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Tetrapod appendicular skeletal elements from the Early Carboniferous of Scotland

Éléments appendiculaires de squelette de tétrapodes en provenance du Carbonifère inférieur d'Écosse

Timothy R. Smithson*, Jennifer A. Clack

University Museum of Zoology, Downing Street, CB2 3EJ Cambridge, UK

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ABSTRACT

Tetrapod postcranial bones are described from Scotland: from the Limestone Coal Group (Early Carboniferous, Serpukhovian) at the Dora open cast site, Fife, and from beds equivalent to the Burdiehouse Limestone (Early Carboniferous, Visean) on the island of Inchkeith, Firth of Forth. The elements from Dora are derived relative to Devonian and Tournaisian tetrapods in having a diamond-shaped interclavicle with no parasternal process, a humerus with a triangular-shaped entepicondyle, a rod-like ilium lacking a post-iliac process and a gracile femur with a prominent internal trochanter but no adductor blade. These bones share characters with their homologues in colosteids and temnospondyls and may be attributable to *Doragnathus woodi*. The femur from Inchkeith most closely resembles that of the embolomere *Proterogyrinus scheelei*.

RÉSUMÉ

Des os postcrâniens de tétrapodes d'Écosse sont décrits: ils proviennent du groupe Limestone Coal (Carbonifère inférieur, Serpukhovien) au site de Dora, Fife, et de dépôts équivalant à la Limestone Burdiehouse (Carbonifère inférieur, Viséen) sur l'île d'Inchkeith, Firth of Forth. Les éléments de Dora sont issus de tétrapodes du Dévonien et du Tournaisien, présentant une zone interclaviculaire en forme de losange, sans processus parasternal, un humérus à entépicondyle triangulaire, un ilium en forme de tige, sans processus post-iliaque, et un fémur gracile avec un trochanter interne proéminent, mais sans lame adductrice. Ces os partagent des caractères avec leurs homologues chez les colostéidés et les temnospondyles et peuvent être attribués à *Doragnathus woodi*. Le fémur d'Inchkeith ressemble davantage à celui de l'embolomère *Proterogyrinus scheelei*.

1. Introduction

Stan Wood's discovery of tetrapod fossils at the Dora open cast site near Cowdenbeath (Fife, Scotland) in 1974

* Corresponding author.
E-mail address: ts556@cam.ac.uk (T.R. Smithson).

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was the first major addition to our knowledge of British Carboniferous tetrapods for nearly a century (Andrews et al., 1977, Smithson, 1985a). Since then, important finds have been made at the Tan Pit Slip open cast site near Wigan, Lancashire (Milner and Lindsay, 1998), the foreshore at Gullane, East Lothian (Paton et al., 1999), the Northumberland coast (Clack, 2003), and most notably at East Kirkton Quarry, near Bathgate, West Lothian, from which many genera have been reported (e.g., Clack, 1998a, 2011; Milner et al., 1986; Rolfe et al., 1994; Wood et al., 1985). Meanwhile, specimens that had not been recognised as tetrapods at the time of collection have been prepared and described including some of the oldest recorded Carboniferous taxa (Clack, 2012; Clack and Ahlberg, 2004; Clack and Finney, 2005). Most recently, new localities in Tournaisian deposits in the Scottish borders have yielded several taxa that are currently under study (Smithson et al., 2012).

Almost all of the tetrapod material collected at the Dora site between 1974 and 1976 has been prepared and described. Seven tetrapod taxa have been identified: *Crassigyrinus* (Clack, 1998b; Panchen, 1985; Panchen and Smithson, 1990), the anthracosaurs *Eoherpeton* (Smithson, 1985b) and *Proterogyrinus* (Smithson, 1986), the baphetid *Spathicephalus* (Beaumont and Smithson, 1998), *Adelogyrinus* (Andrews and Carroll, 1991) and *Doragnathus* (Smithson, 1980). However, several isolated postcranial elements are still awaiting description. Among them are bones that may have formed part of the appendicular skeleton of *Doragnathus woodi*.

Doragnathus woodi was the name given to a number of upper and lower jaw specimens from Dora and a lower jaw from Niddrie (Smithson, 1980). All the specimens are characterized by a marginal dentition comprising a large number of similar sized, sharp, lingually curved teeth. There has been some dispute as to whether *Doragnathus* is a valid taxon. Lebedev (in Lebedev and Clack, 1993 and in Ahlberg et al., 1994) has suggested that *Doragnathus* is synonymous with *Spathicephalus* but this has been refuted by Beaumont and Smithson (1998). *Sigournea multidentata* (Lombard and Bolt, 2006), from the Mississippian (Asbian) of Iowa, USA, although similar in some ways, clearly belongs to a separate taxon, based on differences in the dentition.

The purpose of this paper is to describe the postcranial elements from Dora that may be assignable to *Doragnathus*, and similar material from the Early Carboniferous of Inchkeith, and to compare them with other early tetrapods. These specimens add to the range of morphologies found among Early Carboniferous tetrapod postcrania, and show that diversification of locomotory styles was well under way by this time.

2. Materials and methods

The Dora open cast site material is from the Mississippian Dora Bone Bed horizon (Smithson, 1985a) – (Serpukhovian; equivalent to Pendleian, basal Namurian (Gradstein et al., 2004). For further horizon information and geological details see Smithson (1985a). The specimens were extracted from the bone bed using the "hot water technique" devised by Smithson and Wood (Smithson, in Boyd and Turner, 1980). Remaining matrix was removed using an airbrasive machine and sodium bicarbonate powder.

Inchkeith is a small uninhabitated island in the middle of the Firth of Forth, Scotland. Tetrapod fossils were first reported by Davies (1936) in a review of the geology of the island. An isolated femur was recovered from the north-eastern end of the island in an ashy mudstone that was otherwise devoid of fossils, in beds considered equivalent to the Burdiehouse Limestone (Asbian, mid Viséan). It was briefly described by Swinton (in Davies, 1936, pp. 780) but was not figured. A second tetrapod horizon was discovered in 1978 (Smithson, 1985a). Disarticulated vertebrate remains were found in a band of volcanic ash on the western side of the island. These include pectoral girdle bones and a humerus similar to the isolated elements that may be attributed to *Doragnathus*. Matrix was removed using a dental mallet and mounted needles.

A clavicle (NMS G 1898.176.42) from the shale overlying the South Parrot Coal Seam at Niddrie and a femur (NMS F624) from the Burdiehouse Limestone may also be attributable to *Doragnathus*.

All the material described below is in the collection of the National Museum of Scotland (NMS), Edinburgh, prefix NMS G, apart from the femur from Inchkeith which is housed in the Natural History Museum (BMNH), London, prefix NHMUKR.

3. Description

3.1. Dora material

3.1.1. Pectoral girdle

The pectoral girdle is represented by the interclavicle and clavicle. These are among the most common tetrapod bones recovered from the Dora Bone Bed (see Appendix A). The diamond-shaped interclavicles (Fig. 1) are slightly longer than wide, lack a parasternal process and vary in maximum width from 35 mm to 70 mm although most are in the 50–60 mm wide range. The ventral surface of the interclavicles is ornamented with the pattern of ridges and grooves radiating from the centres of ossification (Fig. 1A–C, H–I) that has been described in colosteids (Godfrey, 1989; Hook, 1983; Panchen, 1975) and many temnospondyls (Holmes, 2000, and refs therein). The degree of ornamentation varies. In some specimens it is quite delicate with a central network of low ridges and hollows radiating out into a pattern of fine ridges and grooves, whilst in others of the same size it is more open with larger and deeper hollows and grooves. The ornamented area extends to the anterior and posterior tips of the interclavicles.

