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Age of the basal 'Lower Old Red Sandstone' Stonehaven Group of Scotland: the oldest reported air-breathing land animal is Silurian (late Wenlock) in age

Charles H. Wellman[1]*, Gilda Lopes[1], Zoë McKellar[2] and Adrian Hartley[2]

[1] School of Biosciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK
[2] Department of Geology and Geophysics, University of Aberdeen, Aberdeen AB24 3UE, UK
CHW, 0000-0001-7511-0464
* Correspondence: c.wellman@sheffield.ac.uk
Present addresses: ZM, 182a Main Street, Greytown, 5712, New Zealand

Abstract: The basal upper Silurian–Lower Devonian 'Lower Old Red Sandstone' deposits of the Midland Valley of Scotland contain several important fossil biotas, including that from the Cowie Harbour Fish Bed. This biota is of great significance because it represents one of the oldest known examples of a fossilized terrestrial ecosystem and includes the oldest reported air-breathing land animal (the myriapod *Pneumodesmus newmani* Wilson and Anderson, 2004). Based on biostratigraphical evidence from dispersed spores this biota is dated as late Wenlock (late Silurian) in age. Recently, however, this age constraint was challenged, based on ^{238}U–^{206}Pb radiometric analysis of zircons, and it was proposed that these deposits are much younger (Early Devonian: Lochkovian). This proposal has serious implications regarding (1) the composition and nature of early terrestrial ecosystems and (2) the geological setting with respect to the timing of terrane accretion and the onset of 'Lower Old Red Sandstone' sedimentation. We report on newly discovered dispersed spore assemblages and additional zircon data that confirm a late Wenlock (late Silurian) age. This age designation establishes the importance of the biota of the Cowie Harbour Fish Bed and is more compatible with both its biotic composition and the regional geological setting.

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The northern 'Strathmore' basin of the Midland Valley of Scotland contains an estimated 9km thick sequence of 'Lower Old Red Sandstone' non-marine terrestrial–fluviatile–lacustrine deposits (Campbell 1913; Armstrong and Paterson 1970; Gillen and Trewin 1987; McKellar and Hartley 2021) (Figs 1 and 2). These are age constrained based on a number of fossiliferous horizons dispersed through the sequence that yield plant megafossil–dispersed spore assemblages and/or fish–arthropod faunas (Browne *et al.* 2002) and previous radiometric age constraints (Richardson *et al.* 1984; Thirlwall 1988). The oldest deposits of this sequence belong to the Stonehaven Group and unconformably overlie the Cambrian–Ordovician Highland Border Complex at the Highland Boundary Fault (Figs 2 and 3). Age dating of the Stonehaven Group is based primarily on dispersed spore assemblages recovered from an inland exposure, separated from the type section that is exposed along the coast (Marshall 1991; Wellman 1993). The dispersed spore flora belongs to the *brevicosta–verrucatus* Zone (probably *Hispanaediscus lamontii* Sub-Zone) of Burgess and Richardson (1995) indicating a late Wenlock (Homerian) age (Wellman 1993; Lavender and Wellman 2002). This age constraint is significant as it dates the onset of 'Lower Old Red Sandstone' facies deposition in Scotland and indicates that the Stonehaven Group contains one of the oldest known non-marine biotas. Importantly, this includes the oldest reported air-breathing land animal (the myriapod *Pneumodesmus newmani* Wilson and Anderson, 2004).

Recently, however, the age of these deposits has been challenged and it was suggested that the biota is much younger based on ^{238}U–^{206}Pb radiometric analysis of zircons recovered from the coastal section (Suarez *et al.* 2017). They suggest an age of 413.7 ± 4.4 Ma; that is, an Early Devonian (Lochkovian) age. Shillito and Davies (2017) also preferred a younger age based on their study of non-marine trace fossils from the sequence. A younger age has serious implications regarding both the interpretation of the Stonehaven Group biota as representing one of the oldest known terrestrial ecosystems and the geological setting of the region. Not only does the biota shed light on the composition and nature of the earliest terrestrial ecosystems, but also many of the fossils present are the oldest representatives of various taxonomic levels and have therefore been utilized in the calibration of influential molecular clock analyses (see Wolfe *et al.* 2016; Brookfield *et al.* 2020). In terms of geological setting it would require that 'Lower Old Red Sandstone' facies sedimentation commenced much later in the Midland Valley of Scotland, which has implications regarding the timing of movements along the Highland Boundary Fault and hence the emplacement of the terranes that form Scotland. It also suggests that a series of unrelated slices of strata are juxtaposed adjacent to the Highland Boundary Fault (Shillito and Davies 2017): the spore-bearing slice of late Wenlock age (which is an extremely rare example of non-marine strata of this age) and a slice of Lochkovian age that yields the trace fossils and Cowie Harbour Fish Bed.

