CHAPTER 2.
THE APPENDICULAR SKELETON OF ERYOPS MEGACEPHALUS COPE, 1877 (TEMNOSPONDYLI: ERYOPOIDEA) FROM THE LOWER PERMIAN OF NORTH AMERICA

Abstract. The appendicular skeleton of the Lower Permian temnospondyl Eryops megacephalus Cope, 1877, described and figured in detail, is similar to that of most temnospondyls, except that it is highly ossified. It displays terrestrial adaptations, including a reduced dermal pectoral girdle and comparatively large limbs, characterized by well-developed processes for muscle attachment. While many features that were previously unknown or uncommon among temnospondyls were identified, no apomorphies of the appendicular skeleton particular to Eryops were found. Some characteristics of the endochondral postcranial skeleton found in well-ossified temnospondyls, such as Eryops, are absent in less well-ossified temnospondyls due to immaturity or paedomorphism. The effects of heterochronic processes on the morphology of the postcranial skeleton of temnospondyls and the implications for cladistics are discussed; the appendicular skeleton of Eryops is considered hypermorphic. Within the Temnospondyli, the Eryops appendicular skeleton is most similar to that of the Dissorophoidea, and most dissimilar to both the most plesiomorphic temnospondyls and the secondarily aquatic Mesozoic stereospondyls. The appendicular skeletons of well-ossified Late Permian and Mesozoic temnospondyls are not as robust as that of Eryops. Surprisingly, Eryops, in common with other well-ossified temnospondyls, shares many derived features of the appendicular skeleton with seymouriamorphs and diadectomorphs. The presence of these previously unrecognised synapomorphies (relative to stem tetrapods and embolomeres) provides evidence for an alternative hypothesis of relationships of early tetrapods, suggesting that the Temnospondyli and seymouriamorphs plus diadectomorphs are sister taxa.

INTRODUCTION

Eryops megacephalus Cope, 1877; from the Lower Permian of North America, is among the most common and best-known temnospondyl amphibians. Temnospondyls are the most numerous and diverse group of the archaic Palaeozoic ‘labyrinthodont’ amphibians. There has been much debate over the last two decades involving temnospondyls, concerning the origin of terrestrial vertebrates (summarised in Clack, 2002a), the phylogenetic relationships of early tetrapods, and the origin of modern lissamphibians and amniotes (summarised in Ruta et al., 2003). Among temnospondyls the postcranial skeleton varies from heavily ossified, with obvious terrestrial adaptations in the stratigraphically oldest taxa, Balanerpeton woodi (Milner and Sequeira, 1994) and Dendrerpeton acadianum Owen, 1853 (Carroll, 1967; Holmes et al., 1998), to poorly ossified and paedomorphic (sensu McNamara, 1986) in most of the Mesozoic taxa (Pawley and Warren, 2004).

Recent work has brought to light some unexpectedly well ossified and terrestrialy adapted postcranial skeletons in basal stereospondyls (Pawley and Warren, 2005), which are monophyletic, mainly Mesozoic radiation of temnospondyls (Yates and Warren, 2000), prompting further investigation into previously undescribed postcranial material among temnospondyl taxa. During this research, it became apparent that many previous descriptions of temnospondyl postcranial elements are inadequate for detailed
comparative work, including cladistic analysis. As part of a more inclusive long term study of the temnospondyl postcranial skeleton, a comprehensive description of the postcranial elements of a member of each major temnospondyl clade was undertaken in order to determine the polarity of postcranial characters and to tease out homoplasy associated with terrestriality. This particular study aims to assist resolution of the issues outlined above, by providing data for large-scale analyses both of relationships within the Temnospondyli and the position of the Temnospondyli within the tetrapods.

Previous descriptions of Eryops megacephalus

*Eryops* Cope, 1877 is a medium sized temnospondyl, reaching a length of 2m or more, and is one of a minority of temnospondyls with postcranial skeletons obviously capable of terrestrial locomotion. Cope (1877) first described the skull and mentioned some features of the vertebrae. Cranial material was revised by Sawin (1941), while the axial skeleton was described by Case (1911a), Olson (1936a), and Moulton (1974). Many partial descriptions of the appendicular postcranial material have been published (Cope, 1878, 1880, 1884, 1888; Williston, 1899; Moodie, 1910; Case, 1911a, 1915; Cope and Matthew, 1915; Gregory et al., 1923; Gregory and Raven, 1941; Gregory, 1949; Langston, 1953). Various morphogenetic stages of the humerus were described by Case (1915) and Bakker (1982). *Eryops* has become a standard reference in anatomical studies of early tetrapods, and its osteology has provided a basis for restorations of musculature. In particular Romer (1922) and Miner (1925) restored musculature in the pectoral (Romer, 1922; Miner, 1925) and pelvic (Romer, 1922) regions.

Cope (1882a) erected the family Eryopidae, based on *Eryops megacephalus*. All recent phylogenetic analyses that have included *Eryops* (Milner, 1990; Yates and Warren, 2000; Ruta et al., 2003) have agreed in their placement of *Eryops* within the Euskelia Yates and Warren, 2000. Taxa included by Yates and Warren (2000) in Euskelia were *Eryops* plus Zatrachyidae Williston 1910a, and *Dissorophus* Cope, 1895 plus Trematopidae Williston 1910b.

Paleoenvironment

*Eryops* is a common component of the bone beds of north-central Texas, deposited in lushly vegetated swampy environments. The vertebrate fauna in these sites is predominantly aquatic or semi-aquatic (Sander, 1987, 1989), while in New Mexico, *Eryops* is found in faunal assemblages dominated by both aquatic and terrestrial vertebrates (Berman, 1993).

Terrestrial adaptations

Case (1915) first considered that *Eryops* was likely to be aquatic because the eyes and nostrils are dorsally positioned on the skull, however, *Eryops* possesses no other obvious aquatic adaptations. Conversely, Romer (1947: p 134.), considered *Eryops megacephalus* to be “as well adapted for terrestrial life as many of its reptilian contemporaries”. The following morphological features, present in *Eryops megacephalus*, have been regarded as adaptations for a terrestrial lifestyle in other taxa: absence of lateral line sulci; absence of any trace of an ossified branchial system; presence of a large tympanic ear and a relatively rod like stapes suggesting the ability to perceive high frequency sound; short trunk and tail; limb bones with well developed articulation surfaces and comparatively
FIGURE 10. Main specimens of *Eryops megacephalus* Cope, 1877 used in reconstructions. 1, MCZ 2675 interclavicle; 2, MCZ 1900 interclavicle; 3, MCZ 7766 interclavicle; 4, MCZ 1883 left clavicle fragment; 5, MCZ 1900 interclavicle; 6, MCZ 1421 right clavicle; 7, MCZ 1984 right cleithrum; 8, AMNH 4203 left radius; 9, AMNH 4862 left ulna; 10, AMNH 4203 right tibia; 11, AMNH 23449 left fibula. Scale bar = 50 mm.
high degree of ossification; and ossified carpus and tarsus (Olson, 1941; de Mar, 1968; Milner and Sequeira, 1994; Holmes, 2000; Carroll, 2002; Vallin and Laurin, 2004). This evidence suggests that *Eryops* was adaptable and probably amphibious, living part of the time in the water. It was undoubtedly capable of sustained terrestrial locomotion.

Despite the use of *Eryops* as a classical textbook example of both a temnospondyl and an early tetrapod, the plethora of previous research, and the availability of extensive collections of well-preserved material, many features of the postcranial skeleton of *Eryops* remain undescribed. Apart from *Edops craigi* (Romer and Witter, 1942) which possesses few associated postcranial elements, *Eryops* is the only large, well-ossified temnospondyl with obvious adaptations for terrestrial locomotion, and its abundant, usually well-preserved, and often disarticulated remains facilitate comprehensive description. The larger size of *Eryops* enables identification of characteristics which, when present, are less easily observed in smaller taxa.

The postcranial skeletons of the terrestrial *Balanerpeton woodi* (Milner and Sequeira, 1994) and *Dendrerpeton acadianum* (Carroll, 1967; Holmes et al., 1998), traditionally considered the most basal taxa in the Temnospondyli, are either too poorly preserved (*Balanerpeton woodi*), or described in insufficient detail (*Dendrerpeton acadianum*) for comprehensive comparative work (Holmes, 2000). The next more derived terrestrial clade is the Euskelia. Various euskelian taxa smaller than *Eryops* are known from associated postcranial material [e.g. *Acanthostomatops vorax* (Credner, 1883) Kuhn, 1961 (Boy, 1989), *Acheloma cumminsi* (*Trematops milleri*) Cope, 1882b (Williston, 1909a; Olson, 1941), *Dissorophus angustus* (Carroll, 1964a), *D. multicinctus* Cope, 1895 (de Mar, 1968), *Ecolsonia cutlerensis* Vaughn, 1969 (Berman et al., 1985), and *Phonerpeton pricei* (Olson, 1941) Dilkes, 1990 (Dilkes, 1990)]. However, these specimens are often not particularly well preserved, and the articulated nature of the specimens conceals some sides of the elements. Hence, *Eryops* remains the most suitable example of a terrestrial temnospondyl for comparative study of postcranial material.

