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Some considerations on the forebrain of the bipulmonate Dipnoi

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Biologia. — *Some considerations on the forebrain of the bipulmonate Dipnoi* (*). Nota di ERNESTO CAPANNA e PIERRE CLAIRAMBAULT, presentata (**) dal Socio A. STEFANELLI.

RIASSUNTO. — Lo studio dell'encefalo anteriore dei Dipnoi e degli Anfibi ha motivato il presente scritto inteso a proporre un modello ipotetico di encefalo attribuibile a quei Vertebrati ittiomorfi del Paleozoico che possono essere già considerati sulla linea evolutiva che conduce ai Tetrapodi. Questo modello è stato essenzialmente costruito sulla base delle nostre personali osservazioni condotte su *Protopterus annectens* e *P. dolloi*. Il telencefalo di *Protopterus* è infatti completamente invertito e vi si possono riconoscere tutte le quattro fondamentali aree palliali e subpalliali; il diencefalo è caratterizzato da tutte le strutture epitalamiche dei vertebrati inferiori e da un ipotalamo molto esteso. Il sulcus medialis divide il talamo in una area talamica dorsale ed in un talamo ventrale; queste due aree diencefaliche si prolungano senza interruzione con il tetto mesencefalico e con il tegmento rispettivamente. Questa peculiarità neuroanatomica ci ha indotto a proporre l'ipotesi di una struttura neurale meso-diencefalica, molto primitiva, che precede la differenziazione delle aree mesencefaliche e diencefaliche nell'evoluzione delle strutture neurali dei Vertebrati inferiori. La morfologia del cervelletto di *Protopterus* ricorda l'organizzazione cerebellare degli Anfibi; un ben distinto Nucleus isthmi è presente al confine tra mesencefalo e metencefalo.

For a number of years we have been investigating the telencephalon of Amphibians for the purpose of shedding light on its cytoarchitectural features [1-9], the features determining its morphogenesis [10-14] as well as peculiarities in its fibre connections [15]. However, we were also careful not to lose sight of the wider problem of the evolution of the nerve structures of the lower vertebrates at that particular moment in their evolution which is marked by the conquest of the subaerial environment.

After our recent observations on the brain of Dipnoi [16], it seemed to us that, in relation to the above phyletic problem, it was possible to sum up our empirical knowledge in the form of the model of a primitive brain which would be able to give us some idea of the neural structures of the ichthyomorphous species at the origin of the evolution of land vertebrates.

The possibility of making such a model is based on the comparative neurological study of those living vertebrates which represent truly preserved evolutionary stages differing only slightly from the Devonian species at the origin of both the Sarcopterygian radiations and the Tetrapod line. (Capanna, 1969 [17]). However, not all segments of the neuraxis lend themselves to an investigation of this type; the hindbrain (rhombencephalon) and the spinal cord are two structures which vary very little throughout the whole evolution-

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ary process. Although in the various Vertebrates it undergoes deep changes in morphology and in its nerve connections, even the cerebellum itself is unsuited to phyletic considerations and speculation as the modifications in cerebellar structures are due to far-reaching functional modifications (Stefanelli, 1944 [18]; 1948 [19]) and do not give a true picture of the evolutionary position of the taxa they belong to.

The forebrain is quite a different matter. Indeed, already in the case of the telencephalon the process of eversion and inversion of the telencephalic walls (Ariens Kappers, 1908 [20]) provides a good example of a basic dichotomy in the evolutionary development of the Vertebrates. The diencephalon itself follows telencephalic evolution, either exhibiting massive structures fused with the basal telencephalic formations in the Actinopterygian line, or structures compressed perlaterally and bilateralized because of the presence of a large median ventricle which cuts it medio-sagittally in the Tetrapod line.

The question of the mesencephalic tectum is a rather complex one. Although the morphology and histology of this nervous centre are very similar in all the Vertebrates, the organization shown in *Protopterus*, especially when compared with the mesencephalic tectum structures of the Urodeles, could suggest interesting considerations pertaining to the discussion of the problem of evolutionary neurological affinities as set out in the present paper.