However, the new age dating is contentious. For example, McKellar *et al.* (2020) reported a range of ^{238}U–^{206}Pb detrital zircon ages from the same coastal exposures that are more consistent with a Silurian age. Although it is noted that provenance studies based on detrital zircon ages alone can be ambiguous, particularly if potential source terranes are characterized by coeval magmatic events (McKellar *et al.* 2020, 2021), it is important to consider all available data in assessing the age of these strata. The debate regarding the age of the Stonehaven Group deposits has prompted a reinvestigation of the palynology–palaeobotany of these strata, during which we discovered new dispersed spore assemblages that are the first from the coastal type section. In addition, we review the available detrital zircon age data and, in conjunction with an assessment of the newly acquired spore assemblages, provide a discussion of the likely age of the Stonehaven Group.

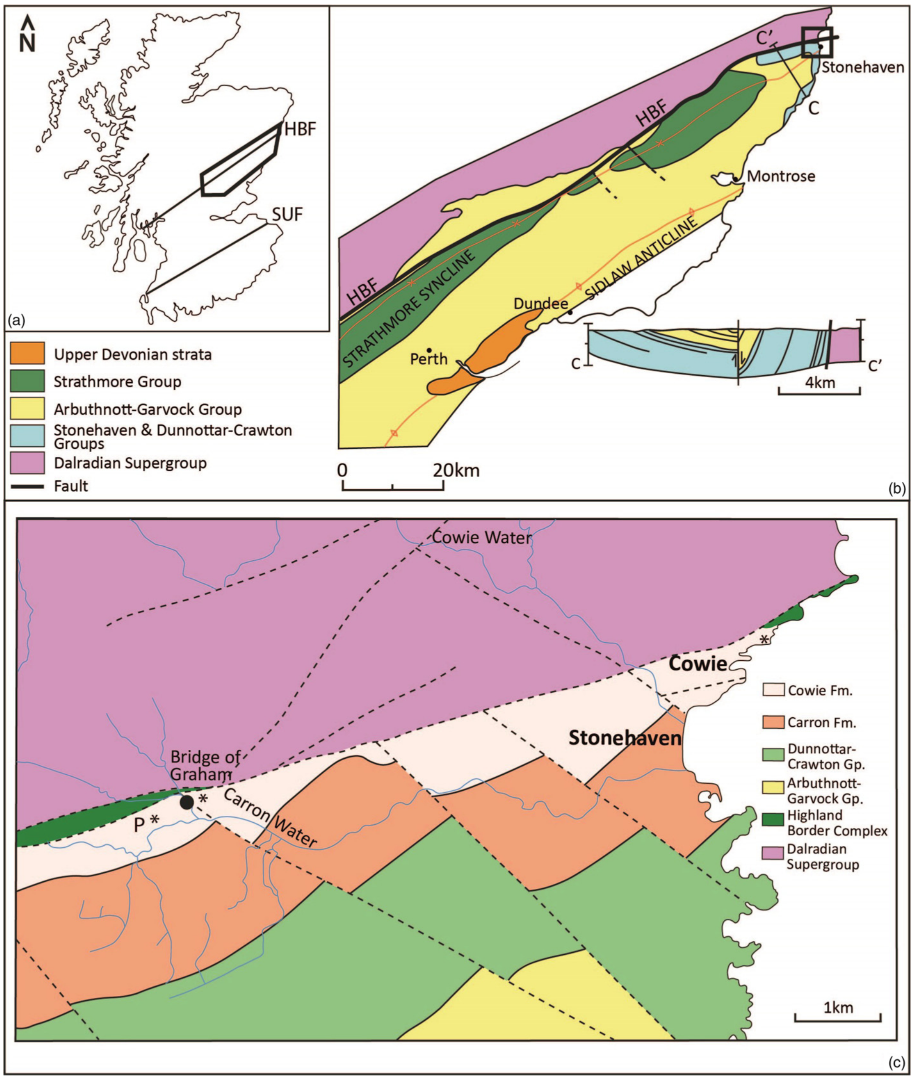

Fig. 1. Locality and geological maps of the Stonehaven Group outcrop and adjacent strata. (**a**) Map of Scotland showing the position of the Midland Valley bounded by the Highland Boundary Fault (HBF) and Southern Upland Fault (SUF). (**b**) Geological map of the demarcated area in (**a**) showing the 'Lower Old Red Sandstone' and adjacent deposits in the NE Midland Valley of Scotland. A geological section C–C' is provided. (**c**) Geological map of the area demarcated in (**b**) showing a more detailed geological map of the Stonehaven Group outcrop. Asterisks mark the location of palynological samples from the coast near Cowie and inland at the Bridge of Graham and on Carron Water. Asterisk marked with a P indicates the location of the plant megafossil assemblage along Carron Water west of Tewel. Sources: figure modified from Shillito and Davies (2017) and McKellar and Hartley (2020).

