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EVOLUTIONARY TRENDS AMONG MOLLUSK FECAL PELLETS

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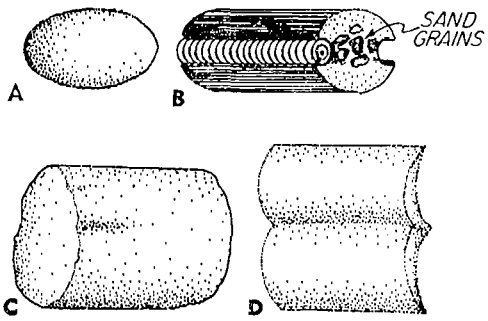
In the study of invertebrate fossils such as gastropods and pelecypods direct knowledge of soft parts must come from inferences drawn from features of the shell that reflect some quality or position of a soft part of the animal. Muscle scars and the pallial sinus of the clam shell come in this category. Occasionally the paleontologist's knowledge of soft parts is aided by an unusual preservation such as the fossilized gastropod intestine

described by Casey (1960) from the Lower Cretaceous, but such finds are indeed rare. Another way to learn about soft parts of fossils is by studying fecal pellets. These have been described from many geologic formations, but have not been viewed as objects useful in reconstructing the internal anatomy of fossil organisms.

Many biologists and geologists have noted that invertebrates produce feces having a characteristic shape and consistency that is quite uniform for members of a species (for review see Moore, 1939). Manning & Kumpf (1959), after comparing feces from many invertebrates, conclude that "Most of the animals in a given group, usually at the generic level, shed similar pellets." Abbott (1954a) used the shape and position of feces of the gastropod genus *Echininus*, along with other criteria, as a basis for removing *Echininus* from the family Modulidae and placing it in the family Littorinidae. Abbott states that "The feces of many, if not all, Littorinidae are relatively short (2 or 3 times as long as wide) and are lined up in the rectum, one directly behind the other," but Abbott did not feel that this character is necessarily of phylogenetic importance. The present report is the result of an investigation based upon the hypothesis that shape of fecal pellets may indeed be of phylogenetic importance and, therefore, be useful in deriving the relationship between invertebrate stocks.



TEXT-FIG. 1—Examples of fecal pellets.

A. Oval pellet from *Cerithium muscarum*. Pellet is light tan with brown spots. Length 1 mm. Pellet was obtained from a living specimen collected in the vicinity of Bimini, Bahamas.

B. Sculptured rod from *Cittarium pica*. Pellet is light brown. The pellet contains two longitudinal surface grooves; one groove contains a spiral tube. Faint ridges run the length of the pellet. Coarser sediment grains are concentrated near center of pellet beneath spiral tube. Pellet length is 4 mm. Pellet was obtained from a living specimen collected in the vicinity of Bimini, Bahamas.

C. Unsculptured rod from *Nerita fulgurans* (from Manning & Kumpf, 1959, fig. 3a). Pellet length varies from 1–3 mm., width 0.71 mm.

D. Ribbonlike pellet from *Brachidontes exustus* (from Manning & Kumpf, 1959, fig. 1c). Pellet length if 0.95 mm., width 0.25 mm.

GASTROPODA

The feces of Gastropoda can be divided according to shape into various types. Manning & Kumpf (1959) classified gastropod pellets as: ovoid or ellipsoid, ellipsoid to rodlike; rodlike, rod with external longitudinal sculpture, rod with spiral sculpture, rod with transverse and longitudinal sculpture, and pellets of undiscernable shape. Pellet classification used in the present paper is: oval pellets, unsculptured rods, sculptured rods, and shapeless pellets for those pellets which have a loose consistency and do not maintain a consistent form. Examples of fecal pellets are shown in Text-figure 1.

