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 referrable 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.

Contents

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.

Historical Review of the Supraspecific Classification of the Scaridae

Forsskål (1775) erected the genus *Scarus* to incorporate ten new species from the Red Sea. Of these, six were scarids; the remaining four have subsequently been placed in the families Labridae and Siganidae. From the original six parrotfish species described by Forsskål, Jordan & Gilbert (1882) designated *Scarus psittacus* as the type species of the genus *Scarus*. However, the actual identity of this species was not resolved until 1978 (Randall & Ormond, 1978). *Scarus* was established as the first genus of the family following the International Commission on Zoological Nomenclature decision (Opinion 261) to invalidate names in Gronow's *Zoophylacii Gronoviani....*(1763), which included the parrotfish genus *Callyodon*. The name was non-binomial, parrotfish merely being referred to as "les callyodons".

Gronow's *Callyodon* was subsequently followed by *Callyodon* Scopoli (1777), *Callyodon* Bloch (1788), and *Calliodon* Bloch & Schneider (1801) all after *Callyodon* Gronow (1763). Walbaum (1792) contrasted the generic characters of *Scarus* and *Callyodon* as described by Gronow, Forsskål and Bloch. The earlier scarid genera *Mormyra* Browne (1789) and *Novacula* Catesby (1771) were not included in this appraisal.

Callyodon was widely used until 1959. Smith (1959) was the last major work to use the name, and noted its replacement by *Scarus*. Despite the invalidity of the name *Callyodon* it may still occasionally be found in more recent literature (eg, Jones & Kumaran, 1980; Suvatti, 1981).

In his extensive study of monocardian animals, Swainson (1839) recognised 16 genera in the subfamily Scarinae (family Percidae), eight of which were new. Of the 16 genera, six contained only labrids and one was erected to accommodate a siganid. Of the remaining nine genera, Swainson recognised the existing *Callyodon* and *Scarus* and erected seven new genera: *Leptoscarus, Hemistoma, Petronason, Erychthys, Chlorurus, Sparisoma,* (Swainson 1839:224-227), and *Chloregaster* (Swainson, 1839:172).

Despite the number of existing scarid genera, Bleeker (1859b) recognised only two, *Scarus* and *Callyodon*, but erected three new genera, *Scarichthys* in 1859a (and 1859b) and *Pseudoscarus* and *Callyodontichthys* in 1861. The three genera *Callyodon, Scarus* and *Pseudoscarus* were subsequently accepted as the 'typical' scarid genera and were widely used and frequently interchanged.

Post-1861 several unusual scarid specimens were collected and new genera were erected to accommodate them, namely, *Cryptotomus* Cope (1871), *Calotomus* Gilbert (1890), *Scaridea* Jenkins (1903) and *Xenoscarus* Evermann & Radcliffe (1917). In addition, Jordan & Evermann (1896) erected two new genera, *Loro* and *Euscarus*, to accommodate two previously described Atlantic species. Fowler (1915) subsequently subdivided *Cryptotomus*, placing several species in a new subgenus *Nicholsina*. *Nicholsina* was accorded full generic status by Schultz (1958).

From 1860 to 1940, the generic classification of the Scaridae was relatively stable, albeit unclear. Most genera were relatively small, each containing a few distinctive species. Most 'typical' scarid species were placed in the 'catchall' genera *Scarus, Pseudoscarus* or *Callyodon*.

In the 1950s two major works on the taxonomy of the Scaridae were published. The first was a review of the parrotfishes of the Western Indian Ocean by J.L.B. Smith (1956). The second was a comprehensive review of the family by L.P. Schultz (1958). The two workers, Smith and Schultz, had disparate backgrounds and approached the problems of scarid taxonomy in markedly different ways.

Although he examined the fish collections of several museums, most of Smith's scarid work was based on observations on fresh and preserved material collected on the numerous trips he made along the east coast of Africa, from South Africa to Kenya, and offshore to Aldabra, and the Seychelles. Smith's collections were intensive but were restricted to the western Indian Ocean. He provided detailed descriptions and numerous colour plates, with the primary aim of identifying forms. Species identifications and groupings were based on morphology, colour patterns and a personal knowledge of their field biology.