In the larger specimens, recessed areas of overlap for the clavicles are visible along the anterolateral margins of the interclavicle ventral surface. To ensure there is a plane surface across the articulated clavicles and interclavicle (Fig. 1B, H, I), the overlap area is slightly recessed. The posterior part of this overlap area is excavated into a broad groove that receives a ridge on the undersurface of the clavicle extending anteromesially from the base of the

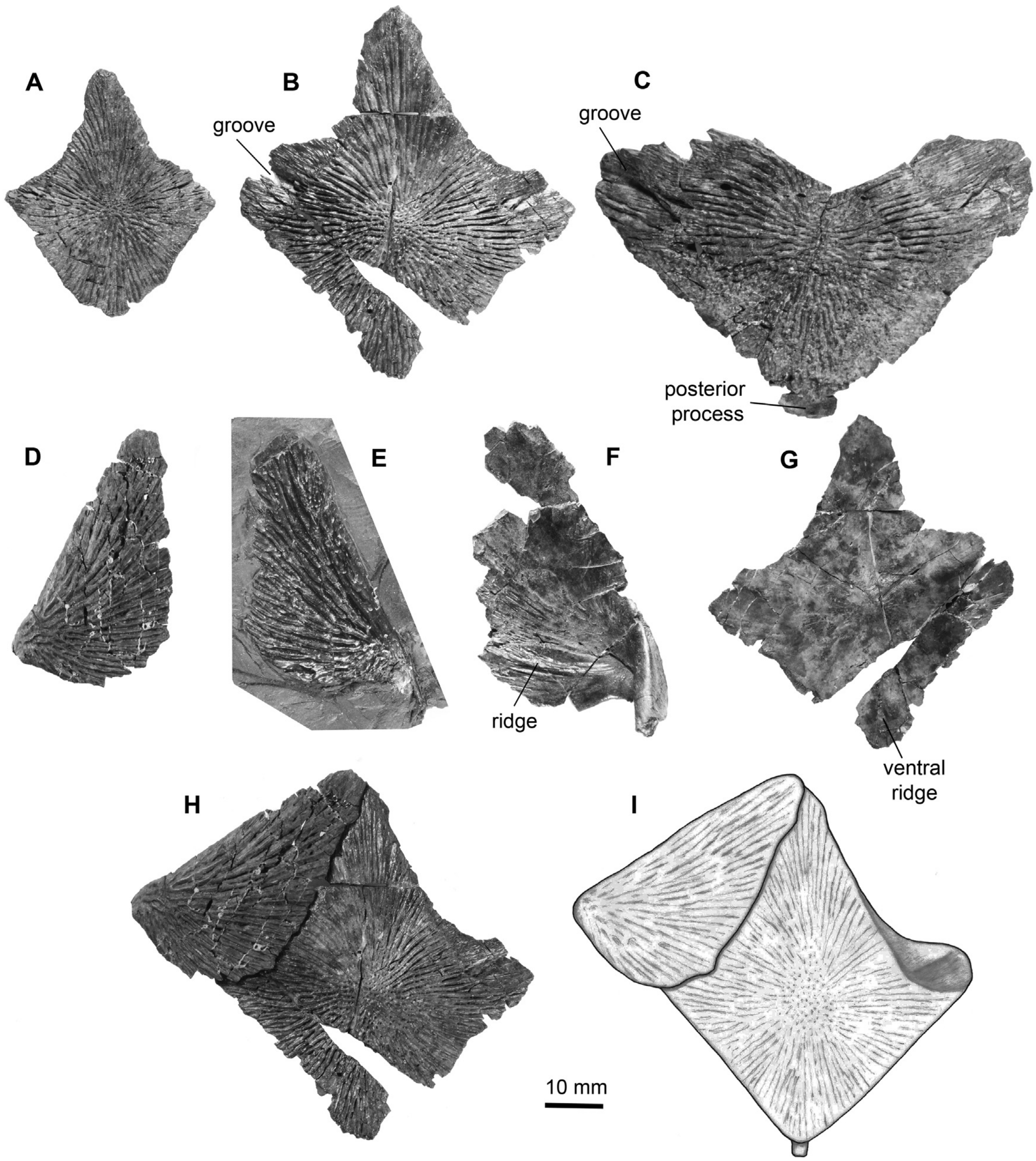


Fig. 1. Pectoral girdle elements from Dora and Niddrie. A–C. Interclavicles from Dora in ventral view. A. NMS G 2012.22.2, B. NMS G 2012.22.1, C. NMS G 2012.22.4. D. Right clavicle from Dora NMS G 2012.22.6 in ventral view. E. Left clavicle from Niddrie NMS G 1898.176.42 in ventral view. F. Right clavicle from Dora NMS G 2012.22.7 in dorsal view. G. Interclavicle from Dora NMS G 2012.22.1 in dorsal view. H. Interclavicle NMS G 2012.22.1 and right clavicle NMS G 2012.22.6 from Dora in ventral view. I. Reconstruction of interclavicle and right clavicle in ventral view. Scale bar: 10 mm.

Fig. 1. Éléments de la ceinture pectorale en provenance de Dora et Niddrie. A–C. Fragments interclaviculaires de Dora, en vue ventrale. A. NMS G 2012.22.2, B. NMS G 2912.22.1. C. NMS G 2012.22.4. D. Clavicule droite de Dora NMS G 2012.22.6, en vue ventrale. E. Clavicule gauche de Niddrie NMS G 1898.176.42, en vue ventrale. F. Clavicule droite de Dora NMS G 2012.22.7, en vue dorsale. G. Fragment interclaviculaire de Dora NMS G2012.22.1, en vue dorsale. H. Fragment interclaviculaire NMS G 2012.22.1 et clavicule droite NMS G 2012.22.6 de Dora, en vue ventrale. I. Reconstitution d'un fragment interclaviculaire et clavicule droite, en vue ventrale. Barre d'échelle : 10 mm.

clavicular stem (see below). The surface of overlap area is reminiscent of overlapping roof tiles.

The dorsal (internal) surface of the interclavicle is smooth but not flat. Its contours match those of the ventral surface. Extending laterally from the centre of the bone are broad ridges that lie above the grooves on the ventral surface that receive the clavicular ridge. In addition, extending posteriorly from the centre is a raised area that in larger specimens becomes a prominent ridge (Fig. 1G). In some specimens, for example NMS G 2012.22.3 and NMS G 2012.22.4, this ridge extends beyond the edge of the ornamented surface as a short posterior tongue-like process (Fig. 1I). Both of these features were helpful in identifying the interclavicles collected from Inchkeith (see below).

The clavicle is triangular (Fig. 1D–F). The long anterolateral edge and shorter posterolateral edge form a right angle where they meet at the base of the clavicular stem. The medial edge that abuts against the interclavicle is straight for most of its length but in dorsal view is gently rounded where it meets the posterolateral edge. When articulated with the interclavicle, the posterolateral edge of the clavicle forms a continuation of the posterolateral edge of the interclavicle (Fig. 1). As in *Greererpeton* (Godfrey, 1989), the centre of ossification of the clavicle is around the base of the clavicular stem. The stem projects dorsally from the clavicular plate at an angle of about 45 degrees. Projecting from its posterior edge is a thin lamina of bone that forms a dorsal continuation of the posterolateral edge of the clavicle. It lacks the reticulate ornament of the clavicular plate and is instead slightly striated. The posterior edge of this lamina is vertical. These features are most clearly seen in NMS G 2012.22.5 and NMS G 2012.22.7.

