

Vertebral Development of Modern Salamanders Provides Insights Into a Unique Event of Their Evolutionary History

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ABSTRACT The origin of salamanders and their interrelationships to the two other modern amphibian orders (frogs and caecilians) are problematic owing to an 80–100 million year gap in the fossil record between the Carboniferous to the Lower Jurassic. This is compounded by a scarcity of adult skeletal characters linking the early representatives of the modern orders to their stem-group in the Paleozoic. The use of ontogenetic characters can be of great use in the resolution of these questions. Growth series of all ten modern salamander families (a 120 cleared and stained larvae) were examined for pattern and timing of vertebral elements chondrification and ossification. The primitive pattern is that of the neural arches developing before the centra, while the reverse represents the derived condition. Both the primitive and derived conditions are observed within the family Hynobiidae, whereas only the derived condition is observed in all other salamanders. This provides support to the claims that Hynobiidae is both the most basal of modern families and potentially polyphyletic (with *Ranodon* and *Hybobius* forming the most basal clade and *Salamandrella* being a part of the most derived clade). This provides insight into a unique event in salamander evolutionary history and suggests that the developmental pattern switch occurred between the Triassic and the mid-Jurassic before the last major radiation. *J. Exp. Zool. (Mol. Dev. Evol.)* 312B:1–29, 2009. © 2008 Wiley-Liss, Inc.

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Salamanders are common model-organisms for fields ranging from developmental genetics (Torok et al., '98) to ecology and toxicology (Welsh and Droege, 2001). Despite modern families being well studied and understood (Petranka, '98), their origins and relationships to the two other living groups of amphibians, frogs (Anura) and caecilians (Gymnophiona), remain controversial (Carroll et al., '99; Schoch and Carroll, 2003). The problem stems from the complete absence of fossils attributable to the modern orders in the late Permian, the time period when they are most likely to have differentiated (Milner, '93; Carroll, 2001). This, combined with the fact that representatives of the modern orders look essentially modern when they appear in the Early and Middle

Jurassic (Ivachnenko, '78; Rocek, 2000), leads one to search for other alternatives than adult characters for the resolution of lissamphibian relationships.

Ontogenetic characters and transformation series are increasingly used in phylogenetic

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reconstructions and have been proved not only to add a new source of information but also to uncover sequence heterochronies (Steyer, 2000). As a part of a larger project to describe ontogenetic characters to be used in the reconstruction of a “total evidence” tree for the resolution of lissamphibian interrelationships, vertebral development in modern and Paleozoic amphibians was studied by Carroll et al. ('99). Preliminary studies of cleared and stained material of the hynobiid salamander *Ranodon tsinpaensis* contradicted Carroll et al.'s claim that all salamanders developed their vertebral centra first and their neural arches later. To understand if this otherwise very conserved character (Carroll et al., '99) was consistent within Urodela and if vertebral development pattern is, indeed, a phylo-

genetically significant character, 29 growth series or isolated individuals from all ten living families were cleared, stained and described. The two resulting patterns of vertebral development were mapped on two recent phylogenies to understand their distributions and suggest which pattern is most likely to be primitive for salamanders. This research shows that a character change from neural arches developing before centra to centra developing before arches occurred early in the diversification of salamanders. It gives insight into a unique event that most likely occurred between the Triassic and the mid-Jurassic (Milner, '83; Gao and Shubin, 2003) and it gives insight into the dispersal patterns of stem-urodeles before their last diversification event.

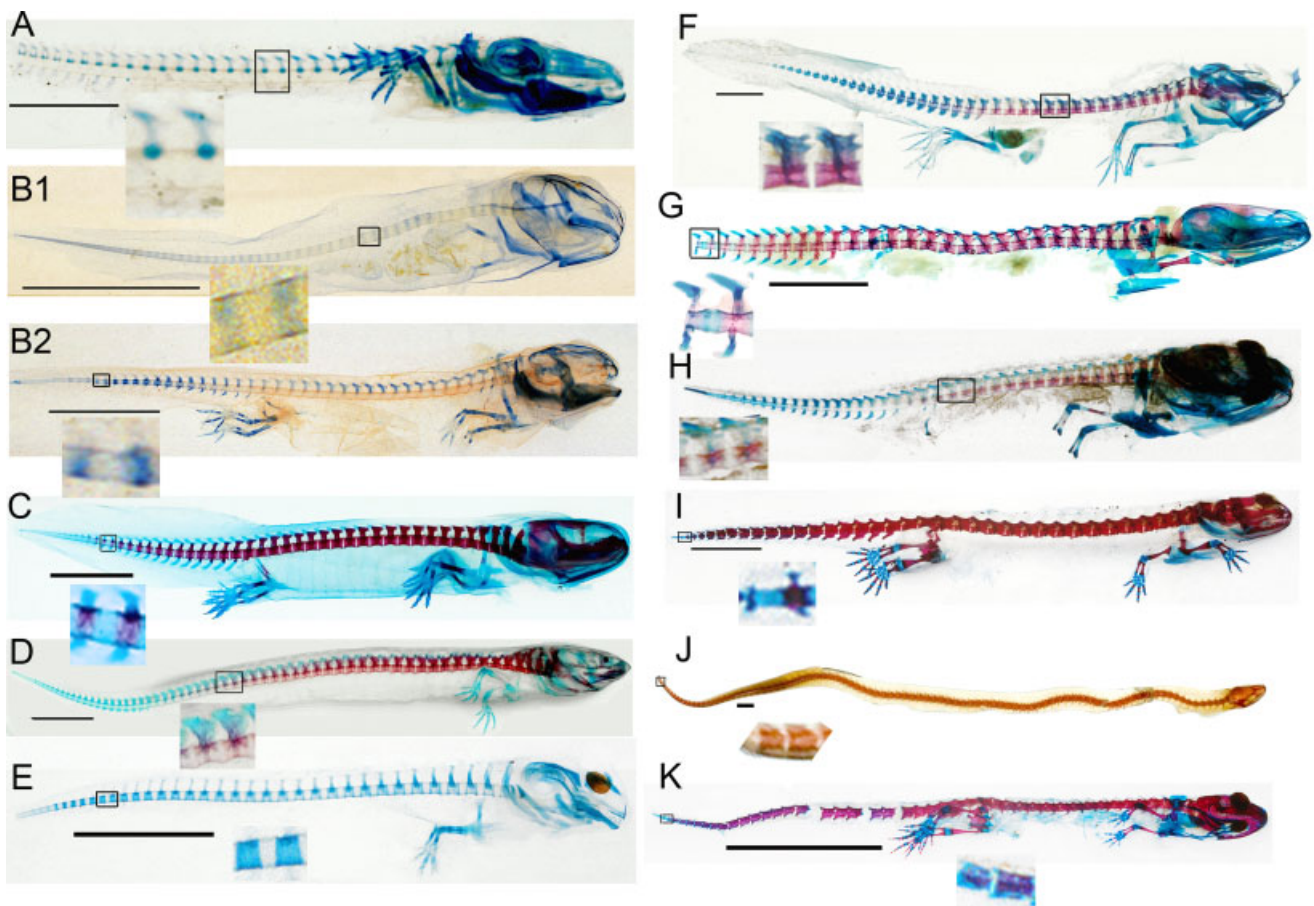


Fig. 1. The primitive pattern of vertebral development is shown by (A) the hynobiid *Ranodon tsinpaensis*. The derived developmental pattern of centra developing before arches is shown by all other salamanders: (B) the hynobiid *Salamandrella keyserlingii*; (C) the cryptobranchid *Cryptobranchus alleganiensis alleganiensis*; (D) the sirenid *Siren intermedia nettingi*; (E) the proteid *Necturus maculosus*; (F) the salamandrid *Notophtalmus viridescens*; (G) the dicamptodontid *Dicamptodon tenebrosus*; (H) the ambystomatid *Ambystoma*; (I) the ryacotritonid *Rhyacotriton*; (J) the amphiumid *Amphiura means*; (K) the plethodontid *Desmognathus fuscus fuscus*. Boxed areas are enlarged for each individual. All scale bars = 5 mm.

MATERIALS AND METHODS

A series of *Ambystoma maculatum* (RM # 4524–4544) was obtained from eggs on Mont St-Hilaire, near Montréal (permit issued to Martin Ouellet, number 2001 03 30 111 16 S F) and raised in the lab. The eggs hatched between 30/05/2002 and 12/06/2002 and were then transferred to an aquarium aerated by a water bubbler, at a temperature varying between 20 and 23°C. The larvae were fed live brine shrimps every other day. The larvae were sacrificed between 05/06/2002 and 17/07/2002 by transferring them to a solution of MS222 (Tricaine methane sulfonate, an anaesthetic). Most of the material for this study was provided by the following institutions: California Academy of Sciences, Canadian Museum of Nature, Chicago Natural History Museum, Florida Museum, Field Museum of Natural History, Museum of Comparative Zoology, Redpath Museum, University of Florida, University of Michigan Museum of Zoology. All the larvae were fixed in formaldehyde before clearing and staining according to procedures derived from Dingerkus and Uhler ('77) and Taylor and Van Dyke ('85).

Specimens were examined and described using a Spencer microscope under refracted and direct light. They were then photographed with a Leica R8 camera with a 100 mm macroscopic lens mounted on extension tubes. For the smallest specimens, extra magnification was provided by mounting the camera to a microscope.

Additional data about vertebral development in modern and fossil salamanders were taken from the literature (Fox, '59; Schmalhausen, '68; Vorobyeva and Antipenkova, 2002; Gao and Shubin, 2003), and the developmental patterns were mapped on two recent phylogenies as in Nishikawa (2000). The phylogeny of salamander families of Wiens et al. (2005) (Fig. 2A) was chosen because it combines molecular and morphological characters for members of all ten living families and takes into account the effects of paedomorphism, while being well supported and well resolved. As the goal of this research is to interpret the results within an evolutionary context, the phylogeny of extant and extinct amphibians of Anderson et al. (2008) was chosen to illustrate the breadth of developmental data in the fossil record. This helps put the results into perspective as well as to polarize characters.

