Earliest Carboniferous tetrapod and arthropod faunas from Scotland populate Romer's Gap

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Devonian tetrapods (limbed vertebrates), known from an increasingly large number of localities, have been shown to be mainly aquatic with many primitive features. In contrast, the post-Devonian record is marked by an Early Mississippian temporal gap ranging from the earliest Carboniferous (Tournaisian and early Viséan) to the mid-Viséan. By the mid-Viséan, tetrapods had become effectively terrestrial as attested by the presence of stem amniotes, developed an essentially modern aspect, and given rise to the crown group. Up to now, only two localities have yielded tetrapod specimens from the Tournaisian stage: one in Scotland with a single articulated skeleton and one in Nova Scotia with isolated bones, many of uncertain identity. We announce a series of discoveries of Tournaisian-age localities in Scotland that have yielded a wealth of new tetrapod and arthropod fossils. These include both terrestrial and aquatic forms and new taxa. We conclude that the gap in the fossil record has been an artifact of collection failure.

Ballagan Formation | end-Devonian mass extinction | terrestriality | rhizodonts | lungfish

A wide range of Late Devonian taxa from around the world document the earliest phases of limbed vertebrate evolution close to the fish-tetrapod transition. These animals do not closely resemble modern forms but were fully or partially aquatic, retaining primitive features, such as fish-like bony fin webs on the tail, and where known, the limbs were paddle-like and polydactylous (1). Devonian limbed tetrapods were mainly around 1 to 2 m in size with dorsoventrally compressed heads that were large relative to their snout-vent length (2). By the mid-Carboniferous, terrestrial tetrapods had diversified into a wide range of morphologies and ecologies that are recognizably modern in aspect. By the mid-Viséan, limbs were penta- or tetradactylous, or secondarily reduced or lost, with small limbed forms about 100 mm in length appearing (3). In the amniote stem lineage, heads had become smaller and deeper relative to snout-vent length or skull width, a feature associated with the evolution of costal ventilation (2). Unfortunately, our understanding of the patterns and processes behind their evolution and diversification has long been hampered by a gap in the continental fossil record of many millions of years from the end of the Devonian (359 Ma) through to the mid-Viséan (~365 Ma Early Carboniferous, Mississippian). The hiatus was recognized by A. S. Romer in 1956 (4). At the time he was writing, it represented a period of about 30 million years covering almost the entire Tournaisian and Viséan stages. Although a few tetrapods from Asbian-age (late Viséan) localities were known (5), their aberrant aspect and aquatic habits did not cast direct light on the earliest phases of tetrapod terrestrialization. Over recent decades, the gap has been narrowed to about 15 million years by the discovery of many new finds from the earlier half of the Viséan. Terrestrial assemblages of tetrapods from the mid-late Viséan (Asbian/Brigantian) have been discovered that, according to many analyses, include basal members of the crown group of tetrapods (6–10). Alternative phylogenies, despite differing in major respects from the above, likewise place the origin of the crown group no later than the mid-Viséan (11, 12). Among recent discoveries from the mid-Viséan is the small amniote-like *Casineria kiddi* (3) documenting the earliest known pentadactyl forelimb. Thus, although the "gap" is closing, we have lacked information about the crucial early part of the period during which terrestriality, defined simply as the ability to support the body and locomote completely out of water, may have been achieved.

Among several explanations for the hiatus is one that took the fossil record to reflect the actual pattern of evolution, marked by the absence of animals from terrestrial ecosystems (13). Recent work has also documented a dramatic changeover in global vertebrate faunal assemblages, coinciding with the end-Devonian mass extinction (EDME) that wiped out many vertebrate groups (14). The EDME (Hangenburg crisis) was driven by a severe glacial episode during which regression and low-latitude continental aridity were followed by a significant marine transgression (Hangenburg Black Shale) that caused ecosystem collapse (15). Among the vertebrate groups affected were many major aquatic forms, such as the placoderms, acanthodians, and several sarcopterygian groups, which, if not entirely exterminated, were seriously reduced in abundance (14). Subsequently, other groups, such as actinopterygians, chondrichthyans, and ultimately tetrapods, increased in numbers and diversity to produce a faunal balance more like that of today (14). How atmospheric or climatic conditions affected all these faunal changes remains to be tested.

