CHAPTER 4.
MORPHOGENESIS OF THE POSTCRANIAL SKELETON IN TEMNOSPONDYLS (TETRAPODA: TEMNOSPONDYLI): IMPLICATIONS FOR PHYLOGENETIC ANALYSIS OF EARLY TETRAPODS

Abstract. Morphogenetic changes in the endochondral postcranial elements of temnospondyls are described in order to distinguish between interspecific (phylogenetic) and intraspecific (morphogenetic and phenotypic) variation in the postcranial skeleton. The morphology of the postcranial skeleton of many temnospondyls is not static; morphogenesis of the endochondral postcranial skeleton involves continual, progressive morphogenetic changes until a high degree of ossification of the whole endochondral postcranial skeleton is apparent. Significant morphogenetic changes are observable in the endochondral postcranial skeleton of temnospondyls, and many morphogenetic changes involve the development of phylogenetically important characteristics. Assessment of the morphogenetic stage of the endochondral postcranial skeleton is imperative in interpretation of phylogenetically significant characteristics. Paedomorphosis of the endochondral postcranial skeleton (retention of morphogenetically immature stages in adults) is common in temnospondyls, and results in the terminal deletion of characteristics that develop later in morphogenesis. The reason for the absence of some derived characteristics of the postcranial skeleton in morphogenetically immature specimens is consequently indeterminate, as absence may be due to either phylogenetic or morphogenetic variation. The cartilaginous parts of the temnospondyl centrum are reconstructed as amphicoelous pleurocentral and intercentral discs.

INTRODUCTION

Recent studies have described extensive, unexpected morphogenetic changes in the postcranial skeleton of some temnospondyls, which are particularly obvious in paedomorphic taxa. Bystrow & Efremov (1940: 138) observed that “In aquatic and ‘land’ Labyrinthodonts the main differences in the postcranial skeleton consist in its greater ossification in the latter”, but previous overviews of the temnospondyl postcranial skeleton (Nilsson, 1939; Romer, 1947; Warren and Snell, 1991), have assumed that all morphological variation of the postcranial skeleton is phylogenetic. The basis for phylogenetic analysis is interspecific (phylogenetic) variation, rather than intraspecific (phenotypic or monogenetic) variation. A number of morphogenetic series of the postcranial skeleton of temnospondyls exist (see below). Comparison of these morphogenetic series with the range of morphological variation observed in temnospondyls implies that much of the described variation in the postcranial skeleton of temnospondyls may be morphogenetic, rather than phylogenetic. Certainly, no previous worker has attempted to differentiate between interspecific (phylogenetic) and intraspecific (morphogenetic and phenotypic) of the postcranial skeleton within the Temnospondyli or other early tetrapods.
Phylogenetic analyses

There has been much debate over the last two decades concerning the origin of terrestrial vertebrates (summarised in Clack, 2002a; Long and Gordon, 2004), the phylogenetic relationships of early tetrapods, and the origin of modern lissamphibians and amniotes (analyses up to 2002 summarised in Ruta et al., 2003; Klembara and Ruta, 2004a; Schoch and Milner, 2004; Vallin and Laurin, 2004). The large scale computer based analyses of temnospondyl relationships (Yates and Warren, 2000; Ruta et al., 2003) have disagreed regarding the relationships of major temnospondyl clades. On initial examination, some of the phylogenetic characters used in these analyses apparently describe morphogenetic (ontogenetic) rather than phylogenetic variation in the postcranial skeleton. Steyer (2000) demonstrated that using ontogenetically variable characters of the cranial skeleton of temnospondyls for phylogenetic analysis can have marked effects on resulting cladogram topologies, and cautioned their use in taxonomy.

The preliminary results of Pawley and Warren (2002) were an initial attempt to separate phylogenetic and non-phylogenetic variation of the postcranial skeleton, particularly of temnospondyls, but including other early tetrapods. That analysis yielded a new, well-supported hypothesis of early tetrapod relationships that proposed that temnospondyls were among the first vertebrates capable of efficient terrestrial locomotion. Another surprising result was the reduced amount of homoplasy in the scoring of postcranial characters, supporting the initial notion that not all the postcranial characters used in previous analysis pertained specifically to phylogenetic variation. Pawley and Warren (2004) proposed that some derived postcranial characteristics may be universally present within the Temnospondyli, but unexpressed in many specimens due to their immature morphogenetic stage. As the preliminary results of Pawley and Warren (2002) were promising, a more inclusive investigation of the types and extent of variation in the postcranial skeleton of temnospondyls was warranted. Phylogenetic analysis is only concerned with phylogenetic variation; it is therefore crucial to identify which characteristics describe phylogenetic, rather than other types of variation. The purpose of this study is to define morphogenetic and phenotypic variation in the postcranial skeleton of temnospondyls, which will assist in defining taxonomically useful characteristics for phylogenetic analysis of temnospondyls (Chapter 5), and the relationships of temnospondyls to other early tetrapod groups (Chapter 6).

Morphogenesis of phylogenetically significant characteristics

The postcranial skeleton of temnospondyls develops from both dermal and endochondral bone, and conforms to the typical tetrapod bauplan. The pectoral elements of the interclavicle, clavicle, and cleithrum are dermal in origin; all other postcranial elements are endochondral (preformed in cartilage). The limb bones of temnospondyls lack secondary centres of ossification and epiphyseal plates, and the presumably cartilaginous epiphyses would have allowed indeterminate growth (Haines, 1934, 1969).

Skeletochronological analyses of the proximal limb bones of derived temnospondyls (Olsen, 1951; Steyer et al., 2004) show that, after an initial rapid growth phase, they continue to increase in size during their lifespan. This continual growth means that the morphology of the endochondral postcranial skeletons of many temnospondyls is not static, rather it is subject to ongoing morphogenesis (development of body shape and form during ontogeny) (Pawley and Warren, 2004; Pawley, in press). As morphogenesis proceeds, morphological characteristics develop that were absent in previous stages. Development of new morphological characteristics ceases only when the postcranial
skeleton becomes well ossified and osteologically mature i.e. adult (Pawley and Warren, 2004, 2006; Pawley, in press), although the skeleton may become even more robust with increasing age. Some temnospondyls have paedomorphic postcranial skeletons that never become osteologically mature (Schoch, 2002d; Pawley and Warren, 2004, 2006). The changes that occur in the endochondral skeleton during morphogenesis are sometimes dramatic, so that the morphology of an immature morphogenetic stage may be quite different to that of later morphogenetic stages.

The morphogenetic changes that occur in the postcranial skeleton may be taxonomically significant, because derived characteristics that are absent in immature morphogenetic stages may develop in later morphogenetic stages of the same taxon. These morphogenetic changes have a particularly significant effect on the characteristics of the terminal portions (generally articulation surfaces) of endochondral elements, which are the last to ossify in morphogenesis.

**Heterochronic effects on morphology**

Heterochronic processes are usually determined within a group of organisms relative to the ancestral condition (McNamara, 1986), but 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 effects of heterochrony on the postcranial skeleton are therefore here defined in terms of comparative osteological maturity within temnospondyls (Pawley and Warren, 2006). Heterochronic effects (sensu McNamara, 1986) cause differing rates of development of morphological characteristics. In temnospondyls, the postcranial skeleton may be affected by different processes from those of the cranial skeleton of the same taxon.

Of particular concern in regard to the postcranial skeleton is the effect of paedomorphosis (morphogenetic retardation, resulting in retention of morphogenetically immature stages in the largest specimens), through the process of neoteny (sensu McNamara, 1986), which is common in temnospondyls (Schoch, 2002d; Pawley and Warren, 2004, 2006). 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.

Paedomorphosis is observable in the postcranial skeletons of obligatorily aquatic temnospondyl taxa, which includes most taxa within the Dvinosauria (Pawley, in press) and Stereospondyli (Pawley and Warren, 2004). Paedomorphic effects are only easily determined in elements that are preformed in cartilage (endochondral). If paedomorphic effects are present in the dermal pectoral elements (clavicle, interclavicle and cleithrum), they are difficult to determine. The endochondral elements of morphogenetically immature taxa retain imperfectly ossified articulation surfaces, and lack enlarged processes for muscle attachment, and the coracoid, pubis, carpal and tarsal elements remain entirely unossified, even in the largest specimens. It is only possible to determine if paedomorphosis is affecting the postcranial skeleton of a particular taxon from observation of a large number of specimens of differing sizes, otherwise the available specimens may simply be immature. For this reason, paedomorphosis, or other heterochronic effects *per se*, are not particularly useful phylogenetic characteristics.

Paedomorphosis may result in the terminal deletion of characteristics that develop later in morphogenesis, derived character states that develop later in morphogenesis may be absent due to the immature morphogenetic state of even the largest and presumably most mature specimens available. Postcranial characteristics that develop late in morphogenesis are present in non paedomorphic taxa (Pawley and Warren, 2004; Pawley,
in press). Other heterochronic effects, in particular the peramorphic processes of acceleration and hypermorphosis (sensu McNamara, 1986) can be observed in well ossified, morphogenetically and osteologically mature terrestrial temnospondyls (Pawley and Warren, 2006).

Acceleration, which is the opposite of neoteny, is an increase in the rate of morphological development, which results in a smaller, but morphogenetically and osteologically mature adult, examples are amphibamids such as *Doleserpeton annectans* (Bolt, 1969) and *Micropholis huxleyi* (Broili and Schröder, 1937). Hypermorphosis is an extension of late ontogenetic 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 and osteological maturity. The only known temnospondyl postcranial skeleton affected by hypermorphosis is that of *Eryops megacephalus* (Pawley and Warren, 2006).

**Larval temnospondyls**

Temnospondyls do not have a definite metamorphosis (Schoch, 2002d; Witzmann and Pfretzschner, 2003; Schoch and Fröbisch, 2006), and no clear definition exists of what constitutes a particular growth stage in a temnospondyl. Despite this, various authors have described morphogenetic changes in the cranial and postcranial skeletons of ‘larval ‘to’ post metamorphic temnospondyls. Examples include *Archeosaurus decheni* (Witzmann, 2006b), branchiosaurids (Watson, 1963; Boy, 1972, 1974; Schoch, 1992), *Micromelerpeton credneri* (Boy, 1995; Witzmann and Pfretzschner, 2003), *Onchiodon labyrinthicus* (Witzmann, 2005), and *Sclerocephalus hauseri* (Schoch, 2003). The postcranial skeletons of these larval specimens are all in the earliest morphogenetic stages of ossification.

