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CHARACTERS, CONGRUENCE AND QUALITY: A STUDY OF NEUROANATOMICAL AND TRADITIONAL DATA IN CAECILIAN PHYLOGENY

BY MARK WILKINSON

School of Biological Sciences, University of Bristol, Bristol, BS8 1UG, UK

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ABSTRACT

Previous phylogenetic analyses of caecilian neuroanatomical data yield results that are difficult to reconcile with those based upon more traditional morphological and molecular data. A review of the literature reveals problems in both the analyses and the data upon which the analyses were based. Revision of the neuroanatomical data resolves some, but not all, of these problems and yields a data set that, based on comparative measures of data quality, appears to represent some improvement over previous treatments. An extended data set of more traditional primarily morphological data is developed to facilitate the evaluation of caecilian relationships and the quality and utility of neuroanatomical and more traditional data. Separate and combined analyses of the neuroanatomical and traditional data produce a variety of results dependent upon character weighting, with little congruence among the results of the separate analyses and little support for relationships among the 'higher' caecilians with the combined data. Randomization tests indicate that: (1) there is significantly less incompatibility within each data set than that expected by chance alone; (2) the between-data-set incompatibility is significantly greater than that expected for random partitions of characters so the two data sets are significantly heterogeneous; (3) the neuroanatomical data appear generally of lower quality than the traditional data; (4) the neuroanatomical data are more compatible with the traditional data than are phylogenetically uninformative data. The lower quality of the neuroanatomical data may reflect small sample sizes. In addition, a subset of the neuroanatomical characters supports an unconventional grouping of all those caecilians with the most rudimentary eyes, which may reflect concerted homoplasy. Although the neuroanatomical data may be of lower quality than the traditional data, their compatibility with the traditional data suggests that they cannot be dismissed as phylogenetically meaningless. Conclusions on caecilian relationships are constrained by the conflict between the neuroanatomical and traditional data, the sensitivity of the combined analyses to weighting schemes, and by the limited support for the majority of groups in the majority of the analyses. Those hypotheses that are well supported are uncontroversial, although some have not been tested previously by numerical phylogenetic analyses. However, the data do not justify an hypothesis of 'higher' caecilian phylogeny that is both well resolved and well supported.

Key words: caecilians, Gymnophiona, phylogeny, characters, congruence, parsimony, compatibility, randomization tests, character weighting.

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I. INTRODUCTION

Phylogeneticists search constantly for previously underexploited evidence of relationships. This has led, most importantly, to the generation of much molecular data, but increasingly also to phylogenetic explorations of non-traditional morphological and behavioural data. The increasing diversity of types of data available for phylogenetic inference has spawned discussion of how best to analyse multiple data sets, particularly whether they should be analysed separately and the separate results examined for taxonomic congruence (e.g. Miyamoto & Fitch, 1995) or in combination (e.g. Kluge, 1989), or perhaps using a conditional approach where data are combined only when the partitions are judged sufficiently homogenous (e.g. Huelsenbeck, Bull & Cunningham, 1996). Wake (1993) used phylogenetic methods to investigate 'non-traditional' characters derived from her studies of the neuroanatomy of caecilians (Wake, 1985, 1992; Fritzsch & Wake, 1988; Schmidt & Wake, 1990). She described four separate neuroanatomical data sets, and reported the results of both separate and combined parsimony analyses of these data, but stressed that her analysis was preliminary and exploratory. Thus, while she aimed to be both speculative and provocative, she cautioned that she was not 'presenting herein what I construe to be solid phylogenetic hypotheses' (Wake, 1993, p. 43). More recently, Wake (1994) discussed the general problems of 'non-traditional' morphology in systematics and used her caecilian neuroanatomical research to illustrate these problems.

Many of the relationships suggested by Wake's (1993) analyses of her neuroanatomical data are difficult to reconcile with current views on the phylogeny of caecilians based on more traditional morphological data (Nussbaum, 1977, 1979; Duellman & Trueb, 1986; Hillis, 1991; Wilkinson & Nussbaum, 1996) and on recent

molecular studies using DNA sequence data (Hedges, Nussbaum & Maxson, 1993; Wilkinson, 1996*a*). These discrepancies prompt a number of questions that warrant further attention. Why do the non-traditional neuronanatomical data support non-traditional hypotheses of relationships? Do the neuroanatomical data differ in quality from more traditional morphological data? Can analyses of the neuroanatomical and more traditional morphological data be combined or used in tandem to resolve caecilian phylogenetic relationships more fully? Here I build upon Wake's (1993) preliminary study, briefly reviewing its limitations and re-evaluating the neuroanatomical characters used. Revised neuroanatomical data and more traditional data are analysed separately and in combination and subjected to a variety of randomization tests to enable comparison of the utility of non-traditional neuroanatomical and more traditional morphological characters in caecilian phylogenetics.

II. MATERIALS AND METHODS

(1) *Data*

Original neuroanatomical data are from Wake (1993). A revised neuroanatomical data set was compiled from Wake (1993), and from the primary literature, particularly Wake (1985, 1992), Fritzsch & Wake (1988) and Schmidt & Wake (1990). Traditional data, extended from that of Wilkinson & Nussbaum (1996), are based on the literature, dissections and observations of dry and cleared and stained skeletal material. Multistate characters were ordered by the method of intermediates (Wilkinson, 1992*a*) where possible, or otherwise left unordered. Complex characters were mostly interpreted as character complexes and represented using a reductive coding strategy (Wilkinson, 1995*a*).

(2) *Phylogenetic analyses*

Parsimony analyses were performed using PAUP 3.1.1 (Swofford, 1993). Except in constrained and bootstrap analyses, heuristic searches employed 10 random addition sequences and tree bisection and reconnection branch swapping, arbitrary resolutions were suppressed, and all most-parsimonious trees (MPTs) were retained subject to the limitations of available memory. Bootstrap (100 replicates) and constrained analyses, used to determine bootstrap proportions (Felsenstein, 1985) and Bremer support (Bremer, 1988; Källersjö *et al.*, 1992) used the CLOSEST addition sequence and retained a maximum of 100 MPTs. Bootstrap analyses with differential character weighting resampled characters with an equal probability and maintained their prespecified character weights. Bremer support values, the additional tree length required to overturn clades in MPTs, are expressed as percentage increases over MPT lengths to facilitate comparisons across analyses using different character weights. Strict and majority-rule component consensus trees were constructed using PAUP. Reduced cladistic consensus trees (Wilkinson, 1994, 1995*b*) and partition table summaries of common *n*-taxon statements (Wilkinson, Suter & Shires, 1996) were used to summarize unambiguous agreement among sets of MPTs using REDCON 2.0 (Wilkinson, 1995*c*). Safe taxonomic reduction (Wilkinson, 1995*d*, Wilkinson & Benton, 1995, 1996) was used to eliminate problematic underdetermined taxa in the revised neuroanatomical data without affecting the parsimonious interpretation of relationships

among the retained taxa. Relations of taxonomic equivalence were determined using TAXEQ2 (Wilkinson, 1995*e*).

A series of parsimony analyses were performed exploring different combinations of characters, and different character-weighting schemes. The original neuroanatomical, revised neuroanatomical, and traditional data sets were analysed with all characters equally weighted with multistate characters either ordered or unordered (additive or non-additive). Parallel analyses were performed on combined revised neuroanatomical and traditional data, supplemented by analyses using Farris's (1969) successive approximations approach to character weighting (SACW), a compatibility-based (LQP) approach using only characters with low Le Quesne probabilities (see below), and combinations of these approaches, in order to investigate the robustness of phylogenetic inferences to variations in character weighting (Wilkinson & Benton, 1996, Wilkinson, 1996*b*). Character weights based on best, average, or worst character rescaled consistency indices derived from MPTs with all characters weighted equally, were used in separate parallel SACW analyses.

The Le Quesne probability is a test statistic for the null hypothesis that a character is no less incompatible with the rest of the data than comparable random and phylogenetically meaningless characters. It is determined by random permutation of the character states of the character to taxa and comparison of the incompatibility count (number of pairwise incompatibilities between this and other characters) for the original character and the random permutations, i.e. it is a permutation tail probability (PTP). It is defined as the proportion of incompatibility counts (for the original and random permutations) having incompatibility counts as low or lower than that of the original unpermuted character (Wilkinson, 1992*b*, 1995*f*; Wilkinson & Nussbaum, 1996). The Le Quesne probability test is analogous to the randomization/permutation tests described by Archie (1989*a*) and by Faith & Cranston (1991) except that it is compatibility-based and is a test of individual characters rather than of entire data sets. Except for trivial differences, such as the focus on incompatibility rather than compatibility, the Le Quesne probability is equivalent to the frequency of compatibility attainment independently developed by Meacham (1994). Characters with Le Quesne probabilities greater than 0·05, determined using 9999 random permutations and PICA95 (Wilkinson, 1995*f*), were excluded in the LQP analysis, which was performed only with the unordered treatment of multistate characters.

Combined LQP and SACW analyses, also using only the unordered treatment of multistate characters, applied the variant SACW protocols described above, but used the LQP trees as initial estimates of phylogeny and character quality. Each combined analysis was performed using either only the reduced set of characters that pass the Le Quesne probability test, or all characters. The latter analyses provide an opportunity for characters excluded on the basis of their incompatibility counts to be reintroduced into the analysis.

The hypothesis that the Rhinatrematidae is the sister group of all other extant caecilians is supported by numerous traditional morphological characters (Nussbaum, 1977, 1979; Wilkinson & Nussbaum, 1996; Wilkinson, 1992*c*, 1996*c*) and is accepted here. Except for reanalyses of the original data (see Appendix) all analyses are performed without consideration of character polarity, and the trees are rooted so as to place the rhinatrematids as a monophyletic sister group of all other caecilians. Reference to Wake and/or the original study is to Wake (1993) unless otherwise noted.

(3) *Randomization tests*

In addition to the Le Quesne probability test, a number of other randomization tests were employed to assess congruence and data quality within and between data sets. Parsimony-based randomization tests (Archie, 1989*a*; Faith & Cranston, 1991) yielded parsimony permutation tail probability (PTP) test statistics (Faith & Cranston, 1991; Archie, 1989*b*) and homoplasy excess ratio (HER) descriptive statistics (Archie, 1989*c*). The tests were performed using the mhennig* heuristic search strategy of Henning86 (Farris, 1988) to analyse the data and PERMUTE (Wilkinson, 1992*d*) to prepare 99 randomly permuted data sets and to summarize the analyses. Compatibility-based randomization tests of entire data matrices yielded pairwise compatibility (PC) PTPs (Wilkinson, 1992*b*, 1995*f*), which can be defined as the proportion of data sets (original and randomly permuted) that have incompatibility counts lower or as low as the original. The PCPTP is identical to a test statistic, C, independently developed by Alroy (1994). Two compatibility-based descriptive statistics, analogous to the parsimony-based HER of Archie (1989*c*) were developed to compare data sets. The first of these incompatibility excess ratios (IER_1) is the mean incompatibility count for randomly permuted data minus the incompatibility count of the original data, divided by the mean count for randomly permuted data. The second (IER_2) is analogous but with the mean incompatibility count for randomly permuted data replaced with the 95% cut-off point in the distribution of incompatibility counts (i.e. the number of incompatibilities that is exceeded by 95% of the randomly permuted and original data). Compatibility-based randomization tests were performed with PICA95 using 999 random permutations. In all these randomization tests, missing entries were maintained in their original positions (i.e. not included in the random permutation) and logically or interdependent characters were tied so as to maintain their necessary mutual compatibility during the random permutation.

Farris *et al*. (1995) proposed a parsimony-based test of the congruence between data sets or partitions. In this test, the difference in lengths between MPTs for the combined data and the sum of the lengths of MPTs for each partition is used as a measure of conflict between the data sets. A parametric test of the significance of this conflict measure is determined by comparing it to that achieved by random partitions of the data into equivalently sized subsets of characters. Thus, this approach tests the null hypothesis that conflict between data partitions is no greater than it would be for random partitions. Here, I use an analogous compatibility-based test in which the measure of conflict is the between-partition incompatibility count (the sum of the pairwise incompatibilities of characters between data sets or partitions). An additional test in which the between-partition incompatibility count is compared to that achieved by random permutations of the assignments of character states to taxa for one of the partitions was used to test the null hypothesis that a given set of characters is no more congruent or compatible with a second set of characters than it would be by chance alone.

Given measures of data quality such as Le Quesne probabilities and the final weights of characters in the SACW analyses, the same random partitioning of data sets can be used to assess the significance of any differences in character quality. Here, I use average Le Quesne probabilities or character weights, and the numbers of characters of maximum weight as overall measures of the quality of the traditional and revised

neuroanatomical data sets, and compare this to these values for random partitions of the combined data. Each of these tests used 999 random partitions.

III. NEUROANATOMICAL DATA

(1) *Review of the original analyses*

Wake (1993) presented majority-rule component consensus trees with compatible minority components and selected tree statistics for her separate and combined parsimony analysis of the four neuroanatomical data sets. Her descriptions of the characters used and the distributions of character states across taxa are presented in the Appendix. Here, I present only a cursory review of her results, focusing primarily upon her analysis of the combined neuroanatomical data (see Appendix).

As Wake (1993) noted, the consensus tree for her combined analysis (Fig. 1, her fig. 5) includes several groups that are uncontroversial. For example, the rhinatrematids *Epicrionops bicolor* and *E. petersi* group together as do the two species of *Boulengerula* and all the ichthyophiids. In contrast, many other relationships are highly surprising and difficult to reconcile with current understanding of caecilian taxonomy and phylogeny based on more traditional characters. For example, the ichthyophiids nest within a heterogeneous assemblage of caeciliids, typhlonectids and scolecomorphids, whereas it is generally accepted that they are outside this group (Nussbaum, 1979, 1991; Duellman & Trueb, 1986; Nussbaum & Wilkinson, 1989; Wilkinson & Nussbaum, 1996; Hillis, 1991; Hedges *et al.* 1993; Walsh, 1986). Similarly, the representatives of three groups that are considered to be clades on the basis of morphological, cytogenetic and/or DNA sequence data (Nussbaum, 1986; Nussbaum and Ducey, 1988; Wilkinson, 1989; Hedges *et al.* 1993), the typhlonectids (*Chthonerpeton indistinctum*, *Nectocaecilia haydee* and *Typhlonectes natans*), the scolecomorphids (*Scolecomorphus uluguruensis*, *S. vittatus* and *S. kirkii*) and the Seychellean caeciliids (*Hypogeophis rostratus* and *Grandisonia alternans*) are not recovered as clades.

Majority-rule consensus trees, as used to summarize the original analyses, have important limitations. They tend to be well resolved whether there is a strong signal in the data or not, and the frequencies of occurrence of groups in MPTs is an extremely poor guide to the strength of inferred relationships (Wilkinson & Benton, 1996). Wake's (1993) consensus tree includes only seven nodes that occur in all (100%) of the fundamental trees. Thus only these relationships are supported unambiguously by the parsimonious interpretation of the data, and yet all of these nodes identify groups that are at odds with current understanding of caecilian phylogeny. Conversely, those groupings that are less controversial do not occur in all MPTs and are not well supported by the data, e.g. they all have zero Bremer support. Wake (1993, p. 50) concluded that the neuroanatomical data may be 'useful in particular at the generic level of analysis, since species within a genus often group together', although they equally often do not group together. More importantly, she suggested that the incongruence between her results and more conventional views may identify areas of surprising neuroanatomical convergence (e.g. between *Typhlonectes natans* and *Scolecomorphus kirkii*) that warrant further study.

Given the rather poor correspondence between relationships supported by the neuroanatomical data and those recognized on the basis of molecular and more

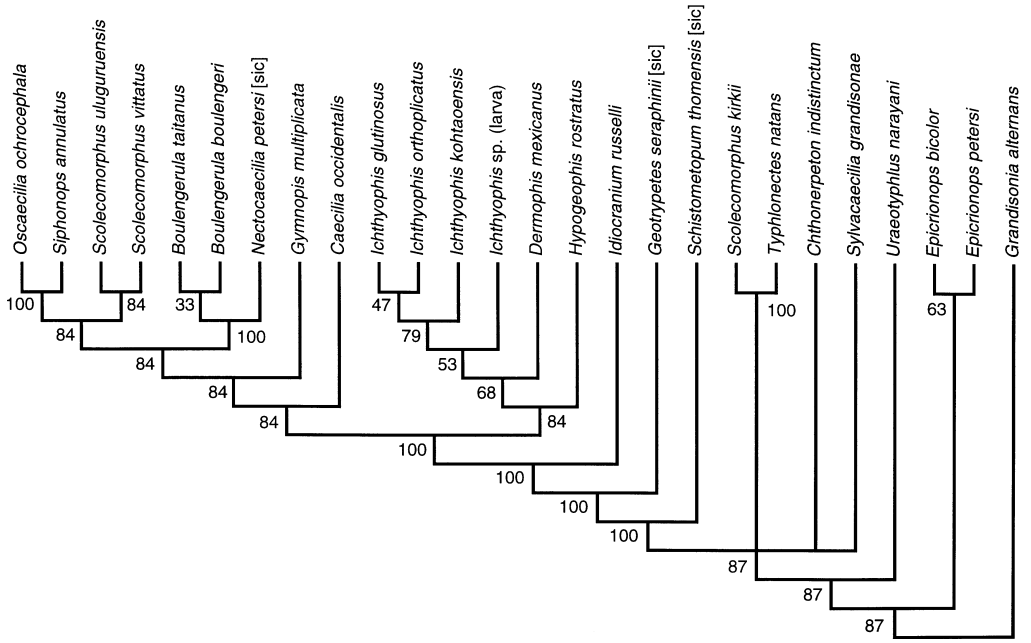


Fig. 1. Majority-rule component consensus tree with minority compatible components for the original combined neuroanatomical data. After Wake (1993).

traditional morphological data, and the ambiguity in the results of the parsimony analysis, the utility of neuroanatomical data for inferring caecilian phylogeny would seem rather limited, and perhaps also somewhat suspect. Certainly, Wake (1993) realized many of these limitations and did not seek to draw firm phylogenetic conclusions from her analyses. Equally, she did not dismiss the neuroanatomical data as phylogenetically uninformative, and such dismissal would be premature. There is no *a priori* reason to suspect that neuroanatomical data would be any less useful for phylogenetic inference than any more traditional morphological data. Further, as Wake (1993) stressed, the original study was only preliminary, and no attempt was made to compare the neuroanatomical data with more traditional morphological data. Unfortunately, the original analysis also suffers a number of problems that limit the conclusions that can be drawn from its results. Chief among these are issues of character construction and coding, methodological aspects of which have been discussed elsewhere (Wilkinson, 1995*a*). These problems are addressed below in a comprehensive revision of the neuroanatomical data. Other problems concern the repeatability of the original results.