The internal surface of the clavicle is relatively smooth apart from a conspicuous ridge that extends medially from the clavicular stem, parallel to the posterior edge of the clavicle. This ridge interlocks with the groove on the overlap area of the interclavicle, making a firm junction.

3.1.2. Forelimb

The forelimb is represented by two humeri (Fig. 2), both unusually small: NMS G 2012.22. 8, and the even smaller NMS G 2012.22.9 (Fig. 2A–D). Both are from the left side and the description is based on the larger of the two. It is 19 mm long, well ossified and well preserved. In most regards it is similar to the humeri of the earliest tetrapods like *Acanthostega* (Coates, 1996), *Pederpes* (Clack and Finney, 2005) and *Whatcheeria* (Lombard and Bolt, 1995), but differs from them in one notable respect: it lacks the characteristic large, square-shaped entepicondyle. Instead, it has a small, triangular entepicondyle, a shape normally associated with juvenile specimens. In this respect, it is most like that of the large *Baphetes* humerus described by Milner and Lindsey (1998) who commented on the unusual shape of the condyle. The entepicondyle projects backwards from a prominent ectepicondylar ridge and is pierced by an entepicondylar foramen. Superficially, NMS G 2012.22.8 resembles the humerus from a juvenile *Greererpeton* illustrated by Godfrey (1989, Fig. 19). The latter specimen is similar in size to the smaller Dora humerus and is clearly immature, poorly ossified and lacks many adult features. Presumably, a more extensive entepicondyle was continued as cartilage. The posterior edge of the entepicondyle is gently rounded and extends posterodistally at an angle of about 45 degrees to the ectepicondylar ridge. This is a similar orientation to that in *Acanthostega* (Coates, 1996, Fig. 16). In contrast, the angle in *Greererpeton* is closer to 90 degrees (Godfrey, 1989, Fig. 18). The distal end of the humerus, from the ectepicondylar ridge to a position level with the entepicondylar foramen, is thickened and unfinished and presumably formed the area of articulation with the radius and ulna.

The proximal head of the humerus of NMS G 2012.22.8 is a strap of unfinished bone that is broadest posteriorly (Fig. 2I). Its dorsal edge is gently concave and its ventral edge gently convex and the head narrows to a point anteriorly at the start of the deltopectoral crest. Its ventral edge is angled slightly medially such that part of the articulating surface is visible in dorsal view. Both dorsal and ventral surfaces are featureless apart from fine striations on the ventral side of the humeral head. There is no sign of a latissimus dorsi process.

The sinuous, narrow and blade-like anterior edge expands distally where it joins the epicondyles (Fig. 2G). In dorsal view this anterior edge is convex and at its apex on the dorsal surface is a shallow depression that probably marks the insertion of the deltoideus muscle. Below the depression on the ventral surface, the bone is thickened to form a prominent ridge that extends posteriorly across the humerus to end abruptly as a raised boss. This ridge probably marks the insertion of the pectoralis muscle.

3.1.3. Pelvic girdle

The pelvic girdle is represented by the ilium (Fig. 3). Initially, the ilia recovered from the Dora Bone Bed were thought to be rhizodont fin supports and it was not until one of us (TRS) had the opportunity to study *Greererpeton* (Godfrey, 1989; Smithson, 1982) that they were correctly identified. Specimens of different sizes have been collected (Fig. 3A–F). Measured from the tip of the iliac blade to the junction with the pubis and ischium, the smallest is 17 mm long and the largest is 84 mm long. The majority are between 35–50 mm long, which is similar to the size range of the femora (see below).

The ilium is a well ossified rod of bone. It is broadest where it joins the pubis and ischium, then tapers above the acetabulum before expanding to form the iliac blade (see below). The anterior portion of the acetabulum is preserved as an area of unfinished bone above the junction with the pubis. It is most clearly seen in the largest specimen NMS G 2012.22.12. In this area the ilium is at its thickest and represents a marked distal expansion of the bone when observed in anterior view (Fig. 3I). Above the acetabulum there is a deep depression which is bounded anteriorly by a ridge that extends backwards from the front of the acetabulum across the iliac blade to the middle of the shaft. This ridge may be the transverse line that separates the axial musculature above from the limb musculature below. Behind and above the acetabulum there is a distinct notch in the posterior edge of the ilium. The medial surface of the iliac blade is smooth and featureless and there is no evidence of attachment of the sacral rib.

3.1.4. Hind limb

The hind limb is represented by the femur. Four femora recovered from the Dora Bone Bed are thought to belong to the same species and this description is based on NMS G 2012.22.14 and NMS G 2012.22.15 (Fig. 4). All specimens are between 35–45 mm long. They are generally well preserved, although the proximal and distal ends are poorly ossified and slightly crushed. The bone is long and slender (Fig. 4) with expanded proximal and distal ends. In anterior