**Assessment of morphogenetic maturity**

Size independent assessment of osteological maturity of the postcranial skeleton in temnospondyls is possible by observation of the endochondral elements. The postcranial characteristics display a definite morphogenetic sequence, and the degree of ossification is uniform across the whole endochondral postcranial skeleton, so that ossification of morphogenetically immature specimens is ubiquitously poor throughout the postcranial skeleton, and morphogenetically mature specimens show a high degree of ossification of the whole endochondral postcranial skeleton. The cessation of morphogenetic changes defines osteological maturity, which occurs in taxa with well-ossified articulation surface on the limb bones, and fully ossified coracoid, pubis, carpus, and tarsus. Specimens with morphogenetically mature postcranial skeletons are uncommon in temnospondyls. Examples are basal temnospondyls such as *Balanerpeton woodi* (Milner and Sequeira, 1994) and *Dendrerpeton acadianum* (Carroll, 1967; Holmes et al., 1998), members of the more derived Euskelia, such as *Acheloma cumminsii* (*Trematops milleri*) (Olson, 1941), *Eryops megacephalus* (Gregory et al., 1923; Pawley and Warren, 2006), and the amphibamids *Doleserpeton annectans* (Bolt, 1969) and *Micropholis huxleyi* (Broili and Schröder, 1937).

Temnospondyls with paedomorphic, osteologically immature postcranial skeletons have linear growth trajectories with increasing size throughout growth stages, as found in the stereospondyls (metoposaurs) *Buettneria perfecta* (Olsen, 1951), and *Dutuitosaurus* (*Metoposaurus*) *ouazzouii* (Steyer et al., 2004). Morphogenetic changes in the postcranial skeletons of these taxa are continual and progressive (Pawley, in press), and do not
plateau with increasing size, which would be expected if they reached morphogenetic maturity. Although growth series of the postcranial skeleton are not available for most temnospondyl taxa, it is usually possible to determine the relative stage of morphogenetic maturity of the postcranial skeleton from the comparative size of the specimen. Some stereospondyls reach lengths in excess of six metres (Damiani, 1999; Schoch, 1999a; Steyer and Damiani, 2005), so it is not unreasonable to imply that relatively large specimens of two or three metres may be sub adult. Conversely, as discussed above, some specimens with morphogenetically mature postcranial skeletons are tiny in comparison.

**Morphogenesis of the cranial skeleton**

Morphogenetic changes in the cranial skeletons of temnospondyls have been described, including those of *Acanthostomatops vorax* (Boy, 1989), *Cheliderpeton latirostre* (Boy, 1993; Werneburg and Steyer, 2002), *Dendrerpeton acadianum* (Godfrey et al., 1987; Holmes et al., 1998), dissorophids (Bolt, 1977), *Onchiodon labyrinthicus* (Boy, 1990), *Sclerocephalus haeuseri* (Boy, 1988; Werneburg, 1992; Schoch, 2003), and the mastodonsaurid *Watsonisuchus* (*Parotosuchus*) spp. (Warren and Hutchinson, 1988; Warren and Schroeder, 1995; Steyer, 2003).

**Morphogenesis of the postcranial skeleton in post larval temnospondyls**

Taxa which provide evidence for morphogenetic changes in the postcrania1 skeletons of temnospondyls include: the basal temnospondyl *Balanerpeton woodi* (Milner and Sequeira, 1994); the dvinosaurs *Dvinosaurus* spp. (Nikitin, 1995, 1997), and *Trinerorhachis insignis* (Pawley, in press); the euskeliains *Acanthostomatops vorax* (Boy, 1989), *Acheloma cumminsii* (Williston, 1909a; Olson, 1941; Sullivan et al., 2000), *Amphibamus (Miobatrachus) grandiceps* (Watson, 1940; Gregory, 1950), *Eryops megacephalus* (Cope, 1878; Case, 1911a, 1915; Miner, 1925; Bakker, 1982; Pawley and Warren, 2006), *Onchiodon labyrinthicus* (Credner, 1893; Boy, 1990; Werneburg, 1993b; Witzmann, 2005), and *Platyrynops (Amphibamus) lyelli* (Carroll, 1964a; Hook and Baird, 1984; Daly, 1994; Carroll et al., 1999); the archegosaurs *Archegosaurus decheni* (Meyer, 1857; Witzmann, 2006a) and *Sclerocephalus haeuseri* (Broili, 1926; Meckert, 1993; Lohmann and Sachs, 2001); and the stereospondyls, notably *Benthosuchus sushkini* (Bystrow and Efremov, 1940), *Buettneria perfecta* (Sengupta, 2002), *Dutuitsaurus ouazzoui* (Dutuit, 1976; Steyer et al., 2004), *Gerrothorax pustuloglomeratus* (Hellrung, 2003), *Lydekkerina huxleyi* (Watson, 1919; Pawley and Warren, 2005), *Mastodonsaurus giganteus* (Schoch, 1999a), and rhinesuchids (Haughton, 1915; van Hoepen, 1915; Broom, 1930; Pawley and Warren, 2004). In all these taxa increase in skull size correlates with an increasing degree of ossification of the postcranial skeleton, and increasing enlargement and rugosity of processes for muscle attachment.

**Morphogenesis of the postcranial skeletons in non-temnospondyl taxa**

Size independent criteria have been used to assess relative osteological maturity, assist taxon determination, and clarify phylogenetic relationships in other non-temnospondyl taxa. Brinkman (1988) used various morphogenetic stages as a way of recognizing the relative osteological age of specimens, and found that size is not a reliable method of estimating the state of maturity of a specimen. Studies of other basal tetrapods include those of lepospondyls, including the nectridian *Sauropleura* spp. (Bossy and Milner, 1998); and stem amniotes, including captorhinomorphs (Kissel et al., 2002; O’Keefe et al.,
2005, Diadectes spp. (Berman and Henrici, 2003), the seymouriamorhps Discosauriscus austriacus (Klembara and Bartik, 2000) and Seymouria spp. (Sullivan and Reisz, 1999; Berman et al., 2000; Klembara et al., 2001), and the eosuchan reptile Thadeosaurus colcanapi (Currie and Carroll, 1984). Morphogenetic series of the postcranial skeletons of more distantly related taxa include those of crocodilians (Brochu, 1995, 1996), mosasaurid reptiles (Caldwell, 1996), and pelycosaurs (Brinkman, 1988).

The major aim of this study is to assess the extent of morphogenetic variation within the postcranial skeleton, in order to differentiate between the various sources of morphological variation in the postcranial skeleton of the Temnospondyli. This study also aims to revaluate relevant cladistic characters, previously used in phylogenetic analysis of temnospondyls and early tetrapods, in the light of this information.

MATERIALS AND METHODS

Data sources

As noted above, this study is only concerned with characteristics pertaining to phenotypic and morphogenetic variation within temnospondyls, and was largely based on observations taken from the literature. Some of the morphogenetic changes in the postcranial skeleton of temnospondyls were observed in the specimens listed, along with repository information, in Appendix 5.

Institutional abbreviations


Choice of taxa

Morphogenetic changes are only described for post larval specimens. A temnospondyl ‘larva’ is defined here as a specimen that lacks ossified vertebral centra and has a rod shaped humerus. The postcranial morphology of larval specimens is ubiquitously underdeveloped, almost completely phylogenetically uninformative, and difficult to compare with that of later morphogenetic stages. No attempt was made to divide specimens into ontogenetic stages as described by Brinkman (1988).
Terminology

Terminology in morphological descriptions follows Romer (1922), Bystrow and Efremov (1940), Coates (1996), Pawley and Warren (2004; 2005; 2006), and Pawley (in press), unless otherwise noted.

Identification of phylogenetic characters affected by morphogenesis

Where relevant, phylogenetic character identifiers (e.g. INTCLA 1) are included to facilitate identification of phylogenetic characters affected by morphogenesis. Character states in plain type (e.g. TRU VER 1) were previously published and their distribution discussed by Ruta et al. (2003). Character identifiers marked ‘YW’ plus a state number (e.g. YW 103) were originally used by Yates and Warren (2000) in their large scale analysis of temnospondyl relationships. Characters used in other previously published analyses (Sequeira and Milner, 1993; Carroll, 1995; Lebedev and Coates, 1995; Coates, 1996; Paton et al., 1999; Anderson, 2001; Damiani, 2001a; Gardner, 2001; Klembara and Ruta, 2004b; Pawley and Warren, 2004; Sequeira, 2004; Clack and Finney, 2005; Pawley and Warren, 2005) have only the numbers in bold (e.g. TRU VER 28). Characters used for the first time in phylogenetic analyses of temnospondyls and early tetrapods (Appendix 8, Appendix 14) are entirely in bold (e.g. INTCLA 7).

Identification of phylogenetic characters mistakenly describing morphogenetic variation

Characters marked with a strikethrough (e.g. SCACOR 3), describe morphogenetic variation rather than phylogenetic variation, and should not continue to be used in phylogenetic analysis of temnospondyls or other early tetrapods. Note that many phylogenetic analyses of temnospondyls and early tetrapods confuse morphogenetic and phylogenetic variation, but only the postcranial characters used by Ruta et al. (2003) and Yates and Warren (2000) have been marked here (e.g. SCACOR 3) as examples, to highlight the prevalence and significance of this problem.

Morphological Description

General observations

The endochondral elements are the postcranial elements most affected by morphogenetic changes. Ossification proceeds from the diaphyses (centres of ossification) and proceeds towards the distal edges (in limb elements, the epiphyses). The endochondral elements increase in overall size and length as ossification proceeds (HUM 16, HUM 18). Morphological features furthest from the diaphyses are last to ossify, and appear latest in the morphogenetic sequence. In immature specimens the articulation surfaces are concave, becoming convex in well ossified, osteologically mature specimens.

In paedomorphic taxa, the articulation surfaces, and features of them, such as the radial condyle may never ossify, even in the largest specimens. An exception is the degree of ossification of the vertebral centrum, which may be inconsistent with that of the rest of the endochondral postcranial skeleton. For example, the anterior presacral intercentra of Mastodonsaurus giganteus and metoposaurs are fully ossified discs (Figure 36), although the rest of the postcranial skeleton is morphogenetically immature.
Vertebrae

Morphogenetic series of a complete vertebral column are observable in *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001), and of the intercentra in *Benthosuchus sushkini* (Bystrow and Efremov, 1940). Apart from the atlas and axis, regional differentiation is minor, but some variation along the vertebral column is present in many temnospondyls. Unfortunately, complete vertebral columns are known for few temnospondyls, and descriptions are all composite, so that the extent of regional variation and its phylogenetic significance within the Temnospondyli is difficult to assess. Examples of composite vertebral columns include *Eoscyopus lockardi* (Daly, 1994), *Eryops megacephalus* (Moulton, 1974), and *Mastodonsaurus giganteus* (Schoch, 1999a).

The vertebrae of temnospondyls consist of a neural arch and two centrum components, an anterior intercentra and posterior pleurocentra, which are typically paired. Temnospondyl vertebrae are thus diplospondylous (Arratia et al., 2001) i.e. with two components per vertebral centrum. The only exception is the trunk centra of *Peltobatrachus pustulatus* (Panchen, 1959) which lack intercentra, so that there is a single centrum.

