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A review paper-on pharyngeal jaw apparatus of family cichlidae

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Abstract

Pharyngeal jaw apparatus is complex musculo-skeletal system which are modification of gill arch elements that is useful for masticating and transporting of food material. It consist of two independent upper plate and single fused lower plate that are containing various types of unicuspid, bicuspid or molariform dentition. Relationship between pharyngeal jaw for feeding and sound production may have profound evolutionary implications. It has serving as a possible mechanism for sound production; trophic biology and reproductive biology could be directly linked by this structure. Consequently, the dual use of the pharyngeal jaw may serve as a mechanism mediating the sympatric speciation of cichlid fishes. Intraspecific pharyngeal variations also occurred in some fishes that helpful to understanding lineage relationships.

Keywords: Pharyngeal apparatus, sound production, evolution, lineage relationship, cichlidae

Introduction

Cichlids are members of a suborder known as Labroidei, along with the wrasses (Labridae), damselfishes (Pomacentridae), and surferperches (Embiotocidae). Cichlids are a species-rich clade of acanthomorph fishes that have captured the attention of ecologists, ethologists, and micro and macro-evolutionary biologists (Keenleyside, 1991; Barlow, 2000; Kornfield and Smith, 2000) [29, 7, 31]. Kullander (1998) [32] recognizes eight subfamilies of Cichlids: the Astronotinae, Cichlasomatinae, Cichlinae, Etroplinae, Geophaginae, Heterochrominae, Pseudocrenilabrinae and Retroculinae. Cichlids are one of the most diverse lineages of freshwater fishes with more than 1,600 species (McMahan *et al.*, 2013) [43]. They represent the largest clade of freshwater euteleosts (Nelson, 2006) [48] and exhibit a Gondwanan distribution, with representatives found throughout Africa, South and Middle America, Madagascar, India, Sri Lanka, Cuba, Hispaniola, Syria, Israel, and Iran (Stiassny, 1991; Chakrabarty, 2004; Sparks and Smith, 2004) [57, 12, 56].

The South Asian Cichlidae are composed of two clades that together represent the sister group of the Madagascan genus *Paretroplus* (Bleeker). *Chaetodon suratensis* (Bloch) and *Etroplus canarensis* (Day) are retained in *Etroplus* (Cuvier), while *Chaetodon maculatus* (Bloch) is allocated to *Pseudetroplus* (Bleeker). South Asian cichlids represent an interesting example of transoceanic Gondwanan variance (Sparks & Smith 2005; Friedman *et al.* 2013) [55, 17]. Three species have been recognized: *Etroplus suratensi*; type species of *Etroplus* Cuvier, *E. maculatus* and *E. canarensis*. The former two species occur in the lowlands of Sri Lanka and southern peninsular India whereas the third is restricted to the Netravati River in Karnataka State, India. The ubiquity of omnivores among cichlids may be largely an adaptive response to environmental conditions throughout their evolutionary history and therefore may also represent an ancestral condition. Convergence infers that natural selection has independently selected similar traits and thus provides strong evidence for their adaptive quality; such traits may be associated with increased fitness or positive selection (Losos, 2011; Elmer & Meyer, 2011) [42, 16]. The pharyngeal jaw apparatus of family cichlidae is complex musculo-skeletal system which are modification of gill arch elements that is useful for masticating and transporting of food material. Labroid fishes contain the synapomorphy of a well-developed pharyngeal jaw apparatus with fused with fifth ceratobranchials forming a single lower pharyngeal jaw plate that is evolutionary key innovation for the success of Labroid fishes (Kaufman & Liem, 1982; Liem, 1973; Liem & Greenwood, 1981; Stiassny & Jensen, 1987) [28, 39, 38, 58].

Pharyngeal jaws shows evolutionary diversification among cichlids not only by increasing functional capacity, efficiency and versatility but also by releasing the oral jaws from many functional demands associated with processing food (Liem, 1973) [39]. In cichlid fishes, tooth shapes and structures also provide important taxonomic and evolutionary characters (Trewavas, 1983) [62]. Cichlid dentition has evolved rapidly and convergent in association with diversification of foraging modes (Ruber *et al.*, 1999; Streelman *et al.*, 2003) [50, 59]. A review paper on this concept very helpful for taxonomic evolution of fishes and establishment of phylogenetic tree of the fishes from family cichlidae.

Role of PJA in relation to feeding

In Cichlids, the pharyngeal jaw apparatus consist of two independent upper plate and single fused lower plate that are containing various types of unicuspid, bicuspid or molariform dentition (Casciotta & Arratia, 1993; Hulsey, 2006) [11, 26]. Pharyngeal jaw apparatus to increase the functional capacity, efficiency and versatility of the fishes (Wainwright, 2012) [65]. Oral and pharyngeal jaws developmentally & functionally decoupled, that are derived from the first and seventh pharyngeal gill arch respectively (Liem, 1973; Hulsey, 2006) [39, 26]. The lower pharyngeal jaw, shape and structure are highly associated with the dietary characteristics of the species and thus displays the variation in shape and dentition (Meyer, 1989) [44]. During the prey-processing, structural stress is concentrated along the posterior midline of pharyngeal jaw, where the most dentition specialized for crushing is located. The degree that the pharyngeal bone is reinforced and the size and shape of dentition greatly depending on the degree to which the species exploits hard-shelled prey and thus the degree of stress incurred during mastication (Hulsey, 2006) [26]. Some fishes that do not require crushing force for prey, often associated with the reduced pharyngeal jaws that possess conical recurved teeth suitable for grasping and manipulating prey that consumed whole (Helling *et al.*, 2010; Burrell *et al.*, 2013) [25, 10]. These relatively atrophied pharyngeal bones probably precludes these species from exploitation of difficult to manipulate prey items such as molluscs that possess shells that require crushing force (Mittelbach, 1984) [45].

