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CYRTOLITES CONRAD, 1838 AND ITS POSITION AMONG THE MONOPLACOPHORA (MOLLUSCA)

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A s t r a c t. The muscle scars of *Cyrtolites* CONRAD, 1838 are described in detail. From their morphology, *Cyrtolites* is regarded as a representative of the *Monoplacophora* rather than the *Gastropoda*. The question of *Amphigastropoda,* and others concerning the phylogeny of the primitive *Mollusca* are discussed.

Introduction

During my visit to the British Museum (Natural History), London in October 1965 I had an opportunity to study — although very briefly — the rich collections of the Paleozoic gastropods deposited there. Besides several interesting new genera of *Bellerophontina,* I found a small collection of cyrtolitids, labelled as *Cyrtolites ornatus* CONRAD from the Ordovician of Canada. Several specimens possess well preserved muscle scars giving evidence of the morphology of the soft body, so important in these primitive molluscs.

I am grateful to the workers of the British Museum (Natural History) for making possible the study of this valuable material as well as for permitting its preparation in Prague. These are Dr. W. T. Dean, Dr. L. R. Cox and S. Ware. As far as the stimulating, critical and even sceptical discussions are concerned, I would like to thank my friend Dr. Ellis L. Yochelson (U. S. National Museum, Washington, D. C.). The excellent preparation of the specimens studied is due to the extraordinary patience of Mr. F. Bastl, the assistent of the Paleontological Department, National Museum, Prague.

The paper is divided into two parts. The first part concerns with the morphology of *Cyrtolites ornatus,* as well as with its position among the specialized monoplacophorans. The second contains a discussion pointing out several important problems in the phylogeny of the primitive molluscs, namely the monoplacophorans and gastropods, during late Paleozoic times. The second part is rather speculative, showing the greatest gaps in our knowledge; however, the new finds recall several old theories, for example, the question of the existence of *Amphigastropoda,* and it seems useful to discuss several problems once more. We

should not forget that the geological record of the primitive molluscs is incomplete; therefore, each new find is very valuable and can help us to complete the phylogeny. There are still mistakes in our interpretation; however, they are limited in time being depended on the number of carefully studied finds.

The organisation of Cyrtolites

About 30 specimens have been studied in the collection of the Paleontological Department of the British Museum (Natural History), London. This material becomes from the collection of J. G. HINDE (1918), from the Ordovician of Canada (Cincinnati Formation, Weston and Hudson River Formation, Humber River, Ontario). The fossils are beautifully preserved in green-grey calcitic siltstone or cryptocrystalline limestone. They are thick-shelled, and the lamellar shell is easily removed from the internal casts. The preparation of 5 specimens has been done in Prague, with the help of a Burgess Vibro-tool. These specimens are deposited in the British Museum (N. H.) in London, under the numbers PG 3660 up 3662 and G 27635—6. The original designation of the species *Cyrtolites ornatus* CONRAD given on the labels has been compared with the figure and the description published by J. B. Knight (1941) and seems to be correct. However, the collection contains several different groups of shells; this may be due to the strong variability, which is common among these primitive molluscs. The variability is well expressed in the morphology of the keel and the transverse undulations of the shell which may be absent. Such questions must be studied by American specialists.

Description of the specimens studied

1. PG 3660. Cincinnati Formation, Weston, Ontario, Canada. Max. length 26.8 mm., width 14.2 mm. Internal cast. Pl. 2, fig. 4.
Nearly adult specimen, internal cast with prepared right side. Transverse undulation well expressed. 2½ whorls. Muscle scars not visible except the ventral ones, indicated by the different glossiness of the cast surface. Keel sharp, doubled in the adult stage. Aperture not preserved.

2. PG 3661. Cincinnati Formation, Weston, Ontario, Canada. Max. length 25.2 mm., width 17.0 mm. Internal cast with partly preserved shell. Pl. 1, figs. 1—3.
Adult specimen with prepared dorsal and right dorsolateral region so that the internal cast is exposed; left side with preserved shell illustrating the outer surface. Shell thick (max. 1.2 mm. on the lateral angulation), lamellar; outer surface with numerous transverse crowded ribs traversed by discontinuous spiral ribs; the transverse ribs pass the main lateral angulation and the dorsal keel almost straightly; the umbilical wall of the whorl is interrupted by a low angulation not shown on the internal cast; the apertural margin apparently has a very wide, short insinuation, as shown by the shape of the transverse ribs; transverse undulation very slightly developed; at least 2 whorls present; muscle scars strong, easily visible on the dorsal and right dorsolateral side;
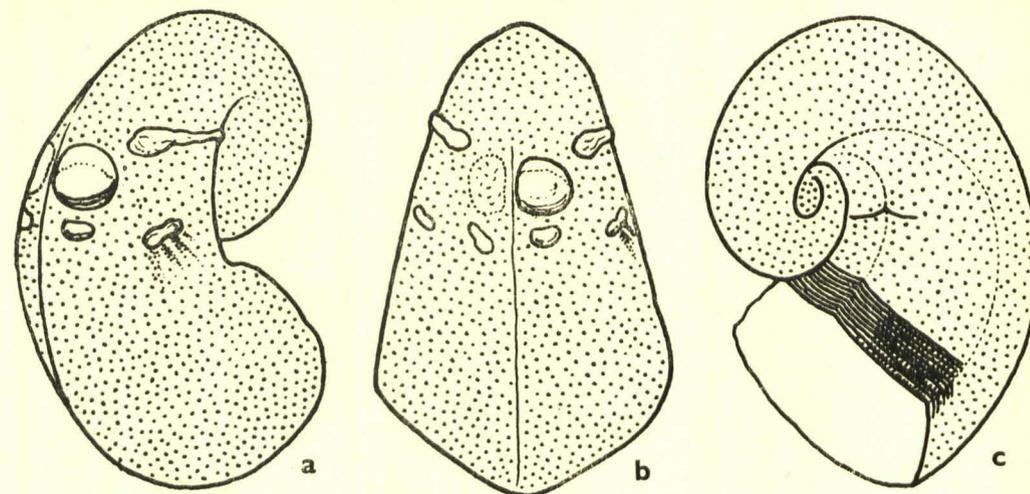

Fig. 1.
Cyrtolites ornatus CONRAD. Specimen PG 3661. a— right dorsolateral, b — dorsal, c — left ventrolateral views. Comp. with pl. I, figs. 1—3. × 2.5.

left anterodorsal scar corraded, the right anterolateral scar narrowing anterolaterally, well separated from the ventral scar; the posterolateral scars composed of two distinct particles fused in the central part; fine irregular radiating scars diverge posteriorly from all scars, namely the posterolateral (muscle impressions?); keel rounded except in the adult stage between the scar zone and the aperture, where it is sharp, with weak parallel lines passing along; whorls apparently not in contact, the ventral groove not visible. Apertural margin not preserved.

