

# The Evolution of the Zygomatic Bone From Agnatha to Tetrapoda

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## ABSTRACT

Establishing the homology of the zygomatic or jugal bone and tracing its origin and early evolution represents a complex issue because of large morphological gaps between various groups of vertebrates. Using recent paleontological findings, we discuss the deep homology of the zygomatic or jugal bone in stem gnathostomes (placoderms) and examine its homology and modifications in crown gnathostomes (acanthodians, chondrichthyans and osteichthyans). The discovery of the placoderm *Entelognathus* from the Silurian of China (~423 million years ago) established that the large dermal plates in placoderms and osteichthyans are homologous. In *Entelognathus*, the jugal was joined by a new set of bones (premaxilla, maxilla, and lachrymal), marking the first appearance of the typical vertebrate face found in tetrapods including humans. In non-*Entelognathus* placoderms, the jugal (homologized with the suborbital plate) occupied most of the cheek region and covered the palatoquadrate laterally. In antiarch placoderms (the most basal jawed vertebrates), the jugal (represented by the ventrally positioned mental plate) functioned as part of the upper jaw. In osteichthyans, the preopercular arose as a novel bone and separated the jugal from the opercular in piscine osteichthyans. A single bone in basal osteichthyans, the preopercular may have divided into two or three elements (the preopercular, the squamosal and/or the quadratojugal) in several later osteichthyan groups. Subsequent modifications of the jugal in the fish-tetrapod transition (its enlargement leading to its contact with the quadratojugal and the separation of the squamosal from the maxilla) brought the vertebrate face to the typical model we see in living tetrapods. *Anat Rec*, 300:16–29, 2017. © 2016 Wiley Periodicals, Inc.

**Key words:** zygomatic; agnathans; gnathostomes; tetrapods; homology

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## INTRODUCTION

The term “zygomatic” derives from the Greek *zygoma* or *zygon*, which means “yoke” because the zygomatic bone in mammals meets the zygomatic process of the temporal bone to form a conspicuous yoke-like arch (the zygomatic arch). In humans, the zygomatic bone (also known as the malar or zygoma) is the cornerstone of the craniofacial skeleton. It joins the maxillary, the frontal and the temporal bones to form parts of the infraorbital margin, the lateral orbital margin, and the zygomatic arch. The zygomatic bone plays a vital role in maintaining the facial

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contour, protecting the eye, providing attachment for facial expression muscles, and withstanding forces incurred during jaw movements (Thiagarajan et al., 2013; Ross et al., 2015). In non-mammalian vertebrates, the equivalent bone is generally known as the jugal bone and the zygomatic arch as seen in mammals is absent. In this article, we use “jugal” in non-mammalian vertebrates to agree with long-established usage in comparative anatomy and to avoid the descriptive inference of a zygomatic arch (Jollie, 1962). Cuvier probably was the first writer to notice the consistency of the zygomatic region in various vertebrate classes in his *Leçons d'anatomie comparée* (Cuvier, 1799–1805). Slade later summarized the chief modifications that the zygomatic underwent in the various mammalian orders (Slade, 1895). In tetrapods (mammals, birds, reptiles, amphibians, and their fossil relatives), the zygomatic bone or its equivalent (the jugal bone) is easy to identify because its topological relationship to other bones and its general function have been quite stable over time. However, establishing the homology of the zygomatic and tracing its origin and early evolution become an increasingly complex issue as one goes back to the early chapters in vertebrate evolution. This is due to a combination of factors such as the morphological gaps between different groups, secondary modifications among the surviving members of many groups, incomplete character suites among extinct groups as well as the inherent uncertainties in reconstructing phylogenetic relationships. In this article we trace the origin and early evolution of the zygomatic among the various early vertebrate groups. We will present recent paleontological findings that have extended the homology of the zygomatic to the basal jawed vertebrates (placoderms) as early as the Silurian period (ca. 423 million years ago; Zhu et al., 2013).

In terms of the number of bones, the diversity of skeletal type and the mode of articulation, the fish skull is far more complex than the skulls of amphibians, reptiles, birds, and mammals (Benjamin, 1990; Cabbage and Mabee, 1996). Although Westoll (1943) transferred the terminology of skull bones from tetrapods (where it was first established in humans) to fishes, conflicts or uncertainties in homologizing skull bones between bony fishes and early tetrapods have long existed (Schultze, 2008). In addition, whether the dermal bone pattern of bony fishes (osteichthyan fishes) can be further extended to placoderms (stem gnathostomes) has been in debate for more than one century (Goodrich, 1909; Denison, 1978; Forey, 1980, 1998; Jarvik, 1980a; Gardiner, 1984a, 1984b; Forey and Gardiner, 1986; Young, 1986, 2010; Friedman, 2007). All this has long impeded our understanding of the origin and evolution of the zygomatic or jugal bone among the various groups of early vertebrates.

Better understanding of the molecular developmental mechanism of the zygomatic bone and new paleontological findings represent two important areas in which further progress can be made in tracing the ontogenetic and the phylogenetic innovations of the zygomatic bone. Recent developmental study indicates that the zygomatic, maxillary, quadratojugal, palatine and pterygoid bones can be regarded as derivatives of the maxillary primordium (Richman and Lee, 2003; Santagati and Rijli, 2003; Lee et al., 2004). The facial region of higher vertebrates (reptiles, birds, and mammals) develops from five primordia that appear in the fourth week: the

frontonasal prominence, the two maxillary prominences, and the two mandibular prominences, which initially consist of buds of undifferentiated mesenchyme (Lee et al., 2001; Richman and Lee, 2003; Sylvia et al., 2003; Moore et al., 2013). For a long time, the traditional view holds that the maxillary processes are derived embryologically from the first pharyngeal arch (Smith and Schneider, 1998; Sperber, 2001; Sylvia et al., 2003; Moore et al., 2013). Recent precise developmental fate maps indicate that the maxillary prominence and its skeletal derivatives including the zygomatic bone are not derived from the first pharyngeal arch but rather from a separate maxillary condensation that occurs between the eye and the maxillomandibular cleft (Cerny et al., 2004). The new embryonic origin of the maxillary prominences probably can shed light on the homology of the zygomatic or jugal in various vertebrate groups. However, more specific comparative studies involving different model organisms are needed in order to use molecular development data to bear directly on the homology of the zygomatic or jugal bone in different vertebrate groups.

**Anatomical Abbreviations** - cir, circumorbital bone; de, dentary; de + ide, dentary plus infradentaries; e, eye; ifc, infraorbital canal; ifc.sb, suborbital division of infraorbital sensory groove; ju, jugal; lac, lachrymal; me, mental; ml, main lateral line; mx, maxilla; op, opercular; pmx, premaxilla; po, postorbital; prsm, preoperculosubmandibular; ps, prespiracular; qj, quadratojugal; scl, sclerotic plate; sm, submarginal plate; so, suborbital plate; sq, squamosal; ssq, subsidiary squamosal.

## THE DEEP HOMOLOGY OF THE ZYGOMATIC IN STEM GNATHOSTOMES

The vertebrates include jawless fishes (agnathans, comprising hagfishes, lampreys, and ostracoderms) and jawed vertebrates (comprising placoderms, acanthodians, chondrichthyans, and osteichthyans). The jawless ostracoderms and the jawed placoderms are now consistently resolved as the stem gnathostomes (Fig. 1), that is, the phylogenetic intermediate of cyclostomes and crown gnathostomes (Maisey, 1986; Janvier, 1996a; Donoghue and Smith, 2001; Gai and Zhu, 2012). They are the earliest vertebrates that have large dermal plates (dermatocranium) covering the endocranium (Janvier, 1996b; Gai et al., 2011). Essentially, the zygomatic or jugal bone is a dermal plate of the circumorbital series that covers the endocranium laterally to form the cheek region. As such, it is conceivable to trace the ancestry of the zygomatic bone to some specialized dermal bones around the eyes in ostracoderms and placoderms.