Smith was primarily concerned with descriptions, and took pains to accurately describe the various colour forms, providing both colour descriptions of fresh material and colour plates. Correct nomenclature was of secondary importance. He regarded many of the early types as unidentifiable, the descriptions being "utterly inadequate". He preferred to describe a species as new rather than use an existing name based on a poor description.

In comparison, Schultz based most of his work on museum specimens, and was much more concerned than Smith with nomenclatural procedure. He regarded Smith's failure to put existing species names to his specimens as "pandering to inadequacy and inefficiency". Their differences were not resolved.

Although Smith (1956) and Schultz (1958) were aware of sexual dimorphism in scarids, neither worker knew the extent of sexual dimorphism and the protogynous life history of most scarids.

In terms of their generic classifications, both workers found the existing generic system unsatisfactory. Smith (1956) accepted some existing genera, but noted that most workers placed Indo-Pacific species into one polymorphous genus, either *Callyodon* or *Scarus*. Smith (1956) chose to adopt the former and, in addition, erected several new genera: *Xanothon, Bolbometopon, Margaritodon, Cetoscarus* and *Hipposcarus*, stating that "Our acquaintance with living Parrot fishes indicates that narrower generic limits for the Indo-Pacific forms are justified, [and] are indeed supported on both taxonomic and ecological grounds". Smith based his groupings on morphology, colour patterns and field

ecology.

In terms of higher classifications within the family, Schultz (1958) selected several genera stating that "Since my studies indicate that certain characters are important in grouping parrotfishes into phyletic lines, it seems advisable to recognise certain of these groups of species as full genera and others as subgenera". Schultz's generic and sub-generic groupings were based on morphological characters which are traditionally used when examining preserved specimens in museum collections. They are therefore based primarily on external characters. Such characters form the basis of traditional museum-based systematics, but are fraught with problems when applied to the parrotfishes, where meristic values and squamation patterns are very conservative. Schultz (1958) provided a presumed phylogeny, but this was undertaken prior to the widespread application of Hennigian principles (after Hennig, 1966). Schultz (1958) rejected all of Smith's new genera, stating that Smith "ignored many of the rules of zoological nomenclature" and that his newly erected genera are synonyms of already valid genera. Schultz erected one new genus *Scarops* and two subgenera, *Ypsiscarus* and *Xenoscarops*. Schultz (1958) also divided the family into two subfamilies, the Sparisomatinae and the Scarinae. This division was based on a proposed phylogeny which highlighted a division within the family in the distribution of a number of internal and external characters.

These studies were followed by a re-evaluation by both workers.

In his re-evaluation of the parrotfishes of the western Indian Ocean, Smith (1959) commended Schultz (1958) for attempting the task of reviewing the whole family and providing illustrations for all species, and welcomed the use of internal morphological characters, but he noted that Schultz had made "grievous errors", primarily in the examination of types. Smith reaffirmed his confidence in his earlier (1956) genera but incorporated two of Schultz's subgenera, *Ypsiscarus* and *Scarops*.

In Schultz's second (1969) revision of the Scaridae, he accepted Smith's genus *Bolbometopon* but rejected *Xanothon*, *Margaritodon*, *Cetoscarus* and *Hipposcarus*. Of his own genera, he raised *Ypsiscarus* to full generic status.

Both Smith and Schultz agreed that the main problem in the recognition of scarid genera was the lack of diagnostic external characters, and agreed that internal morphological characters were particularly useful for higher classification. Despite this, they both continued to erect and recognise genera based solely on a limited number of external morphological characters. The generic classification of the Scaridae remained confused, with the two principal workers, Smith and Schultz, recognising six and four Indo-Pacific genera respectively, but of these they failed to agree on the extent of a single genus. Even if the same generic name was used, it was applied to different species or species groups.

