

TERMINAL FUSIONS OF SKELETAL ELEMENTS AS INDICATORS OF MATURITY IN SQUAMATES

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ABSTRACT—Terminal fusions—fusions of skeletal elements thought to mark the cessation of significant growth—can be used to estimate the relative maturity of fossilized individuals. Little is known of how the absolute timing of terminal fusions relates to sexual and skeletal maturity in squamates. Examination of postnatal ontogenetic series of extant representatives of 14 crown squamate clades reveals that no terminal fusion universally coincides with the achievement of either sexually or skeletally mature size; however, certain fusions may serve as benchmarks of maturity within particular crown clades. Complete fusion of the braincase is a reliable benchmark for skeletal maturity in scleroglossans, but not iguanians. Complete fusion of long bone epiphyses will indicate that a squamate individual is within roughly 20% of maximum size, whereas complete fusion of the scapula and coracoid, the pelvis, and the astragalus and calcaneum can be taken as evidence only that an individual has achieved at least half of the maximum size of its species.

INTRODUCTION

In studies of fossil vertebrates, the ability to estimate the relative maturity of individual specimens is critical for determining whether those specimens represent different stages of a single ontogenetic trajectory, or represent different species (e.g., Colbert, 1990; McIntosh, 1990; Brochu, 1996). The ability to distinguish between ontogenetic and interspecific variation is, in turn, critical for the accurate assessment of a variety of paleobiological parameters, such as species-level diversity through time (e.g., Archibald, 1992, 1993). Although body size can provide a first indication of the maturity of a specimen, evaluating maturity based on size is potentially problematic. For example, the adults of dwarf taxa could be mistaken for juveniles of larger taxa that are closely related (Brochu, 1996). Furthermore, in many reptilian taxa, individuals may begin to breed at only half of their eventual size (Bellairs, 1970). Thus, sexual maturity (the attainment of a species' reproductive size) and skeletal maturity (the attainment of a species' maximum size) are not generally coincident.

As an alternative to estimating specimen maturity based on body size, a number of size-independent maturity criteria have been delineated for a diverse range of taxa including basal synspsids (Brinkman, 1988), crocodylians (Brochu, 1995, 1996), ichthyosaurs (Johnson, 1977), pterosaurs (Bennett, 1993), dinosaurs (Galton, 1982; Callison and Quimby, 1984), and squamates (Estes et al., 1988; Gauthier et al., 1988). These criteria include terminal fusions between skeletal elements. Terminal fusions (for example, between the scapula and coracoid, and between the epiphyses and diaphyses of the long bones) are thought to mark the cessation of significant growth (e.g., Haines, 1969; Andrews, 1982). However, how these fusions relate to sexual maturity and skeletal maturity is poorly understood, particularly in squamates. The few long-term field studies of extant squamate species indicate that there is a considerable intraspecific range of individual maximum sizes (e.g., Fitch, 1954; Davis, 1967; Stamps, 1977); however, the magnitude of this range is unknown for the majority of squamate species. Furthermore, how size-independent criteria for evaluating maturity (like terminal fusions) vary phylogenetically within this clade is largely unexplored.

The detailed study of postnatal skeletal development in a variety of squamate crown clades (Maisano, 2000) provides the opportunity to critically examine the relationship between terminal fusions and sexual and skeletal maturity. The purpose of this investigation is to determine: 1) whether any terminal fusions consistently coincide with sexual maturity across all included species; and 2) the range of sizes over which terminal fusions are complete within and across species, or, just how "terminal" terminal fusions are. Such indicative terminal fusions then could serve as benchmarks for interpreting the ontogenetic status of fossil squamates.

MATERIALS AND METHODS

Species were selected for study based on several criteria. The main objective was to sample as many crown squamate clades as possible. The 21 species examined represent 14 crown clades (Fig. 1). Within each clade, an attempt was made to select species that are generally considered basal, in order to shorten branch lengths and thereby closely bracket ancestral nodes. Another criterion was the availability of life history data in the literature for each species, to enable analysis of the relationship of terminal fusions to sexual maturity and maximum size. The fourth and most compulsory criterion was the relative abundance of each species in major American herpetological collections, from which specimens were borrowed for clearing and staining. Specimens were cleared and double-stained following a modified version of the protocol of Pothoff (1984).

Densely-sampled growth series of each species were constructed based on the snout-vent length (SVL) of individuals, and all references to size herein refer to SVL. The series (see Maisano, 2000:appendix 1) consist of individuals of both sexes and from diverse localities. Because of this, potential effects of gender and population variation on the following observations cannot be isolated. Thus, the following discussion generalizes, across genders (which cannot generally be determined in fossil squamates) and populations, for species.

