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# Evolutionary Relationships in the Family Salamandridae

DAVID B. WAKE AND NECLÂ ÖZETI

Data on 40 characters, 27 relating to feeding mechanisms, were assembled in order to analyze evolutionary relationships in the family Salamandridae. In most instances, primitive and derived states were identified, and in many cases, state phylogenies for each character were hypothesized. Phenetic schemes of character analysis, including single and average linkage techniques and the results of inclusion and exclusion of primitive character states, were compared. There are significant differences, and exclusion of primitive character states is recommended. We put most emphasis on a combinatorial analysis of our own, which takes into account the changes in the feeding system as a single complex unit and also makes use of the phenetic methods in which primitive character states are excluded. The result is the placement of the 14 genera in four groups: A. *Salamandra*, *Chioglossa*, *Salamandrina*; B. *Triturus*, *Euproctus*, *Neurergus*, *Paramesotriton*, *Cynops*, *Hypselotriton*, *Pachytriton*, *Taricha*, *Notophthalmus*; C. *Pleurodeles*; D. *Tylototriton*. The very primitive groups C and D are slightly modified remnants of ancient groups. Group A is the most derived group. *Chioglossa* and *Salamandrina* are the most specialized genera. Of two computer methods for deducing phylogenies, one compares well with these results, but the other does not.

## INTRODUCTION

THE family Salamandridae includes 14 genera and about 43 species, distributed broadly throughout the Holarctic region. Considerable information concerning salamandrid anatomy and evolutionary relationships appeared in the German literature of the 1930's, and the monograph by Herre (1935) remains the most authoritative reference on the family. The work of Herre and others resulted in the inclusion in the family Salamandridae of the genera previously placed in the family Pleurodelidae, and the distribution of regionalized groups of species of *Triturus* to several genera. Their statements concerning salamandrid evolution have not been reevaluated, but von Wahlert (1953) and others added new information that has, in general, tended to corroborate their findings. Nevertheless, many aspects of evolution in the family have not been studied, including feeding and locomotor systems. Data accumulated during our study on feeding mechanisms (Özeti and Wake, 1969) are used in this paper to reinvestigate salamandrid relationships and to attempt to deduce the phylogeny of the group.

Descriptive portions of our comparative morphological paper are condensed here to 27 characters. To these we add an additional 13 that either have been used by others or

which, for various reasons, appear to carry useful information. Our data from feeding mechanisms do not indicate whether we are dealing with an integrated system under a relatively simple genetic control, or whether the parts (our 27 characters) are discrete and evolving independently. Probably state changes in several characters are due to responses to a single selection pressure, but this cannot now be determined. We think that careful analysis of such an adaptive complex will provide useful information for the deduction of the phylogeny. Feeding is an extremely important activity and several clearly adaptive trends in the system are associated with ecological shifts. In deducing phylogeny, knowledge of community of descent is sought, and we feel that very complex systems, where the chance of parallelism and convergence is reduced, offer the best sources for such information. Biological information for systems other than the feeding system has been added, for we wish to make this study as comprehensive as our present knowledge of the group permits.

Our working hypothesis is that information concerning relationship in primary groups (e.g., the family Salamandridae) is contained only in derived character states. Resemblance that results from characters shared in states that are primitive for the primary

group has no phylogenetic information. We are interested in community of descent with change, and retention of primitive conditions is essentially non-descent and provides no information. Derived states which occur only in single taxa similarly have no information concerning relationships, but they do provide information concerning degree of derivation of a group; five of our 40 characters fall into this category.

Analysis of the 40 characters has been based on the premise that a character state of universal occurrence in related, primitive families, or in early fossil ancestors, is primitive for the group under consideration. We have rigorously applied this standard, and feel that the following analysis is conservative in this regard. Where there is doubt, we have not identified a primitive state, except where an apparently clear evolutionary trend exists within the primary group. To facilitate computer analysis we have coded the characters in the following manner (Table 1): primitive state (0), derived states (1, 2, etc.), character not present or inapplicable or no information (9). Reference to primitive salamander families applies to the families Hynobiidae, Cryptobranchidae, and Ambystomatidae, unless specified.

In some instances data have been obtained from the literature, especially in regard to osteology (data from Bolkay, 1928; Herre, 1932, 1933, 1935, 1939; Wolterstorff and Herre, 1935).