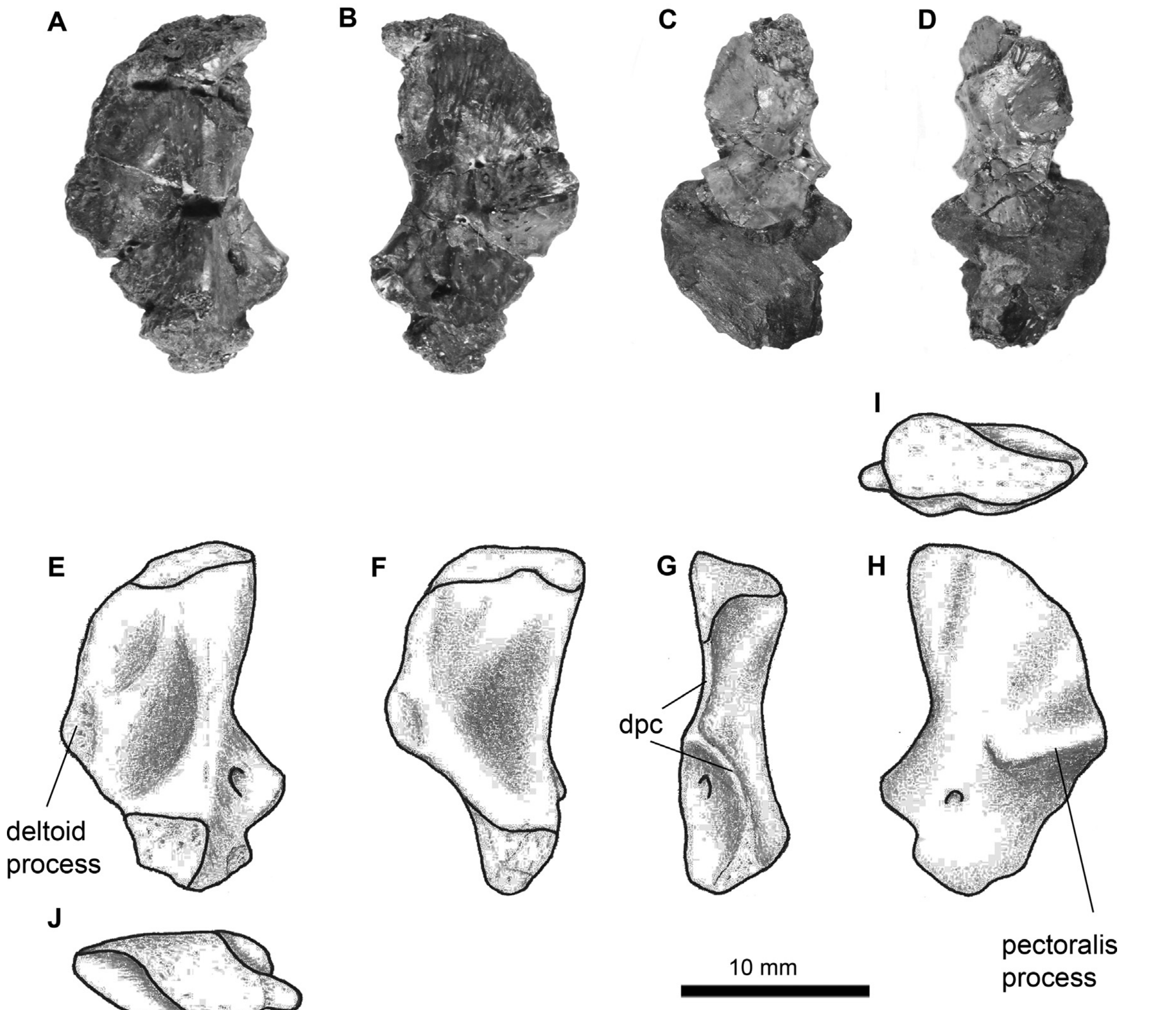


Fig. 2. Humeri from Dora. A. Left humerus NMS G 2012.22.8 in dorsal view. B. Left humerus NMS G 2012. 22.8 in ventral view. C. Left humerus NMS G 2012.22.9 in dorsal view. D. Left humerus NMS G 2012.22.9 in ventral view. E–J. Drawing of left humerus, slightly restored. E. Dorsal view in the plane of the distal ventral surface. F. Dorsal view in the plane of the proximal dorsal surface. G. Anterior view. H. Ventral view in the plane of the distal ventral surface. I. Proximal view. J. Distal view. Scale bar: 10 mm.

Fig. 2. Humérus de Dora. A. Humérus gauche NMS G 2912.22.8, en vue dorsale. B. Humérus gauche NMS G 2012.22.8, en vue ventrale. C. Humérus gauche NMS G 2012.22.9, en vue dorsale. D. Humérus gauche NMS G 2012.22.9, en vue ventrale. E–J. Dessins d'humérus gauche légèrement restauré. E. Vue dorsale dans le plan de la surface distale ventrale. F. Vue dorsale dans le plan de la surface proximale dorsale. G. Vue antérieure. H. Vue ventrale dans le plan de la surface distale ventrale. I. Vue proximale. Vue distale. Barre d'échelle : 10 mm.

view the femur is shallow and reaches its maximum depth at the position of the internal trochanter.

The most striking and potentially diagnostic feature of the femur is the large internal trochanter. It projects inwards and downwards from the centre of the adductor fossa just in front of the midline. It forms a distinct, rounded boss below the proximal condyle (Fig. 4G–I) and divides the adductor fossa into two areas, a large posterior depression and a smaller anterior one. There is no adductor blade. In its place is a low ridge which extends along the undersurface of the femur from the internal trochanter towards the popliteal area. A rugosity at the proximal end of the ridge marks the position of the fourth trochanter.

The distal end of the femur is broader than the proximal end. The condyles for the tibia and fibula are terminal and little of their articulating surfaces is visible in either dorsal or ventral view. There is a deep intercondylar groove on the dorsal surface of the femur (Fig. 4F) that is matched by a low intercondylar ridge on the ventral surface.

3.2. *Inchkeith material*

3.2.1. *Femur*

The right femur NHMUKR 5601 (Fig. 5A and B , E–J) is well preserved. It is a much stouter and more heavily ossified element than the femora from Dora and most closely resembles the femur of *Proterogyrinus scheelei* illustrated

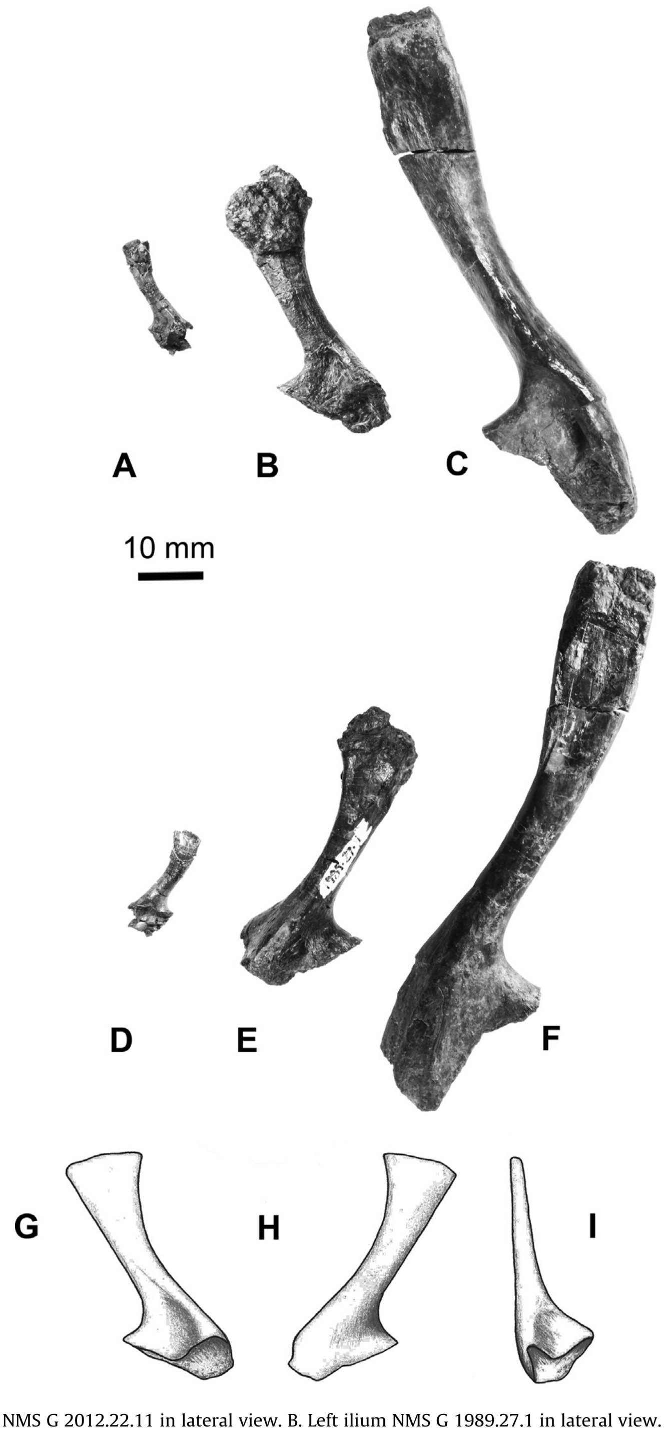


Fig. 3. Ilia from Dora. A. Left ilium NMS G 2012.22.11 in lateral view. B. Left ilium NMS G 1989.27.1 in lateral view. C. Right ilium NMS G 2012.22.13 in lateral view reversed to appear from left. D. Left ilium NMS G 2012.22.11 in medial view. E. Left ilium NMS G 1989.27.1 in medial view. F. Right ilium NMS G 2012.22.13 in medial view reversed. G–I. Drawing of left ilium, slightly restored. G. Lateral view. H. Medial view. I. Anterior view. Scale bar 10 mm.
Fig. 3. Iliaques de Dora. A. Iliaque gauche NMS G 2012.22.11, en vue latérale. B. Iliaque gauche NMS G 1989.27.1, en vue latérale. C. Iliaque droit NMS G 2012.22.13, en vue latérale retournée pour apparaître de la gauche. D. Iliaque gauche NMS G 2012.22.11, en vue médiale. E. Iliaque gauche NMS G 1989.27.1, en vue médiale. F. Iliaque droit NMS G 2012.22.13, en vue médiale retournée. G–I. Dessins d'iliaque gauche légèrement restauré. G. Vue latérale. H. Vue médiale. I. Vue antérieure. Barre d'échelle : 10 mm.

by Holmes (1984, Fig. 33). It is 57 mm long, 21 mm broad across the proximal condyle and 30 mm broad across the distal condyles. In dorsal view, at its narrowest, the shaft is 9 mm wide.

