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REINVESTIGATION OF THE ENIGMATIC CARBONIFEROUS SPHENOPHYTE STROBILUS *CHEIROSTROBUS* SCOTT AND IMPLICATIONS OF *IN SITU RETUSOTRILETES* SPORES

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Premise of research. Cheirostrobus pettycurensis Scott is an early Carboniferous sphenophyte known only from its anatomically-preserved strobili, which bear highly dissected “sporophylls” comprising a lower vegetative part and an upper fertile part bearing inwardly facing sporangia. Since Scott’s pioneering work over 100 years ago, the genus has not been reinvestigated such that it remains poorly characterised and its systematic position enigmatic. We reinvestigate *Cheirostrobus* providing new insights into its structure, anatomy and *in situ* spores, and thereby addressing long-standing questions concerning its considerable systematic and evolutionary importance.

Methodology. Historically prepared slides of *Cheirostrobus* from museum collections were examined using transmitted light microscopy to facilitate detailed description using modern terminology, allowing more effective comparisons and interpretations.

Pivotal results. The strobilus axis comprises a stellate protostele with 9-13 protoxylem poles showing exarch maturation. Protoxylem has circular and metaxylem scalariform pitting. Main vascular bundles depart from the stele in superposed whorls and divide vertically close to the cortex, from which the lower (abaxial) daughter bundle supplies two or three bracts and the upper (adaxial) daughter bundle supplies two or three sporangiophores, with each bract subtending one sporangiophore. Individual sporangiophores have a foliar apex and typically bear four inwardly facing, longitudinally elongated sporangia, disposed in two vertical rows. *In situ* spores are homosporous, trilete, have a prominent margo with leavigate exine and range from 48–77 µm in diameter. Spores conform to the *sporae dispersae Retusotriletes incohatus* Sullivan 1964.

Conclusions. Cheirostrobus has organization similar to members of the Sphenophyllales and Calamitales; it is interpreted as a member of the Sphenophyllales that is on the evolutionary stem lineage leading to the stratigraphically younger Calamitaceae. *Retusotriletes*-type spores are reported *in situ* for the first time within sphenophytes, having previously been found within rhyniophytes, zosterophylls, trimerophytes and algae, further emphasizing its polyphletic nature and convergent spore evolution across multiple lineages. *Retusotriletes incohatus* in the dispersed record ranges from the late Famennian (Devonian) to the late Viséan (Carboniferous) and is common in basal Carboniferous deposits suggesting that *Cheirostrobus* (or closely related plants producing the same kind of spores), had a longer stratigraphic range than was previously recognized and an earliest Carboniferous acme.

Keywords: Cheirostrobus, Sphenophyta, Carboniferous, Cheirostrobales, fertile appendage, sporangiophore, homospory, palynostratigraphy

Introduction

In 1896 D. H. Scott established *Cheirostrobus pettycurensis* Scott to accommodate anatomically preserved strobili from the Mississippian (lower Carboniferous) Pettycur Limestone in southern Scotland (Scott 1896). He considered these strobili to have features that were a mixture of characters typical of the Sphenopsida and Lycopsida (Scott 1896). Although Scott proceeded to publish in close succession two further accounts of the genus that considered its occurrence and reviewed its botanical affinity (Scott 1897*a*, 1898), it was not until his classic 1897*b* paper that for the first time *Cheirostrobus* was illustrated and described in detail (Scott 1897*b*). According to Scott (1897*b*), *Cheirostrobus* comprised a polyarch stele with 9–

12 ribs, each rib having an exarch protoxylem pole with centripetal development that produced tightly spaced, whorled “sporophylls”. Scott’s “sporophylls” each comprised a lower vegetative lobe and an upper fertile lobe, with both vegetative and fertile lobes dividing in three lateral segments organized in such a way that individual vegetative segments subtend a single fertile segment. Individual vegetative segments (sometimes termed sterile segments, e.g. Scott 1897*b*, pg. 3) comprised mesophyll laminae that are horizontal for the most part but have two projecting extensions of which the upward orientated extension is longer than the downward projecting extension (Scott 1897*b*, pgs. 2, 20). Each fertile segment comprised a peltate sporangiophore apex bearing two rows of sporangia that contained numerous *in situ* circular, trilete spores. Comparisons presented by Scott (1897*b*) ultimately led to conclusions that *Cheirostrobus* belonged within the Sphenopsida where it was distinct from all other members of the group. Scott concluded that it had greatest similarity with the stratigraphically younger Carboniferous genera *Sphenophyllum* and *Calamostachys*.

Although Scott’s (1897*b*) account was detailed and extremely well-illustrated for its time, it is often hard to comprehend exactly what Scott meant in relation to what he was describing; the terminology used was often inconsistent and in places is overly complicated, making it difficult to understand. Overall, Scott (1897*b*) considered the “sporophylls” of *Cheirostobus* to be “remarkably complex, more so than any strobili of Cryptogram at present known” (Scott 1897*b*, pg. 3). By contrast, Sporne (1962) disagreed, remarking that the organization of the vascular bundles to supply bracts and sporangiophores led “some morphologists to suggest a more complicated interpretation of the cone structure than is really necessary” - a sentiment with which we wholeheartedly agree.

Present understanding of *Cheirostrobus* is to a large extent based on the excellent diagrammatic reconstruction of the strobilus provided by Scott 1897*b* (pg. 7) that has been widely reproduced subsequently in paleobotany text-books (e.g. Seward 1910; Stopes 1910; Sporne 1962; Boureau 1964; Ogura 1972; Meyen 1987). However, the accuracy of this reconstruction remains uncertain, as do any systematic conclusions based upon it. Many features of the strobilus are unknown, and in particular, detailed morphology of its spores are unknown, preventing more comprehensive comparison. Potonié (1962, 1965) and later Chaloner (1967) placed its spores in the dispersed spore genus *Calamospora* based on analysis of photographic evidence from Scott's (1898*b*) paper, but Potonié (1970) subsequently examined specimens with *in situ* spores and considered that they conformed to the genus *Punctatisporites* (Potonié 1970; Balme 1995).

The information presently available on *Cheirostrobus* has made comparisons with other plants difficult, obscuring its systematic relationships. Scott (1897*b*) concluded that *Cheirostrobus* belonged within the Sphenophylls, whereas Seward (1910) placed it within the sphenopsid Family Cheirostrobeae. Sporne (1962), Boureau (1964), and Bierhorst (1971) assigned *Cheirostrobus* to the Family Cheirostrobaceae within the Order Sphenophyllales, and Ogura (1972) considered it to be the sole representative of the Family Cheirostrobaceae within the Order Cheirostrobales. Meyen (1987) concluded it probably had *Sphenophyllum* type leaves and was allied to the Bowmanitidae, and Cleal and Thomas (1995) considered it to be more closely related to members of the Bowmanitales. Taylor et al. (2009) placed the genus more loosely within the Order Sphenophyllales. As such, there is now no systematic consensus.