Methods

Palynology

Numerous samples for palynological analysis have been collected from throughout the outcrop of the Stonehaven Group during numerous field trips since 1990. For each sample 20 g of fresh rock was cleaned and demineralized using standard palynological HCl–HF–HCl maceration techniques. Sieving was undertaken using a 20 µm mesh. The residue was then subjected to heavy mineral separation, using zinc chloride, to remove any remaining mineral matter. The residues were strew mounted onto glass coverslips and attached to glass slides using epoxy resin. The new productive samples described in this paper were recovered from the coastal type section of the Stonehaven Group from (1) a grey sandy-siltstone exposed in the wave-cut platform [grid reference HO88290/87036] and (2) a large (20 cm) clast of dark grey siltstone within a sandstone [grid reference HO88420/07136] (see Figs 1–3). These strata belong with the Castle of Cowie Member of the Cowie Formation. These are the first palynological assemblages to be recovered from the coastal type section of the Stonehaven Group. They are clearly continental in origin and contain only land plant spores and phytodebris. The palynomorphs are moderate to well preserved and of moderate thermal maturity (Thermal Alteration Index (TAI) = 3 based on the standard colour scheme of Traverse 2007). Oxidation for 20 min in fresh Schultz solution lightened the palynomorphs to a translucent brown suitable for light microscope analysis. All materials are curated in the Centre for Palynology of the University of Sheffield.

Palaeobotany

Land plant megafossils were collected from a small temporary quarry exposed in the north bank of Carron Water at the root base of a tree that had fallen [grid reference NO82173/85182]. All slabs containing plant megafossils are curated in the Centre for Palynology of the University of Sheffield.

Radiometric age dating

Zircon U–Pb age data were obtained from the analyses conducted by McKellar (2017), and a brief description of the method is provided here. Arbitrary and presumed representative zircons were hand-picked from four bulk heavy mineral samples and mounted on double-sided tape for analysis (NO88648725, Cowie Sandstone Fm (just above the basal unconformity); NO88518720, Castle of Cowie Mb, Cowie Sandstone Fm; NO88168678, Cowie Sandstone Fm; NO87948519, Carron Sandstone Fm, Stonehaven Harbour). U–Pb data were acquired via laser ablation single collector magnetic sector field inductively coupled plasma mass spectrometry at the Central Analytical Facility, Stellenbosch University, South Africa. All age data referenced here were obtained by single-spot analyses with spot diameters of 30 µm and crater depths of 10–15 µm. The 91500 zircon reference was used for quality control analyses, and the results were consistently in excellent agreement with published isotope dilution thermal ionization mass spectrometry ages. Concordia ages were obtained using Isoplot/Ex 3.0. A full

