

AMPHORISPERMUM AN ENIGMATIC ASSEMBLAGE

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ABSTRACT

A specimen showing packets of the small Caytonia-like seed *Amphorispermum* is described from the middle Jurassic of Yorkshire, England. *Amphorispermum* seeds had previously been found in large numbers but in isolation. Although some of the packets consist of about ten seeds with their flat sides in contact no tissue connecting them is preserved but the possibility that the assemblage represents a decayed fructification is suggested.

Possible leaves of the plant are considered but though *Ctenis* is mentioned the evidence to connect them is inadequate.

Key-words — *Amphorispermum*, *Caytonia*, Seeds, Middle Jurassic (England).

सारांश

एक रहस्यमय समुच्चय से एम्फोरिस्पर्मम् - टॉम एम० हेरिस

इंग्लैंड में यॉर्कशायर के मध्य जुरेसिक से केटोनिया-सदृश छोटे बीज, एम्फोरिस्पर्मम्, के संवेष्ट प्रदर्शित करता हुआ एक प्रादर्श वर्णित किया गया है। एम्फोरिस्पर्मम् के बीज बहुत संख्या में, परन्तु पार्थक्य, पहले भी पाये गये थे। यद्यपि कुछ संवेष्टों में चपटे पहलुओं पर सटे हुए लगभग 10 बीज हैं जिनको संयोजित करने वाला कोई अतक परिरक्षित नहीं है, तथापि यह सम्भावना कि समुच्चय क्षीण फलन निरूपित करता है, प्रस्तावित की गई है।

AMPHORISPERMUM is a genus of seeds which resemble *Caytonia* seeds but were only known isolated. They were first extracted by bulk maceration from the Rhaetic and Lower Liassic rocks of E. Greenland (Harris, 1926, p. 128; 1932, p. 14; 1937, p. 36) and later from Yorkshire, England (Harris, 1964, p. 28). They have not been found elsewhere perhaps because the bulk-maceration methods were little used for seeds though similar methods have been much used for lycopod megaspores and on an enormous scale for miospores.

All the Greenland specimens were extracted by oxidative maceration followed by alkali as were most of the Yorkshire ones and as a result the extracted fossils consisted of cuticles alone. But some from the Gristhorpe Bed, Yorkshire had been extracted undamaged by maceration in water. The small specimen described here, also from the Gristhorpe Bed, is the first on which *Amphorispermum* had been seen on a rock surface. Hamshaw Thomas collected it many years ago; he left no notes but had evidently studied it as it shows

needle marks and some seeds had been removed. Though unlabelled, its matrix and associated plants are those of the Gristhorpe Bed at its most typical and I have no doubt that that was its origin.

This new specimen makes some contribution to knowledge but leaves very much open; it is offered in the hope that someone will be able to add more. It is also offered as a tribute to Dr Surange's work on the puzzling fructifications associated with *Glossopteris*.

Genus — *Amphorispermum*

Type Species — *A. ellipticum* Harris, 1932.

Emended Diagnosis — (Main axis and branches of fructification unknown, terminal branches inferred). Each group of about 10 seeds about 1 cm long, seeds placed parallel and with their flat sides in contact and their micropyles pointing the same way; possibly a second set present behind the first set.

Seed orthotropous oval or rounded, in different species 1.0-2.0 mm long, up to 1.5 mm broad (but never broader than

long); 0.5 mm thick. Both ends rounded, neither micropyle nor hilum prominent. Integument apparently single about 100 μm thick at lateral margins but thinner over flat surfaces; at lateral margins dense tissue present in integument but not over flat surfaces. External cuticle of integument firm about 2 μm thick showing strongly projecting lateral and end walls of nearly isodiametric cells in longitudinal files, cell size smaller at ends of seed. In unmacerated state, cell walls prominent giving the seed a pitted surface. Vertical and bottom walls of epidermal cells thick. Inner cuticle of integument not recognised but a deep cuticle of unknown morphological nature present outside nucellus and overlapping inner end of micropylar canal, the 'spotted membrane'. Cells of spotted membrane isodiametric or slightly elongated, their outlines feebly marked but interior of each cell, occupied by dark granular matter. Nucellar cuticle robust up to 4 μm thick, its cells elongated, pointed, lateral walls straight or slightly waved, prominent, at micropylar end cells becoming short, walls very thickly cutinised, top flattened, no chamber discernible. At chalazal end cells also short but cuticles not thickened, then ceasing abruptly to leave a round hole.

