Evolution of the Vertebrate Central Nervous System: Patterns and Processes[1]

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SYNOPSIS. As brains do not fossilize, most proposed phylogenetic sequences for central nervous system characters must be based on the patterns of variation of those characters in living organisms. Similarly, hypotheses regarding how brains change through time, and the evolutionary processes that produce these changes, are ultimately based on the character patterns recognized. It is critical in these analyses to distinguish between homologous and homoplasous characters if errors in the reconstruction and interpretation of phylogenies are to be minimized. Definitions of homology and homoplasy are reviewed, as are the concepts that bear on their application. Cladistic definitions are adopted, and criteria for distinguishing homologous from homoplasous characters are discussed. Analysis of a number of CNS characters that are usually assumed to be homologous reveals that homoplasous characters appear among them. As in other organ systems, homoplasous characters are actually common. A number of previous hypotheses regarding CNS evolution are reviewed in the context of new data on neural connections and their cladistic analysis. Some of these hypotheses may be falsified by a cladistic treatment of CNS characters, whereas sufficient data do not exist to evaluate others.

INTRODUCTION

The ability to describe phylogenetic changes in any character (*i.e.,* any definable attribute of an organism) is based on the pattern of character variation observed among different taxa. Equally important, elucidation of evolutionary mechanisms or processes is based on the kinds of character patterns that can be recognized. In both of these analyses, it is critical to distinguish a character and its subsequent phylogenetic transformations (homologous characters) from other characters that may appear similar but have different evolutionary histories (homoplasous characters) if errors in interpretation are to be minimized.

In this paper, I review several definitions of homology and homoplasy, discuss concepts necessarily inherent to any useful set of definitions, and adopt definitions to which the remainder of the paper will adhere. I then review criteria for distinguishing homologous characters from homoplasous characters and analyze a

number of central nervous system (CNS) characters in the context of these definitions and criteria. Finally, I evaluate several published hypotheses regarding CNS evolution, using data from the literature as well as data presented herein, and conclude that previous hypotheses are primarily descriptions of patterns of character variation, not hypotheses outlining evolutionary processes.

CONCEPTS OF CHARACTER COMPARISON

Although there is an extensive literature defining the concepts of homology and homoplasy (*cf.,* Owen, 1843; Lankester, 1870; Osborn, 1902; Haas and Simpson, 1946; Simpson, 1961; Smith, 1967; Bock, 1969; Mayr, 1969; Campbell and Hodos, 1970; Ghiselin, 1976; Hailman, 1976; Wiley, 1981; Patterson, 1982), there is little agreement in formal definitions. Most discussions do, however, focus on character similarity and common ancestry. Owen (1843, p. 379) defined homologue as "The same organ in different animals under every variety of form and function." Owen's definition is clearly pre-evolutionary, and— following the rapid spread of Darwin's theory of evolution—many morphologists saw the need to base the concept of homology on a phylogenetic foundation. Thus
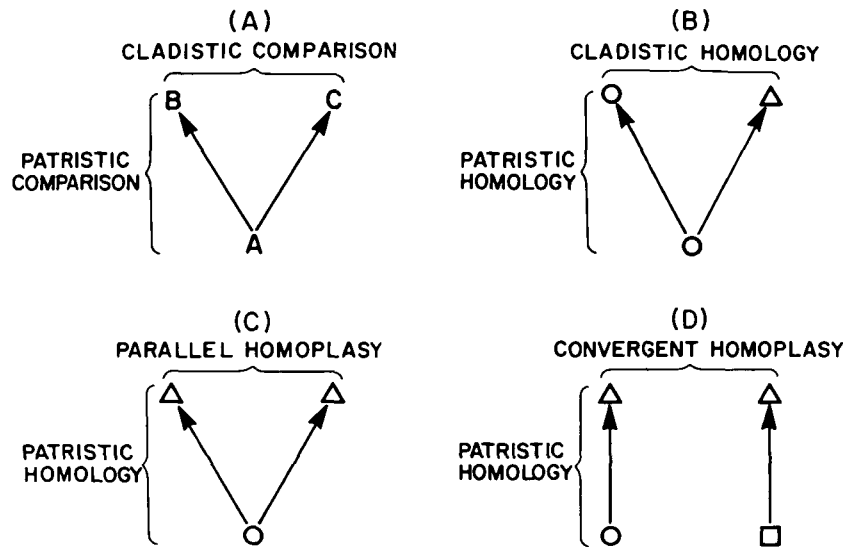
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Fig. 1. Diagrammatic representation of homology, homoplasy due to parallelism, and homoplasy due to convergence. Symbols denote characters and letters denote taxa. Sibling or cladistic comparisons are enclosed by a horizontal bracket and patristic comparisons by a vertical bracket.

Lankester (1870) proposed to call "structures which are genetically related, in so far as they have a single representative in a common ancestor" homogenous, and the relation between such structures homogeny.

The advent of evolutionary theory complicated morphological comparisons in a number of ways. Previously, comparisons were conceived among living sibling or cladistic taxa, as they are now termed (taxa B and C in Fig. 1A). However, the concept of evolving species suggested a second type of comparison, that of patristic species (taxa A to B, or A to C, in Fig. 1A). Thus any definition of homology should include statements involving both cladistic and patristic comparisons (Smith, 1967) which should not be contradictory.

The use of character similarity as a criterion for defining homology is also problematical. Many workers have interpreted Owen's "same organ in different animals" to mean resemblance between organs in different animals. Thus Simpson (1961, p. 78) defined homology as "resemblance due to inheritance from a common ancestry." Simpson's definition, taken literally, would exclude characters that do not resemble each other, such as those in Figure 1B, the

relationship that probably includes most of the structures cited as examples of homologues in comparative anatomy texts. More importantly, his definition could also include cases that he himself defined as parallelism (Fig. 1C) and included under the category of nonhomology (homoplasy). Mayr's definition (1969, p. 85), "Homologous features (or states of features) in two or more organisms are those that can be traced back to the same feature (or state) in the common ancestor of these organisms," avoids the criterion of similarity but does not exclude parallelism which Mayr, like Simpson, lists as a subcategory under nonhomology (which Mayr calls analogy). In short, although both Simpson and Mayr stated that parallelism is a type of nonhomology (see also Haas and Simpson, 1946), neither's definition of homology specifically excludes many cases of parallelism. Thus, based on Simpson's and Mayr's definitions, many misinterpretations of homology and parallelism have become part of the literature.

I believe that any definition of homology should satisfy certain requirements: 1) allow both patristic and cladistic comparisons with no internal inconsistency; 2) not be restricted to characters that exhibit simi-

larity; and 3) include characters that share common ancestry while excluding cases of the phenomenon commonly defined as homoplasy. Wiley's definition of homology (1981, pp. 121–122) appears to satisfy these criteria and is adopted in the subsequent discussion: "A character of two or more taxa is homologous if this character is found in the common ancestor of these taxa, or, two characters (or a linear sequence of characters) are homologous if one is directly (or sequentially) derived from the other(s)."

Given any three taxa with one the common ancestor (taxon A in Fig. 1A) of two descendent taxa (B and C), there are only two character patterns in which both cladistic and patristic homology exist. The first pattern is one in which a character in the ancestral taxon is retained in both descendent taxa, and the second pattern (Fig. 1B) is one in which a character (character "circle") in the ancestral taxon is retained in one descendent taxon but is transformed (into character "triangle") in the other descendent taxon. An important consequence of Wiley's definition is that two different characters in two taxa can be cladistically homologous if one of the characters is retained from the last common ancestor, a condition met by most cladistic homologies commonly recognized in the comparative anatomical literature.

