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Evolution of novel jaw joints promote trophic diversity in coral reef fishes

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We investigated the functional morphology and ecology of biting among the squamipinnes, an assemblage of nine successful and distinctive reef fish families. We demonstrate that an intramandibular joint (IMJ) may have evolved at least three and possibly five times in this assemblage and discuss the impact of this recurring innovation in facilitating prey-capture by biting. Using character mapping on a supertree for the squamipinnes, we reveal up to seven gains or losses of intramandibular flexion, all associated with trophic transitions between free-living and attached prey utilization. IMJs are basal in six of the studied families whereas the origin of intramandibular flexion in the Chaetodontidae (butterflyfishes) coincides with a transition from ram-suction feeding to benthic coral feeding, with flexion magnitude reaching its peak (49 ± 2.7°) in the coral scraping subgenus *Citharoedus*. Although IMJs generally function to augment vertical gape expansion during biting behaviours to remove small invertebrates, algae or coral from the reef, the functional ecology of IMJs in the Pomacanthidae (angelfishes) stands in contrast. Pomacanthid IMJs exhibit over 35° of flexion, permitting gape closure when the jaws are fully protruded. We demonstrate the widespread IMJ occurrence among extant biters to result from a complex convergent evolutionary history, indicating that the IMJ is a major functional innovation that enhances biting strategies in several prominent reef fish groups. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **93**, 545–555.

ADDITIONAL KEYWORDS: acanthuroid – biomechanics – biting strategies – chaetodontoid – ecomorphology – foraging – key innovation – nutritional ecology – ram-suction feeding.

INTRODUCTION

Reef fish assemblages differ from many other fish faunas especially by the dominance of taxa using a diverse range of biting strategies to either graze or scrape the substratum (Wainwright & Bellwood, 2002). The most dominant group of reef biters is the squamipinnes, comprising the Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), Acanthuridae (surgeonfishes), Siganidae (rabbitfishes), and their relatives (Tyler & Sorbini, 1999). Other biting groups include the scarine parrotfishes (Bellwood, 1994) and a few smaller lineages (Turingan, Wainwright & Hensley, 1995; Grubich, 2003). Some of these biting reef fish taxa possess a joint between the lower jaw dentary and articular bones, such as girellids (Vial & Ojeda, 1990), pomacanthids (Konow & Bellwood, 2005), and acanthurids (Purcell & Bellwood, 1993). Similar joints also occur in three scraping scarine genera (Bellwood, 1994; Alfaro, Janovetz & Westneat, 2001) and in a detritus-combing blenniid genus (Springer, 1988; Konow & Bellwood, 2005).

Flexion at this intramandibular joint (IMJ) increases the mechanical complexity of the feeding

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apparatus and appears a likely key-element in promoting the trophic performance and diversification of squamipinnes taxa. Repeated associations with biting strategies have prompted suggestions that IMJs may represent an adaptation to feeding on sturdily attached or structurally resilient prey (Bellwood, Hoey & Choat, 2003). Despite the wide range of novel dislodging strategies in biting fishes (Norton & Brainerd, 1993; Ferry-Graham *et al*., 2002), the function of IMJs and their role in the evolutionary ecology of coral reef fishes largely remains an enigma (but see Alfaro *et al*., 2001).

Functional evidence strengthening the link between an IMJ and biting was recently provided with the description of gape-restricting IMJ kinematics in pomacanthids, coupled with their use of an unusual grab-and-tearing feeding strategy (Konow & Bellwood, 2005). It is peculiar that pomacanthids exhibit a restricted feeding morphological and functional disparity with IMJ-possession being a shared derived trait (Konow, 2005). Despite a restricted structural disparity, the family is characterized by a pronounced trophic diversification (Allen, Steene & Allen, 1998).

Analyses of the chaetodontids, the putative pomacanthid sister-family, have revealed unusual functional traits in the feeding mechanisms of several generalized ram-suction feeders (Motta, 1985; Motta, 1988; Ferry-Graham, Wainwright & Bellwood, 2001a; Ferry-Graham *et al*., 2001b). However, the putative chaetodontid crown-group is yet to be examined in a functional context (Ferry-Graham *et al*., 2001b; Smith, Webb & Blum, 2003), in spite of the well-known coral biting feeding ecology (Motta, 1985, 1989) of several taxa belonging to the *Chaetodon* clade (Ferry-Graham *et al*., 2001a; Smith *et al*., 2003). Whether intramandibular flexion exists in chaetodontids remains a particularly important question, the answer to which will further reflect trends in the evolutionary ecology of functional traits among closely related biting taxa.

In the present study, we used analyses of videos and dissections to examine the functional ecology of IMJs in reef fishes belonging to the squamipinnes. Specifically, we ask: (1) what is the function of IMJs and (2) how are these joints ecologically associated with reef fish feeding guilds? Using supertree methods, we assemble a phylogeny of the squamipinnes and, in light of this tree, we address questions concerning the evolution of IMJs as well as feeding guilds of the squamipinnes: (1) did IMJs evolve convergently and (2) if so, in how many instances? In unison, these methods allow an evaluation of whether convergent IMJ evolution has resulted in convergent IMJ function to promote the use of biting behaviours among reef fishes.

MATERIAL AND METHODS

Analysis of mandible morphology and kinematics

Study taxa were selected for subgeneric representation (Appendix), which was previously determined to reflect trends in ecological diversification (Bellwood, Van Herwerden & Konow, 2004). The methods used here have been described in detail previously (Konow & Bellwood, 2005; Konow, 2005). Manipulations and dissections were conducted on at least two, mostly three fresh specimens of all study taxa (Appendix). For preparation of anatomical diagrams, both dissected and intact specimens were fixed in formalin and clear-stained for bone and cartilage.