Reanalysis of the original combined data set fails to replicate the original results. With all characters ordered, 1265 MPTs were found, and the majority-rule component consensus with compatible minority components (Fig. 2), with all characters ordered and rooted on a hypothetical ancestor, differs considerably from the original (Fig. 1). Of the 22 nodes in the original, only 13 are also present in the reanalysis. In the reanalysis, only two nodes are present in 100% of the MPTs, and these are not among the seven such nodes in the original tree. With all characters unordered, PAUP yielded 27 200 MPTs before the available memory was exhausted. The corresponding majority-

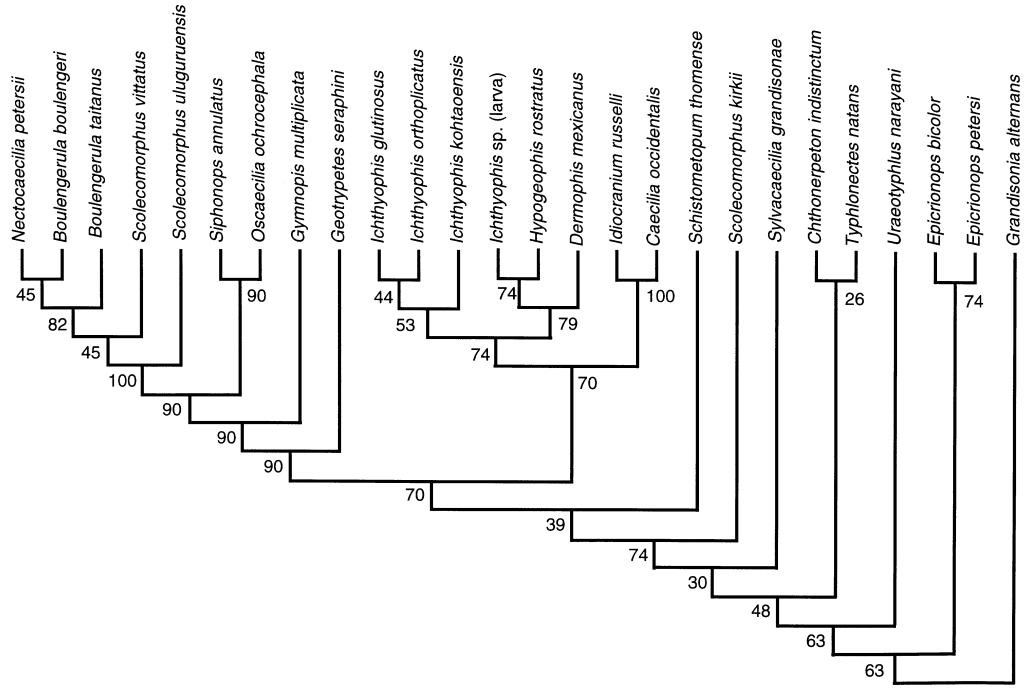


Fig. 2. Majority-rule component consensus tree with minority compatible components from 1265 MPTs produced in the ordered reanalysis of the original Wake (1993) combined neuroanatomical data.

rule component consensus with compatible minority components (Fig. 3) includes no nodes that are unambiguously supported by the parsimonious interpretation of the data, only two nodes in common with the original analysis, and only three nodes in common with the re-analysis with characters ordered. Noteworthy differences between the original and the re-analyses are the failure to recover an ichthyophiid clade and the recovery of a typhlonectid clade in both the reanalyses. Similarly, separate reanalyses of each of the four neuroanatomical data sets fail to yield the original results (see Appendix). I shall not dwell on the problem of repeatability. However, there is a clear need for a thorough review of the significance of the neuroanatomical data, and this must begin with a reconsideration of the characters.

(2) *Revised neuroanatomical data*

My revision of the neuroanatomical data is intended to produce a set of neuroanatomical characters comprising discrete character states taken as putative homologies for the phylogenetic analyses. This leads to some differences from the original treatment reflecting alternative strategies of character construction, the delimitation of character states, and ordering of multistate characters. Although I believe the changes wrought provide an improvement upon the original, some subjectivity is inevitable (Wilkinson, 1995*a*), and the changes should not be interpreted as criticisms of the approaches adopted in the original analysis. The revised data also differ from the original because of inconsistencies in the literature. Some of the inconsistencies between character states reported by Wake (1993) and earlier

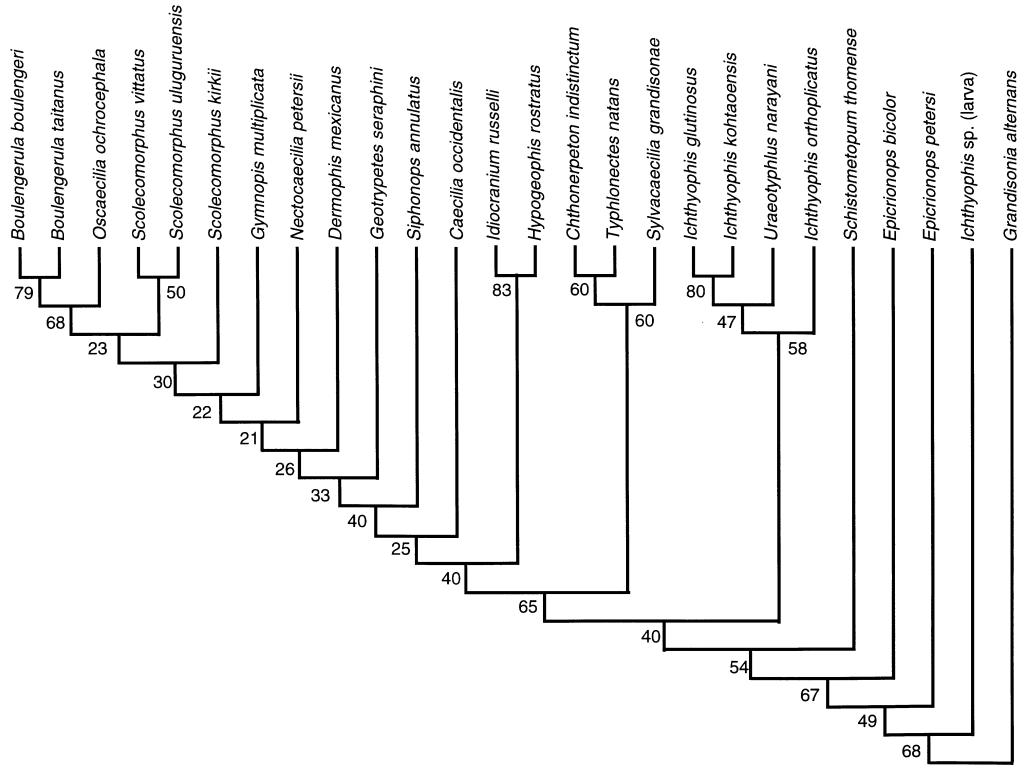


Fig. 3. Majority-rule component consensus tree with minority compatible components from 27 200 MPTs produced in the unordered reanalysis of the original Wake (1993) combined neuroanatomical data.

descriptions may be due to additional observations that could not be reported fully in Wake (1993) because of space constraints (M. H. Wake, personal communication). However, as we shall see, the existence of extensive contradictory reports indicates considerable difficulty in determining some character states confidently. In general, I have taken a conservative approach so that if the inconsistencies cannot be resolved convincingly based on published information, characters have been discarded or problematic taxa scored as equivocal (using missing entries) or eliminated. I have not succeeded in resolving all problems, some of which require detailed study of histological material and, as Wake (1993) noted, would benefit greatly from increased sample sizes. I provide no consideration of character polarity. Characters are numbered following Wake's (1993) treatment with an additional alphabetic identifier, E, A, H, O for the eye, ear, hypoglossal and olfactory-vomeronasal data sets, respectively. Where original characters are divided into more than a single character this numbering is supplemented by a decimal (e.g. E2 becomes E2·1 and E2·2). Multistate characters are ordered based on intermediacy unless otherwise stated. An asterisk indicates that no modification of the original treatment is proposed. Three of Wake's (1993) characters (A8, O2 and O5) are uninformative under parsimony in the context of this treatment and are not considered further here. The revised neuroanatomical data are summarized in Table 1.

Table 1. *Revised neuroanatomical data for caecilians. E, A, H and O indicate the eye, ear, hypoglossal and olfactory-vomeronasal characters respectively. X indicates coding as either {1, 2} for PAUP analyses or as missing. Details of characters are given in the text*

Taxa	E 1·1–6	E 2	E 3	E 4	E 6	E 10	A 1	A 2	A 3	A 5	A 9	A 10	H 1·1–4	H 2	H 5	O 1	O 3	O 4	O 6
Epicrionops bicolor	000000	0	0	0	0	0	0	0	0	0	0	0	011	1	2	?	?	?	?
Epicrionops petersi	000000	0	0	0	0	0	0	0	0	0	0	0	001	1	2	1	0	2	0
Ichthyophis glutinosus	000000	0	0	0	0	0	0	0	0	1	0	0	???	?	?	1	0	0	0
Ichthyophis kohtaoensis	??????	0	?	?	?	?	0	0	0	1	0	0	001	1	2	1	0	0	0
Ichthyophis orthoplicatus	000000	0	0	0	0	0	0	?	?	?	?	?	???	?	?	?	?	?	?
Uraeotyphlus narayani	000000	0	0	0	0	0	0	0	0	1	0	0	001	?	0	0	0	1	0
Scolecomorphus uluguruensis	111111	1	1	0	1	1	1	0	1	?	0	2	011	0	2	2	0	0	0
Scolecomorphus kirkii	11?1?1	1	1	1	1	0	1	0	1	?	0	2	???	?	?	2	0	0	0
Scolecomorphus vittatus	??????	1	?	?	?	?	1	?	?	?	?	?	011	0	2	?	?	?	?
Typhlonectes natans	??00?0	0	1	0	0	0	0	1	1	?	0	1	011	0	0	0	1	0	1
Chthonerpeton indistinctum	001010	0	1	1	0	0	0	1	1	?	0	0	011	1	?	0	1	0	1
Schistometopum thomense	100011	0	1	0	0	0	0	?	?	?	?	?	???	?	?	2	?	?	?
Siphonops annulatus	??????	0	?	?	?	?	0	?	?	?	?	?	011	0	?	2	?	?	?
Caecilia occidentalis	11??11	0	1	1	0	0	0	0	1	?	0	0	01?	1	1	0	0	1	0
Oscaecilia ochrocephala	11??11	0	1	0	1	1	0	1	1	?	1	0	01?	1	0	0	0	1	0
Hypogeophis rostratus	000000	0	1	1	0	0	0	0	1	?	0	0	011	1	1	0	0	1	0
Grandisonia alternans	??????	0	?	?	?	?	0	?	?	?	?	?	011	1	0	2	?	?	?
Dermophis mexicanus	000000	0	0	0	0	0	0	0	1	?	0	0	011	0	0	2	0	2	0
Gymnopis multiplicata	111111	0	1	1	0	0	0	0	1	?	0	0	011	0	0	2	0	2	0
Gegeneophis ramaswamii	111111	0	1	?	?	?	0	?	?	?	?	?	101	1	?	0	?	?	?
Boulengerula boulengeri	111111	0	1	1	1	2	0	1	1	?	1	0	110	1	2	0	0	0	0
Boulengerula taitana	111111	0	1	1	1	2	0	1	1	?	1	0	???	?	?	X	0	0	0
Geotrypetes seraphini	00?0??	0	1	1	0	0	0	0	1	?	0	0	011	0	0	2	0	1	0
Sylvacaecilia grandisonae	00?0??	0	1	1	0	0	0	?	?	?	?	?	???	?	?	0	0	0	0
Idiocranuium russelli	?000??	0	1	1	1	0	0	0	1	?	0	0	010	1	1	0	0	1	0

(*a*) *Taxonomic problems*

Firstly, some taxonomic problems must be addressed. Taxon names were transposed accidentally in two of the original data matrices leading to a mismatch between taxa in the data matrices and those in the corresponding trees, although this did not affect the analyses (M. H. Wake, personal communication). Here, the eye data reported for *I. kohtaoensis* are attributed to *I. orthoplicatus*, and ear data reported for *I. orthoplicatus* are attributed to *I. kohtaoensis*. The original study also included data for a larval *Ichthyophis* sp. Given that ichthyophiids undergo a metamorphosis and that comparisons across different life-history stages may obfuscate phylogenetic relationships (Hennig, 1966), I have not included this taxon in the revised data set.

The hypoglossal nerve data matrix includes '*Nectocaecilia haydeii*' [sic] (transposed to *N. petersii* on the corresponding tree). This taxon is not one of those examined by Wake (1992); rather, the information for this taxon is based on Leutenegger (1972). *Nectocaecilia haydee* had been considered a taxon of doubtful validity (Wilkinson, 1988, 1989; Nussbaum & Wilkinson, 1989), and recent examination of the holotype confirms that it is a junior synonym of the aquatic caecilian *Typhlonectes natans* (Wilkinson, 1996*d*). *T. natans* is also included in Wake's (1993) hypoglossal nerve data matrix, and is reported as differing from *N. haydee* in having spinal 2 incorporated into the hypoglossal. Given that *N. haydee* is now known to be a synonym of *T. natans*, and assuming that the reported observations are not in error, there are two possible conclusions: (1) there is intraspecific variation in the composition of the hypoglossal nerve in *T. natans*; or (2) the specimen examined by Leutenegger (1972) was not *T. natans*, but a representative of some other species. Intraspecific variation would not be surprising, but the alternative is also a realistic possibility given the difficulty of identifying typhlonectid caecilians (see Wilkinson, 1981, 1988, 1989, 1991, 1996*d*, *e*). I have excluded *N. haydee* from this treatment. *Typhlonectes natans* is included in all four of Wake's (1993) data sets, but in her original study of caecilian eyes (Wake, 1985), it is *T. compressicauda* that is listed in the material examined. Fritzsch & Wake (1988) list *T. natans* as the *Typhlonectes* species they examined, but the legend to their Fig. 4*b* refers to *T. compressicauda*. In fact, all such neuroanatomical observations reported by Wake and her co-workers discussed in this paper are based on *T. natans* (M. H. Wake, personal communication, see Wilkinson, 1991 for further comment).

The hypoglossal data set includes *Gegeneophis ramaswamii*, but this taxon is not included in the corresponding tree and was not included in the original analyses (M. H. Wake, personal communication). It is included here. Wake's (1993) data for this terminal taxon are from Ramaswami (1943), who reported working on another species, *G. carnosus*. Taylor (1964) described *G. ramaswamii* and noted that this was presumably the species that was studied by Ramaswamii (1943). I follow Taylor (1964) and Wake (1993) in attributing Ramaswami's (1943) observations to *G. ramaswamii*, and also draw upon his observations to code this species for characters E1 and E3.

(*b*) *Eye characters*

E1·1: Rectus externus present (0), or not (1).
E1·1: Rectus internus present (0), or not (1).

E1·3: Rectus superior present (0), or not (1).
E1·4: Rectus inferior present (0), or not (1).
E1·5: Superior oblique present (0), or absent (1).
E1·6: Inferior oblique present (0), or not (1).

Characters E1·1–1·6 are the reductive coding of Wake's (1993) multistate composite character E1. In essence, composite coding identifies combinations of features, such as the extrinsic eye musculature, seen in terminal taxa as character states of a complex multistate character (one character state for each observed combination). In contrast, reductive coding breaks the variation down into separate characters (e.g. the condition of each intrinsic eye muscle) that are part of a character complex. The distinction between reductive and composite coding was not current at the time of the original analysis, but Wilkinson (1995*a*) has discussed this in some detail and illustrated the approaches with examples drawn from the original neuroanatomical data. He also elaborated reasons for a general preference for reductive coding when the reductive characters do not covary.

There are three main sources of information on the extrinsic eye muscles of caecilians, the individual species descriptions and the discussion of Wake (1985) and Wake's (1993) data matrix. There are several inconsistencies between these sources. Inconsistencies between Wake (1993) and Wake (1985) may reflect additional unpublished observations of additional material (M. H. Wake, personal communication). However, inconsistencies within Wake (1985) suggest that some character states for some taxa may be difficult to determine and are best considered uncertain and in need of further study. Wake (1985, p. 292) states that all six muscles are present in *Typhlonectes natans*, *Geotrypetes seraphini*, *Sylvacaecilia grandisonae* and *Idiocranium russelli*, and that, in the latter three, the superior oblique is attenuate and slips of the rectus externus are difficult to separate from the retractor tentaculi. In contrast, *T. natans* has only five muscles (rectus internus absent) according to the description (p. 284). However, Wake (1985, p. 284) also states that there are possibly a few fibres of this muscle in the same plane as the retractor tentaculi which, referring back to her discussion, would be true of the rectus externus. In the data matrix, *T. natans* is coded as having all six muscles and, in contrast to the discussion, it is the only taxon coded with an attenuate superior oblique. There is thus some uncertainty over the presence/absence of the rectus externus and rectus internus and the condition of the superior oblique, and I have coded *T. natans* as uncertain (with missing entries) for the corresponding characters (E1·1, E1·2 and E1·5) and ignored variation in the development of the superior oblique when present.

Wake's (1985, p. 280) description of *Geotrypetes seraphini* also contradicts the discussion (Wake, 1985, p. 292), reporting just four muscles (rectus externus, rectus internus, rectus inferior and one, unspecified, obliquus). The matrix corresponds to this description with the identity of the obliquus specified (as an inferior oblique). I have scored those muscles that may (discussion) or may not (description and matrix) be present as uncertain. Parallel contradictions in the various reports of *Sylvacaecilia grandisonae* and *Idiocranium russelli* also introduce missing entries into the revised data.

In the original composite treatment, character E1 includes seven character states but no taxon is scored with state 1e (only the rectus inferior present). Wake (1985, p. 282) reported finding 'One postero-ventral extrinsic muscle present, another may be

represented by a stout connective tissue strand' in *Oscaecilia ochrocephala*. In *Caecilia occidentalis*, Wake (1985, p. 280) reported 'Only the rectus inferior identifiable of extrinsic muscles; present as a few fibres only on the right orbit, absent from the left in my sections' but later (p. 292) reported that there were three muscles ('recti superior, inferior and medialis'). In the data matrix, these two taxa are scored with state 1d (rectus superior and rectus inferior present). Given that Wake (1985) did not originally identify the muscle of *O. ochrocephala* as the rectus inferior and was unsure if another muscle was represented or not, and that she found this muscle on only one side of a single specimen in *C. occidentalis*, I have scored both taxa as uncertain with respect to the presence or absence of both the rectus inferior and rectus superior (E1·3 and E1·4).

Wake (1985, p. 282) reported for *Scolecomorphus kirkii* that 'Two attenuate extrinsic muscles attach to orbit, probably retractor [sic] inferior and superior oblique'. However, the matrix indicates the presence of the rectus inferior and rectus superior. Given the confusion as to whether the second muscle is a rectus superior or a superior oblique, I have scored both as uncertain.

E2: Eye in orbital chamber (0), or riding on the tentacle (1).

In scolecomorphids, 'the eye in the young is covered solidly by bone and is imbedded in the internal structure of the tentacle. As the tentacle grows forward, it pulls the eye forward into the tentacular groove or trench and often completely from under the bone' (Taylor, 1968, p. 632). The peculiar association between eye and tentacle, which is one of several highly unusual derived features of the Scolecomorphidae, was not included in the original data. The original E2 is an associated osteological character, describing whether the eye is covered with bone or not, that has been included in more traditional morphological data matrices (e.g. Nussbaum, 1979). In the original, the scolecomorphids are coded as having the primitive condition of E2, eye under skin. Although this coding is literally correct for adult scolecomorphids, given the original formulation of the character, the formulation ignores the lack of positional homology between the eyes of scolecomorphids and other caecilians.

