# Descriptive osteology of *Gymnocorymbus ternetzi* (Teleostei: Characiformes: Characidae)

## N.G. Bogutskaya, A.M. Naseka & I.V. Golovanova

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The purpose of this paper is giving an extensive overview of the cranial skeleton of *Gymnocorymbus ternetzi* (Boulenger, 1895) in a form of a formalized scheme that reflect its *Bauplan* (German for building plan, blueprint; plural: bauplane or bauplaene), a term in biology referring to the common new and original [homologous] properties of the members of a systematic group [taxon]). Each element of the *Bauplan* can be described by a set of parameters, *i.e.*, size, shape, structure, material composition and position. Though *Bauplan* is undoubtedly an abstraction, it is a necessary abstraction to be used in phylogenetic analysis with preference to "ingroup" and "outgroup" comparisons. The cranial osteology of black tetra *Gymnocorymbus ternetzi* (Boulenger, 1895) is described based on the study of larvae, juvenile and adult specimens. Provided are Latin terms and some English equivalents as well *remarks on origin, homology and terminology* for each cranial bone discussed.

N.G. Bogutskaya, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg 199034, Russia. E-mail: nbogutskaya@rambler.ru

A.M. Naseka, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg 199034, Russia. E-mail: dr\_naseka@rambler.ru

I.V. Golovanova, St. Petersburg State University, Universitetskaya nab. 7/9, St. Petersburg 199034, Russia.

# Introduction

Fishes are known to have a morphologically complex and highly kinetic skull (Ferry-Graham & Lauder, 2001). The cranial musculo-skeletal system of adult teleost fishes consists of about 60 interconnected skeletal parts that are moved by an approximately equal number of muscles (Aerts, 1991). Morphological studies on the skeletal morphology of Ostariophysi have already been done by many authors, although the nomenclature of the skeletal, especially cranial, structures in these papers demonstrated a high degree of inconsistencies, which required an initial priority of this study: to provide a conclusive nomenclature, which allowed comparison with other taxa. Besides, the ontogeny of the skull could provide substantial information concerning the origin of bones, whereas the study of the cranial lateral-line system could give data on the true nature of canal bones.

Regan (1911a, 1911b) considered the Ostariophysi to be a group of species which share the common feature of the Weberian apparatus. The Ostariophysi, according to Regan (1911a, 1911b) comprised the suborders Cyprinoidea and the Siluroidea. The Characiformes, belonging to the Cyprinoidea, were regarded as the least specialised group. A close relationship between the group, until then referred to as the Ostariophysi, and the Gonorhynchiformes, was demonstrated by Rosen & Greenwood (1970), based on evidence of the caudal skeleton, the presence of a fright reaction mechanism, swimbladder morphology, presence of nuptial tubercles and a striking similarity in the mouth opening mechanism in Phractolaemus ansorgii (Gonorhynchiformes, Phractolaemidae) and Bivibranchia (Characiformes, Hemiodontidae). The fact, however, that in Gonorhynchiformes no "real sign of vertebral differentiation that would suggest a condition paralleling the development of Weberian ossicles", could be observed that convinced them of similar functionality, in a broad sense, as the Weberian apparatus, resulted in the subdivision of the Ostariophysi in the Anotophysi (Gonorhynchiformes) and the Otophysi (Ostariophysi s.s.) (Rosen & Greenwood, 1970). A first detailed survey of the ostariophysan interrelationships was given by Roberts (1973). He stated that "evidence from caudal skeleton morphology supports relationships between Clupeomorpha and Ostariophysi, and between Clupeomorpha and Gonorhynchiformes, as well as between Gonorhynchiformes and Ostariophysi." He opposed against the notion that characins and cyprinids would be more closely related to each

other than to the catfishes, consequently raising the latter to the same level as the former two. His order of Cypriniformes than corresponds with the Otophysi of Rosen & Greenwood (1970), containing the three suborders: (1) Characoidei, (2) Cyprinoidei and (3) Siluroidei. A more extensive comparison of ostariophysan groups by Fink & Fink (1991, 1996) lead to a new classification of ostariophysans. Fink & Fink (1996) gave strong morphological evidence for the phylogenetic relationships of the Otophysi (comprising herein four orders, the Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes). Their results show, of the major clades, the fossil Chanoides to be sister to all remaining members of otophysans (placed in the Cypriniphysi), with the Cypriniformes being the primitive sister taxa to the remaining three groups (the Characiphysi), and Characiformes being sister to the clade (the Siluriphysi) of Siluriformes and its sister group the Gymnotiformes.

Several hypotheses have been proposed concerning the evolutionary distribution pattern of ostariophysan fishes. As for today, not all groups of ostariophysans show an identical distribution. The Siluriformesshow a cosmopolitan distribution, whereas the Gymnotiformes are confined to South America. The majority of the ostariophysans can be categorised as primary freshwater fishes. Secondary fresh water fishescan be found in Cypriniformes (Cyprinidae), Characiformes and Siluriformes (e.g., Clariidae, Siluridae, Claroteidae, Pangasiidae, Loricariidae), whereas peripheral species have been observed Gonorhynchiformes(Chanidae, in Gonorhynchidae) and Siluriformes (Aspredinidae, Ariidae and Plotosidae) only (Roberts, 1975; Teugels, 1996; Nelson, 2006).

The Otophysi included (as calculated in 2005, Nelson, 2006) 64 families, 1,068 genera, and 7,894 species. It is now included four orders, Cypriniformes (eight families: Cyprinidae, Psilorhynchidae, Gyrinocheilidae, Catostomidae, Balitoridae, Cobitidae, Nemacheilidae and Botiidae; two latter families had earlier been treated as subfamilies of Cobitidae, later of Balitoridae, and now as distinct family, e.g. Nalbant & Bianco, 1998; Tang et al., 2006; Slechtová et al., 2008), Characiformes (18 families), Siluriformes (about 15 families). About 64% of all freshwater fishes can be grouped within the Ostariophysi, where they can be found world wide, with exception of Antarctica, Greenland and New Zealand.

There are many publications, including classical ones, on descriptive and comparative osteology of fishes of the group Otophysi (e.g. Nawar, 1954; Harrington, 1955; Weitzman, 1962; Vandewalle, 1977; Cabuy et al., 1999; Huysentruyt & Adriaens, 2005; Serra & Langeani, 2006). Ontogenetic development of the skeleton has been described in a number of papers on cyprinids (e.g. Vandewalle et al., 1992; Cubbage & Mabee, 1996; Bird & Mabee, 2003), characids (e.g. Bertmar, 1959; Vandewalle et al., 2005; Miquelarena et al., 2005) and catfish (e.g. Bamford, 1948; Geerinckx et al., 2005, 2008) (see also references cited in these publications).

The purpose of this paper is giving an extensive overview of the skeleton of *Gymnocorymbus ternetzi* (Boulenger, 1895) in a form of a formalized scheme that reflect its *Bauplan* (German for building plan, blueprint; plural: bauplane or bauplaene), a term in biology referring to the common new and original [homologous] properties of the members of a systematic group [taxon]). Each element of the *Bauplan* can be described by a set of parameters, *i.e.*, size, shape, structure, material composition and position (Verraes, 1981; Adriaens, 1998). Though *Bauplan* is undoubtedly an abstraction, it is a necessary abstraction to be used in phylogenetic analysis with preference to "ingroup" and "outgroup" comparisons.

The nomenclature used for the developing skeletal structures is based principally on the works of de Beer (1937), Harrington (1955), Daget (1964), Patterson (1977) and Geerinckx et al. (2005). A discussion on homologies and terminology of the bones is given below in respective places.

#### **Material and Methods**

The ontogeny of the bones was observed in the developmental stages of *Gymnocorymbus ternetzi*. Specimens, obtained from an aquarium shop, were fixed in a 4% buffered formaldehyde solution, and used for in toto clearing and staining at different time intervals according to Hanken & Wassersug (1981), with trypsine replaced by a 3% KOH solution. The examined material ranges from 4.0 mm norochord length (NL) larvae (9 days after hatching) to 65.0 mm standard length (SL) adults (three months after hatching).

## Categories of skeletal structures in terms of bone histology and embryonic development

Several different types of **cartilage** could be distinguished in Teleostei: (1) cell rich hyaline cartilage, (2) matrix rich hyaline cartilage, (3) fibro/cellrich cartilage, (4) elastic/cell rich cartilage, (5) 'Zellknorpel' (could be observed in the oral barbells and the gill filaments), (6) scleral cartilage (supporting the eye ball) (Benjamin, 1989, 1990). The larval skeleton of fishes is constituted of cartilaginous structures. In the whole skeleton, there are about 60 cartilage precursors that further develop into ossified structures. The cranial cartilage may be divided into the chondrocranium cartilage and the pharyngeal arch cartilage which respectively develop into chondral bone elements of the neurocranium and the splanchnocranium. The pharyngeal arch cartilage includes cartilages of seven pharyngeal (or visceral) arches which are also called the mandubular arch, the hyoid arch, and five branchial (or gill) arches. Each arch possesses its own cartilage components. The chondrocranium cartilage consists of neurocranial trabecula, parachordal cartilage, ethmoid cartilage, otic capsule and other components. Most cartilage precursors of the bones described in the paper are mentioned in respective places below.

