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Review Article

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THE EVOLUTION OF TEMPOROMANDIBULAR JOINT

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ABSTRACT

Evolution is the dynamic process through which changes occur in genetic structures with resultant changes in phenotypes over time. These changes or addition of new features, which are necessary for the progeny of a species to cope with the environmental factors, bring about the variations seen in animal kingdom. These variations have implications in modern anthropology, medical and forensic sciences. Mammals are distinguished from other vertebrates by many features, one of which is the structure and function of the jaw joint. The purpose of this review is to highlight the underlying mechanisms that are responsible for the distinctive features and adaptations of the mammalian jaw joint in terms of form and function.

KEYWORDS: temporomandibular joint, evolution, mammalian jaw.

INTRODUCTION

The theory of evolution is the cornerstone of the modern biological sciences. The innumerable variations in living organisms are the cumulative results of the long-standing evolutionary processes. Natural selection which is the fundamental concept of theories of evolution proposed by Charles Darwin, is the process through which the living organisms, more adapted to the changed environment, survive and pass the favourable traits on their progeny over time which bring differences and divergence in the process of evolution. The temporomandibular joint (TMJ) is a unique feature of the class mammalia as it is not seen in other vertebrates. The joint is formed between the squamous part of the temporal bone and the mandibular condyle, hence called as temporomandibular joint. The distinctive features of the mammalian jaw joint as compared to invertebrates and other vertebrates has long been studied and compelling evidences have been found by comparative anatomists, embryologists and oral biologists which describe the evolution of the mammalian TMJ. This review highlights the mechanisms that brought the structural and functional changes which in turn resulted in the mammalian jaw joint.

Significance of studying the evolution of TMJ

Biology is always dynamic in nature. The epigenetic factors bring about the changes in the functioning of a biological system which eventually leads to changes at molecular level that are inheritable. Modern sciences help us finding the “normal” as well as the “deviations” from it, the causative factor/s and the “cure” to get back to the normal. By studying evolution, correlations can be made amongst the developmental attributes, normal functioning and environmental factors for the occurrence of deviations from normal in a system. Studying the evolution of TMJ may help us in.

1. Determining normal development and functioning of TMJ.
2. Finding the effects of occlusion and environmental factors e.g., eating habits.
3. Knowing how the existing TMJ problems evolved and choosing the most appropriate available treatment option.
4. Tracing the expected changes and diseases in future and finding new treatment modalities.

The basic concept of jaws in vertebrates

Most of the vertebrate animals are having cartilaginous or bony upper and lower jaws opposing vertically, which are derivatives of the two most anterior pharyngeal arches. One of the earliest models of the subphylum vertebrata, the agnathans (e.g., hagfish) don’t have well defined jaws, instead a cyclostomic (circular) structure with teeth forms the mouth.

The gnathostomes are the initial members of the subphylum vertebrata which have the vertically opposing upper and lower jaws with teeth. This evolution was likely to support the gill arches. The movement of the jaws in gnathostomes would help pushing the water over the gills for efficient gaseous exchange. The repetitive use of jaws helped some gnathostomes to develop the skill of biting.[1]

In tetrapods (e.g., amphibians, reptiles) further development of the jaw structure occurred and apprehension of preys followed by biting and swallowing became the primary function of the jaws. The upper jaw bones (quadrate, jugal, quadratojugal, maxilla and premaxilla) became fused to the skull bones and the lower jaw bones (articular, surangular, angular, preangular, spenial and dentary) together formed the lower component of the feeding apparatus (Fig. 1). The lower component articulates with the upper one via a hinge joint exhibiting various degrees of mobility.[2]

In the transition from reptiles to the mammals the single bone (homologous to dentary) formed the lower jaw and some of the bones (articular and quadrate) previously forming the jaw system, got incorporated in the middle ear.

