Observations on the Brain of the Coelacanth *Latimeria chalumnae:* External Anatomy and Quantitative Analysis

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ABSTRACT   New data on the brain of *Latimeria* indicate that previous estimates of the brain weight were too high by a factor of two. Our data suggest a brain weight of 1.1-1.5 grams for a specimen with a body weight of 30 kilograms. Quantitative data on major divisions of the brain are presented for the first time, and the relative size of the major brain divisions is similar to that of sturgeons and generalized sharks (such as hexanchids and squalids). Examination of brain component weight(s): body weight plots in a sample of non-teleost actinopterygian fishes indicates that all major divisions of the brain, except the telencephalon, are larger than in *Latimeria*. Brain component sizes in *Latimeria* are more similar to those extrapolated for amphibian brains than to those for actinopterygians. However, the cerebellum of *Latimeria* is considerably larger than that of amphibians.

Coelacanths, thought to be extinct since the late Cretaceous, were known only from the fossil record prior to 1938 when J. L. B. Smith described the first living specimen. The anatomy of *Latimeria* is particularly interesting to evolutionary biologists because this species appears to be the sole living representative of the Crossopterygii, a group of bony fishes that gave rise to land vertebrates. More than 70 *Latimeria* have been captured during the last 30 years. Millot and Anthony, in particular, have devoted several years to investigating the general anatomy of these specimens and have reported on this work in several monographs. The nervous system has received their attention as well (Millot and Anthony, '56, '65, '67); however, to our knowledge, the only detailed illustration and description of the external anatomy of the brain of *Latimeria* is that of Millot and Anthony ('65) in which the brain is figured with meninges and blood vessels intact. These tissues are so extensive that little detail of the actual brain surface can be recognized.

An international expedition, resulting from French, British and American cooperation, captured a live coelacanth in March, 1972, and immediately dissected and preserved tissues. We were fortunate to receive the brain of this specimen, thus allowing us to report details of the external anatomy of the brain of *Latimeria* and to compare the brain with those of other vertebrates. This report also includes the first quantitative measurements on major divisions of the *Latimeria* brain. Our comparisons are primarily phenetic rather than phylogenetic due to the paucity of comparative studies, particularly experimental studies, on the brains of bony fishes. Far more information is needed on the brains of these forms before neural trends and their polarity can be established. We have excluded the brains of teleosts, as well as those of amniotic vertebrates, from comparison with *Latimeria* because they are distinctly different from *Latimeria* and the other fishes.

MATERIALS AND METHODS

Three specimens of *Latimeria* were available for our study. Specimens 1 and 2 were provided by the Field Museum of Natural History in Chicago, and no locality or museum numbers are available. The brain of specimen 1 was removed in 1969 by RGN and prepared in serial cross sections by the Bodian method. Specimen 2 was a male with a total length of

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128 cm and a preserved body weight of 30 kg. Both specimens were initially preserved in 10% formalin, then stored in 70% ethanol. Following excision, the brains were stored in AFA (80% ethanol:100% formalin:glacial acetic acid; 90:5:5). Neither brain was adequately fixed for histology, but they did allow examination of the origin and intracranial course of the cranial nerves.

Specimen 3 was caught at Iconi, Grande Comoro on March 22, 1972, under the auspices of the French-British-American expedition. The brain was removed shortly after death and immersed in a gluteraldehyde EM fixative (Locket, '73). This specimen was an immature female with a total length of 85 cm. Unfortunately, no body weight was recorded.

The illustrations of external brain anatomy, by camera lucida and graphic reconstruction methods, are based on both specimens 2 and 3, as each was partly damaged prior to our receipt. After analysis of the external anatomy, the brain of specimen 2 was divided into the following components for weighing: olfactory bulbs, telencephalic hemispheres (including olfactory peduncles), diencephalon, mesencephalon, cerebellum, and medulla. The caudal boundary of the telencephalon was considered to be a plane extending from the rostral border of the habenular nuclei to the rostral border of the optic chiasm. The caudal boundary of the diencephalon was considered to be a plane extending from the rostral pole of the optic tectum to the caudal pole of the infundibulum. The optic nerves were not included in the weight of the diencephalon, but were transected within 2 mm of the chiasm. The cerebellum was considered to include all tissue lying dorsal to a rostro-caudal transection just below the ventral lip of the cerebellar auricle. The caudal boundary of the medulla was set at the level of the first complete cervical spinal nerve. All cranial nerves were transected at the base of the brain, and neither they nor the meninges, blood vessels or choroid plexus of the fourth ventricle were included in the brain division weights.

Measurements of the brain divisions of specimen 2 contain a sizable error factor, as this brain was badly desiccated and shrunken at excision. The same series of measurements could not be performed on brain specimen 3 because the olfactory bulbs, part of the olfactory peduncles, and the dorsal half of the epithalamus had been removed prior to our re-

ceiving the brain. However, these parts contribute only slightly to the total brain weight (fig. 4). Therefore, the weighing of brain specimen 3, with its meninges, blood vessels, and choroid plexus of the fourth ventricle removed, allowed us to estimate a correction factor for the shrinkage of the brain of specimen two. To form another basis for estimating a correction factor, we transected brain specimen three at the mesen-cerebellar junction and recorded the combined weight of the cerebellum and medulla. We did not perform any finer dissection of brain specimen three because of its histological value. Finally, brain specimen three was sectioned in the transverse plane for histological analysis and was used to check our initial determination of cranial nerves.