The neural arches typically ossify before the centra, and the trunk vertebrae ossify before the caudal vertebrae (Romer, 1939; Boy, 1974; Milner, 1982a; Schoch, 2003; Witzmann, 2005, 2006a). As is normal for early tetrapods, the vertebral elements are endochondral (Carroll, 1989), and ossify initially from paired antimeres. Paired neural arches are present in larval temnospondyls, for example *Sclerocephalus haeuseri* (Schoch, 2003), branchiosaurs (e.g. Carroll et al., 1999), and the brachyopoid *Platycepsion wilkinsoni* (Warren and Marsicano, 1998). In the intercentra, these paired antimeres are observable in larval temnospondyls such as *Micromelerpeton credneri* (Boy, 1995), and temnospondyls with paedomorphic postcranial skeletons such as *Rewana quadricuneata* (Howie, 1972a). Paired intercentra can be observed in *Balanerpeton woodi* (Milner and Sequeira, 1994), *Micromelerpeton credneri* (Boy, 1995) and *Rewana quadricuneata* (Howie, 1972a). Vertebral development was also discussed by Witzmann (2006b).

Considerable variation in the morphology of the ossified parts of the vertebral centrum is present within temnospondyls, with some characteristics of the centrum so phylogenetically variable that they are not taxonomically significant within the Temnospondyli (Yates and Warren, 2000). The rhachitomous type, with a crescentric ventral intercentra and paired pleurocentra, is the most common. Departures from the rhachitomous centrum in temnospondyls always involve an increased degree of ossification, sometimes to the extent that the centra become amphicoelous discs (Figure 36).

Centrum types (Figure 36) include two types of diplospondylous centra, (TRU VER 33), rhachitomous and embolomeres (both pleurocentra and intercentra form complete amphicoelous discs). Two other types of centra are essentially monospondylous (TRU VER 33): gastrocentrous (intercentra highly reduced or absent in the trunk region), and stereospondylous (pleurocentra highly reduced, but never absent). The majority of temnospondyls have rhachitomous vertebrae, but all of the previously listed variations are sufficiently common that they are not aberrant. Embolomeres centra (Figure 36.6) are present in tupilakosaurs such as *Thabanchua oomie* (Warren, 1998b) and *Tupilakosaurus* spp. (Nielsen, 1954; Shishkin, 1961, 1973). Gastrocentrous centra (Figure 36.1, Figure 36.2) occur independently in *Peltobatrachus pustulatus* (Panchen, 1959), the dissorophoid *Fayella chickashaensis* (Olson, 1972), and the amphibamid *Doleserpeton annectans* (Bolt, 1969). Stereospondylous centra (Figure 36.3, Figure 36.4), although considered typical of derived temnospondyls, are present in the presacral vertebrae of the
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eukelians *Paroioxys ferriculus* (Moustafa, 1955a). Within the Stereospondyli they are known only in the superstereospondyls (Chapter 5), including the mastodonsaurids *Mastodonsaurus giganteus* (Ochev, 1972; Schoch, 1999a), *Eryosuchus tverdochlebovi* (Ochev, 1972; Shishkin, 1991), all metoposaurs (e.g. Sawin, 1945; Dutuit, 1976), the brachyopoid *Gobiops desertus* (Shishkin, 1991; Maisch and Matzke, 2005), and the chigutisaur *Koolasuchus cleelandi* (Warren et al., 1997). Note that the intercentra of another species of *Eryosuchus*, *E. (Parotosuchus) pronus* (Howie, 1970), are rhachitomous, not stereospondylyous.

Carroll et al. (1999) observed that ossification of the vertebral column in temnospondyls occurs in an anteroposterior direction. Carroll et al. based their diagnosis on the branchiosaur *Branchiosaurus salamandroides*; which retains a larval morphology throughout all known growth stages. In the stereospondyl *Mastodonsaurus giganteus*, which has a paedomorphic endochondral postcranial skeleton, the extent of ossification is regionally differentiated along the vertebral column (Schoch, 1999a). The anterior trunk vertebrae are complete discs; the sacral intercentra almost so, but the lateral edges of the anterior caudal intercentra do not approach each other dorsally (Figure 36.3). The morphology of the vertebral column of *Mastodonsaurus giganteus* is consistent with an anteroposterior ossification sequence, observable even in an extremely large temnospondyl that may reach up to six metres in length (Schoch, 1999a).

Dorsal and ventral fusion of the pleurocentra around the notochord is observed in *Eryops megacephalus* (Romer, 1947; Moulton, 1974) and *Trimerorhachis insignis* (Romer, 1947). Fusion of the pleurocentra and intercentra to each other is known to occur in large specimens of *Dvinosaurus* spp. (Bystrow, 1938), *Eryops megacephalus* (Moulton, 1974), and *Benthosuchus sushkini* (Bystrow and Efremov, 1940).

**Neural spine**

The shape of the neural spine (TRU VER 29) is affected by morphogenetic stage. In larval specimens the paired neural spines are low, and may be triangular in outline rather than rectangular, and the pre and postzygapophyses are poorly developed. The neural spines increase in height (TRU VER 27, YW 105) with morphogenesis in *Archegosaurus decheni* (Meyer, 1857; Witzmann, 2006a), *Onchiodon labyrinthicus* (Witzmann, 2005), and *Sclerocephalus hauseri* (Lohmann and Sachs, 2001). This increase in height can be substantial, as noted in the growth series of *Onchiodon labyrinthicus* (Witzmann, 2005). The buttresses on the lateral surfaces and the dorsal tips of the neural spines increase in ossification associated with expansion of the tips in *Eryops megacephalus* (Moulton, 1974). The neural arches of the trunk vertebrae fuse to the pleurocentra during morphogenesis (TRU VER 11) in *Doleserpeton annectans* (Bolt, 1969; Carroll et al., 2004) (Figure 36.1).

**Intercentra**

The atlas intercentrum forms a ring around the notochord in mature specimens of *Dissorophus multicinctus* (de Mar, 1968). In *Acheloma cumminsi* (Williston, 1909a; Olson, 1941) and *Ecolsonia cutlerensis* (Berman et al., 1985) (Figure 36.5) the mid dorsal fusion of the trunk intercentra (TRU VER 14 / YW 104) is phenotypically variable, with regional differentiation along the vertebral column, although some intercentra are dorsally fused, in others the dorsal edges approach each other, but do not meet.
Pleurocentra

All temnospondyls possess pleurocentra, which articulate with the neural arch, though they may be highly reduced (YW108), as in *Mastodonsaurus giganteus* (Schoch, 1999a). In *Australerpeton cosgriffi* (Dias and Schultz, 2003), the pleurocentra increase in size and degree of ossification during morphogenesis (YW108). Taxa in which the pleurocentra fuse dorsally (TRU VER 8) and ventrally (TRU VER 9) are described above.

Proatlas

An ossified proatlas is present in *Sclerocephalus haeuseri* (Boy, 1988) and *Eryops megacephalus* (Moulton, 1974), but is otherwise unknown in temnospondyls. As both these taxa are relatively derived within temnospondyls, this implies that a cartilaginous proatlas was present in most temnospondyls, but may be absent in stereospondyls, as the atlas lacks articulation facets (CER VER 10) for the proatlas in these taxa.

Ceratobranchials

Ossified ceratobranchials (YW121) are uncommon in temnospondyls, they are present in obligatorily aquatic taxa such as the plesiomorphic temnospondyls *Dvinosaurus primus* (Sushkin, 1936; Bystrow, 1938), *Kouerpeton bradyi* (Olson and Lammers, 1976), *Thabanchuia oomie* (Warren, 1998b), *Trimerorhachis insignis* (Olson, 1979), and the derived stereospondyl (plagiosaurid) *Gerrothorax pustuloglomeratus* (Hellrung, 2003). As part of the splanchnocranium, ceratobranchials are preformed in cartilage. The presence of ossified ceratobranchials in a derived temnospondyl such as plagiosaurids strongly implies that ceratobranchials were present in all temnospondyls in a cartilaginous form, and that their presence in an ossified state is not phylogenetically significant. Branchial denticles (gill teeth) are present in larval specimens of *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001; Schoch, 2003), but are absent in the ‘juvenile’ stage. The sequence of ossification, and subsequent loss of ossification of the ceratobranchials in larger specimens of *Onchiodon labyrinthicus* was described by Witzmann (2005).

Ribs

Morphogenetic series of the ribs are known in *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001). Regional differentiation of the ribs, corresponding to position along the vertebral column, has been noted in many temnospondyls, particularly *Archeosaurus decheni* (Meyer, 1857; Witzmann, 2006a), *Buettneria perfecta* (Sengupta, 2002), *Eryops megacephalus* (Moulton, 1974), *Onchiodon labyrinthicus* (Credner, 1893; Witzmann, 2005), and *Mastodonsaurus giganteus* (Schoch, 1999a). In larval temnospondyls, for example branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992), *Micromelerpeton credneri* (Boy, 1995; Witzmann and Pfretzschner, 2003), and *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001; Schoch, 2003), the ribs are short, straight, poorly ossified, slender rods (RIB 7). Indicators of osteological maturity are difficult to determine for ribs, as their morphology is quite variable even within a single specimen.

The degree of ventral curvature of the ribs (RIB 3) increases with increasing ossification of the distal ends of the ribs. During morphogenesis, the ribs are initially straight in small specimens of *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001; Schoch, 2003), but become longer as the specimens become more mature. The distal ends of the trunk ribs posterior to the scapulocoracoid are truncate in smaller specimens of
Sclerocephalus haeuseri (Lohmann and Sachs, 2001; Schoch, 2003), but elongate and become parallel sided distal to the uncinate processes. In Sclerocephalus haeuseri, small uncinate processes (RIB 5) are present only in larger specimens (Lohmann and Sachs, 2001; Schoch, 2003), becoming large hook-like processes in the largest specimens, which also have ossified carpal elements, and hence are morphogenetically mature.

### Interclavicle

Morphogenetic series of the interclavicle are known in Benthosuchus sushkini (Bystrow and Efremov, 1940), Dutuitosaurus ouazzoui (Dutuit, 1976), Eryops megacephalus (Pawley and Warren, 2006), Onchiodon labyrinthicus (Boy, 1990), Sclerocephalus haeuseri (Boy, 1988; Meckert, 1993; Schoch, 2003). The morphology of the interclavicle remains similar throughout morphogenesis, including those of larval morphology e.g. Micromelerpeton credneri (Boy, 1995; Witzmann and Pfretzschner, 2003) and Sclerocephalus haeuseri (Schoch, 2003). Osteological maturity is not determinable in the interclavicle, as it is a dermal bone, and not preformed in cartilage.

