A *CLASSOPOLLIS*-CONTAINING MALE CONE ASSOCIATED WITH *PSEUDOFRENELOPSIS*

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ABSTRACT. The male cone and pollen attributed to the conifer shoot *Pseudofrenelopsis parceramosa* (Fontaine) Watson is described from the Wealden (Berremian) of the Isle of Wight. Comparison is made with the several earlier described *Classopollis*-containing male cones and a new genus is proposed for such cones found unattached. Aspects of the palaeoecology of the Cheirolepidiaceae (Hirmeriellaceae) are discussed.

OLDHAM (1976) in his cuticle analysis of plant debris beds in the English Wealden reported that a certain type which he identified as '30 CHEIR MaA' was one of the most frequent and abundant of the cuticle species recorded. Watson (1977) has shown that '30 CHEIR MaA' is identical to *Pseudofrenelopsis parceramosa* (Fontaine) Watson. On the basis of impressive association Oldham suggested that this cuticle type probably belonged to a conifer bearing *Classopollis* pollen.

We have collected an abundance of shoot remains of this conifer together with associated male cones at two localities in the Isle of Wight: (1) between Compton Grange Chine and Hanover Point, and (2) Chilton Chine, just east of Hanover Point. At the former locality well preserved compressed shoots (e.g. Pl. 96, figs. 1–4), decorticated twigs (Pl. 96, fig. 5) ranging up to massive logs as much as 40 cm or more in diameter, are abundant in lignite-rich layers of light grey siltstone. The layers are exposed both in the cliffs and on the shore at low tide. The male cones described here are all from the Compton Grange Chine locality.

METHODS

Occasional hand specimens of assembled shoots and detached cones have been collected but the general fragmentary nature of the material has necessitated the use of a bulk maceration procedure. Blocks of plant-rich matrix, once dried, break down readily when wetted; the material can then be sieved, washed, and examined under a dissecting microscope. In this way some eight specimens of male cones and cone fragments have been recovered. Specimens for microscopical examination are cleaned in hydrofluoric acid. Cuticles are prepared using Schultze's macerating fluid followed by alkali. For SEM observations macerated cuticles are dried down on to double-sided 'Sellotape' on stubs and coated either by evaporation of gold-palladium or with gold in a Polaron sputter coater.

DESCRIPTION

Vegetative material. To the detailed description of the vegetative features of *P. parceramosa* given by Watson (1977) we would add only a few points concerning the material with which the male cones are associated.

The great bulk of the material consists of more or less disarticulated shoot segments,

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but specimens with up to ten connected segments are frequent. Plate 96, fig. 1 shows a typical specimen with seven internodes. Such specimens are usually unbranched, 2–7 mm in diameter, with internodes 1–3 times longer than broad. Occasionally specimens are seen which show evidence of branching (Pl. 96, fig. 3). Terminal portions of shoots are fairly frequent (Pl. 96, fig. 4). Larger specimens, up to about 1 cm in diameter, have been observed in which the cortex including the cuticle has become ruptured and discontinuous and in which, as a result, the segmentation is ill-defined. Also present are numerous completely decorticated twigs (e.g. Pl. 96, fig. 5) which sometimes show evidence of branching, often whorled. More massive logs up to 40 cm in diameter also occur; some of these are partially petrified. We yet have no positive evidence that all this debris represents the same species of conifer, but the anatomy of the material is under investigation. At Hanover Point, about 100 m to the east of the main locality are found the well known 'pine-raft' petrified logs.

The male cone. Of the several specimens observed, all but three were incomplete. Two of these are shown on Pl. 96, figs. 7–9. The cone in fig. 7 is round but obliquely compressed so that the morphological apex is seen just below the top in the photograph. The specimen in figs. 8 and 9 is laterally compressed and its shape suggests that the cone may have been somewhat broader than long. However, the specimen has an opened longitudinal crack at the base and also some sporophylls may be missing from the base. Originally, therefore, it was probably more or less spherical. This specimen, after maceration in nitric acid without subsequent alkali treatment, was dissected. The pollen-sacs showed no tendency to rupture, remaining attached to the sporophylls (text-fig. 1C and D); they were filled with a dense mass of pollen which appeared to be either immature or abortive. This specimen enabled us to determine unequivocally the number of pollen sacs as three.