3. PG 3662. Cincinnati Formation, Weston, Ontario, Canada. Max. length 24.0 mm., width 16.7 mm. Internal cast. Pl. 2, fig. 8.
Nearly adult specimen with prepared umbilical regions. Transverse undulations well developed. Internal cast smooth, the scars not visible except the ventral ones, indicated by less glossy islets; keel more rounded in younger stages; at least 2 whorls developed; the matrix preserved between the walls of the whorls in the umbilical area indicates that the whorls were not in touch; the ventral groove apparently not developed (?); aperture not preserved.

4. G 27635. Hudson River Formation, Humber River, Ontario, Canada. Max. length 25.0 mm., width 16.2 mm. Internal cast. Pl. 1, figs. 4—7.
Adult specimen, well prepared internal cast showing the morphology of the ventral side. No transverse undulations. The surface of the cast smooth, the initial part of the shell recrystallized and therefore lost; 2½ whorls before breakage; the dorsal whorl almost rounded in the younger stages; profile slightly arched, the lateral angulation rounded,
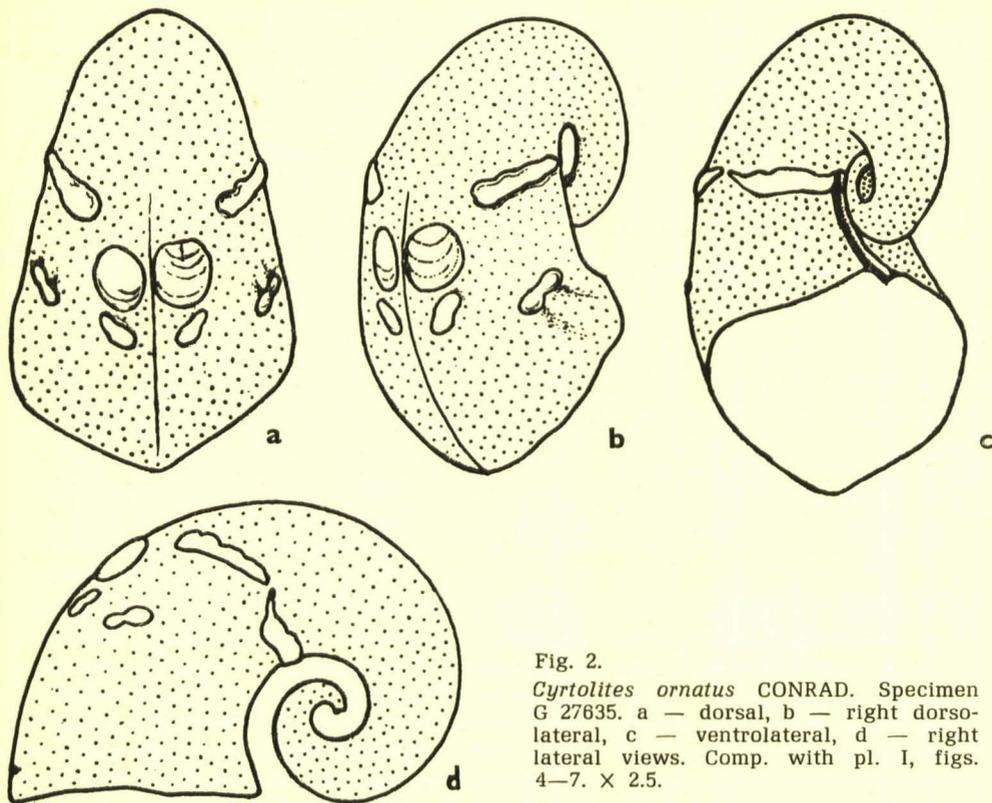
Fig. 2.
Cyrtolites ornatus CONRAD. Specimen G 27635. a — dorsal, b — right dorso-lateral, c — ventrolateral, d — right lateral views. Comp. with pl. I, figs. 4—7. × 2.5.

the ventral side regularly rounded in younger stages, but with narrow ventral groove with relatively sharp margins, and very slightly concave ventrolateral sides in adult stage; muscle scars strong, sharply limited, the anterodorsal scars flat, not absolutely symmetrical, the right one shifted to the keel; both with well developed structures of growth; the left anterolateral scar corraded, the right one composed of three particles, the borders of which extend anteriorly; both posterolateral scars composed of two particles, showing short "migration scars" located anteriorly; ventral scars nearly touching the anterolateral ones, regular, simple, band-like, narrowing laterally, closing the anterior end of the ventral groove; apertural margin lost.

5. G 27636. Hudson River Formation, Humber River, Ontario Canada. Max. length 23.6 mm., width 14.7 mm. Internal cast with fragments of shell near the aperture. Pl. 2, figs. 5—7.