The classification of Gastropoda has recently been modified in *The Treatise on Invertebrate Paleontology* (1960), but as Recent genera have not been treated fully in that work, it has been more convenient to use here the classification in Abbott (1954). The gastropod subclass Prosobranchia is divided into three orders: Archaeogastropoda, Mesogastropoda and Neogastropoda (*The Treatise on Invertebrate Paleontology* includes the last two in the order Caenogastropoda). The order Archaeogastropoda, which is considered to be a primitive stock beginning in the Lower Cambrian, contains four superfamilies with representations in today's seas, the Patellacea, the Neritacea, the Pleurotomariacea and the Trochacea. The order Mesogastropoda (Caenogastropoda, part), which is considered to have sprung from Archaeogastropoda, ranges through Mesozoic rocks but increases in numbers in the Cenozoic. The order Neogastropoda

(Caenogastropoda, part) is mostly confined to Cretaceous and post-Cretaceous deposits. The fecal pellet forms produced by species of prosobranchs are summarized in a histogram in Text-figure 2. The data suggest that the rod pellet, both unsculptured and sculptured, is the primitive type and the oval pellet and shapeless pellet are more advanced types.

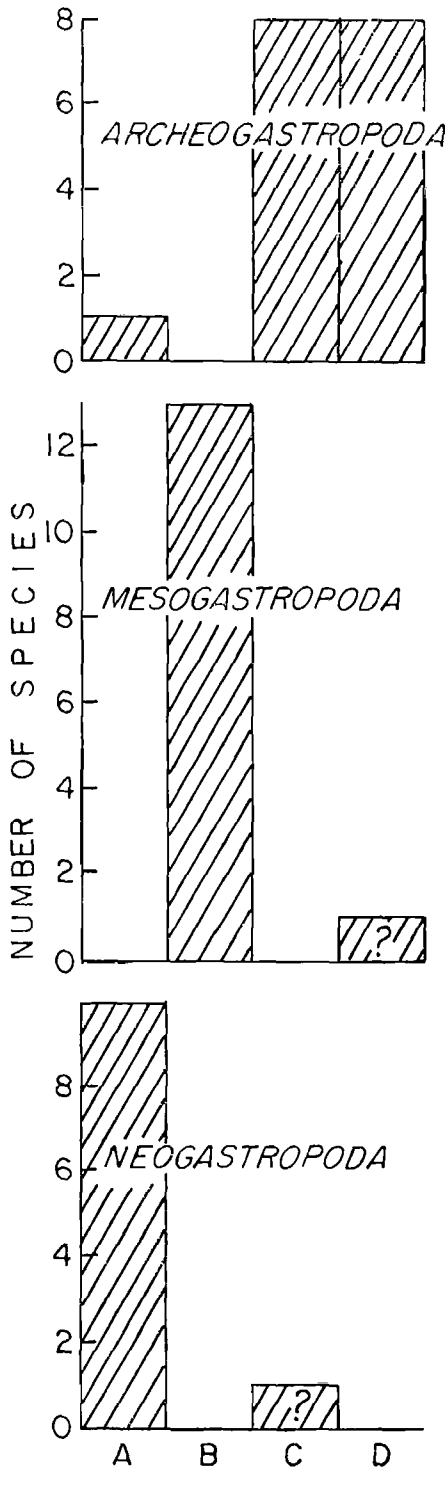
PELECYPODA

The nature of the gills is used by the zoölogist in subdividing the class Pelecypoda. The order Protobranchia, which contains the suborder Nuculacea, is considered primitive; the order Filibranchia containing the suborders Taxodonta and Anisomyaria is considered to be more advanced; the order Eulamellibranchia, which contains the suborders Schizodonta, Heterodonta, Anapedonta and Anomalodesmacea, is a further advance.