#### CHARACTER ANALYSIS

1. Premaxillary fusion. Premaxillary bones are paired in primitive tetrapods and in primitive salamanders. Two premaxillaries are considered primitive (0) and fused premaxillaries derived (1).
2. Frontosquamosal arch. Frontosquamosal arches are found only in the family Salamandridae. There are many fossil salamandrids, but most are represented only by vertebral fragments. Some are known from complete skulls and the earliest of these (*Tylotriton weigelti*, Middle Eocene; *Paleotaricha oligocenia*, Upper Oligocene; *Oligosemia spinosa*, Oligocene; *Heliarchon furcillatus*, Lower Miocene) have well developed arches. The general trend is for bone reduction in salamanders, and the arches are undergoing apparent reduction in certain genera (e.g., *Triturus*). However, frontosquamosal arches do not occur in primitive salamander groups other than salamandrids. Nevertheless, presence of the arch is considered primitive (0), partial development a derived state (1), and absence a more derived state (2).
3. Maxillary length. The toothed portion of the maxillary bone of amphibians is primitively very long. In the most primitive salamandrid state the maxillary extends virtually to the quadrate, or falls just short of that bone (0). In a derived state the maxillary extends past the eye but falls far short of the quadrate (1). A more derived state finds the maxillary falling short of the posterior margin of the eye (2).
4. Nasal bone contact. In hynobiid and cryptobranchid salamanders the nasals are in broad median contact. Such a condition is considered to represent the primitive state in salamandrids (0). Narrow contact is considered a derived condition (1), and no contact is a more derived state (2).
5. Operculum. Opercula are ossified in primitive salamanders. In salamandrids ossification or mineralization is considered primitive (0), and unmineralized cartilage is derived (1).
6. Caudosacral ribs. There is a general evolutionary trend in amphibians for reduction and loss of postsacral ribs, borne on caudosacral vertebrae. Accordingly, caudosacral ribs are considered to represent a primitive state (0) and absence is derived (1).
7. Fifth toe. Loss of the fifth toe and fifth distal tarsal is clearly a derived condition (1), since all generalized salamanders have five toes (0).
8. Lung reduction. Well developed lungs are primitively present in salamanders (0). Lung reduction and loss is considered to be derived (1; see Lüdi, 1955).
9. Skin texture. It is not possible to ascertain whether or not rough skin such as that encountered in the terrestrial newts is primitive or derived. However, since it seems to be associated with a primitive way of life and is absent only in those groups that have diverged from that pattern, we consider roughened, keratinized skin to be primitive (0) and smooth skin to be derived in one direction in terrestrial environments (1) and in another in aquatic habitats (2).
10. Egg size. Primitively salamanders lay large numbers of small eggs. Such a pattern is considered primitive (0), and the laying of medium-sized eggs is considered to be de-

rived (1). Large eggs constitute the most derived state (2) (some data from Wolterstorff and Herre, 1935).

11. Courtship pattern. Salthe (1967) has described three courtship patterns in the family Salamandridae. He considers that found in *Euproctus* to be primitive (0), and we have followed him. He recognizes two derived states (1 and 2).

12. Reproductive pattern. Oviparity is primitive in amphibians (0). Ovoviviparity or viviparity are considered derived (1).

13. Second basibranchial. The second basibranchial is present primitively in salamanders and its presence here is considered primitive (0). Presence of occasional rudiments is considered derived (1) and total absence is a more derived state (2).

14. Epibranchial. Presence of an epibranchial is a primitive state in salamanders (0). Fusion or loss is considered derived (1).

15. Radii. Since the first pair of radii represents an apparent remnant of the hypohyals, elements present in more primitive salamanders and in larvae, we consider two pairs of radii to represent a primitive state (0). Loss of the anterior pair is a derived state (1).

16. Interradial cartilage. The interradial cartilage is a functionally significant element found only in forms that have lost the first pair of radii. Thus absence of the element may be considered primitive (0). We recognize three derivative states. The least derived finds the element very well developed (1). The intermediate state is an element of reduced size (2). The most advanced state is presumed loss of the element in a single genus (*Notophthalmus*) that is a member of the group in which the element is otherwise found (3).

17. First basibranchial. The first basibranchial is primitively ossified (0). A derived state finds a cartilaginous element that is mineralized (1), and in the most derived state the element is unmineralized cartilage (2). The first basibranchials of *Chioglossa* and *Salamandrina* are probably secondarily ossified in response to pressures exerted by the enlarged basiradialis muscles during tongue flipping, but in the absence of conclusive evidence they are called primitive.

18. First ceratobranchial. This element is primitively bony (0) in salamanders. It is cartilaginous in the derived state (1).

19. Second ceratobranchial. There is evidence that the last three elements have separate histories in the family. Since all are subjected to unique mechanical pressures, it is likely that different selective pressures are also operative. Primitively the element is ossified (0). A derived state finds the element partially mineralized (1), and the element is unmineralized cartilage in the more derived state (2).

20. Ceratohyal. This element is partially ossified primitively (0). It is entirely unmineralized cartilage in the derived state (1).

21. Length of first ceratobranchial. This element primitively extends about to the posterior tip of the second ceratobranchial (0). It is very much longer in the derived state (1).

22. Form of rectus cervicis profundus. The derived condition is characterized by the presence of a distinct lengthening loop (1), which is not present primitively (0).

23. Insertion of rectus cervicis profundus. In primitive salamanders this muscle has several heads (0). In certain salamandrids a derived condition is found that is characterized by a single insertion (1).