The jawless armored ostracoderms are considered to have a small suborbital plate such as in the heterostracan *Anglaspis* (so, Fig. 2A; Kiaer, 1932; Blicek and Heintz, 1983), or a small circle of dermal bones surrounding the orbit such as in the astraspid *Astraspis* (cir, Fig. 2B; Elliott, 1987; Sansom et al., 1997) and the anaspid *Pharyngolepis* and *Rhyncholepis* (cir, Fig. 2C,D; Blom et al., 2002; Blom, 2008; Ritchie, 1980). This circle of dermal bones is identified to be circumorbital rather than sclerotic plates because some sensory canals or openings from sensory canals are observed on the dermal bones surrounding orbits in *Astraspis* and *Rhyncholepis* (Elliott, 1987, Ritchie 1980). The jugal bone

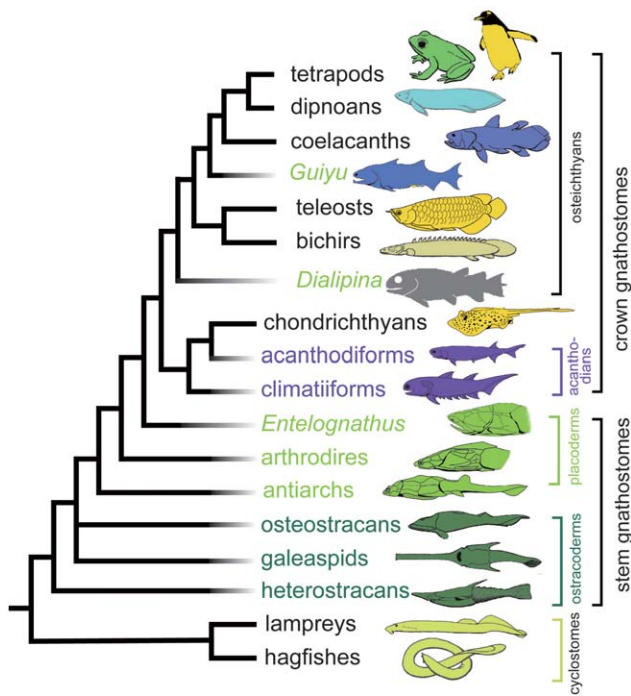


Fig. 1. Simplified phylogeny of vertebrates (modified from Zhu, 2014). Agnathans (jawless fishes) include hagfishes, lampreys, and ostracoderms. Gnathostomes (jawed vertebrates) include traditionally defined groups or assemblages known as placoderms, acanthodians, chondrichthyans (cartilaginous fishes) and osteichthyans (bony fishes and tetrapods). Ostracoderms and placoderms are stem gnathostomes. Crown gnathostomes contain the chondrichthyan total group (acanthodians and chondrichthyans) and the osteichthyan total group (stem taxa, actinopterygians and sarcopterygians). Faded branches represent extinct taxa.

possibly arose from one of the circumorbital bones of ostracoderms, but specific bone-to-bone homology is hard to establish because the extensive dermal armor of ostracoderms is, in most cases, difficult to compare to the dermal elements of jawed fishes and tetrapods.

Except for the jawless ostracoderms, the armored placoderms are the earliest jawed vertebrates that have macromeric dermal skeletons dominated by large bony plates (Maisey, 1988; Janvier, 1996b; Zhu et al., 2013) (Fig. 3). It is documented that many placoderms have both dermal sclerotic and circumorbital plates (Denison, 1978; Burrow et al., 2005; Young, 2008). However, until recently, the homology of the jugal was difficult to establish between placoderms and osteichthyans because these two groups differ completely in the dermal bone pattern, with totally different nomenclature being applied to each case (Denison, 1978; Jarvik, 1980a; Young, 1986, 2010). For example, placoderms have fewer bones in the cheek and gill cover, and have no equivalent of infraorbital or supraorbital series of dermal bones (Janvier, 1996b). Although many paleontologists attempted to establish the homologies of dermal bone pattern between the two groups (Goodrich, 1909; Gardiner, 1984a,b; Forey and Gardiner, 1986; Friedman, 2007), and some even tried to apply osteichthyan terminology to certain dermal bones of placoderms (Stensiö, 1945, 1947, 1959, 1969), such efforts were either largely ignored (Forey, 1980, 1998; Jarvik,

1980a) or were strongly criticized (Jarvik, 1980a; Young, 1986, 2010). In addition, the prevalent phylogenetic hypotheses at the time placed all or some of the micromeric acanthodians as the sister group of osteichthyans, implying that the macromeric dermal skeleton of osteichthyans arose from a micromeric condition and thus is not homologous with the dermal skeleton of placoderms (Brazeau, 2009; Davis et al., 2012).

Fortunately, the huge morphological gap between placoderms and osteichthyans has been reduced by recent discoveries of placoderm-like features among early osteichthyans from the Siluro-Devonian of China. For instance, the eyestalk, a feature previously unknown in osteichthyans, was found in *Achoania* and *Psarolepis* (Zhu et al., 2001), while *Psarolepis* and *Guiyu* (Figs. 1 and 4D) revealed dermal pelvic girdles and multipartite dermal shoulder girdles with spinal plates, again features previously limited to non-osteichthyans (Zhu et al., 1999, 2009, 2012; Zhu and Schultze, 2001). The presence of placoderm-like features in some earliest osteichthyans suggests a conservation of pattern between the placoderm and osteichthyan macromeric dermal skeletons (Gardiner, 1984a,b; Forey and Gardiner, 1986; Zhu et al., 2013; Zhu, 2014).

A recent breakthrough in establishing the homology of the dermal bone pattern between placoderms and osteichthyans came with the discovery of *Entelognathus* (Fig. 1), an osteichthyan-like placoderm from the Silurian Xiaoxiang Vertebrate Fauna of China (~423 million years ago, Zhu et al., 2013, Choo et al., 2014). *Entelognathus* is characterized by the placoderm-like dermal skull roof, braincase and trunk armour, but has osteichthyan-like dermal marginal jaw bones (premaxilla, maxilla and dentary) and operculogular series (Fig. 3A), features previously restricted to osteichthyans. As many aspects of the dermal bone pattern of *Entelognathus* are consistent with those of osteichthyans, the jugal (ju, Fig. 3A) in *Entelognathus* can be identified based on recognizable similarity in topological relationship and sensory canal distribution. The small orbital fenestra is enclosed by a large oblong sclerotic ring, which comprises three intimately fused sclerotic plates as in antiarchs (the most basal group of placoderms; Brazeau, 2009; Zhu et al., 2012, 2013; Davis et al., 2012; Dupret et al., 2014; Long et al., 2015). The elongate jugal bone has loose anterior contacts with the sclerotic ring and lachrymal, but its ventral suture with the maxilla is so tight that the bones are difficult to distinguish except by their ornament patterns (for more details see Zhu et al. 2013, figs. 2–4). The infraorbital canal (ifc, Fig. 3A) enters the jugal dorsally, runs ventrally to join the supraorbital canal, and then continues anteroventrally via the slender lachrymal to terminate below the orbit. A small, roughly triangular ossification, tentatively identified as a quadratojugal, lies at the posterior tip of the cheek complex, and is firmly sutured with the adjacent maxilla and jugal (for more details see Zhu et al., 2013, figs. 2–4).

The new phylogenetic hypothesis resolved the placoderm *Entelognathus* as the sister group of crown gnathostomes (Fig. 1) and thus revived the homology of dermal skeleton between placoderms and osteichthyans. The large dermal plates found in placoderms and osteichthyans are regarded as general features of jawed vertebrates, which have been secondarily lost in

