

A LOWER CRETACEOUS GASTROPOD WITH FOSSILIZED INTESTINES

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ABSTRACT. *Margarites (Atira) mirabilis* sp. nov. is a small trochid gastropod of Lower Cretaceous (Albian) age and is found in the Lower Greensand (Folkestone Beds) of Kent and Surrey. A unique feature in the description of this fossil gastropod is an account of the digestive tract, based on discovery of a specimen in which the contents of the gut have been phosphatized, thus reproducing as a mould the form and internal structures of the organ. The presence of the intestinal groove with bordering typhlosoles, minor longitudinal folds of the intestine, and an anal sphincter are all clearly demonstrable. Similarities with the gut of Recent Trochidae suggest that ecology and feeding habits of the family have remained unchanged. From the arcuate course of the rectum it is inferred that the left hypobranchial gland, missing in living species of *Margarites*, if ever present, was probably lost already in Lower Cretaceous times.

FROM time to time attention is drawn to the freak preservation of internal organs or other portions of the soft anatomy of animals known in the fossil state normally by shells, bones, or other hard parts or by traces only. A prime example is the Tremadocian annelid described by Whittard (1953) which has retained the form of the gut, the jaw apparatus, and minute details of the surface of the skin. Among mollusca, Roger (1944) has illustrated and described a dibranchiate cephalopod from the Upper Cretaceous of Syria in which indications of the stomach, intestines, and other organs can be made out. More recently, Cox (1959) has confirmed observations made by Gavey (1853) on the preservation of moulds of the intestines in nuculid lamellibranchs from the Lias of Gloucestershire.

The occurrence of remains of the gut in a fossil species of *Margarites*, described herein, is believed to be a unique record in the Gastropoda. The specimen was collected by the author in 1945 from a phosphatic concretion in the Lower Greensand (Folkestone Beds) of Sandling Junction, near Hythe, Kent, and was presented to the Geological Survey Museum, London, in 1946. The discovery is all the more remarkable in view of the rarity and generally poor condition of fossils in the Folkestone Beds.

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SYSTEMATIC DESCRIPTION

Family TROCHIDAE

Genus MARGARITES Gray 1847

Subgenus ATIRA Stewart 1927

Margarites (Atira) mirabilis sp. nov.

Plate 41, figs. 1-3, 5-8; text-fig. 1A, B.

Trochus sp., Wright and Wright 1942, p. 86.

Holotype. Geological Survey Museum No. 97302, Lower Greensand, Folkestone Beds (*tardefurcata* Zone, *Farnhamia* horizon), Coxbridge pit, Farnham, Surrey.

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Description. Shell small, nacreous internally, helicoidal, trochiform, consisting of five or six moderately convex whorls separated by simple sutures; apical angle about 85° . Body-whorl large, three-quarters the total height. Base very gently convex, with a funnel-shaped, rapidly expanding umbilicus, angular at the rim. Aperture elliptical, holostomous, having a small sinus corresponding to the umbilical rim. Peristome disconnected, the outer and inner lips being joined only by a film of nacreous material. Outer lip thin, inclined at about 60° to the suture. Inner lip in the same plane as the outer lip, smooth, not reflected. Spire and body-whorl with numerous fine spiral ridges which are traversed obliquely by the growth-lines, giving a subdued trellis-like pattern to the surface. Ornament intensified just below the suture, where the ridges are delicately nodulated. Base finely striated concentrically. Umbilical walls and rim with weak spiral ridges and vertical riblets, minutely beaded at their points of intersection.

Measurements of holotype. Total height 10 mm., height of body-whorl 7.5 mm., diameter of base 10 mm., width of umbilicus 4.9 mm.