Considerable confusion in the literature has resulted from analysis of the phyletic case (Fig. 1C) in which character "circle," found in the ancestral taxon, independently transforms into character "triangle" in the descendent taxa. All current definitions of homology would require that a patristic homology be recognized between character "circle" and the characters "triangle." However, Wiley's definition would not allow recognition of a cladistic homology between the characters "triangle," whereas both Mayr's and Simpson's definitions would. Further, the cladistic comparison in Figure 1C would be described as parallel homoplasy by Simpson (1961) or parallel analogy by Mayr (1969). Lankester (1870) coined the term homoplasy to deal with this specific kind of cladistic comparison, but he did not clearly distinguish whether it should be included

within the category of homologous or non-homologous comparisons. Haas and Simpson (1946, p. 325) state that homoplasy ". . . may be defined to comprise all evolutionary processes bringing about similarities between organisms or their parts, organs or structures, which are not due to common ancestry, but to independent acquisition of similar characters." Similarly, Haas and Simpson (1946, p. 328) state that, "In our opinion, however, homology should be recognized only where there is clear observational evidence of a common origin of the similar characters; wherever new characters are independently acquired in different lineages, no assumption of some inherited latent or potential predisposition to similar changes should be deemed sufficient to consider those characters homologous instead of merely homoplastic."

Thus Haas and Simpson clearly divided character similarities into two mutually exclusive categories: homology *versus* homoplasy. Certainly, cladistic comparisons that involve character similarities due to parallelism should not be interpreted as homology, as this results in errors in the recognition of characters and the reconstruction and interpretation of phylogenies. Simpson (1961, p. 78) defined homoplasy as "resemblance not due to inheritance from a common ancestry," and he recognized five different conditions that might result in homoplasy: parallelism, convergence, analogy, mimicry, and chance similarity. Mayr (1969, pp. 85, 202) came to a similar conclusion but termed the category "analogy." Both Simpson and Mayr restricted their respective categories of homoplasy and analogy to characters that resemble each other. If homoplasy is to constitute a category mutually exclusive from that of homology, both should include characters that are not similar as well as not homologous. Wiley's definition of homoplasy (1981, p. 122)—"A character found in two or more species is homoplasous (non-homologous) if the common ancestor of these species did not have the character in question, or if one character was not the precursor of the other"—satisfies this requirement.

Few workers (Haas and Simpson, 1946;

Simpson, 1961; Ghiselin, 1976; Hailman, 1976) have dealt with the conditions that result in homoplasy or its specific subcategories. Although Simpson (1961) recognized five conditions that might result in homoplasous characters, Mayr (1969) listed only parallelism and convergence, and Patterson (1982) has suggested that analogy, mimicry, and chance similarity should be included under the term convergence. In this paper, I will confine considerations of homoplasy to parallelism and convergence, but further attention should be directed toward the conditions that result in homoplasous characters and the predictive value of recognizing such characters.

Simpson (1961, p. 78) distinguished parallelism from convergence based on presumed differences in the genetic bases of the characters. Thus he assumed that convergent characters were similar characters based on different genes, whereas parallel characters were similar characters based on the same genes. In most cases, we do not know the genetic bases of the characters being examined. Biologists have usually concluded that observed similarities occurring independently in widely separated taxa are due to convergence; if similarities occur in closely related taxa, they are due to parallelism. This "rule of thumb" is clearly an artificial and arbitrary distinction that lends itself to extreme fragmentation. Wiley (1981, p. 12) has redefined convergence and parallelism, based on phenotypic criteria which appear to be more satisfactory, and his definitions are adopted here: Convergence (Fig. 1D) is "the development of similar characters from different pre-existing characters," and parallelism is "the independent development of similar characters from the same plesiomorphic [primitive] character." It should be noted that parallelism and convergence usually characterize only cladistic relationships, and that two characters in different taxa may be cladistically homoplasous (due either to parallelism or convergence) and patristically homologous (Fig. 1C, D). Furthermore, in the case of convergence illustrated in Figure 1D, character "circle" in the one taxon might be cladistically homologous or homoplasous

to character "square" in the second taxon, depending on whether or not these taxa share an immediate common ancestor and what the nature of the character is in that ancestor.

Criteria for Recognition of Homologous and Homoplasous Characters

Since Darwin, homology has been defined one way but tested in another way. Definitions of homology have been based on common ancestry, but criteria for recognizing homologues have generally rested on phenetic similarity (Remane, 1956; Simpson, 1961; Mayr, 1969; Bock, 1977). Remane (1956) suggested that suspected homologues should exhibit similarity in topographical position, exhibit a high degree of resemblance (*i.e.*, level of resemblance should not be superficial; characters should be similar in detail), and exhibit continuance of similarity throughout intermediate species. These criteria are sufficient to distinguish homology (Fig. 1B) from homoplasy due to convergence (Fig. 1D), as the degree of similarity between convergent characters is only superficial, and convergent characters rarely, if ever, occur among intermediate species. However, criteria based on phenetic similarity cannot, by themselves, distinguish between homology (Fig. 1B) and homoplasy due to parallelism (Fig. 1C). Hypotheses regarding these relationships can only be tested by examining the groups' phyletic relationships (Hennig, 1966; Eldredge and Cracraft, 1980; Wiley, 1981; Patterson, 1982). Patterson (1982) correctly claimed that homologous features are those which characterize monophyletic groups. Shared derived characters (synapomorphies) characterize a monophyletic group. Thus synapomorphies are sibling homologies, and every hypothesis of homology is actually a hypothesis regarding a monophyletic group. Conversely, independently derived characters cannot characterize sibling taxa and cannot be homologous. This view does not exclude primitive characters (plesiomorphies) nor shared primitive characters (symplesiomorphies) from consideration as possible homologues, as such characters can

be viewed as those whose level of synapomorphy has not been resolved. As more groups of organisms are included in an analysis, characters initially viewed as symplesiomorphies become synapomorphies defining a monophyletic set of organisms at a higher level. A critical test of a particular hypothesis of homology is possible by testing the congruence of this hypothesis, expressed as a synapomorphy, with other hypotheses of synapomorphy. It is generally assumed that the hypothesis of monophyly that exhibits the largest number of synapomorphies is the most probable (parsimonious) hypothesis. Other hypotheses are said to be falsified, and their "synapomorphies" are assumed to be due to homoplasy.

In order to recognize shared derived characters, it is necessary to determine the direction of change or polarity (*i.e.*, primitive *versus* derived condition) of the characters that are suspected to be homologous on the basis of phenetic similarity. Three phylogenetic criteria are frequently given by cladists to determine the polarity of characters: 1) out-group rule, 2) ontogenetic character precedence (von Baer's theorem), and 3) geological character precedence. The last criterion is of limited value in the study of CNS characters, as little information regarding these characters can be gleaned from the fossil record.

The out-group rule, initially proposed by Hennig (1966), states that given two characters that are homologues and found within a monophyletic group, the character that is also found in the sister group is the primitive (plesiomorphic) character, whereas the character found only within the monophyletic group is the derived (apomorphic) character. As an example of the out-group rule applied to CNS characters, let us consider the distribution of the corpus callosum in mammals. Marsupial and placental mammals are considered sister groups; marsupials do not possess a corpus callosum, whereas placentals do. Is the absence of a corpus callosum a primitive character? Or has this character been lost in marsupials which would, therefore, represent the derived condition? Monotreme mammals are considered the sister

group to other mammals, and they do not possess a corpus callosum. Thus the absence of this structure would be considered the primitive condition for mammals, and the corpus callosum would be considered a derived character for placental mammals.

