

LIMPET GRAZING ON CRETACEOUS ALGAL-BORED AMMONITES

by ETIE BEN AKPAN, GEORGE E. FARROW, and NOEL MORRIS

ABSTRACT. Phosphatized internal moulds of *Anahoplites* sp. and *Euhoplites* sp. reveal sets of six-toothed radula marks closely comparable to those scratched on to Recent molluscs by *Acmaea* (*Tectura*) *virginea* in water depths of up to 25 m on the muddy inshore shelf of western Scotland. Both the Recent and Cretaceous acmaeid marks truncate algal borings. Depth of the Gault sea during the Spathi subzone (M. Albian) was probably between 8 and 30 m, i.e. within the euphotic zone. Subsequent to lithification and phosphatization the moulds were bored by phoronids and scraped by regular echinoids.

FARROW and Clokie (1979) have recently drawn attention to the close association between the Recent limpet *Acmaea* (*Tectura*) *virginea* (Müller 1776) and the shell-boring alga 'conchocelis' on which it feeds. 'Conchocelis' is the resting phase of red seaweeds of the family Bangiaceae: use of the term is as in Farrow and Clokie (1979). In this paper we describe a similar association from the Lower Cretaceous which gives an indication of the depth of deposition of part of the Gault Clay and additionally demonstrates the persistence of acmaeid radula design. The fossil material consists of both shells and ammonite steinkerns bearing grazing traces: nearly all come from the Spathi Subzone of the Middle Albian, only one specimen from Dunton Green being of uncertain horizon. The grazing traces were collected from Copt Point, Folkestone, and are found on ten out of fifty-eight phosphatic internal moulds of hoplitid ammonites.

We outline the evidence for our interpretation of these traces, and document their occurrence alongside the only known species of Acmaeidae from the British Gault.

CHARACTERISTICS OF THE ASSOCIATED FAUNA

The form of the grazing traces from the Gault with their six parallel incised grooves preserved as negatives has led us to conclude that they probably belonged to an acmaeid. Patelliform shells are uncommon in the north-west European Albian, and particularly so in the Gault facies. There is one exception, however, *Patella tenuistriata* Michelin, 1838. This species is recorded from Folkestone by Price (1879) from his beds 2 II, 2 V, 2 VI, 2 VII, and 7 VIII, that is, scattered through the Middle Albian. We have examined nine specimens from the Gault at Folkestone with no further locality information. Of these, two are preserved on ammonite or nautiloid shells. Their protoconchs appear to have been lost during life and no epifauna or epiphyte is apparent. Further specimens of particular interest are two specimens from the Hampden Park borehole, Sussex, from the Spathi Subzone, the same subzone as our grazing trails. Another specimen, from an uncertain horizon of the Gault at Dunton Green, Kent (IGS Z5013), has a well-preserved muscle scar which confirms their identification as Acmaeidae. The only other limpet-like forms from the British Gault are attributed to the Calyptraeacea. Since these are suspension feeders, they are unlikely to have produced the incised traces we describe.

The clays of the Spathi Subzone occur widely across south-east England and have an extremely restricted benthonic fauna preserved. We are indebted to Adrian Morter of the I.G.S. for information concerning the faunas of this horizon, put together from information from several boreholes in East Anglia. Morter's Bed 3 contains common *Birostrina concentrica* and '*Ostrea*' cf. *incurva*, and less commonly the brachiopod *Moutonithyris*, the gastropods *Anticonulus* and *Rissoina*, the bivalves *Entolium*, *Inoceramus*, *Pycnodonte*, *Ludbrookia*, *Neithea*, *Pectinucula*, and the echinoid *Hemiaster*.