Remarks. This gastropod is a characteristic fossil of the Folkestone Beds (Lower Albian) of Kent and Surrey and occurs principally in the *jacobi* Subzone of the *nodosocostatum* Zone and the basal part of the *tardefurcata* Zone. Preservation is generally poor. The holotype, a perfect shell, was isolated by hardening the fossil and its sandy matrix with nitrous cellulose and then applying amyl acetate as a solvent to small areas at a time, removing the sand-grains when loosened, and rehardening the shell as each portion was cleaned.

The shell has the general aspect of Recent *Margarites* but possesses the angular umbilical border diagnostic of the subgenus *Atira*. This border is not coarsely crenulated as in *Garramites*, nor ridged as in *Solariella*. The present species differs from the type-species of *Atira*, *Margarites (A.) ornatissimus* (Gabb) of the Upper Cretaceous of California (Stewart 1927, pl. 24, fig. 1), chiefly in its less angular whorl-profile; and the same character distinguishes it from species of *Margarites* described from the Cretaceous of Japan by Nagao (1939) and from Texas by Stanton (1947). *Margarites (A.) inornatus* (Gabb), also from the Californian Upper Cretaceous, resembles the Lower Greensand form in its rounded whorls but has a much lower, smaller spire. 'Turbo' *moniliferus* J. de C. Sowerby of the Upper Greensand (Upper Albian) of Blackdown, Devon, is superficially similar to *M. (A.) mirabilis*, though it is a taller species with grosser ornament, a canaliculated suture, and subcircular aperture.

THE ECOLOGY AND THE ALIMENTARY SYSTEM OF THE TROCHIDAE

The Trochidae, of which family *Margarites* is regarded as the most primitive member (Thiele 1929), are everywhere characteristic of the intertidal fauna of rocky shores and find an ideal environment on the hard surfaces of coral reefs. Retention of the aspidobranch ctenidium probably debars them from life on a soft substratum with much suspended sediment in the water (Yonge 1947, p. 473). They are microphagous and live mostly under stones and seaweed, browsing on diatoms, algae, and algal debris (Graham 1955), which, together with mineral and other detritus, is rasped into the mouth by the action of the radular teeth. *Margarites helycinus* (Fabricius), the type species of the genus, is a common boreal form of the laminarian and lower littoral zones which attains its southwards range on the northern shores of the British Isles (Cooke 1895, p. 365). Spawn-masses of *Margarites*, each with a hundred or more eggs, have been collected

with the adults from the under surfaces of stones at Cullercoats, Northumberland (Fretter 1955, p. 162).

Following the work of Robert (1900) and Randles (1904) the gross morphology of the alimentary system of the Trochidae is well known. The mouth leads to a buccal cavity or crop, which in turn is connected by a thick-walled oesophagus with a stomachal cavity. The last-named is the principal dilation of the digestive tract and is furnished at its posterior end with a coiled caecum. Owing to the torsion of the visceral mass undergone by the Gastropoda, the digestive tube doubles back from the stomach to the anterior end of the animal, via a long, more or less cylindrical intestine, thrown into coils. Like the stomach, this part of the gut is lined with ciliated epithelium, and it bears an intestinal groove, bordered on either side by a prominent fold (typhlosole), which runs along the gut to the anus. The origin of this groove and accompanying typhlosoles in the stomach is well illustrated by Graham (1949). The rectal continuation of the intestine may be of uniform calibre throughout its length or it may be distended as depicted in Pl. 41, fig. 4, and it is often provided with an anal constriction or sphincter. It ascends to the roof of the mantle-cavity to discharge on the right (exhalent) side of the cavity.

