
Oxroad Bay

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Highlights

Oxroad Bay has yielded a wide variety of plant petrifications that give a remarkable insight into Early Carboniferous plants, particularly among the lycopsids, sphenopsids and pteridosperms. They are yielding the first rigorous whole-plant reconstructions for the Early Carboniferous, as well as establishing details of the plant communities and their environments. This is clearly a palaeobotanical site of international importance (Figure 5.16).

Introduction

This remarkable palaeobotanical locality in Tournaisian volcanoclastic strata on the coast near North Berwick (Figure 5.17), Lothian Region [NT 599 848], was discovered in 1930 by W.T. Gordon, who provided the earliest accounts of its plant fossils (Gordon, 1938, 1941). P.D.W. Barnard then applied the rapid acetate peel technique to the petrifications collected by Gordon. His doctoral thesis (Barnard, 1960a) resulted in several publications (Barnard, 1959, 1960b, 1962). Barnard's work prompted A.G. Long to collect a considerable amount of new material from the site (276 new blocks by 1976 — Long, 1977b), described in a series of important studies (Barnard and Long, 1973, 1975; Long, 1962, 1975, 1976a, 1977a, b, 1979b, 1984, 1986, 1987). Alvin (1965) described a new lycopsid from here, and Alvin, (1966) and Pettitt (1969) undertook maceration studies on lycopsids and pteridosperms respectively. Most recently, the site has been investigated by R.M. Bateman, G.W. Rothwell and A.C. Scott, who have integrated palaeobotanical (including maceration and SEM analyses) and sedimentological work. Their main aims have been to reassess the diversity of dispersed organs, reconstruct them into biologically meaningful plants, and establish details of plant communities and their environments of growth and deposition. The project has resulted in the collection of a further 590 blocks containing petrifications, together with numerous impressions. Some of the results are summarized by Bateman (1988, 1991, 1992), Bateman *in* Cleal (1991), Bateman and Rothwell (1990) and Bateman and Scott (1990).

Description

Stratigraphy

The Oxroad Bay sequence is about 38 metres thick and belongs to the North Berwick Member of the Garleton Hills Volcanic Formation ((Figure 5.18); McAdam and Tulloch, 1985; Davies *et al.*, 1986). Its complex sedimentology is discussed by Scott and Rex (1987), Bateman (1988; *in* Cleal, 1991) and Bateman and Scott (1990). The sediments are reworked volcanoclastics deposited along the margins of an active volcano. The plant fossils occur mainly on several discrete bedding-planes, each representing a distinct terrain. Three of these were dominantly lacustrine, the fourth volcanically-induced mass-flow. Palynological evidence suggests that the strata are upper Tournaisian (Tn3, Upper Courceyan — Scott *et al.*, 1984), although some of the plant megafossils are more characteristic of the lower Visean (Bateman, 1988, Appendix 4).

Palaeobotany

All but the most recent species list published for this locality (Barnard and Long, 1973; Long, 1984; Scott *et al.*, 1984) included taxa identified from loose blocks, which were transported into Oxroad Bay from the nearby Castleton Bay and Gin Head plant beds (described by Scott and Galtier, 1988; see also (Figure 5.17)). The following list of petrifications is based on material recognized as *in situ* by Bateman (1988) and Bateman and Rothwell (1990), although it uses a different supra-generic nomenclature.

Lycopsida:

Oxroadia gracilis Alvin

O. conferta Bateman

Equisetopsida:

Protocalamites longii Bateman

Protocalamostachys farringtonii Bateman

Filicopsida:

Cladoxylon cf. *waltonii* Long

Stauropteris cf. *berwickensis* Long

Gymnosperms:

Amyelon bovius Barnard

Tetrastichia bupatides Gordon

Bilignea cf. *solida* D.H. Scott

Eristophyton beinertianum Zalessky

Buteoxylon gordonianum Barnard and Long

Triradioxylon primaevum Barnard and Long

Oxroadopteris parvus Long

Calathopteris heterophylla Long

aff. *Tristichia ovensii* Long

Lyginorachis waltonii Calder

Lyginorachis sp. nov.

Calathospermum fimbriatum Barnard

Pullaritheca longii Rothwell and Wight

Salpingostoma dasu Gordon

Dolichosperma cf. *sexangulatum* Long

Tantallasperma setigera Barnard and Long

Hydrasperma tenuis Long

cf. *Spbaerostoma* sp. nov.

Stamnostoma oliveri Rothwell and Scott

cf. *Eurystoma burnense* Long

Eosperma oxroadense Barnard

cf. *Eccroustosperma langtonense* Long

Deltasperma fouldenense Long

cf. *Telangium* sp.

cf. *Melissiotheca* sp.

Two species of lycopsid megaspore have also been described (Alvin, 1966). Bateman (1988) recognized at least eight other (probably new) species of petrifications from Oxroad Bay that have yet to be named. He also described, but did not name, several adpression taxa, including a lycopsid (stem), a probable filicopsid (stem and foliar organ) and pteridosperms (one stem, two petioles, four foliar organs, four ovules and one pollen-organ).

Interpretation

According to Bateman and Scott (1990) the vegetation was growing in a hostile, volcanic environment in which the substrate was unstable. It resulted in a patchwork of subcommunities that consequently yielded an unusually wide range of plants.

Oxroadia axes are distinguished from most pene-contemporaneous lycopsids by their consistently small size and prominent protoxylem strands (Figure 5.5) and (Figure 5.19)b. *Paurodendron* is similar but has unbranched vasculature in its rootstock and much smaller tracheids in the central metaxylem of the axes. Bateman (1992) and Bateman *et al.* (1992) argued that *Oxroadia* and *Paurodendron* are small-bodied lepidodendrids derived by pedomorphosis from relatively primitive arboreous species. Bateman recognized two form-species each of stems, strobili and megaspores (*Setispora*), and reconstructed them to form two whole-plant species of *Oxroadia*. These two lycopsids are mutually exclusive at Oxroad Bay, both stratigraphically and (probably) ecologically. Together with *Protocalamites longii* (Bateman, 1991), they are of particular interest as the first fully reconstructed Lower Carboniferous plants.

Alvin's (1965) original description of *Oxroadia gracilis* Alvin was based on a loose block containing a strobilus, seven megaspores and about 12 axes. Additional loose-block material from both here and Berwickshire was described by Long (1971, 1986) to provide details of the leaf bases and rhizomorphs. A further several hundred axes and 43 strobilus fragments from Oxroad Bay were used by Bateman (1992) to reconstruct the bizarre 'pseudoherbaceous' gross morphology of the plant, which possessed a very short stem, strongly and basally concentrated secondary thickening and wide-angle axial dichotomies that suggest a scrambling mode of growth. The leaves were ligulate but lacked sophisticated abscission zones (details of their anatomy are shown in (Figure 5.20)a,c). The rhizomorph resembled a small, compact *Stigmaria* (Long, 1986; Bateman, 1992). The strobili were c. 120 mm long, of the bisporangiate *Flemingites*-type (cf. Brack-Hanes and Thomas, 1983), and were probably borne upright. The megasporangia typically contained four megaspores of the *Setispora subpalaecristata*-type with prominent, anastomosing laesural crests and c. 60 µm-long spines (Alvin, 1965, 1966; Spinner, 1984; Bateman, 1988, 1992).