In no specimen have we been able to determine definitely the arrangement of the sporophylls, but they seem most likely to have been in 3+5 parastichies.

The incomplete specimen in Pl. 97, fig. 1 yielded mature pollen, but the walls of the pollen-sacs disintegrated on maceration (text-fig. 1A). The cuticle preparations and pollen on which the diagnosis of our new species is based are from this specimen which we accordingly designate the holotype.

Although a number of male cones containing *Classopollis* pollen have been described, most of these have only been named by reference to the vegetative shoots with which they have been found associated. In the absence of organic connection this seems an unsatisfactory practice. Barnard (1968) proposed that *Classopollis*-containing male cones should be classified in the form-genus *Masculostrobus* Seward

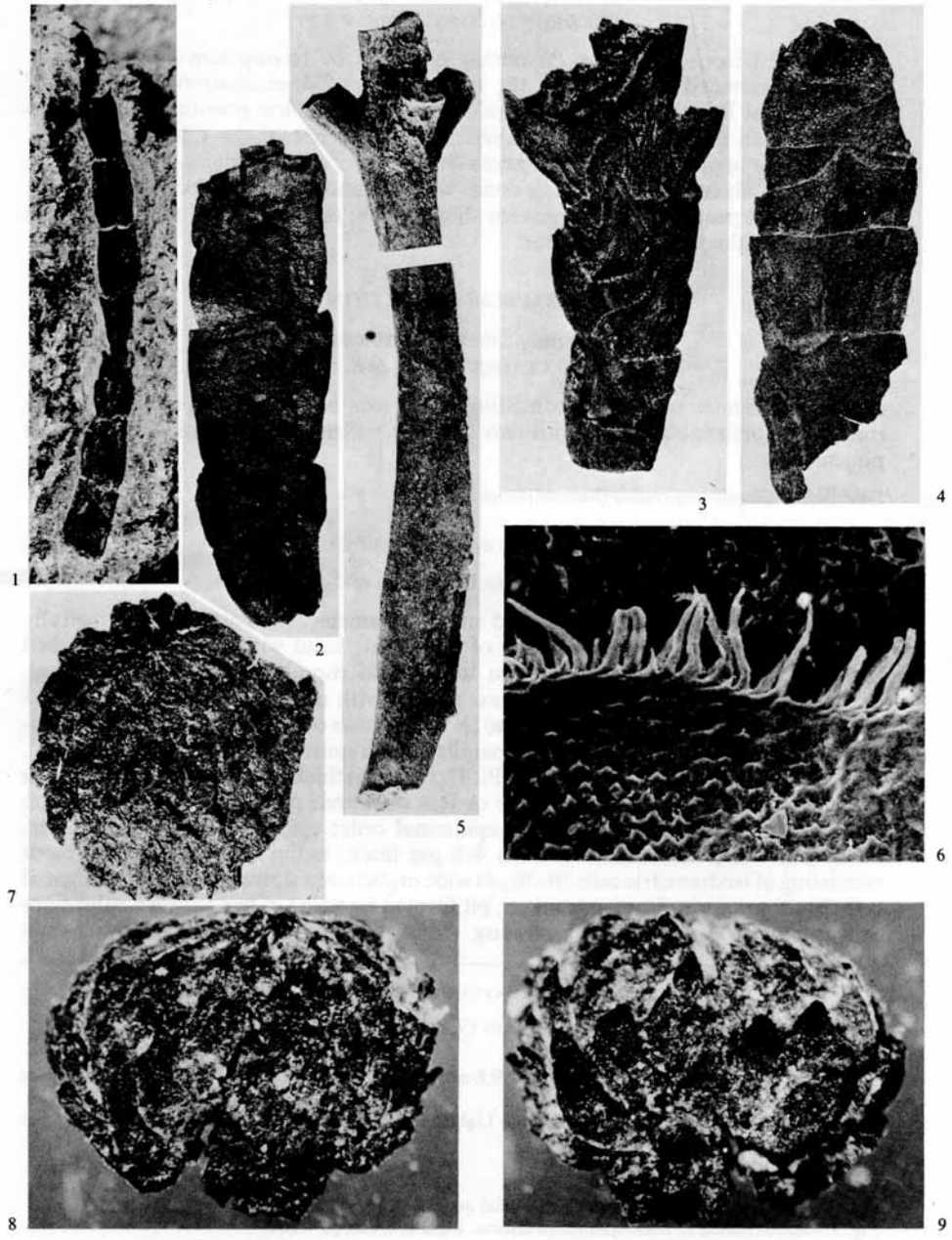
EXPLANATION OF PLATE 96

All specimens from Compton Grange Chine, Isle of wight.

Figs. 1–4, 6. *Pseudofrenelopsis parceramosa* (Fontaine) Watson. 1–4, range of shoot fragments. 6, hairs at edge of leaf. 1, ×1; 2, ×5; 3, ×4; 4, ×4; 6, ×150.

Fig. 5. ?*Pseudofrenelopsis parceramosa* (Fontaine) Waston. Decorticated twig showing a whorl of three branches.

Figs. 7–9. *Classostrobus comptonensis* gen. et sp. nov. 7, specimen V 59116. ×10. 8, 9, two sides of specimen V 59117. ×12.



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distinguished from the genus *Pityanthus* Nathorst by having non-saccate pollen. We have examined the slides of the type-species of *Masculostrobus* (*M. zeilleri* Seward) in the British Museum (Natural History) and confirm previous observations that its pollen is non-saccate. However, it is clearly not of the *Classopollis* type; rather does it appear similar to *Tsugaepollenites mesozoicus* Couper. *Masculostrobus* should be retained for conifer male cones which cannot be more precisely classified, but we would propose a new genus for those which, on the basis of their pollen are assignable to the Cheirolepidiaceae.

