Senckenbergiana marit. | 6 | (1) | 1—31 | Frankfurt a. M., 15. 8. 1974

Faecal Pellets of Amphineura and Prosobranchia (Mollusca) from the Caribbean Coast of Columbia, South America.

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With 14 Text Figures.

Abstract.

Faecal pellets of Caribbean Amphineura and Prosobranchia from the north coast of Columbia are described and figured. The shapes of the faeces can be classified as: plain rod, sculptured rod, plain ovoid, annulated ovoid, and mucus follicle; soft lumps or flocculent masses also occur.

Amphineura produce plain ovoid and ellipsoid pellets, Archaeogastropoda plain or sculptured rods, Mesogastropoda mainly plain and sculptured ovoids and spindles, and Neogastropoda — with very few exceptions — soft, mucoid faeces. The possibilities of preservation of the faecel pellets of the 109 species studied are discussed in respect to both their durability and the habitat of the producer. The type of food and the kind of feeding are considered in relation to pellet form and consistence.

For the distinction of higher taxonomic units, the shapes of faecal pellets are of great value. In contrast, lower taxonomic units cannot easily be distinguished by the shapes of faecal pellets. Differences in the sculpture of the pellets are observed only in genera of the order Archaeogastropoda. These differences are particularly marked in some species of the superfamily Trochacea.

The combination of different types of pellets shed by amphineuran and prosobranch populations in typical littoral environments are figured and possible applications for the fossil record are discussed.

Übersicht.

Kotpillen karibischer Amphineura und Prosobranchia von der Nordküste Kolumbiens werden beschrieben und abgebildet. Die Formen der Kote lassen sich in glatte oder skulpturierte Würste, glatte oder geringelte Pillen, Schleimbeutel und weiche Klumpen oder flockige Massen unterteilen.

Amphineura erzeugen glatte, ovale und elliptische Pillen, Archaeogastropoda glatte und skulpturierte Würste, Mesogastropoda vorwiegend glatte und geringelte Pillen und Neogastropoda mit sehr wenigen Ausnahmen weiche und verschleimte Kote. Möglichkeiten zur Erhaltung von Kotpillen aller 109 erwähnter Arten werden erläutert in Hinblick auf die Festigkeit der Pillen und auf den Lebensort der Erzeuger. Nahrung und Ernährungsweise werden mit der Form und Zusammensetzung der Kotpillen in Beziehung gesetzt.

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Bei der Unterscheidung höherer taxonomischer Einheiten ist die Form der Kotpillen von großem Wert. Bei niedrigeren Einheiten dagegen unterscheiden sich nur in der Ordnung Archaeogastropoda Kote verschiedener Gattungen und in der Überfamilie Trochacea oft sogar noch Kote verschiedener Arten.

Die typische Zusammensetzung verschiedener Kotformen von Amphineura und Prosobranchia aus verschiedenen Lebensgemeinschaften wird für einige küstennahe Lebensräume dargestellt. Mögliche Anwendungen für die Paläontologie werden aufgezeigt.

Contents.

Introduction.

Scope of the Study.

The object of this investigation was to show the possibilities of distinguishing between the various types of faecal pellets occurring in the Amphineura and Prosobranchia. Beyond this, the present study, concerning material from the Caribbean Sea, supplements the results of MANNING & KUMPF (1959) obtained on faecal pellets of the south Florida area. My aim is to suggest possible biological interpretations of the characteristic form of faecal pellets in relation to feeding habits, modes of life, and to palaeontological application, and to determine whether these forms can be divided according to shape and consistence into various groups that may enable us to draw phylogenetic conclusions.

In fine muds, such as those in many lagoons and sheltered bays in the Caribbean, the formation of gastropod faecal pellets is a factor of great sedimentological importance. One example is described by KORNICKER & PURDY (1957) from a Bahamian lagoon where up to 90 % of the bottom sediments are composed of faecal pellets of one gastropod species (see also FOLK & ROBLES 1964). The composition of gastropod communities varies considerably with different environments, and therefore the type of faecal pellet association also varies. I have tried to demonstrate this with examples from the Columbian coast and to suggest that the study of shape and composition of pellets may give results applicable to palaeoecological problems.

Methods.

The animals were collected at several stations in the sea close to the Instituto Colombo Aleman (ICAL) in Santa Marta, Columbia, South America. The samples were carried into the laboratory in plastic buckets, the animals never leaving the water. In the laboratory the freshly caught animals were kept separated, by species, in different jars, with fresh clean water, and large enough to enable free movement. Those pellets which were shed first were taken to be typical, reflecting the normal consistence of pellets produced at the living-place of the animals. Depending on the frequency and amount of defecation, the animals were kept in their jars from 30 minutes to one day. Usually 10 to 15 animals of one species were kept together at once.

Examinations of the pellets were carried out under a binocular microscope right after defecation. They were measured, described, and drawn. For determination of firmness, inner structure, and consistence, the faeces were dissected with a needle and cut with a blade. For determination of durability the faeces were shaken in water. For experiments, only adult animals were used, unless noted differently in the text.

Amphineura.

Description.

All of the species observed shed oval pellets of the same general shape. The surface of the pellets is unsculptured, and they consist mainly of compacted detritus without internal structure. Usually both ends are equally bluntly rounded.

Acanthochitona hemphilli PILSBRY (Fig. 1 A).

Soft, up to 3 mm long, well shaped, smooth, greenish-gray, ovoid pellets, easily disintegrating, fragile and preservable only in very favourable, quiet environments.

Ischnochiton limaciformis Sowerby (Fig. 1 B).

Solid, up to 1.5 mm long and 0.35 mm wide, calcareous, pure white, cylindrical pellets of very rigid consistence and great durability.

Ischnochiton papillosus C. B. Adams (Fig. 1 C).

Solid, up to 0.8 mm long and 0.3 mm wide, gray, ovoid pellets of firm consistence; very preservable.

Ceratozona squalida C. B. Adams (Fig. 1 D).

Firm, up to 1.3 mm long and 0.5 mm wide, gray, ovoid to eggshaped pellets containing many large grains in a fine matrix; very preservable.

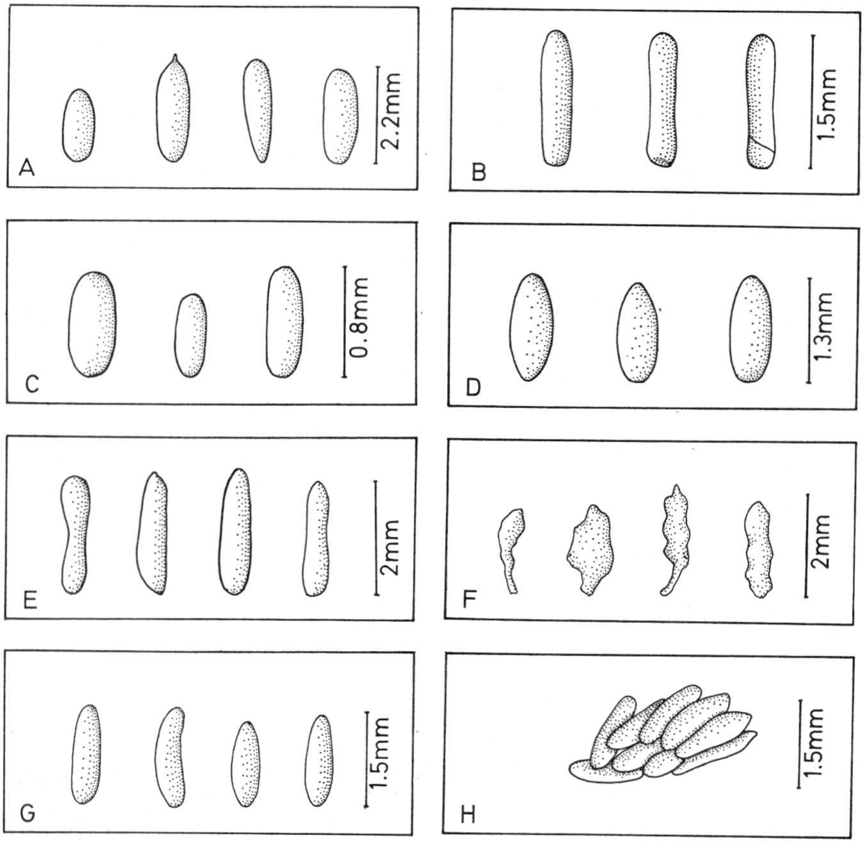

Fig. 1. Faecal pellets of Amphineura. — A. *Acanthochitona hemphilli;* B. *Ischnochiton limaciformis;* C. *Ischnochiton papillosus;* D. *Ceratozona squalida;* E. *Acanthopleura granulata;* F. *Calloplax janeirense;* G. and H. *Chiton marmoratus.*

Abb. 1. Kotpillen der Amphineura. — A. *Acanthochitona hemphilli;* B. *Ischnochiton limaciformis;* C. *Ischnochiton papillosus;* D. *Ceratozona squalida;* E. *Acanthopleura granulata;* F. *Calloplax janeirense;* G. und H. *Chiton marmoratus.*

Acanthopleura granulata GMELIN (Fig. 1 E).

Smooth, solid, up to 3 mm long and 0.8 mm wide, greenish-gray to greenish-brown, cylindrical pellets. The centre measures less in diameter than the bluntly rounded ends; very durable.

Calloplax janeirense GRAY (Fig. 1 F).

Firm to soft, up to 3 mm long, gray to brown pellets with irregular surface and either rounded or pointed ends. Large particles in the matrix cause an irregular pellet surface. Fragile if more organic[1]) durable if more detrital[2]).

Chiton marmoratus LINNÉ (Fig. 1 G, H).

Smooth, solid, up to 1.5 mm long and 0.5 mm wide, light gray to dark-brown, regularly ovoid pellets of great durability.

Chiton tuberculatus LINNÉ.

Soft mucoid pellets, or brown, flocculent faecal mass. Not preservable.