Wherever the eye is covered with bone it is due to bony closure of the orbit. In scolecomorphids, the orbit is similarly closed but the eye is not covered with bone (in adults) because of its anterior migration out of the orbit (a derived feature). The effect of the original treatment is to score those taxa with both bony closure of the orbit (derived) and eyes in the orbit (primitive) as having the derived condition, and those with either (*a*) no bony closure of the orbit (primitive), or (*b*) both bony closure of the orbit (derived) and eyes that have migrated from the orbit (derived) as having the primitive condition. In the present treatment, E2 describes the relationship between the eye and the tentacle. Variation in the bony closure of the orbit is represented in the traditional morphological data (T28) and is not repeated here. I have also added data for those taxa that were not included in the original eye data set.

E3: Optic nerve well developed (0), attenuate or absent (1).

In the original treatment, this character has three states (0, 1a, and 1b – well developed, attenuate and absent). In the matrix, *Schistometopum thomense* is scored '1' but should have been '1a' (M. H. Wake, personal communication). Wake (1985, p. 290) wanted to 'await better material of *Boulengerula boulengeri* and *Scolecomorphus uluguruensis* before declaring the nerve absent', but Wake (1993) treated absence of the nerve as a separate state for these two taxa. M. H.Wake (personal communication) now

considers the attenuate an inappropriate (non-homologous) character state and I have not made use of the distinction between attenuate and absent here.

E4*: Vitreous body present (0), or absent (1).

E5: In the original treatment, this character describes the organization of the retina. This variation is also encompassed in characters E7–E9 (see below) which describe the organization of the separate cell layers of the retina. Thus, E5 was redundant in the original analysis and may have resulted in overweighting. This and the other retinal characters (E7–E9) are not included here (see below).

E6*: More than 5000 retinal cells (0), or less (1).

E7–E9: Characters E7–E9 partitioned variation in the number of cell layers in different regions of the retina. As with the extrinsic eye muscles, there are three sources of information on the numbers of cell layers in the different regions of the retina (E7–9), the individual species descriptions and a summary table (p. 290) of Wake (1985), and the matrix of Wake (1993). Wake (1993) described variation in the outer layer (E7) with a three-state character (0, 1a and 1b, corresponding to 2, 1-2 and 2-3 cell layers), but in the data matrix two taxa, *Boulengerula taitanus* and *B. boulengeri* are coded as an undefined state 1c. Wake (1985, pp. 282, 290) did not report the number of cell layers for these taxa because the retina is vestigial and the layers cannot be readily distinguished, a condition that was intended to correspond with the undefined state 1c (M. H. Wake, personal communication). Both *Scolecomorphus uluguruensis* and *Uraeotyphlus narayani* are reported to have a single outer layer in the species descriptions of Wake (1985) but as having two layers in the accompanying summary table and in the matrix. The original ordering of this character is surprising because it implies a sequence of evolutionary transformations that begins with a decrease in the number of cell layers and is followed by an increase to more than the original primitive number of cell layers without any discussion of what evidence might support this hypothesis over the alternative scenario in which there is an initial increase and subsequent decrease in the number of cell layers.

In the original treatment, E8 is a six-state character (3-4, 3, 3-2, 2, 1, and 0 cell layers in the inner cell layer), and E9 is a five-state character (2, 1-2, 1, > 2, and 0 cell layers in the ganglionic cell layer). As with E7, the original ordering of E9 is not sensible. No taxa are coded as state 1e (no cell layers) of E8, and the two *Boulengerula* species and *Scolecomorphus uluguruensis* which appear to fit this character state (Wake, 1985) are coded as state 1d (1 cell layer). In E9, *B. boulengeri* is coded as having 1-2 cell layers. Wake (1993) distinguished 2 or > 2 as separate character states for the ganglionic layer (E9). *Ichthyophis glutinosus*, *I. orthoplicatus*, *Typhlonectes natans* and *Hypogeophis rostratus* are coded as having > 2 ganglionic cell layers in the matrix but are reported to have two cell layers in the description and summary table. Finally, *T. natans* is also described as having two outer and three inner cell layers in the species description (Wake, 1985, p. 284) but 1-2 and two respectively in the summary table and matrix.

Given the overlap between many of the original character states, uncertainty over the condition in several taxa in each of the three characters that is not easily resolved, and the small sample sizes on which the observations are based (typically a single specimen), I have not included these problematic characters here. Rehabilitation of any of these characters requires additional observations.

E10: Lens present (0), rudimentary (1), or absent (2).

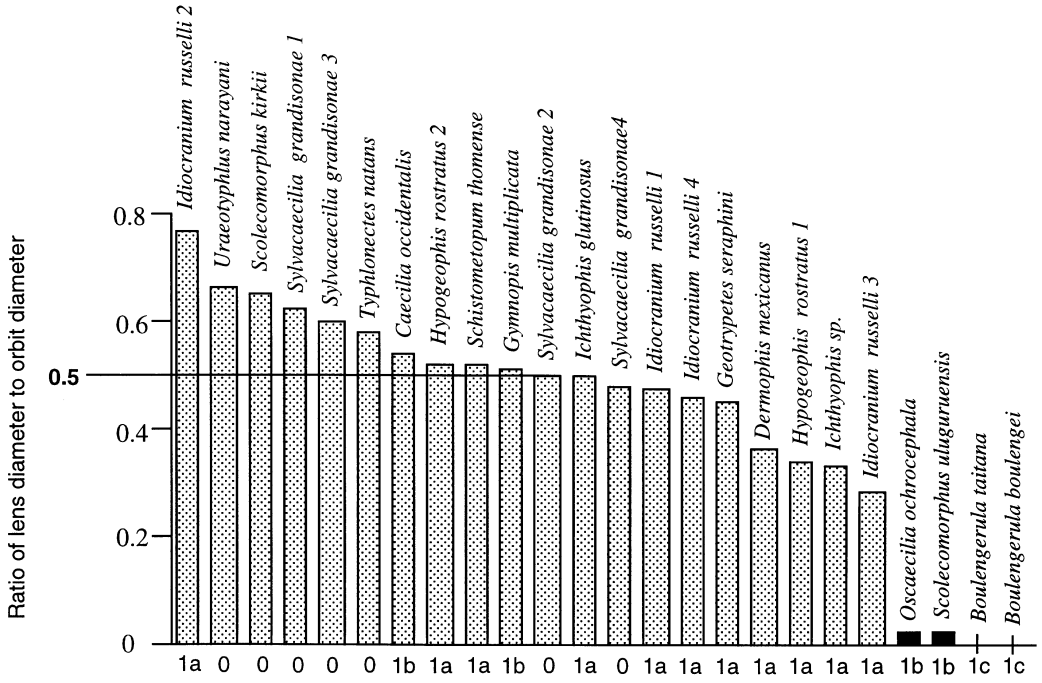


Fig. 4. Ratios of the size of the lens to the size of the orbit for caecilian taxa based on the data of Wake (1985) and the character coding (lens ⩾ half orbit diameter [0]; < half orbit diameter [1a]; absent [1b], state 1c not explained) employed by Wake (1993). Solid boxes indicate a vestigial lens, lines indicate absence of the lens.

The original character states of E10 reflected differences in the ratio of the size of the lens to the size of the orbit with a cut-off between states 0 and 1a where this ratio is 0·5. Fig. 4 shows the distribution of this ratio relative to the 0·5 cut-off based on the data of Wake (1985). Where taxa are represented more than once this reflects alternative ratios based on reported dimensions of an asymmetric orbit and/or lens. There is no break in the distribution of these ratios that supports the use of 0·5 as a boundary between character states. Further, the assignment of *Sylvacaecilia grandisonae*, *Hypogeophis rostratus* or *Idiocranium russelli* to one of these states must depend on which measures of the orbit or lens are used. Finally, some of the character states used in the original do not fit the data of Wake (1985). For example, the *Boulengerula* species are coded as state 1c but there is no corresponding state description, and *Gymnopis multiplicata* and *Caecilia occidentalis* are erroneously coded as lens absent. In view of these problems, I have recoded the character to reflect the three states that can be clearly differentiated, and have ignored variation in the lens/orbit ratio.

E11–E13: Character E11–13 (and E10 described above) describe variation in the size, shape, composition and attachment of the lens and are not entirely independent. In the original formulation, 'lens absent' was a terminal character state in E10–12 (although not in E13) and was thus repeated and overweighted. Tables 2–4, provide summaries of characters E11–13, respectively. Each Table includes a summary of the individual species description provided by Wake (1985) together with an attempt to predict the character state used in the original study based on these descriptions (i.e. the character

Table 2. *Summary of character E11 describing the shape of the lens. 0, round*; *1a, spheroid*; *1b, amorphous*; *1c, absent. D, individual species description from Wake (1985)*; *P, character state predicted based on D*; *T, character state based on summary table of Wake (1985)*; *M, character state in matrix of Wake (1993)*

Taxon	D	P	T	M
Ichthyophis glutinosus	Slightly spherical	1a?	1a	1a
Ichthyophis orthoplicatus	Same as *I. glutinosus*	1a?	1a	1a
Ichthyophis sp. (larva)	A sphere	1a?	1a	0
Uraeotyphlus narayani	Round	0	0	1a
Dermophis mexicanus	Spherical	1a?	1a	0
Caecilia occidentalis	Amorphous	1b	—	1a
Hypogeophis rostratus	Slightly spherical	1a?	1a	0
Geotrypetes seraphini	Round	0	1a	0
Sylvacaecilia grandisonae	Virtually round	0?	0	1a
Schistometopum thomense	Spheroid	1a	1a	1a
Idiocranium russelli	Somewhat flattened	?	1a	0
Oscaecilia ochrocephala	Amorphous	1b?	—	1b
Gymnopis multiplicata	Amorphous	1b	—	1a
Boulengerula taitanus	Absent	1c	—	1b
Boulengerula boulengeri	Absent	1c	—	1b
Scolecomorphus kirkii	Round	0	0	1a
Scolecomorphus uluguruensis	Rudimentary	1b?	—	1b
Typhlonectes natans	Round	0	0	1a

Table 3. *Summary of character E12 describing the structure of the lens. 0, crystalline*; *1a, cellular peripherally, crystalline medially*; *1b, crystalline peripherally, cellular medially*; *1c, cellular amorphous*; *1d, rudimentary*; *1e, absent. Other abbreviations as in Table 2*

Taxa	D	P	T	M
Ichthyophis glutinosus	Crystalline, cellular laterally	1a	1b	1a
Ichthyophis orthoplicatus	Cellular internally, laminate peripherally	1b	1b	1a
Ichthyophis sp. (larva).	Crystalline, cellular laterally	1a	1a	1b
Uraeotyphlus narayani	Cellular centrally, lamellar laterally	1b	1b	1a
Dermophis mexicanus	Somewhat cellular	1c?	1c	1d
Caecilia occidentalis	Cellular amorphous	1d	1d	0
Hypogeophis rostratus	Cellular centrally, laminar peripherally	1b	1b	1a
Geotrypetes seraphini	Cellular centrally, laminar peripherally	1b	1c	1c
Sylvacaecilia grandisonae	Vestigially cellular	1c?	1b	1a
Schistometopum thomense	Acellular centre, lamellar peripherally	0?	1a	1a
Idiocranium russelli	Crystalline few nuclei	0	1a	1a
Oscaecilia ochrocephala	Vestigial, few nuclei	1e	1e	1d
Gymnopis multiplicata	Amorphous	1d?	1d	1d
Boulengerula taitanus	Absent	1f	1f	1f
Boulengerula boulengeri	Absent	1f	1f	1f
Scolecomorphus kirkii	Cellular (few)	1c?	1c	0
Scolecomorphus uluguruensis	Rudimentary	1e	1e	1d
Typhlonectes natans	Slightly cellular	1c?	1c	0

state interpreted as closest to the descriptions) and the actual character state assigned by Wake (1993). In each case, the descriptions are only poorly correlated with the assigned character states and there are additional problems. For example, in E13 (Table 4), taxa lacking a lens are coded as having it attached to the cornea and retina. Some of

Table 4. *Summary of character E13 describing the relation of the lens to the cornea and retina. 0, free; 1a, attached to cornea; 1b, attached to cornea and retina. Abbreviations as in Table 2*

Taxa	D	P	M
Ichthyophis glutinosus	Free of cornea, adjacent peripherally	0	1a
Ichthyophis orthoplicatus	Attached to cornea and retina	1b	1a
Ichthyophis sp. (larva)	Not adherent to cornea or retina	0	0
Uraeotyphlus narayani	Adheres to cornea, and to retina except centrally	1b?	1a
Dermophis mexicanus	Adherent to cornea	1a	0
Caecilia occidentalis	Fused to cornea and retina	1b	1a
Hypogeophis rostratus	Adherent to cornea and retina	1b	1a
Geotrypetes seraphini	Adherent to cornea and retina	1b	1a
Sylvacaecilia grandisonae	Adheres to cornea	1b?	1a
Schistometopum thomense	Free of cornea, held to retina by connective tissue strands	0	0
Idiocranium russelli	Fused to cornea and medial aspect to retina	1b?	1a
Oscaecilia ochrocephala	Vestigial	?	1b
Gymnopis multiplicata	In contact with presumed reduced cornea	1a?	1a
Boulengerula taitanus	Absent	?	1b
Boulengerula boulengeri	Absent	?	1b
Scolecomorphus kirkii	Adherent to cornea and retina	1b	1b
Scolecomorphus uluguruensis	Adheres to retina and connective tissue	1b?	1b
Typhlonectes natans	Adheres to cornea, peripherally to retina	1b?	1b

the discrepancies may be explained by the unpublished observations of additional specimens (M. H. Wake, personal communication), but their extent suggests that there is considerable difficulty in assigning taxa to character states and that, in practice, the boundaries between character states are not clear. I have excluded all three of these characters from the revised data. Their rehabilitation will require additional observations.

(*c*) *Ear characters*

A1: Stapes present (0), or absent (1).

This character has been used in analyses of more traditional morphological data (Nussbaum, 1979) and essentially is unproblematic. I have added data for those taxa not included in the original ear data set where possible.

A2*: Lagena sensory epithelium present (0), or absent (1).

A3: Well-developed lagenal recess with a median recess at saccular orifice and associated basilar papilla present (0), or lagenal recess reduced and basilar papilla absent (1).

In the original treatment, A3 describes the development of a lagenal recess and A4 describes the presence or absence of the basilar papilla. The basilar papilla is housed in the lagenal recess whenever it occurs and no taxa are known with a poorly developed recess that retain a papilla. The covariance of these topologically, and presumably functionally, related traits suggests the correlated evolution of a complex character and I have not retained A3 and A4 as separate characters here to avoid potential overweighting.

A5: Basilar papilla on limbic tissue (0), or not (1).

In the original treatment, those taxa that lack a basilar papilla are coded as not having

it on limbic tissues. Here, they are coded as equivocal with respect to the associations of their non-existent basilar papilla. A5 and A3 (incorporating A4) are not entirely independent, and can be conceived of as the binary factors of an incompletely ordered multistate character with uncertainty over the relations between absence of the basilar papilla and the variation in the disposition of the basilar papilla when present.

A6–A7: In the original, A6 and A7 describe variation in the numbers of hair cells in the papilla neglecta and the papilla amphibiorum, respectively. As Fritzsch & Wake (1988, p. 202) point out, they did not correct for double counting and their estimates of hair cell numbers should be considered a crude approximation. Further, they noted that hair cell numbers are correlated with overall size and so they made use of comparisons of the relative numbers of hair cells in each papillus rather than absolute numbers. Character A10 (see below) is based on the relative numbers of hair cells, so that the A6 and A7 are perhaps redundant to some extent as well as suffering from the difficulties raised by Fritzsch & Wake (1988). They have been excluded from the revised data.

A9*: Papilla neglect a near utriculus-sacculus foramen (0), or not (1).

A10*: Number of hair cells in papilla neglecta less than half (0), approximately equal to (1), or more than twice (2) the number in the papilla amphibiorum.

(*d*) *Hypoglossal characters*

H1·1: Spinal 1 contributes to hypoglossal (0), or not (1).

H1·2: Spinal 3 contributes to hypoglossal (0), or not (1).

H1·3: Vagal ramus X-1 contributes to hypoglossal (0), or not (1).

H2*: Occipital nerve present (0), or not (1).

Characters H1·1–1·3 are the reductive coding of the original composite multistate character H1, discussed by Wilkinson (1995*a*) subject to some modification. In the original treatment, H1 includes three states (1b, 1c and 1d) that include the occipital as one of the components of the hypoglossal. A second character, H2 describes the presence or absence of the occipital and is therefore not independent logically of H1 (because the occipital cannot be incorporated into the hypoglossal if it is not present). Wake (1992, p. 45) reports that the occipital is free on one side in the single specimen of *Gymnopis multiplicata* examined. Such intra-individual variation suggests that the distinction between occipitals that are free and those that are part of the hypoglossal is unlikely to reflect discrete evolutionary stages that are clearly related to phylogeny and that the original coding of *G. multiplicata* was to some extent arbitrary. With the exception of the variable *G. multiplicata*, all taxa that have an occipital have it incorporated into the hypoglossal. In this treatment, only a single occipital character (H2) is retained in order to avoid potential overweighting and the arbitrary assignment of taxa to character states.

Of the original character states, state 1c (spinal 2 not contributing to the hypoglossal) is characteristic of only '*Nectocaecilia haydee*' which is excluded from this treatment. Hence, this state is not considered further. Only *Ichthyophis kohtaoensis* and *Uraeotyphlus narayani* are coded as state 1d, but this contradicts their coding as lacking an occipital in H2. Wake's (1992, pp. 40, 43) report supports the absence of an occipital nerve in *I. kohtaoensis* which is coded as such here, but is equivocal over its presence in *U. narayani* which is coded as uncertain here. Wake (1992, p. 45) also describes *Caecilia occidentalis* and *Oscaecilia ochrocephala* as having the generalized pattern for

caecilians. However, in the matrix they are coded differently (states 1f and 0 respectively, and six steps apart in the ordered treatment). The attributed states differ only with respect to the contribution of vagal ramus 1-4, and these taxa have been coded as uncertain for my corresponding character (H1·3).

H3–H4: In the original treatment, H3 and H4 are binary characters that describe the distance between the atlas and hypoglossal fusion and the length of the fusion in absolute terms (mm). They are not included here because they are likely to be highly dependent upon head size and stage of development, and because this information is not available from Wake (1992).

H5: Hypoglossal in the tongue bifurcated (0), straight with branches along its length (1), branched at tip only (2).

This character is not ordered readily by the method of intermediates and is treated as unordered in all the analyses. Wake (1992, p. 47) reported that in *Chthonerpeton indistinctum* 'the hypoglossal does not bifurcate, but branches extensively throughout'. This contradicts the coding in her matrix which indicates that the hypoglossal is branched only at its tip. I have coded *C. indistinctum* as uncertain for this character.