SYSTEMATIC SECTION

Family CHEIROLEPIDIACEAE

Genus CLASSOSTROBUS gen. nov.

Diagnosis. Conifer male cone consisting of an axis bearing sporophylls of peltate (radial or dorsiventral) form with two or more pollen-sacs containing *Classopollis* pollen.

Type species. Classostrobus rishra (Barnard) comb. nov.

Classostrobus comptonensis sp. nov.

Plate 96, figs. 7–9; Plate 97, figs. 1–7; Plate 98, figs 1–6; text-fig. 1, A–D

Cone approximately spherical, 4–5 mm in diameter. Microsporophylls spirally arranged, peltate in form, consisting of a laminate head with a centrally attached stalk 0·2 mm in diameter and 1 mm long. Head rhomboidal, 1·5–2·0 mm long, 0·5–1·0 mm wide; outer surface convex; margin with unicellular hairs, more or less adnate, up to 60 μm long (text-fig. 1A, B); lower portion of head bearing three cylindrical pollen-sacs, 1 mm long, oriented parallel to the sporophyll stalk (text-fig. 1C, D).

Abaxial cuticle of sporophyll head (Pl. 97, figs. 3–6) thick, papillose, with stomata in ill-defined longitudinal rows or more or less scattered; papillae conical, 10–15 μm long, arising singly from individual epidermal cells; epidermal cells isodiametric, 20–30 μm wide, with anticlinal walls 4–8 μm thick; cutinized hypodermis present consisting of isodiametric cells 20–30 μm wide or, between stomatal rows, of elongated cells 10–20 μm wide. Stomata sunken; pit formed by a ring of five to seven subsidiary cells each with a papilla 10–15 μm long. Adaxial cuticle (Pl. 97, fig. 7) thinner than

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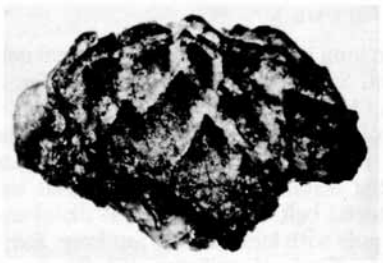
EXPLANATION OF PLATE 97

Classostrobus comptonensis gen. et sp. nov. from Compton Grange Chine, Isle of Wight.