Adult specimen with well prepared left umbilicus. Transverse undulations slightly developed, the surface of the cast irregularly arched in the dorsal region; keel more rounded in the younger stages; 3½ whorls, well exposed in the left umbilicus with perfectly prepared initial part
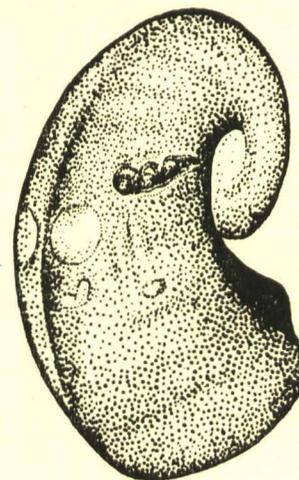
Fig. 3.
Cyrtolites ornatus CONRAD. Specimen G 27636. Right dorsolateral view. Comp. with pl. II, 5. × 2.5.

of the shell which is rather thin; protoconch not visible but probably small; the muscle scars, although weak, are visible, with the exception of the right anterolateral scar which is undoubtedly composed of at least three particles showing gradual increase in size; apertural margin partly preserved indicating a slight tendency to flare, the anterior part of the aperture with either slightly reflected (impressed) preceding whorl or the ventral groove.

Generalized description of the species

S h e l l. — Lamellar, thick, the maximum thickness at the lateral angulation (1.2 mm.). Outer surface with numerous crowded transverse ribs crossed by discontinuous spiral grooves; two ventral keels in adult stages indicating places of very shallow insinuations, not reflected on the internal cast; whorls apparently free during the whole ontogeny numbering 3½. The apertural margin probably slightly flaring in gerontic specimens. Strong transverse undulation often developed, well reflected on the internal side of the shell.

I n t e r n a l c a s t. — Internal cast completely smooth and rounded in the young stages. The adult specimens possess well developed muscle scars, their depth depending on age. Keel much sharper and angulate in adult stages than before the reaching the muscle scars zone where it is rounded. The dorsal sides of the whorl gently arched in adult stage, the lateral angulation rounded, the lateroventral sides sligthly concave; narrow, relatively deep, ventral furrow may be present in adult stage, reaching the main muscle ring where it dies out quite abruptly.

Muscle scars arranged in one main and one secondary ring. The most important scars are developed on the dorsal side of the shell.

The main ring consists of three symmetrical pairs of scars: the dorsal pair, the lateral pair and the ventral pair. The dorsal scars are flat, nearly rounded, located close to the central angulation or keel, and often bear lines of growth. The lateral scars are elongated, deep, narrowing towards the lateral angulation of the shell where they die out; they are composed of at least three particles corresponding to the main muscle attachments. The ventral scars band-like, flat, smooth,

narrowing laterally towards the lateral shell angulations and nearly touching the external ends of the lateral scars. Both the ventral scars may be continuous but when passing the median part of the whorl they are separated by the ventral furrow.

The secondary or posterior ring is incomplete consisting of two symmetrical scars multiplying the dorsal and lateral scars, but much smaller; the posterodorsal scars are usually flat, the posterolateral deep; both seem to be composed of two particles.

There are secondary muscle structures visible on the cast. The first one is due to the migration of scars developed anteriorly; the second one — the ray-like scars diverging posteriorly — might be explained as lateral impressions of the scars located close to the shell wall.

There is no doubt that the development of deep scars appears at the moment when the shell is adult; neither scars nor structures indicating their migration were observed in the younger stages of the shell. They must have been weak and overlain by later layers of the shell material.

The general configuration of the shell indicates that we are concerned with heavy animals creeping on the sea bottom. The shell is perfectly symmetrical resembling the sinuitid bellerophontaceans.,

The main features differing *Cyrtolites* from the bellerophontaceans are:

1. Absence of sinus in the apertural margin in *Cyrtolites.*

2. No parietal inductura developed in *Cyrtolites.*

3. 5 pairs of muscle scars located mainly in the dorsal region of th shell in *Cyrtolites* (only one pair of the columellar scars has been observed in *Bellerophontacea*).

The above mentioned features distinguish *Cyrtolites* from the more advanced bellerophontaceans (e. g., *Sinuites* and its allies). They are insufficient for distinguishing the genus from the imperfectly known *Helcionellacea.*

As no modern revision of *Cyrtolites* has been published in North America, we cannot draw too many conclusions concerning the limitation of the species and the extent of variability. It seems probable that species of *Cyrtolites* will prove to be rather variable as far as the coiling and external ornamentation are concerned. There will probably be a continuous line between the "species" *C. disjunctus* U. et S., 1897 and *C. ornatus* CONRAD, 1838. However, the paper of Ulrich and Scofield 1897 indicates that there are several similar species in the Middle and Upper Ordovician of North America. From the presence of the dorsal insinuation, some of them may belong among the true bellerophontaceans. However, the question of the presence or absence of this insinuation in the genus *Cyrtolites* must be carefully studied in the American material, together with the muscle scars which are the most important feature.

Relations of Cyrtolites

According to the Treatise on Invertebrate Paleontology, Part I, 1, *Cyrtolites* is distributed from Middle to Upper Ordovician. No species are known from the Lower Ordovician.

Seeking the phylogenic roots of *Cyrtolites,* we must consider the bilaterally symmetrical shells occuring through the Cambrian and Lower Ordovician time. There are two groups of molluscs from which the ancestors of *Cyrtolites* may be derived, *Helcionellacea* and *Archinacellida,* and the arguments in favour of one or the other are as follows:

1. The *Helcionellacea* manifested themselves phylogenetically during Lower Cambrian times, and are believed to be primitive *Bellerophontina*. There is as yet no evidence of their muscle scars; as they seemingly had undergone torsion, their muscle scars should be similar to that of *Sinuites* (one pair of columellar retractors). No helcionellaceans are known from rocks younger than Upper Cambrian. I regard the Middle and Upper Cambrian *Helcionellacea* to be a not progressive surviving group of molluscs giving no origin of more advanced groups.