RESULTS AND DISCUSSION

Developmental sequence of element formation and patterns

The development of hemal arches, ribs and spinous processes can be generalized for members of all families. Haemal arches follow the development of caudal centra and they start chondrifying when most, if not all caudal centra have chondrified and ossify in a similar manner, forming almost simultaneously to centra as development proceeds posteriorly. Ribs follow the chondrification and ossification of trunk centra and arches,

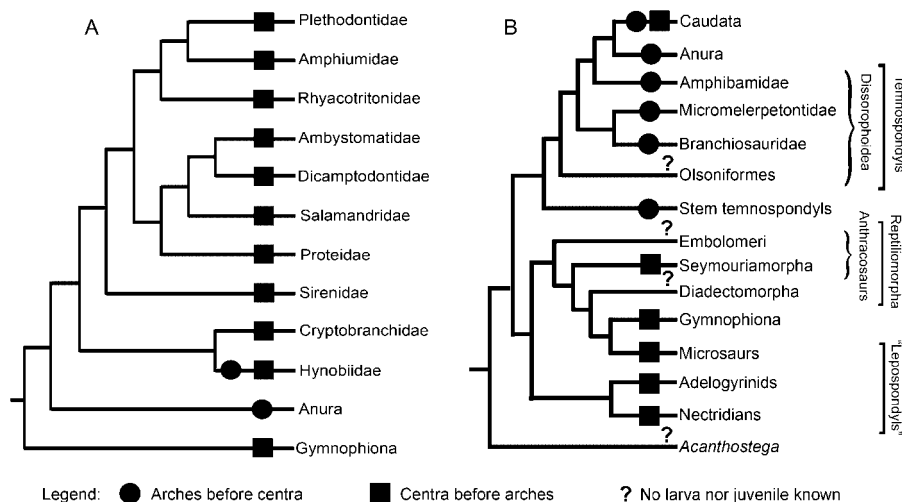


Fig. 2. (A) Vertebral development patterns mapped on Wiens et al. (2005)'s phylogeny of salamander relationships. (B) Vertebral development of extant and extinct amphibians mapped on a phylogeny simplified from Anderson et al. (2008) showing the primitive development pattern for Batrachia and Gymnophiona.

TABLE 1. Vertebral development in ambystomatid salamanders

Arch (Atlas)	Centrum		Arch (Atlas)	Centrum		Arch (Atlas)	Centrum		Arch (Atlas)	Centrum	
	1(Atlas)	2(Trunk)		1(Atlas)	2(Trunk)		1(Atlas)	2(Trunk)		1(Atlas)	2(Trunk)
3	3	3	3	3	3	3	3	3	3	3	3
4	4	4	4	4	4	4	4	4	4	4	4
5	5	5	5	5	5	5	5	5	5	5	5
6	6	6	6	6	6	6	6	6	6	6	6
7	7	7	7	7	7	7	7	7	7	7	7
8	8	8	8	8	8	8	8	8	8	8	8
9	9	9	9	9	9	9	9	9	9	9	9
10	10	10	10	10	10	10	10	10	10	10	10
11	11	11	11	11	11	11	11	11	11	11	11
12	12	12	12	12	12	12	12	12	12	12	12
13	13	13	13	13	13	13	13	13	13	13	13
14	14	14	14	14	14	14	14	14	14	14	14
15	15	15	15	15	15	15	15	15	15	15	15
16	16	16	16	16	16	16	16	16	16	16	16
17	17	17	17	17	17	17	17	17	17	17	17
18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)	18(Sacral)
19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)	19(Caudal)
20	20	20	20	20	20	20	20	20	20	20	20
21	21	21	21	21	21	21	21	21	21	21	21
22	22	22	22	22	22	22	22	22	22	22	22
23	23	23	23	23	23	23	23	23	23	23	23
24	24	24	24	24	24	24	24	24	24	24	24
25	25	25	25	25	25	25	25	25	25	25	25
26	26	26	26	26	26	26	26	26	26	26	26
27	27	27	27	27	27	27	27	27	27	27	27
28	28	28	28	28	28	28	28	28	28	28	28
29	29	29	29	29	29	29	29	29	29	29	29
30	30	30	30	30	30	30	30	30	30	30	30
31	31	31	31	31	31	31	31	31	31	31	31
32	32	32	32	32	32	32	32	32	32	32	32
33	33	33	33	33	33	33	33	33	33	33	33
34	34	34	34	34	34	34	34	34	34	34	34
35	35	35	35	35	35	35	35	35	35	35	35
36	36	36	36	36	36	36	36	36	36	36	36
37	37	37	37	37	37	37	37	37	37	37	37
38	38	38	38	38	38	38	38	38	38	38	38
39	39	39	39	39	39	39	39	39	39	39	39
40	40	40	40	40	40	40	40	40	40	40	40
41	41	41	41	41	41	41	41	41	41	41	41
42	42	42	42	42	42	42	42	42	42	42	42
43	43	43	43	43	43	43	43	43	43	43	43
44	44	44	44	44	44	44	44	44	44	44	44
45	45	45	45	45	45	45	45	45	45	45	45
46	46	46	46	46	46	46	46	46	46	46	46
47	47	47	47	47	47	47	47	47	47	47	47
48	48	48	48	48	48	48	48	48	48	48	48
49	49	49	49	49	49	49	49	49	49	49	49
50	50	50	50	50	50	50	50	50	50	50	50
51	51	51	51	51	51	51	51	51	51	51	51
52	52	52	52	52	52	52	52	52	52	52	52
53	53	53	53	53	53	53	53	53	53	53	53
54	54	54	54	54	54	54	54	54	54	54	54
55	55	55	55	55	55	55	55	55	55	55	55

Arch	Centrum	
	1(Atlas)	2(Trunk)
	1	2
	2	3
	3	4
	4	5
	5	6
	6	7
	7	8
	8	9
	9	10
	10	11
	11	12
	12	13
	13	14
	14	15
	15	16
	16	17
	17	18
	18	19
	19	20
	20	21
	21	22
	22	23
	23	24
	24	25
	25	26
	26	27
	27	28
	28	29
	29	30
	30	31
	31	32
	32	33
	33	34
	34	35
	35	36
	36	37
	37	38
	38	39
	39	40
	40	41
	41	42
	42	43
	43	44
	44	45
	45	46
	46	47
	47	48
	48	49
	49	50
	50	51
	51	52
	52	53
	53	54
	54	55

Ambystoma sp. CMN #23335 (10)

Arch	Centrum	
	1(Atlas)	2(Trunk)
	1	2
	2	3
	3	4
	4	5
	5	6
	6	7
	7	8
	8	9
	9	10
	10	11
	11	12
	12	13
	13	14
	14	15
	15	16
	16	17
	17	18
	18	19
	19	20
	20	21
	21	22
	22	23
	23	24
	24	25
	25	26
	26	27
	27	28
	28	29
	29	30
	30	31
	31	32
	32	33
	33	34
	34	35
	35	36
	36	37
	37	38
	38	39
	39	40
	40	41
	41	42
	42	43
	43	44
	44	45
	45	46
	46	47
	47	48
	48	49
	49	50
	50	51
	51	52
	52	53
	53	54
	54	55

Ambystoma sp. CMN #23335 (9)

Arch	Centrum	
	1(Atlas)	2(Trunk)
	1	2
	2	3
	3	4
	4	5
	5	6
	6	7
	7	8
	8	9
	9	10
	10	11
	11	12
	12	13
	13	14
	14	15
	15	16
	16	17
	17	18
	18	19
	19	20
	20	21
	21	22
	22	23
	23	24
	24	25
	25	26
	26	27
	27	28
	28	29
	29	30
	30	31
	31	32
	32	33
	33	34
	34	35
	35	36
	36	37
	37	38
	38	39
	39	40
	40	41
	41	42
	42	43
	43	44
	44	45
	45	46
	46	47
	47	48
	48	49
	49	50
	50	51
	51	52
	52	53
	53	54
	54	55

Ambystoma sp. CMN #23335 (8)

Arch	Centrum	
	1(Atlas)	2(Trunk)
	1	2
	2	3
	3	4
	4	5
	5	6
	6	7
	7	8
	8	9
	9	10
	10	11
	11	12
	12	13
	13	14
	14	15
	15	16
	16	17
	17	18
	18	19
	19	20
	20	21
	21	22
	22	23
	23	24
	24	25
	25	26
	26	27
	27	28
	28	29
	29	30
	30	31
	31	32
	32	33
	33	34
	34	35
	35	36
	36	37
	37	38
	38	39
	39	40
	40	41
	41	42
	42	43
	43	44
	44	45
	45	46
	46	47
	47	48
	48	49
	49	50
	50	51
	51	52
	52	53
	53	54
	54	55

Ambystoma sp. CMN #23335 (7)

Arch	Centrum	
	1(Atlas)	2(Trunk)
	1	2
	2	3
	3	4
	4	5
	5	6
	6	7
	7	8
	8	9
	9	10
	10	11
	11	12
	12	13
	13	14
	14	15
	15	16
	16	17
	17	18
	18	19
	19	20
	20	21
	21	22
	22	23
	23	24
	24	25
	25	26
	26	27
	27	28
	28	29
	29	30
	30	31
	31	32
	32	33
	33	34
	34	35
	35	36
	36	37
	37	38
	38	39
	39	40
	40	41
	41	42
	42	43
	43	44
	44	45
	45	46
	46	47
	47	48
	48	49
	49	50
	50	51
	51	52
	52	53
	53	54
	54	55

Ambystoma sp. CMN #23335 (6)

Arch	Centrum	
	1(Atlas)	2(Trunk)
	1	2
	2	3
	3	4
	4	5
	5	6
	6	7
	7	8
	8	9
	9	10
	10	11
	11	12
	12	13
	13	14
	14	15
	15	16
	16	17
	17	18
	18	19
	19	20
	20	21
	21	22
	22	23
	23	24
	24	25
	25	26
	26	27
	27	28
	28	29
	29	30
	30	31
	31	32
	32	33
	33	34
	34	35
	35	36
	36	37
	37	38
	38	39
	39	40
	40	41
	41	42
	42	43
	43	44
	44	45
	45	46
	46	47
	47	48
	48	49
	49	50
	50	51
	51	52
	52	53
	53	54
	54	55

TABLE 2. Vertebral development in amphiumid salamanders

Amphiuma meieri FL # 130203	Arch	Centrum
	1 (Atlas)	3 (Atlas)
	2 (Trunk)	2 (Trunk)
	3	3
	4	4
	5	5
	6	6
	7	7
	8	8
	9	9
	10	10
	11	11
	12	12
	13	13
	14	14
	15	15
	16	16
	17	17
	18	18
	19	19
	20	20
	21	21
	22	22
	23	23
	24	24
	25	25
	26	26
	27	27
	28	28
	29	29
	30	30
	31	31
	32	32
	33	33
	34	34
	35	35
	36	36
	37	37
	38	38
	39	39
	40	40
	41	41
	42	42
	43	43
	44	44
	45	45
	46	46
	47	47
	48	48
	49	49
	50	50
	51	51
	52	52
	53	53
	54	54
	55	55
	56	56
	57	57
	58	58
	59	59
	60	60
	61 (Sacral)	61 (Sacral)
	62 (Caudal)	62 (Caudal)
	63	63
	64	64
	65	65
	66	66
	67	67
	68	68
	69	69
	70	70
	71	71
	72	72
	73	73
	74	74
	75	75
	76	76
	77	77
	78	78
	79	79
	80	80
	81	81
	82	82
	83	83
	84	84
	85	85
	86	86
	87	87
	88	88
	89	89
	90	90
	91	91
	92	92
	93	93
	94	94
	95	95

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

beginning to chondrify when all the trunk vertebrae have chondrified and only finishing ossification toward the end of the animal's development. The spinous processes follow the development of the neural arches, only starting to chondrify when all the trunk arches have done so and developing almost simultaneously to the neural arches toward the end of the tail. They start to ossify when all the trunk arches have done so. As the development of those vertebral elements is linked to that of centra or other vertebral elements, they do not provide phylogenetically significant information about sequence heterochronies as the relative timing of centra and arches do, which is why the rest of this article will focus on the latter.