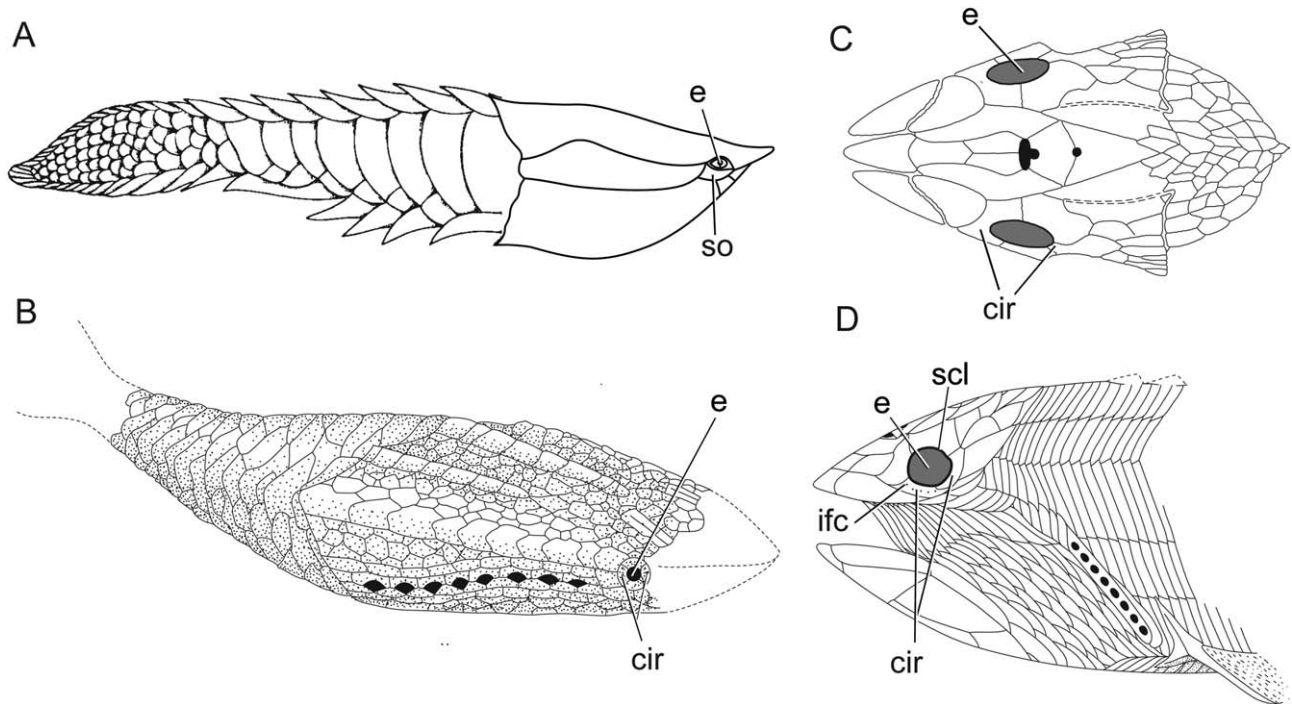


Fig. 2. Representative jawless fishes with either a small suborbital plate or a series of circumorbital bones. A. *Anglaspis* (after Janvier, 1996b); B. *Astraspis* (after Sansom et al., 1997); C. *Pharyngolepis* (after Blom et al., 2002; Blom, 2008), in dorsal view; D. *Rhyncholepis* (after Ritchie 1980), in lateral view.

acanthodians and chondrichthyans (Maisey, 1988, 2004, 2013; Zhu et al., 2013 contra Brazeau, 2009; Davis et al., 2012). Zhu et al. (2013) provided a tentative framework for the homology of large dermal plates across sarcopterygians, actinopterygians, *Entelognathus* and non-*Entelognathus* placoderms.

The cheek plates of non-*Entelognathus* placoderms (such as arthrodires, acanthothoracids and ptyctodontids) are composed of the suborbital, postsuborbital, and submarginal plates (in traditional placoderm terms; Fig. 3B,C). Anteriorly, the suborbital plate (so, Fig. 3B,C) is very large and located beneath the eye, and firmly attached to the palatoquadrate laterally. The main lateral line (ml, Fig. 3B–D) extends from the body onto the skull roof in the region of the dermal shoulder girdle articulation and continues as the infraorbital line postero-ventrally on the suborbital plate beneath the orbit (ifc, Fig. 3B,C). In some advanced coccosteomorphs, the suborbital and postsuborbital plates are fixed to the skull-roof (Janvier, 1996b). The posterior mobile submarginal plate (sm, Fig. 3B,C) is the functional equivalent of the osteichthyan opercular. Primitively, the submarginal is free (e.g., ptyctodontids and primitive arthrodires), but in advanced arthrodires, it is enclosed in the cheek and sutured with surrounding bones (Schultze, 1993). Based on recent fossil findings and new phylogenetic frameworks (Zhu et al., 2013; Dupret et al., 2014; Long et al., 2015), the suborbital and submarginal plates of non-*Entelognathus* placoderms are considered homologous with the jugal and opercular bones of osteichthyans respectively. The combination of placoderm-like and osteichthyan-like features in *Entelognathus* makes it possible to apply a uniform set of terminology to some

plates in placoderms and osteichthyans including tetrapods. In osteichthyans, a series of separate dermal bones such as the premaxillary, maxillary, lachrymal, jugal, squamosal, and quadratojugal join together to form the cheek region (Figs. 4–6). By contrast, the lachrymal, premaxillary, maxillary, squamosal, and quadratojugal are absent in non-*Entelognathus* placoderms, while the jugal plate (i.e., suborbital) covers most of the cheek region and is fused with the palatoquadrate laterally (Fig. 3B,C) implying a considerable strengthening of the upper jaw, an increasing inflexibility of the jaw mechanism and a change in the position of insertion of the adductor musculature (Miles, 1969; Schaeffer, 1975, Janvier, 1996b; Young, 2010).

Antiarchs are a peculiar placoderm group occupying the most basal position of jawed vertebrates (Fig. 1; Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Dupret et al., 2014; Long et al., 2015, Giles et al., 2015). The eyes of antiarchs are housed dorsally in an oval orbito-nasal fenestra in the center of the skull-roof (e, Fig. 3D). Thus, no structure can be recognized in antiarchs that has the topological relationship comparable to that of the suborbital or jugal plate in other placoderms. Stensiö (1948) suggested that the lateral plate is a candidate to be homologized with the jugal plate, whereas Young (1984) demonstrated that the so-called mental plate (me, Fig. 3D) of antiarchs (a dermal bone located on the ventral side of the head forming the upper part of the jaw) is homologous with the suborbital or jugal of other placoderms (so, Fig. 3B,C). This is corroborated by the fact that the mental plate of *Bothriolepis* bears the suborbital division of infraorbital sensory groove (ifc.sb, Fig. 3D) and the palatoquadrate is attached to its inner margin

