UNIVERSITY OF KANSAS PALEONTOLOGICAL CONTRIBUTIONS

MOLLUSCA, ARTICLE 5, PAGES 1-11, PLATES 1, 2, FIGURE 1

ORIGIN AND ADAPTATION OF PLATYCERATID GASTROPODS

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ABSTRACT

The Paleozoic gastropods *Platyceras, Cyclonema, Naticonema,* and possibly *Dyeria* are shown to have been sedentary mollusks that lived on the tegmen of crinoids or cystoids, feeding on the waste products of these echinoderms. The association suggests that the gastropods mentioned were exclusively coprophagous (eating faecal matter). Their attached mode of life is reflected in features of shell form, and similarity in adaptation is judged to denote genetic relationship. Accordingly, they are assembled in the family Platyceratidae.

Cyclonema, which first appears in Black River strata (Middle Ordovician), and *Naticonema,* first known in slightly younger (Trenton) rocks, are found attached to crinoids having a nearly smooth tegmen, and they exhibit only slight irregularities of the apertural margin. Shells of *Platyceras,* stratigraphically distributed from Middle Silurian to Upper Permian, show moderate to strong projections and indentations of the apertural margin, which are correlated with protuberances of the crinoid tegmens beneath them. The earlier species of *Platyceras* bear surface markings of the shell similar to those that characterize *Cyclonema* and *Naticonema,* but later ones lack these features. Taken as a whole, the platyceratid gastropods furnish evidence of progressive adaptation to a coprophagous mode of life and thus they became highly specialized. The correspondence in shell characters and peculiar mode of life, which previously has not been recognized, indicates a common origin from an Early Ordovician or older stock. Disappearance of the group near the end of Paleozoic time coincides with the extinction of various hosts among the camerate and inadunate crinoids, which indicates the possibility that vanishing of the crinoids may account for the termination of these specialized gastropods.

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INTRODUCTION

PURPOSE OF INVESTIGATION

Several years ago when Dr. J. BROOKES KNIGHT, specialist of the Smithsonian Institution on studies of Paleozoic gastropods, was discussing with me the subject of habits and probable evolution of *Platyceras* (Middle Silurian to Upper Permian), our attention was directed to *Cyclonema* (Middle Ordovician to Middle Silurian) as a possible ancestor. A reason for this suggestion was similarity in the living habits of the two genera, for representatives of both are found closely associated with the calyces of crinoids. Dr. KNIGHT suggested that I search the large collection of crinoids in the U. S. National Museum for specimens having gastropods attached to them, and then study the mode of attachment and any seemingly correlated shell characters of the gastropods to learn more of the adaptation and evolution of such gastropods. This paper reports observations and conclusions resulting from the investigation thus undertaken. In addition to specimens of *Platyceras* and *Cyclonema* attached to crinoids, shells belonging to *Naticonema* (Middle Ordovician to Middle Silurian) were found to demonstrate similar association and so are included in the study. Among several other genera that are assigned by Dr. KNIGHT to the family Platyceratidae, none were found to be represented in the U. S. National Museum collection by specimens joined to crinoids or cystoids. Except *Dyeria* (Middle and Upper Ordovician), which will be discussed briefly, the platyceratids not yet definitely known to have lived like *Platyceras* are excluded from consideration in this paper.

PREVIOUS STUDIES

The earliest discovered mention of an association between mollusks and crinoids is by AUSTIN & AUSTIN (1843-49, p. 73). These authors believed that the crinoids were carnivorous and that, as suggested by observed fossils, death overtook some of the crinoid individuals while they were in the act of feeding on a gastropod. KEYES (1888a, p. 233) reports that YANDELL & SHUMARD (1847), YANDELL (1855), and OWEN (1862) held similar views. BILLINGS (1870), on the other hand, judged that the gastropod *Platyceras*[1] was a carnivore that fed on crinoids. DE KONINCK (1842-44), TRAUTSCHOLD (1867), WEATHERBY (1879), and WHITEAVES (1889) mention the close association of specimens of *Platyceras* with various crinoids but do not offer interpretation of its meaning.

MEEK & WORTHEN (1866, p. 386) seem to have been the first to realize that *Platyceras* was a sedentary gastropod that lived on the tegmen of a crinoid, feeding at least partly on excrement ejected by the host crinoid. Later discussions by these authors (MEEK & WORTHEN, 1868, p. 331-334) and especially by KEYES (1888a, 1888b, 1889, 1890, 1892), who published detailed descriptions of the irregular apertures of *Platyceras* specimens attached to crinoids and interpretation of their significance, served to establish clearly this explanation of the association of gastropod and crinoid. HINDE (1885) described specimens of *Platyceras* fixed on the tegmen of *Arthroacantha* from Middle Devonian strata near Arkona, Ont., with illustration of a form identified as *P. dumosum* CONRAD in such association (HINDE, 1885, pl. 6, fig. 1). CLARKE (1908) discussed what he termed the dependent parasitism of gastropods on crinoids and cystoids, citing the association of *Cyclonema* with *Glyptocrinus* shown by fossils from Upper Ordovician strata and furnishing illustrations. Subsequently, he (CLARKE, 1909) described and figured an unusually large *Platyceras tortuosum* attached to the tegmen of a specimen of *Melocrinus micmac;* these fossils come from the Lower Devonian of the Gaspé region in eastern Quebec. Various other authors have noted similar occurrences, but no comment is made generally on adaptation of the gastropod that led to its unusual mode of life.

1. As used in this paper, the name *Platyceras* Conrad (1840) includes subgenera, such as *Orthonychia, Platyostoma,* and *Visitator,* as well as numerous synonyms (*Platycerina, Diaphorostoma, Exogyroceras, Igoceras, Palaeocapulus, Geronticeras, Saffordella,* and several others).