Since Scott's pioneering work on *Cheirostrobus* (Scott 1896 *et seq.*), the genus has not been subjected to detailed reinvestigation. As far as we are aware, additional specimens from the type locality have not been found, nor has the genus been identified from other localities globally (Rex and Scott, 1987; Cleal and Thomas, 1995). As currently characterized, *Cheirostrobus* is a distinctive but rare component of the Mississippian floras of Scotland, presently recognized from a single location and stratigraphic horizon (see below). Here we reinvestigate *Cheirostrobus* using the original materials available to Scott, and provide a redescription and diagnosis using modern terminology, enabling meaningful comparisons with other taxa. We pay particular attention to the *in situ* spores and provide details of their morphology, thereby allowing them to be identified to a *sporae dispersae* species based on up to date comparisons. We consider spore size distribution in order to test previous inferences about its homosporous reproduction (Scott 1897*b*; Bateman and DiMichele 1994), and also evaluate the biostratigraphical and geographical distribution of its *in situ* spores to assess the temporal and spatial distribution of the *Cheirostrobus* plant. Finally, we evaluate the systematic and evolutionary importance of *Cheirostrobus* within the Sphenopsida.

Materials and Methods

All specimens of *Cheirostrobus pettycurensis* were prepared historically as petrological ground thin sections (Hass and Rowe 1999) commercially by W. Hemmingway and J. Lomax and in the late 19th Century (Howell 2006). This method involves slicing rock samples containing petrified fossil plants into sections that are each then mounted on a glass slide. The reverse surface of the slide exposing the rock sample is subsequently ground away to make thin sections that vary from 40–100 μm thick, their thickness largely depending on the opacity of the plant organs to be observed. From these preparations incident light can be transmitted through the specimen to reveal cellular details under light microscopy. Although this partially destructive method can yield high-quality slides for optical microscopy, it has the disadvantage of destroying much of the fossil through the cutting and grinding processes. It is difficult to reconstruct fossil specimens prepared in this way, as the gaps between adjacent thin sections are often both substantial and irregular in thickness (Spencer et al. 2013). Reconstructing specimens of *Cheirostrobus* is further compounded by problems noted by Howell (2006), whereby slides prepared by 1were distributed amongst various museums and universities worldwide for which no inventory exists. Consequently, it is almost impossible to find adjacent slide preparations in order follow structures developing through adjacent slides and study the fossils comprehensively. We have therefore used the previously available sections rather than making new preparations that could have revealed specific features in specific positions and orientations (e.g., Spencer et al. 2013).

Beyond the material studied and figured by Scott (1897), deposited at the Natural History Museum in London (Slides SC 519 to SC 532, SC 2097 to SC 2099, SC 2748, SC 555–12 to SC 555–18, SC 555–25[a], SC 555–63, SC 555–70 to 555–72, SC 578–A, and OC 483 to OC 487), we have examined additional slides of *Cheirostrobus* at the Lapworth Geological Museum (University of Birmingham: D3/8, D3/9 (these slides represent, respectively, the slides number 555-B6 and 555-38 made by W. Hemingway)), at the National Museum of Scotland (Edinburgh, Scotland) (Slides 555–48 to 555–52 and 555–F10), and slides from the British Geological Survey. These specimens were all available to Scott to draw on for his study and include the type and figured materials (Scott 1897*b*).

Slides were studied under transmitted light microscopy at the Natural History Museum (London) using a Leica M–800 optical microscope with attached camera IC 80 HD for lower magnification, and a Nikon Eclipse H 550L for higher magnification. All other slides were examined at the University of Birmingham. Low magnification images were taken using a Zeiss Tessovar macrocamera system, and higher magnification images including spore analysis were obtained using a Zeiss Axioscope; in each case images were captured using a Canon EOS D40 DSLR camera. Images were processed (cropped, rotated, tone, balance and contrast adjusted) and plates were composed using Corel Draw version X6.

In the following account we have not repeated every feature noted in Scott's (1897*b*) seminal monograph on *Cheirostrobus*, but instead have focussed on the salient points and those subject to confusion or disagreement. In addition, we illustrate only those features that are not clearly seen in Scott's account.

Locality and geological information

Specimens were historically collected from the Pettycur Limestone from Pettycur, on the north shore of the Firth of Forth in southern Scotland (Rex and Scott 1987; Cleal and Thomas 1995; Fig. 1). *Cheirostrobus* is not known from other localities and recent trips to the site have not yielded additional fossils. At Pettycur permineralized fossil plants are preserved at the base of basaltic lava flows or within pyroclastic deposits of the Kinghorn Volcanic Formation, and are believed to have been preserved in an *in situ* peat (Rex and Scott 1987; Cleal and Thomas 1995). Although not stated elsewhere, we consider the Pettycur Limestone to represent a lithostratigraphic Member of the Kinghorn Volcanic Formation. Fossil plants in the Pettycur Limestone are permineralized by a combination of calcium carbonate and silica and have exceptionally high levels of anatomical preservation, the high-fidelity of the preservation limited by low levels of organic decay of the plant tissues prior to their preservation.

The Pettycur Limestone was deposited during the Albian regional substage of the Viséan global stage (Mississippian, Carboniferous) according to Scott et al. (1984) and Rex and Scott (1987), and represents the DP (mid Asbian) subzone of the NM (mid–upper Asbian) miospore biozone (Scott et al. 1984). This places the Pettycur Limestone biostratigraphically in the upper part of the Viséan Stage of the Carboniferous, approximately 340 Ma.

Terminology

Scott (1897b) defined “sporophylls” as “foliar structures, which ultimately bear sporangia” (Scott 1897*b*, pg. 3) and considered individual “sporophylls” to comprise a lower vegetative part (his vegetative or sterile lobe) and an upper fertile part (his fertile lobe) (Scott 1897*b*, pg. 3, *et seq*.), with sporangia borne on the fertile part and never directly on the vegetative part. Scott’s definition of a “sporophyll” is therefore not in accordance with the modern definition of a sporophyll in which sporangia are born directly on a leaf homologue (e.g., Sporne 1962; Bierhorst 1971; Ogura 1972). We follow Sporne (1962) in considering the individual structures bearing multiple sporangia to be sporangiophores, and consider these sporangiophores to be born in the axils of bracts. We argue that each vascular bundle departing from the stele supplies a single fertile appendage, which comprises two to three bracts, each bract subtending two to three sporangiophores, and each sporangiophore subtending 4, rarely 5, sporangia. In this way, Scott's inconsistently used terms "vegetative lobes", "sterile segments", "sterile lobes", "vegetative segments", "fertile lobes", "fertile segments" (Scott 1897b, pg. 3–4 *et seq*.) and the term "sporophylls" become unnecessary. This terminology broadly follows that used by Arnold (1958), Good (1978), Gastaldo (1981) and Wang et al. (2005), and others for members of the Sphenophyllales, although in none of these examples are bracts and sporangiophores produced in groups of three. This organisation is different from that applied to equisetophytes where sporangiophores and bracts occur in distinct whorls (Sporne, 1962), leading Riggs and Rothwell (1985) to conclude that the sporangiophores of equisetophytes and sphenophylls are not strictly homologous.

