

# BIOLOGY OF PARROTFISHES



EDITORS  
ANDREW S. HOEY  
ROBERTA M. BONALDO



A SCIENCE PUBLISHERS BOOK

# **Biology of Parrotfishes**



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# Biology of Parrotfishes

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*Clockwise from top left:*

*Bolbometopon muricatum* (João Paulo Krajewski)

*Chlorurus bleekeri* (João Paulo Krajewski)

*Scarus perrico* (Kendall D. Clements)

*Sparisoma amplum* (Kendall D. Clements)

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## Foreword

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No one questions that parrotfishes have evolved from wrasses, and we show this close relationship by grouping them in the same suborder, Labroidei (Nelson, 2006). Parrotfishes were recognized as a distinct group by Aristotle who wrote, "All fishes are saw-toothed excepting the Scarus" and "of all fishes the so-called Scarus, or parrrot, is the only one known to chew the cud like a quadruped." He was, of course, referring to the unique pharyngeal mill of scarids that grinds limestone fragments ingested with turf algae into a fine sand, and at the same time reducing the algae to more digestible fragments. Another unique scarid character that facilitates digestion is the very long intestine and the lack of a stomach. Parrotfishes have evolved to utilize a new resource of nutrition that is denied other herbivores. Once the herbivorous acanthurids, siganids, and pomacentrids have grazed algae to a low stubble, the scarid fishes still have a food resource. Surely this, the morphological differences, and being recognized as a family for 215 years support recognition as a family. The divers and fishermen readily distinguish parrotfishes from wrasses. If we tell them a parrotfish belongs in the wrasse family, they will think we are joking.

**Jack Randall**  
**Honolulu**



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# Preface

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Parrotfish are found on almost every coral reef in the world. It is this ubiquity, coupled with their brilliant colouration and fused 'beak-like' jaws, that have long attracted the attention of those looking and working on tropical reefs. Parrotfishes also have an incredibly diverse and complex array of reproductive and mating strategies that vary both among and within species. However, it is their unique feeding action that has stimulated much scientific endeavour. The morphological innovations of the oral jaws allow parrotfishes to bite through reef carbonates, while the pharyngeal jaws allow them to grind ingested carbonates into sand particles. These innovations not only enable parrotfishes to access nutritional resources that are largely unavailable to other fishes, but make them one of the most important groups of fishes within coral reef ecosystems. No other group of fishes is so inextricably linked to the structural dynamics of their ecosystem. Despite their importance to reef ecosystems, the threats to parrotfish are numerous and severe: from the global effects of ocean warming and acidification to the local effects of overfishing, pollution and habitat degradation.

The aim of this book is to synthesise what is currently known about the biology of parrotfishes, and to consider why are parrotfishes so important to the ecology of coral reefs? The book provides a series of reviews that are intended to provide a firm grounding in the understanding of the morphology, diet, demography, distribution, functional ecology, and current threats of this group. Importantly, it provides new insights into their diet and food processing ability, their life-histories, and the influence of habitat and environment on parrotfish populations, and also identifies emerging research topics and future directions. We hope this book will appeal to students, early-career and established researchers, alike, and will stimulate further investigation into this fascinating and unique group of fishes.

Lastly, we wish to thank to all of those who contributed to this book. We invited the international authorities on various aspects of the biology of parrotfishes to contribute to the book and were overwhelmed by their positive and enthusiastic responses. We would also like to thank David Bellwood for initiating our interest in parrotfishes, sharing his extensive knowledge, and guiding our scientific development. We sincerely thank the reviewers of each chapter of this book for their constructive and insightful comments. Finally, we are extremely grateful for the ongoing support from our families (especially Jess, Kiara, Caelen, and João) for their ongoing support that has enabled us to undertake important and interesting scientific pursuits.

**Andrew Hoey (Townsville, Australia)**  
**Roberta Bonaldo (Campinas, Brazil)**





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# Cranial Specializations of Parrotfishes, Genus *Scarus* (Scarinae, Labridae) for Scraping Reef Surfaces

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## Introduction

Parrotfishes (family Labridae) forage by excavating or scraping surfaces of rocks and carbonate substrate that are encrusted with algae, bacterial mats, and detritus (Bellwood 1994, Choat et al. 2004, Rice and Westneat 2005), often leaving scratches and scars on the rock and coral surfaces (Cousteau 1952, Newell 1956, Clements and Bellwood 1988, Bellwood and Choat 1990, Bellwood 1994, 1996b). Ingested material is then ground into a slurry by their impressive pharyngeal jaws, that have been described to be “like a cement mixer in reverse” (Bellwood 1996b). Analysis of their gut contents indicates that they consume staggering quantities of inorganic residue (Randall 1967, Clements and Bellwood 1988, Bellwood 1995a, 1995b, Choat et al. 2002), accounting for over 70% of the gut volume in some cases (Gobalet 1980), and recent work has shown this residue is a major contributor to island-building sediments (Perry et al. 2015). The unique morphology of parrotfish feeding apparatus has facilitated the functional decoupling of the mandibular and pharyngeal jaws, with the mandibular jaws collecting the materials that are pulverized by the pharyngeal jaws.

Parrotfishes have distinctive modifications of their skulls associated with feeding on massive quantities of abrasive material that is scraped from resistant surfaces. Several early studies describing the anatomical features of parrotfishes largely focused on the mandibular, or oral, jaws (Cuvier and Valenciennes 1839, Boas 1879, Lubosch 1923, Gregory 1933, Monod 1951, Board 1956). In the last few decades there have been several more extensive studies of the mandibular and pharyngeal jaws, as well as the associated musculature (Tedman 1980a, b, Clements and Bellwood 1988, Bellwood 1994, Monod et al. 1994, Bullock and Monod 1997, Wainwright et al. 2004, Price et al. 2010). However, the connective tissue elements of the jaws of labroid fishes have been minimally addressed (for exceptions see van Hasselt 1978, Tedman 1980b, Bellwood and Choat 1990, Bellwood 1994). In this chapter the specializations of the bones, joints and ligaments of the mandibular jaws

of parrotfishes, that allow them to withstand the stress generated during frequent contact with hard surfaces, are described and interpreted along with other elements of the head. The investigators cited above have also noted many of the features described here, but what makes this study noteworthy is the detail of the study and the elaboration of the connective tissue features. In particular, I provide detailed anatomical descriptions of five parrotfish species that reside in the southern Gulf of California (Thomson et al. 1979): the azure parrotfish *Scarus compressus*, bluechin parrotfish *Sc. ghobban*, bumphead parrotfish *Sc. perrico*, bicolor parrotfish *Sc. rubroviolaceus*, and loosetooth parrotfish *Nicholsina denticulata*.

The study of these species complement Clements and Bellwood (1988) and Bellwood (1994) who included one or more of these species in their authoritative studies. The descriptions presented here are a refinement and substantial update of Gobalet (1980). I fully agree with Clements and Bellwood (1988) that in the absence of any data from electromyography, cine radiology, or readings from force transducers, much of the interpretation made here is logical but speculative. It is hoped that this chapter stimulates additional investigations on this unique group of fishes.

## Materials

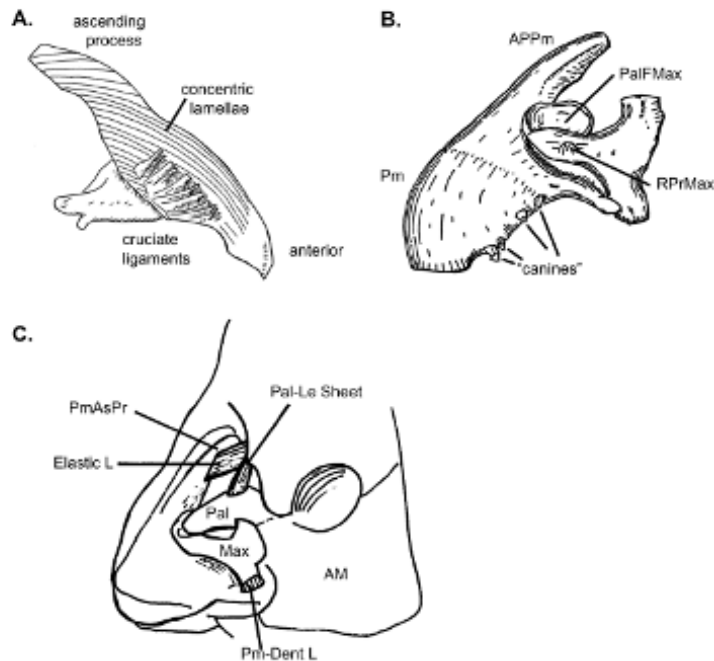
The specimens examined in this study were collected while spear fishing from the coast of the Baja Peninsula, Mexico. Most of the specimens were collected near Danzante Island (just south of Loreto and east of Puerto Escondido, Baja California, Sur). Additional specimens were collected from Pulmo Reef located between La Paz and Cabo San Lucas just north of Punta Los Frailes. For the study, 19 *Sc. compressus* (Standard Length (SL) range: 206-559 mm), 25 *Sc. ghobban* (SL 206-482 mm), 18 *Sc. perrico* (SL 263-540 mm), 10 *Sc. rubroviolaceus* (SL 206-394 mm), a single *Nicholsina denticulata* (SL 291mm), 17 *Mycteroperea rosacea* (Epinephelidae, SL 349-610 mm) and small numbers of several other labrids, and epinephelids were collected (see Gobalet 1980 for details). Dissections were completed on fresh material and specimens preserved for later study. Skeletonized material supplemented the dissections, most of which are now housed at the Ichthyology Department, California Academy of Sciences, San Francisco. The skeletons were prepared by maceration, enzyme digestion, or with the use of dermestid beetles. Identifications follow Rosenblatt and Hobson (1969) and the nomenclature follows Page et al. (2013). The terminology for skeletal elements generally follows Rognes (1973) or Patterson (1977). The features described below are for *Scarus* except where indicated otherwise. The anatomical differences between these four *Scarus* species are subtle at best.

## Results and Discussion

Detailed and technical descriptions of the hard and soft connective tissue elements of the cranium of parrotfishes are present in the appendix to this chapter, as is a table of abbreviations used in the figures. Parrotfishes are not delicate nibblers, but feed by forceful scraping or excavating chunks of algae-bearing substrate. Their feeding requires a coordinated action of the locomotor, sensory, and mandibular jaws (Rice and Westneat 2005). When their open jaws come in contact with rock surfaces, often the whole body thrashes to maintain contact with what is often an irregular substrate. Though they propel themselves toward the substrate with their pectoral fins in typical labriform motion, they break prior to contact. Rice and Westneat (2005: p 3512) provide a classic description of parrotfish feeding: "During many *Scarus* bites, it appears as though the fish is slamming

its head into the rock". Grooves may actually be left on the rocks (Cousteau 1952, Newell 1956, Bellwood and Choat 1990) depending upon whether or not the species is a browser, excavator, or a scraper (Bellwood 1994). Chunks were missing from the scraping edges of the jaws of many specimens in this study and a large *Sc. compressus* had a longitudinal fracture across the palatine-ectopterygoid suture and ventral palatine. Bonaldo et al. (2007) quantified the dental damage to three species of *Sparisoma* off the coast of northeastern Brazil, and suggested the frequency of damage was related to the harder composition of the basaltic rock substratum at this marginal reef environment. Irrespective, these injuries testify to the hazards of this feeding behavior.

There are numerous connective tissue elements that encircle and tightly interconnect the bones surrounding the comparatively small mouth of parrotfishes. Ligaments and connective tissue bands encircle the snout within the lips and attach to the mass of connective tissue between the broad posterolateral surface of the coronoid process and the maxilla. These findings are consistent with Board's (1956) assessment that these bands collectively serve to resist distortion of the jaws during contact with the substrate and during jaw closing. They apparently help to prevent the dorsal displacement of one premaxilla (upper jaw) relative to the other during feeding and complement the interpremaxillary cruciate ligament (Fig. 1A) in this function. Further, the maxillary-dentary ligaments that attach to elements of the upper and lower jaws (Fig. 1C) are too substantial to serve only for mandibular-maxillary coupling that leads to upper jaw protrusion in actinopterygian fishes (Schaeffer and Rosen 1961). Alfaro and Westneat (1999) have documented upper jaw protrusion in *Sc. iseri* despite the inferences of Bellwood (1994) and Wainwright et al. (2004) that it is limited in parrotfishes.



**Fig. 1.** Mandibular jaws and connective tissues of parrotfishes. A. *Scarus perrico* (530 mm SL): medial view of the left premaxilla. B. *Scarus ghobban* (482 mm SL): maxilla and premaxilla in lateral view. C. *Scarus ghobban*: dorsolateral view of the rostrum showing the elastic ligament and maxillary-dentary ligament (Pm-Dent L).