PLATYCERAS

OCCURRENCE ON THE TEGMEN OF VARIOUS CRINOIDS

The conclusion that the observed association of *Platyceras* and allied gastropods with crinoids is not accidental must be regarded as demonstrated by the many known specimens showing the gastropod seated on the crinoid tegmen, with the aperture over the crinoid's anal vent. The *Platyceras* shell is not adjoined in random fashion to some part of the dorsal cup or stem. Furthermore, irregularities of the apertural margin of the attached *Platyceras* invariably fit closely to irregularities of the tegmen of the host. Several examples of this gastropod preserved *in situ* on crinoids, which are illustrated in this paper (Pl. 2, figs. *1b,c, 5, 6a,b*), show how closely the apertural margin of the shell conforms to the surface of the crinoid. One of these specimens, identified as *Platyceras dumosum rarispinum,* from Middle Devonian beds in western Ontario, is attached to a species of the camerate *Arthroacantha,* the edge of the shell being indented so as to fit exactly various irregularities of the ventral surface of the crinoid (Pl. 2, figs. *1a,b*). Re-entrants of the aperture coincide in position with five radiating ridges of the crinoid tegmen, indicating that growth

of the gastropod shell was retarded in these places. A re-entrant on the left posterior side of the aperture fits over the anterior ridge of the tegmen, and a prominent salient at the front of the gastropod aperture covers the anal opening of the crinoid, extending downward also over part of the posterior interradial area of the dorsal cup. This anterior salient is unusually wide, for it corresponds to the posterior interradius of *Arthroacantha*, which has distinctly greater width than other interradial areas. Re-entrants that occur above the left anterior and left posterior ridges of the crinoid tegmen (Pl. 2, fig. 2) are located on the right side of the gastropod aperture (Pl. 2, fig. *1c*). Those covering the right posterior and right anterior tegminal ridges occur on the left side of the attached *Platyceras* aperture. Thus, it is evident that the five re-entrants of the apertural margin are due to retarded growth of the shell where it impinges on the five ridges of the crinoid tegmen. HINDE (1885) first pointed out this conformity of the apertural margin of *Platyceras* to the tegmen of *Arthroacantha* and its relation to the anus of the crinoid.

Two specimens of *Agaricocrinus iowensis* in collections of the U. S. National Museum (no. S4,636) have *Platyceras* shells attached to their calyces; these come from Lower Mississippian rocks of Indiana. The gastropod on one of the crinoids covers the posterior interradial area and exhibits two wide re-entrants of the apertural edge that fit over strongly protuberant rays of *Agaricocrinus* (Pl. 2, figs. *6a, b*). The other *Platyceras* specimen (not illustrated) is located on the crinoid tegmen with the anterior part of its aperture produced into a long salient above the crinoid's anus and reaching down over part of the posterior area of the dorsal cup. Nine small re-entrants of the apertural margin correspond to nine small rounded tegminal plates. It is obvious that the difference in number, shape, and size of irregularities of the shell margin of these two gastropods is explained by difference in their positions on the crinoids. The number and shape of re-entrants and salients of the apertures of species belonging to *Platyceras* lack taxonomic significance.

A specimen of *Platyceras haliotis* PHILLIPS from Middle Silurian (Wenlock) limestone of central England is enclosed completely within the arms of *Marsupiocrinus coelatus* (Pl. 1, figs. *12a,b*). The gastropod is attached to the crinoid tegmen with the anterior part of its aperture located over the anal opening of the host crinoid.

A shell of *Platyceras chesterense* attached to the tegmen of a species of *Pterotocrinus*, from Upper Mississippian rocks, is illustrated by KEYES (1890, pl. 2). The apertural margin of this gastropod has five prominent re-entrants that fit closely around five large tegminal spines of the crinoid.

Another specimen, identified as *Platyceras formosum*, from Lower Mississippian beds in Iowa, is joined to an individual of *Aorocrinus* (Pl. 2, fig. 5). A drawing of this gastropod published by KEYES (1890) shows the aperture extending to the extreme borders of the crinoid tegmen all around; but erroneously it indicates an equal spacing of small re-entrants in the gastropod aperture. Actually, indentations of the shell edge are uneven and the surface of the shell bears five inequidistant flat folds that conform to the elevated rays of the crinoid. The gastropod aperture has a pentagonal outline with re-entrants of the margin corresponding to the five folds just mentioned. The shell surface is depressed sharply between the folds, the depressions being extended as narrow projections between the crinoid rays. Each broad marginal re-entrant of the aperture is divisible into four smaller ones that mark the position of minor folds overlying the four arms of each ray of the crinoid. The anterior part of the gastropod aperture constitutes a wide salient above the crinoid's anal opening and this salient also covers part of the posterior interradial area of the cup. The apertures of *Platyceras* shells attached to specimens of *Aorocrinus* or similarly constructed crinoids have a diagnostic shape, which is characterized by five flat folds on the surface that correspond in position to five broad re-entrants of the margin, each marked by four smaller ones. This is explained by the grouping of four arms in each of the five rays of the crinoid. The anterior salient of the apertural edge is the widest, and this invariably is directed toward the posterior side of the crinoid, covering the anus. Many specimens of *Platyceras* from the Burlington limestone (Lower Mississippian) in collections of the U. S. National Museum exhibit the form just described; they are judged to have lived on the tegmen of *Aorocrinus* or another crinoid having raised rays and grouped arms.

KEYES (1890, pl. 2, fig. 7) has illustrated a specimen of *Strotocrinus* (Lower Mississippian) that shows scars on the tegmen presumably made by an attached *Platyceras* shell. Because the tegmen of *Strotocrinus* is composed of many small plates with smooth surfaces, the aperture of the associated gastropod probably lacked well-defined re-entrants in its margin.

A specimen of *Platyceras infundibulum* attached to the calyx of *Platycrinites hemisphericus* (Mississippian) shows the anterior part of its apertural margin covering the crinoid's anus (CLARKE, 1908, pl. 6, fig. 7). The edge of the gastropod shell is irregular, fitting closely over many small tubercles of the plates and depressions along plate sutures of the crinoid.

CLARKE (1908, pl. 6, figs. 3, 4) also has figured a *Platyceras* shell attached to the poster side of the cup of an inadunate crinoid (*Cromyocrinus*). This specimen shows the margin of the aperture produced into angular projections that precisely conform to the deeply incised sutures between plates of its host.

A *Platyceras* shell on the tegmen of *Megistocrinus* exhibits a smooth apertural margin, because the central part of the crinoid tegmen has smooth even plates (CLARKE, 1908, p. 23). The left margin of the aperture margin has some re-entrants, however, for this part fits over folds above ambulacra at the edge of the tegmen.

The aperture of a *Platyceras* from Lower Mississippian beds at Crawfordsville, Ind., is observed to enclose the dorsal cup and arm bases of *Cydrocrinus*, an inadunate crinoid; this specimen (U. S. National Museum no. S2,593) shows the posterior part of the gastropod aperture almost completely surrounding the crinoid stem.

Many other examples of *Platyceras* with apertures conforming exactly to the surface of the host crinoid could be cited, but evidence here stated seems to indicate very clearly that species belonging to this genus were sedentary gastropods that lived on the calyx of crinoids, generally attached to the tegmen in a manner so as to cover the anal opening of the crinoid.