Live individuals of 26 squamipinnes species found to exhibit some degree of intramandibular flexion (for species names, see Appendix; for species authorities, see http://www.fishbase.org) were video recorded at 200 Hz during feeding for quantification of jaw kinematics (Fig. 1A, B). Video of at least three feeding events was analysed for each individual. Three landmarks were digitized in *Movias* 1.5: (1) the dentary tip; (2) the IMJ at the dentary-articular articulation; and (3) the common lower jaw, or quadrate-mandibular joint (Fig. 2). From the resultant triplets of coordinate pairs, frame-by-frame angular measurements of intramandibular flexion throughout the feeding event were extracted, indicating the timing of onset, duration and magnitude of intramandibular flexion in kinematic plots (Fig. 1C, D). These plots were condensed to maximum values (± SD) for each taxon (Fig. 3) with negative intramandibular flexion values indicating gape-restrictive and positive values indicating gape-expansive kinematics properties (Fig. 1).

IMJs of sacrificed specimens from several video recorded taxa were also manipulated to evaluate the utility of the manipulation techniques for estimating IMJ motion during feeding in taxa where live individuals were unavailable (Appendix). Video and manipulation results matched closely, and manipulation studies were deemed useful in quantifying intramandibular flexion, although video data variance exceeded manipulation variance (e.g. *Coralloch-aetodon lunulatus*: *t*-test, $p = 0.968$; $\mathrm{SD}_{\mathrm{video}} = 1.51$; $\mathrm{SD}_{\mathrm{manipulation}} = 0.50$).

Supertree construction and tracing of character-origins

The supertree method, matrix-representation with parsimony (MRP; Baum, 1992; Doyle, 1992; Ragan, 1992) was used to combine the topological information from smaller source trees with overlapping taxon sets (Tang *et al*., 1999; Smith *et al*., 2003; Bellwood *et al*.,

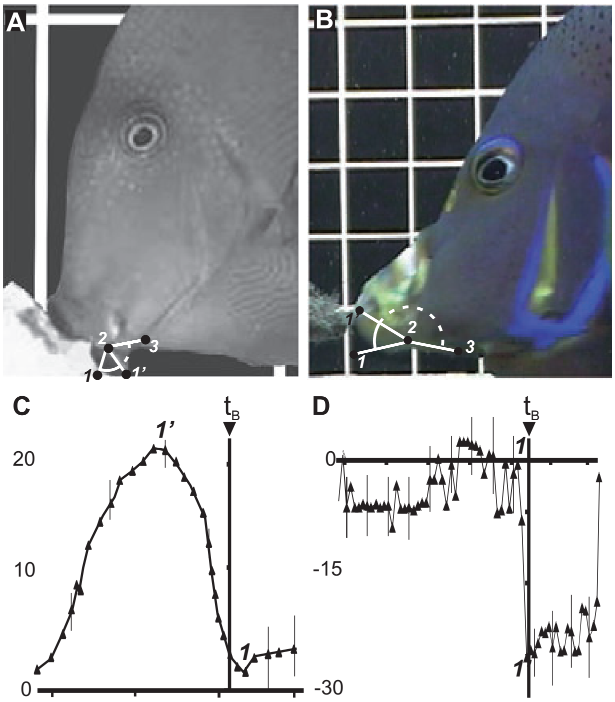

Figure 1. Video images showing maximally rotated intramandibular joints during feeding in (A) the acanthurid *Ctenochaetus striatus* and (B) the pomacanthid *Pomacanthus semicirculatus*, with plots of the associated performance profile of intramandibular joint (IMJ) kinematics for (C) the common gape-expanding IMJ, and (D) the unique gape-restricting IMJ of angelfishes. Marker-points: 1, dentary relaxed; 1′, dentary rotated; 2, IMJ; 3, quadrate-articular joint. In (C) and (D) the *x*axis indicates relative feeding-event duration, with time of jaw occlusion at the *y*axis intercept. The *y*axis indicates degree of intramandibular flexion, with positive values reflecting gape-expanding, and negative values reflecting gape-restricting IMJ kinematics.

2004; Clements, Gray & Choat, 2003; Klanten *et al.*, 2004) into an estimate of squamipinnes relationships. We weighted source-tree contributions in MRP by nodal support, which is shown to recover relationships as well as total-evidence or supermatrix approaches (Bininda-Emonds & Sanderson, 2001; Kennedy & Page, 2002; Salamin, Hodkinson & Savolainen, 2002; Bininda-Emonds, 2003). The resulting character matrix was examined in PAUP 4.0b10 (Swofford, 2003) under parameter settings from Kerr (2005). We inferred the number of times that IMJs and the biting feeding mode evolved over the supertree using both parsimony and likelihood ancestral-state reconstructions as implemented, respectively, in MacClade, version 4.03 (Swofford & Maddison, 1987; Maddison & Maddison, 2001), Mesquite, version 1.06 (Maddison & Maddison, 2005) and MultiState, version 0.08 (Pagel, 1994; Pagel, 2003). Data on trophic guild (i.e. feeding mode) for species in the analysis are personal field observations (N. Konow, unpubl. data) supplemented with information from Allen *et al*. (1998) and FishBase (Froese & Pauly, 2007).

In likelihood reconstruction, branches were assigned 'Grafen' lengths, where the sum of integral valued branch lengths between any taxon and the root is minimized and equal across the tree (Grafen, 1989). A range of affine transformations of branch lengths provided qualitatively similar results; hence, we only report reconstructions based on untransformed lengths. Likelihoods of ancestral states for the IMJ were calculated over all possible states for *Luvarus*, whose condition is unknown, and for three possible positions of the Girellidae.