Discussion.

With the exception of *Acanthochitona hemphilli* and *Chiton tuberculatus,* all Amphineura studied shed very solidified, preservable faecal pellets of the same general shape.

The pellets of *Ischnochiton floridanus* PILSBRY and *Acanthopleura granulata* from south Florida (MANNING & KUMPF 1959) fit well into this group, on the basis of shape. The latter species must have devoured mainly calcareous algae because the pellets were pure white, as was found for the species *Ischnochiton limaciformis* in Santa Marta.

Chances of preservation of faeces differ with the habitat of the species, *Acanthochitona hemphilli, Ischnochiton limaciformis, I. papillosus,* and *Calloplax janeirense* are found on the lower sides of rocks, on large shell fragments, on shells of living *Atrina* and *Pinna*, and under rubble in lagoons and quiet bays. Conditions for preservation are good in these environments. *Acanthopleura granulata, Chiton marmoratus, C. tuberculatus,* and *Ceratozona squalida* settle mainly on exposed rocky shores. Therefore, the conditions of preservation even of solid pellets are much less favourable here and can be expected only in more quiet environments close by.

Archaeogastropoda.

Description.

The faecal pellets of this group usually consist of straight to slightly but evenly bowed, cylindrical or ribbon-like rods that show broken ends. According to their external sculpture, this group is divisible into five subgroups.

1) Organic = soft organic remains and slime.

2) Detrital = inorganic and/or organic hard particles.

1. Plain unsculptured rods with round cross sections like those of *Acmaea pustulata* (Fig. 2 A).

Hemitoma octoradiata Gmelin.

Firm, up to 4 mm long and 0.7 mm wide, smooth, mostly slighty bowed cylinders with fine irregular transverse articulation. Pellets consist of fine detritus coagulated by mucus and are very preservable.

Acmaea pustulata Helbing (Fig. 2 A).

Firm, up to 1.2 mm long and 0.2 mm wide, perfect cylinders made of pure white, calcareous material of great durability.

Acmaea antillarum Sowerby.

Identical in size and consistence with *A. pustulata.*

Diodora listeri Orbigny (Fig. 2 B).

Mostly soft, rarely firm, up to 2.5 mm long and 0.8 mm wide, irregularly stuffed cylinders. When composed mainly of coarse detrital or organic particles, the pellets disintegrate rapidly after defecation either into soft lumps of detritus or greenish organic flocculent masses. Only faeces with fine detrital material coagulated by organic material are firm and can be preserved.

Diodora minuta Lamarck.

Soft, roundish fragments of disintegrated, cylindrical faeces, which fall apart right after production.

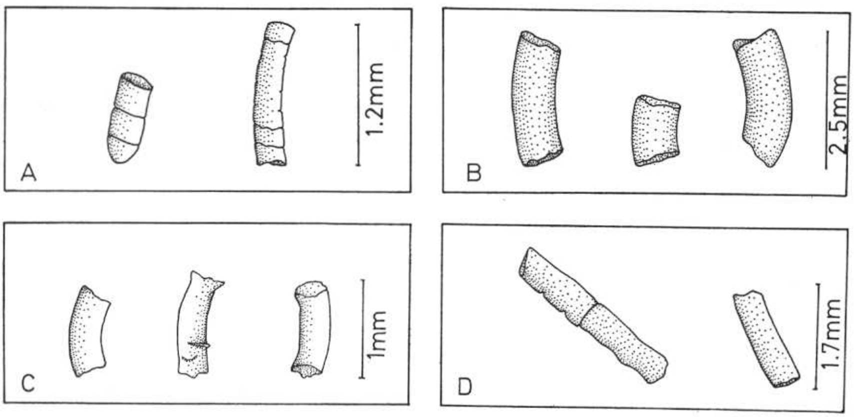

Fig. 2. Faecal rods of patelloid Archaeogastropoda. — A. *Acmaea pustulata;* B. *Diodora listeri;* C. *Lucapinella limatula;* D. *Lucapina suffusa.*

Abb. 2. Kot-Würste napfförmiger Archaeogastropoda. — A. *Acmaea pustulata;* B. *Diodora listeri;* C. *Lucapinella limatula;* D. *Lucapina suffusa.*

Fissurella nodosa BORN.

Either soft, up to 3 mm long and 0.5 mm wide, mostly organic rods with pointed ends, easily disintegrating, or firm, up to 5 mm long and 0.3 mm wide, greenish to light gray cylinders with transverse cracks and broken ends, containing much calcareous material and showing great durability.

Fissurella angusta GMELIN.

Soft, up to 3 mm long and 0.5 mm wide, mucoid cylinders with both ends rounded or drawn out into mucus points. In the opaque mucoid matrix, larger plant remains and detrital particles are seen. Not preservable.

Calliostoma sarcodum DALL (Fig. 4 A).

Plain rods, up to 1.7 mm long and 0.3 mm wide, often composed of opaque mucus and irregularly stuffed, greenish or brownish particles. Mostly soft and often glued to each other.

2. Round rods sculptured with a longitudinal ribbon or furrow like those of *Nerita tessellata* (Fig. 3 B).

Lucapinella limatula REEVE (Fig. 2 C).

Firm rods, up to 1 mm long and 0.2 mm wide, fine in texture and often with a longitudinal groove or suture. The very preservable rods contain many sponge spicules.

Lucapina suffusa REEVE (Fig. 2 D).

Solid rods, up to 10 mm long and 3 mm wide, without internal structure, irregular, transversely stuffed appearence, often with a longitudinal groove that can be up to 0.1 mm wide, or only with a suture.

Nerita fulgurans GMELIN (Fig. 3 A).

Solid rods, up to 10 mm long and 3 mm wide, without internal structure, mostly showing broken ends, but some with pointed ends tapering out in a mucus tip. White, gray, and green, fine-grained rods show a longitudinal mucoid ribbon in a shallow straight or slightly bent groove.

Nerita tessellata GMELIN (Fig. 3 B).

Firm, up to 20 mm long and 1.5 mm wide, bent and irregularly stuffed rod with a longitudinal mucus ribbon that is either narrow, with wide meandering curves, or a broad band of tight meanders of a smaller ribbon.

Nerita peloronta LINNÉ (Fig. 3 C).

Durable, up to 20 mm long and 1 mm wide, bowed, stuffed rod with a longitudinal mucus ribbon in a shallow groove. The mucus ribbon is either curved in wide bends, or it forms a broad band composed of a tightly meandering ribbon that shows each loop touching the next.

Nerita versicolor GMELIN (Fig. 3 D).

Firm, up to 15 mm long and 0.5 mm wide, tightly stuffed, bowed rod with a widely curving, longitudinal mucus ribbon usually situated on the inside bend of the bowed rods. In rods consisting largely of mucus inside of an enveloping mucoid skin, irregularly meandering thin tubes occur, which are pressed tightly to each other.

Neritina virginea LINNÉ (Fig. 3 E).

Firm to soft, up to 5 mm long and 1 mm wide, tightly stuffed rods, sculptured by a longitudinal mucus ribbon that is bordered by a deep pointed furrow on one side. Rods with much fine detritus are firmer than those constructed mainly of organic material.

Neritina piratica RUSSEL (Fig. 3 F).

Firm to soft, up to 3 mm long and 2 mm wide, greenish rods with an irregular longitudinal furrow.

Smaragdia viridis viridemaris MAURY.

Soft mucoid rods, easily disintegrating and showing chlorophyll grains and remains of the cell-walls from turtle grass eaten by the animal. Not preservable.

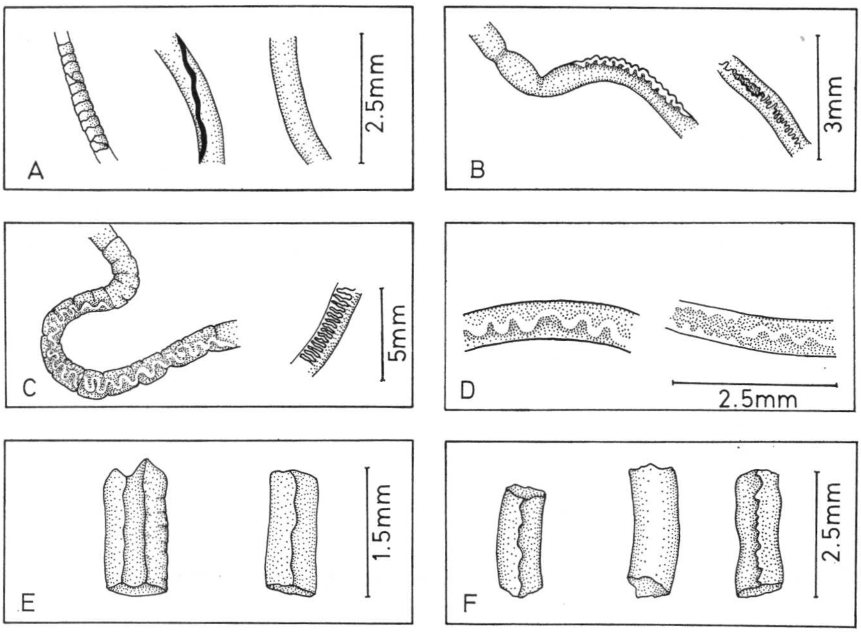

Fig. 3. Faecal rods of the Neritidae. — A. *Nerita fulgurans;* B. *Nerita tessellata;* C. *Nerita peloronta;* D. *Nerita versicolor;* E. *Neritina virginea;* F. *Neritina piratica.*

Abb. 3. Kot-Würste der Neritidae. — A. *Nerita fulgurans;* B. *Nerita tessellata;* C. *Nerita peloronta;* D. *Nerita versicolor;* E. *Neritina virginea;* F. *Neritina piratica.*

3. Straight rods with a broad longitudinal groove that has a longitudinal ridge in its centre. Pellets of fine consistence show transverse plate-like inner structure, like *Astraea caelata* (Fig. 4 B).