Fig. 1. Holotype. ×12.
Fig. 2. Part of adaxial side of a microsporophyll from the holotype showing part of the stalk where it joins the laminal portion. SEM ×160.
Fig. 3. Abaxial cuticle of sporophyll lamina. Light microscope. Specimen V 59115A (from holotype). Light microscope ×400.
Fig. 4. Inside abaxial cuticle. SEM ×400.
Fig. 5. Outside abaxial cuticle. SEM ×800.
Fig. 6. Oblique inside view of cut edge of abaxial cuticle. SEM ×800.
Fig. 7. Adaxial cuticle of microsporophyll lamina. Light microscope ×800.



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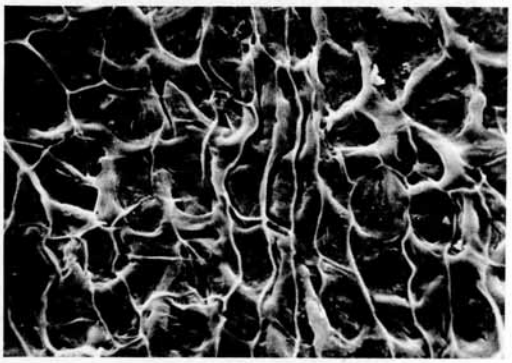

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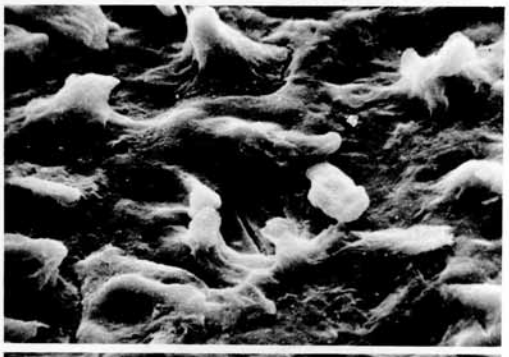

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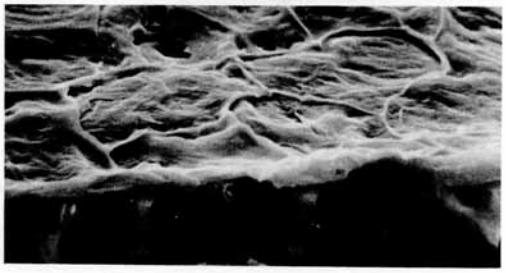

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abaxial, beset with conical papillae up to 40 μm long in distal region; epidermal cells isodiametric, not well marked; stomata absent. Stalk of sporophyll (Pl. 97, fig. 2) smooth; epidermis of elongated cells, 60–80 μm long, 15–30 μm wide.

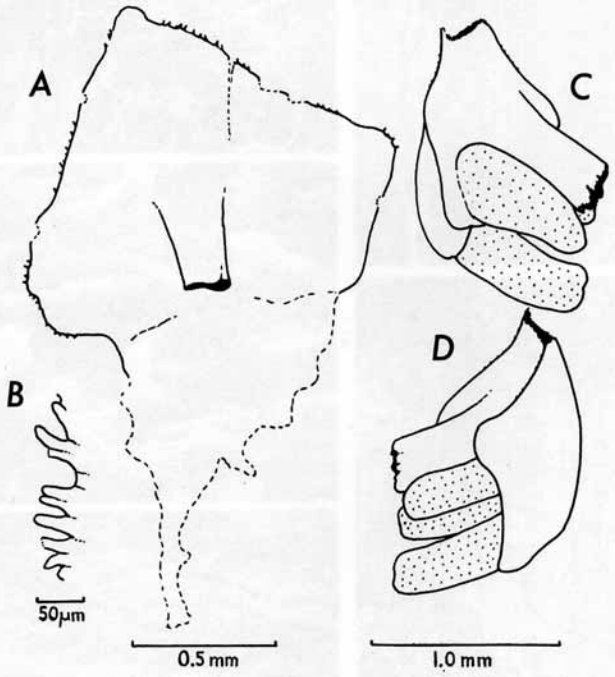
Pollen (Pl. 98) of *Classopollis* type, spheroidal with flattened poles, diameter (30–)36(–40) μm × (23–)25(–27) μm (15 grains measured), divided into two unequal caps by a subequatorial furrow situated at the distal edge of an equatorial belt (8–)11(–12) μm wide; 9–12 striations in equatorial belt. Pseudospore at distal end 6–11 μm in diameter. Trilete mark at proximal pole with laesurae 5–7 μm long. Exine thickness 1·3 μm; equatorial thickening 2·5 μm. External sculpture (Pl. 97, fig. 6) fine, of small blunt spines, about 25 elements per sq. μm. Internal sculpture (Pl. 98, figs. 1, 3) vermiculate.