Morter's Bed 2, a grey clay bioturbated with *Chondrites* and other traces, contains the bivalves *Birostrina*, *Inoceramus*, *Mesosacella*, *Pectinucula*, *Pseudolimea*, *Pycnodonte*, *Rastellum*, the brachiopods *Kingena*, *Moutonithyris*, and *Tamarella*, and the solitary coral *Cyclocyathus*. These faunas are typical of the Spathi Subzone benthos. One or two additions are known from Folkestone, including *Oistotrigonia fittoni* (Deshayes), which seems to be restricted to the clay facies.

We suggest that the fauna was limited by the fine-grained sediments. These were, however, not always oxygen-deficient, as nuculoid infaunal deposit feeders form a significant part of the fauna. Shells of nektonic cephalopods are present in sufficient numbers to have provided a substrate for epifaunal grazers and this would have been the case for the acmaeids. The trochaceans and rissoaceans may also have browsed on shell fragments, or storm-derived algae or sponges.

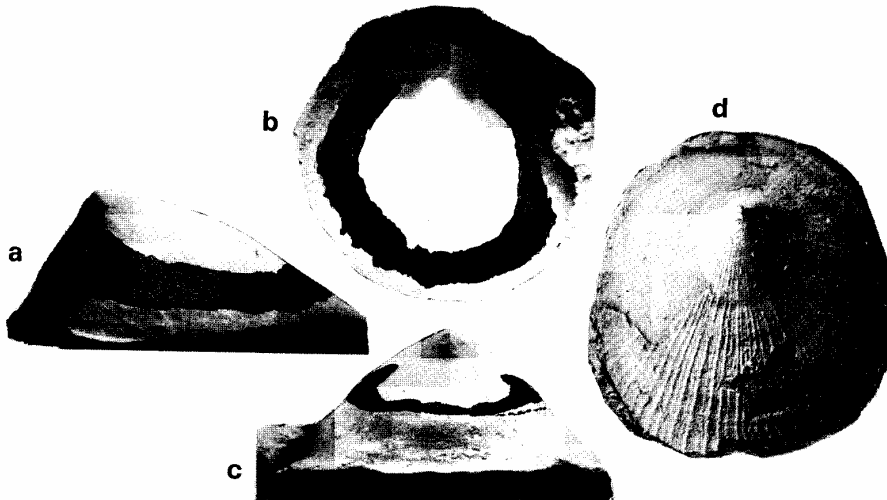
We feel that the coincidence of the occurrence of *Acmaea*-like grazing traces and the records of the only known species of Acmaeidae from the British Middle Albian is sufficient to justify our interpretation as one being the product of the other.

SYSTEMATIC DESCRIPTION

Acmaea tenuistriata (Michelin, 1838)

Material. Shells: nine specimens from the Gault of Folkestone (M.-U. Albian) BM(NH) GG.19971-19978; two specimens from the Spathi Subzone, M. Albian, Hampden Park borehole, Sussex, IGS, BDL 6727 and 6731; one specimen from an unspecified nodule bed in the Gault, Dunton Green, Kent, IGS Z5013.

Description. Broad, oval, bilaterally symmetrical, limpet-like shells with the apex approximately half-way between the mid-point and the anterior margin. The height is approximately one-third of the length. The largest specimen is about 15 mm in length. There is a radiating ornament of fine ribs with wide inter-spaces. No protoconchs are preserved. The shell structure is partly preserved in two specimens, BM(NH) GG.19977-19978 (text-fig. 1*d*), and consists of concentrically arranged cross lamellae which appear like vertical prisms in radial section. The shell is preserved entirely in a pinkish form, typical of Gault shells originally formed entirely of aragonite. The body and foot attachment scar is well preserved in IGS Z5013 and is illustrated in text-fig. 1*a-c*. It consists of a broad horseshoe-shaped area of scar joined at its anterior by a thinner line.



TEXT-FIG. 1. *Acmaea tenuistriata* (Michelin). *a-c* steinkern with muscle attachment scar inked in: IGS Z5013, unspecified nodule bed, Gault, Dunton Green, $\times 4$. (*a*) view of left side, (*b*) dorsal, (*c*) view of anterior. (*d*) specimen with part of the shell preserved: BM(NH) GG.19977, Middle-Upper Albian, Copt Point, Folkestone, $\times 3$, dorsal view.