Traditionally the postcranial skeletons of temnospondyls have been neglected in the literature. When described at all, individual elements are rarely illustrated in sufficient detail to allow complete inter taxon comparisons. The aim of this description is to improve our understanding of the appendicular skeleton of a well ossified terrestrial temnospondyl, and to describe potential characteristics for use in future cladistic analyses.

**MATERIALS STUDIED**

**Locality and repository information**

All specimens examined, with repository, location, and stratigraphic information, are listed in Appendix 3. The specimens of *Eryops* used in this description are mostly from the Nocona and Petrolia Formations of Texas, with one specimen from the Lower Archer City Formation of Texas, and another from the Cutler Formation of New Mexico.

**Institutional abbreviations**

AMNH, American Museum of Natural History, New York; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
Specific designation

Known specimens of *Eryops* cover the whole of the Lower Permian (Olson and Vaughn, 1970), although various species of *Eryops* have been described, Case (1911a), Romer (1947), and Moulton (1974) established that only *E. megacephalus* is valid. More recently, Milner (1996) considered that the cranial material of *Eryops* was referable to four species and allocated it to successive stratigraphic zones. The features used to distinguish species included skull shape, tooth differentiation, and sculpture pattern, with some overlap of characteristics between species. However, no formal taxonomic revision was provided, so the material used in this study cannot be assigned to species recognised by Milner. Pending revision, all specimens in this study are referred to the type species *E. megacephalus* Cope, following Moulton (1974).
Criteria for reconstructions

Reconstructions of individual elements were based primarily on the specimens shown in Figure 10 and Figure 11; other specimens examined are listed in the captions of Figure 13-Figure 20. The least damaged and distorted specimens were used, while larger and better-ossified specimens were considered most likely to belong to adults, to minimize the possibility of describing morphogenetic features. The pectoral girdle (Figure 14.2) was reconstructed using the following criteria. Cope (1888: figure 1.2) described the ventral portion of a slightly distorted, articulated pectoral girdle. The relative proportions of the various elements in Cope’s figure were used to scale the elements from different specimens in our reconstruction. The clavicular facets on the interclavicle (Figure 12.1) indicate that the clavicle blades are oriented laterally, and a little dorsally (see below). The cleithrum is frequently preserved in articulation with the scapulocoracoid, so that the ventral portion of the cleithral shaft must be located posterior to the dorsal clavicular process and anterior to the scapulocoracoid.

Some specimens displayed anomalies, discussed below as paleopathologies. Identification and orientation of distal limb elements was determined by comparison with articulated specimens of the forelimb [AMNH4186 ventral surface figured in Gregory and Raven (1941)], and hind limb (MCZ7555). Descriptive terminology follows Romer (1922; 1956), Bystrow and Efremov (1940), Coates (1996), and Pawley and Warren (2004), unless noted otherwise.

The manus and pes were not described in this study. While specimens are available (see above), they are all too incomplete to allow a full description and reconstruction. The authors consider this would be best undertaken as part of a detailed study and comparison with the few other well ossified specimens of temnospondyl autopodia e.g. Acheloma cumminsi (Williston, 1909a; Schaeffer, 1941) and Sclerocephalus Goldfuss, 1847 (Boy, 1988), and outgroups.

Preparation

Specimens were prepared when necessary using an Aro airscribe. Repairs were made with Zap® cyanoacrylate glue.

Morphological description

TEMNOSPONDYLI Zittel 1888 (sensu Yates and Warren, 2000)
Euskelia Yates and Warren 2000
Eryopidae Cope 1882a
ERYOPS Cope 1877
ERYOPS MEGACEPHALUS Cope 1877

This description of the appendicular skeleton of Eryops, while considerably more detailed, does not depart significantly from the original descriptions of the elements of E. megacephalus by Cope (1880; 1888). Moodie, in a description of E. willistoni (Moodie, 1910), figured several fragmented postcranial elements, none of which differ substantially from those described by Cope (1878; 1880) or Case (1911a) or from those figured in this study. It should be noted that this species was not recognized in assessments of the genus by Case (1911a), Moulton (1974), or Milner (1996). Langston (1953), in describing postcranial material that he assigned to E. grandis Marsh, 1878, lists no discrete
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FIGURE 12. Interclavicle of *Eryops megacephalus*. Reconstruction of interclavicle: 1, ventral; 2, dorsal and 3, anterior views. Abbreviations: air, anterior interclavicular ridge; fel, clavicular facet; lit, lateral interclavicular trabecula; pf, pectinate fringe; sit, sternal interclavicular trabecula. Interclavicle reconstruction based on AMNH 4186; MCZ 1900 (two specimens), 2675, 7279 and 7766.
anatomical features of the postcranial skeleton that differentiate it from that of *E. megacephalus*. All the supposed differences between these taxa are easily attributable to individual variation, morphogenetic variation, or size differences.

**Interclavicle**

The interclavicle (Figure 10, Figure 12.1) is roughly ovoid, slightly wider than long, with the anterior border drawn out into a pectinate fringe. The lateral and posterior margins of the interclavicle are thin, and covered with a fine pattern of ridges, which radiate from the main body of the interclavicle. Posteriorly, the border is semicircular, and grades gently into the main body. The length of the anterior portion of the interclavicle, measured at the level of the posterior border of the clavicular facets, is much longer than the posterior portion. Deeply cut into the anterior border, the prongs of the pectinate fringe have bluntly rounded tips, some of which are bi- or trifurcate towards their ends. A low ridge (herein termed the anterior interclavicul ar ridge, abbreviation = air) separates the clavicular facets anteriorly (Figure 12.1). In ventral view (Figure 12.1), the clavicular facets are oriented laterally, while in anterior view (Figure 12.3), the clavicular facets are oriented slightly dorsally. The center of ossification is anterior to the posterior border of the clavicular facets, approximately in the center of the interclavicle. Ornament on the main body of the interclavicle consists of transverse coarse ridges, with grooves in between. A pit is present at the medial extremity of most grooves. Several larger, deeper pits are present also on the clavicular facets. In dorsal view (Figure 12.2), the gently hollowed surface of the interclavicle is featureless except for a few large scattered pits around the center of ossification. The lateral and sternal interclavicular trabeculae (sensu Howie, 1970) are difficult to observe. There is considerable non-morphogenetic individual variation in the proportions of the interclavicle among the specimens observed. For example, while the example chosen for description is intermediate in morphology, the ornamented portion of the interclavicle between the clavicular facets of MCZ 7766 (Figure 10.3) is wider, while MCZ 1900 (Figure 10.5) is longer.

**Clavicle**

The clavicle (Figure 10, 13) has a narrow, wedge shaped ventral blade that is anteroposteriorly shorter than wide. The ornamented central portion of the ventral surface of the blade (Figure 13.1) bears shallow, transversely oriented grooves with pits similar to those of the interclavicle. These decrease in size and depth towards the center of ossification at the junction of the dorsal clavicular process and the ventral blade. On the ventral surface the ornament radiates from the center of ossification, while on the dorsal surface near the center of ossification, there are deep pits in some specimens. A broad, shallow clavicular groove occupies the anterior border of the blade (Figure 13.1, Figure 13.6), terminating at the level of the center of ossification. In lateral view (Figure 13.3), the clavicular process dorsal to the center of ossification is smooth and unornamented; there is a shallowly recessed area, herein termed the clavicular recess (abbreviation = clr) in the middle of the posterior lamina.

In anterior view (Figure 13.6) the dorsal clavicular process, comprising a narrow clavicular rod (new term, abbreviation = dcr) and a posterior lamina, joins the ventral blade in a smooth curve. The clavicular rod is robust and gently twisted anteriorly at its most distal end, and measured from the center of ossification, is approximately the same length as the ventral blade.
In dorsal view (Figure 13.2), the clavicular rod runs smoothly into the anterior edge of the ventral blade. The dorsal surface of the ventral blade is marked with fine striations, which radiate from the center of ossification, and are deepest near the medial edge. Fine, posterodorsally directed striations cover the medial surface of the dorsal clavicular rod and extend along the medial edge of the posterior lamina, where they deepen into small grooves (Figure 13.2, Figure 13.4).