The proximal articulating surface is roughly rectangular in outline. It is gently convex dorsally and almost flat ventrally. The inclined anterior corner projects ventrally, at right angles to the anteroposterior axis of the

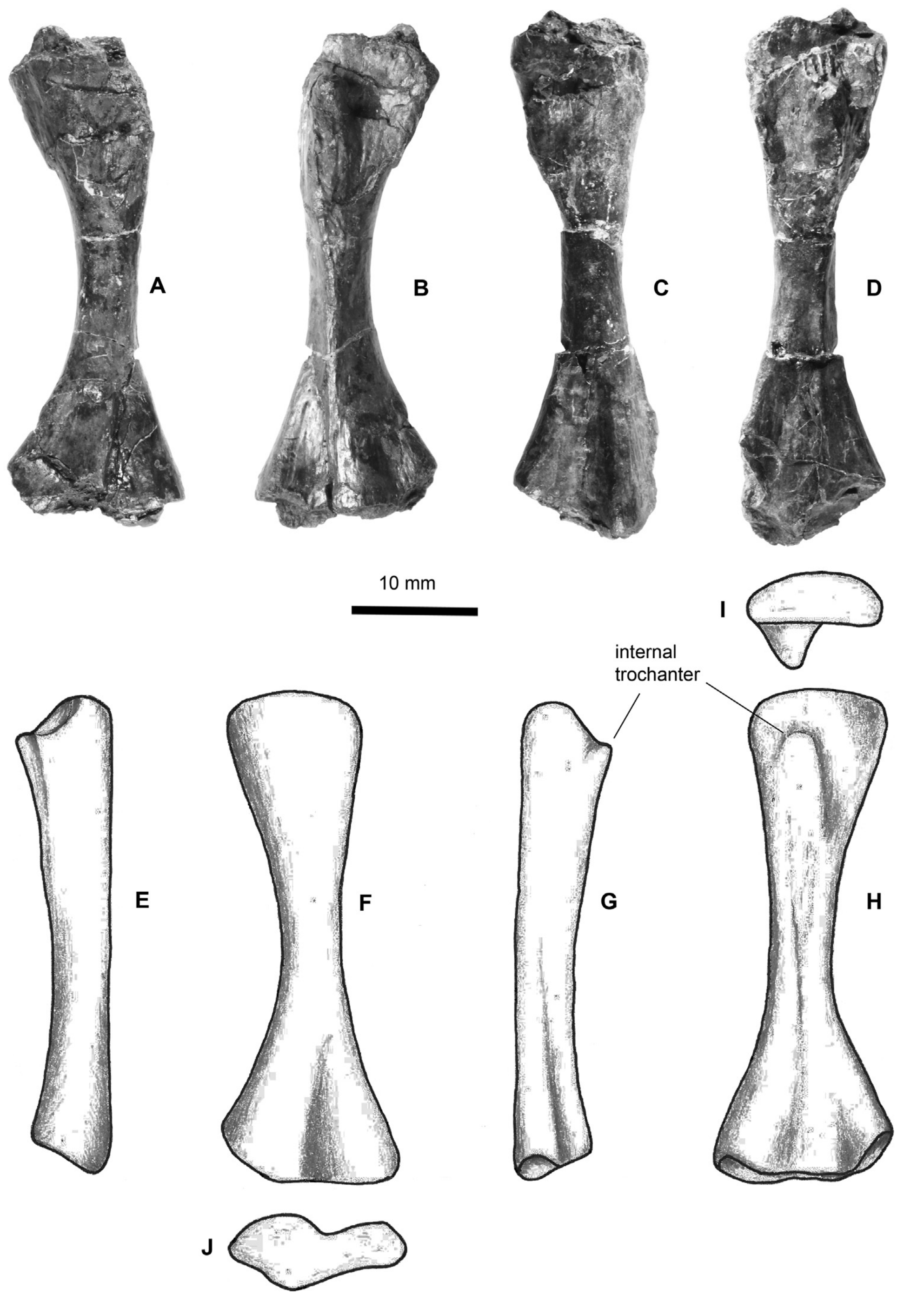
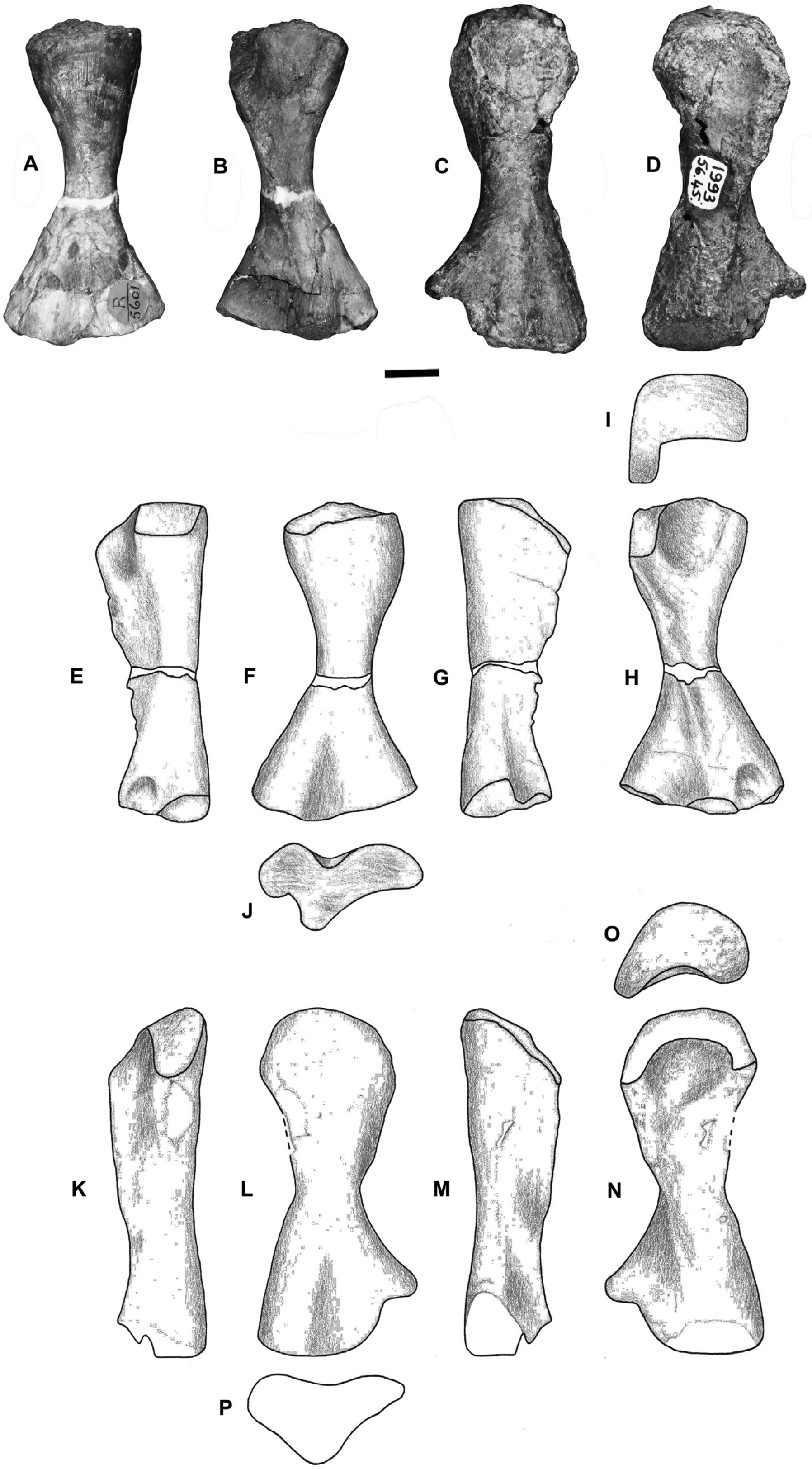