Distinguished are three main categories of **bones**: (1) cartilage bone, (2) dermal bone, and (3) membrane bone (e.g. Patterson, 1977) though the two latter types are often considered as one type called intermembranous bone, or dermal bone, with twothree subtypes. A fourth type, which could not be grouped in one of them, involves the so called chondroid bone (Huysseune, 1986; Huysseune & Verraes, 1990). Of all four types of bone, separate representatives have been observed in G. ternetzi. Additionally, fusions occurred between the different types of bone: 1 - perichondral bone and membranous bone, 2 - perichondral bone and dermal bone, 3 - perichondral bone and chondroid bone, 4 - dermal bone and dermal bone. These categories of bones are reviewed by Adriaens (1998).

CARTILAGE BONE (or cartilage replacement bone). Bones developed from a cartilage precursor. During ontogeny perichondral osteoprogenitor cells differentiate into osteoblasts (Meunier & Huysseune, 1992). As they surround the cartilaginous structure, they initiate *perichondral ossification*, which is the primal phase of ossification. By producing a thin layer of osteoid, the osteoblast may or may not become enclosed in this matrix, which may subsequently become mineralised by hydroxy-apatite crystals. Whether osteoblasts become enclosed, consequently differentiating into osteocytes, or remain at the surface of the continuously added bone matrix, results in the presence of cellular or acellular bone. Lower teleost fishes, including ostariophysans (zebrafish), are reported to lack acellular bone (Parenti, 1986), whereas acellular bone is most frequently observed in higher taxa (again with some exceptions) (Meunier & Huysseune, 1992). At a later stage, cartilage has been observed to become mineralised as well, at the close connection with the perichondral bone. Resorption of this cartilage is generally preceded by perichondral ossification. Such chondroclastic resorptions may be accompanied by the invasion of a blood vessel into the cartilage, consequently supplying new osteoblasts. The thus formed intracartilaginous canal may become lined with bone. Even more, the cavity formed within the perichondral bone, as a result of extensive cartilage resorption, may be filled with bony trabeculae. Such an intracranial ossification is then referred to as endochondral ossification. The latter category of ossifications is quite rare; in Clarias gariepinus, for example, it was found only in the hyoid bar (Adriaens, 1998). Apart from perichondral bones (and endochondral bones), the socalled **parachondral bones** can be observed in some skeletal regions. Parachondral ossification, although lying closely against cartilage or perichondral bone, is still separated from it by at least a layer of perichondrium and periosteum, or two layers of periosteum, respectively.

*INTRAMEMBRANOUS BONE* develops directly from a mesenchymal condensation and lacks any cartilaginous precursors, neither ontogenetically nor phylogenetically (Patterson, 1977). Intramembranous bones that are formed superficially (in connection with the ectoderm) are commonly referred to as *dermal bones* and those lying deep in the mesoderm as *membrane bones*.

Dermal bones may enclose a canal of the cranial lateral-line system or may not. A canal bearing bone consists of the membranodermal component and the neurodermal component that fuse together in ontogeny. Early dermal bones all are simple and platelike. Growth and bone deposition appears to occur especially at the margins of these plates, reflected by the concentration of osteoblasts. Later on, dermal bones start to form apolamellae as well, perpendicular to its surface.

Membrane bones are those bones that ossify "in membrane deep in the mesoderm, with no ontogenetic or phylogenetic connection with the ectoderm" (Patterson, 1977). These bones involve those that are homologous with cartilage bones in more primitive vertebrates, as well as sesamoid bones and outgrowths of cartilage bones. Only three bones are referred to as membrane bones in *Danio (Brachydanio) rerio,* intercalary (in the oric region), and claustrum and tripus (in the Weberian apparatus) (http://zfin.org/action/anatomy).

*CHONDROID BONE.* At many articulations, an unusual kind of tissue, closely resembling cartilage invaded by bone, can be observed. These articulations involve those between (1) the maxillary bone and the autopalatine bone, (2) the autopalatine bone and the lateral ethmoid bone, (3) the autopalatine bone and the antorbital bone, (4) the lower jaw and the suspensorium, (5) two dental bones (Adriaens, 1998; Gill et al., 2006).

# **Description and discussion**

As Romer (1947) has pointed out, the determination of precise homologies between the skull bones of different groups of fishes presents great difficulties. The homology of many teleost skull bones is in question. The latest trend in Anglicising of scientific language is a major contributor to term proliferations (*e.g.*, dental, dentary or lacrymal, lachrymal, lacrimal). In an ontogenetic context, this gives even more problems, *e.g.*, dentary is sometimes used when referring to both the (1) os dentale, (2) the fused complex between the os mentomeckelian and the os dentale, or (3) the fused complex between the latter two and the os spleniale (Adriaens, 1998). We provide Latin terms and some English equivalents as well *remarks on origin, homology and terminology* for each cranial bone discussed below.

In general, the skeleton can be defined and subdivided as all the cartilaginous and bony elements comprising the exoskeleton (or dermoskeleton) which includes the dermocranium, secondary pectoral girdle and scales, and the endoskeleton. The latter has a somatic axial component comprising the neurocranium, vertebral column and paraxial elements, a somatic appendicular component comprising the median fins, paired fins, radials, pterygiophores and fin rays, and a visceral component, the splanchnocranium (or viscerocranium), comprising the mandibular arch, the hyoid arch and the branchial arches (Coad, 2008).

#### Cranium: neurocranium

#### Ethmoid region [=olfactory region] (Figs 1, 2).

*Os ethmoideum* [os mesethmoideum]. The ethmoid [mesethmoid or median ethmoid] is a median unpaired bone of the mixed origin being composed of both supraethmoidal (dermethmoidal) component and a contribution from the ethmoid cartilage that ossifies as a perichondral lamellae ensheathing the nasal septum anterodorsally and laterally. In cyprinids, the dermal and chondral ossification are commonly treated as separate elements, os supraethmoideum (supraethmoid) and os mesethmoideum (mesethmoid).

The ethmoid projects forward from under the anterior edge of the frontals, meets the lateral ethmoids posterolaterally, and the vomer and parasphenoid ventrally in synostoses. Anteriorly the ethmoid bone ends in a pointed process which forms the anteriormost portion of the neurocranium (Fig. 1, eth). This part of the anterodorsal region of the ethmoid is called the "ethmoidal spine" by Weitzman (1962); laterally from the ethmoidal spine the flattened plates serve as joint surfaces for the reception of the ascending processeses of the premaxillaries. In the dorsal aspect, the ethmoid is narrow, about two times longer than wide. Its posterior part is about as wide as the anterior part, and the posteriormost extremety is markedly concave forming two horns (latero-dermethmoids of some authors) extending posteriorly to contact the frontals. Thus, the posterior ethmoid margin forms a part of the anterior margin of the anterior (prepineal) fontanel (the anterior part of the large dorsomedial cranial fontanel) (Fig. 1, ppf). No or few foramina pierce the surface of the ethmoid.

*Os ethmoideum laterale* [os ethmoidale laterale; lateroethmoideum]. The lateral ethmoid is a large, paired bone of the mixed origin. The lateral ethmoid wing, or lateral process, is composed largely of intramembranous prefrontal derivation (Weitzman, 1962) while the medial portion is apparently of endochondral origin from the cartilages separating the olfactory region from the orbit (the laminae orbitonasales). It was shown for cyprinids that it arises from both perichondral and endochondral ossifications (Harrington, 1955). Compaing the developmental stages of *G. ternetzi* we found two origins of ossifications which spacially correspond to the chondral and dermal prefrontal ossifications.

Bordered by the ethmoid anteriorly and overlain by the frontal dorsolaterally, the lateral ethmoid forms the upper anterior wall of the orbit. Each lateral ethmoid projects downward from under the anterior region of each frontal, and lies lateral to the anterior part of the rhinosphenoid. Although the lateral ethmoids approach each other medially, they do not reach the midline and do not contact each other but do contact the anterior edge of the rhinosphenoid and the ethmoid. On its anterior surface and between its median and lateral regions, the lateral ethmoid bears a very narrow spur that extends anteriorly and medially to contact the dorsoposterior surface of the rectangular portion of the vomer. The lateral portions of the lateral ethmoids extend downward as a wide triangular process (Figs 1, 2, *leth*) to the upper lateral edge of the ectopterygoids. The posterior surface of the ethmoid above the rhinosphenoid has a median fossa, the anterior myodome, for the origin of the superior oblique eve muscles. The lateral ethmoid forms one half (the lower one) of the outer margin of the olfactory foramen which is rather large. The posterior section of the lateral ethmoid contribution to the olfactory foramen is formed by the bone itself while the anterior section by the spur contacting the lateral margin of the vomer. Ligamentous tissue suspends the upper anterior tip of the maxillary bone to the lateral ethmoid wing.