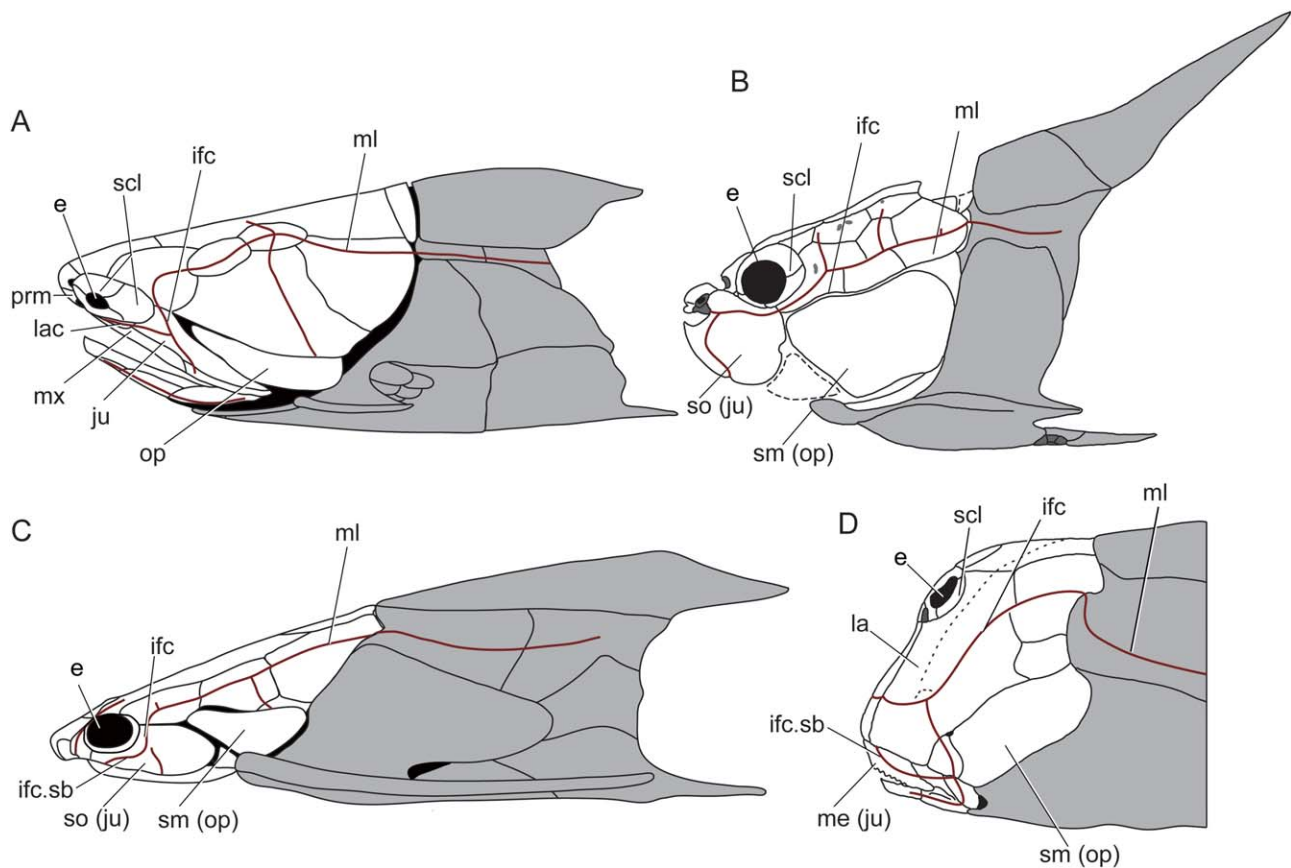


Fig. 3. *Entelognathus* and non-*Entelognathus* placoderms with the jugal. A. *Entelognathus* (after Zhu et al., 2013); B. acanthothoracid *Romundina* (after Goujet and Young, 2004); C. arthrodire *Dicksonosteus* (after Goujet, 1984); D. antiarch *Bothriolepis* (after Young and Zhang, 1996).

as in other placoderms (Young, 1984; Young and Zhang, 1996). It is noteworthy that the jugal in antiarchs was modified as a functional equivalent of the osteichthyan upper jaw by having a cutting edge biting against the lower jaw. It probably represents a specialized condition related to its benthic lifestyle.

### THE HOMOLGY OF THE ZYGOMATIC IN CROWN GNATHOSTOMES

Crown gnathostomes include traditional groups known as acanthodians, chondrichthyans and osteichthyans (Jarvik, 1980a; Maisey, 1986; Janvier, 1996b), the last of which comprise some stem taxa (e.g. *Lophosteus*, *Dialipina*) and two major lineages, the actinopterygians lineage (ray-finned fishes) and the sarcopterygian lineage (lobe-finned fishes and tetrapods) (Friedman, 2007; Zhu et al., 2013; Giles et al., 2015; Figs. 1 and 7). The cheek bone patterns in crown gnathostomes are considerably different, making it difficult to establish an overall homology scheme (Andrews et al., 2006). Schultze (2008) summarized some basic criteria to build the homology of dermal bone across different vertebrate groups, for example the relative position to other structures. The cheek bones of crown gnathostomes generally include lachrymal, jugal, postorbital/dermosphenotic, squamosal, quadratojugal, and preopercular. Posteroventral to the orbit, the

jugal is centered to join together the disparate portions of the cheek, for example articulating with lachrymal and/or maxilla (anteriorly), quadratojugal and/or squamosal (posteriorly), and postfrontal and/or postorbital (dorsally). In addition, fishes and early tetrapods possess lateral sensory-line canal or pit-line which passes through the center of ossification of the dermal bones, and induces their formation (Janvier, 1996b), thus the dermal head bones that bear such a canal or a pit line have been widely used as landmarks for identifying other adjacent bones. Generally, the lachrymal, jugal, postorbital/dermosphenotic carry the infraorbital canal beneath the eye, and the preoperculum carries the preopercular canal from the cheek to the mandible; the squamosal carries the jugal canal (a horizontal portion of the preopercular canal) forward from the preoperculum to join the infraorbital canal within the jugal bone (Forey, 1998). The last has therefore been widely used as a landmark for identifying the jugal. In this section, we will use these criteria to discuss the homology of cheek bones in crown gnathostomes.

### Chondrichthyans

The conventionally defined chondrichthyans (taxon I, Fig. 7) have only cartilaginous components in skulls and jaws and completely lack large dermal plates including the jugal (Maisey, 1984; Schultze, 1993).

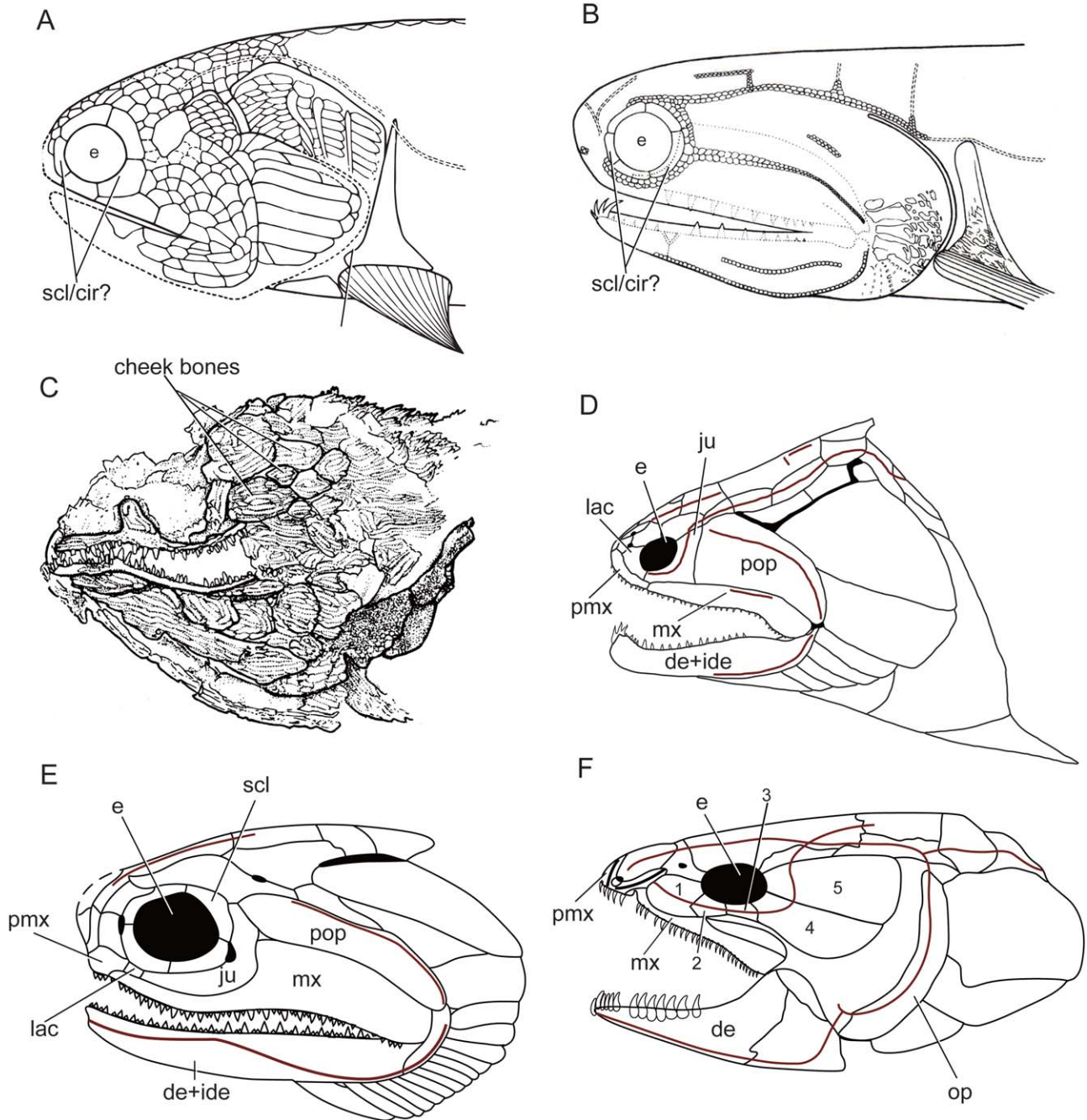


Fig. 4. Cheek bone pattern in acanthodians, stem osteichthyans, stem sarcopterygians and actinopterygians. A. acanthodian *Brachyacanthus* (after Watson, 1937); B. acanthodian *Ischnacanthus* (after Watson, 1937); C. stem osteichthyan *Dialipina* (after Schultze and Cumbaa, 2001); D. stem sarcopterygian *Guiyu* (after Zhu et al., 2009); E. actinopterygian *Cheirolepis* (after Arratia and Cloutier, 1996); F. actinopterygian *Amia* (after Jarvik, 1980a), Infraorbital 3 stipulated as homologous with the jugal (Schultze, 2008).