Fig. 4. Femora from Dora. A. Right femur NMS G 2012.22.14 in dorsal view. B. Right femur NMS G 2012.22.14 in ventral view. C. Left femur NMS G 2012.22.15 in dorsal view. D. Left femur NMS G 2012.22.15 in ventral view. E–J. Drawings of right femur, slightly restored. E. Posterior view. F. Dorsal view. G. Anterior view. H. Ventral view. I. Proximal view. J. Distal view. Scale bar 10 mm.

Fig. 4. Fémurs de Dora. A. Fémur droit NMS G 2012.22.14, en vue dorsale. B. Fémur droit NMS G 2012.22.14, en vue ventrale. C. Fémur gauche NMS G 2012.22.15, en vue dorsale. D. Fémur gauche NMS G 2012.22.15, en vue ventrale. E–J. Dessins de fémur droit, légèrement restauré. E. Vue postérieure. F. Vue dorsale. G. Vue antérieure. H. Vue ventrale. I. Vue proximale. J. Vue distale. Barre d'échelle : 10 mm.

articulating surface, to form the anterior wall of an otherwise shallow adductor fossa. Its proximal edge is unfinished. This ventrally directed wall marks the proximal end of a ridge, essentially a low adductor crest, which extends across most of the undersurface of the femur. There is no adductor blade. Proximally, rugosities mark the positions of the internal and fourth trochanters, and the ridge continues distally as the adductor crest,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fading out before reaching a prominent intercondylar ridge.

The distal articulating surface is roughly v-shaped in outline. The dorsal surface is marked by a deep intercondylar fossa, which lies slightly in front of the ventral intercondylar ridge. The articulating surface is unfinished and there is no clear distinction between the tibial and fibular condyles. A deep depression behind the intercondylar ridge, the fibular fossa, extends mesially beyond the posterior edge of the articulating surface. The popliteal area in front of the intercondylar ridge is shallow and featureless.

A previously undescribed femur from Dora, unlike those described above, is similar to the Inchkeith femur and is described here for completeness. The left femur NMS G 1993.56.45 (Fig. 5 C and D, K–P) is well preserved. It was damaged during recovery from the bone bed, but its key diagnostic features are preserved. It is a stout, well ossified bone 62 mm long, 26 mm broad across the proximal condyle and 30 mm broad across the distal condyle. In dorsal view, at its narrowest, the shaft is 12 mm wide.

The proximal end of the femur has a gently rounded outline in dorsal view. The articulating surface forms a dorsally convex strap of unfinished bone which is deepest posteromesially. The entire articulating surface is orientated ventrodistally and is visible in ventral view. The adductor fossa is shallow. Its anterior edge is formed by the proximal end of the adductor crest. The crest is thickened in the areas of the internal and fourth trochanters but narrows distally, fading out in front of the intercondylar ridge. The distal articulating surface is damaged but is roughly v-shaped in outline. The intercondylar groove is shallow and lies above the intercondylar ridge. There is no evidence of a fibular fossa and the popliteal area is featureless.

3.2.2. Interclavicle

Two interclavicles were collected from Inchkeith; an incomplete specimen NMS G 2012.22.17 (Fig. 6D) 60 mm wide preserved in dorsal view and a larger specimen NMS G 2012.22.16 (Fig. 6B) 70 mm wide preserved in part and counterpart on a block with a number of other bones including a jaw that may be of *Doragnathus* (Smithson, 1985a). In both specimens the anterior portion of the interclavicle is missing. The smaller element is clearly identified as an interclavicle by the broad ridges on the dorsal surface seen in the interclavicles from Dora. In the larger specimen, all the posterior half of the bone is preserved including as impression the tongue-like continuation of the central posterior ridge seen in some interclavicles from Dora. Little true external surface is exposed but it is possible to make out the reticulate ornament on the ventral surface.

3.2.3. Clavicle

A single left clavicle NMS G 2012.22.18 (Fig. 6A), preserved in part and counterpart, is identical in shape to NMS G 2012.22.7 (Fig. 1F). It is larger than any of the specimens recovered from the Dora Bone Bed: its anterior edge is 60 mm long compared with 50 mm in NMS G 2012.22.7. The ornamentation of the ventral surface is slightly more pronounced than on the specimens from Dora, but the clavicular stem bears a similar bony lamina along its posterior edge.

3.2.4. Humerus

A single left humerus, NMS G 2012.22.19 (Fig. 6C), is 32 mm long and much larger than the specimens recovered from the Dora Bone Bed. It is preserved in ventral view and no attempt has been made to remove it from the surrounding intractable matrix. The area around the insertion for m. pectoralis is damaged as is the area immediately in front of the entepicondylar foramen, but otherwise the bone surface is well preserved.

In outline the Inchkeith humerus is very similar to the larger specimen from Dora NMS G 2012.22.8 (Fig. 2A and B), but differs from the latter in that the deltopectoral crest is relatively shorter in the Inchkeith specimen and in the size of the entepicondyle, which is more developed especially in relation to the position of the entepicondylar foramen. As in the Dora specimen there are no obvious muscle scars on the ventral surface and it lacks any other diagnostic features.

4. Discussion

4.1. Comparison of the Dora material with the appendicular skeletons of other early tetrapods

4.1.1. Interclavicle

The interclavicles from Dora are very similar in shape to the interclavicle attributed to the colosteid *Pholidogaster* (Panchen, 1975) and those of the earliest temnospondyl *Balanerpeton* (Milner and Sequeira, 1994). They differ from the interclavicle of most other earlier tetrapods. In these the anterior portion is shorter than the posterior. In *Acanthostega* (Coates, 1996) and *Pederpes* (Clack and Finney, 2005) the interclavicle is almost kite-shaped. This is the likely primitive condition (Clack and Finney, 2005). In *Ossinodus* (Warren and Turner, 2004) the posterior portion of the interclavicle is more elongate, but in *Ichthyostega* (Jarvik, 1996), *Whatcheeria* (Lombard and Bolt, 1995) and *Eldeceeon* (Smithson, 1994) this area is even more developed, extending backwards as a long, narrow parasternal process. This pattern is also found in later microsaurs

Fig. 5. Femora from Inchkeith and Dora. A. Right femur NHMUKR 5601 from Inchkeith in dorsal view. B. Right femur NHMUKR 5601 from Inchkeith in ventral view. C. Left femur from Dora NMS G 1993.56.45 in dorsal view. D. Left femur from Dora NMS G 1993. 56.45 in ventral view. E–J. Drawings of right femur NHMUKR 5601from Inchkeith. E. Posterior view. F. Dorsal view. G. Anterior view. H. Ventral view. I. Proximal view. J. Distal view. K–P. Drawings of left femur from Dora NMS G 1993.56.45 slightly restored and reversed to appear from the right. K. Posterior view. L. Dorsal view. M. Anterior view. N. Ventral view. O. Proximal view. P. Distal view. Distal view left unshaded due to surface damage. Scale bar: 10 mm.