2. The *Archinacellida* are known from the Upper Cambrian to ? Silurian (probably only to uppermost Ordovician). Their family *Archinacellidae* has its acme during the Lower and Middle Ordovician. The archinacelloid monoplacophorans represent typical cyclomyans which have developed a more or less complete ring of muscle scars, often fused to form a continuous band. As far as height is concerned, the shells of *Archinacella* are variable and we know several species with quite high shells. I regard, therefore, the genus *Cyrtonellopsis* YOCHELSON, 1958 as being related to the archinacellid monoplacophorans,
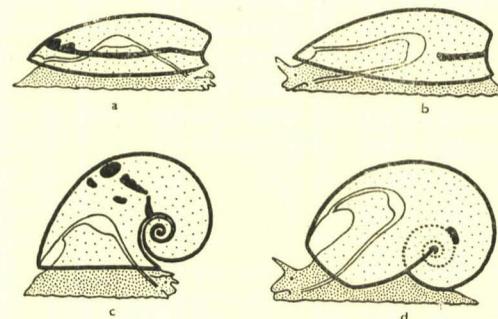

Fig. 4.
Restoration of the representatives of two convergent lines: the cyclomyan monoplacophorans (a—c) and the gastropods (b—d), a — *Archinacellina,* Upper Ordovician, Eu.; b — *Palaeoscurria* or *Lepetopsis,* Ordovician — Carboniferous, Eu., N. Am.; c — *Cyrtolites,* Ordovician, N. Am.; d — *Sinuites,* Ordovician, cosmop. — Note the position and the shape of the muscle scars (black). Orig., schem.

though this presumption is not supported by the muscle scars which are not known yet in this genus. *Cyrtonellopsis* is known from the Lower Ordovician of North America and from the Llanvirnian of Central Europe (Bohemia). If we compare this genus with *Cyrtonella* HALL, 1879 or *Cyrtolites* CONRAD, 1838 we shall find almost no differences apart from the coiling, which seems to be a progressive feature. Thus, if we believe that the archinacellids were untorted, we must accept

Cyrtolites as an untorted mollusc, a suggestion which does not seem very plausible. However, my previous opinion about the repeated torsion in different groups and different time should be revised (see R. J. Horný 1963, p. 43).

The muscle organization of *Cyrtolites* is very similar to that of *Archinacella,* with the main scars arranged in a nearly continuous circle. The additional scars probably do not express any metamery but repetition caused by a strongly changed, coiled shell. The scars of *Cyrtolites* can be regarded as strongly specialized and the decomposition of the continuous archinacellan band-like scar is probably also due to the changed mechanism of coiled shell.

Not being torted the cyrtolitid molluscs never played an important part in mollusc phylogeny. During their time there was strong competition between similar but torted bellerophontaceans well adapted to different surroundings, producing rich populations and providing an origin for several new groups of more advanced gastropods. Nevertheless, we can find several descendants of *Cyrtolites* or its allies during Silurian and even Devonian times.

The best known Silurian representative is *Yochelsonia* HORNÝ, 1962, several species of which occur in the Silurian of Bohemia. It is distinguished from *Cyrtolites* by smaller, strongly ribbed shell which is carinate during the young stages; the lateral angulations are often lacking, the shell being more rounded in transverse section in the adult stage. Muscle scars not known in detail; the anterodorsal ones very similar to those in *Cyrtolites,* the anterolateral passing to peculiar trilobate "migration scars"; the posterior scars not observed. (The interpretation of the scars of *Yochelsonia* illustrated by me in 1963 (p. 93) was incomplete, strongly overemphasizing the "migration scars".)

The stratigraphically younger genus *Cyclocyrtonella* HORNÝ, 1962, from the uppermost Silurian, possesses one pair of scars corresponding to the anterolateral scars of *Cyrtolites.* The youngest, Devonian genera are *Cyrtonella* HALL, 1879 and *Neocyrtolites* HORNÝ, 1965.
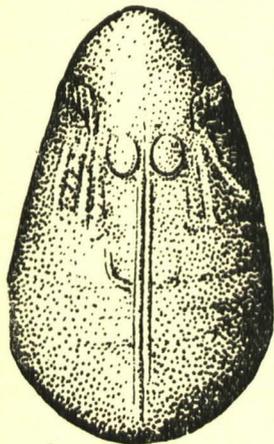

Fig. 5.
Yochelsonia fallax (PERNER). Dorsal view showing the scars. Comp. with pl. II, figs. 1—3. × 4.

A reconsideration of the relationships of the primitive Mollusca

Considering the phylogeny of the primitive gastropods, J. B. Knight (1952) discussed the problem of the existence of *"Amphigastropoda".* This question has been revived by the find of multiple paired scars in *Cyrtolites.* As I will show below, there is no reason to speak about the monoplacophorans as direct ancestors of the bellerophontaceans. The idea of *Amphigastropoda* sensu W. Wenz (1940), concentrating the monoplacophorans and the bellerophontaceans in one subclass, is evidently wrong and as such was criticized by Knight (1952, p. 50). *Cyrtolites* and its allies, however, represent a beautiful sample of the *Amphigastropoda,* including the coiled shells with the scars possessing certains signs of monoplacophoran character. Nevertheless, we must consider the fact that *Cyrtolites* and its allies represent a highly specialized group of molluscs which never took part in any important evolutionary trend and never led to *Gastropoda.* I do not use, therefore, the profaned name *Amphigastropoda* it the present systematics.

The main differences between the classes Monoplacophora and *Gastropoda* have been clearly defined in the Treatise on Invertebrate Paleontology, Part I, 1. There is no doubt that the *Monoplacophora* really represent an independent, well defined class. However, it would be quite wrong to presume that the monoplacophorans, as we know them from the fossil record, represent the ancestors of *Gastropoda.* Both classes developed and existed side by side from early Cambrian. The monoplacophorans are rare as fossils, and never underwent any important distribution or "explosive evolution". As far as the organisation of the soft body is concerned, they resemble, however, the hypothetical ancestor of certain classes, for example the *Bivalvia, Polyplacophora* and *Gastropoda.*

Seeking the phylogenic roots of the classes of *Mollusca* we must go back to Precambrian times. This is, of course, an ideal field for hypotheses and speculations as there are no fossils available for study (except those which are not comparable with anything similar to *Mollusca*).