RESULTS

INTRAMANDIBULAR MORPHOLOGY AND KINEMATICS

IMJs are present in the biting chaetodontids belonging to the derived genus *Chaetodon*. The IMJ is particularly well developed in the crown-subgenera *Corallochaetodon* and *Citharoedus* (Fig. 2A), where intramandibular flexion occurs prior to peak jaw protrusion, thereby augmenting gape expansion by additional dentary rotation of approximately 16° and 49°, respectively (Fig. 3). *Chaetodon* mandibles have a prominent flanging of the primordial articular process (Fig. 2A, B) lateral to the ligaments connecting to the upper jaw (not illustrated).

Similarly, in acanthurids (Fig. 2E), siganids (Fig. 2F), and in *Girella* (Fig. 2H), IMJs also augment gape expansion (Fig. 3) and bear anatomical resemblance to scarine and blennid IMJs (Fig. 2I, J) with steep resting angles between the dentary and articular bones. However, these articular bones, and those of pomacanthids (Fig. 2C, D) lack the primordial process flange.

Among pomacanthid taxa, intramandibular flexion is broadly comparable (Fig. 3), with a mean ± SD rotation of –35 ± 4.8° and rotation-onset lagging 5–6 ms after peak-jaw protrusion. This is part of a unique timing-sequence of the feeding event, where protruded jaw closure precedes a high-velocity jaw retraction. Divergence from this pattern exists among zooplanktivores, such as *Genicanthus* (Figs 3, 4) where non-attached prey elicit reduced IMJ kinematics, with mean rotation of –7 ± 4.8°. Still, attached prey elicits intramandibular flexion of –26.5 ± 4.7°, comparable to the grab-and-tearing taxa. Within the Acanthuridae, manipulations of IMJs in zooplankton feeding members of the Nasinae also suggested reduced intramandibular flexion of 11.1 ± 2.1° from the acanthuroid mean of 18.7°.

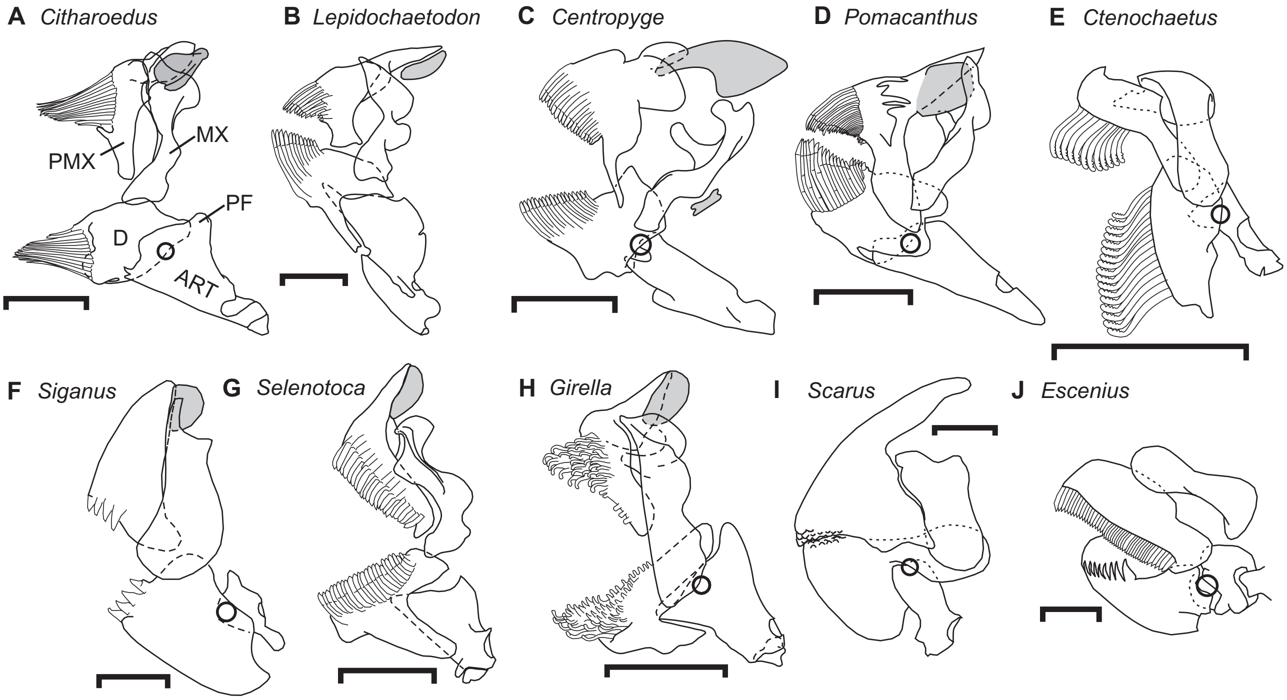

Figure 2. Jaw morphologies in the study families. Open circles indicate the presence and position of intramandibular joints. PMX, premaxillary bone; MX, maxillary bone; D, dentary bone; ART, articular bone; PF, primordial flange on articular bone. Rostral cartilage in grey where present. Chaetodontidae: A, *Chaetodon* [*Citharoedus*] *ornatissimus*; B, *Chaetodon* [*Lepidochaetodon*] *unimaculatus*; Pomacanthidae, C, *Centropyge* [*Centropyge*] *bicolor*; D, *Pomacanthus* [*Arusetta*] *semicirculatus*; E, Acanthuridae (*Ctenochaetus striatus*); F, Siganidae (*Siganus doliatus*); G, Scatophagidae (*Selenotoca multifasciata*); H, Girellidae (*Girella laevifrons*; redrawn from Vial & Ojeda, 1990); I, Scaridae (*Scarus flavipectoralis*); and J, Blennidae (*Escenius bicolor*) are shown for comparison. A–I, scale bar = 10 mm; J, scale bar = 0.1 mm.