For comparison, brains from a number of vertebrate species (table 1) were fixed in situ in AFA. All specimens were adults based on gonadal tissue and reported adult body lengths. Following fixation, the brains were divided and weighed according to the criteria established for *Latimeria*. Data reported in table 1 are based on a single specimen of each species. Six specimens of *Necturus* were measured to assess intraspecific variation in brain weight. Their body weights ranged from 103 – 131 gm, and the mean brain weight was 0.1068 gm with a S.E. of 3.9%. The reliability of our comparisons might be improved by increasing the number of species, particularly amphibians, examined; however, our coefficients of allometry for urodele brain divisions closely agree with those in the extensive study of Thireau ('76) who examined 43 species of urodeles.

Brains of the species being compared to *Latimeria* were first fixed in AFA because unfixed neural tissue is almost impossible to manipulate without considerable distortion. Fixation in AFA results in an 8-9% reduction in brain weight, and the brain division weights reported are not corrected for this reduction.

Fig. 1 Dorsal view of the brain of *Latimeria*. Olfactory bulbs of the telencephalon not pictured. a lat, anterior lateral line nerve; au, auricle of cerebellum; ce, corpus of cerebellum; cer, cervical spinal nerve; inf, infundibulum of the hypothalamus; obl, medulla oblongata; occ, occipital (hypoglossal) nerves; on, optic nerve; op, olfactory peduncle (tract); p lat, posterior lateral line nerve; pit, pituitary gland; tec, optic tectum; tel, telencephalon; III, oculomotor nerve; IV, trochlear nerve; V_1, profundus nerve; $V_{2,3}$, trigeminal nerve; VI, abducent nerve; VII, facial nerve; VIII, acoustico-vestibular nerve; IX, glossopharyngeal nerve; X, vagus nerve.
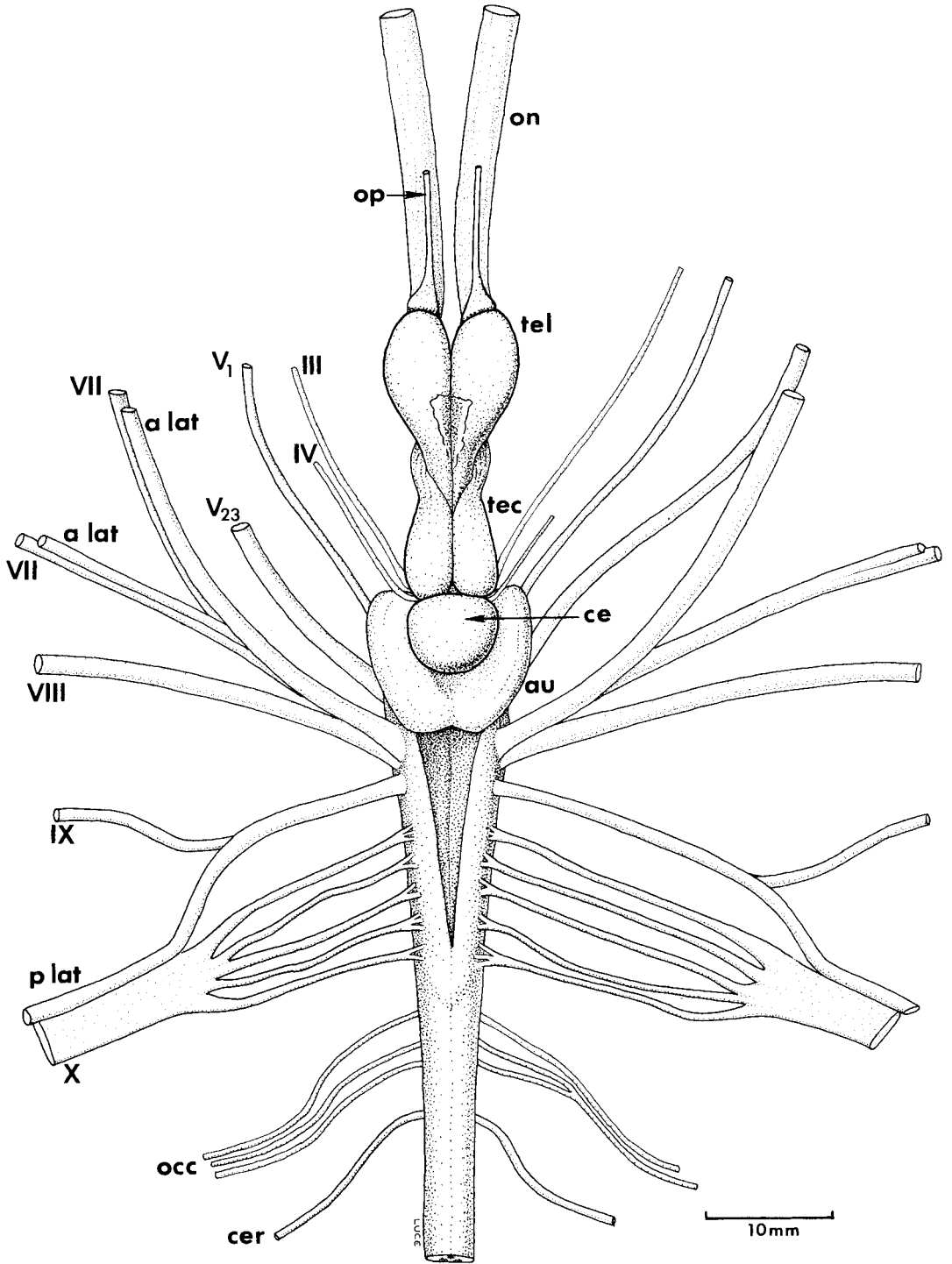
Figure 1

