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MORPHOLOGICAL FEATURES OF CEPHALIC SKELETON OF THE ADULT BLACK SEA TURBOT (KALKAN) *SCOPHTHALMATUS MAXIMUS* VAR. *MAEOTICA* (PLEURONECTIFORMES, SCOPHTHALMIDAE)

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Morphological Features of Cephalic Skeleton of the Adult Black Sea Turbot (Kalkan) *Scophthalmus maximus* var. *maeotica* (Pleuronectiformes, Scophthalmidae). Yelnikov D. V., Khanaychenko A. N. — For the first time the full description of neural and visceral cephalic skeleton of adult Black Sea turbot (kalkan), *Scophthalmus maximus* (Pallas) has been carried out. The detailed outline of the norm of development of cephalic skeleton in adult Black Sea turbot with up-to-date nomenclature of bone elements is offered as a basis to conduct further studies on variability of skeleton elements and abnormalities among the Black Sea turbot morphotypes from natural populations and artificially reared specimens.

Key words: the Black Sea turbot, morphological features, cephalic skeleton.

Морфологические особенности строения головного отдела скелета черноморской камбалы калкан, *Scophthalmus maximus* var. *maeotica* (Pleuronectiformes, Scophthalmidae). Ельников Д. В., Ханайченко А. Н. — Впервые представлено полное описание нормы строения черепной коробки и висцерального скелета взрослых особей черноморской камбалы калкан, *Scophthalmus maximus* (Pallas). С учётом современной номенклатуры составлена подробная схема стандартного строения головного отдела скелета калкана, которую в дальнейшем предлагается использовать как основу нормы строения скелета при изучении изменчивости морфотипов и аномалий скелета особей черноморского калкана из природных популяций и выращенных в искусственных условиях.

Ключевые слова: черноморская камбала калкан, морфологические особенности, скелет головы.

Introduction

Morphological peculiarities of fish skeleton should be undoubtedly considered while carrying out analysis of intraspecific variability of the species within its natural habitat, and for analysis of deformities induced during early ontogenesis under adverse environmental parameters in natural, or in artificial conditions. Studies of morphological variability in *Scophthalmus maximus* (syn. *Psetta maximus*) *var. maeotica* (Pallas, 1814) (Pleuronectiformes, Scophthalmidae) (kalkan, or Black Sea turbot, further referred to as BST) carried out in the Institute of Biology of Southern Seas, Sevastopol, Ukraine since 2006 revealed various abnormalities in morphology (including skeleton) of BST from natural population (Khanaychenko et al., 2008), and comparative study of abnormalities in the wild and artificially reared specimens in order to reduce skeleton deformities in larviculture reared BST juveniles, was carried out (Khanaychenko et al., in prep.). In the only publication concerning morphology of BST skeleton (Kalinina, 1959), the incomplete description of the cranial part of cephalic skeleton of BST was presented that was considered insufficient for analysis of intraspecific variability and skeleton pathologies of this species.

Both trends of morphological research require standardized approach to analysis of skeleton morphology. Detailed description of the normal structure of cephalic skeleton of BST according to up-to-date nomenclature should contribute to better further analysis of the levels of morphological variability and pathology of these species both from nature and aquaculture.

Material and method

Biological analysis of 214 wild BST specimens caught during scientific ichthyological survey in Sevastopol coastal area (North-Western shelf off Crimea — NWC, Black Sea) in 2008 during their natural spawning period (March–June) at the depths 40–70 m was carried out. Among the sampled fish, 12 mature specimens of both genders, of the standard length varying from 36.5 to 51.0 cm without any observed abnormalities in skeleton structure were selected to describe standard normal morphological features of cephalic skeleton of adult BST. The cranium was separated from the soft tissues by processing the fish skulls in the hot water, followed by washing in running tap water. The bones were disarticulated after natural maceration in a tap water in closed vessels, followed by careful washing in running tap water. Otoliths for fish aging were extracted through the large occipital foramen prior to disarticulation of the bones. BST age was determined by counting the annual rings on the medial side of the sagittal otolith under the microscope MBS–10 under transmitted light. Selected for description of morphological features of BST fishes were aged after otolith analysis from 4 to 8 years old.

Determination of specific bones and their spatial location in the skeletons of investigated specimens was carried out basing on the standard description of the bony fish skeleton after Gourtovoy et al. (1976). Generalized layout of standard BST cephalic skeleton was proposed after specialized scheme of the skeleton structure of Atlantic Pleuronectidae (Diaz de Astarloa, 2005). The nomenclature used to present the generalized scheme of the adult BST cephalic skeleton features followed the up-to-date descriptions of a multi-species anatomy ontology for teleost fishes (Whetzel et al., 2011) and after Dictionary of ichthyology (Coad, McAllister, 2007) and specialize descriptions of the flatfish cephalic skeleton (Chanet, 2003; Diaz de Astarloa, 2005).