The reestablishment of both aquatic and terrestrial ecosystems, as well as their component faunas and floras, following the EDME is a phenomenon of great evolutionary significance. By the mid-Viséan, tetrapods that are generally considered to have been terrestrial had appeared (8–10) and the base of the crown group had been founded. Unfortunately, we are currently largely ignorant of the exact chronology and dynamics of these early phases of terrestrialization and diversification in tetrapod evolution. To discover significant numbers of fossil sites representing this period would mark a major breakthrough in our understanding of this crucial period in Earth history.

Results

We report the discovery of a suite of tetrapod fossils from four localities in southern Scotland, dated as Tournaisian (16–19), of which three have also yielded terrestrial arthropods. These localities are the coastal section at Burnmouth north of Berwick on Tweed, the banks and bed of the Whiteadder River near Chirnside, the banks of the Tweed River near Coldstream (all

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Data deposition: Some fossil material has been placed in the University Museum of Zoology, Cambridge, and some will be placed in the National Museum of Scotland.

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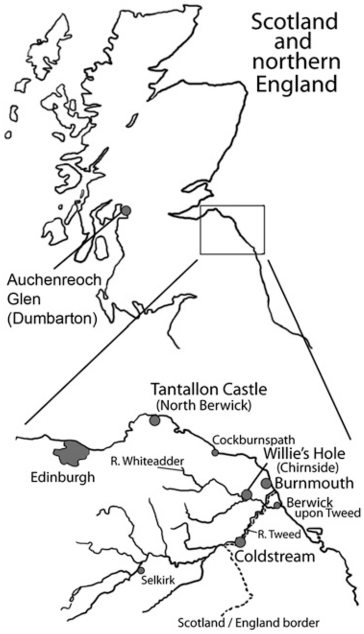

Fig. 1. Map of southern Scotland and northern England to show the locations of Tournaisian sites in Scotland. Large gray circles represent sites, and small gray circles represent other towns.

Tweed basin, Borders Region), and the sedimentary strata near Tantallon Castle on the south shore of the Firth of Forth (Midland Valley basin, East Lothian Region) (Fig. 1). In addition, two previously known Tournaisian localities have yielded tetrapod fossils: Dumbarton in western Scotland and Blue Beach near Horton Bluff in Nova Scotia. These augment the scope of our discoveries and help to give a fuller picture of events. Our discoveries strongly suggest that the apparent gap in the fossil record does not reflect an accurate pattern of evolutionary events but has been the result of the lack of, or at least the lack of successful, collecting effort from appropriate sedimentary rocks and localities (16, 17).

All but the Nova Scotia site derive from the Tournaisian argillaceous dolostone-bearing mudstone succession of Scotland. Formerly known as the Cementstone Group (the lower part of the Calciferous Sandstone Measures in Scotland), these rocks have now been assigned to the Ballagan Formation [Inverclyde Group (19)]. Most belong to the claviger-macra (CM) palynozone, dated as 348 to 347.6 Ma (20). The Blue Beach deposits are dated as pretiosus-clavata (PC) palynozone, late Tournaisian (21), approximately contemporary with or slightly earlier than the Scottish localities.

Burnmouth. The sedimentary rocks consist of a succession of near-vertical strata passing up the sequence from west to east. The oldest bed so far dated is verrucosus-incohatus (VI) palynozone, and the sequence records a conformable (although condensed) series of time slices through the Tournaisian, although the Devonian-Carboniferous boundary and the base of the Tournaisian may not be present. An Old Red Sandstone facies (possibly Kinnesswood Formation) marks the base of the succession, but its relation to the Tournaisian strata is uncertain. These strata are overlain by the Viséan Fell Sandstone Formation. The Ballagan Formation as exposed at Burnmouth dominantly comprises mudstone, with interbedded sandstone and thin beds of "cementstone," and represents cyclical deposition. Plant material from some beds has been described previously (22), and the presence of a few "fish" fragments has been noted (19, 23).