**Figure 13.** Left clavicle of *Eryops megacephalus*. Reconstruction: 1, ventral; 2, dorsal; 3, lateral; 4, medial; 5, posterior; 6, anterior views. In 1 and 2 the anterior surface is uppermost. Abbreviations: cgr, clavicular groove; clr, clavicular recess; co, center of ossification; dcp, dorsal clavicular process; dcr, dorsal clavicular rod; pl, posterior lamina. Clavicle reconstruction based on AMNH 4186, 4774; MCZ 1421, 1883. Scale bar = 50 mm.
Cleithrum

The cleithrum (Figure 10, Figure 14) is a slender and relatively delicate element, sometimes found co-ossified with the much more massively constructed scapulocoracoid in larger specimens (e.g., AMNH 4307). When articulated with the scapulocoracoid, the cleithral shaft extends ventrally to the level of the glenoid. The expanded, laterally compressed dorsal cleithral process caps the anterodorsal edge of the scapulocoracoid (Figure 14.2). A thin flange, the cleithral crest, forms the anterodorsal margin of the dorsal cleithral process (Figure 14.1). A smaller flange, the suprascapular lamina, is located on the posteroverentral margin of the dorsal cleithral process (Figure 14.3); it extends a short distance lateral to the ventral groove for articulation with the scapulocoracoid. In some specimens, deep pits are located at the center of ossification of the dorsal cleithral process.

The scapular flange of the cleithral shaft forms the posterolateral border of the laterally flattened cleithral shaft. The anterior surface of the shaft (Figure 14.2), which articulates with the dorsal process of the clavicle, is smoothly rounded. In medial view (Figure 14.3), the posterior edge of the shaft is shallowly recessed for articulation with the scapular blade. Fine striations cover the ventral most portion of the cleithral shaft and the medial surface of the scapular flange; these become more pronounced ventrally, and form shallow grooves.

Scapulocoracoid

The scapulocoracoid (Figure 11, Figure 14.2, Figure 15) is a robust element with no visible sutures between the scapula and coracoid regions. In lateral view (Figure 15.1), the scapular portion is dorsally flared and narrowest just above the supraglenoid fossa. Even in the largest specimens, the dorsal edge of the scapula is unossified, indicating the presence of a cartilaginous extension. The lateral supraglenoid ridge is continuous with the posterior border of the scapular blade so that it meets the posterodorsal margin of the glenoid.

The posterior border of the scapular blade (continued ventrally by the lateral supraglenoid ridge), and the anterior edge of the glenoid cavity, align in lateral view (Figure 15.1). The glenoid arches medially above the infraglenoid fossa, and narrows to approximately two-thirds of its width at a point just below the level of the supraglenoid fossa. The anterior part of the glenoid is oriented posteriorly, while the posteroverentral surface is oriented dorsally. Within the infraglenoid fossa, the infraglenoid recess (sensu Pawley and Warren, 2005) is deeply concave under the midpoint of the glenoid, lateral to the low infraglenoid ridge (sensu Pawley and Warren, 2005) which is medial to the coracoid and glenoid foramina. The anterior edge of the scapula (Figure 15.2) narrows to a sharp edge at the level of the supraglenoid fossa, where it joins the thickened coracoid portion. The anterior border of the scapular blade is finished in periosteal bone down to its narrowest portion, however the margin of the coracoid region is unossified, indicating that the surface continued in cartilage in life.

The paths of three foramina through the scapulocoracoid are similar to those observed in other early tetrapods. The supraglenoid foramen is located in the middle of the deep supraglenoid fossa; the internal opening is located in the upper part of the subscapular fossa (Figure 15.2). The ventrally located glenoid and coracoid foramina are located on the coracoid (Figure 15.1, Figure 15.4), from where the coracoid foramen passes dorsally to the mid portion of the subscapular fossa (Figure 15.2), while the glenoid foramen passes to the middle of the supraglenoid buttress (Figure 15.3). CT scans facilitated the identification of the passage of coracoid and glenoid foramina through the
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FIGURE 14. Left cleithrum of *Eryops megacephalus*. Reconstruction: 1, lateral; 2, anterior; 3, medial; 4, posterior views. Reconstruction of pectoral girdle of *Eryops megacephalus*: 5, left lateral; 6, ventral views. Abbreviations: cc, cleithral crest; co, center of ossification; dcthp, dorsal cleithral process; cs, cleithral shaft; lss, suprascapular lamina; sfcs, scapular flange of cleithral shaft. Cleithrum reconstruction based on AMNH 4211, MCZ 1900 (two specimens), 1984, 7768. Scale bar = 50 mm.
bone. A smoothly rounded, thickened ridge, herein termed the scapular torus (abbreviation = sctor) (Figure 15.3), is most obvious medially, passing from the anterodorsal corner of the scapula to the supraglenoid buttress. This buttress is robust, broadly flattened, and widens into the ventral infraglenoid buttress from a position above the glenoid. The anterior face of the supraglenoid buttress is smoothly rounded and dorsoventrally oriented, concealing the openings for the supraglenoid and coracoid foramina within the deep subscapular fossa when the scapulocoracoid is observed in medial view. In posterior view (Figure 15.4), the main axis of the scapula meets the main axis of the coracoid at slightly greater than a right angle. The cancellous surface of the coracoid forms the posterior border of the scapulocoracoid directly posterior to the glenoid. The angle at which the coracoid plate joins the scapular blade in lateral view is much greater in some individuals. Most of the specimens observed exhibited some degree of lateral flattening which increased the angle between the coracoid plate and scapular blade; however, the specimen on which the reconstruction is based, AMNH4307, is considered to be relatively uncrushed.

Humerus

The description of the various surfaces of the humerus (Figure 11.3, Figure 16) follows the terminology of Romer (1922). The nature of the articulation of the humerus with the glenoid has been described in various taxa by Romer (1922), Miner (1925) and Holmes (1977). The massively built humerus has a typical tetrahedral shape, such as was described by Romer (1922), with widely expanded proximal and distal ends set at almost right angles to each other. The short, thick humeral shaft is somewhat laterally compressed, and roughly quadrangular in cross section.

Most prominent on the extensor surface (Figure 16.1) are the large ectepicondyle and entepicondyle. The ectepicondyle is a steep sided crest, which projects anteriorly beyond the radial condyle; cancellous bone forms the distal surface. The smoothly rounded posterior border of the entepicondyle is not perforated by an entepicondylar foramen. On the anterior side of the extensor surface, the rounded ectepicondylar ridge runs distally from the head of the humerus to the proximal portion of the ectepicondyle. On the posterior side, a low, rounded ridge, herein termed the entepicondylar ridge (abbreviation = entr) passes from below the proximal articulation surface on the entepicondyle. Between the ectepicondylar and entepicondylar ridges is a shallow groove that originates just below the articulation surface of the caput humeri, and expands distally into the deeply hollowed area between the ectepicondyle and entepicondyle. Just posterior to the midline of the proximal anterior surface (Figure 16.2) is the scapulohumeral ridge (new term, abbreviation = shr), the most elevated portion of which is recessed and formed of cancellous bone. This ridge probably divides the attachment area for the scapulohumeralis muscle from that of the more posteriorly located subcoracocapsularis muscle (after Holmes, 1977). The rugose, elevated deltoid crest is located on the flexor side of the anterior surface; the dorsal most part is conspicuously well developed. On the extensor side, the latissimus dorsi process is a sharp spike of bone, oriented proximodorsally, with a deeply rugose dorsal surface, indicating a strong muscle attachment.

On the flexor surface (Figure 16.3) the proximal humeral ridge is sharp-edged and finished in periosteal bone. It joins the proximal articulation surface with the deltopectoral area. Distal to the proximal humeral ridge, the deltopectoral crest separates into two distinct regions, the deltoid crest, and the pectoralis attachment, separated by a cancellous bone surface. The sharp-edged anterior humeral keel crosses the shaft from the distal side
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FIGURE 15. Left scapulocoracoid of *Eryops megacephalus*. Reconstruction: 1, lateral; 2, anterior; 3, medial; 4, posterior views. Abbreviations: fcor, coracoid foramen; fgl, glenoid foramen; fsgl, supraglenoid foramen; gl, glenoid fossa; igb, infraglenoid buttress; igf, infraglenoid fossa; igr, infraglenoid ridge; igs, infraglenoid recess; lsr, lateral supraglenoid ridge; sgb, supraglenoid buttress; sgf, supraglenoid fossa; ssf, subscapular fossa; sctor, scapular torus. Scapulocoracoid reconstruction based on AMNH 4180, 4183, 4215, 4307; MCZ 2712, 7559. Scale bar = 50 mm.
of the deltid and pectoral areas to the flexor side of the supinator process. The robust, bluntly rectangular supinator process is anterodorsomedially oriented. It lies below the humeral shaft anterior to the radial condyle. The most prominent feature of the distal flexor surface is the large, convex, ovoid, anterolaterally oriented capitulum for the radius, surfaced in cancellous bone. The proximal and posterior borders of the capitulum recess below the periosteal flexor surface, resulting in a lip between the radial condyle and the entepicondyle.

