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Paul A. Garner
Biblical Creation Trust

Jonathan Asher
Biblical Creation Trust

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BARAMINOLOGICAL ANALYSIS OF DEVONIAN AND CARBONIFEROUS TETRAPODOMORPHS

Paul. A. Garner, Biblical Creation Trust, P.O. Box 325, Ely, CB7 5YH United Kingdom paul@biblicalcreationtrust.org
Jonathan Asher, Independent scholar

ABSTRACT

According to evolutionary theory, the origin of tetrapods (or limbed vertebrates) from a fish-like ancestor during the Devonian Period was one of the major events in the history of life. Devonian sediments have yielded several families of tetrapod-like fishes, including the elpistostegids which range from the Givetian to Frasnian of the Middle to Upper Devonian and are regarded as close to the evolutionary ancestry of tetrapods. Two of the best-known 'early' tetrapods are *Ichthyostega* and *Acanthostega*, first described from fossil material discovered in the Famennian (uppermost Upper Devonian) sediments of East Greenland. These taxa (and others subsequently described) display mosaic combinations of fish-like and tetrapod-like characters, along with some unique traits (such as polydactyly) not found in more 'derived' tetrapods. Creationists have claimed that these organisms are not evolutionary intermediates, but were rather the inhabitants of aquatic environments associated with a pre-Flood floating forest biome, with morphologically intermediate traits that equipped them for life in an environment that was itself intermediate between the sea and the land. This paper evaluates the baraminic status of a range of Devonian and Carboniferous fishes and tetrapods using the techniques of statistical baraminology. Baraminic distance correlation (BDC) and three-dimensional multidimensional scaling (MDS) are applied to six previously published character-taxon matrices. The results reveal little evidence of continuity, and significant evidence of discontinuity, between the elpistostegids and tetrapods such as *Ichthyostega* and *Acanthostega*, consistent with the creationist claim of separate ancestry. However, further work will be required to elucidate the baraminic relationships within these presumably apobaraminic groups.

KEY WORDS

tetrapods, tetrapodomorphs, Devonian, Carboniferous, baraminic distance, multidimensional scaling, discontinuity

INTRODUCTION

According to evolutionary theory, the origin of tetrapods from a fish-like ancestor during the Devonian Period (conventionally 419.2-358.9 million years ago) was one of the major events in the history of life (Clack 2012). In this paper, we will use the term 'tetrapod' to refer to a vertebrate with limbs rather than paired fins. The more inclusive term 'tetrapodomorph' is used to refer to tetrapods plus some tetrapod-like fishes. Devonian sediments have yielded several families of these tetrapod-like fishes, including the elpistostegids which range from the Givetian to Frasnian of the Middle to Upper Devonian and are regarded as close to the evolutionary ancestry of tetrapods (Ahlberg and Johanson 1998; Table 1). *Elpistostege* from the Frasnian Escuminac Formation of Quebec, Canada, was originally described as a tetrapod based on a partial skull roof (Westoll 1938) and only recognized as a fish when more complete material was discovered half a century later (Schultze and Arsenault 1985). *Panderichthys*, from the Frasnian Gauja Formation of Latvia and Estonia, is much better known. Complete specimens reveal that *Panderichthys* has paired fins, a set of opercular bones and other fish-like features of the braincase and lower jaw (Ahlberg and Clack 1998; Ahlberg et al. 1996; Boisvert 2005; Boisvert 2009; Boisvert et al. 2008). However, in other respects its appearance is quite tetrapod-like, with a dorsoventrally flattened body and skull, dorsally placed orbits with supraorbital ridges, a large spiracular opening, frontal bones in the skull roof and an elongated snout with marginal nares (Vorobyeva 1977; Vorobyeva 1980; Vorobyeva 1992; Vorobyeva and Kuznetsov 1992; Vorobyeva and Schultze 1991). Even more tetrapod-like is *Tiktaalik* from the Frasnian Fram Formation of Nunavut Territory, Canada. *Tiktaalik* was described from multiple, articulated specimens preserved in three dimensions, all from a single site on southern Ellesmere Island (Daeschler et al. 2006; Downs et al. 2008; Shubin et al. 2006; Shubin et al. 2014). Like *Panderichthys*, *Tiktaalik* has paired fins and a dorsal surface covered with overlapping rhombic scales. However, the snout is even more elongated, the spiracle is even larger and there is no bony opercular cover. Furthermore, *Tiktaalik* is distinguished from other tetrapodomorph fishes by possession of imbricate ribs, and a pectoral girdle with enlarged scapular and coracoid elements and highly mobile elbow-like and wrist-like joints. The head is also detached from the shoulder girdle, allowing flexure in the neck region. These features would have allowed the animal to support itself on a substrate using its pectoral fins in a limb-like manner.

The earliest tetrapods to appear in the fossil record constitute a paraphyletic grade (i.e. not a clade) and may be referred to as ichthyostegalians (Table 2). Two of the best-known are *Ichthyostega* and *Acanthostega*, first described from fossil material discovered in the Famennian sediments of East Greenland (Jarvik 1952; Jarvik 1965; Jarvik 1996; Säve-Söderbergh 1932). Although the anatomy of *Ichthyostega* is known in considerable detail, no single specimen possesses a complete vertebral column and so the relative proportions of the body, including those of the head and limb girdles, have been reconstructed from partial, overlapping specimens (Ahlberg et al. 2005a). *Ichthyostega* is about one metre

Table 1. Devonian elpistostegids mentioned in this paper. Givetian is a subdivision of the Middle Devonian and Frasnian is a subdivision of the Upper Devonian. Fm = Formation.

Taxon	Stratigraphic unit	Age	Location	Material	Reference(s)
Elpistostege	Escuminac Fm	Frasnian	Quebec, Canada	Partial dermal skull roofs and part of axial skeleton	Schultze (1996); Schultze and Arsenault (1985); Westoll (1938)
Tiktaalik	Fram Fm	Frasnian	Nunavut Territory, Canada	Multiple articulated specimens	Daeschler et al. (2006); Downs et al. (2008); Shubin et al. (2006); Shubin et al. (2014)
Panderichthys	Gauja Fm	Givetian	Latvia and Estonia	Complete specimens	Ahlberg and Clack (1998); Ahlberg et al. (1996); Boisvert (2005); Boisvert (2009); Boisvert et al. (2008); Brazeau and Ahlberg (2006); Vorobyeva (1977); Vorobyeva (1980); Vorobyeva (1992); Vorobyeva (1995); Vorobyeva (2000); Vorobyeva and Kuznetsov (1992); Vorobyeva and Schultze (1991)

long with flanged, imbricate ribs anterior to a more flexible lumbar region, an arrangement similar to that seen in the Carboniferous tetrapods *Pederpes* and *Whatcheeria* (Clack 2002a; Clack and Finney 2005; Lombard and Bolt 1995). The differentiation of the trunk into thoracic, lumbar, postsacral and caudal regions would have permitted dorsoventral flexion of the body, and a distinctive form of locomotion on land (Ahlberg et al. 2005a). New ichthyostegid material, including a well-preserved and articulated hind limb, collected by an expedition to East Greenland in 1987, revealed that *Ichthyostega* was polydactylous, with seven digits on the hind limb (Coates and Clack 1990). The pectoral and pelvic girdles are large and the hind limb paddle-like, with flattened bones and an inflexible ankle (Pierce et al. 2012). Fish-like characteristics of *Ichthyostega* include a lateral line system, a tail with bony fin rays and an ear region specialized for underwater hearing (Clack et al. 2003).