The sequence has now yielded isolated and partially associated tetrapod, lungfish, and arthropod material, including, unusually for Early Carboniferous deposits, small individuals. Tetrapod remains have so far been recorded in five different horizons in circa 40 m of strata exposed in the upper third of the sequence. The most significant of these is a small (10 mm across the metapodial series) pentadactylous autopod (identity as manus or pes cannot yet be determined). It derives from a horizon a few meters above one that has been dated as CM palynozone. Its morphology strongly suggests that its owner was a terrestrial tetrapod [specimen University Museum of Zoology Cambridge (UMZC) 2011.8] (Fig. 2). The proportions of the metapodials and preserved phalanges, being elongate and gracile, are most similar to those of the Viséan forms *Silvanerpeton*, *Eldeceeon*, and *Balanerpeton*, as well as the Late Carboniferous anthracosaur *Gephyrostegus*, all of which are usually considered to have been terrestrial (8, 24). They are quite unlike those of other Early Carboniferous forms, such as *Pederpes* (25, 26), *Crassigyrinus* (27), *Greererpeton* (28), or *Proteroygyrinus* (29).

Two or three meters above this, a partial *Crassigyrinus*-like jaw (specimen UMZC 2011.9.1) (Fig. 2), a large rhizodont shoulder girdle (specimen UMZC 2011.9.3), numerous large lungfish elements (e.g., specimens UMZC 2011.9.6–7), and *Gyracanthus* spines have been found, together with a wealth of fossil charcoal. *Crassigyrinus* is a large tetrapod previously known only from the late Viséan and early Namurian of Scotland (30, 31). The newly discovered jaw ramus is almost exactly the same size as the known specimens, has almost identical external ornamentation,

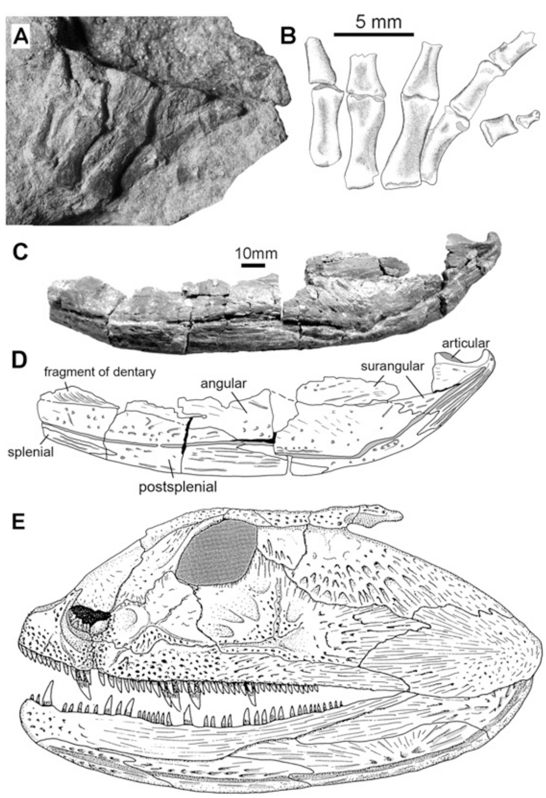

Fig. 2. Burnmouth specimens. (*A* and *B*) Pentadactylous autopod (specimen UMZC 2011.8). *A* and *B* are to the same scale. (*A*) Photograph. (*B*) Interpretive drawing. (*C*) Photograph of a *Crassigyrinus*-like partial lower jaw (specimen UMZC 2011.9.1) in an external view. Anterior end and tooth-bearing bones are missing. (*D*) Interpretive drawing of the specimen. (*E*) Reconstruction of the skull of *Crassigyrinus scoticus* from the Viséan of Scotland (based on ref. 31) to the same scale as the lower jaw in *C*.

and differs from the known specimens in only minor details of the internal structure. This gives *Crassigyrinus* a temporal distribution comparable to that of the whatcheeriid family, which occurs at Blue Beach (32). This Burnmouth horizon confirms the presence, by this early date, of large vertebrates whose affinities are with later Carboniferous rather than Devonian forms.

Willie's Hole Near Chirnside. Gently dipping Ballagan Formation strata, consisting of sandstones, mudstones, shales, and thin cementstones, crop out in the bed of the River Whiteadder (19). From it, three separate conformable horizons have yielded a wealth of tetrapods, rhizodonts, lungfish, actinopterygians, *Gyracanthus* spines, myriapods, crustaceans, scorpions, and eurypterids. The base of the tetrapod-bearing sequence is the Willie's Hole Shrimp Bed (33). This gray mudstone contains predominantly plant remains (bed 3). A second gray mudstone unit separates it from an overlying second tetrapod-bearing horizon (bed 2). This dark siltstone contains tetrapods, lungfish, rhizodonts, and arthropods, the richest of the three horizons. Above that is a third horizon yielding mainly actinopterygians (bed 1, Fig. 3 *A* and *B*). The site is about 2 miles from the contemporary locality of Foulden, which does not preserve tetrapods but includes many fish taxa common between the two sites (34).