(*e*) *Olfactory-vomeronasal characters*

O1: Undivided (0), slightly divided (1), or divided (2) main nasal cavity.

Ramaswami (1943) reported that *Gegeneophis ramaswamii* lack eminentia olfactoria dividing the nasal cavities, Els (1963) and Straub (1985) report the presence of a conchiod process in *Schistometopum thomense* and *Grandisonia alternans*, respectively, and Weidersheim's (1879) illustrations of *Siphonops annulatus* show a divided main nasal cavity. These observations have been added to the matrix. Schmidt & Wake (1990, p. 257) report that *Boulengerula taitanus* has a 'slightly divided nasal cavity' but this species is coded as divided in the matrix. I have scored *B. taitanus* as {1, 2} for the PAUP analyses, and as equivocal for other analyses.

O3*: Respiratory epithelium posterolaterally (0), or throughout (1) the main nasal cavity.

O4: Vomeronasal organ mediolateral (0), mediolateral with lateral projection (1), or lateral (2).

This character is not readily ordered by the method of intermediates and is treated as unordered in all the analyses.

O6*: Vomeronasal organ moderate (0), or large (1).

(3) *Analyses of the revised neuroanatomical data*

Some summary statistics for compatibility analyses and permutation tests on the revised neuroanatomical data are summarized in Table 5. In both ordered and unordered treatments of multistate characters, the data have a PCPTP of 0·001, the minimum possible given the number of random permutations, allowing rejection of the null hypothesis that the data show no less incompatibility (incongruence) than is expected for random (and thus phylogenetically uninformative) data. Parsimony-based randomization tests (Table 6) also support this result.

Parsimony analysis of the revised neuroanatomical data with all characters unordered yields over 30000 MPTs. The high number of MPTs partly reflects the abundant missing data and the underdetermination of particular taxa. Using TAXEQ2, three taxa,

Table 5. *Summary statistics for compatibility analyses and randomization tests. O, observed incompatibility count, Range, range for randomly permuted data; Mean, mean ± standard deviation for randomly permuted data; 95%, 95% significance cut-off; PCPTP, pairwise compatibility permutation tail probability; ND, normal deviate; IER_1, IER_2, incompatibility excess ratios*

Data	Treatment	O	Range	Mean	PCPTP	95%	ND	IER_1	IER_2
Neuroanatomical	Unordered	103	144–209	178·77 ± 9·61	0·001	163	7·88	0·43	0·37
Neuroanatomical	Ordered	135	189–263	222·77 ± 11·73	0·001	204	7·48	0·39	0·34
Traditional	Unordered	200	728–846	786·61 ± 16·90	0·001	785	34·71	0·75	0·75
Traditional	Ordered	215	835–950	890·34 ± 18·60	0·001	860	36·31	0·76	0·75
Combined	Unordered	673	1615–1798	1702·60 ± 27·21	0·001	1657	37·84	0·60	0·59
Combined	Ordered	736	1846–2102	1948·14 ± 32·31	0·001	1898	37·51	0·62	0·61

Table 6. *Summary statistics for parsimony-based randomization tests. PTP, permutation tail probability; HER, homoplasy excess ratio. 'Original' data are from Wake (1993)*

Data	Treatment	PTP	HER
Original eye	Ordered	0·01	0·397
Original eye	Unordered	0·01	0·407
Original ear	Ordered	0·01	0·531
Original ear	Unordered	0·01	0·614
Original hypoglossal	Ordered	0·36	0·055
Original hypoglossal	Unordered	0·53	0·037
Original olfactory-vomeronasal	Ordered	0·11	0·416
Original olfactory-vomeronasal	Unordered	0·02	0·605
Original combined	Ordered	0·01	0·200
Original combined	Unordered	0·01	0·291
Revised neuroanatomical	Ordered	0·01	0·529
Revised neuroanatomical	Unordered	0·01	0·536
Traditional	Ordered	0·01	0·769
Traditional	Unordered	0·01	0·764
Combined traditional and revised neuroanatomical	Ordered	0·01	0·659
Combined traditional and revised neuroanatomical	Unordered	0·01	0·674

Ichthyophis orthoplicatus, *Scolecomorphus vittatus* and *Siphonops annulatus*, were identified as taxonomic equivalents that could be eliminated from the analysis under the constraints of safe taxonomic reduction (i.e. without affecting relationships among the remaining taxa, see Wilkinson, 1995*d*). Analysis with these taxa excluded yielded 456 MPTs with lengths (*L*) of 57, consistency indices (CI) of 0·54, and retention indices (RI) of 0·75. The strict component consensus (Fig. 5*a*) includes only three clades: a poorly resolved clade including all caeciliids, typhlonectids and scolecomorphids corresponding to the 'higher' caecilians of Nussbaum (1991) and uncontroversial groupings of typhlonectids and of scolecomorphids.

Table 7 is a summary of all *n*-taxon statements that are common to the 456 MPTs, together with their Bremer support values, expressed both as numbers of extra steps and as percentage increases over MPT length. An incomplete graphical representation of these relationships is provided by the single primary strict reduced cladistic

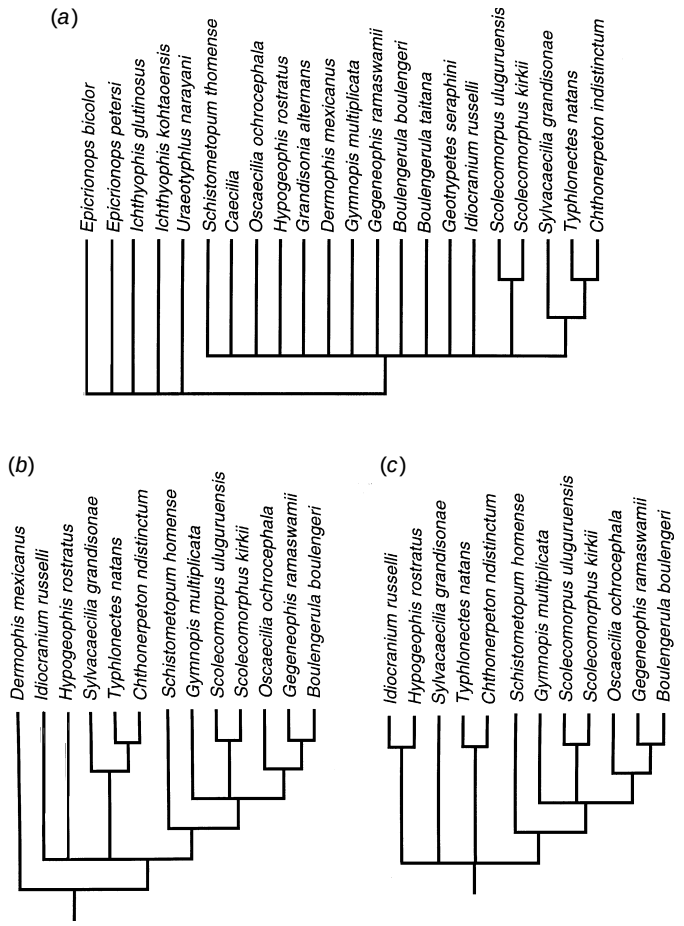


Fig. 5. Relationships common to MPTs found in the analyses of the revised neuroanatomical data. (*a*) Strict component consensus of the unordered analysis after exclusion of *Ichthyophis orthoplicatus*, *Scolecomorphus vittatus* and *Siphonops annulatus*. (*b*) Primary strict reduced consensus (part). (*c*) Primary strict reduced consensus (part) of the corresponding ordered analysis.

consensus tree (Fig. 5*b*) which displays additional resolution at the expense of the exclusion of four particularly underdetermined taxa, *Boulengerula boulengeri*, *Caecilia occidentailis*, *Grandisonia alternans*, and *Idiocranium russelli*. This tree includes an unconventional grouping of all the remaining caeciliid and scolecomorphid taxa that have rudimentary eyes, and that have the orbit covered with bone. In previous studies, the scolecomorphids have been recovered as the sister-group of a caeciliid–typhlonectid clade (Nussbaum, 1979; Duellman & Trueb, 1986; Hillis, 1991; Wilkinson & Nussbaum, 1996), implying convergent rudimentation of their visual systems. The basal position of *Dermophis mexicanus* within the 'higher' caecilians and its great separation from *Gymnopis multiplicata* are also surprising. *Dermophis* and *Gymnopis* have been considered probable sister genera (e.g. Nussbaum and Wilkinson, 1989), and they have a complex taxonomic history in which *Dermophis* has been repeatedly synonymized with *Gymnopis*. Relationships within the 'higher' caecilians are generally

Table 7. *Summary of all* n*-taxon statements common to all 456 MPTs for the revised neuroanatomical data with multistate characters treated as unordered. 1 indicates taxa that are more closely related to each other than to any taxa denoted by 0. BS = Bremer Support. % = Bremer support expressed as a percentage of MPT length. Taxa*: 1, Epicrionops-bicolor; *2*, E. petersi; *3*, Ichthyophis glutinosus; *4*, I. kohtaoensis; *5*, Uraeotyphlus narayani; *6*, Scolecomorphus uluguruensis; *7*, S. kirkii; *8*, Typhlonectes natans; *9*, Chthonerpeton indistinctum; *10*, Schistometopum thomense; *11*, Caecilia; *12*, Oscaecilia ochrocephala; *13*, Hypogeophis rostratus; *14*, Grandisonia alternans; *15*, Dermophis mexicanus; *16*, Gymnopis multiplicata; *17*, Gegeneophis ramaswamii; *18*, Boulengerula boulengeri; *19*, B. taitanus; *20*, Geotrypetes seraphini; *21*, Sylvacaecilia grandisonae; *22*, Idiocranium russelli

Taxa 1111111111222 12345678901234567890 12	BS	%
00000110000000000000000	3	5·26
00000001100000000000000	2	3·51
00000001100000000000010	1	1·75
00000111111111111111111	1	1·75
00000111111111?01111111	1	1·75
00000000000000011?000	1	1·75
00000000000010?00111000	1	1·75
00000011000?10?01111000	1	1·75
00000011001?10?01111?00	1	1·75
00111??????????????????	1	1·75

poorly known, but analyses of the available DNA sequence data provide fairly strong bootstrap support for the conflicting hypothesis that *Dermophis mexicanus*, *Hypogeophis rostratus* and *Schistometopum thomense* are related to each other more closely than they are to *Typhlonectes natans* (Hedges *et al*. 1993; Wilkinson, 1996*a*). The recovery of the caeciliid *Sylvacaecilia grandisonae* as more closely related to the typhlonectids than to the other caeciliids is also unconventional. Bremer support for relationships that are common to all the MPTs is low, with only the scolecomorphid and typhlonectid groupings having values greater than the minimum possible.

Parsimony analysis with all multistate characters (except H5 and O4) ordered, and with the problematic *Ichthyophis orthoplicatus*, *Scolecomorphus vittatus* and *Siphonops annulatus* deleted, yielded 2691 MPTs ($L = 61$, CI = 0·51; RI = 0·74). The strict component consensus of these MPTs includes the scolecomorphid and typhlonectid clades found in the unordered analysis but no other groups. Table 8 provides a summary of all *n*-taxon statements common to all the MPTs and their Bremer support. A single primary strict reduced cladistic consensus (Fig. 5*c*), produced through the exclusion of five underdetermined taxa (*Boulengerula taitanus*, *Caecilia occidentalis*, *Dermophis mexicanus*, *Geotrypetes seraphini* and *Grandisonia alternans*), mostly parallels the unordered analysis in recovering a 'higher' caecilian group and the same association of those caeciliids and scolecomorphids with rudimentary eyes. As in the unordered analysis, only the scolecomorphid and typhlonectid groupings have Bremer support greater than the minimum possible. Notable differences in the ordered and unordered analyses are the more poorly resolved relationships of *Sylvacaecilia grandisonae* and the

Table 8. *Summary of all* n*-taxon statements common to all 2691 MPTs for the revised neuroanatomical data with multistate characters treated as ordered. Format and abbreviations as in Table 7*

Taxa 1111111111222 12345678901234567890 12	BS	%
00000110000000000000000	4	6·56
00000001100000000000000	2	3·28
00000000000010?00111000	1	1·64
00000000000000011?000	1	1·64
0000000000?01000000001	1	1·64
00000000000100000 11?000	1	1·64
00000111111111??11111111	1	1·64
00000110000?10?01111000	1	1·64
00000110001?10?01111?00	1	1·64
0000011??111??01111???	1	1·64
0011????????????????????	1	1·64

association of *Hypogeophis rostratus* and *Idiocranium russelli* in the former, and the overlapping but different sets of underdetermined taxa that are excluded form the reduced consensus tree.

(4) *Comparison of analyses of the revised and original neuroanatomical data*

As with the original data, there are rather few clades that are supported unambiguously by the parsimonious interpretation of the revised neuroanatomical data, although, unlike the original, those clades that are supported correspond to relatively uncontroversial hypotheses of relationships. The important question of whether the revision of the neuroanatomical data affects character quality is difficult to address based on comparison of consensus trees, but some indication is provided by comparative performance in parsimony-based randomization tests (Table 6). Tests of the original eye, ear, and combined neuroanatomical data allow rejection of the null hypotheses that these data sets are random ($P = 0{\cdot}01$). In contrast, both ordered and unordered treatments of the original hypoglossal data and the ordered treatment of the olfactory-vomeronasal data do not allow the null hypotheses that these data sets are random to be rejected ($P > 0{\cdot}05$). This may well reflect the small numbers of characters in these data sets rather than any more profound deficiency in the data. In comparison of the original combined neuroanatomical data and the revised neuroanatomical data, although both are significantly different from random, the HER values for the original combined data are dramatically lower than those for the revised neuroanatomical data. While this does not necessarily indicate any significant improvement in data quality with the revision of the neuroanatomical data, the magnitude of the differences in HER values is suggestive of this, and indicates that the revision is most unlikely to have produced an overall reduction in data quality.

Table 9. *Traditional caecilian data. Details of characters are given in the text*

Taxa	1111111112222222233333333444444444555555551234567890345567890024578901235689023456789012345678 ab ab
Epicrionops bicolor	0100011010000000000100000000000000000000000????00000
Epicrionops petersi	0100011010000000000100000000000000000000000000000000000
Ichthyophis glutionsus	0110000101101010111011111010000000000011111110000000000
Ichthyophis kohtaoensis	0110000101101010111011111010000000000011111110000000000
Ichthyophis orthoplicatus	0110000101101010111011111010000000000011111110000000000
Uraeotyphlus narayani	0020000101101011111011111020000000000011111100000000000
Scolecomorphus uluguruensis	1020001102117?11?113111111210100010111000000????11010
Scolecomorphus kirkii	1020001102117?11?113111111210100010111000000????11010
Scolecomorphus vittatus	1020001102117?11?113111111210100010111000000010011010
Typhlonectes natans	1021111102102021112011110101011100001000010010101010
Chthonerpeton indistinctum	1021111102102021112011110101011100001000010??0101010
Schistometopum thomense	1021111101102021112011110101000100011000000110000100
Siphonops annulatus	1021111101102021112011110101100101001000000010001110
Caecilia occidentalis	1021111101102021112011110201001100 1??000000101 0?111
Oscaecilia ochrocephala	1021111101102021112011111201001100 1??000000101001111
Hypogeophis rostratus	1021111101102021112011110201001000001000000112?00100
Grandisonia alternans	1021111101102021112011110101001000001000000112000100
Dermophis mexicanus	1021111101102021112011110101100101011000000010000110
Gymnopis multiplicata	1021111101102021112011111101000000011000000011000110
Gegeneophis ramaswamii	1021111101102021112011111101001000001000000111000110
Boulengerula boulengeri	1021111101102021120111111101100100001000000111011110
Boulengerula taitanus	1021111101102020112011111101000000001000000111011110
Geotrypetes seraphini	1021111102102021112011110201001100011000000010000100
Sylvacaecilia grandisonae	1021111101102021112011110101001000000000??00????00100
Idiocranium russelli	1021111101102021112011110201001000000100??00????00100

IV. TRADITIONAL DATA

(1) *Characters*

More-traditional character data, drawn from external morphology, life-history variation and musculoskeletal, cardiovascular and respiratory systems have been used in previous studies of caecilian phylogeny (Nussbaum, 1979; Duellman & Trueb, 1986; Hillis, 1991; Wilkinson & Nussbaum, 1996). The 'traditional' data matrix presented here (Table 9) is based primarily on Wilkinson & Nussbaum (1996), which in turn was developed from Nussbaum's (1979) pioneering cladistic study. In order to facilitate comparison and combination with the revised neuroanatomical data, new data for those taxa included in the revised neuroanatomical matrix but not included in Wilkinson & Nussbaum's (1996) matrix have been added. Comprehensive observations were not possible for *Caecilia occidentalis*, and unlike in the revised neuroanatomical data, observations for *Caecilia* represent a composite of observations on several species. In Wilkinson & Nussbaum (1996), multistate characters were ordered and represented by their binary factors. Here, they are presented mostly as multistate characters to facilitate unordered treatments. To facilitate cross referencing, the numbering of characters follows Nussbaum (1979) and Wilkinson & Nussbaum (1996), but with character numbers prefixed by a T. Characters are listed below and discussion is limited to departures from the latter study that are more than trivial modifications of descriptive

terminology. Several of Nussbaum's (1979) characters or character states were excluded by Wilkinson & Nussbaum (1996) because they were uninformative in the context of their analyses. Those that are informative in the context of the present analysis because of its increased taxonomic scope are reintroduced. Four of Wilkinson & Nussbaum's (1996) characters (11, 12, 23, 37) provided difficult to score for the new taxa and, in lieu of any redefinition of their character states, are not included here. Nine additional characters (T50–58), including four (T50–53) from the Nussbaum & Naylor (1982) study of variation in the trunk musculature of caecilians, have been added to the data. The resulting matrix represents the most comprehensive array of traditional caecilian data to date, both in its taxonomic scope and number of characters.

T1: True tail (postcloacal vertebrae and annuli) present (0), or absent (1).
T2: Tertiary annuli absent (0), or present (1).
T3: Mouth terminal (0), slightly subterminal (1), or strongly subterminal (2).
T4: Premaxillae and nasals separate (0), or fused (1).
T5: Septomaxillae present (0), or not (1).
T6: Prefrontals present (0), or not (1).
T7: Postfrontals present (0), or not (1).
T8: Squamosal and frontal in contact (1), or not (1).
T9: Squamosal notch – os basale process absent (0), or present (1).
T10: Zygokrotaphic with the musculus adductor mandibulae externus major extending through the fossa and meeting at the dorsal midline of skull (0), stegokrotaphic (1), or zygokrotaphic but the adductor muscle not extending dorsally through the fossa (2).
T13: Parasphenoid parallel sided (0), or converging anteriorly (1).
T14: Orbitosphenoid vertical (0), or oblique (1).
T15a: Quadrate and maxillopalatine separated ventrally by large pterygoid (0), by small pterygoid and pterygoid process of quadrate (1), by pterygoid process only [pterygoid absent] (2).
T15b: Mediopalatinal canal expanded [pterygoid and pterygoid process of quadrate absent] (1), or not (0).