Intramandibular flexion is absent in the Scatophagidae, Microcanthidae, Ephippidae and amongst generalized ram-suction feeding chaetodontids. Marginal flexion is found in *Drepane* (Fig. 3; jaw anatomy in Tyler *et al.*, 1989; fig. 37C), whereas the invertebrate-picking *Zanclus*, a monotypic sister-taxon to the Acanthuridae, lacks intramandibular flexion, which apparently is an exception to the widespread pattern of intramandibular flexion in biting squamipinnes members.

PHYLOGENETIC DISTRIBUTION OF INTRAMANDIBULAR FLEXION AND FEEDING MODE

MRP returned 349 optimal trees of length 646 with 83 ingroup taxa, a strict consensus of which is shown in Figure 4. Parsimony reconstructed ram-suction feeding use of free-living prey as ancestral with three to five independent acquisitions of biting (via ACCTRAN versus DELTRAN parsimony mappings). Pagel (1994) suggests that a ratio of the state likelihoods over 7 : 1 provides significant support for the most probable state. The likelihood analysis also recovered free-living prey use as ancestral with at least two, and possibly four independent acquisitions of biting strategies. Similarly, IMJ absence is recovered as the ancestral squamipinnes trait, with up to five independent IMJ acquisitions. The likelihood reconstruction highlights the uncertainty in the parsimony reconstructions concerning IMJ evolution and the complex evolution of feeding modes along the acanthuroid branch (Fig. 4).

Character mapping recovered the gape-expanding IMJ character state as the earliest IMJ-origin (irrespective of alternative positions of the Girellidae) and showed IMJ-possession to be the basal state among pomacanthids, siganids and acanthurids. However, among chaetodontids, gape-expanding intramandibular flexion originates deep in the phylogeny, at the transition from ram-suction feeding to biting in the subgenus *Chaetodon* [*Radophorus*] (Fig. 4). Within the *Chaetodon* crown-group (Fig. 4), the magnitude of flexion culminates in the stout-jawed coral feeders (Fig. 3).

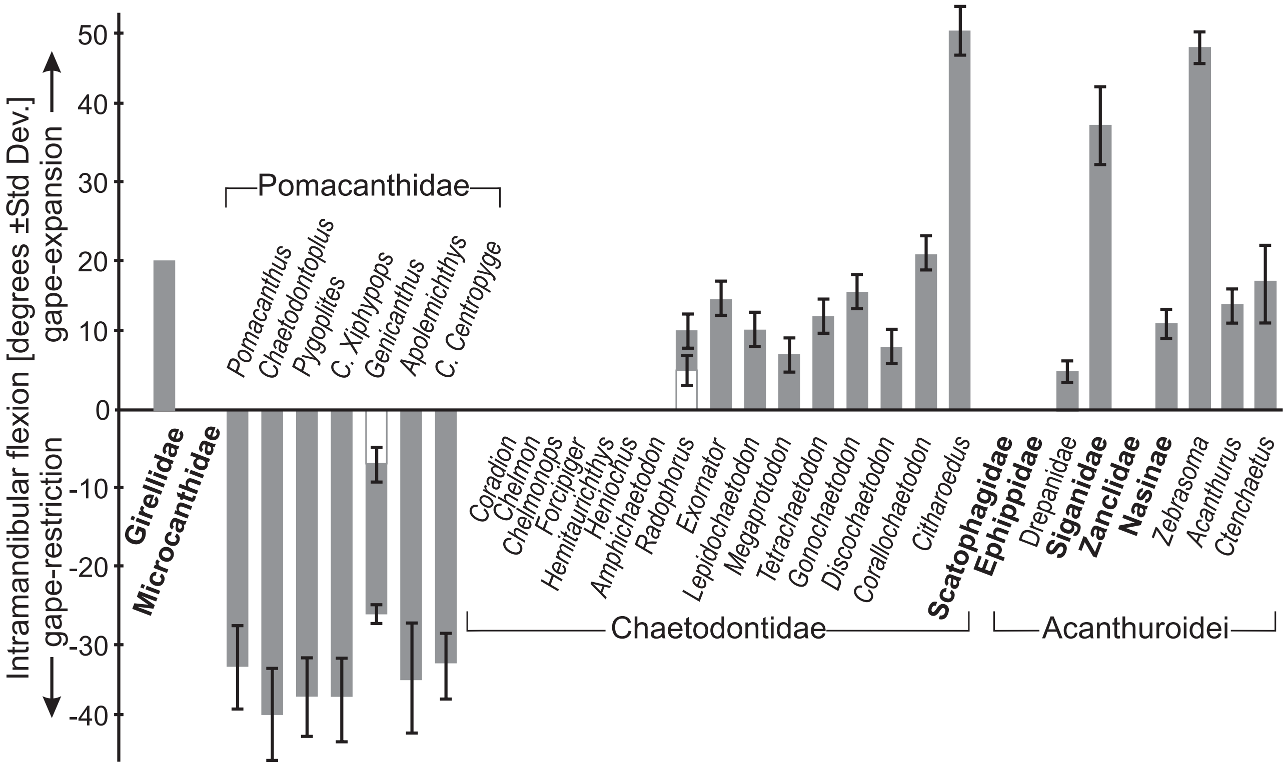

Figure 3. Clade-means of intramandibular flexion based on kinematics and biomechanical analyses of $N = 3$ specimens (horizontal axis, see Appendix), with value-polarity (vertical axis) indicating gape-restricting (negative) or expanding augmentation (positive) by intramandibular flexion. For *Chaetodon* [*Radophorus*], the grey column represents *Chaetodon* [*Radophorus*] *melannotus* and the white column the remaining taxa. In *Genicanthus*, the grey column represents attached and white column free-living prey. *Girella* values were measured from mandible drawings in Vial & Ojeda (1990).