Dated as the lower part of the CM zone, the Willie's Hole succession represents a whole ecosystem changing through time. The tetrapod collection includes about 100 samples of large and small semiarticulated tetrapod skeletons and isolated bones.

One of the small individuals (specimen UMZC.2011.7.2, new taxon A) is one of the few tetrapod specimens to have been recovered from the horizon of bed 1. A small individual, it preserves a lower jaw, representing a skull about 75 mm long, with enough of the cheek preserved to allow a provisional skull reconstruction (Fig. 4). There are also two sclerotic plates and numerous elongate gastral scales. The reconstructed skull has a deep quadratojugal, a large squamosal, and a narrow suborbital process to the jugal underlying a large orbit, consonant with the 4-mm-long sclerotic plates. The snout is short, and the teeth are conical but with "labyrinthodont" enamel. Its proportions most closely resemble those of the Viséan *Silvanerpeton* (35) or the Late Carboniferous *Gephyrostegus* (24). The specimen preserves a disrupted but probably pentadactyl manus, of which the metacarpal and phalangeal proportions are quite different from those of specimen UMZC.2011.8, in being short and squat (Fig. 4). These proportions also rule out its identity as either of the latter named genera. Its distinct dermal sculpturing and well-ossified phalanges suggests that it was not a juvenile of one of the larger forms.

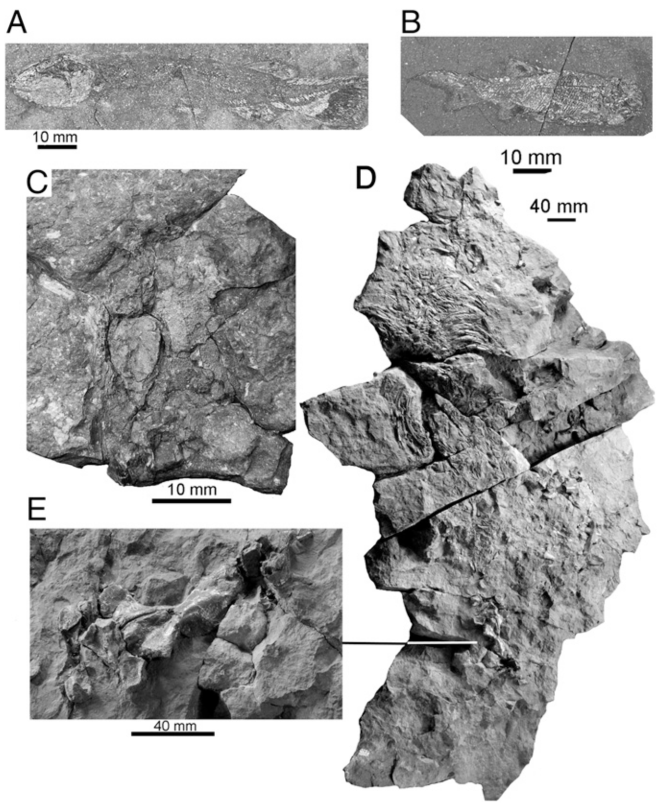

Fig. 3. Willie's Hole specimens. (*A*) Actinopterygian *Phanerosteon ovensi* (UMZC 2011.7.11). (*B*) Actinopterygian *Aetheretmon valentiacum* (UMZC 2011.7.12). (*C–E*) Willie's Hole Level 2 specimens. (*C*) Skull in natural mould showing orbit and outline of skull (SPW 4034). (*D*) New tetrapod taxon B "Ribbo" (SPW 4165). (*E*) Inset showing femur, tibia, and fibula.

Bed 2 has yielded by far the majority of tetrapod remains, including several semiarticulated skeletons and numerous isolated bones. One of the largest specimens [specimen from the collections made by S.P.W. (SPW) 4165, new taxon B] from this bed preserves a disrupted postcranial skeleton with conspicuous curved ribs, part of a forelimb, and both hind limbs, with some pedal elements and a few associated skull bones (Fig. 3 *D* and *E*). Although the hind limb elements show some similarities to those of *Pederpes*, the ribs are not flanged as they are in that taxon, and they are longer and more robust in specimen SPW 4165 (26). The hind limb elements are larger, relative to the ribs, than they are in *Crassigyrinus* (27). As the only two comparable taxa from the Early Carboniferous, these differences rule out specimen SPW 4165 as a member of either of these genera, but only further study will elucidate their relationships. A complete description of this specimen should help resolve some of the conflicting positions for *Pederpes* and *Crassigyrinus* at the base of the stem tetrapod tree (6, 7, 35).