Oxroadia conferta has a similar rhizomorph, but the vegetative axes exhibit fewer protoxylem strands and more closely-spaced branching (Bateman, 1988, 1992). The single known strobilus was shorter (c. 30 mm long) and its sporangia contained more megaspores (?16) of smaller diameter ((Figure 5.20)d). Dispersed megaspores of this type were described as '*Triletes pannosus*' by Alvin (1966), and later reclassified as *Setispora pannosa* by Spinner (1984). They have coarser, more profoundly fused laesural fimbriae, and longer (c. 200 µm) spines than the megaspores of *O. gracilis*. All of the aerial organs of these two *Oxroadia* species can be distinguished, and they are mutually exclusive at individual stratigraphical levels within the Oxroad Bay sequence (Bateman, 1992). This almost certainly reflects an early example of ecological control on the spatial distribution of two closely-related species.

Stems of a third lycopsid were described by Barnard (1960a) as cf. *Paurodendron*; small fragments occur sparsely throughout the sequence here (Bateman and Rothwell, 1990). The xylem lacks wood and the stele is deeply incised into

7–10 rounded lobes. It thus resembles *Asteroxylon* (from the Lower Devonian Rhynie Chert — see Chapter 4) and *Leclercqia* (Banks, 1960; Grierson and Bonamo, 1979), rather than supporting Barnard's comparison with *Paurodendron*.

Equisetopsida

Petrified equisetopsid remains were first reported here by Bateman (1988). Vegetative axes were named *Protocalamites longii* and reproductive structures *Protocalamostachys farringtonii* (Bateman, 1991). They represent a single whole-plant species with short, slender stems. The tuberoid stem bases generated dense root-balls and were interconnected by rhizomes. The woody stems subtended at least one order of branching and bore repeatedly dichotomizing leaves. Strobili were probably small, with three vertical rows of paired sporangiophores. The sporangia were small and the plant heterosporous, this being the earliest evidence of heterospory amongst the sphenophytes (Figure 5.19)d. The thick-walled megaspores vary greatly in diameter from 100–320 µm. They resemble *Protocalamostachys pettycurensis* Chaphekar (1963) more closely than *P. arranensis* Walton (1949b).

Filicopsida

Two filicopsid species have been reported from here (Bateman, 1988; Bateman and Rothwell, 1990). *Cladoxylon* cf. *waltonii* Long (1968b) is represented by a few polystelic stem bases that are greatly expanded and exhibit weakly-developed secondary xylem. Other stem fragments are smaller than the largest petiole-like primary branches, which are adaxially concave and appear to undergo initial equal dichotomies. The more distal branches exhibit typical *Hierogramma*-type anatomy and bear pinnae with clepsydropsid vascular traces. Possible stem and foliar correlatives occur in the adpression assemblages, and resemble those of *Cladoxylon scoparium* (Leclercq, 1970) and *Pseudosporochnus nodosus* (Leclercq and Banks, 1962). These cladoxylalean fragments re-assemble to form a short, stocky, infrequently branched, upright plant.

Several rachises with a characteristic four-lobed stele have been identified as *Stauropteris berwickensis* Long (1966). Also tentatively placed in this species was a single fragment of a larger axis with a five-lobed stele. No filicopsid reproductive organs have been found at Oxroad Bay.

Pteridosperms

There has been much speculation concerning possible whole-plant restorations of pteridosperms from the assemblages of isolated, petrified organs at Oxroad Bay. A hypothetical *Calathopteris–Calathospermum–Salpingostoma* plant postulated by Long (1976a) is in danger of becoming enshrined in the literature as a genuine reconstruction (cf. Retallack and Ditcher, 1988). Other postulated vegetative-reproductive (stem-ovule) correlations were *Buteoxylon* with *Tantaloosperma* (Barnard and Long, 1973), and *Tetrastichia* with *Eosperma* (Barnard, 1959, 1960a). Unfortunately, these hypotheses are based only on histological similarity and comparisons with preconceived bauplans. The abundance of pteridosperm organs of all types at Oxroad Bay permits an enormous number of theoretical combinations.

More recent studies (Bateman, 1988; Bateman and Rothwell, 1990) have yielded much information on how to interpret associations of organs from different exposures and different horizons within exposures, thus reducing the number of likely combinations of organs. Individual plants are being reconstructed by organic connection, though the most difficult correlation (megasporangiate and microsporangiate reproductive organs to stem via petiole) has yet to be achieved unequivocally for any Lower Carboniferous pteridosperm. However, sufficient evidence has accumulated to suggest that five or six species of whole plant were present. This is more consistent with the numbers of petioles (4), pollen-organs (4) and ovulate cupules (4) currently recognized at Oxroad Bay. The reported number of taxa of stem (9) has probably been inflated by the use of different names for different ontogenetic stages of the same species (Long, 1984; Wight, 1987; Bateman and Rothwell, 1990). Despite many previous assertions to the contrary, all of these reconstructed plants will probably prove to be lagenostomean. The large number of recorded isolated ovules (10) probably reflects greater dispersal potential of disseminules (Bateman and Rothwell, 1990; Bateman and Scott, 1990; Bateman in Cleal, 1991). In the absence of an unequivocal correlation between them, the following discussion will treat each of the pteridosperm organ-types separately.

Such evidence has stimulated ideas concerning early cupule organization and structure (Matten and Lacey, 1981), the reproductive biology of early pteridosperm ovules (Andrews, 1940; Walton, 1954; Smith, 1964), and the ontogeny of these ovules (Bateman, 1988; Rothwell and Wight, 1989). An important result of this work has been the development of the 'hydrasperman reproduction' concept, in which pollination was facilitated by an elongate extension of the pollen chamber wall (the lagenostome or salpinx) rather than by a micropyle formed by the integument, and the presence of a specialized structure (the central column) that sealed the pollen chamber after fertilization had occurred (Rothwell, 1986). This work also prompted the controversial ideas on angiosperm origins, put forward by Long (1966, 1975, 1977b, 1985; see discussion on the Whiteadder, above).

Rooting structures

Barnard (1962) attributed certain gymnosperm roots to the form-species *Amyelon bovius* Barnard. The diversity of pteridosperms at the locality obscures their affinities.