Salamanders, as all other tetrapods (Carroll et al., '99), develop their vertebral column in an anterior to posterior direction. In the specimen of hynobiid salamander *R. tsinpaensis* studied here, all neural arches are chondrified but there is no sign of developed centra (Fig. 1A, detail, Fig. 2 and Table 5b). This suggests that the arches develop first and well in advance of the centra. This assumption is confirmed by the observation of this pattern in the hynobiids *R. sibericus* (Vorobyeva and Antipenkova, 2002), *Hynobius maculosus* (Fox, '59) and in an incompletely ossified fossilized larvae recently discovered in the Middle Jurassic of China (Gao and Shubin, 2003). This "small larval Cryptobranchoid" (superfamily including the Hynobiidae and Cryptobranchidae) has not been identified to the family level, but is most likely to be a basal member of the Hynobiidae on the basis of cranial morphology. In contrast, the centra of the hynobiid *Salamandrella keyserlingii* (Fig. 1B, Fig. 2 and Table 5a) chondrify first and it is only after several centra have chondrified that the arches begin to appear. This lag between the appearance of centra and arches shortens at the end of the tail, allowing the arches to "catch up." The first centra start ossifying when most, if not all, vertebrae have finished chondrifying and the arches start ossifying when at least a few centra are already ossified. The latter is a general rule for the nine other salamander families (Figs. 1C–K, 2, Tables 1–4, 6–10). There is some degree of variation in the timing of centra and arches development across families, ranging from a very long delay between the ossification of arches and centra in Amphiumidae (Figs. 1J, 2 and Table 2) to an almost simultaneous chondrification and ossification of the centra and arches in Plethodontidae (Fig. 1K, 2 and Table 6).

Primitive developmental pattern and lissamphibian relationships

Until very recently, the common consensus on lissamphibians (frogs, salamanders and caecilians) was that they formed a monophyletic group and that they were a sister-group to the Paleozoic amphibian group Temnospondyli (Milner, '93; Ahlberg and Milner, '94; Ruta et al., 2003). However, a recent phylogeny including a transitional stem amphibian shows that salamanders and frogs (Batrachia) are closely related to temnospondyls, whereas caecilians are more closely related to "lepospondyls" and reptiliomorphs,

TABLE 3. Vertebral development in cryptobranchid salamanders

	Arch		Centrum	
	1 (Atlas)	2 (Trunk)	1 (Atlas)	2 (Trunk)
<i>Cryptobranchus alleganiensis</i> FMNH 84162	3	4	3	4
	5	6	5	6
	7	8	7	8
	9	10	9	10
	11	12	11	12
	13	14	13	14
	15	16	15	16
	17	18	17	18
	19	20	19	20
	21	22	21	22
	23	24	23	24
	25	26	25	26
	27	28	27	28
	29	30	29	30
	31	32	31	32
	33	34	33	34
	35	36	35	36
	37	38	37	38
	39	40	39	40
41	42	41	42	
43	44	43	44	
45	45	45	45	
<i>Cryptobranchus alleganiensis</i> FMNH 84153	3	4	3	4
	5	6	5	6
	7	8	7	8
	9	10	9	10
	11	12	11	12
	13	14	13	14
	15	16	15	16
	17	18	17	18
	19	20	19	20
	21	22	21	22
	23	24	23	24
	25	26	25	26
	27	28	27	28
	29	30	29	30
	31	32	31	32
	33	34	33	34
	35	36	35	36
	37	38	37	38
	39	40	39	40
41	42	41	42	
43	44	43	44	
45	45	45	45	
<i>Cryptobranchus alleganiensis</i> CMNH 84154	3	4	3	4
	5	6	5	6
	7	8	7	8
	9	10	9	10
	11	12	11	12
	13	14	13	14
	15	16	15	16
	17	18	17	18
	19	20	19	20
	21	22	21	22
	23	24	23	24
	25	26	25	26
	27	28	27	28
	29	30	29	30
	31	32	31	32
	33	34	33	34
	35	36	35	36
	37	38	37	38
	39	40	39	40
41	42	41	42	
43	44	43	44	
45	45	45	45	
<i>Cryptobranchus alleganiensis</i> CMNH 84154	3	4	3	4
	5	6	5	6
	7	8	7	8
	9	10	9	10
	11	12	11	12
	13	14	13	14
	15	16	15	16
	17	18	17	18
	19	20	19	20
	21	22	21	22
	23	24	23	24
	25	26	25	26
	27	28	27	28
	29	30	29	30
	31	32	31	32
	33	34	33	34
	35	36	35	36
	37	38	37	38
	39	40	39	40
41	42	41	42	
43	44	43	44	
45	45	45	45	
<i>Cryptobranchus alleganiensis</i> CMNH 84154	3	4	3	4
	5	6	5	6
	7	8	7	8
	9	10	9	10
	11	12	11	12
	13	14	13	14
	15	16	15	16
	17	18	17	18
	19	20	19	20
	21	22	21	22
	23	24	23	24
	25	26	25	26
	27	28	27	28
	29	30	29	30
	31	32	31	32
	33	34	33	34
	35	36	35	36
	37	38	37	38
	39	40	39	40
41	42	41	42	
43	44	43	44	
45	45	45	45	
<i>Cryptobranchus alleganiensis</i> CMNH 84154	3	4	3	4
	5	6	5	6
	7	8	7	8
	9	10	9	10
	11	12	11	12
	13	14	13	14
	15	16	15	16
	17	18	17	18
	19	20	19	20
	21	22	21	22
	23	24	23	24
	25	26	25	26
	27	28	27	28
	29	30	29	30
	31	32	31	32
	33	34	33	34
	35	36	35	36
	37	38	37	38
	39	40	39	40
41	42	41	42	
43	44	43	44	
45	45	45	45	

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

TABLE 4. Vertebral development in dicamptodontiid salamanders

	Arch		Centrum	
	1(Atlas) 2(Trunk)	3	1(Atlas) 2(Trunk)	3
<i>Dicamptodon tenebrosus</i> CAS 210348	3	3	3	3
	4	4	4	4
	5	5	5	5
	6	6	6	6
	7	7	7	7
	8	8	8	8
	9	9	9	9
	10	10	10	10
	11	11	11	11
	12	12	12	12
	13	13	13	13
	14	14	14	14
	15	15	15	15
	16(Sacral)	16(Sacral)	16(Sacral)	16(Sacral)
	17(Caudal)	17(Caudal)	17(Caudal)	17(Caudal)
	18	18	18	18
	19	19	19	19
	20	20	20	20
21	21	21	21	
22	22	22	22	
23	23	23	23	
24	24	24	24	
25	25	25	25	
26	26	26	26	
27	27	27	27	
28	28	28	28	
29	29	29	29	
30	30	30	30	
31	31	31	31	
32	32	32	32	
33	33	33	33	
34	34	34	34	
35	35	35	35	
36	36	36	36	
37	37	37	37	
38	38	38	38	
39	39	39	39	
40	40	40	40	
41	41	41	41	
42	42	42	42	
43	43	43	43	
44	44	44	44	
45	45	45	45	
46	46	46	46	
47	47	47	47	
48	48	48	48	
49	49	49	49	
50	50	50	50	
<i>Dicamptodon tenebrosus</i> CAS 210347	3	3	3	3
	4	4	4	4
	5	5	5	5
	6	6	6	6
	7	7	7	7
	8	8	8	8
	9	9	9	9
	10	10	10	10
	11	11	11	11
	12	12	12	12
	13	13	13	13
	14	14	14	14
	15	15	15	15
	16	16	16	16
	17(Sacral)	17(Sacral)	17(Sacral)	17(Sacral)
	18(Caudal)	18(Caudal)	18(Caudal)	18(Caudal)
	19	19	19	19
	20	20	20	20
21	21	21	21	
22	22	22	22	
23	23	23	23	
24	24	24	24	
25	25	25	25	
26	26	26	26	
27	27	27	27	
28	28	28	28	
29	29	29	29	
30	30	30	30	
31	31	31	31	
32	32	32	32	
33	33	33	33	
34	34	34	34	
35	35	35	35	
36	36	36	36	
37	37	37	37	
38	38	38	38	
39	39	39	39	
40	40	40	40	
41	41	41	41	
42	42	42	42	
43	43	43	43	
44	44	44	44	
45	45	45	45	
46	46	46	46	
47	47	47	47	
48	48	48	48	
49	49	49	49	
50	50	50	50	
<i>Dicamptodon tenebrosus</i> CAS 93958	3	3	3	3
	4	4	4	4
	5	5	5	5
	6	6	6	6
	7	7	7	7
	8	8	8	8
	9	9	9	9
	10	10	10	10
	11	11	11	11
	12	12	12	12
	13	13	13	13
	14	14	14	14
	15	15	15	15
	16(Sacral)	16(Sacral)	16(Sacral)	16(Sacral)
	17(Caudal)	17(Caudal)	17(Caudal)	17(Caudal)
	18	18	18	18
	19	19	19	19
	20	20	20	20
21	21	21	21	
22	22	22	22	
23	23	23	23	
24	24	24	24	
25	25	25	25	
26	26	26	26	
27	27	27	27	
28	28	28	28	
29	29	29	29	
30	30	30	30	
31	31	31	31	
32	32	32	32	
33	33	33	33	
34	34	34	34	
35	35	35	35	
36	36	36	36	
37	37	37	37	
38	38	38	38	
39	39	39	39	
40	40	40	40	
41	41	41	41	
42	42	42	42	
43	43	43	43	
44	44	44	44	
45	45	45	45	
46	46	46	46	
47	47	47	47	
48	48	48	48	
49	49	49	49	
50	50	50	50	
<i>Dicamptodon ensatus</i> CMN 29370-1	3	3	3	3
	4	4	4	4
	5	5	5	5
	6	6	6	6
	7	7	7	7
	8	8	8	8
	9	9	9	9
	10	10	10	10
	11	11	11	11
	12	12	12	12
	13	13	13	13
	14	14	14	14
	15	15	15	15
	16(Sacral)	16(Sacral)	16(Sacral)	16(Sacral)
	17(Caudal)	17(Caudal)	17(Caudal)	17(Caudal)
	18	18	18	18
	19	19	19	19
	20	20	20	20
21	21	21	21	
22	22	22	22	
23	23	23	23	
24	24	24	24	
25	25	25	25	
26	26	26	26	
27	27	27	27	
28	28	28	28	
29	29	29	29	
30	30	30	30	
31	31	31	31	
32	32	32	32	
33	33	33	33	
34	34	34	34	
35	35	35	35	
36	36	36	36	
37	37	37	37	
38	38	38	38	
39	39	39	39	
40	40	40	40	
41	41	41	41	
42	42	42	42	
43	43	43	43	
44	44	44	44	
45	45	45	45	
46	46	46	46	
47	47	47	47	
48	48	48	48	
49	49	49	49	
50	50	50	50	