An almost complete skull roof is represented by specimen SPW 4034, and it probably represents a further new taxon (Fig. 3*C*). It has a rounded but short snout with large orbits and ornamentation reminiscent of that of a temnospondyl, but only further study could confirm or refute such an assignment. If corroborated, it would represent the earliest member of the group by about 15 million years.

The myriapods (specimen SPW 762 and specimens UMZC 2011.7.2–3, Fig. 5) are among the earliest known from the Carboniferous and probably include two new taxa. The presence of myriapods demonstrates the potential of the site to preserve terrestrial elements of the fauna. Scorpions (specimen SPW G765, Fig. 5), eurypterids, and myriapods have been recovered from bed 2. Bed 3, in addition to plants, yielded tetrapods, a rhizodont, actinopterygians, crustaceans, and two small gastropods.

Coldstream. Fossils include tetrapod skull bones and vertebrae, as well as lungfish and rhizodont elements, *Gyracanthus* spines, and scorpion fragments. The nearby locality of Lennel Braes has yielded the myriapod *Anthracodesmus*, previously dated as Viséan (36) and considered as such by Ward et al. (13). The most recent survey by the British Geological Survey has redated the sequence as Tournaisian (37).

Tantallon Castle, East Lothian. Sedimentary rocks close to the fossil plant localities of Castleton Bay and Oxroad Bay (38) have yielded isolated vertebrate bones and teeth, including tetrapod elements, such as a partial large lower jaw (specimen National Museum of Scotland G 1977.43.3) (39).

Dumbarton, Western Scotland. *Pederpes finneyae*, represented by an almost complete articulated skeleton, is an isolated occurrence in the Ballagan Formation of the area (25, 26). Virtually no other tetrapod or even vertebrate elements have been found there. Its