24. Myocommata in rectus cervicis profundus. Primitively many myocommata are present in salamander muscles. The most primitive state in salamandrids finds three myocommata between the sternum and insertion (0). A derived state finds but one (1), and in a more derived state there are none (2).

25. Heboosteoypsiloideus. We consider the less differentiated state to represent the primitive state (0), and the more differentiated to represent a derived state (1).

26. Inter-ossa-quadrata. Primitive salamanders have a well developed muscle (0). One derived state is represented by a distinct reduction of the muscle with only a few muscle fibers extending to the medial raphe (1). A more derived state finds all fibers falling short of the raphe (2).

27. Tongue. Tongues of four general types can be recognized in salamandrids. The most primitive type is similar to that found in primitive hynobiids and ambystomatids, and has a well developed tongue pad but lacks a free posterior flap (0). One derived state (1) is found in *Pachytriton*, an aquatic form that lacks a differentiated tongue pad. In another direction, evolutionarily, is a tongue pad with somewhat free posterior

margins (2). The most derived state of this trend is a tongue pad with a large, free posterior flap (3).

28. Basiradialis. Primitively this muscle is rather small and weak to relatively well developed (0). In the derived state the muscle is very well developed and strong (1).

29. Rib protrusion. Rib processes either protrude (1) or do not (2) from the body wall. The processes occur in many fossil salamandrids and may be primitive features of the family, but we are unsure of this. Protrusion is not found in other families of salamanders, and we prefer not to identify one or the other of these states as primitive at this time.

30. Rectus abdominis profundus. Maurer (1892) first demonstrated differences in the degree of differentiation of the trunk muscles of salamanders, but he emphasized only *Triturus* and *Salamandra* among the salamandrids. From our dissections and analysis of histological sections, we have been able to extend these observations somewhat. In primitive salamanders this muscle is not distinct from the rectus abdominis superficialis (0). In the derived state the two muscles are differentiated and separate (1).

31. Medial superficial fibers of genioglossus. Primitively the superficial fibers are extensive and include medial fibers that insert in the vicinity of the tips of the ceratohyals (0). The medial fibers are absent, but the lateral ones are relatively well developed in the derived state (1).

32. Relation of geniohyoideus to genioglossus. Primitively the geniohyoideus muscles are attached to well differentiated genioglossal muscles by dense beds of connective tissue lying at the anterior ends of the ceratohyals (0). In one derived state the connection is absent (1). In an entirely different trend the connection is present but the geniohyoideus is not differentiated (2).

33. Insertion of the rectus cervicis superficialis. Two states are found. In the first (1) the muscle inserts primarily in the vicinity of the attachment of the first ceratobranchial to the first basibranchial, and in the second (2) a well developed slip extends far anteriorly to insert near the tip of the first basibranchial. The simpler state (1) is probably primitive, but we have no good evidence.

34. Insertion of the rectus cervicis profundus. The rectus cervicis profundus has

slips that attach to the posterior part of the first basibranchial (2), to that part and to the radii (3), or to neither part (1). We are not certain which, if any, is the primitive state; states 1 and 2 are found in other primitive salamanders.

35. Radioglossus and hyoglossus. The primitive state has but a single, undifferentiated and unpaired muscle (0). In one direction the muscle differentiates and both parts, but particularly the radioglossus, are well developed (1). In another direction the muscle is differentiated and a single hyoglossus and a paired radioglossus are found (2). The radioglossals are not well developed. In a third derived state (3) the muscles are greatly reduced.

36. Depressor mandibulae. This muscle may have a single part (3), two skeletal heads (2), or a skeletal head and a cutaneous head (1). We cannot identify a primitive state.

37. Subhyoideus. The muscle is either not attached to the mandible (3), attached by muscle fibers to the mandible (2), or attached to the mandible by a tendon (1). The state that lacks mandibular attachment is probably the primitive one, since the muscle is derived from hyoidean constrictors, but we cannot be certain.

38. Interradialis. Primitively the muscle is present (0), but it may be very well developed (1) or absent (2).

39. Ratio of epibranchial to ceratobranchial. The epibranchial is either shorter (1) or longer (2) than the ceratobranchial. The short epibranchial is likely the primitive state, since lengthening of the epibranchial in other groups is associated with derivative features of tongue protrusion. However, we have not identified either state as primitive.

40. Maxillary-ptyergoid joint. A maxillary-ptyergoid joint is either present (1) or absent (2). Primitive salamanders lack such joints and state 2 may be primitive; in the absence of good evidence we have not identified either state as primitive.