Stems

Bateman and Rothwell (1990) list nine pteridosperm stem species, which probably represent five or six whole-plant species. The first four are clearly distinct:

Tetrastichia bupatides Gordon (1938) has a distinctive, cruciform protostele ((Figure 5.19)a). They are mostly small stems, probably from shrubby plants, and only the largest exhibit secondary xylem (Gordon, 1938; Barnard, 1960a). Dichotomously branching, *Lyginorachis*-like petioles with few abaxial corrugations were borne in four vertical columns of sub-opposite pairs (Gordon, 1938; Wight, 1987). The fronds have been compared with *Sphenopteris affinis* Lindley and Hutton (Gordon, 1938; Andrews, 1948) and *Adiantites*, but the evidence is equivocal. Elsewhere, the form-genus *Tetrastichia* has only been reported from the lower Tournaisian at Ballyheigue, Irish Republic (Matzen *et al.*, 1984b).

Billignea cf. *solida* Scott, consisting of stems up to 70 mm in diameter with a distinctive pith of short tracheids, was first reported by Long (*in* Scott *et al.*, 1984). Attached lyginopterid petioles reported by Bateman (1988), confirm the lagenostomean affinities of this pteridosperm tree.

The assignment of *Eristophyton beinertianum* Zalesky to the lagenostomean pteridosperms similarly resulted from studies of Oxroad Bay material. Originally described as calamopityalean by Gordon (1941), it was first recognized as *Eristophyton* by Barnard (1960a). Long (1987) demonstrated that the stems reach 100 mm in diameter and possess a parenchymatous pith that extends into the lateral branches. Associated *Lyginorachis waltonii* petioles are large, with several stelar corrugations that separate near the base; Long (1987) suggested correlation with the adpression frond genus *Diplothemema*.

Stem I of Bateman and Rothwell (1990) resembles a similarly unnamed pteridosperm axis with three sympodia recovered from Visean strata at Kingswood End by Scott *et al.* (1986). A single short length of narrow fusainized axis exhibits parenchymatous pith in intimate association with five mesarch sympodia. They are surrounded by a secondary xylem cylinder of narrow tracheids interspersed with abundant small, uniseriate rays. In the absence of attached petioles, its familial affinities are unclear.

It is uncertain whether *Buteoxylon gordonianum* Barnard and Long represents an additional whole-plant species or should be synonymized with the taxa listed below. The single specimen described from here by Barnard and Long (1973, 1975) was the apical portion of a small stem with a mixed pith and numerous attached petioles. The petioles possessed single protoxylem strands in the centre of both arms of the characteristic Y-shaped stele, and apparently did not dichotomize. A much larger axis of this species with well developed wood was reported by Bateman and Rothwell (1990). Barnard and Long (1975) used *Buteoxylon* and *Triradioxylon* to erect a new family, the Buteoxylonaceae, which they suggested might belong to the progymnosperms. The discovery of protostelic, triradiate stems associated with pteridosperm ovules (Rothwell and Erwin, 1987) renders this less probable.

Although originally described as separate genera, the four remaining pteridosperm stem taxa probably belong to only one whole-plant species (Bateman and Rothwell, 1990; Rothwell and Scott, 1992b). Although not yet fully reconstructed, it

has been tentatively interpreted as scrambling or lianascent.

1. *Oxroadopteris parvus* Long (1984) is a small axis with a pith of elongate tracheids. It bears *Lyginorachis*-type petioles that bifurcate close to the stem and possess few stelar corrugations.
2. *Calathopteris beterophylla* Long (1976a) is also small, has a mixed pith and bears two types of petiole. The more numerous, *Lyginorachis*-type petioles have few stelar corrugations and were probably vegetative. The remainder have three-ribbed xylem strands that trichotomize within the cortex of the stem, and were probably fertile (Long, 1976a).
3. Stem H of Bateman and Rothwell (1990) was ascribed to *Tristichia ovensii* by Long (1962). However, *T. ovensii* as defined by Long includes several different species of protostelic axes, and is clearly in need of revision. The Oxroad Bay stems of this type emit in 1/3 phyllotaxis *Lyginorachis*-type petioles that dichotomize close to the stem.
4. *Triradioxylon primaevum* Barnard and Long (1975) (cf. '*Aneuromyton*' of Barnard, 1960a) resembles Stem H in stelar anatomy. Attached petioles are widely spaced along the stem; each has a Y-shaped stele and a single, central protoxylem strand. Barnard and Long (1975) asserted that these petioles did not dichotomize, and were thus similar to *Rhacopteris* fronds with possible progymnosperm affinities. However, Bateman and Rothwell (1990) have shown that a dichotomy is present and that *Triradioxylon* is thus a pteridosperm.

Other foliar organs

Only four isolated, pteridospermous foliar organs have been named from Oxroad Bay (Bateman and Rothwell, 1990):

- Barnard's (1960a) *Lyginorachis* sp. A probably represents secondary racheis and therefore is not strictly comparable with the petioles that were used to characterize most other *Lyginorachis* species.
- Barnard's (1960a) *Lyginorachis* sp. B has since been identified with *L. waltonii* Calder and shown to be attached to *Eristophyton* stems (Long, 1987). It possesses dorsiventrally shallow vascular traces with several abaxial corrugations that divide into discrete bundles near the base.
- *Lyginorachis* sp. nov. of Bateman (1988) occurs in organic connection with *Biligneia* cf. *solida* Scott. It lacks sclerotic nests, and possesses vascular traces with four corrugations that remain connected at the base.
- Foliar organ A of Bateman and Rothwell (1990) encompasses a wide range of triradiate axes formerly attributed to *Tristichia ovensii* Long. They have yet to be partitioned into biologically meaningful species.

Compressed petioles and frond segments have not been successfully correlated with the more informative petrified material.

Ovulate cupules

Two types of ovulate cupule found at Oxroad Bay have generated more discussion than any other species present. *Calathospermum fimbriatum* Barnard (1960b) is a large, apparently solitary and bilaterally symmetrical cupule that is dissected into many lobes and probably contained numerous ovules. It was interpreted by Barnard (1960b) and Smith (1964a) as a modified frond borne on an apparently unbranched but otherwise *Lyginorachis*-like petiole. Long (1975) interpreted *Calathospermum* as a 'megacupule', resulting from the fusion of a pair of radially symmetrical cupules. He also argued that it is a possible precursor of the angiosperm carpel (Long, 1966, 1975, 1977b, 1985). Matten and Lacey (1981) interpreted branching of the cupule lobes distal to the basal-most dichotomy as pseudomonopodial. *In situ* ovules reported by Barnard (1960a, b) and Long (1975) resemble *Salpingostoma dasu* Gordon in pattern of organization but are much smaller; they may have been abortive. However, Bateman and Rothwell (1990) report *in situ* ovules more closely resembling *Tantalosperma setigera* Barnard and Long.

A.G. Long (pers. comm. 1988) argued that specimens with unusually long axes that appear to lack pinnae may constitute a second species of *Calathospermum* here. Study of similar compressed cupules from Oxroad Bay may help resolve this question.