Results

Cephalic skeleton (cranium, or skull) of BST as in all Teleosts consists of two main parts: Neurocranium (axial skeleton of the head, or the braincase) and Viscerocranium (syn. Splanchnocranium, or facial skeleton of the head). Neurocra-

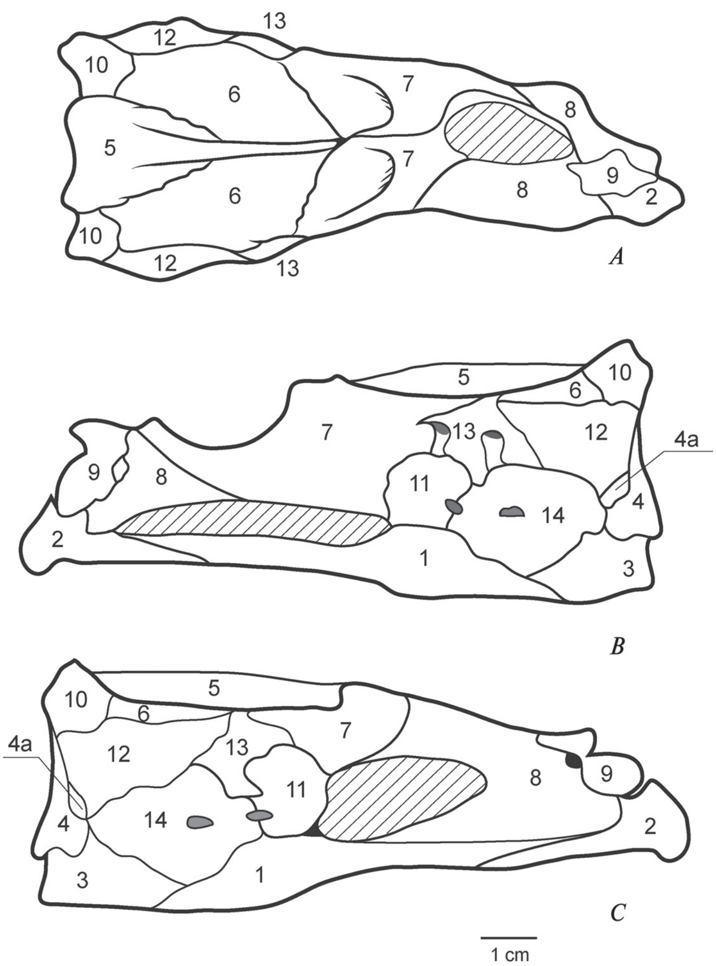

Fig. 1. Structure of *Neurocranium* of the Black Sea turbot: *A* — dorsal view; *B* — left lateral view; *C* — right lateral view. 1 — parasphenoideum; 2 — vomer; 3 — basioccipitale; 4 — exoccipitale laterale; 4a — intercalare; 5 — supraoccipitale; 6 — parietale; 7 — frontale; 8 — ethmoideum laterale; 9 — mesethmoideum; 10 — epioticum; 11 — pterosphenoideum; 12 — pteroticum; 13 — sphenoticum; 14 — prooticum. Original drawing of D. V. Yelnikov edited by A. V. Drapun.

Рис. 1. Строение черепной коробки черноморского калкана (*P. m. maeotica*): *A* — вид сверху, *B* — вид слева, *C* — вид справа. 1 — parasphenoideum; 2 — vomer; 3 — basioccipitale; 4 — exoccipitale laterale; 4 a — intercalare; 5 — supraoccipitale; 6 — parietale; 7 — frontale; 8 — ethmoideum laterale; 9 — mesethmoideum; 10 — epioticum; 11 — pterosphenoideum; 12 — pteroticum; 13 — sphenoticum; 14 — prooticum. Оригинальный рисунок Д. В. Ельникова. Художник-оформитель — А. В. Драпун.

nium is composed of the skull roof (or cranial dome) and the base of the braincase; sphenoid, occipital (syn. basicranial), orbital, olfactory (syn. ethmoid) and otic regions. Viscerocranium is presented by visceral arches: the jaws, hyoid and gill arches. The general peculiarity of the adult BST is the left-right asymmetry of cephalic skeleton resulted from remodeling induced by metamorphosis.

Structure of BST Neurocranium

At the base of Neurocranium (fig. 1: 1), two unpaired bones: parasphenoideum (fig. 1: 1) and vomer (fig. 1: 2) are located. Parasphenoideum playing the role of the main beam of the cranium, stretches along the entire length of Neurocranium, and its rostrum is fastened tightly to vomer under the eye-socket and to the main occipital bone, basiocciopitale in its back part (fig. 1: 3 — basiocciopitale). On both sides of parasphenoideum, its plate-like extensions are connected at their midpart with frontale and pterosphenoideum, postero-laterally it articulates with prooticum and, posteriorly with basioccipitale. In its rostral part, parasphenoideum is bended slightly towards the ocular part of the body that is common to all flatfishes. In *Psetta* (or syn. *Scophthalmus*) genus, BST including, the right eye, as a rule (excluding abnormal, reversed specimens), migrates during metamorphosis to the left side of the body and, correspondingly, parasphenoid bends, with minor variations, towards the left side. Vomer, located in front of parasphenoideum is significantly smaller than the latter and is extended in its rostral part. Lateral thickenings of vomer are joined with the upper jaw, and on its lower part the teeth are located.