DISCUSSION

IMJs are surprisingly widespread among reef fishes belonging to the squamipinnes. These secondary lower jaw joints have evolved independently up to five times in close association with a wide range of biting strategies. Despite their rather uniform morphology, IMJs exhibit divergent kinematics, and function to augment either jaw occlusion or gape expansion during feeding. Extant IMJ-bearers are typically substratum biters, except in several instances of secondary reversal to planktivory.

Overall, it appears that few major radiations of biting reef fishes lack IMJs. Prior to the present study, IMJs were infrequently described and best known from three parrotfish genera (Bellwood, 1994; Streelman *et al*., 2002; Bellwood *et al*., 2003). Among the squamipinnes, IMJs were established as a symplesiomorphic trait in pomacanthids (Konow & Bellwood, 2005; Konow, 2005),and otherwise only known in two acanthurids (Purcell & Bellwood, 1993) and one girellid (Vial & Ojeda, 1990). The present study identified three additional reef fish families, the Drepanidae, Siganidae, and Acanthuridae, where IMJs are symplesiomorphic traits and one, the Chaetodontidae, where an IMJ is a synapomorphic trait in the crown-group, genus *Chaetodon*.

Those biting taxa that lack an IMJ tend to be robust excavators (e.g. some parrotfishes; Bellwood, 1994; Streelman *et al*., 2002; Bellwood *et al*., 2003) or durophages (e.g. Tetraodontiformes; Turingan *et al*., 1995). In durophages, fusion of jaw elements yield increased structural stability of the jaw apparatus, a trend that is also seen among coral-excavating chaetodontids; *Lepidochaetodon unimaculatus* has the most robust chaetodontid jaws (Fig. 2B) and exhibits restricted intramandibular flexion (Fig. 3).

FUNCTIONAL ECOLOGY OF IMJS

Pomacanthids are unique among fishes, and perhaps among animals, in their ability to bite with their jaws protruded (Fig. 5C), and this capability results from their derived gape-restrictive IMJ kinematics (Fig. 5A–D), which couple with considerable jaw protrusion (Fig. 5B) and a high-velocity retraction of the occluded jaws (Fig. 5C, D). This unique functional

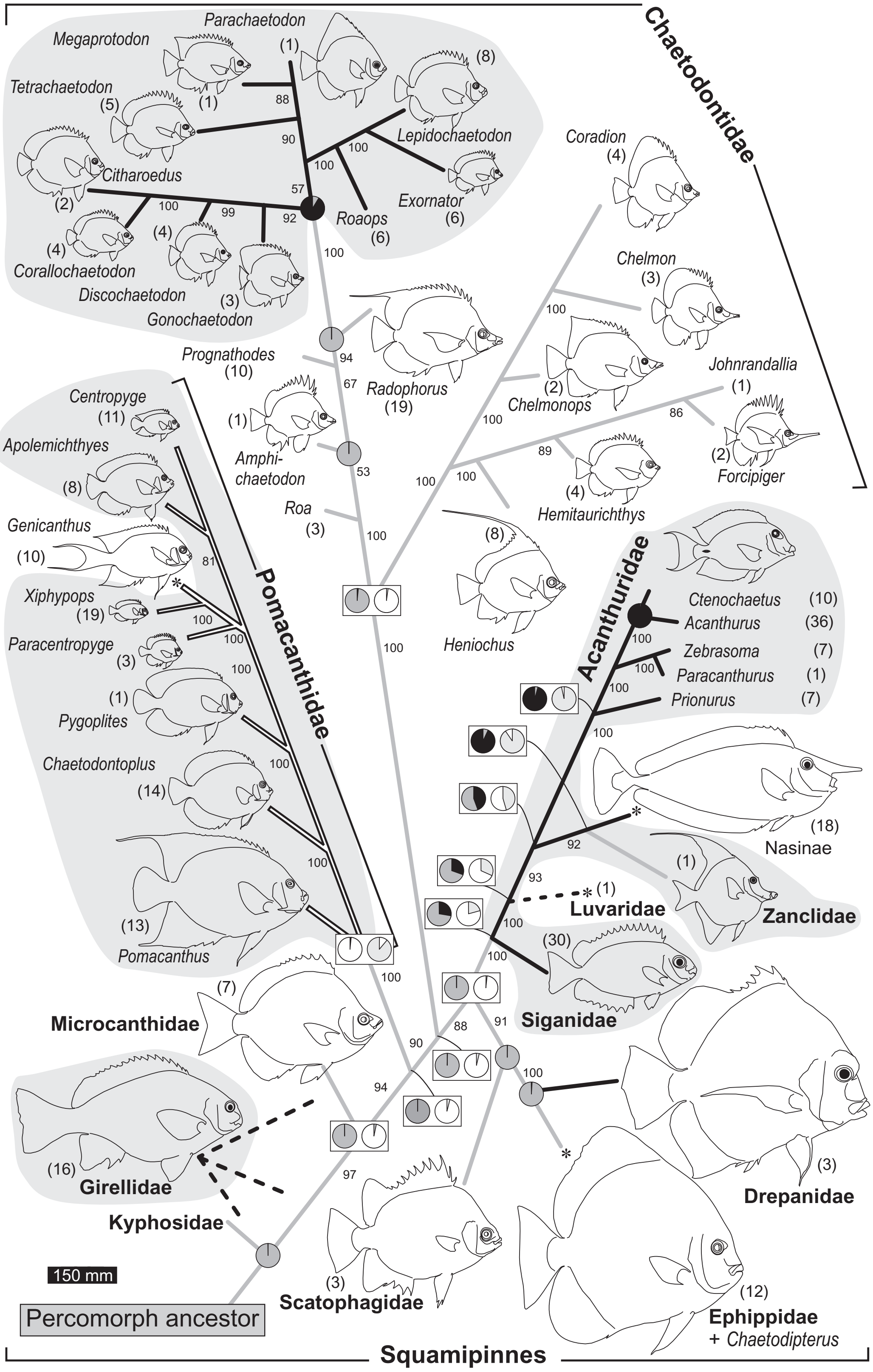
Chaetodontidae
Parachaetodon
Megaprotodon
(1)
(8)
Tetrachaetodon
(5)
(1)
88
90
100
Lepidochaetodon
100
Coradion
(4)
Citharoedus
57
Exornator
(2)
100
99
92
Roaops
(6)
(4)
(4)
(6)
Corallochaetodon
Discochaetodon
(3)
Gonochaetodon
100
Chelmon
(3)
100
Prognathodes
(10)
94
67
Radophorus
(19)
Johnrandallia
(1)
(2)
Chelmonops
100
86
Centropyge
(11)
(1)
Apolemichthyes
Amphi-
chaetodon
53
89
(2)
Forcipiger
(8)
100
100
(4)
Hemitaurichthys
Roa
(3)
100
Genicanthus
(8)
(10)
81
Xiphypops
*
(19)
100
Pomacanthidae
Paracentropyge
100
(3)
100
Heniochus
Acanthuridae
Ctenochaetus (10)
Acanthurus (36)
100
Zebrasoma (7)
100
Paracanthurus (1)
(1)
Pygoplites
100
Prionurus (7)
100
Chaetodontoplus
100
(14)
*
(18)
92
Nasinae
100
(1)
93
* (1)
Luvaridae
Zanclidae
(13)
Pomacanthus
100
(30)
100
100
Siganidae
(7)
Microcanthidae
88
91
90
100
94
(16)
Girellidae
97
*
(3)
Drepanidae
Kyphosidae
150 mm
(3)
Scatophagidae
(12)
Ephippidae
+ Chaetodipterus
Percomorph ancestor
Squamipinnes