Pullaritheca longii Rothwell and Wight (1989) represents cupule aggregates containing *Hydrasperma tenuis* Long ovules ((Figure 5.19)c). They compare with adpression cupules usually identified as *Sphenopteris bifida* Lindley and Hutton (Long, 1977b; Bateman and Rothwell, 1990). Identical ovules have also been reported *in Kerryia* cupules from the Irish

Republic (Matten *et al.*, 1980), which differ from *Pullaritheca* in symmetry, branching pattern and number of ovules enclosed (Bothwell and Scheckler, 1988; Rothwell and Wight, 1989). Nomenclatural instability in the past (cf. Long, 1977a; Matten *et al.*, 1975; Matten *et al.*, 1980; Matten *et al.*, 1984a) reflects reluctance to take full account of ontogenetic variation in the ovules and to treat separately the taxonomy of the ovules and of the cupules. Many of the *Pullaritheca* cupules collected by Bateman and Rothwell (1990) contained several abortive ovules, and a few contained more mature individuals (Bateman, 1988; Rothwell and Wight, 1989).

Long (1977a, b, 1979b) recognized two modes of arrangement of the cupules (paired 'hemicupules' and unpaired 'megacupules') that were both considered to represent an entire mega-sporophyll, and necessitated revision of his 'cupule-carper theory'. However, Rothwell and Wight (1989) and Bateman and Rothwell (1990) reported a gradation between these two extremes. Comparison of *Pullaritheca* with adpressions assigned to *Sphenopteris bifida* Lindley and Hutton led Long (1979b) to suggest that both bore cupules in similar fashion, as aggregates attached to the median axes of trichotomous petioles. Indeed, clusters of up to eight *Pullaritheca*-like cupules occur in adpression assemblages at Oxroad Bay (Bateman, 1988). One petrified *Pullaritheca* cupule found by Long (1977a) contained both ovules and deformed sporangia. This suggests a developmental anomaly reflecting the homologous architecture of pollen-organ aggregates that were probably borne on other trifurcating petioles of the same plant (Bateman, 1988; Bateman and Rothwell, 1990; Bateman and DiMichele, in press).

An open, frequently and irregularly dichotomous, hirsute cupule contains *Dolichosperma* cf. *sexangulatum* Long ovules (Bateman, 1988). Its branching pattern resembles that of the cupules bearing the ovule *Eurystoma burnense* (Long, 1960b, 1965).

A similarly open, but pseudomonopodially branched, cupule bears *Stamnostoma oliveri* ovules in aggregates of up to four (Bateman and Rothwell, 1990; Rothwell and Scott, 1992a).

Isolated ovules

Bateman (1988) and Bateman and Rothwell (1990) list ten species of isolated petrified ovule. All appear to be distinct, though an ontogenetic relationship between *Tantalosperma* and *Dolichosperma* is credible. Some potential correlatives occur in the adpression assemblages, notably the ovule megaspore studied by Pettitt (1969), which probably represents *Eosperma oxroadense* Barnard (Bateman, 1988).

Salpingostoma dasu Gordon (1941) is the largest known Lower Carboniferous ovule, up to 50 mm long and 6 mm wide (Bateman and Rothwell, 1990). It usually had six integumentary vascular bundles extending into lobes that project well beyond the tall, narrow lagenostome. The integument also bore large, antapically concentrated trichomes. Gordon (1941) erroneously endowed *Salpingostoma* with an atypical pollen-receiving apparatus (Rothwell, 1986).

Dolichosperma cf. *sexangulatum* was first reported from Oxroad Bay by Bateman (1988). It typically had six integumentary bundles and lobes that extend well beyond the lagenostome and was covered with evenly distributed, coarse tri-chomes. Very similar but rather smaller is *Tantalosperma setigera*, which possessed four (rarely five or six) vascular bundles, integumentary lobes that extend well beyond the lagenostome, and an even covering of coarse trichomes. Since the two are essentially distinguished only on size and number of integumentary lobes, they may conceivably be ontogenetic stages of the same species.

Hydrasperma tenuis Long was reported by Long (1977a, b, 1979b). It had 8–12 integumentary lobes that extended only slightly beyond the lagenostome, which is the widest part of the ovule. Dispersed *H. tenuis* ovules exhibit a wide range of ontogenetic variation at Oxroad Bay, and were erroneously segregated as *H. longii* by Matten *et al* (1980).

Cf. *Sphaerostoma* sp. nov. (Bateman, 1988; Bateman and Rothwell, 1990) is characterized by an integument with eight vascular bundles, but no lobes. It differs from *S. ovale* Benson (1914; see also Long, 1961b) in its thicker, denser integument and sparser, but coarser, trichomes.

The 'cf. *Sphaerostoma* sp.' of Barnard (1960a) differs from bona fide *Sphaerostoma* in having a morphologically distinct pollen chamber, and an integument that forms an open collar surrounding the lagenostome. It was therefore assigned to

Stamnostoma huttonense Long by Barnard and Long (1973; see also Rothwell, 1986). However, it differs from *S. huttonense* Long in having a smaller length:breadth ratio and papillae on the integument. Consequently, it has been referred to a new species, *Stamnostoma oliveri* Rothwell and Scott (1992a).

Cf. *Eurystoma burnense* Long has been reported by Bateman (1988). Elsewhere, Long (1966, 1969) has recognized both pre-prothallial and prothallial ontogenetic phases. Its distinctive, triangular transverse section reflects its three vascular bundles and associated wide lateral keels, which terminate as short lobes projecting slightly beyond the lagenostome.

Eosperma oxroadense Barnard (1959) has only two integumentary vascular bundles and lacks integumentary lobes; short spiny trichomes occur on some specimens. Pettitt (1969) demonstrated attachment of three abortive megaspores to a compressed functional megaspore that probably belonged to *Eosperma*.

Bateman (1988) has demonstrated the presence of cf. *Eccroustosperma langtonense* Long from *in situ* strata, the report by Long (1987) having been based on a loose block that was probably transported from nearby Castleton Bay. It has two vascular traces terminating in fairly short integumental lobes that do not extend beyond the lagenostome. Bateman (1988) observed that Oxroad Bay specimens are more strongly curved than those from elsewhere (cf. Long, 1961b, 1975), and may represent the pre-prothallial ontogenetic stage of *Campptosperma berniciense* Long (1961a).

Deltasperma foulidenense Long (1961a) was first recognized as fusainized material macerated by Bateman (1988) ((Figure 5.20)d). Two vascular strands terminate in fairly short integumental lobes that do not exceed the lagenostome. Characteristically large superficial cells cover the whole of the more convex face, and the apical region of the less convex face.

Pollen-organs

Three of the four pollen-organs listed by Bateman (1988) and Bateman and Rothwell (1990) appear to be synangiate: cf. *Telangium* sp., cf. *Melissiotheca* sp. and 'pollen-organ C'. The *Telangium*-like synangia terminate repeatedly dichotomous axes. They typically comprise eight, basally-fused, bilaterally-arranged synangia containing finely tuberculate pre-pollen. They therefore share characters with several *Telangium*-like form-genera (e.g. Eggert and Taylor, 1971; Long, 1979a; Millay and Taylor, 1979; Meyer-Berthaud and Galtier, 1986a).