No cutinised megaspore membrane present (matter enclosed in nucellus indefinite and amorphous).

DESCRIPTION

When I first saw Thomas' specimen it showed numerous seeds in groups and degagement revealed further seeds (Text-fig. 1). There was no sign of any tissue connecting the adjacent seeds to one another or between the groups of seeds. I term the groups packets since this has no morphological implications. There were many plant fragments around but all seemed irrelevant. Bits of each fragment were macerated and a few proved to be of common Gristhorpe Bed leaves but most gave no cuticle. They may have been fern fragments.

After being photographed the specimen was transferred when the same seeds were revealed from the opposite side and a good many additional seeds were seen. Many seeds or bits of seed packets were loose in the liquor. Still there was no sign of tissue

connecting the seeds, disappointingly. Fragments of the leaf *Ctenis falcata* L. & H. the commonest fossil in the block lie close to the seeds but there is no connection. The most striking seed packets are ones which show the flat sides of seeds but I believe those which show the edges of closely placed seeds are the least distorted. The packets are numbered for description but I suspect that some of the numbers may merely mark the parts of a single packet.

Packets 1 and 2 — These were visible in the original specimen but only recognised as relevant in the transfer. The packets are orientated at right angles to most others, and the seeds are compressed from end to end; one seed was removed and macerated to confirm that it really was *A. pullum*; its cuticles were normal and characteristic. It is likely that the packets each consists of seeds packed side by side and possibly the two packets are parts of a single structure having two rows of seeds.

Packets 3 and 4 (possibly a single long packet) — In packet 3, seeds lie irregularly, some present their edges, some their flat sides and some are beneath others, but in packet 4 with more regularly placed seeds there are none underneath. The seed on the right was removed and macerated; its micropyle pointed downwards. A little black matter between packets 3 and 4 yielded no cuticles.

Packet 5 has six tilted but not displaced seeds and a separate seed on the right.

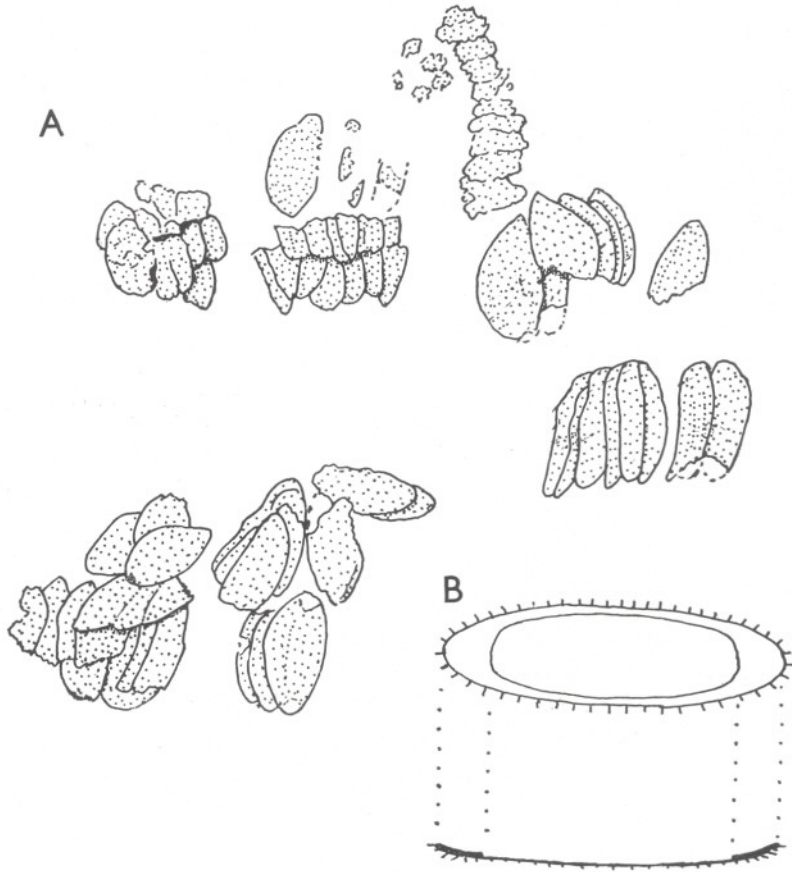
Packet 6 has about 12 seeds, some little displaced and preserved with an edge pointing upwards but others displaced and lying beneath another seed.