In the last two decades the taxonomy of scarid species

has stabilised. Following the discovery of sex reversal in scarids (Brock & Yamaguchi, 1954), field studies in the 1960s and 1970s (Randall, 1963; Choat, 1969; Choat & Robertson, 1975) established the extent of sex reversal in scarids and greatly assisted in the subsequent linking of sexual colour phases. Nomenclatural stability also resulted from: 1) a detailed re-examination of types, which established the identity of type specimens and linked the species in original descriptions with currently recognised forms (Randall & Ormond, 1978; Randall & Nelson, 1979); 2) geographically extensive collections which have resolved differences between geographic variants and closely related but geographically isolated species eg, *S. tricolor/forsteni*; 3) detailed regional reviews (eg, Rosenblatt & Hobson, 1969; Randall, 1983a,b; Randall & Bruce, 1983; Choat & Randall, 1986).

Despite the increased species stability, genera continued to be selected on an ad-hoc basis. Most studies recognised the generic classification of Schultz (1969) with the exception of *Scarops* and the addition of Smith's *Cetoscarus* and *Hipposcarus* (eg, Randall 1983b; Randall & Bruce, 1983; Choat & Randall, 1986).

Since the major works of Smith and Schultz, only two studies have specifically considered the status of scarid genera. In the same year as Schultz's final revision of the Scaridae, Rosenblatt & Hobson (1969) working on the Scarinae of the eastern Pacific, considered the status of many scarin genera to be uncertain. They concluded that, "Until such time as the internal anatomy of a large number of parrotfish species is known, the most reasonable way to arrange the species of the Scarinae is to recognise only two genera....*Bolbometopon* and *Scarus*".

In 1985, Bruce & Randall revised two scarid genera, *Calotomus* and *Leptoscarus*. They diagnosed the two genera and placed *Scaridea* in the synonymy of *Calotomus*. Although detailed descriptions of each genus and the component species were given, these were based almost entirely on external morphological characters. Bruce & Randall (1985) emphasised the need for a detailed study of other scarid groups before any comments on the relationship between these two genera and other sparisomatine genera could be made.

All of the recent workers have emphasised the need for a reclassification of the Scaridae and all have recognised the value of internal morphological characters in such an undertaking. None of the studies to date have assessed relationships in a phylogenetic framework utilising cladistic methodologies. The use of such methodologies can provide a clear indication of the limits and interrelationships of scarid species groups, and will give a rational basis for selecting scarid genera.

This study represents the first detailed examination of the family based on analyses of both internal and external morphological characters using cladistic methodologies.

Status of the Family Scaridae

The Scaridae was first recognised as a distinct family by Bleeker (1859b) who later, in 1862, provided detailed descriptions of the two families: the Scaroïdes (parrotfishes) and the Labroïdes. Prior to this classification, the two groups were both placed in a single family, the Labridae (eg, Cuvier & Valenciennes, 1840; Kner, 1860; Günther, 1862). Bleeker's classification formed the basis for all subsequent classifications, with the Scaridae being widely accepted as a distinct family. Nevertheless, the close relationship between the Labridae and Scaridae was still recognised. In Norman's (1966) classification, the Labridae, Scaridae and Odacidae comprise a single division, the Labriformes. In the classification of Greenwood et al. (1966) the three families form a single sub-order the Labroidei.

Recently, the status of the Labroidei has received considerable attention. The first major change was in 1981, when Liem & Greenwood (1981) suggested that the Cichlidae, Embiotocidae, Labridae, Scaridae and Odacidae represent a monophyletic assemblage, with the latter three families (the Labroidei sensu Greenwood et al., 1966) forming a distinct (monophyletic) lineage. This work was followed by that of Kaufman & Liem (1982), who presented evidence to suggest that the Cichlidae, Embiotocidae, Labridae, Scaridae, Odacidae and the Pomacentridae are a monophyletic assemblage and proposed that all six families be included in the Labroidei. This classification, unless stated otherwise, is followed in the present study (however, see Rosen & Patterson, 1990 for a discussion of the status of the Labroidei). Within this 'expanded' Labroidei it was argued that the Labridae, Scaridae and Odacidae should be recognised as a single family, the Labridae, "since the monophyletic nature of this assemblage is strongly indicated by both morphological and functional characters". Kaufman & Liem (1982) did not state the reason for the proposed fusion beyond evidence of monophyly.