*Os vomer* [os vomerale]. The vomer is a frequently median unpaired or paired dermal bone in the middle of the roof of the mouth covering the ethmoid ventrally and in front of the parasphenoid. There is still a big debate about the using of the name *vomer* for it was shown long ago that the vomer in mammals is homologous with with the parassphenoid rather than with this bone in fishes. Many authors use the name *os praevomer* [os praevomerale] (prevomer). Compaing the developmental stages we found no paired precursors of the vomer.

The vomer is toothless; it is somewhat convex dorsally and concave ventrally. The upper anterior portion of the vomer is in contact with the parts of the lateral ethmoid wings by a synchondral joint surface. The vomer is located almost vertically because of the big difference between the depths of the ethmoid and sphenotic regions of the neurocranium. The dorsal surface of the anterior region of the prevomer contacts the ventral surface of the ethmoid. The posterior, triangular portion is thin. This portion, the shaft of the vomer, inserts in a well defined concavity on the anteroventral surface of the parasphenoid. The anterior, widened, portion of the prevomer is thickened, has a slightly concave anterior margin, and dorsally forms a synchondral joint surface for the ethmoid. Two anterolateral projections of the vomer extend toward the upper tips of the maxillaries and lie below lateral wings of the ethmoid bone. Centrally and in the sagittal plane the vomer bears a dorsal lamella that contacts a similar lamella of the ethmoid. The vomerine lamella is rather deep and of almost the same size as the ethmoidal lamella. These lamellae together form the deep internasal septum.

*Os nasale*. The nasal is a paired dermal bone, positioned lateral to the dorsal surface of the ethmoid.

The nasal bone is transversed by the anteriormost part of the supraorbital sensory canal; in *G. ternetzi* it is tubular being presented by only the neurodermal component while any membranodermal component is lacking. The nasal is long, its anterior end lies laterally to the upper end of the premaxillary ascending process, and the posterior end abuts the frontal (Fig. 1, n). It encloses two canal segments, and the single pore is located in the middle of the bone.

A part of the ethmoid region is also the paraspenoid which is discussed below in the *sphenoid region*. The parasphenoid and the vomer may be also classified as bones of the *basicranium*, the base of the braincase.

#### Orbital region (Fig. 2).

*Os frontale*. The frontal bone is a large paired dermal bone that constitutes a great part of the cranial roof. Though as noted in Janvier (1996), what are commonly termed the frontals and parietals in actinopterygians, originally taken from human anatomy, are homologous with the parietals and postparietals, respectively, of early tetrapods, most authors keep using the term *frontal* in the traditional meaning (Nelson, 2006).

Extending from the ethmoid caudad to the parietal, posterolaterally each frontal overlaps its respective pterotic, and just anterior to the pterotic each covers its respective sphenotic. The paired frontal bones in all specimens examined and at all growth stages are largely separated by a well-developed dorsomedian cranial fontanel that is divided by the epiphyseal bar [infrafrontal bar] that is completely ossified only in the adults (Fig. 1, eb). In the smaller specimens the frontal bones are relatively farther apart than in the older specimens. Ventrally the frontal bears the orbital lamella, which lies external to and is applied to the dorsolateral surface of the pterosphenoid, the orbitosphenoid, and the anterior region of the sphenotic. The supraorbital sensory canal after leaving the nasal enters the frontal at its anterior edge. The canal then passes backward having two main branches, the mesial, or epiphyseal branch, and the posterior one. The epiphyseal branch (Fig. 1, ebc) extends medially over the epiphyseal bar and opens by a terminal pore with no communication to its counterpart. The posterior branch continues backward in the frontal to enter the parietal bone at the middle of its anterior edge.

The frontal bone(s) is a part of the cranial roof composed of the dermal bones covering the neurocranium, the nasal, the frontal, the supraorbital, the parietal and the supraoccipital bones.

*Gymnocorymbus ternetzi* has an orbital ring of seven bones (Fig. 3); the anteriormost one does not bear a sensory canal while six others are associated with the infraorbital canal. The supraorbital bone (*os supraorbitale*) commonly present in most Otophysi is a paired dermal bone that commonly forms the anterodorsal margin of the orbit is absent in *G. ternetzi*.

Os antorbitale. The antorbital is a paired dermal bone lying lateral to the nasal bone in front of the eye. This bone lies in the posterior wall of the nasal sac and is closely associated posteriorly with the supraorbital if the latter is present. The antorbital in characids is not associated with the infraorbital sensory canal except presumably secondarily in some highly modified forms and perhaps cannot be compared directly to the antorbital of Amia. However, its topographic position is the same and Gosline (1961) apparently concluded that the best name for the bone in characids and many other fishes is antorbital. Homologization of the bone and its terminology in characids and cyprinids in comparison with other lower fishes reviewed by Harrington (1955), Gosline (1961) and Weitzman (1962). Gosline (1961) supposed that the lachrymal of cyprinids is a compound bone made up of the fused lachrymal and antorbital. It is because of the difficulty of homologization of elements of the infraorbital series that Weitzman (1962) designated the infraorbital elements posterior to the antorbital in characids simply by number, starting with the first bone bearing the canal (apparently an equivalent to the lachrymal).

The antorbital bone in *G. ternezi* is a small triangular bone considerably narrow and pointed in its dorsal part and widened in the ventral part. It does not have any contact with the first infraorbital bone (Fig. 3, *anto*).

*Ossa infraorbitalia* [ossa suborbitalia] (Fig. 3). The infraorbital bones [suborbitals bones] are dermal bones that are situated under and posterior to the eye and associated with the infraorbital sensory canal. Name applied to six or more of the circumorbital bones; in caracids, the following bones are commonly distinguished: infraorbital 1 (lachrymal or preorbital by some), infraorbital 2 (jugal by earlier authors), infraorbital 3 (great suborbital by some), infraorbital 4 and 5, and infraorbital 6 (dermosphenotic).

*Os infraorbitale 1* [os lacrymale] (Fig. 3, *io1*). The infraorbital 1 in *G. ternetzi* is a very shallow bone with a poorly ossified both membranodermal and neurodermal components. The canal has two segments on the bone. The very posterodorsal end of the bone overlaps only the very anterior extremety of the infraorbital 2.

*Os infraorbitale 2.* The infraorbital 2 is considerably longer than the infraorbital 1 and deep in its posterior part. A very limited posteriordorsal portion of the bone overlaps the infraorbital 3.

*Os infraorbitale 3* (Fig. 3, *io3*). The infraorbital 3 is the largest element of the infraorbital series. Its ventral and posterior margins are separated from the horizontal and vertical limbs of the preoprcle by a clear distance. The canal has 3 to 5, commonly 4, segments on the bone.

*Os infraorbitale 4* and *os infraorbitale 5*. The both infraorbitals 4 and 5 are relatively narrow, with poorly ossified neurodermal component. They do not over lap either each other or the neighbouring bones.

Os infraorbitale 6 (Fig. 3, io6). The infraorbital 6 is a short bone, its width being about the width of the infraorbital 5 or slightly larger. The bone bears one canal segment which is a terminal segment of the infraorbital canal. The canal ends by a pore at the upper margin of the infraorbital 6 and does not communicate with the supraorbital canal. Thus, the infraorbital canal in *G. ternetzi* lacks the most characteristic feature of the dermosphenoticum – an anastomose of the infraorbital canal posterior to the parietal branch of the latter (for discussion on os dermosphenoticum see, e.g. Harrington, 1955 and Bogutskaya, 1989).

*Sclerotic bones*, a pair of small dish-shaped bones that cap the anterior and posterior margin of the eyeball. They are weakly calcified in *G. ternetzi*.

**Sphenoid region** (Figs 1, 2), cranium bones which together form the floor and sidewalls of the middle part of the neurocranium.

*Os orbitosphenoideum.* The orbitosphenoid is a large median unpaired cartilage bone consisting of two diverging plates. The orbitosphenoid develops from the taenia marginalis anterior and forms the

anterior and anterolateral boundary of the orbital foramen and constitutes a part of the sidewalls and floor of the cranial cavity. It is bordered by the frontals dorsally, the pterosphenoid posteriorly, and the rhinosphenoid anteriorventrally (Fig. 2, *orbsph*); it is positioned medial to the upper part of the eye.

*Os rhinosphenoideum.* The rhinosphenoid is a median cartilage bone which ossified separately from both the ethmoid and the orbitosphenoid. According to Weitzman (1962), an a specimen of *Brycon meeki* of 32 mm in standard length, the rhinosphenoid consisted of two thin discs set side by side, sandwiching a disc of cartilage; in larger specimens the two lamellar halves of this bone were fused along their dorsal edges.