Parasphenoideum is the basis for several Neurocranium regions — sphenoid region, where conjoining with pterosphenoideum it forms the basis and the side walls of the middle part of the cranium; conjoining with ethmoidale laterale, mesethmoideum and vomer it provides support to olfactory region; conjoining with frontale, it supports the orbital region.

Occipital (syn. basicranial) region of the head is formed by basiocciopitale, exooccipitale and supraoccipitale (fig. 1: 3—5) delimiting the walls of the principal occipital foramen (foramen occipitale magnum).

As a result of asymmetric remodeling and body torsion of BST during metamorphosis, the main unpaired occipital bone, forming the floor of foramen magnum, basioccipitale (fig. 1, B: 3 and fig. 1, C: 3) is shifted significantly from its longitudinal axis; it is attached to parasphenoideum by its rostral extension, and its hind concave surface compatible with the surface of vertebrae centrum, serves a place of articulation with the first precaudal vertebra. Ventrally basioccipitale is linked to parasphenoid forming parasphenoid-basioccipitale joint, anteriorly it articulates with exooccipitale.

Above the dorsal surface of basioccipitale, and strongly articulated dorsally with it, two paired practically symmetrical, pyramidal-like from the lateral view, forming the lateral sides of foramen magnum, exoccipitals (exooccipitale, syn. = exoccipitale= occipitale laterale) — fig. 1, B: 4 and fig. 1, C: 4) are located. Together with basioccipitale, they form basioccipitale-exoccipitale joint. At the place of this joint exooccipitale forms two overhanging processes. The right exooccipitale could exceed the left one in size. Both have two large foramina allowing the passage of two cranial nerves — glossofaryngeal and vagus. Anteriorly exooccipitale is bordered with prooticum, and with small membrane bone intercalare laterally (fig. 1: 4a), the latter found in-between these larger bones. Dorsally exooccipitale borders the ventral surface of epioticum.

Unpaired upper occipital bone (fig. 1: 5 — supraoccipitale), located at the dorsal part of the occipital region of the cranium, postero-ventrally articulates with exooccipitales, and completes the bony ring around the foramen magnum, forming its dorsal margin. On its top, supraoccipitale forms the high crest-like apophysis (fig. 1: 5), stretched forward far beyond the lower part of the bone thus separating the right and the left parietal and frontal bones. Front lateral edges of supraoccipitale are joined with the small, slightly asymmetrical paired parietal bones of otic region (parietale — fig. 1: 6) located dorsally in the back of the skull. The latter looks like trapezoid bony plate with thickened outer edges, and the smaller left stretches forward the larger right one. These bones cover the top of the head over otic region. Parietale is articulated to frontale anteriorly, and extensively overlaps the edge of pteroticum alongside the posterolateral edge of the Neurocranium.

Orbital region

Axial torsion of BST Neurocranium (as a rule to the left, up to 90°) takes place simultaneously with the migration of the right eye to the left side during metamorphosis, and leads to significant modification (relocation and deformation), and as a result, to asymmetry of all bones of the periorbital area: the frontal bones and the bones of olfactory region. Frontal bones (frontale — fig. 1: 7), which form the orbital area, are altered most significantly during metamorphosis and are transformed into asymmetrical cup-like spongy bone plates with the crescent-shaped processes in their front lower part. The right frontale (fig. 1, B: 7) undergoes significant displacement and torsion along its longitudinal axis: it is deeper and more elongated lengthwise; its crescent-shaped process is longer, narrower and flatter than that of the left frontale, and sheathed in the latter. The crescent-shaped process of the right frontale together with the bones mesethmoideum and the right ectoethmoideum forms the posterior border of the orbit of the right eye.

The left frontale (fig. 1, C: 7) is wider and shorter than the right one. The laminated, large, crescent-shaped process located in the lower part of the left frontale is connected anteriorly with the left lateral olfactory bone (ectoethmoideum), and separates the left and the right eye-sockets. The left eye is not bordered by its own real eye-socket; it is located directly on the jaw muscles, outside the axial skull (neurocranium). The plexus of the bones of Viscerocranium forms the bottom of the orbit of the left eye.

Lacrimal bone (lacrimale, fig. 2: 24) is a small bone lamina located at the front edge of the orbital foramen, above the junction of two visceral bones — palatinum (fig. 2: 21) and ectopterygioideum (fig. 2: 22). The group of small orbital bones (infraorbitalia) is typical for the orbital part of Neurocranium in bony fishes (Teleosts) with lateral symmetry of the body (Gurtovoy et al., 1976). Most of these bones except one of them — small lacrimale, are indistinguishable in the skeleton of adult BST. Other infraorbitalia apparently fused with the neighbouring bones, either been reduced or lost in early ontogenesis.