Astraea tecta SOLANDER.

Very coarse-grained, easily disintegrating rods with a round side and a broad longitudinal groove. Poor chances for preservation.

Astraea caelata GMELIN (Fig. 4 B).

Firm rods, up to 1 mm wide and 2 mm long, consisting of fine to coarse grained detritus. Rods constructed of fine grains show a broad longitudinal groove with a prominent, transversely segmented, sharp median ridge, and seven smaller longitudinal shallow grooves sculpturing the sides.

Astraea phoebia RÖDING (Fig. 4 C).

Firm, straight rods, up to 2 mm long and 0.8 mm wide, with a rounded side and a wide longitudinal groove that has a mucus ridge in its centre consisting of a row of mucus knots that are connected to each other with a fine mucus blade. Pellets of fine grained consistence show a transverse inner structure of irregular plates of differently coloured material. Durable and very preservable.

Turbo castanea GMELIN (Fig. 4 D).

Firm and durable rods, up to 2.5 mm long and 1 mm wide, with rounded, smooth sides and a steep longitudinal groove having a sharp median ridge on a broad base in its centre. The rod is evenly grained, without inner structure.

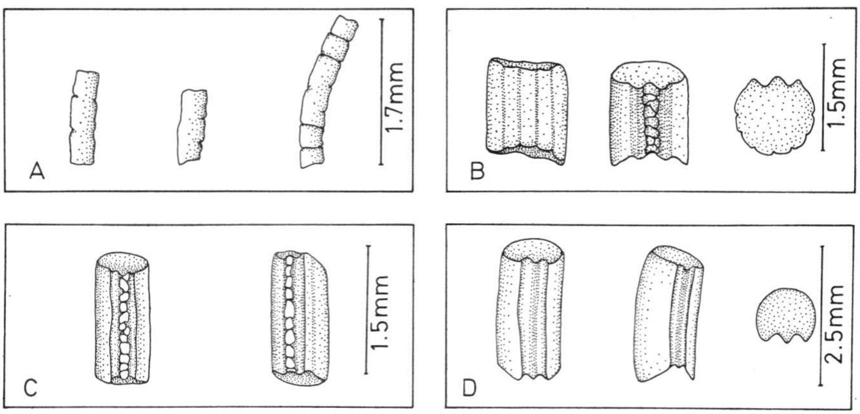

Fig. 4. Faecal rods of the Trochacea (1). — A. *Calliostoma sarcodum;* B. *Astraea caelata;* C. *Astraea phoebia;* D. *Turbo castanea.*

Abb. 4. Kot-Würste der Trochacea (1). — A. *Calliostoma sarcodum;* B. *Astraea caelata;* C. *Astraea phoebia;* D. *Turbo castanea.*

4. Plain or longitudinally striped rods or ribbons with a deep longitudinal furrow or canal, like *Tricolia tessellata* (Fig. 5 E).

Arene tricarinata STEARNS (Fig. 5 A).

Firm, up to 1 mm long and 0.1 mm wide, straight to slightly bowed rods with typically 8-10 longitudinal grooves on the rounded side, and a deep triangular longitudinal canal on the other side. The grooves on the rounded side are not always present, depending on the size of the detrital particles forming the pellet; but if present, they are rounded and separated by a sharp ridge. Sometimes, transverse internal differentiation into fine plates is visible.

Arene cruentata MÜHLFELD (Fig. 5 B).

Firm rods, up to 1.7 mm long and 0.4 mm wide, with one smooth rounded side and a rounded, shallow, broad, longitudinal groove on the other. Very preservable.

Tricolia bella M. SMITH (Fig. 5 C).

Firm rods, up to 1 mm long and 0.2 mm wide, with one side rounded, the other side either sculptured by a narrow pointed groove or a deep rounded canal. In the latter case, the pellet has the shape of a ribbon that, in cross-section, shows the two lateral wings rolled up.

Tricolia affinis C. B. ADAMS (Fig. 5 D).

Firm ribbon, up to 0.7 mm long and 0.15 mm wide, the sides mostly fused in a narrow groove; some are an open ribbon with rolled up sides.

Tricolia tesselata POTIEZ (Fig. 5 E).

Firm ribbons, up to 0.2 mm long and 0.05 mm wide, laterally enrolled, with rounded sides and a deep, longitudinal canal; U-shaped in cross-section.

5. All rods have two deep V-shaped, longitudinal grooves with an upstanding ridge between them, and have a sculpture of smaller ridges that are thrown into more or less tightly packed lateral undulations, as in *Cittarium pica* (Fig. 5 F).

Cittarium pica LINNÉ (Fig. 5 F).

Firm rods, up to 15 mm long and 3 mm wide, with two longitudinal grooves on opposite sides, one wide and rounded and the other wedge-shaped and narrow. The outside of the rod is sculptured with 20 grooves and rounded ridges. These ridges consist on the inside of a broad longitudinal groove of colourless, opaque, mucoid material, and are straight. On the outside of the rod they are thrown into undulations that are tighter the farther away they are from the broad longitudinal groove. These meandering sculpture ridges consist mainly of fine detrital material and are separated from each other by mucoid material in the intervening grooves. With larger particle size, the sculpture is lost. Pellets shed by young animals show scaly mucus structures in the broad median groove, and only 12 to 15 ridges are visible on the outside. The rods are well consolidated and are brownish or greenish in colour.

Tegula viridula GMELIN (Fig. 5 G).

Firm rods, up to 0.5 mm long and 0.15 mm wide. When constructed of fine grained material, they show 10 longitudinal, rounded ridges with sharp grooves between them on the rounded side. If made of coarser material, the rounded side has only one longitudinal median ridge or groove. The other side is occupied by a broad, longitudinal, rounded groove with a row of mucus knots connected to each other by a central blade-like ridge.

Tegula fasciata BORN.

The faeces of *T. fasciata* are identical to those of *T. viridula*. Usually, the pellets of *T. fasciata* are of finer consistence than those of *T. viridula* because

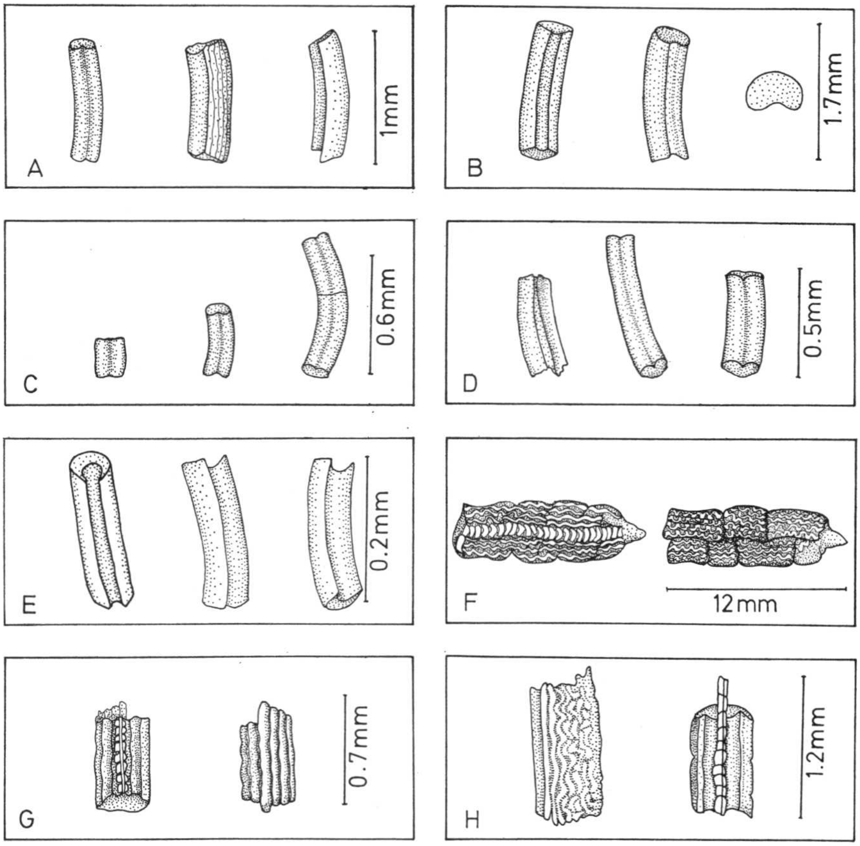

Fig. 5. Faecal rods of Trochacea (2). — A. *Arene tricarinata;* B. *Arene cruentata;* C. *Tricolia bella;* D. *Tricolia affinis;* E. *Tricolia tessellata;* F. *Cittarium pica;* G. *Tegula viridula;* H. *Tegula excavata.*

Abb. 5. Kot-Würste der Trochacea (2). — A. *Arene tricarinata;* B. *Arene cruentata;* C. *Tricolia bella;* D. *Tricolia affinis;* E. *Tricolia tessellata;* F. *Cittarium pica;* G. *Tegula viridula;* H. *Tegula excavata.*

the former lives under rocks in shallow, calm turtle-grass environment, whereas the latter nestles under rocks just below surf in highly agitated water.

Tegula excavata LAMARCK (Fig. 5 H).

Firm rods, well preservable, up to 1.2 mm long and 0.5 mm wide, with a longitudinal groove having a ridge which consists of mucus knots connected to each other with a sharp mucus blade. Pellets of very fine consistence show 15 more or less regularly folded grooves and ridges on the sides; these are straight near to the longitudinal mucus ridge, but farther away from it, they grade into undulations.

Discussion.

Lucapina, Lucapinella, and *Calliostoma* produce very few faecal pellets in comparison to all other Archaeogastropoda mentioned here. These three species probably feed on crusts of sponges, tunicates, and other animal colonies. All other Archaeogastropoda live mainly on algal growths, which they (1) scrape off rocks, like *Hemitoma, Acmaea, Diodora, Fissurella, Astraea, Turbo, Cittarium, Tegula, Arene,* and *Nerita,* (2) pick from soft bottoms or rotting plant material, like *Neritina,* or (3) graze off the leaves of *Sargassum* and turtle-grass, like *Tricolia.* Only *Smaragdia* bites out parts of the actual leaves of turtle-grass.