Table 1 shows the published average size at sexual maturity (MAT SVL, averaged for both sexes unless otherwise noted) and maximum size (MAX SVL, averaged for both sexes unless otherwise noted) for each species, as well as the largest specimen examined (EXAM SVL, gender indicated if known). Size at sexual maturity is unknown for *Agama a. lionotus*, *Acanthodactylus boskianus*, *Chalcides ocellatus*, *Lepidophyma gaigeae*,

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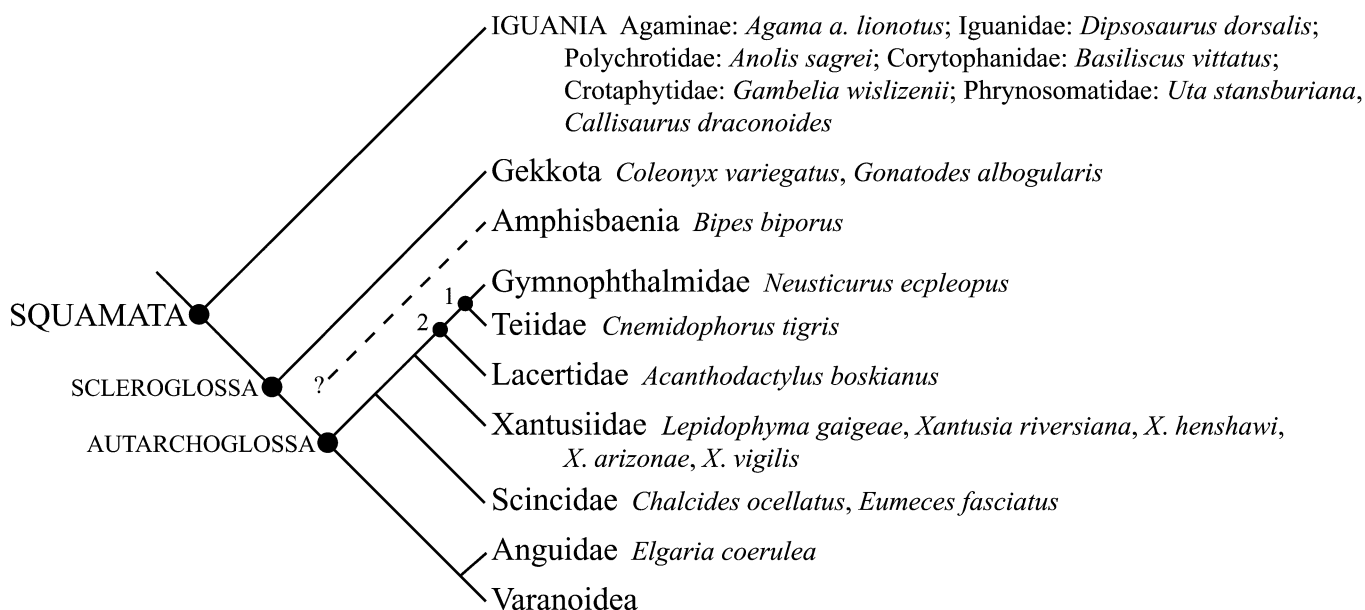


FIGURE 1. Simplified hypothesis of squamate relationships showing species investigated. Node 1, Teiioidea; node 2, Lacertiformes. After Estes et al. (1988), with iguanian nomenclature of Frost and Etheridge (1989).

and *Xantusia arizonae*. However, this size can be estimated because size at sexual maturity, mean adult size, and maximum size are strongly correlated in squamates (Andrews, 1982). Using regression equations (Andrews, 1982:fig. 3) and the largest specimen of each series as a proxy for that species' maximum size (or, in the case of *L. gageae*, the maximum size reported in the literature, which is slightly larger), the mean size of each species can be estimated, then used to estimate size (averaged for both sexes) at sexual maturity.

The timing of onset and completion of fusions was determined visually rather than histologically. Fusions are termed "complete" when sutures are no longer discernible. Fusions are described as correlating with sexual maturity if their onset/completion falls within 10% of the average size at sexual maturity

(from Table 1); fusions falling outside of this range are described as occurring before or after sexual maturity. The relationship of terminal fusions to skeletal maturity is discussed in terms of the percentage of maximum size (from Table 1) at which they occur. The caudal vertebrae are not included in this discussion because many specimens lack tails.

Institutional Abbreviation—CJB, personal collection, Christopher J. Bell, The University of Texas, Austin.