The pedicellate synangia of cf. *Melissiotheca* sp. are shallowly divided into at least two lobes, each consisting of 30–100 basally-fused sporangia that are embedded in a parenchymatous cushion, and contain rugulate pre-pollen (Bateman, 1988; Bateman and Rothwell, 1990). The sporangia are smaller and exhibit less profound lateral fusion than those of *Melissiotheca longiana* Meyer-Berthaud (1986). Numerous compressed synangia from Oxroad Bay are difficult to apportion between cf. *Telangium* sp. and cf. *Melissiotheca* sp. (Bateman, 1988).

Pollen-organ C of Bateman and Rothwell (1990) is a large, hirsute, oviform organ that superficially resembles the ovulate cupule *Calathospermum fimbriatum* Barnard in size and branching pattern. Large sporangia form asymmetrical synangia and enclose dimorphic pre-pollen; the larger pre-pollen morph is considered fertile and the smaller abortive (Bateman, 1988). Similar pre-pollen has frequently been found in the lagenostome of *Salpingostoma dasu* Gordon (Long, 1975; Bateman, 1988). Pollen-organ C was incorrectly referred to cf. *Telangium* by Barnard (1960a) and subsequent workers, and should not be confused with the cf. *Telangium* described above.

Pollen-organ D of Bateman and Rothwell (1990) is a single terete branching axis terminated by a small, thick-walled sporangium. It is associated with abundant foliar organs showing similar histology. Spores found in the sporangium have sparse, blunt-tipped spines, and compare with forms found in the lagenostome of *Deltasperma* (Bateman, 1988).

General remarks

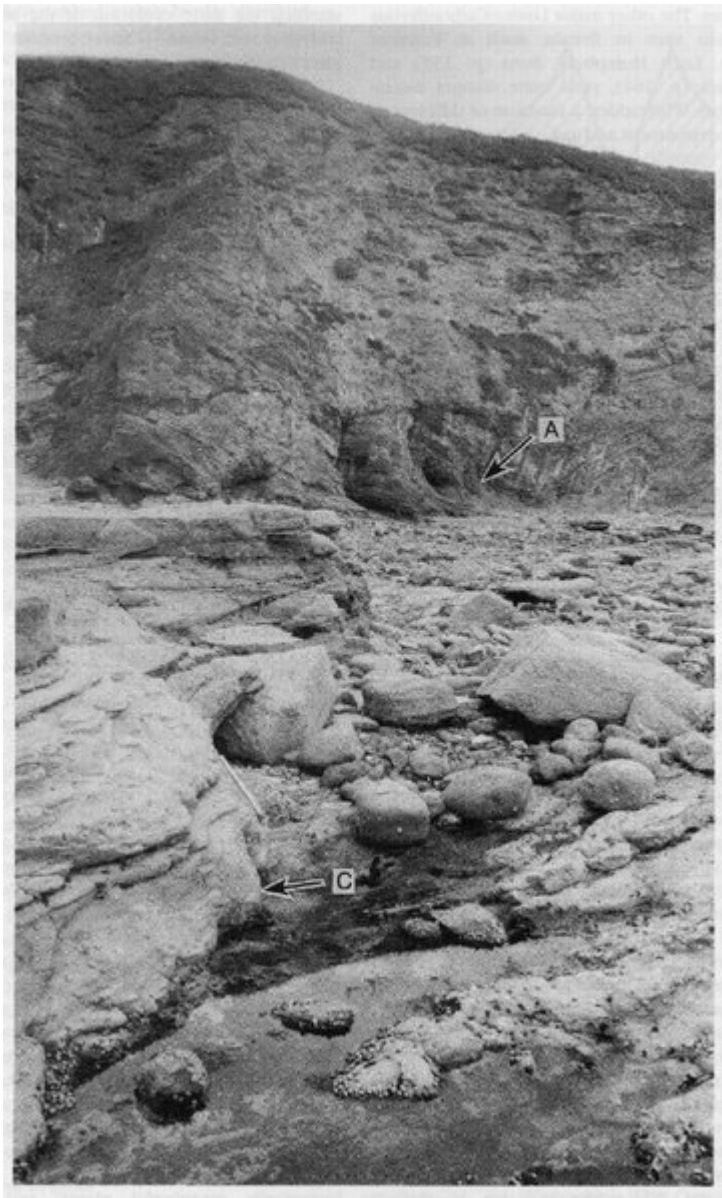
At least 11 whole-plant species of tracheophyte grew at Oxroad Bay, and these have produced one of the most diverse assemblages of Early Carboniferous petrifications. In Britain, it is second in estimated partial-plant diversity only to the Whiteadder (see above, and Scott *et al.*, 1984; Bateman *in* Cleal, 1991). Other taxonomically similar petrification

assemblages occur at nearby Castleton Bay (Scott and Galtier, 1988); the upper assemblage at Loch Humphrey Burn (see below); Kingswood (see below); and Ballyheighue, Irish Republic (Matten *et al.*, 1980; Matten *et al.*, 1984b). These occurrences vary considerably in age (Strunian to possible early Asbian), sedimentological regime and geographical location, but evidently reflect similar ecological and taphonomic constraints. However, none of the above localities matches Oxroad Bay in whole-plant diversity, or in the potential for correlating petrification, adpression and fusain fossils of the same plant organ.

