

An 'Intracranial Joint' in Frogs

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The intracranial joint /sensu Romer/ or the intracranial juncture apparatus /sensu Bjerring/ is a complex articulatory system separating the orbitotemporal and otic regions of the endocranium of crossopterygian fishes. No other group of fish possesses such cranial division. It was hitherto even supposed that crossopterygians are the only vertebrates that have the skull so peculiarly divided into anterior and posterior moieties. Only some authors /Gardiner, 1970, 1973, 1984; Gardiner and Bartram, 1977; Miles 1971, 1973, 1975, 1977; Patterson 1975; Schaeffer, 1968/ believe the ventral otic fissure in actinopterygians is homologous with the crossopterygian intracranial joint /see Fig. 1/. However, Bjerring /1978/ has denied this homology.

In osteolepiform and porolepiform fishes the apparatus lies at the level of the anterior tip of the notochord, between the posterior margin of the frontal and the anterior margin of the parietal /or underneath the compound bone where the frontal and parietal are dominant elements/. In coelacanthiforms the location of the apparatus is rather different, and hence it cannot be considered homologous with that in the former groups /Bjerring, 1978 : 208, fig. 6/.

The topographic relations of the apparatus may be well exemplified in Eusthenopteron /Fig. 2/, the best known representative of the osteolepiforms.

The same condition can be found in certain ontogenetic stages of frogs. For instance in *Pelobates* the tadpoles before metamorphosis /stages 55-57/ have the lateral walls of the braincase in the orbitotemporal region separated from the otic capsule by a distinct slot called the fissura prootica /Roček, 1981, fig. 15/. This fissure is rather widened within part of its extent; the ganglion trigeminofaciale is located in this space. Anterior to the fissura prootica is the proc. ascendens palatoquadrati. It is worthy of note that in the investigated specimen the ganglion trigeminofaciale runs out from the braincase above the proc. ascendens on one side, but underneath it on the opposite side. From this it can be deduced that the position of the foramen prooticum is not yet well established in this species. The slot itself reaches up to the floor of the braincase.

The fissura prootica is very distinct until the last stages of metamorphosis. The proc. ascendens desintegrates close to its basis /cf. Plasota, 1974 : 119, 124/ so that the posterior part of the palatoquadrate lacks direct connection with the braincase in adults. The dorsal part of the fissura prootica is closed by the taenia tecti marginalis, and the whole area of the former slot becomes covered by membrane, thus forming the fontanella prootica.

In *Xenopus* /Fig. 3/, the prootic fissure is even better developed. An originally firm connection between the orbitotemporal braincase and the otic capsules becomes inter-

rupted as a consequence of considerable reduction of the braincase walls. The floor of the braincase immediately anterior to the notochordal canal displays a large fenestra, anterior to which there is a large area consisting of a thin membranous layer only. The palatoquadrate lacks any connection either with the braincase or /in contrast to Pelobates/ with the otic capsule where the proc. oticus palatoquadrati disappears completely. This results in a peculiar situation, where the orbitotemporal and otic sections of the endocranium are entirely separate, except for narrow strips of membrane on the ventral wall of the braincase. Thus it may be supposed that these endocranial divisions would theoretically be movable, if these motions were not prevented by developing exocranial bones /especially by the parasphenoid and the frontoparietal/.

At the end of metamorphosis /stage 66/ the connection of the orbitotemporal braincase with the otic capsule, as well as that between the palatoquadrate and the otic capsule are newly constituted. However, the braincase walls remain membranous to a considerable extent, with the large prootic foramen that serves not only for housing the ganglion trigeminofaciale but also for the optic and oculomotorius nerves. The palatoquadrate also becomes newly fixed to the otic capsule, both by the processus oticus /which is not, however, homologous with that in the tadpole/, and the processus basalis. One branch given off from the above-mentioned ganglion is enclosed by the latter process in a newly arisen foramen.

Disregarding the time of appearance, and not taking into account the striking differences between larval cranial structures /see e.g. the ethmoidal region of the endocranium, the viscerocranium, etc./, the fissura prootica seems to be present in tadpoles of all frog groups /see Kraemer, 1973 for discoglossids, De Jongh, 1968 for ranids, etc./.

It should be emphasized that the fissura prootica is not the remnant of an early embryonic state, when both the trabeculae cranii and the palatoquadrate lacked any connection with the capsula otica. After the formation of the capsula, the lateral walls of the orbitotemporal region of the neural endocranium, as well as the posterior end of the palatoquadrate, become firmly attached to the capsula, so that before metamorphosis /stage 56/ the neural endocranium is a compact structure. Only later does the fissura prootica start to develop.

The question now arises whether it is possible to homologize the fissura prootica in tadpoles with the intracranial juncture apparatus of the osteolepiform fishes. Evidence supporting this homology derives from the fact that both these slots lie at the most anterior level reached by the notochord in the course of ontogeny. The same holds for their topographic relation to the areas occupied by frontal and parietal ossification centers. The main difference between the two structures is that whereas in the osteolepiforms the nervus trigeminus passes through a separate foramen which lies posterior to the intracranial juncture apparatus, in tadpoles it passes through the fissura prootica. However, this difference may be due to the fact that in most frogs /except for the Leiopelmatidae and Discoglossidae/ there is a relatively large ganglion trigeminofaciale instead of the two separate trigeminus and facialis nerves. The relatively large size of this ganglion, together with a considerable shortening of the anterior part of the otic region /Shishkin, 1973: 166/ could have been responsible for the fusion of an originally separate foramen with the fissura prootica.

The assumption that the intracranial juncture apparatus and the prootic fissure are homologous is also supported by the topographical relations of the posterior part of the palatoquadrate to the neural endocranium.

It follows from the above that the anatomical condition found in adult osteolepiforms is present in metamorphosing tadpoles. The structural changes that occur during the concluding stages of metamorphosis are the additions acquired during phylogenetic development from Devonian crossopterygians to frogs, via some not-yet-exactly-known group of Palaeozoic amphibians.

If the homology of the two structures in question is proved correct, then it may serve as a further piece of evidence for the theory of the origin of tetrapods from crossopterygian fishes, because none of the other fish groups, including dipnoans, possess any structure similar to the intracranial juncture apparatus.

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Fig. 1: Neurocranium of *Mimia* /Actinopterygii, Palaeonisciformes/ in sinistral view. Signs of cranial division marked by an arrow. After Gardiner /1984/. Fig. 2: Neural endocranium of *Eusthenopteron* /Crossopterygii, Osteolepiformes/ in sinistral view. After Jarvik /1981/. Fig. 3: Endocranium of *Xenopus* /Anura, Pipidae/ tadpole, stage 62, in sinistral view. Drawn not to scale. II - V: passages of cranial nerves.