Figure 4. Supertree for the squamipinnes, based on available phylogenetic evidence (see text), which was combined using matrix-representation with parsimony. Bootstrap values for nodes are given alongside branches the lengths of which were chosen for clarity of presentation. Representative study taxa (for Chaetodontidae at subgenus, Pomacanthidae and Acanthuridae at genus, and the remainder at family level) are shown with thumbnails scaling to maximum total length, to illustrate the evolution of body-plans. Numbers in parenthesis indicate the number or species within clades, and asterisks indicate secondary reversal from biting to planktivory. Intramandibular joint (IMJ) character-states are optimized to branches: filled, gape-expanding IMJ; open, gape-restricting IMJ; shaded, no IMJ; stippled, ambiguous. Feeding mode is mapped to clades using shading to delineate biting taxa while all other taxa utilize free-living prey. Likelihood reconstructions of ancestral states are illustrated using pie charts at relevant nodes with shading according to the branch optimizing colour scheme. Relative likelihoods (as approximate posterior probabilities) are given for feeding mode (right charts) and for the dominant IMJ state, including the second most probable state when the probability is greater than 0.05 (left or solitary charts).

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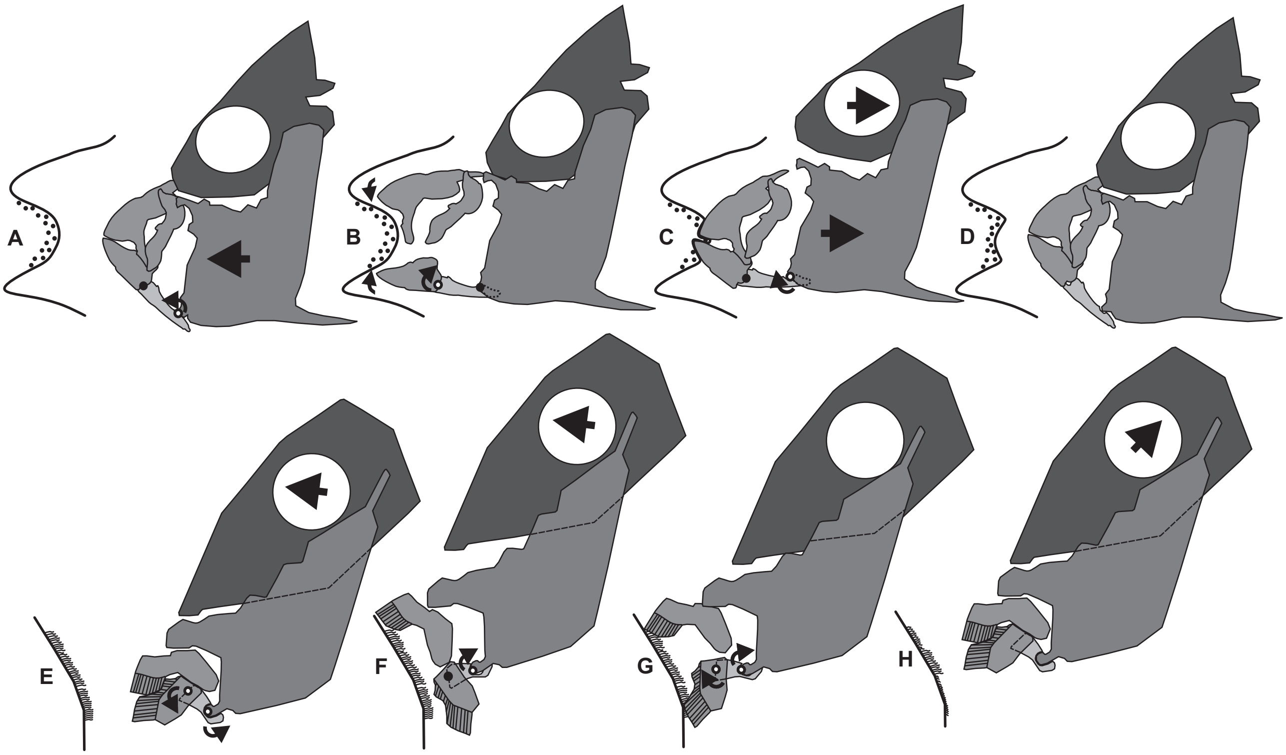