The rhinosphenoid projects forward to between the median edges of the lateral ethmoids and forms a septum between the olfactory nerves as they issue from the orbitosphenoid. All joints of this bone are synchondral (Fig. 2, *rsph*).

Below both the rhinosphenoid and orbitosphenoid and just above the parasphenoid in the interorbital septum is a small round unpaired ossification (Fig. 2), which appears in specimens of about 35 mm SL.

*Os parasphenoideum.* The parasphenoid is a long unpaired median dermal bone that runs almost the entire length of the neurocranium.

The parasphenoid contacts the vomer anteriorly, and the prootic and basioccipital posteriorly. It is markedly curved in about the middle of its length where it bears a pair of ascending flanges, or ascending wings, which suture with the pterosphenoids and prootics of each respective side. The posterior myodome lies above the posterior portion of the parasphenoid and between ventral extensions of the prootic. The carotid foramen which occurs between the anteroventral region of the prootic and the parasphenoid just posterior to the scending process is relatively large, two thirds of its margin is formed by the notch at the parasphenoid. The ventral keel, which is located along the midline just in front of the ascending wings, is deep and well developed (Fig. 2, *vkp*).

*Os pterosphenoideum* [os pleurosphenoideum; os alisphenoideum]. The pterosphenoid [also called pleurosphenoid or alisphenoid but these bones in mammals and reptiles respectively are not homologous] is a paired bone which develops from the taenia marginalis posterior; this cartilage bar (bilaterally paired) is first visible as an anterior extension of the auditory capsule. It grows anteriorly toward the middle of the orbit where it is connected to its counterpart on the other side by the epiphyseal bar.

The pterosphenoid forms the posterior upper region of the orbit. Internally the pterosphenoid constitutes a part of the base for the arch of the epiphyseal bar. Laterally the pterosphenoid is bordered by the frontal, posteriorly by the sphenotic, ventrally by the prootic, and anteriorly by the orbitosphenoid. The foramen for the trochlear nerve is relatively large and located between the frontal and dorsal parts of the margins of the pterosphenoid and the orbitosphenoid.

**Otic region** [cranial vault] (Figs 1, 2). It is mostly formed from *capsula auditiva* (auditory, or otic, capsule) that is a cartilaginous skeleton about the inner ear in Elasmobranchii or a chondral skeleton in bony fishes comprised of the prootic, opisthotic (or its replacement), intercalar, epiotic, exoccipital, sphenotic, pterosphenoid and basisphenoid as walls and floor with the parietals as the roof.

*Os parietale.* The parietal bone is a paired dermal bone that covers the hind part of the cranium, overlapping the dorsal edge of the sphenotic, pterotic, epiotic and the anterior edge of the supraoccipital. The parietals are overlapped anteriormedially by the frontals.

The two rather narrow parietals in *G. ternetzi* are sheets of bone that do not meet along the midline, but are separated by the large posterior (postpineal) fontanel (the posterior part of the large dorsomedial cranial fontanel). A posterior branch of the supraorbital sensory canal system passes backward in the median part of the frontal continuing through the parietal as the parietal sensory canal and opens to the exterior over the supratemporal canal. Thus, the very end of the supraorbital canal tube almost or completely overlaps the supratemporal canal tube but does not communicate with the latter.

*Os extrascapulare* [extrascapula; os tabulare; os supratemporale] (Figs 2, 4, *esc*). The extrascapular [tabular, supratemporal, or scale bone] is a paired dermal bone that contacts the parietal at the lower posterior region where the supratemporal sensory canal leaves the parietal. At the same time, the extrascapula receives the sensory canal from the pterotic bone being a place of the interconnection of the two main canals of the posterior part of the head into a single canal that goes further caudad into the posttemporal bone.

*Os posttemporale* [suprascapula, suprascapular, supracleithrum I] (Fig. 1, *ptt*). The posttemporal is a paired superficial dermal bone that attaches the pectoral girdle to the skull. The posttemporal bone is treated by some (e.g. Weitzman, 1962) as a part of the pectoral girdle.

It is attched to the neurocranium via two projections, or processes, the upper pointed one extending upward and forward over the epiotic along the posteriorventral edge of the parietal, the lower, smaller process extending inward toward the opisthotic to which it is attached by a ligament. The posttemporal carries the main laterosensory canal also called the posttemporal canal.

*Os sphenoticum* [os autosphenoticum]. The sphenotic bone is a paired chondral ossification that develops from the taenia marginalis posterior and the tectum synoticum (an unpaired thin dorsal sheet of cartilage that partially covers the posterior chondrocranium).

The sphenotic lies below the frontals and the upper portions of the pterotics that contain the sensory canals. The frontal and pterotic overlaps the sphenotic to a certain extent forming the dilator fossa. The dilator fossa is formed mainly from the sphenotic and provides the surface of origin for the dilator operculi muscle. Laterally the sphenotic has a strong spinous process, directed almost ventrally rather than laterally (Fig. 2, *spho*). The levator arcus palatine muscle arises from the posterior surface of the sphenotic spine.

*Os pteroticum.* The pterotic consists of both cartilaginous (autopterotic) and intramembranous (supratemporal-intertemporal, or dermopterotic) components. The autopterotic is developed from the otic capsule and encloses the horizontal semicircular canal of the inner ear. The neurodermal component is represented by the canal that connects the frontal canal and the extrascapular canal and receives the mandibular-preopercular canal from the suprapreopercle (Fig. 4, *pto*).

Dorsally the pterotic is overlaid by the respective parietal and frontal. Anteriorly the pterotic contacts the sphenotic, ventromedially the prootic, posteroventrally the exoccipital and posteriorly the epiotic. The prootic, sphenotic, exoccipital and epiotic joints of the pterotic are synchondral, and the parietal and opisthotic are synchondral, and the parietal and opisthotic are synchondral surface is grooved by the rear portion of the hyomandibular fossa. There is no foramen between the sphenotic and pterotic.

*Os prooticum.* The prootic is a paired chodral bone developed from the otic capsule and the parachordal cartilage (a rod-shaped paired cartilage on either side of the notochord; paired cartilages unite, forming the base of the chondrocranium and are replaced by the prootic bones).

The prooticum is an extensive bone of the complicated structure that lies between the parasphenoid, prootic of the other side, the basioccipital, exoccipital, pterotic and sphenotic. The bone is pierced by foramina that accommodate branches of the trigeminal and facial nerves. The auditory foramen as seen from the lateral view is the largest one and extends along the most part of the lateral surface of the prootic. The subtemporal fossa is a very shallow depression in the posterior region of the suture between the prootic, pterotic, and basioccipital.

*Os epioticum* [os epioccipitale]. The epiotic [epioccipital] bone is a paired chondral bone developed from the otic capsule and situated on the posterior surface of the neurocranium. It encloses the posterior semicircular canal of the inner ear.

The epiotic contacts the supraoccipital and parietal dorsally, and the exoccipital ventrally. The lower anterior region of the epiotic contacts the pterotic, while a process of the epiotic extends to contact the parietal above and the pterotic below. This epiotic process that bridges the posttemporal fossa is very narrow in *G. ternetzi*. Ascin most characins, the posttemporal fossae are well developed, being actually fontanels, the deepest part covered by a strong membrane for the origin of epaxial muscles.

*Os intercalare* [os opistoticum]. The intercalar bone [intercalary; opistotic] is a small membrane bone that may be homologous with a cartilage bone in more basal fishes (Patterson, 1977).

The intercalary is very thin and poorly ossified in G. ternetzi; it is located on the surface in the region of the suture between the prootic, pterotic and the exoccipital and associated with the ventral process of the posttemporal.

#### Occipital region (Figs 1, 2).

*Os supraoccipitale.* The supraoccipital bone is of a mixed origin. The main body of the bone is a chondral ossification that develops from the tectum synoticum (an unpaired thin dorsal sheet of cartilage that partially covers the posterior chondrocranium). It is large constituting the postero-dorso-median surface of the cranial roof. It bears an enlarged, posteriorly pointed, triangular process commonly called the supraoccipital crest that extends posterodorsally; the crest is an ossification of the connective median septum separating the anterior trunk muscles.

The supraoccipital is considerable notched along the medial anterior margin forming the posterior edge of the postpineal foramen (posterior part of the dorsal cranial fontanel). Laterally and anteriorly it sends an arch under the posterior median portion of the parietal. The supraoccipital crest is well developed extending upward and caudad relative to the posterior cranial surface (Figs 1, 2, *so*).