Little morphogenetic or phenotypic variation is observable in growth series of the interclavicle, except for minor differences in the relative length and width of the interclavicle, observable in Eryops megacephalus (Pawley and Warren, 2006) and Onchiodon labyrinthicus (Boy, 1990). The anterior interclavicular ridge is more pronounced in larger specimens of Eryops megacephalus (Pawley and Warren, 2006). In the trematosaur Trematolesistes hagdorni (Schoch, 2006), the interclavicle becomes elongated with increasing size.

### Clavicle

Morphogenetic series of the clavicle are found in Benthosuchus sushkini (Bystrow and Efremov, 1940), Dutuitosaurus ouazzoui (Dutuit, 1976), and Sclerocephalus haeuseri (Broili, 1926; Meckert, 1993; Lohmann and Sachs, 2001). The morphology of the clavicle remains similar throughout morphogenesis, including larval stages e.g. Micromelerpeton credneri (Boy, 1995; Witzmann and Pfretzschner, 2003) and Sclerocephalus haeuseri (Boy, 1990; Schoch, 2003). Osteological maturity is not determinable for the clavicle, as it is a dermal bone, and not preformed in cartilage. Only minor morphogenetic and phenotypic variation is observable in growth series of the clavicular blade, for example, in Benthosuchus sushkini (Bystrow and Efremov, 1940) growth is somewhat greater medially. The anterior clavicular flange (CLA 5 / YW 112) develops with morphogenesis; it is present only in larger specimens of Trimerorhachis insignis (Pawley, in press) and Benthosuchus sushkini (Bystrow and Efremov, 1940).

### Cleithrum

Morphogenetic series of the cleithrum are known in, Buettneria perfecta (Sengupta, 2002), and Dutuitosaurus ouazzoui (Dutuit, 1976), Onchiodon labyrinthicus (Credner, 1893; Witzmann, 2005), Mastodonsaurus giganteus (Schoch, 1999a), rhinesuchids (van Hoepen, 1915; Broom, 1930; Pawley and Warren, 2004), and Sclerocephalus haeuseri (Broili, 1926; Meckert, 1993; Lohmann and Sachs, 2001). The morphology of the cleithrum remains similar throughout morphogenesis, including larval stages, for example branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992) and Sclerocephalus haeuseri (Lohmann and Sachs, 2001; Schoch, 2003). As the cleithrum is a dermal bone, osteological maturity is not determinable. Minor phenotypic variation in the size and
general shape of the dorsal cleithral process is observable in specimens of *Sclerocephalus haeuseri* (Meckert, 1993). Only minor morphogenetic variation is observable in growth series of the cleithrum. The dorsal cleithral process (CLE 4) extends slightly further over the scapulocoracoid with increasing morphogenetic stages of *Benthosuchus sushkini* (Bystrow and Efremov, 1940), *Mastodonsaurus giganteus* (Schoch, 1999a), and *Sclerocephalus haeuseri* (Meckert, 1993). The scapular flange of the cleithral shaft increases slightly in depth in larger specimens of *Dutuitosaurus ouazzoui* (Dutuit, 1976) and *Mastodonsaurus giganteus* (Schoch, 1999a). The suprascapular lamina (sensu Bystrow and Efremov, 1940) merges with the extended scapular flange of the cleithral shaft in large specimens of *Mastodonsaurus giganteus* (Schoch, 1999a). The cleithrum of temnospondyls is initially always separate from the scapulocoracoid, although in very large specimens of *Eryops megacephalus* they sometimes fuse (Pawley and Warren, 2006).

**Scapulocoracoid**

Morphogenetic series of the scapulocoracoid (Figure 37) are known in *Archegosaurus decheni* (Meyer, 1857; Witzmann, 2006a), *Benthosuchus sushkini* (Bystrow and Efremov, 1940), *Dutuitosaurus ouazzoui* (Dutuit, 1976), *Dvinosaurus* spp. (Nikitin, 1997) (Figure 37.2), *Eryops megacephalus* (Figure 37.4), *Gerrothorax pustuloglomeratus* (Hellrung, 2003), *Mastodonsaurus giganteus* (Schoch, 1999a), *Onchiodon labyrinthicus* (Credner, 1893; Boy, 1990; Witzmann, 2005), *Platyrhinops iyelli* (Carroll, 1964a; Daly, 1994; Carroll et al., 1999), rhinesuchids (Haughton, 1915; van Hoepen, 1915; Broom, 1930; Pawley and Warren, 2004), *Sclerocephalus haeuseri* (Broili, 1926; Boy, 1988; Meckert, 1993; Lohmann and Sachs, 2001) (Figure 37.3), and *Trimerorhachis insignis* (Pawley, in press) (Figure 37.1).

The scapulocoracoid of temnospondyls is usually considered to have only one centre of ossification (e.g. Meckert, 1993; Holmes et al., 1998). The single coracoid of temnospondyls ossifies late in morphogenesis. The coracoid is present as a separate ossification (SCACOR—1) in one specimen of *Mastodonsaurus giganteus* (Schoch, 1999a), but in larger specimens the scapular blade and coracoid plate become indistinguishably fused. This indicates that two separate scapulocoracoid ossifications are probably present in temnospondyls, but evidence for this is not easy to detect because the presence of two ossifications is a transitional ontogenetic feature (also discussed by Schoch, 1999a). The scapular portion ossifies much earlier in morphogenesis than the coracoid, which apparently ossifies rapidly, as a partly ossified coracoid is unknown in temnospondyls.

An ossified coracoid plate fully fused to the scapular blade indicates osteological maturity of the scapulocoracoid (Figure 37.4.2). The centre of ossification of the scapula is located immediately dorsal to the supraglenoid foramen; the centre of ossification of the coracoid is unknown. The initial ossification of the scapula portion in larval temnospondyls, for example in branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992) and *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001; Schoch, 2003), is lunate (Figure 37.3.1); the ossification of the lateral supraglenoid ridge and dorsal blade follows (Figure 37.4.1). The scapular blade (SCACOR 6) develops with morphogenesis, expanding as it enlarges dorsally; it ossifies before the glenoid (Figure 37.4.1). Only when the scapular blade is close to morphogenetic maturity does the separate ossification of the coracoid proceed. With increasing age, the anterior edge of the scapular blade becomes finished in periosteal bone.
FIGURE 37. Morphogenetic series of the temnospondyl scapulocoracoid. 1, left scapula of *Trimerorhachis insignis* in a, lateral and b, medial views (from Pawley, in press). 2, left scapula of *Dvinosaurus* in lateral view (after Nikitin, 1997). 3, left scapulocoracoid of *Sclerocephalus haueieri* in lateral view (after Meckert, 1993). 4, left scapulocoracoid of *Eryops megacephalus* in a, lateral and b, medial views, 4.1 MCZ 1900, 4.2 from Pawley and Warren (2006). Abbreviations: cor, coracoid, fcor, coracoid foramen, fgl, glenoid foramen, fsbl, supraglenoid foramen, gl, glenoid fossa, igb, infraglenoid buttress, igr, infraglenoid ridge, igs, infraglenoid recess, lsr, lateral supraglenoid ridge, sb, scapular blade, sc, scapular tubercle, sgb, supraglenoid buttress, sgf, supraglenoid fossa, ssf, subscapular fossa, sctor, scapular torus. Scale bar = 25 mm.
In *Trimerorhachis insignis* (Pawley, in press), the posterior edge of the supraglenoid buttress develops with morphogenesis (Figure 37.1b), hiding the medial opening of the supraglenoid foramen in medial view (SCACOR 15). The infraglenoid buttress (SCACOR 4), which is a ventral extension of the supraglenoid buttress, develops with the ossification of the glenoid and coracoid. Only the larger specimens of *Trimerorhachis insignis* (Pawley, in press) and *Dvinosaurus* spp. (Nikitin, 1997) possess a scapular tubercle (SCACOR 9), which is small protuberance on the posterior surface of the supraglenoid buttress (Figure 37.1.3a).

The lateral supraglenoid ridge is absent in early morphogenetic stages, in which the scapula is lunate (Figure 37.1, Figure 37.3.1), becoming well developed only in specimens with an ossified dorsal scapula blade (the anterior edge of the scapular blade is finished in periosteal bone). The position of the external opening of the supraglenoid foramen changes as the lateral supraglenoid ridge develops. Initially, in specimens with a lunate scapula; it is located anteroventral to the lateral supraglenoid ridge. As the lateral supraglenoid ridge ossifies, enclosing the supraglenoid fossa (SCACOR 8), the supraglenoid foramen becomes located dorsal to the lateral supraglenoid ridge.

Plesiomorphic temnospondyls such as *Trimerorhachis insignis* (Pawley, in press) (Figure 37.1) never have a ventrally open supraglenoid foramen (SCACOR 5 / YW 111). In the stereospondyl *Mastodonsaurus giganteus* (Schoch, 1999a) the supraglenoid foramen is open ventrally in the specimen which lacks a coracoid, but in the later morphogenetic stages, where an enlarged scapular blade is present, the supraglenoid foramen may be ventrally enclosed, indicating that this characteristic is only observable in early morphogenetic stages of stereospondyls. Coracoid and glenoid foramina (SCACOR 3), the infraglenoid fossa, infraglenoid ridge (SCACOR 12) and infraglenoid recess (SCACOR 13), are only present in specimens that possess an ossified coracoid (Figure 37.4.2).

**Humerus**

Morphogenetic series of the humerus (Figure 38) are known in *Acheloma cumminsi* (Olson, 1941) (Figure 38.3), *Benthosuchus sushkini* (Bystrow and Efremov, 1940), *Dvinosaurus* spp. (Nikitin, 1995), *Eryops megacephalus* (Case, 1911a, 1915; Miner, 1925; Bakker, 1982; Pawley and Warren, 2006) (Figure 38.2), *Mastodonsaurus giganteus* (Schoch, 1999a), *Sclerocephalus haeuseri* (Broili, 1926; Boy, 1988; Meckert, 1993; Lohmann and Sachs, 2001), rhinesuchids (Haughton, 1915; van Hoepen, 1915; Pawley and Warren, 2004), *Trimerorhachis insignis* (Pawley, in press) (Figure 38.1), and the metoposaurs *Buettneria perfecta* (Olsen, 1951; Sengupta, 2002) and *Dutuitosaurus ouazzoui* (Dutuit, 1976).

