

Structure features and structural transformations of the maxillary bones in the Baikal cottoid fish

Tolmacheva Yu.P.*, Bun M.M.

Limnological Institute, Siberian Branch of the Russian Academy of Sciences, Ulan-Batorskaya Str., 3, Irkutsk, 664033, Russia

ABSTRACT. In this paper, we study morphogeometric parameters and histostructure of maxillary bones in three coastal Baikal Cottoidei species belonging to different trophic groups. The results of the study revealed that the main trend in the transition from benthography to ichthyography is the sequential elongation of jaws and reduction in the mouth thrust accompanied by a consistent change in the form and internal structure of bone elements. A detailed analysis of data revealed that the changes mostly concern additional morphological structures (processes) of the bones directly connected with musculoligamentous apparatus and experiencing the highest tension during the functioning of the maxillary system. The distinctive features of the structural transformations maxillary bones in different fishes is a consequence of the uneven effect of power load that changes when the body adapts to certain habitat conditions.

Keywords: cottoid fish, maxillary apparatus, morphogeometric parameters, histostructure, structural adaptation, external power load

Introduction

The study of trophic adaptations in Baikal fish represents a bulk of closely related species. This is very interesting due to the peculiarities of the Baikal ecosystem owing to its age and diversity of underwater landscapes. The cottoid group, whose representatives occupy at present practically all biotopes and trophic niches of the lake, has a special status amongst the Baikal fish. Three species of the family Cottidae, *Paracottus knerii*, *Leocottus kesslerii* and *Batrachocottus baicalensis* (Taliev, 1955; Sideleva, 2003), inhabit the littoral zone (from the water edge up to the depths of 250–300 m). The study of dietary habits within this biotopical group revealed two main trends of trophic adaptation, allowing these species to coexist in a single biotope: zoophagy and zoophagy + ichthyophagy (Taliev, 1955; Sideleva and Mekhanikova, 1990; Sideleva, 2003; Dzyuba, 2004; Miyasaka et al., 2006; Tolmacheva, 2008). Each species formed its morphofunctional features in the structure of the anterior digestive system as a result of adaptation to a specific trophic behavior (Taliev, 1955; Yabe, 1985; Sideleva and Mekhanikova, 1990; Sideleva, 2003; Tolmacheva, 2010). As any change in the function and structure of the system is followed, above all, by certain changes in its separate parts, it is relevant to apply the detailed approach to study latent regularities of these structural transformations in the closely related species of fish.

The present paper concerns a comparative morphometric and histological study of the maxillary bones and analysis of potential causes of their structural transformations in the Baikal cottoid fish from various trophic groups.

Materials and research methods

Osteological specimens of the maxillary bones of three species of cottoid fish from the Baikal littoral zone, *Paracottus knerii* (Dyb., 1874), *Leocottus kesslerii* (Dyb., 1874) and *Batrachocottus baicalensis*, were used in this study. Thirty specimens of each species were examined in total.

The standard methods for osteological analysis were used to study the shape of the maxillary bones (Standard methods... 1976). The soft tissues were removed from the fish skulls with a 10% solution of NaOCl; the cleaned bones were stored in glycerol. The comparative analysis included 16 measurements (% of the bone length) of the anguloarticulare, dentale and praemaxillare. The method for constructing allometric networks similar to the approach used previously in analyzing the variability of the body shape of fish (Strauss and Bookstein, 1982; Strauss and Fuiman, 1985; Tolmacheva, 2011) was used to create geometric structures of the maxillary bones. The geometric design was performed via the Autocad 2010 software (<http://www.autodesk.ru>) (Fig. 1).

*Corresponding author.

E-mail address: tjul78@mail.ru (Yu.P. Tolmacheva)

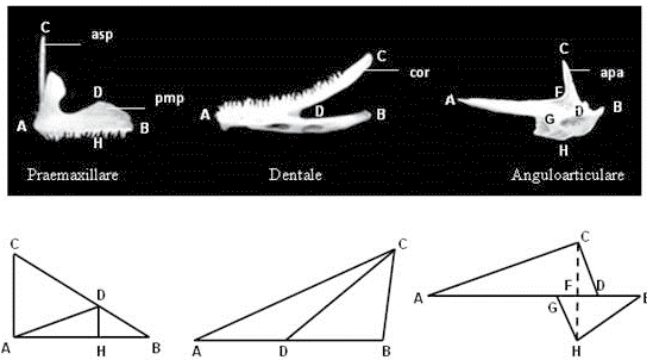


Fig. 1. The construction scheme of morphogeometric design of the maxillary bones in cottoid fish: a) the measurement scheme in osteological analysis; b) projection of measurements (in % of bone length) in morphogeometric design. Legend: Praemaxillare: asp – pmx ascending process, pmp – pmx maxillary process, (AC – asp height, AH – pmp location, DH – pmp height); Dentale: cor – den coronoid process (BC den height, AC – location of the cor posterior end, DC – cor length, BD – den notch depth); Articulare: apa – superior art process (CH – art height, AD – location of suprascapular notch (base of superior process), CD – height of superior process, CF – location of superior process: AG – location of inferior notch).