TABLE 1

Brain weight: body weight data

Species	Body weight in kg	Brain weight in gm	Brain component weights in gm					
			Olfactory bulbs	Telen-cephalon	Dien-cephalon	Mesen-cephalon	Cere-bellum	Medulla
Ambystoma maculatum	0.022	0.0328	0.0033	0.0143	0.0057	0.0018	0.0009	0.0068
Ambystoma tigrinum	0.040	0.0590	0.0073	0.0252	0.0079	0.0042	0.0010	0.0134
Amia calva	0.727	0.3485	0.0330	0.0707	0.0424	0.0841	0.0288	0.0895
Bufo americanus	0.070	0.0604	0.0054	0.0185	0.0079	0.0100	0.0016	0.0170
Bufo marinus	0.193	0.1225	0.0200	0.0392	0.0119	0.0203	0.0032	0.0279
Cryptobranchus alleganiensis	0.400	0.1611	0.0242	0.0606	0.0153	0.0090	0.0020	0.0500
Dicamptodon ensatus	0.052	0.0760	0.0082	0.0259	0.0098	0.0087	0.0011	0.0223
Hyla septrionalis	0.014	0.0474	0.0050	0.0150	0.0066	0.0085	0.0008	0.0115
Latimeria chalumnae	30	1.2596	0.0320	0.3014	0.1176	0.1316	0.2200	0.4570
Lepidosiren paradoxa	0.642	0.4109	0.0365	0.2443	0.0320	0.0159	0.0088	0.0734
Lepisosteus osseus	1.065	0.6026	0.0362	0.1252	0.0629	0.1239	0.1404	0.1140
Necturus maculosus	0.103	0.1064	0.0214	0.0361	0.0165	0.0063	0.0016	0.0245
Polypterus palmas	0.075	0.1080	0.0130	0.0410	0.0108	0.0151	0.0054	0.0227
Rana catesbeiana	0.427	0.2178	0.0200	0.0476	0.0345	0.0556	0.0046	0.0555
Rana pipiens	0.035	0.1019	0.0068	0.0277	0.0137	0.0233	0.0019	0.0285
Scaphirhynchus platorynchus	0.510	0.2362	0.0314	0.0291	0.0469	0.0326	0.0254	0.0708
Sphyrna lewini	55.71	59.880	4.1916	31.1376	2.3952	3.5928	11.3772	7.1856
Squalus acanthias	1.252	2.9377	0.2365	0.6242	0.2679	0.4977	0.6170	0.6944

Each brain was dissected while immersed in the fixative, and each brain part was blotted immediately prior to weighing on a Mettler analytical balance (Model H10). The accuracy of ten repeated measurements on the smallest brains (0.03 g) was ± 0.3%; while accuracy on small brain divisions (0.003 g) was ± 1.6%. Recorded body weights are from fresh material.

RESULTS

General observations

The brain of *Latimeria* is considerably elongated with little trace of the cephalic flexures seen in most bony fishes except dipnoans. As Millot and Anthony ('65) noted, the brain is housed in an expansive neurocranium, and a centimeter or more of the peripheral course of most of the cranial nerves is observable within the neurocranium.

The olfactory peduncles (figs. 1-3) are extremely long, and the olfactory bulbs are directly apposed to the nasal cavity. The swellings at the rostral poles of the telencephalic hemispheres do not represent the olfactory bulbs. This was determined at the time of dissection and confirmed by subsequent histological examination. In this respect *Latimeria* clearly differs from the lepidosirenid lungfishes in which the olfactory bulbs arise from, and are in direct continuity with, the telencephalon. Elongated peduncles also occur in some

actinopterygians and in most cartilaginous fishes, as well as in *Neoceratodus*.

The telencephalon of *Latimeria* is relatively longer than that of actinopterygian fishes with the exception of *Polypterus* (Nieuwenhuys, '69; Braford and Northcutt, '74), and its shape is more similar to the telencephalon in dipnoans. The general similarity is further reinforced by an obvious lateral swelling of the ventral telencephalon (figs. 2, 3) which is even more pronounced in the Dipnoi (Holmgren and van der Horst, '25; Nieuwenhuys, '69; Clairambault and Capanna, '73; Northcutt, '77a).

The pituitary of *Latimeria* appears unique among that of vertebrates we have examined, as it extends rostrally rather than caudally from the infundibulum. This condition, noted previously (Millot and Anthony, '65; Nieuwenhuys, '69), has been interpreted as a consequence of skull growth rapidly out-distancing brain growth and the rostral shifting of the hypophyseal fenestra.