In the past used different terms have been used for the distal foliar portions of the sporangiophore including "peltate structure", "peltate head", "quadrangular shield", "quadrangular peltum" and a "mushroom-like form" (e.g. Scott 1897a; Hickling 1907; Baxter 1950). However, to clearly demonstrate if the apex was peltate, it is necessary to examine this feature in tangential sections. Lacey (1943) and Taylor (1967) described strobili of *Calamostachys binneyana* that were apparently peltate, but tangential sections revealed they were in fact cruciate, comprising of four arms each subtending a single sporangium. Without new tangential sections of *Cheirostrobus*, we refer to this structure as a foliar apex and make no further inferences about it being peltate or cruciate.

Results

Class – Sphenopsida C. Agardh 1825

Order – Sphenophyllales Boureau 1964

Family – Cheirostrobaceae Boureau 1964

Genus – Cheirostrobus DH Scott 1896 emend. Neregato et *Hilton*

Emended generic diagnosis. Cone consisting of a cylindrical axis, bearing numerous fertile appendages arranged in verticils as successive superposed whorls. Individual fertile appendages divided, almost nearly to their base, producing two or three bracts that each subtends a single sporangiophore. Bracts comprise a mesophyll that is subhorizontal and bifurcates into a shorter lower and a longer upper extension. Sporangiophores elongate, bearing inwards facing sporangia attached to the inner surface of a foliar apex. Spores homosporous, circular, trilete. Cone axis protostelic with exarch protoxylem. Metaxylem tracheids with spiral, scalariform, and circular bordered wall pitting.

Remarks. We have emended the generic and specific diagnosis in order to (1) include additional information identified during the course of this research relating to the structure of the cone and organisation of the strobilus, and (2) update the descriptive terminology used by Scott (1896; 1897*a*, *b*; 1920) to simplify it and to enable more effective comparisons with other taxa.

Species – Cheirostrobus pettycurensis D. H. Scott 1896 emend. Neregato et Hilton

Emended specific diagnosis. Strobilus 30–40 mm diameter, seated on a distinct peduncle. 9–13 fertile appendages per whorl. Fertile appendages comprising two or three bracts that each subtend a sporangiophore. Sporangiophore terminating in a foliar apex that bears on its internal surface four (rarely five) sporangia, organized in two vertical rows. Sporangia densely crowded; sporangial walls uniseriate, comprising thin, columnar cells. Spores homosporous, circular, trilete, 48(66)77 μm in diameter, laevigate, with prominent margo and imperfectae curvaturate.

Remarks. As noted by various authors (e.g., Taylor 1967; Good 1978), the number of protoxylem poles varies along a strobilus axis. We have expanded the diagnosis to include the observed variation within the species, although Scott's conclusion that 12 were present is the most common arrangement.

Locality. Pettycur foreshore, southern Scotland (Rex and Scott 1987).

Horizon. Pettycur Limestone Member, Kinghorn Volcanic Formation.

Stratigraphic age. Upper Viséan, Carboniferous, approximately 340 Ma.

Description

In the following description we illustrate key specimens that demonstrate specific features pertinent to our analysis; we do not repeat all of the illustrations provided by Scott (1897*b*) and here only illustrate key features to diagnose and interpret the plant.

Gross morphology. The strobilus is at least 100 mm long, approximately 22 mm in diameter at the base, 30 mm in the middle, and 17 mm close to the apex, showing at least 26 whorls (Fig. 2). In transverse section the strobilus is elliptical, measuring 30–40 x 15 mm in diameter, with the central axis approximately 7.5 mm in diameter (Fig. 3, A, B); we consider the elliptical outline to be taphonomic artefact from an original circular organisation. The strobilus axis comprises a stellate protostele (Fig. 3, A, B) from which vascular traces arise in tightly spaced whorls with successive departures in vertical rows. Individual bundles arising from the stele (α) supply a single fertile appendage and divide vertically close to the cortex to generate two daughter bundles, of which the abaxial (β) supplies the bracts and the adaxial (γ) supplies the sporangiophores (Fig. 3, C; Fig. 4, A, B). Sporangiophores bear four, rarely five, inwardly facing sporangia with a distal foliar apex (Fig. 4, A, E).

Strobilus axis. In transverse section the strobilus axis is approximately 7.5 mm in diameter, composed of a central vascular cylinder surrounded by parenchymatous cells of a thin cortex (Fig. 3, A). The cortex is generally poorly-preserved; we cannot identify phloem and cortical cells individually. The periphery of the axis is rendered crenulated by the divergence of fertile appendages (Fig. 2, Fig. 4 A, B). The vascular cylinder is approximately 2.8 mm in diameter and has a stellate protostele 2.3 mm in diameter, exhibiting 9–13 protoxylem poles (Fig. 3, A–C). Protoxylem cells in transverse section are polygonal, ranging from 14–32 µm in diameter, and metaxylem cells are circular–elliptical, 44–72 µm in diameter (Fig. 3, B, C). Protoxylem is located at the tips of the vascular cylinder and has uniseriate and multiseriate circular pitting, whereas the metaxylem occurs toward to the centre and has spiral and scalariform pitting (Fig. 4, C, D). Although Scott (1897*b*, pg. 9; his Plate 3, photograph 17 and Plate 4, photograph 2) remarked that multiseriate circular pitting seen in some tracheids is in fact bordered pitting (1897*b*, pg. 9), we have not observed bordered pits and so discount this interpretation. Due to the protoxylem position, maturation was centripetal. In longitudinal section, protoxylem and metaxylem are arranged in longitudinal files several millimetres long.