EFFECT OF SEDENTARY LIVING HABIT ON THE APERTURE

The irregularity and variability of *Platyceras* shells make taxonomic treatment of them rather difficult. It should be remembered that the many variations shown by these shells reflect their stationary living habit. If the surface on which they grew was smooth, their apertural margin also was smooth, but if the surface of attachment was uneven, the edge of the aperture was marked by re-entrants and salients corresponding to irregularities of this surface. The irregularities of the attachment surface are recorded also in growth lines of the shell. Strong re-entrants of the apertural margin correspond in position and shape to sinuosities of the growth lines traced backward toward the apex. Such traces on some shells superficially resemble the anal fasciole (selenizone) of the pleurotomarians, to which they are neither analogous nor homologous.

Some students of gastropods have expressed the opinion that the prominent re-entrant of *Platyceras* shells corresponds to the single anal emargination of the pleurotomarians. TERMIER & TERMIER (1952, p. 387) go so far as to homologize each and every re-entrant in the margin of platyceratid shells with the single anal slit of dibranchiate gastropods such as the pleurotomarians, and thus they postulate that a ctenidium bordered each re-entrant of the platy-

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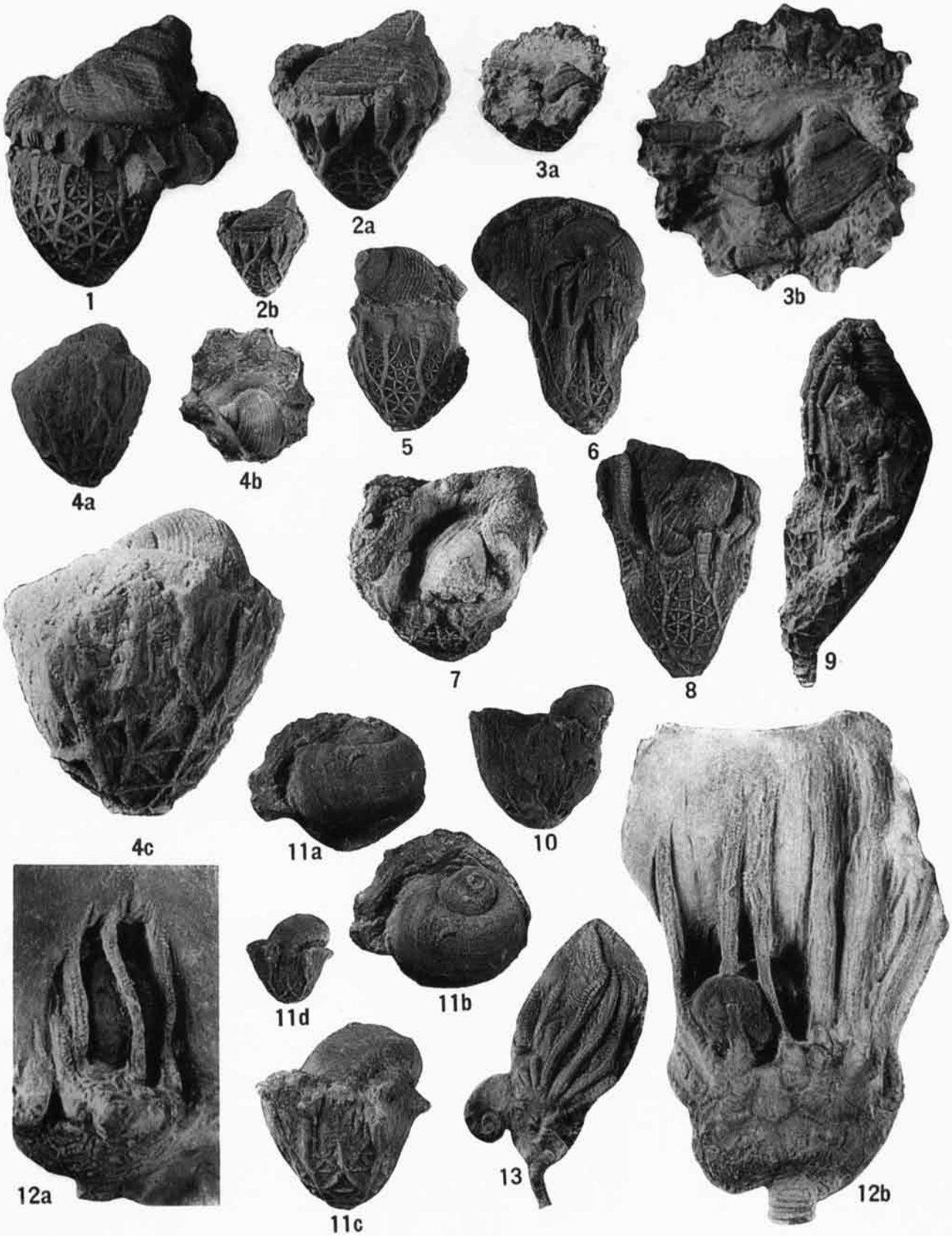
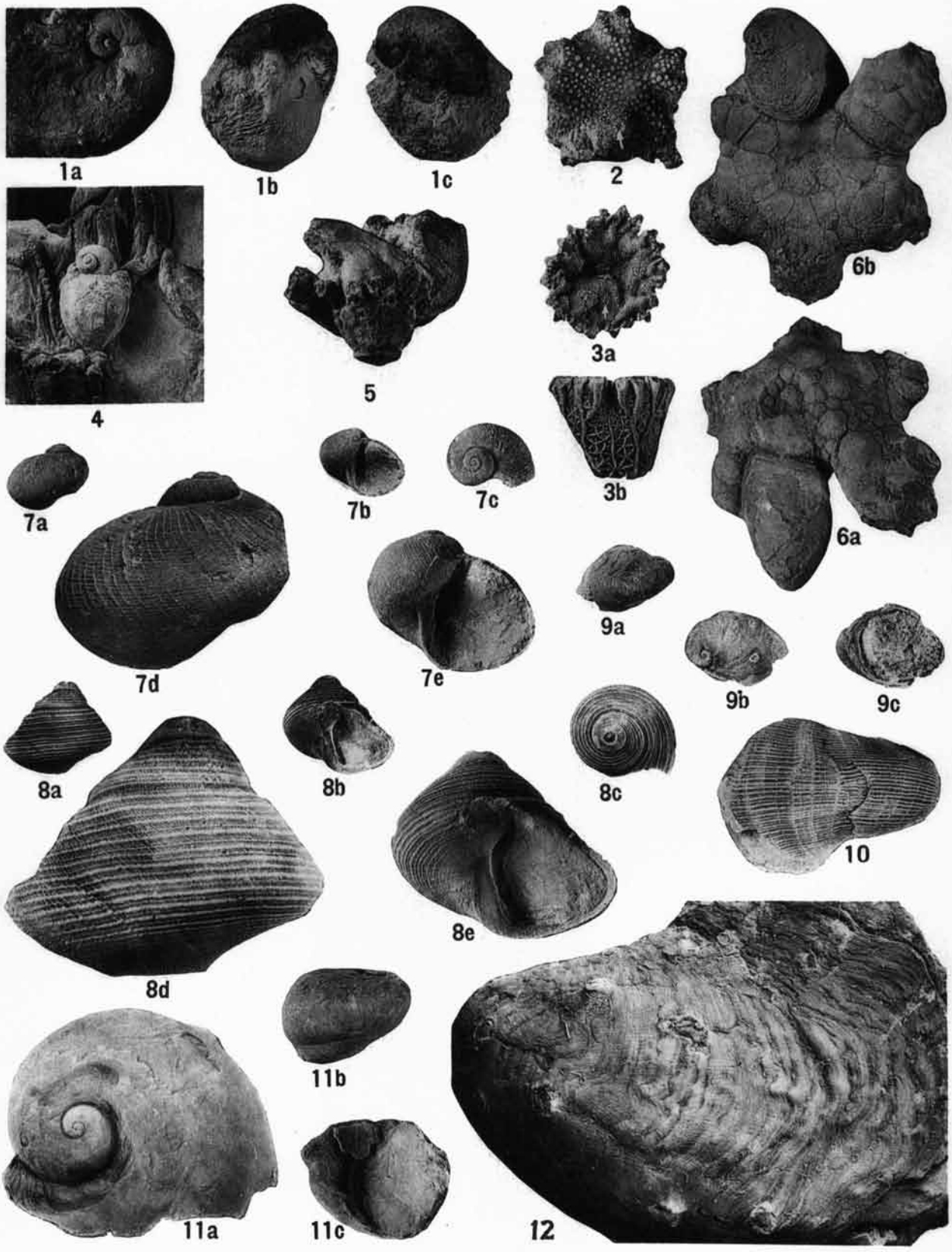
EXPLANATION OF PLATE 1