Distribution of character states in the salamandrid genera is summarized in Table 1. Table 2 summarizes the character state trees, or the presumed direction of change or evolutionary trends for each character. Information in these tables is used below to aid in outlining major patterns of phenetic relationships, and, in the following section, in elucidating phyletic patterns. Our data are mainly from systems related to feeding

TABLE 1. DISTRIBUTION OF CHARACTER STATES IN SALAMANDRID GENERA.  
See text for coding.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40				
<i>Salamandra</i>	0	2	0	0	1	1	0	0	1	2	1	1	0	1	0	0	2	1	2	1	0	0	1	2	1	2	2	0	2	1	1	1	2	1	3	2	3	2	9	2				
<i>Chioglossa</i>	0	2	2	0	1	1	0	1	1	2	9	0	0	1	1	0	0	1	2	1	1	0	1	1	1	1	1	3	1	2	1	0	1	1	3	2	1	0	9	2				
<i>Salamandrina</i>	0	0	0	2	1	0	1	1	0	9	0	2	1	1	0	0	1	2	1	0	1	2	1	2	1	2	3	1	1	1	0	1	1	1	1	1	1	1	2	1	9	2		
<i>Pleurodeles</i>	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	2	0	2	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	1	3	3	0	2	2	2	2			
<i>Tylotriton</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	2	0	3	0	2	2	2			
<i>Euproctus</i>	1	0	2	2	1	1	0	1	0	2	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	3	3	3	0	2	1	1			
<i>Triturus</i>	1	1	2	2	1	1	0	0	0	1	2	0	2	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	3	2	3	2	0	2	2	2		
<i>Neuregus</i>	1	1	2	2	1	1	0	0	0	2	9	0	2	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	3	3	3	0	1	2	0	1	2		
<i>Notophthalmus</i>	1	0	1	1	1	1	0	0	0	1	2	0	2	0	1	3	1	0	1	0	0	0	0	0	0	0	0	0	0	2	9	0	0	1	3	2	3	3	0	1	2	0	1	
<i>Taricha</i>	1	0	0	2	0	1	0	0	0	1	2	0	2	0	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0	2	9	0	0	1	3	3	3	0	1	2	0	1	2	
<i>Cynops</i>	1	0	2	0	0	1	0	0	0	2	2	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	3	3	3	2	0	2	2	2	2	
<i>Paramesotriton</i>	1	0	0	2	1	1	0	0	0	2	9	0	2	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	2	9	0	0	1	3	2	3	3	0	1	2	0	1	2
<i>Hypselotriton</i>	1	0	2	1	0	0	0	2	9	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	9	0	0	1	3	3	3	0	2	2	2	2	2	
<i>Pachytriton</i>	1	0	2	2	1	1	0	0	2	2	9	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	9	2	1	3	3	3	0	2	1	2	1

TABLE 2. CHARACTER STATE TREES.

State relation	Character (see text)
0 → 1	1,5,6,7,8,12,14,15,18,20,21,22,23,25,28,30,31
0 → 1 → 2	2,3,4,10,11,13,17,19,24,26
0 → 1 — 2 → 3	16
0 ↗ <sup>1</sup> ↘ <sup>2</sup>	9,32,38
0 ↗ <sup>1</sup> ↘ <sup>2 → 3</sup>	27,35
1 — 2	29,33,39,40
1 — 2 — 3	34,37
1,2,3	36

and this, of course, places limitations on our interpretation. The body of data is relatively large and is derived from an examination of all genera. We have therefore prepared an analysis of evolutionary relationships.

Similarity matrices are presented in Table 3. Total similarity (in roman type) and similarity based on characters shared in other than known primitive states (in italics) are presented. In addition, on the diagonal (in bold face) is presented the percentage of characters for each genus that are in other than known primitive states; this is at least a rough approximation of the relative degree of divergence from a presumed common ancestor. Genera are listed from top to bottom in increasing degree of primitiveness. From the data in this table, we may select four generic groups for discussion: A. *Chioglossa*, *Salamandrina*, *Salamandra*; B. *Neurergus*, *Pachytriton*, *Notophthalmus*, *Triturus*, *Taricha*, *Euproctus*, *Paramesotriton*, *Hypselotriton*, *Cynops*; C. *Pleurodeles*; D. *Tylototriton*.

*Chioglossa*, *Salamandrina*, and *Salamandra* are about equally derived (by our gross estimation, Table 3, diagonal) from a presumed familial ancestor. These genera are considerably more derived in the characters analyzed than the remaining genera. Among the remainder, *Neurergus* and *Pachytriton* are the most derived, and *Tylototriton* is the most primitive.

Based on the percentage of total characters shared in the same state, regardless of

whether the states are primitive or derived, *Hypselotriton* and *Cynops* have the greatest phenetic similarity (89%). The lowest similarity among genera of group B is 68% between *Pachytriton* and *Notophthalmus*. In contrast, the highest similarity in group A is 63% (*Chioglossa-Salamandra*) and the lowest is 46% (*Salamandrina-Salamandra*). The highest similarity between members of groups A and B is 43% (*Chioglossa-Neurergus*) and the lowest is 25% (*Pachytriton-Salamandrina*). *Pleurodeles* is most similar to *Salamandra* (49%) and least to *Chioglossa* (42%) among genera of group A, and to *Hypselotriton* (68%) and *Pachytriton* (50%) respectively among group B. *Tylototriton* is most similar to *Salamandra* (39%) and least to *Chioglossa* (32%) among genera of group A, and to *Hypselotriton* and *Taricha* (68%), and to *Pachytriton* (50%) respectively among group B. *Pleurodeles* and *Tylototriton* share 85% of their characters in the same state.