On the posterior surface (Figure 16.4), the finely striated area dorsal to the cancellous area on the anterior edge is suggestive of a pectoralis muscle attachment. The ventral humeral ridge is low and difficult to discern at its origin on the posterior side of the cancellous area on the flexor surface of the deltopectoral crest but, as it passes onto the flexor surface of the entepicondyle, it swells to form a low, but distinct, ventral entepicondylar ridge (new term, abbreviation = ver).

The well-ossified proximal articulation surface (Figure 16.5) is gently convex, and divided by a ridge into an anteroventrally oriented portion and a posterodorsally oriented portion. The cancellous distal articulation surface (Figure 16.6) is elongate with the radial capitulum located at the anterior edge, directly ventral to the ectepicondyle, while the ulnar condyle is located directly posterior to this in the middle of the distal surface. The posterodistal edge of the entepicondyle forms the posterior half of the distal surface.

**Radius**

The radius (Figure 10, Figure 17.1) is a stout, pillar like element, with flared proximal and distal ends. The distal portion is flattened between the extensor and flexor surfaces (Figure 17.1.2, Figure 17.1.4) and broader than the proximal head (Figure 17.1.1, Figure 17.1.2). The extensor surface (Figure 17.1.1) is gently convex in transverse section, with the anterior edge flatter than the posterior edge. The dorsomedial radial ridge and proximoventral radial ridge that are common to stem tetrapods (sensu Warren and Ptasznik, 2002) are absent. A sharp-edged ventromesial radial ridge (sensu Warren and Ptasznik, 2002) passes down the midline of the anterior surface (Figure 17.1.2), terminating distally in an area of cancellous bone confluent with the distal articulation surface. It should be noted that the radius of *Ossinodus pueri* Warren and Turner, 2004, described by Warren and Ptasznik (2002) is here reinterpreted as a left radius, following comparison with *Acanthostega gunnari* Jarvik, 1952 (Coates, 1996).

On the flexor surface (Figure 17.1.3), the ventral radial crest is located slightly medial to the posterior edge. It originates well below the expanded humeral articulation surface, and runs into the distal border medial to the posterior edge. The proximal and distal portions of the flexor surface are convex, while the shaft is concave in transverse section. A broad low ridge, herein termed the radial flexor ridge (abbreviation = rfr), originates below the midpoint of the shaft, and increases in depth distally.

The humeral articulation surface (Figure 17.1.5) is subrectangular, gently concave, and narrows rapidly into the anteroposteriorly compressed shaft. The distal articulation surface (Figure 17.1.6) is complex, with three convex articulation facets for the radiale, centrale, and intermedium. The radiale facet extends from the anterior surface of the extensor surface to the distal side of the ventromesial radial ridge. The facet for the centrale is the largest of the three, extending from the extensor surface to the anterior distal surface of the radial flexor ridge. The facet for the intermedium is small and located almost entirely on the flexor side.
FIGURE 16. Left humerus of *Eryops megacephalus*. Reconstruction: 1, extensor; 2, anterior; 3, flexor; 4, posterior; 5, proximal; and 6, distal views. In 5 and 6 the extensor surface is uppermost. Abbreviations: ahk, anterior humeral keel; avph, anteroventral proximal humeral articulation surface; delt, deltoid crest; ect, ecteroid condyle; ent, ecteroid condylar ridge; ent, entepicondyle; entr, entepicondylar ridge; hur, ventral humeral ridge; ldp, latissimus dorsi process; pdphs, posterodorsal proximal humeral articulation surface; pect, attachment area for pectoralis muscle; phr, proximal humeral ridge; rac, radial condyle; shr, scapulohumeral ridge; sup, supinator process; ulc, ulna condyle; ver, ventral entepicondylar ridge. Humerus reconstruction based on AMNH 4183, 4186, 4204, 4255; MCZ 7551. Scale bar = 50 mm.
Ulna

The ulna (Figure 10, Figure 17.2) is relatively slender when compared to the radius, anteroposteriorly flattened, and exceeds the radius by the in length of the olecranon process. In extensor view (Figure 17.2.1) the most prominent feature is the proximal portion of the ulnar extensor keel (new term, abbreviation = uek), which is highly rugose for the attachment to the triceps muscle but narrows distally into a steep keel, terminating at the distal articulation surface. In anterior view (Figure 17.2.2) the humeral articulation surface forms an angle of approximately 45º to the shaft, and the distal surface is broadly flared and as wide as the proximal surface. On the posterior surface (Figure 17.2.4) a low posterior ulnar crest (new term, abbreviation = puc) originates below the posterior humeral articulation surface, and curves distally down the midline of the posterior surface. It branches at the midpoint of the shaft into another low ridge, the posterolateral ulnar crest (new term, abbreviation = pluc).

In proximal view (Figure 17.2.5) the humeral articulation surface is approximately quadrangular. In all specimens examined, the dorsal surface of the olecranon process is incompletely ossified lateral to the humeral articulation surface. In distal view (Figure 17.2.6), the laterally flattened articulation surface carries posterior and anterior articulation surfaces for the ulnare and intermedium, respectively.

Pelvis

The pelvis (Figure 11, Figure 18) is a robust element, with no discernible sutures separating the ilium, ischium, and pubis. As a whole, it is narrow in anterior and posterior views, the two halves becoming co-ossified in larger specimens. Dorsal to the acetabulum (Figure 18.1), the dorsal iliac blade is anteroposteriorly expanded and oriented slightly anteriorly. The puboischiadic plate meets the acetabular area at a shallow angle, so that much of the plate is visible in lateral view. The overall outline of the blade resembles that of a chopper or hatchet. The posteroventral border of the iliac blade extends into a sharp-edged flange, herein termed the sacral flange (abbreviation = sacf), which gives the iliac blade a rectangular outline in ventrolateral view (Figure 18.1). This flange does not appear to be a remnant of the post-iliac process seen in many early tetrapods as a post-iliac process is posterodorsally directed while the sacral flange extends posteroventrally. The transverse pelvic ridge is a short crest directly anterior to, and not extending posterior to, the prominent supractabular buttress. The acetabulum is large with the ventral border occupying more than half the length of the puboischiadic plate. A posterior supractabular notch is present posterior to the supractabular buttress. The anteriormost edge of the acetabular cavity is confluent with the anterior surface of the pubis. The cancellous surface of the acetabulum extends anteriorly onto the lateral surface of the pubis, a feature that may be subject to morphogenetic change, as the anteriormost edge of the acetabulum in some specimens (e.g., MCZ 1219) is finished in periosteal bone. The postacetabular buttress is prominent and thickened at the posterior acetabular edge, but thins rapidly into the sharp-edged posterior border of the ischium. The single obturator foramen opens close to the ventral border of the acetabulum.

The anterior border of the puboischiadic plate (Figure 18.2) is bluntly rectangular, widest at the posterior edge of the acetabulum, and bordered in cancellous bone. In dorsomedial view (Figure 18.3) the anterior edge of the broadened mesial iliac ridge passes down the anterior border of the pelvis to form the anterior edge of the pubis, so
FIGURE 17. Left radius and ulna of *Eryops megacephalus*. Reconstruction: 1, extensor; 2, anterior; 3, flexor; 4, posterior; 5, proximal; and 6, distal views. Reconstruction of left ulna of *Eryops megacephalus*: 7, extensor; 8, anterior; 9, flexor; 10, posterior; 11, proximal; and 12, distal views. In 5, 6, 11 and 12 the extensor surface is uppermost. Abbreviations: cenf, centrale facet; intf, intermedial facet; ol, olecranon process; pluc, posterolateral ulnar crest; puc, posterior ulnar crest; radf, radiale facet; rfr, radial flexor ridge; tri, attachment area for triceps muscle; uek, ulnar extensor keel; ulnf, ulnar facet; vmrr, ventromesial radial ridge; vrc, ventral radial crest. Radius reconstruction based on AMNH 4186, 4203, 4754, ulna reconstruction based on ANNH 4186, 4754, 4862; MCZ 1137. Scale bar = 50 mm.
that the obturator foramen opens onto the anterior surface. The clearly defined facet for the sacral rib on the medial surface of the dorsal iliac process (Figure 18.3) has a smooth surface, showing little evidence for muscle or ligament attachment. There is considerable individual variation in the shape of the dorsal iliac process, with some specimens much more elongate than others, e.g., MCZ 1858 (Figure 11.5) and MCZ 7773 (Figure 11.4).