The optic nerves are large and appear relatively larger than do those of most bony fishes. They are far larger than those of any of the living dipnoans (Holmgren and van der Horst, '25; Schnitzlein and Crosby, '68). The optic tectum is clearly paired and possesses slightly developed lateral recesses and well developed cellular and fibrous laminae (Northcutt and Neary, '75). The internal organization of the
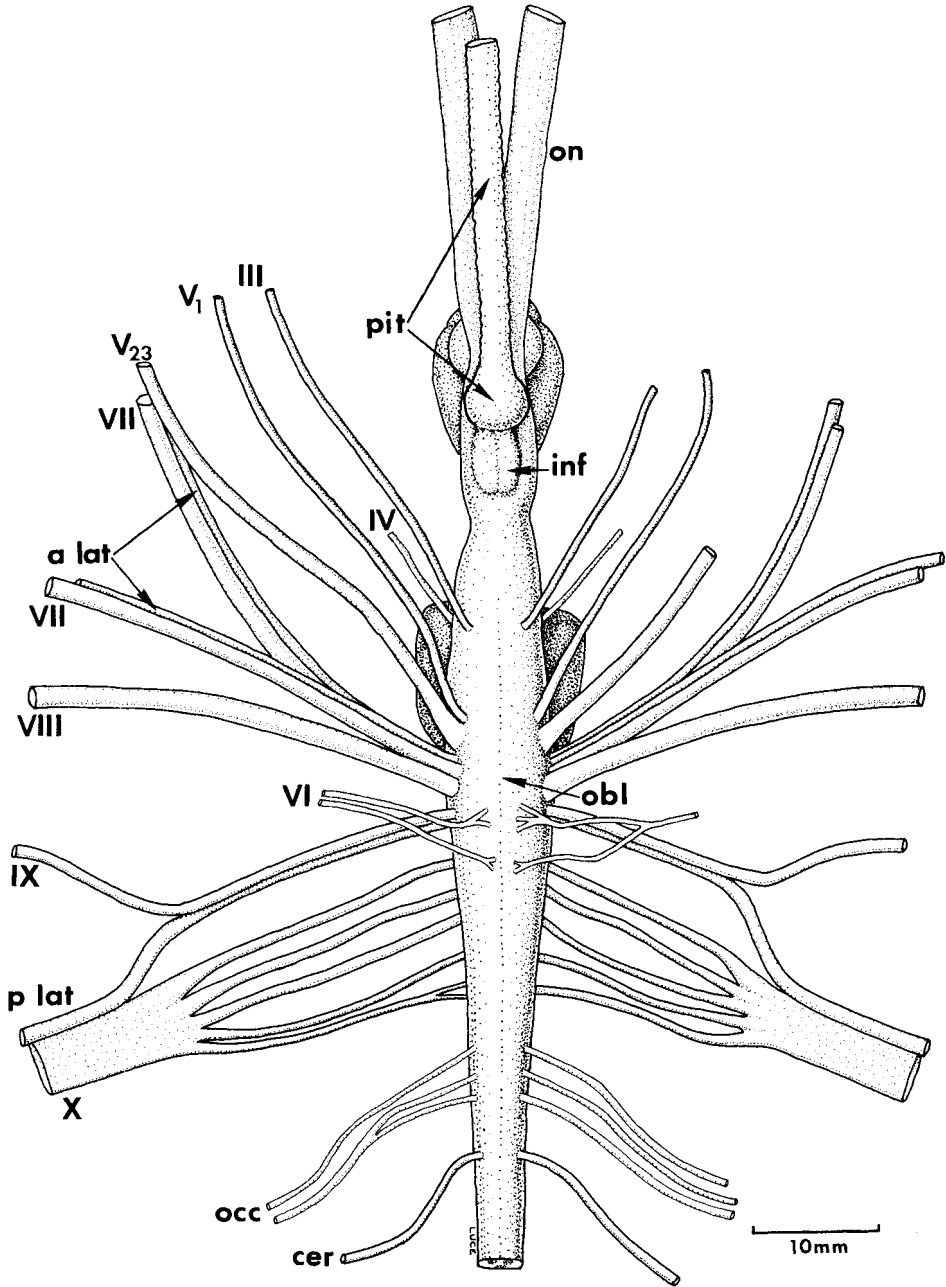
Fig. 2 Ventral view of the brain of *Latimeria*. Abbreviations same as figure one.

tectum of *Latimeria* reveals more extensive differentiation than the tecta of dipnoans and salamanders (Holmgren and van der Horst, '25; Herrick, '48; Northcutt, '77a).

The large cerebellum (figs. 1-3) is the most striking feature of the general morphology of the *Latimeria* brain. The corpus is a large spherical dome surrounded laterally and caudally by pronounced auricles, and the cerebellum is larger than in living amphibians.
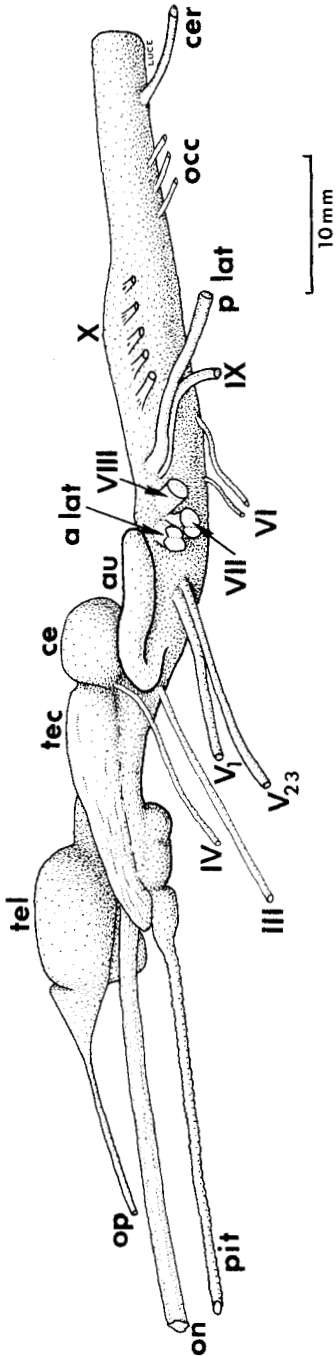
Fig. 3   Lateral view of the brain of *Latimeria*. Abbreviations same as figure one.

Latimeria has all three somatic motor cranial nerves, innervating the extrinsic eye muscles; and they arise from the same brain stem areas as in other vertebrates. The abducent nerve is unusual as it arises from multiple roots, and the most caudal ramus is considerably removed from the other rami (fig. 2).