Together with the bones of olfactory region frontal bones cover the most of BST skull and frames (peri)orbital region of the skull.

Olfactory, or ethmoid region is located directly above vomer and is attached to it. It is formed by paired lateral olfactory bones: ectethmoideum (= ethmoideum laterale = parethmoideum = pleurethmoideum = = praefrontale = exethmoideum (Dias de Astarloa, 2005; McAlister, 2007) — fig. 1: 8) — left (fig. 1, B: 8) and right (fig. 1, C: 8) and unpaired mesethmoideum (fig. 1: 9). Lateral ethmoids lie deeply in front of the orbits, and present the most significant size asymmetry among the bones of BST ethmoid region. They undergo significant transformation during metamorphosis and differ from each other both in shape and size. Contrary to BST frontal bones, the BST right ethmoideum (fig. 1, C: 8) is robust, considerably (almost twice) larger than the left one (fig. 1, B: 8), and has a massive wing-like expanded process that is connected with the right frontale.

Unpaired intermediate olfactory bone (fig. 1: 9 — mesethmoideum) is located in the front part of the skull (anterior part of the braincase) between two lateral olfactory bones. It is a bony bilobed plate curved in longitudinal direction. At the place of its junction with the lateral olfactory bones (fig. 1: 8 — ectoethmoideum) it forms the inner walls of olfactory capsules. Olfactory capsules are located at the top of the head, in front of frontale, between the bones of Splanchnocranium and mesethmoideum. From above they are covered with the paired nasal bones (nasalia, fig. 2: 20) separated by mesethmoideum. Three bones (unpaired mesethmoideum and two paired ectoethmoideum) are connected together in front of the skull and are joined with the upper part of vomer.

Otic region (or auditory capsule) is located in postero-lateral of BST Neurocranium and is comprised of series of paired bones located at each lateral side of the head, participating in formation of the walls of the otic capsule and supporting the vestibulo-auditory system. Most of these paired bones present only minor signs of asymmetry.

Upper elements of otic capsule, paired bones (fig. 1: 10 — epioticum = = epioccipitale), locate at the back top of Neurocranium and look like sharply outlined irregular frusto-conical tubercles. The epioticum is surrounded by the following bones: exoccipitale (fig. 1: 4) (ventrally), supraoccipitale (fig. 1: 5) (laterally, along its axis), parietale (fig. 1: 6) (dorso-laterally), pteroticum (fig. 1: 12) (laterally). The shoulder girdle joins to epioticum through posttemporale (not shown on the scheme of the BST cranium, since these bones are included into the shoulder girdle scheme). Together with prooticum and pteroticum it forms the auditory capsule encasing the semicircular canals of the inner ear where 3 pairs of otoliths are located.

Pterosphenoideum (fig. 1: 11) — is a paired, slightly asymmetric flat and hexagonal-shaped bone plate (the left — more circular and the right — more rectangular) belonging to several regions: to sphenoid region — lying on the lateral expansion of parasphenoid and forming parasphenoideum-pterosphenoideum joint as part of the lateral borders of the cranium; to orbital region joining with frontale anteriorly; to otic region — sutured to prooticum posteriorly and, thus forming prooticum-pterosphenoideum joint and, dorso-posteriorly joins with sphenoticum. Foramina of pterosphenoideum give the route to facial nerves.

Large dense wing-shaped triangular paired bones (pteroticum fig. 1: 12) occupy the forepart of the otic region. Practically symmetrical, still the body of the left pteroticum is insignificantly larger and has wider but shorter wing-like process than the right one. Together with parietale (fig. 1: 6) which locates immediately above pteroticum and slightly overlaps it, they present very special finger- like curved surface which forms the postero-lateral border of the Neurocranium. From the front the wing-like process of pteroticum is connected to frontale. Pteroticum is sutured to postero-lateral surface of prooticum (fig. 1: 14) and, anteriorly to posterior surface of sphenoticum (fig. 1: 13), with exoccipitale (fig. 1: 4) posteriorly, and postero-ventrally at a very restricted surface, with intercalare (fig. 1: 4a), and is covered by epioticum (fig. 1: 10) dorso-posteriorly.

Sphenoticum syn. autosphenotic (fig. 1: 13) — is a paired bone practically untouched by asymmetry resulted from the torsion of the cranium in BST. It has typical saddle-like form with wing-like processes extended on both sides from its central part. Separating the orbital region from the otic region of the cranium, it is articulated with pterosphenoideum antero-ventrally, with frontale dorso-medially, with pteroticum dorso-posteriorly and with prooticum ventrally; dorso-posterior part of sphenoticum very shortly sutures with parietale. Together with the latter, sphenoticum participate in formation of the articulation fossa of hyomandibulare.