It has been generally accepted that the Labroidei (sensu Kaufman & Liem, 1982) is monophyletic, although the interrelationships between the families within this assemblage remain unclear (Stiassny & Jensen, 1987). Likewise it is widely accepted that the Labridae, Scaridae and Odacidae represent a monophyletic assemblage. The fusion of the Labridae, Scaridae and Odacidae into a single family, however, is still a topic of active discussion. Fusion was first suggested by Gomon & Russell in an oral presentation at the inaugural International Conference on the Systematics and Evolution of Indo-Pacific Fishes held in Sydney, September 1981. Some workers followed Gomon & Russell and Kaufman & Liem (1982) and included the Scaridae in the Labridae, eg, Stiassny & Jensen (1987). Others questioned this decision. Richards & Leis (1984) cautioned against fusion of the three families, based on observations on the early life history characters of several labroid families. Bruce & Randall (1985) retained the Scaridae arguing that their unique dentition, lack of a true stomach and herbivorous habit warrant familial status. Choat & Randall (1986) likewise rejected a fusion of the three families.

In the present study, fusion of the Labridae, Scaridae and Odacidae is also rejected. Monophyly is a prerequisite to the recognition of a family but does not, alone, warrant such recognition. Despite the rejection of Kaufman & Liem's (1982) proposal it is recognised that the current status of the three families is unsatisfactory. Combining them into a single family, however, is only one possible solution. An alternative solution, recognising several families within the Labridae, must also be considered. Although a familial revision is justified, any action at this time is regarded as premature. Such action must await a more detailed and critical study of the interrelationships of the Labridae, Scaridae and Odacidae so that the two alternative classifications may be adequately appraised. In this study therefore, the conventional system will be followed, recognising the Scaridae, Labridae and Odacidae as separate families.

The status of the three families is discussed below.

LABRIDAE

The status of the Labridae is less well defined than the Odacidae or Scaridae. The Labridae (sensu Norman, 1966; Greenwood et al., 1966) appears to be a paraphyletic assemblage. There are presently no recognised synapomorphies uniting the Labridae. The insertion of the Adductor Mandibulae section A1 via a tendon to the tip of the premaxillary process of the maxilla was regarded by Stiassny (1981) as a synapomorphy uniting the Labridae. However, the status of this character was later questioned by Stiassny & Jensen (1987) who reported that this condition was approached by some embiotocids and cichlids. In view of this similarity, and the presence of a comparable insertion mode in some scarid genera (character 116, below), Stiassny & Jensen (1987) are followed and this character is rejected as a synapomorphy uniting the Labridae sensu stricto. The lack of a synapomorphy uniting the Labridae highlights the need for a detailed revision of the Labroidei (sensu Greenwood et al., 1966).

Kaufman & Liem (1982) proposed a fusion of the three families, whilst Gomon & Russell (1981, oral presentation) have proposed a classification of the genera within such a family. However, in an oral presentation at the Third International Conference on the Systematics and Evolution of Indo-Pacific Fishes, in Wellington, New Zealand, 1989, Bellwood presented evidence (given in Bellwood, 1990) to suggest that two distinct lineages exist within the Labridae and that the recognition of several labrid families may be warranted.

ODACIDAE

The Odacidae has been recently reviewed by Gomon & Paxton (1985). They presented evidence which suggested that the family is monophyletic. The Odacidae

was retained as a family to avoid confusion, but the authors supported the inclusion of the family Odacidae, along with the monotypic genus *Chelio*, as a tribe Odacini within the Labridae following Gomon & Russell (1981, oral presentation; cited in Gomon & Paxton, 1985).

SCARIDAE

Upon examination, many of the characters traditionally considered diagnostic for the Scaridae (eg, fused jaw teeth, loss of the supraneurals (predorsal bones), presence of an articulatory articular-dentary joint) are absent from the more basal genera, whilst others (eg, the lower pharyngeal jaw form, and the form of the first haemal spine) appear to be present in some labrids (eg, *Pseudodax*). Nevertheless, the monophyly of the Scaridae is strongly supported by a wide range of derived character states, many of which are unique and unreversed. In this study, the Scaridae is retained as a family, however, it is acknowledged that a re-evaluation of the familial status of labroid taxa is necessary.

