THE SEXUAL ORGANIZATION OF CRETACEOUS *PERMOCALCULUS* (CALCAREOUS ALGAE)

by G. F. ELLIOTT

ABSTRACT. *Permocalculus ampullacea* Elliott, from the lower part of the Lower Cretaceous of Algeria and Iraq, is believed to be based on plants of the sexual generation of the botanical species, including female plants; and associated fossils are interpreted as representing both male and asexual plants, so indicating a sexual organization like that of the comparable living chaetangiacid alga *Galaxaura*.

IN the living marine chaetangiacid alga *Galaxaura* separate individuals are either of dioecious sexual plants or asexual plants: the two categories are often morphologically dissimilar, and were originally classified as different taxonomic sections of the genus. Howe (1917, 1918) assumed from this that the two were related on the basis of an alternation of generations. The recognition of sexual and asexual forms of the same species has, however, proved very difficult, and in spite of very detailed studies Svedelius (1953) concluded that only by experimental spore-culture could such a relationship be definitely established. For this reason the writer (Elliott 1956, 1960), dealing with largely fragmentary remains of the extinct alga *Permocalculus*, similar to *Galaxaura*, stressed the impossibility of classifying these fossils other than on a strictly morphological basis. From the Cretaceous of Iraq three such species were described, distinguishable on average typical pore-diameter, size and shape of whole segments, and the nature of typical fragments, which depends on calcification and size of segment. These species (Elliott 1956, 1958, 1959) are *P. ampullacea* (Valanginian–Hauterivian), *P. inopinatus* (Barremian–Aptian), and *P. irenae* (Albian–Cenomanian). The present note deals primarily with the first of these.

Remains of Permocalculus ampullacea Elliott. This species occurs in north Iraq from the Jurassic–Cretaceous passage level through Valanginian and Hauterivian, as evidenced by its occurrence in the local Zangura, Garagu, Lower Sarmord, and Lower Qamchuqa formations of various deep wells in the Mosul and Kirkuk areas. In Algeria the species also occurs at these Lower Cretaceous levels.

As described from the type material (Elliott 1959), *P. ampullacea* is a species of 'waxing-and-waning' morphology, roughly circular in cross-section, with variable calcification, and fine surface pores of about 0·012 mm. diameter (Pl. 11, fig. 1). Occasional specimens show scattered internal sporangial cavities (fig. 4). Associated commonly with it are fragments and debris of a much more coarsely pored but thin-walled form, with pore-diameter of 0·025–0·040 mm. (fig. 4). This has not yet been found as a complete segment, but certain pieces suggest that the segments were probably circular in cross-section. Also, rarely, there are associated remains of peculiar structures, flattened in cross-section, showing very numerous crowded cavities, smaller in size than the sporangial cavities of *P. ampullacea* s. str.; the mesh between these cavities is sometimes partly disintegrated (figs. 2, 3).

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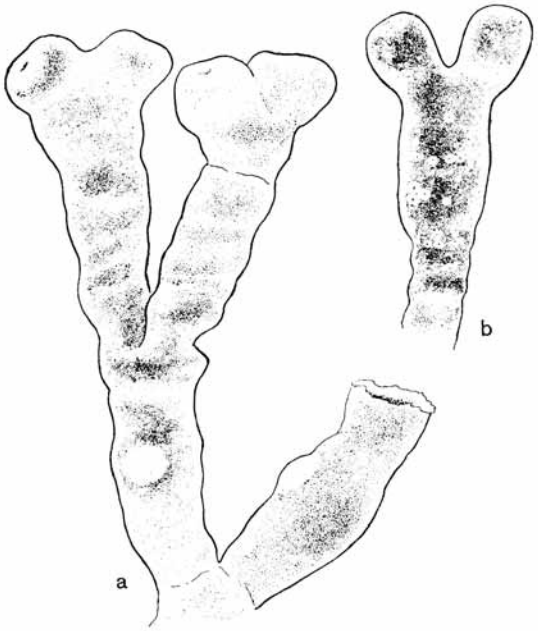
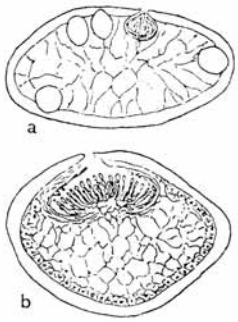
Comparison of Galaxaura and Permocalculus. Now in living *Galaxaura* the reproductive cavities (cystocarps) of female plants of the sexual generation are scattered in segments of the plant which are more or less rounded in cross-section (text-figs. 1*a*, 2*b*), and which are mechanically as stout as other segments. In the male plants, however, the cavities are smaller than in the female, and crowded in special, rather fragile, terminal segments