Fig. 5. Fémurs d'Inchkeith et de Dora. A. Fémur droit NHMUKR 5601d'Inchkeith, en vue dorsale. B. Fémur droit NHMUKR 5601 d'Inchkeith, en vue ventrale. C. Fémur gauche de Dora NMS G 1993.56.45, en vue dorsale. D. Fémur gauche de Dora NMS G 1993.56.45, en vue ventrale. E–J. Dessins de fémur droit NHMUKR 5601 d'Inchkeith. E. Vue postérieure. F. Vue dorsale. G. Vue antérieure. H. Vue ventrale. I. Vue proximale. J. Vue distale. K–P. Dessins de fémur gauche de Dora NMS G 1993.56.45, légèrement restauré et tourné pour apparaître de la droite. K. Vue postérieure. L. Vue dorsale. M. Vue antérieure. N. Vue ventrale. O. Vue proximale. P. Vue distale. La vue distale n'a pas été ombrée, en raison de la surface endommagée. Barre d'échelle : 10 mm.

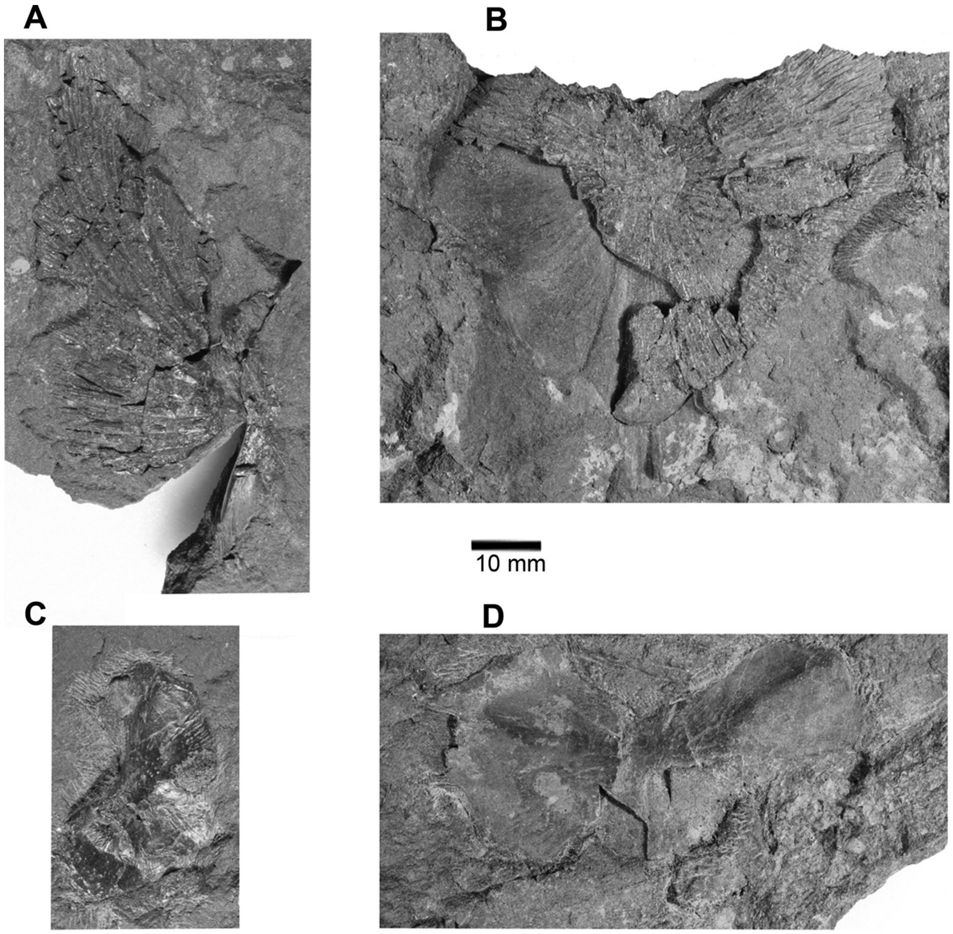

Fig. 6. Pectoral girdle and limb elements from Inchkeith. A. Right clavicle NMS G 2012.22.18 in dorsal view. B. Incomplete interclavicle NMS G 2012.22.16 in dorsal view. C. Left humerus NMS G 2012.22.19 in ventral view. D. Incomplete interclavicle NMS G 2012.22.17 in ventral view. Scale bar: 10 mm.
Fig. 6. Ceinture pectorale et éléments de membre d'Inchkeith. A. Clavicule droite NMS G 2012.22.18, en vue dorsale. B. Fragment interclaviculaire incomplet NMS G.2012.22.16, en vue dorsale. C. Humérus gauche NMS G 2012.22.19, en vue ventrale. D. Fragment interclaviculaire incomplet NMS G 2012.22.17, en vue ventrale. Barre d'échelle : 10 mm.

(Carroll and Gaskill, 1978), seymouriamorphs (Klembara, 2000; White, 1939) and early amniotes (Carroll, 1970).

The interlocking groove on the overlap area of the interclavicle and the ridge on the internal surface of the clavicle, are the most distinctive features of the dermal shoulder girdle and have not been described in other early tetrapods. This arrangement suggests that the clavicles and interclavicle were strongly joined in life and formed a ventral shield that both protected the organs of the anterior thorax and gave rigidity to the pectoral girdle. It would have effectively prevented any form of girdle rotation, an important feature of early amniote locomotion.

4.1.2. Humerus

The humeri from Dora differ from those of most early tetrapods in lacking the large, square-shaped entepicondyle. This is most likely due to immaturity and incomplete ossification of the bone, although humeri of similar size in other early tetrapods, for example *Eldeceeon* (Smithson, 1994) and *Silvanerpeton* (Ruta and Clack, 2006), display a typical entepicondyle.

4.1.3. Ilium

The ilia from Dora are very similar to those of the temnospondyl *Balanerpeton* (Milner and Sequeira, 1994) and the colosteid *Greererpeton* (Godfrey, 1989). It is a simple rod expanded at the acetabulum. In the earliest tetrapods, including *Acanthostega* (Coates, 1996), *Ichthyostega* (Jarvik, 1996), *Pederpes* (Clack and Finney, 2005), *Ossinodus* (Warren and Turner, 2004) and *Crassigyrinus* (Panchen and Smithson, 1990), the ilium is biramous with distinct dorsal and post-iliac processes. This condition is probably plesiomorphic for tetrapods. One of these processes has been lost in the ilia from Dora. It is unclear which of the two it is, but in the earliest tetrapods the dorsal process forms part of the sacrum and it is likely that this area of the ilium has been retained in the ilia from Dora, as well as those of colosteids and temnospondyls, and that the post-iliac process has been lost (see also Panchen, 1975).