Latimeria, like other bony fishes, possesses a distinct profundus branch (V_1) of the trigeminal complex. However, V_1 separates very proximally from the mandibular and maxillary branches ($V_{2,3}$). The facial cranial nerves are obvious and divide into rostral and caudal branches (figs. 1-3). Both branches are closely associated with branches of the anterior lateral line nerves in their course toward neurocranial exit. However, the anterior lateral line nerves are distinct cranial nerves possessing separate entry into the medulla dorsal to the facial rami (fig. 3).
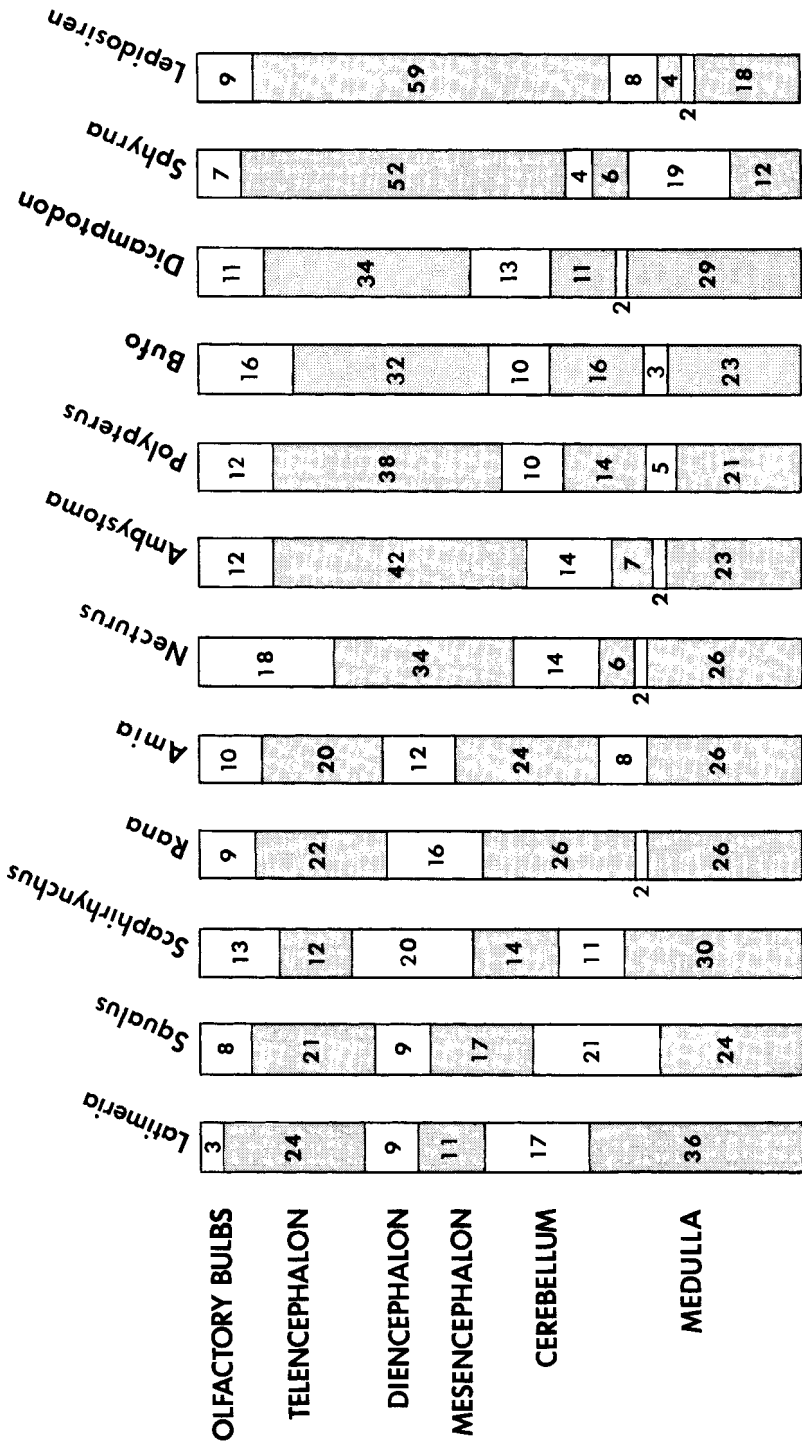
The eighth cranial nerves consist of a single ramus with entry caudal to the anterior lateral line nerves (fig. 3). *Latimeria* is similar in this respect to most other bony fishes.

The posterior lateral line nerves are well developed and are first seen in close association with the vagal nerves as they enter the neurocranium (figs. 1, 2). However, the posterior lateral line nerves rapidly arc rostrally and run with the glossopharyngeal nerves. In *Latimeria* there can be no question that the anterior and posterior lateral line nerves are distinct and separate cranial nerves. These lateral line nerves are clearly not components of the facial and vagal nerves, even though they have frequently been said to be components of these branchiomeric nerves (see Goodrich, '58 for general review).

The vagal nerves are well developed and, as in other vertebrates, arise from a series of rootlets (figs. 1-3). *Latimeria,* like other bony fishes, possesses a number of spino-occipital nerves which innervate the hypobranchial musculature and are probably homologous to the hypoglossal nerves of land vertebrates.