We must try to forget the existence of *Monoplacophora,* and perhaps more with the help of philosophy than phylogeny to immagine or to restore the common Precambrian ancestor of the true molluscs. Let us consider several assumptions:

1. The Precambrian ancestor possessed certain features characteristic of the annelid worms. The ventral and dorsal sides were distinguishable, and the head was more or less separated. The body was segmented, and many organs were arranged metamerically. The ventral side was adapted for either creeping on the sea-bottom or more less active swimming or even ploughing up the sediment. The dorsal side was not calcified. This ancestor inhabited the newly created litorals during several Precambrian orogenies and adapted itself to different conditions by means of morphological differentiation. The greatest adaptation, which took place sometime between the end of Precambrian and the beginning of Cambrian time, was caused by deep changes of climatic, biochemic and probably even cosmic character. It seems probable that several groups of the "praemolluscs" were differentiated even before these main changes. However, the emergence of the first true mollusc depended on the formation of a shell, and the conditions suitable for this took place sometime "between" the Precambrian and Cambrian. Thus,

several groups of molluscs were defined even before the Cambrian, whilst some originated during the Lower Cambrian or even later.

Of course there were several time-levels of radiation in space during the Precambrian — Cambrian "interregnum", though these are poorly known stratigraphically, and this is the reason for the inequality of the classes in the *Mollusca*.

As was pointed out above, some of the "praemolluscs" were adapted for creeping, some for active swimming, and some for burrowing or ploughing up the sediments. These three groups are shown in different classes of *Mollusca*. There is no doubt that during early Cambrian times there existed more classes or groups of *Mollusca,* the organisation and morphology of which are still unknown or imperfectly known (i. g., *Cambridioidea*). A careful investigation carried out in the limestone facies of the Lower Cambrian should produce many new finds concerning these "unsuccessful" extinct molluscs.

2. The most closely related groups of *Mollusca* are the *Bivalvia, Polyplacophora, Monoplacophora* and *Gastropoda,* and it is useful to recapitulate the main features distinguishing or defining them:

*Bivalvia:* bivalved shell, head not developed (secondarily?);

Polyplacophora: shell consisting of several (generally 7—8) particles. Head developed;

Monoplacophora: single shell, rudimentary metamery may be present, head developed;

Gastropoda: single torted shell so that the anal opening becomes anterior in position. Head developed.

3. The main feature causing a qualitative change in the evolution and distinguishing the classes *Monoplacophora* and *Gastropoda* is the torsion. As I have written elsewhere, I do not regard metamery as the main criterion for distinguishing these classes, as we can demonstrate gradual disappearance of metamery during the evolution of the *Monoplacophora*. Further, according to E. L. Yochelson (written communication), it is difficult to speak about true metamery within the class *Monoplacophora,* even in the order *Tryblidioidea*. Fossil material gives us at least evidence of the muscle attachments whilst other important features have to be inferred. The position for distinguishing both classes is complicated as the primitive molluscs are strongly homeomorphous. The difficulties concerned with the Cambrian *Helcionellacea* are well known.

4. According to the morphology and development of the shell it is possible to say that the shape of the shell is very important. The animal possessing a shell supporting the soft body survives much easily, has opportunities for the widest adaptation, and, therefore, has more possibilities of morphological differentiation which manifests itself in the evolutionary process. Among the shell-bearing *Mollusca*, the monoplacophorans were originally inadequately supported by the shell, and this may be the reason for their minority in fossil and even Recent assemblages.
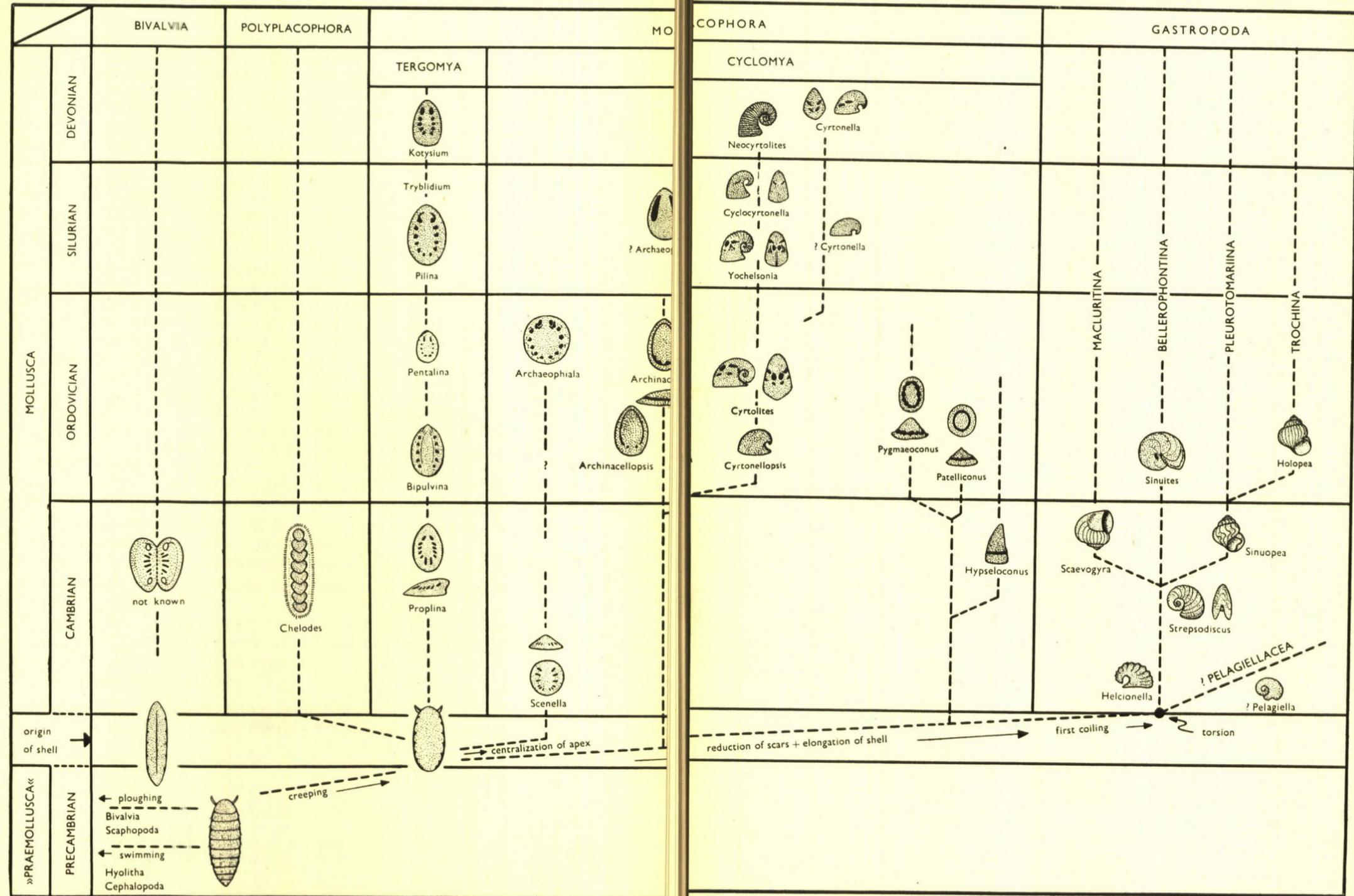
Recapitulation