The pelvic symphysis is finished in periosteal bone, with the symphysial surface deep anteriorly, shallowing abruptly on the posterior border of the mesial iliac ridge, and tapering to the posterior border of the ischium.

**Femur**

The femur (Figure 11, Figure 19) is robust and longer than the humerus, with a relatively narrow, anteroposteriorly flattened shaft, and expanded ends. In extensor view (Figure 19.1), the shaft is narrowest directly above the adductor blade but flares out distally towards the tibial and fibular condyles.

The posterior caput femoral fossa (new term, abbreviation = pcff) occupies the proximoposterior surface of the extensor side of the femoral head (Figure 19.1). A small ridge distal to this fossa is presumably the attachment for the ischiotrochantericus muscle (Romer, 1922). On the fibular side of the intercondylar fossa, the sharp-edged intercondylar crest (new term, abbreviation = icc) originates on the proximal side, and passes down the length of the fossa before terminating abruptly proximal to the fibular condyle.

In flexor view (Figure 19.3), the intertrochanteric fossa is gently concave. On either side of this fossa, confluent with the proximal articulation surface, but not visible in proximal view, are the cancellous, recessed areas of the anterior caput femora fossa (new term, abbreviation = acff) and the posterior caput femoral fossa, which are separated from the proximal articulation surface by low ridges. The edge of the intertrochanteric fossa, abutting the anterior caput femora fossa, is smoothly rounded, while the edge abutting the posterior caput femoral fossa is sharp. The massive processes of the adductor blade on the anterior side, and the posterior intertrochanteric ridge on the posterior side, bound the intertrochanteric fossa distally and meet at the adductor crest. Both the posterior intertrochanteric ridge and adductor blade are similar in thickness and ventral expansion. The ventrally oriented adductor blade (Figure 19.2) has the typical internal and fourth trochanters on the ventral surface. A trough of periosteal bone separates the internal trochanter from the cancellous area of the anterior caput femoral fossa. The boss of the internal trochanter is shallowly concave and filled with cancellous bone, while the surface of the fourth trochanter is tuberculate.

The adductor crest (Figure 19.3) is deepest and broadest immediately posterior to the junction of the posterior intertrochanteric ridge and adductor blade. It passes down the midline of the shaft, becoming narrower and shallower until it branches to form the anterior popliteal ridge on the proximal side of the popliteal area. A low distal continuation of the adductor crest turns around the posterior side of the popliteal area and passes to the ventralmost portion of the fibular condyle. The anterior popliteal ridge curves sinuously around the anterior side of the popliteal area to terminate at the ventralmost portion of the tibial facet. The fibular fossa on the posterior surface of the femur is shallowly recessed and much narrower than the popliteal area.

In proximal view (Figure 19.5), the articulation surface is smoothly convex and dorsoventrally flattened. In distal view (Figure 19.6), the deeply incised intercondylar fossa is oriented ventrally towards the midline of the popliteal area. The tibial and fibular facets are continuous, and aligned almost at right angles to each other. The tibial
FIGURE 18. Left pelvis of *Eryops megacephalus*. Reconstruction: 1, ventrolateral; 2, anterior; 3, dorsomedial; 4, posterior views. Abbreviations: dip, dorsal iliac process; isch, ischium; mir, mesial iliac ridge; obt, obturator foramen; pab, postacetabular buttress; psan, posterior supracetabular notch; pub, pubis; sab, supracetabular buttress; sacf, sacral flange; srf, sacral rib facet; symph, symphysial surface; tpr, transverse pelvic ridge. Pelvis reconstruction based on AMNH 4183; MCZ 1219, 1858, 7773. Scale bar = 50 mm.
condyle is gently biconcave for articulation with the dumbbell-shaped proximal tibial surface (Figure 20.5), while the fibular condyle is convex.

Tibia

The tibia (Figure 10, Figure 20.1) is wedge-shaped with a greatly expanded femoral head, which narrows rapidly to a thin shaft, with the distal articulation surface gently expanded relative to the shaft. The proximal and distal ends are set at approximately 30° to each other.

In extensor view (Figure 20.1.1), the large, steep-sided cnemial crest dominates the anterior side with a deeply hollowed cnemial trough (new term, abbreviation = cnt) lying posterior to it along the midline of the tibia. A lower, rounded ridge forms the posterior side of the extensor surface. Distal to the cnemial crest, the shaft is anteroposteriorly compressed, so that it is deepest between the extensor and flexor surfaces. While the posterior border of the shaft curves deeply around the interepipodial space, the vertical axis through the center of the tibia is straight, in contrast to the bowed midline of the fibula.

The flexor surface (Figure 20.1.3) bears a series of crests: the anterior tibial flexor crest (new term, abbreviation = atfc) and the posterior tibial flexor crest (new term, abbreviation = ptfc) originate in the upper third of the flexor surface and converge towards the distal end to form the distal tibial flexor crest (new term, abbreviation = dfc). The anterior tibial flexor crest is low and poorly defined at its extremities, while the posterior tibial flexor crest is more sharply defined and steep-sided at its midpoint. Between these two crests, on the midpoint of the flexor surface, lies a deep fossa, the puboishiotibialis tibial fossa (new term, abbreviation = pittf), for the insertion of the puboishiotibialis muscle (Romer, 1922). The distal tibial flexor crest continues to the medial side of the articulation surface.

The femoral articulation surface (Figure 20.1.5) is dumbbell-shaped, its anterior surface is gently convex in proximal view, and its posterior surface is concave. The cnemial trough forms a deep constriction on the extensor side of the femoral articulation surface, marking the boundary between the anterior and posterior articulation surfaces, but the flexor side of the tibial head (Figure 20.1.3) is gently constricted. The distal articulation surface (Figure 20.1.6) is ovoid and strongly convex, with continuous facets for articulation with the tibiale and intermedium.

Fibula

The fibula (Figure 10, Figure 20.2) is a relatively slender element, approximately as long as the tibia. In extensor view (Figure 20.2.1), the proximal and distal ends are similar in width; in proximal view, the proximal surface twists at approximately 45° to the distal surface. The broad fibular extensor ridge (new term, abbreviation = fer) bulges out from the femoral articulation surface, and passes directly distally down the proximal head. A short ridge, the anterior fibular ridge (new term, abbreviation = afr), is located on the anterior proximal surface (Figure 20.2.2), so that the proximal head of the fibula has a rectangular outline in extensor view. The anterior fibular ridge is probably the insertion area for the medial ligament to the tibia (Romer, 1922). The flexor surface of the shaft (Figure 20.2.3) is concave along its length. A shallow fibular sulcus crosses the anterodistal corner. The posterior fibular ridge (new term, abbreviation = pfr) runs along the posteromedial edge of the bone from just below the proximal third of the shaft to the distal facet for the fibulare; this low ridge is tuberculat e along most of its length.
FIGURE 19. Left femur of Eryops megacephalus. Reconstruction: 1, extensor; 2, anterior; 3, flexor; 4, posterior; 5, proximal; and 6, distal views. In 5 and 6 the extensor surface is uppermost. Abbreviations: acff, anterior caput femora fossa; adb, adductor blade; ade, adductor crest; apr, anterior popliteal ridge; ffo, fibula fossa; fibc, fibular condyle; icc, intercondylar crest; icf, intercondylar fossa; intr, internal trochanter; istr, attachment for ischirotrochantericus muscle; itf, intertrochanteric fossa; pcff, posterior caput femora fossa; pir, posterior intertrochanteric ridge; ppa, popliteal area; tibe, tibial condyle; tr4, fourth trochanter. Femur reconstruction based on AMNH 4183 (two specimens), 4203. Scale bar = 50 mm.
In posterior view (Figure 20.2.4), the bone narrows below the proximal head, while distally it is constant in width.

The femoral articulation surface is concave (Figure 20.2.5) and meets the extensor surface of the bone at a steep angle. The distal articulation surface (Figure 20.2.6) is bipartite; the medial side is convex for articulation with the intermedium, while the lateral portion is concave for articulation with the fibulare.