The Biology of the Scaridae

Ecology. Although several scarid species may be found in subtropical waters, the vast majority of species are to be found in tropical regions in the immediate vicinity of coral reefs. Most species live in shallow waters, with the greatest abundance being between 1 and 10 m (Bouchon-Navaro & Harmelin-Vivien, 1981; Russ, 1984). However, some species may be found down to 180 m (Bruce & Randall, 1985). Five genera, *Scarus*, *Chlorurus*, *Hipposcarus*, *Bolbometopon* and *Cetoscarus*, encompass 63 species, most of which occur solely on or around coral reefs. In addition, two genera, *Calotomus* and *Sparisoma*, have four reef-associated species. The remaining species in these two genera and the four species in the remaining three genera (*Cryptotomus*, *Nicholsina* and *Leptoscarus*), are found on rocky reefs or in seagrass beds; *Cryptotomus* and *Nicholsina* in the Caribbean and *Leptoscarus* in the Indo-Pacific.

Food and feeding. All scarid species are diurnal herbivores. The vast majority of reef-dwelling species feed on the short epilithic (turf) algae that covers the reef substratum. However, there are at least two distinct functional groups within this assemblage: excavators and scrapers (Bellwood & Choat, 1990). Excavators have powerful oral jaws which excavate the substratum, leaving distinct grazing scars. Scrapers have less powerful jaws and rarely scar the substratum. Excavating species include: all *Chlorurus* species, *Bolbometopon*, *Cetoscarus*, and *Sparisoma viride*. The scrapers include all *Scarus* and *Hipposcarus* species. Within the scraping species a distinct subgroup of *Scarus* species may be recognised which occasionally feed on the surface of the sand in

the immediate vicinity of reefs (Bellwood & Choat, 1990). Several reef-dwelling species have also been reported to eat the faeces of other reef species (Bailey & Robertson, 1982).

There have been several reports of scarids feeding on live corals (eg, Hiatt & Strasburg, 1960; Glynn *et al.*, 1972; Frydl, 1979). However, it has been found that live coral represents a major dietary constituent (greater than 50%) in only one species, *Bolbometopon muricatum* (Bruce, 1979; Bellwood, 1986; Bellwood & Choat, 1990).

The diet of those species that live in seagrass beds (*Nicholsina*, *Calotomus*, *Leptoscarus* and *Sparisoma* species), is composed primarily of seagrasses (Randall & Bishop, 1967; Bruce & Randall, 1985). The diet of *Cryptotomus*, another seagrass dwelling species, and the sub-tropical rocky reef species *Sparisoma cretense* and *S. strigatus* have not been determined quantitatively. However, the former appears to feed primarily on seagrasses and associated epiphytes, whilst the latter two species include algae and a large amount of inorganic material in their diet (DRB unpublished data).

During feeding, many reef-dwelling scarid species remove large quantities of inorganic material. As a result, scarids are a major bioeroding agent on coral reefs. It has been estimated that up to 9 kg/m^2/yr may be removed by scarid grazing on the Great Barrier Reef (Kiene, 1988). The importance of scarids in primary erosion, sediment reworking and habitat modification have been the focus of a number of recent studies (Frydl & Stearn, 1978; Keine, 1988; Bellwood & Choat, 1990).

Colour phases and reproductive biology. Most scarids are protogynous hermaphrodites and undergo a complex series of colour pattern changes associated with their sexual ontogeny. There are typically three distinct colour phases: the juvenile phase, initial phase (IP) and terminal phase (TP). IPs are sexually subadult, female or primary males (ie, males which are not the result of sexual inversion). The colour pattern of IPs is typically drab comprising dull browns and greys. TPs are sexually males. They may be either primary males which have simply undergone a colour change, or secondary males which have synchronously changed both their sex and colour pattern. The colour patterns of TPs are usually bright, with green and blue predominating. Juvenile colour patterns are extremely variable and often bear no resemblance to the adult IP or TP colour patterns (Bellwood & Choat, 1989). The reproductive biology of parrotfishes is considered in detail in Choat & Robertson (1975), Robertson & Warner (1978) and Robertson *et al.* (1982).