Considerable part of otic department is presented by the large paired prooticum (fig. 1: 14), the bone shaped as improper square, or squared flower with a non-ossified cartilage area in its central part and perforated by foramen for trigeminal nerve. Thin foliated delicate posterior surface of prooticum is sutured ventrally with the thin anterior surfaces of basioccipitale forming together with it the chamber where the sagittal otoliths are located. Postero-dorsally prooticum is sutured densely with pteroticum. Antero-dorsally prooticum is connected to the ventral part of sphenoticum, and at the boundary of their joining the articulation of hyomandibulare is located. Antero-ventrally prooticum is articulated with the lateral extensions of parasphenoid, and anteriorly it borders with pterosphenoideum; while dorso-posteriorly it borders with exoocipitale and, slightly with intercalare (fig. 1: 4a).

The smallest bone of the otic region, cone-form, intercalare (syn. opisthoticum = paroccipitale (fig 1: 4a) is bordered with anterior surface of exooccipitale and posterior surface of pteroticum, and, shortly, with prooticum, serving the posterior wall of otic capsule. Intercalare is often not easily found and often lost among the Neurocranium bones of BST in case of absence of preliminary maceration of the skull prior to disarticulation of the bones.

Small, slightly asymmetrical paired parietal bones of otic region (parietale — fig. 1: 6) locate dorsally in the back of the skull. Those are trapezoid bony plates with thickened outer edges: the lighter and smaller left is stretched slightly forward than the larger right one; and both articulating medially cover the top of the head over otic region, posteriorly to supraoccipitale. Parietale is articulated with frontale from ahead and extensively overlaps the edge of pteroticum alongside the posterolateral edge of the Neurocranium.

Structure of BST Splanchnocranium (branchiocranium, or visceral cranium)

All bones of Splanchnocranium including the jaws, hyoid and branchial regions (fig. 2—4), are paired in Teleosts including Scophthalmidae. What is distinctive for the visceral skeleton of BST, as for *Psetta* (*Scophthalmus*) genus in general, is that the bones of the blind side (normally, the right one) have lesser (minor) spatial curvature than the bones of the ocular side (normally, the left one). In other aspects (the differences in location and size characteristics of the left-right bones) are almost negligible.

Mandibular (jaws) arch (or arcus mandibularis) is represented by the upper and lower jaws (upper and lower jaw elements).

Lower jaw. Dentary bone (dentale, fig. 2: 17) lies in the rostral part of the lower jaw and bears numerous small teeth. By its lower and more elongated process, dentale attaches to articulare. Articulare (fig. 2: 18) is located in the posterior part of the mandible. Upper jaw bone — quadratum (fig. 2: 23) is adjustably fixed in articular bursa of the rear top of articulare. Small angulare (fig. 2: 19) terminates the lower jaw. It almost adheres to the inner surface of the lower rear edge of articulare. The asymmetry of the bones of the lower jaw arch is negligible; the bones of the right (blind) side — dentale, articulare and angulare — are slightly more massive than similar bones of the left (ocular) side.

Upper jaw is articulated with the lower jaw through the primary bones of the upper jaw, quadrates (quadratum, fig. 2: 23). Despite the name, those are triangle shaped osseous trabecula with a comb-like crest at their ventral side. The articular surface of quadratum epiphysis is located at the apex of the triangle of quadratum; the bony lamina of quadratum is stretched between two robust beams of almost isoscales triangle. The left quadratum is slightly wider and shorter than the right one. The upper bound of quadratum is attached to the outside of ectopterygoideum (fig. 2: 22). Ectopterygoids are the narrow curved paired boomerang-like bones (the right one