T15b describes a distinctive condition that is restricted to scolecomorphids (Nussbaum, 1986) and was excluded from Wilkinson & Nussbaum's (1996) analysis because it was uninformative. Nussbaum (1979) included this as part of his character 15. 15a and 15b are not entirely independent, and can be conceived of as a single multistate character. Scolecomorphids are coded as equivocal for T15a, reflecting uncertain relations of their condition to the other states in T15a.

T16: Basipterygoid process absent (0), weakly developed (1), or well developed (2).
T17: Stapes perforate (0), or imperforate (1).

Nussbaum (1979) included absence of the stapes as an additional character state in his character 17. This was ignored by Wilkinson & Nussbaum (1996) because it was uninformative in the context of their analysis. Presence or absence of the stapes is included in the revised neuroanatomical data (A1) and is not repeated here. Nussbaum (1979) included T17a and T17b as a single multistate character. A1 and T17 are not independent and are treated as interdependent in randomization tests.

T18: Quadrate and maxillopalatine in contact laterally (0), or not (1).
T19: Retroarticular process short and straight (0), or long and recurved (1).

T20a: Posterior glossal skeleton reduced in size, ceratobranchial (cb) 4 absent (0), cb 3 and 4 fused and a little expanded (1), cb 3 and 4 fused and much expanded (2).
T20b: ceratobranchials 3 and 4 fused enclosing larynx (1), or not (0).

Fused ceratobranchials enclosing the larynx is a characteristic of scolecomorphids and was excluded from Wilkinson & Nussbaum's (1996) analysis. Nussbaum (1979) included T20a and T20b as a single multistate character. The coding here reflects the uncertainty concerning the relation of the scolecomorphid condition to the states in T20a.

T22: Anterior fibres of m. interhyoideus anterior insert on ceratohyal (0), or not (1).
T24: M. interhyoideus posterior in one (0), or two (1) bundles.
T25: M. interhyoideus posterior predominantly oblique (0), or predominantly horizontal (1).
T27: M. depressor mandibulae predominantly vertical (0), or predominantly longitudinal.
T28: Orbit open (0), or covered in bone (1).
T29: Tentacular aperture adjacent to eye (0), between eye and naris (1), or beneath naris (2).
T30: Phallodeum aspinous (0), or spinous (1).
T31: Vent longitudinal (0), or transverse or circular (1).
T32: Splenial teeth present (0), or absent (1).
T33: Choanal openings small (0), or large (1).
T35: Narial plugs absent (0), present (1).

In Nussbaum (1979), *Hypogeophis rostratus* was mistakenly coded as lacking narial plugs, a typographic error that was replicated in Wilkinson & Nussbaum (1996). The coding has been corrected here.

T36: Mesethmoid covered dorsally (0), or exposed between frontals (1).
T38: Prevomerine teeth without (0), or with (1) a medial diastema.
T39: Choanae not completely encircled by maxillopalatine (0), or completely encircled (1).
T40: Some or all premaxillary-maxillary teeth relatively small (0), all enlarged (1).
T42: Oviparous (0), or viviparous (1).
T43: Larval stage (0), or direct development (1).
T44: Atria not divided externally (0), or divided externally (1).
T45: Anterior pericardial space short and small (0), or long and extensive (1).
T46: Posterior internal flexures in m. rectus laterales less than two (0), or two (1).
T47: Internal flexures on m. subvertebralis none (0), or one (1).
T48: Tracheal lung absent (0), or present (1).
T49: Anterior annuli orthoplicate (0), or angulate (1).
T50: Paired m. rectus laterales meet mid-dorsally (0), or separated (1).
T51: One (0), or no (1) anterior internal flexures in m. rectus lateralis.
T52: 'Myosepta' in m. obliquus externus superficialis well developed (0), dorsal only (1), or absent (2).
T53: Origin of ventral part of m. subvertebralis from midcentrum (0), or subvertebralis (1).

Hypogeophis rostratus is atypical in its origin from the basapophysis (Nussbaum & Naylor, 1982), and is coded as equivocal with respect to this character.

T54: Terminal keel absent (0), or present (1).

A vertical keel is present on the body termini of species of *Boulengerula* and *Scolecomorphus*. Nussbaum & Hinkel (1994) discussed this character.

T55: Annular scales, secondary annuli and segmented body termini present (0), or absent (1).

The presence and absence of annular scales, secondary annuli and segmented body termini covary and are treated as a single complex character here.

T56: M. interhyoideus posterior short (0), or elongate (1).

In all caeciliids, the m. interhyoideus posterior has an elongate origin that extends up to seven trunk segments behind the head. In all other caecilians the muscle is shorter, extending to only the fourth trunk segment (M. Wilkinson & R. A. Nussbaum, unpublished data).

T57: Anterior dentary teeth bicuspid (0), or monocuspid (1).

Phylogenetic implications of variation in the number of cusps or caecilian teeth have been discussed by Greven (1984), Wilkinson (1991), and Nussbaum & Hinkel (1994). In lieu of a more thorough and comprehensive survey, I have made only limited use of the known variation here.

T58: Vomeropalatine tooth rows forming a semicircle (0), or an angle (1), anteriorly.

State 1 of this character describes an unusual arrangement of teeth that is unique to the species of *Caecilia* and *Oscaecilia* (Nussbaum & Wilkinson, 1989).

(2) *Analysis of the traditional data*

Some summary statistics for compatibility analyses and permutation tests of the traditional data are summarized in Table 5. In both ordered and unordered treatments of multistate characters, the data have a PCPTP of 0·001, the minimum possible given the number of random permutations, allowing rejection of the null hypothesis that the data show no less incompatibility than is expected for random data. Parsimony-based randomisation tests also support this result (Table 6).

With all multistate characters ordered, parsimony analysis yields 12 MPTs ($L = 93$, CI = 0·63, RI = 0·85), and with all multistate characters unordered parsimony analysis yields 23 MPTs ($L = 92$, CI = 0·64, RI = 0·85). The strict component consensus is identical for both sets of trees (Fig. 6*a*). As in Wilkinson & Nussbaum's (1996) analysis, the Uraeotyphlidae is the sister group of a monophyletic Ichthyophiidae, and these are the sister group of a 'higher' caecilian clade. Within the higher caecilian clade, the scolecomorphids, typhlonectids and caeciliids are each monophyletic, with the typhlonectids the sister group of the caeciliids and the scolecomorphids the sister group of the typhlonectid-caeciliid clade. The caeciliid clade is poorly resolved with only three pairs of sister taxa identified. Of these, the *Caecilia–Oscaecilia ochrocephala* pair and the *Boulengerula* groupings are uncontroversial. The separation of *Dermophis mexicanus* and *Gymnopis multiplicata*, as in the analysis of the neuroanatomical data, is more surprising, as is the recovery of a monophyletic Caeciliidae. Analyses of DNA-sequence data provide strong bootstrap support for the hypothesis that *Caecilia* is more closely related to *Typhlonectes natans* than it is to other caeciliids, and that the Caeciliidae is paraphyletic, and since Nussbaum (1977) it has been generally accepted that typhlonectids evolved from a caeciliid ancestor.

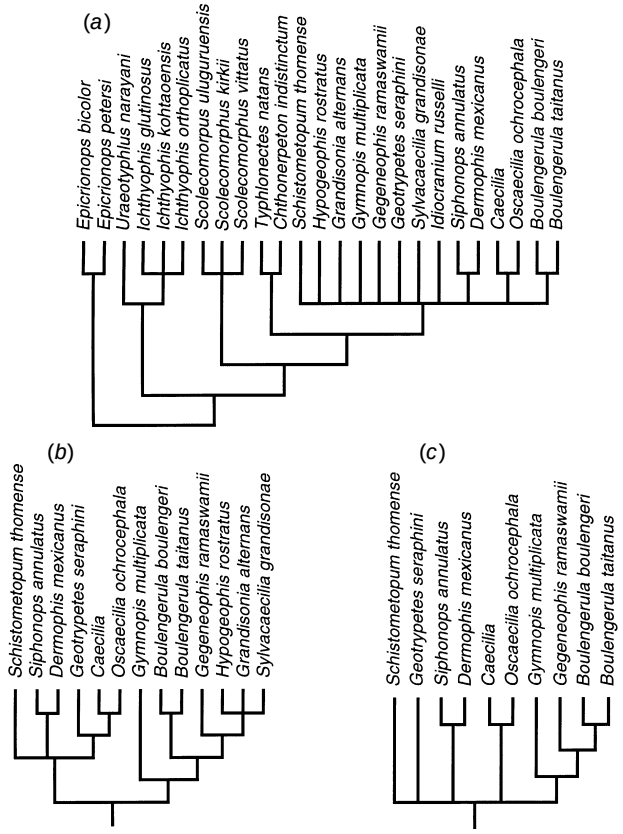


Fig. 6. Relationships common to MPTs found in the analyses of the traditional data. (*a*) strict component consensus (*b*) primary strict reduced consensus (in part) of the ordered analysis. (*c*) primary strict reduced consensus (in part) of the corresponding unordered analysis.

Table 10 summarizes all *n*-taxon statements common to the 12 ordered MPTs and their Bremer support. A corresponding primary strict reduced cladistic consensus (Fig. 6*b*) achieves much greater resolution of the caeciliid clade (six more nodes) at the expense of the exclusion of only *Idiocranium russelli*. This consensus includes two main caeciliid clades, which, apart from the position of *Caecilia*, are consistent with DNA-sequence phylogenies (Hedges *et al*. 1993; Wilkinson, 1996*a*). The Seychellean caecilians, represented here by *Hypogeophis rostratus* and *Grandisonia alternans*, which are considered monophyletic on the basis of molecular, immunological and cytogenetic data (Hedges *et al*. 1993; Haas, Nussbaum & Maxson, 1993; Nussbaum & Ducey, 1988), group together with the Ethiopian *Sylvacaecilia grandisonae* (a taxon not included in these other studies). Bremer support for some relationships, particularly the caeciliid clade and much of the resolution within this clade, are minimal, but more conventional relationships, including those at the base of the tree, have more impressive support values.

Table 11 summarizes all *n*-taxon statements common to the 23 unordered MPTs and their Bremer support. There is a single primary strict reduced cladistic consensus (Fig. 6*c*) in which exclusion of *Idiocranium russelli*, *Hypogeophis rostratus*, *Grandisonia*

Table 10. *Summary of all* n*-taxon statements common to all 12 MPTs for the traditional data with multistate characters treated as ordered. Taxa: 1*, Epicrionops bicolor; *2*, E. petersi; *3*, Ichthyophis glutinosus; *4*, I. kohtaoensis; *5*, I. orthoplicatus; *6*, Uraeotyphlus narayani; *7*, Scolecomorphus uluguruensis; *8*, S. kirkii; *9*, S. vittatus; *10*, Typhlonectes natans; *11*, Chthonerpeton indistinctum; *12*, Schistometopum thomense; *13*, Siphonops annulatus; *14*, Caecilia; *15*, Oscaecilia ochrocephala; *16*, Hypogeophis rostratus; *17*, Grandisonia alternans; *18*, Dermophis mexicanus; *19*, Gymnopis multiplicata; *20*, Gegeneophis ramaswamii; *21*, Boulengerula boulengeri; *22*, B. taitanus; *23*, Geotrypetes seraphini; *24*, Sylvacaecilia grandisonae; *25*, Idiocranium russelli. *Format and other abbreviations as in Table 7*

Taxa 1111111111222222 12345678901234567890123456	BS	%
00111000000000000000000000	1	1·08
00111100000000000000000000	3	3·23
00000011100000000000000000	9	9·68
00000000011000000000000000	4	4·30
00000000000001100000000000	3	3·23
00000000000010000100000000	2	2·15
00000000000000000000011000	2	2·15
00000000001111111111111111	1	1·03
00000000011111111111111111	2	2·15
00000011111111111111111111	4	4·30
00111111111111111111111111	15	16·13
00000000000000011011110?1	1	1·08
00000000000111100100001?0	1	1·08
00000000000000011000000?1	2	2·15
00000000000000011001000?1	1	1·08
00000000000000011000000?0	1	1·08
00000000000000011001110?1	1	1·08

Table 11. *Summary of all* n*-taxon statements common to all 23 MPTs for the traditional data with multistate characters treated as unordered. Format and abbreviations as in Table 10*

Taxa 1111111111222222 12345678901234567890123456	BS	%
00111000000000000000000000	2	2·17
00111100000000000000000000	4	4·35
00000011100000000000000000	8	8·70
00000000011000000000000000	4	4·35
00000000000010000100000000	3	3·26
00000000000001100000000000	2	2·17
00000000000000000000011000	2	2·17
00000000001111111111111111	1	1·09
00000000011111111111111111	2	2·17
00000011111111111111111111	3	3·26
00111111111111111111111111	12	13·04
00000000000000011000000?1	1	1·09
00000000000000??011110??	1	1·09
00000000000000??001110??	1	1·09

alternans and *Sylvacaecilia grandisonae* allows some additional resolution that parallels one of the main caeciliid groupings found in the ordered analysis but those taxa included in the other main caeciliid clade remain part of an unresolved basal caeciliid polytomy. As in the ordered analyses, Bremer support values are high for some conventional relationships but mainly minimal for resolution within the caeciliid clade.

V. COMPARISON OF SEPARATE TRADITIONAL AND NEUROANATOMICAL ANALYSES AND DATA

There are some obvious differences, and relatively few similarities, between relationships supported by the parsimonious interpretations of the revised neuroanatomical and the more traditional data. The neuroanatomical data provide no resolution of basal relationships within the Gymnophiona, whereas the traditional data provide their strongest support for relationships within this part of the tree. Both types of data lend support to a traditional 'higher' caecilian grouping of scolecomorphids, caeciliids and typhlonectids and, within this group, both support the integrity of typhlonectids and of scolecomorphids. Both data sets offer some additional resolution of relationships within the 'higher' caecilians but, apart from an association between *Boulengerula* and *Gegeneophis ramaswamii*, and to a lesser extent with *Gymnopis multiplicata*, these differ substantially. The neuroanatomical data support a grouping of all those taxa with rudimentary eyes (with *Caecilia occidentalis* equally parsimoniously included or not). This is not replicated with the traditional data where scolecomorphids are excluded from the caeciliid–typhlonectid clade. Judged by their limited Bremer support, neither the alternative placements of the scolecomorphids is compelling. Most of the relationships supported by the revised neuroanatomical data have minimal Bremer support, as do most of the alternative resolutions of relationships within the Caeciliidae supported by the traditional data. Consequently, none of these poorly supported hypotheses deserves much confidence.

Both data sets are significantly different from random data, but the neuroanatomical data have rather lower HER and IER values than the traditional data suggesting relatively higher levels of incompatibility/incongruence and thus lower data quality. Differences in the retention indices for the two data sets also suggest a difference in data quality. However, given that there are twice as many characters (52) in the traditional data, differences in these descriptive statistics might also reflect differences in the amount of, rather than the quality of, the data. This was tested further by determining the incompatibility counts for 999 subsets of half the traditional characters, selected randomly without replacement. There are 103 incompatibilities in the neuroanatomical data (multistate characters unordered). Subsets of the traditional data have a mean incompatibility count of 50·07, and only one subset had an incompatibility count equal to or greater than the neuroanatomical data. This indicates that the incompatibility in the neuroanatomical data is significantly higher, and data quality significantly less, than for the traditional data when variation in amount of data are taken into account.

VI. ANALYSIS OF THE COMBINED DATA

Some summary statistics for compatibility analyses and permutation tests of the combined neuroanatomical and traditional data are summarized in Table 5. In both ordered and unordered treatments of multistate characters, the data have a PCPTP of

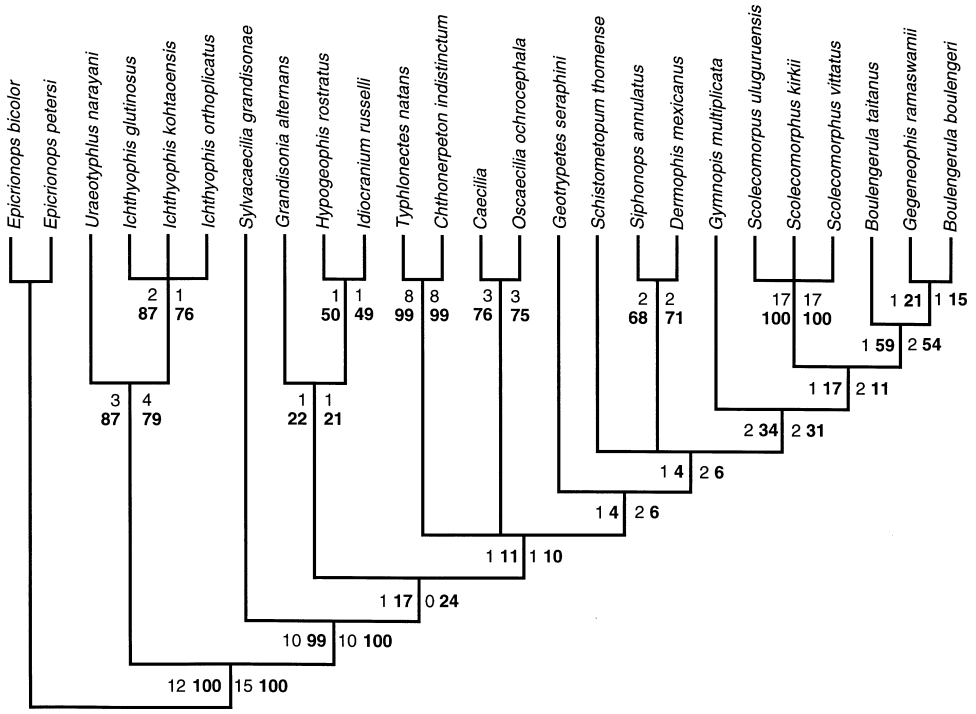


Fig. 7. Strict component consensus tree for the parsimony analysis of the combined data using equal weights. Numbers in plain text are Bremer support values as a percentage of tree length, those in bold are bootstrap proportions. Numbers to the left of branches are from the ordered, and those to the right from the unordered analyses.

0·001, the minimum possible given the number of random permutations, allowing rejection of the null hypothesis that the data show no less incompatibility than is expected for random data. Parsimony-based randomisation tests (Table 6) also support this conclusion.

(1) *Parsimony analysis with equally weighted characters*

Parsimony analysis of the combined data, with all multistate characters (except H5 and O4) ordered, yields 36 MPTs ($L = 168$, CI = 0·54, RI = 0·77). With all multistate characters treated as unordered, parsimony yields 27 trees ($L = 161$, CI = 0·56, RI = 0·78). The strict component consensus for these MPTs are virtually identical (Fig. 7) and include elements of both the neuroanatomical and traditional trees. Relationships at the base of the tree replicate those supported by the traditional data alone. As expected, those groups that are supported in both the separate analyses, the 'higher' caecilians, typhlonectids, scolecomorphids and the *Boulengerula–Gegeneophis ramaswamii* association are also recovered in the combined analysis. Most interesting are the relationships between those caecilians with the most rudimentary eyes. These were grouped together by the neuroanatomical data, whereas the traditional data identified the scolecomorphids as an independent radiation. The combined data reunite the main rudimentary-eyed caecilians, with the exception of *Oscaecilia ochrocephala*.