Conditions for preservation of the faeces vary greatly for the different species of Archaeogastropoda, depending on the consistence of the pellets and the habitat of the pellet-producing animal. *Diodora minuta, Fissurella angusta,* and *Smaragdia viridis* shed soft pellets that disintegrate immediately after production into small unidentifiable grains. *Fissurella nodosa, Cittarium pica, Tegula excavata, Nerita versicolor,* and *N. fulgurans* live on exposed rock cliffs, therefore their pellets have no chances for preservation in their habitat. *Hemitoma octoradiata, Acmaea antillarum, A. pustulata, Diodora listeri, Lucapinella limatula, Lucapina suffusa, Calliostoma sarcodum, Astraea tecta, A. caelata, A. phoebia, Turbo castanea, Arene tricarinata, A. cruentata, Tegula viridula, T. fasciata, Tricolia bella, T. affinis, T. tessellata, Nerita tessellata,* and *N. peloronta* live on hard substrates, on coral reefs, in rubble of reefs and cliffs, and on plants growing in this general environment, so that the faeces of this group can be preserved only near the habitat of the producers, in numerous cavities among corals and rocks.

The faeces of *Neritina* have very good chances for preservation in the shallow lagoons between the mangrove trees and in the muds within their root systems. Here *Neritina* usually thrives, so that a large percentage of the bottom sediment is transformed into its pellets.

The published descriptions of faecal pellets of Archaeogastropoda from south Florida (MANNING & KUMPF 1959) reveal very few differences from those of Santa Marta. In Florida, the general composition of pellets seems to be more coarse grained, so that many fine elements of sculpture are lost, e. g. the median ridge in the longitudinal groove in *Astraea* pellets, or the longitudinal ribbon on *Nerita* rods. The same trend is observable for pellets from *Cittarium pica* figured by KORNICKER (1962) from the Bahamas. Here, the lateral sculpture is not visible.

Faeces described by MOORE (1931, 1932) from Europe show a resemblance of *Patella vulgata* LINNÉ with *Acmaea*, of *Calliostoma ziziphinum* LINNÉ with *Calliostoma sarcodum*, and of *Gibbula* and *Cleandella* with *Cittarium* and *Tegula*.

Mesogastropoda.

Description.

The mesogastropod faecal pellets can be grouped, according to the animals' modes of life, into pellets shed by herbivorous, carnivorous, and filtering species.

Herbivorous Mesogastropoda.

Littorina angulifera LAMARCK (Fig. 6 A).

Durable, brown to gray, drop- to ovoid-shaped, irregularly annulated pellets, up to 2 mm long and 1 mm wide. The ringed structure is caused by alternating layers richer in organic or detrital matter, respectively.

Littorina nebulosa LAMARCK (Fig. 6 B).

Firm ovoid pellets, up to 1.5 mm long and 0.7 mm wide, often with small stalks at both ends. Mostly composed of organic material, often showing wood fibres and irregular internal annulations in places having different grain sizes.

Littorina ziczac GMELIN (Fig. 6 C).

Firm ovoid pellets, up to 1.2 mm long and 0.4 mm wide, without internal structure and composed of fine grained detritus, often containing mica flakes.

Littorina lineolata ORBIGNY (Fig. 6 D).

Firm pellets, up to 1 mm long and 0.4 mm wide, brownish, smooth, without internal structure and with many mica flakes in the fine detritus.

Nodilittorina tuberculata MENKE (Fig. 6 E).

Solid, smooth, ovoid pellets, up to 1 mm long and 0.4 mm wide, without internal structure, often containing large grains of sand.

Tectarius muricatus LINNÉ (Fig. 6 F).

Smooth, firm, ovoid pellets, up to 1.2 mm long and 0.5 mm wide, without internal structure.

Planaxis lineatus DA COSTA (Fig. 7 A).

Firm spindles, up to 0.7 mm long, showing inner differentiation into transverse plates, typically smooth and composed of homogenous fine grained detritus well-consolidated by mucoid material.

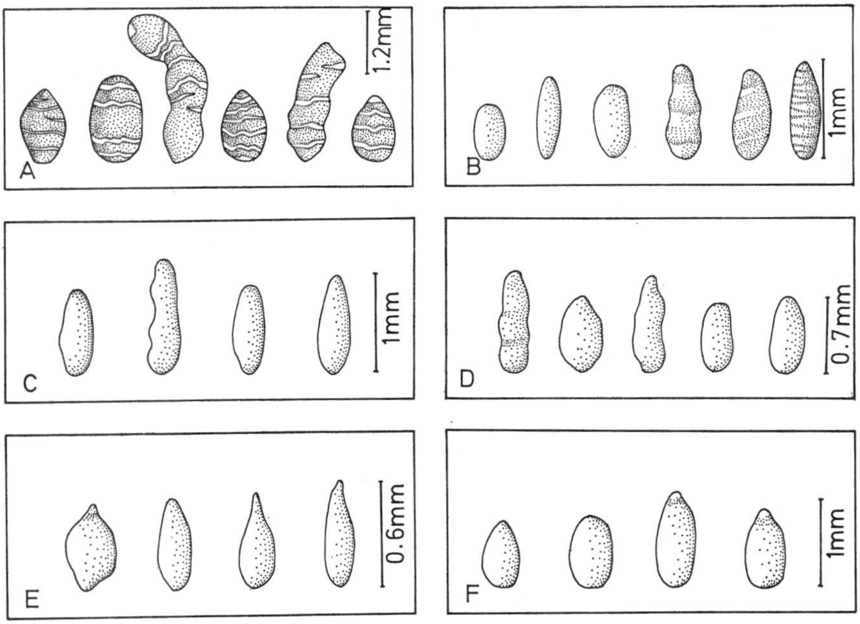

Fig. 6. Faecal pellets of Littorinidae. — A. *Littorina angulifera;* B. *Littorina nebulosa;* C. *Littorina ziczac;* D. *Littorina lineolata;* E. *Nodilittorina tuberculata;* F. *Tectarius muricatus.*

Abb. 6. Kotpillen der Littoinidae. — A. *Littorina angulifera;* B. *Littorina nebulosa;* C. *Littorina ziczac;* D. *Littorina lineolata;* E. *Nodilittorina tuberculata;* F. *Tectarius muricatus.*

Planaxis nucleus BRUGUIÈRE (Fig. 7 B).

Well consolidated, light gray to dark green, spindle-shaped pellets, up to 1.5 mm long, broader on one end than on the other. Depending on the coarseness of the material composing them, the pellets may show up to 25 transversal discs that are often separated from each other by a fine mucus layer.

Modulus modulus LINNÉ (Fig. 7 F).

Well consolidated, ellipsoid pellets, up to 2.5 mm long, some showing internal structure in transversely inclined compartments.

Alaba incerta ORBIGNY.

Firm, yellowish opaque, cylindrical pellets, up to 5 mm long and 0.1 mm wide, with one wide, rounded end and another narrow pointed end. Pellets are composed mainly of plant remains and many show internal, straight, transverse annulation.

Batillaria minima GMELIN (Fig. 7 C).

Very resistant pellets, up to 1 mm long and 0.2 mm wide, with one end wider than the other and with internal annulation in the form of 10 to 13 inner plates, often extending through to the surface of the pellets.

Cerithium variabile C. B. ADAMS (Fig. 7 D).

Firm, spindle-shaped pellets, up to 1 mm long and 0.3 mm wide, with one blunt and another pointed end. Small pellets, up to 0.8 mm long, usually show no transverse differentiation; larger pellets have up to 15 internal, inclined

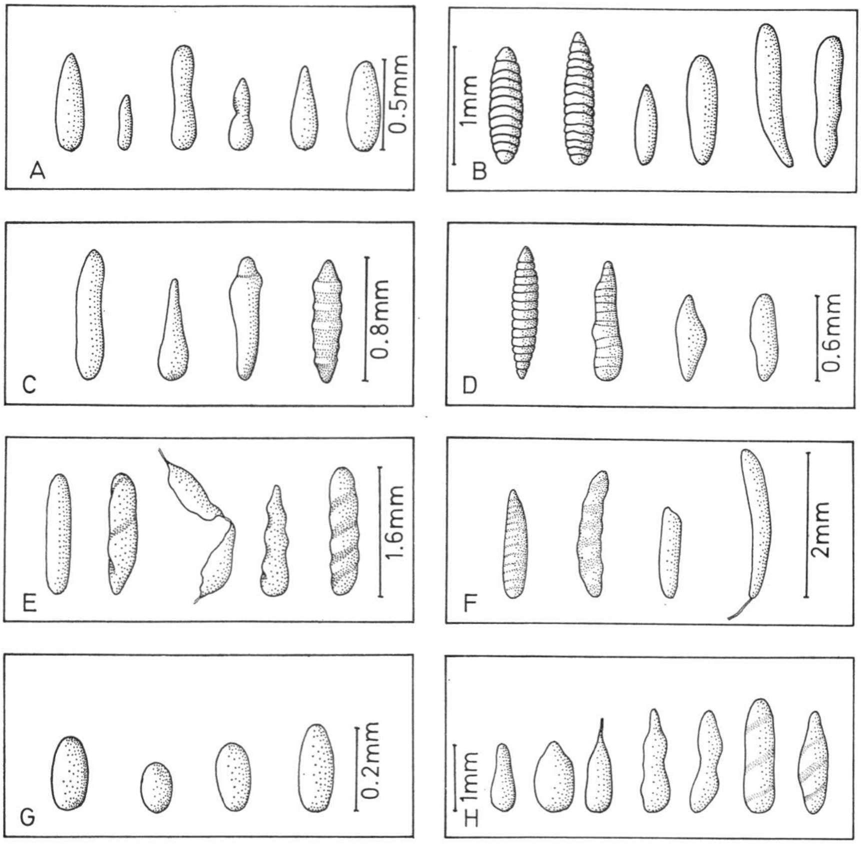

Fig. 7. Faecal pellets of herbivorous Mesogastropoda. — A. *Planaxis lineatus;* B. *Planaxis nucleus;* C. *Batillaria minima;* D. *Cerithium variabile;* E. *Cerithium eburneum;* F. *Modulus modulus;* G. *Caecum antillarum;* H. *Ampullarius* cf. *monticolus.*

Abb. 7. Kotpillen pflanzenfressender Mesogastropoda. — A. *Planaxis lineatus;* B. *Planaxis nucleus;* C. *Batillaria minima;* D. *Cerithium variabile;* E. *Cerithium eburneum;* F. *Modulus modulus;* G. *Caecum antillarum;* H. *Ampullarius* cf. *monticolus.*

plates, each differentiated into finer material toward the blunt end and coarser material toward the pointed end of the pellet. Colour mostly grayish brown.