In correlation with the opening of the anus into the mantle-cavity (essentially a respiratory chamber) there is elaborate intestinal mechanism for consolidation of the faeces into compact pellets too heavy to be drawn in by the inhalent current (Yonge 1947). In vegetarian animals faecal matter is always bulky and it is probable, as postulated by Graham (1932) in the case of *Patella*, that the long coiled intestine of herbivorous feeders like the Trochidae is concerned chiefly, if not exclusively, with the formation of firm faeces. Indigestible and undigested matter is compacted together into a string, cemented by secretions from the secretory cells of the digestive gland, and driven along the gut by ciliary action. In *Patella* Graham has noted that the cilia on the double folds of the mid-gut beat into the groove between, along which a current runs to the anus. The faeces are voided as rod-shaped masses which break into lengths four or five times the diameter (Moore 1932). Moorhouse (1932), speaking of *Trochus niloticus* from

EXPLANATION OF PLATE 41

- Figs. 1-3, 5-8. *Margarites (Atrina) mirabilis* sp. nov. 1, Specimen with body-whorl broken open and exposing a mould of the gut. The specimen is seen in oblique lateral aspect with the spire pointing upwards and the base tilted slightly into the field of view. The terminal half of the body-whorl, on the observer's left, is filled with detritus and the aperture lies buried in the matrix. Lower Greensand (Folkestone Beds) (*nodosocostatum* Zone, *jacobi* Subzone), Sandling Junction sandpit, near Hythe, Kent (Geological Survey Museum No. Zm 490; author's coll.), $\times 6$. 2, Pencil sketch of same specimen to clarify relationship of internal organs to shell morphology. 3, Portion of same specimen enlarged $\times 24$, showing anal sphincter (A), rectum (R), with impressions of longitudinal folds on the dorsal surface, and, on the ventral surface, a mould of the intestinal groove and pair of typhlosoles (T); a loop of the intestine (L) protrudes from below the right side of the rectum and its descending limb may be followed to a convolution indicated at C; the buccal cavity and part of the oesophagus may be represented by the structures lettered B and O respectively. 5, 6, 7. Three views of holotype to show aperture (5), side (6), and base (7). Lower Greensand (Folkestone Beds) (*tardefurcata* Zone, *Farnhamia* horizon), Coxbridge pit, Farnham, Surrey (Geological Survey Museum No. 97302; author's coll.), $\times 4$. 8, Portion of same specimen enlarged $\times 6$ to show details of ornament.
- Fig. 4. Gut of *Trochus turbinatus* (Born.), seen from above and with the rectum (R) laid over to the right. The anterior part of the buccal cavity (B) and the posterior part of the stomach (S) are omitted, and the stomach is opened to show the intestinal groove and bordering typhlosoles (T). Other parts are lettered as in fig. 3. Redrawn from Robert 1900, \times about 5.

the Great Barrier Reef, says: 'Feeding appears to proceed at every opportunity, so that the amount of faecal matter deposited is very great.' Rao (1939) dissected scores of specimens of this species and found that the stomach and intestines were always full, even though the oesophagus was empty. Individuals starved for a few hours under laboratory conditions were found on dissection to contain very little food material in the stomach, although the intestinal loops were nearly always full.

Clark (1958), in a study of the mantle-cavities of some Trochidae and Turbinidae, has observed that there is an association between the course of the rectum across the roof of the mantle-cavity and the development of the hypobranchial glands (organs which secrete mucus to bind the fine sediment carried in with the respiratory current). In species with a straight rectum the right gland is small, while in species where the rectum takes an arcuate course the right gland is variously developed. The greater the arc of the rectum, the larger is the right hypobranchial gland, since it appears always to occupy the whole of the space available between the right side of the rectum and the point where the roof and floor of the mantle-cavity meet. Fretter (1955) showed that in *Margarites helycinus* the left hypobranchial gland is entirely lacking, while the right is well developed. Dissections of *Margarites groenlandicus* carried out by the author confirmed the extreme condition of disparity of development of these glands and also the strongly arcuate shape of the rectum in this genus (text-fig. 1D).