Symbiotic relations between *Cyclonema* and Ordovician crinoids, *Naticonema* and Ordovician and Silurian crinoids, and *Platyceras* and a Silurian crinoid. The illustrations on this plate show gastropods preserved *in situ* as they lived on the tegmen of their host crinoid.



BOWSHER — Adaptation of Platyceratid Gastropods



BOWSHER — Adaptation of Platyceratid Gastropods

ceratid aperture. They recognize that the slit or sinus of pleurotomarian gastropods lies just over the anal tube, but the logical consequence of interpreting the several re-entrants of the platyceratid shell as anal slits (namely, that these gastropods possessed several anal vents) is not mentioned. It should be pointed out that the terms "capuliform" and "holobranch" as used by DELPEY (1940a) and TERMIER & TERMIER (1952) lack taxonomic significance. A gastropod may have a capuliform shell either as a primitive character or as a secondary adaptation, commonly in response to a sedentary habit. The term holobranch is employed to distinguish gill structures extending the full length of the gastropod aperture, whether these structures consist of true ctenidia or of pallial branchiae. The TERMIERS (1952) consider holobranch gastropods to be primitive, neglecting the fact that many holobranch forms such as *Patella* clearly are highly specialized and appear late in geologic time. Available evidence seems not to support views on evolution and classification of the gastropods based on the concept that *Platyceras* represents a primitive, holobranchiate stem from which all members of the class are presumed to have developed.

FEEDING HABITS

If, as seems to be indicated, platyceratid individuals lived their post-larval existence fixed to the calyx of a crinoid, it is reasonable to suppose that their chief food supply was faecal matter discharged from

EXPLANATION OF PLATE 2

Symbiotic relations between *Platyceras* and Devonian and Mississippian crinoids, tegminal structure of an Ordovician and a Devonian crinoid, and shell characteristics of the gastropods *Cyclonema, Naticonema,* and *Platyceras.*

FIGURE — PAGE

1a-c—*Platyceras* on *Arthroacantha carpenteri* Hinde, from the Arkona beds of Hamilton age, Middle Devonian, at Arkona, Ont., Canada (USNM no. 50,489). *1a,* Apex of the *Platyceras* showing ornamentation of the earliest whorls, × 2. *1b,* Anterior ray of the crinoid showing the strong re-entrant on the left posterior margin of the gastropod where it fits closely over the ridge on the crinoid tegmen formed above the anterior ambulacrum, × 1. *1c,* Oblique view from above the left posterior ray showing the irregular apertural margin of the *Platyceras* conforming to the shape of the crinoid tegmen. The re-entrants of the aperture can be traced back along the shell by the growth lines, × 1 . . . . . 2, 3, 9

2—Tegmen of *Arthroacantha* sp., from the Silica shale (of Stewart), Hamilton age, Middle Devonian, at Sylvania, Ohio (USNM no. 111,578). The minute anal opening (marked by white arrow) is situated atop a small anal protuberance, × 1 3

3a,b—*Glyptocrinus decadactylus* Hall, from the Maysville group (Cincinnatian), Ordovician, at Cincinnati, Ohio (USNM no. S179). *3a,* Top view of the crinoid showing character of the tegmen (anal vent marked by white arrow) and a concentric groove which may mark the position occupied by a coprophagous gastropod (*Cyclonema* or *Naticonema*), × 1. *3b,* Posterior side of crinoid, × 1 7

4—*Naticonema* over the anal opening of *Caryocrinites ornatus* Say, from the Niagara group, Silurian, Lockport, New York (USNM no. S4,634), × 1 8

5—*Platyceras* over the anal opening of *Aorocrinus immaturus* (Wachsmuth & Springer) from the Hampton formation (Laudon, 1931), Lower Mississippian, LeGrand, Marshall County, Iowa (USNM no. S590), × 2 . . 2, 3

6a-c—*Platyceras* on the anal opening of *Agaricocrinus iowaensis* Miller & Gurley, from the Edwardsville formation (Osagian), Lower Mississippian, Crawfordsville, Indiana (USNM no. S4,636). *6a,* Oblique view of the tegmen of *Agaricocrinus* showing the irregular aperture of the gastropod over the anal opening, which is located in the posterior interradial area, conforming to the shape of the crinoid. *6b,* Oblique view of the base of the *Agaricocrinus* showing the re-entrant on the right side of the gastropod where the apertural margin fits against the side and the right posterior ray of the crinoid, × 1 . . . . . 2, 3, 9

7a-e—*Naticonema cyclostomatum* (Hall) from the Waldron clay member of Wayne formation (Niagaran), Silurian, Newsom, Tennessee (USNM no. 99,420), for comparison with *Cyclonema* and *Platyceras. 7a,* Side view, × 1. *7b,* Apertural view, × 1. *7c,* Top view, × 1. *7d,* Side view showing typical *Naticonema* ornamentation, × 1. *7e,* Apertural view showing columellar lip, × 2 . . 8, 9