RESULTS

Figure 2 and Table 2 summarize the ontogeny of skeletal fusions in each growth series as they relate to sexual and skeletal maturity, respectively.

TABLE 1. Published size at sexual maturity (MAT SVL), published maximum size (MAX SVL), and largest specimen examined (EXAM SVL), for species in this study (in mm). Unless gender is indicated, MAT SVL and MAX SVL are averaged for both. ** denotes sizes derived using the regression equations of Andrews (1982).

Species	MAT SVL	MAX SVL	EXAM SVL	Source(s)
<i>Agama a. lionotus</i>	72.1**		106.2 (♂)	this study
<i>Uta stansburiana</i>	45	57 (♂)	54.5 (♂)	Tinkle, 1967
<i>Callisaurus draconoides</i>	69	93	80.5 (♂)	Pianka and Parker, 1972; Tanner and Krogh, 1975
<i>Anolis sagrei</i>	34.5	52	63.9 (♂)	Duellman and Schwartz, 1958; Schoener and Schoener, 1978
<i>Basiliscus vittatus</i>	82	137.5 (?)	110.7 (♀)	Hirth, 1963; Fitch, 1973
<i>Gambelia wislizenii</i>	100	131.5	110.9 (♀)	Parker and Pianka, 1976; McGuire, 1996
<i>Dipsosaurus dorsalis</i>	112	143.5	122.7 (♂)	Mayhew, 1965, 1971
<i>Coleonyx variegatus</i>	54	68	72.8 (♀)	Parker, 1972a
<i>Gonatodes albogularis</i>	36	48	43.8 (♂)	Fitch, 1973
<i>Bipes biporus</i>	185 (♀)	240	231.0 (♂)	Papenfuss, 1982
<i>Acanthodactylus boskianus</i>	55.5**		79.5 (♂)	this study
<i>Cnemidophorus tigris</i>	68.5	99.2	105.3 (♂)	Parker, 1972b; this study
<i>Neusticurus ecleopus</i>	52.5	67	63.2 (♂)	Sherbrooke, 1975
<i>Elgaria coerulea</i>	76		110.7 (♀)	Fitch, 1935; Stewart, 1985; Vitt, 1973
<i>Chalcides ocellatus</i>	76.9**		114.0 (♂)	this study
<i>Eumeces fasciatus</i>	52		74.3 (♂)	Vitt and Cooper, 1986
<i>Lepidophyma gageae</i>	44.9**	63 (?)	61.5 (?)	Mosauer, 1936; Gonzalez, 1995
<i>Xantusia riversiana</i>	67.5	105.8	93 (?)	Goldberg and Bezy, 1974; Fellers and Drost, 1991
<i>X. henshawi</i>	53	67.5	62 (?)	Lee, 1975
<i>X. arizonae</i>	40.7**	56.5	56.6 (?)	Bezy, 1967
<i>X. vigilis</i>	37	47.5	50 (?)	Miller, 1951; Zweifel and Lowe, 1966

	<i>Agama</i>	<i>Uta</i>	<i>Callisaurus</i>	<i>Anolis</i>	<i>Basiliscus</i>	<i>Gambelia</i>	<i>Dipsosaurus</i>
	< = >	< = >	< = >	< = >	< = >	< = >	< = >
exoccipital/opisthotic							
otooccipital/basioccipital							
prootic/basisphenoid							
prootic/otooccipital (ventral)							
prootic/otooccipital (dorsal)							
basisphenoid/basioccipital							
supraoccipital/otooccipital							
supraoccipital/prootic							
neurocentral suture							
neural suture							
scapula/coracoid							
ilium/ischium/pubis							
stylo. & zeugo. epiphyses							
auto. epiphyses							
astragalus/calcaneum							
	<i>Coleonyx</i>	<i>Gonatodes</i>	<i>Bipes</i>	<i>Acantho.</i>	<i>Cnemidoph.</i>	<i>Neusticurus</i>	<i>Elgaria</i>
	< = >	< = >	< = >	< = >	< = >	< = >	< = >
exoccipital/opisthotic							
otooccipital/basioccipital							
prootic/basisphenoid							
prootic/otooccipital (ventral)							
prootic/otooccipital (dorsal)						?	
basisphenoid/basioccipital							
supraoccipital/otooccipital						?	
supraoccipital/prootic							
neurocentral suture							
neural suture							
scapula/coracoid							
ilium/ischium/pubis			?				
stylo. & zeugo. epiphyses							
auto. epiphyses							
astragalus/calcaneum			NA				
	<i>Chalcides</i>	<i>Eumeces</i>	<i>Lepidophy.</i>	<i>X. rivers.</i>	<i>X. henshawi</i>	<i>X. arizonae</i>	<i>X. vigilis</i>
	< = >	< = >	< = >	< = >	< = >	< = >	< = >
exoccipital/opisthotic							
otooccipital/basioccipital							
prootic/basisphenoid							
prootic/otooccipital (ventral)							
prootic/otooccipital (dorsal)			?	?	?	?	?
basisphenoid/basioccipital							
supraoccipital/otooccipital							
supraoccipital/prootic			?	?	?	?	?
neurocentral suture							
neural suture							
scapula/coracoid							
ilium/ischium/pubis							
stylo. & zeugo. epiphyses							
auto. epiphyses							
astragalus/calcaneum							