FOSSILIZATION OF THE GUT IN *MARGARITES (ATIRA) MIRABILIS*

The specimen which forms the nucleus of this paper was obtained from a phosphatic concretion in the Folkestone Beds of Sandling Junction sandpit, near Hythe, Kent (horizon 3 of Casey 1939). This horizon falls within the *jacobi* Subzone of the *nodosocostatum* Zone, here taken as the basal zone of the Albian. Above and below the bed in question are unfossiliferous sands exhibiting well-marked current-bedding. Concretions from this bed are one of the few sources of abundant fossils in the Folkestone Beds and within their sandy and pebbly matrix contain a varied fauna of mollusca, bryozoa, echinodermata, and brachiopoda. They appear to represent aggregations of organic debris that accumulated in hollows on the sea-floor and were cemented by syngenetic formation of calcium-phosphate, the shell-substance of mollusca and other carbonate being converted to collophane. Ammonites and gastropods are usually hollow, and the preservation and mode of occurrence of the fossils suggest that the shells were buried rapidly more or less where they died.

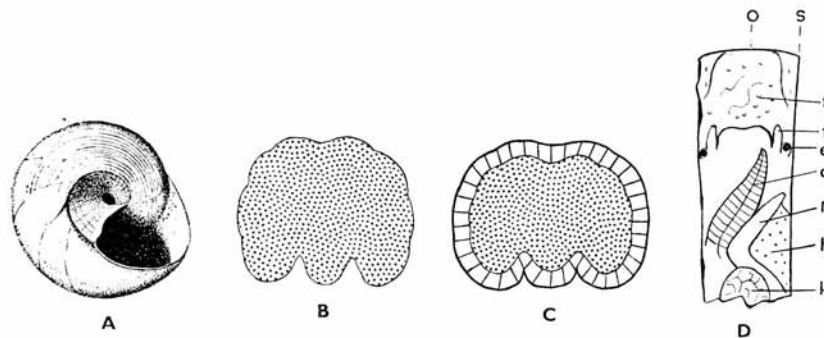
Margarites (Atira) mirabilis is the commonest gastropod in this bed and it is not unusual to find a dozen or more specimens in the space of a few cubic inches. The body-whorl of a hollow specimen was accidentally punctured, revealing inside the cavity, about half a turn back from the aperture, a minute worm-like structure of problematical origin. Enlargement of the 'window' resulted in exposure of the structure illustrated in Pl. 41, figs. 1-3, which is now interpreted as a mould of the intestines of the animal.

From data discussed in the preceding section it is apparent that retention of food and faecal matter in the alimentary tract after death is normal in the Trochidae. Moreover, it seems likely that this singular example of fossilization was made possible in the first place through the habit of these gastropods of consolidating the contents of the intestines. Material in the gut must have been firm enough to have stayed intact after decomposition of the surrounding tissues and to have remained in that condition long enough to

become involved in the process of phosphatization. In this manner the form of the gut and its internal features have been preserved as a mould in much the same way as the internal moulds of hollow shells are formed by compaction of infilling sediment. Contents of the digestive tract being of much finer grain than detrital sediment, minute structural detail of the gut is faithfully reproduced.

When comparing the fossil specimen with the gut of *Trochus* (Pl. 41, fig. 4) it must be borne in mind that in the fossil we see the organ as it is disposed when the animal is retracted in its shell, while in the living form it is shown spread out.

Reference to Pl. 41, fig. 3 will identify the anus, with well-marked sphincter-muscle (A), lying adjacent to the suture of the whorl and directed to the anatomically right side of the animal. The cylindrical rectum (R), about 0.4 mm. in diameter, takes a strongly



TEXT-FIG. 1. A, B, *Margarites (Atira) mirabilis* sp. nov. Base of holotype (A) showing details of aperture and umbilicus, $\times 3$; and (B) cross-section of mould of the rectum of specimen figured in Pl. 41, figs. 1-3, \times about 70. C, D, *Margarites groenlandicus* (Chemnitz) var. *umbilicalis* (Posselt), Angonagsalik, East Greenland (British Museum, Natural History, No. 1939. 7. 25. 456), cross-section of rectum (C), \times about 50; and (D) view of animal in retracted position, the shell and part of the mantle removed, $\times 5$. s = whorl-suture of shell, o = operculum, f = foot, t = cephalic tentacle, e = eye, c = ctenidium, r = rectum, h = right hypobranchial gland, k = kidney.