Acanthostega is also much more completely known as a result of material collected by the 1987 expedition, including the first postcranial remains (Bendix-Almgreen et al. 1988; Bendix-Almgreen et al. 1990; Clack 1988). Several articulated specimens in a mass-death assemblage appear to represent juvenile *Acanthostega* with humeri displaying varying degrees of ossification in an ontogenetic series (Sanchez et al. 2016). The remarkable preservation also means that some delicate structures, not often preserved in fossil tetrapods, are known in *Acanthostega*. The braincase and ear region are tetrapod-like (Clack 1989; Clack 1994a; Clack 1994b; Clack 1998). However, the gill skeleton is fish-like, indicating that *Acanthostega* had internal gills somewhat similar to those of the Australian lungfish (*Neoceratodus*) (Coates and Clack 1991). Indeed, *Acanthostega* appears to have been more aquatic than *Ichthyostega*, with a longer tail and more numerous lepidotrichia (Coates 1996). Unlike *Ichthyostega*, the ribs are small and straight with little differentiation along the vertebral column, suggesting that its primary mode of locomotion was tail-propelled swimming. This conclusion is supported by the morphology of the fore and hind limbs, which are difficult to interpret as load-bearing structures. An articulated fore limb revealed that *Acanthostega* had eight digits arranged in a paddle-like fashion (Coates and Clack 1990).

Since the discovery of *Ichthyostega* and *Acanthostega*, our knowledge of Devonian tetrapods has been greatly expanded, with many new taxa being described (Table 2). Thirteen genera are now known from Greenland, Scotland, Latvia, Russia, the USA, Australia and China, and there is additional unnamed material from the USA, Russia and Belgium (Olive et al. 2016). Like *Ichthyostega* and *Acanthostega*, these taxa display mosaic combinations of fish-like and tetrapod-like characters, along with some unique traits (such as polydactyly) not found in more ‘derived’ tetrapods. Furthermore, new discoveries are beginning to populate the previously depauperate interval covering the Tournaisian and most of the Viséan, a part of the Lower Carboniferous record known as ‘Romer’s Gap’ after the great vertebrate palaeontologist Alfred Sherwood Romer (Coates and Clack 1995). The diverse tetrapod assemblages of the upper Viséan include fully terrestrial forms with five or fewer digits, quite unlike the polydactylous, aquatic and semi-aquatic tetrapods of the Frasnian and Famennian. Until recently, however, the only tetrapod fossils from the intervening Tournaisian were isolated skeletal elements, trackways and a single articulated skeleton of the whatcheeriid *Pederpes* (Clack 2002a; Clack and Finney 2005; Smithson et al. 2012). However, Clack et al. (2016) have now described five new Tournaisian tetrapods from two localities (*Perittodus*, *Ossirarus*, *Diploradus*, *Koilops* and *Aytonerpeton*). Other taxonomically indeterminate taxa have also been recovered.

In addition to body fossils, putative trackways of tetrapods have been documented from a number of Devonian localities in Australia, South America and Europe (Clack 1997; Lucas 2015; Table 3). The most securely identified are the Genoa River trackways in New South Wales, Australia (Warren and Wakefield 1972) and the Valentia Island trackways in southwestern Ireland (Stössel 1995; Stössel et al. 2016). Niedźwiedzki et al. (2010) described trackways in the Zachełmie Quarry in Poland that are Middle Eifelian in age, and thus predate the earliest tetrapod body fossils by 14 million years and the oldest elpistostegids by 5 million years (Narkiewicz and Narkiewicz 2015). Lucas (2015) argued that these ichnofossils did not have the diagnostic characteristics expected of Devonian tetrapod tracks and trackways and re-interpreted them as fish feeding traces/nests (*Piscichnus*). However, Qvarnström et al. (2018) have defended the tetrapod identification, based on the well-preserved morphology and new data indicating a

Table 2. Named genera of Devonian tetrapods ('ichthyostegalians'). Most are represented by single specimens; *Ichthyostega* and *Acanthostega* represent stratigraphic ranges. Frasnian and Famennian are subdivisions of the Upper Devonian. Fm = Formation. Gp = Group. After Olive et al. (2016).

Taxon	Stratigraphic unit	Age	Location	Material	Reference(s)
Ichthyostega	Aina Dal Fm Britta Dal Fm	Upper Famennian	East Greenland	Skulls, skeletal elements, some articulated	Ahlberg et al. (2005a); Blom (2005); Blom et al. (2005); Blom et al. (2007); Clack et al. (2003); Clack et al. (2012); Coates and Clack (1990); Jarvik (1952); Jarvik (1965); Jarvik (1996); Pierce et al. (2012); Pierce et al. (2013); Save-Söderbergh (1932)
Acanthostega	Britta Dal Fm	Upper Famennian	East Greenland	Skulls, articulated skeletons	Ahlberg and Clack (1998); Blom et al. (2005); Blom et al. (2007); Clack (1988); Clack (1989); Clack (1994a); Clack (1994b); Clack (1998); Clack (2002b); Coates (1996); Coates and Clack (1990); Coates and Clack (1991); Jarvik (1952); Porro et al. (2015); Sanchez et al. (2016); Save-Söderbergh (1932)
Tulerpeton	Khovanshchina Beds	Upper Famennian	Tula Region, Russia	Fore and hind limbs, partial pectoral and pelvic girdles, skull fragments	Lebedev (1984); Lebedev (1985); Lebedev and Clack (1993); Lebedev and Coates (1995); Mondéjar-Fernández et al. (2014)
Ventastega	Ketleri Fm	Upper Famennian	Latvia	Skull fragments, girdle fragments	Ahlberg and Lukševičs (1998); Ahlberg et al. (1994); Ahlberg et al. (2008); Esin et al. (2000); Lukševičs and Zupiņš (2003); Lukševičs and Zupiņš (2004); Witzmann (2010)
Hynerpeton	Catskill Fm	Upper Famennian	Pennsylvania, USA	Pectoral girdle, skull fragments	Daeschler (2000); Daeschler et al. (1994); Daeschler et al. (2009)
Densignathus	Catskill Fm	Upper Famennian	Pennsylvania, USA	Lower jaw	Daeschler (2000); Daeschler et al. (2009)
Jakubsonia	Zadonskian Beds	Lower Famennian	Oryol Region, Russia	Partial skull roof, partial lower jaw, cleithrum, partial femur	Esin et al. (2000); Lebedev (2004)
Ymeria	Talus specimen, Celsius Bjerg Gp	Famennian	North-east Greenland	Lower jaws, maxillae, premaxillae, partial palate and shoulder girdle	Blom et al. (2007); Clack et al. (2012)
Metaxygnathus	Cloghnan Shale	Frasnian to Famennian	New South Wales, Australia	Lower jaw	Ahlberg and Clack (1998); Ahlberg et al. (1994); Campbell and Bell (1977); Young (1993); Young (1999); Young (2006)
Obruchevichthys	Ogre Beds	Upper Frasnian	Latvia	Lower jaw fragments	Ahlberg (1991); Ahlberg (1995); Ahlberg and Clack (1998); Clément and Lebedev (2014)
Webererpeton	Smota Lovat' Fm	Upper Frasnian	Leningrad Region, Russia	Lower jaw	Ahlberg (1991); Ahlberg (1995); Clément and Lebedev (2014)
Elginerpeton	Scat Craig Beds	Middle or Upper Frasnian	Scotland	Ilia, limb bones, skull and pectoral girdle fragments	Ahlberg (1991); Ahlberg (1995); Ahlberg (1998); Ahlberg and Clack (1998); Ahlberg et al. (2005b)
Sinostega	Zhongning Fm	Frasnian	Ningxia Hui, China	Incomplete left mandible	Zhu et al. (2002)

Table 3. Putative trackways of tetrapods in the Devonian. Eifelian and Givetian are subdivisions of the Middle Devonian, Frasnian and Famennian are subdivisions of the Upper Devonian, and Tournaisian is a subdivision of the Lower Carboniferous. Fm = Formation. Gp = Group. After Lucas (2015).