As discussed earlier, we believe that more information concerning phylogeny is to be derived from an analysis in which character states known to be primitive for the primary group as a whole are excluded (such as italicized matrix in Table 3), than one in which these states are included. When states known to be primitive are excluded, the similarity matrix is considerably modified, especially among those genera which retain many primitive characters. The highest degree of similarity now is 47% (*Chioglossa-Salamandra*) and occurs within group A rather than group B. The lowest similarity

TABLE 3. SIMILARITY MATRICES<sup>1</sup> FOR SALAMANDRID GENERA.

		Genus													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	<i>Chioglossa</i>	<b>74</b>	57	63	43	35	30	37	30	40	38	36	40	42	32
2	<i>Salamandrina</i>	43	<b>73</b>	46	31	25	28	35	31	30	39	28	30	46	38
3	<i>Salamandra</i>	47	35	<b>72</b>	32	30	26	27	29	26	35	28	28	49	39
4	<i>Neurergus</i>	27	17	19	<b>53</b>	78	79	84	82	82	87	78	82	55	55
5	<i>Pachytriton</i>	22	14	16	41	<b>53</b>	68	76	70	87	78	81	82	50	50
6	<i>Notophthalmus</i>	16	14	13	34	27	<b>51</b>	80	87	69	84	76	74	56	62
7	<i>Triturus</i>	21	22	13	37	34	33	<b>50</b>	77	78	87	78	85	55	58
8	<i>Taricha</i>	16	14	13	37	30	39	31	<b>46</b>	72	84	78	80	64	68
9	<i>Euproctus</i>	24	14	15	37	42	23	30	26	<b>45</b>	82	81	83	53	58
10	<i>Paramesotriton</i>	22	19	19	40	35	34	37	32	32	<b>45</b>	78	82	63	66
11	<i>Hypselotriton</i>	19	11	14	32	33	27	30	27	30	27	<b>41</b>	89	68	68
12	<i>Cynops</i>	21	14	13	34	34	26	35	28	30	29	32	<b>40</b>	63	63
13	<i>Pleurodeles</i>	21	22	23	16	16	13	15	15	13	16	19	15	<b>38</b>	85
14	<i>Tylototriton</i>	11	14	13	11	11	13	13	13	13	13	14	10	23	<b>30</b>

<sup>1</sup> Roman type—total similarity (per cent); *italics*—similarity (per cent) in characters shared in other than known primitive states; **bold face**—percentage of characters that occur in states other than known primitive states.

among genera of group A (35%, *Salamandra-Salamandrina*) is high relative to the family as a whole. The highest degree of similarity among genera of group B is 42% (*Euproctus-Pachytriton*) and the lowest is 23% (*Euproctus-Notophthalmus*). The average similarity within group B is now 30%, which contrasts strikingly with the average of 77% when primitive states are included (Figs. 3, 4). By contrast, average similarity within group A has dropped only from 51% with primitives included to 39%. The highest similarity between members of groups A and B is 27% (*Chioglossa-Neurergus*) and the lowest is 11% (*Salamandrina-Hypselotriton*). *Pleurodeles* is almost equally similar to all members of group A (21–23%), but is most similar to *Hypselotriton* (19%) and least similar to *Euproctus* and *Notophthalmus* (13%) among genera of group B. *Tylototriton* and *Pleurodeles* share only 23% of their characters in states other than those known to be primitive. This is a figure equivalent to the lowest similarity within group B. *Tylototriton* has so few non-primitive states that further comparisons are relatively meaningless (range from 10–14%).

#### EVOLUTIONARY PATTERNS AND RELATIONSHIPS

From the data presented in the comparative parts of this paper, from our analysis of functional morphology, and from the character analysis presented above we have formulated an hypothesis concerning the

phylogenetic relationships within the family Salamandridae. The family is represented by a rather good fossil record (for list of currently recognized species see Brame, 1967). Most of the fossils are represented only by vertebrae, however, and these are currently being studied by several workers. In addition, studies are being conducted on vertebral morphology of recent forms in the laboratory of the senior author and these indicate that modern salamanders are so poorly known in terms of vertebral variation that meaningful interpretation of fossil vertebrae is not possible at this time. For these reasons and because very little information concerning those anatomical features that we have studied is available from the fossils, we have chosen to use a deductive approach, utilizing as the primary data those presented in our previous paper (Özeti and Wake, 1969). We have sought character correlations and in this search we have been greatly aided by computer programs prepared by Joseph Felsenstein and Glenn Sharrock, both of the University of Chicago. These procedures have enabled us to view our data from several standpoints, and the result of this analysis is the cladogram, discussed below, presented in Fig. 7. Four phenograms (Figs. 1–4), prepared by single and average linkage clustering methods (Sokal and Sneath, 1963) are useful in illustrating phenetic relationships. Two cladograms (Figs. 5, 6) have been generated by electronic digital computers. One (Fig. 5) was prepared by