**Paleopathology**

The surface of the sacral rib attachment area on both the ilia of MCZ 7773 are deeply pitted, with smooth-edged pits thus possibly indicating osteomyelitis (Ortner, 2003). The bilateral occurrence of these pits is interesting, however the two sides are differentially affected, with the left side more affected than the right. The femur, AMNH 4203 (Figure 11.6) and fibula, AMNH 23449 (Figure 10.11), which are possibly from the same individual, display irregular processes consistent with myositis ossificans traumatica of the lateral collateral ligament (Ortner, 2003). Two recessed conical marks on the lateral surface of the scapula of AMNH 4211 (Figure 11.1) are interpreted as bite marks. Given the number of possible perpetrators no guesses can be taken as to the possessor of the teeth. Comparison of these elements with many others of the same genus and other unrelated taxa indicates that the above conditions are aberrant, and at least some of them are likely to be pathological rather than normal features.

**DISCUSSION**

**Comparisons with previous work**

The restoration of the pectoral girdle (Figure 14.2) is close to the unrestored girdle figured by Cope (1888), but differs considerably from that of Romer (1922) and Miner (1925), in that these authors restore much smaller clavicles and interclavicle. Miner’s reconstruction shows the clavicles as posterolaterally oriented on the interclavicle. The position of the clavicular facets of the interclavicle (Figure 12.1.1) indicates that the clavicular blades are correctly oriented transversely, consistent with the situation in other euskelians preserved as articulated specimens such as *Anconastes vespers* (Berman et al., 1987a), *Dissorophus multicinctus* (de Mar, 1968), and *Micropholis stowi* Huxley, 1859 (Broili and Schröder, 1937). Overall the revised pectoral girdle (Figure 14.2) is similar in proportions to that of *Micropholis stowi* (Watson, 1913), and *Dendrerpeton acadianum* (Holmes et al., 1998) although the interclavicle is posteriorly extended in *Dendrerpeton*.

The present study disagrees with the work of Miner (1925) in many respects. Miner’s restoration of the interclavicle was rhomboidal in outline, but the many specimens examined indicate that this configuration is incorrect; the outline is subcircular (Figure 12). There is no evidence for Miner’s depiction of the dorsal process of the cleithrum as completely capping the dorsal surface of the scapular blade. The posterodorsal corner of the scapular blade appears to be broken in Romer’s (1922: figure 33.1) specimen; complete scapular blades examined in this study possessed a sharp posterodorsal corner (Figure 15.1).

Miner (1925) did not give a catalogue number for the *Eryops* humerus used in his illustrations. These show no differentiation between the cancellous and periosteal bone surfaces, giving the impression that all bone surfaces are periosteal. The radial condyle appears to have been crushed on this humerus as it is much more bulbous in undamaged
FIGURE 20. Left tibia and fibula of *Eryops megacephalus*. Reconstruction: 1, extensor; 2, anterior; 3, flexor; 4, posterior; 5, proximal; and 6, distal views. Reconstruction of left fibula of *Eryops megacephalus*: 7, extensor; 8, anterior; 9, flexor; 10, posterior; 11, proximal; and 12, distal views. In 5, 6, 11 and 12 the extensor surface is uppermost. Abbreviations: afr, anterior fibular ridge; atfc, anterior tibial flexor crest; cn, cnemial crest; cnt, cnemial trough; dtfc, distal tibial flexor crest; fer, fibular extensor ridge; ff, fibulare facet; fs, fibular sulcus; intf, intermedial facet; pitf, fossa for the tibial insertion of the puboishiotibialis; pfr, posterior fibular ridge; ptfc, posterior tibial flexor crest; tibf, tibiale facet. Tibia reconstruction based on AMNH 4198, 4203, 4754; MCZ 2092, 7555, 7797; fibula reconstruction based on AMNH 23449; MCZ 6475, 7555. Scale bar = 50 mm.
specimens (Figure 16). Bakker (1982) found that several features of the *Eryops* humerus changed with morphogenesis, including the ossification of proximal and distal articulation surfaces, the development of the convex radial condyle and supinator process, and ossification of the proximal humeral ridge, while the pectoral surface of the deltopectoral crest remained unossified (Figure 16.3). The specimen illustrated by Schoch (1999a) had a subadult morphology. Schoch compared this specimen with mature specimens of other temnospondyl taxa; some of the morphological differences depicted by Schoch are therefore morphogenetic rather than phylogenetic.

Attachment of the deltoid and pectoralis muscles to the anterior face of the deltopectoral crest (Romer, 1922; Miner, 1925) seems unlikely, given that the cancellous surface would have been covered in cartilage in life. An attachment of the pectoralis muscle to the striated area on the proximoventral surface of the deltopectoral crest (Figure 16.4) is more probable. The description of the attachment area for the scapulohumeralis muscle by Romer (1922) was disputed by Miner (1925) and Holmes (1977), who suggested that a subcoracoscapularis muscle was present dorsal to the scapulohumeralis. The area of cancellous bone (scapulohumeral ridge) (Figure 16.2) between the two areas for muscle attachment suggests their presence in *Eryops*.

The present description agrees with that of Case (1911a) except for the ulna (Figure 17) which was described by Case as possessing an ossified tip to the olecranon process. The large and apparently mature specimen used in the original description of forelimb epipodials by Cope (1888) (AMNH 4186) was examined. The dorsal surface of the olecranon process is in fact unossified, as in all other ulnae examined in this study. This characteristic is found in other members of the Euskelia such as *Ecolsonia cutlerensis* (Berman et al., 1985).

The short transverse pelvic ridge (Figure 18.1) was not depicted by Cope (1878; 1880), or Cope and Matthew (1915). The extended transverse pelvic ridge described in *Eryops* (Romer, 1922) was not found in any specimen. The fourth trochanter of the femur was figured by Romer (1922) as being on the posterior side of the intertrochanteric fossa, on the posterior intertrochanteric ridge. It is more consistent with our general understanding of the placement of the caudifemoralis muscle that the fourth trochanter be located on the ventral surface of the adductor blade distal to the internal trochanter, on the anterior side of the femur (Figure 19.3).

Features of *Eryops megacephalus* that are uncommon in temnospondyls

As previously noted, the scapulocoracoid is co-ossified with the cleithrum in some large and exceptionally well-ossified specimens. In *Eryops*, the cleithrum is of the typical temnospondyl type with a long ventral shaft and is usually separate from the large scapular blade, thus the co-ossification is a late morphogenetic feature not seen in small specimens. This characteristic is not homologous with the co-ossified cleithrum and scapulocoracoid of Devonian tetrapods such as *Ichthyostega stensoei* Säve-Söderbergh, 1932 (Jarvik, 1996) or *Acanthostega gunnari* (Coates, 1996), which have a different morphology. In these taxa, the cleithral shaft is absent, the scapular blade is comparatively undeveloped, and the cleithrum and scapulocoracoid are co-ossified in all specimens.

Holmes (1980) considered that derived temnospondyls only possessed one coracoid foramen, with the exception of *Dissonorophus angustus* (Carroll, 1964a). As noted by Moodie (1910), all temnospondyls in which the coracoid is ossified, possess three scapulocoracoid foramina, including two coracoid foramina; other examples include the euskelians *Acheloma cumminsi* (Williston, 1909a) and *Dissonorophus multicinctus* (Williston, 1910b), the archegosaur *Sclerocephalus* (Boy, 1988), and the basal
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stereospondyls *Peltobatrachus pustulatus* (Panchen, 1959) and *Lydekkerina huxleyi* (Lydekker, 1889) Broom, 1915 (Pawley and Warren, 2005). The restoration of *Dendrerpeton acadianum* (Holmes et al., 1998) displays only a coracoid foramen, however as noted by Carroll (1967) and Holmes et al. (1998), the area of the coracoid foramen is either not preserved or covered by gastralia in all specimens.

The humerus of *Eryops* has been described as the archetypal primitive tetrapod humerus (Romer, 1922; Miner, 1925; Gregory, 1949; Andrews and Westoll, 1970). Recent discoveries of indisputably more plesiomorphic Devonian tetrapods such as *Ichthyostega stensioei* (Jarvik, 1952, 1996), *Acanthostega gunnari* and *Tulerpeton curtum* Lebedev, 1984 (Lebedev and Coates, 1995) have rendered the morphology of the humerus of *Eryops*, and the interpretations of gait based on it (Romer, 1922; Miner, 1925), characteristic of some more derived subgroups of tetrapods.