Locality	Stratigraphic unit	Age	Description	Reference(s)	Comments
Eastern Greenland	Kap Graah Group	Devonian	Two trackways of symmetrically arranged impressions without median traces.	Friend et al. (1976)	Friend et al. (1976) discussed but rejected a tetrapod interpretation. Lucas (2015) attributes the traces to an arthropod, probably *Diplichnites*.
Orkney Islands	Upper Old Red Sandstone	Devonian	Two parallel but separated marks with symmetrical lateral projections.	Westoll (1937); Wilson et al. (1935)	Leonardi (1987) attributed the trace to a rhipidistian fish. Rogers (1990) suggested an arthropod trackway. Lucas (2015) interprets it as a zosterophyll stem with attached sporangia.
Genoa River, New South Wales, Australia	Combyingbar Fm	Frasnian	Two trackways with alternating pattern, one with median drag impression. Manus (smaller) and pes (larger) with at least five digits.	Leonardi (1987); Warren and Wakefield (1972); Young (2006)	Pridmore (1995) and Lucas (2015) suggest the same animal moving at different speeds made the two trackways.
Easter Ross, northern Scotland	Upper Old Red Sandstone	Givetian to Tournaisian	Trackway with alternating impressions. Manus (smaller) and pes (larger).	Rogers (1990)	Clack (1997) and Lucas (2015) agree this is a tetrapod trackway but the stratigraphic age is uncertain.
Valentia Island, southwestern Ireland	Valentia Slate Fm	Givetian to Famennian	Long meandering trackway without median drag impression. Alternating pattern with 150 manus and pes impressions showing size differentiation.	Stössel (1995); Stössel et al. (2016)	Clack (1997) and Lucas (2015) agree that this is a tetrapod trackway.
Tibagi, Paraná, Brazil	Ponta Gross Fm	Givetian or Lower Frasnian	Single "left manus" track with four long, curved "digits".	Leonardi (1983)	Roček and Rage (1994) noted some similarity to ophiuroid trace fossils. Lucas (2015) rejects tetrapod interpretation.
Zachełmie Quarry, Poland	Wojciechowice Fm	Middle Eifelian	Numerous trackways and isolated impressions, varying greatly in appearance.	Niedźwiedzki et al. (2010); Narkiewicz and Narkiewicz (2015)	Lucas (2015) regards these as fish feeding traces or nests. However, Qvarnström et al. (2018) have defended the tetrapod identification.
Glenisla, Grampians Range, Australia	Grampians Gp	Lower Devonian or Upper Silurian	Twenty-three impressions in a ladder-like pattern.	Turner (1986); Warren et al. (1986); Warren (1991); Young (2006)	Roček and Rage (1994) identified this as a "rhipidistian" trace lacking the median body drag. Gourmanis et al. (2003) attributed it to *Diplichnites*, an arthropod trackway. Clack (1997) and Lucas (2015) also reject tetrapod interpretation.

non-marine paleoenvironment (rather than the marginal marine setting originally inferred). Other Devonian trackways have been incorrectly ascribed to tetrapods or their stratigraphic age is uncertain (Table 3).

Wise (1995) defined a stratomorphic series as a sequence of species or higher taxa in the fossil record, where each taxon is a morphological intermediate between the taxa stratigraphically below and above it. In the case of the Devonian fish-tetrapod series, the 'least derived' elpistostegid *Panderichthys* appears in the Givetian (Ahlberg et al. 2000), the 'most derived' elpistostegids *Elpistostege* and *Tiktaalik* in the Frasnian (Ahlberg et al. 2000; Daeschler et al. 2006) and the ichthyostegalians in the upper Frasnian (Ahlberg 1991; Ahlberg 1995; Ahlberg 1998). Despite some possibly conflicting data, such as the Zachełmie trackways in the Middle Devonian and the poorly-known taxon *Livoniana*, which seems 'more derived' than *Panderichthys* but is contemporary with it (Ahlberg et al. 2000), the agreement between phylogeny (inferred from morphology) and stratigraphy seems fairly robust and the fish-tetrapod series thus provides a good example of a stratomorphic series *sensu* Wise (1995).

From an evolutionary perspective, this stratomorphic series is interpreted as an evolutionary sequence documenting the step-wise acquisition of key tetrapod characters during a major morphological transition (e.g. Blieck et al. 2010; Clack 2006; Clack 2009; Clack 2012). However, Garner (2003) highlighted a number of difficulties with the evolutionary interpretation and concluded that the Devonian tetrapodomorphs were morphological intermediates, though not evolutionary intermediates. Wise (2003) proposed a creationist interpretation, in which the Devonian tetrapodomorphs were inhabitants of aquatic environments associated with a pre-Flood floating forest biome, and equipped with morphologically intermediate traits suitable for life in an ecosystem that was itself intermediate between the sea and the land.

Furthermore, Garner (2003) claimed that Devonian tetrapods such as *Ichthyostega* and *Acanthostega* remained separated from elpistostegids such as *Panderichthys* by a significant morphological (and, by inference, phylogenetic) discontinuity. However, this claim has not until now been tested with a statistical analysis. Here, we examine six character matrices from Ahlberg and Clack (1998), Daeschler et al. (2006), Ruta (2011), Swartz (2012), Sookias et al. (2014) and Clack et al. (2016) using baraminic distance correlation (BDC) and three-dimensional MDS (multidimensional scaling). These methods should allow us to detect any morphological discontinuities that may exist between these organisms, and to draw some conclusions regarding their baraminic status from a creationist perspective.

METHODS

BDISTMDS version 2.0 was used to carry out a BDC analysis on the datasets (Wood 2008a). Baraminic distance is the percentage of character states that two organisms have in common (Robinson and Cavanaugh 1998). The BDC correlates the distances between taxa using linear regression to derive a statistical significance of the similarity of two organisms. Ideally, baraminologists hope to identify well-defined groups of taxa that are united by significant, positive correlation (interpreted as evidence of continuity) and separated from the outgroup taxa by significant, negative correlation (interpreted as evidence of discontinuity). For baraminic distance calculations, characters are omitted that do not meet a minimum criterion of character relevance (the percentage of taxa for which a character state is known). In the present analysis, we used a character relevance cutoff of 75%, and bootstrap values were obtained from 100 pseudo-replicates of each character set (see Wood 2008b). Our baraminic distance correlations were supplemented with the application of classical MDS, as described by Wood (2005a). MDS converts a matrix of Euclidean distances between objects into a set of k-dimensional coordinates of the objects, where k is a predetermined dimensionality. One major advantage of MDS is the introduction of the concept of *stress*, a measure of how the observed baraminic distances are distorted by the reduction in dimensionality. The smaller the stress, the better the fit between the baraminic distances and the distances inferred from the classical MDS.