The histological structures of the maxillary tissues were studied according to the standard methods (Merkulov, 1969). The material was fixed in a 10% buffer formalin solution, which was decalcified with a 5% nitric acid solution and put into wax-paraffin. The 10- μm thick sections were stained with hematoxylin-eosin. The anatomical structure of each bone was presented as longitudinal and transverse sections. Morphometric analysis of the specimens was performed using a binocular light microscope (S. Zeiss) and ImageScope Color Image Analysis software (Moscow, 2008). The following parameters were chosen for the analysis: bone area, cartilage and bone cavity (thousand μm^2 /area of one field of view). The average area of one field of view was 1.73 μm^2 at 125-fold magnification. Each specimen was analyzed in 10 areas of view.

Results and discussion

The objects studied were closely related species of cottoid fish that inhabit the littoral zone of Lake Baikal and have a similar feeding behavior. The previous investigations of the maxillary apparatus of these fish revealed the growth of its linear parameters in the following direction: *Paracottus knerii* - *Leocottus kesslerii* - *Batrachocottus baicalensis*. This was due to the consumption of prey with different size and incomplete transition to ichthyophagy (Tolmacheva, 2010) (Fig. 2).

Morphogeometrical parameters. The morphometric analysis together with a geometric approach made the set of linear measurements more illustrative and enabled to investigate the simple regularities that are not always apparent without visualization (Fig. 2):

Upper jaw (*praemaxillare* + *maxillare*). Elongation of the upper jaw is followed by a consistent reduction of its ascending process of *praemaxillare*. This is often observed in other fish species. The relative height of the ascending process in the zoophage *P. knerii* and *L. kesslerii* was 81% and 70%, respectively, of the *praemaxillare* length, whereas it was 52% in the facultative ichthyophage *B. baicalensis*.

Lower jaw (*dentale* + *anguloarticulare*). The main differences in the relative parameters of the lower jaw amongst the studied species are limited to the reduction of the bone height. The relative height

of the *dentale* in *P. knerii* and *L. kesslerii* was 41.6 and 43%, respectively, and 35% – in *B. baicalensis*. It is noteworthy that the *anterior process* of *anguloarticulare* is consistently retracted (70%, 77% and 71% in *P. knerii*, *L. kesslerii* and *B. baicalensis*, respectively) and dislocated in a more horizontal position (Fig. 2). The anterior process (70 - 71%) and the lower process (62%) remain in unaltered position.

The measurements show that the consistent elongation of the jaw and reduction of the mouth protrusion in the studied species is followed by an appropriate change in mouth shape and the ratio of its morphological structures (Taliev, 1955; Sideleva and Mekhanikova, 1990; Sideleva, 2003; Tolmacheva, 2008; 2010). The power load, which changed during evolution, is the main factor that affects the morphogenesis of the bone tissue (Wolff, 1892). Hence, a transformation of the bone shape should primarily occur in the regions of the maximum stress during the functioning of the maxillary apparatus.

The protrusion of the upper jaw in the cottoid fish results from gliding the ascending processes of *praemaxillare* along the *ethmoideum*. The degree of the protrusion depends on two interdependent features: the length of the *praemaxillare* and the height of the ascending process (Gregory, 1933; O’Kamura, 1970; Voskoboinikova, 1986). The ascending processes of *praemaxillare* carry the maximum power load, resulting

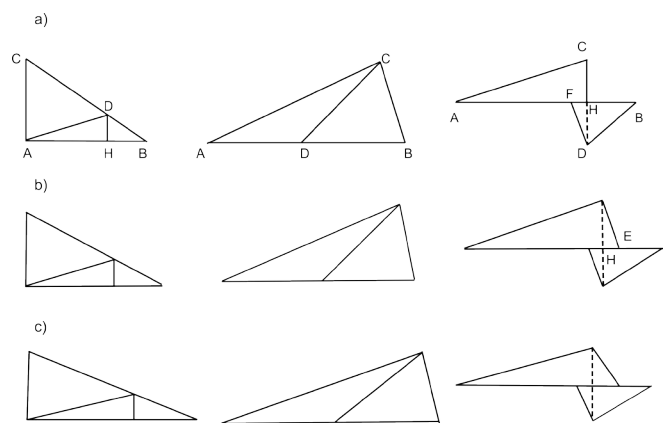


Fig. 2. Morphogeometric design of jaw apparatus bones in littoral species of Cottoidei belonging to different trophic groups: a) *Paracottus knerii*; b) *Leocottus kesslerii*; c) *Batrachocottus baicalensis*.