**Heterochronic processes in temnospondyls**

*Eryops* is unusual in that it is both large and well ossified for a temnospondyl. Temnospondyls display indeterminate growth in that, after an initial rapid growth phase, they continue to increase in size during their lifespan (Steyer et al., 2004). Previous studies of heterochronic processes within temnospondyls (McNamara, 1988; Schoch, 1995) have focused exclusively on cranial characteristics. Heterochronic processes are determined within a group of organisms relative to the ancestral condition (McNamara, 1986). As current conflicting large scale phylogenies of temnospondyl taxa (Yates and Warren, 2000; Ruta et al., 2003) make determination of the ancestor-descendant relationships within temnospondyl taxa uncertain, the discussion below is limited to generalized comparisons. Heterochronic processes are not quantifiable (it is not possible to determine the extent of the effect of each process) or phylogenetically significant in the present context.

Various heterochronic processes (changes in relative time of appearance and rate of development of characters already present in ancestors) (McNamara, 1986) may have produced the large size and well-developed morphology of the postcranial skeleton of *Eryops*. Pawley and Warren (2004) discussed morphogenetic development of the postcranial skeleton among stereospondyls, which are paedomorphic through the process of neoteny (sensu McNamara, 1986). Neoteny is a reduced rate of morphological development resulting in an extension of the duration of the growth phase, often accompanied by an increase in overall size, e.g. *Mastodonsaurus giganteus* Jaeger, 1828 (Schoch, 1999a) is almost three times the size of *Eryops* at 6m long, and *Siderops kehli* (Warren and Hutchinson, 1983) is 3m long. Only the endochondral postcranial skeleton displays evidence of morphogenetic immaturity, as evidence of incomplete ossification is not observable in the ornamented dermal bones. In temnospondyls with paedomorphic postcranial skeletons, the morphology of the postcranial elements remains essentially immature, never reaching the stage of development seen in *Eryops*. The ends of the bones remain imperfectly ossified and they lack enlarged processes for muscle attachment. Some elements such as the coracoid and pubis may never ossify, or may only develop in the largest specimens (Pawley and Warren, 2004). Temnospondyls with paedomorphic postcranial skeletons often possess other adaptations for an aquatic lifestyle such as lateral line sulci, ossified ceratobranchials and enlarged, anteriorly expanded interclavicle and clavicles.

Two peramorphic processes (occurrence of the ancestral adult morphology in a descendant juvenile stage of development), acceleration and hypermorphosis (McNamara, 1986), are relevant. Acceleration, which is the opposite of neoteny, is an increase in the
rate of morphological development, which often results in a smaller but morphogenetically mature adult. Morphogenetic maturity is indicated by the well-ossified ends to the limb bones and fully ossified coracoid, pubis, carpus, and tarsus.

This process appears to be common among temnospondyls; many well-ossified temnospondyls are relatively small, less than 1m long, compared to the large paedomorphic taxa listed above. Examples include: *Balanerpeton woodi* (Milner and Sequeira, 1994), the euskelian *Acheloma cumminsi* (Williston, 1909a), and the basal stereospondyl *Lydekkerina huxleyi* (Pawley and Warren, 2005). These small, well-ossified temnospondyls often display the other adaptations for a terrestrial lifestyle listed above. Hypermorphosis is an extension of late morphogenetic development, caused by a delay in the onset of maturation (McNamara, 1986). This process results in attainment of a larger adult size, accompanied by morphogenetic maturity. Hypermorphosis is the most likely heterochronic process to have produced the large size and well-ossified morphology of *Eryops*. The larger size of *Eryops* has not resulted in the development of any structures that are not present in other smaller taxa (see below).

From the evidence presented above there is no correlation between the degree of ossification of the postcranial skeleton and overall size in temnospondyls. Complete ossification of the appendicular skeleton, particularly the carpus and tarsus, appears to define morphogenetic (not necessarily reproductive) maturity in temnospondyls. Absolute size alone cannot be taken as an indicator of morphogenetic maturity, as noted by Brinkman (1988) for pelycosaurs.

*Morphogenetic vs. phylogenetic variation*

In temnospondyls, there are two major causes of differing postcranial morphology, morphogenetic and phylogenetic variation. Pawley and Warren (2004) discussed growth series and the development of postcranial characteristics with morphogenesis in stereospondyls. In paedomorphic taxa where growth series are available, some characteristics of the postcranial skeleton develop only in the largest and most mature specimens. An example of a postcranial character used in phylogenetic analysis of temnospondyls is the absence (plesiomorphic state) or presence (derived state) of a supinator process of the humerus. The supinator process is developed in small specimens of *Eryops* (Bakker, 1982) and *Acheloma* (Olson, 1941) but is only present in the largest specimens of paedomorphic taxa such as *Mastodonsaurus giganteus* and *Bentosuchus sushkini* Efremov, 1937 (Bystrow and Efremov, 1940). In temnospondyls, there is a direct correlation between the degree of ossification of the humerus and the development of a supinator process. Humeri of the most immature morphogenetic stages are readily identifiable using other characteristics besides their generally poorly ossified condition: the proximal humeral ridge is unossified, and the distal edge of the entepicondyle is rounded rather than square (for more detailed explanations, see Pawley and Warren, 2004).

In contrast, the humerus of taxa with an ‘L’ shaped humerus such as the stem tetrapod *Greererpeton burkemorani* Romer, 1969 (Godfrey, 1989a) and the embolomere *Proterogyrinus scheeli* Romer, 1970 (Holmes, 1984), considered to be similar (Holmes, 1980; Lebedev and Coates, 1995), display the plesiomorphic state (absence of a supinator process). Growth series indicate that even the largest, most well-ossified specimens never develop the derived state, a supinator process.
Confounding morphogenetic variables

In phylogenetic analyses, comparison of the humerus of smaller sized specimens of a paedomorphic taxon such as *Mastodonsaurus giganteus* which display the plesiomorphic state (absence of a supinator process) would imply similarities with taxa with an ‘L’ shaped humerus, but not well ossified temnospondyl taxa such as *Eryops* (which possess the derived state). Conversely, comparison of a larger sized specimen of *Mastodonsaurus giganteus* (which possesses a supinator process) implies similarities with *Eryops*, but not taxa with an ‘L’ shaped humerus. This presents problems for cladistic analysis.

It is more parsimonious to suggest that the derived state (presence of a supinator process) is ubiquitous among temnospondyls, and that this state is absent in some taxa due to the immature or paedomorphic morphology of the specimens, rather than that the sporadic distribution of the supinator process within temnospondyls is due to homoplasy (as suggested by some phylogenetic analyses, for example Yates and Warren, 2000; Ruta et al., 2003). For example, their coding of the presence of a supinator process on the humerus has in some cases confused morphogenetic with phylogenetic variation. Examination of these analyses indicates that the postcranial skeletons of all temnospondyl taxa that possess the plesiomorphic condition (absence of a supinator process) display characteristics of morphogenetic immaturity (discussed in more detail in Pawley and Warren, 2004).

Steyer (2000) demonstrated that using morphogenetically variable cranial characters in phylogenetic analysis can have marked effects on the resulting cladogram topologies. Taxa that develop postcranial characteristics late in morphogenesis have inherited the potential to display the derived state. It is vital to take into account the morphogenetic stage of the postcranial skeleton (which is often inconsistent with that of the skull) when making comparisons between taxa, in order to reduce confounding morphogenetic variables.

Thus, when comparing the morphology of the postcranial skeletons of immature or paedomorphic temnospondyl taxa with well-ossified taxa such as *Eryops*, the differences are mostly morphogenetic rather than phylogenetic. In contrast, the differences between taxa with an ‘L’ shaped humerus and temnospondyl taxa such as *Eryops* are phylogenetic.

Morphological comparisons

It is not aim of this study to compare exhaustively the postcranial skeleton of *Eryops* with that of other tetrapods, but rather to contribute to work in progress on the temnospondyl postcranial skeleton. Only characteristics that are present in morphogenetically mature specimens, and are thus considered to be of phylogenetic significance will be discussed below.