Ahlberg and Clack's (1998) matrix consisted of 26 taxa scored for 50 mandibular characters. The taxa included the elpistostegid *Panderichthys*, seven Devonian tetrapods and a sampling of other Carboniferous to Permian tetrapods. We used a modified version of the matrix with character states for the Carboniferous taxon *Whatcheeria* rescored by Lombard and Bolt (2006). We performed two calculations. The first was on the whole dataset. After filtering at 0.75 character relevance cutoff, we used 41 characters to calculate baraminic distances. The second was on a subset of 11 taxa; 15 Carboniferous and Permian taxa were excluded in order to avoid spurious positive distance correlations caused by the inclusion of excessive outgroups (c.f. Wood 2005b). After filtering at 0.75 character relevance cutoff, we used 37 characters to calculate baraminic distances.

Daeschler et al.'s (2006) matrix consisted of 9 taxa scored for 114 cranial, mandibular and postcranial characters. Characters 1-61 were taken from Ahlberg and Johanson (1998) and characters 62-83 from Ahlberg et al. (2000). The taxa included three elpistostegids, two Devonian tetrapods and four Devonian sarcopterygian fishes belonging to other families. We analysed the full dataset of 9 taxa. After filtering at 0.75 character relevance cutoff, we used 86 characters to calculate baraminic distances. A sampling of cranial, mandibular and postcranial characters was retained after filtering.

Ruta's (2011) matrix consisted of 44 taxa scored for 157 characters of the appendicular skeleton, including the pectoral and pelvic girdles and the paired appendages. The taxa included two elpistostegids, four Devonian tetrapods and a sampling of other Devonian to Permian tetrapods and fishes. Two taxa (Catskill humerus, *Caerorhachis*) were excluded from the analysis because too few character states were known. For our calculations, we excluded another 29 taxa and used a subset of 13 taxa. The excluded taxa were Devonian, Carboniferous and Permian forms representing multiple families. As with the Ahlberg and Clack (1998) dataset, this was to eliminate excessive outgroups. After filtering at 0.75 character relevance cutoff, we used 51 characters to calculate baraminic distances. A sampling of characters of the pectoral girdle and paired appendages was retained after filtering, but all the pelvic girdle characters were eliminated.

Swartz's (2012) matrix consisted of 47 taxa scored for 204 cranial, mandibular and postcranial characters. Of the 204 characters, 197 were taken from Ahlberg and Johanson (1998), Ahlberg et al. (2008), Coates and Friedman (2010), Daeschler et al. (2006), Long et al. (2006) and Zhu and Ahlberg (2004), several of them with modifications. The taxa included three elpistostegids, four Devonian tetrapods and a sampling of other Devonian to Permian tetrapods and fishes. For our calculations, we excluded 37 taxa and used a subset of 10 taxa. The excluded taxa were Devonian, Carboniferous and Permian forms representing multiple families. As with the Ahlberg and Clack (1998) dataset, this was to eliminate excessive outgroups. After filtering at 0.75 character relevance cutoff, we used 101 characters to calculate baraminic distances. A sampling of cranial, mandibular and postcranial characters was retained after filtering.

Sookias et al.'s (2014) matrix consisted of 25 taxa scored for 115 cranial, mandibular and postcranial characters. The matrix was modified from Clack et al. (2012), which in turn was based on the matrix of Callier et al. (2009). Callier et al. (2009) modified the matrix of Ahlberg et al. (2008), deleting six characters to reduce redundancy and adding four humeral characters. The taxa included three elpistostegids, seven Devonian tetrapods and a sampling of other Devonian to Carboniferous tetrapods and fishes. For our calculations, we excluded 14 taxa and used a subset of 11 taxa. The excluded taxa were Devonian and Carboniferous forms representing multiple families. As with the Ahlberg and Clack (1998) dataset, this was to eliminate excessive outgroups. After filtering at 0.75 character relevance cutoff, we used 40 characters to calculate baraminic distances. Most characters of the lower jaw and lower jaw dentition were retained, but all but one character of the palatal dentition, and all the skull roof, braincase and postcranial characters were eliminated, including the new characters introduced by Callier et al. (2009).

Clack et al.'s (2016) matrix consisted of 45 taxa scored for 213 cranial, mandibular and postcranial characters. Characters were sourced from Ahlberg and Clack (1998), Clack (1998), Clack et al. (2012), Clack and Finney (2005), Klembara et al. (2014), Ruta and Clack (2006) and Ruta et al. (2002), several of them with modifications and with the addition of five new characters. The taxa included two elpistostegids, six Devonian tetrapods and a sampling of other Devonian to Carboniferous tetrapods and fishes. We performed our calculations on two subsets of taxa. In both cases, several Carboniferous and Permian taxa representing multiple families were removed in order to eliminate excessive outgroups. Our first analysis excluded 32 taxa and used a subset of 13 taxa, including two of the new Tournaisian tetrapods (*Perittodus*, *Diploradus*) described by Clack et al. (2016). A third (*Ossirarus*) had to be eliminated because it had too few characters in common with the other taxa. After filtering at 0.75 character relevance cutoff, we used 32 characters to calculate baraminic distances. All postcranial and upper dentition characters were eliminated after filtering, as were most of the palatal and general skull characters. Our second analysis excluded 36 taxa and used a subset of 9 taxa, and included only the Devonian tetrapods, the elpistostegids and *Eusthenopteron*. After filtering at 0.75 character relevance cutoff, we used 50 characters to calculate baraminic distances. All postcranial characters were eliminated after filtering, along with most of the palatal and general skull characters.

RESULTS

The baraminic distance correlation results for Ahlberg and Clack's (1998) whole matrix are summarized in Figure 1. Two blocks of positive correlation are evident, one comprising the 'more derived' Carboniferous and Permian taxa and a second smaller one comprising the Devonian taxa plus one Lower Carboniferous taxon (*Whatcheeria*). Almost all members of the first group are negatively correlated with all members of the second group, with only three exceptions: *Greererpeton*, *Megalocephalus* and *Crassigyrinus*. *Megalocephalus* is negatively correlated with all but one member of the Devonian group. However, *Greererpeton* is negatively correlated with only four of the nine members of the Devonian group, and *Crassigyriunus* is negatively correlated with only one of the Devonian taxa. Moreover, *Crassigyrinus* is the only taxon that does not show positive correlations with all other members of its own group. Bootstrap values are generally good, ranging from 27% to 100% with a median value of 94%. The 3D MDS results indicate the same groupings (Figure 2), with an obvious cluster of Carboniferous and Permian taxa separated from a cluster of Devonian taxa + *Whatcheeria*. The Devonian taxa include seven tetrapods plus one elpistostegid (*Panderichthys*). The Carboniferous and Permian taxa represent multiple families of tetrapods. The 3D stress was 0.133 with minimal stress of 0.121 at four dimensions.