Materials and Methods

The analyses in this study were based on the external examination of 65 scarid species, with dissections and/or examinations of osteological

preparations of 63 species. This represents approximately 81% and 79%, respectively, of the 80 extant scarid species recognised in this study (listed in the revised classification genera of Scaridae). These species included representatives of all genera and sub-genera of previous authors (*Scaridea* excepted). The species examined were classified into ten groups based on shared character state distributions. All ten groups corresponded with previously recognised genera. In all cases the species examined included the type species from each of these genera. Care was taken to ensure that, in cases where the type species has a wide geographical distribution, the material examined included specimens from the geographic region which encompasses the type location of the type species (ie, Red Sea specimens of *Chlorurus gibbus*, *Hipposcarus harid* and *Scarus psittacus*). The material examined is listed in Appendix I, with details of material held in museum collections given in Appendix II.

Throughout the text generic terms are employed in their revised sense. The body of this study is based on a survey of the comparative morphology of the Scaridae with a phylogenetic analysis of the morphological characters and their character states. The results of these analyses are presented as a cladogram. This cladogram describes interrelationships between species groups within the family and indicates that changes to the current generic classification of the Scaridae are necessary. To clarify these changes, generic diagnoses, synonymies, a key, and an annotated list of valid extant species are given in the revised classification of genera of Scaridae.

The terminology of the following studies was used in the descriptions: (i) external morphology – Choat & Randall (1986), (ii) osteology – Gomon & Paxton (1985), Russell (1988), with details following Rognes (1973) and Barel *et al.* (1976), (iii) myology – Winterbottom (1974), unless stated otherwise, (iv) intestinal morphology – Bellwood (1986).

Preparation of material. Most of the osteological material examined was obtained by hot water maceration of fresh or frozen specimens followed by bacterial digestion. Fresh or fully thawed frozen specimens were placed in hot water at 80 to 100°C for three to ten minutes until the flesh was loose. The specimen was removed, allowed to cool and excess flesh carefully washed off or removed using forceps. The bones were then placed in fresh water for four to ten days (at approximately 25°C) to allow any remaining flesh to be softened by bacterial digestion. The water was changed every one to two days and any loose flesh washed off. The water was buffered with calcium carbonate to prevent excessive acid buildup. Care was taken to ensure that the bony elements of the suspensorium, neurocranium and vertebral column did not disassociate. In whole preparations, all disarticulated bones, including ribs and fin elements, were retained. Once all the flesh was removed, the bones were sterilised and connective tissues fixed by brief immersion in buffered 20% formaldehyde (2-4 hrs), before being washed, air dried and labelled for storage. If necessary, the bones were subsequently degreased by washing in toluene.

Fully articulated osteological preparations were prepared from fresh or frozen material. Specimens were gutted, scaled and cleaned of as much flesh as possible, taking care not to disturb any bones. For ease of examination, the left mandibular, palatine and hyoid arches were dissected free, along with the intact branchial basket. All material was air dried for several days or weeks and placed in a dermestid beetle colony to remove the remaining flesh.

To obtain clean disarticulated bones from dry articulated skeletons or from whole preserved specimens, bones were carefully removed, placed in distilled water for 24 to 48 hours, cleaned of excess flesh, and placed in a narrow deep flask of hot water to which sodium perborate had been added (approximately 30g/l). The bones were left in this solution for 48 hours then the softened flesh washed or brushed off. The perborate treatment was repeated if necessary.

Enzyme cleared counterstained specimens were prepared using the alcian blue-alizarin red S method of Dingerkus & Uhler (1977). Some specimens were subsequently dissected to clearly expose internal structures. A few specimens were dissected prior to clearing.

Osteological details of type material and additional specimens were based on analyses of radiographs stored in the Ichthyology Department of the National Museum of Natural History, Smithsonian Institution.