The theory of ontogenetic character precedence (von Baer's theorem) establishes character polarity based on comparison of developmental patterns rather than distribution of characters among adults in closely related taxa. Von Baer's theorem states that members of two or more closely related taxa will follow the same course of development to the stage of their divergence. Thus characters observed to be more general are assumed to be primitive, whereas those that are less general are assumed to be derived. A neurological example of ontogenetic character precedence can be seen by comparing the development of the telencephalon in amphibians and reptiles. The telencephalon of reptiles differs from that of amphibians by possessing a dorsal ventricular ridge. Is the absence of this ridge in amphibians a primitive or a derived condition? Examination of the embryology of the telencephalon in amphibians and reptiles, as well as many other anamniotes, reveals that the early development of this structure is almost identical among amphibians and reptiles. However, neuronal development of the lateral wall of the telencephalon in amphibians is characterized by differentiation of the neuroblasts *in situ*; in reptiles a portion of the neuroblasts migrates laterally to form a lateral cortical plate that is the target of the lateral olfactory tract, whereas the remaining matrix zone continues to undergo cellular division *in situ*, resulting in the dorsal ventricular ridge. Thus, absence of the ridge appears to be the primitive condition in tetrapods, and the presence of a dorsal ventricular ridge is the derived condition.

VARIATION IN SOME CNS CHARACTERS

For the most part, statements of possible homology between CNS characters have been based solely on phenetic similarity. As pointed out above, this is sufficient to discriminate homology from convergent

homoplasy, but phenetic criteria are inadequate to discriminate homology from parallel homoplasy. Such discrimination can best be accomplished by out-group comparisons and acceptance of an hypothesis that requires the fewest number of transformations. This requires that the distribution and variation of the characters being considered be sampled in a large number of groups. Not many CNS characters have been so thoroughly sampled, but there are a few whose distribution and variation are relatively well documented: the lateral line system, ascending spinal projections, and long efferent pathways from the telencephalon. These characters will now be reviewed and examples of both homology and homoplasy suggested for each.

Lateral Line System

In most anamniotes, mechanoreceptive neuromasts are distributed over the head and body and are innervated by branches of the anterior and posterior lateral line nerves, respectively (Bullock et al., 1982; McCormick, 1982). In all anamniotes that have been examined experimentally, the lateral line nerve fibers that innervate the mechanoreceptors enter the medulla and terminate in a nucleus that is alar-derived, occupies the same topographical position in the medulla, and is termed the medial octavolateralis nucleus. This nucleus (Fig. 2) occurs in all anamniotic vertebrates (except most adult anurans) and is absent, as are lateral line nerves, in other chordates, all of which suggests that the medial octavolateralis nucleus is homologous among anamniotic vertebrates and probably arose at the time of the origin of vertebrates.

In many anamniotic vertebrates, a second class of receptors (electroreceptors) comprises part of the lateral line system. The electroreceptive system exhibits several patterns of organization in terms of receptor morphology, peripheral innervation, and central projections within the medulla. Lampreys, cartilaginous fishes, chondrosteans, cladistians, actinistians, lungfishes, apodans, and salamanders are believed to possess ampullary receptors with kinocilia and cathodal excitation (Bul-
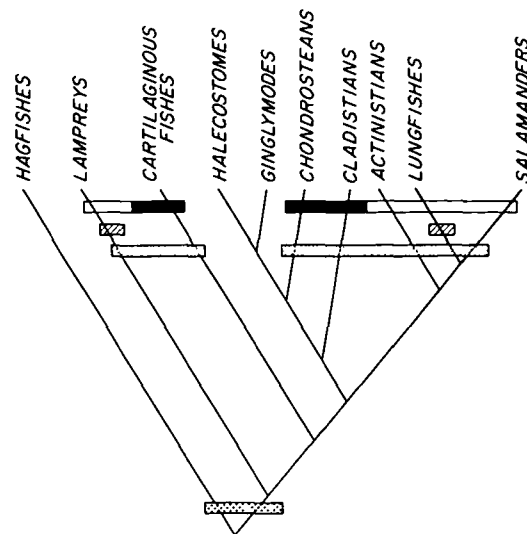

Fig. 2. A branching diagram (cladogram) showing the relationships among major groups of vertebrates. Various CNS characters are indicated by a bar at the appropriate level: medial octavolateralis nucleus (stippling), dorsal octavolateralis nucleus (random dashes), recurrent ramus of the anterior lateral line nerve (hatching), medullary electroreceptive nuclear projection to the optic tectum (solid bar), suspected distribution of this projection (open bar).

lock et al., 1982, 1983). Halecomorphs and ginglymodes, however, do not possess electroreceptors; only a few teleost taxa (Fig. 3) possess electroreceptors, and their morphology and excitatory properties differ from those in the other anamniotes.

The electroreceptors of anamniotes other than teleosts are innervated only by the anterior lateral line nerve, and these electroreceptive fibers enter the medulla by a separate dorsal root and terminate in a dorsal octavolateralis nucleus (Boord and Campbell, 1977; Bodznick and Northcutt, 1980, 1981; Fritzsch, 1981; New, 1981; Münz et al., 1982; Bullock et al., 1983; Northcutt, 1983). Electroreceptors in teleosts (Fig. 3) may be innervated by either or both the anterior and posterior lateral line nerves, and the electroreceptive fibers enter the brain stem and terminate in the electroreceptive lateral line lobe (ELLL), a nucleus that does not occupy the same topological position in the medulla as the dorsal octavolateralis nucleus in other
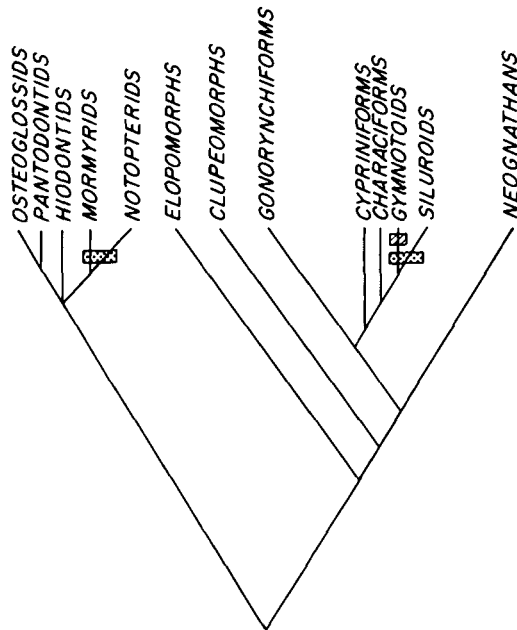
FIG. 3. A cladogram showing the relationships among teleost fishes. Various CNS characters are indicated by a bar at the appropriate level: electroreceptive lateral line lobe (stippling), recurrent ramus of the anterior lateral line nerve (hatching).

anamniotes (Bullock *et al.*, 1982, 1983; McCormick, 1982).

An out-group analysis of the distribution of a dorsal octavolateralis nucleus (Fig. 2) and parsimony suggest that this nucleus is homologous among anamniotes, and that it probably arose in the common ancestor of lampreys and gnathostomes. The absence of electroreceptors and a dorsal octavolateralis nucleus in ginglymodes and halecomorphs suggests that the dorsal octavolateralis nucleus is not homologous to the electroreceptive lateral line lobe of teleosts but that the two structures represent a case of homoplasy. Similarly, the distribution of an ELLL among teleosts (Fig. 3) suggests that the ELLL of osteoglossomorphs is homoplasous to the ELLL of ostariophysines. There are insufficient data to resolve the homologous or homoplasous relationships of the ELLL in mormyrids and notopterids, or in gymnotoids and siluroids.