*Os exoccipitale*. The exoccipital is a paired chondral bone that develops from the occipital arch

cartilage and parachordal cartilage. It bears a large foramen (lateral occipital foramen), contacts the supraoccipital dorsally, the epiotic laterally and the basioccipital ventrally, forms the posterior hind margin of the cranium and borders the lateral and posterior margins of the foramen magnum.

Internally and externally the exoccipital forms the dorsal portion of the bony lagenar capsule. Just above the lagenar capsule is a large foramen for the tenth cranial (vagus) nerve. Just anterior to this foramen are few small and minute foramina. Through the largest of these (though it is very small relative to the foramen for the tenth nerve) passes the ninth cranial (glossopharyngeal) nerve.

*Os basioccipitale*. The basioccipital is a median unpaired chondral bone that develops from the parachordal cartilages. It contacts the prootics anteriorly, the parasphenoid ventromedially, and the exoccipitals dorsally, and forms the posteroventral hind margin of the cranium, articulating with the centrum of the first vertebra.

The lower anterior portion of the basioccipital is divided into two bilateral lamellae of bone that contact the two posterior processes of the parasphenoid below. Between the bony lamellae formed by the prootics and basioccipital, above the parasphenoid, and between the bilateral posterior projections of the parasphenoid, lies the large posterior myodome. The myodome is open ("floorless" sensu Weitzman, 1962) posteriorly.

# *Cranium: splanchnocranium* (viscerocranium) (Figs 4, 5).

**Mandibular arch** (jaw, jaw cartilage, oral jaw skeleton, pharyngeal arch 1 skeleton, visceral arch 1): skeletal and cartilagenous elements of the first pharyngeal arch. The manibular arch is subdivided into the dorsal part (palatoquadrate arch, dorsal visceral arch 2, upper jaw or upper pharyngeal jaw) and the ventral part (ventral mandibular arch, or lower jaw). In a specimen of 4.2 mm NL the metapterygoid and symplectic are slightly ossified while the ectopterygoid, entopterygoid and qudrate start to progressively calcify since 5.5 mm NL. The only bone which appears much later is the palatine (in specimens since 7.2-8.6 mm SL). A very late ossification of the palatine was also found in *Brycon moorei* (Vandewalle et al., 2005).

*Os palatinum* [os palatine]. The palatine [palatal] bone is a paired chondral bone on the roof of the mouth lateral to the vomer that may properly be called *os autopalatinum* (the autopalatine) that derives from the pars autopalatine of the palatoquadrate cartilage but apparently in characiforms lacks the dermal component (*os dermopalatinum*), which is often dentigerous in higher teleosteans.

In *G. ternetzi* the autopalatine is a toothless dorsoventrally depressed sand-glass-like bone slightly elongated anteroposteriorly (Fig. 4, *pl*). Its anterior end bears a deep articulatory surface that is attached with the anterolateral margin of the vomer. In two cases, one of the two lamellae forming the articulatory facet is penetrated by a very small foramen though in most cases the autopalatine is not fenestrate. If present, the foramen is much smaller than that shown in *Bryconamericus* by Serra & Langeani (2006).

*Os ectopterygoideum.* The ectopterygoid is a paired dermal bone located at the anterior part of the palatoquadrate.

In adults *G. ternetzi* it is a long thin bone that is very narrow anteriorly where it meets the autopalatine and slightly wider at its posterior synostosis with the quadrate.

*Os entopterygoideum* [os endopterygoideum; os mesopterygoideum]. The entopterygoid is a paired dermal bone that forms the anteroventral and ventral surface of the orbit. It develops in the membrane dorsomedial to the palatoquadrate cartilage.

In *G. ternetzi* it is roughly triangular, with its posteroventral margin almost straight (Fig 4, *entpt*).

Os metapterygoideum. The metapterygoid is a chodral bone that develops from the palatoquadrate cartilage. The posterior edge of the metapterygoid meets by means of cartilage the dorsoposterior surface of the symplectic and the lower anterior portion of the hyomandibular. The anterior edge of the metapterygoid meets by means of cartilage the quadrate and overlaps the entopterygoid.

As is typical for characids, the metapterygoid and the quadrate, and, to a much lesser degree, the symplectic form the borders of a large, central circular foramen (Fig. 4.).

*Os quadratum.* The quadrate bone is a chondral bone that develops from the palatoquadrate cartilage. The body of the quadrate ossifies first at the ball-and-socket articulation with the anguloarticular (Fig. 5).

In adult *G. ternetzi* the quadrate has a markedly concave dorsal margin to form the border of the foramen and a very poorly pronounced posterior process that is represented by a deep rounded structure not elongated or pointed.

*Os maxillare*. The maxilla [maxillary bone] is a paired dermal bone that forms a distal part of the upper jaw.

In *G. ternetzi* the maxillar is toothless. Its upper arm moves at the lateral portion of the premaxilla. Just at the of the upper arm is a small facet for articulating with the lateral extremity of the premaxilla. The body of the maxillar blow the joint is elongated and oval-shaped. In general, the maxillar is not long. The posterior tip of the maxillary does not extend to the posterior border of the second infraorbital.

*Os praemaxillare.* The premaxilla [premaxillary bone] is a paired dermal bone that forms a proximal part of the upper jaw.

The premaxilla is a very thick L-like heavy bone. The premaxilla is immovably joined to its counterpart and to the ethmoid behind by very short ligaments. Its lateral limb is almost equal to the vertical limb [premaxilla ascending process]. The ascending process fits into a groove on the dorsolateral surface of the ethmoid. The premaxillar bears two rows of teeth along the anterior edge. The outer row has 4-6 tricuspid teeth which are slightly smalle than teeth of the inner row. The teeth in the inner row are commonly five, tricuspid, the second one (from the midline) is the largest and the most lateral teeth is the smallest.

**Ventral mandibular arch** (lower part of mandibular arch, lower jaw, mandible, mandibular series): the ventral portion of the first pharyngeal arch, comprising the lower jaw.

Since Haines (1937), Lekander (1949) and Harrington (1955) the terminology used for the bones of the lower jaw of the teleosts seems to be settled as given below.

Os dentale. Lekander (1949) found that the dentary bone (dental bone) in *Phoxinus phoxinus* (Cyprinidae) is formed from several primordia and is of both dermal and endochondral origin. However it is still not clear if a chondral element takes any part in the formation of the dentary. It forms the anterolateral part of the lower jaw and develops outside from the Meckel's cartilage appearing first at the anterior part of the latter; it is apparently formed by a membranodermal component and a neurodermal component that develops into a sensory mandibular canal. In the adult, the dentary meets its counterpart anteriorly at the mandibular symphysis. The dentary abuts the retroarticular posteriorly, and surrounds the anguloarticular.

In *G. ternetzi* the dentary completely lacks the coronoid process. The sensory canal goes along the whole lower margin of the bone, well ossified, and commonly consists of five segments (Fig. 5, *d*, *dc*). In adults the dentary bears four large teeth, the second one (from the midline) being the largest. The teeth have commonly five cusps, the lower ones being very small. Posterior to the last large tooth is a series (3-4) of small unicuspid teeth. In smaller specimens (as the specimen figured) the size difference between the large teeth and small teeth is not

so marked and the transition from large teeth to small teeth is more gradual than in large specimens. The symphysis of the lower jaw consists of three convoluted bony folds. The folds on one side fit into the spaces formed by the folds of the other side as described by Weitzman (1962).

Os angulo-articulare [os articular]. The anguloarticular, together with the dentary, coronomeckelian, retroarticular and Meckel's cartilage, constitute the mandible. It is a paired bone of a mixed (compound) origin that results of the fusion of the dermal angular and the cartilaginous articular. The angular part ossifies initially on the posterolateral surface of Meckel's cartilage near the articulation with the quadrate (Vandewalle et al., 2005; our data). Posteroventrally, the anguloarticular is ligamenttously connected to both the interopercular bone and the posterior ceratohyal. The posterior end of the articular bears a socket for the condylar surface of the quadrate. A segment of the canal on the anguloarticular is located just below the articular surface being a continuation of the canal on the dentary onto the preopercle (Fig. 5, aart, aartc).

*Cartilago Meckeli*. The Meckel's cartilage [ceratomandibular cartilage, also called mandibular cartilage or primary mandible], the embryonic lower jaw of bony fishes which ossifies in a number of bones different in different groups of fishes. In lower teleosts, it ossifies at least in part as the coronomeckelian, articular and retroarticular. It remains in some adult fishes, including characids, as a pointed rod embedded in the dentary and anguloarticular. The Meckel's cartilage extends along the floor of the median mandibular fossa. Part of the median face of the coronomeckelian bone is in contact with Meckel's cartilage.

Os coronomeckeli [sesamoid angular, supraangular, sesamoid articular, articular sesamoid, splenial, os meckeli or d bone]. The corono-meckelian bone is one of the derivates of the Meckel's cartilage.

It is a small round bone lodged in the medial inner surface of the anguloarticular just at the level of the dentary margin (Fig. 5, *cm*). Posterodorsally it bears a crest for attachment of a portion of the adductor mandibulae muscle.