The possible evolution of the phyllum *Mollusca* (mainly the "creeping groups) is illustrated in the table. The class *Monoplacophora* is emphasized in order to show the probable phylogeny. It is necessary to point out that the „boundary" between Precambrian and Cambrian is, for technical reasons, rather widened, and indicated by "origin of shell". During this time a great radiation of the "praemolluscs" took place, and we can speak about a great "expansion into space". Several groups of *Mollusca* have evolved, since that time: the creeping (or "monoplacophoran") stem, the more or less swimming stem *(Hyolitha; Cephalopoda)*, the ploughing stem *(Scaphopoda; ? Bivalvia)* and the burrowing stem, not recorded *(Aplacophora*-like). During the end of the Precambrian-Cambrian "interval" representatives of these stems developed solid shells and then continued their molluscan evolution. The origin of *Gastropoda* was apparently somewhat later, as they were derived from molluscs with an existing shell, at about the Lower Cambrian boundary. Even the origin of *Bivalvia,* may have similar character. The groups of the monoplacophoran molluscs known above the Precambrian-Cambrian boundary have never manifested themselves in the praemolluscs — gastropods phylogeny. They represent surviving specialized groups of molluscs having no occasion and no possibility for more dynamic evolution and depending on quantitative changes only (e. g., fusing of scars, elongation of the shell, etc.). Only the torsion can be treated as a new, progressive qualitative change causing the origin of a new class. However, each surviving group *(Tryblidiida, Archinacellida* etc.) had an ancestor, which had existed before the beginning of Cambrian time and which belonged to the main phylogenic trend leading to the *Gastropoda.* This is why we cannot speak about the true monoplacophorans as the direct ancestors of *Gastropoda.*

The main evolutionary stem from the "praemollusca" towards *Gastropoda* is shown by the following points:

I. origin of a flat shell in the dorsal region ("tergomyan stage"),

II. centralization of the apex according to the muscle zone (primitive "cyclomyan stage"),

III. elongation of the shell + reduction and specialization of the muscle scars (more advanced or specialized "cyclomyan stage"),

IV. torsion (= origin of *Gastropoda*),

V. next development of shell.

One of the most important points in gastropod evolution was the centralization of the apex according to the more or less cyclical muscle
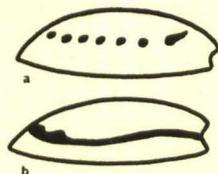

Fig. 6.
Development of the scar zone in *Cyclomia* (a — *Drahomira*) and *Tergomya* (b — *Archinacellina*). Schem.

zone, and this made possible the next development of an elongated, high shell. The typical monoplacophorans have the muscle scars arranged in a more or less complete circle located posteriorly towards the apex which remains above the head of the animal (*Tergomya*). The position of *Scenella* and *Archaeophiala* is not yet clear, but they are representatives of *Cyclomya,* having the apex inside the muscle scar zone. The more advanced cyclomyan molluscs of *Patelliconus*-like or *Hypseloconus*-like shell were probably the molluscs standing just before the torsion, which took place together with the first signs of coiling.

The recapitulation presented above illustrates only the present stage of our knowledge, and no doubt new finds will eliminate the speculative hypotheses.

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CYRTOLITES CONRAD, 1838 A JEHO SYSTEMATICKÁ POZICE MEZI PŘÍLIPKOVCI (MOLLUSCA, MONOPLACOPHORA)

V anglické části práce je zevrubně popsána morfologie vnitřní stěny schránky druhu *Cyrtolites ornatus* CONRAD, 1838 ze svrchního ordoviku Severní Ameriky. Svalové vtisky byly nalezeny na několika exemplářích, které jsem měl možnost studovat v roce 1964 ve sbírkách British Museum (Natural History) v Londýně. Rod *Cyrtolites* CONRAD byl dříve považován za primitivního belerofontida, jako typický představitel čeledi *Cyrtolitidac*. Analýza párových svalových vtisků (celkem pět párů zrcadlově souměrných vtisků), uspořádaných v kruhu obemykajícím celý obvod schránky a nejsilněji zakotvených v dorzální oblasti, potvrdila můj dřívější předpoklad, že rod *Cyrtolites* CONRAD představuje zástupce vysoce specializované vývojové větve přílipkovců, u kterých nastala následkem prodloužení a stočení ulity redukce a specializace svalových úponů. Důsledky plynoucí z těchto poznatků pro fylogenezi a systematiku jsou popsány v anglickém textu, kam odkazuji.