Also the choice of the material requires some explanation. The study of the only living Crossopterygian, *Latimeria chalumnae* (Millott and Anthony, 1962 [21], 1966 [22]) and of the Branchiopterygians (Nieuwenhuys, 1963 [23]) has clearly shown that the telencephalon of these species has already begun the process of eversion of the telencephalic walls which is to characterize the Actinopterygian line. On the other hand, also among the Dipnoi the monopulmonate evolutionary line (Ceratodontidae: *Neoceratodus forsteri*) displays a telencephalon that although it cannot be described as everted, is indicative of a peculiar condition (Nieuwenhuys and Hicky, 1965 [24]) which already dismisses it as a possible precursor of amphibian forms. On the contrary, the line of the bipulmonate Dipnoi (Lepidosirenidae: genera *Protopterus* and *Lepidosiren*) with their distinctly inverted telencephalon which repeats forms and connections typical of tetrapod neural organization, seems to present itself as the possessor of that very neuro-anatomic model we set out to look for.

However, there still remains the doubt expressed by Bertmar (1968 [25]) and by Jarvik (1968 [26]) that this and other anatomical characteristics which are reminiscent of batrachomorphic structures are merely examples of evolutionary convergence. Nevertheless it must be pointed out that recent cytotaxonomic data (Ohno and Atkin, 1966 [27]; Morescalchi, 1970 [28]; Denton and Howell, 1973 [29]; Capanna and Cataudella, 1973 [30]) tend to demonstrate the close resemblance of the karyotype among Dipnoi, Branchiopterygians and Amphibians and that such a character can hardly be imagined to have been shaped by convergence and is instead the expression of a derivation from a hypothetical common Gnathostome ancestor.

On the other hand, because of their morphological features, the Dipnoi are considered (Schmalhausen, 1968 [31]) as being more primitive than the Polypterinae and even than the Crossopterygii. What is even more important, these characters of primitiveness such as the persistence of the notochord and the aspondylous vertebral situation have remained unchanged down to the present-day Dipnoi. Thus everything seems to indicate that even the anatomic structures that have left no fossil traces—and in this particular case we are interested in the encephalon—have remained unchanged from the mid-Devonian down to the present time.

For these reasons, and within the scope of these evolutionary problems, we thus think it of interest to give a brief outline of our interpretation of the architectural make-up of the forebrain of the bipulmonate Dipnoi as can be inferred from our observations on *Protopterus annectens* (Owen) and *P. dolloi* Boulenger.

As mentioned earlier, the inversion of the telencephalic walls and the bilateralization of the telencephalic hemispheres are complete in *Protopterus*. In addition, the presence of the four foundamental sulci in the lateral ventricles allows the pallial and sub-pallial telencephalic areas typical of the Amphibians to be detected. What does differ from the neural organization of the Amphibians, but which could also well be a primitive character of the telencephalic structures of the lower Vertebrates as it is found in the Actinopterygian line, is the predominant development of the basal areas as compared with the pallial ones. One consequence of this hyperdevelopment is the truly unusual peculiarity of an olfactory bulb being pushed upwards because of a subpallial blind end which bulges out. As a result the olfactory bulb has no room below for its extensive development due to the large amount of primary olfactory fibres and so several bulbar structures such as the mitral cells slide backwards followed by the primary olfactory fibres, thus forming a grey magnocellular layer along the whole of the lateral pallial wall.

This subpallial hyperdevelopment gives rise to a peculiar situation also in the basal region, i.e. the superimposition of a striatal grey layer over the septal periventricular grey layer in the more ventral area of the hemisphere. This is the formation we referred to as " Superpositio ventralis " (Clairambault and Capanna, 1973 [16]) thereby replacing the ambiguous denomination of " olfactory tubercle " given to this basal area by numerous Authors (Elliot Smith, 1908 [32]; Rudebeck, 1945 [33]; Schnitzlein and Crosby, 1963 [34]) on the strength of an absurd homology with the olfactory tubercle of Mammals. What is of greatest interest as far as the superpositio ventralis is concerned is the continuity of this striatal formation with two large ventro-lateral neuropilary masses which we interpret as amygdalae because their neuroanatomic connections correspond to the primitive position of the amygdalae in the Amphibians. In the latter, the amygdalae are displaced slightly upwards because of pallial development into two occipital cones projecting the telencephalic masses backwards and upwards so that the foraminal and postforaminal striatal grey mater (i.e. the amygdalae) is superimposed on the diencephalic nuclei.