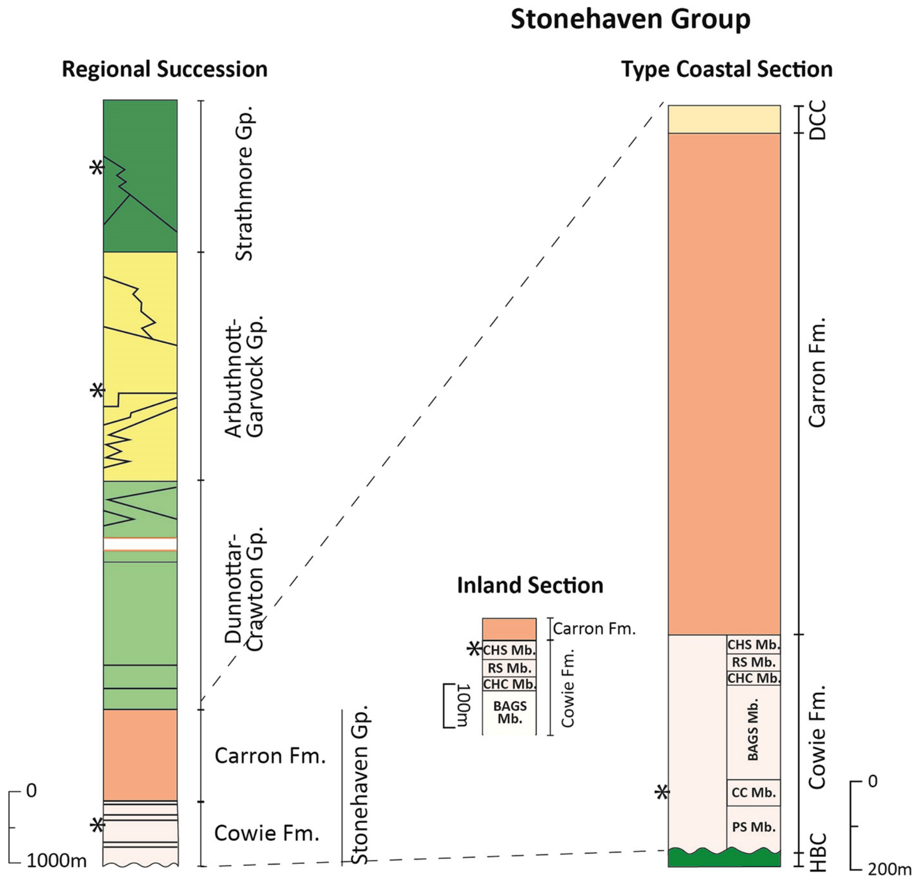

Fig. 2. Stratigraphic sequence of the 'Lower Old Red Sandstone' deposits of the Strathmore Basin in the northern Midland Valley of Scotland. Asterisks mark the presence of fossiliferous horizons in the Cowie Formation of the Stonehaven Group (Cowie Harbour Siltstone Member and Castle of Cowie Member), Arbuthnott–Garvock Group and Strathmore Group, which all yield fishes, arthropods, plants and dispersed plant spores. Relative thicknesses for the inland exposures are estimated from geological mapping. PS Mb., Purple Sandstone Member (includes Basal Breccia Member); CC Mb., Castle of Cowie Member; BAGS Mb., Brown and Grey Sandstone Member; CHC Mb., Cowie Harbour Conglomerate Member (= Volcanic Conglomerate Member); RS Mb., Red Sandstone Member; CHS Mb., Cowie Harbour Siltstone Member (= *Dictyocaris* Member) (includes Cowie Harbour Fish Bed); HBC, Highland Border Complex; DCC, Dunnottar–Crawton Group.

description of methods used for analysis and data processing has been given by McKellar *et al.* (2020).

Results

Palynological analysis

The newly discovered dispersed spore assemblages are dominated by moderate- to well-preserved spores of thermal maturity TAI = 3 (Traverse 2007) and phytodebris (cuticle-like sheets and tubular structures, including banded tubes) (Wellman 1995) (Fig. 4; Table 1). Although less well preserved than the previously described dispersed spore assemblage it is clear that all are very similar in composition and belong with the *brevicosta–verrucatus* Zone of Burgess and Richardson (1995), indicating a late Wenlock (Homerian) age. The smaller number of taxa reported in the new assemblages may reflect poorer preservation (most likely) or the fact that they are from slightly lower in the sequence and slightly older (less likely). Thus the spore-bearing inland exposures (which contain rare biota) can be directly correlated with the type section for the Stonehaven Group, which is better exposed along the coast and yields more abundant biota. The dispersed spore zonation scheme developed for the Silurian is based largely on investigations from the independently age-constrained type sections for the Llandovery, Wenlock and Ludlow Series (Burgess 1991; Burgess and Richardson 1991, 1995) and has subsequently been utilized throughout Avalonia, Laurentia and Baltica, and indeed worldwide, and shown to be highly reliable (Wellman *et al.* 2013).

Palaeobotanical analysis

The siltstones–fine sandstones of the newly discovered plant bed were extensively quarried and found to contain numerous horizons covered in plant debris (so-called 'tea leaf beds'). A single bifurcating plant axis was discovered (Fig. 4) that is notable for its small size. In fact, all (unbranching) axes that were present are of this size with none more than 1 mm in diameter. The plant debris is associated with *Dictyocaris* remains, as is the case in the coastal exposures of the Cowie Harbour Siltstone Member (= *Dictyocaris* Member) (which contains the Cowie Harbour Fish Bed). Campbell (1913) and most subsequent workers mapped the inland exposures in this area as correlatives of the *Dictyocaris* Member exposed in the coastal section. Strata from near this locality have also yielded a fish spine (Campbell 1913).