In larval temnospondyls, for example branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992), *Micromelerpeton credneri* (Boy, 1995; Witzmann and Pfretzschner, 2003), *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001; Schoch, 2003) and the earliest stage of *Trimerorhachis insignis* (Pawley, in press) (Figure 38.1.1), the humerus is a featureless column of bone. Indicators of osteological maturity of the humerus are an ossified convex radial condyle, and periosteal bone separating the distal surface of the ectepicondyle from the radial condyle. The developmental sequence of ossification is subject to both phenotypic and phylogenetic variation. For example, in *Acheloma cumminsi* (Olson, 1941), the supinator process ossifies prior to the proximal humeral ridge; in *Trimerorhachis insignis* (Pawley, in press) this sequence is reversed. Most temnospondyls have the proximal and distal ends of the humerus set at approximately right angles (HUM 19). Phenotypic variation in the degree of humeral torsion is known to occur
Figure 38. Morphogenetic series of the temnospondyl humerus. 1, left humerus of *Trimerorhachis insignis* in a, extensor and b, anterior views (from Pawley, in press). 2, left humerus of *Eryops megacephalus* in a, flexor, b, extensor and c, distal views, 2.1-2.4 after Bakker (1982), 2.5 from Pawley and Warren (2006). 3, left humerus of *Acheloma cumminsi* in flexor view (after Olson, 1941). Abbreviations: delt, deltoid crest, ect, ectepicondyle, ent, entepicondyle, hur, ventral humeral ridge, ldp, latissimus dorsi process, pect, attachment area for pectoralis muscle, phr, proximal humeral ridge, rac, radial condyle, sup, supinator process, ulc, ulna condyle, ver, ventral entepicondylar ridge. Scale bar = 25 mm.
(occasionally), as in Buettneria perfecta (Olsen, 1951), Dvinosaurus spp. (Nikitin, 1995), Mastodonsaurus giganteus (Schoch, 1999a), and Trimerorhachis insignis (Pawley, in press). In these taxa, the degree of torsion varies from approximately a right angle to significantly less. In immature specimens, the proximal humeral articulation surface is flat in lateral view, rather than anteroposteriorly curved.

The proximal humeral ridge ossifies during morphogenesis (Figure 38), it is unossified in smaller specimens. As it ossifies, it separates the proximal articulation surface from the deltoid and pectoral crests. Small areas of the anterior edge of the proximal humeral ridge may remain unossified in larger specimens (Figure 38.1.6b). In Trimerorhachis insignis (Pawley, in press), the deltoid and pectoral crests are obvious even in small specimens, and they increase in depth and rugosity during morphogenesis. The degree of rugosity is phenotypically variable, with specimens of the same degree of ossification displaying differing degrees of development (Figure 38.1). The scapulohumeral ridge remains unossified in Eryops megacephalus (Pawley and Warren, 2006). This feature is not known in other temnospondyls, and it often remains unprepared in specimens of Eryops megacephalus, so it may have been overlooked or dismissed as damage in other taxa (Pawley and Warren, 2006).

In the smallest specimens of Trimerorhachis insignis (Pawley, in press) (Figure 38.1), the latissimus dorsi process (HUM 1, HUM 24, HUM 25) is absent because it was located in the unossified proximal area of the humerus, but in other specimens it is conspicuous. With increasing size the latissimus dorsi becomes more distant from the proximal articulation surface and increasingly robust. The morphology of the latissimus dorsi process is also subject to phylogenetic variation, it is highly reduced or absent (HUM 20) in most stereospondyls. The presence of a conspicuous latissimus dorsi process in early morphogenetic stages of a plesiomorphic taxon such as Trimerorhachis insignis indicates that the reduction of the latissimus dorsi process in the Stereospondyli is not a paedomorphic feature (Pawley, in press).

The distal end of the ectepicondyle enlarges anteriorly (HUM 7) during morphogenesis (YW 115), and the distal surface becomes finished in periosteal bone in osteologically mature specimens, separating it from the radial condyle (Figure 38.2.5c); the most distal tip of the ectepicondyle is the slowest to ossify. In later morphogenetic stages, the anterior edge of the ectepicondyle extends anterior to the radial condyle (HUM 26) as in Eryops megacephalus (Case, 1911a, 1915; Miner, 1925; Pawley and Warren, 2006).

The shape of the entepicondyle changes dramatically throughout morphogenesis. In the smallest specimens, it is barely developed. With increasing size, the outline of the entepicondyle becomes triangular and then, as the distal border becomes increasingly ossified, the outline of the entepicondyle becomes squared off. In the largest specimens, the posterolateral margin of entepicondyle lies distal to the area of the radial-ulnar facets (HUM 13). The width of the entepicondyle also increases proportionally with morphogenesis (HUM 15). The posterior edge of the entepicondyle always remains unossified. The presence of an entepicondylar foramen (HUM 6) may be phenotypically variable among plesiomorphic temnospondyls. An entepicondylar foramen is present near the most dorsal edge of the entepicondyle in one specimen of Dvinosaurus spp. (Gubin, 2004), but is not known in other specimens of this taxon.

The ventral entepicondylar ridge (Pawley and Warren, 2006) is only developed in the largest specimen of Benthosuchus sushkini (Bystrow and Efremov, 1940), which implies it develops later in morphogenesis. The ventral humeral ridge (HUM 3), which in temnospondyls is obscured somewhat by torsion of the humerus, develops with morphogenesis. It is present as a low ridge in the largest specimens of Trimerorhachis
insignis (Pawley, in press) (Figure 38.1.7b), but is easily observed in late morphogenetic stages of well ossified taxa such as *Eryops megacephalus* (Pawley and Warren, 2006).

In immature specimens, the supinator process (HUM 2) is confluent with the distal end of the anterior humeral keel, and is not a separate process. With increasing size and ossification of the distal articulation surface, the supinator process becomes prominent and separated from the distal articulation surface by periosteal bone (Figure 38.1.6b). Initially the anterior edge of the supinator process is finished in cancellous bone, in specimens with a well-ossified radial condyle, such as *Acheloma cumminsi* (Olson, 1941), the anterior edge becomes finished in periosteal bone (Figure 38.3.). In the larger specimens of paedomorphic taxa such as *Benthosuchus sushkini* (Bystrow and Efremov, 1940), *Dvinosaurus* spp. (Nikitin, 1995), *Mastodonsaurus giganteus* (Schoch, 1999a), rhinesuchids (Pawley and Warren, 2004), and *Trimerorhachis insignis* (Pawley, in press) (Figure 38.1), the supinator process remains small and triangular and the distal edge remains unossified. In well-ossified taxa such as *Acheloma cumminsi* (Olson, 1941) (Figure 38.1) and *Eryops megacephalus* (Case, 1911a, 1915; Miner, 1925; Bakker, 1982; Pawley and Warren, 2006) (Figure 38.2), the supinator process develops early in morphogenesis, is prominent and rectangular in shape, and well separated from the distal end of the humerus by a broad band of periosteal bone.

In temnospondyls, an ossified radial condyle (HUM 11) is always located distal to the supinator process, so that specimens that lack a supinator process also lack an ossified radial condyle. The radial condyle often remains unossified throughout morphogenesis in paedomorphic taxa like *Trimerorhachis insignis* (Pawley, in press) (Figure 38.1), its absence may be mistaken for the radial condyle being distally located on the humerus (YW 116). Well-ossified taxa such as *Acheloma cumminsi* (Olson, 1941) and *Eryops megacephalus* (Pawley and Warren, 2006) develop large convex radial condyles in larger specimens (Figure 38.2). The presence of an ossified ulnar condyle is difficult to determine. In well-ossified taxa such as *Eryops megacephalus*, the ulnar condyle indents into the distal articulation surface (Pawley and Warren, 2006) (Figure 38.2.5b-c).

**Radius**

Morphogenetic series of the radius are known only in *Dutuitosaurus ouazzoui* (Dutuit, 1976) (Figure 39.1). In larval temnospondyls, for example branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992) and *Sclerocephalus haeuweri* (Lohmann and Sachs, 2001; Schoch, 2003), the radius is a featureless column of bone. Indicators of osteological maturity of the radius are the ossification of the proximal and distal articulation surfaces.

The radius is a relatively featureless element and no morphogenetic changes can be observed except for the increasing ossification and definition of the articulation surfaces, as seen in *Eryops megacephalus* (Pawley and Warren, 2006).

**Ulna**

Morphogenetic series of the ulna (Figure 39) are known in *Australerpeton cosgriffi* (Dias and Schultz, 2003), *Buettneria perfecta* (Sengupta, 2002), *Dutuitosaurus ouazzoui* (Dutuit, 1976) (Figure 39.4), *Ecolsonia cutlerensis* (Berman et al., 1985) (Figure 39.3), and *Trimerorhachis insignis* (Pawley, in press). In larval temnospondyls, for example branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992) and *Sclerocephalus haeuweri* (Lohmann and Sachs, 2001; Schoch, 2003), the ulna is a featureless column of bone. Indicators of osteological maturity of the ulna are a strip of periosteal bone separating the dorsal tip of the olecranon process from the humeral articulation surface, and the
intermedial and ulnare facets are distinct and juxtaposed at right angles (in anterior and posterior views) on the distal end of the ulna, as in well ossified taxa such as *Ecolsonia cutlerensis* (Berman et al., 1985) and *Eryops megacephalus* (Pawley and Warren, 2006).

The olecranon process (ULNA 1) is subject to morphogenetic development, it is almost absent in immature specimens (Figure 39.4.1). During morphogenesis, the degree of extension of the lateral surface of the olecranon process above the medial edge of the articulation surface increases. The dorsal tip of the olecranon process is separated from the humeral articulation surface by a strip of periosteal bone in larger specimens of

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**Figure 39. Morphogenetic series of the temnospondyl radius and ulna.** 1, left radius of *Dutuitosaurus ouazzoui* in extensor views (after Dutuit, 1976). 2, left radius of *Eryops megacephalus* in a, extensor and b, flexor views (from Pawley and Warren, 2006). 3, left ulna of *Ecolsonia cutlerensis* in a, flexor, b, extensor, c, anterior, and d, posterior views (after Berman et al., 1985). 4, left ulna of *Dutuitosaurus ouazzoui* in posterior view (after Dutuit, 1976). 5, left ulna of *Eryops megacephalus* in a, anterior and b, posterior views (from Pawley and Warren, 2006). Abbreviations: intf, intermedial facet, ol, olecranon process, pluc, posterolateral ulnar crest, puc, posterior ulnar crest, radf, radiale facet, tri, attachment area for triceps muscle, uck, ulnar extensor keel, ulnf, ulnar facet. Scale bar = 25 mm.
Ecolsonia cutlerensis (Berman et al., 1985) (Figure 39.3.2).

The posterior ulnar crest is rugose in well-ossified taxa such as *Ecolsonia cutlerensis* (Berman et al., 1985) and *Eryops megacephalus* (Pawley and Warren, 2006), these rugosities are absent in osteologically immature specimens. The posterolateral ulnar crest (ULNA 2) (Figure 39.5a) is present in specimens of *Buettneria perfecta* (MCZ 1923) which lack a well-developed olecranon process. The triceps attachment area on the proximal end of the ulnar extensor keel is rugose even in morphogenetically immature specimens, however the rugosities are deeper and extend down the whole length of the ulnar extensor keel in well-ossified taxa such as *Eryops megacephalus* (Pawley and Warren, 2006) (Figure 39.5b).