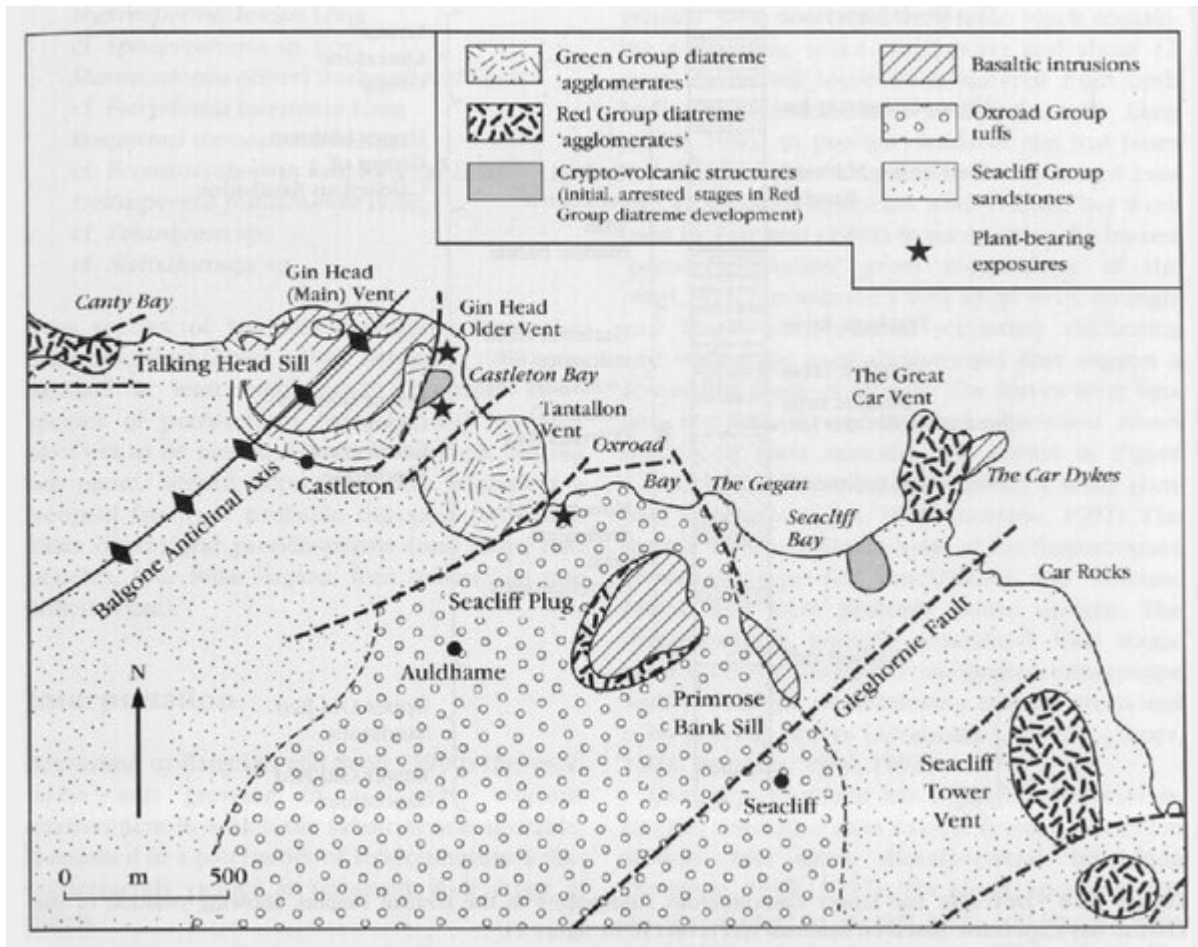
Conclusion

Oxroad Bay is one of a series of basal Carboniferous sites in southern Scotland that yield anatomically-preserved plant fossils (about 350 million years old). Taken together, they are the most important global source of information on vegetation of this age. This site is especially important for allowing the first rigorous reconstructions for Early Carboniferous representatives of these plant groups. Studies of the club-mosses and horsetails have been completed, but work continues on the more diverse (and thus more problematic) early seed plants and on the ferns. Integration of the reconstructions with palaeoenvironmental data from this unstable volcanic setting has led to recognition of several distinct plant communities. Increasing knowledge of their structure and dynamics will allow comparison with extant vegetation.

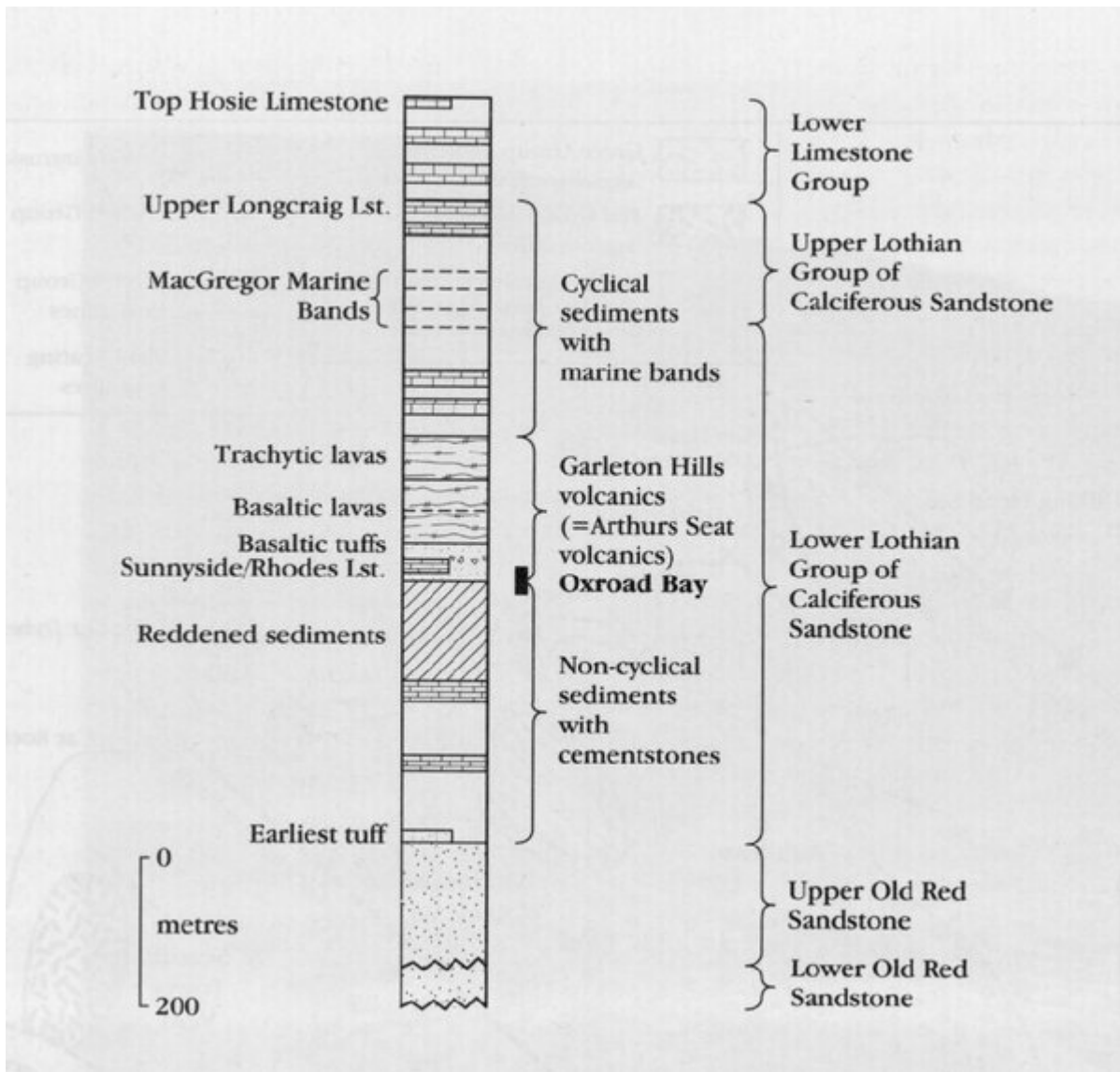
[References](#)