Packet 7 has 4 seeds in position and one separate; the axis of this packet like 1 and 2 is longitudinal.

Packet 8 has 9 considerably displaced seeds showing their flat sides and there are some seeds beneath others. A separate seed above and a group of 3 on the right may belong to this packet.

DISCUSSION

Thomas' specimen is the only block showing *Amphorispermum* on its surface but there is evidence that seed packets occur

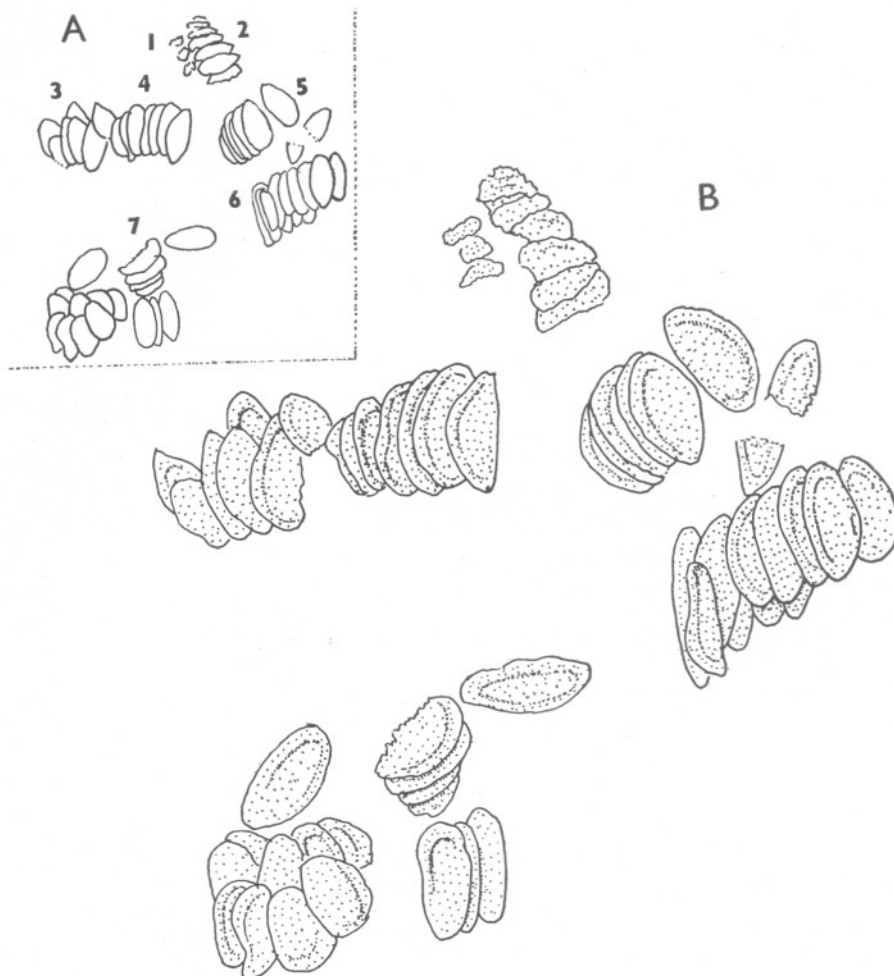


TEXT-FIG. 1—A. Outline drawing of the seeds visible in Pl. 1, fig. 1, omitting plant fragments considered extraneous. One of the seeds in the bottom left group shows its micropyle (black) $\times 11$. B. Diagram of the compression of an *Amphorispermum* seed, based on Walton, 1936. The matrix is compressed to $1/3$, the solid substance of the testa to $1/20$, the seed contents have vanished. The originally elliptical seed has collapsed into its mould in the matrix beneath, the matrix above has followed. The lower surface is weakly convex and shows cell walls as low ridges, the upper surface is weakly concave, it scarcely shows cell walls but the thickened edge forms a rim. For simplicity the number of surface cell is reduced and their walls are exaggerated. There is no lateral movement apart from small shear distortions which are omitted.

elsewhere. Many bulk macerations of Yorkshire Bajocian rocks have yielded *A. pullum* seeds but usually just a few from a kg of rock and I believe that these few lay separately in the matrix, but three localities each gave a pair of seeds adhering by their flat sides. These happen to be localities rich in species. They are Hasty Bank near the base of the Lower Deltaic (prepared by C. Hill), the Middle Deltaic Gristhorpe Bed and the Middle Deltaic Cloughton Solenites Bed, the two last being classic localities of nineteenth century collectors. In none of these are *A. pullum*

seeds abundant, many macerations gave none and the richest less than 10 per kg. Mere chance would scarcely give seed pairs.