Figure 5. The divergent roles of intramandibular joints (IMJ) in the feeding ecology of biting coral reef fishes. Biomechanical models of the gape-restricting IMJ unique to pomacanthids (A–D) and the common gape-expanding IMJ found in other biters (E–H) are superimposed on video frames of feeding individuals. Large black arrows indicate the motion of the predator (and of the highly protrusible pomacanthid suspensorium). Solid circles indicate joint inactivity and joint flexion is indicated by open circles, with curved arrows indicating the resultant kinematics (displayed in the subsequent frame). Shading from dark to light corresponds to: neurocranium – suspensorium – oral jaws – articular bone. For the purported role of muscles and ligaments in these models, see Purcell & Bellwood (1993) and Konow & Bellwood (2005).

system appears to provide a sufficiently novel and versatile basis to promote pomacanthid ecological diversification. The resultant ‘grab-and-tearing’ feeding behaviour has evidently allowed pomacanthids to exceed ‘ecological thresholds’ formed by structural resilience and sturdy attachment of prey that furthermore is typically found in confined habitats; all traits that otherwise make such prey unavailable to all but a few durophageous reef taxa (Konow & Bellwood, 2005).

Despite their conservative feeding morphology and kinematics, pomacanthids are trophically diverse with three major ecomorphological patterns. Larger, more robust taxa procure structurally resilient prey using the characteristic 'grab-and-tearing' feeding behaviour (Konow & Bellwood, 2005). Smaller, more gracile taxa use their gape-restrictive IMJ kinematics to tear or shear turf algae, or more delicate invertebrate prey (Allen *et al*., 1998; Konow, 2005). Interestingly, several pomacanthids show a third pattern in being plankton feeders [e.g. genus *Genicanthus*, most *Holacanthus* species (not examined herein) and *Pomacanthus rhomboides*; N. Konow, unpubl. data]. These taxa, as well as planktonic members of the Nasinae and *Chaetodon*, show a tendency towards stiffening of the IMJ-bearing mandible and the results obtained in the present study confidently recovered these ram-suction feeding lifestyles as atavistic, and accompanied by a secondary reduction in IM-flexion stiffening the mandible (Konow, 2005).

The gape-expanding IMJ (Fig. 5E, F, G, H) is by far the most widespread type and exhibits a much wider range of flexion-magnitude across taxa than the gape-restricting pomacanthid IMJ type (Fig. 3). This variability may reflect different optima in feeding musculoskeletal systems, or disparate ecological advantages related to the feeding guilds associated with each IMJ type.

Mechanical models of the teleost lower jaw describe a lever system where the distance from the lower jaw joint to the teeth is the output lever through which adductor muscle contraction forces are transmitted to the biting surface of the teeth (Wainwright *et al*., 2004). All else being equal, if the jaw is short, a greater force is transmitted, yet a short mandible limits vertical gape expansion, thereby restricting the contact surface area of the teeth onto the feeding substratum. Thus, although a short mandible is mechanically well equipped for forceful biting, an inevitable trade-off is a restriction in the amount of substrate that can be covered during each bite. The reduced gape distance is at least partly mitigated by an IMJ that, through sequential jaw rotation at two separate joints, permits gape expansion followed by occlusion (Fig. 5E, F).

The secondary IMJ also enables its bearer to actively modulate the angle of the lower jaw engaging the feeding substrate, which may allow IMJ-bearing chaetodontids, girellids, acanthurids, and scarines to effectively scrape a larger surface with each bite (Fig. 2G, H; Vial & Ojeda, 1990; Purcell & Bellwood, 1993; Bellwood, 1994; Bellwood, 2003). Additionally, in taxa with ventrally directed jaw protrusion [e.g. the pomacanthid pygmy-angelfishes *Centropyge* (*Xiphypops*), Konow, 2005], an IMJ enables the fish to maintain a body position more parallel with the substratum, thereby enhancing its predator evasion capability and allowing a stable orientation to ambient water flow (Alexander, 1967; Motta, 1984; Purcell & Bellwood, 1993). In unison, these potential benefits of an IMJ, coupled with its repeated appearance coinciding with the origin of substrate biting, suggest that a joint subdividing the mandible is an important functional adaptation, which is an innovation that enhances biting performance.

A high degree of intramandibular flexion appears to facilitate coral-tissue scraping in *Chaetodon* crown-taxa, which have stout jaw morphologies and bristle-shaped teeth. Nevertheless, relatively modest intramandibular flexion is characteristic in many other *Chaetodon* taxa, corresponding well with altered biomechanical requirements towards jaw stability for coral polyp browsing using more pincer-like jaws with anteriorly directed bristle teeth (Motta, 1989). Interestingly, most taxa in the basal-most *Chaetodon* subgenus, *Radophorus* are invertebrate pickers (Allen *et al*., 1998) and these exhibit only slightly more intramandibular flexion than in a mandible with suturing of the dentary to the articular bone (approximately 4°; N. Konow, unpubl. data). Yet, a sole obligate coral feeding species, *Chaetodon* [*Radophorus*] *melannotus*, exhibits more pronounced flexion (approximately 10°). This species also appears superficially distinct from other *Radophorus* taxa, questioning the taxonomical classification of this taxon.