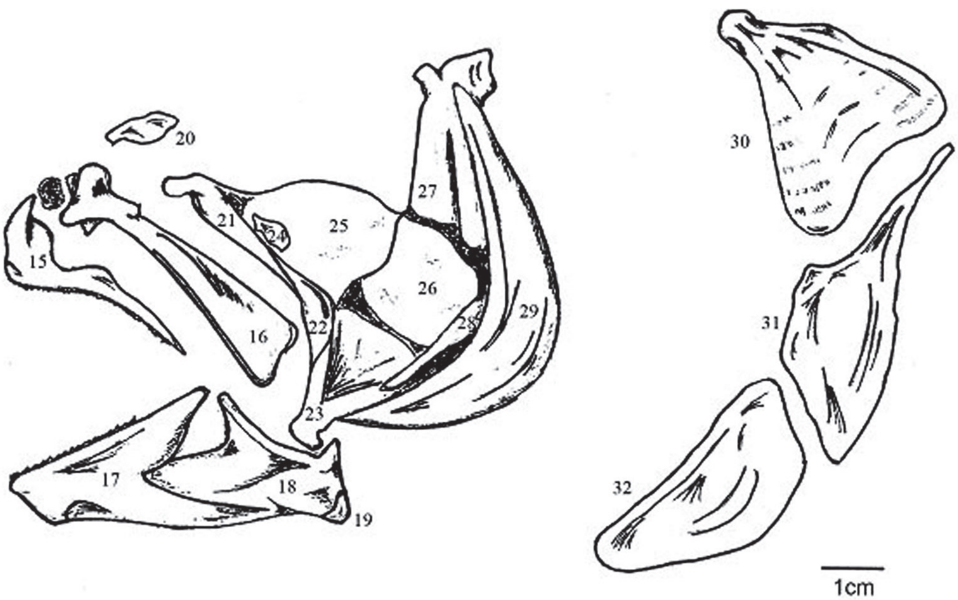

Fig. 2. Structure of mandibular arch of the Black Sea turbot (*P. m. maeotica*): 15 — praemaxillare; 16 — maxillare; 17 — dentale; 18 — articulare; 19 — angulare; 20 — nasale; 21 — palatinum; 22 — ectopteryogoideum; 23 — quadratum; 24 — lacrimale; 25 — entopteryogoideum; 26 — metapteryogoideum; 27 — hyomandibulare; 28 — symplecticum. Gill cover structure: 29 — praeoperculum; 30 — operculum; 31 — suboperculum; 32 — interoperculum. Original drawing of D. V. Yelnikov edited by A. V. Drapun.

Рис. 2. Строение челюстной дуги черноморского калкана (*P. m. maeotica*): 15 — praemaxillare; 16 — maxillare; 17 — dentale; 18 — articulare; 19 — angulare; 20 — nasale; 21 — palatinum; 22 — ectopteryogoideum; 23 — quadratum; 24 — lacrimale; 25 — entopteryogoideum; 26 — metapteryogoideum; 27 — hyomandibulare; 28 — symplecticum. Строение жаберной крышки: 29 — praeoperculum; 30 — operculum; 31 — suboperculum; 32 — interoperculum. Оригинальный рисунок Д. В. Ельникова. Художник-оформитель — А. В. Драпун.

slightly stronger than the left one) connected by its interior surface to metapterygoideum; from their front side they are connected with palatinum. Hook-like bones — palatinum (fig. 2: 21), the right slightly larger than the left one, are movably attached by their anterior part to Neurocranium through vomer articulation. The interweaving of three pterygoid bones forms the left eye-socket. The thin round lamina of internal pterygoid bone — entopterygoideum (= mesopterygoideum, fig. 2: 25) is fixed to the hind part of ectopterygoideum. Posterior pterygoid bone (metapterygoideum, fig. 2: 26) is located between entopterygoideum and quadratum.

Secondary upper jaw is formed by two pairs of bones: premaxillary (fig. 2: 15 — praemaxillare = intermaxillary = surmaxillary = bimaxillary) and maxillary (fig. 2: 16 — maxillare). Premaxillary bones located at the tip of upper jaw, are the thin curved laminas with several processes (ascending, articular, postmaxillary and caudal); both premaxillary bare small teeth. Maxillaries — are the curved laminas, expanded in their posterior part, with articular formations in their anterior part. Both pairs of bones of the secondary upper jaw are joined movably together by the rostral cartilage in one point of Neurocranium above vomer. Insignificant asymmetry of the bones of the upper jaw of BST is the following: the bones of the ocular side of the body, especially, maxillare, are more robust and more curved than the bones of the blind side.

Hyoid region of Splanchnocranium, lying between the jaws and gill arches is represented by the upper branch, called otherwise dorsal hyoid branch, and the lower branch, otherwise known as ventral hyoid branch.

The basis of the upper branch is hyomandibulare (fig. 2: 27) which serves as articulation of the jaws apparatus (suspension) to the otic department of neurocranium, connecting the lower jaw with the skull. The anterior part of hyomandibulare

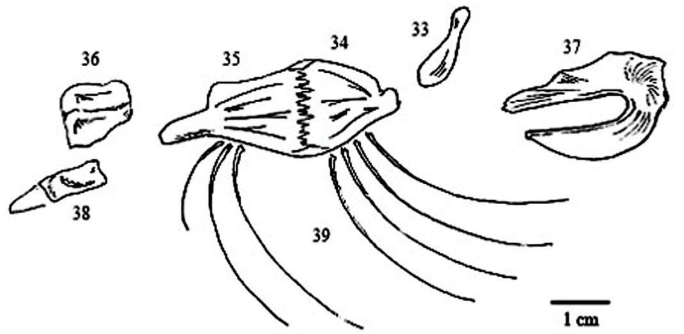

Fig. 3. Structure of hyoid arch of the Black Sea turbot (*P. m. maeotica*): 33 — interhyale; 34 — epihyale; 35 — ceratohyale; 36 — hypohyale; 37 — urohyale; 38 — basihyale; 39 — radii branchiostegii. Original drawing of D. V. Yelnikov edited by A. V. Drapun.