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

TABLE 5. Vertebral development in hynobiid salamanders

<i>Salamandrella keyserlingii</i> RM 4545		<i>Salamandrella keyserlingii</i> RM 4546		<i>Salamandrella keyserlingii</i> RM 4547		<i>Salamandrella keyserlingii</i> RM 4548		<i>Salamandrella keyserlingii</i> RM 4549		<i>Salamandrella keyserlingii</i> RM 4550		<i>Salamandrella keyserlingii</i> RM 4551	
Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum
1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)
2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)
3	3	3	3	3	3	3	3	3	3	3	3	3	3
4	4	4	4	4	4	4	4	4	4	4	4	4	4
5	5	5	5	5	5	5	5	5	5	5	5	5	5
6	6	6	6	6	6	6	6	6	6	6	6	6	6
7	7	7	7	7	7	7	7	7	7	7	7	7	7
8	8	8	8	8	8	8	8	8	8	8	8	8	8
9	9	9	9	9	9	9	9	9	9	9	9	9	9
10	10	10	10	10	10	10	10	10	10	10	10	10	10
11	11	11	11	11	11	11	11	11	11	11	11	11	11
12	12	12	12	12	12	12	12	12	12	12	12	12	12
13	13	13	13	13	13	13	13	13	13	13	13	13	13
14	14	14	14	14	14	14	14	14	14	14	14	14	14
15	15	15	15	15	15	15	15	15	15	15	15	15	15
16	16	16	16	16	16	16	16	16	16	16	16	16	16
17	17	17	17	17	17	17	17	17	17	17	17	17	17
18	18	18	18	18	18	18	18	18	18	18	18	18	18
19	19	19	19	19	19	19	19	19	19	19	19	19	19
20	20	20	20	20	20	20	20	20	20	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)
21	21	21	21	21	21	21	21	21	21	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)
22	22	22	22	22	22	22	22	22	22	22	22	22	22
23	23	23	23	23	23	23	23	23	23	23	23	23	23
24	24	24	24	24	24	24	24	24	24	24	24	24	24
25	25	25	25	25	25	25	25	25	25	25	25	25	25
26	26	26	26	26	26	26	26	26	26	26	26	26	26
27	27	27	27	27	27	27	27	27	27	27	27	27	27
28	28	28	28	28	28	28	28	28	28	28	28	28	28
29	29	29	29	29	29	29	29	29	29	29	29	29	29
30	30	30	30	30	30	30	30	30	30	30	30	30	30
31	31	31	31	31	31	31	31	31	31	31	31	31	31
32	32	32	32	32	32	32	32	32	32	32	32	32	32
33	33	33	33	33	33	33	33	33	33	33	33	33	33
34	34	34	34	34	34	34	34	34	34	34	34	34	34
35	35	35	35	35	35	35	35	35	35	35	35	35	35
36	36	36	36	36	36	36	36	36	36	36	36	36	36
37	37	37	37	37	37	37	37	37	37	37	37	37	37
38	38	38	38	38	38	38	38	38	38	38	38	38	38
39	39	39	39	39	39	39	39	39	39	39	39	39	39
40	40	40	40	40	40	40	40	40	40	40	40	40	40
41	41	41	41	41	41	41	41	41	41	41	41	41	41
42	42	42	42	42	42	42	42	42	42	42	42	42	42
43	43	43	43	43	43	43	43	43	43	43	43	43	43
44	44	44	44	44	44	44	44	44	44	44	44	44	44

Ranodon tsinpaensis CNHM 50982

Arch	Centrum
1(Atlas)	1(Atlas)
2(Trunk)	2(Trunk)
3	3
4	4
5	5
6	6
7	7
8	8
9	9
10	10
11	11
12	12
13	13
14	14
15	15
16	16
17	17
18	18
19	19
20(Sacral)	20(Sacral)
21(Caudal)	21(Caudal)
22	22
23	23
24	24
25	25
26	26
27	27
28	28
29	29
30	30
31	31
32	32
33	33
34	34
35	35
36	36
37	37
38	38
39	39
40	40
41	41
42	42
43	43
44	44

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

TABLE 6. Vertebral development in plethodontid salamanders

Plethodon cinereus CMN#22231+2		Plethodon cinereus CMN#22231-6		Plethodon cinereus CMN 23497(1)		Plethodon cinereus CMN 23497(2)	
Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum
1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)	1(Atlas)
2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)
3	3	3	3	3	3	3	3
4	4	4	4	4	4	4	4
5	5	5	5	5	5	5	5
6	6	6	6	6	6	6	6
7	7	7	7	7	7	7	7
8	8	8	8	8	8	8	8
9	9	9	9	9	9	9	9
10	10	10	10	10	10	10	10
11	11	11	11	11	11	11	11
12	12	12	12	12	12	12	12
13	13	13	13	13	13	13	13
14	14	14	14	14	14	14	14
15	15	15	15	15	15	15	15
16	16	16	16	16	16	16	16
17	17	17	17	17	17	17	17
18	18	18	18	18	18	18	18
19	19	19	19	19	19	19	19
20	20	20	20	20	20	20	20
21	21	21	21	21	21	21	21
22	22	22	22	22	22	22	22
23(Sacral)	23(Sacral)	23(Sacral)	23(Sacral)	22(Sacral)	22(Sacral)	23(Sacral)	23(Sacral)
24(Caudal)	24(Caudal)	24(Caudal)	24(Caudal)	23(Caudal)	23(Caudal)	24(Caudal)	24(Caudal)
25	25	25	25	25	25	25	25
26	26	26	26	26	26	26	26
27	27	27	27	27	27	27	27
28	28	28	28	28	28	28	28
29	29	29	29	29	29	29	29
30	30	30	30	30	30	30	30
31	31	31	31	31	31	31	31
32	32	32	32	32	32	32	32
33	33	33	33	33	33	33	33
34	34	34	34	34	34	34	34
35	35	35	35	35	35	35	35
36	36	36	36	36	36	36	36
37	37	37	37	37	37	37	37
38	38	38	38	38	38	38	38
39	39	39	39	39	39	39	39
40	40	40	40	40	40	40	40
41	41	41	41	41	41	41	41
42	42	42	42	42	42	42	42
43	43	43	43	43	43	43	43
44	44	44	44	44	44	44	44
45	45	45	45	45	45	45	45
46	46	46	46	46	46	46	46
47	47	47	47	47	47	47	47
48	48	48	48	48	48	48	48
49	49	49	49	49	49	49	49
50	50	50	50	50	50	50	50
51	51	51	51	51	51	51	51
52	52	52	52	52	52	52	52
53	53	53	53	53	53	53	53
54	54	54	54	54	54	54	54
55	55	55	55	55	55	55	55

Eurycaca bis/mesata CMN 23506(1)	Arch		Centrum		Arch	Centrum		Arch	Centrum	
	1(Arch)	2(Trunk)	1(Arch)	2(Trunk)		1(Arch)	2(Trunk)		1(Arch)	2(Trunk)
	4	4	5	5	4	4	4	3	3	10(Sacral)
	5	5	6	6	5	5	5	4	4	11(Sacral)
	6	6	7	7	6	6	6	5	5	12(Caudal)
	7	7	8	8	7	7	7	6	6	21
	8	8	9	9	8	8	8	7	7	22
	9	9	10	10	9	9	9	8	8	23
	10	10	11	11	10	10	10	9	9	24
	11	11	12	12	11	11	11	10	10	25
	12	12	13	13	12	12	12	11	11	26
	13	13	14	14	13	13	13	12	12	27
	14	14	15	15	14	14	14	13	13	28
	15	15	16	16	15	15	15	14	14	29
	16	16	17	17	16	16	16	15	15	30
	17	17	18	18	17	17	17	16	16	31
	18	18	19	19	18	18	18	17	17	32
	19(Sacral)	19(Sacral)	20(Caudal)	20(Caudal)	19(Sacral)	19(Sacral)	20(Caudal)	19(Sacral)	19(Sacral)	33
	20(Caudal)	20(Caudal)	21	21	20(Caudal)	20(Caudal)	21	20(Caudal)	20(Caudal)	34
	21	21	22	22	21	21	21	20	20	35
	22	22	23	23	22	22	22	21	21	36
	23	23	24	24	23	23	23	22	22	37
	24	24	25	25	24	24	24	23	23	38
	25	25	26	26	25	25	25	24	24	39
	26	26	27	27	26	26	26	25	25	40
	27	27	28	28	27	27	27	26	26	41
	28	28	29	29	28	28	28	27	27	42
	29	29	30	30	29	29	29	28	28	43
	30	30	31	31	30	30	30	29	29	44
	31	31	32	32	31	31	31	30	30	45
	32	32	33	33	32	32	32	31	31	46
	33	33	34	34	33	33	33	32	32	47
	34	34	35	35	34	34	34	33	33	48
	35	35	36	36	35	35	35	34	34	49
	36	36	37	37	36	36	36	35	35	50
	37	37	38	38	37	37	37	36	36	51
	38	38	39	39	38	38	38	37	37	52
	39	39	40	40	39	39	39	38	38	53
	40	40	41	41	40	40	40	39	39	54
	41	41	42	42	41	41	41	40	40	55
	42	42	43	43	42	42	42	41	41	
	43	43	44	44	43	43	43	42	42	
	44	44	45	45	44	44	44	43	43	
	45	45	46	46	45	45	45	44	44	
	46	46	47	47	46	46	46	45	45	
	47	47	48	48	47	47	47	46	46	
	48	48	49	49	48	48	48	47	47	
	49	49	50	50	49	49	49	48	48	
	50	50	51	51	50	50	50	49	49	
	51	51	52	52	51	51	51	50	50	
	52	52	53	53	52	52	52	51	51	
	53	53	54	54	53	53	53	52	52	
	54	54	55	55	54	54	54	53	53	
	55	55			55	55	55	54	54	