8a-e—*Cyclonema pyramidale* James, from the Maysville group (Cincinnatian), Ordovician, at Morrow, Ohio (USNM no. 45,776), for comparsion with *Naticonema* and *Platyceras. 8a,* Side view, × 1. *8b,* Apertural view, × 1. *8c,* Top view, × 1. *8d,* Side view showing typical cyclonematid ornamentation, × 3. *8e,* Apertural view showing columellar lip, × 2 9

9a-c—*Platyceras dumosum* Hall, from the Arkona beds, Hamilton age, Middle Devonian, at Arkona, Ont., Canada (USNM no. 50,489). *9a,* Side view, × 1. *9b,* Top view, × 1. *9c,* Apertural view, × 1 8

10—*Dyeria costatus* (James), from Corryville shale member, McMillan formation, Maysville group (Cincinnatian), Ordovician, Cincinnati, Ohio (USNM no. 45,796), showing irregular growth lines characteristic of this gastropod, × 2 8

11a-c—*Platyceras haliotis* (Phillips), from the Wenlock (Middle Silurian), at Dudley, England (USNM no. 9,982), for comparison with *Cyclonema* and *Naticonema. 11a,* Top view, × 3. *11b,* Side view, × 1. *11c,* Apertural view, × 1 9

12—Surface sculpture on a specimen of *Platyceras rarispinum(?)* Hall, from the Silica shale (of Stewart), Hamilton age, Middle Devonian, Sylvania, Ohio (USNM no. 12,338), showing the fine *Naticonema*-like ornamentation of the shell, × 2 9

the alimentary canal of their host. The deduction that *Platyceras* was a coprophagous [2] invertebrate is based on the observation that shells of this gastropod found attached to crinoids are almost invariably so placed that the mantle cavity would cover the anal opening of the host crinoid.

Nothing is known of the nature of faecal waste of extinct crinoids. GISLÉN (1924) has studied the excrement of some living comatulid crinoids in order to learn about their nourishment. He reported that the ejected waste consists of undigested food particles held together by a jelly-like substance so as to form mucous balls. These faecal pellets normally fall onto the tegmen, from which they are dislodged by water currents or by movements of the crinoid. They contained a mixture of organic detritus, such as threads of algae, macerated leaves, and other plant remains, diatoms, peridinians, crustacean larvae, copepods, ostracodes, fragments of hydroid colonies, and myzostomids—all more or less digested—as well as some living infusorians.

The faeces of many extinct crinoids probably were evacuated as pellets, for otherwise the excrement ejected from the anus would have contaminated the sea water immediately adjacent to the food-gathering arms. Because the anal vent is located on the tegmen near the base of the arms, the ciliated ambulacral grooves of the arms would return the contaminated sea water to the mouth. This unsanitary condition would be avoided, however, if the excrement were extruded as faecal pellets. If we may assume that the Paleozoic crinoids, like modern comatulids, emitted waste from their alimentary tract in the form of pellets, these pellets would furnish a constantly available source of food for a *Platyceras* individual that was located so as to cover the anus of the crinoid. The gastropod probably was not suctorial but had to wait passively until the crinoid was ready to "serve" it with a faecal pellet. This inference is based on the observation that exceptionally well-preserved crinoids belonging to various genera have an area of crowded tiny plates, probably moveable, in the position of the anus. The area resembles the periproct of an echinoid, and it is presumed to have functioned in closing or opening the anal orifice.

The Paleozoic crinoids probably required well-oxygenated sea water around them. If coprophagous gastropods associated with them fed on faecal pellets, it seems unlikely that they possessed unusual means for evacuation of their own body wastes or that these affected the crinoid; also, probably they had no special gill structures.

SELECTIVITY IN CHOICE OF HOST

The rather considerable variation in shell characters shown by individuals belonging to *Platyceras* makes specific identifications difficult. This statement is generally applicable, and it gives reason for expression of doubt concerning the correctness of several specific identifications reported by KEYES (1890). If one accepts his identifications, however, the conclusion is warranted that species of *Platyceras* were not selective in choosing a particular genus or species of crinoid as their host. For example, KEYES reports that *Capulus* (= *Platyceras*) *equilateralis* is variously found on the tegmens of *Strotocrinus, Agaricocrinus, Poteriocrinites, Platycrinites,* and two different species of *Gilbertsocrinus.* He also cites the occurrence of *Capulus* (=*Platyceras*) *dumosum* and *Capulus* (= *Platyceras*) *erectus* on the tegmens of specimens belonging to *Arthroacantha punctobrachiata.* Perhaps the choice of a host crinoid is controlled only by the presence of a reasonably smooth place of attachment for the gastropod close to the anus of the crinoid. *Platyceras* seems not to have lived on any crinoids provided with a long, slender anal tube (such as *Cactocrinus, Teleiocrinus, Steganocrinus,* and others).

Because the shape and ornamentation of a crinoid tegmen make an impression on apertural characters of an attached *Platyceras* shell, the nature of irregularities of the gastropod's aperture may provide diagnostic clues to the type of crinoid that served as host. This is an important observation, for it is obvious that many *Platyceras* shells become disassociated from their host, as when the plates of the crinoid fall apart after death, and this scattering of crinoid skeletal parts is the rule, rather than the exception.

2. The term "coprophagous" (faeces-eating) is applied to any animal that feeds on dung or waste matter derived from another animal. It is appropriately used to designate platyceratid gastropods, which subsisted mainly, if not exclusively, on the excrement of crinoids and cystoids.

CYCLONEMA

DIAGNOSTIC FEATURES

The genus *Cyclonema* HALL (1852) is distinguished by the subquadrate shape of the shell aperture, with oblique outer lip and with columellar lip excavated and thickened; the base of the shell is rounded or slightly flattened and the spire is moderately elevated; an umbilicus and callus are lacking; and the exterior of the shell bears many rather coarse revolving threads or cords, which are crossed by fine irregularly undulating transverse threads and growth lines. The stratigraphic range of *Cyclonema* is from Middle Ordovician (Black River) to Middle Silurian.

Many species of post-Niagaran Paleozoic gastropods that have been referred by various authors to *Cyclonema* are thought to be assignable actually to other genera; they do not belong to *Cyclonema.* The forms discussed in this paper as members of the genus are closely related to the type species, *C. bilix* (Conrad).