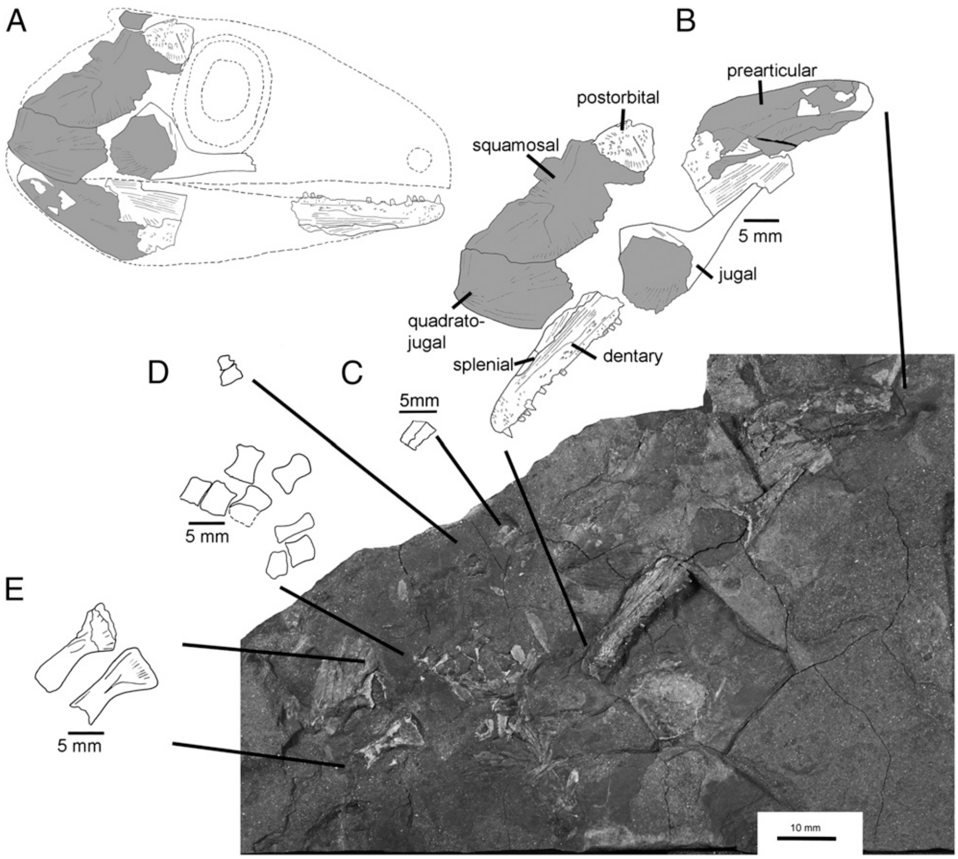

Fig. 4. Willie's Hole, new tetrapod taxon A: UMZC 2011.7.2. A photograph of part of the specimen, with interpretive diagrams from part and counterpart, is shown. (*A*) Reconstruction of skull. (*B*) Diagram of the cheek and lower jaw used to create the reconstruction, in position on the specimen. (*C*) Two sclerotic plates. (*D*) Digit elements as distributed on the specimen. (*E*) Radius and ulna. In *A* and *B*, the gray shading indicates the natural mold.

phylogenetic position is basal to almost all post-Carboniferous tetrapods, with the possible exception of *Crassigyrinus* (6, 7, 31, 35), and it appears to have had hind limbs adapted for walking on land (26). In part, its importance lies in providing identification of isolated elements from other localities, including Blue Beach (32).

Blue Beach, Nova Scotia. Known for many years, this locality has yielded isolated elements, some resembling *Pederpes* and others that are more similar to Devonian forms (32, 40). They may indicate that some known Devonian tetrapod taxa survived the EDME. Equally significant, many horizons yield subaerially produced pentadactyl and tetradactyl tetrapod trackways representing at least six different forms of both large and small animals. Their clarity and depth indicate that the animals could walk unsupported by water. These attest to the great diversity reached by terrestrially capable tetrapods as early as the PC zone (41, 42). There are also large rhizodont and lungfish elements comparable to those in Scotland, as well as actinopterygians. Identification of the some of the isolated bones can be aided by description of the recently discovered Scottish material.

Discussion

The hypotheses put forward by Ward et al. (13) should, in future, be testable against our new records. Those authors associated the absence of fossil tetrapods from this period with a corresponding absence of terrestrial arthropods. By estimating the diversity and origination rates of tetrapods ("stegocephalians" in the authors' terms) and arthropod groups during the Early Carboniferous, they suggested that the lack of fossils was related to low atmospheric oxygen levels pertaining at that time, as modeled by Berner (43). These low levels, it was postulated, inhibited the animals from leaving the water because of poorly developed respiratory structures, and also restricted their diversity.

Our discoveries clearly demonstrate that multiple localities yielding terrestrial arthropods and probably terrestrial tetrapod fossils from the Tournaisian do exist, thus providing evidence that the gap was indeed the result of collection failure. The contention in the study by Ward et al. (13) that tetrapods might have been confined to the water during this time does not explain the existence of the hiatus in fossil discoveries. Most fossil tetrapods are found in deposits laid in aquatic environments, from which they are more, rather than less, likely to be recovered. Furthermore, our recent finds suggest that there may be no need to postulate low atmospheric oxygen levels at this time to explain the absence of fossils. The discovery of charcoal-bearing beds in the Burnmouth sequence challenges some of the implications of the study by Berner (43) with respect to oxygen levels (44).

Our new records, combined with those from trackways, suggest that tetrapods appear to have recovered relatively rapidly from the EDME by the mid-Tournaisian. Fish groups had evolved, or reevolved, into new large forms (e.g., rhizodonts, lungfishes). By the mid-Viséan, not only had tetrapods appeared that are usually considered terrestrial (8–10, 35) and the base of the crown group been established (6–12), but highly specialized secondarily aquatic forms had also evolved (45).

By examining the earlier parts of the Burnmouth sequence, we can test the hypothesis of the "Lilliput effect" (46) on vertebrate evolution; that is, following the EDME, vertebrates underwent an evolutionary stage constrained to small size by adverse conditions, such as aridity or other climatic conditions. We can provide a maximum time (less than 10 million years) by which they had overcome such a constraint.