Cerithium eburneum BRUGUIÈRE (Fig. 7 E).

Firm spindle-shaped pellets, up to 1.5 mm long and 0.3 mm wide, with mostly one blunt and one pointed end, some with both ends pointed. Short pellets, up to 0.8 mm long, show no internal annulation; larger pellets have up to 5 internal, inclined plates, each differentiated into finer material toward the blunt end and coarser material toward the pointed end.

Ampullarius cf. *monticolus* VERNHOUT (Fig. 7 H).

Firm spindle-shaped pellets, up to 3 mm long and 0.8 mm wide, with variable colouring. Some are purely organic, others mostly sandy. If of alternating composition, inclined compartments of more sandy, light coloured rings and more organic, dark coloured plates are developed.

Ampullarius porphyrostomus REEVE.

Mostly purely organic, spindle-shaped pellets, up to 3 mm long, rarely showing internal annulation of inclined plates. Animals just hatched from the egg mass shed ovoid to spindle-shaped pellets, up to 4 mm long and 0.2 mm wide. These are composed of the walls of the egg cases, eaten by the juveniles, and are of pure white colour and great durability.

Xenophora conchyliophora BORN.

Well formed, bean-shaped, durable pellets, up to 1 mm long and 0.5 mm wide, shed in great numbers in connected lumps. Larger detrital grains sometimes are incorporated into the pellets and distort their shape. No internal structure.

Strombus raninus GMELIN (Fig. 9 A).

Ovoid to spindle-shaped pellets (up to 1 mm long and 0.4 mm wide) are packed into a rod (up to 7 mm long and 2 mm wide) with one rounded side and a broad longitudinal groove. These rods disintegrate easily, and firm, readily preservable pellets are strewn about.

Strombus gigas LINNÉ and *Strombus pugilis* LINNÉ produce the same type of rods, composed loosely of durable ovoid pellets without internal structure.

Mesogastropod Filter-feeders.

This group combines genera from the superfamilies Hipponicacea, Calyptraeacea, and Cerithiacea, which live a sedentary life and feed on floating particles that they filter from the water. *Bittium varium* and *Caecum antillarum* use fine algal thickets in feeding diatoms and other small plants and plant particles that have been entangled in them. In this way, these two species may also be grouped together with herbivorous species.

Hipponix antiquatus LINNÉ (Fig. 8 A).

Firm, egg-shaped pellets, up to 1 mm long and 0.2 mm wide, with a hard shiny outer crust.

Cheilea equestris LINNÉ.

Ovoid to egg-shaped, brownish-gray pellets, up to 0.7 mm long and 0.3 mm wide, with a hard, shell-like, smooth surface.

Crucibulum auriculum GMELIN.

Smooth, egg-shaped pellets, up to 0.4 mm long and 0.2 mm wide, with a firm outer hull.

Crepidula convexa SAY (Fig. 8 B).

Perfectly egg-shaped pellets, up to 0.3 mm long; very durable.

Crepidula plana SAY.

Egg-shaped pellets, up to 0.4 mm long, some with more irregular shapes, but all rounded and firm.

Petaloconchus mcgintyi OLSSON & HARBISON (Fig. 8 C).

Smooth, ovoid pellets, up to 1.5 mm long, with points on both ends.

Petaloconchus erectus DALL (Fig. 8 D).

Firm, egg-shaped pellets, up to 1.2 mm long, durable, with a smooth hull.

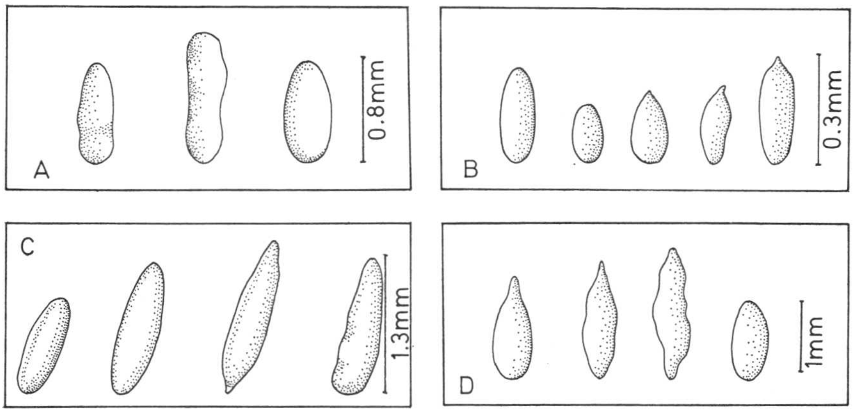

Fig. 8. Faecal pellets of filter feeding Mesogastropoda. — A. *Hipponix antiquatus;* B. *Crepidula convexa;* C. *Petaloconchus mcgintyi;* D. *Petaloconchus erectus.*

Abb. 8. Kotpillen von Mesogastroproda mit filternder Ernährungsweise. — A. *Hipponix antiquatus;* B. *Crepidula convexa;* C. *Petaloconchus mcgintyi;* D. *Petaloconchus erectus.*

Bittium varium PFEIFFER.

Very firm, drop-shaped pellets, up to 0.05 mm long, made of very fine detrital material, without internal structure.

Caecum antillarum CARPENTER (Fig. 7 G).

Very small, ovoid to egg-shaped, smooth pellets, up to 0.2 mm long, made of fine detrital particles without internal structure; very durable.

Carnivorous Mesogastropoda.

This group contains species of the superfamilies Triviacea, Cypraeacea, Tonnacea, and Cymatiacea, which produce either ovoid pellets or soft mucus follicles and flocculent masses.

Trivia pediculus LINNÉ (Fig. 9 B).

Firm, spindle-shaped pellets, up to 1 mm long and 0.25 mm wide, with both ends pointed; internal articulations divide the pellets into irregular, transverse sheets of olive-gray and brownish-gray material.

Cyphoma gibbosum LINNÉ (Fig. 9 C).

Egg-shaped, bilaterally compressed, well rounded pellets, up to 1 mm long, made up of olive-gray organic material that tightly agglutinates violet skeletal fragments of gorgonians. Some pellets show regular to irregular transverse annulations and are shed in bundled masses that fall apart immediately after defecation.

Cymatium pileare LINNÉ (Fig. 9 D).

Egg-shaped, firm, smooth pellets, up to 0.8 mm long, durable, brown in colour.

Bursa cubaniana ORBIGNY (Fig. 9 E).

Mostly egg-shaped, durable pellets, up to 1.5 mm long and 0.8 mm wide, showing irregular, internal, transverse annulation; some have irregularly rounded shapes.

Cypraea cinerea GMELIN.

Mucoid follicles of soft organic material, up to 3 mm long, irregularly tangled.

Cypraea spurca acicularis GMELIN.

Mucous follicle containing red organic grains and profuse sponge spicules.

Tonna galea LINNÉ.

The skeletal remains of sea cucumbers are shed in an unsolidified lump along with flocculent organic faecal masses.

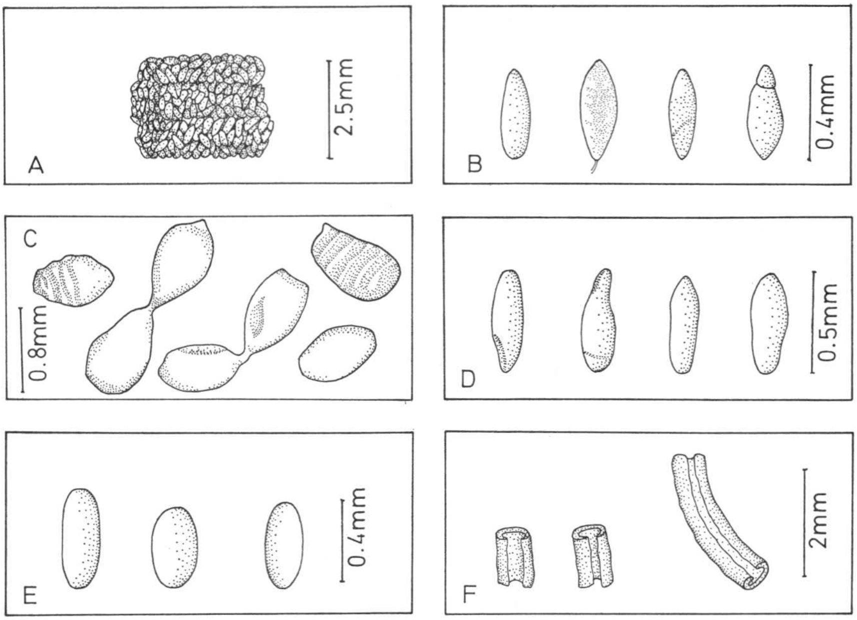

Fig. 9. Faecal pellets of five mesogastropods and one neogastropod. — A. *Strombus raninus;* B. *Trivia pediculus;* C. *Cyphoma gibbosum;* D. *Cymatium pileare;* E. *Bursa cubaniana;* F. *Nitidella laevigata.*

Abb. 9. Kotpillen von fünf Mesogastropoden und einer Neogastropode. — A. *Strombus raninus;* B. *Trivia pediculus;* C. *Cyphoma gibbosum;* D. *Cymatium pileare;* E. *Bursa cubaniana;* F. *Nitidella laevigata.*

Charonia variegata LAMARCK.