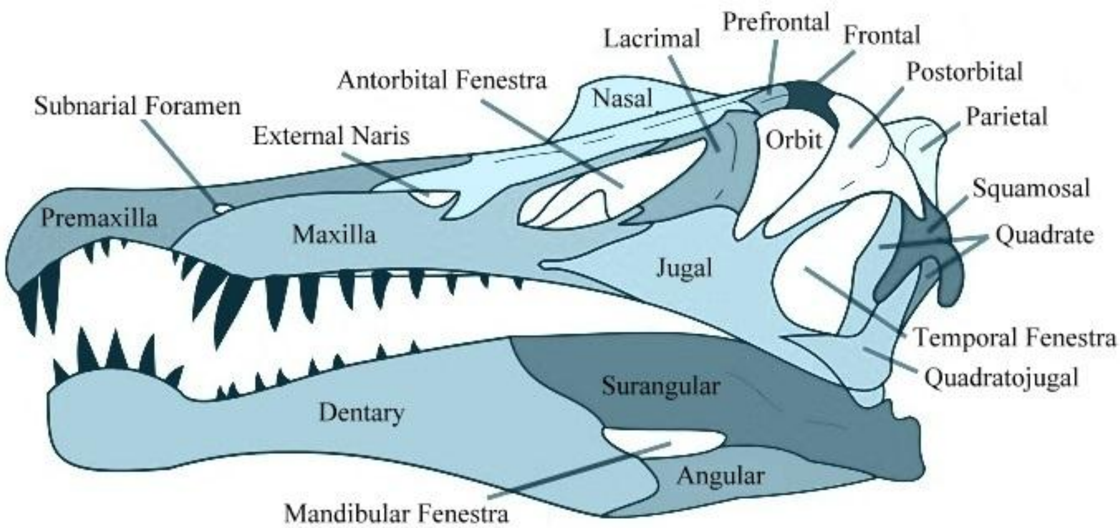

Fig. 1: Reptilian skull; multiple bones fuse together to form the upper and the lower jaws.

Morphological types of joints in the process of evolution

(i) Synarthroses: Simplest form of joint. The two skeletal parts are attached together by connective tissue, fibro-tendinous tissue, cartilage or fibrocartilage. In jawless fishes (agnathans) a thin plate of fibrocartilage connects the two cartilaginous joint elements and merges with its perichondrium peripherally forming a synarthrosis.
(ii) Schizarthroses: A number of separate fluid-filled cavities appear in the connective tissue between the two skeletal elements.
(iii) Hemidiarthroses or Periarthroses: In this type of joint a single cavity occupies the centre of the joint and the articulating skeletal elements are united at the periphery of the joint.
(iv) Eudiarthroses: This is the definitive diarthroidal joint. Articulating skeletal elements are separated from one another by the joint cavities. The synovial tissues limit the joint periphery. This type of jaw joint is primitive in some bony fishes (teleosts) and tetrapods.[3]

The evolution of the TMJ anatomy

The mammalian lower jaw is comprised of a single bone, the mandible, whereas in non-mammals, it is formed by multiple bones. Thus, an important distinguishing feature of mammalian lower jaw is the reduction in number of bones. This reduction occurred slowly over approximately 120 million years.

A number of transformations took place in the feeding apparatus as the divergence of species underwent giving rise to the mammals. These include reduction in the sizes of post-dentary bones of lower jaw, caudal extension of the dentary and switching of the primary articulation site from the quadrate-articular to the dentary-squamosal. These transformations can be illustrated in three different stages.

(A) Basal condition: Dimetrodon[4] (Fig-2A)
(i) The lower jaw is composed of multiple bones
(ii) The dentary is restricted to the rostral part of lower jaw
(iii) Single articulation site on the articular

(B) Intermediate condition: Diarthrognathus [5] (Fig-2B)
(i) The lower jaw is comprised of multiple bones
(ii) The post-dentary bones, reduced in size, are restricted to the caudal part of lower jaw
(iii) The relative size of dentary has increased
(iv) Two sites of articulation: One on the articular and the other on the dentary

(C) Derived mammalian condition: Monodelphis[6] (Fig-2C)
(i) Lower jaw is formed by a single bone, which is homologous with the dentary
(ii) The articular (=malleus) and the quadrate (=incus) have been incorporated into the middle ear (Fig. 3)
(iii) Single articulation site on the dentary (=mandible)