Vascular system and organization of fertile appendages. To understand the organization of the strobilus it is first necessary to determine its vascular architecture. The vascular system is composed of a solid protostele with 9-13 tips (Fig. 3, A–C) from which individual vascular bundles (α) depart from the axis in an angle of 30^o in a whorled disposition along the strobilus (Fig. 4, A, B; Fig. 5). In the cortex, approximately 2.7 mm from the inner margin, the α bundles divide in a vertical plane in relation to the cone axis, producing a lower derived bundle (β) that runs in a more or less horizontal course and supplies the bracts, while the upper derived bundle (γ) also follows a more or less horizontal course and supplies the sporangiophores (Fig. 4, A, B; Fig. 5). Due to the limited number of sections available, exacerbated by their often oblique nature and the small size of the individual bundles making them difficult to distinguish in the crowded cone organisation, it has not been possible to determine the precise course of the derived bundles passing through the mid to distal parts of the fertile appendages. The best information comes from tangential sections through the cone that show small lacunae surrounding vascular bundles organized adjacent to each other, producing three derived bundles (Fig. 5, A-B). In generating this organisation both the bract bundle (β) and sporangiophore bundle (γ) divide horizontally in a palmate fashion, as noted by Scott (1897b). The β bundle divides to producing two or three daughter bundles (β1, β2, β3), that each supply the bract and the heel of the bract (see below), while γ bundles also divides to produce two or three daughter bundles (γ1, γ2, γ3), that each supply a single sporangiophore. The palmate divisions are demonstrated by the bundles dividing in tangential section (Fig 5, A) where bundles γ1, γ2 and γ3 occur in groups of two or three after the first division whereas the β bundles occur in two or three after the second division (Fig. 5, C, D).

Bracts. Individual bracts comprises a laminar mesophyll between 0.2–0.34 mm thick (Fig. 4, A) that extends horizontally before dividing in a vertical plane to produce a longer, upwardly orientated extension and a shorter, downwardly orientated extension that is here termed the heel. Unfortunately, we have been unable to locate specimens that illustrate clearly the sporophyll heels as described by Scott (1897b); these are visible in Scott's 1897b paper in his Pl. 2 Fig. 10 where a heel is labelled st^3. The upper extension of the bract overlaps the whorl of fertile appendages above, and the heel encloses the sporangiophore apex. In this organization the bracts above and below tightly enclose the sporangiophores in the fertile appendage (Fig. 5, B; Fig. 6, B).

Fertile appendages. Fertile appendages are inserted at a slightly inclined angle in relation to the axis and are born in whorls spaced 1.7–2.2 mm apart. They divide rapidly from their departure from the axis into a lower vegetative part (bracts) and an upper fertile part (sporangiophores). Both the vegetative and fertile parts rapidly divide horizontally, the vegetative part comprising two or three bracts whereas the fertile part comprising two or three sporangiophores. Bracts are larger than the sporangiophores and so form the most voluminous structures in the fertile appendages (Fig. 4, A; Fig. 6).

In transverse section the number of fertile appendages per whorl is unclear, but as each of the vascular strands in the stele supplies a single fertile appendage, we consider that each whorl contains between 9–13 fertile appendages, thus having between 18–39 bracts each of which subtend a single sporangiophore (Fig. 7). Scott's (1897*a*, p.3) calculation of 12 "sporophylls" per whorl used the same evidence but did not include the variation in the number of protoxylem poles noted in the present account.

Sporangiophores. Sporangiophores are slightly inclined relative to the cone axis and are parallel to and are tightly constrained by the position of the bracts, with each bract subtending a single sporangiophore. Sporangiophore pedicels are seen in tangential sections through the cone and are approximately 0.4 mm in diameter (Fig. 4, E); they are closely surrounded by the sporangia and are difficult to see in many sections. Individual sporangiophores are long and slender in longitudinal section (Figs. 2; 3, A; 4, A), and are terminated by a foliar apex (Figs 4, A; 6). On the inwards facing surface of the apex, sporangiophores bear sporangia in two vertical rows. Sporangiophores bear four (rarely five) sporangia of which two are positioned on the adaxial row (inferior sporangia *sensu* Scott), whereas two are positioned on the abaxial row (superior sporangia *sensu* Scott) (Figs 4, E; 5, C; 6).

Sporangia. Individual sporangia are polygonal-hexagonal in transverse section, 0.6–1.3 mm wide (Fig. 4, E), and in longitudinal section are elongate-cylindrical, 15–24 mm long. The abaxial (inferior) sporangial row tends to be slightly longer than the adaxial (superior) sporangia row (Figs 4, A; 5, C; 7). With each whorl bearing 18–39 sporangiophores, each bearing 4–5 sporangia, each whorl in the strobilus would thus contain 72–195 sporangia; with at least 26 whorls per strobilus, each strobilus would contain at least 1,872–5,070 sporangia. Sporangial walls are uniseriate, composed of rectangular columnar cells, approximately twice as high as they are wide, with no differentiation between inner, outer and lateral walls (Fig. 8, A, B). No evidence of a dehiscence mechanism has been observed. Sporangial cavities from all sporangia from the inferior and superior rows on the sporangiophore contain abundant, densely packed spores (Figs 3, A; 4, A; 6). Abortive sporangia or those that have shed their spores are absent.

In situ spores. Spores of *Cheirostrobus* have a circular to slightly sub-circular amb with a distinct margo that extends almost into the equatorial margin (Fig. 8, C–H). The majority of the spores have *imperfectae* c*urvaturae* and few have *perfectae* c*urvaturae.* Spores are laevigate on both their distal and proximal surfaces. Measuring complete spores with no sign of distortion or damage provides equatorial diameters that range from 48–77 µm (n = 245; mean = 66.7 µm; mode = 68 µm) with a normal size distribution (Fig. 9). Spores have a thin exine that ranges between 2.0–4.0 µm (n = 73; mean = 2.48 µm; mode = 2.0 µm). Laesurae are subdued and reach 1/2 to 3/4 of the spore radius and are accompanied by a distinct margo 2.0–4.0 µm wide (n = 21; mean = 2.24 µm; mode = 2.0 µm). The spores confirm to the *sporae dispersae* species *Retusotriletes incohatus* Sullivan 1964.

Discussion

Accuracy of Scott's (1897) diagrammatic reconstruction

Scott's (1897) hand-drawn reconstruction of *Cheirostrobus* has been widely reproduced in text-books (e.g., Scott 1920; Seward 1910; Boureau 1964) or used as the basis for more simplified depictions of the organization of its strobilus (e.g., Stopes 1910; Ogura 1972; Meyen 1987). Much of our previous understanding of *Cheirostrobus* has been gained from this diagram, although its accuracy is has not previously been questioned. Scott had direct access to the specimens prepared by Hemmingway and Lomax would have been provided with details of how the specimens were prepared (including section orientations and dimensions) that are no longer available (Howells, 2006). We therefore assume that his reconstruction was as accurate as possible for the time.