### Acanthodians

The presence of the jugal bone in acanthodians is still enigmatic. Most acanthodians have four to six large dermal bones around the orbits (Fig. 4A,B; Denison, 1979; Schultze, 1993), but it is difficult to decide whether these bones are circumorbital bones (Watson, 1937;

Denison, 1979; Janvier, 1996b) or sclerotic plates (Burrow et al., 2011). Maisey (1984) and Zhu et al. (2013) placed acanthodians as paraphyletic plesions on the stem segment of the chondrichthyan total-group (Figs. 1 and 7). This indicates that the macromeric dermal skeleton is a general feature of jawed vertebrates. Thus the

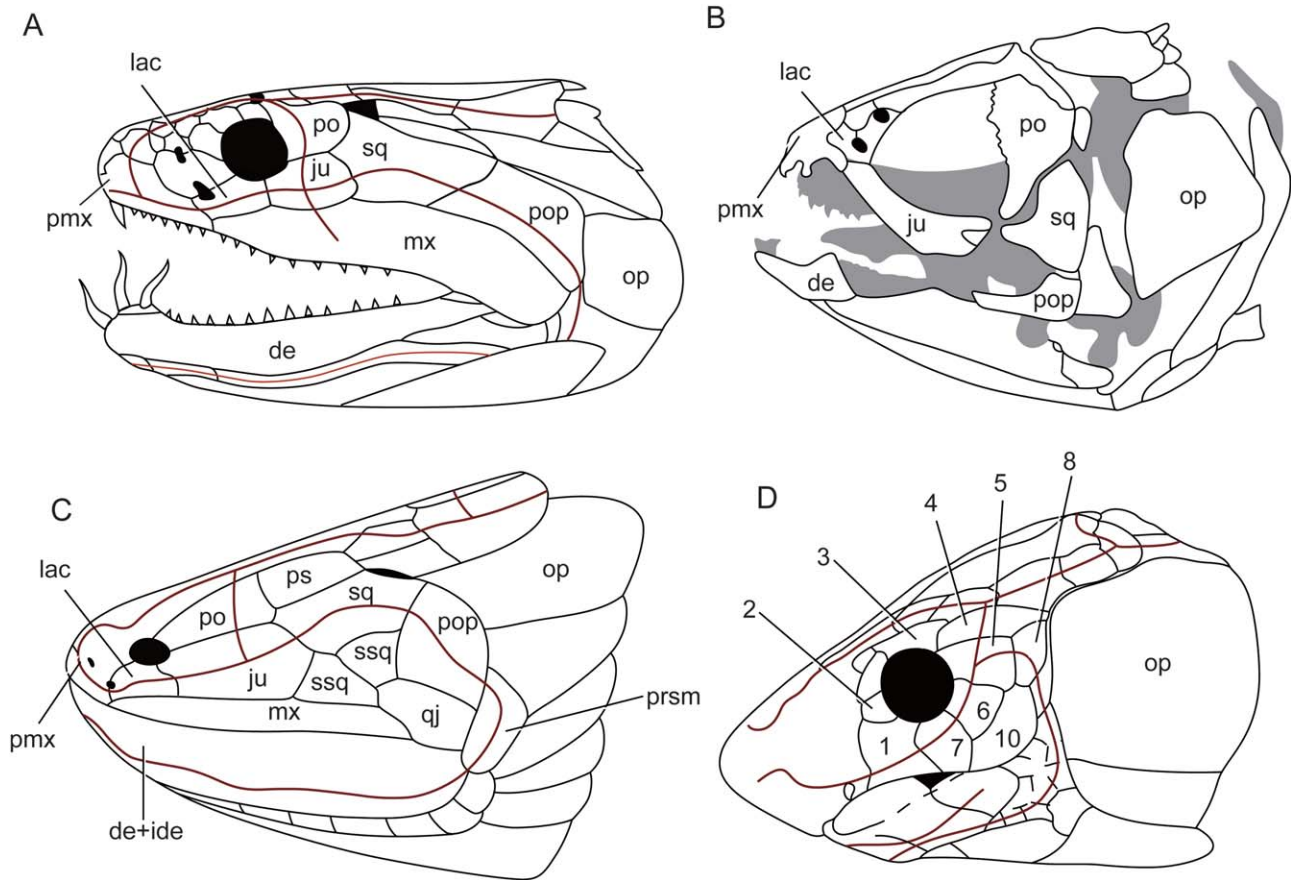


Fig. 5. Cheek bone pattern in onychodonts, actinistians, porolepiforms and dipnoans. A. onychodont *Onychodus* (after Long, 2001); B. actinistian *Latimeria* (after Forey, 1998); C. porolepiform *Porolepis* (after Janvier, 1996b); D. dipnoan *Chirodipterus* (after Miles, 1977).

last common ancestor of crown gnathostomes had a macromeric condition and acanthodian dermal skeleton probably underwent reduction (taxa H, Fig. 7), ultimately leading to the condition in chondrichthyans (taxa I, Fig. 7). While this interpretation is supported by many recent fossil findings, the partly micromeric cheek and jaw condition of the stem osteichthyan *Dialipina* (cheek bones, Fig. 4C, taxa G in Fig. 7) (Schultze and Cumbaa, 2001) as well as the micromeric regions found among the large skull plates of some placoderms (e.g., *Gemuendina*; Gross, 1963; Janvier, 1996b) and in the snouts of some sarcopterygians (e.g., *Powichthys*; Jessen, 1975; Clément and Janvier, 2004) have to be treated as independent origin of the micromeric condition in different taxa. Further research on the chondrichthyan total group may indicate that micromeric conditions represent a derived condition among crown gnathostomes while the large dermal bone patterns reflect the general conditions of the gnathostome total group.

### Actinopterygians

The primitive actinopterygians (e.g., *Cheirolepis*, *Mimipiscis*) have a small number of cheek bones consisting of the jugal, lachrymal, preopercular, premaxillary, and maxillary bones (Figs. 4E and 7; Jollie, 1962;

Ahlberg, 1991; Arratia and Cloutier, 1996; Choo, 2012). The preopercular (pop, Fig. 4E) is much larger than the jugal (ju, Fig. 4E) in *Cheirolepis*, and reaches far dorsally to contact the skull roof and carries the preopercular canal that connects with the otic canal. The squamosal is absent in all actinopterygians. In advanced actinopterygians (e.g., neopterygian *Amia*, Figs. 4F and 7, and teleost *Elops*, taxon M in Fig. 7), the jugal and the lachrymal are divided into smaller bones known as infraorbitals (usually designated as infraorbitals 1–5, Fig. 4F; Harder, 1975; Nybelin, 1979; Jarvik, 1980a). Schultze (2008) proposed that the infraorbital 1 is homologous with the lachrymal, and the infraorbital 3 is homologous with the jugal (Figs. 4F and 7). He stipulated that infraorbitals 2, 4, and 5 are new formations that arose independently within the actinopterygian lineage.

### Stem Sarcopterygians

The sarcopterygian lineage or the sarcopterygian total-group comprises stem sarcopterygians and crown sarcopterygians, from the latter of which evolved early tetrapods or land vertebrates.