Rather than beginning immediately following "Romer's Gap," we can now test the hypothesis that diversification and terrestrialization of tetrapods had been taking place during the 15 or more million years that it represents. Our discoveries and other

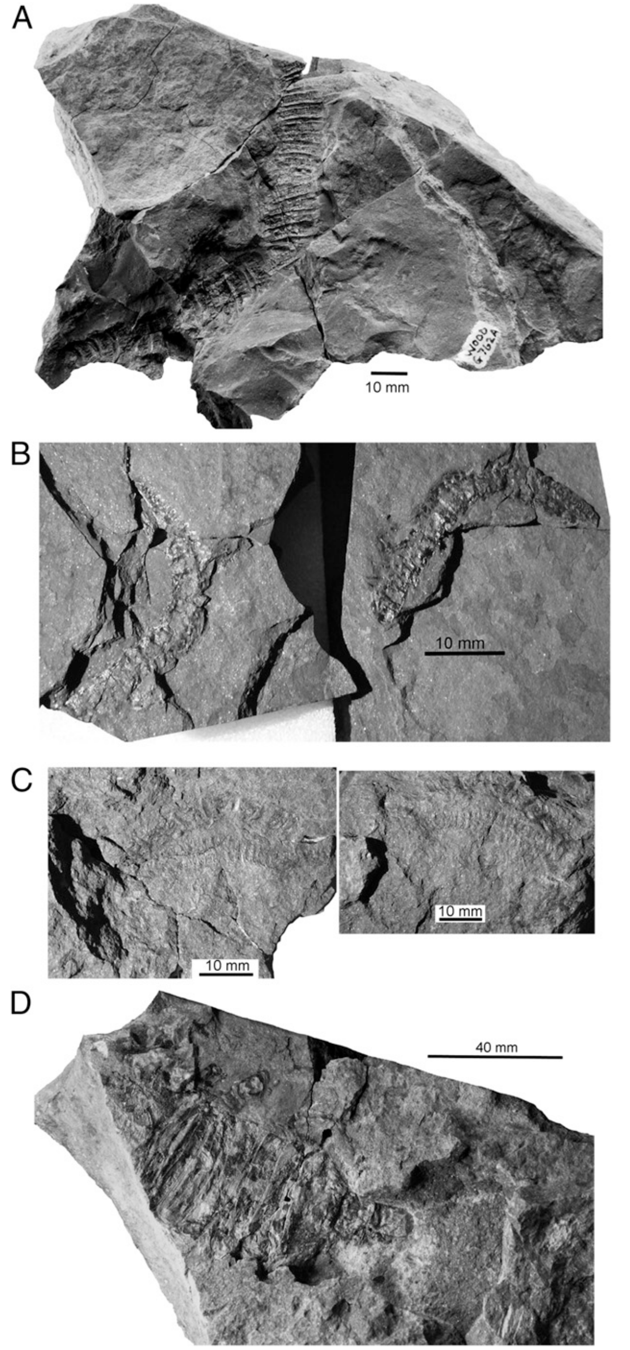

Fig. 5. Willie's Hole arthropods. (*A–C*) Myriapods. (*A*) Specimen SPW 762. (*B* and *C*) Specimens UMZC 2011.3–4 in part and counterpart. (*D*) Scorpion specimen SPW 765.

