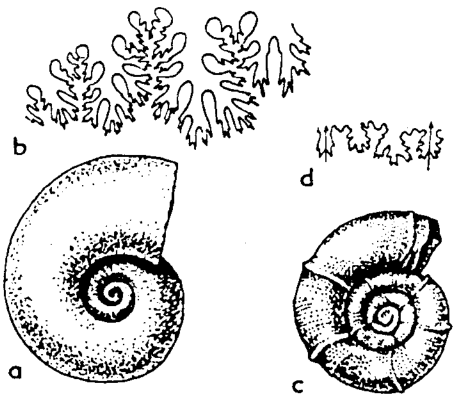

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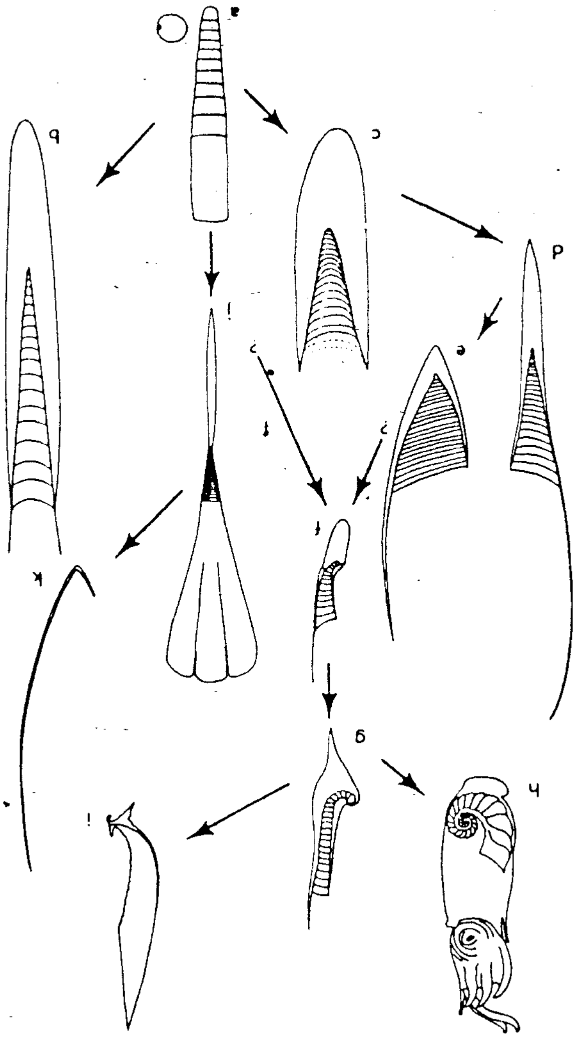
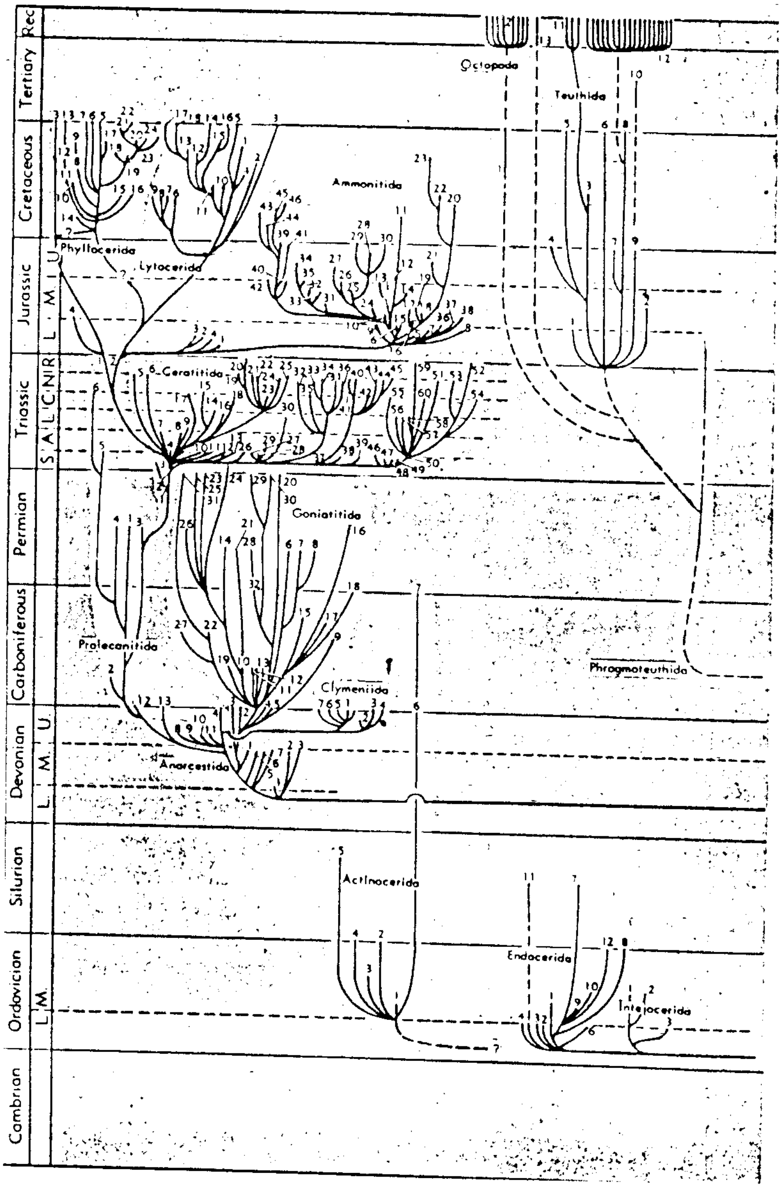