Locality. Between Compton Grange Chine and Hanover Point, near Freshwater, Isle of Wight.

Horizon. Barremian.

Holotype. Pl. 97, figs. 1–7; Pl. 98, figs. 1–6; text-fig. 1, A, B.

Depository of specimens. British Museum (Natural History). Nos. V 59115–59117.



TEXT-FIG. 1. *Classostrobus comptonensis* gen. et sp. nov. A, microsporophyll from the holotype, adaxial side. B, marginal hairs from holotype. C, D, opposite side views of a single microsporophyll from specimen (V 59117) shown on Pl. 96, figs. 8, 9.

Discussion. The attribution of this new male cone to *Pseudofrenelopsis parceramosa* is based on close association and on cuticle similarities between the microsporophyll and the leaf.

The great abundance of shoot remains of this conifer in the Isle of Wight bed which has yielded the male cones is impressive. We estimate that less than 1% of the identifiable plant fragments represent different plants. Of these the commonest is another conifer, a *Brachyphyllum*, the cuticle of which is quite different from that of *Pseudofrenelopsis* and resembles that which Oldham (1976) compares with *B. obesum* Seward. The only other plants present are occasional fragments of Bennettitalean leaflets.

There is a considerable similarity between the abaxial cuticle of the sporophyll and that of the *Pseudofrenelopsis* leaf. Both are papillate, have rather similar stomata and a well developed hypodermis. The adaxial cuticles are similar in having long, hair-like papillae; in the shoot, this hairiness is confined to the leaf itself. The margin of the leaf and sheath as well as that of the sporophyll has unicellular, often somewhat laterally united hairs.

Male cones of several Cheirolepidiaceae containing *Classopollis*-type pollen have now been described. Harris (1957) described male cone remains from 'Rhaeto-Liassic' fissure deposits in Carboniferous Limestone from South Wales, which he attributed to *Hirmeriella muensteri* (Hörhammer). These cone fragments and the shoots with which they were associated were later attributed by Muir and van Konijnenburg-van Cittert (1970) to their new species *H. airelensis*. Here, though no complete specimen is known, the cone is apparently similar in general form to our new species, but the number of pollen sacs on the microsporophyll was judged to be only two. According to Hörhammer (1933) and Jung (1968) the male cone of *H. muensteri* has peltate microsporophylls with a ring of some twelve pollen-sacs. Barnard (1968) described a *Classopollis*-containing male cone as *Masculostrobus rishra* which he tentatively attributed to *B. expansum* (Sternberg) Seward and in which the microsporophyll was said to bear six to eight pollen sacs. Barnard and Miller (1976) have since identified the parent plant as *Cupressinocladus pseudoexpansum* Barnard and Miller.

Van Konijnenburg-van Cittert (1971) described the male cone attributed to *B. crucis* Kendall; she found evidence of only two pollen sacs on the microsporophyll.

Hluštík and Konzalová (1976) were not able to determine the number of pollen sacs in the male cone of *Frenelopsis alata* (K. Feistmantel) Knobloch.