The skeletal remains of sea stars or sea cucumbers are shed along with flocculent organic masses, if the prey had been a sea star or a sea cucumber. When the prey were sea urchins, a violet suspension of faecal material is shed. This can dye the water of an aquarium for quite a while.

Discussion.

Only four members of the Mesogastropoda from Santa Marta produced unformed or irregularly formed faeces. Defecation in these four is rare, and in the case of *Charonia* and *Tonna,* occurs only after one or more prey animals have been devoured. The faeces of *Tonna* are shed in the same environment (sandy bottoms) prefered by both prey and predator. Skeletal remains of Echinodermata can be transported out of their actual habitat by *Charonia,* which moves, for example, from turtle-grass lagoons into reefs and rocky cliffs.

The two species of *Cypraea* feed on animal colonies fixed to the lower sides of rocks, mainly tunicates and sponges. Faeces are produced in small numbers, mostly in an environment that is favourable for preservation, except for the mostly organic follicle masses.

All other members of the Mesogastroproda studied here shed ovoid pellets that mostly are quite durable and are produced in great numbers. With the exception of *Cymatium, Bursa, Trivia* and *Cyphoma,* all live on plants as grazers or filter feeders. Strangely, *Bursa* and *Cymatium* produce durable pellets in greater numbers, although their main food in aquaria were other mollusks, flesh of fish, and annelids. *Trivia* and *Cyphoma* live from colonial animals. *Trivia* seems to prefer the same kind of food as *Cypraea,* but in contrast to *Cypraea,* it produces large numbers of durable pellets. *Cyphoma* eats the polyps of gorgonian colonies, biting off all pink skeletal elements and leaving only the black, inner supporting system.

The populations of herbivorous Mesogastropoda usually are large, each individual eats continuously, and therefore faecal pellets are produced in huge numbers.

Faecal pellets of the different species of Littorinidae are very similar to each other, mostly an ovoid to drop-shape. All Littorinidae that live on rocky surfaces compose their pellets mainly of fine detritus, often consisting of mica flakes and rock fragments that they scrape from the surface while rasping off algae. The pellets of the two species, *Littorina angulifera* living on mangrove roots, and *L. nebulosa* living on dead tree-trunks, show irregular internal annulation due to alternation of more organic and more detrital layers. These two species also live in environments that are more favourable to preservation of their faeces than other species that live on exposed rocky shores. In the latter environment, the bottoms of tidal pools are sometimes covered with sediment composed mainly of the faeces of littorinids.

The shape of pellets of European Littorinidae are equivalent to those from Columbia. Pellets with and without internal structure also are found (Moore 1931).

In the superfamily Cerithiacea, except for those members that filter feed, all individuals shed spindle-shaped faecal pellets. If these consist of fine grained material, they usually show regular internal annulations. The pellets shed by grazing Cerithiacea have a very good chance of being preserved because they are firm and are produced in great numbers and in the proper environments. The pellets of *Planaxis* could be deposited in the system of cavities between rocks. Pellets of *Cerithium eburneum* compose much of the muddy sediments in quiet bays and open lagoons, in the turtle-grass meadow environment, along with those of *Modulus* and *Alaba.* In some mangrove lagoons the pellets of *Batillaria minima* are of great importance, as are the pellets of *Cerithium variabile* in shallow parts of the coral reef lagoons.

Members of the group of filter feeders belonging to different superfamilies of the Mesogastropoda produce ovoid to egg-shaped pellets, mostly of very uniform consistency and with a very firm, smooth, shiny outer skin. These pellets are easily preserved because of their great durability, but only the individuals of *Petaloconchus, Bittium,* and *Caecum* are so numerous that large amounts of faecal pellets can be produced.

Ampullarius, a member of the superfamily Viviparacea, lives in quiet (*A. porphyrostomus*) and running (*A. monticolus*) freshwater and their pellets are of importance to sediments being formed in both environments.

The marine genera *Xenophora* and *Strombus* are also herbivorous, but only the latter genus occurs in such numbers on turtle-grass bottoms and sandy or muddy bay floors that faecal pellets are produced in significant quantities. The original pellet rod (also described by ROBERTSON 1961) may be preserved only in very favourable muddy environments, but single pellets are durable and are strewn about in great numbers.

The remaining genera, *Trivia, Cyphoma, Cymatium* and *Bursa,* produce pellets that may well be preserved in the system of cavities in coral reefs and rubble.

Neogastropoda.

Description.

With very few exceptions, the usual type of faeces produced by the Neogastropoda are soft organic rods and lumps, flocculent masses, and mucoid follicles.

Murex brevifrons LAMARCK, *Murex pomum* GMELIN, *Risomurex roseus* REEVE, *Ocenebra intermedia* C. B. ADAMS, *Purpura patula* LINNÉ, *Thais deltoidea* LAMARCK, *T. haemastoma* CONRADI, *Melongena melongena* LINNÉ, *Leucozonia nassa* GMELIN, *L. ocellata* GMELIN, and *Drupa nodulosa* C. B. ADAMS form pellets that in general are roundish, tightly packed, dark olive, brown and red; these organic rods have a stuffed structure of pressed plates and lumps, and mostly disintegrate immediately after production.

Engeniophus guadelupense PETIT, *Nitidella nitida* LAMARCK, *Olivia reticularis* LAMARCK, *Persicula pulcherrima* GASKOIN, *Conus mus* HWASS, *C. jaspideus* GMELIN, *Terebra taurinus* SOLANDER, *Anachis pulchella* SOWERBY, *Cantharus tinctus* CONRAD, and *Xancus angulatus* SOLANDER produce mucoid rods and follicles lacking a characteristic form, and sometimes also flocculent masses without mucus.

Columbella mercatoria LINNÉ, *Anachis brasiliana* V. MARTENS, *A. obesa* C. B. ADAMS, *A. sparsa* REEVE, *Coralliophila caribaea* ABOTT, *Engina turbinella* KIENER, *Pisania pusio* LINNÉ, *Mitrella ocellata* GMELIN, *Nassarius vibex* SAY, *Fasciolaria tulipa* LINNÉ, *Crassispira fusescens* REEVE, and *Fusilatirus cayohuesonicus* SOWERBY shed waste products in the form of a suspended flocculent mass. These faeces are of yellow, green, brown, or black colour.

Olivella petiolita DUCLOS.

Spherical to cylindrical, firm pellets of a variety of rounded shapes, up to 0.8 mm long and 0.2 mm wide. The outer skin is smooth, and the internal structure homogeneous.

Nitidella laevigata LINNÉ (Fig. 9 F).

Plates of light brown to greenish brown organic material, curled up on both sides. Not very firm, but chances of preservation exist in favourable environments.

Discussion.

Neogastropod faeces from Columbia are, with two exceptions, soft and not preservable. Preservation of these faeces would be possible only in very quiet, muddy environments, in authochtonous position, or if shed inside the sediment. *Nitidella laevigata* eats *Sargassum*, and *Olivella petiolita* takes up much detrital particles with its food, which probably consists of endobenthonic worms.

Systematic and Environmental Relationships.

Comparison with Known Pellets from Florida and the Bahamas.

Amphineuran and prosobranch faecal pellets were described by MANNING & KUMPF (1959) from south Florida, and by KORNICKER (1962) from the Bahamas. Most of the species studied by these authors were also found in Santa Marta; others were represented by closely related species of the same genus. The differences in shape and consistency are compiled in Fig. 10 which shows that many pellets from the northern and the southern Caribbean realms are identical, but also, that pellets from the Columbian north coast usually are more differenciated with respect to internal structure and external sculpture. For example, the sculpture in the faeces of *Cittarium pica*, described by KORNICKER (1962), and of the genera *Astraea, Turbo,* and *Nerita,* described by MANNING & KUMPF (1959), is much simpler than that of Columbian representatives. Internal structures can be found in Santa Marta, in many pellets of the genera *Planaxis, Modulus, Batillaria,* and *Cerithium,* but were not noted from south Florida. The reason for this difference may be that the Floridian and Bahamian pellets were, in general, composed of more coarse-grained detrital material, so that formation of fine structures were not possible there.

Relationship between Mollusk Taxonomy and Shape of Faecal Pellets.

Fig. 11 clearly demonstrates that faecal pellets of Amphineura and Prosobranchia show shapes that are specific to higher taxonomic units and thus are relevant phylogenetically (in contrast with the conclusions of SCHÄFER 1953, resulting from studies in the North Sea).

It is apparent that the systematic value of the faecal pellets is not always positive. Although the nature and form of the amphineuran and prosobranch faecal pellets are variable, generally they are uniform within a family.