Fig. 19


Rec
Tertiary
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Jurassic
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Triassic
S A L C N R
Permian
Carboniferous
Devonian
L M U
Silurian
Ordovician
L M
Cambrian
Octopoda
Teuthida
Phylloceratida
Lytoceratida
Ammonitida
Ceratitida
Goniatitida
Prolecanitida
Clymeniida
Anarcestida
Actinocerida
Endocerida
Intejocerida
Phragmoteuthida

Fig. 20

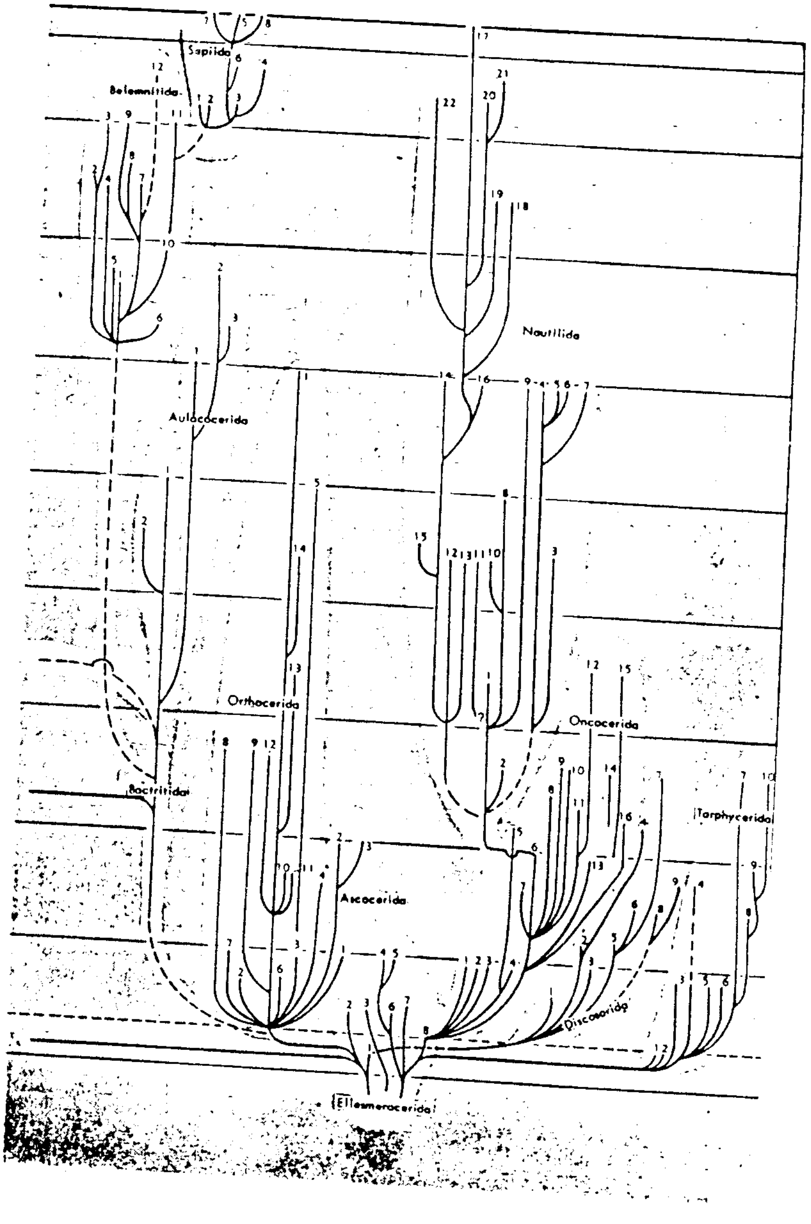
Sapiida
Belemnitida
Aulacocerida
Nautilida
Orthocerida
Oncocerida
Bactritida
Tarphycerida
Ascocerida
Discosorida
Ellesmerocerida

Fig. 20 (cont.)

Table 1

Adaptive Devices to Regulate Buoyancy

Device	Occurs in
Crowding of septa	Ellesmerocerida, Orthocerida, Oncocerida, Discosorida, Bactritoidea, Ammonoidea
Lengthening of body chamber	Bactritoidea (Bactritidae), Ammonoidea
Reducing size of phragmocone	Oncocerida, Discosorida, Parabactritidae
Truncation of posterior shell portion	Orthocerida, Ascocerida
Endosiphuncular deposits	Actinoceratoidea, Endoceratoidea, Orthocerida, Discosorida, Oncocerida
Cameral deposits	Actinoceratoidea, Orthocerida, Discosorida, Belemnitida
Gas-filled chambers in dorsal portion of body chamber	Ascocerida
Liquid in chambers	Sepiida, Nautilida, probably others
Complex folding of septa	Ammonoidea
Elaborate ornamentation, spines, flanges	Ammonoidea, Nautilida (rare)
Hollow keel, nodes and spines	Ammonitida
Thinning of shell and septa	Discosorida, Ammonoidea
Construction of rostrum	Many Coleoidea

Table. 1