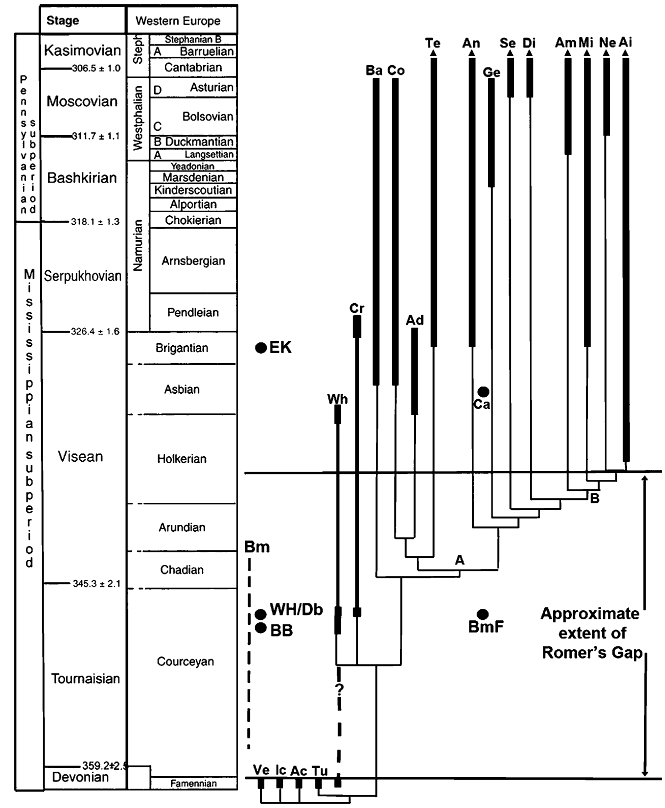

Fig. 6. Carboniferous time scale with superimposed family tree of tetrapods, including recent data on occurrences and allowing for uncertainty in parts of the tree. Arrows at the top of lines indicate that groups persisted into the Permian. The Devonian tetrapod tree is based on the study by Callier et al. (47). The Carboniferous tetrapod tree (6, 7, 35) is shown with the node for the origin of the crown group on those phylogenies marked by A. Alternative phylogenies (11, 12) place the node for the origin of the crown group at B. All phylogenies imply an origin for the crown group no later than the early to mid-Viséan. *Casineria* is placed *incertae sedis* among the stem amniotes, and the Burnmouth foot is placed outside the tree. Whatcheeriids may extend into the Late Devonian (48), "microsaurs" into the Brigantian (49), and *Crassigyrinus* into the Tournaisian (this paper). Dating is according to the study by Gradstein et al. (20). Ad, adelogyrinids; Am, amiotes; An, anthracosaurs; Ai, aïstopods; Ba, baphetoids; BB, Blue Beach; Bm, Burnmouth; BmF, Burnmouth foot; Ca, *Casineria*; Co, colosteids; Cr, *Crassigyrinus*; Di, diadectids; EK, East Kirkton; Ge, gephyrostegids; Mi, microsaurs; Ne, nectrideans; Se, seymouriamorphs; Te, temnospondyls; Wh, whatcheeriids; WH/Db, Willie's Hole/Dumbarton.

recent new records from elsewhere certainly suggest that many tetrapod lineages have their origins much earlier than previously appreciated, and their earliest appearances may well be extended back in time as the result of further research. Fig. 6 shows a family tree against a Carboniferous time scale taking the recently discovered data into account.

These new finds will ultimately throw light on the ecological and environmental circumstances under which the establishment of modern terrestrial faunas took place. The discoveries will allow us to test the hypothesis put forward by Ward et al. (13), following careful phylogenetic as well as diversity and disparity analyses envisaged for the future. These finds will allow us to put forward refined hypotheses, testable by further finds and analyses. The wealth of material from several different sites and environments will provide the opportunity to investigate the causes and consequences of the EDME. Our initial results suggest that reestablishment of at least some components of the tetrapod fauna was achieved within 10 million years. We have established that pentadactyly arose about 20 million years earlier than previously documented (3). Studies may now examine the interlinkage of environmental and atmospheric changes to faunal turnover, the timing of ecosystem recovery, the sequence of acquisition of terrestrial characters by tetrapods, resolution of the problems of relationships among early tetrapods (and thus the recalibration of the phylogenetic tree), and the time of appearance of crown group tetrapods, based on the presence, rather than the absence, of fossil data.

Materials and Methods

T.R.S. prospected, collected, and prepared material, using mechanical and acid digestion techniques, from Burnmouth and Coldstream over a period of 23 y, starting in 1988. S.P.W. prospected, collected, and prepared material, using mechanical, airbrasive, and acid digestion techniques, from Willie's Hole, Burnmouth, and Tantallon Castle. Willie's Hole material was recovered by him from the bed of the River Whiteadder between 2008 and 2009. J.A.C. and R. N. G. Clack collected and prepared material, using mechanical techniques, from Burnmouth in 2010 and 2011. J.E.A.M. provided paleontological analyses and dating of the new sites. Rough-crushed dark mudstone samples were treated with 30% HCl, followed by decant washing with water to neutral and then 60% HF, a further decant washing to neutral, and then sieving at 15 μm. Neoformed fluorides were removed by a single short treatment with hot HCl, followed by a further sieving. The organic residue was then permanently mounted using Elvacite 2044 (Lucite International Ltd.). Photographs were taken by S.P.W., J.A.C., J. Gundry, and R. Stebbings (UMZC), and figures were prepared by J.A.C. Those specimens not already in the possession of the UMZC are being purchased and will be housed by the National Museum of Scotland.

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