Recent discoveries of stem sarcopterygians such as *Guiyu*, *Achoania*, and *Psarolepis* from the Siluro-Devonian of China, especially the oldest articulated

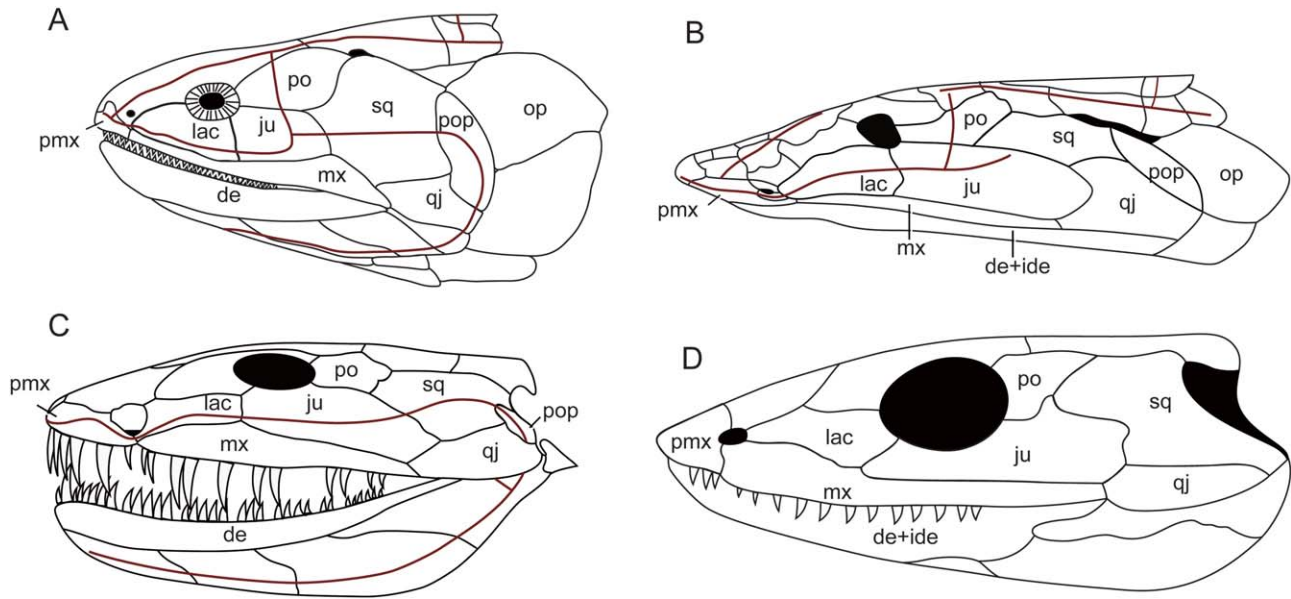


Fig. 6. Cheek bone pattern in osteolepiforms, elpistostegids and early tetrapods. A. osteolepiform *Eusthenopteron* (after Jarvik, 1980a); B. elpistostegid *Panderichthys* (after Vorobyeva and Schultze, 1991); C. Devonian tetrapod *Ichthyostega* (after Jarvik, 1996); D. Carboniferous tetrapod *Dendrerpeton* (after Carroll, 1967).

osteichthyan *Guiyu* shed new light on homologizing dermal bones (Zhu et al., 1999, 2001, 2009). The cheek plates of *Guiyu* consist of lachrymal, jugal, preopercular, premaxilla, and maxilla (Figs. 4D and 7). The jugal (ju, Fig. 4D) is located postero-ventral to the orbit, and articulates anteriorly with a separate triangular bone enclosing the posterior nostril. This triangular bone was termed the preorbital as a skull roof bone by comparison to primitive actinopterygians (Zhu et al., 2009; Qiao and Zhu, 2010). However, this bone might alternatively be compared to the condition in early sarcopterygians such as *Onychodus* (Long, 2001; Andrews et al., 2006) and *Porolepis* (Ahlberg, 1991; Janvier, 1996b). Consequently, it is likely to be a lachrymal based on parsimonious interpretations of available fossil evidences (lac, Fig. 4D).

Posteriorly, the jugal contacts with a very large trapezoid plate, the preopercular (pop, Fig. 4D), which carries the preopercular canal from the cheek to the mandible. There is no evidence for the presence of squamosal and quadratojugal in *Guiyu* and other related forms. A single large preopercular is also present in *Psarolepis* (Zhu and Schultze, 1997; Yu, 1998; Zhu et al., 1999), *Styloichthys* (Zhu and Yu, 2002), *Youngolepis* (Chang, 1982, 1991), *Tungsenia* (Lu et al., 2012), and *Kenichthys* (Chang and Zhu, 1993; Zhu and Ahlberg, 2004) (Fig. 7). This large cheek plate in *Youngolepis* was regarded to be the fusion of preopercular, squamosal and quadratojugal (Chang, 1991; Chang and Zhu, 1993). The out-group comparison (with stem sarcopterygians and primitive actinopterygians) suggests that this is a single bone (preopercular) rather than a fusion of three bones. By comparison to the condition in placoderm *Entelognathus*, the preopercular is a novel bone in osteichthyans that shapes the cheek by articulating with the jugal anteriorly.

### Onychodonts

Onychodonts are considered basal members of crown sarcopterygians (Zhu et al., 2009). The cheek plates of *Onychodus* consist of the lachrymal, jugal, squamosal, preopercular, premaxilla and maxilla (Figs. 5A and 7), but the quadratojugal is either absent or very small (Jessen, 1966; Long, 2001; Andrews et al., 2006). The jugal (ju, Fig. 5A) is identified by its position, its relationship to the orbit, and by the fact that it contains the junction of the infraorbital and postorbital lateral lines. A large bone, the squamosal (sq, Fig. 5A), separates the preopercular (pop, Fig. 5A) from the jugal. Compared with the condition in stem sarcopterygians such as *Guiyu* and *Psarolepis*, the squamosal of *Onychodus* is presumably a novel bone for crown sarcopterygians.

### Actinistians

Actinistians or coelacanth (represented by *Latimeria* and its fossil relatives) have reduced cheek plates with no maxilla and quadratojugal (Figs. 5B and 7). The jugal (ju, Fig. 5B), the squamosal (sq, Fig. 5B) and the preopercular (pop, Fig. 5B) in coelacanth have no direct contact with each other. The jugal (ju, Fig. 5B) is a large plate-like bone forming the lower margin of the orbit and covering much of the side of the cheek and the upper jaw. As the jugal is very large and occupies the territory of both the lachrymal and the jugal in other sarcopterygians, the absence of the lachrymal was explained as the result of a fusion between the lachrymal and the jugal (Forey, 1998). However, Qiao and Zhu (2010) suggested that the “lacrimojugal” of coelacanth should be interpreted as a single bone (jugal). By comparison to *Guiyu* and *Onychodus*, we propose that the