FIGURE 2. Ontogeny of skeletal fusions as they relate to sexual maturity in species examined. A thin line indicates that a fusion is ongoing; a thick line indicates that a fusion is complete. Abbreviations: <, before sexual maturity; =, at sexual maturity; >, after sexual maturity (stages as defined in text); ?, cannot be determined; NA, not applicable.

TABLE 2. Percentage maximum size at earliest completion of fusions in species examined. Percentages based on the larger of published maximum size or largest specimen examined (see Table 1). “>” indicates that sutures are still discernible in the largest specimen examined.

	Braincase	Neurocentral suture	Neural suture	Scapula/coracoid	Ilium/ischium/pubis	Stylo. & zeugo. epiphyses	Auto. epiphyses	Astragalus/calcaneum
<i>Agama</i>	>100	27	39	>100	>100	>100	>100	78
<i>Uta</i>	86	62	70	70	79	>100	86	70
<i>Callisaurus</i>	70	45	48	59	63	63	63	58
<i>Anolis</i>	63	53	54	54	54	>100	100	55
<i>Basiliscus</i>	>80	55	66	>80	>80	>80	80	80
<i>Gambelia</i>	70	50	52	67	67	82	70	67
<i>Dipsosaurus</i>	>81	49	34	70	70	>81	81	81
<i>Coleonyx</i>	>100	65	55	68	72	82	82	72
<i>Gonatodes</i>	>91	66	66	66	66	91	>91	66
<i>Bipes</i>	38	38	38	38	?	76	79	NA
<i>Acanthodactylus</i>	100	70	80	80	80	>100	86	100
<i>Cnemidophorus</i>	100	35	37	87	83	87	87	78
<i>Neusticurus</i>	>94	33	34	83	83	>94	94	83
<i>Elgaria</i>	100	64	64	67	67	67	100	67
<i>Chalcides</i>	100	63	52	93	78	>100	86	86
<i>Eumeces</i>	100	73	73	77	77	100	100	73
<i>Lepidophyma</i>	>98	77	77	77	77	94	94	78
<i>X. riversiana</i>	>88	80	66	66	80	>88	>88	80
<i>X. henshawi</i>	>92	61	60	61	73	92	92	73
<i>X. arizonae</i>	>100	82	77	79	82	98	>100	88
<i>X. vigilis</i>	100	64	58	62	64	90	90	64

Braincase

The squamate braincase (Fig. 3) consists of nine bones: the unpaired supraoccipital, basisphenoid, and basioccipital; and the laterally paired exoccipitals, opisthotics, and prootics. Fusion of the exoccipital and opisthotic into a compound bone, referred to here as the otooccipital, is a prenatal or early postnatal event in squamates (Estes et al., 1988; Gauthier et al., 1988; Maisano, 2000, 2001).

The braincase is already completely fused in neonatal *Bipes*. The otooccipital and basioccipital, the prootic and basisphenoid, and the supraoccipital and prootic begin to fuse before sexual maturity in all species examined. All braincase fusions begin before sexual maturity in phrynosomatids, *Gambelia*, *Dipsosaurus*, *Chalcides*, and *Xantusia henshawi*. All braincase fusions except that of the prootic and otooccipital ventrally begin before sexual maturity in the remaining iguanians and in lacertiforms and *X. riversiana*. The onset of fusion of the prootic

and otooccipital ventrally correlates with sexual maturity in *Agama*, *Anolis*, *Basiliscus*, gekkotans, teioids, *Elgaria*, *Eumeces*, and xantusiids except *X. henshawi*. The onset of fusion of the prootic and otooccipital dorsally correlates with sexual maturity in gekkotans and *Eumeces*. The onset of fusion of the basisphenoid and basioccipital correlates with sexual maturity in *Coleonyx*, *Elgaria*, *Eumeces*, *Lepidophyma*, and *X. arizonae*. The onset of fusion of the supraoccipital and otooccipital correlates with sexual maturity only in *X. vigilis* and *X. arizonae*.