Overall, we find Scott's reconstruction remarkably accurate in terms of depicting the organization of the strobilus, although the spacing of the successive fertile appendage departures from the cone axis is unrealistic; this has been expanded to improve clarity of the diagram by inaccurately removing overcrowding. Moreover, it is clear from the specimens that the morphology of the bracts and sporangiophores tightly constrain the position and size of the sporangia, presenting a much denser arrangement that lacks the spaces between the individual sporangia, sporangiophore pedicels or the bracts that appear in Scott's diagram. The radial organization of the cone is therefore much more similar to that presented here as Figure 7 than to Scott's original reconstruction. The organization in transverse section is, however, remarkably accurate, although the divisions of the vascular bundles vary to show two zones (Fig. 5 C, D). Moreover, the number of sporangia per sporangiophore shown in Figure 7 accommodates our new interpretation (Fig. 7). New specimens combined with non-destructive tomographic techniques (e.g., Spencer et al. 2013) will be required to fully reconstruct the strobilus in full detail.

Whole-plant considerations

Other organs belonging to the *Cheirostrobus* whole-plant are currently unknown. Early accounts suggested that *Cheirostrobus* may have been associated with leaves of *Pseudobornia* Nathorst (e.g., Seward, 1910). Orlova and Jurina (2014) recently described the primary xylem of *Pseudobornia schweitzeri* from the Upper Devonian Russia as having spiral, annular, scalariform and pitted cell-wall thickenings, whereas *Cheirostrobus* lacks annular and pitted wall thickenings. Cleal and Thomas

(1995) concluded that an association between *Cheirostrobus* and *Pseudobornia* was unlikely as *Pseudobornia* is only known from the Devonian and is unknown in Scotland. Following criteria specified by Bateman and Hilton (2009), there is no evidence to reliably associate *Pseudobornia* with *Cheirostrobus*.

Within the Pettycur Limestone two kinds of sphenopsid strobilus and two kinds of sphenopsid stems/leaves are present, suggesting that the assemblage includes at least two sphenopsid whole-plant species. From Pettycur, archaeocalamitalean stems of *Archaeocalamites goeppertii* and strobili of *Protocalamostachys pettycurensis* (Rex and Scott 1987) are protostelic with mesarch primary xylem maturation (Table 2) and can be reliably associated as parts of a single whole-plant species based on this evidence and information from other localities (Bateman 1991). This plant is clearly both vegetatively and reproductively distinct from *Cheirostrobus*. Sphenophyllalean stems and leaves of *Sphenophyllum insigne* from Pettycur are protostelic and have centripetal and exarch primary xylem maturation, as also seen in *Cheirostrobus*. However, *Sphenophyllum insigne* has a triangular protostele while other species of the genus can have up to six poles, whereas in *Cheirostrobus* this structure is more stellated, with 9–13 poles. Also, the protoxylem cells in *Cheirostrobus* have uniseriate and multiseriate circular pitting, whereas *Sphenophyllum* has spiral pitting, and secondary xylem in *S. insigne* is limited to scalariform pitting, but *Cheirostrobus* demonstrates more diverse pitting including spiral, scalariform, and bordered pits. Species of *Sphenophyllum* have a more complex stem structure in which there is clear division of the secondary body into fascicular wood composed of tracheids (located in front of the protoxylem tips) and parenchymatous cell comprising interfascicular rays between the protoxylem tips (Baxter 1948). Such differentiation is absent from *Cheirostrobus,* suggesting that its stems and leaves were not assignable to *Sphenophyllum insigne*.

Interestingly, vegetative organs of *Cheirostrobus* and fertile organs of *Sphenophyllum insigne* are both unknown at Pettycur. Although an intuitive association could be made between these organ-taxa by assuming that they represent different parts of the same whole-plant species, at other localities *Sphenophyllum* is strongly associated with sphenophyllalean cones including *Peltastrobus reedae* (Baxter 1950; Leisman and Graves 1964; Baxter 1972), *Sentistrobus goodii* (Riggs and Rothwell 1985) and *Bowmanites* (Hoskins and Cross 1943), all of which are anatomically and morphologically different from *Cheirostrobus*. The answer to the question of the identity of the other parts of the *Cheirostrobus* plant are unlikely to come from the existing materials prepared from the Pettycur Limestone; future collecting and identification of evidence such as specimens demonstrating organic attachment between multiple organs, or shared histological similarities that allow them to be reliably associated with one another, are now required. Likewise, complimentary investigation from other sites in the Mississippian of southern Scotland and northern England is desirable seeking anatomical information from sphenophylalean cones that are present.

Spores of *Cheirostrobus*

Based on analysis of photographic evidence from Scott's 1897*b* paper, spores from *Cheirostrobus* were previously assigned to the dispersed genera *Calamospora* Schopf, Wilson and Bentall 1944 (Potonié 1962, 1965; Chaloner 1967), but later assigned to *Punctatisporites* Schopf, Wilson and Bentall 1944 by Potonié (1970) based on examination of *Cheirostrobus stobili*. However, *Calamospora* and *Punctatisporites* lack the prominent curvaturae present in the spores of *Cheirostrobus* thus contradicting these identifications. *In situ* spores of *Cheirostrobus* conform to the features of *Retusotriletes* as originally described by Naumova (*in* Jansonius and Hills, 1976) as a semicircular, trilete spore with three differentiated flattened contact surfaces. However, Streel (1964) subsequently emended the genus to restrict it to spores with a smooth exine such as those of *Cheirostrobus*.

Species of *Retusotriletes* range stratigraphically from the Late Silurian to the Mississipian (Table 1). Those with the greatest similarity to the spores of *Cheirostrobus* include *R. anfractus*, *R. mirabilis* and *R. delicatus* which share a thin exine and margo, and *R. goensis* which also has a thin exine but lacks a margo. *Retusotriletes tenerimedium* and *R. rugulatus* have a moderately thin exine (1.5 and 1.5–3.0 µm respectively), but the margo is thin in both of these species (Fig. 10). The spores of *Cheirostrobus* conform most closely to *Retusotriletes incohatus* (G. Clayton, pers. com. 2014) that has an exine and margo of approximately 2 µm (Sullivan, 1964), but dispersed spores of *R. incohatus* (35–50 µm; Fig. 11) are smaller than the *in situ* spores of *Cheirostrobus* (48–77 µm). This size difference may be related to taphonomic size sorting of dispersed species. Moreover, it is widely appreciated that i*n situ* spores do not readily conform to species concepts for dispersed spores that have been subjected to post–dispersal taphonomic sorting by wind and water. The *in situ* spores of *Cheirostrobus* provide botanically significant information pertaining to a biological species (*sensu* Bateman and Hilton, 2009) in which natural variation is encountered, in this case, having larger spores than those found in the dispersed record. Alternatively, this variation could be related to the permineralized preservation of *Cheirostrobus* that is distinct from that of dispersed spores that preserve the sporopollenin. Silica permineralized i*n situ* spores from the Rhynie chert and *in situ* spores in Devonian aged charcoalified plants tend to be smaller than those of the same species in the dispersed record (Wellman et al., 1998; Wellman et al., 2006), suggesting that the larger size of permineralized spores in *Cheirostrobus* is not related to mineralization. We are unaware of comparable studies in carbonate permineralized *in situ* spores which more representative of the situation in the Pettycur Limestone that combines both carbonate and silicate preservation (Rex and Scott, 1987). Alternatively, dispersed spores may shrink during desiccation.