Рис. 3. Строение гиоидной дуги черноморского калкана (*P. m. maeotica*): 33 — interhyale; 34 — epihyale; 35 — ceratohyale; 36 — hypohyale; 37 — urohyale; 38 — basihyale; 39 — radii branchiostegii. Оригинальный рисунок Д. В. Ельникова. Художник-оформитель — А. В. Драпун.

connects to pterygoids and its posterior part is articulated with the bones of operculum. Paired bone symplecticum (fig. 2: 28) is attached to the lower part of hyomandibulare. It is a strong thin elongated arcuately curved, bilaterally sharpened bone expanded in the curved part. The lower part of symplecticum binds tightly to the bones of the upper jaw, to the lower compacted edge of quadratum. Ventral hyoid arch (fig. 3) is attached to hyomandibulare through interhyale (fig. 3: 33), a relatively small, elongated bone thickened ventrally, attached by cartilage to the lower bone — epihyale (fig. 3: 34). This triangular-like bone at the upper end of hyoid arch together with ceratohyale (fig. 3: 35) forms a tight entity with a barely noticeable crest-like joint in its middle part. Wide connecting suture (in the form of a crest-lock) between these two bones widen towards the lateral parts and generates the triangular cartilage densification at its edges (fig. 3: 34, 35). The paired hypohyale (fig. 3: 36) composed of upper and lower tightly fused parts, is joined with the long process of the anterior part of ceratohyale.

Below, under the branchial apparatus, the unpaired bone urohyale (fig. 3: 37, syn. basibranchiostegale) is fastened to a group of major branchial bones and the bones of shoulder girdle with the help of the tendon.

Another unpaired bone of elongated form with a cone-shaped cartilage at its anterior edge (basihyale, syn. glossohyale, fig. 3: 38) is located at the front end of the distal part of the hyoid arch. Hyoid arches are movably attached to the recesses in posterior part of basihyale.

Branchiostegal rays, or radii branchiostegii (fig. 3: 39) branch off epihyale and ceratohyale and serve the basis for branchial membrane. All of the above mentioned bones of hyoid arch (with exception of basihyale) at both sides of the body are paired and practically symmetrical. Minor differences in all paired bones of hyoid arch on the right and left sides of the body are found in various density in some parts of certain bones and in directions of their bending and jointing.

Gill arch supports (branchial apparatus)

The central part of BST gill apparatus is comprised of three main/ principal axial unpaired branchial bones (basibranchiale = copula, fig. 4: Bb.1–Bb.3), tightly held together by means of strong cartilaginous joints. Paired symmetrical gill arches are attached to the principal branchial bones. Three pairs of the upper branchial arches are attached, respectively, to each side of three basibranchiale. The short bones (hy-

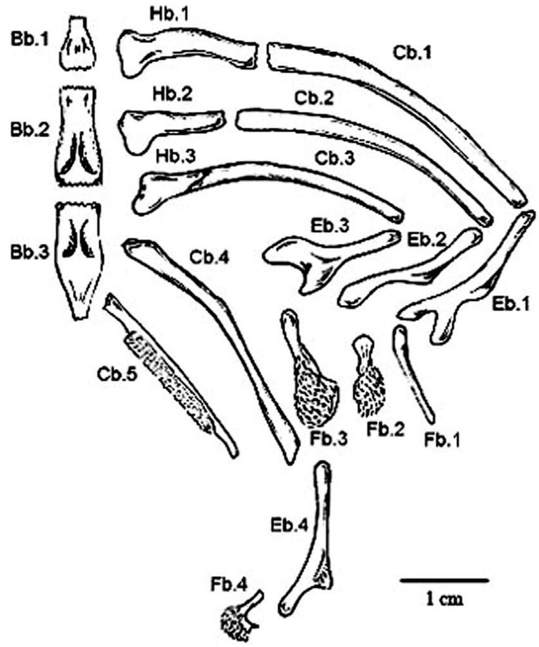

Fig. 4. Gill arch structure of the Black sea turbot (dorsal view, left side). Bb.1—Bb.3 — basibranchiale; Cb.1—Cb.5 — ceratobranchiale; Eb.1—Eb.4 — epibranchiale; Fb.1—Fb.4 — pharyngobranchiale; Hb.1—Hb.3 — hypobranchiale. Original drawing of D. V. Yelnikov edited by A. V. Drapun.

Рис. 4. Строение жаберной дуги черноморского калкана (вид сверху, левая сторона тела). Bb.1—Bb.3 — basibranchiale; Cb.1—Cb.5 — ceratobranchiale; Eb.1—Eb.4 — epibranchiale; Fb.1—Fb.4 — pharyngobranchiale; Hb.1—Hb.3 — hypobranchiale. Оригинальный рисунок Д. В. Ельникова. Художник-оформитель — А. В. Драпун.

pobranchiale, fig. 4: Hb.1—Hb.3), are adjustably fastened to the first three branchial arches. The fourth and fifth gill arches are attached through cartilage to the ventral inferior end of the last basibranchiale.