We suspected that most of the Carboniferous and Permian taxa were so different from the Devonian taxa that they were obscuring any discontinuities among the Devonian taxa. We therefore removed most of the Carboniferous and Permian forms from the analysis and ran it again, with a subset of 11 taxa comprising the Devonian forms plus *Whatcheeria*, *Greererpeton* and *Crassigyrinus*. The baraminic distance correlation results for this subset of Ahlberg and Clack's (1998) matrix are summarized in Figure 3. There are two blocks of taxa, one comprising the Devonian tetrapods + *Whatcheeria* and another comprising *Greererpeton* + *Crassigyrinus*. Only one Devonian tetrapod (*Obruchevichthys*) is correlated negatively

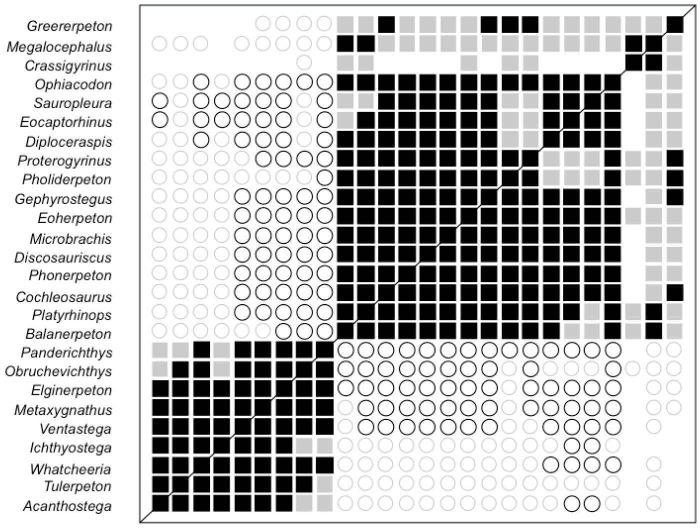

Figure 1. BDC results for Ahlberg and Clack's (1998) whole matrix, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90% in a sample of 100 pseudoreplicates. Grey symbols represent bootstrap values <90%.

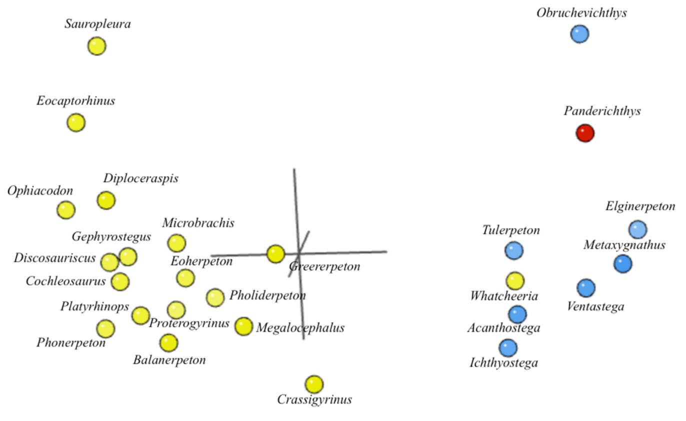

Figure 2. Three dimensional MDS applied to Ahlberg and Clack's (1998) whole matrix. Devonian tetrapods are shown in blue, elpistostegids in red and Carboniferous and Permian tetrapods in yellow.

with another taxon, namely *Crassigyrinus*. *Panderichthys* is not positively correlated with any other taxon, although it is negatively correlated with both *Crassigyrinus* and *Greererpeton*. However, bootstrap values for all taxon-pair correlations are low, ranging from 46% to 84% with a median value of 60%; none reaches >90%. The 3D MDS results indicate the same groupings (Figure 4), with an obvious cluster of Devonian tetrapods + *Whatcheeria* separated from *Greererpeton* + *Crassigyrinus*. *Panderichthys* stands apart from both of these groupings. The 3D stress was 0.157 with minimal stress of 0.104 at four dimensions.

The baraminic distance correlation results for Daeschler's (2006) matrix are summarized in Figure 5. There are three main clusters, comprising (1) the Devonian tetrapods (*Ichthyostega* + *Acanthostega*), (2) the elpistostegids (*Panderichthys* + *Tiktaalik* + *Elpistostege*), and (3) the other fishes (*Glyptolepis* + *Megalichthys* + *Gooloogongia* + *Eusthenopteron*). Each member of Group 1 is negatively correlated with each member of Group 3, although there are no negative correlations between members of Groups 1 and 2. One member of Group 2 (*Tiktaalik*) is negatively correlated with one member of Group 3 (*Glyptolepis*). Bootstrap values range from 47% to 100%, with a median value of 86.5%. The positive correlation between *Glyptolepis* and *Gooloogongia* has the lowest bootstrap value (47%); all others were 72% or above. The same groupings are evident in the 3D MDS results (Figure 6), with clear separation between the three clusters. The 3D stress was 0.071 with minimal stress of 0.049 at five dimensions.

The baraminic distance correlation results for Ruta's (2011) matrix are summarized in Figure 7. Two clusters are evident, one comprising all the tetrapods (including the Devonian forms) and another comprising all the fishes (including the elpistostegids). The two clusters are separated by significant negative correlation. Bootstrap values range from 47% to 100%, but are generally good with a median value of 97%. The lowest bootstrap values are associated with the negative correlations between some fishes and tetrapods (e.g. 50% between *Gogonasus* and *Hynerpeton*; 53% between *Panderichthys* and *Crassigyrinus*) and the positive

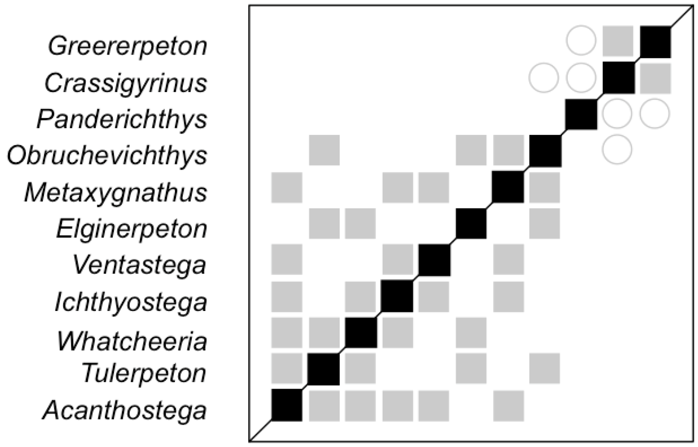

Figure 3. BDC results for Ahlberg and Clack's (1998) matrix with a subset of 11 taxa, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90% in a sample of 100 pseudoreplicates. Grey symbols represent bootstrap values <90%.

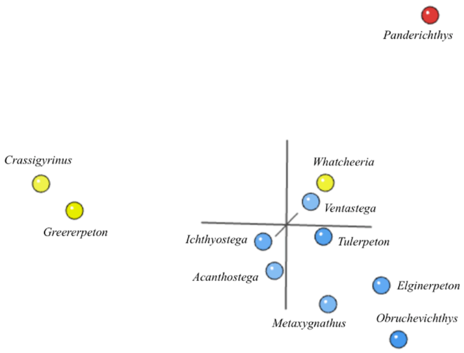

Figure 4. Three dimensional MDS applied to Ahlberg and Clack's (1998) matrix with a subset of 11 taxa. Devonian tetrapods are shown in blue, elpistostegids in red and Carboniferous tetrapods in yellow.

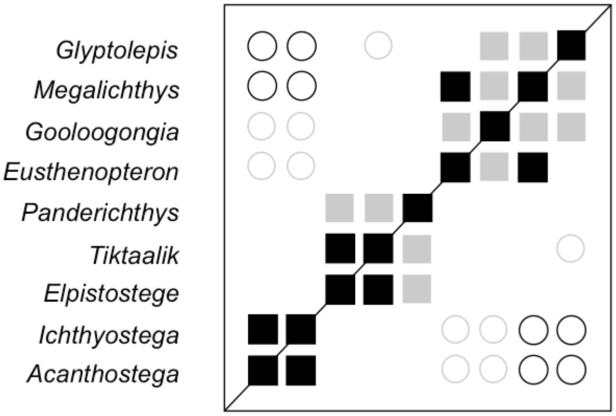

Figure 5. BDC results for Daeschler et al.'s (2006) whole matrix, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90% in a sample of 100 pseudoreplicates. Grey symbols represent bootstrap values <90%.