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

TABLE 7. Vertebral development in proteid salamanders

Necturus alabamensis MCZ 108631		Necturus alabamensis MCZ 108637		Necturus maculosus CMN 30734 17310		Necturus maculosus CMN 30734 17311	
Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum
1(Atlas)	2(Trunk)	1(Atlas)	2(Trunk)	1(Atlas)	2(Trunk)	1(Atlas)	2(Trunk)
3	3	3	3	3	3	3	3
4	4	4	4	4	4	4	4
5	5	5	5	5	5	5	5
6	6	6	6	6	6	6	6
7	7	7	7	7	7	7	7
8	8	8	8	8	8	8	8
9	9	9	9	9	9	9	9
10	10	10	10	10	10	10	10
11	11	11	11	11	11	11	11
12	12	12	12	12	12	12	12
13	13	13	13	13	13	13	13
14	14	14	14	14	14	14	14
15	15	15	15	15	15	15	15
16	16	16	16	16	16	16	16
17	17	17	17	17	17	17	17
18	18	18	18	18	18	18	18
19	19	19	19	19	19	19	19
20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20	20	20	20
21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21	21	21	21
22	22	22	22	22	22	22	22
23	23	23	23	23	23	23	23
24	24	24	24	24	24	24	24
25	25	25	25	25	25	25	25
26	26	26	26	26	26	26	26
27	27	27	27	27	27	27	27
28	28	28	28	28	28	28	28
29	29	29	29	29	29	29	29
30	30	30	30	30	30	30	30
31	31	31	31	31	31	31	31
32	32	32	32	32	32	32	32
33	33	33	33	33	33	33	33
34	34	34	34	34	34	34	34
35	35	35	35	35	35	35	35
36	36	36	36	36	36	36	36
37	37	37	37	37	37	37	37
38	38	38	38	38	38	38	38
39	39	39	39	39	39	39	39
40	40	40	40	40	40	40	40
41	41	41	41	41	41	41	41
42	42	42	42	42	42	42	42
43	43	43	43	43	43	43	43
44	44	44	44	44	44	44	44
45	45	45	45	45	45	45	45
46	46	46	46	46	46	46	46
47	47	47	47	47	47	47	47
48	48	48	48	48	48	48	48
49	49	49	49	49	49	49	49
50	50	50	50	50	50	50	50

Necturus maculosus CMN31688-7	Arch		Centrum	
	1(Atlas) 2(Trunk)	2(Trunk)	1(Atlas) 2(Trunk)	2(Trunk)
	3	4	3	4
	4	5	4	5
	5	6	5	6
	6	7	6	7
	7	8	7	8
	8	9	8	9
	9	10	9	10
	10	11	10	11
	11	12	11	12
	12	13	12	13
	13	14	13	14
	14	15	14	15
	15	16	15	16
	16	17	16	17
	17	18	17	18
	18	19	18	19
	19	20(Sacral)	19(Sacral)	20(Sacral)
	20(Sacral)	21(Caudal)	20(Caudal)	21(Caudal)
	21(Caudal)	22	21	22
	22	23	22	23
	23	24	23	24
	24	25	24	25
	25	26	25	26
	26	27	26	27
	27	28	27	28
	28	29	28	29
	29	30	29	30
	30	31	30	31
	31	32	31	32
	32	33	32	33
	33	34	33	34
	34	35	34	35
	35	36	35	36
	36	37	36	37
	37	38	37	38
	38	39	38	39
	39	40	39	40
	40	41	40	41
	41	42	41	42
	42	43	42	43
	43	44	43	44
	44	45	44	45
	45	46	45	46
	46	47	46	47
	47	48	47	48
	48	49	48	49
	49	50	49	50

Necturus maculosus CMN31688-9	Arch		Centrum	
	1(Atlas) 2(Trunk)	2(Trunk)	1(Atlas) 2(Trunk)	2(Trunk)
	3	4	3	4
	4	5	4	5
	5	6	5	6
	6	7	6	7
	7	8	7	8
	8	9	8	9
	9	10	9	10
	10	11	10	11
	11	12	11	12
	12	13	12	13
	13	14	13	14
	14	15	14	15
	15	16	15	16
	16	17	16	17
	17	18	17	18
	18	19	18	19
	19	20	19(Sacral)	20(Caudal)
	20	21	20(Caudal)	21(Caudal)
	21	22	21	22
	22	23	22	23
	23	24	23	24
	24	25	24	25
	25	26	25	26
	26	27	26	27
	27	28	27	28
	28	29	28	29
	29	30	29	30
	30	31	30	31
	31	32	31	32
	32	33	32	33
	33	34	33	34
	34	35	34	35
	35	36	35	36
	36	37	36	37
	37	38	37	38
	38	39	38	39
	39	40	39	40
	40	41	40	41
	41	42	41	42
	42	43	42	43
	43	44	43	44
	44	45	44	45
	45	46	45	46
	46	47	46	47
	47	48	47	48
	48	49	48	49
	49	50	49	50

Necturus maculosus CMN31688-11	Arch		Centrum	
	1(Atlas) 2(Trunk)	2(Trunk)	1(Atlas) 2(Trunk)	2(Trunk)
	3	4	3	4
	4	5	4	5
	5	6	5	6
	6	7	6	7
	7	8	7	8
	8	9	8	9
	9	10	9	10
	10	11	10	11
	11	12	11	12
	12	13	12	13
	13	14	13	14
	14	15	14	15
	15	16	15	16
	16	17	16	17
	17	18	17	18
	18	19	18	19
	19	20	19(Sacral)	20(Sacral)
	20	21	20(Sacral)	21(Sacral)
	21	22	21(Caudal)	22(Caudal)
	22	23	22(Caudal)	23(Caudal)
	23	24	23	24
	24	25	24	25
	25	26	25	26
	26	27	26	27
	27	28	27	28
	28	29	28	29
	29	30	29	30
	30	31	30	31
	31	32	31	32
	32	33	32	33
	33	34	33	34
	34	35	34	35
	35	36	35	36
	36	37	36	37
	37	38	37	38
	38	39	38	39
	39	40	39	40
	40	41	40	41
	41	42	41	42
	42	43	42	43
	43	44	43	44
	44	45	44	45
	45	46	45	46
	46	47	46	47
	47	48	47	48
	48	49	48	49
	49	50	49	50

Necturus maculosus CMN31688-10	Arch		Centrum	
	1(Atlas) 2(Trunk)	2(Trunk)	1(Atlas) 2(Trunk)	2(Trunk)
	3	4	3	4
	4	5	4	5
	5	6	5	6
	6	7	6	7
	7	8	7	8
	8	9	8	9
	9	10	9	10
	10	11	10	11
	11	12	11	12
	12	13	12	13
	13	14	13	14
	14	15	14	15
	15	16	15	16
	16	17	16	17
	17	18	17	18
	18	19	18	19
	19	20	19(Sacral)	20(Caudal)
	20	21	20(Caudal)	21(Caudal)
	21	22	21	22
	22	23	22	23
	23	24	23	24
	24	25	24	25
	25	26	25	26
	26	27	26	27
	27	28	27	28
	28	29	28	29
	29	30	29	30
	30	31	30	31
	31	32	31	32
	32	33	32	33
	33	34	33	34
	34	35	34	35
	35	36	35	36
	36	37	36	37
	37	38	37	38
	38	39	38	39
	39	40	39	40
	40	41	40	41
	41	42	41	42
	42	43	42	43
	43	44	43	44
	44	45	44	45
	45	46	45	46
	46	47	46	47
	47	48	47	48
	48	49	48	49
	49	50	49	50

Necturus maculosus CMN31688-11	Arch		Centrum	
	1(Atlas) 2(Trunk)	2(Trunk)	1(Atlas) 2(Trunk)	2(Trunk)
	3	4	3	4
	4	5	4	5
	5	6	5	6
	6	7	6	7
	7	8	7	8
	8	9	8	9
	9	10	9	10
	10	11	10	11
	11	12	11	12
	12	13	12	13
	13	14	13	14
	14	15	14	15
	15	16	15	16
	16	17	16	17
	17	18	17	18
	18	19	18	19
	19	20	19(Sacral)	20(Sacral)
	20	21	20(Sacral)	21(Sacral)
	21	22	21(Caudal)	22(Caudal)
	22	23	22(Caudal)	23(Caudal)
	23	24	23	24
	24	25	24	25
	25	26	25	26
	26	27	26	27
	27	28	27	28
	28	29	28	29
	29	30	29	30
	30	31	30	31
	31	32	31	32
	32	33	32	33
	33	34	33	34
	34	35	34	35
	35	36	35	36
	36	37	36	37
	37	38	37	38
	38	39	38	39
	39	40	39	40
	40	41	40	41
	41	42	41	42
	42	43	42	43
	43	44	43	44
	44	45	44	45
	45	46	45	46
	46	47	46	47
	47	48	47	48
	48	49	48	49
	49	50	49	50