Some fishes possess electroreceptors that

are located on the trunk but innervated by rami of the anterior lateral line nerves (Figs. 2, 3). Lampreys (Ronan and Northcutt, 1982), lungfishes (Northcutt, 1983) and gymnotoids (Maler *et al.*, 1974) each possess such recurrent rami, but the number of these rami and their central terminations differ. An out-group analysis and parsimony suggest that the presence of a recurrent trunk ramus of the anterior lateral line nerve in these taxa is a case of homoplasy.

Congruence should exist among homologous characters that characterize natural groups, whereas homoplasous characters are not congruent. The dorsal nucleus in cartilaginous fishes (Boord and Northcutt, 1982), chondrosteans (R. G. Northcutt and J. G. New, unpublished observations), and cladistians (Northcutt, unpublished observations) projects directly to the optic tectum and to a deeper midbrain nucleus. The ELLL of mormyrids (Bell *et al.*, 1981), notopterids (Braford, 1982), gymnotids (Maler *et al.*, 1982) and siluroids (T. E. Finger, personal communication) projects to a deeper midbrain nucleus but does not project to the optic tectum. Again, an out-group analysis of a medullary electroreceptive nuclear projection to the optic tectum (Fig. 2) suggests that this pathway is homologous in cartilaginous fishes and primitive bony fishes. Furthermore, the distribution of this pathway supports the hypothesis that the dorsal nucleus is homoplasous to the ELLL of teleosts, and it also allows us to predict that the pathway will be present in all anamniotes that possess a dorsal octavolateralis nucleus.

ASCENDING SPINAL PATHWAYS

Ascending spinal pathways have been determined experimentally in hagfishes (Ronan, 1983), lampreys (Northcutt and Ebbesson, 1980; Ronan, 1983), cartilaginous fishes (Hayle, 1973; Ebbesson and Hodde, 1981), ray-finned fishes (Hayle, 1973; Northcutt, unpublished observations), lungfishes (R. G. Northcutt and M. C. Ronan, unpublished observations), salamanders (Nieuwenhuys and Cornelisz, 1971), anurans (Ebbesson, 1976; Neary and Wilczynski, 1977), reptiles (Ebbesson 1967,

1969, 1978; Pedersen, 1973; Pritz and Northcutt, 1980; Ebbesson and Goodman, 1981; Hoogland, 1981; Künzle and Woodson, 1982), birds (Karten, 1963) and mammals (see Willis and Coggeshall, 1978, for a recent review). The distribution of ascending pathways, combined with outgroup comparison, allows us to reach a number of conclusions.

Spinoreticular pathways occur in all vertebrate species examined and likely represent a shared primitive character that arose with the origin of vertebrates. Spinocerebellar pathways occur in all jawed vertebrates and represent a shared primitive character for gnathostomes. It is not clear whether or not hagfishes and lampreys possess spinocerebellar pathways, as it is not certain that they possess a cerebellum. Spinotectal pathways occur among most vertebrate radiations but do not appear to exist in lampreys, ray-finned fishes, or anuran amphibians. Given the distribution of spinotectal projections as presently known, it seems most likely that lampreys, ray-finned fishes, and anurans have independently lost such projections. However, additional details regarding the cells of origin for spinotectal projections, their transmitters, and their termination within the tectum are needed to strengthen this hypothesis. Spinothalamic projections have been reported only for an advanced shark (Ebbesson and Hodde, 1981) and for amniotic vertebrates. Given this distribution, it is most likely that spinothalamic pathways in sharks are homoplasous to those of amniotes. Again, additional details are needed to substantiate the probable homology of spinothalamic pathways among amniotic vertebrates.

Telencephalic efferents

Information on long descending projections from the telencephalon of various vertebrates has accumulated from studies using ablation or injection of tracers into telencephalic areas or other brain parts. Data presently exist for hagfishes and lampreys (Ronan, 1983; Ronan, unpublished observations), cartilaginous fishes (Ebbesson, 1972; Smeets and Timerick, 1981), ray-finned fishes (Echteler and Saidel, 1981;

Northcutt, 1981; Kimmel et al., 1982; Murakami et al., 1983), lungfishes (Ronan and Northcutt, 1983), salamanders (Kokoros and Northcutt, 1977), anurans (Northcutt and Kicliter, 1980; ten Donkelaar et al., 1981; ten Donkelaar, 1982; Wilczynski and Northcutt, 1983), reptiles (Butler, 1980; Halpern, 1980; Wolters et al., 1982; Woodson and Künzle, 1982; L. Bruce, personal communication), birds (see Benowitz, 1980, for a recent review), and mammals (see Kuypers and Martin, 1982, for a recent review).

The distribution of descending spinal pathways (Fig. 5), combined with out-group comparisons, allows us to reach a number of conclusions. Telencephalic projections to the diencephalon and midbrain tegmentum characterize all vertebrate species and likely represent a shared primitive character that arose with vertebrates. Striospinal pathways have been reported in anuran amphibians (ten Donkelaar et al., 1981) and lizards (L. Bruce, personal communication). If a similar pathway occurs in salamanders, it is probable that striospinal pathways characterize tetrapods and have been lost independently in birds and mammals. A striomedullar or spinal pathway may exist in cartilaginous fishes, as Ebbesson (1972) described a long descending pathway to the caudal medulla in nurse sharks (a group of advanced sharks) following extensive ablations of the telencephalon. The telencephalic cells that give rise to this pathway, however, might be located within the pallium, in which case these sharks would possess a palliomedullar pathway. Smeets and Timerick (1981) did not report telencephalic projections to the medulla of Raja and Scyliorhinus, generally considered to be primitive. Thus, whether a striomedullar or palliomedullar pathway exists in nurse sharks, such a pathway would be considered an independently derived character and homoplasous to long descending pathways in tetrapods. Similarly, their distribution would indicate that the pathways that arise in the telencephalon and project to the optic tectum are homoplasous. Elasmobranch fishes have tectal projections the cells of origin of which are in the central nucleus, a dorsal pallial

division of the telencephalon. Teleost fishes possess a similar pathway, but the cells of origin are located in the central zone of area dorsalis which has been homologized to part of the striatum of amniotes (Northcutt and Braford, 1980). A similar pathway also exists in amphibians, but the cells of origin are in the anterior entopeduncular nucleus, a suspected homologue of part of the striatum of amniotes. Telencephalic neurons that give rise to tectal projections in amniotes that possess such projections (birds, turtles, and mammals) are located within homologues of the dorsal pallium. Thus it is difficult to reach conclusions regarding the homologous/homoplasous relationships of telencephalotectal projections among vertebrates. Their known distribution would suggest that striotectal projections arose in tetrapods and were subsequently lost in theropsid vertebrates. The palliotectal pathways in cartilaginous fishes and theropsids would then be interpreted as independently evolved pathways. Alternatively, "striatal" cells that project to the optic tectum in anurans and teleosts could be viewed as displaced pallial cells that migrated into the striatum. To support this hypothesis, one would have to demonstrate that such migration actually occurs ontogenetically and account for why it did not occur in cartilaginous fishes.

Palliospinal pathways occur in mammals (corticospinal tracts) and birds (projections of the hyperstriatum accessorium and "archistriatum"). However, similar pathways apparently do not exist in reptiles or other sarcopterygians. Given this distribution, the palliospinal pathways in birds and mammals must be viewed as independently evolved and homoplasous. If subsequent studies reveal that the long telencephalic efferents of sharks arise within the pallium, their occurrence would constitute an additional case of homoplasy.