I do not discuss the morphology of Thomas' specimen considered as a fructification because I am uncertain that it is a fructification. I have, however, considered the possibility that the seeds in their packets were connected by tissue and that the packets were connected to one another by further tissue but that this tissue was soft and rotted away or was consumed by animals which at the same time disturbed some of the seeds.



TEXT-FIG. 2 — A. Simplified diagram of the seed packets of B, numbered as described in the text. B. Outline drawing of the seeds exposed in transfer (Pl. 2, fig. 3) but photo reversed for comparison with Text-fig. 1. One of the seeds of packet 4 shows its micropyle (black). Several seeds show compression borders $\times 11$.

Early oxidative decay certainly occurred in the matrix of Thomas' block as in much of the Gristhorpe Bed. The associated *Ctenis* fragments are just light brown cuticle, all their mesophyll has vanished and their veins are merely darker streaks. Tissue connecting the *Amphorispermum* seeds could have vanished but I am indebted to Dr Krassilov (by letter) for a different idea, that the specimen was not a fructification damaged by small animals but seeds assembled by an animal (such as a caddis fly larva, Ephemeroptera). I have seen caddis cases armoured with small seeds, sometimes rather neatly, but never packed side to side.

I bear this idea in mind; it is an additional reason for not discussing the morphology of the whole fossil.

Some new facts are available about the seeds. Though I had earlier studied Gristhorpe Bed seeds extracted by water maceration and undamaged I had not noticed that there is often a difference between their flat sides. One side is slightly convex, shows no marginal rim and its surface is strongly pitted because epidermal cell walls stand up. The other is slightly concave, has a marked marginal rim and the epidermal cells are less well-marked. I consider that the two flat sides were originally

exactly alike but a difference was imposed by the strong compression of their tissues in a less compressible fine-grained matrix (Walton, 1936). The diagram (Text-fig. 1B) illustrates the effects but I point out that since there is no record of how the block faced in the bed there is no proof that the convex surface faced downward.

Amphorispermum is so like a *Caytonia* seed that there was at first doubt whether it should be distinguished but now after nearly 50 years we know more differences. There is no general difference in size but the substance of the *Caytonia* testa is thicker. The outer cuticle of the testa in *Amphorispermum* though not thick, is more robust than in *Caytonia* the top of the nucellus is often raised but flat in *Amphorispermum*. The inner cuticle named the 'spotted layer' is better developed in *Amphorispermum* where it is occasionally detachable as a cutinised membrane. Its nature is unknown, it is not the cutinised lining of a single integument because it overlaps the micropylar canal which ends blindly below. In *Caytonia*, occasional seeds show endosperm cell contents (as resinous blocks), nothing of the kind has been seen in *Amphorispermum*. Above all, in *Caytonia*, pollen grains are often to be seen in the micropyle and occasionally in some sort of cavity at the top of the nucellus. I have never seen a pollen grain in the micropylar canal of *A. pullum*, but Harris (1932, pp. 15, 17) states that 'badly preserved spores' were present in certain of the Greenland *Amphorispermum* seeds. I cannot exclude the possibility that pollen may be concealed in a cavity in the dark and confused cell walls of the top of the nucellus.

Thus the differences are relative or inferences. The points of agreement are very numerous (see Harris, 1958, p. 93) for the fullest account of the *Caytonia* seed and far closer than with any other seed so far described. But clearly if Thomas' fossil is truly a fructification it is very different from *Caytonia*, though possibly not so different as to exclude comparison.

THE LEAF OF THE *AMPHORISPERMUM* PLANT

A main aim of my palaeobotanical work has been to link separate fossil organs. I have failed to do this for *Amphorispermum*.

When describing the Greenland specimens I concluded that they and the *Selaginella*-like megaspores that accompanied them were an extraneous element in their plant bed not belonging to the plants represented by leaves. This may be true also for the Yorkshire *A. pullum* (Harris, 1932, p. 14; 1964, p. 28).