TABLE 7. Continued

Necturus maculosus CMN20233-1	Arch		Centrum		Necturus maculosus CMN20233-2	Arch		Centrum		Necturus maculosus CMN20233-3	Arch		Centrum		Necturus maculosus CMN20233-4	Arch		Centrum		Necturus maculosus CMN20233-5	Arch		Centrum		Necturus maculosus CMN20233-6	Arch		Centrum		
	1(Alias) 2(Trunk)	2(Trunk)	1(Alias) 2(Trunk)	2(Trunk)		1(Alias) 2(Trunk)	2(Trunk)	1(Alias) 2(Trunk)	2(Trunk)		1(Alias) 2(Trunk)	2(Trunk)	1(Alias) 2(Trunk)	2(Trunk)		1(Alias) 2(Trunk)	2(Trunk)	1(Alias) 2(Trunk)	2(Trunk)		1(Alias) 2(Trunk)	2(Trunk)	1(Alias) 2(Trunk)	2(Trunk)		1(Alias) 2(Trunk)	2(Trunk)	1(Alias) 2(Trunk)	2(Trunk)	1(Alias) 2(Trunk)
	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4
	5	6	5	6	5	6	5	6	5	6	5	6	5	6	5	6	5	6	5	6	5	6	5	6	5	6	5	6	5	6
	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8
	9	10	9	10	9	10	9	10	9	10	9	10	9	10	9	10	9	10	9	10	9	10	9	10	9	10	9	10	9	10
	11	12	11	12	11	12	11	12	11	12	11	12	11	12	11	12	11	12	11	12	11	12	11	12	11	12	11	12	11	12
	13	14	13	14	13	14	13	14	13	14	13	14	13	14	13	14	13	14	13	14	13	14	13	14	13	14	13	14	13	14
	15	16	15	16	15	16	15	16	15	16	15	16	15	16	15	16	15	16	15	16	15	16	15	16	15	16	15	16	15	16
	17	18	17	18	17	18	17	18	17	18	17	18	17	18	17	18	17	18	17	18	17	18	17	18	17	18	17	18	17	18
	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20
	21	22	21	22	21	22	21	22	21	22	21	22	21	22	21	22	21	22	21	22	21	22	21	22	21	22	21	22	21	22
	23	24	23	24	23	24	23	24	23	24	23	24	23	24	23	24	23	24	23	24	23	24	23	24	23	24	23	24	23	24
	25	26	25	26	25	26	25	26	25	26	25	26	25	26	25	26	25	26	25	26	25	26	25	26	25	26	25	26	25	26
	27	28	27	28	27	28	27	28	27	28	27	28	27	28	27	28	27	28	27	28	27	28	27	28	27	28	27	28	27	28
	29	30	29	30	29	30	29	30	29	30	29	30	29	30	29	30	29	30	29	30	29	30	29	30	29	30	29	30	29	30
	31	32	31	32	31	32	31	32	31	32	31	32	31	32	31	32	31	32	31	32	31	32	31	32	31	32	31	32	31	32
	33	34	33	34	33	34	33	34	33	34	33	34	33	34	33	34	33	34	33	34	33	34	33	34	33	34	33	34	33	34
	35	36	35	36	35	36	35	36	35	36	35	36	35	36	35	36	35	36	35	36	35	36	35	36	35	36	35	36	35	36
	37	38	37	38	37	38	37	38	37	38	37	38	37	38	37	38	37	38	37	38	37	38	37	38	37	38	37	38	37	38
	39	40	39	40	39	40	39	40	39	40	39	40	39	40	39	40	39	40	39	40	39	40	39	40	39	40	39	40	39	40
	41	42	41	42	41	42	41	42	41	42	41	42	41	42	41	42	41	42	41	42	41	42	41	42	41	42	41	42	41	42
	43	44	43	44	43	44	43	44	43	44	43	44	43	44	43	44	43	44	43	44	43	44	43	44	43	44	43	44	43	44
	45	46	45	46	45	46	45	46	45	46	45	46	45	46	45	46	45	46	45	46	45	46	45	46	45	46	45	46	45	46
	47	48	47	48	47	48	47	48	47	48	47	48	47	48	47	48	47	48	47	48	47	48	47	48	47	48	47	48	47	48
	49	50	49	50	49	50	49	50	49	50	49	50	49	50	49	50	49	50	49	50	49	50	49	50	49	50	49	50	49	50
	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)	20(Sacral)	21(Caudal)

Necturus CMN20238-7		Necturus CMN20238-8		Necturus CMN20238-9		Necturus CMN20238-10		Necturus CMN20238-11		Necturus CMN20238-16	
Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum	Arch	Centrum
1(A)BS	1(A)BS	1(A)BS	1(A)BS	1(A)BS	1(A)BS	1(A)BS	1(A)BS	1(A)BS	1(A)BS	1(A)BS	1(A)BS
2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)	2(Trunk)
3	3	3	3	3	3	3	3	3	3	3	3
4	4	4	4	4	4	4	4	4	4	4	4
5	5	5	5	5	5	5	5	5	5	5	5
6	6	6	6	6	6	6	6	6	6	6	6
7	7	7	7	7	7	7	7	7	7	7	7
8	8	8	8	8	8	8	8	8	8	8	8
9	9	9	9	9	9	9	9	9	9	9	9
10	10	10	10	10	10	10	10	10	10	10	10
11	11	11	11	11	11	11	11	11	11	11	11
12	12	12	12	12	12	12	12	12	12	12	12
13	13	13	13	13	13	13	13	13	13	13	13
14	14	14	14	14	14	14	14	14	14	14	14
15	15	15	15	15	15	15	15	15	15	15	15
16	16	16	16	16	16	16	16	16	16	16	16
17	17	17	17	17	17	17	17	17	17	17	17
18	18	18	18	18	18	18	18	18	18	18	18
19	19	19	19	19	19	19	19	19	19	19	19
20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)	20(Sacral)
21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)	21(Caudal)
22	22	22	22	22	22	22	22	22	22	22	22
23	23	23	23	23	23	23	23	23	23	23	23
24	24	24	24	24	24	24	24	24	24	24	24
25	25	25	25	25	25	25	25	25	25	25	25
26	26	26	26	26	26	26	26	26	26	26	26
27	27	27	27	27	27	27	27	27	27	27	27
28	28	28	28	28	28	28	28	28	28	28	28
29	29	29	29	29	29	29	29	29	29	29	29
30	30	30	30	30	30	30	30	30	30	30	30
31	31	31	31	31	31	31	31	31	31	31	31
32	32	32	32	32	32	32	32	32	32	32	32
33	33	33	33	33	33	33	33	33	33	33	33
34	34	34	34	34	34	34	34	34	34	34	34
35	35	35	35	35	35	35	35	35	35	35	35
36	36	36	36	36	36	36	36	36	36	36	36
37	37	37	37	37	37	37	37	37	37	37	37
38	38	38	38	38	38	38	38	38	38	38	38
39	39	39	39	39	39	39	39	39	39	39	39
40	40	40	40	40	40	40	40	40	40	40	40
41	41	41	41	41	41	41	41	41	41	41	41
42	42	42	42	42	42	42	42	42	42	42	42
43	43	43	43	43	43	43	43	43	43	43	43
44	44	44	44	44	44	44	44	44	44	44	44
45	45	45	45	45	45	45	45	45	45	45	45
46	46	46	46	46	46	46	46	46	46	46	46
48	48	48	48	48	48	48	48	48	48	48	48
49	49	49	49	49	49	49	49	49	49	49	49
50	50	50	50	50	50	50	50	50	50	50	50

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

TABLE 8. Vertebral development in rhyacotritonid salamanders

	Arch	Centra		Arch	Centra		Arch	Centra
<i>Rhyacotriton olympicus</i>	1(Atlas)	1(Atlas)	<i>Rhyacotriton olympicus</i>	1(Atlas)	1(Atlas)	<i>Rhyacotriton olympicus</i>	1(Atlas)	1(Atlas)
CMN 34784-1	2(Trunk)	2(Trunk)	CMN 34784-1	2(Trunk)	2(Trunk)	CMN 34784-3	2(Trunk)	2(Trunk)
3502	3	3	3502	3	3	3504	3	3
	4	4		4	4		4	4
	5	5		5	5		5	5
	6	6		6	6		6	6
	7	7		7	7		7	7
	8	8		8	8		8	8
	9	9		9	9		9	9
	10	10		10	10		10	10
	11	11		11	11		11	11
	12	12		12	12		12	12
	13	13		13	13		13	13
	14	14		14	14		14	14
	15	15		15	15		15	15
	16	16		16	16		16	16
	17(Sacral)	17(Sacral)		17(Sacral)	17(Sacral)		17(Sacral)	17(Sacral)
	18(Caudal)	18(Caudal)		18(Caudal)	18(Caudal)		18(Caudal)	18(Caudal)
	19	19		19	19		19	19
	20	20		20	20		20	20
	21	21		21	21		21	21
	22	22		22	22		22	22
	23	23		23	23		23	23
	24	24		24	24		24	24
	25	25		25	25		25	25
	26	26		26	26		26	26
	27	27		27	27		27	27
	28	28		28	28		28	28
	29	29		29	29		29	29
	30	30		30	30		30	30
	31	31		31	31		31	31
	32	32		32	32		32	32
	33	33		33	33		33	33
	34	34		34	34		34	34
	35	35		35	35		35	35
	36	36		36	36		36	36
	37	37		37	37		37	37
	38	38		38	38		38	38
	39	39		39	39		39	39
	40	40		40	40		40	40
	41	41		41	41		41	41
	42	42		42	42		42	42
	43	43		43	43		43	43
	44	44		44	44		44	44
	45	45		45	45		45	45

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

supporting the hypothesis of a diphyletic origin of lissaphibians (Fig. 2B). The sister-relationship of caecilians and microsaurians (Carroll and Currie, '75; Carroll, 2000) and that of Batrachia with temnospondyls (Milner et al., '86; Trueb and Cloutier, '91) had been supported before but the divergence time of those groups was unclear. Despite the different sister-group relationships of caecilians and Batrachia, the monophyly of lissamphibia was still compatible as long as these groups formed a clade excluding amniotes. Anderson et al. (2008) show that this is not the case and estimate that caecilians and batrachians diverged at the split between temnospondyls and "lepospondyls" in the late Carboniferous (328–335 Myr ago).

Divergences in vertebral development pattern can be seen between those two major groups when mapped on a simplified version of Anderson et al.'s (2008) phylogeny (Fig. 2B). Data about extant salamanders were taken from this study, whereas the pattern of arches first in frogs was studied by Carroll et al. ('99) from growth series and immature individuals of the following families: Ascaphidae, Pipidae, Dendrobatidae, Hylidae, Mi-

crohylidae, Leptodactylidae. The centra of caecilians developing first was discovered in *Epicrionops* and the caeciliid *Schistometopum* by Marvalee and David Wake (Wake and Wake, '86, 2000) and reported by Carroll et al. ('99). Thanks to many growth series and incompletely ossified individuals, vertebral development pattern of Palaeozoic amphibians is available for most groups and is stable enough within each group to be generalized from data at hand.