Discussion. The shape of this shell and the form of its muscle scar are characteristic of the Family Acmaeidae. The general shape of this species, with its apex placed anterior to the mid-point, and its fine radial striae, are reminiscent of the subgenus *Acmaea* (*Tectura*) Gray, type species *A. virginea* (Müller), quoted as *Patella parva* da Costa (jun. sub. syn.) rather than *Acmaea* s.s., type species *A. mitra* (von Eschscholtz), a Californian species with a taller shell and central apex. However, without a thorough revision of the fossil members of the family we feel unable to place this species in a particular subgenus.

Grazing traces

Seven specimens are in the BM(NH); four collected by EBA and GEF, GG 19979–19982, and three collected by H. Lister, GG 19983–19985. The grazing traces are preserved as exquisitely detailed protruberances on the surfaces of the phosphatic moulds (Pl. 37, figs. 2–4). Individual markings, up to 200 μm wide by 400 μm long when fully developed, consist of six relatively broad ridges separated by narrow furrows. Overlapping of adjacent marks, however, rarely permits the full complement of ridges to be appreciated, and sets of sub-parallel ridges are the norm, their orientation being more consistent on some specimens (Pl. 37, fig. 4) than on others (Pl. 37, fig. 3). Successive truncation of sets of ridges suggests at least three phases of trace activity, the lowest being poorly preserved and having a smoothed appearance.

Borings

Three types seem to be present. The first consists of a widespread fine granulation on the surface of moulds where radula traces occur, in the form of small upstanding mounds of circular cross-section (Pl. 37, fig. 4). These represent the infilling of borings into the original ammonite shell. Having an approximate diameter of 6 μm they are probably algal in origin.

The second and third types represent unfilled borings into the lithified phosphatic moulds. The former are oval in cross-section, 500 μm in diameter, and penetrate deeply into the moulds: the latter are tunnels very close to the surface of the moulds which clearly truncate grazing traces in places (Pl. 37, fig. 3). The tunnels measure about 100 μm in depth and between 180 and 300 μm in maximum diameter, and are visible for a few millimetres before disappearing, only to reappear. These are probably the work of phoronids (Bromley 1970).

COMPARISON WITH RECENT TRACES

The Gault traces are similar to Recent *A. (Tectura) virginea* radula marks incised into mollusc shells (Pl. 37, fig. 1) but are preserved in a negative form. The comparison extends from over-all similarity of shape to details of six broadly incised elements, demonstrating a closer affinity in radula design between the presumed Gault acmaeid and the Recent *A. (T.) virginea* than between living *A. virginea* and *A. tessulata* (Müller 1776), whose radula is of four-pronged construction.

However, the Gault grazing traces are wider and less consistent in orientation than are those of the Recent *A. (T.) virginea*. This size difference is a reflection of the sizes of the causative limpets. For example, the longest Gault acmaeid measures 15 mm whereas the Recent British *A. (T.) virginea* is scarcely more than 7 mm long. Variation in the size of Recent *Acmaea* dictates the width of the grazing traces produced, 'scoops' ranging from 80 to 100 μm wide.

DEPTH OF DEPOSITION OF THE GAULT CLAY

The similarity between the fossil and Recent grazing traces is the more remarkable on account of the further association between the grazing marks and the fine granulation seen on the Gault specimens—the negative of the algal borings seen pitting the Recent examples. It is this association that sheds light on the depositional environment of the Gault during the Spathi Subzone, and in order to assess the probable depth of water it is necessary to consider something of the ecology of living *Acmaea*.