MOORE (1931) and MOORE & KRUSE (1956) considered the various forms of pellets to be modifications of the unsculptured rod, oval or ellipsoidal pellets

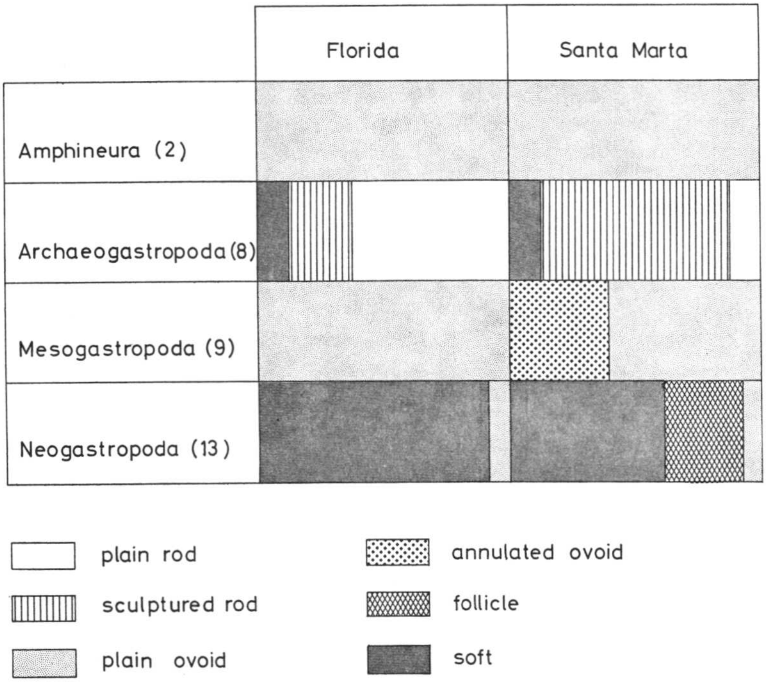

Fig. 10. Comparison of pellet forms of the same or closely related species from south Florida (MANNING & KUMPF 1959) with those from Columbia. — Parentheses indicate the numbers of species compared, each field representing 100%.

Abb. 10. Gegenüberstellung von Kotpillen-Formen gleicher oder vergleichbarer Arten Südfloridas (MANNING & KUMPF 1959) und Kolumbiens. — In Klammern steht die Anzahl der miteinander verglichenen Arten. Jede Fläche entspricht 100%.

being produced by way of the constricted rod. KORNICKER (1962) and ARAKAWA (1970) concluded that the various types of pellets may be simplifications of the sculptured rod, because of the predominance of such rods among both primitive gastropods and bivalves. In this study it is shown that Amphineura, which are considered to be phylogenetically more primitive than prosobranchs and bivalves, shed oval to ellipsoidal pellets. Therefore, generalisations concerning the form of the most primitive molluskan faecal pellet should be taken with caution.

KORNICKER'S (1962) statement that faecal pellet shape and composition may be of phylogenetic importance is true in some cases. ABBOTT (1954), for example, successfully employed the faecal characters, together with other indices, as a basis for removing the gastropod genus *Echinius* from the family Modulidae and placing it in the Littorinidae. TAYLOR (1966) demonstrated a difference in faecal characters between the gastropod families Bithyniidae and Hydrobiidae.

In general, only certain families of Archaeogastropoda show pellets that are characteristic for genera, some even for species. Here, further studies of faecal pellets of members of the superfamily Trochacea may help to clear the picture. All other amphineuran or prosobranch faecal pellet forms are characteristic only for superfamilies or groups of superfamilies, as in most Archaeogastropoda and some Mesogastropoda. Here, faecal pellets are more characteristic of feeding types. In the Neogastroproda, the faeces are rarely or not at all characteristic.

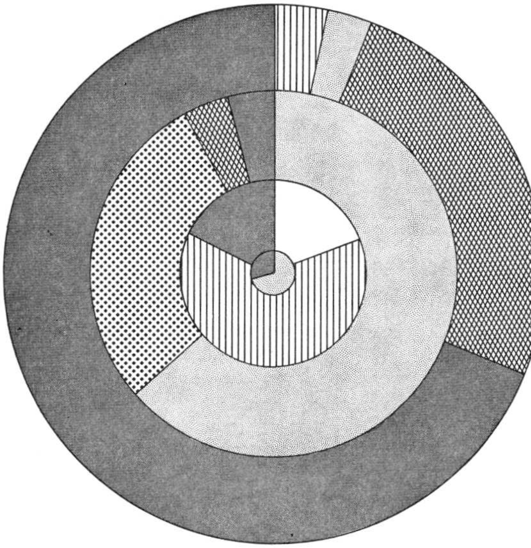

Fig. 11. The different faecel pellet-forms of the Amphineura (inner circle), Archaeogastropoda (next circle), Mesogastropoda (next circle), and Neogastropoda (outer circle), related to each other. — The thickness of each ring-plate reflects the number of analysed species; the whole surface of one ring-plate equals 100%. — Legend see Fig. 10.

Abb. 11. Die verschiedenen Kotformen der Amphineura (innerer Kreis), der Archaeogastropoda (nächster Kreis), der Mesogastropoda (nächster Kreis) und der Neogastropoda (äußerer Kreis) sind zueinander in Beziehung gesetzt. Die Dicke einer jeden Ringscheibe entspricht der Zahl der untersuchten Arten, und die Fläche einer jeden Ringscheibe entspricht 100%. — Legende siehe Abb. 10.

Relationship between Ecology and Faecal Pellet Shape.

Moore (1939) found that, in general, carnivorous animals tend to produce faeces of loose consistency, vegetable feeders tend to produce firmer ones, and pellets of deposit feeders tend to the most resistant.

In this study it is shown that the firmest, most durable faecal pellets are shed by filter-feeding gastropods. These animals take up very uniform, fine grained particles from the seawater. Often their faecal pellets are protected from destruction by an especially firm, smooth, outer skin.

Deposit feeders or herbivorous animals that take up appreciable detritus along with their plant food usually produce firm pellets. But so also do carnivorous animals that ingest sufficient detritus or skeletal material with their food. Perhaps it would be more concise to speak of a grazing mode of life for this group.

Gastropods feeding upon pure plant material, like *Smaragdia viridis* and *Nitidella laevigata,* shed organic feaces having little chances of preservation. *Smaragdia* feeds only upon fresh leaves of turtle-grass (*Thallassia*), and *N. laevigata* consumes the leaves of *Sargassum;* therefore, neither takes up detritus with its food.

Carnivorous gastropods feeding upon animal prey lacking skeletal material, or avoiding their prey's skeletal tests, produce soft faeces. Because of the high nutritive value of the food, these faeces are produced in small amounts. In contrast to the animals feeding on pure plant material, the herbivorous and carnivorous grazers and filter feeders have to take up food almost continuously and therefore produce large numbers of pellets equally continuously.

Schäfer (1953) suggested that all sedentary or slow-moving gastropods necessarily form hard solid pellets or mucoid follicles in order to avoid contaminating their own environment with floating or soft faeces. The littoral molluskan fauna of the Caribbean contains many species that disproove this idea for tropical sea animals. *Charonia,* for example, is quite slow in its movements but from time to time extrudes large amounts of flocculent and liquid faeces, with no ill effects imparted to the producer. Even animals kept in an aquarium with seawater running only half the day indicated no difficulties living for quite a while in water made murky by purple clouds of faecal material.

Coralliophila caribaea remains stationary in populations of up to 20 animals intimately living together between the basal parts of a gorgonian colony, on which it feeds. Even their flocculent faeces are shed into the small, restricted cavities without having ill effects on the producers.

Many more examples could be given to proove that flocculent or liquid faecal masses are not necessarily disadvantageous to gastropods living in shallow-water environments.

Prosobranch or amphineuran species show a well marked zonation, reflecting specific adaptations to depth of water, turbulence, salinity, substratum, food, enemies, temperature of water or substratum, and many other factors. Therefore, in the littoral environments of the Columbian coast typical populations are found, which naturally produce a typical assemblage of faecal pellet shapes. In Fig. 12 and 13, the localities containing a typical population, and the shapes of pellets produced by its members, are related to each other. If one neglects the soft and mucoid faeces and looks only at the preservable pellets, some generalities can be demonstrated. Plain rods are produced mainly on hard substrates, such as rocky cliffs, coral reefs, and coral rubble, by plant feeding Archaeogastropoda. Sculptured rods may be found in the mangroves, on cliffs, and hardgrounds, but not in muds and on sand bottoms because the plant-rasping Nertitacea and Trochacea are absent here. The plain ovoid pellets are found everywhere from rocky cliffs to muddy bottoms, produced by grazing and filter feeding Mesogastropoda. Annulated ovoids are absent in rocky cliffs and sandy bottom environments and rare on most hard substrates, because either too much coarse grained material hinders the formation of internal platy structures, or the pellets are formed by filter feeders.

From Fig. 14 it is apparent that an ecologically more differentiated sequence of environments could be achieved, with the help of faecal pellets of Archaeogastroproda, especially for areas of hard substrates. Different parts of reef structures, with associated lagoons and mangrove forests, can be differentiated by their Archaeogastropoda faecal pellet association.

Application to the Fossil Record.

Schäfer (1953, 1962), in his study on faecal pellets of animals from the North Sea, reaches certain conclusions concerning the validity of gastropod faeces in taxonomy that contrasted with those offered in studies on the same

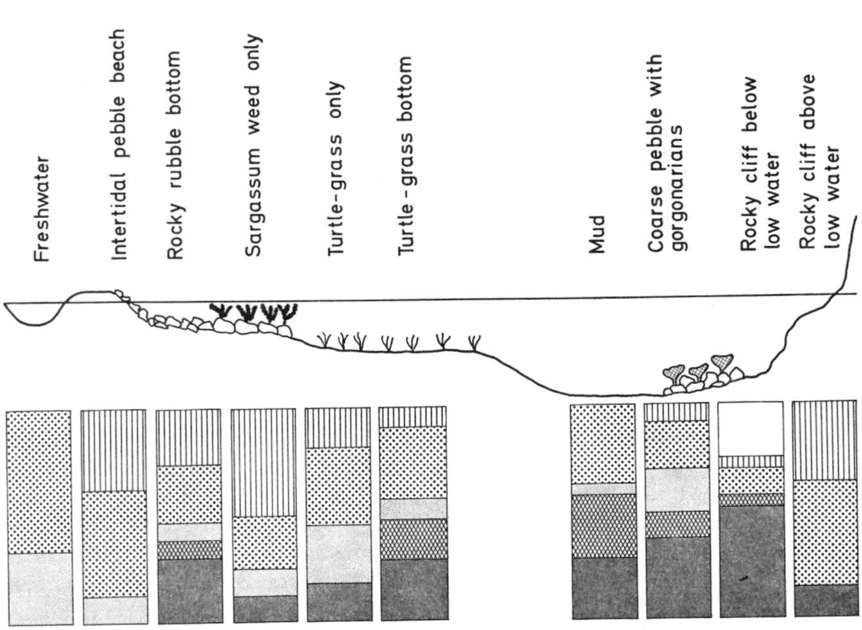

Fig. 12. Schematic transect from a freshwater pond, across the beach, rubble, turtlegrass meadows, into a muddy deep, and ending at a rocky cliff. — The faecal pellet assemblage of populations of Amphineura and Prosobranchia for the different environments noted are compiled in columns, all calculated to 100%. — Legend see Fig. 10.