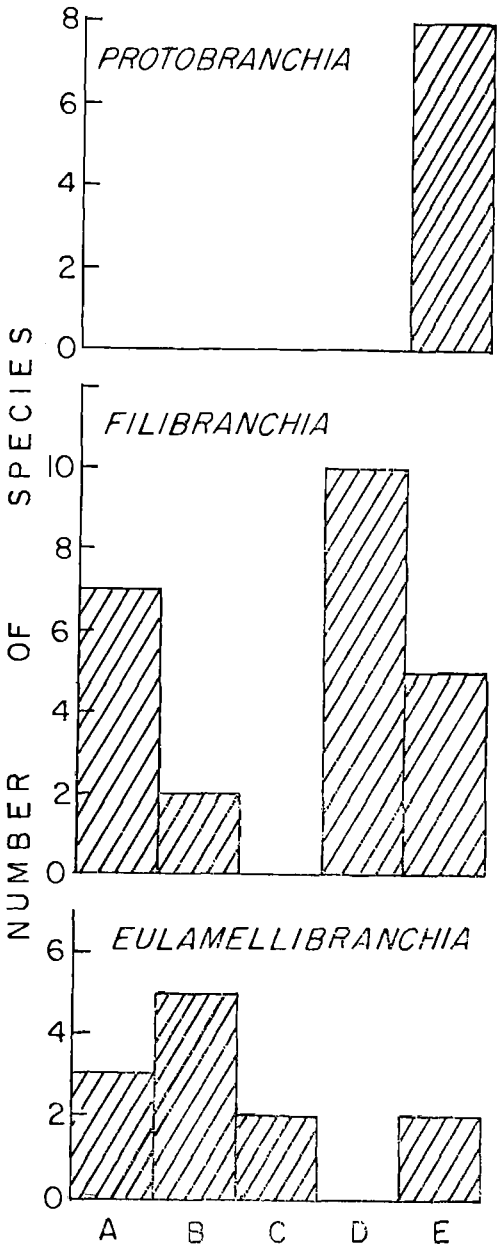
Some pelecypods produce a ribbonlike fecal pellet that has not been reported from gastropods; otherwise the pelecypod and gastropod pellets are quite similar. The fecal pellet forms produced by species of Pelecypoda are summarized in a histogram in Text-figure 3. The data suggest that the sculptured rod is the primitive type.

ANNELIDA

Yonge (1960, p. 4), after consideration of the structure of *Neopilina*, states "Now, no doubt remains that the Mollusca must have separated from the Annelida *after* the appearance of segmentation; the affinities between the two phyla are much closer than was previously suspected." Therefore, of interest here are the feces of the annelid *Eurythoe complanatus* which is described by Manning & Kumpf (1959, p. 304) as a short



TEXT-FIG. 2—Histograms of types of fecal pellets produced by the gastropod orders Archaeogastropoda, Mesogastropoda and Neogastropoda. Column A—shapeless feces. Column B—oval pellets. Column C—unsculptured pellets. Column D—sculptured pellets. Data mostly from literature.



TEXT-FIG. 3—Histograms of types of fecal pellets produced by pelecypod orders Protobranchia, Filibranchia and Eulamellibranchia. Column A—shapeless pellets. Column B—oval pellets. Column C—unsculptured pellets. Column D—ribbonlike pellets. Column E—sculptured pellets. Data mostly from literature.

rod with a longitudinal groove on both the dorsal and ventral surfaces. Although all annelids do not produce sculptured rods, *e.g.*, *Arenicola marina* extrudes rods without sculpture (Moore, 1955, p. 516), the fact that an annelid is capable of excreting a sculptured rod, which is characteristic of many gastropods and pelecypods of primitive stock, supports the possibility of the sculptured rod being a primitive type.

EVOLUTIONARY DEVELOPMENT OF FECAL PELLETS

Moore (1939, p. 517) considers the various shapes of fecal pellets to be modifications of the unsculptured rod. Because of the predominance of sculptured rods among both primitive gastropod and pelecypod stocks, it is the present writer's opinion that the various types of fecal pellets may be simplifications of the sculptured rod. The unsculptured rod may be a type transitional between the sculptured rod and oval pellets and shapeless pellets, but the scarcity of unsculptured rods among pelecypods suggests that oval and shapeless pellets may have evolved directly from sculptured pellets. If, as suggested here, the primitive fecal pellet is the sculptured rod type, there has been considerable similarity in the development of fecal pellet types among diverse groups.

Primitive feces seem to be extruded as long rods, which then tend to break up into shorter rods because of mechanical weakness of the longer rod. A major change in organs producing fecal pellets must have taken place when oval pellets were evolved. In the Littorinidae the oval pellets are lined up in the gut (Abbott, 1954a), showing that in this group they are formed before reaching the anus. In general, oval pellets are not completely isolated from each other, but appear like strung beads, one connected to the other. After elimination, the slender connecting links are broken and the oval pellets become discrete bodies.