Trabeculae of bone are laid down along lines of stress (Murray 1936) and the concentric laminae of the medial premaxillae (Fig. 1A) look like a diagrammatic representation of the stress lines one would expect if a load were applied by the premaxillary tip (e.g. see images in Kardong 2006: p 151). The most superficial laminae arch almost the complete length of the bone and the laminae of the posterior portion of the robust ascending process are oriented almost perpendicular to the rostrum so they contact the rostral cartilage when the upper jaw is abducted with the laminae and cartilage dampening the forces. The premaxillary-frontal elastic ligament (Fig. 1C: Elastic L) apparently stretches during abduction and protrusion and could help dampen the dorsal deflection of the anterior tip of the premaxilla while the ascending process is anteroventrally positioned. It may also recoil to retract the upper jaw across the substrate.

Though many parrotfishes scrape flat or convex surfaces (Choat and Bellwood 1985, Konow and Bellwood 2005), shearing forces resulting from feeding on heterogeneous surfaces might tend to dislocate the premaxillae or dentaries (i.e., upper and lower oral jaws) relative to each other. Cruciate ligaments are positioned to resist shearing forces (Beecher 1979) and the cruciate ligaments between the premaxillae (Fig. 1A) are radially arranged and probably can resist shearing forces over a range of positions. The symphysis between the dentaries is broad and bears a series of long interdigitating ridges and grooves (for illustrations, see Bellwood 1994: p 16). The ridges are perpendicular to the radius of curvature of the outer edge of the beak, an orientation that increases the area of contact and thus the surface for transmission of forces from one bone to the other (Herring 1972). Stresses would thus be minimized through the serrate joint and the cruciate ligaments.

A forward thrust with abducted jaws against an unyielding substrate will force the premaxilla against the premaxillary condyle of the maxilla; the maxilla against the palatine; and the ascending process of the premaxilla against the rostrum. Menisci are present between maxilla and premaxilla, maxilla and vomer, and the rostral cartilage between the premaxilla and rostrum are positioned to provide cushioning. Consistent with the findings of Clements and Bellwood (1988) there is no synovial connection between the neurocranium and anterior suspensorium as exists in the less derived epinephelids. The lateral ethmoid-palatine ligament and bands (Fig. 1C: Pal-Le Sheet), and the endopterygoid-lateral ethmoid ligament restrict free motion of the anterodorsal portion of the suspensorium. These connections also would transmit forces from the palatine to the neurocranium as well as limit suspensorial abduction consistent with the reduced suction feeding (Clements and Bellwood 1988, Alfaro and Westneat 1999, Wainwright et al. 2004). Therefore, there appears to have been an evolutionary tradeoff between the selective forces encouraging reinforcement of the skull versus the generation of suction (Alfaro and Westneat 1999).

The palatine must withstand the forces transmitted to it. Longitudinal forces from the upper jaws will also be directly transmitted to the neurocranium because the posterior palatine fits in a notch on the lateral ethmoid. This is noteworthy in large specimens of *Sc. compressus* and *Sc. perrico*, which have a high posterior edge of the palatine. The maxillary condyle of the palatine is a particularly conspicuous and robust feature in large specimens (Fig. 2A: PaMax). Trabeculae within the anterior palatine generally have an orientation that reflects the application of longitudinal forces (Hildebrand and Goslow 2001). The lachrymal (Fig. 2B: La) is tightly bound to the preorbital process by the lachrymal-lateral ethmoid bands and ligaments. Anteriorly the tough lachrymal-palatine ligament connects the lachrymal with the lateral surface of the palatine. Stresses may also be dissipated along the track from the palatine to the preorbital process of the neurocranium via these bones and ligaments.

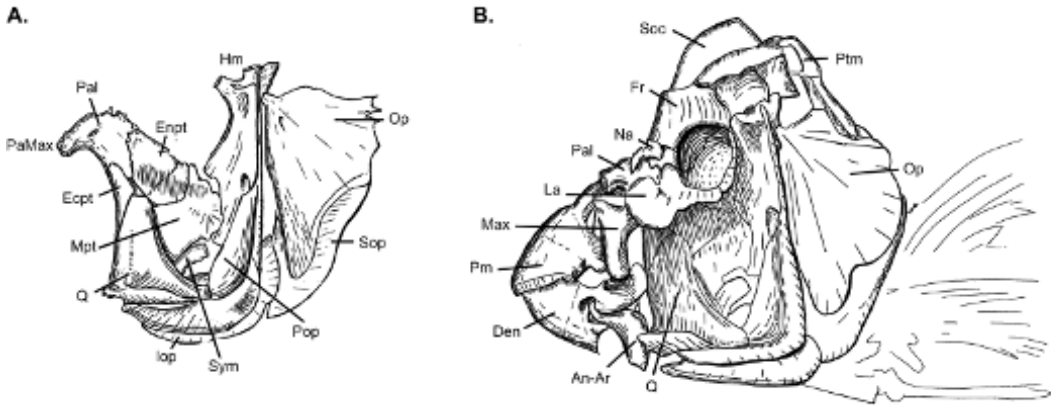


Fig. 2. A. Lateral view of left suspensorium and opercular series of *Scarus compressus* (477 mm SL); B. Lateral view of skull of *Scarus perrico* (510 mm SL).

Attention has deservedly been given to the intramandibular joint of derived percimorphs (Konow and Bellwood 2005, Konow et al. 2008, Price et al. 2010). In pomacanthids this novel joint between the dentary and anguloarticular allows 35 degrees of motion and permits gape closure when the mandibles are fully protruded (Konow et al. 2008). More derived parrotfishes (*Hipposcarus*+*Chlorurus*+*Scarus*) possess this intramandibular joint (Streelman et al. 2002) and it has been treated as a key portion of a unique four-bar linkage (Bühler 1977, Wainwright et al. 2004). Price et al. (2010) pose that the modulation of this joint may allow parrotfishes to maintain a consistent orientation with a wide gape on the surface throughout the scraping bite. The parrotfish innovations of the intramandibular joint and the pharyngeal jaws together led to rapid diversification of the oral jaws (Price et al. 2010). Parrotfishes have higher jaw-closing lever ratios than the wrasses, reflecting the greater force required to scrape hard substrata (Bellwood 2003, Wainwright et al. 2004, Westneat et al. 2005). These previous evaluations were made on the mechanics of the entire mandible with a pivot between the quadrate and mandible. I suggest that the mechanics is even more complicated because it is a double lever. Wainwright et al. (2004) hinted at this. Of particular interest are modifications of the mandible that enhance force applied at the dentary tip. A distinctive syndesmosis between the dentary and anguloarticular is present along with a shift in the insertion of the A2 of the adductor mandibulae to the coronoid process from the typical actinopterygian insertion on the ascending process of the anguloarticular (Winterbottom 1973). The consequence is a shortened out-lever of the mandible with the intramandibular joint as the pivot from that seen in generalized percimorphs like *Mycteroperca* (Fig. 3). The quadrate-mandibular articulation is the other joint. The A3 subdivision of the adductor mandibulae attaches to the medial anguloarticular (Fig. 4B, C) and is in a position to effect adduction around the quadrate-mandibular joint but it likely has only a minor role because it is quite thin. The A2 subdivision of the adductor mandibulae, on the other hand, is in a position to adduct the dentary on its pivot at the intramandibular joint. The A2 thus would be an important adductor of the dentary as previously noted by Lubosch (1923). In generalized percimorphs like *Mycteroperca* the A2 inserts on the ascending process of the anguloarticular, close to the quadratomandibular joint, which is thus the fulcrum of a third class lever and being close to the pivot is positioned to enhance speed rather than force. In *Scarus* the insertion of A2 is on the coronoid process of the dentary, and the fiber direction is almost parallel with the anterodorsal ramus of the anguloarticular (Figs. 3B, 4A). With this orientation it can generate little force that would



cause mandibular rotation around the quadrate-mandibular joint and being roughly perpendicular to the coronoid process has a mechanically optimal orientation at least during limited rotation. Therefore, this is a first class lever with a shortened out-lever arm ( $L_o$  in Fig. 3B). Its in-lever of the dentary is also lengthened as a result of the elongation of the coronoid process. For a given in-force generated by the adductor mandibulae, the out-force at the tip of the dentary will be three times that of the generalist which feeds by inertial suction (Fig. 3). The Aw muscle is also in a position to abduct (Fig. 4C: Aw ab) or adduct (Fig. 4C: Aw ad) the dentary around the intramandibular joint. The muscle is delicate, however, and likely functions to modulate the position of the dentary rather than generate much force.

Considering the presence of only subtle anatomical differences among the members of the genus *Scarus* studied here, one can speculate on how these sympatric species divide the resources because it does not appear to be on the basis of their feeding. The gut content of *Scarus* spp. is composed primarily of fine particles (Hoey and Bellwood 2008, Bonaldo et al. 2014), with over 70% of the gut contents of the *Scarus* species in this study passing through a 630  $\mu\text{m}$  mesh (Gobalet 1980). This small particle size makes it extremely difficult to evaluate what they are targeting, and it would take a creative, perhaps molecular, approach to discriminate what exactly has been pulverized and resides in the intestines (see Clements and Choat, Chapter 3). Considering that parrotfishes have been estimated to spend in excess of 84-91% of the daylight hours feeding (*Chlorurus* spp: Bellwood 1995a) and their impact on reefs can be bioerosion in excess of 5,000 kg per individual per year (Bellwood et al. 2003, 2012) it is logical that they are going to possess anatomical features consistent with the forceful cropping of chunks of inorganic materials. Collectively, the numerous structural adaptations in parrotfishes described above contribute to a spectacular eating machine.

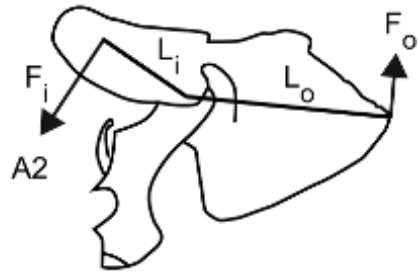
A1A2



**A. *Mycteroperca rosacea***

$$F_i \times L_i = F_o \times L_o$$

$$F_o = 0.16 F_i$$

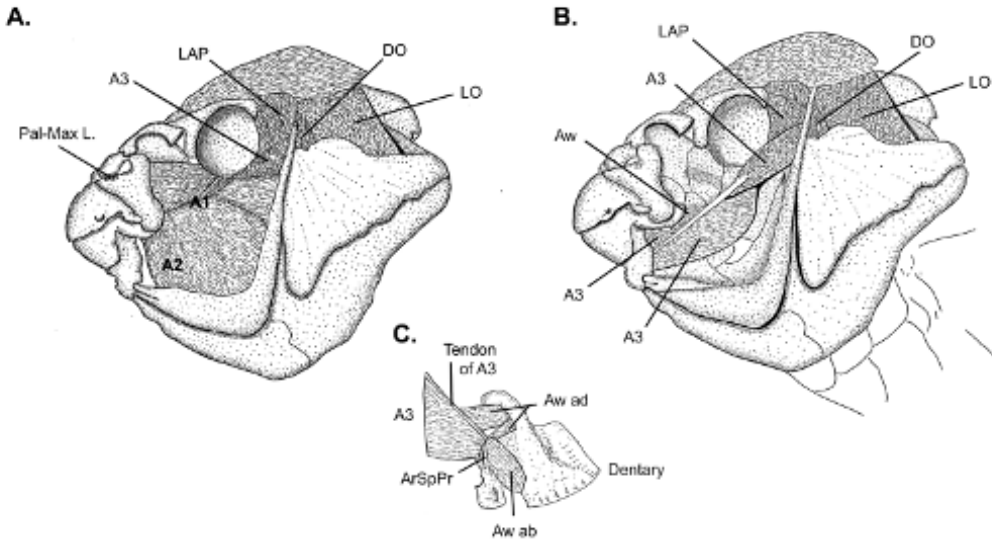


**B. *Scarus compressus***

$$F_i \times L_i = F_o \times L_o$$

$$F_o = 0.47 F_i$$

**Fig. 3.** Comparison of the lower oral jaw of a generalized percimorph and *Scarus*. A. Lateral view of the right mandible of *Mycteroperca rosacea* (610 mm SL); B. Lateral view of the right mandible of *Scarus compressus* (457 mm SL).  $F_i$  = in-force generated by the adductor mandibulae;  $F_o$  = out-force at the tip of the dentary,  $L_i$  = in-lever (distance from fulcrum to the point of application of the in-force);  $L_o$  = out-lever (distance from the fulcrum to the point of application of the out-force). *Scarus* demonstrates three times the mechanical advantage as in the generalist, *Mycteroperca*.



**Fig. 4.** Muscles of the head of *Scarus*. A. Lateral view of the muscles of the head of *Scarus ghobban* (460 mm SL). Connective tissue of the A1A2 to the premaxillary symphysis has been removed. B. Lateral muscles of the head of *Scarus ghobban* (460 mm SL) with the A1A2 complex of the adductor mandibulae removed. C. Medial complex of the left adductor mandibulae of *Scarus perrico* (540 mm SL) in medial view. Anterior is to the right.