Complete fusion of the braincase correlates with sexual maturity in phrynosomatids, *Gambelia*, and *Dipsosaurus*. Complete fusion of the prootic and basisphenoid correlates with sexual maturity in gekkotans, *Lepidophyma*, and *Xantusia vigilis*. Complete fusion of the prootic and otooccipital dorsally and of the supraoccipital and prootic correlates with sexual maturity only in *Gonatodes*. Complete fusion of the supraoccipital and otooccipital correlates with sexual maturity in *Gonatodes*, *Lep-*

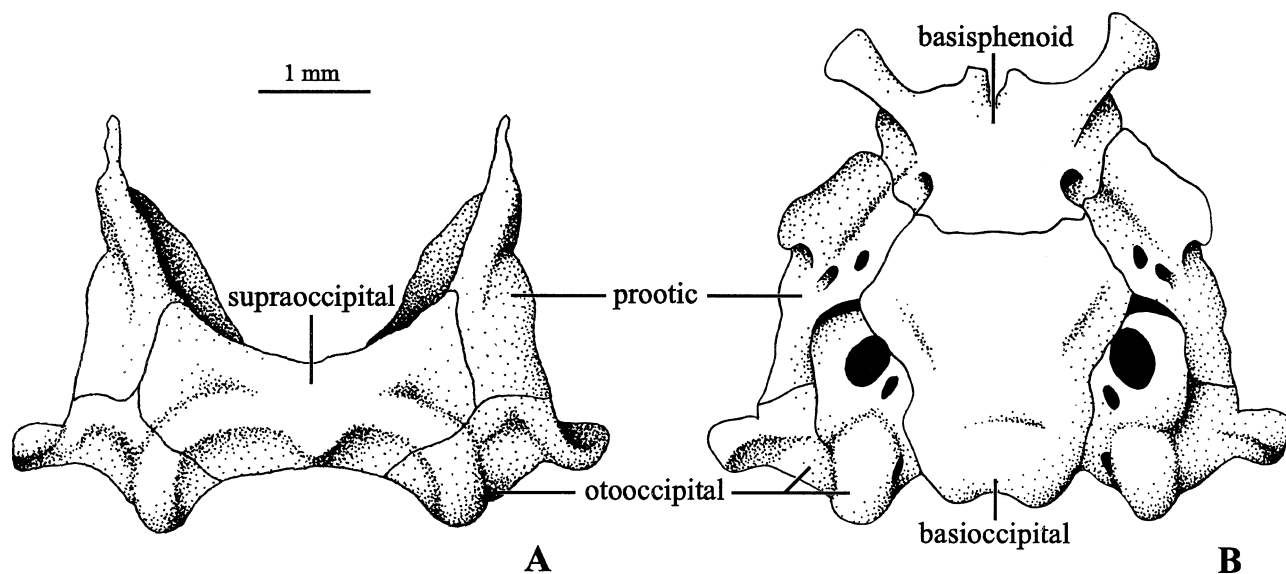


FIGURE 3. Dorsal (A) and ventral (B) views of the braincase of a sexually immature *Coleonyx variegatus* (CJB 52, 69% MAX SVL).

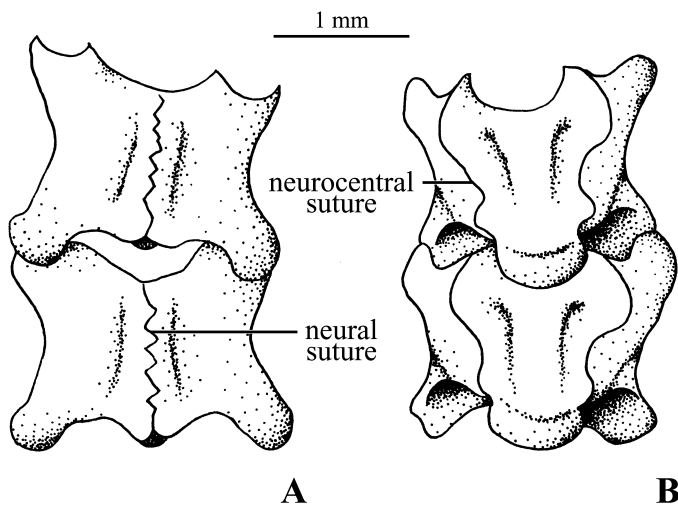


FIGURE 4. Dorsal (A) and ventral (B) views of two trunk vertebrae of a sexually immature *Callisaurus draconoides* (CJB 103, 49% MAX SVL).

idophyma, and *X. vigilis*. In all other cases, braincase fusions are not complete until after sexual maturity, if at all. Thus, if all braincase fusions in an individual are complete, such that the sutures are no longer discernible, it is almost certainly sexually mature. However, the absence of such fusion is not evidence that an individual is sexually immature, except in some iguanians.