4.1.4. Femur

The femur from Inchkeith resembles most closely that of *Archeria* (Romer, 1957) and, in particular, *Proterogyrinus*

(Holmes, 1984). The anterior edge of the adductor fossa is considerably deeper in the Inchkeith femur and the intercondylar ridge has a slightly more posterior position, but otherwise the shape and proportions of the condyles, the positions of the internal and fourth trochanters and depth and orientation of the adductor crest are identical. It is the oldest known femur to lack an adductor blade (see below). In the absence of other material, it is probably unwise to speculate on its affinities, but the Inchkeith femur may represent the earliest known record of an anthracosaur *sensu stricto* (Klembara, Clack, Milner and Ruta ms in revision).

The stout femur from Dora is superficially similar to the femur from Inchkeith but there are notable differences. The proximal condyle is broader and more rounded in the Dora femur and the shaft is relatively wider. The anterior edge of the adductor fossa is less deep and is more like that of *Proterogyrinus*. The proximal end of the adductor crest, in the region of the internal and fourth trochanters, is also thicker but the intercondylar groove is shallower. There is no fibular fossa in the Dora femur. It is possible that the Dora femur is that of *Proterogyrinus pancheni* (Smithson, 1986), also from Dora, but in the absence of other pelvic elements, it is also probably unwise to speculate further on its affinities.

Among early tetrapods, the gracile femora from Dora are most like those of the colosteids *Greererpeton* (Godfrey, 1989) and *Pholidogaster* (Romer, 1964) in being relatively simple cylinders of bone expanded at each end. Each is characterized by a prominent internal trochanter in the centre of the adductor fossa, whose position on the undersurface of the femur is similar to that in *Acanthostega* (Coates, 1996). In contrast, the internal trochanter in *Caerorhachis* (Ruta et al., 2002), *Greererpeton* (Godfrey, 1989), *Pederpes* (Clack and Finney, 2005) and *Proterogyrinus* (Holmes, 1984) lies closer to the anterior edge, and in *Crassigyrinus* (Panchen and Smithson, 1990) the trochanter is much enlarged and projects as a distinct process from the anterior edge of the femur. The Dora femora also differ from the femora of the earliest tetrapods, including *Acanthostega* (Coates, 1996), *Ichthyostega* (Jarvik, 1996) *Tulerpeton* (Lebedev and Coates, 1995), by the complete absence of an adductor blade. A distinct adductor blade is retained in many early tetrapods but the earliest records of its absence are in the Inchkeith femur, *Crassigyrinus* (Panchen and Smithson, 1990) and in the Dora femora.

4.2. Likely affinities of the Dora appendicular elements

The derived characters of the appendicular elements from Dora noted above make it unlikely that they should be assigned to any of the taxa currently known from the Devonian. Similarly, it is unlikely that they belong with whatcheeriids, anthracosaurs or baphetids. Furthermore, they show no features that suggest they may belong with microsaurs or nectrideans. Instead, they share a number of characters with colosteids and the earliest temnospondyls, in particular an interclavicle lacking a parasternal process and the rod-like ilium lacking a post-iliac process.

Colosteids are distinguished from other early tetrapods by four unique characters (Bolt and Lombard, 2010; Smithson, 1982):

- a dentary notch that accommodates;
- a premaxillary tusk;
- an elongate Meckelian fenestra on the internal surface of the lower jaw;
- a pattern of bones in the snout in which an elongate prefrontal separates the nasal from the lacrimal.

None of these characters has been observed in the cranial material from Dora and there is no evidence that colosteids were present in the fauna.

Early temnospondyls are characterized by (Milner and Sequeira, 1994) the presence of:

- large rounded interpterygoid vacuities in the palate;
- flat vomers overlapped or sutured with a slender cultriform process;
- an otic notch between the skull table and cheek that may have supported a tympanum.

None of these features has been observed in the cranial material from Dora either, although few specimens are sufficiently well preserved to show them.

The most common tetrapod recorded from Dora is *Doragnathus* (Smithson, 1980). It is represented by a number of jaw elements containing the characteristic incurved teeth. In contrast, other tetrapod taxa appear to be represented by no more than three individuals (Beaumont and Smithson, 1998; Panchen, 1985, Panchen and Smithson, 1990; Smithson, 1985b, 1986). It is therefore plausible to assume that the numerous appendicular elements described here could also be assigned to *Doragnathus*. Weight is given to this suggestion by the presence at Niddrie of a *Doragnathus* lower jaw (Smithson, 1980) and a clavicle indistinguishable for those described above from Dora (see above Fig. 1E). However, we do not intend to propose here to assign to *Doragnathus* the appendicular elements from Dora. This may create a chimaera – colosteid-like postcranial elements associated with a lower jaw that is distinctly uncolosteid-like – and produce erroneous results in cladistic analyses. Instead, we will leave them in open nomenclature and hope that the future discovery of more articulated material will help resolve their affinities.

5. Conclusions

In summary, the appendicular elements from Dora are derived with respect to the earliest tetrapods in having:

- a diamond-shaped interclavicle with no parasternal process;
- a rod-like ilium lacking a post-iliac process;
- a gracile femur with a prominent internal trochanter but lacking an adductor blade.

To judge from the interlocking junction between the clavicle and interclavicle, the broad strap-like humeral and femoral heads, and the lack of torsion in the humeri, it appears that the range of motion in the limbs of these animals was rather restricted. The capability for long axis rotation, required for efficient walking, was very limited (Pierce et al., 2012). However, the range of morphologies found among Early Carboniferous tetrapod elements hints at an early diversification in locomotory styles and capabilities.

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Appendix A. Specimens studied

Dora open cast site

'Doragnathus'

Interclavicle: NHMUK R9244, NHMUK R9245, NHMUK R9944, NHMUK R9945, NHMUK R9946, NMS G.1976.19.47, NMS G.1977.46.41, NMS G.1979.51.23, NMS G.1979.51.24, NMS G.1993.56.66, NMS G.1993.56.67, NMS G.1993.56.68, NMS G.1993.56.70, NMS G.2012.22.1, NMS G.2012.22.2, NMS G.2012.22.3, NMS G.2012.22.4.

Clavicle: Left; NHMUK R9247, NHMUK R9942, NHMUK R9947, NMS G.1976.19.39, NMS G.1977.46.43, NMS G.1979.51.25, NMS G.1979.51.26, NMS G.1993.56.73, NMS G.1993.56.75, NMS G.1993.56.76, NMS G.1993.56.77, NMS G.1993.56.78, NMS G.1993.56.81, NMS G.1993.56.83, NMS G.1993.56.84, NMS G.2012.22.5. Right; NMS G.1976.19.33, NMS G.1976.19.45, NMS G.1977.46.45, NMS G.1978.4.20, NMS G.1979.51.22, NMS G.1993.56.80, NMS G.2012.22.6, NMS G.2012.22.7.

Humerus: Left; NMS G.2012.22.8, NMS G.2012.22.9.

Ilium: Left; NMS G.2012.22.10, NMS G.2012.22.12, NMS G.2012.22.13. Right; NMS G.1989.27.1, NMS G.1989.27.2, NMS G.1989.27.3, NMS G.2012.22.11.

Femur: Left; NMS G.1993.56.10, NMS G. 2012.22.15. Right; NMS G.1978.4.25, NMS G. 2012.22.14.

Other elements: **Femur**: Left; NMS G. 1993.56.45.

Inchkeith: Interclavicle: NMS G.2012.22.16.1 + 2, NMS G.2012.22.17.1 + 2. **Clavicle**: Left; NMS G.2012.22.18.1 + 2. **Humerus**: Left; NMS G.2012.22.19. **Femur**: Right; NHMUK R5601.

Niddrie: Clavicle: Left; NMS G.1898.176.42.

Burdiehouse: Femur: Left; F624 Hugh Miller Collection (housed in the NMS).

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