In situ spores of *Retusotriletes incohatus* in *Cheirostrobus* range from 48–77 µm in diameter and have a unimodal size distribution (Fig. 9) characteristic of homospory, as previously interpreted by Scott (1897b) and Bateman and DiMichele (1994). Biostratigraphically dispersed spores of *R. incohatus* range from the LN biozone of the late Famennian (Upper Devonian) to the end of the Viséan stage (Mississippian), but is most common in the Tournaisian (Keegan 1981; Waters et al. 2011; D. McLean, pers. com. 2014–15). It is widespread though the Tournaisian–Viséan deposits of southern Scotland where it is an index species for the *Vallatisporites vallatus–Retusotriletes incohatus* (VI) basal Tournaisian miospore biozone (e.g., Keegan 1981; Waters et al. 2011), but is also present up to the NM Asbian biozone in which the Pettycur Limestone occurs near the end of its stratigraphic range. We consider that the late Famennian-Viséan stratigraphic range of *R. incohatus* is likely to coincide with the stratigraphic range of *Cheirostrobus pettycurensis* or closely related species with the same kind of spore, extending the accepted stratigraphic range of *Cheirostrobus* from the NM biozone of the Viséan that was based solely on the age of the Pettycur fossil plant assemblage (Rex and Scott 1987). The abundance of *R. incohatus* spores in the Tournaisian suggests this represented the acme of *Cheirostrobus* or closely related species.

While we can now associate *Retusotriletes incohatus* spores with the *Cheirostrobus* plant*,* other species of *Retusotriletes* have previously been found *in situ* in members of strongly contrasting plant groups, including rhyniophytes (Eggert 1974;

Gensel 1976; Fanning et al. 1991a; Wellman et al. 2006), zosterophylls (Edwards 1969; Gensel et al. 1975), trimerophytes (Banks 1975; Banks et al. 1975), lycophytes (Kerp et al. 2013), and algae (Chaloner and Orbell 1971; Ronney et al. 2013) (Table 3). From this phylogenetic distribution it is evident that spore genus *Retusotriletes* is not monophyletic and represents morphological convergence from unrelated lineages; the present account expanding this taxonomic range into the Sphenopsida for the first time.

Species of *Retusotriletes* in the dispersed record (Fig. 10) vary considerably in size from small species such as *R. warringtonii* (18–36 µm) and *R. simplex* (22–42 µm) up to much larger species such as *R. distinctus* (113–218 µm) and *R. loboziakii* (168–209 µm). Considering the massively polyphyletic nature of *Retusotriletes*, we have considered morphological features that may indicate different morphological groupings within the genus in order to enable its subdivision into systematically significant groupings. We have considered spore diameter, exine thickness and also the presence of a *curvatura perfecta*. Exine thickness influences water and environmental tolerance in that thicker exines are more resistant to desiccation but a thinner exine is more easily dispersed by anemophily, whereas a *curvatura perfecta* suggests strong attachment between spores within the tetrahedral tetrad prior to dispersal. There is a strong positive correlation ($r^2 = 0.51$) between spore diameter and exine thickness in which larger spores have thicker exine (Fig. 10). However, attempts to find statistically reliable groupings within *Retusotriletes,* including Detrended Correspondence Analysis using features of the *curvatura perfecta* have proven unsuccessful.

In Figure 10 we offer in contrasting colours our interpretation of the different dispersal mechanisms but emphasize that these lack strong statistical support in the present analysis. Species in Group 1 have a thin exine, 0.5–1.5 µm in thickness, *curvaturae perfectae* and *imperfectae*, being interpreted as dispersed individually or collectively by wind due to their small size and thin exine that together implies a low weight. These species include *R. minor*, *R. nigritellus*, *R. delicatus*, *R. semizonalis* and *R. biarealis*, and range stratigraphically from the Middle Silurian to the early Middle Devonian; we suggest this group represents a primitive organization within *Retusotriletes*. Species in Group 2 are the most diverse and are mid to large-sized, with exine up to 8 µm thick, and with both *curvaturae perfectae* and imperfectae, ranging stratigraphically from the Late Silurian to the Mississippian. We interpret this group to have been dispersed in tetrads or individually by water or wind. By contrast, Group 3, (*R. distinctus* and *R. loboziakii*) form a notable outlier from the other species and range stratigraphically from the Middle to Late Devonian. These species possess *curvaturae perfectae* and a very thick (9-15 µm) exine, consequently having a greater weight and stronger environmental resilience. In exceeding 200 µm in diameter both of these species can be classified arbitrarily as megaspores (Traverse 1988; Bateman and DiMichele 1994). On this basis we consider their inclusion within the genus *Retusotriletes* inappropriate. From their morphology we interpret that they were dispersed by water and produced by aquatic heterosporous plants. Ultrastructural information from different species may in the future allow botanically significant groupings to be identified within the artificial genus *Retusotriletes*.

Affinity of Cheirostrobus

Although Scott (1896, 1897*a*, *b*) initially considered *Cheirostrobus* to display features of both lycophytes and sphenopsids, the organization of the strobilus comprising successive whorls arranged in vertical rows and with sporangia born on sporangiophores is characteristic of sphenopsids. This differs markedly from lycophytes in which leaves and sporophylls are helically inserted with sporangia born directly on sporophylls (Table 2).

Within Sphenopsida *Cheirostrobus* also has similarities with members of Archaeocalamitaceae (Table 2) which are also protostelic (Bateman 1991). However, Archaeocalamitales are distinguished by their mesarch protoxylem maturation and absence of bracts or sporophylls, having sporangiophores born directly on the cone axis (Bateman 1991). *Cheirostrobus* is distinct from the probable Permian archaeocalamitacean *Peltotheca* Escapa et Cúneo (Escapa and Cúneo 2005; Elgorriaga et al. 2018) that has reproductive organs composed of internodes covered in peltate sporangiophores and lacking bracts. It also differs from the Mesozoic/Cenozoic–extant genus *Equisetum* which is eustelic (Table 2) and has cones that lack bracts and sporophylls with sporangiophores born directly on the cone axis (Sporne 1962).