Comparison of the appendicular skeleton of *Eryops* with that of the earliest known temnospondyls *Balanerpeton woodi* (Milner and Sequeira, 1994) and *Dendrerpeton acadianum* (Carroll, 1967; Holmes et al., 1998) is hampered by their state of preservation (Holmes, 2000). Discernable features of their appendicular skeletons differ from the more derived *Eryops* in that they retain plesiomorphic characteristics. These include the presence of an entepicondylar foramen of the humerus, a post-iliac process on the ilium (more derived temnospondyls retain only the portion of the ilium for sacral rib attachment), the extension of the pubis anterior to the mesial ridge of the puboischiadic plate, the adductor crest of the femur passing distally to the fibular condyle, and the expanded distal extremity of the fibula.
The appendicular skeleton of *Eryops* is most similar to that of other members of the Euskelia (Yates and Warren, 2000), in particular the Dissorophoidea. Within the Euskelia, taxa with described postcranial material include: *Acheloma cumminsi* (Williston, 1909a; Olson, 1941); *Anconastes vesperus*; *Ecolsonia cutlerensis*; *Phonerpeton pricei* (Dilkes, 1990); *Tambachia trogallas* (Sumida et al., 1998); *Dissoropus angustus* (Carroll, 1964a) and *D. multicinctus* (Williston, 1910b; de Mar, 1968); the amphibamids (Carroll, 1964a; Daly, 1994); and the enigmatic *Parioxys ferricolus* Cope, 1878 (Moustafa, 1955b) and *P. bolli* (Carroll, 1964b). *Eryops* shares with members of this clade the reduced interclavicle with laterally oriented, wedge-shaped clavicles and robust, well-ossified limbs. All trematopids and dissorophoids possess some features not found in *Eryops*, such as an expanded dorsal process of the cleithrum that covers the dorsal surface of the scapulocoracoid, an expanded, rounded iliac blade, and, on the femur, a massive fourth trochanter with a flattened ventral face, while they lack the intercondylar crest of the femur and sacral flange of *Eryops*.

The features of *Eryops* not seen in dissorophoids can be found in other members of the Euskelia: the intercondylar crest on the femur can be seen in *Parioxys bolli*, while the sacral flange is seen in *Platyrhinops* (Amphibamus) *lyelli* Wyman, 1858 (Carroll, 1964a), a somewhat surprising observation due to the comparatively small size of this taxon.

The extensive adaptations attributed to an aquatic existence seen in most of the more derived temnospondyl taxa, including the stereospondyls, complicate comparisons with the postcranial skeleton of *Eryops*. Generally, these modifications include expansion of the dermal pectoral girdle and simplification and paedomorphic reduction of the limb elements.

Some archegosaurs, such as *Sclerocephalus haeseuri* (Broili, 1908; Meckert, 1993), and basal stereospondyls possess well-ossified postcranial skeletons (at least in the most mature specimens). Notable are *Peltobatrachus pustulatus*, *Uranocentrodon senekalensis* Van Hoepen, 1911 (Haughton, 1915; van Hoepen, 1915), and *Lydekkerina huxleyi* (Pawley and Warren, 2005), but overall their appendicular skeletons are not as robust as that of *Eryops*. They all differ from *Eryops* in the possession of an enlarged anteriorly expanded interclavicle, with the center of ossification level with the posterior border of the clavicular facets; anteriorly expanded clavicular blades; absence of the cleithral crest; absence of the convex radial condyle of the humerus [present in *Sclerocephalus haeseuri* (Meckert, 1993)]; and the absence of the enlarged posterior intertrochanteric ridge of the femur.

Ongoing research indicates that other unrelated taxa such as diadectomorphs share many derived similarities of their postcranial skeletons with temnospondyls, which implies, as suggested by Pawley and Warren (2002), that they share a common ancestor above the level of stem tetrapods (sensu Ruta et al., 2003), and the Anthracosauria Säve-Söderbergh 1934 (sensu Panchen, 1970).

The differences between the skulls and vertebrae of the seymouriamorphs plus diadectomorphs and those of temnospondyls are well known, and phylogenetically temnospondyls and seymouriamorphs plus diadectomorphs are considered to have evolved independently from separate groups of stem tetrapods (most recently revised in Ruta et al., 2003; Vallin and Laurin, 2004). Within the seymouriamorphs and diadectomorphs, genera with described postcranial material include *Seymouria* spp. Broili, 1904 (White, 1939; Berman et al., 1987b; Berman et al., 2000), *Diadectes* spp. Cope, 1878 (Case, 1905, 1911b; Romer, 1956; Berman et al., 1998; 2004), *Diasparactus zenos* Case, 1910 (Case and Williston, 1913), *Limnoscelis* spp. Williston, 1911b (Williston, 1911a, 1911b, 1912; Romer, 1946; Berman and Sumida, 1990) and *Orobates*
Williston (1911a) commented on the close resemblance of the humerus of *Eryops* to that of *Limnoscelis* and *Diadectes*. Romer (1946; 1957) noted that in many respects the appendicular skeleton of *Eryops* resembled that of seymouriamorphs and diadectomorphs more closely than the ‘L’ shaped humerus of the embolomere *Archeria crassidisca* Cope, 1884 (Romer, 1957). Embolomeres are usually considered to be more closely related to amniotes than are temnospondyls (summarized in Ruta et al., 2003; see also Vallin and Laurin, 2004). Heaton (1980) observed that the humerus of *Eryops* is only distinguishable from that of the seymouriamorphs and diadectomorphs by the absence of the entepicondylar foramen, and quite distinct from the ‘L’ shaped humeri of the ‘anthracosaurs’ *Archeria crassidisca*, *Proterogyrinus scheeli* and *Gephyrostegus bohemicus* Jaekel, 1902 (Carroll, 1970), which are more similar in morphology to those of stem tetrapods (sensu Ruta et al., 2003) (Holmes, 1980; Lebedev and Coates, 1995).

There are many derived similarities, in comparison with stem tetrapods, between the appendicular skeletons of seymouriamorphs, diadectomorphs, and *Eryops*. All of the following are seen in all well ossified temnospondyls, seymouriamorphs and diadectomorphs (irrespective of size): of the clavicle, posterior border of the posterior lamina is convex; loss of anterior and medial cleithral ridges; scapula blade extended dorsally and flared, scapular ridge on the posterior surface of the supraglenoid buttress absent, supraglenoid foramen anteroposteriorly oriented and located dorsal to the midpoint of the glenoid within a deep supraglenoid fossa, supraglenoid foramen hidden in medial view, glenoid twisted so that the posterior most surface is oriented almost dorsally, infraglenoid ridge and fossa present; humerus with a waisted shaft, proximal and distal articulation surfaces set at right angles to each other, absence of ventral humeral ridge and humeral process 2 (Jarvik, 1996), anterior humeral keel originates distal to the deltopectoral crest, supinator process present, ectepicondyle projects anterior to the enlarged, convex, and ventrally situated radial condyle; the dorsomedial ridge and proximoventral ridge of the radius absent; on the pelvis, mesial iliac ridge aligns with iliac neck; of the femur, enlarged posterior intertrochanteric ridge joins ventrally oriented adductor blade at its junction with the adductor crest, fibula fossa narrow and hidden in ventral view; tibial shaft cylindrical, cnemial extensor flange, anterior tibial crest, and posterior tibial keel of the tibia absent, a steep-sided cnemial crest which runs parallel to the anterior border is present, tibial flexor crests join at the midline of the flexor surface; medial surface of the femoral articulation surface of the fibula concave.

The following characters, not observed in all temnospondyls, but found in the Euskelia, seymouriamorphs and diadectomorphs may be convergent terrestrial adaptations: body of interclavicle wider than long; narrow, laterally oriented cleithral blades; femur with an enlarged posterior intertrochanteric ridge; and of the tibia, posterior femoral articulation surface enlarged and similar in size to the anterior surface.

The findings of this study indicate that *Eryops* is not an unusual or plesiomorphic temnospondyl. The presence of the synapomorphies described above in many well ossified temnospondyls, including derived temnospondyls, such as *Eryops*, and stereospondyls, is considered evidence for their possible presence in all temnospondyls. The absence of these synapomorphies in some temnospondyls is due to their immature or paedomorphic condition, hence the presence of these derived characteristics is not homoplastic within temnospondyls.

It is quite surprising to find so many similarities between temnospondyls, seymouriamorphs and diadectomorphs in the appendicular skeleton because many of these characteristics appear to be homoplastic if mapped onto established phylogenies.
(summarized in Ruta et al., 2003). However, these phylogenies have used very few of the anatomical structures described in this paper. We consider that these characteristics are in fact synapomorphies, i.e. shared derived characters of *Eryops* (and other well ossified temnospondyls), seymouriamorphs and diadectomorphs.

This paper has extended the list of potential postcranial characters for use in cladistic analysis of early tetrapods, and the use of these characters may result in the temnospondyls and stem amniotes being sister taxa, thus altering our current understanding of early tetrapod relationships. The distribution of characteristics of the postcranial skeleton among basal tetrapod groups is the subject of ongoing research, and the implications of these results will be subjected to a detailed analysis elsewhere.

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