**Pelvis**

Morphogenetic series of pelvic elements (Figure 40) are known in *Acanthostomatops vorax* (Boy, 1989), *Balanerpeton woodi* (Milner and Sequeira, 1994), *Benthosuchus sushkini* (Bystrow and Efremov, 1940), *Buettneria perfecta* (Sengupta, 2002), *Dendrerpeton acadianum* (Carroll, 1967; Holmes et al., 1998) (Figure 40.1), *Eryops megacephalus* (Pawley and Warren, 2006) (Figure 40.3), *Lydekkerina huxleyi* (Watson, 1919; Pawley and Warren, 2005), *Mastodonsaurus giganteus* (Schoch, 1999a), and *Onchiodon labyrinthicus* (Boy, 1990; Witzmann, 2005), and *Trimerorhachis insignis* (Pawley, in press) (Figure 40.2).

In larval temnospondyls, for example branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992), *Micromelerpeton credneri* (Boy, 1995; Witzmann and Ppretzschner, 2003), and *Sclerocephalus haeusleri* (Lohmann and Sachs, 2001; Schoch, 2003), only the ilium is ossified. The pubis is the last pelvic element to ossify, and indicates morphogenetic maturity of the pelvis when it encloses the obturator foramen. Presence of the pubis is correlated with the state of ossification of the whole postcrani al skeleton; specimens with an ossified pubis also have ossified coracoids, carpus and tarsus. It is present in only the largest specimens of *Balanerpeton woodi* (Milner and Sequeira, 1994), *Dendrerpeton acadianum* (Carroll, 1967; Holmes et al., 1998) (Figure 40.1), *Eryops megacephalus* (Pawley and Warren, 2006) (Figure 40.3), *Mastodonsaurus giganteus* (Schoch, 1999a), and *Sclerocephalus haeusleri* (Boy, 1988; Lohmann and Sachs, 2001; Schoch, 2003).

The available growth series also indicate significant phenotypic variation in the shape of the dorsal iliac process, for example in *Benthosuchus sushkini* (Bystrow and Efremov, 1940), *Eryops megacephalus* (Pawley and Warren, 2006) (Figure 40.3), and *Trimerorhachis insignis* (Pawley, in press). In *Trimerorhachis insignis*, the dorsal iliac process becomes more strongly dorsally flared in larger morphogenetic stages (Pawley, in press) (Figure 40.2). The post iliac process (ILI 2), which in temnospondyls is only known in the most plesiomorphic taxa, *Balanerpeton woodi* (Milner and Sequeira, 1994) and *Dendrerpeton acadianum* (Carroll, 1967; Holmes et al., 1998), is barely developed in the smallest specimens of *Dendrerpeton acadianum* (Carroll, 1967; Holmes et al., 1998) (Figure 40.1).

The anterior and posterior supracetabular notches become more prominent with increasing ossification of the ventral part of the ilium. The postacetabular buttress (ILI 6) is absent in specimens in which the pelvic elements are not fused.

The sacral flange, although uncommon in temnospondyls and known only in *Eryops megacephalus* (Cope, 1878; Pawley and Warren, 2006) and *Platyrhinops lyelli* (Carroll, 1964a; Hook and Baird, 1984), develops before the ilium fuses to the ischium and pubis (Figure 40.3).

The transverse pelvic ridge (ILI 7) is both phylogenetically and phenotypically
FIGURE 40. Morphogenetic series of the temnospondyl pelvis. 1, left pelvis of *Dendrerpeton acadianum* in lateral view, 1.1 and 1.3 after Carroll (1967) 1.2 after Holmes et al. (1998). 2, left pelvic elements of *Trimerorhachis insignis* in lateral view, 2.1-2.3 ilium, 2.4 ischium (from Pawley, in press). 3, left pelvis of *Eryops megacephalus* in lateral view, 3.1 MCZ 7770, 3.2 from Pawley and Warren (2006). Abbreviations: asan, anterior supracetabular notch, dip, dorsal iliac process, isch, ischium, obt, obturator foramen, pab, postacetabular buttress, pop, post iliac process, psan, posterior supracetabular notch, pub, pubis, sacf, sacral flange, tpr, transverse pelvic ridge. Scale bar = 25 mm.
variable within the Temnospondyli. In basal temnospondyals, such as *Dendrerpeton acadianum*, it extends from the anterior surface of the supracetabular buttress to the posterior side of the ilium (Carroll, 1967; Holmes et al., 1998) (Figure 40.1.3). In some more derived temnospondyals such as *Eryops megacephalus* (Pawley and Warren, 2006) and *Trimerorhachis insignis* (Pawley, in press) (Figure 40.2.3) the transverse pelvic ridge is shortened and does not extend posterior to the supracetabular buttress. In *Benthosuchus suckini* (Bystrow and Efremov, 1940) and *Trimerorhachis insignis* (Pawley, in press) the presence of the transverse pelvic ridge is phenotypically variable, and in some specimens it is absent.

**Femur**

Morphogenetic series of the femur (Figure 41) are known in *Acheloma cumminsi* (Williston, 1909a; Olson, 1941; Sullivan et al., 2000) (Figure 41.2), *Balanerpeton woodi* (Milner and Sequeira, 1994), *Benthosuchus suckini* (Bystrow and Efremov, 1940), *Lydekkerina huxleyi* (Watson, 1919; Pawley and Warren, 2005), rhinesuchids (Haughton, 1915; van Hoeven, 1915; Pawley and Warren, 2004), *Trimerorhachis insignis* (Pawley, in press) (Figure 41.1), and the metoposaurs *Buettneria perfecta* (Sengupta, 2002) and *Dutuitosaurus ouazzoui* (Dutuit, 1976). In larval temnospondyls, for example branchiosaurids (e.g. Boy, 1972; Boy, 1974; Schoch, 1992), *Micromelerpeton credneri* (Boy, 1995; Witzmann and Pfretzschner, 2003), and *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001; Schoch, 2003), the femur is a simple column of bone. Indicators of osteological maturity of the femur are a well-developed anterior and posterior caput femoral fossa, which are an indication of a well-ossified femoral head.

The adductor blade deepens with morphogenesis, as does the adductor crest, which is low and almost absent in immature specimens. A low adductor crest associated with a well-developed internal trochanter, as in *Trimerorhachis insignis* (Pawley, in press) (Figure 41.1a), is a phylogenetically significant characteristic (FEM 6). The small protuberance considered to mark the attachment for the ischiotrochantericus muscle is only present within temnospondyls in large, well ossified specimens of *Eryops megacephalus* (Pawley and Warren, 2006) (Figure 41.3a), and is therefore probably not a phylogenetically significant characteristic.

The anterior and posterior caput femoral fossae on the proximal femoral articulation surface are only present in osteologically mature specimens (Figure 41.3). The posterior intertrochanteric ridge (FEM 7) increases in prominence with morphogenesis. It is possible that the development of this feature into a structure similar in size to the internal trochanter is a feature of late morphogenesis, as it is only known in temnospondyls in highly ossified taxa such as *Ecolsonia cutlerensis* (Berman et al., 1985) and *Eryops megacephalus* (Cope, 1878; Pawley and Warren, 2006).

In morphogenetically immature specimens, the internal trochanter lacks a distinct process (FEM 1) and is not distinct from the proximal articulation surface (FEM 2). The degree of rugosity of the fourth trochanter (FEM 3) is phenotypically variable, being rugose only in some of the larger specimens of *Trimerorhachis insignis* (Pawley, in press), which indicates that this characteristic is probably not phylogenetically useful. In *Acheloma cumminsi* the fourth trochanter is expanded with a deeply concave ventral surface, a characteristic developed only in larger specimens (Williston, 1909a; Olson, 1941; Sullivan et al., 2000) (Figure 41.2.2b). The intercondylar fossa develops with morphogenesis; it is a small, shallow, vaguely defined depression in osteologically immature taxa (Figure 41.1), but deep and sharply defined in well-ossified specimens (YW 119) (Figure 41.3). The anterior popliteal ridge develops late in morphogenesis, and
FIGURE 41. Morphogenetic series of the temnospondyl femur. 1, left femur of *Trimerorhachis insignis* in a, extensor and b, flexor views (from Pawley, in press). 2, left femur of *Acheloma cumminsi* in a, extensor and b, flexor views (after Sullivan et al., 2000). 3, left femur of *Eryops megacephalus* in a, extensor and b, flexor views (from Pawley and Warren, 2006). Abbreviations: acff, anterior caput femora fossa, adb, adductor blade, adc, adductor crest, apr, anterior popliteal ridge, ffo, fibula fossa, fibc, fibular condyle, icf, intercondylar fossa, intr, internal trochanter, istr, attachment for ischirotrochantericus muscle, pcff, posterior caput femora fossa, pir, posterior intertrochanteric ridge, ppa, popliteal area, tibc, tibial condyle, tr4, fourth trochanter. Scale bar = 25 mm.
is only observable in well ossified taxa such as *Eryops megacephalus* (Cope, 1878; Case, 1911b; Pawley and Warren, 2006) (Figure 41.3b). The popliteal area increases in size, and the fibula fossa is deeper in osteologically more mature specimens, consistent with increasing ossification of the distal end of the femur.

The tibial and fibular condyles are ill defined in osteologically immature specimens. In small specimens, they are confluent, so the distal end of the femur is flat. With morphogenesis, they become set at right angles to each other in extensor view. In well-ossified specimens, the dorsal surface of the tibial and fibular condyles project distal to the intercondylar fossa in extensor view (Figure 41.3a).

**Tibia**

Morphogenetic series of the tibia (Figure 42) are known in *Eryops megacephalus* (Case, 1911b; Pawley and Warren, 2006) (Figure 42.2), *Mastodonsaurus giganteus* [in which the 'fibula' (Schoch, 1999a: fig. 48) is an inverted immature right tibia], *Trimerorhachis insignis* (Pawley, in press), and the metoposaurs *Dutuitosaurus ouazzoui* (Dutuit, 1976) (Figure 42.1) and *Buettneria perfecta* (Sengupta, 2002). In larval temnospondyls, for example branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992) and *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001; Schoch, 2003), the tibia is a featureless column of bone. Indicators of osteological maturity of the tibia are the distal end of the tibia being expanded to approximately twice the width of the shaft, and the intermedial and tibiale facets are set at almost right angles to each other.

Observed in all temnospondyls, the cnemial crest is a large, steep sided ridge with sides set at right angles to each other. It increases in height and prominence during morphogenesis, correlated with increasing ossification of the proximal articulation surface. Correspondingly, the cnemial trough deepens as the proximal articulation surface ossifies (Figure 42.2a).