The embryological development of TMJ in mammals is similar to the evolutionary history as described above. The malleus (=articular) which originates as a part of lower jaw initially, gets separated from lower jaw at later stages of development. Suckling is seen at very immature stage in young marsupials, when the articular and incus form the functional jaw joint. At later stages of development these two bones move into middle ear after the establishment of contact between dentary and temporal bone.[7]

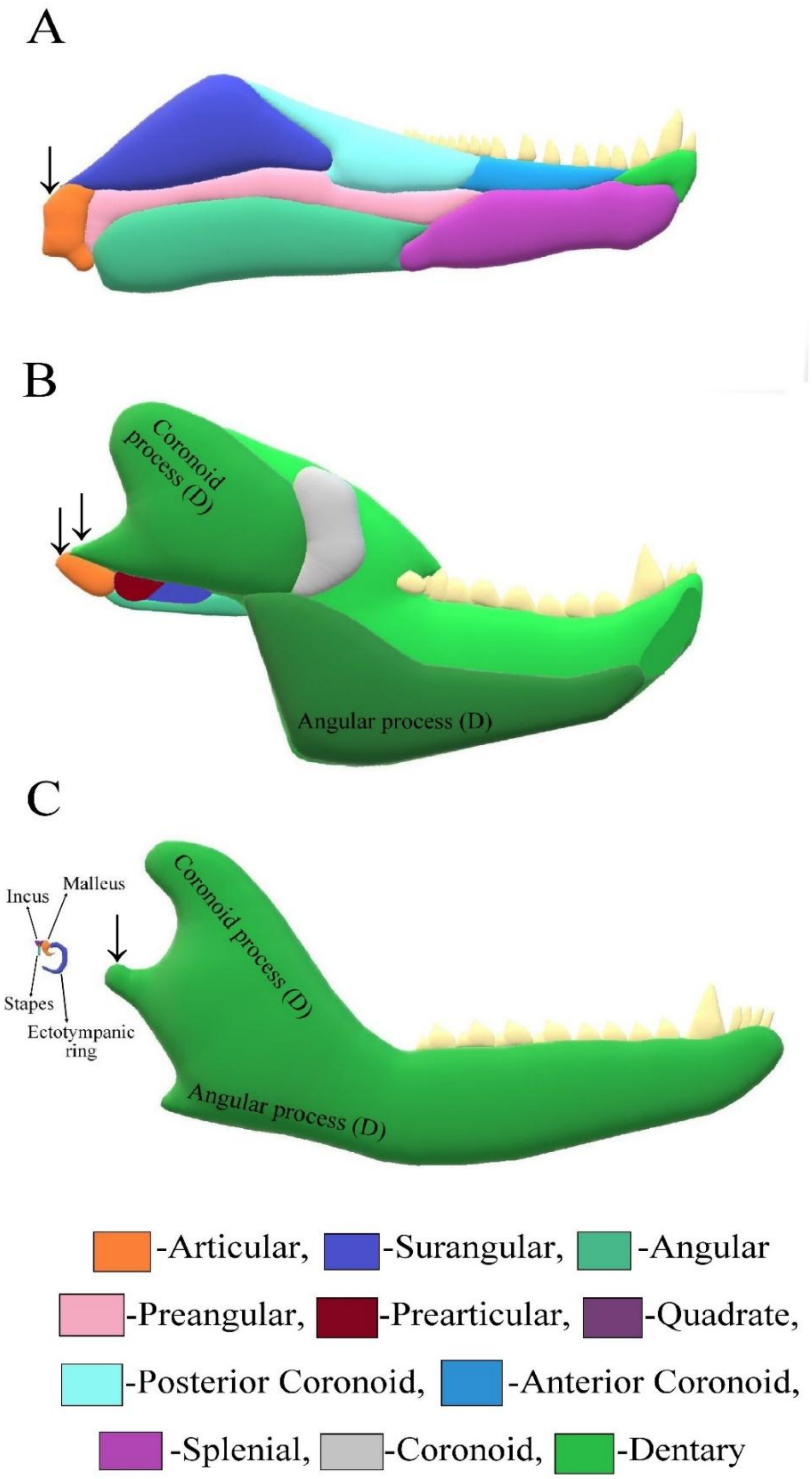

Fig. 2: Illustration of the transition to mammalian jaw joint from basal condition. Mandibles from Dimetrodon (A), Diarthrognathus (B) and Monodelphis (C) are shown in medial view. Arrows indicate site(s) of articulation.