arcuate course convex to the left (corresponding to its course over the roof of the mantle-cavity) and then plunges down through the space that was once occupied by the visceral mass. Here, inside the bend, on the ventral side of the rectum may be seen very clearly the mould of the intestinal groove and its bordering typhlosoles (T). A loop of the intestine (L), homologous with that indicated in the figure of *Trochus*, lies underneath the rectum; its contents have been fractured, presumably owing to the sharp folding consequent to retraction of the animal at death. It is not possible to follow the posterior prolongation of the intestine beyond the obscure convolution indicated at C. Passing below both rectum and intestinal loop is another length of digestive tract that might conceivably be part of the buccal cavity (B) and the oesophagus (O). In addition to the typhlosoles, there were about eight minor longitudinal folds on the lateral and dorsal areas of the rectum and intestine; these are reproduced as shallow, parallel grooves on the mould, and between these grooves the surface is broken into microscopic, closely spaced undulations, the whole resembling in texture a peeled banana. Anteriorly, these structures end at the mass of detrital and mineral matter that fills the apertural half of

the whorl. It is possible that a mould of the stomach is preserved out of sight in the depths of the body-whorl.

Moore, in a series of papers, has shown that the faecal pellets of a variety of invertebrates have characteristic shapes and structures. His studies of the Trochidae have special bearing on the present work in that they demonstrate striking similarities between the fossil mould of the rectum of *Margarites (A.) mirabilis* and the faecal pellets of Recent members of the family. Moore (1932) found that in *Gibbula umbilicalis* (Da Costa) and *G. cineraria* (Linné) animals with shells of diameter 15 mm. formed pellets with an average diameter of 0.6 mm.; in *Cantharus clelandi* (Wood) an animal with a shell of 10 mm. produced pellets of 0.4 mm. diameter, which are precisely the sizes of the shell and the rectal diameter of *Margarites (A.) mirabilis*. Pellets from the two species of *Gibbula* mentioned above are roughly circular in section but on the ventral side are two deep V-shaped longitudinal grooves with an upstanding ridge between them. These are obviously moulded by the intestinal groove and the typhlosoles. The ventro-lateral lips bordering the ventral grooves are smooth, but the rest of the dorsal and lateral regions of the surface are cut by furrows into longitudinal panels. These panels are thrown into tightly packed lateral undulations of varying degrees of regularity and coarseness. Pellets taken from the littoral zone were found to have the undulations coarse and irregular; those from depths of 5 to 20 fathoms were more regular and finer in texture. The mould of the rectum of *Margarites (A.) mirabilis* (text-fig. 1B) agrees closely in cross-section with that of faecal pellets of *Gibbula umbilicalis* illustrated by Moore, but in the finely sculptured undulations of the panels it compares better with pellets of *Cantharus clelandi*. A cross-section of the rectum of *Margarites groenlandicus* (Chemnitz) is also figured in text-fig. 1 for comparative purposes.

The known ecology of the Trochidae, and of *Margarites* in particular, is consistent with our knowledge of the environment of deposition of the Folkestone Beds, namely near-shore, shallow-water conditions, and absence of very fine detritus. From the long coiled intestine of *Margarites (A.) mirabilis* it may be inferred that this species, like its living relatives, was a microphagous and herbivorous animal, and from the other details of its alimentary anatomy it would appear that its constitution closely resembles that of the family as living today. If the relationship noted by Clark between the course of the rectum and the development of the hypobranchial glands is valid throughout the family, we are permitted to infer also that the left hypobranchial gland, missing in Recent *Margarites*, was either never present or had been lost already by Lower Cretaceous times.

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