Zircon analysis

The results of the palynological and palaeobotanical analyses were considered alongside previously published zircon U–Pb data (McKellar 2017; McKellar *et al.* 2020). Zircon data were derived from four samples collected from the Stonehaven Group for detrital zircon geochronology, three of which were obtained from the basal section of the Cowie Formation and one from the overlying Carron Formation. A total of 456 grains from the four samples yielded 427 concordant (90–110%) analyses that fall into three main age groups: Archean ($n = 11$, 2.6% of all analyses), Proterozoic ($n = 329$, 77.0% of all analyses) and Phanerozoic ($n = 87$, 20.4% of all analyses). All samples have a marked absence of zircon grains aged *c.* 2500–2100 and 800–600 Ma. The lowermost sample from the basal Cowie Formation is dominated by Phanerozoic zircon grains aged between 512 ± 5 and 439 ± 4 Ma, whereas the remaining three samples are dominated by Proterozoic and Phanerozoic grains aged between 2882 ± 20 and 430 ± 6 Ma. The presence of common age peaks among the samples and the similarities in broad temporal trends (e.g. limited Archean grains) suggests that the data are largely representative of the Stonehaven Group as a whole. The Sheinwoodian–Homerian boundary is currently considered to be 430.5 Ma.

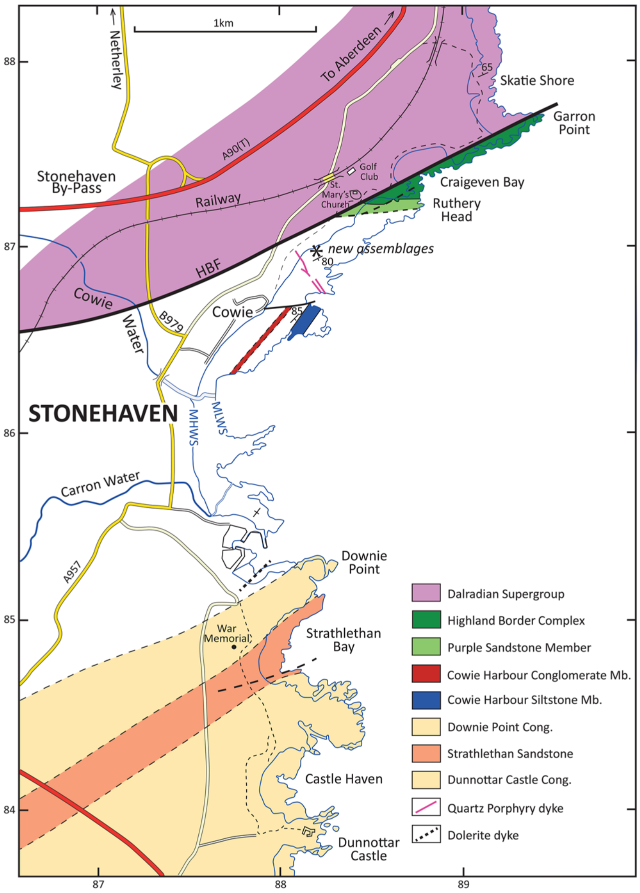

Fig. 3. Geological map of the coastal type section of the Stonehaven Group. The Stonehaven Group outcrop between the Highland Boundary Fault (HBF) and Highland Border Complex to the north and Downie Point Conglomerate to the south is uncoloured except for important marker horizons. The location of the new dispersed spore assemblages is indicated with an asterisk. MHWS, mean high water springs; MLWS, mean low water springs. Source: after Gillen and Trewin (1987).

Discussion

Confirmation of the age of the Stonehaven Group biota is hugely significant in terms of our understanding of the earliest terrestrial ecosystems. The dispersed spore assemblages are composed entirely of non-marine forms (dispersed spores and phytodebris) and represent an extremely rare example of a pre-Devonian spore assemblage from continental deposits (Wellman *et al.* 2013). Although associated sediments contain abundant plant fragments, plant axes are exceedingly rare and constitute diminutive axes, with a solitary bifurcating example, only millimetres in size (Fig. 4). The size of these axes is entirely consistent with a Late Silurian age. Plants of Early Devonian (Lochkovian) age include much larger forms, such as those reported from higher in the sequence from the Arbuthnott–Garvock Group (e.g. Edwards 1975). Larger 'patches' of plant material that are not axial in nature occur in the Stonehaven Group and probably represent microbial mats (Tomescu *et al.* 2006) and/or nematophyte remains (Lang 1926).