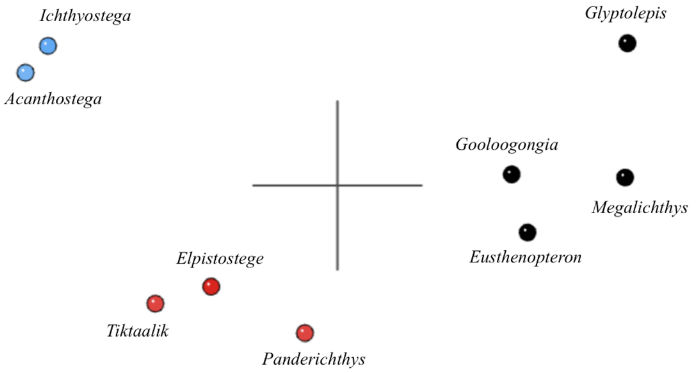

Figure 6. Three dimensional MDS applied to Daeschler et al.'s (2006) whole matrix. Devonian tetrapods are shown in blue, elpistostegids in red and other fishes in black.

correlation between *Acanthostega* and *Tulerpeton* (47%). In the 3D MDS results (Figure 8), there is also a clear separation between the two clusters, but perhaps also some indications of discontinuities within each cluster. For example, *Tiktaalik* + *Panderichthys* seem to be somewhat separated from *Gogonasus* + *Eusthenopteron*, and *Marsdenichthys* is separated from all the other fishes. Likewise, *Ichthyostega* + *Acanthostega* + *Hynerpeton* are slightly separated from the Carboniferous tetrapods + *Tulerpeton* (which seem to form a tight 'sub-cluster'), and *Ossinodus* is separated from all the other tetrapods. The 3D stress was 0.205 with minimal stress of 0.169 at two dimensions.

The baraminic distance correlation results for Swartz's (2012) matrix are summarized in Figure 9. Two clusters are evident, one comprising the Devonian tetrapods (*Ichthyostega* + *Ventastega* + *Acanthostega*) and the other comprising the Devonian fishes (*Osteolepis* + *Gogonasus* + *Eusthenopteron* + *Panderichthys* + *Tiktaalik*). Every member of Group 1 is negatively correlated with every member of Group 2, apart from *Tiktaalik*. *Elginerpeton* is not positively correlated with any other taxon, but is negatively correlated with *Osteolepis* and *Eusthenopteron*. *Elpistostege* is not positively or negatively correlated with any other taxon. Bootstrap values range from 36% to 100%, but are generally good with a median value of 94%. The lowest bootstrap values are seen with the negative correlations between *Elginerpeton* and, respectively, *Eusthenopteron* (36%) and *Osteolepis* (45%). The 3D MDS results (Figure 10) show the same clusters, with *Elginerpeton* probably part of the Devonian tetrapod cluster and *Elpistostege* standing apart from both clusters. There may also be an indication of discontinuity between the elpistostegids and the other fishes. The 3D stress was 0.1098 with minimal stress of 0.1097 at four dimensions.

The baraminic distance correlation results for Sookias et al.'s (2014) matrix are summarized in Figure 11. Two clusters can be seen, one comprising the Devonian fishes (including the elpistostegids) and

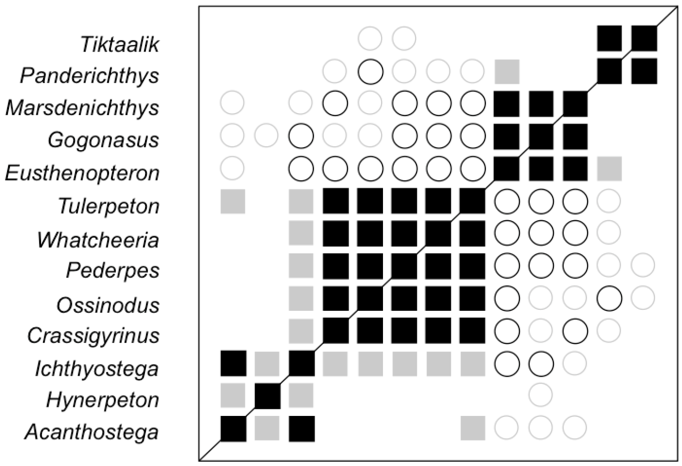

Figure 7. BDC results for Ruta's (2011) matrix with a subset of 13 taxa, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90% in a sample of 100 pseudoreplicates. Grey symbols represent bootstrap values <90%.

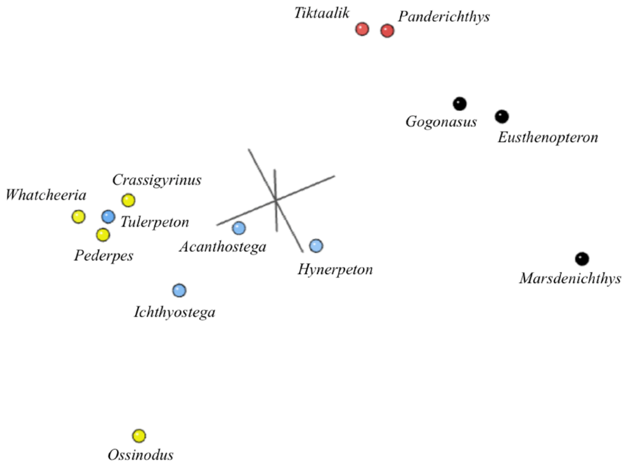

Figure 8. Three dimensional MDS applied to Ruta's (2011) matrix with a subset of 13 taxa. Devonian tetrapods are shown in blue, elpistostegids in red, Carboniferous tetrapods in yellow and other fishes in black.

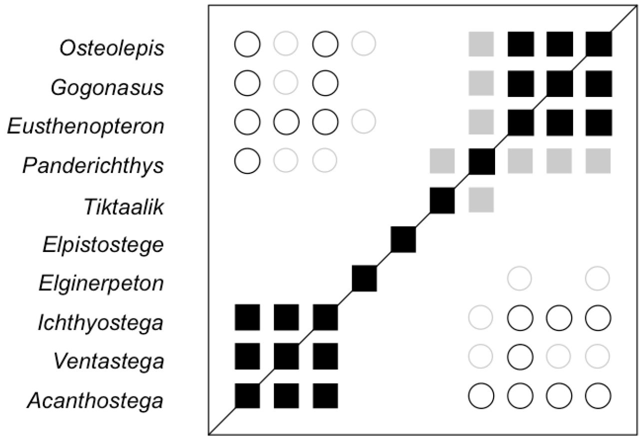

Figure 9. BDC results for Swartz's (2012) matrix with a subset of 10 taxa, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90% in a sample of 100 pseudoreplicates. Grey symbols represent bootstrap values <90%.

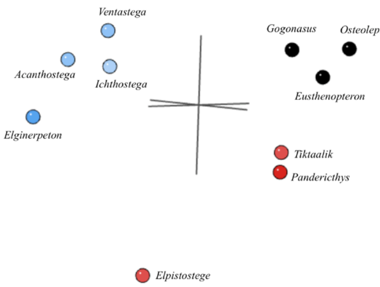

Figure 10. Three dimensional MDS applied to Swartz's (2012) matrix with a subset of 10 taxa. Devonian tetrapods are shown in blue, elpistostegids in red and other fishes in black.

the other comprising the Devonian tetrapods. Every member of Group 1 is positively correlated with every other member of the group; the same is true of Group 2. Furthermore, every member of Group 1 is negatively correlated with every member of Group 2, with the sole exception of *Tiktaalik* with *Ymeria*. *Elginerpeton* is neither positively nor negatively correlated with any other taxon in the dataset. Bootstrap values range from 24% to 100%, with a median value of 65%. The lowest bootstrap values (24%-65%, with a median of 44%) are associated with the negative correlations between the Devonian fishes and a subset of the tetrapods (comprising *Ymeria* + *Metaxygnathus* + *Densignathus* + *Ventastega*). Bootstrap values for the negative correlations between the fishes and *Ichthyostega* + *Acanthostega* are generally higher (64%-99%, with a median of 88.5%). The 3D MDS results (Figure 12) show the same clusters, with *Elpistostege* a little separated from the other fishes. *Elginerpeton* stands apart from both clusters. The minimal stress was at three dimensions (0.171).