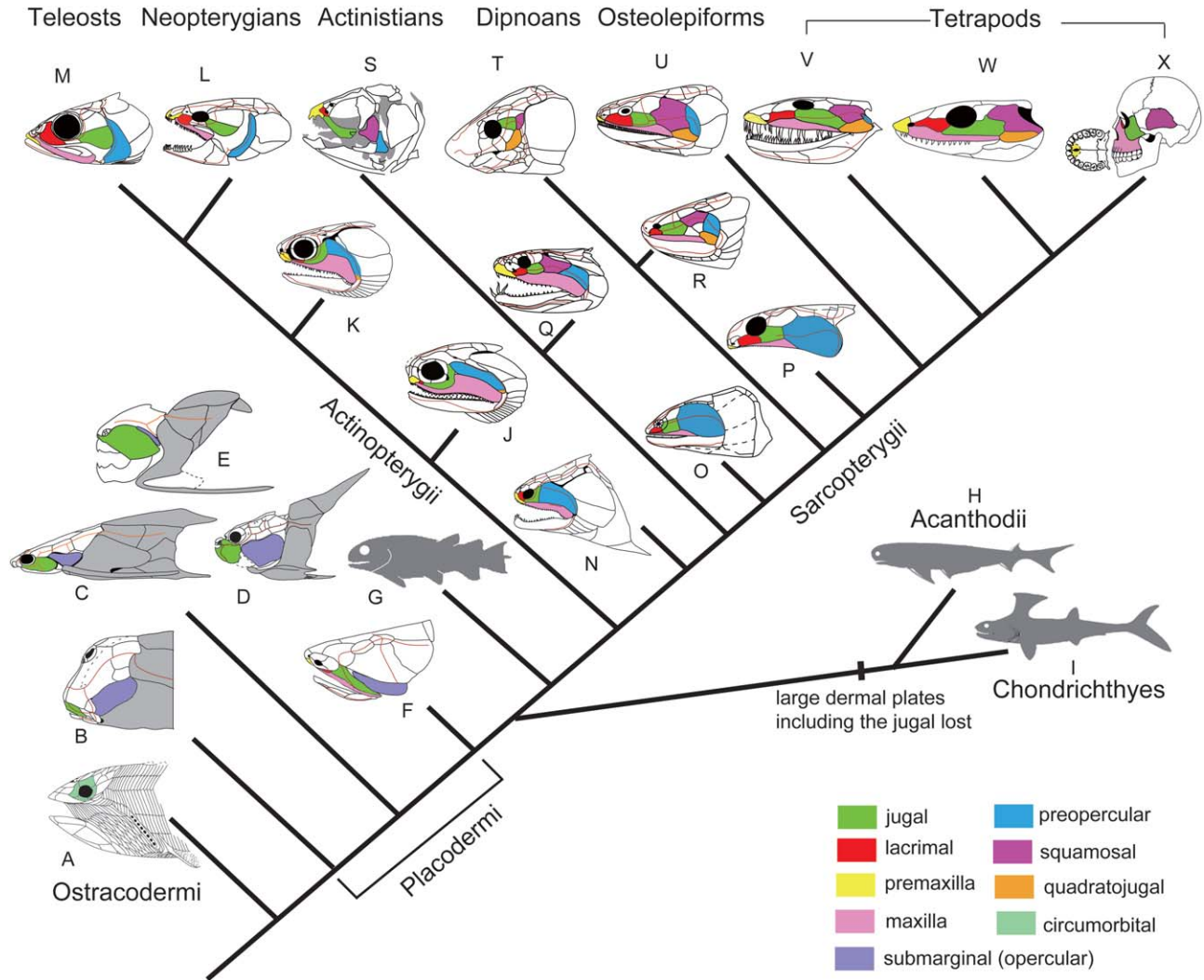


Fig. 7. Character transition of the zygomatic or jugal and related cheek and jaw bones in various vertebrate groups. A. *Rhyncholepis* (after Ritchie, 1980); B. *Bothriolepis* (after Young and Zhang, 1996); C. *Dicksonosteus* (after Goujet, 1984); D. *Romundina* (after Goujet and Young, 2004); E. *Dunkleosteus* (after Young, 2010); F. *Entelognathus* (after Zhu et al., 2013); G. *Dialipina* (after Schultze and Cumbaa, 2001); H. *Acanthodes* (after Denison, 1979); I. *Akmonistion* (after Coates and Sequeira, 2001); J. *Cheirolepis* (after Arratia and Cloutier,

1996); K. *Mimipiscis* (after Choo, 2012); L. *Amia* (after Jarvik, 1980a); M. *Elops* (after Nybelin, 1979); N. *Guiyu* (after Zhu et al., 2009); O. *Styloichthys* (after Zhu and Yu, 2002); P. *Kenichthys* (after Zhu and Ahlberg, 2004); Q. *Onychodus* (after Long, 2001); R. *Porolepis* (after Javier, 1996b); S. *Latimeria* (after Forey, 1998); T. *Chirodipterus* (after Miles, 1977); U. *Eusthenopteron* (after Jarvik, 1980a); V. *Ichthyostega* (after Jarvik, 1996); W. *Dendrerpeton* (after Carroll, 1967); X. *Homo* (courtesy of Brian Choo).

lacrimal (lac, Fig. 5B) in actinistians is represented by a small triangular bone, which was interpreted as the preorbital wedged between the jugal and the tectal (Forey, 1998).

Like *Onychodus*, actinistians lack a quadratojugal. Andrews et al. (2006) proposed that the quadratojugal is probably fused with the preopercular, and that this fusion is a derived feature of actinistians and onychodonts. However, Long (2001) proposed that the quadratojugal of primitive actinopterygians is homologous to the squamosal in actinistians and onychodonts. Based on the very small size of the quadratojugal in primitive actinopterygians (Pearson and Westoll, 1979) as well as the absence

of the quadratojugal in many early sarcopterygians such as *Guiyu* (Zhu et al., 2009), *Psarolepis* (Zhu and Schultze, 1997; Yu, 1998; Zhu et al., 1999), *Styloichthys* (Zhu and Yu, 2002), *Youngolepis* (Chang, 1982, 1991), *Tungsenia* (Lu et al., 2012) and *Kenichthys* (Chang and Zhu, 1993; Zhu and Ahlberg, 2004), we stipulate that the squamosal of *Onychodus* represents a novel bone found in crown sarcopterygians, as mentioned above.

The remaining taxa of crown sarcopterygians are usually divided into two subgroups, dipnomorphs (comprising porolepiforms and dipnoans) and tetrapodomorphs (comprising osteolepiforms and tetrapods) (Fig. 7), each with its own characteristic cheek bone pattern.

## Porolepiforms

The cheek plates of porolepiforms consist of the jugal, lacrymal, squamosal, preopercular, quadratojugal, maxilla, subsidiary squamosals, prespiracular, and preoperculosubmandibular (Figs. 5C and 7), with the last three bones considered as novel elements unique to porolepiforms (Ahlberg, 1991). The jugal (ju, Fig. 5C) of porolepiforms is considerably larger than the lacrymal and the postorbital (lac, po, Fig. 5C). The preopercular (pop, Fig. 5C) is a broad bone with a long suture against the quadratojugal (qj, Fig. 5C), and the posterior end of the maxilla (mx, Fig. 5C) is shallow. The preopercular-jugal

canal passes through three bones, that is, the squamosal, the preopercular and the preoperculosubmandibular, and these three bones occupy the same region as the preopercular of *Youngolepis*, *Kenichthys*, *Tungsenia*, *Styloichthys* and stem sarcopterygians.

## Dipnoans

The bone arrangement in dipnoans is so different from other bony fishes that the traditional names could not be applied (Forster-Cooper, 1937; Jarvik, 1967). Dipnoans have 10 or more bones in a short cheek region