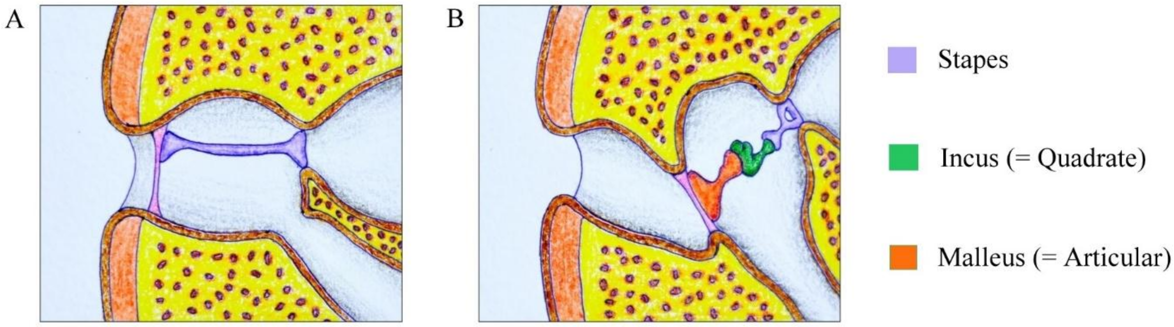

Fig. 3: Reptilian (A) and mammalian (B) middle ear bones. The articular and the quadrate have been incorporated into the mammalian middle ear.

Histologic evolution of the TMJ

A review of developmental and comparative anatomy provides important data suggesting important changes in histology over time. The Meckel's cartilage, which is thought to act as a scaffold for the development of the musculoskeletal infrastructure of the mammalian lower jaw[8], acts somehow differently in non-mammalian vertebrates. In non-mammalian vertebrates, the articular bone (which forms the lower part of jaw joint) ossifies endochondrally from the Meckel's cartilage[9], thus making the cartilage lining the jaw joint hyaline-like, lacking fibrous perichondrium or any organized bundles of fibrous matter.[10]

In contrast, the distal part of condylar process (dentary) in mammals undergoes endochondral ossification from secondary cartilage.[11] Shibata et al showed that in mice, the progenitor cells of mandibular condylar cartilage, are derived from the periosteum of developing mandible.[12] Thus, the articular and prechondroblastic layers possess fibrocartilaginous properties having organized bundles of fibroblast-like cells and type-I collagen.[13] The composition of the cartilaginous lining on the temporal fossa is similar to the condylar cartilage. The underlying chondroblastic layer have hyaline-like properties, unlike the articular or prechondroblastic layers.[13]

Another evolutionary change in jaw joint is the incorporation of intra-articular disc in metatherian mammals (marsupials) and eutherian mammals, which is absent in non-mammals and protherian (basal condition) mammals.[14] The intra-articular disc is thought to be the result of the mesenchymal condensation between the condyle and fossa[15] or the mesenchymal separation from condylar blastema.[16]

Comparison between reptilian and mammalian jaw joints.