*Os retroarticular* [angular, Bridge's ossicle *a*, lower articular or angulo-retroarticular]. The retroarticular is a paired cartilage bone that forms at the posteroventral tip of Meckel's cartilage where the interoperculomandibular ligament attaches.

It is small, roughly triangular in shape, and located at the very posteroventral end of the lower jaw (Fig. 5, *rart*). The retroarticular is ligamentously connected to the interopercle and preopercle posteriorly and abuts the ventral shelf of the dentary anteriorly.

**Pharyngeal arch 2 skeleton** (arcus hyoideus). The hyoid arch, or bar, is the arch lying between the jaws and gill arches, with which it is believed homologous and which helps support the floor of the mouth cavity. It is subdivided into the dorsal part (dorsal hyoid arch) and the ventral part (ventral hyoid arch) and composed of the paired exo- and endoskeleton elements.

The **dorsal hyoid arch** (dorsal visceral arch 2) is a part of pharyngeal arch 2 skeleton and suspensorium at the same time. It includes the opercular series, hyomandibular, and symplectic.

*Opercular series* (gill cover; opercular flap; opercular apparatus) (Fig. 4). All four bones of the opercular series are already partly ossified in the smallest specimens (4.0 mm of notochord length, 9 days after hatching).

*Os praeoperculum* [os praeoperculare]. The preopercle [preopercular bone] is a paired dermal bone which lies in front of the gill cover and which bears the upper part of the preoperculo-mandibular sensory canal.

It is clearly L-shaped with the preopercle horizontal limb (the lower, horizontal portion of the preopercle bone) and the preopercle vertical limb (the upper, vertical portion of the preopercle bone). The anterior end of the preopercle fits into a groove on the median lower region of the quadrate, while the dorsal end lies between the infraorbital bones and the opercle. The upper end of the preopercle does not fuse to the suprapreopercle.

*Os suprapraeoperculum* [os supraoperculum]. The suprapreopercle is a dermal bone located right above the upper end of the preopercle.

The suprapreopercle is a long tubular bone represented by a neurodermal component and completely lacking any membranodermal component (Fig. 4, *spop*). It is not fused to the preopercle even in the adult specimens examined.

*Os operculum* [os operculare]. The opercle [opercular bone] is a paired dermal bone that is the principle and largest component of the gill cover comprising its upper part.

The opercle is a fairly deep, smooth bone on the lateral part of the face and below the posterior region of the hyomandibular. It forms a ball-andsocket joint with the hyomandibular that is located at the anterior margin of the bone about one third of the bone depth below its upper margin. *Os suboperculum* [os suboperculare]. The subopercle [subopercular bone] is a paired dermal bone lying below the opercle in the gill cover.

It is relatively deep and moderately curved along the ventral margin of the opercle. The subopercle extends in front of the opercle and bears at the anterodorsal end a small rounded process.

*Os interoperculum* [os interoperculare]. The interopercle [interopercular bone] is a paired dermal bone of the lower gill cover below the horizontal arm of the preopercle and in front of the subopercle.

The anterior end of the interopercle is ligamentously connected to the posterior surface of the retroarticular of the lower jaw.

Hyomandibula [os hyomandibulare]. The hyomandibula [hyomandibular] is a paired chondral bone that develops from the hypotymplectic cartilage [hyomandibular cartilage]. This paired large cartilage articulates with the chondrocranium dorsally, the opercle posteriorly, and the palatoquadrate cartilage anteriorly. The hyomandibula is the large, dorsal-most member of the hyoid arch. It begins ossifying in the dorsal edge of the hyosymplectic cartilage near the hyomandibular foramen (5.0 mm NL). In the adult, the hyomandibula has cartilage-capped anterior and posterior articulating heads that meet the hyomandibular fossa of the cranium in synovial joints. The posterior knob of the bone capped in cartilage, forms a synovial joint with the opercle similar to the state describe for zebrafish (Cyprinidae) (http://zfin.org/action/anatomy/). Its lower arm is short, ending just in front of the corner formed by the sharp bend in the orbital edge of the preopercle. The lower arm attaches through cartilage to the elongate symplectic and the interhyal.

*Os symplecticum.* The symplectic is a paired chondral bone that develops from the hyosymplectic cartilage [hyomandibular cartilage]. As in most characiniforms and cyprinids the symplectic is a rod-shaped bone articulating with the hyomandibular and quadrate; the anterior part of the symplectic lies on a depression on the inner face of the quadrate.

#### Ventral hyoid arch.

*Os interhyale* [also called *os stylohyale* but not homologous with the stylohyal of Tetrapoda]. The interhyal bone is a paired chondral ossification that develops from the interhyal cartilage.

The interhyal is a small rod-like element that connects the ventral and dorsal parts of the hyoid arch. It articulates laterally with the posterior end of the epihyal and medially at the cartilaginous junction between the hyomandibula and the symplectic. A strong ligament conncts the interhyal with the median surface of the preopercle. It is well ossified in *G. ternetzi*.

*Os epihyale*. The epihyal (also called dorsal ceratohyal or posterior ceratohyal as it is considered to be the dorsal ossification of the ceratohyal; may or may not be homologous with the epal element of the branchial arches) is a paired chondral ossification on the anterior surface of the posterior end of the ceratohyal cartilage near the site of articulation with the interhyal.

The epihyal is a flat bone with a large foramen almost in the center. Anteriorly, the epihyal contacts the ceratohyal along a long suture, while the fourth branchiosteial ray is attached to the lower lateral surface of the epihyal. The epihyal starts to ossify in specimes of 5.0-5.5 mm NL.

*Os ceratohyale.* The ceratohyal (also called anterior ceratohyal, ceratohyal anterior, rostral ceratohyal) is a paired chondral bone that develops from the anterior portion of the ceratohyal cartilage.

The posterior end markedly broadens and meets the epihyal via a layer of cartilage. The anterior end broadens and bifurcates, the lateral arm abutting the ventral hypohyal and, dorsally, contacting a small portion of the dorsal hypohyal. The anterodorsal head forms a synchondrosis with the dorsal hypohyal and the anteroventral head forms a synchondrosis with the ventral hypohyal. Two anterior branchiostegal rays articulate with the ventral edge of the ceratohyal, and the third one with the lower lateral surface of the ceratohyal. The ceratohyal is the first chondral bone of the hyoid arch starting to ossify in specimes of 4.2-5.0 mm NL almost simultaneously with the branchiostegal rays.

*Ossa hypohyalia.* The hypohyals, two on each side, develop from the ceratohyal cartilage – the dorsal hypohyal at the anterodorsal tip and the ventral hypohyal at the anteroventral tip of the ceratohyal cartilage. The hypohyals are the most anterior of the bilaterally paired ventral hyoid arch elements.

A large foramen lies between the ventral hypohyal and the two anterior arms of the ceratohyal. Strong paired ligaments attach the anterior end of the urohyal and medial surfaces of the ventral hypohyals. The ventral hypohyal starts to ossify earlier than the dorsal one, in few examined specimens from 4.6-4.8 mm NL but largerly from 5.5 mm NL, while the dorsal hypohyal starts to ossify in few examined specimens from 6.2-6.4 mm SL but largerly from 6.7-6.8 mm SL.

*Os basihyale* [basihyoideum]. The basihyal [basihyoid; glossohyal] is a median unpaired bone that develops from the basihyal cartilage (the anteriormost cartilage of the hyoid arch), joining both branches of the hyoid series and forming the tongue skeleton in Teleostei. It is located between the anterior tips of the ceratohyal cartilages, anterior to the first copula. The anterior tip of the bone remains cartilaginous.

The basihyal tooth plate [*os glossohyale*] is absent. The bone is rod-shaped. The anterior tip of the basihyal extends anteriorly past the ventral hypohyals; the posterior edge does not reach the posterior extent of the dorsal hypohyals. The basihyal ossification appears comparatively late; a very initial ossification was found in a specimen of 7.6 mm SL while most specimens display the basihyal ossification only from 8.9 mm SL.

*Os urohyale.* The urohyal is a median dermal bone that ossifies in the membrane between the paired sternohyoideus muscles ventral to the anterior end of copula 1.

It is an unpaired ossification of the tendon of the sternohyoideos muscles. In *G. ternetzi* the urohyal is a vertical lamella with a poorly developed (reduced) ventral plate which is very narrow and only presented just posterior the head of the bone. The urohyal starts to ossify in a few examined specimens of 4.6-4.8 mm NL but largerly from 5.5 mm NL.

*Radii branchiostegii.* The branchiostegal rays are thin dermal bones that support the branchiostegal membrane.