Qualitative observations

In figure 4, the relative size of the major brain divisions of *Latimeria* is compared to that of other vertebrates. Brains most like that of *Latimeria* are located in adjacent columns, while those most different are clustered to the right side of the figure. The brain of *Latimeria* is most similar to those of gen-

Fig. 4 Relative development of major brain divisions in *Latimeria* compared to selected vertebrates: *S. acanthias, S. plato-rynchus, R. catesbeiana, A. calva, N. maculosus, A. tigrinum, P. palmas, B. marinus, D. ensatus, S. lewini, L. paradoxa.*

eralized sharks belonging to the families Squalidae and Hexanchidae (Daniel, '34). However, *Latimeria* is clearly unlike the advanced sharks such as *Sphyrna* (fig. 4). *Latimeria* can be characterized by an evaginated telencephalon and well developed visual and lateral line systems. However, the telencephalic pallium of *Latimeria* does not undergo an inversion as in land vertebrates (Niewenhuys, '69). Unlike most actinopterygians, *Latimeria* does not possess an elaborate optic tectum, but the tectum is better developed than in the neotenic salamanders, such as *Ambystoma* and *Necturus,* or the lepidosirenid lungfishes.

Quantitative observations

The data in figure 4 illustrate the relative size of major brain divisions among taxa, but they convey no information regarding the changes in absolute brain volume among taxa. Clearly the latter is an important measure of information processing in the central nervous system and thus a significant measure of brain evolution (Jerison, '73). Unfortunately, we still do not possess adequate information on the brain weight:body weight ratio of *Latimeria.* The most widely cited estimate is that reported by Millot and Anthony ('65) for their specimen C3, a 129-cm, 40-kg male, in which the fresh weight of the brain plus meninges did not exceed three grams. Our second specimen was a 30-kg male, and the preserved weight of the brain plus meninges and blood vessels was 2.68 g. However, following removal of the meninges, blood vessels, and cranial nerves the brain weight of specimen two was only 0.62 g. Since this brain specimen had obviously desiccated, brain specimen 3 was used to estimate a shrinkage correction factor. Estimates of this correction factor were based on: (1) the weight of brain specimen 3 with the meninges, blood vessels, and cranial nerves removed (1.13 gm); and (2) the combined weight of the cerebellum and medulla (0.6901 gm). For the estimate, the weight of the missing brain parts was considered to equal, at most, the weight of the olfactory bulbs and diencephalon, i.e., 12% of the total brain weight (fig. 4). Thus, we arrived at an *intact* brain weight for specimen three of (1.13) (12/88) + (1.13) = 1.28 gm, giving an estimated correction factor of (1.28) / (0.62) = 2.06. For the second estimate, we divided the combined weight of the cerebellum and medulla in brain specimen 3 by their weight in

brain specimen 2, arriving at a correction factor estimate of (0.6901) / (0.3385) = 2.04. To simplify calculation, we rounded off both correction factors to 2.0 and multiplied all raw brain component weights of specimen 2 by this amount. Although specimen 3 was considerably smaller than specimen 2 or Millot and Anthony's specimen C3 (85 cm *vs*. 128 cm and 129 cm), a comparison of the dimensions of brain specimen 3 with the mid-sagittal photograph of the brain of Millot and Anthony's specimen C3 (Millot and Anthony, '65, Plate IV) showed only 0-10% differences.

The corrected weights of the major brain components of *Latimeria* are plotted and compared to those for other anamniotic vertebrates in figure 5. While the body weight of *Latimeria* falls outside the range of the other plotted body weights, visual inspection indicates that the brain component weights of *Latimeria* are within an extrapolated range of those of many anamniotes. Further comparisons are difficult without numerical extrapolations, particularly if comparisons are attempted with specific anamniotic groups. Three specific numerical extrapolations are presented in figure 6. The brain components of *Latimeria* are compared to a least-squares fitted line for the brain components of non-teleost actinopterygian fishes (fig. 6A), urodeles (fig. 6B), and anurans (fig. 6C). The slope (interspecific coefficient of allometry) and the coefficient of determination were calculated for each brain component line. These vertebrate groups were chosen for analysis since their brains show the greatest similarity to that of *Latimeria.* Lungfishes are not included as the present sample is inadequate.