The genus *Acmaea* occurs widely in intertidal and shallow water-shelf habitats and there is much evidence for an algal grazing habit. Craig (1968) has described *A. pelta* living on micro- and macro-algae. Black (1976) described *A. incessa* living exclusively on the kelp *Egregia*, and many intertidal species graze upon epilithic algae (Kozloff 1973; Carefoot 1976). Fretter and Graham (1976) recorded *A. virginea* on algal-coated shell debris off the British coast. While these observations suggest that the depth was within the photic zone, it is possible to make a more refined estimate by looking in more detail at a single area.

Living Acmaea virginea on the Scottish continental shelf

Farrow and Clokie (1979, Table 1) working in the Firth of Clyde, found *A. virginea* down to only 18 m, coincident with the local limit of the euphotic zone as measured biologically by the last record of 'conchocelis' (Clokie, Boney, and Farrow 1979). This correlation is well established regionally, *Acmaea* extending into deeper water where substrates are coarser, environmental energy higher, and water clearer, as off the Orkney Islands where the euphotic limit is 38 m (Farrow, Allen, Akpan, and Brown 1981). A muddier, Firth-of-Clyde or Firth-of-Lorne-type environment is more appropriate as a Gault analogy, although the present latitude of 56° N is further north than that of Folkestone in the Albian, which was more like 33° N (Smith, Briden, and Drewry 1973, fig. 7, map 2).

Evidence on *A. virginea* distribution in one area of the Firth of Clyde is summarized on text-fig. 2. It is clear that the limpet extends down to within a few metres of the euphotic limit. Since, however, *Acmaea* grazing is intensive only where algal infestation is heavy we may conclude that deposition of the Gault Clay during this part of the Spathi Subzone was well within the euphotic zone. Depth was unlikely to have been greater than 30 m and could even have been as shallow as 8 m.