The anterior and posterior tibial ridges are present in immature specimens of the paedomorphic *Trimerorhachis insignis* (Pawley, in press), but not in more derived temnospondyls, which indicates that they may be phylogenetically significant, and develop early in morphogenesis. The anterior, posterior, and distal tibial flexor crests (TIB 4) are barely discernable in osteologically immature specimens. In osteologically mature specimens, they form a ‘Y’ shaped set of narrow ridges on the flexor surface of the tibia (Figure 42.1.1b).

The distal end of the tibia expands in width relative to the shaft as the degree of ossification increases. In well ossified taxa, such as *Eryops megacephalus* (Pawley and Warren, 2006) (Figure 42.1), the distal end of the tibia is expanded to approximately twice the width of the shaft in all views (Figure 42.2). In immature specimens, the intermedial and tibiale facets are confluent and the distal end of the tibia is essentially flat (Figure 42.2).

**Fibula**

Morphogenetic series of the fibula (Figure 42) are known in *Trimerorhachis insignis* (Pawley, in press #1095) (Figure 42.3), and the metoposaurs *Buettneria perfecta* (Sengupta, 2002) and *Dutuitosaurus ouazzoui* (Dutuit, 1976). In larval temnospondyls, for example branchiosaurs (e.g. Boy, 1972; Boy, 1974; Schoch, 1992) and *Sclerocephalus haeuseri* (Lohmann and Sachs, 2001; Schoch, 2003), the fibula is a simple column of bone. Indicators of osteological maturity of the fibula are a well-defined, medially angled
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FIGURE 42. Morphogenetic series of the temnospondyl tibia and fibula. 1, left tibia of *Eryops megacephalus* in a, extensor and b, flexor views, 1.1 (from Pawley and Warren, 2006),1.2 AMNH 4198. 2, left tibia of *Buettneria perfecta* MCZ 1922 in a, extensor and b, flexor views. 3, left fibula of *Trimerorhachis insignis* in flexor view (from Pawley, in press). 4, left fibula of *Eryops megacephalus* in a, extensor and b, flexor views (from Pawley and Warren, 2006). 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, intf, intermedial facet, pfr, posterior fibular ridge, ptfc, posterior tibial flexor crest, tibf, tibiale facet. Scale bar = 25 mm.
femoral articulation surface and the intermedial and fibulare facets have a sigmoid outline in ventral view.

The anterior fibular ridge (Figure 42.4a) develops with the ossification of the proximal end of the fibula, along with the fibular extensor ridge (Figure 42.4a). The posterior fibular ridge (FIB 3) is present in all temnospondyl specimens, but it is phenotypically variable in degree of prominence. It is often abraded in water worn specimens. Rows of tubercles (FIB 4) along the posterior fibular ridge are observable in exceptionally well ossified specimens of Eryops megacephalus (Pawley and Warren, 2006) (Figure 42.4b), which indicates that this is a characteristic which develops very late in morphogenesis, and is not phylogenetically useful.

The distal end of the fibula is curved in osteologically immature specimens, and with increasing ossification becomes sigmoid in ventral view. The intermedial facet becomes more deeply recessed, and the ventral outline of the fibulare facet flattens during morphogenesis (Figure 42.3).

Manus and Pes

Morphogenetic series of the carpus and tarsus are known in Sclerocephalus haeuseri (Boy, 1988; Lohmann and Sachs, 2001). The carpal and tarsal elements do not all ossify (TAR 1) at the same time, with only a few of the proximal elements ossified (TAR 2) in Mastodonsaurus giganteus (Schoch, 1999a) and Uranocentrodon (Myriodon) senekalensis (van Hoepen, 1915). In the manus of Uranocentrodon senekalensis, there are two ossified carpal elements, which are indeterminable, in the pes of the same specimen (van Hoepen, 1915), the intermedium, proximal centrale, fibulare, and tarsal three are ossified. These are the largest elements of the fully ossified temnospondyl tarsus (Schaeffer, 1941). Osteological maturity of the manus and pes is indicated by the presence of the full complement of 11 carpal (Gregory et al., 1923; Olson, 1941) and 12 tarsal (Schaeffer, 1941) elements.

Digits

Morphogenetic series of the digits are present in larval specimens, but details of morphogenetic development are elusive.

Dermal ossifications

The cycloid dorsal scales and ventral scutes differentiate with growth in larval Sclerocephalus haeuseri (Schoch, 2003), and are not present in early morphogenetic stages of Balanerpeton woodii (Milner and Sequeira, 1994), Platyrhinops lyelli (Clack and Milner, 1993) and Archegosaurus decheni (Witzmann, 2006b).

Enlarged, laterally expanded paramedian osteoderms articulating with the neural spines, are present in dissorophids and Peltobatrachus pustulatus (Panchen, 1959). Bolt (1974d) considered that the single paramedian osteoderm (internal series) per neural spine of Broiliellus spp. (Williston, 1914; de Mar, 1966) may represent an immature morphogenetic stage of Dissorophus multicinctus, which has two paramedian osteoderms (internal and external series) per neural spine (Williston, 1910b; de Mar, 1968).
DISCUSSION

Most of the morphogenetic series presented represent display continual, progressive morphogenetic development from larval to osteologically mature specimens. Much of the morphological variation observed in previous overviews of the temnospondyl postcranial skeleton (Nilsson, 1939; Warren and Snell, 1991), is morphogenic rather than phylogenetic. The ossification sequences observed in the endochondral postcranial skeleton of temnospondyls generally supports the hypothesis of Brinkman (1988), who considered that the morphogenetic sequence of the postcranial skeleton observed in pelycosaurs was probably typical of early tetrapods. However, some differences between the postcranial skeletons of temnospondyls and those of other early tetrapods are noted below.

Differences in morphogenetic sequences of other early tetrapod taxa

Anterior humeral keel

The only growth series known for taxa with an ‘L’ shaped humerus are those of the stem tetrapod *Greererpeton burkemorani* (Godfrey, 1989a) and the anthracosaur *Proterogyrinus scheeli* (Holmes, 1984). The anterior humeral keel is unossified in immature specimens of these taxa, ossifying in larger specimens. In contrast, the anterior humeral keel is ossified in the smallest specimens of all taxa with waisted humeri, including temnospondyls, as noted here, and seymouriamorphs (Klembara et al., 2001).

Coracoid

A single coracoid is characteristic of basal tetrapods (Ruta et al., 2003). The only temnospondyl known to display this is *Mastodonsaurus giganteus* (Schoch, 1999a). In stem amniotes such as *Petrolacosaurus kansensis* (Reisz, 1977) and *Thadeosaurus colcanapi* (Currie and Carroll, 1984) two coracoid ossifications per side are present in early or all morphogenetic stages, which indicates a phylogenetic difference.

Astragalus

The tibiale, intermedium and proximal centrale fuse together in late morphogenetic stages of stem amniotes and microsaurs to produce the astragalus (Rieppel, 1993; Kissel et al., 2002; Berman and Henrici, 2003), which is unknown in temnospondyls.

Implications for phylogenetic analysis

Morphogenetic stage has a considerable affect on the morphology of the postcranial skeleton. Specimens of many temnospondyl taxa are not morphogenetically mature, and their osteologically underdeveloped condition must be considered when making morphological comparisons. The range of morphogenetic variation observed in the endochondral skeleton of temnospondyls could create problems for interpretation of postcranial characteristics used in phylogenetic analysis. Determination of the absence or presence of particular characteristics may depend on the morphogenetic stage of specimens examined (Pawley and Warren, 2004, 2006; Pawley, in press). The basis for hypotheses of phylogenetic relationships is interspecific (phylogenetic) variation, not intraspecific (phenotypic or morphogenetic) variation.
As noted in the above description of morphogenetic changes in the temnospondyl postcranial skeleton, several characters previously used in phylogenetic analysis of temnospondyls describe morphogenetic, not phylogenetic variation e.g. \( YW_{115} \). Another example would be the coding of the phylogenetic character \( FEM_2 \). 'absence (0) or presence (1) of condition: internal trochanter separated from femur by a distinct trough-like space' (Ruta et al., 2003). Both states of this character are observable in the morphogenetic series of some taxa described here. This is not a polymorphism, because the character states describe morphogenetic (ontogenetic), not phylogenetic, variation. The earlier morphogenetic stages display state (0), the later morphogenetic stages, state (1). Specimens displaying state (0) are of a morphogenetically less mature stage, rather than plesiomorphic, whereas specimens displaying state (1) are of a morphogenetically more mature stage, rather than derived.

Some characters that describe morphogenetic rather than phylogenetic variation are easily eliminated, however other characteristics develop with morphogenesis and require the morphogenetic age of specimens to be taken into account when coding specimens. An example of a characteristic subject to both morphogenetic and phylogenetic variation is the presence or absence of a supinator process (HUM 2 / YW 114). The supinator process is absent (state = 0) in well ossified, morphogenetically mature stem tetrapods (sensu Ruta et al., 2003), but is ubiquitous among temnospondyl specimens that have achieved a sufficient stage of morphogenetic maturity (state = 1) (Pawley and Warren, 2004, 2006). An example of potential confusion of this type can be seen in the treatment by various workers of the presence or absence of a supinator process of the humerus of the basal temnospondyl \textit{Dendrerpeton acadianum} (Carroll, 1967). Comparison of the humerus specimen described by Carroll (1967) with the growth series of temnospondyls described here indicates that the specimen described by Carroll (1967) is morphogenetically immature, and would not be expected to have developed a supinator process. The description of a much larger tibia of the same taxon by Carroll (1967) supports this hypothesis. Whether the supinator process is present or not in larger specimens of \textit{Dendrerpeton acadianum}, such as that described by Holmes et al. (1998) is unknown, as the anterior surface of the humerus in this specimen has not been prepared.

Both the large scale phylogenetic analyses of Yates and Warren (2000) and Ruta et al. (2003) code the supinator process of \textit{Dendrerpeton acadianum} (Carroll, 1967; Holmes et al., 1998) as absent, the plesiomorphic condition (state = 0). The morphogenetic evidence presented here implies that it is just as parsimonious to suggest that a supinator process is absent in the \textit{Dendrerpeton acadianum} described by Carroll (1967) due to its immature morphogenetic stage. It is not possible to determine whether the supinator process in \textit{Dendrerpeton acadianum} is absent due to morphogenetic or phylogenetic variation, and it would be prudent in this case to exercise caution and code the presence or absence of a supinator process in \textit{Dendrerpeton acadianum} unknown (state = ?) in future phylogenetic analyses.