from the functioning of the maxillary apparatus in the anamniotes (Lebedkina, 1980). An elongation of the *praemaxillare* in ichthyophages significantly increases the pressure on the ascending processes and, thus, leads to their gradual reduction.

The lesser degree of protrusion requires more efforts to close the mouth (Aleev, 1963). This process is carried out with the *musculus adductor mandibulae* (A2, A3 and AW), whose portions are predominantly attached to the internal side of the *anguloarticulare* and the anterior process (Dobben, 1935; Yabe, 1985). The transformation of the *anguloarticulare* shape and the consistent dislocation of the anterior process in a horizontal plane is due to the increasing power stress from the muscles. In turn, the dislocation of the anterior process of *anguloarticulare* in a horizontal plane reduces the *dentale* that contacts with it in the region of the coronoid process.

Histostructure. The histological analysis shows that rough fibrous tissue typical of the bony fish represents the microstructure of maxillary bones in the studied species (Meunier and Desse, 1986). There are compacted portions of cartilaginous tissue in the contact areas. The surface of each bone represents a compact structure above bone cavities that are connected by anastomoses and form a single network (Fig. 3a). Inside the cavities, there are fragments of osteoblasts that were destroyed during the preparation of the specimens.

The number and size of the cavities significantly vary within the same bone (Fig. 3a, Fig. 3b). E.g., many small cavities, making 30-43% of the total area in a vertical section of the bone, represent the network structure inside the bones. The internal structure of the processes (*ascending process of praemaxillare*, *anterior process of anguloarticulare* and *coronoid process of dentale*) represent a single large cavity (50-69% in area) that is encircled by a layer of a dense coarse fibrous tissue.

Bias in the external mechanical load on the formation of the bone tissue induces the heterogeneity of the network structure (the bone cavities become fewer and larger) in different portions of the same bone. In the study of the internal structure of the maxillary apparatus in the Scaridae, the area of the cavities increased in the region of the maximum stress (Bogachik, 1999). We determined this regularity in the microstructure of the processes of the maxillary bones that are the most affected by the muscular-ligamentous apparatus.

Conclusion

Thus, changes in functional requirements in a specific environment cause the adaptive transformations of the maxillary apparatus of the fish. The main trend observed in the Baikal cottoid fish at the transition from benthos feeding to ichthyophagy is a consistent elongation of the jaw and reduction of the upper jaw protrusion followed by an appropriate change in the shape, size and internal structure of the main bone elements. The transformation of the bone shape and

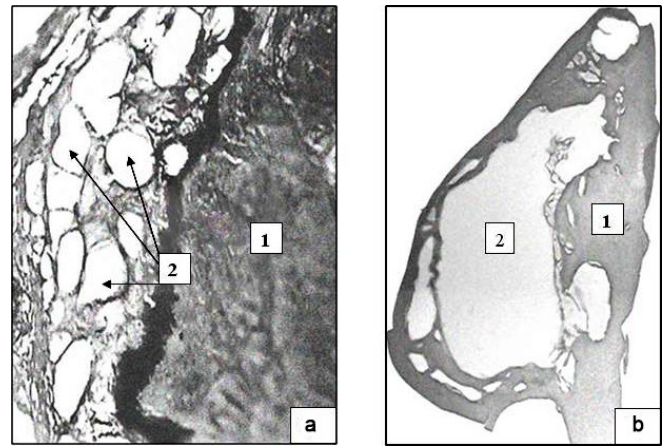


Fig. 3. Anguloarticulare histostructure of the bighead sculpin *Batrachocottus baicalensis*: a) transverse section of the bone; b) transverse section of the anguloarticulare superior process. 1 – compact tissue, 2 – medullary cavities. Magnification x125.

internal structure occurs in the regions of the maximum stress that occurs during the functioning of the maxillary apparatus. It mainly concerns supplementary elements (processes) of the maxillary bones that are directly connected to the muscular-ligamentous apparatus and most exposed to external forces. Overall, the peculiarities of the structural transformations of the maxillary system in different species is a result of uneven power load that changes during adaptation of an organism to a specific environment.

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