HYPOTHESES OF CNS EVOLUTION

Phylogenetic sequences, particularly for soft tissues that do not fossilize, are formulated on the pattern of observed variation for homologous characters in living organisms. Similarly, hypotheses regarding how brains have changed through time,

and the evolutionary mechanisms that produced these changes, are ultimately based on the character patterns recognized. Four major hypotheses have been proposed in comparative neurobiology to establish phylogenetic sequences and/or explain how these sequences occurred. These hypotheses can now be evaluated in the context of substantially increased data on neural connections and advances in the theory and methodology of systematics generated over the last few years.

Encephalization hypothesis

Encephalization is a vague and ambiguous, albeit frequently used, term. The original concept appears to have arisen with studies of relative brain size (Lartet, 1868; Marsh, 1874; Dubois, 1897), where the term was used to describe a supposed process by which brain volume relative to body volume increases through geological time. Subsequently, the term encephalization has also been used to describe the increase in some forebrain areas (cortex and thalamus), and their functions, in more "progressive" species, and the shift of "higher" functions to more rostral brain areas in a linear sequence of evolution from "fish to amphibians to reptiles to mammals" (Romer, 1970; MacLean, 1978; Sarnat and Netsky, 1981). Thus the term has been used to refer to at least three phenomena and has also become enmeshed in a tangled, finalistic view of evolution with connotations of Scala naturae.

The data on brain-body allometry support the concept of increased brain size (as well as forebrain size) relative to body size through time (Jerison, 1973; Ebbesson and Northcutt, 1976; Bauchot, 1978; Northcutt, 1978, 1981). However, the distribution of large brain size relative to body size suggests that this phenomenon has occurred in some advanced members of each vertebrate radiation, and that encephalization—as a neural character—has occurred independently and must therefore be viewed as a homoplasous character. It is likely that corticalization in mammals (Hofman, 1982) is also homoplasous, and that cortical volumes have increased in many mammalian lineages

independently. Furthermore, it is not clear what selective pressures and adaptive value are associated with increased brain size and/or relative increases in cortices (Armstrong, 1983) and whether they are the same in each case. Similarly, there are few, if any, data that support the concept of a more rostral shift of so-called higher functions (Macphail, 1982).

Invasion hypothesis

This hypothesis proposes that vertebrate brains change through time by the addition of new pathways, which occurs when axon collaterals of a neuronal population form connections with other neuronal populations not previously (in phylogeny) innervated by the first population (Herrick, 1948; Bishop, 1959; Noback and Shriver, 1969). Subsequently, the "older" connections are said to be retained in some intermediate species and then lost in the most advanced species of a radiation. Thus, lemniscal pathways might be compared in rats, cats, and monkeys and these species assumed to represent a linear series of mammals approximating a phylogenetic sequence. Perhaps the most popular application of the invasion hypothesis has been to the evolution of the telencephalon, and a proposed phylogenetic sequence has resulted: The telencephalon of fishes received only olfactory input; fibers first invaded the striatum in amphibians; thalamic fibers subsequently invaded the pallium of reptiles (Ariëns Kappers *et al.*, 1936). Experimental neuroanatomical studies in the last twenty years have refuted many of the supposed phylogenetic sequences based on presumed invasion of new fiber systems (see Northcutt, 1981, for a recent review). Many, if not most, neural pathways appear to be very stable phylogenetically, and the majority of these pathways appear to have arisen with the origin of vertebrates or, shortly after, with the origin of jawed vertebrates. This is not surprising, as such origin and stability are true of most elements of other vertebrate body systems.

Among vertebrate species, variation in the termination of a given neural pathway—the expected result of invasion—is
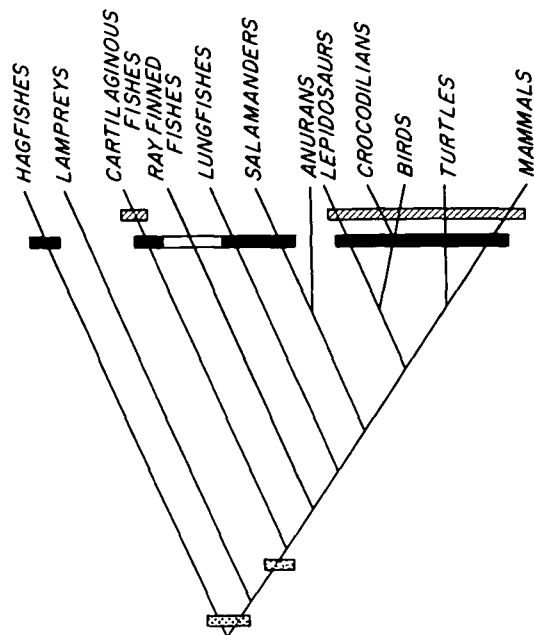

Fig. 4. A cladogram showing the relationships among major groups of vertebrates. Various CNS pathways are indicated by a bar at the appropriate level: spinoreticular (stippling); spinocerebellar (random dashes); spinotectal (solid bars); uncertain spinotectal (open bar); spinothalamic (hatching).

encountered so rarely that Ebbesson (1980) argued that such a phenomenon does not occur and that differences in neural connections are brought about only by the selective *loss* of connections. Clearly, several of the projections cited as examples in the preceding section are most parsimoniously interpreted as the result of invasion of new areas. The known distribution of spinothalamic pathways (Fig. 4) can be explained by two independent invasions of the thalamus, whereas five separate evolutionary events would be required to account for this distribution by loss of the connections. Similarly, the evolution of palliospinal pathways can be explained by invasion of the spinal cord twice, three times if sharks possess such a pathway, whereas an explanation by loss requires eight separate evolutionary events. The available data on interspecific variation in neural pathways are consistent with the following interpretation: New pathways *can*
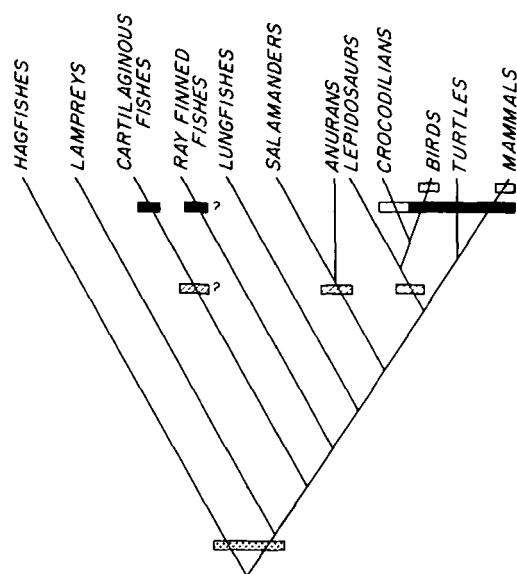
Fig. 5. A cladogram showing the relationships among major groups of vertebrates. Various CNS pathways are indicated by a bar at the appropriate level: telencephalo-diencephalic and tegmental (stippling); striomedullar or spinal (hatching); palliotectal (solid bars); uncertain palliotectal (open bar); palliospinal (random dashes); question marks indicate telencephalic pathways but pallial or subpallial origin uncertain.

arise by the invasion of neural areas; that this event has apparently occurred only rarely does not preclude its being of major importance in the evolution of CNS characters.