Some herbivorous species have relatively well-developed pharyngeal jaw that often possess large conical teeth, these large teeth may generate the crushing or tearing force necessary to efficiently manipulate husks or seed associated with many fruits. Pharyngeal jaw are functionally linked to the aforementioned benthic shifting foraging strategy that is ubiquitous among cichlids. Shifting species utilize the pharyngeal jaw much like a rake to help separate food from mouthfuls of sediment and thus may be associated with various pharyngeal morphologies depending on the degree of sifting and target prey (Drucker & Jensen, 1991) [15]. The lower teleost and more derived teleost differ in their pharyngeal myology which directly affects the functional properties of pharyngeal complex (Vandewalle *et al.*, 2000) [64]. For investigation of pharyngeal anatomy and function, cichlids have remained the model taxon. There are many examples of detailed anatomical description of pharyngeal myology for cichlids (Liem, 1973; Anker, 1978; Claes & Aerts, 1984; Aerts *et al.*, 1986; Galis & Ducker, 1996; Smiths *et al.*, 1996a) [39, 5, 13, 1, 19].

It has been well documented that the pharyngeal teeth in cichlids are morphologically plastic in response to prey type

(Greenwood, 1991; Witte & Barel, 1976; Witte, 1984; Witte *et al.*, 1990; Huysseune, 1995; Smits *et al.*, 1996a, b) [22, 67, 66, 68, 27, 54]. In cichlids that have more durophagous diet, the pharyngeal teeth will become much thicker and resemble those of a molluscivore, 1973; Witte and Barel, 1976) [21, 67]. This may be response of a limit of pharyngeal muscles ability to crush different prey items by contraction force alone. This diet induced plasticity and trophic adaptability is thought to be a substrate for speciation in cichlid fishes (Kornfield & Smith, 2000) [31].

Role of PJA in relation to sound production

A large number of fishes produce sounds in different social context such as agonistic interactions, courtship and competitive feeding (Amorim *et al.*, 2003; Amorim & Hawkins, 2005; Bertucci *et al.*, 2010; Colleye & Parmentier, 2012; Ladich, 1997; Lobel, 1998; Longrie *et al.*, 2013; Parmentier *et al.*, 2010) [4, 3, 8, 14, 8, 40, 41, 49]. Sound production does not rely on the same kind of mechanism in all teleost fishes that have evolved a high diversity of sound producing mechanism (Amorim, 2006; Ladich & Fine, 2006) [2, 33]. Stridulation is a widespread mechanism in fishes that is based on friction of skeletal elements such as teeth, fin rays and vertebrae (Ladich & Fine, 2006; Moulton, 1958; Salmon *et al.*, 1968, Burkenroad, 1930; Tavalga, 1971) [33, 46, 51, 9, 61]. Stridulation sounds are composed of a series of rapidly produced and irregular transient pulses, containing a wide range of frequencies (Hawkins, 1993) [24].

In many fishes without obvious sound-producing elements, the sonic mechanism has been attributed to sounds that result from the friction of pharyngeal teeth (Ballantyne and Colgan, 1978; Lanzing, 1974) [6, 37]. Although acoustic communication appears to be an integral part of cichlid behaviour (Amorim, 2006) [2], cichlids speciation has usually been associated with, morphological plasticity of pharyngeal jaw apparatus originating in tropic adaptation, and sexual selection based on female recognition of conspecific male colour pattern (Seehausen & Van-Alphen, 1998; Turner *et al.*, 2001; Kocher, 2004) [53, 63, 30].

According to Amorim (Amorim, 2006) [2], cichlid sounds can be grouped into three classes, probably associated with the sound-producing mechanism: (1) growls, low-frequency pulse usually associated with both agonistic and courtship context; (2) chewing sound, broad-frequency-band stridulatory sounds that can be heard when the fish are eating and are threatening conspecifics, and (3) thump-like sounds produced apparently as a result of body movements such as head nodding. Stridulatory mechanism are based on friction of skeletal elements such as teeth, fin, rays and vertebrae (Burkenroad, 1930; Tavalga, 1971b) [9, 60]. Stridulation sounds are raps and creaks, often composed of a series of rapidly produced and irregular transient pulses, containing a wide range of frequencies (Hawkins, 1993) [23].

Feeding sounds have been investigated in several species and generally correspond to pulsed chewing sounds that occur during food and manipulation by teeth of the pharyngeal jaws (Ladich & Fine, 2006) [33]. The interception and localization of these feeding sounds could be a major advantages for foraging fishes but a disadvantage for the sender (Scholz & Ladich, 2006; Myberg, 1981) [52, 47]. The relationship between pharyngeal jaw for feeding and sound production may have profound evolutionary implications. The pharyngeal jaw serving as a possible mechanism for sound production; trophic biology and reproductive biology could be directly

linked by this structure. Consequently, the dual use of the pharyngeal jaw may serve as a mechanism mediating the sympatric speciation of cichlid fishes (Kornfield & Smith, 2000)^[31].

Conclusion

Polymorphisms in pharyngeal jaw structure will be useful for accessing the ecological divergence & trophic polymorphisms of the species. Intraspecific pharyngeal variations also occurred in some fishes that helpful to understanding lineage relationships. The clarity in the cichlids systematic, Inter-relationships between two subfamilies and phylogenetically more information on the morphology of oral Jaw and pharyngeal jaw bones.

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