TEXT-FIG. 1. *Galaxaura glabriuscula* Kjellm. Recent; ×4. *a*, Female branch with cystocarps; *b*, male branch with spermatangial cavities. After Svedelius (1953).



TEXT-FIG. 2. *Galaxaura glabriuscula* Kjellm. Recent; ×23. Cross-sections of *a*, male branch; *b*, female branch. After Svedelius (1953).

which are flattened in cross-section (text-figs. 1*b*, 2*a*): these segments, after discharge of the spermatangial contents, probably drop off (Svedelius 1953, p. 17) and are replaced by proliferation shoots. In the asexual plants the little tetraspores are borne amongst the coarse threads or hairs of the surface, and leave no reproductive cavities in the subdermal calcification comparable with those of the sexual plants.

It is therefore suggested that *Permocalculus ampullacea* as described is based on plants of the sexual generation of the botanical species, female when the sex is recognizable; that the rare structures described above represent reproductive segments from male plants; and that the abundant coarsely pored debris is from the asexual plants. The analogies on size and arrangement of cavities, and on the form of the containing segments, already indicated above between sexual *Galaxaura* and *Permocalculus*, are supported by the rarity of the fragile spent male structures, shed before the break-up

of the whole plant which provides most of the debris for fossilization, and by the very coarsely pored presumed asexual debris. For as already stated, the asexual plants of *Galaxaura* differ markedly in appearance from the sexual ones, and the coarsely pored thin subdermal calcification in the fossil *Permocalculus* is what one would expect from a hairy rough-surfaced plant, such as is known in *Galaxaura*. It may also be of significance that Howe (1917, p. 622) records that in dried herbarium specimens of the Recent *Galaxaura* only the single superficial cell-layer exfoliates in sexual plants, whereas in the asexual plants two outer cell-layers come away. Possibly this mechanical consequence of cell-structure correlates with the differentiated fragmentation seen in the fossils.

This tripartite association has not yet been seen in the later Cretaceous species, *P. inopinatus* and *P. irenae*. This may be remedied by future collecting, but an alternative explanation is possible. Svedelius (1953, pp. 10, 50) has indicated the possibility of various Recent *Galaxaura spp.* being able to exist without alternation of generations, either solely in the sexual phase or solely as spore-producing individuals. Algae are primitive plants, and it may well be that the evolution of *Permocalculus* during the Cretaceous included a simplification of reproductive mechanism.

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Note. Similar structures have recently been seen in *Permocalculus inopinatus* from the Barremian–Aptian of the Hadhramaut, Southern Arabia.