But if Thomas' specimen is a fructification of delicate construction it could not have withstood the rough treatment I had envisaged, decay on a forest floor and then transport by heavy rain to a river before ultimate burial in a delta pool. Even the seed pairs suggest rather local origin and this encourages a fresh search for the leaf; it must be search with an open mind because there is no leaf classified as a *Caytonia*-plant ally common to Yorkshire and Greenland apart from *Sagenopteris* species, already assigned to *Caytonia* itself.

The guiding principles are:

1. The four known species of *Amphorispermum* are taken to belong to a natural genus, so their leaves should be a single genus.

2. This genus should have two species in the Greenland Rhaetic, sometimes at least associated with *A. ellipticum* and *A. rotundum* and one species in the Lower Lias associated with *A. major*. But, experience with *Caytonia* and *Sagenopteris* in bulk-macerations shows that we should tolerate separate occurrences.

3. The leaf must not be one firmly placed in an unlikely family for instance the conifers nor one which I feel confident is already linked with a different seed.

Three genera only of leaves fit these principles; *Ctenis* the likeliest, then *Raphidopteris* Barale (formerly *Stenopteris*) then *Ptilozamites* and *Ctenozamites* which I take for this purpose as one genus. All three are provisionally classified and no seeds have been assigned to them. *Ctenis* has all along been taken as a Cycad the other two are included in the vague class, the Mesozoic Pteridosperms.

The case for *Ctenis* — In the Greenland Rhaetic, *Ctenis nilssoni* Nathorst and *C. minuta* Florin are sometimes associated with both *A. ellipticum* and *A. rotundum* but in beds rich in other species. They often occur separately. In the Lower Lias there is *C. stewartiana* which in one rich bed is associated with *A. major*. This is

not impressive, but if it were shown for the Swedish Rhaetic where all three species of *Ctenis* occur, that the matrix contained corresponding seeds it would be rather impressive.

In the Yorkshire Bajocian *Ctenis falcata* L. & H. (= *sulcicaulis* Phillips) is widespread, a similar species *C. kaneharai* is less common except locally. The only example known of locally abundant seed and leaf fragments is on Thomas' Gristhorpe block but I consider in particular the other two localities where seed pairs are known from bulk macerations. These are Hasty Bank, where in some layers *C. kaneharai* is abundant and at Cloughton Wyke where *C. falcata* is locally common. There are several localities where *Ctenis* leaf fragments and *A. pullum* were found in the same bulk maceration but far more localities where they were not found together. There are no records of local abundance in particular macerations. If the association of *A. pullum* with *Ctenis kaneharai* at Hasty Bank and of *C. falcata* with it at Gristhorpe represent original connection then *A. pullum* would be composite, the similar seeds of two species.

The case for *Rhaphidopteris* — This case is weaker because in the Greenland Rhaetic there is just one rare species *R. astartensis* but there is another rare leaf named *Andrupia stenodonta* which might be closely allied. Each occurs in a rich bed which includes the one or both of the seeds. In the Lower Lias there is one rather commoner leaf, *R. dinosaurensis* which is associated with *A. major* in one locality.

In Yorkshire *R. williamsoni* is rather widespread and locally common and does occur in the three localities which gave seed pairs and I have a note that in one Gristhorpe maceration abundant fragments of *R. williamsoni* occurred with *A. pullum*. The case is stronger for the Yorkshire than for the Greenland species.

The case for *Ptilozamites* + *Ctenozamites* — This is the weakest because there are too few species of leaves in Greenland. In the Greenland Rhaetic *P. nilssoni* is common and is associated in several localities with one other or both seeds. But there is no other leaf of this group and in the Lower Lias nothing of the kind is known though *Ctenozamites cycadea* occurs elsewhere. In Yorkshire *Ctenozamites* occurs widely, at least as fragments, *C. cycadea* at Hasty Bank and *C. leckenbyi* in the Gristhorpe but not Cloughton. No close association has been noted anywhere.

I mention these possibilities which arise from field associations as ones to be borne in mind. I expect that suitable bulk macerations done systematically in other regions might yield *Amphorispermum* seeds and repeated association with a leaf genus in an otherwise different flora would indeed be impressive. It may be recalled that the case made by Thomas for linking *Caytonia* with *Sagenopteris* at first failed to convince a good many palaeobotanists but they were convinced when the same association was noted in other localities, some of them remote from Yorkshire and in floras of different age.