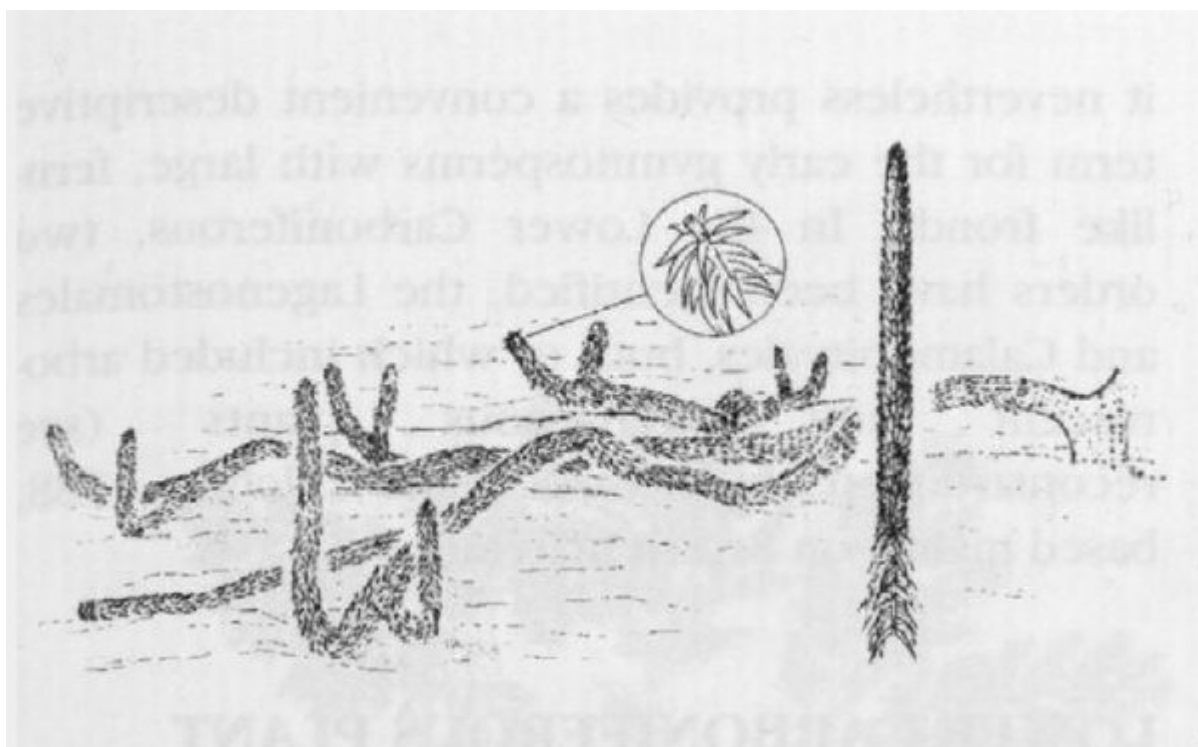
(Figure 5.16) Oxroad Bay. View south across the foreshore, with Dinantian lacustrine sediments in the foreground overlain by reworked volcanigenics exposed in the cliffs. Two of the four horizons yielding anatomically-preserved plants are shown: (A) was discovered by W.T. Gordon in 1930, (C) by R.M. Bateman in 1984. Hammer is 0.3 metres long. (Photo: R.M. Bateman.)



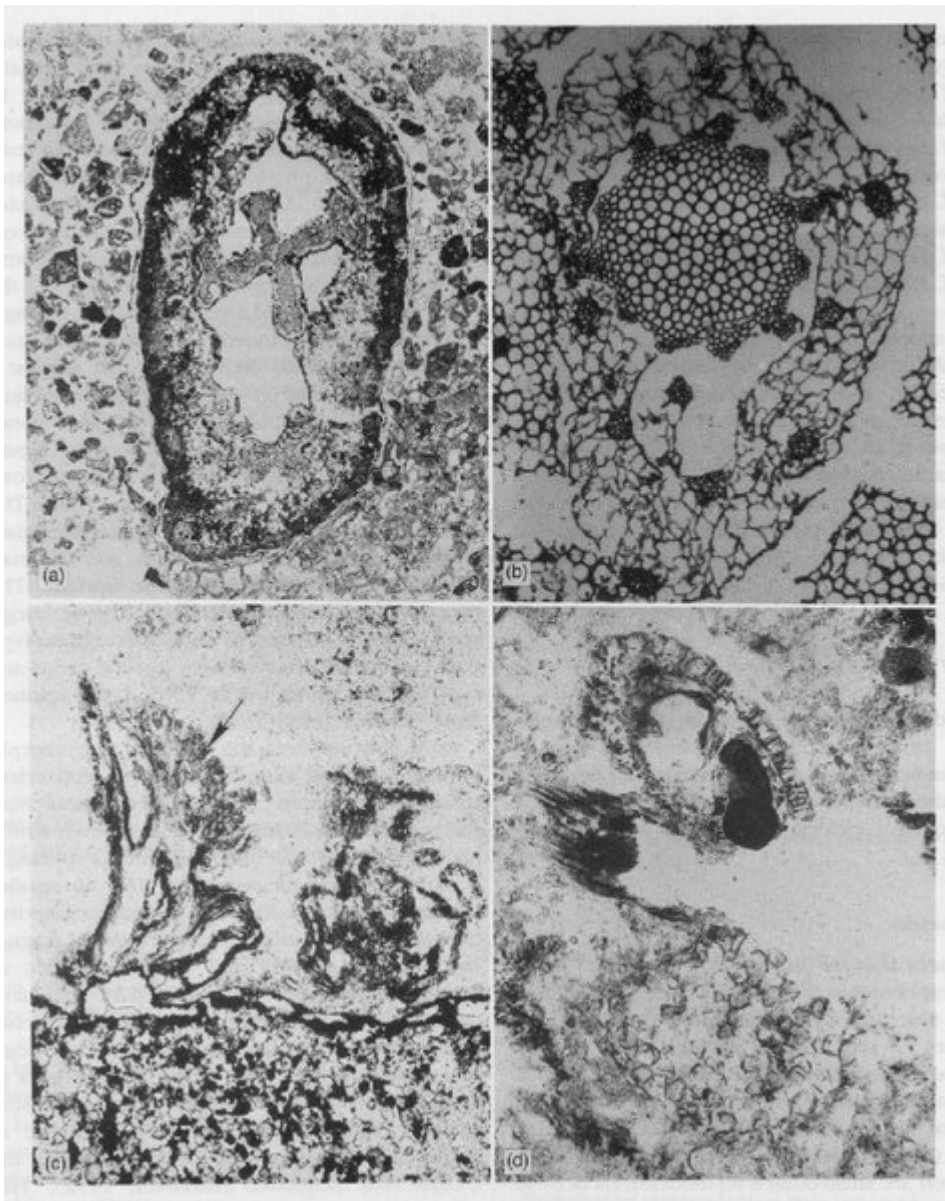
(Figure 5.17) Geological map of the Tantallon area of East Lothian, showing location of palaeobotany sites including Oxroad Bay. Based on Bateman and Scott (1990, figure 2).