EVIDENCE CONCERNING MODE OF LIFE

Like *Platyceras,* shells belonging to *Cyclonema* are found closely associated with crinoids. CLARKE (1908, p. 22) was the first to point out the occurrence of *Cyclonema* on the tegmen of Late Ordovician crinoids and in a later paper (CLARKE, 1921) he considerably expanded his description and discussion. In preparation for the present paper, numerous examples similar to those reported by CLARKE were found and studied. Commonly, the gastropod shells are attached to calyces of species of the monobathran camerate, *Glyptocrinus.*

As usually preserved, the arms of *Glyptocrinus* effectively conceal a gastropod shell attached to its tegmen, but some specimens of this crinoid are observed with the arms bowed outward just above the dorsal cup, in manner that would cover a moderately large gastropod. Only when one or more of the arms of such a crinoid are removed, can the gastropod located between the arm bases be seen. This removal may be effected by natural causes during weathering after the fossil has become exposed; this is common. Also, the presence of a *Cyclonema* on the tegmen of *Glyptocrinus* may be discovered by breaking away some of the arms which hide it.

The tegmen of *Glyptocrinus* is nearly smooth, and accordingly the apertural edge of an attached *Cyclonema* shell is relatively even. Irregularities of the apertural margin do exist, but they are too inconspicuous to permit identification of the tegminal elevations that are responsible for very shallow broad indentations of the shell margin. It is significant, however, that the magnitude and general configuration of irregularities in the apertural margin of *Cyclonema* agree closely with the slight elevations and depressions of the tegmen of *Glyptocrinus.*

Another feature of specimens of *Cyclonema* found on crinoid tegmens is that most of them are placed with the aperture of the gastropod over the anus of the crinoid. Unlike *Platyceras,* however, which was forced to adopt certain stable positions on the irregular tegmen of its host, the shells of *Cyclonema* show no preferred orientation on the nearly featureless tegmen of *Glyptocrinus.* The gastropod may be seated in almost any orientation above the anal opening of the crinoid.

In order to study this seemingly random placement of *Cyclonema,* it is desirable to examine the tegmen of its host in more detail. Illustrations are given of a typical specimen of *Glyptocrinus* (Pl. 2, figs. *3a, b*). The ventral view shows the tegmen oriented in conventional manner with the posterior side downward, and near this edge the location of the very small anal opening is indicated by a white arrow. In studying the tegmen, the position of the anus is distinguishable only by the presence of many small plates which are crowded around it. The tegmen as a whole is slightly arched or nearly flat. The specimen illustrated has a roughly circular depression on the tegmen that may have been covered by the aperture of a *Cyclonema* shell. No ridges on the tegmen are observable except within a few millimeters of its edge, and these are weakly defined. The tegminal plates are small and their smooth surface lies nearly flat; sutures between the plates are not indented. Evidently, a gastropod attached to this tegmen should have an almost smooth apertural margin, and if the aperture was located so as to surround the anus of the crinoid, a part of the shell margin should be joined to the tegmen near the outer edge of the posterior interradius.

Three figured specimens of *Cyclonema* attached to the summit of *Glyptocrinus* individuals that are given in this paper (Pl. 1, figs. *2a,b, 4a-c, 6*) do not indicate conclusively that placement of the gastropods agrees exactly with their position in life. This is hardly surprising in view of the lack of any organic connection between the gastropod and its host that would anchor it in place after death. Several other associated pairs of *Cyclonema* and *Glyptocrinus* which are illustrated (Pl. 1, figs. *1, 3a,b, 5, 7-9, 11a-d*) show the gastropod in place above the anus of the crinoid, and these seem to indicate that the *Cyclonema* individuals are preserved where they lived, with little or no shift in position on the crinoid tegmen. These and many other examples are interpreted to establish beyond reasonable doubt the coprophagous habit of *Cyclonema.* The undulating growth lines observed on the surface of most *Cyclonema* shells reflect a sedentary mode of life, and they may be cited as additional evidence that species belonging to this genus were probably all sedentary on crinoids or cystoids and were coprophagous.

ULRICH & SCOFIELD (1897, p. 1057) have suggested that the shell of *Cyclonema* differed in composition from that of most other Ordovician gastropods, and in their opinion species of *Cyclonema* lacked an operculum, or if they had an operculum, it was not suited for preservation. In various beds one may find well-preserved shells of *Cyclonema* associated with other gastropods that are represented only by "steinkerns"; the same is true of *Platyceras.* Lack of an operculum may be explained by the sedentary habit of these gastropods.

NATICONEMA

DIAGNOSTIC FEATURES

Naticonema PERNER (1903) is a Middle Ordovician to Devonian genus of *Cyclonema*-like gastropods that are distinguished mainly by their round aperture with thickened and excavated columellar lip, rather low spire, round base, large body whorl of somewhat variable shape, absence of an umbilicus or callus, and by surface ornamentation consisting of many fine revolving threads and moderately strong undulating transverse threads and growth lines.

Many species of Ordovician and Silurian gastropods from North America that have been referred by various authors to *Platyceras, Strophostylus, Diaphorostoma* and *Platyostoma* actually belong to *Naticonema.*

MODE OF LIFE

An examination of Ordovician crinoids in collections of the U. S. National Museum to determine possible association with gastropods revealed specimens of *Cyclonema* but no other genus. Specimens of crinoids borrowed from the University of Cincinnati also showed a decided predominance of *Cyclonema* on the tegmen of *Glyptocrinus,* but two gastropods belonging to an undescribed species of *Naticonema* were discovered in place on the summit of crinoid calyces (Pl. 1, figs. *10, 11a-d*). The association of individuals illustrated in Pl. 1, fig. *10,* does not furnish conclusive evidence of the coprophagous habit of *Naticonema,* for the aperture of the gastropod is located a little to the right side of the crinoid's anus. The orientation of this shell corresponds, however, to that of gastropods that feed on faeces discharged by their host. The specimen figured in Pl. 1, figs. *11c,d,* on the other hand, clearly shows the *Naticonema* shell located over the anus of the crinoid. Accordingly, it seems very probable that this species of *Naticonema* was coprophagous.

Search of the Silurian crinoid collections of the U. S. National Museum resulted in finding only three gastropods attached to the calyces of crinoids. Two of the specimens are *Naticonema niagarense* HALL and they are attached to the tegmens of individuals identified as *Macrostylocrinus ornatus* HALL (Pl. 1, fig. *13*). They come from Niagaran beds at Lockport, N. Y. The shape of the crinoid tegmen and configuration of the arm trunks of *Macrostylocrinus* allowed little latitude for placement of the gastropod with its aperture covering the anus of the crinoid; in fact, only two positions are possible, and the *Naticonema* that is illustrated chose the seemingly more natural one. A specimen of *Naticonema* from the Waldron shale of Indiana is here illustrated to show characters of the genus (Pl. 2, fig. *7a-e*); this form closely resembles *N. niagarense,* of which no free specimens from Lockport are available. The third specimen of a Silurian gastropod on a crinoid in the U. S. National Museum collections (no. S1,291) is attached to the calyx of *Marsupiocrinus coelatus* PHILLIPS, from Middle Silurian (Wenlock) limestone at Dudley, England. It bears faint ornamentation similar to that of *Naticonema* but is identified as *Platyceras haliotis* PHILLIPS (Pl. 2, fig. *9a-c*).