## Summary

In this chapter I have presented the details of the anatomy of parrotfishes of the genus *Scarus* that emphasize the features of the head that resist the forces applied during the scraping of rocky substrates that are encrusted with the organic materials they ingest. These descriptions and interpretations complement the growing literature on this monophyletic group of almost 100 species (Parenti and Randall 2011). The connective tissue elements (ligaments, menisci, fascia, joints) were emphasized with the following specializations being of particular interest: within the tissues surrounding the mouth, and likely deeper, are connective tissue bands and ligaments that encircle the snout; serrate joints between the dentaries and cruciate ligaments between the ascending processes of the premaxillae are positioned to resist dislocations; the intramandibular joint between the dentary and anguloarticular is a syndesmosis that likely functions to dampen forces generated during the scraping of the rigid surfaces upon which parrotfishes feed; this joint also enhances the leverage of the system powered by the A2 portion of the adductor mandibulae acting on the enlarged coronoid process; menisci are present between the premaxillae and maxillae, maxillae and vomers, and between the ascending processes of the premaxillae and the rostrum; the boney structure of the ascending processes of the premaxillae are concentrically laminar to resist compressive forces; there are unique elastic ligaments interconnecting the frontals with the ventral surfaces of the premaxillary ascending processes. Along with a highly derived pharyngeal grinding apparatus, the impressive mandibular jaws and their associated connective tissues have contributed to the parrotfishes having a substantial influence on the turnover of substrate in tropical and subtropical reefs.

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## APPENDIX

The abbreviations used in the figures are as follows:

Am	adductor mandibulae
A1	portion of adductor mandibulae
A2	portion of adductor mandibulae
A3	portion of adductor mandibulae
An-Ar	anguloarticular
APPm	ascending process of premaxilla
Ar	articular
ArSpPr	splint process of anguloarticular
AStF	anterior subtemporal fossa
Aw	portion of adductor mandibulae
Aw ab	abducting portion of Aw
Aw ad	adducting portion of Aw
BH	basihyal (glossohyal)
BPhGr	basipharyngeal groove of neurocranium
BrStg	branchiostegal rays
CCMax	cranial condyle of maxilla
CH	ceratohyal
Den	dentary
DenCorPr	coronoid process of dentary
DHPPR	dorsal hypohyal posterior process
D.Intrahyoid Lig.	dorsal intrahyoid ligament
DO	dilator operculi
DOF	dilator operculi fossa
DPFr	dorsal process of frontal
DStF	deep subtemporal fossa
Ecpt	ectopterygoid
EH	epihyal
Enpt	endopterygoid
EoPtfa	posttemporal facet of epiotic
Epo	epiotic
Eth	ethmoid
Exs	extrascapular
Fm	foramen magnum
Fr	frontal
Hm	hyomandibula
HmSoc	hyomandibular sockets
HyoHyAbd 1&2	hyohyoideus abductores
Ic	intercalcar
IH	interhyal
IOF	infraorbital foramen
Iop	interopercle
La	lachrymal
LAP	levator arcus palatini

LEth	lateral ethmoid
LO	levator operculi
LOcF	lateral occipital fossa
Max	maxilla
MaxCr	maxillary crest
MOcF	medial occipital fossa
Mpt	metapterygoid
Na	nasal
OccCon	occipital condyle
Op	opercle
Pal	palatine
PalFMax	palatine fossa of maxilla
Pal-Le sheet	sheet of connective tissue between palatine and lateral ethmoid
Pal-Max L.	palatine maxillary ligament
PaMax	maxillary condyle of palatine
Par	parietal
ParCr	parietal crest
Pm	premaxilla
PmAsPr	ascending process of premaxilla
PmCMax	premaxillary condyle of maxilla
Pm-Dent L	premaxillary-dentary ligament
Pop	preopercle
PPtoF	fossa of the posterior face of the pterotic
ProSp	ventral spike of prootic
Psp	parasphenoid
PtF	posttemporal fossa
Ptm	posttemporal
Pto	pterotic
PtoPopPr	preopercular process of pterotic
PtoCr	pterotic crest
PtF	posttemporal fossa
Q	quadrate
QMJLF	quadrato-mandibular joint lateral fossa
QMJMF	quadrato-mandibular joint medial fossa
Rar	retroarticular
RoF	rostral fossa
RPr Max	rostral process of maxilla
Soc	supraoccipital
SoCr	supraoccipital crest
Sop	subopercle
Spo	sphenotic
StF	supratemporal fossa
Sym	symplectic
VHH	ventral hypohyal
VOcF	ventral occipital fossa
Vo	vomer
VoF	ventral fossa of vomer
VoMaxFa	maxillary facet of the vomer

## Detailed Anatomy of the Parrotfish Head

### Skeleton

**Neurocranium.** The neurocranium is highly sculptured with ridges and concavities that provide for the attachment and muscle mass of the cranial and trunk musculature (Fig. 5). A rostral fossa extends back to the level of the orbit and is divided by a low midline crest (Fig. 5A: RoF). A posterodorsally asymmetrically expanded supraoccipital crest extends the length of the supraoccipital (Fig. 5B: SoCr). In *Scarus compressus* and *Sc. perrico*, the crest is high in association with their prominently enlarged foreheads. The anterior edge of the crest is nearly vertical in *Sc. perrico*, which has the most developed hump. The crest is quite low in *Sc. rubroviolaceus* and of intermediate height in *Sc. ghobban*. The parietal crest (Fig. 5A, B: ParCr) angles laterally in *Sc. rubroviolaceus*, and dorsolaterally in *Sc. perrico*, *Sc. ghobban*, and *Sc. compressus*. In *Sc. perrico*, the parietal crest is higher, extends more anteriorly, and curves to the midline along the anterior edge of the frontal. The pterotic crest angles dorsolaterally and terminates at the posterior edge of the orbit, except in *Sc. perrico*, where it curves medially on the frontal to join the parietal crest. The posterior ends of the pterotic and parietal crests are joined superficially by an extrascapular that covers

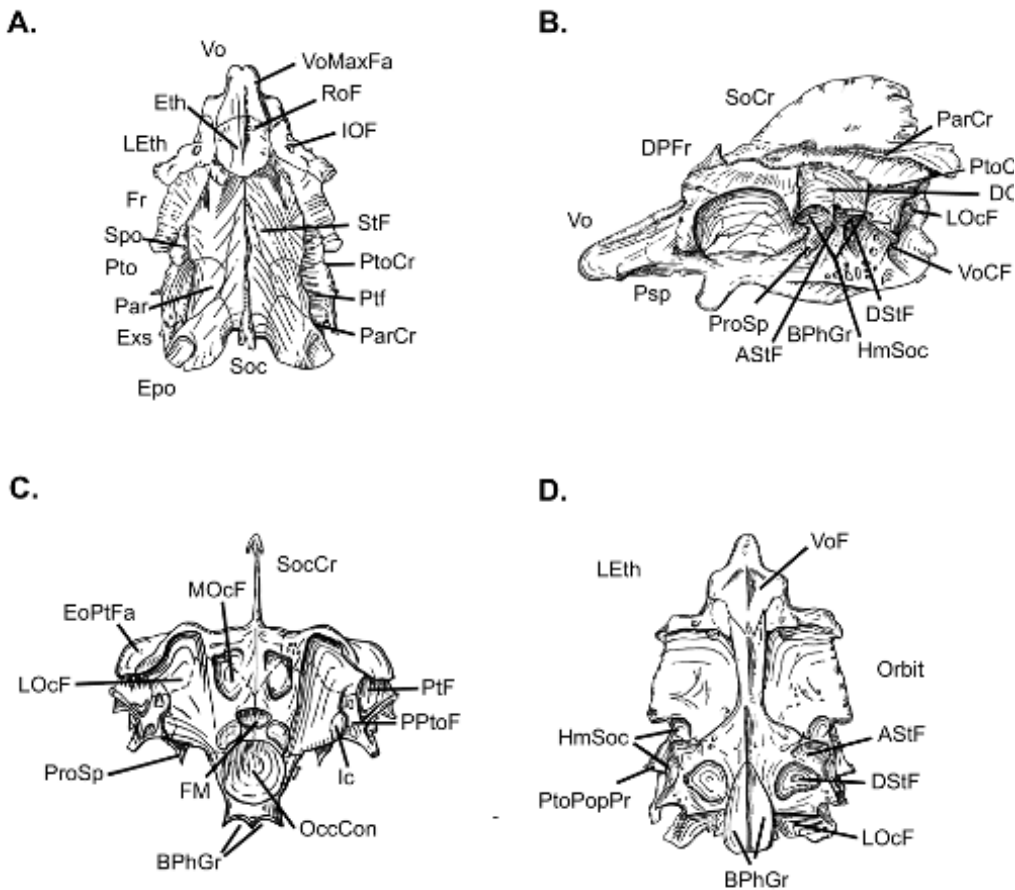


Fig. 5. Neurocranium of *Scarus compressus* (478 mm SL): A. dorsal view; B. lateral view; C. posterior view; D. *Scarus rubroviolaceus* (342 mm SL) ventral view.



the posterior end of the posttemporal fossa between the two crests (Fig. 5A: Exs). The supratemporal fossa lies between the parietal and the supraoccipital crests (Fig. 5A: StF).

Three prominent fossae are present in the postorbital region of the ventral neurocranium. Between the sockets of the neurocranial-hyomandibular joint is the anterior subtemporal fossa (Fig. 5D: AStF). Posterior and medial to this fossa is the deep subtemporal fossa (Fig. 5D: DStF). Bellwood (1994) considers these fossae unique to scarines, but dramatic subtemporal fossae are present in such distantly related groups including cyprinids and elopids. Thin laminae of the supraoccipital, epiotic, parietal, and pterotic separate the deep subtemporal fossa from the posttemporal and supratemporal fossae. Most of the greatly enlarged fourth levator externus muscle originates from the anterior and deep subtemporal fossae (Gobalet 1989, Bellwood 1994). The lateral occipital fossa (Fig. 5C: LOcF) is as deep as the deep subtemporal fossa and is the dominant feature of the posterior aspect of the neurocranium. The medial portion of the elevator posterior muscle originates from the lateral occipital fossa (Gobalet 1989). A small fossa on the posterior face of the pterotic, and lateral to the opisthotic, is the site of the fleshy origin of the lateral portion of the levator posterior muscle (Gobalet 1989). In *Nicholsina denticulata* this fossa is triangular and deep. It is well defined only in large specimens of *Scarus*.

The medial occipital fossae, visible in posterior view (Fig. 5C: MOcF), are limited to the region dorsal to the foramen magnum and are separated in the midline by a ventral extension of the supraoccipital crest. Cranial to the first vertebra on the posterolateral neurocranium is the ventral occipital fossa (Fig. 5B: VOcF). The supratemporal, posttemporal, ventral occipital and medial occipital fossae are points of attachment for trunk muscles. A dilator fossa is present posterior to the postorbital process (Fig. 5B: DOF). The posterolateral pterotics bear fossae of the levator operculi. The preopercular process of the lateral pterotic (Fig. 5D: PtoProPr) separates the dilator fossa from the levator fossa.

The anterolateral vomer has a broad convex surface against which the cranial condyle of the maxilla abuts. Posterior to this surface is a lateral expansion to which the vomeropalatine and vomeroendopterygoid ligaments attach. In anterior view, the vomer of *Sc. rubroviolaceus* is the shape of an inverted "V." It is more rounded in the other three species of *Scarus*. The ventral vomer has a sharp midline ridge that is the anterior extension of the keel of the parasphenoid (Fig. 5B: Psp) to which the anterior fibers of the adductor arcus palatini muscle attach.

A cartilaginous interspace noted by Starks (1926) in two parrotfish species separates the posterior edge of the ethmoid from the frontal in *Sc. compressus*, *Sc. perrico* and *Sc. rubroviolaceus*. This cartilaginous interspace is lacking in *Sc. ghobban*. The ethmoid is outwardly convex in *N. denticulata* and there is no cartilaginous interspace.

In *Scarus*, the ethmoid appears to be a bone of multiple origins. At least three ossification centers are indicated, a subcircular dorsal plate [the rostrodermethmoid plus supraethmoid (Patterson 1975)] which covers the ethmoid cartilage and paired cones of cartilage bone which form the medial portion of the anterior myodome. In large specimens these centers grow together. Starks (1926) describes the endochondral components of the ethmoid as remaining separate in three species of *Callyodon*, a genus since subsumed within *Scarus* (Bellwood 1994). This pattern of formation of the ethmoid, and the dominance of the endochondral ethmoid as a major bone of the anterior myodome, may be taxonomically and phylogenetically important features. The condition of the ethmoid in *Mycteroperca rosacea* (Epinephelidae) and *Morone saxatilis* (Moronidae) is that of a single rostrodermethmoid-supraethmoid that doesn't form the anterior myodome and does not separate the lateral ethmoids. In representative labrids (*Labrus*, *Symphodus*, *Ctenolabrus* and *Centrolabrus*; Rognes 1973), and in *Halichoeres nicholsi*, *Bodianus diplotaenia* and *Semicossyphus pulcher*, the

anterior myodomal component of the ethmoid forms as a pair of posteroventrally-directed growths from the dorsal plate and the separation of the lateral ethmoids is not as complete as in *Scarus*. A third endochondral ossification between the lateral ethmoids is present in *N. denticulata* in the midline ventral to the two described for *Scarus*.