The baraminic distance correlation results for Clack et al.'s (2016) matrix with a subset of 13 taxa are summarized in Figure 13. At least two and possibly three clusters can be seen: (1) the elpistostegids + *Eusthenopteron*, (2) *Tulerpeton* + *Pederpes*, and (3) the rest of the tetrapods. All members of Group 2 are negatively correlated with all members of Group 1. However, there are no negative correlations between Group 3 and either of the other two groups, and one member of Group 3 (*Ymeria*) is positively correlated with one member of Group 1 (*Tiktaalik*). Overall, bootstrap values are very low, ranging from 19% to 97% with a median value of 64%. The 3D MDS results (Figure 14) reveal a diffuse cluster of tetrapods separated from the elpistostegids + *Eusthenopteron*, with *Tulerpeton* and *Pederpes* the furthest from the elpistostegids. The 3D stress was 0.155 with minimal stress of 0.146 at four dimensions.

The baraminic distance correlation results for Clack et al.'s (2016) matrix with a subset of 9 taxa are summarized in Figure 15. Two clusters can be seen, one comprising the Devonian fishes (including the elpistostegids) and the other comprising four of the Devonian

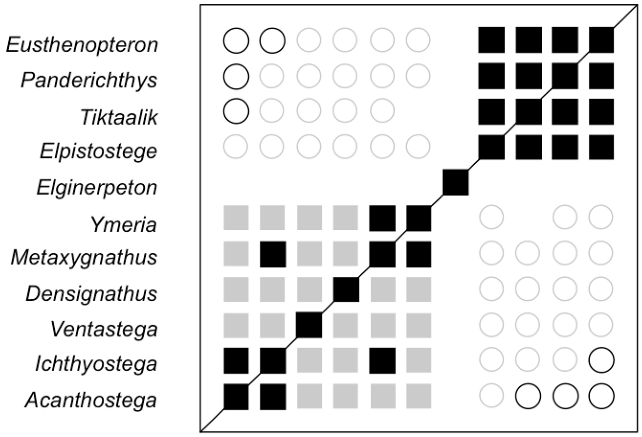

Figure 11. BDC results for Sookias et al.'s (2014) matrix with a subset of 11 taxa, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90% in a sample of 100 pseudoreplicates. Grey symbols represent bootstrap values <90%.

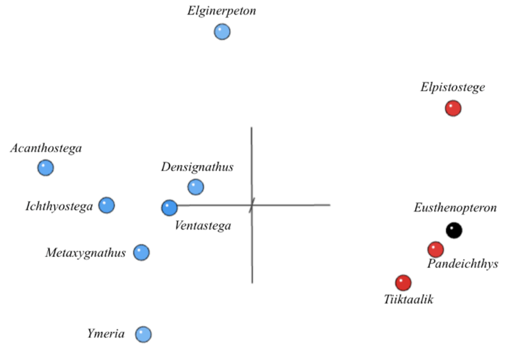

Figure 12. Three dimensional MDS applied to Sookias et al.'s (2014) matrix with a subset of 11 taxa. Devonian tetrapods are shown in blue, elpistostegids in red and other fishes in black.

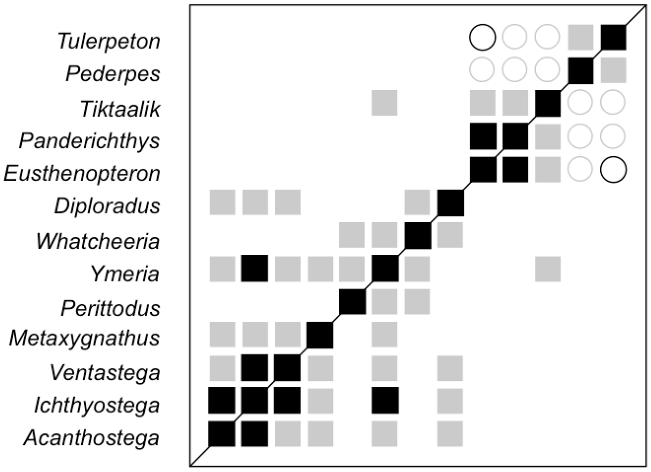

Figure 13. BDC results for Clack et al.'s (2014) matrix with a subset of 13 taxa, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90% in a sample of 100 pseudoreplicates. Grey symbols represent bootstrap values <90%.

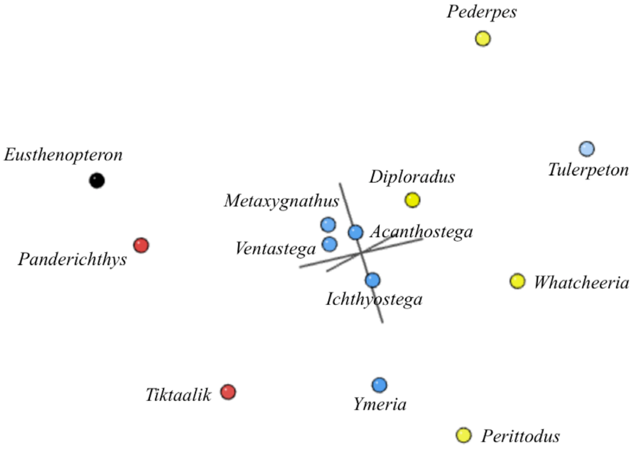

Figure 14. Three dimensional MDS applied to Clack et al.'s (2016) matrix with a subset of 13 taxa. Devonian tetrapods are shown in blue, elpistostegids in red, Carboniferous tetrapods in yellow and other fishes in black.

tetrapods (*Ventastega* + *Ichthyostega* + *Ymeria* + *Acanthostega*). However, there are no negative correlations between members of these two groups. *Tulerpeton* is not positively correlated with any other taxon in the dataset, but is negatively correlated with two members of Group 1 (*Panderichthys*, *Eusthenopteron*) and one member of Group 2 (*Acanthostega*). *Metaxygnathus* is neither positively nor negatively correlated with any other taxon. Again, bootstrap values are very low, ranging from 30% to 97% with a median value of 60%. The 3D MDS results (Figure 16) show the same two clusters, with *Tulerpeton* standing apart from both. The 3D stress was 0.130 with minimal stress of 0.113 at five dimensions.