Reptilian Jaw Joint	**Mammalian Jaw Joint**
Reptiles have only one bone in middle ear (the stapes) and the lower jaw is made up of at least 7 bones.	Mammals have 3 bones in the middle ear and a single-boned (the mandible/dentary) lower jaw.
The teeth are supported by the reptilian dentary which is followed by a series of post-dentary bones.	The teeth are supported by the mandible only and there are no post-dentary bones.
In reptiles jaw joint is formed between the last post-dentary bone (the articular which is homologous to malleus) and a skull bone, the quadrate (which is joined to the temporal bone).	In mammals jaw joint is formed between the single bone of the lower jaw, the dentary and the temporal bone of the skull.
The cartilage lining of lower jaw (at the jaw joint) is hyaline-like, which lacks fibrous perichondrium.	In the condylar cartilage, articular and prechondroblastic layers possess fibrocartilaginous properties while the chondroblastic layer possesses hyaline-like properties. The cartilage is lined by fibrous perichondrium continuous with the periosteum of mandibular ramus.
All bones of lower jaw except the articular, are dermally derived from and develops around Meckel's cartilage. The articular undergoes endochondral ossification from Meckel's cartilage.	Mandibular body (dentary) undergoes intramembranous ossification while the distal portion of condylar process undergoes endochondral ossification from the secondary cartilage. Meckel's cartilage acts as a scaffold for development of musculoskeletal infrastructure.
Reptiles and other non-mammals don't have intra-articular disc in the jaw joint.	All eutherian and some taxa of metatherian mammals (marsupials) have the intra-articular disc. All protherian (monotremes) mammals, which represent the basal condition in mammals, lack this unique feature.

Evolution of the muscular elements surrounding the jaw joint

The mechanics of reptilian jaw joint is like a third-class lever in which the joint acts as a "fulcrum", the bite force acts as "load" and the jaw closing muscles act as "force". As the muscles (force) are closer to the joint than the point of bite (load), greater forces pass vertically through the joint than the forces generated between teeth at the biting point.

The reptilian jaw-closing muscles insert on the lower, inner and upper surfaces of the lower jaw, which pull the jaw forward and inward or upward and inward. Unilateral contraction tends to medial deflection of the lower jaw which is limited by the pterygoid flanges. The mechanics of the jaw joint and the requirement of limiting the medial deflection on unilateral contraction of closing muscles necessitates for a larger jaw joint to withstand the forces passing through it. For example, crocodiles and other reptiles have jaw joints relatively larger than their skull sizes.[7]

In mammals, the morphology of the teeth with multiple opposing shearing surfaces makes the jaw movement rather complex. In order to be able to chew food, combination of movements or complex movements are necessary for the shearing surfaces to glide/contact precisely over/on the other. This is made possible due to the fact that the position and orientation of the mammalian jaw closing muscles are different from those of reptiles. A "sling of muscles" surrounds each side of lower jaw.[17] Unlike reptiles, the mammals have large masseter on the outer surface of lower jaw which acts as the counterpart of the pterygoids inserted on the inner side. The temporalis provides additional biting force while chewing food. The selective contraction of the two "slings of muscles" makes all the complex jaw movements possible in mammals.

Genetic aspect of TMJ evolution

The Hox gene family is responsible for encoding proteins that influence cell proliferation, differentiation, movement, adhesion and cell death resulting in body morphogenesis. The vertebrates with jaws have four clusters of Hox genes (Hox A, B, C and D). The bony fishes and the amniotes have the similar sets of genes with the identical linear sequence in Hox A, B and D clusters suggesting consistency in controlling the gene expressions required for vertebrate morphogenesis.[18]

Two major duplications of Hox genes are thought to have occurred in early evolution of vertebrates. The first during the transition between cephalochordates and agnathans and the second during the transition between agnathans and gnathostomes.[19]

CONCLUSION

The temporomandibular joint is unique in nature when compared to other joints. It's developmental origin and evolutionary pathway possess complex mechanisms which resulted in the modern mammalian jaw joint. These mechanisms are clearly in favour of the improved efficiency of the masticatory function and the auditory acuity in the higher vertebrates, the mammals. The changes in food habits and morphologies of dentition further helped the jaw joint and its surrounding musculature to acquire their modern form and functions. Here the morphologic, histologic, functional and genetic aspects of evolution of the TMJ have been reviewed from the previous studies which help us understand

1. The complex nature of jaw movements and correlate them clinically while restoring the form and function.
2. The tissue engineering required for designing physiologic joint regenerates that may benefit the existing TMJ problems.

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