CLARKE (1908, p. 22, pl. 6, fig. 1) has described from the Rochester shale of New York a so-called *Diaphorostoma* attached to the calyx of the cystoid *Caryocrinites ornatus.* The gastropod was seated over the anus of its host. I examined many specimens of *C. ornatus* from the Rochester shale in the Springer collection, U. S. National Museum, but was able to find only one specimen of this cystoid with a gastropod preserved on its tegmen (Pl. 2, fig. *4*). The gastropod appears to be the same species, *Naticonema niagarense,* as was found on *Macrostylocrinus ornatus* (Pl. 1, fig. *13*). It is possible that this species of *Naticonema* fed also on waste discharged by other crinoids and cystoids. Some species of coprophagous gastropods evidently were not selective in choosing their host, even though symbiosis of this type is usually confined within narrow bounds.

The observations here recorded indicate that *Naticonema* was a coprophagous gastropod, like *Platyceras* and *Cyclonema.*

DYERIA

Gastropods belonging to the genus *Dyeria,* from Upper Ordovician rocks of the Cincinnati region, first were placed in the Bellerophontacea and later with *Platyceras* in the Platyceratidae. *Dyeria* is a low-spired relative of *Cyclonema* having an uncoiled outer whorl (Pl. 2, fig. *10*). ULRICH & SCOFIELD (1897, p. 1044) concluded that *Dyeria* is not a bellerophontid and "not far removed from *Cyclonema.*" They noted that though the margin of the aperture of shells belonging to *Dyeria* (and hence the lines of growth) take on an undulating course, those of *Cyclonema* do not. A study of many specimens of *Cyclonema* shows that most of them actually do have undulating growth lines like those of *Platyceras* except that they are much less conspicuous. This fact seems to be explained by the smoothness of the tegmen of host crinoids. The characters of *Dyeria* suggest that it too was a sedentary form, perhaps coprophagous, but the genus is rare and no specimen has yet been found on a crinoid. *Cyclonema* occurs commonly on *Glyptocrinus,* which may also have been the host for *Dyeria.*

NATURE AND ORIGIN OF THE PLATYCERATIDS

VIEWS ON CLASSIFICATION

ZITTEL-EASTMAN (1937) placed *Cyclonema* and *Dyeria* in the Trochonematidae (suborder Rhipidoglossa) and *Platyceras* in the Capulidae (superfamily Taenioglossa, suborder Platypoda). WENZ (1938) assigned *Platyceras* and *Naticonema* to the family Platyceratidae (superfamily Trochonematacea, order Archaeogastropoda), *Cyclonema* to the family Cyclonematidae (superfamily Trochanematacea) and *Dyeria* to the subfamily Bucanospirinae (family Trochonematidae, superfamily Trochanematacea). J. B. KNIGHT, ELLIS YOCHELSON and ROGER BATTEN are currently preparing a revised classification of Paleozoic gastropods (now in press) and based partly on evidence presented in this report, they are placing *Cyclonema, Dyeria, Naticonema* and *Platyceras* with others in the family Platyceratidae.

RELATIONSHIP OF PLATYCERATID GENERA

Although *Cyclonema, Naticonema,* and *Platyceras* appear to be very different from one another, various observations lead to the conclusion that they are closely related. They possess features of ornamentation in common. They have the same coprophagous habit. Study of the evolution of these genera suggests that *Cyclonema* and *Naticonema* converge as they are traced backward in time. The same is true of *Naticonema* and *Platyceras.*

The ornamentation of *Cyclonema* consists of strong revolving threads and moderately strong transverse ridges (Pl. 2, fig. *8d*). Surface features of *Naticonema* definitely resemble those of *Cyclonema,* differing only in degree. The transverse ridges are stronger than the revolving threads in *Naticonema* (Pl. 2, fig. *7d*), especially on early whorls. In the Silurian, some species currently referred to *Platyceras* seem actually to belong to *Naticonema;* others which are irregularly uncoiled in manner characteristic of *Platyceras* retain ornamentation recalling that of *Naticonema.* Many Devonian species of *Platyceras* have *Naticonema*-like ornamentation. One specimen of *Platyceras* aff. *P. rarispinum* Hall from the Silica shale of Stewart (1927) (U. S. National Museum, no. 123,338) retains distinct revolving lirae, much broken up, reminiscent of that of *Naticonema* (Pl. 2, fig. *12*). Other Devonian species of *Platyceras,* like those of later periods have only growth lines. On some of these smooth shells, weak but distinct transverse ridges are confined to the apex of the shell (Pl. 2, fig. *1a*). Upper Paleozoic platyceratids lack ornamentation, except for growth lines.

The columellar lip of *Cyclonema* is flattened to near straightness on its inner (apertural) side but flaring, with a moderately well-arched outline on the outer (umbilical) side; it has gently concave surface (Pl. 2, fig. *8e*) and lacks a parietal inductura except close to the columella and adjacent to the suture. The columellar lip and parietal inductura of *Naticonema* are very similar to those of *Cyclonema.* These structures are missing on *Platyceras,* probably as a reflection of its more complete modification for the sedentary habit which also resulted in an uncoiled and irregular shell.

The apertural margin and growth lines of *Cyclonema* are generally variable and irregular, but not as variable and irregular as in *Naticonema.* The difference in apertural irregularity of shells belonging to these two genera may be due to the fact that most of the crinoids associated with *Cyclonema,* mainly Ordovician, had nearly smooth tegmens, whereas the tegmens of shells of crinoids associated with *Naticonema,* mainly Silurian, were more irregular. The *Platyceras* shells from Devonian and Mississippian rocks have very irregular apertures, which is correlated with the fact that most of their hosts were characterized by very rugose tegmens. It is also possible that the sedentary habit was a greater influence in the growth of *Naticonema* than of *Cyclonema.*

Cyclonema has a close, helicoidally coiled shell (Pl. 2, figs. *8a,d,* and Pl. 1, fig. 8). *Naticonema* has a low, helicoidally coiled shell with a strongly expanding aperture (Pl. 2, figs. *7d,e*). Early species of *Platyceras* have closely coiled early whorls and rapidly expanding apertures; although the coiling is helicoidal, it appears to be nearly planospiral (Pl. 2, figs. *1a-c, 11a-c*). Later species of *Platyceras* are completely uncoiled and irregular (Pl. 2, figs. *6a,b*). The evolution from close, helicoidally coiled shells to uncoiled irregular ones is a progressive response to the sedentary habit of these gastropods.