Both the *Protopterus* species examined by us lack this superimposition of the telencephalon on the diencephalon which seems to pedunculate at the level of this very junction. It follows that the reciprocal position of the diencephalic parts appears in its most linear, and thus most primitive, situation. Thus in the epithalamus we find two almost symmetrical habenula ganglia which clearly separate two parietal organs, the rear one of which displays cells of the photoreceptor type. The habenulas are followed by a sub- and post-habenular ependymal area which is continuous with the subcommissural organ. A very deep sub-habenular furrow separates the epithalamus from the talamus which, in its turn, is divided by a sulcus medialis into an area thalamica dorsalis and a thalamus ventralis. The sulcus hypothalamicus separates the thalamus from the hypothalamus. The diencephalon of Protopterus is thus disconcertingly schematic, almost as if it had been deliberately created to represent the theoretical design of the diencephalic structures of the Amphibians. However, even in their linearly schematic and primitive nature, the thalamic areas of *Protopterus* possess cyto- and fibro-architectural levels of organization which we find to be characteristic of the Amphibians, such as the stratification of the area thalamica dorsalis and a neuropil whose position and structure recall those of the neuropil of Bellonci in the Anurans. All these structures are thus evidence that, at the level of the thalamus, a position of possible convergence of various kinds of sensitive influences has been reached.

The development of the hypothalamus is enormous, especially the preoptic formations. It must not be forgotten, however, that in the lower Vertebrates the nuclei in the preoptic area play a part in the neuro-endocrine regulation of the water and salt balance and if there were ever animals with a real water balance problem these are the Dipnoi.

The boundary between diencephalon and mesencephalon is extremely hard to make out. The mesencephalic tectum does not extend laterally to produce the characteristic hemispherical formations as in all Vertebrates. Instead, the mesencephalic ventricle remains a narrow slit which continues the diencephalic ventricle without interruption. This slit-like arrangement of the ventricle and the vertical position of the tectal layers is like that of the Urodoles even if, in the latter, the mesencephalic ventricle is rhomboidal in cross section and not a narrow slit as in *Protopterus*. As a result, the position of the posterior commissure is not enough to set the boundary between two areas which appear homogeneous in the grey matter and may be characterized only by a few cyto-architectural peculiarities (e.g. the cells of the mesencephalic nucleus of the fifth nerve or the bipolar tectal cells) found at caudal levels.

In the case of *Protopterus* it is thus possible to speak of a very primitive neural situation consisting of a single sensitive formation, thalamus dorsalis + tectum, and ventral to the sulcus of Hiss, of a single motor unit, thalamus ventralis + tegment. In the course of the evolution of the lower Vertebrates, starting from its more caudal area, this single neural structure probably differentiated into a specialized sensitive district (mesencephalic tectum) independently in the two lines characterized by the inversion and eversion of the telencephalic walls.

This picture of the forebrain of *Protopterus* can thus now be completed by stressing one feature of the more cranial part of the hindbrain: the cerebellum is similar in all respects to that of the Amphibians and between the mesencephalic tectum and the cerebellum a small but distinct nucleus of the isthmus can be identified. The dorsal metencephalic structure thus confirms the primitive nature if the Protopterus encephalon, especially when the cerebellar structure is compared with that of *Latimeria* (Lemire, 1970 [35]; 1971 [36]) and of the Branchiopterygians (Nieuwenhuys, 1967 [37]) where the cerebellum is already shaped after the Actinopterygian model.

If the forebrain scheme we are looking for is thus a primitive one with respect to the radiation of land Vertabrates, it must without doubt be imagined as being very similar to the *Protopterus* encephalon. In addition, the considerations made earlier concerning the meso-diencephalic and metencephalic structures indicate that the model based on the *Protopterus* encephalon is to be considered as primitive and ancestral also with respect to the Actinopterygian radiation itself. Thus our model of the encephalon of a gnathostome vertebrate which may be considered as being ancestral to all the branches of bony fishes can be summed up as having a bilateralized inverted telencephalon (*sensu* Ariens Kappers) followed by a long meso-diencephalic structure which tends to differentiate anteriorly into diencephalic structures (habenulae, parietal organs, anterior thalamus, hypothalamus, etc.) and posteriorly into mesencephalic structures (tectum, ganglion of the isthmus, etc.). In this scheme, the cerebellum is to be conceived as a small laminar formation of the kind found in the Amphibians.