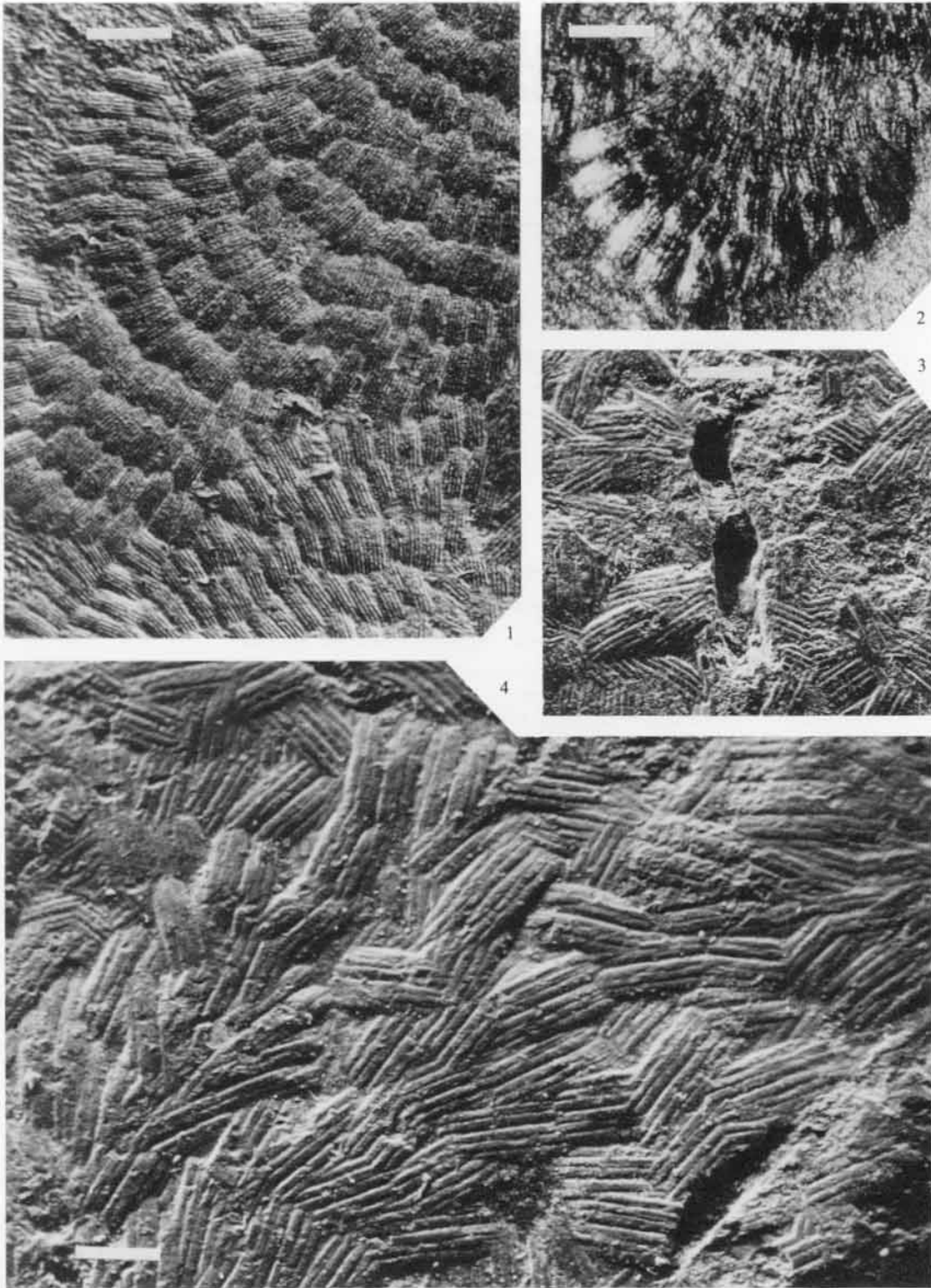
TAPHONOMY

The evidence is clear that these Gault ammonites were infested with shell-boring algae to such an extent that the full thickness of shell must have been riddled with them, for the limpet grazing marks were made on the inside of the body chambers: any on the outside would have had negligible fossilization potential. It remains to be established, however, whether the algae infested dead shells drifting near the ocean surface, maybe for several years (House 1973, p. 309; though cf. Reymont 1958), or whether they bored into the shells when the latter were on the sea bed. Since the environmental interpretation for this part of the Gault hinges on this point, further consideration is necessary. There is some supporting circumstantial evidence.

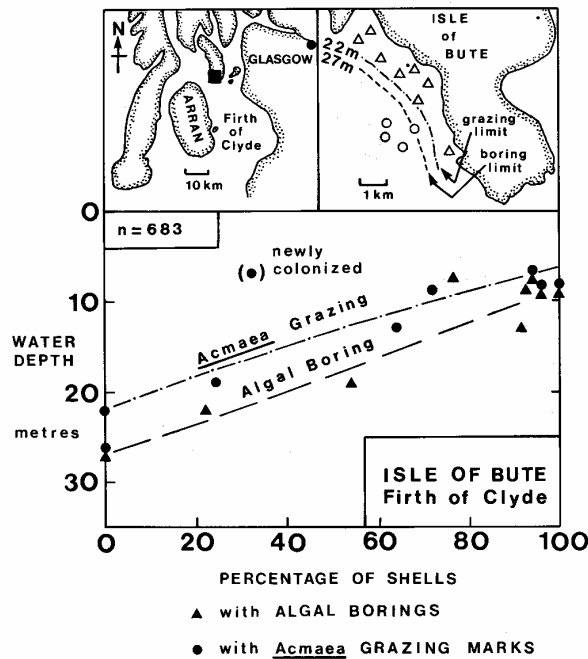
First, there is the occurrence of probable regular echinoid scratches both on the phosphate moulds and on associated shell debris: this scratching is commonest today within the euphotic zone. However, the occurrence of these traces on the ammonite moulds post-dates not only the grazing marks but also lithification of the moulds, and could be ruled misleading. Second, it is to be doubted whether the 'conchocelis' phase of members of the family Bangiaceae (coastal red algae) would be sufficiently dispersed to infest a multiplicity of widely scattered floating cephalopods. It seems easier