The only instances in which complete fusion of the braincase might not indicate skeletal maturity—that an individual has achieved its species' maximum size—are restricted to iguanians and amphisbaenians. Such fusion is already complete in neonatal *Bipes*, and may occur at as early as 63% of maximum size in *Anolis*, and 70% of maximum size in *Callisaurus* and *Gambelia*. In all scleroglossans examined other than *Bipes*, complete fusion of the braincase is not achieved until the largest specimen examined, if at all. Thus, if all braincase fusions in a scleroglossan individual are complete, it is certainly skeletally mature. However, the absence of such fusion is not evidence that it is skeletally immature.

Vertebrae

Each vertebra initially consists of three elements (Fig. 4): the centrum, and bilateral neural arch halves lateral to it that extend dorsally. The centrum is separated laterally from the neural arch halves by the neurocentral suture, and the neural arch halves are separated from each other dorsally by the neural suture.

Closure of the neurocentral suture is already complete in neonatal *Agama*, *Bipes*, and teioids, and begins before sexual maturity in all other species examined. Its closure is complete before sexual maturity in most iguanians, *Coleonyx*, and teioids. Complete closure of the neurocentral suture correlates with sexual maturity in *Anolis*, *Basiliscus*, *Gonatodes*, *Acanthodactylus*, *Elgaria*, skinks, and most xantusiids. Complete closure of the neurocentral suture occurs in specimens that range from as little as 27% to as much as 82% of their species' maximum size. Thus, it can occur too early in ontogeny and over too great a size range to serve as a benchmark for skeletal maturity.

As with the neurocentral suture, closure of the neural suture is already complete in neonatal *Bipes*, and begins before sexual maturity in all other species examined. Its closure is complete before sexual maturity in the same taxa as the neurocentral suture, with the addition of *Xantusia henshawi*. Complete clo-

sure of the neural suture correlates with sexual maturity in the same taxa as the neurocentral suture, with the exception of *Acanthodactylus*, and the addition of *X. riversiana* and *X. arizonae*. Thus, complete closure of the neural suture is a reliable benchmark for sexual maturity in xantusiids. As with the neurocentral suture, complete closure of the neural suture can occur too early and over too great a size range—34%–80% of a species' maximum size—to serve as a benchmark for skeletal maturity in squamates.

Limb Girdles

The scapula and coracoid are completely fused in neonatal *Bipes*. They begin to fuse before sexual maturity in all other species examined except *Agama*, *Basiliscus*, *Cnemidophorus*, *Eumeces*, *Lepidophyma*, and *Xantusia arizonae*; in all of these except *Agama*, the onset of fusion of the scapula and coracoid correlates with sexual maturity. Fusion of the scapula and coracoid is complete before sexual maturity in *Uta*, *Gambelia*, *Gonatodes*, *X. henshawi*, and *X. vigilis*. Their complete fusion correlates with sexual maturity in *Callisaurus*, *Anolis*, *Dipsosaurus*, *Coleonyx*, *Neusticurus*, *Elgaria*, *Eumeces*, *Lepidophyma*, and *X. riversiana*, but it not achieved until after sexual maturity in all other species examined. Thus, if the scapula and coracoid are completely fused in an individual, it is probably sexually mature. However, the absence of such fusion is not evidence that an individual is sexually immature. Complete fusion of the scapula and coracoid occurs in specimens as small as 38% of the maximum size of their species (54% if *Bipes* is excluded), whereas in some series, the suture is still discernible in the largest specimen examined. Thus, such fusion will reliably indicate only that an individual has achieved at least half of its species' maximum size.

The ilium, ischium, and pubis begin to fuse before sexual maturity in most iguanians, *Gonatodes*, lacertiforms, *Elgaria*, *Chalcides*, and *Xantusia vigilis*. The onset of fusion of the pelvic bones correlates with sexual maturity in *Basiliscus*, *Coleonyx*, *Eumeces*, and most xantusiids. Fusion of the pelvic bones is complete before sexual maturity only in *Gambelia* and *X. vigilis*. Their complete fusion correlates with sexual maturity in phrynosomatids, *Dipsosaurus*, gekkotans, *Neusticurus*, *Lepidophyma*, and *X. henshawi*, but is not achieved until after sexual maturity in all other species examined. Thus, complete fusion of the ilium, ischium, and pubis in an individual almost certainly indicates that it is sexually mature. However, the absence of such fusion is not evidence that an individual is sexually immature.