The ventrolateral portion of the preorbital process of the lateral ethmoid bears a rough lachrymal facet and anterior and lateral to the olfactory foramen the lateral ethmoid is notched for the posterodorsal portion of the palatine. Anterior to this notch is a flat facet for the medial palatine.

Posterior and medial to the anterior-most point of the frontal is a dorsal process that is of a form unique to each of the five parrotfishes studied (Fig. 5B: DPFr). In *Sc. perrico* the process is part of the parietal crest. In *Sc. compressus* the process is high and stands alone. A parasagittal ridge rises anteriorly in *Sc. ghobban* to abruptly terminate at a high point. In *Sc. rubroviolaceus* it is a nondescript bump on the transversely flattened frontal. The frontal slopes antero-ventrally at this level in *N. denticulata*.

The supraorbital region of the frontal is sculptured with low outwardly directed ridges. The frontal is robust and cancellous anterior to the dorsal process in *Sc. perrico* and *Sc. compressus*. This region is flatter in *Sc. ghobban* and *Sc. rubroviolaceus*. Ventrally directed laminae of the frontals form part of the medial wall of the orbit. Anteriorly these laminae meet the ethmoid. These laminae angle ventromedially but remain separated across the midline except in *N. denticulata* where they meet at the midorbital level. They also meet in four species of parrotfishes studied by Starks (1926).

Cartilage-fills the cavity between the ventral wings of the frontals in *Calotomus* (Starks 1926), *Scarus* and *N. denticulata*. Transverse, ventrally directed laminae of the frontals below the supraoccipital separate this cartilage from the braincase.

The "Y"-shaped basisphenoid of the midline splits the entrance to the posterior myodome and forms the base of the orbital opening to the cranial chamber. The prootics meet in the midline ventral to the dorsal forks of the basisphenoid where they form the roof of the anterior portion of the myodome. Anteriorly directed laminae of the basioccipital are the roof of the posterior portion of the myodome. The lateral walls of the myodome are formed by the prootics and parasphenoid. The prootic also forms the posterior wall and part of the ventral portion of the incomplete pituitary capsule.

In the posterior-most corner of the neurocranium, as seen in dorsal view, is the slightly convex and spatulate epiotic. Its flattened dorsal surface has a facet for the ventral surface of the dorsal ramus of the posttemporal. The splinter-like intercalcar limb of the posttemporal is bound by ligaments to the intercalcar. The complex exoccipital contributes to the lateral, medial, and ventral occipital fossae, the deep subtemporal fossa, occipital condyle, and walls of the foramen magnum.

The sphenotic forms most of the postorbital process, contributes to the posterior wall of the orbit, to the round anterior socket of the hyomandibula, to the dilator fossa, and contributes to the roof of the anterior subtemporal fossa. I was unable to distinguish a sphenotic distinct from a dermosphenotic as Patterson (1977) stated occurs in the majority of teleosts.

The prootic contributes to the anterior subtemporal fossa, the deep subtemporal fossa, and to the myodome. A prominent spike from which branchial levators originate (Gobalet 1989) projects ventrally from the lateral commissure lateral to the posterior opening of the par jugularis of the trigeminofacialis chamber. The spike is absent from *N. denticulata*.

The medial edge of the pterosphenoid bears a small preotic wing described by Rognes (1973) in some labrids. The preotic wing in *Scarus* is an extension of the pterosphenoid within the connective tissue membrane covering part of the opening of the cranial chamber.

When present, these thin laminae are rarely symmetrical. The preotic wing is absent from *Sc. perrico*. It is a small equilateral triangle and is present in seven of twelve specimens of *Sc. compressus* and only on the left side. Seven *Sc. rubroviolaceus* observed have some bilateral representation of the preotic wing in which it is usually broad and square. In *Sc. ghobban* the preotic wing is typically squared-off on the left side and round on the right. In a 206 mm specimen it is two tiny splinters. It was absent from only one of 13 *Sc. ghobban*. The preotic wing is triangular in the single specimen of *N. denticulata*.

The longest bone in the neurocranium is the parasphenoid, which ventrally has a sharp keel that caudally separates the neurocranial grooves of the synovial basipharyngeal joint (Fig. 5B: Psp, BPhGr). Anteriorly the keel bears a characteristic rudder-shaped process ventrally. The scar of Baudelot's ligament is found dorsal to the neurocranial grooves that receive the upper pharyngeal condyles and in line with the ridge separating the deep subtemporal fossa from the ventral occipital fossa. The neurocranium is highly trabecular and suggestive of considerable reinforcement due to forces applied to it from the action of both the mandibular and pharyngeal jaws.

*Mandibular jaws.* The distinctive jaws of *Scarus* show extreme modifications for their habit of scraping rock and calcareous surfaces. The jaws are short, robust, and the quadratomandibular joint is well anterior of the orbit. The exposed surfaces of the dentary and premaxilla are composed of numerous tiny denticles cemented together into thick outwardly convex beaks with tapered and squared-off cutting edges (Bellwood 1994). Worn denticles are constantly replaced from internal germinative tissues.

The anguloarticular is quite distinctive (Figs. 2, 3B, 6, also see Bellwood and Choat 1990: p 196, Bellwood 1994: p 18). There is a syndesmosis between it and the dentary and a diarthrosis between it and the quadrate. In *Scarus* the vertically oriented anguloarticular consists of two spatulate parts. One medially concave portion is directed ventromedially from the quadrate fossa. A ridge is found on the anterior edge of the medial face. The interopercular-mandibular ligament attaches posterior to this ridge. The posteroventral portion of this arm is ankylosed to the small retroarticular. The anterodorsomedially-directed arm is at an oblique angle to the ventral arm and is twisted forty-five degrees relative to it. This ramus fits in the notch on the lateral dentary and it is called the anterior articular ascending process by Bellwood (1994). I should note what I am naming the anguloarticular is based on Patterson (1977) whereas other investigators (e.g. Bellwood 1994, 2003, Wainwright 2004) use the name articular.

The quadrate fossa of the anguloarticular has medial and lateral facets (Fig. 6: QMJLF). In smaller specimens of all four species the lateral facet is a continuous almost semicircular surface. In large specimens of *Sc. compressus* and *Sc. perrico*, the lateral facet has both posterior-facing and dorsal-facing portions. A raised transverse ridge meets a similar ridge on the lateral mandibular condyle of the quadrate during adduction. The medial facet is directed posterodorsally and is offset posteroventrally relative to the lateral facet. A dorsally projecting process, located just posterior to the fossa, is the attachment point of a quadratomandibular

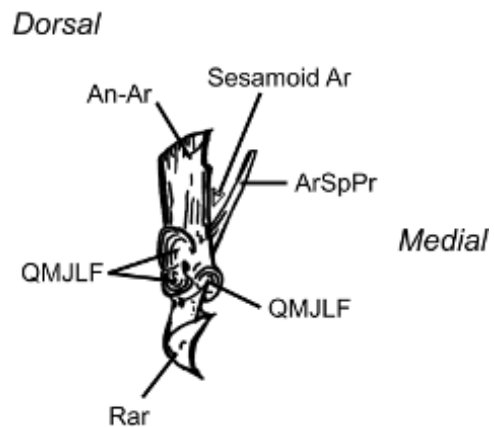


Fig. 6. *Scarus compressus*: posterior view of anguloarticular.

ligament. A unique splint process of the anguloarticular projects dorsally from above the medial facet (Fig. 4C, 6: ArSpPr). This is the articular medial spine of Bellwood (1994). The small pyramidal sesamoid articular tightly adheres to the anguloarticular dorsal to the splint process. No Mechelien groove or cartilage is found in *Scarus*, but is present in the less derived *N. denticulata*.

The dentary symphysis is a long, broad serrate joint (beautifully illustrated in Bellwood 1994: p 16). The dentary is concave inside the tapered scraping edge. Its massive coronoid process projects posteriorly from the denticled portion of the bone and its broad dorsolateral surface is concave, rough, and rounded-off posteriorly. A ventrolateral flange covers the articular notch.

The hemispherical dental surfaces of the premaxillae are similar to those of the dentaries (Fig. 1B, 2: PM). The posterior edge of the premaxilla is squared-off except for the medially positioned ascending process and the notched posterolateral corner. The maxilla is tightly bound to the premaxilla by the maxillary-premaxillary posterior ligament in this notch. The anterior end of the ventral portion of the ascending process bears two sharp parallel ridges. The lateral ridge is expanded at the base into a small maxillary condyle. The medial ridges broaden the contact surfaces between the premaxillae, surfaces tightly bound by cruciate ligaments (see below). Concentric arches of boney laminae are visible on the medial face (Fig. 1A). Large specimens of *Sc. ghobban* and *Sc. rubroviolaceus* bear "canines" on the lateral surfaces of the premaxillae above the corner of the mouth (Fig. 1B). *Sc. perrico* lacks these canines and some *Sc. compressus* have tiny raised denticles in this position.

Only limited motion is possible between the anterior maxilla and the premaxilla (Figs. 1B, 4: Max, Pm). The lateral surface of the maxilla is flattened, and has a thin anteriorly recurved dorsal crest. A rostral process is located lateral to the palatine fossa (Fig. 1B: RPrMax). The dorso-medial edge of the head of the maxilla forms the medial wall of an elongate palatine fossa. The large scar of the adductor mandibulae tendon is located on the posterior face ventral and lateral to the palatine fossa.

The anterior-most portion of the maxilla bears a premaxillary condyle. This condyle has synovial joints anterolaterally with the maxillary facet of the premaxilla, and anteromedially with the broad maxillary-premaxillary anterior ligament. A small flat cranial condyle that glides on the vomer is found on the posterior portion of the medial aspect of the head. The medial surface of the ventrolateral maxilla is grooved for the tough maxillary-dentary and maxillary-premaxillary posterior ligaments.

*Circumorbitals.* The dorsal portion of the medial surface of the broad lachrymal (Fig. 2B: La) is notched for the tight joint with the preorbital process of the neurocranium. The dorsomedial portion of the lachrymal is concave and the dorsal edge is slightly dished in for the olfactory pit. The anterior portion of the medial surface is thickened and scarred from the tough lachrymal-palatine ligament. A thin anteroventral extension covers the dorsal crest of the maxilla.

There are usually three infraorbitals in addition to the lachrymal though in each *Scarus* species an individual was found with four on one side and three on the other. One specimen of *Sc. compressus* had two on each side. Gosline (1968) indicated that this reduction in circumorbital number from the perciform total of six (including the lachrymal) is a specialization.

*Nasal.* The lateral portion of the fan-shaped posterior portion of the nasal is attached to the frontal-lateral ethmoid suture and to the lateral ethmoid, dorsolateral to the olfactory foramen. The nasal is laterally notched around the olfactory pit and is laterally recurved over the dorsal portion of the maxillary process of the palatine.

*Hyoid* (Fig. 7). The hyoid bar is thin, broad, ventrally convex, dorsally deeply recessed and anterodorsally recurved medially. Of the four bones that comprise it, the ventral hypohyal (Fig. 7A: VHH) is unusual in that it underlies 60% of the length of the ceratohyal (in both *Scarus* and *N. denticulata*) and anteromedially meets its opposite at an oval condyle. The dorsal hypohyal bears a posteriorly recurved hook (Fig. 9A: DHPPr) that forms the anterior border of the dorsal recess. Cartilage separates the anterior ceratohyal from the ventral hypohyal. The epihyal (Fig. 7A: IH) is tightly bound to the interopercular thus preventing pivoting around the now vestigial interhyal. This apparent immobility is consistent with the proposal of Bellwood (1994) that scraping parrotfishes have limited suspensorial abduction and gular depression. Five flattened branchiostegal rays attach ventrolaterally to the hyoid bar (Fig. 7A: BrStg).

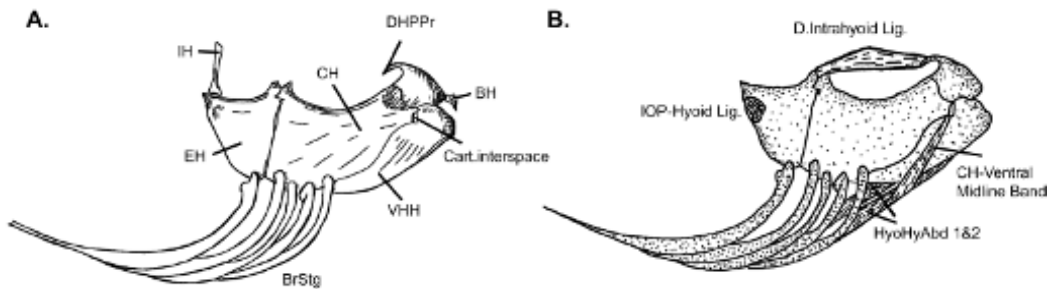


Fig. 7. A. *Scarus perrico* (349 mm S.L.): lateral view of right hyoid, anterior is to the right.