The segregation of coarse sediment particles in one part of a pellet and fine sediment in another has been noted by many investigators (*e.g.*, Manning & Kumpf, 1959; Moore, 1932), and is illustrated in Text-figure 1B of the present paper. In general, the separation of pellet constituents seems to

be a primitive trait with composition being more nearly uniform in advanced forms.

EFFECT OF FOOD HABIT

Moore (1939) states "In general, carnivorous animals tend to produce faeces of loose consistency, vegetable eaters firmer ones, and deposit eaters the most resistant of all." The Neogastropoda are primarily carnivores or omnivorous scavengers and their feces are generally of a loose consistency and not likely to be preserved as fossils. The Mesogastropoda include carnivores, herbivores, detritus feeders and ciliary feeders. In the present study all mesogastropods considered are herbivores and produce oval pellets with the exception of *Strombus*, whose oval pellets are aggregated into short rods (Robertson, 1961). The Archeogastropoda considered in this study are essentially herbivores and produced, with one exception, sculptured or unsculptured rods.

The protobranch genus *Nucula* feeds by gathering detritus by means of flexible proboscides (Abbott, 1954, p. 38). The primitive pelecypod protobranchs on which data are available produce sculptured rods. The Pectinidae, which are suspension feeders, also produce sculptured rods, but many suspension feeders produce shapeless pellets. Although data are too few at present to be very meaningful, it is not unlikely that with further study, the shape, composition and consistency of fecal pellets might prove useful in interpreting the feeding habit and habitat of the animal from which they were excreted.

EXCRETORY ORGANS

The excretory organs of gastropods have recently been discussed by Cox (1960) and those of gastropods and pelecypods by Yonge (1960). Many differences in the excretory systems of the various gastropod and pelecypod subdivisions are described by these authors. For example, Cox states, "A further appendage to the stomach, situated at the opposite end to the style sac, is the posterior caecum, developed in most Archaeogastropoda (but not in Fissurellidae) and in a few opisthobranchs. It is commonly more or less coiled and its function is to assist in the sorting of the contents of the stomach by means of the cilia with which it is lined," and "In some prosobranch and tectibranch genera anal glands open into the rectum close to the anus, and are concerned with the preparation of the feces." Yonge (1960, p. 15) in discussing primitive stages in the evolution of the Mollusca states "The stomach itself probably early contained a ciliated sorting region, an area of cuticle forming a gastric shield, and a 'style-sac' region initially concerned with the consolidation of fecal material—a matter of prime importance when the gut opened into the respiratory (i.e., mantle) cavity. Lengthening of the gut posterior to the stomach was also associated with the formation of firm fecal pellets." Although the literature contains references to the organs responsible for the consolidation of digestive waste into compact feces (*e.g.*, Moore, Lalicker & Fischer, 1952, p. 291), differences in organs causing excretion of sculptured rods by some animals and unsculptured rods and oval pellets by others has evidently received little study. Information such as that reported on *Nucula* by Moore (1931, p. 361) is useful. Moore states "The intestine of *Nucula* shows thickened longitudinal ridges with long cilia, and these form grooves in the smooth surface of the pellet, whose number and position vary according to the species." A better understanding of the relationship between the shape, composition and consistency of fecal pellets and the organs producing them is necessary if paleontologists are to use fecal pellets as a means of reconstructing the soft parts of fossil animals. Such knowledge will also be useful in associating fossil fecal pellets with the animal which excreted them.

CONCLUSIONS

The available data concerning the fecal pellets of invertebrates are still too few for drawing firm conclusions, but the results of this study indicate the following:

1. Fecal pellet shape, and composition, may be of phylogenetic importance.
2. Fossil fecal pellets may be useful to the paleontologist for reconstructing the soft parts of fossil animals.
3. Fecal pellets may prove useful in paleoecology if their shape, composition, and con-

sistency can be related more clearly with feeding habit.

4. The sculptured rod may be the primitive molluscan fecal pellet type.

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