

A Phylogenetic Study of the Parrotfishes Family Scaridae (Pisces: Labroidei), with a Revision of Genera

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ABSTRACT. The comparative morphology of the family Scaridae was examined to provide data which were used to i) assess the monophyly of the family, ii) identify groups of species within the family, and iii) determine the phylogenetic relationships of these groups. Analyses were based on examinations of 69 of the 80 species of Scaridae recognised in this study. In addition, five outgroup taxa from the family Labridae were examined. A total of 143 characters coded as 334 character states were used in the analyses. The characters were drawn from the osteology of the neurocranium, oral jaws, palatine arch, hyoid arch, branchial arches, pectoral girdle, pelvic girdle, axial skeleton, dorsal and anal fins, and the caudal skeleton. In addition, characters were drawn from the soft anatomy of the oral jaws and pharyngeal apparatus, the viscera, reproductive system, colour patterns and external morphology. Phylogenetic analyses of these character states were undertaken using the principle of maximum parsimony. Computational procedures were performed using the program PAUP. Two trees were produced with consistency indices of 0.697 (autapomorphies excluded). The topology and character state distributions of the ingroup are identical in both trees. The analyses strongly supported the monophyly of the Scaridae. The family is defined by 54 synapomorphies, of which 19 are unique and unreversed. Within the family ten groups are recognised. All are referable to previously recognised genera. *Calotomus*, *Leptoscarus*, *Sparisoma*, *Cetoscarus*, *Bolbometopon*, *Chlorurus*, *Hipposcarus* and *Scarus sensu stricto* are hypothesised to be monophyletic based on the possession of unique derived character states. No uniquely derived character states were found to define *Cryptotomus* or *Nicholsina*. A cladogram showing the phylogenetic relationships of these ten taxa is provided. This cladogram is used as a basis for a new classification of the Scaridae. The following ten genera are recognised in this classification: *Cryptotomus*, *Nicholsina*, *Calotomus*, *Leptoscarus*, *Sparisoma*, *Cetoscarus*, *Bolbometopon*, *Chlorurus*, *Hipposcarus* and *Scarus*. The main difference in this classification from that in common usage is in the limits of the genus *Scarus*. The genus *Scarus sensu lato* as previously applied was paraphyletic and included species in two distinct lineages. These two lineages are recognised herein as *Chlorurus* and *Scarus sensu stricto* with *Hipposcarus* being the immediate sister group of *Scarus sensu stricto*. The analyses also indicate that the subfamily Sparisomatinae is paraphyletic. A subfamilial division of the Scaridae is therefore rejected. A diagnosis of supraspecific taxa, with a key to genera and a list of Recent species are provided. Biogeographical analyses based on the cladogram point to a major division between Indo-Pacific and Atlantic/Caribbean scarid taxa and

identify the closure of the eastern Tethys and the formation of the Isthmus of Panama as key vicariance events in the history of the Scaridae. Analyses of habitat associations suggest that scarids first arose in seagrass and that reef dwelling forms are of a more recent origin. An analysis of adult feeding modes suggests that scarids which excavate the substratum when feeding arose from taxa which fed by browsing, and that taxa with a scraping mode arose relatively recently from excavating forms as a result of paedomorphosis.

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Introduction

The parrotfishes (family Scaridae) are a distinctive group of labroid fishes. Members of the family may be found on coral reefs throughout the world. They are present in the tropical Atlantic, Indian and Pacific Oceans, where they are closely associated with coral reefs. In these areas, they form a dominant and conspicuous part of the herbivorous fish community. As such, they have been the focus of a number of studies on the importance and role of herbivores on coral reefs. They have been implicated as major determinants of the benthic community structure of coral reefs (Brock, 1979; Lewis & Wainwright, 1985) and as dominant agents of bioerosion on reefs, both currently (Kiene, 1988; Bellwood & Choat, 1990) and historically (Steneck, 1983a,b). Parrotfishes are a significant component of reef fisheries yields and are a common food item in many tropical regions (Johannes, 1981; Reeson, 1983; Bellwood, 1988).

The Scaridae is relatively small family, with 80 species in ten genera. It comprises small to large species with maximum adult sizes ranging from 110 to 1000 mm SL. Despite the small size and relative importance of the family, the systematics of the Scaridae has been in a state of confusion for many years. This is primarily a result of the conservative nature of the external morphology of the group and has forced most workers to rely on colour patterns as the primary criterion for identifications. This approach is confounded by the complex colour patterns exhibited by most species, as a result of their sexual dichromatism and a propensity for dramatic colour pattern changes both when live and as a result of capture. These colour patterns are usually lost during preservation, thus limiting the utility of preserved specimens.

There has been only one review of the family, by Schultz (1958). Schultz (1958) was aware of sexual dichromatism in the family but not of its extent. In his 1958 revision therefore, sexual stages were often regarded as separate species.

The recent clarification of the status of many scarid species is a result of the linking of the sex-related colour patterns, ie, initial and terminal phase colour patterns (*sensu* Randall & Choat, 1980), and the identification of early types. This has stabilised the taxonomy of the Scaridae at the species level. A clarification of the

supraspecific classification of the family is now of paramount importance.

All recent workers who have addressed the problems of the supraspecific classification of the Scaridae (ie, Smith, 1956, 1959; Schultz, 1958, 1969; Rosenblatt & Hobson, 1969) have recognised the value of internal characters in the resolution of scarid genera. Yet their studies, and all subsequent studies, have relied on generic groupings based almost entirely on external morphological characters or a single internal character state (eg, *Scarops* Schultz, 1958).

To date, there has been no detailed analysis of the interrelationships between scarid genera. Many generic descriptions lack adequate definitions or sufficient diagnostic details to enable the boundaries of groups to be clearly recognised. It is therefore, almost inevitable that scarid genera have been accepted or rejected on a 'ad-hoc' basis.

An examination of the internal morphology of representative species from all ten valid Recent genera and of representatives from several closely related families has provided a foundation upon which it is possible to undertake a major revision of the systematics of the Scaridae.

This will be undertaken as a phylogenetic analysis using a cladistic methodology (Hennig, 1966; Wiley, 1981; Ax, 1987). It is the aim of this study to produce a phylogenetic hypothesis for the Scaridae, and a classification which reflects this phylogeny. To provide a strong basis for the analyses, this phylogenetic study is based on the widest range of available evidence, incorporating both internal and external anatomical features. A classification based on phylogeny is desirable as it permits morphological data to be examined in an evolutionary framework. A phylogeny is also an essential prerequisite to the formulation and testing of hypotheses of the biogeography and evolution of the group.

The objectives of this study are to: 1) determine the phyletic status of the family Scaridae; 2) define the major subgroups within the family; 3) determine the interrelationships of the subgroups; 4) present a generic classification of the Scaridae which reflects these interrelationships.

Introductory aspects of scarid taxonomy and biology will be considered under separate headings: i) historical review; ii) status of the family Scaridae; iii) biology of the Scaridae.