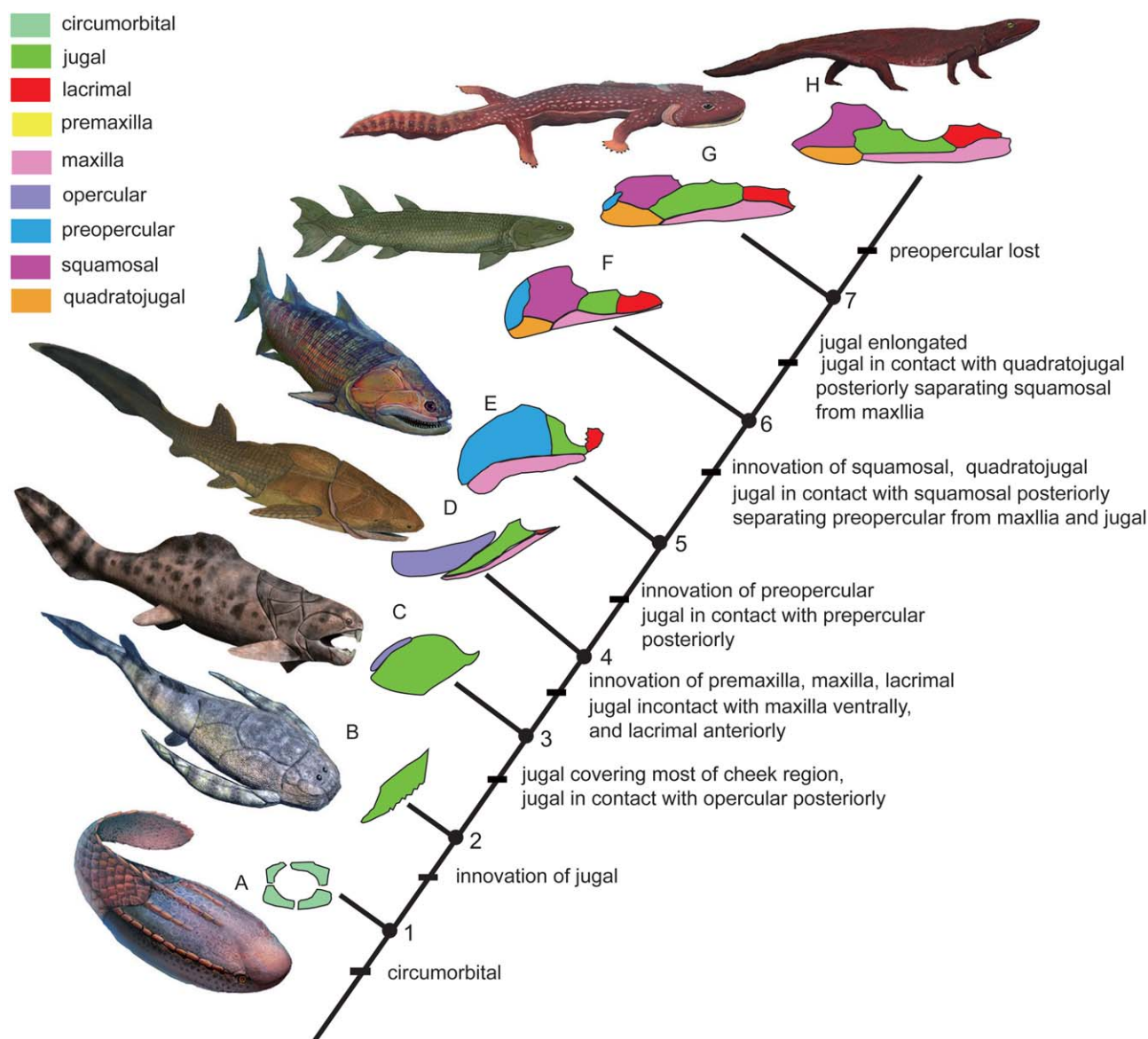


Fig. 8. Major steps in the evolution of the zygomatic or jugal bone from agnathans to tetrapods. The jugal can be traced to the most basal jawed vertebrates (antiarchs). The premaxilla, maxilla, lacrymal and possibly quadratojugal first arose in *Entelognathus*. The preopercular first arose at the base of osteichthyans (bony fishes and

tetrapods) but was subsequently lost in tetrapods. A. *Astraspis*; B. *Bothriolepis*; C. *Dunkleosteus*; D. *Entelognathus*; E. *Guiyu*; F. *Eusthenopteron*; G. *Acanthostega* (life restoration) / *Ichthyostega* (cheek bone pattern); H. *Dendrerpeton*. (A, courtesy of Dinghua Yang; B, C, courtesy of Nobu Tamura, D–H, courtesy of Brian Choo).

(1–10, Fig. 5D), but the maxilla and the premaxilla are absent. The infraorbital canal passes through a series of circumorbital bones (numbered 4, 5, 6, 7, 1) before it reaches the snout (Miles, 1977; Schultze, 1993). However, it is difficult to determine which of these bones may be considered homologous to the jugal in other forms.

### Osteolepiforms

The cheek bones of osteolepiforms (e.g. *Eusthenopteron*, Fig. 6A and 7; Jarvik, 1942, 1980b) comprise the lachrymal, jugal, squamosal, quadratojugal, premaxilla, and maxilla. The cheek is characteristic in showing a relatively short jugal (ju, Fig. 6A), with a large squamosal, a quadratojugal, and a bar-shaped preopercular (sq, qj, pop, Fig. 6A). The quadratojugal (qj, Fig. 6A) separates the maxilla from the preopercular (pop, Fig. 6A). The large squamosal (sq, Fig. 6A) meets the maxilla at the back of the cheek, and separates the quadratojugal from the jugal (Clack, 2002b).

### Early Tetrapods

The main cheek bones of early tetrapods include the lachrymal, jugal, squamosal, quadratojugal, premaxilla and maxilla (Figs. 6C,D and 7; Clack, 2002a,b, 2003). The preopercular is a rather superficial element of the cheek in *Acanthostega* and *Ichthyostega* (pop, Fig. 6C; Jarvik, 1996; Clack, 2002a), and completely lost in other tetrapods (e.g., *Dendropeton*, Fig. 6D; Carroll, 1967). The size of the jugal (ju, Figs. 6C,D and 7) has a great increase in tetrapods so that an isolated jugal bone from an early tetrapod can be distinguished from that of an osteolepiform fish by its size and its proportional contribution to the formation of the orbital margin (Clack, 2002b). Tetrapods also differ from sarcopterygian fishes in that their elongate jugal contacts the quadratojugal and separates the squamosal from the maxilla (Figs. 6C,D and 7). An intermediate condition already existed in varying degrees in the elpistostegid sarcopterygians such as *Elpistostegia*, *Panderichthys* (Fig. 6B) and *Tiktaalik* from the Middle to Late Devonian, which are the closest tetrapod relatives known at present (Schultze and Arsénault, 1985; Vorobyeva and Schultze, 1991; Daeschler et al., 2006).

### SUMMARY: MAJOR STEPS IN THE EVOLUTION OF THE ZYGOMATIC

We can tentatively summarize the major steps in the evolution of the zygomatic or jugal bone from the agnathans to tetrapods based on currently accepted phylogenetic hypothesis (Zhu et al., 2013; Dupret et al., 2014; Long et al., 2015; Giles et al., 2015) (Fig. 8). Further research on more acanthodians may shed light on the loss of jugal and marginal jaw bones which are uniquely seen in *Entelognathus* and crown osteichthyans and presumably existed in the last common ancestor of crown gnathostomes.

The jugal probably arose from some specialized dermal bones (circumorbitals or suborbital plate) in the jawless ostracoderms as early as in the Ordovician (470 million years ago) (Node 1, Fig. 8). The identification of the mental plate as the jugal in antiarchs has extended the homology of jugal bone from osteichthyans to the

most basal jawed vertebrates (Node 2, Fig. 8). In most non-*Entelognathus* placoderms, the jugal (= suborbital plate) occupies most of the cheek region and covers the palatoquadrate laterally, probably representing a primitive condition of the jugal (Node 3, Fig. 8). As non-*Entelognathus* placoderms have fewer cheek bones than crown gnathostomes, the jugal has a simple contact relationship, that is only in contact with the postsuborbital or/and opercular posteriorly.

The discovery of *Entelognathus* from the Silurian of China provides the earliest evidence of osteichthyan-like premaxilla, maxilla, and lachrymal in placoderms (Node 4, Fig. 8). As additional dermal bones (premaxilla, maxilla, and lachrymal) join in the cheek formation, the contact relationship of the jugal becomes more complex. It is now in contact with the lachrymal anteriorly, the maxilla ventrally, and the opercular posteriorly. Thus, *Entelognathus* significantly reduces the morphological gap between placoderms and osteichthyans, and presents a configuration of bones that is unique among known placoderms and presumably marks the earliest appearance of the typical vertebrate face.

In the common ancestor of crown osteichthyans (Node 5, Fig. 8), a large novel bone (the preopercular) began shaping the face by separating the opercular from the jugal. A single large preopercular with no squamosal or quadratojugal is present in advanced actinopterygians, stem sarcopterygians (*Psarolepis*, *Guiyu*, and *Achoania*), stem rhipidistian (*Styloichthys*), primitive dipnomorph (*Youngolepis*), and primitive tetrapodomorphs (*Kenichthys* and *Tungsenia*). This raises the possibility that squamosal, quadratojugal or both arose independently in actinopterygians, actinistians, dipnomorphs and tetrapodomorphs, probably by subsequent division of the single large preopercular. The disassociation of a large single preopercular into an assembly of preopercular, squamosal and/or quadratojugal impacts on the posterior contact relationship of the jugal.

In the lineage leading from stem sarcopterygians to osteolepiforms (Node 6, Fig. 8), the preopercular was subdivided into an assembly of bones including squamosal, quadratojugal, and preopercular. The squamosal, a large novel bone, is in contact with the jugal anteriorly, which separates the preopercular from the jugal, whereas another novel bone, the quadratojugal, separates the preopercular from the maxilla (Node 6, Fig. 8).

During the transition from osteolepiforms to tetrapods (Node 7, Fig. 8), the jugal had an obvious increase in size and contacted the quadratojugal, together separating the squamosal from the maxilla, whereas the preopercular was largely reduced in size in Devonian tetrapods *Ichthyostega* and *Acanthostega*, and was completely lost in later tetrapods. The position of the preopercular was taken up by the expanded contact between the squamosal and quadratojugal bones. After that, the lachrymal, jugal, squamosal, quadratojugal, premaxilla and maxilla became crucial and stable facial components in shaping the face of tetrapods including humans.

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