Equivalent cell hypothesis

This hypothesis postulates that neuronal populations, not necessarily defined nuclei, are homologous when they are interconnected in the same way or have the same histochemical properties (Karten, 1969; Nauta and Karten, 1970). This hypothesis has been invoked to homologize divisions of the avian dorsal ventricular ridge to individual cellular laminae, or groups of laminae, of mammalian isocortex (Karten, 1969) and the avian nucleus basalis of the telencephalon to the mammalian ventral posteromedial thalamic nucleus (Cohen and Karten, 1974), on the basis that both nuclei receive direct projections from the principal trigeminal sensory nucleus. Although the formulation of this hypothesis has had

a profound effect on comparative neurobiology, primarily by shifting attention to cellular details rather than treating nuclei as static units, it is underlaid by a number of problematical assumptions. The hypothesis assumes that the connections and histochemistry of a given cell population are more stable than the position of its cell bodies, an assumption whose validity has not been demonstrated. Secondly, the hypothesis relies solely on phenetic similarity to recognize homologues, without determining the polarity of the similar characters. Thus, although it is possible that nucleus basalis of birds is homologous to the ventral posteromedial nucleus of mammals, it is also possible that direct trigeminal projections to nucleus basalis are a derived character in thecodont vertebrates, resulting from medullary trigeminal fibers directly invading the telencephalon. These hypothesized relationships, and others, can be tested only by out-group comparisons. Connectional and histochemical information obviously must be used in evaluating potential homologues, but neural populations that do not occupy the same topographical position should be considered homologous only if compatible with out-group analysis and the demonstration that one or more of the populations do migrate.

Parcellation hypothesis

This hypothesis proposes that brain connections change through time by the differential loss of connections and the subsequent segregation (parcellation) of more homogenous neural populations. Ebbesson (1980, p. 185) bases this hypothesis on the belief that experimental neuroanatomical studies reveal that "projections vary primarily in quantity and degrees of differentiation, but are principally to the same targets and never to an unusual target like the hypothalamus, telencephalon or the ventral geniculate nucleus." Ebbesson further argues that there is no evidence that new neural structures arise by genetic mutation or by invasion of one system by another. His hypothesis suggests that vertebrate brain evolution proceeds from brains that are diffuse and undifferentiated

to brains that possess more restricted connections and larger numbers of discrete cell groups.

Even a preliminary examination of CNS organization reveals that vertebrate species exhibit a profound range of variation in the size of their brains, the number of discrete cellular populations constituting most brain divisions, and the connections of these populations. Thus there can be no question that differentiation must have occurred in some brain areas of some species through time. The real question is how that differentiation occurs. Ebbesson (1980, p. 206) claimed that loss of neuronal connections is the only mechanism that underlies that differentiation and that this hypothesis is supported by the existing variation in CNS characters. However, a given pattern of variation can only be consistent with, or refute, a phylogenetic hypothesis, and models based on selective loss or invasion could result in dendrograms exhibiting similar character variation. Thus arguments as to which process *most likely* accounts for a given pattern are best based on parsimony. The hypothesis that requires the fewest number of evolutionary events to account for the observed pattern is then the one most likely to explain the evolutionary processes that have occurred. As noted above, many patterns of variation in the CNS can be explained only by a large number of independently occurring losses, whereas the same pattern can be explained by one or two independently occurring events. In these cases, parsimony suggests that invasion rather than loss of connections is more likely. Similarly, Ebbesson's parcellation model predicts that a cell population in a species with a less differentiated brain should exhibit connections to more cell groups than the same population in a species with a more differentiated brain. Assuming that the brains of living vertebrates do not exhibit a single grade of organization, this prediction is not valid.

Finally, Ebbesson's model of parcellation has a theoretical flaw similar to preformation theories of development. If connections are only lost in phylogeny, resulting in an increase in parcellated cell groups, then conversely, the brains of the first vertebrates must have had fewer cell classes than those of modern vertebrates (as Ebbesson claimed), but modern vertebrates could have no connections not exhibited by the first vertebrates. Thus, at some point in phylogeny, organisms might only possess three cell classes, the minimal number to form a network, but these three cell classes must have had all of the connections exhibited by the brains of modern mammals. A less extreme prediction of the hypothesis would be that the cerebellum of early vertebrates consisted of one or two cell classes that possessed all of the connections of the eight cell classes that develop from the matrix zone of the mammalian cerebellum. These would include such diverse connections as those of the pontine and inferior olivary nuclei. It seems far more likely that brain evolution has proceeded by the addition of new cell classes, the collateralization of pathways, and the loss of connections.

Conclusions

Hypotheses of phylogenetic sequences, and the processes that produced them, are formulated on the observed patterns of variation of homologous characters in living organisms. Recognition of homologous CNS characters has usually been based on the degree of phenetic similarity without regard to out-group comparisons and the polarity of the characters being considered. As noted, the degree of phenetic similarity does not allow one to discriminate between homology and homoplasy due to parallelism. When many presumed CNS homologues are re-examined in the context of their polarity, numerous cases of homoplasy, rather than homology, are revealed.

Critical evaluation of current hypotheses concerning CNS evolution reveals that these hypotheses generally describe patterns of character variation and rarely address processes. Encephalization and parcellation hypotheses hold that the brains of earlier vertebrates were characterized by fewer or smaller distinct cell groups with more diffuse connections. Assuming that the brains of living vertebrates reflect various levels of morphological complexity, it

is likely that the brains of the earliest vertebrates were smaller and possessed fewer cell groups than those of most of their descendents. However, there is no evidence that the neural pathways of earlier vertebrates were more diffuse. If such a stage occurred in vertebrate evolution, it must have preceded the level of brain organization that characterizes hagfishes and lampreys.

Both the equivalent cell and parcellation hypotheses assume conservation of connections, though in different respects. The equivalent cell hypothesis assumes that connections rarely, if ever, change but that the cell bodies forming these connections are free to migrate and change their position. The parcellation theory, on the other hand, assumes that axons never invade new territories and that pathways are only lost. Finally, the invasion hypothesis assumes that connections change readily and that new neural areas are constantly invaded in the course of phylogeny.

Migration, invasion, and loss have all undoubtedly occurred in CNS evolution, but none of these phenomena is sufficient, by itself, to explain CNS evolution, and each can be discounted in specific cases. The observed variation in the brains of living vertebrates is, therefore, most consistent with the following interpretation: Some brain areas have increased by the multiplication of existing neuronal classes and/or the addition of new neuronal classes; new levels of organization have emerged by the loss of connections as well as by invasion of new areas. These conclusions, however, do not address the equally important questions of what selective pressures resulted in these phenomena and what advantages were conferred by these changes. Answers to these questions will likely come only as we address very different questions concerning CNS characters. Additional data on interspecific neural populations and their connections are needed if we are to understand the full range of CNS variation and determine the polarity of many of the character complexes already recognized. Equally important, data on intraspecific variation are critical if we hope to gain insights into the

way selection operates on CNS characters in evolving populations. Similarly, information on ontogenetic sequences of character development and the genetic specification of CNS characters is required if we hope to understand how, and with what facility, changes might occur. Finally, our failure to recognize those CNS characters that are derived, and thus characterize monophyletic groups, has prevented us from understanding those features of the CNS associated with major adaptive changes in vertebrate brain evolution.

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REFERENCES

Ariëns Kappers, C. U., G. Huber, and E. C. Crosby. 1936. The comparative anatomy of the nervous system of vertebrates, including man. Reprinted 1960. Hafner, New York.

Armstrong, E. 1983. Relative brain size and metabolism in mammals. Science 220:1302–1304.

Bauchot, R. 1978. Encephalization in vertebrates. A new mode of calculation for allometry coefficients and isoponderal indices. Brain, Behav. Evol. 15:1–18.

Bell, C. C., T. E. Finger, and C. J. Russell. 1981. Central connections of the posterior lateral line lobe in mormyrid fish. Exp. Brain Res. 42:9–22.

Benowitz, L. I. 1980. Functional organization of the avian telencephalon. In S. O. E. Ebbesson (ed.), Comparative neurology of the telencephalon, pp. 389–421. Plenum, New York.