They are four; the two anterior branchiostegal rays have small but clearly defined hooked tips which articulate with the ventral edge of the ceratohyal in special notches; the third one hangs on the lower lateral surface of the ceratohyal with no special articulating tip, and the most posterior ray, branchiostegal 4, inserts externally on the lower lateral surface of the epihyal with no special articulating tip. The branchiostegal rays start to ossify in examined specimens from 4.0 to 5.2 mm NL.

**Branchial arches** (pharyngeal arches 3-7, gill arches 1-5, visceral arches 3-7). The branchial arches are suspended from the cranial base. The first three branchial arches are much alike, each having an epibranchial below the pharyngo-branchial. The pharyngobranchial and the epibranchial form the upper limb of the arch. The lower limb consists of an elongate ceratobranchial and a short hypobranchial. The ceratobranchials, hypobranchials, and the median baslbranchials are joined by cartilage.

*Ossa pharyngobranchialia* [ossa infrapharyngobranchialia]. The pharyngobranchials are the dorsalmost bones of the branchial arches located immediately dorsal and medial to the epibranchials. The pharyngobranchials are paired chondral bones developed from the respective pharyngobranchial cartilages.

The pharyngobranchial 1 lies ventrolateral to the ventral keel of the parasphenoid, which in turn lies below the posterior edge of the orbit. The bone is only ossified in its upper part in specimens larger than 9.9 mm SL. The ossified part of the bone forms an upwardly directed finger-like process. It bears neither gill rakers nor a dentigerous plate. The pharyngobranchial 2 is located in a horizontal plane and ossified only in its lower part where it bears few (1 or 2) gill rakers on both anterior and posterior margins. There is no visible foramen between the pharyngobranchials 2 and 3 and the bones do not overlap each other being separated by a considerable amount of cartilage. The pharvngobranchial 3 is somewhat larger than the pharyngobranchial 2 and bears larger gill rakers (1 to 3) only at its anterior margin; at the posteroventral part of the pharyngobranchial 3 is a small dentogerous pale bearing small conical teeth. The pharyngobranchial 3 is the first pharyngobranchial to appear in specimens of about 6.4-6.8 mm SL. The pharyngobranchial 1-3 are called suspensory pharyngeals by Weitzman (1962).

The pharyngobranchial 4 and 5 are called upper pharyngeals by Weitzman (1962). Any ossificaton of the pharyngobranchial 4 and 5 cartilages are absent. They are tooth-bearing plates that lie close together and may be fused to each other in larger specimens forming a single pad bearing numerous rows of conical teeth. The pharyngobranchial 5 [posterior pharyngeal of Weitzman] is suspended from the ventral surface of the dorsal margin of the ceratobranchial 4. The anterior end of the pharyngeal 4 is supported from above by the anterodorsal arm of the third ceratobranchial via the cartilage.

Ossa epibranchialia [ossa epibranchialia]. The epibranchials 1-4 ossify in the epibranchial cartilages in a posterior to anterior progression (from the forth to the first bone) inspecimens starting from 4.3 mm SL. The medial (upper) tips of the epibranchial 1-3 articulate through cartilage with the lateral ends of the pharyngobranchials 1-3, respectively. The cartilaginous tips of the epibranchials articulate laterally with the cartilaginous tips of the ceratobranchials. Gill rakers are present on the anterior and posterior edges of epibranchials 1-3 and the anterior edge of the epibranchial 4. Uncinate processes are absent on the epibranchials 1 and 2 while they are well developed, large on the posterodorsal margins of the epibranchials 3 and 4. There are no special modifications of the epibranchials. The epibranchial 5 is absent.

*Ossa ceratobranchialia* [ossa ceratobranchialia]. The ceratobranchials 1-5 ossify in the ceratobranchial cartilages in specimens starting from 4.9-5.0 mm SL. Anteromedially ceratobran-



Fig. 1. Dorsal view of the neurocranium of Gymnocorymbus ternetzi, SL 25 mm;

*eb*, epiphysial bar; *ebc*, epiphysial branch of supraorbital sensory canal; *epo*, epiotic; *esc*, extrascapula; *eth*, ethmoid; *f*, frontal; *leth*, lateral ethmoid; *n*, nasal; *p*, parietal; *pma*, premaxilla; *pmap*, premaxillary ascending process; *ppf*, prepineal fontanel; *psoc*, parietal branch of supraorbital sensory canal; *ptpf*, postpineal fontanel; *ptt*, posttemporal; *so*, supraoccipital; *spho*, sphenotic; *stc*, supratemporal sensory canal.



Fig. 2. Lateral view of the neurocranium of *Gymnocorymbus ternetzi*, SL 25 mm; *bo*, basioccipitale; *leth*, lateral ethmoid; *orbsph*, orbitosphenoid; *psph*, parasphenoid; *rsph*, rhinosphenoid; *soc*, supraoccipital crest; *vkp*, ventral keel of parasphenoid.





anto, antorbital; ectpt, ectopterygoid; entpt, entopterygoid; esc, extrascapula; ih, interhyal; io, infraorbital; iop, interopercle; mtpt, metapterygoid; op, opercle; pl, palatine; pop, preopercle; pto, pterosphenoid; q, quadrate; s, symplectic; sop, subopercle.



Fig. 5. Lower jaw, from inside, of *Gymnocorymbus ternetzi*, SL 25 mm; *aart*, angulo-articular; *aartc*, mandibular sensory canal on angulo-articular; *cm*, coronomeckelian bone; *d*, dentary; *dc*, mandibular sensory canal on dentary; *rart*, retroarticular.

chials 1-3 articulate with hypobranchials 1-3; medially they articulate with the cartilage between the basibranchials. Posterolaterally ceratobranchials 1-4 articulate with epibranchials 1-4. Gill rakers are present on the anterior margins of ceratobranchials 1-4 and on the posterior margin of only the ceratobranchial 3 and 4. The ceratobranchial 5 is modified into a structure modified into the lower pharyngeal. The tooth-bearing plate is triangular and located at the posterior edge of the bone. The dorsal surface of the tooth-bearing plate supports about rows of rather irregularly placed, small, sharp-pointed, conic teeth.

*Ossa hypobranchialia* [ossa hypobranchialia]. The hypobranchials are the most medial of the bilaterally paired elements of the branchial arches. The hypobranchial ossifications 1-3 develop in the small hypobranchial cartilages that lie between the medial tips of the ceratobranchials and copula 1 and 2. In the examined specimens ossification of the hypobranchial were late to appear; it starts in the hypobranchial 2 in specimens 7.0-7.2 mm SL and only in specimens 10.0-10.6 mm SL the hypobranchial 3 appears followed by the hypobranchial 1 in specimens of 11.3-12.0 mm SL. The hypobranchials. Both the fourth and fifth arches lack hypobranchials.

The hypobranchial bear gill rakers at their anterior margins. The two anterior bones are about rectangular while the posterior one is clearly conical, or triangular, with its apex orientated ventromesially to below the posteriormost basibranchial.

*Copulae* (1 and 2). They are median cartilaginous elements that are the precursors of the basibranchials. They are not assigned to specific branchial arch numbers.

Ossa basibranchialia [ossa basibranchialia]. The basibranchials (1-4) are median elements that are ossified within copulae and are not assigned to a specific branchial arch number. They start to ossify almost simultaneously in specimens of 6.5-7.0 mm SL, the first-third somewhat earlier than the forth one. They articulate posterolaterally with the hypobranchials. The basibranchial 1 is immediately posterior to the basihyal and joined to that bone by cartilage. The basibranchial 2 immediately follows the first, and consists of a bony rod for the anterior half of its length and a cartilaginous rod overlaid by a thin sheet of bone for a part of the posterior half of its length. The basibranchial of the third arch is bony throughout its length and abuts a large cartilaginous mass immediately posterior to it. This cartilaginous mass contacts the cartilaginous median ends of the fourth and fifth ceratobranchials.

*Spinae branchialia.* The gill rakers are rather long especially on the ceratobranchials 1-3. The gill raker count on the left first arch is 19-22. All rakers are pointed, very well ossified. Almost all rakers have short bony spicules arraged in irregular number along their sides.