All extrapolated brain components of non-teleost actinopterygians are larger than the corresponding brain components of *Latimeria,* with the exception of the telencephalon (fig. 6A). The telencephalon of *Latimeria* is as large as that of non-teleost actinopterygians, and our data support the observation of Nieuwenhuys ('69) that the pallium of *Latimeria* is greatly thickened and suggestive of the everted pallium of actinopterygians. The extrapolated cerebellum of non-teleost actinopterygians is far larger than that of *Latimeria.* In our sample of actinopterygians, the cerebellum exhibits a coefficient of allometry, disproportionate relative to that of other brain components, and this difference would be further exaggerated if teleosts
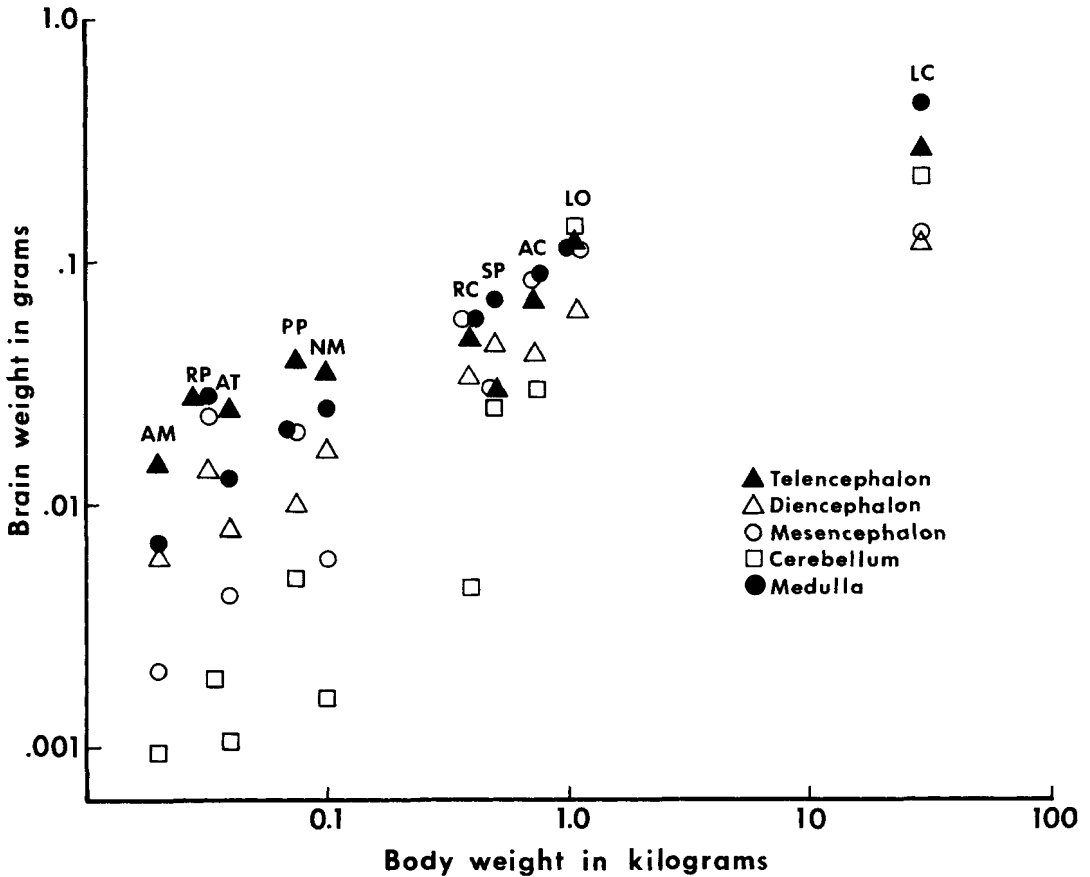
Fig. 5   Double log plots of major brain divisions and body weights for a number of anamniotic vertebrates and *Latimeria*. Am, *Ambystoma maculatum;* RP, *Rana pipiens;* AT, *Ambystoma tigrinum;* PP, *Polypterus palmas;* NM, *Necturus maculosus*; RC, *Rana catesbeiana;* SP, *Scaphirhynchus platorynchus;* AC, *Amia calva:* LO, *Lepisosteus osseus;* and LC, *Latimeria chalumnae.*

were included in the sample (unpublished observations).

The extrapolated telencephalic and medullar sizes of urodele amphibians are larger than the corresponding brain components of *Latimeria* (fig. 6B). The extrapolated diencephalon and mesencephalon of urodeles are only slightly smaller. However, the cerebellum of *Latimeria* is 29 to 30 times larger than the extrapolated cerebellum of urodeles.

The extrapolated mesencephalic size of anuran amphibians is larger than the corresponding brain component of *Latimeria* (fig. 6C). This difference is likely due to the hypertrophy of the visual system in anurans. The cerebellum (6×), medulla (2×), and telencephalon (2×) of *Latimeria* are larger than the corresponding extrapolated components of

anurans. These differences in the rhombencephalon may be due, in part, to the development of the lateral line system. This system is well developed in *Latimeria* and absent in most adult amphibians. However, both *Ambystoma* and *Necturus* retain the lateralis system as adults (Herrick, '48), and thus differences may be, at best, related to the relative development of this system.

The relative sizes of brain components in amphibians and *Latimeria* are comparable, with the exception that the cerebellum of *Latimeria* is 6 to 30 times larger than that of amphibians.

DISCUSSION

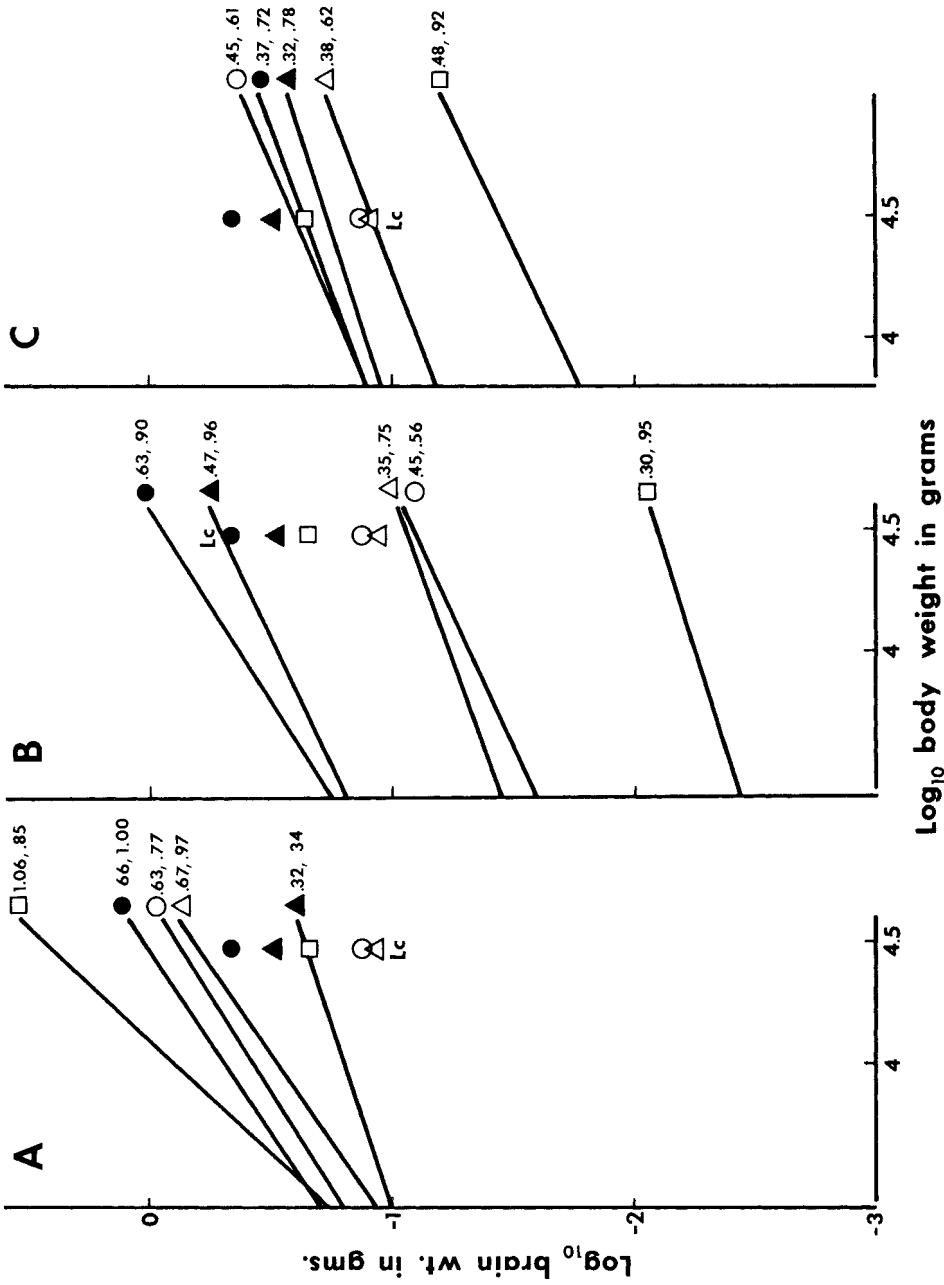Our analysis indicates that the brain of *Latimeria* possesses a number of characters