The gradual change and ultimate loss of the *Cyclonema*-like pattern of ornamentation, loss of columellar lip and parietal inductura, the change from close helicoidally coiled shell to an uncoiled irregular one, and the coprophagous habit of *Cyclonema, Naticonema,* and *Platyceras* are factors which suggest relationships between these genera. For these reasons they are included in the same family.

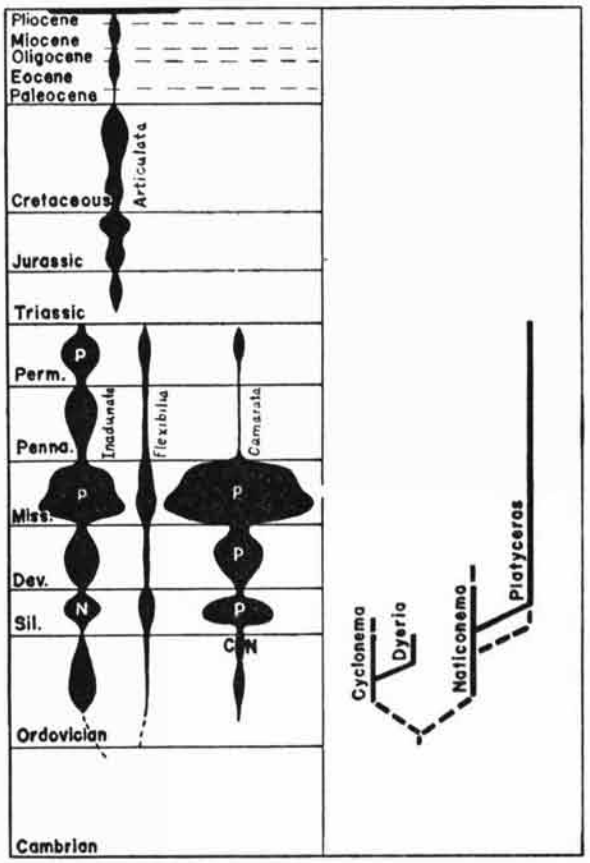


FIGURE 1. Chart showing range and phylogenetic relations of the gastropods *Cyclonema, Dyeria, Naticonema,* and *Platyceras* compared with distribution of crinoids (according to Moore, Lalicker, & Fischer, 1952). Important known occurrences of gastropods attached to the tegmen of crinoids are indicated by the letters "C" for *Cyclonema,* "N" for *Naticonema,* and "P" for *Platyceras.*

ANTIQUITY OF THE COPROPHAGOUS HABIT

Some workers (COSSMANN, 1915; DELPEY, 1940b; TERMIER & TERMIER, 1952) following their predecessors of the pioneer days of paleontology have identified "capuliform" gastropods from Cambrian rocks as *Platyceras*. KNIGHT (1946, p. 281; 1952, p. 44) pointed out that these gastropods were misidentified, belonging neither to *Platyceras* nor to relatives of this genus. He suggested that the Platyceratidae may have been derived from a simple helicoidally coiled form. The study described in this paper supports his conclusion. The terms "capuliform" and "capulid" may be applied to the shells of many platyceratids, as well as to shells of some Cambrian pelagiellids and tryblidiids, providing no taxonomic significance is intended. The fact that both groups were "capuliform" or "capulid" does not mean they are related to each other or to the Capulidae, which did not appear until long after the disappearance of the pelagiellids and tryblidiids. No specimen has been found in the extensive collections of the U. S. National Museum from Cambrian and Ordovician rocks that would be referred to the genus *Platyceras* today, or to the Platyceratidae for that matter. Study of these and other collections suggests that true *Platyceras* did not appear until Niagaran times.

The oldest species of *Naticonema* known to me is represented by undescribed specimens from strata of Trenton age near Pisgah, Ky. (U. S. National Museum, no. 123,330). These have undulating growth lines. *Cyclonema montrealense* BILLINGS (WILSON, 1951, p. 5) from the Lowville (Black River) part of the Ottawa formation, St. Lawrence Lowland, Canada, seems to be the oldest species of *Cyclonema*. The undulating growth lines that characterize *C. montrealense* and the specimens of *Naticonema* from Kentucky suggest that both forms were sedentary and probably coprophagous.

Cyclonema ranged from Middle Ordovician to Middle Silurian, *Naticonema* from Middle Ordovician into the Devonian, and *Platyceras* from Middle Silurian to the end of the Permian. No example of coprophagous gastropods living symbiotically with crinoids has been found in the Mesozoic or Tertiary. Some Recent gastropods, such as *Stilifer, Stylina, Sabinella,* and *Melanella,* live in association with the echinoderms, but they are true parasites and do not have a coprophagous habit.

The appearance of the coprophagous gastropods, in Black River and Trenton times, coincided with the appearance of their crinoid hosts (MOORE, 1952, p. 342, fig. 1). Their distribution and abundance through the Paleozoic era roughly parallels that of their crinoid hosts and both highly specialized invertebrate groups disappeared at the end of the Permian (Fig. 1).

CONCLUSIONS

The coprophagous habit of *Cyclonema* and *Naticonema* is shown to have been established at least by Middle Ordovician time. The ornamentation, nature of the columellar lip and irregular aperture, and the sedentary, coprophagous habit indicates phyletic relations between these forms and *Platyceras*. Accordingly, all these forms may be placed together and with others like them may be classed in the same family. The increasing impact of the coprophagous habit on the life of these gastropods resulted in the loss of initial regularity of coiling of the shell and produced marked irregularity of the apertures. Recognition of the cause of the apertural irregularity with its variable number of re-entrants and salients, militates against considering the platyceratids as holobranchiate or multibranchiate. The primitive Platyceratidae are shown to be simple, helicoidally coiled forms. All are probably diotocardians with a single ctenidium.

The evidence suggests that *Cyclonema* and *Naticonema* were derived from a common Early or Middle Ordovician ancestral stock and that *Platyceras* evolved directly from *Naticonema* in Late Ordovician or Early Silurian times. *Dyeria* probably was derived from *Cyclonema* in Late Ordovician times and may be interpreted as an example of parallel evolution which left no known descendants.

Much interesting information can be obtained about the habits of early forms of *Cyclonema* and *Naticonema* by studying all available specimens of Middle and Upper Ordovician crinoids that are suited to have been the hosts of coprophagous gastropods.

Further study of crinoids from the Cincinnatian rocks of the Ohio area may yield specimens of *Dyeria* or other coprophagous gastropods in place on the tegmen of crinoids.

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