THE SQUAMIPINNES SUPERTREE

Our squamipinnes supertree showed some conflict with earlier morphology-based hypotheses (Winterbottom, 1993). Although resolving some polytomies present in Tyler *et al*. (1989), the chaetodontoid fishes (pomacanthids, chaetodontid, and microcanthids) are placed in paraphyly as sistergroup to the Acanthuroidei. This displacement, and that of *Amphichaetodon*, from a widely accepted position as the basal-most chaetodontid (Ferry-Graham *et al*., 2001b; Smith *et al*., 2003) may be due to restricted outgroup-representation in Bellwood *et al*. (2004). Placement of the Girellidae at the base of our tree is tentative and results from ambiguity of analyses by Yagishita & Nakabo (2003) and Yagishita, Kobayashi & Nakabo (2002). The position of *Zanclus*, as sistergroup to the Nasinae, may result from long-branch attractions in the source trees (Tang *et al*., 1999; Clements *et al*., 2003). The clade with scatopagids as sister to *Drepane*, ephippids, and *Chaetodipterus* only diverges from source trees in the placement of scatophagids (Tang *et al*., 1999; Ferry-Graham *et al*., 2001b; Smith *et al*., 2003). Below, the clade inter-relationships listed must be considered tentative, and therefore favour the most conservative character-optimization interpretations. Emerging molecular evidence may recover a polyphyletic squamipinnes, and evolutionary interpretations resulting from character-optimizations herein likely underestimate the complexity of IMJs and biting evolution. Future results are not, however, likely to compromise the robust evolutionary link between IMJs and biting feeding behaviours.

CONVERGENT, PARALLEL OR DIVERGENT IMJ EVOLUTION?

The present analysis clearly shows the distribution of IMJs among squamipinnes reef fishes to result from convergent evolution. IMJ evolution occurs only in groups that utilize biting strategies, a trend that may extend to other perciform lineages (i.e. the scarines and blenniids). This evidence underscores the need for robust phylogenetic reconstructions. A comprehensive re-examination of the squamipinnes would benefit from clade age-estimates to resolve chaetodontoid common-ancestry and squamipinnes stem-group relationships. The uncertain position of the Girellidae particularly illustrates this requirement. A deeper perciform clade-resolution would help reveal whether intramandibular flexion is a fundamental and basal teleost trait. Regardless, IMJs may have been as important a functional innovation among the squamipinnes as the pharyngeal jaw apparatus has been in the evolution of labroids.

CONCLUSIONS

Reef fishes belonging to the squamipinnes have evolved IMJs for biting strategies with a remarkable convergence frequency of at least three, possibly five instances during their evolution. Adding these novelties to the previously documented case of intramandibular flexion in scarines, and the perfect association between IMJ origin and use of biting prey capture, suggests the role of IMJs as important innovations for advanced biting strategies in reef fishes. A widespread gape-increasing IMJ appears useful for 'lighter' grazing and scraping tasks where it also may permit fine control of jaw orientation throughout the bite. Meanwhile, gape-restricting intramandibular flexion is unique to pomacanthids, among which it facilitates novel prey-utilization involving biting with the jaws fully protruded. The unique pomacanthid IMJ function underpins a substantial trophic diversification of this family in tropical marine reef ecosystems.

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APPENDIX

Species investigated in the present study. We used three individuals for both manipulation studies and video kinematics, unless otherwise indicated in superscript (*kinematics from L. A. Ferry-Graham. For species authorities, see http://www.fishbase.org).

Chaetodontidae (butterflyfishes): genus *Chaetodon: Citharoedus ornatissimus*$^{(3,1)}$, *Corallochaetodon lunulatus*, *Discochaetodon aureofasciatus*$^{(3,0)}$, *Gonochaetodon baronessa*$^{(3,1)}$, *Tetrachaetodon plebius*$^{(3,0)}$, *Megaprotodon trifascialis*$^{(3,0)}$, *Parachaetodon ocellatus*$^{(2,0)}$, *Lepidochaetodon unimaculatus*$^{(3,2)}$, *Exornator xanthurus**, *Radophorus lineolatus*, *Radophorus melannotus*, *Chelmon muelleri*, *Chelmonops curiosus*$^{(3,1)}$, *Coradion altivelis*, *Forcipiger longirostris**, *F. flavissimus**, *Hemitaurichthys polylepis*$^{(3,0)}$, *Heniochus varius*$^{(3,1)}$, *Amphichaetodon howensis*$^{(2,0)}$. Pomacanthidae (angelfishes): *Centropyge* [*Centropyge*] *bicolor*, *C.* [*Xiphypops*] *bispinosa*, *Apolemichthys trimaculatus*, *Genicanthus melanospilos*, *Paracentropyge multifasciata*$^{(3,0)}$, *Pygoplites diacanthus*, *Chaetodontoplus duboulayi*, *Pomacanthus* [*Euxiphipops*] *sexstriatus*, *P.* [*Arusetta*] *semicirculatus*. Scatophagidae (scats): *Selenotoca multifasciata.* Microcanthidae (stripeys): *Tilodon sexfasciatus*$^{(3,1)}$, *Atypichthys latus*$^{(3,0)}$. Ephippidae (batfishes): *Platax orbicularis*$^{(3,2)}$. Drepanidae (sicklefishes): *Drepane punctata*$^{(3,0)}$. Siganidae (rabbitfishes): *Siganus doliatus*$^{(3,0)}$. Zanclidae (Moorish idol): *Zanclus cornutus*$^{(3,2)}$. Nasinae (unicornfishes): *Naso liturathus*$^{(3,0)}$. Acanthuridae (surgeonfishes): *Paracanthurus hepatus*$^{(3,0)}$, *Zebrasoma veliferum*$^{(3,0)}$, *Acanthurus olivaceus*$^{(3,2)}$, *Ctenochaetus striatus*$^{(3,2)}$. Scarinae (parrotfishes): *Scarus flavipectoralis*$^{(3,0)}$, Blennidae (blennies): *Escenius bicolor*$^{(3,0)}$.