Bootstrap proportions and Bremer support for the groups supported by the

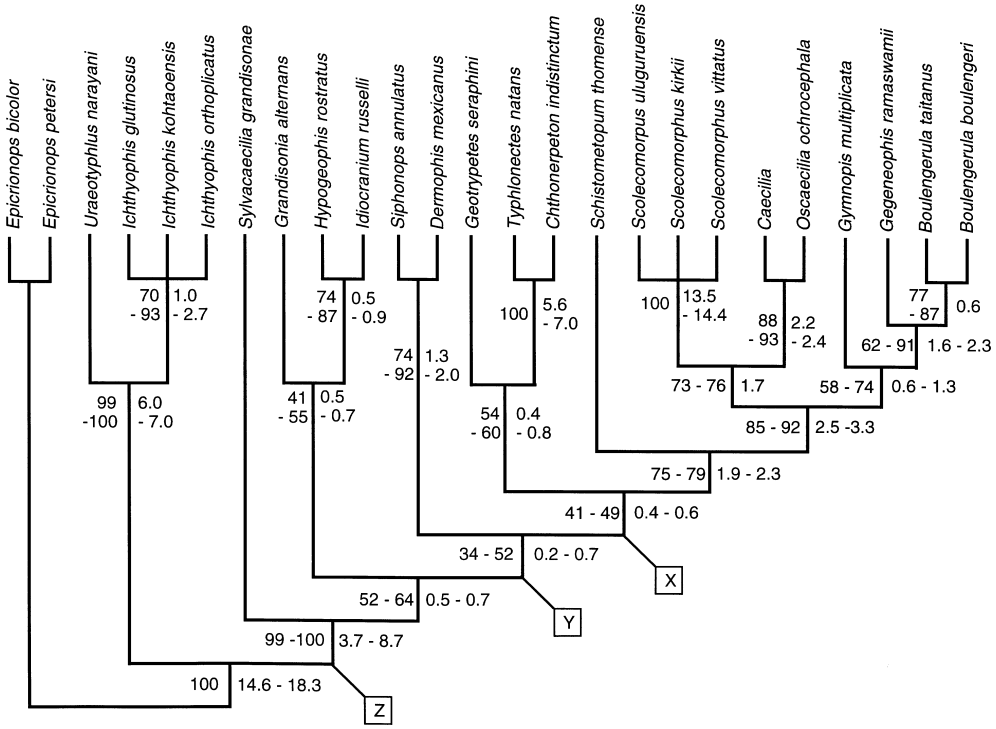


Fig. 8. Strict component consensus tree for the SACW analysis of the combined data using average fits and worst fits with unordered multistate characters. Numbers to the right of the branches are the range of bootstrap proportions; those to the left the range of Bremer support values (as a percentage of tree length) across all the variant SACW treatments that include that branch. X, Y and Z indicate points where the partial trees in Fig. 9 are identical to this full tree.

combined data (Fig. 7) indicate that some groups, primarily those that were best supported by the traditional data alone, are well supported. Most of the other resolutions of relationships within the higher caecilians have little support, certainly insufficient to warrant much confidence that the hypothesized relationships correspond to phylogeny. Note that the scolecomorphids are separated from their more conventional position as the sister group of a caeciliid–typhlonectid clade by six nodes in the combined data consensus tree, but that all of these nodes have low bootstrap proportions and minimal or near-minimal Bremer support. In summary, with all characters weighted equally, the parsimonious interpretation of the combined data provides much resolution. However, apart from two well-supported relationships at the base of the tree (the rhinatrematid – all other caecilians split, and the 'higher' caecilian clade), and a few other groups (typhlonectids, scolecomorphids, and to a lesser extent the ichthyophiid–uraeotyphlid and the *Oscaecilia ochrocephala–Caecilia* clades), the data do not provide us with a phylogenetic hypothesis that is as well supported as it is resolved. Several of the less well-supported relationships, both in the combined and separate analyses, are intriguing, but with equal weighting of characters they are no more than that.

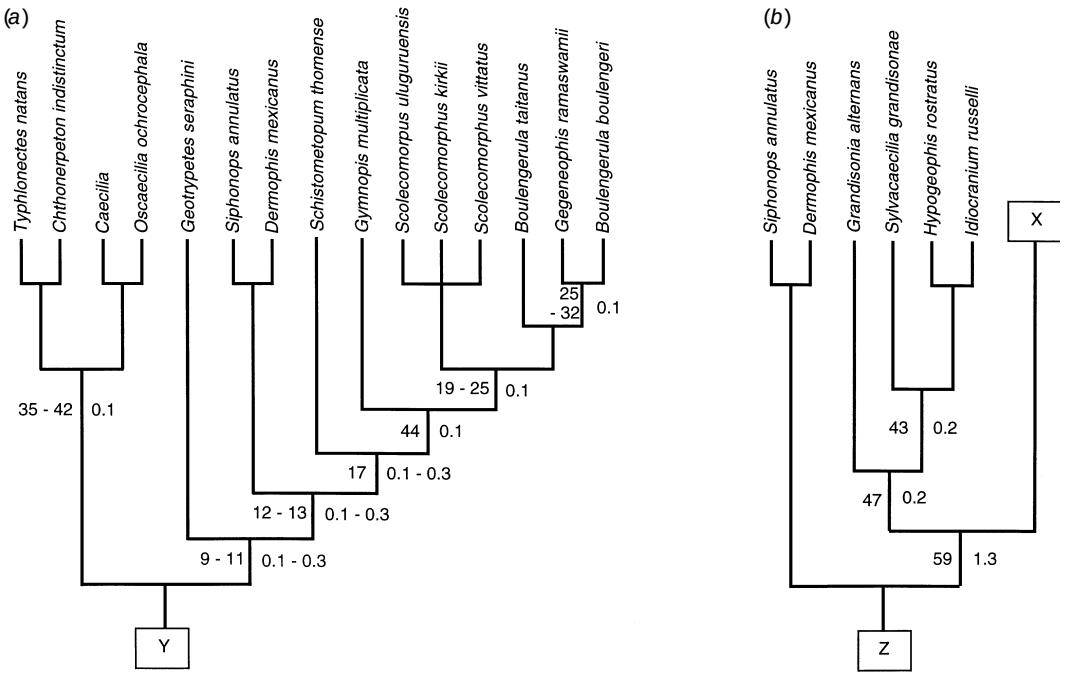


Fig. 9. Strict component consensus trees (in part) for variant SACW analyses of the combined data (*a*) using best fits, and (*b*) using worst fits and ordered multistate characters. X, Y and Z indicate points where the full tree is like that in Fig. 8. format as in Fig. 8.

(2) *SACW analyses*

SACW analyses provide one possible means of enhancing the phylogenetic signal in character data, by giving higher weight to characters that fit initial estimates of phylogeny. Final character weights produced by the six variants of SACW used are summarized in Table 12. Each application resulted in a reduction in the numbers of MPTs. With multistate characters unordered, SACW using average and worst fits of character rescaled consistency yielded the same set of nine MPTs and the same final character weights, SACW using average fits and ordered multistate characters produced a different set of eight MPTs but the same strict component consensus (Fig. 8). Using best fits, with multistate characters ordered or unordered produced a different set of nine MPTs and a slightly different strict component consensus (Fig. 9*a*). Using worst fits with multistate characters unordered yielded a unique set of nine MPTs and a different strict component consensus (Fig. 9*b*).

Relationships at the base of the tree are consistent across all SACW analyses, and reproduce those supported by the equal-weights analyses of the traditional and the combined data. Relationships within the 'higher' caecilian clade vary more with treatment. In all but the ordered–worst-fits analysis, *Sylvacaecilia grandisonae* is the sister taxon of all other higher caecilians, and a clade comprising the Seychellean species plus *Idiocranium russelli* is the sister group of the remaining 'higher' caecilians, as in the combined–equal-weights analyses. In the ordered–worst-fits analysis, this scheme is modified with the *Siphonops annulatus–Dermophis mexicanus* clade recovered as the

Table 12. *Comparative measures of data quality for all characters. LQP, Le Quesne probability; A, B and W, final weights in SACW analyses using average, best and worst fits, respectively. For details of characters, see text*

		Unordered			Ordered		
Character		LQP	B	A/W	B	A	W
1	T1	0·0001	1000	1000	1000	1000	1000
2	T2	0·0001	375	375	375	375	375
3	T3	0·0001	1000	1000	533	533	533
4	T4	0·0003	438	438	438	438	438
5	T5	0·0003	438	438	438	438	438
6	T6	0·0111	417	417	417	417	417
7	T7	0·0001	1000	1000	1000	1000	1000
8	T8	0·0214	1000	1000	1000	1000	1000
9	T9	0·0201	1000	1000	1000	1000	1000
10	T10	0·0058	333	556	333	556	556
11	T13	0·0214	1000	1000	1000	1000	1000
12	T14	0·0011	1000	1000	1000	1000	1000
13	T15a	0·0001	1000	1000	1000	1000	1000
14	T15b	0·0011	1000	1000	1000	1000	1000
15	T16	0·0002	571	571	593	593	593
16	T17	0·0729	200	200	200	200	200
17	T18	0·0214	1000	1000	1000	1000	1000
18	T19	0·0214	1000	1000	1000	1000	1000
19	T20a	0·0001	1000	1000	1000	1000	1000
20	T20b	0·0202	375	375	375	375	375
21	T22	0·0214	1000	1000	1000	1000	1000
22	T24	0·0214	1000	1000	1000	1000	1000
23	T25	0·0214	1000	1000	1000	1000	1000
24	T27	0·0214	1000	1000	1000	1000	1000
25	T28	0·0065	429	429	429	429	429
26	T29	0·0064	185	267	185	267	267
27	T30	0·0011	1000	1000	1000	1000	1000
28	T31	0·0003	438	438	438	438	438
29	T32	0·0556	200	200	200	200	200
30	T33	0·0459	1000	1000	1000	1000	1000
31	T35	0·0003	259	111	259	111	167
32	T36	0·0018	67	28	67	28	28
33	T38	0·0011	1000	1000	1000	1000	1000
34	T39	0·0300	1000	1000	1000	1000	1000
35	T40	0·0236	375	1000	375	1000	1000
36	T42	0·0045	250	250	250	250	250
37	T43	0·0001	1000	1000	1000	1000	417
38	T44	0·0002	1000	1000	1000	1000	1000
39	T45	0·0002	1000	1000	1000	1000	1000
40	T46	0·0002	1000	1000	1000	1000	1000
41	T47	0·0001	1000	1000	1000	1000	1000
42	T48	0·0111	400	400	400	400	400
43	T49	0·0004	1000	1000	1000	1000	1000
44	T50	0·0147	200	200	200	200	200
45	T51	0·0002	1000	1000	1000	1000	1000
46	T52	0·0049	500	1000	333	556	556
47	T53	0·0255	1000	333	1000	333	333
48	T54	0·0243	375	375	375	375	375
49	T55	0·0199	143	143	143	143	143
50	T56	0·0001	267	267	267	267	267

Table 12. (*cont.*)

		Unordered			Ordered		
Character		LQP	B	A/W	B	A	W
51	T57	0·0001	273	273	273	273	273
52	T58	0·0974	1000	1000	1000	1000	1000
53	E1·1	0·0063	438	1000	438	1000	1000
54	E1·2	0·0066	429	1000	429	1000	1000
55	E1·3	0·1362	400	400	400	400	400
56	E1·4	0·0784	1000	1000	1000	1000	1000
57	E1·5	0·0063	417	1000	417	1000	1000
58	E1·6	0·0069	438	1000	438	1000	1000
59	E2	0·0011	1000	1000	1000	1000	1000
60	E3	0·0017	400	400	400	400	1000
61	E4	0·1225	74	74	74	74	111
62	E6	0·0608	200	100	200	100	100
63	E10	0·2069	333	333	250	250	250
64	A1	0·0011	1000	1000	1000	1000	1000
65	A2	0·1025	167	167	167	167	167
66	A3	0·0002	1000	1000	1000	1000	1000
67	A5	0·0264	1000	1000	1000	1000	1000
68	A9	0·1108	250	250	250	250	250
69	A10	0·0365	1000	1000	444	444	444
70	H1·1	0·1189	1000	1000	1000	1000	1000
71	H1·2	0·3948	111	111	111	111	111
72	H1·3	0·3412	0	0	0	0	0
73	H2	0·1348	222	125	222	125	67
74	H5	0·1493	229	143	229	143	143
75	O1	0·0059	280	100	156	62	80
76	O3	0·0519	1000	1000	1000	1000	1000
77	O4	0·3875	143	82	143	82	82
78	O6	0·0519	1000	1000	1000	1000	1000

sister group of all other 'higher' caecilians, and *Sylvacaecilia grandisonae* nesting within the Seychelles–*I. russelli* grouping (Fig. 9*b*). Relationships in the best-fits SACW consensus tree (Fig. 9*a*) are consistent with the combined–equal-weights results (Fig. 7) but with additional resolution uniting the typhlonectids and the *Caecilia–Oscaecilia ochrocephala* clade, as in molecular studies (Hedges *et al.* 1993; Wilkinson, 1996*a*) and further specifying the relationships of *Schistometopum thomense* and the *S. annulatus–D. mexicanus* clade. All other SACW analyses recover the *Caecilia–O. ochrocephala* clade as the sister group of the scolecomorphids, along with several minor modifications to relationships supported by the equal-weights analyses, including moving *Gegeneophis ramaswamii* outside the *Boulengerula* clade, and recovering *Gymnopis multiplicata* as their sister group. These taxa are united in a single clade that includes all those caecilians with the orbit covered with bone and the most rudimentary eyes, together with *Caecilia*, species of which have open orbits but rather rudimentary eyes.

Consideration of bootstrap proportions and Bremer support values for the relationships recovered in the SACW analyses is instructive. Those relationships that were best supported in the combined–equal-weights analyses, remain the best-supported relationships with SACW, and some (the ichthyophiids and the ichthyophiid–uraeotyphlid clade) have increased levels of support. In contrast, the

majority of relationships that were only poorly supported in the combined–equal-weights analyses remain poorly supported in the SACW analyses, indicating that these relationships rest primarily on the parsimonious interpretation of relatively low-weight, and potentially misleading homoplastic characters. Similarly, most of those relationships that are unique to a subset of the SACW analyses have very low levels of support. A notable exception is the clade comprising *Caecilia* and all the caecilians with closed orbits, recovered in the majority of SACW analyses, and supported by impressive bootstrap proportions (85–92) and moderate Bremer support (2·5–3·3 %).

In summary, as in the combined–equal-weights analyses, the various SACW analyses identify the same few well-supported relationships. A few other relationships such as the association of *Gegeneophis ramaswamii* and *Boulengerula*, and that of *Idiocranium russelli* and the Seychelles caecilians are consistently recovered in all analyses but are otherwise not particularly well supported. There are several incompatible hypotheses of relationships within the 'higher' caecilians, each of which is most parsimonious under one or more interpretations of character weights. Generally, these relationships are only poorly supported, primarily by homoplastic and potentially misleading characters, and their sensitivity to character weighting reinforces the impression that compelling resolution of 'higher' caecilian relationships must await additional data.

(3) *LQP and combined LQP and SACW analyses*

Le Quesne probabilities, determined for all characters in the combined data under the unordered interpretation of the multistate characters are summarised in Table 12. Those characters with the highest Le Quesne probabilities, and which do not allow rejection of the null hypothesis that they show no less incompatibility than random characters ($P > 0{\cdot}05$) were excluded (18 characters), and the remaining 70 characters, referred to here as the LQP characters, given equal weight. This unordered analysis produced two MPTs ($L = 109$, CI = 0·633, RI = 0·446), one of which (Fig. 10) is also the strict component consensus of the pair, and is identical to that produced in the ordered–worst-fits SACW analysis (Fig. 9*b*). Relationships between the two trees differ only within the scolecomorphid clade. Application of any of the SACW procedures (best, worst, or average fits of characters) using the two LQP trees as the starting trees and only the LQP characters, has no effect upon inferred relationships (the same two MPTs are produced) and affects only tree statistics. Application of any of the SACW procedures using the two LQP trees as starting trees but including all the characters of the combined data, produces identical sets of nine MPTs that differ only in relationships within the ichthyophiid and scolecomorphid clades. The strict component consensus for these trees is identical to that for the LQP analyses, and the LQP–SACW analyses using only the LQP characters (Fig. 10). Thus, the results are robust to variation in character weighting and to the inclusion or exclusion of the worst characters (as judged by their Le Quesne probabilities).

Bootstrap proportions and Bremer support values for the LQP analyses and LQP–SACW analyses using only the LQP characters are summarized in Fig. 10. As in all previous analyses of the combined data, basal relationships, the 'higher' caecilian clade, the typhlonectids and the scolecomorphids are the best-supported relationships. SACW has a profound positive effect upon the bootstrap proportions for many of the less certain relationships within the 'higher' caecilians.

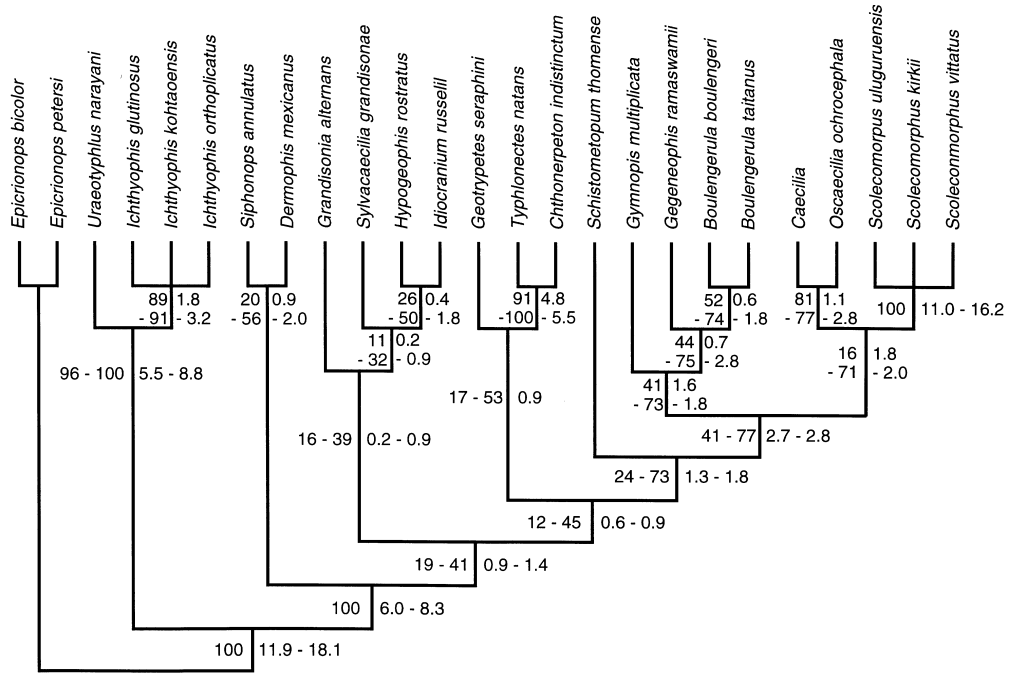


Fig. 10. Strict component consensus tree for the LQP and combined LQP–SACW analyses of the combined data. Format as in Fig. 8.