Kromě uvedených zjištění vyplynula ze studia ještě řada velmi zajímavých poznatků, které dosti podstatně pozměňují naše dosavadní názory na vývoj primitivních měkkýšů. Pro paleogeografické závěry je důležité zjištění, že rod *Cyrtolites* skutečně v českém ordoviku není znám. Pokud byl odtud uváděn, šlo vesměs o záměnu s některými skutečnými primitivními belerofontidy, jako je např. rod *Sinuitopsis* a *Temnodiscus,* a se specializovaným rodem *Yochelsonia.*

Pravděpodobný vývoj části třídy *Mollusca* je graficky znázorněn na přiložené tabulce. Třída *Monoplocophora* (přílipkovci) je zakreslena nejpodrobněji, vzhledem k zaměření celé práce. Hranice mezi prekambriem a kambriem je zobrazena z grafických důvodů mnohem širší; je v tabulce označena „vznik schránky". Během nejvyššího prekambria uskutečnila se rozsáhlá radiace „předměkkýšů"; můžeme zde hovořit o typické „expansi do prostoru". Některé pozdější třídy měkkýšů byly predisponovány již od této doby: lezoucí měkkýši (monoplakoforního charakteru), volně pohybliví nebo plovoucí (hyoliti a hlavonožci), ryjící (kelnatky a snad mlži) a vrtající v nezpevněném sedimentu, jejichž zástupci se nezachovali ve fosilním stavu (aplakoforního charakteru). Teprve na samém konci prekambria tito měkkýši předchůdci získali pevnou schránku a pokračovali ve vývoji jako praví měkkýši. Vznik gastropodů a snad i mlžů je zřetelně poněkud mladšího data, protože byli odvozeni od měkkýšů s již existující pevnou schránkou, a to patrně v nejranějším kambriu.

Monoplakoforní měkkýši, které známe počínaje nejspodnějším kambriem, se ve vývoji měkkýšů již nikdy neuplatnili; to znamená, že žádný z nich netvoří vývojovou řadu vedoucí ke třídě *Gastropoda.* Představují přežívající specializované skupiny měkkýšů, kteří nikdy neměli ani subjektivní, ani objektivní předpoklady k dynamičtější evoluci; jejich další existence byla závislá pouze na kvantitativních morfologických změnách (např. na splývání a redukci svalových vtisků, prodlužování a stáčení schránky, apod.). Jediná torze může být považována za novou progresívní kvalitativní změnu, která vyvolala vznik nové, vývojeschopné třídy — *Gastropoda.* Nicméně je naopak jisté, že většina z přežívajících reliktních skupin měla svého předka, který existoval před počátkem kambria a který skutečně patřil k hlavní vývojové linii, vedoucí od primitivních „předměkkýšů" ke gastropodům. Toto je důvod, proč nemůžeme hovořit o přílipkovcích jako o přímých vývojových předcích gastropodů.

Hlavní vývojová větev vedoucí ke gastropodům může být dokumentována těmito hlavními stádii nebo znaky:

I. vznik ploché schránky v dorzální oblasti (tergomyové stádium),
II. centralizace vrcholu vzhledem ke svalovému poli (primitivní cyklomyové stádium),
III. prodlužování ulity + redukce a specializace svalových vtisků (pokročilé cyklomyové stádium),
IV. torze (=vznik gastropodů),
V. další vývoj schránky, umožněný torzí.

Jedním z nejdůležitějších momentů ve vývoji gastropodových předků je centralizace vrcholu vzhledem k více či méně kruhovitě uspořádané zóně svalových vtisků. To byl základní předpoklad pro vznik prodloužené vysoké schránky. Typičtí přílipkovci mají svalové vtisky uspořádány ve více či méně úplném kruhu umístěném posteriorně vzhledem k vrcholu, který zůstává nad hlavovou částí zvířete. Pozice rodů *Scenella* a *Archaeophiala* není zcela vyjasněna; nicméně je zřejmé, že to jsou zástupci cyklomyové větve, mající vrchol umístěný uvnitř zóny svalových vtisků. Pokročilejší cyklomyární přílipkovci se schránkami patelikonového nebo hypselokonového tvaru stali se pravděpodobně přímými předky gastropodů a byli postiženi torzí, která se objevila zároveň s prvními symptomy stáčení ulity.

Uvedený přehled dokumentuje pouze současný stav našich vědomostí, které nemohou být podepřeny studiem měkkých částí těla. Nelze pochybovat o tom, že nové objevy (zejména ve vápencovém spodním kambriu) přinesou množství nových poznatků, které pomohou eliminovat chyby a spekulativní hypotézy.

PLATE 1

Cyrtolites ornatus CONRAD, 1838

Specimen No. PG 3661. Internal cast with partly preserved shell. X 2.5. 1 — Right dorsolateral view showing the dorsal and lateral muscle scars. Note the ray-like structures diverging posteriorly from the posterolateral muscle scar. 2 — dorsal view. The left anterodorsal scar corraded. The dorsal keel is sharpest between the muscle area and the apertural margin. 3 — left ventrolateral view showing the left side with preserved shell. The ventral keel as well as the fine tranverse striation are well visible.

Specimen No. G 27635. Internal cast. X 2.5. — Right dorsolateral view showing the dorsal and lateral muscle scars. The lateral scars composed of several particles. 5 — dorsal view. The left anterolateral scar slightly corraded; note the lines of growth on the anterodorsal scars. 6 — ventrolateral view showing the right ventral scar and the ventral groove. The median processus of the ventral scar does not belong to the scar itself (comp. fig. 2, page 60). 7 — Right lateral view showing the mutual relationship of the lateral and the ventral scars. The initial part of the shell is broken off.

Cyrtonellopsis elevata (PERNER, 1903)

Specimen No. 3070, Museum of Dr. B. Horák, Rokycany. Internal cast. Loc.: Osek near Rokycany, Šárka Beds, Llanvirnian, Ordovician. 8 — right lateral view showing high, strongly curved shell. X 2.5.