Amphibamidae develop their arches first as seen in a grown series of *Amphibamus lyelli* (Carroll et al., '99). Micromelerpetontidae display the same developmental pattern in a growth series of *Micromelerpeton credneri* (Boy, '72; Witzmann and Pfretzschner, 2003). Many growth series are known for Brachiosauridae and they all show the "arches first" pattern as seen in the growth series of *Branchiosaurus salamandroides* (Carroll et al., '99). There are no larval or immature postcrania known for the olsoniforms *Ecolsonia* and *Acheloma* used in this phylogeny, a question mark is therefore used on Figure 2B. A juvenile specimen of *Balanerpeton* (Carroll, 2001) as well as the

TABLE 9. Vertebral development in salamandrid salamanders

Tritia granulosa CMN 31412 (1)	Centium			Arch			Centium			Arch		
	1 (Atlas)	2 (Trunk)	3 (RM #5011)	1 (Atlas)	2 (Trunk)	3 (RM #5011)	1 (Atlas)	2 (Trunk)	3 (RM #5011)	1 (Atlas)	2 (Trunk)	3 (RM #5011)
	4	4	4	4	4	4	4	4	4	4	4	4
	5	5	5	5	5	5	5	5	5	5	5	5
	6	6	6	6	6	6	6	6	6	6	6	6
	7	7	7	7	7	7	7	7	7	7	7	7
	8	8	8	8	8	8	8	8	8	8	8	8
	9	9	9	9	9	9	9	9	9	9	9	9
	10	10	10	10	10	10	10	10	10	10	10	10
	11	11	11	11	11	11	11	11	11	11	11	11
	12	12	12	12	12	12	12	12	12	12	12	12
	13	13	13	13	13	13	13	13	13	13	13	13
	14	14	14	14	14	14	14	14	14	14	14	14
	15	15	15	15	15	15	15	15	15	15	15	15
	16	16	16	16	16	16	16	16	16	16	16	16
	17	17	17	17	17	17	17	17	17	17	17	17
	18	18	18	18	18	18	18	18	18	18	18	18
	19	19	19	19	19	19	19	19	19	19	19	19
	20	20	20	20	20	20	20	20	20	20	20	20
	21	21	21	21	21	21	21	21	21	21	21	21
	22	22	22	22	22	22	22	22	22	22	22	22
	23	23	23	23	23	23	23	23	23	23	23	23
	24	24	24	24	24	24	24	24	24	24	24	24
	25	25	25	25	25	25	25	25	25	25	25	25
	26	26	26	26	26	26	26	26	26	26	26	26
	27	27	27	27	27	27	27	27	27	27	27	27
	28	28	28	28	28	28	28	28	28	28	28	28
	29	29	29	29	29	29	29	29	29	29	29	29
	30	30	30	30	30	30	30	30	30	30	30	30
	31	31	31	31	31	31	31	31	31	31	31	31
	32	32	32	32	32	32	32	32	32	32	32	32
	33	33	33	33	33	33	33	33	33	33	33	33
	34	34	34	34	34	34	34	34	34	34	34	34
	35	35	35	35	35	35	35	35	35	35	35	35
	36	36	36	36	36	36	36	36	36	36	36	36
	37	37	37	37	37	37	37	37	37	37	37	37
	38	38	38	38	38	38	38	38	38	38	38	38
	39	39	39	39	39	39	39	39	39	39	39	39
	40	40	40	40	40	40	40	40	40	40	40	40
	41	41	41	41	41	41	41	41	41	41	41	41
	42	42	42	42	42	42	42	42	42	42	42	42
	43	43	43	43	43	43	43	43	43	43	43	43
	44	44	44	44	44	44	44	44	44	44	44	44
	45	45	45	45	45	45	45	45	45	45	45	45
	46	46	46	46	46	46	46	46	46	46	46	46
	47	47	47	47	47	47	47	47	47	47	47	47
	48	48	48	48	48	48	48	48	48	48	48	48
	49	49	49	49	49	49	49	49	49	49	49	49
	50	50	50	50	50	50	50	50	50	50	50	50
	51	51	51	51	51	51	51	51	51	51	51	51
	52	52	52	52	52	52	52	52	52	52	52	52
	53	53	53	53	53	53	53	53	53	53	53	53
	54	54	54	54	54	54	54	54	54	54	54	54
	55	55	55	55	55	55	55	55	55	55	55	55

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

TABLE 10. Vertebral development in sirenid salamanders

	Arch	Centrum		Arch	Centrum		Arch	Centrum		Arch	Centrum
<i>Pseudobranchius striatus</i> FMNH 247633 (1)	1(Atlas) 2(Trunk)	1(Atlas) 2(Trunk)	<i>Pseudobranchius striatus</i> FMNH 247633 (2)	1(Atlas) 2(Trunk)	1(Atlas) 2(Trunk)	<i>Pseudobranchius striatus</i> FMNH 247633 (3)	1(Atlas) 2(Trunk)	1(Atlas) 2(Trunk)	<i>Pseudobranchius striatus</i> FMNH 247633 (4)	1(Atlas) 2(Trunk)	1(Atlas) 2(Trunk)
	3	3		3	3		3	3		3	3
	4	4		4	4		4	4		4	4
	5	5		5	5		5	5		5	5
	6	6		6	6		6	6		6	6
	7	7		7	7		7	7		7	7
	8	8		8	8		8	8		8	8
	9	9		9	9		9	9		9	9
	10	10		10	10		10	10		10	10
	11	11		11	11		11	11		11	11
	12	12		12	12		12	12		12	12
	13	13		13	13		13	13		13	13
	14	14		14	14		14	14		14	14
	15	15		15	15		15	15		15	15
	16	16		16	16		16	16		16	16
	17	17		17	17		17	17		17	17
	18	18		18	18		18	18		18	18
	19	19		19	19		19	19		19	19
	20	20		20	20		20	20		20	20
	21	21		21	21		21	21		21	21
	22	22		22	22		22	22		22	22
	23	23		23	23		23	23		23	23
	24	24		24	24		24	24		24	24
	25	25		25	25		25	25		25	25
	26	26		26	26		26	26		26	26
	27	27		27	27		27	27		27	27
	28	28		28	28		28	28		28	28
	29	29		29	29		29	29		29	29
	30	30		30	30		30	30		30	30
	31	31		31	31		31	31		31	31
	32	32		32	32		32	32		32	32
	33	33		33	33		33	33		33	33
	34	34		34	34		34	34		34	34
	35	35		35	35		35	35		35	35
	36	36		36	36		36	36		36	36
	37	37		37	37		37(Sacral)	37(Sacral)		37(Sacral)	37(Sacral)
	38(Sacral)	38(Sacral)		38(Sacral)	38(Sacral)		38(Caudal)	38(Caudal)		38(Caudal)	38(Caudal)
	39(Caudal)	39(Caudal)		39(Caudal)	39(Caudal)		39	39		39	39
	40	40		40	40		40	40		40	40
	41	41		41	41		41	41		41	41
	42	42		42	42		42	42		42	42
	43	43		43	43		43	43		43	43
	44	44		44	44		44	44		44	44
	45	45		45	45		45	45		45	45
	46	46		46	46		46	46		46	46
	47	47		47	47		47	47		47	47
	48	48		48	48		48	48		48	48
	49	49		49	49		49	49		49	49
	50	50		50	50		50	50		50	50
	51	51		51	51		51	51		51	51
	52	52		52	52		52	52		52	52
	53	53		53	53		53	53		53	53
	54	54		54	54		54	54		54	54
	55	55		55	55		55	55		55	55
	56	56		56	56		56	56		56	56
	57	57		57	57		57	57		57	57
	58	58		58	58		58	58		58	58
	59	59		59	59		59	59		59	59
	60	60		60	60		60	60		60	60
	61	61		61	61		61	61		61	61
	62	62		62	62		62	62		62	62
	63	63		63	63		63	63		63	63
	64	64		64	64		64	64		64	64
	65	65		65	65		65	65		65	65
	66	66		66	66		66	66		66	66
	67	67		67	67		67	67		67	67
	68	68		68	68		68	68		68	68
	69	69		69	69		69	69		69	69
	70	70		70	70		70	70		70	70
	71	71		71	71		71	71		71	71
	72	72		72	72		72	72		72	72
	73	73		73	73		73	73		73	73
	74	74		74	74		74	74		74	74
	75	75		75	75		75	75		75	75
	76	76		76	76		76	76		76	76
	77	77		77	77		77	77		77	77
	78	78		78	78		78	78		78	78
	79	79		79	79		79	79		79	79
	80	80		80	80		80	80		80	80
	81	81		81	81		81	81		81	81
	82	82		82	82		82	82		82	82
	83	83		83	83		83	83		83	83
	84	84		84	84		84	84		84	84
	85	85		85	85		85	85		85	85

TABLE 10. Continued

	Arch	Centrum		Arch	Centrum		Arch	Centrum
<i>Siren lacertina</i> UF 14229-1	1(Atlas) 2(Trunk)	1(Atlas) 2(Trunk)	<i>Siren lacertina</i> UMMZ 152254	1(Atlas) 2(Trunk)	1(Atlas) 2(Trunk)	<i>Siren intermedia</i> CMNH84076	1(Atlas) 2(Trunk)	1(Atlas) 2(Trunk)
	3	3		3	3		3	3
	4	4		4	4		4	4
	5	5		5	5		5	5
	6	6		6	6		6	6
	7	7		7	7		7	7
	8	8		8	8		8	8
	9	9		9	9		9	9
	10	10		10	10		10	10
	11	11		11	11		11	11
	12	12		12	12		12	12
	13	13		13	13		13	13
	14	14		14	14		14	14
	15	15		15	15		15	15
	16	16		16	16		16	16
	17	17		17	17		17	17
	18	18		18	18		18	18
	19	19		19	19		19	19
	20	20		20	20		20	20
	21	21		21	21		21	21
	22	22		22	22		22	22
	23	23		23	23		23	23
	24	24		24	24		24	24
	25	25		25	25		25	25
	26	26		26	26		26	26
	27	27		27	27		27	27
	28	28		28	28		28	28
	29	29		29	29		29	29
	30	30		30	30		30	30
	31	31		31	31		31	31
	32	32		32	32		32	32
	33	33		33	33		33	33
	34	34		34	34		34	34
	35	35		35	35		35	35
	36	36		36	36		36	36
	37	37		37	37		37	37
	38	38		38	38		38	38
	39	39		39	39		39	39
	40	40		40	40		40	40
	41(Sacral)	41(Sacral)		41	41		41	41
	42(Caudal)	42(Caudal)		42	42		42	42
	43	43		43	43		43	43
	44	44		44	44		44	44
	45	45		45	45		45	45
	46	46		46	46		46	46
	47	47		47	47		47	47
	48	48		48	48		48	48
	49	49		49	49		49	49
	50	50		50	50		50	50
	51	51		51	51		51	51
	52	52		52	52		52	52
	53	53		53	53		53	53
	54	54		54	54		54	54
	55	55		55	55		55	55
	56	56		56	56		56	56
	57	57		57	57		57	57
	58	58		58	58		58	58
	59	59		59	59		59	59
	60	60		60	60		60	60
	61	61		61	61		61	61
	62	62		62	62		62	62
	63	63		63	63		63	63
	64	64		64	64		64	64
	65	65		65	65		65	65
	66	66		66	66		66	66
	67	67		67	67		67	67
	68	68		68	68		68	68
	69	69		69	69		69	69
	70	70		70	70		70	70
	71	71		71	71		71	71
	72	72		72	72		72	72
	73	73		73	73		73	73
	74	74		74	74		74	74
	75	75		75	75		75	75

Erypoid temnospondyl *Onchiodon* (a much smaller but close relative to *Eryops*) develop their arches first (Schoch, 2002) exemplifying the condition for stem temnospondyls. The primitive pattern for all temnospondyls is therefore that of arches first and it is retained in modern frogs and is the primitive pattern for salamanders.