VII. FURTHER COMPARISONS BETWEEN THE NEUROANATOMICAL AND TRADITIONAL DATA

Le Quesne probabilities, and the final character weights in the SACW analyses provide comparative measures of character quality derived independently of, or as part of, the phylogenetic analyses, using compatibility and parsimony, respectively. Inspection of these values, suggests that the highest Le Quesne probabilities are concentrated particularly in the neuroanatomical characters. Most (15 out of 18) of the characters that were excluded from the LQP analysis are neuroanatomical. Similarly, although to a less-extreme degree, there appear to be disproportionately more low weights among the neuroanatomical characters. The significance of differences in the Le Quesne probabilities and character weights of the 52 traditional and 26 neuroanatomical differences were tested by using the differences in their respective mean values, and, in the case of the character weights, the differences in the total number of characters with maximum weight, as comparative measures of overall data quality, and comparing these against the values for 999 random partitions of the data into subsets of 52 and 26 characters. Comparing the mean values, the traditional data always have a higher average quality than the neuroanatomical data, but the difference is only significantly greater than for random partitions in the comparisons using the Le Quesne probability ($P = 0{\cdot}001$). Comparing the differences in number of characters with maximum weight, the traditional data have significantly more high-weight characters than the neuroanatomical data in both the ordered and unordered–best-fits character-weighting schemes ($P = 0{\cdot}044$ and $P = 0{\cdot}028$, respectively) but not in the

other SACW regimes. Thus, both compatibility (Le Quesne probability) and some parsimony (SACW using best fits) measures of character quality suggest that the neuroanatomical data are of significantly lower quality than the traditional data, although under alternative parsimony measures (SACW using average or worst fits) these differences are not statistically significant.

The above results suggest that congruence/compatibility between the neuroanatomical and traditional data sets should be further investigated. Applying the compatibility-based analogue of Farris *et al.*'s (1995) parsimony-based test of incongruence, the between-data-set incompatibility count is 370, and is significantly higher than that for random partitions ($P = 0{\cdot}002$, mean = 302·34) demonstrating heterogeneity of the traditional and neuroanatomical data sets. Although levels of incompatibility/incongruence within each data set may be significantly less than for randomly permuted data, this does not rule out the possibility that the two data sets may be random with respect to each other. In a final test, the between-data-set incompatibility count was compared with that achieved by 999 random permutations of the neuroanatomical data (with the traditional data unaffected by the permutation procedure). The results of this test demonstrate that there are significantly fewer incompatibilities between the traditional and neuroanatomical data than between the traditional and random data ($P = 0{\cdot}001$) allowing rejection of the null hypothesis that the neuroanatomical data are random with respect to the traditional data.

VIII. DISCUSSION

Of growing concern in phylogenetic inference is the question whether data sets should be combined or analysed separately, followed by investigation of taxonomic congruence. This problem is of practical consideration only if combined and separate analyses produce conflicting results, and is of concern here because separate and combined analyses of the traditional and neuroanatomical data do not yield the same estimates of phylogeny. The combined analyses produce a mixture of inferences supported by each of the separate analyses, together with some novel relationships that are not seen in either. Advocates of combined analyses, have supported their preferred protocol both with philosophical arguments under the banner of 'total evidence' (e.g. Kluge, 1989) and demonstrations that a consensus of separate analyses of partitions can yield results that are wholly inconsistent with those from combined analyses (Barrett, Donoghue & Sober, 1991). Advocates of separate analyses followed by studies of taxonomic congruence (e.g. Miyamoto & Fitch, 1995) stress that separate analyses can reveal additional insights and that agreement among the results of separate analyses of data partitions (particularly different genes) provides particularly strong evidence that the phylogenetic inferences are accurate. The conditional combination approach to this problem (e.g. Huelsenbeck *et al.* 1996) suggests that the potential benefits of neither approach need be abandoned wholesale, and seeks to clarify the conditions under which separate or combined analyses should be pursued. Specifically, Huelsenbeck *et al.* (1996) suggest that data sets should be combined only when they are sufficiently homogeneous, so that the differences between them can be attributed to sampling rather than to fundamentally different evolutionary mechanisms underlying the data. If the data are significantly heterogeneous, they recommend separate analyses and comparison of trees.

The compatibility-based test of random partitions shows that the between-data-set incompatibility of the neuroanatomical and traditional data are significantly greater than that expected for random partitions and that the data are therefore not homogenous. Limited understanding of morphological evolution and of the nature of the differences between the traditional and neuroanatomical data does not permit any compelling explanation of this result. However, the several comparisons of data quality described above suggest that the neuroanatomical data, while not random with respect to themselves or the traditional data, are of lower quality. This might be because the neuroanatomical data are based on smaller sample sizes (Wake, 1993) so that the definition of character states and the coding of particular taxa is a distorted representation of the underlying biological variation. Another possibility is that the neuroanatomical data include many characters that may be correlated but convergent and misleading. A major difference between the traditional and neuroanatomical data sets is the phylogenetic relationships of the Scolecomorphidae. The traditional data set places this group outside a typhlonectid–caeciliid clade, whereas the neuroanatomical data associate the scolecomorphids with those caeciliids, that, like scolecomorphids, have the most rudimentary visual systems. If rudimentation of the visual system has occurred repeatedly in caecilians as a common consequence of a largely subterranean burrowing mode of life, and if this process affects a number of features that are taken as independent evidence of phylogenetic relationships, conflict between the neuroanatomical and traditional data would not be surprising.

Accepting the conditional combination approach, the heterogeneity of the traditional and neuroanatomical data suggests that we should focus on the separate analyses of these data and search for agreement. As we have seen there is some, but overall rather little, agreement. However, given that the neuroanatomical data appear to be of lower quality, resolution of the disagreements might reasonably place greater emphasis upon the traditional data. Indeed, assessment of data quality would seem to be a potentially important adjunct to the methods of taxonomic congruence or conditional combination. While the suggestion that data sets should be combined only if they are sufficiently homogeneous has much merit, it is also possible that combined analyses might provide some reinforcement of whatever weak phylogenetic signal is present in each of the separate data sets, particularly if character-weighting methods are used to enhance such signals. The only way of accommodating this possibility would seem to be by performing a combined analysis of the significantly heterogeneous data and determining whether hypotheses of relationships emerge that are at all well supported (e.g. as measured by Bremer support and/or bootstrapping etc.), and judging the utility of the combined analysis *a posteriori*. In the present case, a fairly clear, if somewhat disappointing, picture emerges from the combined and separate analyses. The strongest signal in the traditional data set provides support for some conventional relationships such as the integrity of the scolecomorphids, the typhlonectids, and the 'higher' caecilians, as well as for other branches at the base of the caecilian tree. The neuroanatomical data provide no resolution at the base of the tree but some support for the former relationships. Neither of the separate analyses identify strong support for their various incongruent resolutions of relationships within the 'higher' caecilians and the combined analyses do not add significantly to this overall picture. Most of the relationships within the 'higher' caecilians remain poorly supported, and the fact that

the various analyses using equal or differential weighting of characters do not produce entirely consistent results further underlines the continuing uncertainty of 'higher' caecilian phylogeny.

There are two interesting exceptions to these general results. The first exception is provided by the consistent results from the SACW analyses with average fits with either ordered or unordered characters, and worst fits with unordered characters. These analyses all produce the same strict component consensus (Fig. 8) and, in contrast to the other analyses, relationships within the 'higher' caecilians are generally supported by more impressive (although still not compelling) bootstrap proportions. The second exception is provided by the LQP analyses and the combined LQP–SACW analyses with the LQP characters either included or not. All of these variant analyses support the same strict component consensus (Fig. 10), demonstrating a fairly impressive insensitivity to differences in methods. These two trees (Figs 8, 10) differ only in the positions of *Sylvacaecilia grandisonae* and a *Dermophis mexicanus–Siphonops annulatus* clade, and it is tempting to recommend a consensus of these trees as a best conservative estimate of relationships based on the available morphological data. However, this is tempered by disagreements between these hypotheses and conclusions based on analyses of DNA sequences, and the limited bootstrap and Bremer support indices for most clades within the higher caecilians. For example, analyses of DNA data suggest that *Schistometopum thomense* and *Dermophis mexicanus* are more closely related to each other than they are to *Siphonops annulatus*, and that *Caecilia* is more closely related to *Typhlonectes natans* than to *S. thomense*. Judged against the expectations from background knowledge (or assumptions), the grouping of *Idiocranium russelli* with the Seychellean caecilians, the separation of *D. mexicanus* and *Gymnopis multiplicata* and the association of all those caecilians with rudimentary visual systems are surprising and suspicious results. Each of these relationships could yet prove compelling in future analyses: conclusions from molecular studies must themselves be tempered by their, as yet, very limited taxonomic scope, and background knowledge may represent little more than biased supposition. However, my conservative conclusion is that the available morphological data do not justify a phylogenetic hypothesis for 'higher' caecilians, that is both well resolved and well supported.

Although the goal of a well-supported morphological phylogeny for caecilians is not an outcome of this study, some progress has been made. It is apparent that the utility of the original neuroanatomical data for phylogenetic analysis was affected by internal inconsistencies and many contradictions with the primary literature (other problems of character coding, ordering, overweighting and unrepeatability also compromise the original analyses). Judged by their comparative HERs, the revised neuroanatomical data set seems to be considerably less noisy than the original data. Given that systematists build upon the work of previous researchers, my revision of the neuroanatomical data may be hoped to provide improved foundations upon which others can build. The many question marks in Table 1 indicate the need for additional observations that may further enhance the neuroanatomical data. At the very least, any future use of the caecilian neuroanatomical data in studies of caecilian phylogeny must take account of the problems identified with the original data.

A fairly unambiguous result is that the revised neuroanatomical data are of lower quality than the traditional data. However, explaining this difference in quality will

require much additional work. It is possible that a subset of the neuroanatomical characters is the product of concerted homoplastic rudimentation of the visual system, but such a conclusion must be based on an, as yet unavailable, well-supported phylogeny. In addition, caecilian taxa may be intraspecifically variable in some of the characters used, but that this variation has not been detected because of small sample sizes, and this must be addressed by increasing the sample sizes. However, despite the apparent low quality of the neuroanatomical data, randomization tests suggest that these data are not so noisy as to be completely phylogenetically meaningless.

The available data do provide fairly good support for some hypotheses of relationships. Best supported among these are the monophyly of four groups, the Scolecomorphidae, Typhlonectidae, the 'higher' caecilians, and the Ichthyophiidae and Uraeotyphlidae. To a lesser extent, the monophyly of the Ichthyophiidae, of *Boulengerula* and of *Oscaecilia ochrocephala* and *Caecilia*, are also reasonably well-supported, although, of these, only the monophyly of *Boulengerula* is supported by the analyses of the neuroanatomical data alone. None of these hypotheses is particularly controversial and several have been supported by previous phylogenetic analyses of traditional and/or molecular data (Nussbaum, 1979; Duellman & Trueb, 1986; Hillis, 1991; Hedges *et al*. 1993; Nussbaum & Hinkel, 1994; Wilkinson, 1996*a*; Wilkinson & Nussbaum, 1996). Progress is most clear with respect to the monophyly of the Typhlonectidae and Scolecomorphidae and the association of *Caecilia* and *Oscaecilia ochrocephala*. Each of these hypotheses is part of the background knowledge (or assumptions) of caecilian systematics (Nussbaum & Wilkinson, 1989) but none has been tested previously by rigorous phylogenetic analyses. Note that all of these groups emerge from the analysis of the traditional data alone and that the neuroanatomical data provide some additional support for a few of these groups but do not provide compelling support for any additional groups.

IX. SUMMARY

(1) Previous preliminary phylogenetic analyses of caecilian data yield results at odds with those supported by more traditional data.

(2) Based on comparative measures of data quality, a revised neuroanatomical data set appears to represent some improvement over previous treatments.

(3) There is little congruence between the results from separate analyses of the neuroanatomical and traditional morphological data.

(4) Randomisation tests indicate that neither the traditional nor the neuroanatomical data are indistinguishable from random data and that they are not random with respect to each other, but that they are significantly heterogeneous.

(5) The neuroanatomical data appear to be of lower quality than the traditional data, but cannot be dismissed as phylogenetically meaningless.

(6) Several uncontroversial hypotheses (e.g. the basal split between rhinatrematids and other caecilians, and the monophyly of the Ichthyophiidae, Typhlonectidae and Scolecomorphidae) are well supported by the combined data.

(7) A subset of the neuroanatomical characters supports an unconventional grouping of all those caecilians with the most rudimentary eyes, which may reflected concerted homoplasy.

(8) Conclusions on relationships within the 'higher' caecilians are constrained by the

conflict between the neuroanatomical and traditional data, the sensitivity of the combined analyses to weighting schemes, and by the limited support for the majority of groups in the majority of the analyses.

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XI. APPENDIX

The original data, including descriptions of characters and their states (Table 13) and the published eye, ear, hypoglossal and olfactory-vomeronasal data matrices (Tables 14–17), are summarized here. Wake (1993) performed both polar and non-polar analyses, with both ordered and unordered (additive and non-additive) treatments of multistate characters. Salamanders were used as a single outgroup for assessing character polarities and multistate characters were conceived as linear transformation series (i.e. $0 \rightarrow 1a \rightarrow 1b$) in the ordered treatments (M. H. Wake, personal communication). 'Analyses with characters polarised and unordered resulted in the most parsimonious sets of trees' (Wake, 1993, p. 44), and the results of these analyses, all of which produced multiple MPTs, were presented in the form of majority-rule component consensus trees.

Each of the original data matrices and a combined data set were reanalysed using PAUP 3.1.1. Polar analyses were performed by including a hypothetical ancestral taxon scored with the primitive character state for each character. Non-polar analyses were rooted so as to reproduce the rooting in the original trees. With three exceptions, the data sets I analysed are exactly as they appear in Wake (1993). The exceptions are (1) the scoring of *Schistometopum thomense* for character E3 was changed from 1 to 1a, (2) *Gegeneophis ramaswamii* was not included in the reanalyses because it was not included in the original analyses (M. H. Wake, personal communication), and (3) I used an integer coding in which 0, 1, 2, etc. correspond to Wake's 0, 1a, 1b etc. The last difference is purely cosmetic and can have no effect upon the results of the analyses.

Wake reported few statistics or indices that would allow a detailed comparison of her analyses and my reanalyses. With the exception of her analysis of the combined data, she reported tree length and numbers of MPTs, but no measures that can be used to assess the fit of data to trees, such as consistency and retention indices. With each consensus tree, Wake reported 'Rohlf's CI', a consensus index (Rohlf, 1982) that is highly dependent upon the degree of resolution in the consensus tree (Swofford, 1991). With the combined data, Wake reported Rohlf's CI_1, but not tree length or number of MPTs. Wake (1994, p. 187) reported these statistics as 'Rohlf's consistency index', suggesting confusion with the consistency index of Kluge & Farris (1969).

I was unable to reproduce the original trees or statistics in my reanalyses of the

Table 13. *Original neuroanatomical character descriptions* (*slightly abbreviated*). *After Wake* (*1993*)

Character	Description
E1	Extrinsic musculature: all six present (0); six present, superior oblique attenuate (1a); rectus externus, r. internus, r. inferior, inferior oblique present (1b); r. superior, r. inferior, r. internus present (1c); r. superior, r. inferior present (1d); r. inferior present (1e); all absent (1f).
E2	Eye under skin (0); eye under skin and bone (1).
E3	Optic nerve well developed (0); attenuate (1a); absent (1b).
E4	Vitreous body present (0); absent (1).
E5	Retina with multiple well-organised layers (0); amorphous (1).
E6	Retinal cell number: > 5000 (0); < 5000 (1).
E7	Number of cell layers in outer cell layer: 2 (0); 1-2 (1a); 1 (1b); > 2 (1c); 0 (1d).
E8	Number of cell layers in inner cell layer: 3-4 (0); 3 (1a); 2-3 (1b); 2 (1c); 1 (1d); 0 (1e).
E9	Number of cell layers in ganglionic cell layer: 2 (0); 1-2 (1a); 1 (1b); > 2 (1c); 0 (1d).
E10	Lens ⩾ half orbit diameter (0); < half (1a); absent (1b).
E11	Lens round (0); spheroid (1a); amorphous (1b); absent (1c).
E12	Lens crystalline (0); cellular peripherally, crystalline medially (1a); crystalline peripherally, cellular medially (1b); cellular amorphous (1c); rudimentary (1d); absent (1e).
E13	Lens free (0); attached to cornea (1a); attached to cornea and retina (1b).
A1	Stapes present (0); absent (1).
A2	Lagena present (0); absent (1).
A3	Lagenar recess large, median recess at saccular orifice (0); lagenar recess variable (1).
A4	Basilar papilla present (0); absent (1).
A5	Basilar papilla on limbic tissue (0); not on limbic tissue (1).
A6	Papilla neglect (PN) with > 100 hair cells (0); < 20 (1a); 20-40 (1b); 40-60 (1c).
A7	Papilla amphibiorum (PA) with > 200 hair cells (0); 88-180 (1a); 50 or fewer (1b).
A8	One fibre tract to PA and PN (0); 2 or more (1).
A9	PN near utriculus and sacculus, foramen in utriculus (0); PN far from foramen, foramen on lateral utriculus wall (1).
A10	Number of hair cells in PN half the number in PA (0); equal (1a); twice as many (1b).
H1	Hypoglossal nerve composed of: spinals 1 and 2 (0); spinals 1, 2 and 3 (1a); spinals 1 and 2 and occipital (1b); spinal 1 and occipital (1c); spinals 1, 2 and 3, and occipital (1d); spinals 1, 2 and 3, and vagal ramus X-1 (1e); spinals 1 and 2 and vagal ramus X-1 (1f); spinal 2 and vagal ramus X-1 (1g); spinals 2 and 3 (1h).
H2	Occipital absent (0); present (1).
H3	Distance from atlas to hypoglossal fusion < 45 mm (0); > 45 mm (1).
H4	Hypoglossal fusion < 40 mm (0); > 40 mm (1).
H5	Hypoglossal in tongue: bifurcated (0); straight with branches along its length (1a); branched only at tip (1b).
O1	Main nasal cavity undivided (0); slightly divided (1a); divided (1b).
O2	Longitudinal axis of main nasal cavity parallel to longitudinal axis of the head (0); at 60° (1).
O3	Respiratory epithelium in the main nasal cavity: concentrated posterolaterally (0); widespread (1).
O4	Vomeronasal organ mediolateral with lateral projection (0); mediolateral (1a); lateral (1b).
O5	Caudal extension to vomeronasal organ: present (0); absent (1).
O6	Vomeronasal organ moderate in size (0); large (1).

original data (data not shown). Generally, the reanalyses produced different numbers of MPTs, with different tree lengths, and majority-rule component consensus trees with greater resolution but fewer nodes than were replicated across all the MPTs than in the original results. The results were also highly sensitive to the treatment of multistate characters as ordered or unordered. Differences between the original and reanalyses are difficult to explain and I shall not dwell on this here. However, in view of the revisions of the neuroanatomical characters described above, and the unrepeatability