The fauna of the Cowie Harbour Fish Bed (Table 2) consists of fish and arthropods (eurypterids, myriapods and potential phyllocarid crustaceans). Although most of the specimens have been recovered from the Cowie Harbour Fish Bed in the coastal section, it is important to note that fish spines are reported from inland exposures in the Carron Water west of Tewel (Campbell 1913) and in Tewel Burn (= Burn of Graham) (Westoll 1945). The Carron water outcrop is the same horizon from which we recovered the bifurcating plant axis that is associated with abundant *Dictyocaris*. The Tewel Burn outcrop is from where the original dispersed spore assemblage was recovered (Wellman 1993). All of the taxa reported from the Stonehaven Group have more in common with Silurian forms from coeval continental strata in the Anglo-Welsh Basin, UK to the south (Edwards and Richardson 2004) and Ringerike, Norway to the north (Bremer *et al.* 2019). Indeed, initial age determinations for the Cowie Harbour Fish Bed, prior to the recovery of spore evidence, almost universally suggested a late Silurian ('Downtonian' = Pridoli) age based on comparisons with fish–arthropod biotas (Campbell 1913; Westoll 1945, 1951). The palynological age date is clearly more compatible with the composition of the fish–arthropod fauna. Fish–arthropod biotas from higher in the sequence, from the famous Early Devonian (Lochkovian) deposits of the Arbuthnott–Garvock Group (Fig. 2), are notably more diverse and evolutionarily 'advanced' (Dineley 1999), as are also the plants (Edwards 1975) and dispersed spores (Richardson *et al.* 1984; Lavender and Wellman 2002).

Radiometric age constraints are scarce in the Lower Old Red Sandstone of the Midland Valley; however, the results of previous geochronological analyses (Thirlwall 1983, 1988) indicate that volcanic rocks in the northern Midland Valley Basin were emplaced during the earliest Devonian. The Lintrathen Tuff Member (previously the Lintrathen Porphyry or Lintrathen Ignimbrite) has been assigned to the top of the Crawton Volcanic Formation of the Dunnottar–Crawton Group (Browne *et al.* 2002) and has yielded a Rb–Sr age of 415.5 ± 5.8 Ma (Thirlwall 1988). Thirlwall also reported Rb–Sr ages of 410.6 ± 5.6 and 411.4 ± 5.6 Ma for rocks from the Ochil Volcanic Formation at the bottom of the Arbuthnott–Garvock Group (Thirlwall 1988), which are consistent within error with the age obtained for the Lintrathen Tuff Member and support an Early Devonian age for the emplacement of these intercalated volcanic rocks, probably near the Silurian–Devonian boundary (Richardson *et al.* 1984). As such, the majority of the Dunnottar–Crawton Group and the Stonehaven Group, which have a thickness of at least 4 km, must have been deposited before this time.

Detrital zircon populations can be used to estimate the maximum depositional ages of strata, where robust radiometric constraints are unavailable, by obtaining the ages of the youngest grains within strata (Rainbird *et al.* 2001; Brown and Gehrels 2007). However, the accuracy of such estimates relies on the means used to obtain the youngest grain ages. Four methods (i.e. youngest single-grain age, youngest graphical age peak, mean age of the two (or more) youngest grains that overlap at 1σ and mean age of the three (or more) grains that overlap at 2σ) have been investigated in a previous study (Dickinson and Gehrels 2009). Single-grain ages were found to yield the least statistically robust maximum depositional ages owing to the possibility that ages are affected by common Pb loss; therefore, they should be used with caution. Youngest single-grain ages of 413.7 ± 4.4 and 414.3 ± 7.1 Ma have been reported from strata immediately below and above the Cowie Harbour Fish Bed (Suarez *et al.* 2017), thus suggesting a Lower Devonian (Lochkovian) maximum depositional age for the Cowie Sandstone Formation. There is, however, some uncertainty with these data as they are based on a limited number of single-grain zircon ages that may not account for common Pb loss, which can produce an anomalously young age. In addition, detailed examination of the zircon age data provided by Suarez *et al.* (2017) reveals that when error limits are taken into account, only two of the 74 single-grain zircon dates yielded a unique Devonian age, four grains are late Silurian in age and the remainder are mid-Silurian or older in age. The single-grain zircon ages of Suarez *et al.* are also inconsistent with the Rb–Sr ages determined for volcanic rocks in the younger Dunnottar–Crawton and Arbuthnott–Garvock groups discussed above (Thirlwall 1983, 1988), which are separated from the Cowie Harbour Fish Bed by several kilometres of sedimentary and volcanic strata (Armstrong and Paterson 1970; Browne *et al.* 2002; McKellar and Hartley 2020; McKellar *et al.* 2021).