Bishop, G. H. 1959. The relation between nerve fiber size and sensory modality: Phylogenetic implications of the afferent innervation of cortex. J. Nerv. Ment. Dis. 128:89–114.

Bock, W. J. 1969. Comparative morphology in systematics. In Systematic biology, pp. 411–488. National Academy of Sciences, Publ. 1692, Washington.

Bock, W. J. 1977. Foundations and methods of evolutionary classification. In M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), Major patterns in vertebrate evolution, pp. 851–895. Plenum, New York.

Bodznick, D. A. and R. G. Northcutt. 1980. Segregation of electro- and mechanoreceptive inputs to the elasmobranch medulla. Brain Res. 195: 313–321.

Bodznick, D. A. and R. G. Northcutt. 1981. Electroreception in lampreys: Evidence that the earliest vertebrates were electroreceptive. Science 212:465–467.

Boord, R. L. and C. B. G. Campbell. 1977. Structural and functional organization of the lateral line system of sharks. Amer. Zool. 17:431–441.

Boord, R. L. and R. G. Northcutt. 1982. Ascending lateral line pathways to the midbrain of the clearnose skate, Raja eglanteria. J. Comp. Neurol. 207: 274–282.

Braford, M. R., Jr. 1982. Electroreceptive and mechanoreceptive afferents of the torus semicircularis in the notopterid fish, Xenomystus nigri. Neurosci. Abstr. 8:764.

Bullock, T. H., R. G. Northcutt, and D. A. Bodznick. 1982. Evolution of electroreception. Trends in Neurosciences 5:50–53.

Bullock, T. H., D. A. Bodznick, and R. G. Northcutt. 1983. The phylogenetic distribution of electroreception: Evidence for convergent evolution of a primitive vertebrate sense modality. Brain Res. Rev's. 6:24–46.

Butler, A. B. 1980. Cytoarchitectonic and connectional organization of the lacertilian telencephalon with comments on vertebrate forebrain evolution. In S. O. E. Ebbesson (ed.), Comparative neurology of the telencephalon, pp. 297–329. Plenum, New York.

Campbell, C. B. G. and W. Hodos. 1970. The concept of homology and the evolution of the nervous system. Brain, Behav. Evol. 3:353–367.

Cohen, D. H. and H. J. Karten. 1974. The structural organization of avian brain: An overview. In I. J. Goodman and M. W. Schein (eds.), Birds. Brain and behavior, pp. 29–73. Academic Press, New York.

Dubois, E. 1897. Sur le rapport du poids de l'encéphale avec la grandeur du corps chez mammifères. Bull. Soc. Anthropol. Paris 8:337–376.

Ebbesson, S. O. E. 1967. Ascending axon degeneration following hemisection of the spinal cord in the Tegu lizard (Tupinambis nigropunctatus). Brain Res. 5:178–206.

Ebbesson, S. O. E. 1969. Brain stem afferents from the spinal cord in a sample of reptilian and amphibian species. Ann. N.Y. Acad. Sci. 167:80–101.

Ebbesson, S. O. E. 1972. New insights into the organization of the shark brain. Comp. Biochem. Physiol. A 42:121–129.

Ebbesson, S. O. E. 1976. Morphology of the spinal cord. In R. Llinás and W. Precht (eds.), Frog neurobiology, pp. 697–707. Springer-Verlag, New York.

Ebbesson, S. O. E. 1978. Somatosensory pathways in lizards: The identification of the medial lemniscus and related structures. In N. Greenberg and P. D. MacLean (eds.), Behavior and neurology of lizards, pp. 91–104. U.S. Dept. Health, Education and Welfare, NIMH, Rockville, Maryland.

Ebbesson, S. O. E. 1980. The parcellation theory and its relation to interspecific variability in brain organization, evolutionary and ontogenetic development, and neuronal plasticity. Cell Tissue Res. 213:179–212.

Ebbesson, S. O. E. and D. C. Goodman. 1981. Organization of ascending spinal projections in Caiman crocodilus. Cell Tissue Res. 215:383–395.

Ebbesson, S. O. E. and K. C. Hodde. 1981. Ascending spinal systems in the nurse shark, Ginglymostoma cirratum. Cell Tissue Res. 216:313–331.

Ebbesson, S. O. E. and R. G. Northcutt. 1976. Neurology of anamniotic vertebrates. In R. B. Masterton, M. E. Bitterman, C. B. G. Campbell, and N. Hotton (eds.), Evolution of the brain and behavior in vertebrates, pp. 115–146. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Echteler, S. M. and W. M. Saidel. 1981. Forebrain connections in the goldfish support telencephalic homologies with land vertebrates. Science 212: 683–685.

Eldredge, N. and J. Cracraft. 1980. Phylogenetic patterns and the evolutionary process. Columbia University Press, New York.

Fritzsch, B. 1981. The pattern of lateral line afferents in Urodeles. Horseradish peroxidase study. Cell Tissue Res. 218:581–594.

Ghiselin, M. T. 1976. The nomenclature of correspondence: A new look at "homology" and "analogy." In R. B. Masterton, W. Hodos, and H. Jerison (eds.), Evolution brain and behavior. Persistent problems, pp. 129–142. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Haas, O. and G. G. Simpson. 1946. Analysis of some phylogenetic terms, with attempts at redefinition. Proc. Am. Phil. Soc. 90:319–349.

Hailman, J. P. 1976. Uses of the comparative study of behavior. In R. B. Masterton, W. Hodos, and H. Jerison (eds.), Evolution brain and behavior. Persistent problems, pp. 13–22. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Halpern, M. 1980. The telencephalon of snakes. In S. O. E. Ebbesson (ed.), Comparative neurology of the telencephalon, pp. 257–295. Plenum, New York.

Hayle, T. H. 1973. A comparative study of spinal projections to the brain (except cerebellum) in three classes of poikilothermic vertebrates. J. Comp. Neurol. 149:463–476.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.

Herrick, C. J. 1948. The brain of the tiger salamander. University of Chicago Press, Chicago.

Hofman, M. A. 1982. Encephalization in mammals in relation to the size of the cerebral cortex. Brain, Behav. Evol. 20:84–96.

Hoogland, P. V. 1981. Spinothalamic projections in a lizard, Varanus exanthematicus: An HRP study. J. Comp. Neurol. 198:7–12.

Jerison, H. J. 1973. Evolution of the brain and intelligence. Academic Press, New York.

Karten, H. J. 1963. Ascending pathways from the spinal cord in the pigeon (Columba livia). Proc. 16th Internat. Congr. Zool., Washington, D.C. 2:23.

Karten, H. J. 1969. The organization of the avian telencephalon and some speculations of the phylogeny of the amniote telencephalon. Ann. N.Y. Acad. Sci. 167:164–179.

Kimmel, C. B., S. L. Powell, and W. K. Metcalfe. 1982. Brain neurons which project to the spinal cord in young larvae of the zebrafish. J. Comp. Neurol. 205:112–127.

Kokoros, J. J. and R. G. Northcutt. 1977. Telencephalic efferents of the tiger salamander Ambystoma tigrinum tigrinum (Green). J. Comp. Neurol. 173:613–628.

Künzle, H. and W. Woodson. 1982. Mesodiencephalic and other target regions of ascending spinal projections in the turtle, Pseudemys scripta elegans. J. Comp. Neurol. 212:349–364.

Kuypers, H. G. J. M. and G. F. Martin. 1982. Anatomy of descending pathways to the spinal cord. (Prog. Brain Res. Vol. 57) Elsevier, New York.

Lankester, E. R. 1870. On the use of the term homology in modern zoology, and the distinction between homogenetic and homoplastic agreements. Ann. Mag. Nat. Hist. 4:34–43.