Table 14. *Original data for caecilian eye characters* (*E1–E13*). *After Wake* (*1993*)

	Characters												
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13
Epicrionops bicolor	0	0	0	0	0	0	0	0	0	1a	0	0	0
Epicrionops petersi	0	0	0	0	0	0	1a	1a	0	1a	1a	0	0
Ichthyophis sp. (larva)	0	0	0	0	0	0	0	1a	1c	1a	0	1b	0
Ichthyophis glutinosus	0	0	0	0	0	0	0	1c	1c	1a	1a	1a	1a
Ichthyophis kohtaoensis	0	0	0	0	0	0	0	1c	1c	1a	1a	1a	1a
Uraeotyphlus narayani	0	0	0	0	0	0	0	0	0	0	1a	1a	1a
Dermophis mexicanus	0	0	0	0	0	0	0	1c	1a	1a	0	0	0
Gymnopis multiplicata	1f	1	1a	1	0	0	1a	1a	1b	1b	1a	1d	1a
Caecilia occidentalis	1d	0	1a	1	0	0	1b	1c	1c	1b	1a	1d	1a
Oscaecilia ochrocephala	1d	1	1a	0	1	1	0	1d	1d	1b	1b	1d	1b
Boulengerula taitanus	1f	1	1a	1	1	1	1c	1d	1d	1c	1b	1f	1b
Boulengerula boulengeri	1f	1	1b	1	1	1	1c	1d	1a	1c	1b	1f	1b
Geotrypetes seraphini	1b	0	1a	1	0	0	0	1b	0	1a	0	1c	1a
Sylvacaecilia grandisonae	1b	0	1a	1	0	0	0	0	0	0	1a	1a	1a
Hypogeophis rostratus	0	0	1a	1	0	0	0	1a	1c	1a	0	1a	1a
Idiocranium russelli	1c	0	1a	1	0	1	0	1c	1a	1a	0	1a	1a
Schistometopum thomense	1c	0	1	0	0	0	0	1a	0	1a	1a	1a	0
Scolecomorphus uluguruensis	1f	0	1b	0	1	1	0	1d	1d	1b	1b	1d	1b
Scolecomorphus kirkii	1d	0	1a	1	0	1	1a	1a	1a	0	1a	0	1b
Typhlonectes natans	1a	0	1a	0	0	0	1a	1a	1c	0	1a	0	1a
Chthonerpeton indistrinctum	1b	0	1a	1	0	0	0	0	0	0	1a	0	1b

Table 15. *Original data for caecilian eye characters* (*A1–A10*). *After Wake* (*1993*)

	Characters									
Taxa	1	2	3	4	5	6	7	8	9	10
Epicrionops bicolor	0	0	0	0	0	0	0	0	0	0
Epicrionops petersi	0	0	0	0	0	0	0	0	0	0
Ichthyophis glutinosus	0	0	0	0	1	1b	1a	0	0	0
Ichthyophis orthoplicatus	0	0	0	0	1	1b	1a	0	0	0
Uraeotyphlus narayani	0	0	0	0	1	?	1a	0	0	0
Dermophis mexicanus	0	0	1	1	1	1c	0	1	0	0
Gymnopis multiplicata	0	0	1	1	1	1b	1a	0	0	0
Caecilia occidentalis	0	0	1	1	1	1b	1a	0	0	0
Oscaecilia ochrocephala	0	1	1	1	1	1c	1a	0	1	0
Boulengerula taitanus	0	1	1	1	1	1a	1b	0	1	0
Boulengerula boulengeri	0	1	1	1	1	1a	1b	0	1	0
Geotrypetes seraphini	0	0	1	1	1	1b	1a	0	0	0
Hypogeophis rostratus	0	0	1	1	1	1c	1a	0	0	0
Idiocranium russelli	0	0	1	1	1	1a	1a	0	0	0
Scolecomorphus uluguruensis	1	0	1	1	1	1a	1b	0	0	1b
Scolecomorphus kirkii	1	0	1	1	1	1a	1b	0	0	1b
Typhlonectes natans	0	1	1	1	1	0	1a	0	0	1a
Chthonerpeton indistinctum	0	1	1	1	1	?	1a	0	0	0

Table 16. *Original data for caecilian hypoglossal nerve characters* (*H1–H5*). *After Wake* (*1993*)

	Characters				
Taxa	1	2	3	4	5
Epicrionops bicolor	0	0	1	1	1b
Epicrionops petersi	1a	0	1	1	1b
Ichthyophis sp. (larva)	0	0	0	1	1b
Ichthyophis kohtaoensis	1d	0	1	1	1b
Uraeotyphlus narayani	1d	0	1	0	0
Dermophis mexicanus	1b	1	0	0	0
Gymnopis multiplicata	1b	1	0	1	0
Caecilia occidentalis	1f	0	1	1	1a
Oscaecilia ochrocephala	0	0	0	1	0
Siphonops annulatus	0	1	?	?	?
Boulengerula boulengeri	1g	0	0	0	1b
Geotrypetes seraphini	1b	1	1	1	0
Grandisonia alternans	0	0	0	0	0
Hypogeophis rostratus	0	0	1	0	1a
Idiocranium russelli	1f	0	0	0	1a
Gegeneophis ramaswamii	1h	0	?	?	?
Scolecomorphus uluguruensis	1b	1	1	1	1b
Scolecomorphus vittatus	1b	1	0	1	1b
Typhlonectes natans	1b	1	1	0	0
Chthonerpeton indistinctum	0	0	0	1	1b
Nectocaecilia haydeii [sic]	1c	1	?	?	?

Table 17. *Original data for caecilian olfactory-vomeronasal characters* (*O1–O6*). *After Wake* (*1993*)

	Characters					
Taxa	1	2	3	4	5	6
Epicrionops petersi	1a	0	0	1b	0	0
Ichthyophis glutinosus	1b	0	0	1a	1	0
Ichthyophis kohtaoensis	1b	0	0	1a	1	0
Uraeotyphlus narayani	0	0	0	0	1	0
Dermophis mexicanus	1b	0	0	1b	1	0
Gymnopis multiplicata	1b	0	0	1b	1	0
Caecilia occidentalis	0	0	0	0	1	0
Oscaecilia ochrocephala	0	0	0	0	1	0
Boulengerula taitanus	1b	0	0	1a	1	0
Boulengerula boulengeri	0	1	0	1a	1	0
Geotrypetes seraphini	1b	0	0	0	1	0
Sylvacaecilia grandisonae	0	0	0	1a	1	0
Hypogeophis rostratus	0	0	0	0	1	0
Idiocranium russelli	0	0	0	0	1	0
Scolecomorphus uluguruensis	1b	0	0	1a	1	0
Scolecomorphus kirkii	1b	0	0	1a	1	0
Typhlonectes natans	0	0	1	1a	1	1
Chthonerpeton indistinctum	0	0	1	1a	1	1

of the original results, I suggest that no conclusions be based on the results of the original analyses.

XII. REFERENCES

ALROY, J. (1984). Four permutation tests for the presence of phylogenetic structure. *Systematic Biology* **43**, 430–437.

ARCHIE, J. W. (1989*a*). A randomisation test for phylogenetic information in systematic data. *Systematic Zoology* **38**, 239–252.

ARCHIE, J. W. (1989*b*). Phylogenies of plant families: a demonstration of randomness in DNA sequence data derived from proteins. *Evolution* **43**, 1796–1800.

ARCHIE, J. W. (1989*c*). Homoplasy excess ratios, new indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. *Systematic Zoology* **38**, 253–269.

BARRETT, M., DONOGHUE, M. J. & SOBER, E. (1991). Against consensus. *Systematic Zoology* **40**, 486–493.

BREMER, K. (1988). The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**, 795–803.

DUELLMAN, W. E. & TRUEB, L. (1986). *Biology of Amphibians*. McGraw-Hill, New York.

ELS, A. J. (1963). Contributions to the cranial morphology of *Schistometopum thomensis* (Bocage). *Annals of the University of Stellenbosch* **38**, 39–64.

FAITH, D. P. & CRANSTON, P. S. (1991). Could a cladogram this short have arisen by chance alone?: On permutation tests for cladistic structure. *Cladistics* **7**, 1–28.

FARRIS, J. S. (1969). A successive approximations approach to character weighting. *Systematic Zoology* **18**, 374–385.

FARRIS, J. S. (1988). *Henning86*, version 1.5. Distributed by the author. Port Jefferson Station, New York.

FARRIS, J. S., KÄLLERSJÖ, M., KLUGE, A. G. & BULT, C. (1995). Constructing a significance test for incongruence. *Systematic Biology* **44**, 570–572.

FELSENSTEIN, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791.

FRITZSCH, B. & WAKE, M. H. (1988). The inner ear of gymnophione amphibians and its nerve supply: a comparative study of regressive events in a complex sensory system (Amphibia: Gymnophiona). *Zoomorphology* **108**, 201–217.

GREVEN, H. (1984). The dentition of *Gegeneophis ramaswamii* Taylor, 1964 (Amphibia, Gymnophiona), with comments on monocuspid teeth in the Amphibia. *Zeitschrift für zoologische Systematik und Evolutionsforschung* **22**, 342–348.

HASS, C. A., NUSSBAUM, R. A. & MAXSON, L. R. (1993). Immunological insights into the evolutionary history of caecilians (Amphibia: Gymnophiona): relationships of the Seychellean caecilians and a preliminary report on family-level relationships. *Herpetological Monographs* **7**, 56–63.

HEDGES, S. B., NUSSBAUM, R. A. & MAXSON, L. R. (1993). Caecilian phylogeny and biogeography inferred from mitochondrial DNA sequences of the 12S and 16S rRNA genes (Amphibia: Gymnophiona). *Herpetological Monographs* **7**, 64–76.

HENNIG, W. (1966). *Phylogenetic Systematics*. University of Illinois Press, Urbana, Illinois.

HILLIS, D. M. (1991). The phylogeny of amphibians: current knowledge and the role of cytogenetics. In *Amphibian Cytogenetics and Evolution* (ed. D. M. Green & S. K. Sessions), pp. 7–31. Academic Press, San Diego.

HUELSENBECK, J. P., BULL, J. J. & CUNNINGHAM, C. W. (1996). Combining data in phylogenetic analysis. *Trends in Evolution and Ecology* **11**, 152–158.

KÄLLERSJÖ, M., FARRIS, J. S., KLUGE, A. G. & BULT, C. (1992). Skewness and permutation. *Cladistics* **8**, 275–287.

KLUGE, A. G. (1989). A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* **38**, 7–25.

KLUGE, A. G. & FARRIS, J. S. (1969). Quantitative phyletics and the evolution of anurans. *Systematic Zoology* **18**, 1–32.

LEUTENEGGER, S. (1972). Hirn, Hirnnerven und Geruchsorgan von *Nectocaecilia haydee* (Gymnophionen). Dissertation, University of Basel.

MEACHAM, C. A. (1994). Phylogenetic relationships at the basal radiation of Angiosperms, further study by probability of character compatibility. *Systematic Botany* **19**, 506–522.

MIYAMOTO, M. M. & FITCH, W. M. (1995). Testing species phylogenies and phylogenetic methods with congruence. *Systematic Biology* **44**, 64–76.

NUSSBAUM, R. A. (1977). Rhinatrematidae: a new family of caecilians (Amphibia: Gymnophiona). *Occasional Papers of the Museum of Zoology, University of Michigan* **682**, 1–30.

Nussbaum, R. A. (1979). The taxonomic status of the caecilian genus *Uraeotyphlus* Peters. *Occasional Papers of the Museum of Zoology, University of Michigan* **687**, 1–20.

Nussbaum, R. A. (1986). Systematics of the caecilians (Amphibia: Gymnophiona) of the family Scolecomorphidae. *Occasional. Papers of the Museum of Zoology, University of Michigan* **713**, 1–49.

Nussbaum, R. A. (1991). Cytotaxonomy of caecilians. In *Amphibian Cytogenetics and Evolution* (ed. D. M. Green & S. K. Sessions), pp. 33–66. Academic Press, San Diego.

Nussbaum, R. A. & Ducey, P. K. (1988). Cytological evidence for monophyly of the caecilians (Amphibia: Gymnophiona) of the Seychelles Archipelago. *Herpetologica* **44**, 290–296.

Nussbaum, R. A. & Hinkel, H. (1994). Revision of East African caecilians of the genera *Afrocaecilia* Taylor and *Boulengerula* Tornier (Amphibia: Gymnophiona: Caeciliidae). *Copeia* **1994**, 750–760.

Nussbaum, R. A. & Naylor, B. G. (1982). Variation in the trunk musculature of caecilians (Amphibia: Gymnophiona). *Journal of Zoology* **198**, 383–398.

Nussbaum, R. A. & Wilkinson, M. (1989). On the classification and phylogeny of caecilians (Amphibia: Gymnophiona), a critical review. *Herpetological Monographs* **3**, 1–42.

Ramaswami, L. S. (1943). An account of the head morphology of *Gegenophis* [sic] *carnosus* (Beddome), Apoda. *Journal of Mysore University* **3**, 205–220.

Rohlf, F. J. (1982). Consensus indices for comparing classifications. *Mathematical Biosciences* **59**, 131–144.

Schmidt, A. & Wake, M. H. (1990). The olfactory and vomeronasal system of caecilians (Amphibia: Gymnophiona). *Journal of Morphology* **205**, 255–268.

Straub, J. O. (1985). *Contributions to the cranial anatomy of the genus* Grandisonia *Taylor 1968* (*Amphibia: Gymnophiona*). Inaugural dissertation, University of Basel.

Swofford, D. L. (1991). When are phylogeny estimates from molecular and morphological data incongruent? In *Phylogenetic analysis of DNA sequences* (ed. M. M. Miyamoto & J. Cracraft), pp. 295–333. Oxford University Press, Oxford.

Swofford, D. L. (1993). *PAUP: Phylogenetic Analysis Using Parsimony*. Version 3.1.1 Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Taylor, E. H. (1964). A new species of caecilian from India (Amphibia, Gymnophiona). *Senckenbergiana Biologica* **45**, 227–231.

Taylor, E. H. (1968). *The Cecilians of the World*. University of Kansas Press, Lawrence.

Wake, M. H. (1985). The comparative morphology and evolution of the eyes of caecilians (Amphibia: Gymnophiona). *Zoomorphology* **105**, 277–295.

Wake, M. H. (1992). Patterns of peripheral innervation of the tongue and hyobranchial apparatus in caecilians (Amphibia: Gymnophiona). *Journal of Morphology* **212**, 37–53.

Wake, M. H. (1993). Non-traditional characters in the assessment of caecilian phylogenetic relationships. *Herpetological Monographs* **7**, 42–55.

Wake, M. H. (1994). The use of unconventional morphological characters in the analysis of systematic patterns and evolutionary processes. In *Interpreting the Hierarchy of Nature* (ed. L. Grande & O. Rieppel), pp. 173–200. Academic Press, San Diego.

Walsh, D. (1986). *Systematics of caecilians*. Ph.D. Thesis, McGill University.

Weidersheim, R. (1879). *Die Anatomie der Gymnophionen*. Jena.

Wilkinson, M. (1981). Notes on a caecilian, *Nectocaecilia* sp. *Herptile* **5**, 22–25.

Wilkinson, M. (1988). The status of *Nectocaecilia cooperi* Taylor, with comments on the genus *Nectocaecilia* Taylor (Amphibia: Gymnophiona: Typhlonectidae). *Journal of Herpetology* **22**, 119–121.

Wilkinson, M. (1989). On the status of *Nectocaecilia fasciata* Taylor with a discussion of the phylogeny of the Typhlonectidae (Amphibia: Gymnophiona). *Herpetologica* **45**, 23–36.

Wilkinson, M. (1991). Adult tooth crown morphology in the Typhlonectidae (Amphibia: Gymnophiona): a reinterpretation of variation and its significance. *Zeitschrift für zoologische Systematik und Evolutionsforschung* **29**, 304–311.

Wilkinson, M. (1992*a*). Ordered versus unordered characters. *Cladistics* **8**, 375–385.

Wilkinson, M. (1992*b*). *Consensus, compatibility and missing data in phylogenetic inference*. Ph.D. Thesis, University of Bristol.

Wilkinson, M. (1992*c*). The phylogenetic position of the Rhinatrematidae (Amphibia: Gymnophiona): evidence from the larval lateral line system. *Amphibia-Reptilia* **13**, 74–79.

Wilkinson, M. (1992*d*). *PERMUTE* software and documentation. Department of Geology, University of Bristol.

Wilkinson, M. (1994). Common cladistic information and its consensus representation: reduced Adams and cladistic consensus trees and profiles. *Systematic Biology* **43**, 343–368.

Wilkinson, M. (1995*a*). A comparison of two methods of character construction. *Cladistics* **11**, 297–308.

Wilkinson, M. (1995*b*). More on reduced consensus methods *Systematic Biology* **44**, 435–439.

WILKINSON, M. (1995*c*). *REDCON 2.0* software and documentation. School of Biological Sciences, University of Bristol.

WILKINSON, M. (1995*d*). Coping with missing entries in phylogenetic inference using parsimony. *Systematic Biology* **44**, 501–514.

WILKINSON, M. (1995*e*). *TAXEQ2* software and documentation. School of Biology Sciences, University of Bristol.

WILKINSON, M. (1995*f*). *PICA95* software and documentation. School of Biological Sciences, University of Bristol.

WILKINSON, M. (1996*a*). Majority-rule reduced consensus methods and their use in bootstrapping. *Molecular Biology and Evolution* **13**, 437–444.

WILKINSON, M. (1996*b*). On the distribution of homoplasy and choosing among trees. *Taxon* **45**, 263–266.

WILKINSON, M. (1996*c*). The heart and aortic arches of rhinatrematid caecilians (Amphibia: Gymnophiona). *Zoological Journal of the Linnean Society* **118**, 135–150.

WILKINSON, M. (1996*d*). Resolution of the taxonomic status of *Nectocaecilia haydee* (Roze) and a key to the genera of the Typhlonectidae (Amphibia: Gymnophiona). *Journal of Herpetology* **30**, 413–415.

WILKINSON, M. (1996*e*). The taxonomic status of *Typhlonectes venezuelense* Fuhrmann (Amphibia: Gymnophiona: Typhlonectidae). *The Herpetological Journal* **6**, 30–31.

WILKINSON, M. & BENTON, M. J. (1995). Missing data and rhynchosaur phylogeny. *Historical Biology* **10**, 137–150.

WILKINSON, M. & BENTON, M. J. (1996). Sphenodontid phylogeny and the problems of multiple trees. *Philosophical Transactions of the Royal Society B* **351**, 1–16.

WILKINSON, M. & NUSSBAUM, R. A. (1996). On the phylogenetic position of the Uraeotyphlidae (Amphibia: Gymnophiona). *Copeia* **1996**, 550–562.

WILKINSON, M., SUTER, S. J. & SHIRES, V. L. (1996). The reduced cladistic consensus method and cassiduloid echinoid phylogeny. *Historical Biology* **12**, 63–73.