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EXPLANATION OF PLATES I–II

Plate I

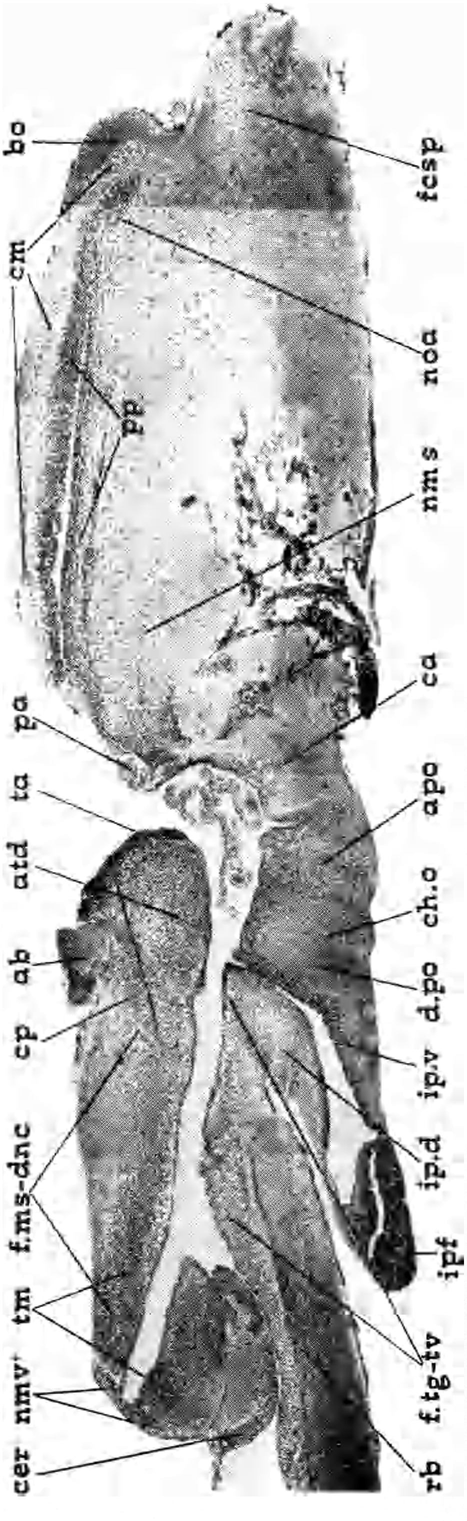
Median sagittal and horizontal sections of the forebrain of *Protopterus dolloi*. The lettering corresponds to the list of abbreviations below.

Plate II

Para–median sagittal section of the forebrain of *Protopterus dolloi* that better shows the telencephalic-areas; for the lettering see the abbreviation list below.