Lartet, E. 1868. De quelques cas de progression organique verifiables dans la succession des temps géologiques sur des mammifères de même famille et de même genre. C. R. Acad. Sci. 66:1119–1122.

MacLean, P. D. 1978. Why brain research on lizards? In N. Greenberg and P. D. MacLean (eds.), Behavior and neurology of lizards, pp. 1–10. U.S. Dept. Health, Education, and Welfare (NIMH), Rockville, Maryland.

Macphail, E. M. 1982. Brain and intelligence in vertebrates. Clarendon Press, Oxford.

Maler, L., T. Finger, and H. J. Karten. 1974. Differential projections of ordinary lateral line receptors and electroreceptors in the gymnotid fish, Apteronotus (Sternarchus) albifrons. 1974. J. Comp. Neurol. 158:363–382.

Maler, L., E. Sas, C. E. Carr, and J. Matsubara. 1982. Efferent projections of the posterior lateral line lobe in gymnotiform fish. J. Comp. Neurol. 211:154–164.

Marsh, O. C. 1874. Small size of the brain in Tertiary mammals. Amer. J. Sci. Arts 8:66–67.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, New York.

McCormick, C. A. 1982. The organization of the octavolateralis area in actinopterygian fishes: A new interpretation. J. Morphol. 171:159–181.

Münz, H., B. Claas, and B. Fritzsch. 1982. Electrophysiological evidence for electroreception in the axolotl Siredon mexicanum Neurosci. Letters 28:107–111.

Murakami, T., Y. Morita, and H. Ito. 1983. Extrinsic and intrinsic fiber connections of the telencephalon in a teleost, Sebastiscus marmoratus. J. Comp. Neurol. 216:115–131.

Nauta, W. J. H. and H. J. Karten. 1970. A general profile of the vertebrate brain, with sidelights on the ancestry of cerebral cortex. In F. O. Schmitt (ed.), The neurosciences. Second study program, pp. 7–26. Rockefeller University Press, New York.

Neary, T. J. and W. Wilczynski. 1977. Ascending

thalamic projections from the obex region in ranid frogs. Brain Res. 138:529–533.

New, J. G. 1981. Central projections of the lateralis nerves in the shovelnose sturgeon, Scaphirhynchus platorynchus. Master's Thesis, University of Michigan, Ann Arbor.

Nieuwenhuys, R. and M. Cornelisz. 1971. Ascending projections from the spinal cord in the axolotl (Ambystoma mexicanum). Anat. Rec. 169:388.

Noback, C. R. and J. E. Shriver. 1969. Encephalization and the lemniscal systems during phylogeny. Ann. N. Y. Acad. Sci. 167:118–128.

Northcutt, R. G. 1978. Brain organization in cartilaginous fishes. In E. S. Hodgson and R. F. Mathewson (eds.), Sensory biology of sharks, skates, and rays, pp. 117–193. Office of Naval Research, Dept. of the Navy, Arlington, Virginia.

Northcutt, R. G. 1981. Evolution of the telencephalon in nonmammals. Ann. Rev. Neurosci. 4:301–350.

Northcutt, R. G. 1983. The primary lateral line afferents in lepidosirenid lungfishes. Soc. Neurosci. Abstr. 9:1167.

Northcutt, R. G. and M. R. Braford, Jr. 1980. New observations on the organization and evolution of the telencephalon of actinopterygian fishes. In S. O. E. Ebbesson (ed.), Comparative neurology of the telencephalon, pp. 41–98. Plenum Press, New York.

Northcutt, R. G. and S. O. E. Ebbesson. 1980. Ascending spinal pathways in the sea lamprey. Soc. Neurosci. Abstr. 6:628.

Northcutt, R. G. and E. E. Kicliter. 1980. Organization of the amphibian telencephalon. In S. O. E. Ebbesson (ed.), Comparative neurology of the telencephalon, pp. 203–255. Plenum Press, New York.

Osborn, H. F. 1902. Homoplasy as a law of latent or potential homology. Amer. Natur. 36:259–271.

Owen, R. 1843. Lectures on comparative anatomy. Longman, Brown, Green, and Longmans, London.

Patterson, C. 1982. Morphological characters and homology. In K. A. Joysey and A. E. Friday (eds.), Problems of phylogenetic reconstruction (Systematics Association Special Volume No. 21), pp. 21–74. Academic Press, New York.

Pedersen, R. 1973. Ascending spinal projections in three species of side-necked turtle: Podocnemis unifilis, Pelusios subniger, and Pelomedusa subrufa. Anat. Rec. 175:409.

Pritz, M. B. and R. G. Northcutt. 1980. Anatomical evidence for an ascending somatosensory pathway to the telencephalon in crocodiles, Caiman crocodilus. Exp. Brain Res. 40:342–345.

Remane, A. 1956. Die Grundlagen des naturlichen Systems der vergleichenden Anatomie und Phylogenetik. Geest und Portig K. G., Leipzig.

Romer, A. S. 1970. The vertebrate body University of Chicago Press, Chicago.

Ronan, M. C. 1983. Ascending and descending spinal projections in petromyzontid and myxinoid agnathans. Ph.D. Diss., University of Michigan, Ann Arbor.

Ronan, M. C. and R. G. Northcutt. 1982. Primary

projections of the lateral line nerves in the northern lamprey. Soc. Neurosci. Abstr. 8:764.

Ronan, M. C. and R. G. Northcutt. 1983. Origins of descending spinal projections in lungfishes. Soc. Neurosci. Abstr. 9:1063.

Sarnat, H. B. and M. G. Netsky. 1981. *Evolution of the nervous system.* Oxford University Press, New York.

Simpson, G. G. 1961. *Principles of animal taxonomy.* Columbia University Press, New York.

Smeets, W. J. A. J. and S. J. B. Timerick. 1981. Cells of origin of pathways descending to the spinal cord in two chondrichthyans, the shark *Scyliorhinus canicula* and the ray *Raja clavata.* J. Comp. Neurol. 202:473–491.

Smith, H. M. 1967. Biological similarities and homologies. Syst. Zool. 16:101–102.

ten Donkelaar, H. T. 1982. Organization of descending pathways to the spinal cord in amphibians and reptiles. *In* H. G. J. M. Kuypers and G. F. Martin (eds.), *Anatomy of descending pathways to the spinal cord* (Prog. Brain Res. Vol. 57), pp. 25–67. Elsevier, New York.

ten Donkelaar, H. J., R. de Boer-van Huizen, F. T.

M. Schouten, and S. J. H. Eggen. 1981. Cells of origin of descending pathways to the spinal cord in the clawed toad (*Xenopus laevis*). Neuroscience 6:2297–2312.

Wilczynski, W. and R. G. Northcutt. 1983. Connections of the bullfrog striatum: Efferent projections. J. Comp. Neurol. 214:333–343.

Wiley, E. O. 1981. *Phylogenetics.* Wiley, New York.

Willis, W. D. and R. E. Coggeshall. 1978. *Sensory mechanisms of the spinal cord.* Plenum Press, New York.

Wolters, J. G., R. de Boer-van Huizen, and H. J. ten Donkelaar. 1982. Funicular trajectories of descending brain stem pathways in a lizard (*Varanus exanthematicus*). *In* H. G. J. M. Kuypers and G. F. Martin (eds.), *Anatomy of descending pathways to the spinal cord* (Prog. Brain Res. Vol. 57), pp. 69–78. Elsevier, New York.

Woodson, W. and H. Künzle. 1982. Distribution and structural characterization of neurons giving rise to descending spinal projections in the turtle, *Pseudemys scripta elegans.* J. Comp. Neurol. 212: 336–348.