Reptiliomorphs, caecilians (Gymnophiona) and “lepospondyls” all display the reverse developmental pattern. There are no postcranial growth series of *Proterogyrinus* known, the only embolomere represented in Anderson et al.’s (2008)

phylogeny and neither are there for *Limnoscelis*, the only Diadectomorph included in the phylogeny. However, the pattern of centra developing first can clearly be seen in representatives of the other groups. A larva of *Gephyrostegus* (Carroll, ’70), immature remains attributed to *Seymouria sanjuanensis* (Klembara et al., 2001) as well as a juvenile of *Utegenia shpinari* display this developmental pattern for Seymouriamorpha. The microsauro *Hylopleosion* (Carroll et al., ’99), an adelogyridid not assigned to genus (Carroll et al., ’99) as well as neotridians (Carroll, ’99), develop

TABLE 10. Continued

	Arch	Centrum		Arch	Centrum		Arch	Centrum		Arch	Centrum		Arch	Centrum
Siren	1(Atlas)	1(Atlas)	Siren	1(Atlas)	1(Atlas)	Siren	1(Atlas)	1(Atlas)	Siren	1(Atlas)	1(Atlas)	Siren	1(Atlas)	1(Atlas)
intermedia	2(Trunk)	2(Trunk)	intermedia	2(Trunk)	2(Trunk)	intermedia	2(Trunk)	2(Trunk)	intermedia	2(Trunk)	2(Trunk)	intermedia	2(Trunk)	2(Trunk)
nettingi			nettingi			nettingi			nettingi			nettingi		
FMNH 245464 (1)			FMNH 245464 (2)			FMNH 245464 (3)			FMNH 245464 (4)			FMNH 245464 (5)		
	3	3		3	3		3	3		3	3		3	3
	4	4		4	4		4	4		4	4		4	4
	5	5		5	5		5	5		5	5		5	5
	6	6		6	6		6	6		6	6		6	6
	7	7		7	7		7	7		7	7		7	7
	8	8		8	8		8	8		8	8		8	8
	9	9		9	9		9	9		9	9		9	9
	10	10		10	10		10	10		10	10		10	10
	11	11		11	11		11	11		11	11		11	11
	12	12		12	12		12	12		12	12		12	12
	13	13		13	13		13	13		13	13		13	13
	14	14		14	14		14	14		14	14		14	14
	15	15		15	15		15	15		15	15		15	15
	16	16		16	16		16	16		16	16		16	16
	17	17		17	17		17	17		17	17		17	17
	18	18		18	18		18	18		18	18		18	18
	19	19		19	19		19	19		19	19		19	19
	20	20		20	20		20	20		20	20		20	20
	21	21		21	21		21	21		21	21		21	21
	22	22		22	22		22	22		22	22		22	22
	23	23		23	23		23	23		23	23		23	23
	24	24		24	24		24	24		24	24		24	24
	25	25		25	25		25	25		25	25		25	25
	26	26		26	26		26	26		26	26		26	26
	27	27		27	27		27	27		27	27		27	27
	28	28		28	28		28	28		28	28		28	28
	29	29		29	29		29	29		29	29		29	29
	30	30		30	30		30	30		30	30		30	30
	31	31		31	31		31	31		31	31		31	31
	32	32		32	32		32	32		32	32		32	32
	33	33		33	33		33	33		33	33		33	33
	34	34		34	34		34	34		34	34		34	34
	35	35		35	35		35	35		35	35		35	35
	36	36		36	36		36	36		36	36		36	36
	37(Sacral)	37(Sacral)		37(Sacral)	37(Sacral)		37(Sacral)	37(Sacral)		37(Sacral)	37(Sacral)		37(Sacral)	37(Sacral)
	38(Caudal)	38(Caudal)		38(Caudal)	38(Caudal)		38(Caudal)	38(Caudal)		38(Caudal)	38(Caudal)		38(Caudal)	38(Caudal)
	39	39		39	39		39	39		39	39		39	39
	40	40		40	40		40	40		40	40		40	40
	41	41		41	41		41	41		41	41		41	41
	42	42		42	42		42	42		42	42		42	42
	43	43		43	43		43	43		43	43		43	43
	44	44		44	44		44	44		44	44		44	44
	45	45		45	45		45	45		45	45		45	45
	46	46		46	46		46	46		46	46		46	46
	47	47		47	47		47	47		47	47		47	47
	48	48		48	48		48	48		48	48		48	48
	49	49		49	49		49	49		49	49		49	49
	50	50		50	50		50	50		50	50		50	50
	51	51		51	51		51	51		51	51		51	51
	52	52		52	52		52	52		52	52		52	52
	53	53		53	53		53	53		53	53		53	53
	54	54		54	54		54	54		54	54		54	54
	55	55		55	55		55	55		55	55		55	55
	56	56		56	56		56	56		56	56		56	56
	57	57		57	57		57	57		57	57		57	57
	58	58		58	58		58	58		58	58		58	58
	59	59		59	59		59	59		59	59		59	59
	60	60		60	60		60	60		60	60		60	60
	61	61		61	61		61	61		61	61		61	61
	62	62		62	62		62	62		62	62		62	62
	63	63		63	63		63	63		63	63		63	63
	64	64		64	64		64	64		64	64		64	64
	65	65		65	65		65	65		65	65		65	65

Each numbered rectangle in the tables represents a vertebra. Notes in parentheses indicate the beginning of each section of the vertebral column. Coding: no shading = unchondrified and unossified; grey shading = chondrified; black = ossified.

centra before arches. It therefore seems to be the primitive developmental pattern for antraco-saurs, reptiliomorphs and “lepospondyls” and is inherited by all caecilians and amniotes (Carroll et al., '99).

Given the fact that there are no known juvenile or growth series for the Devonian tetrapod *Acanthostega* it is difficult to say which developmental pattern is likely to be primitive for all tetrapods. One can look at vertebral development sequences of the tetrapodomorph fish *Eusthenopteron* (closely related to tetrapods), but the authors of the study suggest that its complex and non antero-posterior development is likely to be derived (Cote et al., 2002). All tetrapods develop

their vertebral column in an anterior to posterior direction, after the expression of *Hox* genes. This is not the case for *Eusthenopteron* where development of vertebral elements begin with the ossification of neural arches at the anterior base of the tail, progressing posteriorly into the tail and anteriorly into the trunk until development is halted at the level of the second dorsal fin. The development of trunk neural arches is terminated when the centra (developing in an antero-posterior direction) have ossified. This suggests that centra (intercentra) ossify before neural arches but the authors argue that, as arches are first to appear in evolution, the primitive developmental pattern for tetrapods would be that or arches first

(Cote et al., 2002). In the absence of developmental data for the earliest tetrapods, either (a) the primitive development pattern for all tetrapods is that of arches first and a switch occurred in the ancestor of anthracosaurs+“lepospondyls, (b) the primitive development pattern for all tetrapods is that of centra first and a switch occurred in the ancestor of temnospondyls or (c) each major group inherited their development pattern from tetrapods that had adopted a different development pattern. This would mean that there is no primitive tetrapod development pattern, just two different solutions to developing a vertebral column as a tetrapod. Either way, vertebral development pattern is a very conserved character in tetrapods and switches in state are exceedingly rare. The switch observed in modern salamanders is a unique event in recent tetrapod evolution.

Salamander relationships

Current salamander phylogenies present three congruence problems with regard to the distribution of vertebral ossification patterns: the monophyly of Hynobiidae, the monophyly of Cryptobranchioidea (Hynobiidae+Cryptobranchidae) and, in some phylogenies, the basal position of Sirenidae. As presented above, the apparently primitive ossification pattern of arches before centra occurs among living salamanders exclusively in a subset of Hynobiidae: *Ranodon* and *Hynobius*, but not *Salamandrella*. Cryptobranchids, sireniids and all other salamanders show the derived pattern. Because of this, each of the aforementioned three phylogenetic statements necessitates an additional switch between primitive and derived modes of vertebral ossification. The only phylogenetic pattern that would allow a least homoplastic distribution of vertebral ossification patterns is to have a paraphyletic Hynobiidae at the base of the salamanders, with *Ranodon* and *Hynobius* as sister-groups to *Salamandrella*+all other salamanders. This has recently been supported by a phylogenetic analysis based on the mitochondrial genome of all members of Hynobiidae (Zhang et al., 2006).

Sireniids are placed as the sister-group of all other salamanders in some recent phylogenies (Duellman and Trueb, '86; Larson and Dimmick, '93) but others place Hynobiidae, alone or with other families, in that position (Gao and Shubin, 2001; San Mauro et al., 2005; Wiens et al., 2005). Data from vertebral development gives support to the basal position of Hynobiidae (Noble, '31; Sato,

'43). As for the interrelationships of hynobiids, Hynobiidae has often been hypothesized to be one of the few salamander families to be paraphyletic (Milner, '83; Zhao et al., '88; Trueb and Cloutier, '91). Notwithstanding the current phylogenetic consensus, there is thus some reason to believe that Hynobiidae may form a paraphyletic basal group of living salamanders, and that only a single switch in the pattern of vertebral ossification has occurred during salamander evolution. If this were true, it would imply that the superfamily Cryptobranchioidea (Hynobiidae+Cryptobranchidae) is not a valid taxon. The fossil record of hynobiid and cryptobranchid salamanders (Gao and Shubin, 2003), paleogeographical isolation events (Milner, '83) and divergence times based on molecular evolution (San Mauro et al., 2005), suggest that this unique switch in vertebral development would have taken place between the Triassic and the mid-Jurassic in Asia.

CONCLUSIONS

The retention of the primitive development pattern by some members of Hynobiidae provides support for their position as the most primitive member of the modern order, but raises questions about its monophyly. Some genera included in Hynobiidae may be the sister-taxa to all other modern salamanders and that others may be the sister-taxa to Cryptobranchidae. Consequently, Cryptobranchioidea (Hynobiidae+Cryptobranchidae) may not be a valid taxon. The relationships of the members of those clades should be reassessed using a large species and character sample to elucidate this problem.

This study of vertebral development patterns in all modern families of salamanders has shown that, as in all other tetrapod taxa (Carroll et al., '99; Wake and Wake, 2000), vertebral development pattern is a robust character with phylogenetic significance that can be used in future reconstructions including ontogenetic data. The primitive pattern is that of the development of the arches before the centra and is retained by a putative hynobiid from the mid-Jurassic of China and the modern genera *Ranodon* and *Hynobius*. A switch in the developmental pattern most likely occurred within stem-uroleles between the Triassic and the mid-Jurassic in Asia. This occurred after the group ancestral to the modern genera *Ranodon* and *Hynobius* had evolved, but before the radiation of the group later giving rise to *Salamandrella* and all other salamander families.

The retention of two vertebral development patterns in modern salamanders provides a unique opportunity to explore the causes of a switch in such a robust phylogenetically character.

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