EXPLANATION OF PLATE 37

- Fig. 1. Grazing traces of Recent *Acmaea* (*Tectura*) *virginea* on algal bored *Dosinia* shell: 9 m: Isle of Bute, Firth of Clyde, Scotland. For locality see text-fig. 2.
- Fig. 2. Grazing traces of Lower Cretaceous acmaeid on surface of hoplitid ammonite skeinkern: note the grazing front (cf. fig. 1): BM(NH) GG.19983: Spathi Subzone, Middle Albian, Copt Point, Folkestone.
- Fig. 3. Phoronid boring cutting through acmaeid grazing traces on surface of hoplitid ammonite steinkern: BM(NH) GG.19980: Spathi Subzone, Middle Albian, Copt Point, Folkestone.
- Fig. 4. Grazing traces of Lower Cretaceous acmaeid on surface of hoplitid ammonite steinkern: note their relatively consistent orientation (cf. fig. 3): BM(NH) GG.19979: Spathi Subzone, Middle Albian, Copt Point, Folkestone.



AKPAN *et al.*, Limpet grazing



TEXT-FIG. 2. Depth of occurrence of Recent shells showing algal borings and *Acmaea* grazing marks: Firth of Clyde, Scotland. Note that the limit of grazing is slightly shallower than the limit of algal boring by 'conchocelis' (taken as a biological indication of the limits of the euphotic zone).

to envisage punctured shells being concentrated on the sea bed by winnowing and wave action, thus providing a typical habitat for the acmaeids, which are unknown pseudo-planktonically.

The following taphonomic sequence is therefore suggested:

1. Damaged ammonite shells sink on to muddy sea floor and are colonized by boring algae on their inner and outer surfaces (damage is supported by incomplete preservation: Reyment 1958; Seilacher 1971).
2. Acmaeid limpets colonize the dead shells, feeding on the endolithic algae in 'sweeping' fashion where infestation is high, but with more clearly defined 'scoops' where infestation is lower.
3. Draught filling of very fine mud replicates the body chamber before the limpet grazing has reached such an advanced stage that the weakened shell falls apart: many ammonites may have been grazed to destruction in the absence of an intervening smothering of mud. (Attempts artificially to replicate modern grazing traces with Epotex resin have been markedly less successful than Nature's amazingly high-fidelity moulds in the Gault!)
4. Burial, lithification, and phosphatization (with dissolution of aragonite?).
5. Re-exhumation by winnowing of mud: concentration of nodules without transportation.
6. Boring by polychaetes? and phoronids: biting by regular echinoids.

CONCLUSIONS: BORING ALGAE AND MOLLUSCAN GRAZING TRACES IN THE FOSSIL RECORD

The long geological record of both the boring algae (e.g. *Palaeoconchocelis starmachii* from the Silurian of Poland, Campbell 1980) and the patellaceans (Trias-Rec.) suggests that earlier radula marks may soon come to light. Boekschoten (1967) and Voigt (1977) have recorded a range of

molluscan traces as far back as the upper Jurassic, with chiton marks more frequently encountered than those of limpets. Taylor (1981, pl. 2/3) has figured what are clearly acmaeid radula marks on an *Isognomon* from the Portlandian, *kerberus* Zone. Again they seem to be associated with an algal-bored shell.

The implications of the kind of approach reported in this paper are twofold. First, it shows that when reasonably stringent sampling programmes are put into effect on present-day continental shelves it is possible to refine the determination of palaeoecological parameters, in this instance water depth. As this parameter is a difficult one to assess in clay sequences, this is a step forward, and the result for the Spathi Subzone of the Gault of 8–30 m may come as something of a surprise. The second implication lies in the evidence which is afforded for a remarkable lack of change in radula design or pattern of feeding in the acmaeids since the Lower Cretaceous.

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