Abb. 12. Schematisches Profil ausgehend vom Süßwasser, über Strand, Geröll und Seegraswiese in ein schlammiges Tief und endend an umbrandetem Felsabsturz. — In den Säulen sind auf 100% bezogen die Kotpillengemeinschaften aufgetragen, die von den verschiedenen Lebensgemeinschaften von Amphineura und Prosobranchia an den bezeichneten Stellen erzeugt werden. — Legende siehe Abb. 10.

subject along British Atlantic coast by Moore (1931, 1932) and near the Bahamas by Kornicker (1962). In respect to the tropical gastropod fauna described here, the views of Moore and Kornicker are supported by the results of Arakawa (1970), who provided an extensive study on the faecal pellets of Bivalvia.

Schäfer (1953, 1962) suggested that the only type of faeces characteristic of gastropods is the faecal-pellet trail. If that were the case, no characteristic gastropod faecal remains could be expected in any littoral environment seen in the Santa Marta area, because all trails on the bottom surface are destroyed rapidly by rich communities of mobile benthonic animals. The only possibility of preservation of pellets as lebensspuren would be in infaunal (or intrastratal) environments. Species living here usually produce faeces in the shape of mucoid follicles, e. g., *Olivia, Persicula, Conus jaspideus, Terebra,* and *Crassispira.* These faeces, without characteristic shapes, are produced in small numbers while the animals are burrowing or resting inside the sediment. But palaeontological interpretation of the deformation structures left by the burrowing animal probably

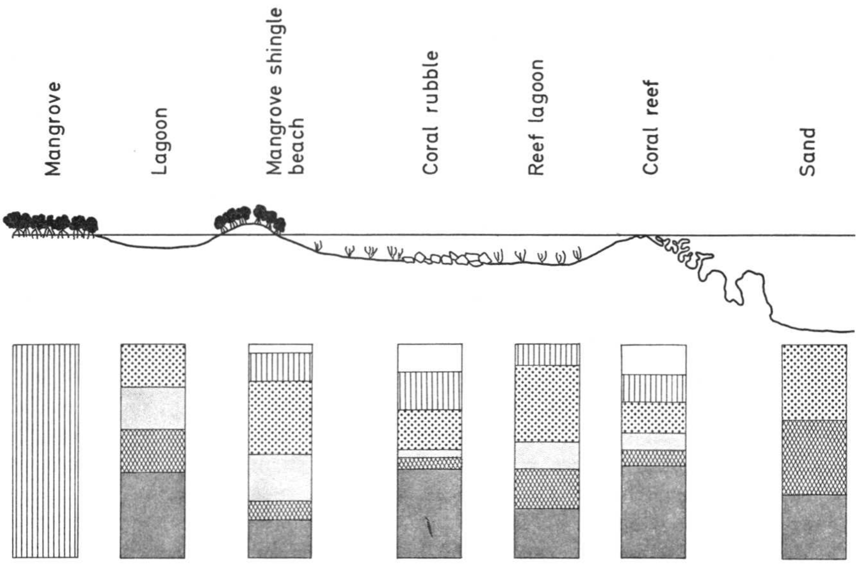

Fig. 13. Schematic transect from a mangrove forest through a restricted lagoon, across the beach-wall into the coral reef lagoon, and across the coral reef. — Faecal pellet assemblages compiled in columns, as in Fig. 12. — Legend see Fig. 10.

Abb. 13. Schematisches Profil vom Mangrovenwald durch eine abgeschlossene Lagune über den Strandwall hinweg in die Lagune des Korallenriffes und über dieses hinweg. — Die Kotpillengemeinschaften sind wieder wie in Abb. 12 dargestellt. — Legende siehe Abb. 10.

have much more taxonomic value than the few noncharacteristic faeces left along the way.

KORNICKER (1962) suggested that fossil faecal pellets may be useful to the palaeontologist for reconstructing the soft parts of the fossil animal, and also may be used palaeoecologically if their shape, composition, and consistence can be related more closely with feeding habitats.

My study suggests that these expectations can be limited a bit further with respect to Amphineura and Prosobranchia. For example, it is difficult to distinguish recent or fossil Amphineura faeces from those produced by Mesogastropoda. Furthermore, many carnivorous Mesogastropoda produce pellets of the same type as those produced by many herbivorous Mesogastropoda.

Also, some variation is seen in the consistence of pellets of the same species living in different environments. Striking variations were found when south Florida and Bahama faeces were compared with those from Santa Marta.

From the study of the Caribbean amphineuran and prosobranch faecal pellets, some suggestions for application in palaeontology, and especially palaeoecology, may be given:

1. Different environments are populated by specific animals that produce a typical assemblage of faecal pellets. This assemblage may be of great value, especially for the interpretation and differentiation of lagoonal and shallow-water limestones. Here, the composition of the pellet assemblages, and the shapes of pellets, can be studied easily with the help of peels and thin sections.

2. The two large gastropod orders Archaeogastropoda and Mesogastropoda can be differentiated by the types of pellets produced by their members. The first shed rod-like pellets, the latter ovoid and spindle-shaped pellets. This difference may proove to be of palaeontologic and phylogenetic importance in the analysis of gastropod faunas.

3. In the order Archaeogastropoda, faecal pellet shapes show much differentiation from genus to genus, some even from species to species. This characteristic can be used to help clarify problems concerning palaeozoic gastropods.

4. The consistence of pellets allows some further interpretations. Ovoid to egg-shaped pellets of very fine consistence, with a smooth, firm, outer hull, suggest a producer that lives by actively or passively filtering the water. Durable pellets of all shapes described, but with a more irregular consistence, suggest a grazing way of life, either herbivorous or carnivorous. Pellets containing large mica flakes, together with sharp-edged rock fragments, in a fine-grained matrix or comparable mixtures, give evidence for animals scraping rock surfaces in order to obtain food (here, many Amphineurans, Littorinidae, and Neritidae).

▶

Fig. 14. Schematic table showing the close relations of archaeogastropod faecal pellet-shapes to the environment. — The rods are drawn in transverse sections.

Abb. 14. Schematische Darstellung der engen Beziehung der Kotpillenformen bei Archaeogastropoden zum Lebensraum. — Die Kot-Würste wurden im Querschnitt-Bild dargestellt.


Rocky cliff, spray zone
Rocky cliff, tidal zone
Rocky cliff, less than 1m below low tide
Rocky cliff, more than 1m below low tide
Rocky cliff, deep rubble
Pebbles, spray zone
Pebbles, tidal zone
Pebbles, shallow water
Pebbles, deep water
Coral reef, algal crest
Coral reef, coral growth
Coral reef, fore-reef rubble
Coral reef, back-reef rubble
Coral reef lagoon
Coral reef lagoon shingle beach
Mangrove
Sand bottom with turtle-grass
Sargassum growths
Mud bottom
Mud bottom with some pebbles

5. Sediments composed of only one, or very few, pellet types are expected to have been formed under special conditions, such as fresh, saline, or brackish water, restricted lagoons, or mangrove forests. One example of this was given by KORNICKER & PURDY (1957) from a Bahamian lagoon. Here, up to 90 % of the sediment was composed of the faecal pellets of *Batillaria minima*.

Conclusions.

The faecal pellets of 8 species of Amphineura, 30 species of Archaeogastropoda, 36 species of Mesogastropoda, and 35 species of Neogastropoda from the area of Santa Marta are described and figured. The faecal pellets of the Amphineura are cylindrical ovoids, without internal structure. Faeces of the Archaeogastropoda are rods with their ends broken off, and are divisible into 5 groups, according to their external sculpture. Mesogastropoda produce mostly ovoid to spindle-shaped pellets. Carnivorous species feeding on large prey shed soft faeces. Mesogastropod faeces are most easily grouped according to their feeding ecology: filter feeders, grazers, and animals feeding upon soft prey. Neogastropoda faeces are, with the exception of one plant-feeding species and one detritus feeder, all soft and irregular in outline.

The Columbian faecal pellets compare well with known Floridian and Bahamian faeces. The former show more detail in both outer sculpture and internal structure, due to their finer consistence. Larger taxonomic units in Amphineura and Prosobranchia can be separated easily, using the shape of the faeces. Thus, Archaeogastropoda are recognized by rods, and Mesogastropoda by ovoid pellets, in all species analysed here. In the order Archaeogastropoda, the shape of the faeces reflect differences among genera, and some even among species. With Mesogastropoda faeces, the type of feeding by the animal seems to be a greater influence than taxonomy.

In general, gastropods that feed on filtered particles produce the most durable pellets; those that feed by grazing also shed durable pellets; those feeding upon pure plant food produce pellets preservable only in favourable environments; and those feeding upon large prey animals shed soft faeces. Typical assemblages of these various faecal pellets must be expected in diverse environments within the littoral sea and the estuary.

Acknowledgements.

The investigations were carried out at the Instituto Colombo Aleman (ICAL) in Santa Marta, Columbia, South America. My work in this marine laboratory was supported by the Deutsche Forschungsgemeinschaft (DFG) under grant ER 4/26.

I am indebted to Robert W. FREY, Athens, Ga., and Uwe MARR, Bonn, who reviewed the manuscript and gave many comments and suggestions. The drawings were made by my wife G. VAN SPAENDONK.

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