Abbreviations used in the plates

ab:	habenula;
amg:	amygdala;
ap:	archipallium;
apo:	area praeoptica;
atd:	area thalamica dorsalis;
bo:	olfactory bulb;
ca:	anterior commissure;
cab:	commissura habenularis;
cer:	cerebellum;
ch.o:	optic chiasma;
cm:	mitral cells;
cp:	commissura posterior;
d.po:	decussatio post–optica;
fcsp:	subpallal blind end;
f.ms–dnc:	meso–diencephalic formation;
f.tg–tv:	tegmentum–ventral thalamus formation;
ip.d:	dorsal hypotalamus;
ipf:	hypophysis;
ip.v:	ventral hypothalamus;
nb:	neuropil of Bellonci;
nls:	nucleus lateralis septi;
nms:	nucleus medialis septi;
nmV°:	mesencephalic nucleus of the 5th nerve;
no:	olfactory nerve;
noa:	anterior olfactory nucleus;
pa:	paraphysis;
pp:	paleopallium;
rb:	rhombencephalon;
ssf:	pars sub–foraminalis septi;
sv:	ventral septum;
su.v:	superpositio ventralis;
ta:	thalamus anterior;
tm:	mesencephalic tectum.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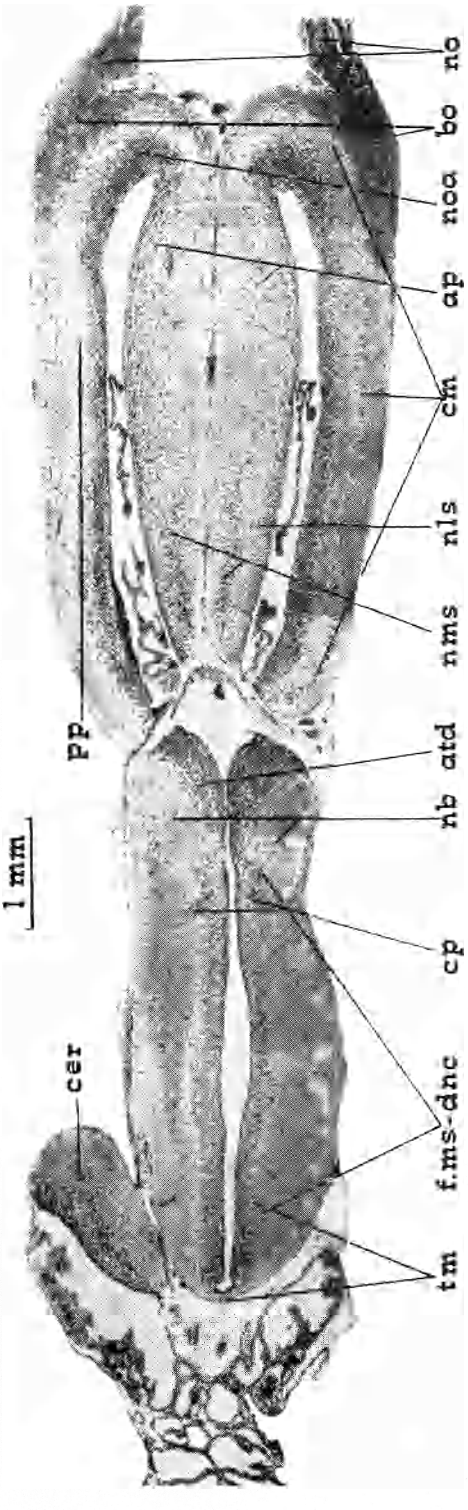
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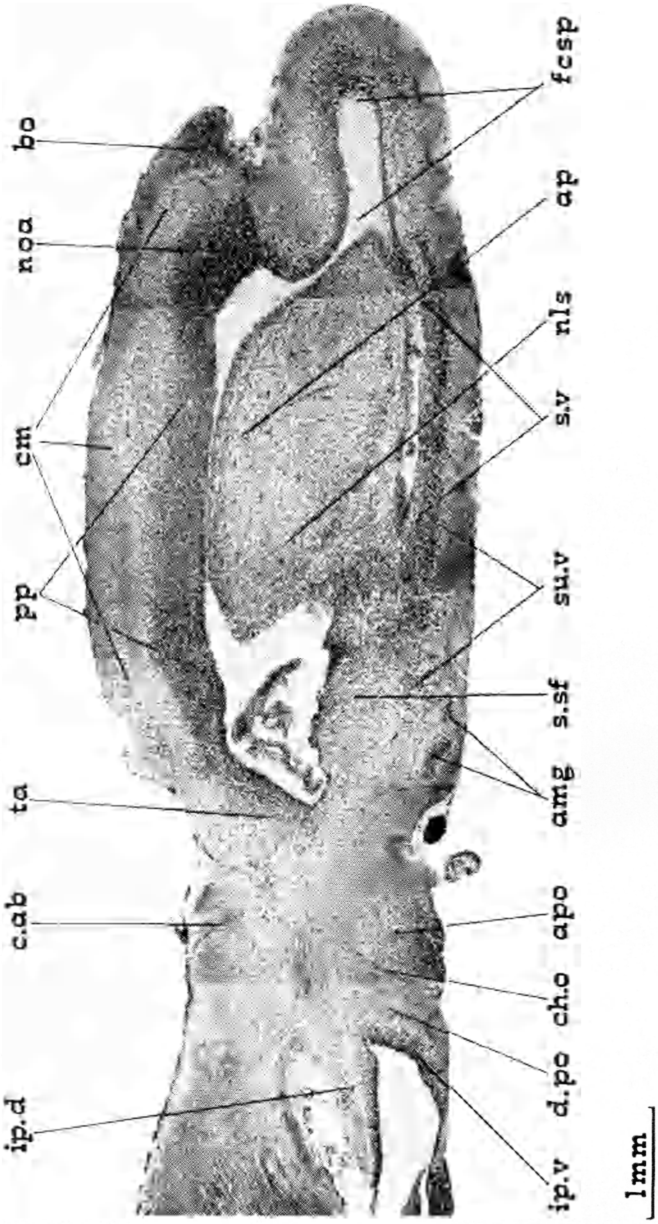
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