Complete fusion of the ilium, ischium, and pubis occurs in individuals as small as 54% of the maximum size of their species, and in some series is never achieved. This contradicts Gauthier et al. (1988), who considered complete fusion of these bones to characterize all skeletally mature rhynchocephalians and squamates with unreduced pelvises. The present investigation shows that such fusion will reliably indicate only that an individual has achieved at least half of the maximum size of its species.

Epiphyses

In squamates, the epiphyses ossify from distinct secondary centers of ossification (Dollo, 1884), and this may be true of lepidosaurs in general (Estes et al., 1988). The epiphyses of the stylopodium (humerus/femur) and zeugopodium (ulna and radius/fibula and tibia) begin to fuse before sexual maturity in phrynosomatids, *Gambelia*, *Gonatodes*, *Bipes*, *Neusticurus*, and *Xantusia vigilis*. The onset of their fusion correlates with sexual maturity in all remaining species; thus, it can serve as a benchmark for sexual maturity in most iguanians, most lacertiforms, skinks, and most xantusiids (this was also reported by Lee,

1975, for *X. henshawi*). Complete fusion of the stylopodial and zeugopodial epiphyses correlates with sexual maturity only in *Callisaurus*, *Gambelia*, *Dipsosaurus*, and *Bipes*. In all other species examined, complete fusion is not achieved until after sexual maturity, if at all. Thus, complete fusion of the stylopodial and zeugopodial epiphyses in an individual indicates that it is sexually mature. However, the absence of such fusion is not evidence that an individual is sexually immature.

Complete fusion of the stylopodial and zeugopodial epiphyses is a relatively reliable benchmark for skeletal maturity. In all species examined except *Callisaurus*, *Bipes*, and *Elgaria* (where fusion is complete at as early as 63%, 76%, and 67% of maximum size, respectively), epiphyseal fusion is complete at the earliest at 82% of maximum size. In three series, fusion of stylopodial and zeugopodial epiphyses is not complete until the largest specimen examined, and in nine series, these sutures are still discernible in the largest specimen. Thus, complete fusion of the stylopodial and zeugopodial epiphyses in an individual will, with rare exceptions, indicate that it is within 20% of the maximum size of its species.

The epiphyses of the autopodium (manus/pes) are already fusing in neonatal *Bipes*, and begin to fuse before sexual maturity in most iguanians, lacertiforms, and *Chalcides*. The onset of autopodial epiphyseal fusion correlates with sexual maturity in *Anolis*, *Basiliscus*, gekkotans, *Elgaria*, *Eumeces*, and xantusiids except *Xantusia arizonae*. The completion of autopodial epiphyseal fusion correlates with sexual maturity in phrynosomatids, *Gambelia*, *Dipsosaurus*, and *Bipes*. In all other species examined, complete fusion is not achieved until after sexual maturity, if at all. Thus, complete fusion of the autopodial epiphyses in an individual indicates that it is sexually mature. However, the absence of such fusion is not evidence that an individual is sexually immature.

In all species examined except *Callisaurus*, *Gambelia*, and *Bipes* (where fusion is complete at as early as 63%, 70%, and 79% of maximum size, respectively), complete fusion of the autopodial epiphyses occurs within 20% of maximum size. In four series, fusion is complete only in the largest specimen examined, and in another four series, it is never complete. Thus, as with the stylopodial and zeugopodial epiphyses, complete fusion of the autopodial epiphyses is a relatively good benchmark for skeletal maturity in squamates.

Astragalus and Calcaneum

In squamates, the astragalus and calcaneum both ossify within a single proximal tarsal cartilage (Sewertzoff, 1908). They begin to fuse before sexual maturity in all species examined except *Lepidophyma*, *Xantusia arizonae*, and *X. vigilis*, in which the onset of this fusion correlates with sexual maturity. Fusion of the astragalus and calcaneum is complete before sexual maturity in phrynosomatids, *Gambelia*, and *Gonatodes*. Their complete fusion correlates with sexual maturity in *Anolis*, *Dipsosaurus*, *Coleonyx*, *Neusticurus*, and most xantusiids, but is not achieved until after sexual maturity in the remaining species examined. Thus, neither the onset nor the completion of fusion of the astragalus and calcaneum is a reliable benchmark for sexual maturity in squamates, except perhaps xantusiids. However, if the astragalus and calcaneum are completely fused in an individual, it is most likely sexually mature.