B. *Scarus* sp.: lateral view of the ligaments of the right hyoid, anterior is to the right.

*Suspensorium and opercular series.* The suspensorium is roughly rectangular in shape with a deeply notched dorsal border. The quadratomandibular joint (Fig. 2A: Q) is positioned nearly as far rostral as the maxillary process of the palatine (Fig. 2A: PaMax). Flanges on the mandibular condyle of the quadrate meet those of the anguloarticular and apparently serve to limit adduction (see description of the anguloarticular fossa above). The hyomandibular articulation with the neurocranium is through synovial joints on two condyles. The posterodorsal hyomandibula projects posteriorly in line with the condyles. A sharp ridge of the hyomandibular arises from the pillar of the anterior condyle runs to the opercular condyle, and defines the ventral boundary of the dilator fossa.

The extensive fossa of the adductor mandibulae muscle is deepest dorsal to the quadrate at the junction of the endopterygoid and metapterygoid. A dorsally concave horizontal ridge of the quadrate defines the ventral edge of the fossa and the angle of the preopercle defines the posteroventral border. The dorsal portions of the convex medial surfaces of the endopterygoid (Fig. 2A: Enpt) and metapterygoid (Fig. 2A: Mpt) are the insertion point of the adductor arcus palatini muscle.

The palatine and endopterygoid are bound at a serrate suture. The stout maxillary condyle of the palatine (Fig. 2A: PaMax) projects at an acute angle to the anterior border of the suspensorium.

The lateral surface of the palatine (Fig. 2A: Pal) bears a scar from the lachrymal-palatine ligament, and the medial surface bears a prominent scar of the vomero-palatine ligament in line with the ventral edge of the maxillary process. The posterior edge of the palatine fits in a notch on the lateral ethmoid anteroventral to the olfactory foramen and a concavity of the posterior portion of the medial surface reinforces the contact.

The opercle (Fig. 2A: Op) is thickened ventral to the hyomandibular socket and a sharp ridge extends posteroventrally from the socket half the breadth of the bone. The adductor operculi and levator operculi attach dorsal to this ridge. The subopercle (Fig. 2A: Sop) has a dorsal process that projects anterior to the ventral portion of the opercle and on the medial interopercle (Fig. 2A: Iop) is a facet against which the epihyal (Fig. 7A: EH) abuts. The ligament to the epihyal attaches to the fossa anterior to the facet.

## Ligaments

The *nasal-frontal ligament* is a band of connective tissue interconnecting the posterior end of the nasal with the anterior edge of the frontal lateral to its anterior-most point and continues laterally onto the lateral ethmoid. The dorsal surfaces of the nasals are interconnected across the midline by tough connective tissue over the ascending processes of the premaxillae. The anterior attachment of these *internasal and interpalatine bands* is on the dorsal edge of the palatine or on the maxillary-nasal ligament. Ventral to the internasal bands, a tough independent sheet interconnects the posterodorsal edges of the palatines.

Connective tissue arises on the medial surfaces of the rostral processes of the maxillae and spreads out medially as its fibers cross the ascending process of the premaxillae. With the interpalatine bands, this *intermandibular cross ligament* forms the dorsal cover of the rostral fossa. Connective tissue interconnects the posterodorsal lachrymal with the anterior lateral ethmoid, the *lachrymal-lateral ethmoid ligaments*. Ligaments also join the notched portion of the lachrymal with the preorbital process, immobilizing the union.

The *nasal-lachrymal bands* are continuous with the subcutaneous connective tissue of the snout that binds the nasal to the lachrymal anterior and posterior to the olfactory pit. A short, tough, *lachrymal-palatine ligament* interconnects the medial surface of the anterodorsal part of the lachrymal with the lateral surface of the palatine, posterior to, and in line with, the ventral edge of the maxillary process. This distinctive ligament was also observed in epinephelids.

Considerable connective tissue attaches to the symphysis of the ascending processes of the premaxillae. The deep layer of this *premaxillae associated connective tissue* arises from between the dentary and the ventral maxilla. The outer layer is a superficial tendon of the adductor mandibulae. It arises from the A1A2 complex posterior to the coronoid process of the dentary. The deep and superficial parts fuse before their attachment to the premaxillary symphysis.

Strong *maxillary-nasal and maxillary-palatine ligaments* join the rostral process of the maxilla to the anterior tip of the nasal, and to the anterolateral surface of the maxillary process of the palatine anterior to the lachrymal-palatine ligament (Fig. 4A: Pal-MaxL). The maxillary-nasal ligament, the nasal bone, and the nasal-frontal ligament form a track that interconnects the maxilla and the neurocranium. It probably functions to limit the forward rotation of the maxilla. The narrow and delicate *anguloarticular-maxillary ligament* (Primordial Ligament) attaches to the ridge of the anguloarticular dorsal to the quadrate fossa. It passes medial to the A2 and lateral to the A3 portions of the adductor mandibulae and joins the massive tendon of A1 that inserts on the posterior face of the maxilla. A distinct band interconnects the ventral portion of the groove of the ventromedial maxilla and the anterodorsal portion of the coronoid process of the dentary. A thick cuff of connective tissue attaches to the posterior border of the lateral face of the coronoid process and covers the posterior and posterolateral portions of the ventral maxilla. This is the *maxillary-dentary ligament and cuff*. The tough *posterior maxillary-premaxillary ligamentous* strap interconnects the medial surface of the notched posterolateral portion of the premaxilla with the dorsal

portion of the groove in the medial surface of the ventral maxilla. This tight connection severely limits independent motion of these elements.

A tough, broad band of parallel fibers connects the medial portion of the head of the maxilla, ventral to the cranial condyle, with the ventral portion of the groove in the posterior aspect of the ascending process of the premaxilla. This is the *anterior maxillary-premaxillary ligament*. The attachment to the ascending process is broader than the attachment to the maxilla. The medial facet of the premaxillary condyle of the maxilla glides on the lateral surface of this band in a synovial cavity. A *maxillary-rostral cartilage ligament* connects the anterolateral portion of the rostral cartilage (described below) with the medial maxilla dorsal to its cranial condyle. The ascending processes of the premaxillae are bound together by a continuous superficial band of *interpremaxillary cruciate ligaments* (Fig. 1A). The broad premaxillary symphysis contains approximately nine pairs of tough crisscrossing ligaments. They are radially arranged and attach ventrally on one element and dorsally on the opposite bone. The cruciate design of ligaments is optimal for resisting shearing forces (Beecher 1979) and Bellwood (1994) also noted them in parrotfishes. These ligaments are also cruciate in *N. denticulata*.

The *premaxillary-frontal elastic ligament* is a cylindrical bundle of elastic fibers that connects the lateral surface of the posterior half of the ascending process of the premaxilla (and, at times, the anteroventral portion of the ascending process) with the anterior tip of the frontal and with the lateral ethmoid ventral to it (Fig. 1C). This extraordinary ligament stretches and recoils with manipulation. It is also found in *N. denticulata*.

The tough *vomero-palatine ligament* is directed dorsally from the edge of the laterally expanded portion of the vomer to the scar on the medial palatine in line with the ventral edge of the maxillary process. This ligament has a transverse orientation in *N. denticulata*. The tough, strap-like *vomero-endopterygoid ligament* attaches to the same ridge as the vomero-palatine ligament on the lateral expansion of the vomer, and is directed posteroventrally to the anterior edge of the medial surface of the endopterygoid. The posterodorsal and posterior edge of the palatine connect to the anterior tip of the frontal, and to the lateral ethmoid by the *palatine-lateral ethmoid ligament and sheet* (Fig. 1C: Pal-Le Sheet). The nasal may attach to the dorsal edge of the connective tissue sheet. The ventrolateral edge of this sheet is a short, tough ligament that connects the ventral portion of the posterior edge of the palatine with the anterior face of the lateral ethmoid, lateral to the palatine notch. The joint between the anterior suspensorium and the preorbital process in this location is not synovial.

The tough, short *lateral ethmoid-endopterygoid ligament* connects the ventral preorbital process, medial to the lachrymal facet, with the dorsal edge of the anterior endopterygoid. This is a ligament that limits suspensorial abduction. The joint capsules positioned between the hyomandibula and sphenotic are surrounded by the *hyomandibulo-neurocranial ligaments* that restrict motion to the medial-lateral plane. The posterior ligaments extend caudally behind the synovial capsule. The *anguloarticular-dentary sheet of connective tissue* connects the anterior edge of the anguloarticular to the rough superficial surface of the bony portion of the posterior dentary. An *interanguloarticular sheet of connective tissue* lies deep within the lower lip and is continuous with the connective tissue mass between the dentary and maxilla. This band interconnects the anterior faces of the anguloarticulars across the ventral midline.

A tough, thick *anguloarticular-dentary ligament* connects the medial face of the anteriodorsal spatulate ramus of the anguloarticular with a rough triangular pedicel on the lateral wall of the dentary. The dorsolateral surface of the anguloarticular is connected to the medial surface of the laterally expanded flange of the coronoid process by a ligament.

Anterior-posterior and medial-lateral motions are possible at this syndesmosis. The tough, wide *interopercular-mandibular ligament* narrows from its attachment to the anterior end of the interopercle to its attachment to the posterior and medial faces of the retroarticular, and the ventromedial anguloarticular. A *quadrato-mandibular ligament* connects the anguloarticular, posterior to the quadrato fossa, with the quadrato concavity ventral to the mandibular condyles. Fine connective tissue also interconnects the quadrato and anguloarticular on the lateral surface of the joint. The medial connection across the joint is a tough band. Additional connective tissue interconnects the anterior preopercle with the anguloarticular.

The *interopercular-hyoid ligament* is an extensive mass of short fibers interconnecting the posterolateral surface of the epihyal with a concave facet on the medial interopercle (Fig. 7B: IOP-Hyoid Lig.). It limits rotation between these elements. These tough, short, circular *urohyal-hypohyal ligaments* interconnect the anterolateral facets of the urohyal to the medial surfaces of the ventral hypohyals. The tough *posterior interhyoid cross ligament* interconnects the dorsomedial processes of the dorsal hypohyals over the joint between the first and second basibranchials. The *anterior interhyoid cross ligament* is a small band that interconnects the cartilages between the ceratohyals and ventral hypohyals across the midline ventral to the urohyal. A tough band forms the dorsal edge of the hyoid bar and interconnects the dorsal processes of the dorsal hypohyal, ceratohyal and epihyal. This is the *dorsal intrahyoid ligament* (Fig. 7B: D. Intrahyoid Lig.). Board (1956) identified this in *Sparisoma* and it is also present in *N. denticulata*. Osse (1968) identified (probably incorrectly) the *hyohyoideus proprius* muscle in this position in *Perca fluviatilis*.

The *ceratohyal-ventral midline band* is transparent and extends ventromedially from the ceratohyal above the cartilaginous interspace between the ceratohyal and ventral hypohyal (Fig. 7B). It is lateral to the first *hyohyoideus adductor* and meets its counterpart in the midline and may extend onto the first branchiostegal rays and ventral urohyal. This ligament is probably the tendon of the *hyohyoideus ventralis par caudalis* in *Haplochromis* described by Anker (1977). The fibers of the *urohyal-first basibranchial ligament* interconnect the flat ventral surface of the first basibranchial with the dorsal spine of the urohyal. Except for Liem's (1970) description of the Nandidae, the *opercular-interopercular ligament* is rarely mentioned. It probably exists in all bony fishes that open the mouth through the levator operculi-opercular series coupling. The ligament arises from most of the anterior edge of the opercle and attaches to the posterolateral surface of the interopercle and may include the dorsal process of the subopercle. The thin *hyomandibular-opercular ligament* encircles this synovial ball-and-socket joint between these two bones. The unusually tough *Baudelot's ligament* interconnects the parasphenoid ventral to the ridge separating the deep subtemporal and ventral occipital fossae with the anterior cleithrum at the base of the elongate dorsal spike.

## Menisci

A thin *maxillary-premaxillary meniscus* is positioned within the synovial joint between the anterolateral face of the premaxillary condyle of the maxilla and the facet on the base of the lateral ridge of the posterior aspect of the ascending process of the premaxilla. As a result, the maxilla and premaxilla also appear to move as a single unit that is also the case in *N. denticulata* even though this meniscus is absent.

A *maxillary-vomerine meniscus* is located between the cranial condyle of the maxilla and the anterolateral facet of the vomer. Connective tissue from the posterior edge of this meniscus attaches to the vomer and connective tissue from the dorsal part of the meniscus



attaches within the groove in the ventral portion of the ascending process of the premaxilla. In *N. denticulata* the maxillary cranial condyle is tiny and the meniscus is absent.