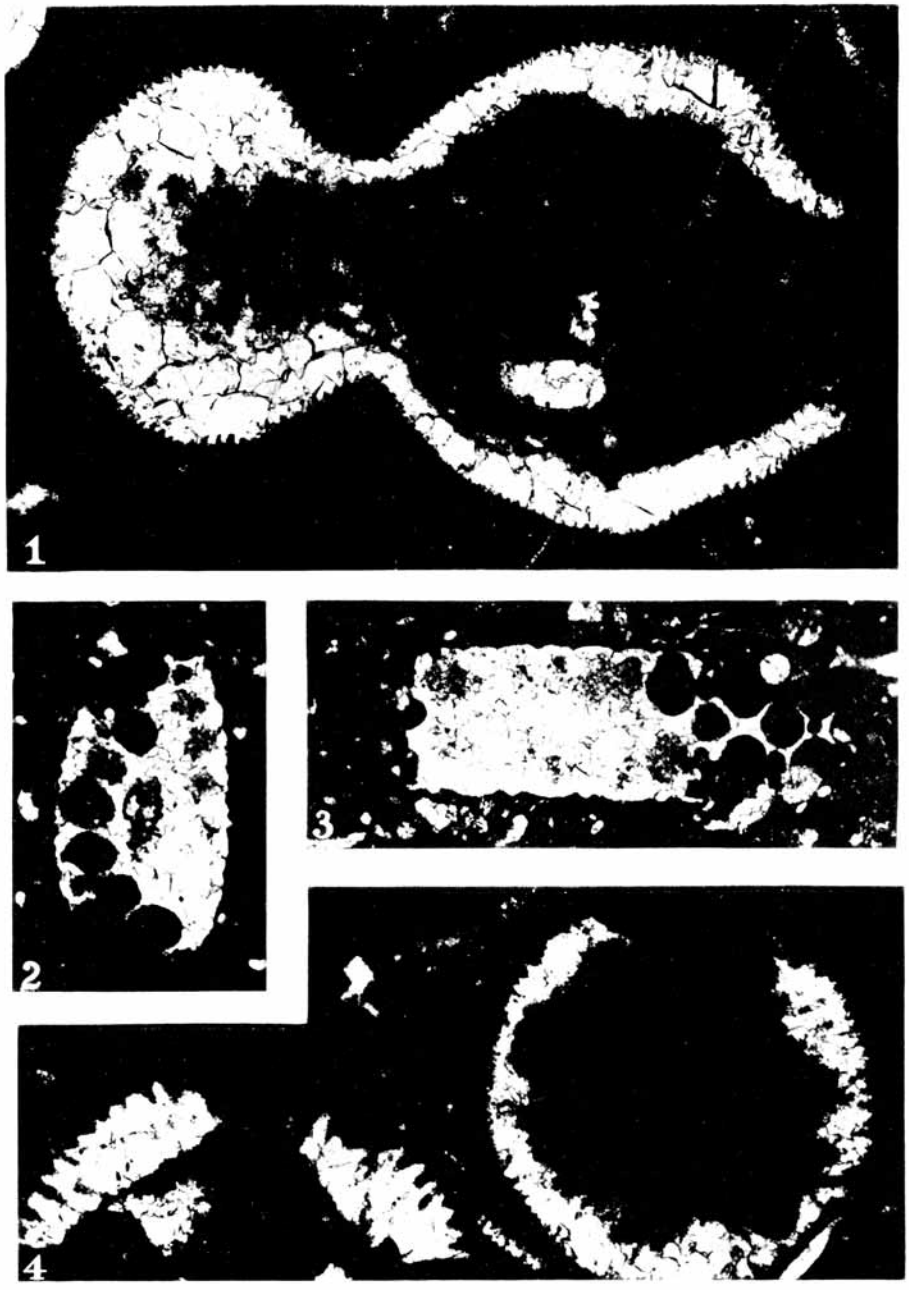
EXPLANATION OF PLATE 11

Fig. 1. *Permocalculus ampullacea* Elliott, longitudinal thin-section, × 50. Lower Cretaceous, Hauterivian; south flank of Djebel Harraza, Algeria. Brit. Mus. (Nat. Hist.) Dept. Palaeont., reg. no. V. 41663.

Fig. 2. Presumed male branch of this species, oblique-transverse thin-section, × 50. Lower Cretaceous, Hauterivian; Kirkuk well no. 116, Iraq. Reg. no. V. 41733.

Fig. 3. Presumed male branch, longitudinal thin-section, × 50. Locality and horizon as for fig. 2. Reg. no. V. 41732.

Fig. 4. Random cut showing presumed female branch with incompletely calcified sporangia on viewer's right, and fragments of coarsely pored presumed asexual form on left, × 50. Locality, horizon, and registered number as for fig. 1.



ELLIOTT, Cretaceous calcareous Algae