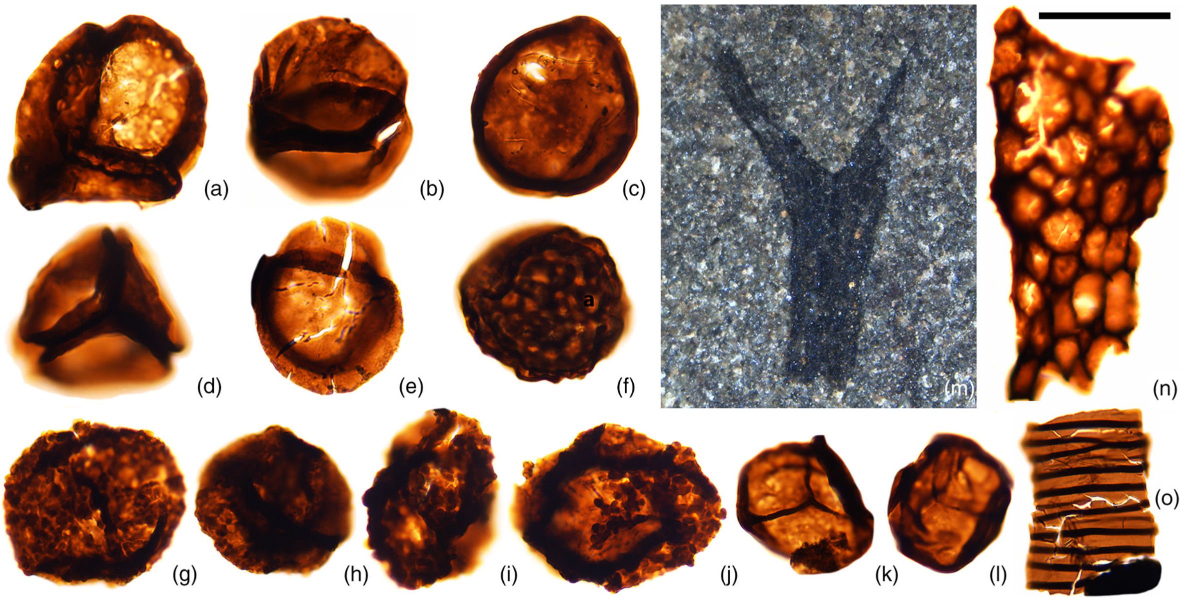

Fig. 4. Dispersed spores (**a–l**), plant megafossil (**m**) and phytodebris (**n**, **o**) from the Stonehaven Group. Palynomorphs are located by slide number followed by England Finder number (in parentheses following each fossil identification). Scale bar represents 30 µm (**a–l**), 1.8 mm (**m**) or 40 µm (**n**, **o**). (**a**) *Tetrahedraletes medinensis* (Strother and Traverse) Wellman and Richardson (1993) (21SCOT13.2, J46). (**b**) *Dyadospora murusdensa* (Strother and Traverse) Burgess and Richardson (1991) (21SCOT13.2, E46). (**c**) *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson (1991) (21SCOT13.R, W32). (**d**) *Cheilotetras caledonica* Wellman and Richardson (1993) (21SCOT13.1, G47/3). (**e**) *Pseudodyadospora petasus* Wellman and Richardson (1993) (21SCOT13.1, V44). (**f**) Hilate cryptospore with reticulate ornament. Pyrite damage has enhanced the reticulation but its original form is evident (21SCOT13.2, H42). (**g**) *Hispanaediscus wenlockensis* Burgess and Richardson (1991) (21SCOT13.1, H42/3). (**h**) *Hispanaediscus wenlockensis* Burgess and Richardson (1991) (21SCOT13.1, H44/3). (**i**) *Hispanaediscus lamontii* Wellman (1993) (21SCOT13.R, S42/3). (**j**) *Hispanaediscus lamontii* Wellman (1993) (21SCOT13.1, U42/1). (**k**) *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister (1969) (21SCOT13.2, N38). (**l**) *Ambitisporites avitus* Hoffmeister (1959) (21SCOT13.1, O43/1). (**m**) Plant megafossil represented by a simple bifurcating axes. (**n**) Banded tube (21SCOT13.1, P44/4). (**o**) Cuticle-like sheet (21SCOT13.1, M32).

In contrast, the youngest single-grain zircon ages derived from the four samples obtained from the Stonehaven Group by McKellar *et al.* (2020), which are based on >100 grains per sample, are 439 ± 4, 478 ± 4, 470 ± 7 and 430 ± 6 Ma (in ascending stratigraphic order), the latter two of which were collected from strata below and above the Cowie Harbour Fish Bed, respectively. These ages are markedly older than those given by Suarez *et al.* (2017), suggesting that an Early Devonian maximum depositional age is unlikely for the Stonehaven Group as a whole. Furthermore, youngest single-grain ages of 478–430 Ma are consistent with derivation from magmatic rocks that were emplaced in Dalradian-like strata during the Grampian and earliest Scandian events (Oliver *et al.* 2008), which is in agreement with the main provenance of the Lower Old Red Sandstone of the northern Midland Valley Basin (Davidson and Hartley 2010; Hartley and Leleu 2015; McKellar *et al.* 2020, 2021). Given the provenance of the Stonehaven Group strata, the lack of robust constraints on an Early Devonian maximum depositional age, the radiometric ages derived from the Dunnottar–Crawton and