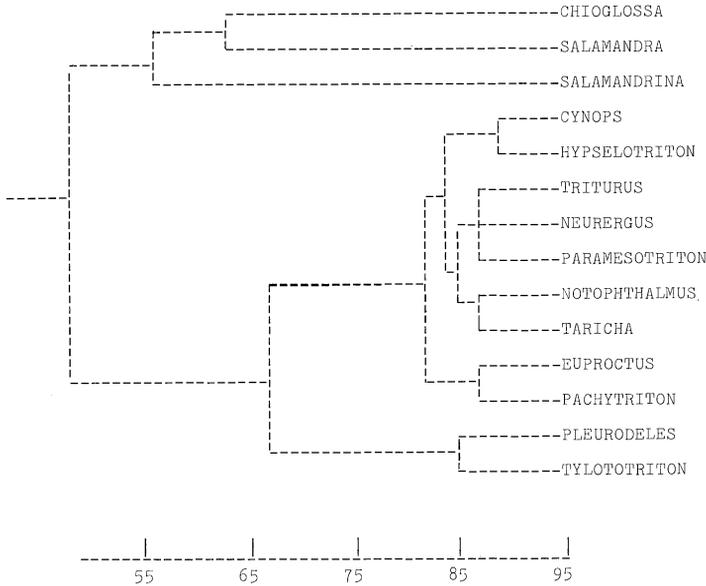


Fig. 1. Relationships of salamandrid genera. Phenogram constructed by single linkage method with primitive states included.

utilizing the minimum evolutionary steps method of Camin and Sokal (1965). The other (Fig. 6) is based on a computer program prepared by Joseph Felsenstein. This method attempts to minimize the number of convergences in the tree. Where convergence cannot be avoided, the convergent taxa are

placed as close together as possible. It utilized the character state trees and is a phylogenetic method (cf. Inger, 1967).

Comparison of phenograms constructed by the same method, but with primitive states included in one case and excluded in the other, is instructive. In Figs. 1 and 3 primi-

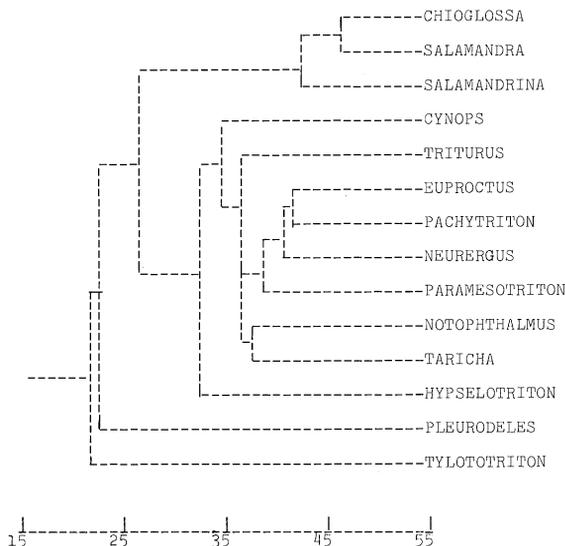


Fig. 2. Relationships of salamandrid genera. Phenogram constructed by single linkage method with known primitive states excluded.

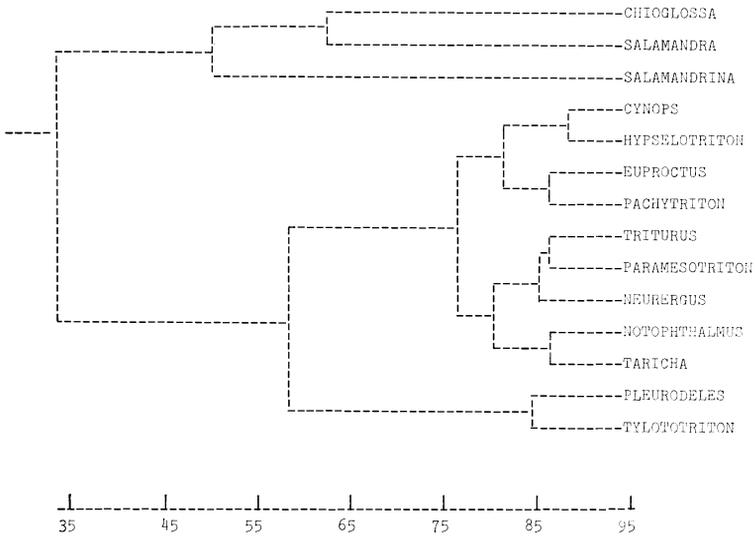


Fig. 3. Relationships of salamandrid genera. Phenogram constructed by average linkage method with primitive states included.