Each branchial arch includes ceratobranchiale (fig. 4: Cb.1—Cb.5) — light elongated bones with the grooves on their distal part which contain blood vessels coming from the branchiostegal rays. The fifth ceratobranchiale bears the small cloves. Paired upper gill bones (epibranchiale, fig. 4: Eb.1—Eb.4), each pair having its proper distinctive form, are located on the first four branchial arches posteriorly ceratobranchiale. Pharyngobranchials (pharyngobranchiale fig. 4: Fb.1—Fb.4) are located in the distal part of the first four branchial arches. Fused together, they form the pharyngeal apparatus. All pharyngobranchials, except for the first pair, are smooth and elongated, and have the bony shields bearing the teeth.

Gill arches are covered by the gill cover, thin solid plate consisted of four dermal paired bones of operculum series (fig. 2: 29—32). The surface of the paired sickle-shaped preopercular bone (praeoperculum, fig. 2: 29) is tightly attached to posterior external part of the hyomandibular bone. The upper edge of the gill cover is formed by the upper side of the anterior edge of opercular bone (operculum, fig. 2: 30) movably attached in the joint of hyomandibular bone. From below operculum adjusts to a small flat bone suboperculum (fig. 2: 31). Interoperculum, (fig. 2: 32) joins along its perimeter with the other three gill cover bones and is connected with angulare of the lower jaw by means of the tendons. Praeoperculum is partly overlying interoperculum (by its horizontal part) and (by its vertical part). Left-right asymmetry of the gill apparatus is weakly expressed — mainly in insignificant difference in sizes and shapes of paired bones.

Conclusions

The most typical morphological features of the cranial skeleton of the Black Sea kalkan, as in all species of Pleuronectiformes is the asymmetrical structure of the left and right sides of neurocranium forming during metamorphosis. Under normal conditions, during the metamorphosis, the right eye totally migrates to the left side, and synchronously with the right eye migration, the bones restructure, and asymmetry in practically all the paired bones of neurocranium develops. Among all the bones of the BST Neurocranium, the bones of periorbital region acquired most significant asymmetry as a result of early eye migration and cranial skeleton torsion towards the ocular left side of the body and main deformations took place in anterior part. The most considerable differences are observed for the paired bones frontale and ectoethmoideum. Several bones of cephalic skeleton — group of orbital bones infraorbitalia (except lacrimale), as well as bones common to most of bony fishes, such as orbitosphenoideum, and basisphenoideum, were not found in BST, probably being reduced, or completely fused with the other bones, or lost as in Gadidae. Left-right asymmetry in the Splanchnocranium in BST is less expressed than asymmetry of the Neurocranium. The asymmetry of the right and left bones of the mandibular apparatus appears in minor dimensional and density characteristics. Bones of hyoid arch are practically symmetrical.

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References

Chanet B. Interrelationships of scophthalmid fishes (Pleuronectiformes: Scophthalmidae). Cybium. — 2003. — **27**, N 4. — P. 275–286.

Coad B. W., McAllister D. E. Dictionary of Ichthyology. — 2007. — http://www.briancoad.com/Dictionary/Complete%20Dictionary.htm.

Diaz de Astarloa J. M. Osteologia craneal comparada de tres especies de lenguado del genero Paralichthys (Pleuronectiformes, Paralichthyidae) del Atlantico suroccidental // Rev. chil. hist. nat. — 2005. — **78**, N 3. — P. 343–391.

Gourtovoy N. N., Matvejev B. S., Dzerzhinsky F. Y. Practical zootomy of the vertebrates (lower vertebrates, agnathous, pisces). Uchebnoye posobiye dlya biologicheskikh spetsial'nostey universtitetov. — Moskva : Vysshaya shkola, 1976. — P. 302–324. — Russian : *Гуртовой Н. Н., Матвеев Б. С., Дзержинский Ф. Я.* Практическая зоотомия позвоночных (низшие хордовые, бесчелюстные, рыбы).

Kalinina E. M. On anatomy of the Black Sea flatfish (Pleuronectiformes) // Trudy Sevastopolskoy biologicheskoy stantsii. — 1959. — **12**. — P. 319–327. — Russian : *Калинина Э. М.* К анатомии черноморских камбалообразных (Pleuronectiformes).

Khanaychenko A. N., Giragosov V. E., Yelnikov D. V., Danilyuk O. N. Pigmentation anomalies in the Black Sea turbot Psetta (= Scophthalmus) maxima maeotica (Pleuronectiformes: Scophthalmidae) // Morskiy Ekologichny Zhurnal. — 2008. — **7**, N 2. — P. 87–95 — Russian : *Ханайченко А. Н., Гирагосов В. Е., Ельников Д. В., Данилюк О. Н.* Аномалии пигментации черноморской камбалы калкана Psetta (= Scophthalmus) maxima maeotica (Pleuronectiformes: Scophthalmidae).

Whetzel P. L., Noy N. F., Shah N. H. et al. BioPortal: enhanced functionality via new Web services from the National Center for Biomedical Ontology to access and use ontologies in software applications // Nucleic Acids Res. — 2011. — doi: 10.1093/nar/gkr469.

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