In contrast, the absence of a supinator process in well-ossified specimens of a non-temnospondyl taxa such as \textit{Captorhinus aguti} (Holmes, 1977) is more likely to be phylogenetic (state = 0). Morphogenetic series have not been described for the postcranial skeleton of \textit{Captorhinus aguti}, but the humerus described by Holmes (1977) possesses all the indicators of morphogenetic maturity observed in the growth series of the early tetrapod taxa listed above. The distal articulation surface is well ossified, with an ossified radial condyle, and the distal surface of the ectepicondyle is separated from the radial condyle by periosteal bone. Further major morphogenetic changes are unlikely in this morphogenetically mature specimen, so that in this case the supinator process is most likely absent due to phylogenetic variation.
Revised lists of postcranial characters used in phylogenetic analysis of temnospondyls are presented in the analysis of interrelationships of the Temnospondyli (Chapter 5, Appendix 8), and an analysis of early tetrapods (Chapter 6, Appendix 14). These character state lists eliminate previous phylogenetic characters identified as erroneously describing morphogenetic variation, and indicate characters affected by morphogenetic development to minimise confusion with plesiomorphic absence states.

**Implications for commonly used phylogenetic characters**

Characteristics of the vertebrae, particularly those of the centrum, have traditionally been used to establish phylogenetic relationships in temnospondyls and other early tetrapods (e.g. Watson, 1919, 1926; Panchen, 1967; Parrington, 1967; Panchen, 1977a). Phylogenetic variation in centrum type is definitely present among temnospondyls, but the range of variation present in any taxon is affected by regional differentiation along the vertebral column as well as morphogenetic stage. Reinterpretation of the cartilaginous parts as amphicoelous discs implies that the most parsimonious explanation for variations in the morphology of the vertebral centrum is variation in the degree of ossification of the centrum. Variations in centrum morphology, although interesting, are unreliable for definitive taxonomic purposes.

**Heterochrony**

As outlined above, various heterochronic processes (sensu McNamara, 1986) affect the postcranial skeletons of temnospondyls. Paedomorphosis is the heterochronic process of greatest importance to phylogenetic analysis, because it results in the absence of derived characteristics. Paedomorphosis of the postcranial skeleton may affect several related species, and consequently be the predominant heterochronic effect on the postcranial skeleton within a clade.

**Phylogenetic significance of heterochrony**

Many taxa within the temnospondyl clades Dvinosauria and Stereospondyli have paedomorphic postcranial skeletons, in contrast to the many well-ossified taxa within the Euskelia. This uneven distribution of the overall degree of ossification of the postcranial skeleton within the Temnospondyli may give the initial impression that characteristics of the degree of ossification of the postcranial skeleton are of phylogenetic significance. As discussed previously, it is often difficult to distinguish between truly paedomorphic taxa and those that are merely immature. Heterochronic effects are therefore not useful for taxonomic purposes, because they are too difficult to quantify objectively.

**Heterochrony and phylogenetic analysis**

When paedomorphosis affects the postcranial skeleton of clades such as the Dvinosauria, the morphology of the postcranial skeleton within the clade may be consistent enough that morphogenetic variation is easily confused with phylogenetic variation.

**Interpretation of unpreserved parts of the vertebral centrum**

Many of the figures of rhachitomous vertebrae apparently have the components of the vertebral column artificially ‘pushed together’ so that there is little space between them.
This may be due to the preservation of the specimen, or because workers are unfamiliar with the large amount of apparent ‘space’ in the rhachitomous vertebral column. Evidence for the ‘pushing together’ of vertebral elements is difficult to find, but observation of the rare temnospondyl vertebral columns that are preserved relatively undisturbed (e.g. AMNH 4280 Eryops megacephalus) indicates that the bases of the neural arch, and the pleurocentra and intercentra are consistently spaced quite some distance apart in the specimens, which in this in this case is as described by Moulton (1974).

Schoch (1999a) described in Mastodonsaurus giganteus a dorsal perforation of the intercentra as the ‘chorda incisure’ or notochordal perforation (Figure 36.3), possibly following the interpretation of Panchen (1967). As the thinnest part of these centra is located in the centre, it seems more plausible that the ‘chorda incisure’ is in fact a remnant of the closure of the two sides of the intercentrum dorsal to the notochord.

**Implications of reinterpreting morphogenesis of the vertebral centrum**

**Evolution of centrum types within the Temnospondyli**

The fossil evidence, consisting of the occurrence of the variety of centrum types (embolomerous, gastrocentrous, and stereospondylous) (Figure 36) within the Temnospondyli supports the hypothesis that the cartilaginous parts of the rhachitomous centra formed amphicoelous pleurocentral and intercentral discs around the notochord, as proposed by Romer (1947), Moustafa (1955a), and Bolt (1979). Embolomerous, gastrocentrous, and stereospondylous centra are easily derivable from rhachitomous centra, simply by an increased degree of ossification (Figure 43). Simple variation, both morphogenetically and phylogenetically, in the degree of ossification from the antimeres, and in the cranio-caudal depth of the cartilaginous pleurocentral and intercentral rings would explain much of the extent of morphological variation of the pleurocentra and intercentra observed in temnospondyls. The rhachitomous type of centrum represents a lower degree of ossification of the pleurocentral and intercentral rings, with ossification proceeding from the pleurocentral and intercentral antimeres, thus the rhachitomous type is a poorly ossified diplospondylous centrum. In embolomerous centra, which are also clearly diplospondylous, both cartilaginous discs become well ossified (Figure 43.5). In gastrocentrous (Figure 36.1, Figure 36.2) and stereospondylous (Figure 43.4) centra only one ring becomes well ossified, a low degree of ossification is retained in the other, so that one centrum is much larger than the other and the vertebral centrum as a whole approaches a monospondylous condition. No major change in morphogenetic development is necessary to derive monospondylous centra from diplospondylous centra (Wake, 1970), merely changes in the proportions of the vertebral components. This evidence suggests that the evolution of centrum types within the Temnospondyli mostly results from changes in the morphogenetic processes involved in centrum formation, but that these changes to morphogenetic processes also have some phylogenetic basis.

**Articulation of centrum components**

Traditional biomechanical interpretations of rhachitomous type centra reconstruct the cartilaginous parts as simple wedges of cartilage covering the cancellous surfaces of the intercentra and pleurocentra (Olson, 1936b; Rockwell et al., 1938; Moulton, 1974; Holmes, 1989b), on an unconstricted notochord. All have assumed that the cartilaginous parts of the centrum form a simple layer over the cancellous internal surface of the
intercentra and pleurocentra. The evidence presented here would suggest that this is not the case for vertebral centra, or for any other endochondral postcranial element. Biomechanically, a simple wedge shaped cartilaginous reconstruction that does not extend around the notochord is inherently unstable, because flexure of the vertebral column would detach the centra away from the notochord (Rockwell et al., 1938). Most importantly, none of the previous hypotheses of reconstruction of the soft tissue components of vertebrae in temnospondyls has compared the soft tissue reconstructions or the method of vertebral articulation in temnospondyls with evidence from extant taxa.

Extant phylogenetic bracketing (phylogenetic inference), infers attributes in fossil taxa based on transferral of known attributes in other taxa, based on an explicit statement of phylogenetic relationships (Bryant and Russell, 1992; Witmer, 1995). In this case, all phylogenetic relationships of early tetrapods to date that have included temnospondyls (most recently reviewed by Ruta et al., 2003) place fish as an outgroup and salamanders and/or lizards as derived taxa. Using extant phylogenetic bracketing, developmental processes and soft tissue components are predictable for temnospondyls and other early tetrapod taxa with rhachitomous vertebrae. Most developmental processes and soft tissue components of the vertebrae are ubiquitous to lower vertebrates, and are thus likely to have been present in temnospondyls.

In extant lower vertebrates, such as most fish, lissamphibians, and primitive reptiles, the centra are typically amphicoelous with biconcave anterior and posterior surfaces. This evidence is consistent with that of the fossil record (above). During development, the medial growth of the centra constricts the notochord, so that it forms biconvex expansions between the centra. The concave internal surfaces of the centra articulate on the intervertebral expansions of the notochord. The centra surround the notochord, preventing lateral and dorsoventral displacement, whereas the biconvex expansion of the notochord between the centra prevents anteroposterior dislocation. Medial growth of the centra may proceed to the point where it completely obliterates the notochordal canal. The notochord then forms biconvex intervertebral discs, held between the centra by the intervertebral fibres connecting adjacent centra (e.g. Werner, 1971; Symmons, 1979). The centra are linked to each other by an external ring of strong intervertebral fibres, connecting the external edges of the centra, and preventing dislocation of the vertebrae (e.g. Williams, 1959; Hoffstetter and Gasc, 1969; Wake, 1970; Laerm, 1976; Symmons, 1979).

Reconstruction of a similar method of articulation is plausible for rhachitomous, embolomerous, gastrocentrous, and stereospondylous centra, which implies that the vertebral columns of taxa possessing this centrum type may have had similar biomechanical properties (in the general sense) to those of extant lower vertebrates. Reconstructing the soft parts of rhachitomous centra as wedges of cartilage that do not extend around the notochord implies that a completely different, unknown method of articulation and prevention of dislocation of centrum elements. This method of articulation is therefore much less likely to have been present than one which is consistent with that of extant taxa. The fossil evidence, consisting of the sporadic phylogenetic development of amphicoelous rhachitomous, embolomerous, gastrocentrous, and stereospondylous centra within the Temnospondyli (Chapter 5), which are likely to have a method of centrum attachment and articulation typical of extant lower vertebrates, provides evidence that a completely different method of centrum attachment and articulation for the rhachitomous type centra is phylogenetically unlikely. The most parsimonious solution to these issues, both phylogenetically and biomechanically, is that the cartilaginous parts of the rhachitomous centra in temnospondyls formed sub equal
amphicoelous pleurocentral and intercentral rings, as proposed by Romer (1947), similar to those of extant lower vertebrates.

ACKNOWLEDGEMENTS

This manuscript forms part of the PhD dissertation of Kat Pawley, who sincerely thanks her supervisor, Dr Anne Warren, for her support and encouragement. An American Museum of Natural History collections visitation grant and an Australian Postgraduate Award provided funding. For hospitality, facilitating visits to, and loans from collections I would like to thank: Prof Bruce Rubidge and Dr Mike Raath of the Bernard Price Institute for Palaeontological Research, Johannesburg, Dr Heidi Fourie of the Transvaal Museum, Pretoria; and Dr Johann Welman and Elize Potgieter of the National Museum in Bloemfontein, Dr G. Gaffney of the American Museum of Natural History, New York, and C. Schaff of the Museum of Comparative Zoology, Harvard University. For assistance with the loan of specimens I would like to thank Lyndon K. Murray and Dr Tim Rowe of the Texas Memorial Museum, Austin, Texas, Dr Pat Holroyd of the Museum of Paleontology, University of California, Los Angeles, California, and Dr Greg Gunnell of the University of Michigan Museum of Paleontology, Ann Arbor, Michigan. I am also grateful to Dr Ernst L. Lundelius Jnr for valuable tips on morphogenetic series of non-temnospondyl taxa.