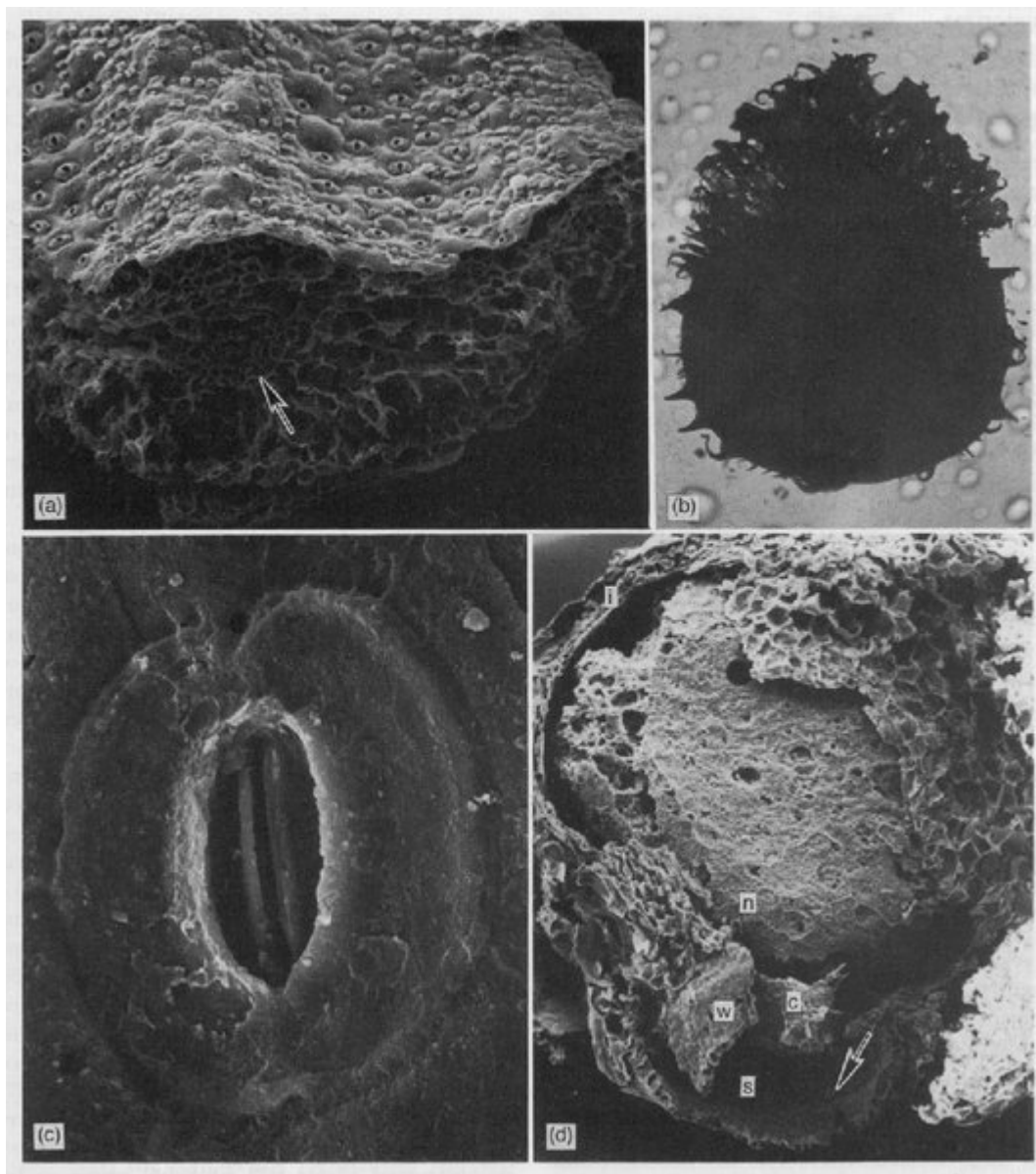
(Figure 5.18) Devonian and Lower Carboniferous stratigraphy in the Lothian Region, showing position of the Oxroad Bay exposures. Based on Bateman and Scott (1990, figure 1).



(Figure 5.5) Reconstruction of an Early Carboniferous herbaceous lycopsid, *Oxroadia gracilis*. Based on Bateman et al. (1992, figure 2D).



(Figure 5.19) Petrified plants from North Berwick Member of the Garlcton Hills Volcanic Formation (Courseyan), Oxroad Bay. (A) *Tetrastichia bupatides* Gordon. Transverse section of stem of shrubby pteridosperm, showing the characteristic four-lobed stele emitting paired leaf traces; Natural History Museum, London, Gordon Collection (holotype). x 8.4. (B) *Oxroadia gracilis* Alvin. Transverse section of a branch of the pseudoherbaceous rhizomorphic lycopsid, showing the coronate stele emitting leaf traces through the inner cortex; Bateman Collection, specimen OBD(?2.15)038bT/2. x 118. (C) *Pullaritheca longii* Rothwell and Wight cupule with *Hydrasperma tenuis* Long ovules attached to the placental margin. Rare example of a developmental anomaly in a fossil plant, where the abortive ovule to the right is normal, whereas the ovule to the left has a deformed, proliferated and nonfunctional pollen chamber (arrowed); Long Collection, Hancock Museum, Newcastle upon Tyne, specimen HM 11718. x 38. (D) *Protocalamostachys farringtonii* Bateman. Sporangiphore axis (left centre) emitting two of four sporangia, the upper being a megasporangium, the lower a microsporangium; Bateman Collection, specimen OBC084gB/5. x 71. (Photo A: G.W. Rothwell; photos B-D: R.M. Bateman.)



(Figure 5.20) Fusainized plants from North Berwick Member of the Garleton Hills Volcanic Formation (Courceyan), Oxroad Bay. (A) *Oxroadia gracilis* Alvin. Transverse section through microphyll leaf of this rhizomorphic lycopsid, showing terete vascular strand (arrowed) surrounded by mesophyll; highlighted abaxial surface shows stomata restricted to two shallow furrows (left, centre right); Bateman Collection, specimen OBD(2.17)176:CP21. x 108. (B) *Setispora pannosa* (Alvin) Spinner. Elaborately ornamented megaspore of the pseudoherbaceous lycopsid *Oxroadia conferta* Bateman; Natural History Museum, London, specimen V.52016e. x 37. (C) *Oxroadia gracilis* Alvin. Detail of stomata of leaf, showing paired sunken guard cells surrounded by putative subsidiary cells; Bateman Collection, specimen OBD(2.17)176:CP21. x 1634. (D) *Deltasperma fouldenense* Long. Platyspermic pteridosperm ovule with one half of the integument (i) removed to reveal the nucellus (n); at the bottom of the photograph is a typical apical pollen chamber; a cylindrical wall (w) surrounds the central column (c) and salpinx (s), containing a single prepollen grain (arrowed); Bateman Collection, specimen OBD(2.26)190:CP17. x 52. (Photos A, C and D: R.M. Bateman. Photo B: C.H. Shute, Natural History Museum, London.)