The *rostral cartilage* is located between the ascending processes of the premaxillae and the vomer. A synovial capsule for the ascending process of each premaxilla is located on the dorsal surface of the cartilage and the grooved ventral surface of the rostral cartilage slides in a synovial joint on the midline ridge of the rostral fossa (5A: RoF). This is effectively a large meniscus. A thin *interhyoid meniscus* is found in the synovial joint between the ventromedial condyles of the ventral hypophyals in the midline.

## Muscles

The A1 and A2 portions of the *adductor mandibulae* (Fig. 4) are distinguished on the basis of their points of insertion because there are not obvious superficial subdivisions (Fig. 4A). None of the superficial adductor mandibulae inserts on the anguloarticular as described by Board (1956) or Tedman (1980b) nor does the internal subdivision described by Lubosch (1923). The A3, which inserts on the anguloarticular (Fig. 4B: A3), and the subdivided Aw (Figs. 4B, C: Aw) are the “deep” portions of the adductor mandibulae. The details described here are consistent with Clements and Bellwood (1988) and Bellwood (1994).

The massive A1 (Fig. 4A: A1) has a fleshy origin from most of the adductor fossa of the suspensorium and from the surface of A3. The A1 inserts by a thick tendon on the posterior maxilla and to the medial portion of the coronoid process of the dentary. Superficial attachments to connective tissue probably also directly influence the premaxillae. There doesn't appear to be a discreet dorsal portion as determined by Clements and Bellwood (1988) in *Sc. rubroviolaceus* and no aponeurotic connection to the anguloarticular was identified.

The fleshy origin of A2 (Fig. 4A: A2) is from the posterior portion of the horizontal ridge of the quadrate. A2 is parallel-fibered and inserts on the medial surface of the posterior end of the coronoid process of the dentary. This is consistent with Lubosch (1923), Clements and Bellwood (1988) and Bellwood (1994). Dorsally its short, flat tendon is continuous with the tendon of A1. This apparently is the A1 alpha muscle of Tedman (1980b). In *Leptoscarus vaigiensis* (Schultz 1958), *Sparisoma cretense* (Board 1956), and *N. denticulata*, the A2 is separate from A1 and inserts along the posterior border of the ascending process of the anguloarticular and on the tip of the coronoid process of the dentary.

Most of the mass of A3 (Fig. 4B) is located posterodorsal to A1 and originates from the lateral surface of the ventral portion of the levator arcus palatini and from the hyomandibula ventral to it. These fibers attach to a long, narrow, and flat tendon that inserts on the sesamoid articular on the medial face of the ascending process of the anguloarticular. A broad, but very thin portion of A3 originates from the metapterygoid and quadrate and attaches to the medial surface of the tendon. A few fibers of A3 that have origins on the ventral quadrate insert directly on the anguloarticular posteroventral to the sesamoid articular, not on the dentary as suggested by Clements and Bellwood (1988) for *Sc. rubroviolaceus*. The insertion of A3 is not on the splint process of the anguloarticular as described by Lubosch (1923). A3 has two points of insertion to the medial surface of the body of the anguloarticular in *N. denticulata*.

The small Aw is subdivided into a ventral abductor (Fig. 4C: Aw ab) and a pair of dorsal adductors (Fig. 4C: Aw ad) and is a more complicated muscle than described by Clements and Bellwood (1988). The abductor portion (Aw beta of Bellwood 1994: p 38) originates along the anterior edge of the splint process of the anguloarticular (Fig. 4C: ArSpPr) and from the bone ventral to the splint. The fleshy insertion is on the posterior edge of the

dentary. One part of the adductor portion of Aw arises from the tendon of A3 and inserts on the coronoid process medial to A2. This is the muscle tendo-dentary of Lubosch (1923) and part of the deep portion of A3 of Board (1956) and possibly Aw gamma of Bellwood (1994: p 38). The other part of Aw arises from the end of the splint process and inserts on the dentary anterior to, and in line with, the fibers that originate on the tendon of A3. This is the muscle artic-dentary of Lubosch (1923) who considers this subdivision of the medial adductor to be a scarid character. Though the anguloarticular of *N. denticulata* is not highly modified (ascending process present; splint process rudimentary; no *Scarus*-like anguloarticular-dentary joint), the Aw subdivision is very close to that of *Scarus*. An additional portion of the medial adductor of *N. denticulata* arises from the medial surfaces of the endopterygoid and quadrate and inserts on the ventral portion of the medial anguloarticular. This is the adductor mandibulae medialis of Lubosch (1923) for *Leptoscarus vaigiensis* (then called *Sc. coeruleopunctatus*) and is present in *Sparisoma cretense* (Board 1956).

The *levator arcus palatini* (Fig. 4A, B: LAP) originates from the postorbital process of the neurocranium and fans out to insert on the hyomandibula dorsal to the transverse ridge. A thin layer of its fibers originate along the superficial edge of the dilator fossa caudal to the orbit, cover the dilator operculi and insert on the caudal end of the transverse ridge. The *dilator operculi* (Fig. 4A, B: DO) originates from the dilator fossa of the neurocranium medial to the adductor arcus palatini and from the hyomandibula dorsal to the transverse ridge. This conical muscle comes together medial to the dorsal process of the preopercle and inserts on the anterodorsal corner of the opercle. It isn't always distinct from the levator operculi caudal to it.

The *levator operculi* (Figs. 4A, B: LO) originates from the levator fossa of the pterotic and from the posterodorsal process of the hyomandibula. There is extensive pinnation within this muscle and the fiber direction is posteroventral toward the insertion on the dorsomedial opercle.

The *adductor arcus palatini* originates from the ventral fossa of the vomer (Fig. 5D: VoF), from the keel of the parasphenoid (Fig. 5B: Psp) and midline anterior to the keel, and from the lateral parasphenoid and prootic dorsal to the keel. It inserts on the dorsomedially-directed portion of the endopterygoid and metapterygoid and on the anterior portion of the medial hyomandibula. The fiber direction is generally posterolateral to posteroventrolateral from the origin.

The pinnate *adductor operculi* has a fleshy origin from the ventral-facing surface of the neurocranium between the lateral occipital fossa and the deep subtemporal fossa and an aponeurotic origin anterodorsal to the ridge separating the ventral occipital fossa from the media wall of the deep subtemporal fossa. The fiber direction is ventrolateral from the origin to its fleshy insertion on the medial opercle. The fascia of the ventral edge of the ovoid insertion is on the crest of the ridge of the medial opercle.

The small *intermandibularis* interconnects the medial surfaces of the dentaries dorsal to the posterior portion of the symphysis. The fleshy attachment is posteroventral to a large foramen, lateral to the insertion of the geniophyoideus, and dorsal to the insertion of the abductor portion of the Aw. It is ovoid in cross section. The *geniophyoideus* originates from all but the dorsal portion of the lateral surface of the posterior ceratohyal, the anterior epihyal, and the heads of the branchiostegal rays. It fuses with its counterpart in the midline anterior to the first branchiostegal ray and inserts on the dentary lateral to the posterior end of the symphysis. The insertion is by a mass of connective tissue medially and by a tendinous band dorsolaterally. This muscle is subdivided in *Sparisoma cretense* (Board 1956).

The *hyohyoideus inferioris* originates from the medial surfaces of the arched ventral portion of the first two branchiostegal rays. The sheet of fibers angles anteromedially and meets its counterpart ventral to the urohyal to which there is a connection through fascia. Fibers may also insert either on the ventrolateral urohyal or on the lateral surface of the hypaxial muscle that is continuous with the sternohyoid muscle. The *hyohyoideus inferioris* and the first *hyohyoideus abductoris* define the anteroventral opening to the opercular chamber.

There are five distinct branchiostegal ray abductors (*hyohyoidei abductores*) that interconnect each ray and the hyoid (Fig. 7B: HyoHyAbd). The first abductor has a fleshy attachment to the anterior edge on the medial surface of the first branchiostegal ray. The attachment on the hyoid bar is tendinous on the ventral hypohyal posterior to the urohyal-ventral hypohyal ligament. There is an attachment to the lateral surface of the anteroventral urohyal. The second abductor originates by a flat tendon from the ventral edge of the ventral hypohyal and its fleshy insertion is on the medial surface of the second branchiostegal ray ventral to its head. The abductors of the three caudal branchiostegal rays have fleshy attachments to the proximal portions of the medial surfaces of their respective rays and tendons of origin from the ventral portion of the medial surface of the hyoid covering the suture between the ventral hypohyal and the ceratohyal. The three thin tendons are slightly staggered anterior to posterior.

The *hyohyoidei adductores* are thin muscles between the distal portions of the branchiostegal rays. The dorsal-most adductor interconnects the dorsal portion of the fifth branchiostegal ray with much of the medial surface of the opercular.

From a tendinous origin from the more ventro-posterior process of the pterotic the *protractor pectoralis* fans out to a long, fleshy insertion on the anterior face of the dorsal elongation of the cleithrum dorsal and lateral to Baudelot's ligament. In *N. denticulata* the *protractor pectoralis* is parallel fibered and inserts on the lateral edge of the cleithrum posterodorsal to the pharyngeal facet. The *protractor pectoralis* may have a role in parrotfish pharyngeal jaw stabilization through the pharyngocleithral joint (Gobalet 1989).

The thin *levator pectoralis* is continuous with the epaxial musculature medial to it. Its origin from the posterodorsal process of the hyomandibula may be either fleshy or aponeurotic. Additional fibers originate from the levator fossa ventromedial to the levator operculi. The insertion is on the anterior edge of the dorsal portion of the supracleithrum, and on the lateral surface of the posttemporal.

The *sternohyoideus* muscle is a ventromedial mass of complex fibers that originate from the anterior surface of the ventral portion of the cleithrum. Fibers from each side meet in the midline on the posterior edge of the urohyal and on the ventral surface of the more dorsal of the two posterior processes of the urohyal. Dorsal to this mass, and also originating from the anteroventral cleithrum and from the connective tissue cover of the medial mass, are anteriorly directed fibers. They also insert on the more dorso-posterior processes of the urohyal. The fiber direction of this sheet is almost parallel to the dorsal edge of the urohyal. The medial mass fans out anteriorly and dorsally. Originating from the lateral surface of the connective tissue cover of the ventromedial mass is a thin sheet of fibers that are continuous with the hypaxial musculature ventral to them. Together they insert in the lateral groove of the urohyal. A narrow tendon extends dorsally from their myocomma covering and inserts on the ventral end of the third hypobranchial. A thin sheet of muscle fibers is found lateral to the myocomma posterior and lateral to the tendon to the third hypobranchial. The tendon is also present in *Sparisoma cretense* arising

from the “isthmus muscle” (Board 1956). Winterbottom (1973) gives an independent name, the sternobranchialis, to a muscle with this connection. Elshoud-Oldenhave and Osse (1976) have called this tendon to the third hypobranchial a ligamentous projection in *Gymnocephalus cernua*. The small tendon to the third hypobranchial in *N. denticulata* arises from the superficial fascia of the sternohyoideus muscle. This connection probably is a modification of the ligamentum urohyal caudale of Anker (1977). Wainwright et al. (2004) consider the sternohyoideus to be reduced in parrotfishes in contrast with the wrasses.