Most of the male cones attributed to the Cheirolepidiaceae show a general cuticle resemblance between the microsporophyll and the leaf of the plant, though in most there are fewer stomata on the microsporophyll. Harris (1957) reported that stomata were not seen on the microsporophyll in his *Hirmeriella* material from South Wales.

The pollen is not dissimilar to that from the cone described by Hluštík and Konzalová and attributed to *F. alata*, but has a somewhat wider equatorial band with more striations. These characters in our pollen are rather closer to those in the pollen of *Classolepis rishra* (Barnard) n. comb., but the grain in that species is somewhat larger in size.

Of the dispersed species of *Classopollis* described in detail by Reyre (1970), none agrees completely with our pollen; the surface sculpture is probably most like that of

C. martinottii Reyre from the Berriasian-Valanginian of Israel, but other characters do not agree.

The pollen associated with Oldham's (1976) '30 CHEIR MaA' cuticle (which we identify as *P. parceramosa*) in the English Wealden appears to be the same kind as our pollen (Hughes, pers. comm.).

The smooth, non-sutured shoot internodes which are a typical feature of what we interpret as the adult foliage form of *Pseudofrenelopsis* is also an essential feature of *Frenelopsis*; it occurs in no other known conifers. This, together with cuticle similarities between the two genera (Alvin 1977; Watson 1977) make it not surprising that they should both be *Classopollis*-producers (i.e. Cheirolepidiaceae). They may represent closely related taxa within the family. Other members, also recognized on the basis of the male cones containing *Classopollis*, while having a more conventional morphology, show, nevertheless, considerable diversity. Among them are species of *Brachyphyllum* and *Pagiophyllum* (Kendall 1952; van Konijnenburg-van Cittert 1971), the *Elatides*-like *Tomaxellia* (Archangelsky 1968), and the cupressaceous-like *Cupressinocladus pseudoexpansum* (Barnard and Miller 1976). Such morphological diversity might well imply ecological diversity. The *Pseudofrenelopsis*/*Frenelopsis* group with their distinctive and indeed unique morphological characters may have been adapted to very different kinds of habitats from those occupied by some other members of the family. Watson (1977) has suggested, on the evidence of the extraordinarily thick cuticles and rather little wood in the shoots of some species, that they may have been succulent halophytes. Oldham (1976) envisaged his '30 CHEIR MaA' (= *P. parceramosa*) as dominating river-margin swamps on the Wealden delta.

The palaeoecology of *Classopollis*-producers has been discussed by numerous authors. Vakhrameev's (1970) review is an invaluable contribution. His conclusions and those of others since have been usefully summarized by Srivastava (1976). Nearly all authors have assumed ecological uniformity and have concluded either that the plants inhabited coastal lowlands (swamps or sand-bars) or that they were components of inland slope vegetation. That the family was widespread geographically and especially abundant at lower latituted in the Mesozoic has been well established.