Table 1. Spore taxa recovered from the Stonehaven Group

Spore taxon	A1	A2
Ambitisporites avitus Hoffmeister, 1959	X	X
Ambitisporites dilutus (Hoffmeister) Richardson and Lister, 1969	X	X
Synorisporites spp.	X	
Archaeozonotriletes chulus (Cramer) Richardson and Lister, 1969	X	X
Chelinospora? sp. A	X	
Cymbosporites sp. A	X	
Laevolancis divellomedium (Chibrikova) Burgess and Richardson, 1991	X	X
Laevolancis plicata Burgess and Richardson, 1991	X	X
Artemopyra brevicosta Burgess and Richardson, 1991	X	
Artemopyra sp. A Burgess and Richardson, 1991	X	
Hispanaediscus lamontii Wellman, 1993	X	X
Hispanaediscus verrucatus? (Cramer) Burgess and Richardson, 1991	X	X
Hispanaediscus wenlockensis Burgess and Richardson, 1991	X	X
Dyadospora murusattenuata (Strother and Traverse) Burgess and Richardson, 1991	X	X
Dyadospora murusdensa (Strother and Traverse) Burgess and Richardson, 1991	X	X
Pseudodyadospora petasus Wellman and Richardson, 1993	X	X
Cheilotetras caledonica Wellman and Richardson, 1993	X	X
Tetrahedraletes medinensis (Strother and Traverse) Wellman and Richardson, 1993	X	X
Murornate permanent tetrads	X	

A1, Assemblage 1 from Bridge of Graham inland exposure (Wellman 1993); A2, Assemblage 2 from the new coastal localities.

Table 2. Fish–arthropod taxa reported from the Cowie Harbour Fish Bed

Fishes
Hemiteleaspis heintzi Westoll, 1945
(a non-cornuate osteostracan; the non-cornuate osteostracans are predominantly Silurian in age)
Traquairaspis campbelli Traquair, 1912
(a traquairaspid heterostracan; there are many species of this genus, mostly known from the Late Silurian of the Welsh Borderland)
Cowielepis richiei Blom, 2008
(a birkeniid anapsid; most birkenids are Silurian in date, with articulated forms known from the late Silurian of Scotland and Ringerike in Norway)
Arthropods (eurypterids and *Dictyocaris*)
Nanahughmilleria norvegica Kiær, 1911
(a eurypterid species that also occurs in the Silurian of Ringerike, Norway)
Dictyocaris slimoni Salter, 1860
(an enigmatic taxon possibly representing a phyllocarid arthropod; this taxon is also found in the Silurian rocks of Lesmahagow, Scotland and Ringerike, Norway)
Arthropods (myriapods)
Albadesmus almondi Wilson and Anderson, 2004
Cowiedesmus eroticopodus Wilson and Anderson, 2004
Pneumodesmus newmani Wilson and Anderson, 2004

Fish data from Campbell (1911, 1912, 1913), Traquair (1912), Westoll (1945, 1951), White (1946, 1950), Ritchie (1960, 1964), Janvier (1981), Dineley (1999) and Blom (2008). Arthropod data from Kiær (1911), Salter (1860), Størmer (1935) and Wilson and Anderson (2004).

Arbuthnott–Garvock groups, and the *c.* 4 km thickness of the dividing strata, a Silurian maximum depositional age for the Cowie Sandstone Formation is indicated.

Conclusions

- The basal upper Silurian–Lower Devonian 'Lower Old Red Sandstone' deposits of the Stonehaven Group of the Midland Valley of Scotland are late Wenlock (late Silurian) in age.
- This provides a reliable age constraint for one of the oldest known terrestrial biotas (which includes the oldest reported air-breathing land animal, the myriapod *Pneumodesmus newmani* Wilson and Anderson 2004). It also has implications regarding the early appearance of various ichnofauna (Shillito and Davies 2017).
- The new age constraint is compatible with the geological setting and recent models regarding the timing of terrane accretion and the onset of 'Lower Old Red Sandstone' sedimentation in Scotland.

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Author contributions **CHW**: conceptualization (equal), formal analysis (equal), writing – original draft (lead); **GL**: formal analysis (supporting), writing – original draft (supporting); **ZM**: formal analysis (equal), writing – original draft (supporting); **AH**: conceptualization (equal), formal analysis (equal), writing – original draft (supporting)

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Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability Zircon data are from McKellar (2017) and McKellar *et al.* (2020) and are available upon request.

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