Cheirostrobus has been previously treated as the sole member of the Family Cheirostrobaceae within sphenopsida (Boureau 1964; Ogura 1972) but has also been placed within the Sphenophyllales by other authors (Sporne 1962; Meyen 1987; Taylor et al. 2009). Sphenophyllales, like *Cheirostrobus,* are protostelic and have mesarch protoxylem maturation (Table 2). However, *Cheirostrobus* differs from the Devonian sphenophyllalean genera *Eviostachya* Stockmans (Stockmans 1948; Leclercq 1957) and *Hamatophyton* Wang et al. (Wang et al. 2006); all lack bracts or sporophylls and have sporangiophores inserted in whorls directly on the cone axis, in a similar fashion to the Archaeocalamitaceae and *Equisetum*. Within Sphenophyllales, *Bowmanites* (Binney) Hoskins et Cross (Hoskins and Cross 1943), *Sphenostrobus* Levittan et Barghoorn (Levittan and Barghoorn 1948) and *Sentistrobus* Riggs et Rothwell (Riggs and Rothwell 1985) have their bracts and the sporangiophores fused at their bases, forming a single organ (sporophylls), vascularized by a single common bundle diverging from the stele.

However, *Cheirostrobus* differs from each of these genera in having bracts and sporangiophores individualized and forming groups of two or three originating from a single bundle in the fertile appendage. *Peltastrobus* (Baxter) Leisman et Graves (Baxter 1950; Leisman and Graves 1964), another genus assigned to the sphenophyllales, comprises a cone organized in superposed whorls with five sporangiophores radiating beside the bract bases. of the sporangiophores one is disposed perpendicularly to the cone axis, two inclined at 45^o above and two inclined at 45^o below the central/perpendicular sporangiophore. This its morphology is markedly different from *Cheirostrobus.*

Although the protostele of *Cheirostrobus* contrasts with the eustele of members of the Calamitaceae (Table 2), *Cheirostrobus* shares several features with members of this family including *Palaeostachya* Weiss (Baxter 1955; Leisman and Bucher 1971), *Weissistachys* Rothwell et Taylor (Rothwell and Taylor 1971*a*,*b*), *Mazostachys* Kosanke (Kosanke 1955), *Calamostachys* Schimper (Taylor 1967) and *Calamocarpon* Baxter (Baxter 1963). In all of these genera, as in *Cheirostrobus,* bracts and sporangiophores are separate structures, the latter arising from the former at different levels. So, if they diverge from the axis, they are supplied by two different vascular bundles that diverge from the main vascular bundle within the strobilus axis. In *Palaeostachya* Weiss (Baxter 1955; Arnold 1958; Leisman and Bucher 1971; Gastaldo 1981; Stewart and Rothwell 1993) and *Weissistachys* Rothwell et Taylor (Rothwell and Taylor 1971*a*,*b*) elongated sporangiophores are inserted at the bract axils lying in an angle of approximately 45 to 60^o at the cone axis; in *Mazostachys* Kosanke (Kosanke 1955) sporangiophores are circular, inserted perpendicularly at the cone axis, slightly above the bracts and in a remarkable pendulant manner along the cone axis. In the other members of Calamitaceae such as *Calamostachys* Schimper (Kosanke 1955; Arnold

1958; Taylor 1967; Taylor et al. 2009) and *Calamocarpon* Baxter (Baxter 1963), elongated sporangiophores are inserted perpendicularly at the cone axis between successive whorled bracts. Besides these features, some species of *Calamostachys* are heterosporous including *C. americana* Arnold (Arnold 1958) as well as *Calamocarpon insignis* that is monomegasporic (Baxter 1963).

Cheirostrobus thus exhibits an unique combination of features (Table 2) but includes some that are characteristic of members of the Sphenophyllales, including being protostelic with mesarch xylem maturation, but others that are more characteristic of the Calamitaceae, including individual vascular bundles supplying the upper fertile and the lower vegetative parts of the fertile appendage. However, its spores are distinct from those of both the Sphenophyllales and Calamitaceae.

Based on the information presently available we consider *Cheirostrobus* to be a member of the Sphenophyllales that is on the evolutionary stem-lineage leading to the stratigraphically younger Calamitaceae, hence, shares features with both clades, potentially in a similar position as occupied by the Archaeocalamites. Its distinction from other sphenopsids is more than adequate to justify the Family Cheirostrobaceae (Boureau, 1964). A morphological and anatomical cladistic analysis of Sphenopsida, integrating extinct and extant taxa, is now required to test this hypothesis of relationships and will be presented elsewhere (Neregato et al., manuscript in progress).

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Figure and table captions

Fig. 1 Outline map of Scotland showing location of Pettycur on the southern coast of Fife.

Fig. 2 Longitudinal section through cone of *Cheirostrobus pettycurensis.* VS = vascular strand; VB = vascular bundles; SP = sporangiophores; FA = foliar apex. The yellow color is a result of the aging of the Canada Balsam mounting medium. The dotted rectangle at the top of the image shows the vascular bundles departure. Scale bar = 5 mm.

Fig. 3 Transverse sections through strobilus of *Cheirostrobus pettycurensis. A.* Section showing axis and disposition of sporangiophores. VS = Stellate vascular strand in strobilus axis; VB = vascular bundles; SP = sporangia within sporangiophores. Specimen 555-50; scale bar = 5 mm. *B.* Stellate stele with 13 ribs corresponding to 13 protoxylem poles. Large arrow indicating protoxylem cells and small arrow indicating metaxylem cells. Specimen OC 487; scale bar = 1 mm. *C*. Oblique section (X–X' in 5C) showing division of the vascular bundles. The main vascular bundle (α) departs from the stele and undergoes its first division generating a lowermost daughter bundle (β) and an uppermost daughter bundle (γ). Specimen SC 519; scale bar = 1 mm.

Fig. 4 Radial and tangential longitudinal sections through the cone of *Cheirostrobus pettycurensis*. *A.* Radial section showing the stele and fertile appendage disposition. VB = vascular bundles; SP = sporangia in sporangiophores; FA = foliar apex. Specimen SC 521; scale bar = 2 mm; *B*. Detail of the vascular system showing its organization. The main vascular bundle (α) departs from the stele generating a lowermost daughter bundle (β) and an uppermost daughter bundle (γ); *C*. Protoxylem tracheids in radial section showing uniseriate and multiseriate circular thickenings in tracheid walls. Specimen SC 521; scale bar = 100 µm. *D*. Radial section showing circular thickenings in the protoxylem (left) and scalariform thickenings in the metaxylem (right). Specimen SC 521; scale bar = 50 µm; *E.* Tangential section probably close to cone periphery showing grouping of sporangiophores with examples of four sporangia per sporangiophore (red dots) and rarely five sporangia (yellow dots). Vascular bundles organized in threes in the bract (green hollow circles) and sporangiophores (amber hollow circles) are shown. Specimen SC 528; scale bar = 2 mm.