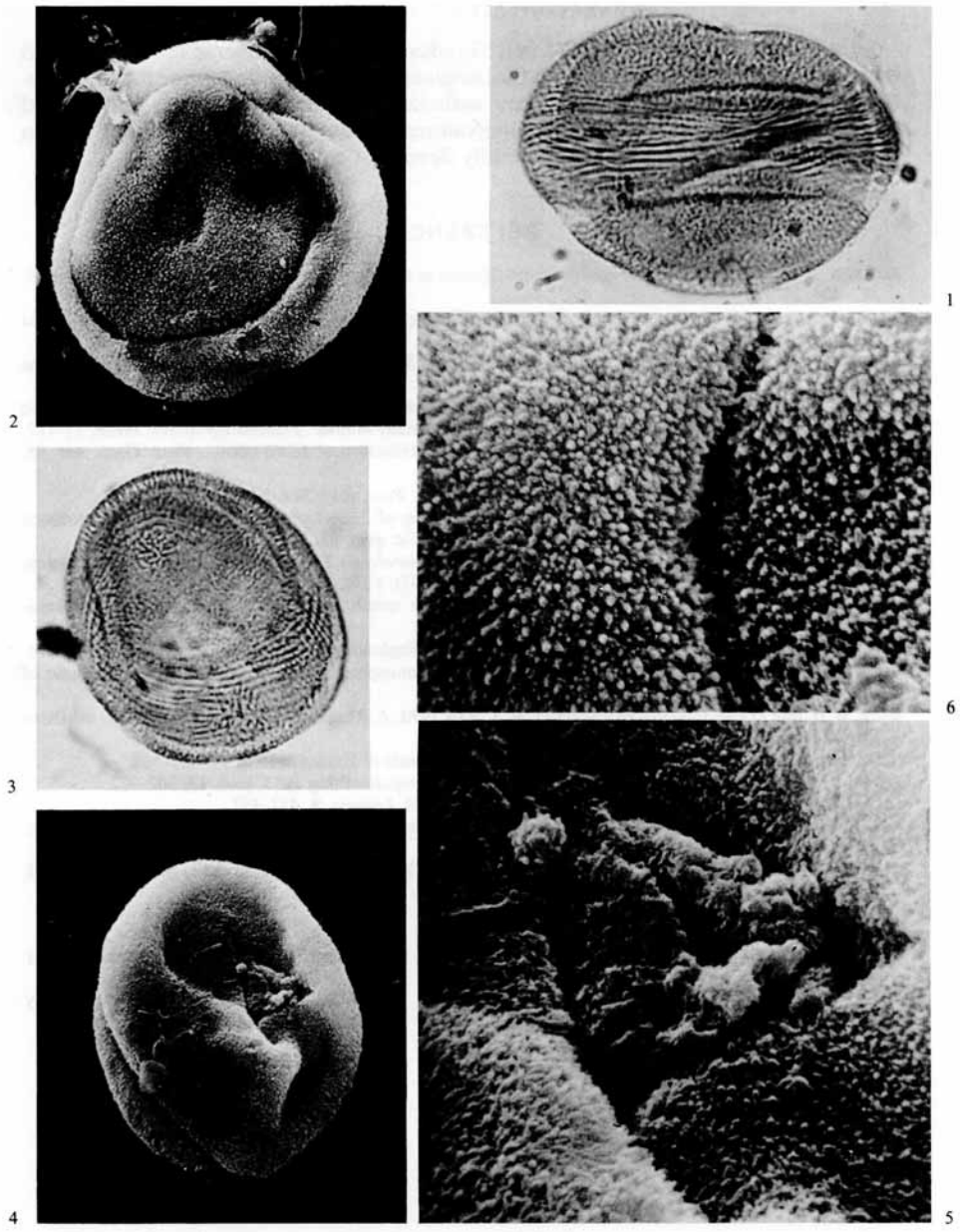
The assumption of ecological uniformity may be quite unjustified. Ecological diversity could account for the apparently conflicting nature of much of the palynological evidence upon which conclusions concerning palaeoecology have generally been based. It is noteworthy that Batten (1974), in interpreting the palaeoecology of the English Wealden, gave four alternative reconstructions of the flora. These included three alternative habitats for *Classopollis*-producers: (1) sandy bars and barrier islands along the coast; (2) mangrove-like communities; (3) flood-plains or upland slopes.

EXPLANATION OF PLATE 98

Classopollis from *Classostrobus comptonensis* gen. et sp. nov. from Compton Grange Chine, Isle of Wight.

Figs. 1, 3. Light microscope views. Slide V 59115B. 1, Equatorial view. ×1500. 2, oblique distal view. ×1500.

Figs. 2, 4–6. SEM views. 2, distal side. ×15000. 4, oblique proximal view. ×15000. 5, triradiate mark. ×7500. 6, detail of surface at the subequatorial furrow. ×9000.



ALVIN, SPICER, and WATSON, *Classopollis* from *Classolepis*

Clearly it is unlikely that the Cheirolepidiaceae were so diverse that they could have occupied the range of habitats that angiosperms do now but, prior to the angiosperm advance, they may have been sufficiently diverse to occupy, and indeed dominate, some variety of different environments, including some important ones in the tropics and sub-tropics now generally devoid of conifers.

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