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EXPLANATION OF PLATES

PLATE 1

1. Part of the original block after some of the matrix has been degaged, photo under oil. × 8.
- 2, 3, 4. Views of a broken packet lying detached in the transfer liquor. The packet has two sets of seeds inclined at an angle to one another. Figs. 2 and 3 are the same but with different lighting,

Fig. 4 is the other side and shows compression borders. × 16.

PLATE 2

- 5, 6. A broken packet from the transfer liquor, seen from two sides. The seed on the right of fig. 6 has a strong compression border. × 16.
7. Transfer of original specimen. × 8.

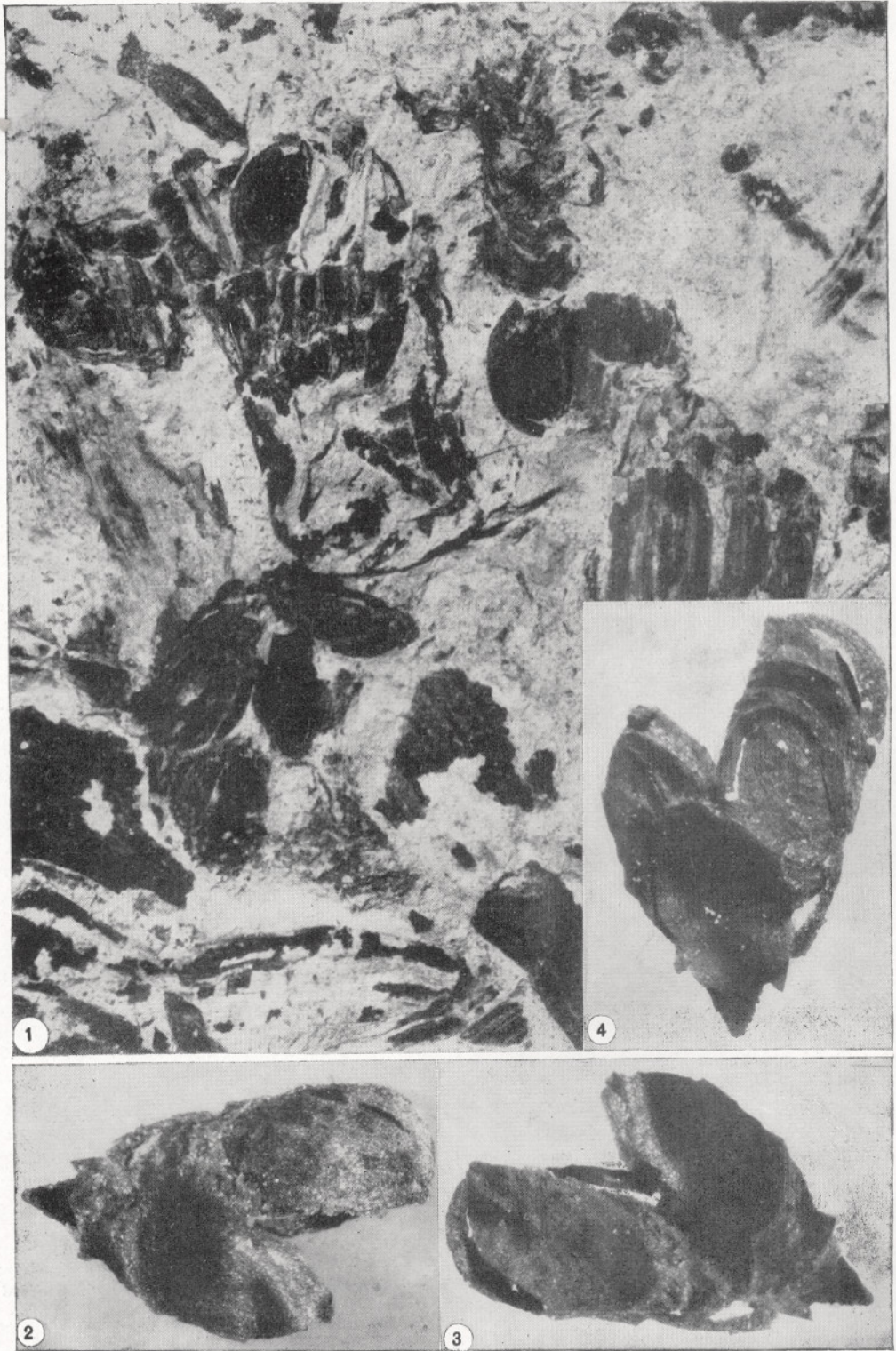


PLATE 1