Fig. 5 Vascularization and apices of the bracts in *Cheirostrobus pettycurensis*. *A*. Tangential section probably close to the axis showing the main vascular bundles before division (arrows). Specimen SC 521; scale bar = 2 mm; *B*. Proposal radial section reconstruction showing the sporangiophores, bracts, and the approximate position of section X–X' in 5B; scale bar = 2 mm. *C*. Proposed three-dimensional reconstruction of the vascular system showing the main vascular bundle and its daughter vascular bundles.

Fig. 6 Radial section through the cone of *Cheirostrobus pettycurensis*. *A*. Distal region of the fertile appendages showing upper sporangia (Up SP), lower sporangia (Lw SP) and foliar apex (FA). Specimen SC 521; scale bar = 1 mm. *B*. Distal part of the fertile appendages showing upper sporangia (Up SP), lower sporangia (Lw SP), foliar apex (FA), bracts (small arrows) and heel (long arrow). Specimen SC 519; scale bar = 1 mm; the dark vertical line is where two coverslips join from the original specimen preparation. *C*. Distal part of two fertile appendages showing the delimitation of a sporangiophore with four sporangia (top) and another one with five sporangia (bottom). Up SP = upper sporangia; Lw SP = lower sporangia; FA = foliar apex (FA). Specimen SC 522; scale bar = 2 mm.

Fig. 7 Reconstructions in transverse section through the strobilus of *Cheirostrobus pettycurensis*. *A*. *S*ection through entire strobilus showing disposition of fertile appendages. *B*. Detail of a single fertile appendage comprising three bracts and three sporangiophores. Scale bars = 5 mm.

Fig. 8 *In situ* spores of *Retusotriletes incohatus* within sporangia of *Cheirostrobus pettycurensis*. *A.* Spore masses within adjacent sporangia (arrows indicate sporangium walls). *B.* Enlargement of 8A showing loosely packed spores within clear chert matrix. *C–G.* Proximal surfaces of individual spores showing range of preserved features including lips, thin exine and *curvaturae imperfecta*. In *E* and *F*, arrows indicate the "ghost circumference" that marks the original spore diameter prior to taphonomic shrinkage. *H.* Distal spore surface showing thick exine and laevigate ornament. All scale bars = 10 µm, except A = 200 µm, B = 100 µm. A, C–F, H = Specimen 555–D3/9; B, G = Specimen 555–D3/8.

Fig. 9 Size frequency distribution of *Retusotriletes incohatus* spore diameters within sporangia of *Cheirostrobus pettycurensis.* The graph shows a normal distribution characteristic of homosporous reproduction. Analysis based on measurements of 247 complete spores, with diameters plotted in 5 µm bins.

Fig. 10 Relationship between average spore diameter and average exine thickness in species of *Retusotriletes* showing a positive correlation ($r^2 = 0.5262$). Species represented by red dots have a thin exine, curvaturae perfectae and imperfectae and are interpreted as being dispersed individually or in tetrads by wind; blue dots represent mid- large-sized species with *curvaturae perfectae* and *imperfectae*, that are interpreted as being dispersed individually or in tetrads by water or wind; yellow dots represent species with *curvaturae perfectae* and a very thick exine, interpreted as being dispersed in tetrads by water that in our view do not belong to the genus (Figure 11). Note that from this figure, species in which exine thickness was not stated in the original papers are excluded (Figure 11, Table 1).

Fig. 11 Size distribution of previously recognized species of *Retusotriletes* showing minimum, maximum, and mean (tick) diameter. Dispersed (black arrow) and *in situ* (red arrow) spores of *R. incohatus* show different size ranges. In this plot *R. distinctus* and *R. loboziakii* form outliers to the size range of other species, from which we conclude it unlikely that they belong to the genus. The 25, 50, and 75 percentiles (to left of size axis) are based on the combined mean values for all species.

Table 1. Comparison of species of *Retusotriletes*; all species based on dispersed spore records except *Retusotriletes incohatus,* which is documented here as both dispersed and *in situ* within *Cheirostrobus pettycurensis* strobili. Species listed from small to large sized, in the same order as represented in Figure 11.

Table 2. Comparison of features of strobili of *Chreirostrobus* with those of Sphenophyllales, Calamitales, *Equisetum*, Lycophytes, and pseudo-strobili of

Noeggerathiales. Information on *Cheirostrobus* based on Scott (1896, 1897 *a*, *b*; 1898; 1920), Seward (1910) and this investigation. Information on Sphenophyllales based on *Bowmanites* (Hoskins and Cross 1943; Good 1978), *Sphenostrobus* (Levittan and Barghoorn 1948), *Peltastrobus* (Baxter 1950), and *Sentistrobus* (Riggs and Rothwell 1985); on Archaeocalamites based on *Protocalamostachys* (Bateman 1991; Taylor et al. 2009) and *Pothocites* (Chaphekar 1965); on Calamitales based on *Calamostachys* (Lacey 1943; Kosanke 1955; Arnold 1958; Taylor 1967; Taylor et al. 2009), *Palaeostachya* (Hickling 1907; Baxter 1955; Arnold 1958; Leisman and Bucher 1971; Gastaldo 1981; Stewart and Rothwell 1993), *Calamocarpon* (Baxter 1963), *Paracalamostachys* (Hibbert and Eggert 1965; Thomas 1969), *Mazostachys* (Kosanke 1955), *Weissistachys* (Rothwell and Taylor 1971a, b); on *Equisetum* based on Duckett (1970), Meyen (1987), Kenrick and Crane (1997); on Lycophytes based on *Lepidostrobus* (Brack-Hanes and Thomas 1983; Thomas 1970; Thomas and Dykto 1980; Thomas and Bek 2014; Bek and Oplustil 1998, 2006), *Minostrobus* (Meng et al. 2013), *Flemingites* (Brack-Hanes and Thomas 1983; Oplustil and Bek 2006; Stevens et al. 2010), *Yuguangia* (Hao et al. 2007), and *Moscvostrobus* (Naugolnykh and Orlova 2006); on Noeggerathiales based on information from Boureau (1964), *Noeggerathiaestrobus* (Šimůnek and Bek 2003), *Discinites* (Bek and Šimůnek 2005; Wang et al. 2004) and *Paratingia* (Wang et al. 2009; Wang et al. 2017, and references therein).

Table 3. Botanical affinities and stratigraphic age of plants previously reported as bearing *in situ Retusotriletes* spores demonstrating plesiomorphic conditions in multiple spore lineages or parallel evolution of spore morphology within multiple lineages.