# Innovation and Diversity of the Feeding Mechanism in Parrotfishes

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## Introduction

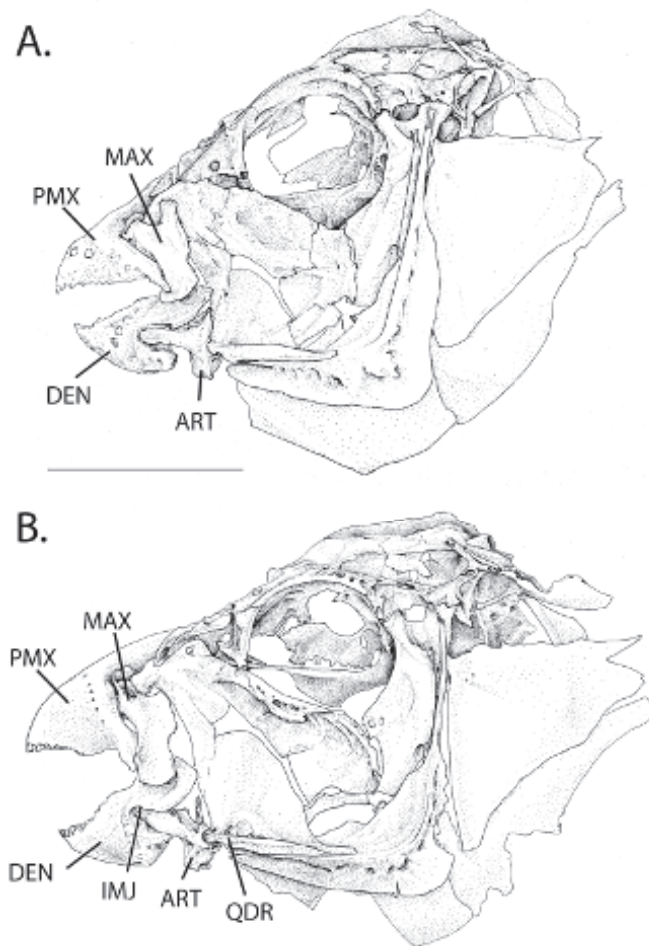
The feeding activities of parrotfishes are one of the fundamental ecological processes in coral reef ecosystems. These activities involve scraping hard rocky surfaces to remove turf algae, detritus, bacteria, and a wide range of encrusting invertebrates. This mixture of dead coral skeletons, the invertebrate and microbial organisms that colonize these surfaces and the detritus of organic debris is then passed to the pharyngeal jaw apparatus of parrotfish where it is mixed with mucous and ground to a fine slurry before being passed to the intestines (Bellwood and Choat 1990, Choat 1991, Choat et al. 2002). Here, nutrients are extracted from the slurry (Crossman et al. 2005) and fine sand is excreted back into the environment (Frydler and Stearn 1978, Bellwood 1995a, 1995b, Bruggenmann et al. 1996). The grazing activities of parrotfishes play a major role in disturbing benthic communities (Burkepile and Hay 2011, Brandl et al. 2014), preventing large algae from getting established and allowing corals and a more diverse community of encrusting organisms to become established and persist. The excretion of sand and concomitant bioerosion of the reef by parrotfishes occurs on a profound level as well, with accounts concluding that parrotfish are the major biological producers of sand in many reef systems (Bellwood 1995a, 1995b, Malella and Fox [Chapter 8](#)). Many groups of reef fishes are herbivores, microbioivores or detritivores but the singular impact of parrotfishes is because they are the only major group that removes the calcareous surface layers of the reef as they graze.

The unique ability of parrotfish to feed in this way is closely linked to the presence of several evolutionary novelties in the feeding mechanism that facilitate their ability to scrape rocky substrates and pulverize these scrapings. In this chapter we will focus on three of these innovations: the parrotfish pharyngeal mill apparatus, the cutting edge of the oral dentition, and the intramandibular joint in the oral jaws. We describe each of the three innovations, review their evolutionary history, their impact on parrotfish feeding abilities, and the impact that each has had on the evolutionary diversification of parrotfishes.

## Major Innovations in the Parrotfish Feeding Mechanism

### The Pharyngeal Mill Apparatus

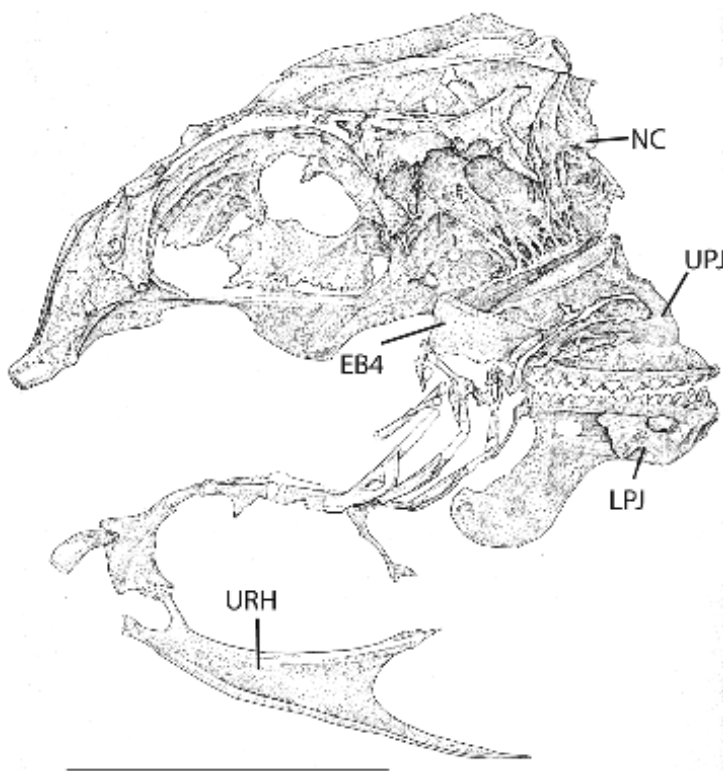
Parrotfishes are phylogenetically nested within the Labridae (Westneat and Alfaro 2005). Herbivory appears to have evolved at least three times within Labridae: once in *Pseudodax*, at least once in the odacines (Clements et al. 2004), and once in parrotfish. Parrotfish (Figs 1 and 2) are by far the largest radiation of herbivorous labrids with about 100 described species. All parrotfish share a derived condition of the pharyngeal jaw apparatus, a pharyngeal mill (Fig. 2) that appears to be crucial to their abilities as herbivores (Gobalet 1989, Bullock and Monod 1997). This system is built on a suite of already existing modifications of the pharyngeal jaw system that are shared by labrid fishes (Kaufman and Liem 1982, Bellwood



**Fig. 1.** Diagrams of the skull of parrotfishes prepared by hand from cleared and stained specimens, A. *Cetoscarus bicolor* and B. *Chlorurus sordidus*. Note that while both of these species possess cutting edge dentition on the jaws, *Cetoscarus* lacks an intramandibular joint between the dentary and articular bones while *Chlorurus* has this novel joint. Scale bars = 10 mm. Abbreviations: ART, articular; DEN, dentary; IMJ, intramandibular joint; MAX, maxilla; PMX, premaxilla; QDR, quadrate. Diagrams prepared by Ian Hart.

1994, Wainwright et al. 2012). The labrid condition, termed pharyngognathly, involves three derived features. (1) Fused left and right lower pharyngeal jaw bones (5th ceratobranchials) into a single structural lower jaw that is stronger and able to withstand higher forces. (2) Well developed joints between the underside of the neurocranium and the dorsal surface of the upper pharyngeal jaws that stabilize the upper jaws when the lower jaw is pulled up against them in biting actions. (3) The presence of a direct muscular connection between the neurocranium and the lower pharyngeal jaw that results in a powerful bite (Kaufman and Liem 1982, Stiassny and Jensen 1987).

The modifications in parrotfish are substantial and include extensive elaboration of the paired fourth epibranchial bones that sit lateral to the pharyngobranchials (the upper jaw bones that bear tooth plates), holding the upper jaws in a medial position while biting occurs, thus stabilizing them and guiding them during anterior-posterior movements of the upper jaw (Gobalet 1989, Chapter 1). The joints between the upper pharyngeal jaws and the neurocranium are extended anterior-posteriorly and are convex, allowing the upper jaws a long scope as they slide forward and backward while the muscular sling generates a biting action (Fig. 2). It is suspected that the characteristic milling action of parrotfishes is produced by an anterior-posterior motion of the upper jaws while the lower jaw bites against it (Gobalet 1989, Wainwright 2005). The teeth on both the upper jaws



**Fig. 2.** Diagram of the pharyngeal mill apparatus of the parrotfish *Chlorurus sordidus*, prepared by hand from a cleared and stained specimen. Note the anterior-posterior elongation of the joint between the neurocranium and upper pharyngeal jaw, and the teeth on both the upper and lower pharyngeal mill. Scale bar = 10 mm. Abbreviations for bone names: EB4, fourth epibranchial; LPJ, lower pharyngeal jaw (5th ceratobranchials); NC, neurocranium; UPJ, upper pharyngeal jaw (pharyngobranchial); URH, urohyal. Diagram prepared by Ian Hart.

and lower jaw are organized into anterior-posterior rows with the newest teeth coming in anteriorly and older teeth being moved posteriorly until they are worn away. This characteristic structure of the pharyngeal jaws is found in all parrotfish (Bellwood 1994) though it varies somewhat among genera and species in terms of the extent of the anterior-posterior elongation of the joint with the neurocranium and the size of the grinding surface on the lower pharyngeal jaw (see figure 12 in Bellwood 1994). The major trend within these features is that the grinding surface and the joint with the neurocranium are more elongate in the anterior-posterior direction in the reef-associated group that includes *Bolbometopon*, *Cetoscarus*, *Hipposcarus*, *Chlorurus* and *Scarus*. Functionally, the key consequence of this large suite of derived traits characteristic of the parrotfish pharyngeal mill is that the system is specialized for milling or grinding actions, as opposed to the crushing and winnowing actions that are more typical of pharyngeal jaw function in other labrids (Liem and Sanderson 1986, Wainwright 1988).

### Cutting Edge on Oral Dentition

Teeth on the upper and lower oral jaws are coalesced into a cutting edge in *Leptoscarus*, *Sparisoma*, *Cetoscarus*, *Bolbometopon*, *Hipposcarus*, *Chlorurus* and *Scarus* (Fig. 1, Bellwood and Choat 1990, Bellwood 1994). Oral jaw teeth in the remaining parrotfish, *Cryptotomus*, *Nicholsina*, and *Calotomus*, are individual, caniniform teeth as in wrasses, though *Calotomus* has somewhat flattened teeth (Bellwood 1994). Referring to the distribution of this trait on the parrotfish phylogeny (Fig. 3), it is somewhat ambiguous whether the absence of the cutting edge in these taxa is a retained primitive trait or a secondary reversal to this condition. However, a maximum likelihood reconstruction upon the phylogeny favors the interpretation that the cutting edge dentition evolved once and has been lost twice. All parrotfish that lack the cutting edge dentition are occupants of seagrass habitats and all taxa with the cutting edge except some *Sparisoma* are reef-dwellers, suggesting that there is a strong relationship between feeding on rocky substrates and the evolution and use of the cutting edge. The cutting edge gives a distinctive beak-like appearance to the jaws that is the basis of the common name 'parrotfish'. This structure is key to the ability of parrotfish to scrape the surface of rock or dead coral, removing the characteristic assemblage of coral skeleton, algae, microbes, detritus and encrusting invertebrates that they feed upon. Whether scraping or excavating, the feeding activities of parrotfish on reefs depend critically on this modified dental arrangement (Clements and Bellwood 1988, Bellwood and Choat 1990).

### Intramandibular Joint

Parrotfish in the genera *Hipposcarus*, *Chlorurus* and *Scarus* have a well-developed joint between the dentary and articular bones of the lower jaw (Fig. 1b). In these taxa, the large section two of the adductor mandibulae muscle has the derived condition of inserting on the dentary rather than the articular bone and thus has the unusual property of crossing two joints, both the quadrate-articular joint and the articular-dentary joint. In other parrotfish and in wrasses the mandible is a single rigid structure formed by a dentary and articular that are held tightly together by many short ligaments (Fig. 1a). The intramandibular joint permits motion at the quadrate-articular joint, as in other teleosts, as well as the joint between the dentary and articular. The introduction of this joint alters the linkage mechanics of the oral jaw system, resulting in a novel four-bar linkage that transmits motion of the lower jaw to the upper jaws (Wainwright et al. 2004). Exactly how the intramandibular joint functions during feeding is not known, although one inferred



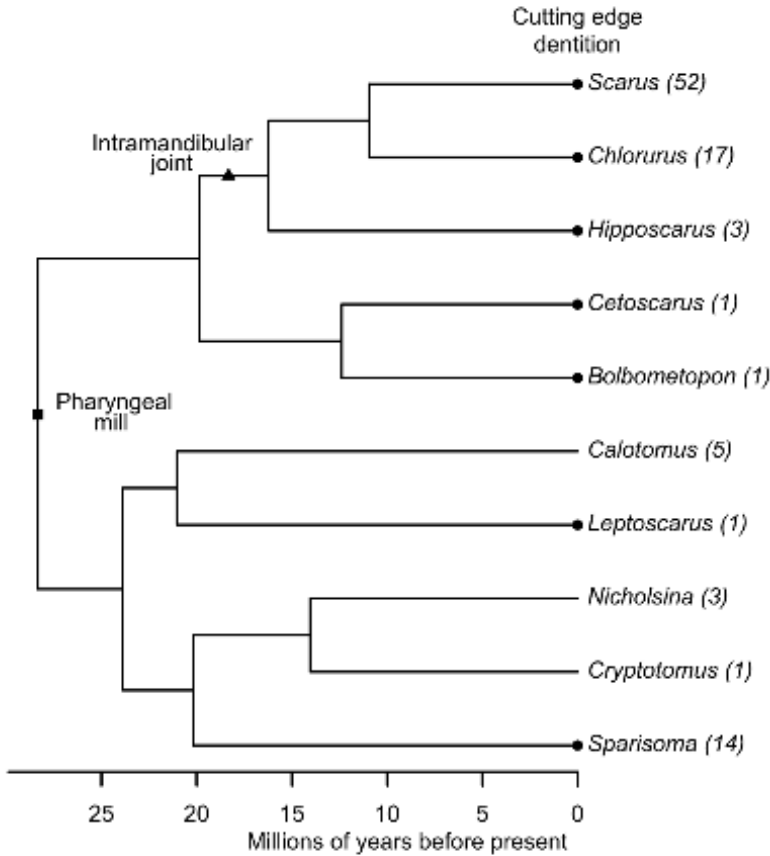


Fig. 3. Time calibrated molecular phylogeny of parrotfish genera (Kazancioğlu et al. 2009). Inferred origins of the parrotfish pharyngeal mill and the intramandibular joint are indicated by a square and triangle respectively. The distribution of the cutting edge dentition among genera is indicated at the tips with dark circle. A likelihood reconstruction of the history of the cutting edge dentition favored a single origin of the trait and two losses.

consequence of the joint and modified attachment of the adductor mandibulae is that the mechanical advantage, or force transmission, of the adductor mandibulae during oral jaw biting is almost twice as high as it is in taxa that lack the joint (Bellwood 1994, Wainwright et al. 2004, see also Gobalet [Chapter 1](#)). At present it is also not known if movement occurs at both joints during normal feeding behavior. If movement occurs at both joints during feeding this could allow fish to modulate the orientation of the dentary during biting actions, maintaining a favorable orientation throughout the scrape. Such a function could result in enlargement of the region of contact between the teeth and substrate during scraping. A better understanding of the function of the intra-mandibular joint will be an important goal in future research.