DISCUSSION

Garner (2003) claimed that there was a morphological discontinuity between even the most fish-like tetrapods and the most tetrapod-like fishes, and our study provides statistical evidence to support that claim. Leaving aside our analysis of Ahlberg and Clack's (1998) whole matrix, which includes too many outgroups, three of our analyses show no positive correlations between tetrapods and elpistostegids (Ahlberg and Clack 1998 with 11 taxa; Clack et al. 2016 with 9 taxa; Daeschler et al. 2006) and three show negative correlations (Ruta 2011 with 13 taxa; Swartz 2012 with 10 taxa; Sookias et al. 2014 with 11 taxa). There was only one analysis (Clack et al. 2016 with 13 taxa) in which a single elpistostegid (*Tiktaalik*) was positively correlated with a tetrapod (*Ymeria*), and when this analysis was re-run with fewer taxa and more characters even this positive correlation vanished. Minimally, therefore, our results suggest the presence of two apobaramins: tetrapods and elpistostegids. Our ability to detect discontinuity between the Devonian tetrapods and the elpistostegids is especially noteworthy, given that the Devonian tetrapods possess many fish-like characters and the elpistostegids possess many tetrapod-like characters. Theoretically, taxa that share characteristics of fish and tetrapods could have bridged the gap between these two groups, but our BDC and MDS analyses support separating them into distinct clusters even when such intermediate forms are included. In this respect our results are reminiscent of Wood's (2010; 2016) finding that statistical baraminology is able to detect discontinuity between humans and non-humans, even though the fossil record includes some humans with ape-like characters and some apes with human-like characters.

Some taxa yielded inconsistent results in our study. For example, *Elpistostege* clustered as expected with other elpistostegids in two analyses (Daeschler 2006; Sookias et al. 2014), but failed to do so in one analysis (Swartz 2012); *Elginerpeton* clustered as expected with the tetrapods in two analyses (Ahlberg and Clack 1998; Swartz 2012), but failed to do so in one analysis (Sookias et al. 2014); *Metaxygnathus* clustered as expected with the tetrapods in three analyses (Ahlberg and Clack 1998; Sookias et al. 2014; Clack et al. 2016 with 13 taxa), but failed to do so in one analysis (Clack et al. 2016 with 9 taxa); and *Tulerpeton* clustered as expected with the other tetrapods in one analysis (Ahlberg and Clack 1998), but in another seemed discontinuous with them (Clack et al. 2016). Moreover, in some of our analyses certain Carboniferous tetrapods clustered with Devonian tetrapods (*Whatcheeria* in Ahlberg and Clack 1998, *Whatcheeria*, *Crassigyrinus* and *Pederpes* in Ruta 2011, *Pederpes*, *Diploradus*, *Whatcheeria* and *Perittodus* in Clack et al. 2016) while in others they clustered separately from them (e.g. *Crassigyrinus* and *Greererpeton* in Ahlberg and Clack 1998). Further work will be needed to elucidate the baraminic status of the taxa within these presumably apobaraminic groups.

Several possible limitations to the current study suggest themselves. The first concerns the non-holistic nature of some of the datasets, a problem exacerbated by the loss of characters after filtering. For instance, Ahlberg and Clack's (1998) matrix consisted of mandibular characters only and Ruta's (2011) matrix of appendicular skeletal characters only. However, missing characters is a perennial problem with fossil data and can only be resolved with the discovery of more fossil material. Moreover, other matrices in our study sampled a greater range of skeletal characters, and in two cases (Daeschler et al. 2006; Swartz 2012) good representation of the character sets was maintained even after filtering. A second concern is the possible non-independence of the character datasets that we analysed. Clearly there is some overlap in the sources used by Daeschler et al. (2006), Swartz (2012), Sookias et al. (2014) and Clack et al. (2016) to construct their matrices, so it is reasonable to ask whether we are actually dealing with six different matrices or merely variants of fewer matrices. However,

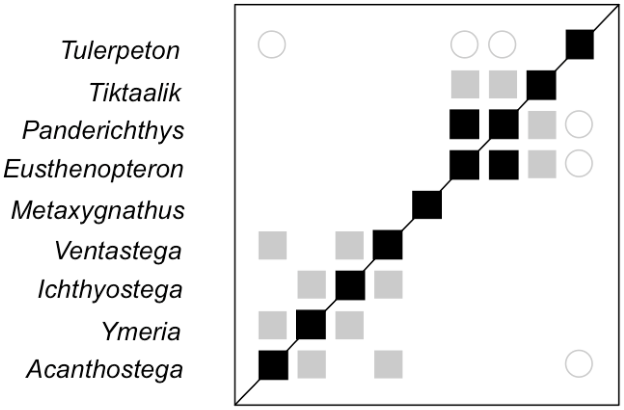

Figure 15. BDC results for Clack et al.'s (2014) matrix with a subset of 9 taxa, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90% in a sample of 100 pseudoreplicates. Grey symbols represent bootstrap values <90%.

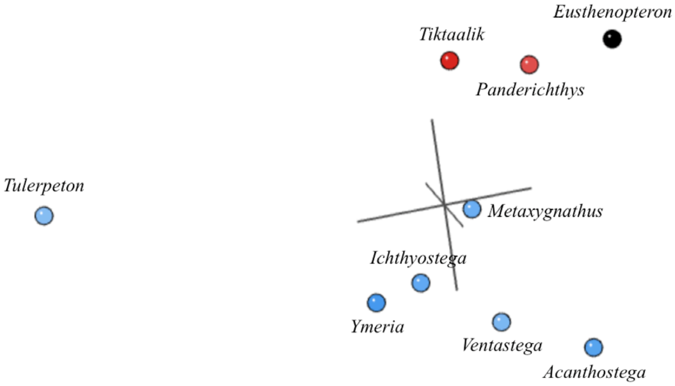

Figure 16. Three dimensional MDS applied to Clack et al.'s (2016) matrix with a subset of 9 taxa. Devonian tetrapods are shown in blue, elpistostegids in red and other fishes in black.

it is worth pointing out that two of our datasets appear to have been newly constructed and not based on earlier matrices (Ahlberg and Clack 1998; Ruta 2011), and those that did draw on previously published matrices rescored or modified some characters and/or used different character-taxon combinations. Overall, we feel that the matrices we selected are sufficiently different to regard them as independent. A third issue concerns the bootstrapping results. Some of our analyses were characterized by poor bootstrap values, in particular those based on the matrices of Ahlberg and Clack (1998), Sookias et al. (2014) and Clack et al. (2016). However, as Wood (2008b) has pointed out, low bootstrap values should not be taken to imply that the correlations are not significant, but rather that they are highly dependent on a particular character set. This highlights where future research may be needed. Moreover, the fact that we obtained similar results with datasets yielding better bootstrap values bolsters our confidence in the conclusions that we have drawn. Finally, a fourth concern is our removal of outgroups, a procedure that raises the question of whether different results might have been obtained had more of those taxa been retained in our analyses. Our rationale for removing these taxa is that they represented multiple families so different from the Devonian taxa in which we were particularly interested, that their presence in our analyses was swamping discontinuities that were otherwise evident among the Devonian forms. However, other analyses could undoubtedly be run with different outgroup selections in order to see whether our results can be replicated.

CONCLUSION

Our studies reveal statistical evidence of morphological discontinuity between Devonian and Carboniferous tetrapods and the Devonian elpistostegids, which we interpret as evidence of phylogenetic discontinuity and, by implication, separate ancestry. Given that this result was consistent across all six of our datasets, we think that our conclusions are robust and will likely withstand future analyses. However, further studies using other datasets with different combinations of taxa and characters are encouraged.

ACKNOWLEDGMENTS

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THE AUTHORS

Paul A. Garner is a full-time Researcher and Lecturer for Biblical Creation Trust in the UK. He has an MSc in Geoscience from University College London, where he specialised in palaeobiology. He is a Fellow of the Geological Society of London and a member of several other scientific societies. His first book, *The New Creationism: Building Scientific Theories on a Biblical Foundation*, was published by Evangelical Press in 2009.

Jonathan Asher is currently studying for a BSc in Biochemistry at a British university.