tive states have been included. In both two very distinct phenetic groups are evident. Similarities are low in the *Chioglossa-Salamandra-Salamandrina* group. The remaining genera fall into two groups, a *Triturus* group in which similarities are very high, and a *Tylostotriton-Pleurodeles* group with the similarity at a very high level. When

resemblances based on shared primitive states are excluded (Figs. 2, 4) the pattern is rather drastically changed. *Pleurodeles* and *Tylostotriton* are joined at a very low level, and the average similarity within the *Triturus* group is also low. The *Salamandra* group is at the relatively highest level of the three. The similarities of genera within the *Salamandra*

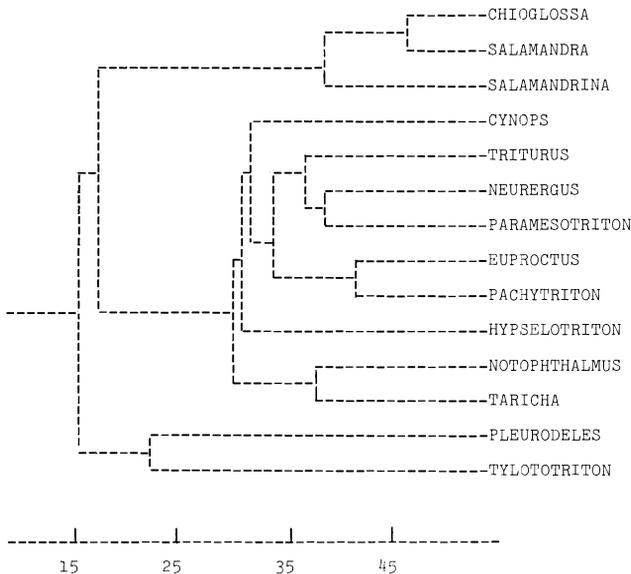


Fig. 4. Relationships of salamandrid genera. Phenogram constructed by average linkage method with known primitive states excluded.





a close relative of *Pachytriton* by some authors (Herre, 1935; Steiner, 1950), but von Wahlert (1953) and Freytag and Petzold (1962) have emphasized the closer relationship of *Pachytriton* to other east Asian genera, especially *Paramesotriton*. Based on overall similarity and especially on similar evolutionary trends in feeding mechanisms, we consider *Pachytriton* to be most closely related to *Hypselotriton*. The two may have arisen from an ancestral stock close to that which gave rise to *Cynops*. *Cynops* is the most generalized and *Pachytriton* the most specialized of these three genera. *Euproctus* was probably derived relatively early from the stock that gave rise to the *Notophthalmus-Taricha* and the *Triturus-Neurergus-Paramesotriton* subgroups. *Euproctus* contains three very distinct species and our generalizations concerning the genus are based on very scanty material. We have been unable to analyze interspecific variation and our statements concerning its relationships must be considered tentative.

*Notophthalmus* and *Taricha* are very distinct genera, but evidence for their close relationship is fairly good. They have been separated from each other for a very long time, for the Oligocene genus *Paleotaricha* is very similar to modern *Taricha* in most details.

We agree with Bolkay (1928), Herre (1932, 1935), von Wahlert (1953), and Steiner (1950) in considering *Neurergus* and *Triturus* to be very closely related.

*Paramesotriton* presents several problems. The genus contains three species, *P. deloustali*, a very distinctive species from Viet Nam, and the closely related *P. hongkongensis* and *P. chinensis*. The last two species were included until recently in the genus *Trituroides* (see Freytag, 1962). We have studied only *P. hongkongensis* which we consider to be more closely related to *Triturus* than to any other genus, but there is also evidence of relatively close relationship to other east Asian genera, especially *Cynops*. Freytag and Petzold (1961), on the basis of their studies on *P. deloustali*, suggested that the genus is closely related to *Cynops*. In terms of the feeding apparatus, however, the relationship of *P. hongkongensis*, at least, to *Triturus* seems closer than that to *Cynops*.

Several authors (e.g., Herre, 1935; von Wahlert, 1953) have considered *Salamandra* to be the most primitive salamandrid. On

the basis of our analysis, we conclude that *Tylostotriton* is the most primitive genus. In terms of feeding mechanisms, *Tylostotriton* is distinctly primitive. If it had a second basibranchial (some individuals apparently have, Noble, 1928), it would have a hyobranchial apparatus that would correspond precisely with our concept of that which was present in ancestral salamandrids. We suggest that a group of salamanders more primitive and generalized than modern *Tylostotriton* was widely distributed in Eurasia during late Mesozoic times. Modern *Tylostotriton* of southeast Asia has remained relatively close to this group in terms of morphological similarity, but the similarity is based on the very conservative, primitive nature of most features of *Tylostotriton*. Primitive salamandrids that were morphologically similar to modern *Tylostotriton* existed in Europe as late as Late Miocene (Noble, 1928; Herre, 1935), but no longer occur there. The ancestral stock of *Pleurodeles* probably diverged rather early; modern *Pleurodeles* has many primitive and generalized features. Today, *Pleurodeles* and *Tylostotriton* represent separate, conservative stocks derived with relatively little change from the Mesozoic ancestors of the family. The two genera have doubtless had very long, separate histories.