## Phylogenetic Distribution of Feeding Innovations

Some lineages of parrotfishes have acquired all three of the innovations described above ([Fig. 3](#)). Parrotfish in the group made up by *Scarus*, *Chlorurus* and *Hipposcarus* have the modified

pharyngeal mill, cutting edge dentition on their oral jaws, and an intramandibular joint. The possession of all three of these innovations appears to be unique among reef fishes and even among teleost fishes, although none of these traits are unique to parrotfishes.

Remarkably, many of the complex modifications found in the parrotfish pharyngeal mill are also found in the herbivorous wrasse *Pseudodax* (Bellwood 1994). Although a labrid, *Pseudodax* is not closely related to parrotfishes and the presence of the pharyngeal mill has evolved independently in this lineage. This is particularly noteworthy as the pharyngeal mill configuration of the pharyngeal jaws is not known to occur in any teleost outside of Labridae. Cutting edge dentition involving a cement layer around coalesced dentition in the oral jaws is found in another labrid, *Odax* (Clements and Bellwood 1988). *Odax* is a temperate herbivore that feeds mostly on large fucoids and laminarian macroalgae (Clements and Bellwood 1988). The pharyngeal jaws of *Odax* show the typical wrasse condition, lacking the modifications characteristic of the pharyngeal mill seen in parrotfishes and *Pseudodax* (Clements and Bellwood 1988, Bellwood 1994). Similarly, *Pseudodax* lacks the cutting edge dentition made of smaller coalesced teeth, although it does have large, flattened incisiform teeth that provide a different type of cutting edge in the oral jaws (Bellwood 1994). A few other teleost lineages have cutting edge dentition formed by coalesced or fused teeth, including members of Oplegnathidae and Tetraodontidae.

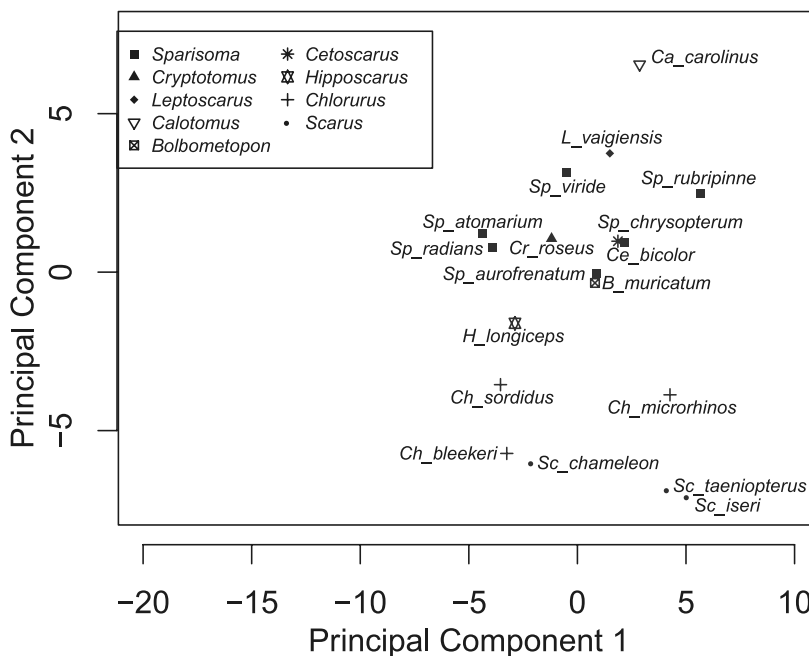
Finally, an intramandibular joint has evolved several times in reef fishes, including some members of Acanthuridae, Pomacanthidae, Chaetodontidae, Blenniidae, Girellidae and Siganidae (Vial and Ojeda 1990, Purcell and Bellwood 1993, Bellwood 2003, Konow et al. 2008, Konow and Bellwood 2005, Ferry-Graham and Konow 2010), and some non-reef lineages: *Helostoma* and some Poeciliidae (Gibb et al. 2008, Ferry et al. 2012). In all cases this trait is associated with feeding by biting the benthos (Konow et al. 2008). Bellwood (2003) noted that these reef lineages, together with parrotfishes, make up the major herbivorous fishes on modern reefs. Given that intramandibular joints have apparently evolved numerous times in benthic feeding reef fishes, there is a need to better understand the functional benefits of this modification in benthic feeding fishes (Konow et al. 2008) and whether the function of the extra joint is similar in each case. Some possible advantages of the additional joint are that it permits (1) a greater angular sweep of the lower jaw, although this trait is normally associated with overall shortening of the lower jaw (Purcell and Bellwood 1993), (2) Modulation of the orientation of the toothed surface of the lower jaw through the sweep of the bite (Price et al. 2010), (3) Effective biting while the upper jaws are protruded (Konow et al. 2008) or (4) that the flexibility and associated complexity in muscular attachments result in greater dexterity in movements of the lower jaw during feeding.

Although all parrotfish possess the grinding pharyngeal mill, many seagrass-dwelling lineages lack the cutting edge on the oral jaws that is essential for scraping hard surfaces on reefs. Only *Scarus*, *Chlorurus* and *Hipposcarus*, a lineage nested inside a larger clade of reef-dwelling parrotfishes, have the mobile intramandibular joint. As discussed in Bonaldo et al. (2014), the phylogeny suggests that parrotfish may have invaded reef habitats twice, once along the branch below the node uniting *Bolbometopon* and *Scarus*, and a second time within *Sparisoma*. Most parrotfish living in seagrass feed in a different manner from those taxa on reefs because of the absence of the ubiquitous hard substrata that promotes scraping behavior. In seagrass, parrotfish feed on blades of seagrass, epiphytes that live on seagrass and large algal plants. These are taken by a browsing behavior in which they are removed from their holdfast or separated from the rest of the plant by cropping or biting and tearing.

## Morphological and Functional Diversity of Parrotfish

The complex phylogenetic distribution of the three innovations discussed above implies the presence of functional diversity among parrotfishes (Fig. 3). There are considerable differences between taxa in their feeding biology, with *Bolbometopon*, *Cetoscarus* and *Chlorurus* digging deep gashes in the reef during forays (termed excavators by Bellwood and Choat 1990) while *Hipposcarus* and *Scarus* feed with much more superficial scrapes of rock or sometimes sandy surfaces, taking less carbonate while they primarily remove epilithic organisms (Bellwood and Choat 1990). The reef-dwelling *Sparisoma* species appear to be superficial scrapers with *Sparisoma viride* and its sister species, *Sp. amplum*, being informally described as an excavator (e.g. Bellwood 1994) and some authors also categorizing *Sp. chrysopterum* and *Sp. rubripinne* as excavators (Bernardi et al. 2000). Within the lineage that possesses the intramandibular joint there is wide diversity in feeding mode, from superficial scraping to excavating. This suggests that the intramandibular joint may have a general benefit to scraping hard substrate that is not specific to either extreme on the axis from deep excavating to superficial scraping.

A functional morphospace for the parrotfish feeding system can be produced by a principal components analysis summarizing eight functional traits of the feeding mechanism in 34 species, including representatives of all genera except *Nicholsina* (Figs 4 and 5). The traits used in this analysis are described in detail elsewhere (Wainwright



**Fig. 4.** Plot of Principal Component 1 vs 2 from a phylogenetic PCA run on nine morphological variables associated with the functional morphology of the parrotfish feeding mechanism. The variables included were mechanical advantage of jaw opening and jaw closing, transmission coefficients of the oral jaws and hyoid 4-bar linkages, oral jaw gape distance, maximum upper jaw protrusion distance, and masses of the adductor mandibulae, sternohyoideus, and levator posterior muscles. Average values of each trait for several specimens per species were corrected for body while accounting for phylogenetic relationships where necessary. Data are from Wainwright et al. 2004 and Price et al. 2010.

et al. 2004) but include the horizontal width of the oral gape, maximum premaxillary protrusion distance, the mechanical advantage of jaw opening and closing muscles, and the transmission coefficient of the four-bar linkage that operates the oral jaws (transmission coefficients are the inverse of mechanical advantage), as well as the mass of three major muscles; the adductor mandibulae complex, the sternohyoideus and the levator posterior. The adductor mandibulae is a complex of muscles that function to adduct the oral jaws during biting, the sternohyoideus is involved in ventral depression of the hyoid bar during suction, which is poorly developed in parrotfish, and the levator posterior muscle is a major biting muscle from the pharyngeal jaw system that pulls the lower pharyngeal jaw up against the upper jaw.

After size-correcting traits by calculating residuals of species means from Log-Log regressions on the cube root of body mass the position of 34 species in principal component space reveals major features of the morphological diversity (Figs 4 and 5). Principal component one (PC1) is negatively correlated with all morphological traits and represents an axis that captures species at one extreme with relatively large muscles, a large mouth, high protrusion distance, and high values of four-bar transmission coefficients and jaw lever mechanical advantage, and species at the other extreme with small values of these traits (Table 1; Fig. 4). Principal component two (PC2) primarily involves a trade-off between jaw lever mechanical advantage and the gape width. In bivariate plots of PC1 vs 2 and PC3 vs 4 a group composed of species of *Scarus* is apparent, and a second group made up of all other parrotfishes with the excavators *Chlorurus* and *Bolbometopon* somewhat is set apart from this group (Figs 4 and 5). Two interesting points are that *Sp. viride* is

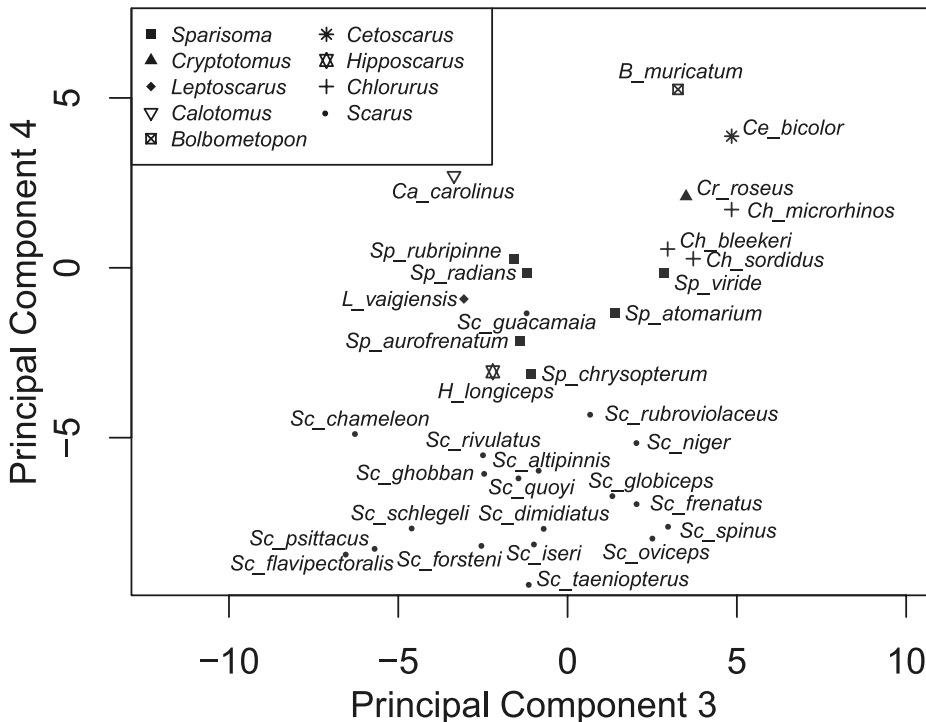


Fig. 5. Plot of Principal Component 3 vs 4 from a phylogenetic PCA run on nine morphological variables associated with the functional morphology of the parrotfish feeding mechanism. See Fig. 4 legend for member variables and Table 1 for loadings and variance explained. Data are from Wainwright et al. 2004 and Price et al. 2010.