Complete fusion of the astragalus and calcaneum prior to skeletal maturity was considered to be a synapomorphy of lepidosaurs by Gauthier et al. (1988). This is supported by the present investigation, although there may be exceptions—in *Basiliscus* and *Acanthodactylus*, this fusion is not complete until the largest specimen examined. Complete fusion of the astragalus and calcaneum occurs in individuals as small as 55% of maximum size; thus, such fusion will reliably indicate only

that an individual has achieved at least half of the maximum size of its species. Gauthier et al. (1988) also stated that fusion of the astragalus and calcaneum precedes fusion of the scapula and coracoid in lepidosaurs. This observation is mostly corroborated by the present investigation, except in gekkotans, xantusiids, and *Elgaria*. In these taxa, the onset of these two fusions is either coincident (*Coleonyx* and *Xantusia vigilis*), or that of the scapula and coracoid slightly precedes that of the astragalus and calcaneum (rest of taxa).

CONCLUSIONS

No terminal fusion is found to be a reliable benchmark for sexual maturity in all species examined. However, some fusions may serve as benchmarks in particular crown squamate clades. Complete fusion of the braincase, of the pelvic bones, and of the autopodial epiphyses correlates with sexual maturity in phrynosomatids. The onset of fusion of the prootic and otooccipital ventrally and of the autopodial epiphyses, and complete fusion of the otooccipital and basioccipital, of the prootic and basisphenoid, and of the pelvic bones, correlate with sexual maturity in gekkotans. The onset of fusion of the prootic and otooccipital ventrally correlates with sexual maturity in teioids. The onset of fusion of the stylopodial and zeugopodial epiphyses, and complete closure of the neural and neurocentral sutures, correlate with sexual maturity in skinks. The onset of fusion of the limb epiphyses, and complete closure of the neural suture, correlate with sexual maturity in xantusiids. No benchmarks for sexual maturity can be confidently identified for the remaining crown clades, as each is represented here by just one species. However, the following is true for the majority of squamate species investigated: if in an individual the braincase, scapula and coracoid, pelvic bones, limb epiphyses, and/or astragalus and calcaneum are completely fused, the individual is probably sexually mature; if not, the individual is not necessarily sexually immature.

Several terminal fusions—especially closure of the neurocentral and neural sutures—may be nowhere near “terminal” in many of the species examined. Complete fusion of the braincase reliably indicates skeletal maturity in scleroglossans (except *Bipes*), whereas in most iguanians it indicates that an individual is within at least 30% of the maximum size of its species. Complete fusion of the limb epiphyses will generally indicate that a squamate individual is within 20% of the maximum size of its species. Complete fusion of the scapula and coracoid (except in *Bipes*), of the ilium, ischium, and pubis, and of the astragalus and calcaneum, indicate only that a squamate individual has achieved at least half of the maximum size of its species.

In all species examined, fusion of most, if not all, of the braincase elements begins before any epiphyseal fusions. This contrasts with the findings of Estes et al. (1988), who considered epiphyseal fusion prior to braincase fusion to be a synapomorphy of scleroglossans. Strict comparison of the present observations with those of Estes and colleagues is not possible because in the present study, the timing of fusions was determined visually, whereas in their study, this timing was determined by whether elements remained associated in disarticulated specimens. However, the braincase elements may remain associated in earlier ontogenetic stages in iguanians due to the precocious onset of fusion of the basisphenoid and basioccipital relative to that in scleroglossans (Maisano, 2000).

Because terminal fusions are thought to mark the cessation of significant growth, it is difficult to understand how individuals could continue to grow after such fusions are complete. This is especially true of the fusion of the long bone epiphyses, which may reach completion in individuals that are only 63% of the maximum reported size for their species (*Callisaurus*).

It may very well be that these individuals have achieved their personal maximum size, and this could be tested via longitudinal allometric studies employing X-radiography. However, even a considerable range in individual maximum size cannot account for the extreme case presented by *Bipes*. In neonates of this fossorial species, the braincase, scapulocoracoid, and vertebral elements are already fused, yet *Bipes* almost triples in length—from 90 to 240 mm SVL—during postnatal ontogeny. How *Bipes* accomplishes this is unknown, but clearly, “terminal” fusions cannot be taken as *de facto* evidence that an individual squamate has stopped growing. Only by continuing to examine the timing of terminal fusions in extant taxa—especially via more longitudinal studies of individual ontogenies—will we gain a better understanding of their relationship to growth, and thus be able to more rigorously utilize them in the interpretation of fossil individuals.

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