*Salamandra*, *Chioglossa*, and *Salamandrina* are the descendants of a third branch of the ancestral salamandrid stock. This branch diverged very early. The major trend within this group has been in the direction of terrestriality, with the extreme being found in the viviparous *Salamandra atra*. Of the three extant genera, ancestors of *Salamandrina* probably represented the first derivative stock. *Salamandrina* has become highly specialized, but within the framework of a primitive, generalized morphology (e.g., separated premaxillary bones, frontosquamosal arch, rough skin, etc.). *Salamandra* has also retained a number of primitive characters, but it has become specialized in several ways and a minor adaptive radiation has occurred within the relatively widespread genus (Özeti, 1967). *Chioglossa* is the most derived of the three genera, and it has many specializations. *Chioglossa* and *Salamandrina* are both highly specialized forms that have relict distributions in southern and western Europe. In general body form, in the relative mobility of the tongue, in its

coloration, and in its smooth skin and long tail, *Chioglossa* is remarkably convergent with plethodontids. The distinctly salamandrid skeleton and the tongue propulsion mechanism, which is very different from that of plethodontids, clearly demonstrates that convergence, rather than common ancestry, accounts for the similarity. In *Salamandrina* and *Chioglossa* tongue pad movements are dominant in feeding. In the adetoglossal plethodontids, the entire hyobranchial apparatus is projected, and tongue pads are neither as elaborated nor as mobile as in the salamandrids.

The remaining genera (*Euproctus*, *Triturus*, *Neurergus*, *Paramesotriton*, *Cynops*, *Hypselotriton*, *Pachytriton*, *Notophthalmus*, and *Taricha*) have probably been derived from an ancestral stock that may have been more similar to *Tylostotriton* than to any other modern salamandrid. Within this group of nine genera (our *Triturus* group) a clear trend in the direction of aquatic feeding specializations is apparent. However, more than simple aquatic habitation is involved, for the generalized *Pleurodeles* is more aquatic than many members of the *Triturus* group, which are structurally and functionally more specialized. The ancestors of the *Triturus* group were perhaps derived later and from a less generalized and less conservative stock than the ancestors of the *Pleurodeles* and *Tylostotriton* groups. However, even within the *Triturus* group, very generalized salamanders (e.g., *Cynops*) have survived, and the relatively extremely specialized forms such as *Pachytriton* are specialized within a framework that is primitive relative to such derived salamandrids as *Chioglossa*.

Differentiation within the *Triturus* group has been relatively extensive and has resulted in many more discrete phyletic lines (as reflected in the number of genera) than in the other three generic groups combined. In species diversity, too, the *Triturus* group is dominant. Of the 43 species of living salamandrids recognized by Brame (1967), 28 are in the *Triturus* group and 9 are species of *Triturus*. Yet the range of differentiation is not great, and, at least in terms of feeding mechanisms, the differences separating any two of the three genera in the *Salamandrina* group are greater than those within the entire *Triturus* group. The ancestral stock of the *Triturus* group probably arose in

western Eurasia and its success may have led to the extinction of the *Tylostotriton*-like populations that occurred in that region at least as late as Late Miocene times. This stock may have become almost world-wide in distribution relatively early, perhaps by the beginning of Tertiary times. Disruption of this widespread group and subsequent differentiation of the isolated stock led to the present evolutionary patterns. Ancestors of *Euproctus* were probably derived relatively early; species of *Euproctus* today occupy montane streams, specialized environments, but they have retained some primitive features, notably the most primitive pattern of breeding behavior in the family (Salthe, 1967), that suggest very early derivation. In east Asia, descendants of a somewhat more derived stock than that which gave rise to *Euproctus* also invaded montane stream environments. From this were derived the specialized genera *Hypselotriton* and *Pachytriton*, the latter the most extremely specialized member of the *Triturus* group. The remaining genera have rather similar ways of life and they represent, in a sense, descendants of a common stock which have evolved partially in parallel. Each has its own unique features which have evolved in response to the selective pressures characteristic of the diverse region they have inhabited. *Triturus* today occupies most of Europe and Asia Minor, extending as far southeast as Israel. Its close relative, *Neurergus*, occupies Kurdistan and neighboring areas in the Middle East, regions peripheral to the south and east of the main *Triturus* range. The ranges of *Paramesotriton* and *Cynops* overlap in east-central China, but generally *Paramesotriton* ranges to the south and west (to North Viet Nam) and *Cynops* to the north and east (to Japan). *Taricha* inhabits western North America and *Notophthalmus* ranges throughout eastern North America and into Mexico. Thus today the more generalized but discrete lines derived from the generalized ancestral stock of the *Triturus* group tend to occupy distinct, sizable geographic regions, and these ranges may reflect the ancient disruption of the once widespread ancestral stock.

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