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# References

- Adriaens, D. 1998. On how a larva becomes an adult catfish: a functional morphological approach to the cranial ontogeny of the African catfish, Clarias gariepinus (Siluriformes, Clariidae). Thesis submitted to obtain the degree of Doctor in Sciences (Biology). Part 1. Universiteit Gent. 240 pp.
- Aerts, P. 1991. Hyoid morphology and movements relative to abducting forces during feeding in Astatotilapia elegans (Teleostei: Cichlidae). Journal of Morphology, 208: 323-345.
- Bamford, T.W. 1948. Cranial development of Galeichthys felis. Proceedings of Zoological Society of London, 118: 364–391.
- Benjamin, M. 1989. Hyaline-cell cartilage (chondroid) in the head of teleosts. *Anatomic Embryology*, **179**: 285-303.
- Benjamin, M. 1990. The cranial cartilages of teleosts and their classification. *Journal of Anatomy*, 169: 153-172.
- Bertmar, G. 1959. On the ontogeny of the chondral skull in Characidae, with a discussion on the chondrocranial base and the visceral chondrocranium in fishes. *Acta Zoologica*, 40: 203–364.
- Bird, N.C. & Mabee, P.M. 2003. The developmental morphology of the axial skeleton of the zebrafish, *Danio rerio* (Ostariophysi: Cyprinidae). *Developmental Dynamics*, 228: 337-357.
- Bogutskaya, N.G. 1989. Cyprinid infraorbital bones and the problem of "dermosphenoticum". Proceedings of Zoological Institute of Academy of Sciences of USSR [Trudy ZIN RAN], 201: 29-44. (In Russian with English Summary).
- Cabuy, E., Adriaens, D., Verraes, W. & Teugels, G.G. 1999. Comparative study on the cranial morphology of *Gymnallabes typus* (Siluriformes: Clariidae) and their less anguilliform relatives, *Clariallabes melas* and *Clarias* gariepinus. Journal of Morphology, 240: 169–194.
- Cubbage, C. & Mabee, P.M. 1996. Development of the cranium and paired fins in the zebrafish Danio rerio (Ostariophysi, Cyprindae). *Journal of Morphology*, 229: 121-160.
- Daget, J. 1964. Le crâne des Téléostéens. Mémoires du Muséum National d'Histoire Naturelle, Série A, 31(2): 163–341.
- **de Beer, G.R.** 1937. *The development of the vertebrate skull.* Clarendon Press, Oxford.
- Ferry-Graham, L.A. & Lauder, G.V. 2001. Aquatic prey capture in ray-finned fishes: a century of progress and new directions. *Journal of Morphology*, 248: 99-119.

- Fink, S.V. & Fink, W.L. 1981. Interrelationships of the ostariophysan fishes (Teleostei). Zoological Journal of Linnean Society of London, 72: 297–353.
- Fink, S.V. & Fink, W.L. 1996. Interrelationships of ostariophysan fishes (Teleostei). *In*: Stiassny, M.L.J., Parenti, L.R. & Johnson, G.D. (Eds.), *Interrelationships of Fishes*. Academic Press, London. P. 209–249.
- Geerinckx, T., Brunain, M. & Adriaens, D. 2005. Development of the osteocranium in the suckermouth armored catfish Ancistrus cf. triradiatus (Loricariidae, Siluriformes). Journal of Morphology, 268: 254–274.
- Geerinckx, T., Brunain, M. & Adriaens, D. 2008. Ontogeny of the Chondrocranium in *Corydoras aeneus* (Gill, 1858) (Callichthyidae, Sluriformes). *Journal of Morphology*, 269: 522–532.
- Gillis, J.A., Witten, P.E. & Hall, B.K. 2006. Chondroid bone and secondary cartilage contribute to apical dentary growth in juvenile Atlantic salmon. *Journal of Fish Biology*, 68(4): 1133-1143.
- Gosline, W. 1961. Some osteological features of modern lower teleostean fishes. *Smithsonian Miscellaneous Collections*, 142(3): 1-42.
- Haines, R.W. 1937. The posterior end of Meckel's cartilage andrelated ossifications in bony fishes. *The Quarterly Journal of Microscopical Science*, 80: 1-38.
- Hanken, J. & Wassersug, R. 1981. The visible skeleton. A new double-stain technique reveals the native of the "hard" tissues. *Functional Photography*, 16: 22-26.
- Harrington, R.W. 1955. The osteocranium of the American cyprinid fish, *Notropis bifrenatus*, with an annotated synonymy of teleost skull bones. *Copeia*, **1955**: 267-290.
- Huysentruyt, F & Adriaens, D. 2005. Descriptive osteology of Corydoras aeneus. Cybium, 29(3): 261-273.
- Huysseune, A. & Verraes, W. 1990. Carbohydrate histochemistry of mature chondroid bone in Astatotilapia elegans (Teleostei: Cichlidae) with a comparison to acellular bone and cartilage. Annales des Sciences Naturelles, Zoologie, Paris 13(11): 29-43.
- Huysseune, A. 1986. Late skeletal development at the articulation between upper pharyngeal jaws and neurocranial base in the fish, *Astatotilapia elegans*, with the participation of a chondroid form of bone. *The American Journal* of Anatomy, **177**: 119-137.
- Janvier, P. 1996. Early Vertebrates. Oxford Monographs on Geology and Geophysics, 33. Oxford Univ. Press, Oxford. 393 pp.
- Lekander, B. 1949. The sensory line system and the canal bones in the head of some Ostariophysi. Acta Zoologica, Stockholm, 30: 1-131.
- Meunier, F.J. & Huysseune, A. 1992. The concept of bone tissue in Osteichthyes. *Netherlands Journal of Zoology*, 42(2-3): 445-458.
- Miquelarena, A., Ortubay, S & Cussac, V. 2005. Morphology, osteology and reductions in the ontogeny of the scaleless characid Gymnocharacinus bergi. Journal of Applied Ichthyology, 21(6): 511-519.
- Nalbant, T. & Bianco, P.G. 1998. The loaches of Iran and adjacent regions with description of six new species (Cobitoidea). *Italian Journal of Zoology*, 65 (Suppl.): 109-123.
- Nelson, J.S. 2006. Fishes of the World, 4th Edition. Wiley, New-York. 642 pp.
- Parenti, L.R. 1986. The phylogenetic significance of bone types in euteleost fishes. Zoological Journal of Linnaean Society of London, 87: 37–51.
- Patterson, C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. *In:* Andrews, S.M., Miles, R.S., Walker, A.D. (Eds.), *Problems in Vertebrate Evolution.* Academic Press, London. P. 77–121.

- Regan, C.T. 1911a. The classification of the teleostean fishes of the order Ostariophysi. 2. Siluroidea. Annals and Magasins of Natural History, Ser. 8, 8(47): 37-577.
- Regan, C.T. 1911b. The classification of the teleostean fishes of the order Ostariophysi. 1. Cyprinoidea. Annals and Magasins of Natural History, Ser. 8, 8(48): 13-32.
- Roberts, T.R. 1973. Interrelationships of ostariophysans. In: Greenwood, P.H., R.S. Miles & C. Patterson (Eds.), Interrelationships of fishes. Zoological Journal of Linnean Society of London, 53, suppl. 1: 373–395.
- Roberts, T.R. 1975. Geographical distribution of African freshwater fishes. Zoological Journal of the Linnean Society, 57(4): 249-319.
- Rosen, D.E. & Greenwood, P.H. 1970. Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorhynchiform fishes. *American Museum Novitates*, 2428: 1-49.
- Serra, J.P. & Langeani, F. 2006. Redescrição e osteologia de Bryconamericus exodon Eigenmann, 1907 (Ostariophysi, Characiformes, Characidae). Biota Neotropica, 6(3): 1-14.
- Šlechtová, V., Bohlen, J. & Perdices, A. 2008. Molecular phylogeny of the freshwater fish family Cobitidae (Cypriniformes: Teleostei): delimitation of genera, mitochondrial introgression and evolution of sexual dimorphism. *Molecular Phylogenetics and Evolution*, 47: 812-831.
- Tang, Q., Liu, H., Mayden, R. & Xiong, B. 2006. Comparison of evolutionary rates in the mitochondrial DNA cytochrome b gene and control region and their implications for phylogeny of the Cobitoidea (Teleostei: Cypriniformes). Molecular Phylogenetics and Evolution, 39: 347-357.
- Teugels, G.G. 1996. Taxonomy, phylogeny and biogeography of catfishes (Ostariophysi, Siluroidei): an overview. *Aquatic Living Resources*, 9: 9-34.
- Vandewalle, P. 1977. Particularités anatomiques de la tête de deux Poissons Cyprinidés Barbus barbus (L.) et Leuciscus leuciscus (L). Bulletin de l'Académie royale des Sciences de Belgique, 5: 469-479.
- Vandewalle, P., Focant, B., Huriaux, F. & Chardon, M. 1992. Early development of the cephalic skeleton of Barbus barbus (Teleostei, Cyprinidae). *Journal of Fish Biol*ogy, **41**: 43–62.
- Vandewalle, P., Germeau, G., Besancenet, P., Parmentier, E. & Baras, E. 2005. Early development of the head skeleton in *Brycon moorei* (Pisces, Ostariophysi, Characidae). *Journal of Fish Biology*, 66: 996–1024.
- Verraes, W. 1981. Theoretical discussion on some functionalmorphological terms and some general reflexions on the explanations in biology. *Acta Biotheorethica*, **30**: 255-273.
- Weitzman, S.H. 1962. The osteology of Brycon meeki, a generalized characid fish, with an osteological definition of the family. Stanfords Ichthyological Bulletin, 8(1): 1-77.

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