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RESEARCH & KNOWLEDGE

Short Communication

Living animals for comparison in studies of Mesozoic fossils.

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Abstract - Lungfish are timeless, starting in the Devonian and still found today. Unfortunately this does not mean that biologists and palaeontologists agree about the functional anatomies of dipnoans. Most lungfish that are sufficiently well preserved have an enlarged rib behind the head, known as the occipital or cranial rib. Biologists describe this rib in living lungfish as an aid to the suctorial activities of the fish, involving feeding, burrowing in the mud or drawing a current of air or water into the oral cavity, activities important to both groups of extant lungfish. The arrangement of the occipital rib in lungfish differs in neoceratodonts and lepidosirenids, because the morphology of the oral cavity and the throat differs in the two groups. Suctorial activities are important in most if not all lungfish, for feeding, breathing in air or water, or digging a hole in the substrate. However, presence of an occipital rib does not mean that the fish would have been an air breather.

Keywords: Continuity of lungfish morphology, occipital rib, suctorial feeding, respiration

1. Introduction

Not every fossil fish has a close living representative, and it can often be difficult to work out the functional anatomy of the extinct specimen if there is no surviving group. It is different with the Dipnoi. Lungfish are timeless, starting in the Devonian and still found today. Unfortunately this does not mean that biologists and palaeontologists agree about the functional anatomies of dipnoans. There are a number of instances of confusion, particularly about early dipnoans, that could be clarified if comparisons were made with either *Neoceratodus forsteri*, the Australian lungfish, or with a lepidosirenid, one of the species of *Protopterus* from Africa or *Lepidosiren paradoxa* from South America.

Most lungfish that are sufficiently well preserved have an enlarged rib behind the head, known as the occipital or cranial rib. Biologists describe this rib in living lungfish as an aid to the suctorial activities of the fish, involving feeding, burrowing in the mud or drawing a current of air or water into the oral cavity, activities important to both groups of extant lungfish (Greenwood, 1987; Bemis, 1987). However, a number of palaeontologists are sure that the presence of an occipital rib indicates that the fish must have breathed air (Clement *et al*., 2016), even if they were benthic fish living in marine waters eighty fathoms deep.

2. Materials and methods

Illustrations of fossil lungfish with occipital ribs preserved, such as *Ceratodus sturii* (Teller, 1891) and *Sagenodus copeanus* (Schultze and Chorn, 1997) were compared with heads of the living lungfish stained with Alcian blue and Alizarin red by the method of Kelly and Bryden (1893) to show jaw structures and occipital ribs in situ. \

3. Results

The arrangement of the occipital rib in lungfish differs in neoceratodonts and lepidosirenids, because the morphology of the oral cavity and the throat differs in the two groups. The two extant groups of lungfish separated in the Permian and are in many ways quite dissimilar (Kemp *et al*., 2017). Neoceratodontids and related lungfish have a wide gap between the prearticular jaw bones, a long basihyal to support the tongue, and a set of complex muscles attached to the ceratohyal and in the operculum to move the tongue forwards, and plug the gap between the prearticular jaw bones (Fig. 1). A further series of muscles are attached to the mandible and to the pectoral girdle, and contraction of these muscles creates a suctorial force to draw food, water or air into the mouth. In this group, the occipital rib is attached to the posterior chondrocranium by an immoveable amphiarthrosis, and is surrounded by hypaxial musculature of the trunk. It is not moveable, and does not reach as far as the pectoral girdle or the muscles associated with the pectoral girdle (Fig. 1). The rib would have little or no influence on the suctorial actions of the jaws.

Lepidosirenids utilize different structures and mechanisms. They have no basihyal, no gap between the tooth plates of either the upper or lower jaws, and the occipital rib articulates with the posterior skull in a

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moveable articulation or diarthrosis (Kemp, 2012). This may assist the suction operated by the jaw muscles, attached to the pectoral girdle and the ceratohyal and jaws.

Some fossils, such as *Sagenodus copeanus* (Schultze and Chorn, 1997) or *Ceratodus sturii* (Teller, 1891), follow the neoceratodontid pattern, with a fixed rib, strong hyoid apparatus and a gap between the prearticular bones. Others, such as *Rhinodipterus kimberleyensis*, which has a gap between the prearticular bones and well developed and apparently moveable occipital ribs (Clement *et al*. 2016), may be similar to neoceratodontids or to lepidosirenids, but the hyoid apparatus is not known in *R. kimberleyensis*, so the actual mechanism of suction in this species is uncertain.

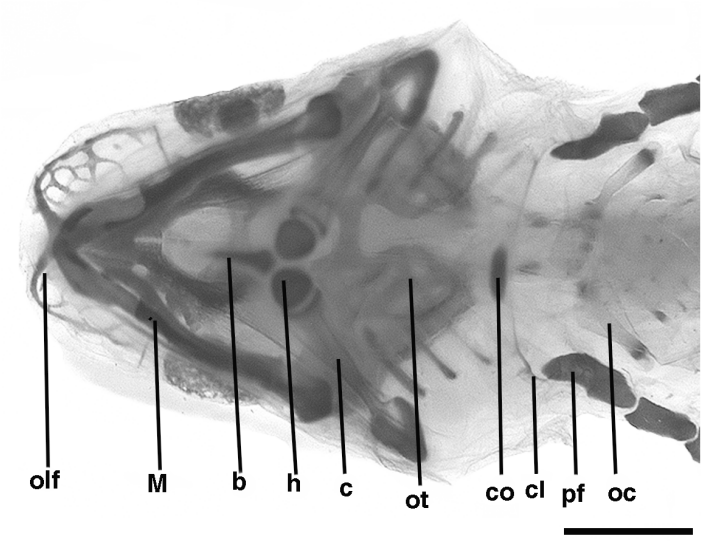

Figure 1. The head of a juvenile lungfish, stained with Alcian blue and Alizarin red. Occipital ribs, partially ossified, are present behind the pectoral girdle (coracoid and cleithrum). b = basihyal, c = ceratohyal, cl = cleithrum, co = coracoid, ex = exoccipital, h = hypohyal , M = Meckel's cartilage, oc = occipital rib, olf = olfactory capsule, ot = otic capsule (membranous labyrinth), pf = base of pectoral fin. Scale bar = 2cm.

4. Discussion

Suctorial activities are important in most if not all lungfish, for feeding, breathing in air or water, or digging a hole in the substrate. However, presence of an occipital rib does not mean that the fish would have been an air breather. Suction involves the structure of the mandible, the ceratohyal and the muscles of the pectoral girdle and operculum. In neoceratodontids, the occipital rib, which does not move and is embedded in muscles, may have no influence on suction. Palaeozoic and Mesozoic dipnoans should not be seen as fundamentally different from living lungfish, and comparisons of functional anatomy among the different groups will enhance understanding of all dipnoans and their environments.

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