PLATE 2

Yochelsonia fallax (PERNER, 1903)

Specimen No. NM L 5586 (National Museum Prague). Internal cast.
Loc.: Barrandian Area (locality unknown), „Orthoceras" limestone of the Kopanina Beds, Silurian. X 4. 1 — Right dorsolateral view showing the doubled median keel, the rounded dorsal and the lateral scar composed of several particles. The diverging grooves or scars probably corresponds to the migration of scars. 2 — dorsal view showing both lateral and dorsal scars, as well as the „migration" grooves. Note the scar-like structures posteriorly of the dorsal scars (comp. fig. 5, page 64). 3 — left dorsolateral view. The lateral scar and different „migration" structures well visible.

Cyrtolites ornatus CONRAD, 1838

Specimen No. PG 3660. Internal cast. X 2.5. 4 — dorsal view showing slightly doubled dorsal keel.
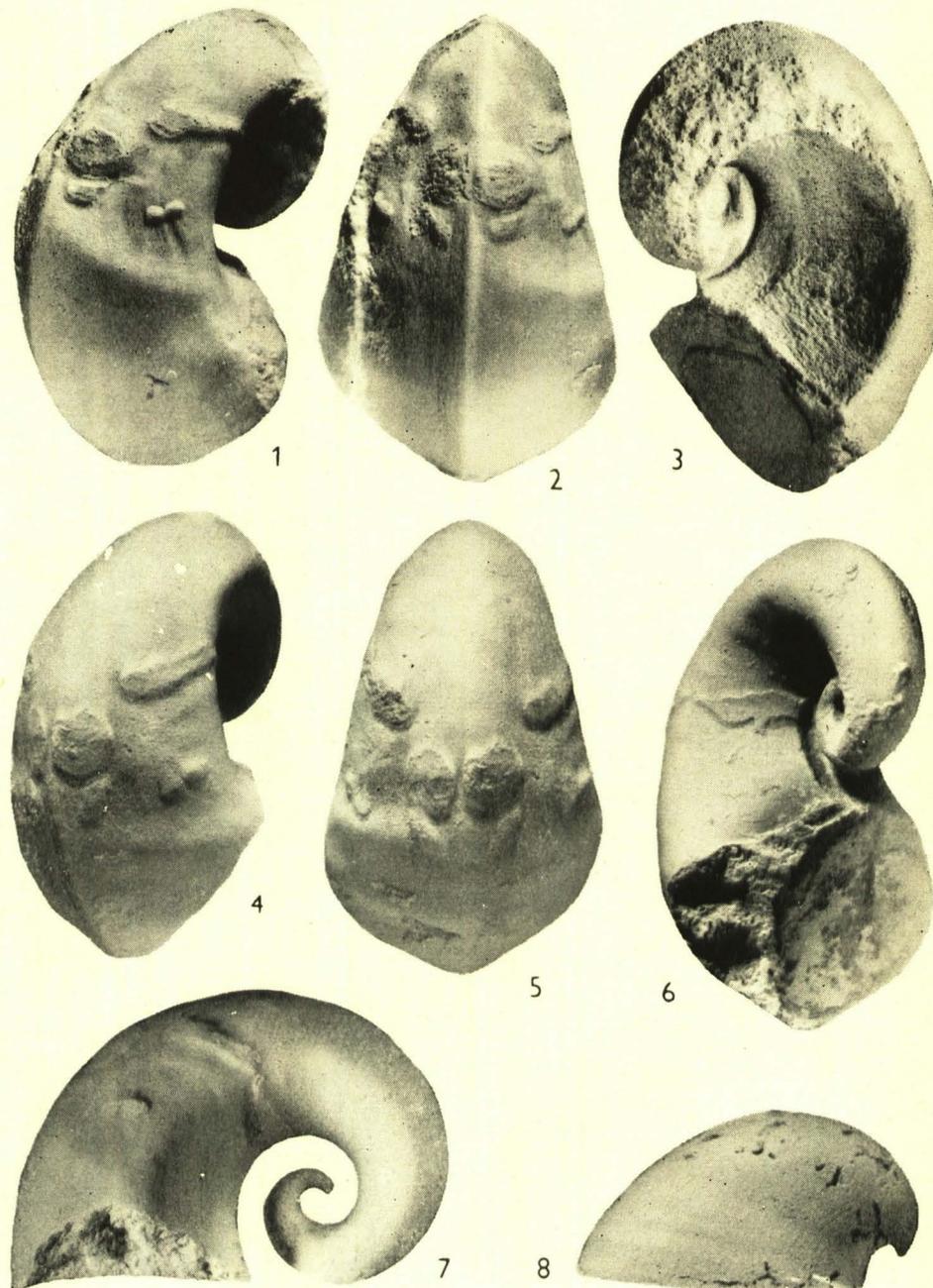
Specimen No. G 27636. Internal cast X 2.5. 5 — right dorsolateral view showing weak dorsal and lateral scars. The right anterolateral scar composed of at least three particles showing structures of growth. 6 — apertural view. Note the slight reflection of the ventral groove inside the aperture. 7 — left lateral view showing the initial part of the shell.
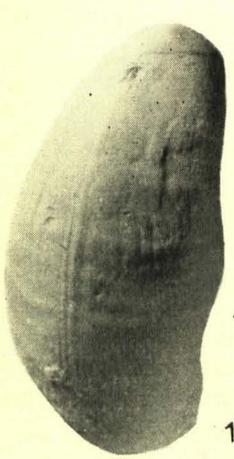
Specimen No. PG 2662. Internal cast. X 2.5 8 — left lateral view. Note the transverse undulation of the shell.

All specimens whitened with ammonium chloride. Photo R. Horný.
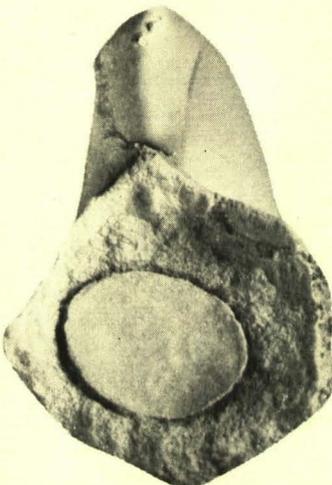
R. J. Horný: Cyrtolites Conrad, 1838.

Plate 1