Fig. 6   Least-squares extrapolated major brain divisions of: (A) non-teleost actinopterygians (*Amia, Lepisosteus, Polypterus* and *Scaphirhynchus*); (B) urodele amphibians (*Ambystoma, Cryptobranchus, Dicamptodon* and *Necturus*); and (C) anuran amphibians (*Bufo, Hyla* and *Rana*) compared to *Latimeria* (Lc) Major brain division symbols same as figure five. Interspecific coefficient of allometry and coefficient of determination for each extrapolated brain division presented to the right of each least-squares fitted line.

in common with those of *Squalus* and *Scaphirhynchus*. The latter taxa both exhibit relative brain proportions that are most similar to *Latimeria*. *Scaphirhynchus* deviates most by conspicuous hypertrophy of the olfactory apparatus and relative reduction in the visual system (unpublished observations). *Latimeria* and the squaliform sharks possess well developed visual systems, lateral line organs, and moderate cerebellar development. Contrary to popular belief, sharks (with the exception of sphyrnids) are not characterized by hypertrophy of the olfactory system (Ebbesson, '72; Northcutt, '77b). Similarly, olfaction in *Latimeria* does not appear as well developed as vision, based on the relative size of the olfactory and optic tracts.

The following neural features characterize *Latimeria;* and they are probably primitive gnathostome features based on their wide distribution in squaliform sharks and non-teleost actinopterygian fishes: (1) moderate to poorly developed olfactory organs; (2) well developed visual system; (3) bilobed mesencephalic tectum with well developed internal lamination; (4) small mesencephalic acustico-lateralis center (torus semicircularis); (5) moderate to well developed cerebellum; (6) well developed lateral line organs supplied by two distinct and separate pairs of cranial nerves; and (7) an evaginated telencephalon. The last feature is not present in actinopterygian fishes, but is present in all other bony fishes, sharks, and agnathans; thus an evaginated telencephalon is most likely the primitive gnathostome condition.

Our data on the brain weight of *Latimeria* suggest that previous estimates are too high by a factor of two, and that errors were introduced by including the weight of the blood vessels, meninges, and parts of the peripheral cranial nerves.

Our calculated brain weight for *Latimeria* (1.1-1.5 gms) falls outside the predicted range for the brain weight: body weight ratios of other anamniotic vertebrates (Jerison, '73; Ebbesson and Northcutt, '76). However, Romer ('37) described the endocranial cavity of *Ectosteorhachis*, a late Carboniferous rhipidistian, and his reconstruction of the probable brain shape bears a number of remarkable similarities to that of *Latimeria*. More importantly, Jerison's ('73) volumetric analysis of the *Ectosteorhachis* endocast suggests that this rhipidistian would also possess a low brain weight: body weight ratio comparable to

that of the sturgeon *Scaphirhynchus*. While *Latimeria* possesses a low brain weight: body weight ratio, these data suggest that such ratios may have generally characterized crossopterygians as well as primitive actinopterygians.

If the brain size of *Latimeria* is comparable to that of the crossopterygians that gave rise to amphibians, then virtually no increase in brain size would have occurred with the transition to the amphibian grade. The only absolute reduction in the size of any brain component would have been in the size of the cerebellum (figs. 4, 6).

Detailed comparisons based on extrapolated lines suggest that most brain components in living actinopterygian fishes are larger than in *Latimeria*. The brain of *Latimeria* is more similar to the extrapolated amphibian brain components.

While such numerical manipulations are necessary to compare taxa with widely different weights, it must be remembered that these comparisons assume no change in selective pressures, except for changes related to size, and thus such extrapolations may be of limited value. Unfortunately, no other numerical comparative methods are presently available.

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