Anatomical illustrations were prepared primarily from drawings made using a camera-lucida mounted on a dissecting microscope. Large structures or whole head dissections of large specimens were drawn using a Grant projector, or were based on photographs of the specimen. In paired bones, those of the left side are figured. Abbreviations used in the text figures are listed in Appendix III.

Comparative Morphology of the Scaridae

Previous descriptions. There have been few comprehensive studies of the internal morphology of parrotfishes. Most studies have been restricted to descriptions of specific structures, particularly the pharyngeal apparatus (Monod, 1951; Nelson, 1967; Yamaoka, 1980; Liem & Greenwood, 1981; Kaufman & Liem, 1982; Gobalet, 1989) and oral jaws (eg, Choat, 1969; Bruce, 1979; Bellwood & Choat, 1990).

To date, there has been no published comparative study which addresses differences between all scarid genera, with the possible exception of Schultz (1958) who figured the pharyngeal bones of several genera and alluded to their utility in supra-specific classifications. General surveys of the oral jaws (Choat, 1969) and of the pharyngeal apparatus (Bruce, 1979) formed the

basis for ecological comparisons but were not examined in a cladistic framework. Detailed studies which consider more than one functional system are invariably restricted to one or a few species, usually from the genus *Scarus* (eg, Gobalet, 1980; Tedman, 1980a,b; Clements & Bellwood, 1988).

The studies outlined above include most of the major works on scarid morphology. Additional descriptions of the morphology of specific structures will be noted in the relevant sections below. In the following section, derived character states are indicated in the text by boldface numbers in parentheses giving the character and character state (eg, **2.1** = character 2 state 1 is derived). Where there is more than one derived state these are indicated in a similar manner (eg, **8.1-2** or **8.3**). Numbering character states 1, 2, 3 etc. does not necessarily indicate a transformation series. The polarity of the characters states was determined during the construction of the cladogram.

Osteology

Neurocranium (characters 1 – 12)

Fig. 1

The form of the neurocranium varies widely within the family, from robust massive structures in *Bolbometopon* to light, fragile structures in some *Scarus* species. The neurocranium of many scarids is well ossified with strong suturing of the bony elements, particularly in large specimens. The basic form of the neurocranium of scarids has been described briefly by Tedman (1984a), Yamaoka (1980), Gobalet (1989) and Clements & Bellwood (1989).

As in the outgroups, the ethmoid-vomerine region is usually relatively short. Although quite variable both within and between genera, elongation of this region is apparent in several genera and is considered derived (**1.1**; region forward of lateral ethmoid greater than 40% of total neurocranuim length). Two pairs of facets are visible on the vomer, a pair of maxillary facets on the anterior lateral surface and a pair of anteriorly facing premaxillary facets near the ethmoid-vomer suture. The orientation of the lateral maxillary facets appears to be of phylogenetic significance. In the outgroups the orientation has an anterior component (face of facet clearly visible when viewed anteriorly), with the loss of this component in scarids apparently being derived (**5.1**). The characteristic depression formed by the ethmoid and frontals in labrids, which forms a fossa for the ascending processes of the premaxillae (Russell, 1988), is represented in scarids by a depression in the ethmoid. The loss of this depression in some scarids is considered derived (**2.1**). In the outgroups and some scarid genera, the ethmoid and frontals are sutured. However, in those scarids which have an ethmoid-frontal depression, the two bones are separate (**3.1**). Because fusion of the bones and the presence of a depression

can co-occur (as in labrids), the two features are regarded as separate characters. The only genus which differs from this basic pattern is *Bolbometopon*, which unlike all other taxa has an enlarged reticulate ethmoid (**4.1**). This forms the base for the unusually large hump in this species although, as in other species, the hump *per se* is composed of fibrous tissue.

Dorsally, two unusual features of the scarid neurocranium are apparent. Firstly, the form of the supraoccipital crest. In most scarids, the supraoccipital crest has distinct lateral flanges (**6.1**). These flanges are absent in the outgroups. In *Calotomus* they are particularly well developed and result in an extended trifid supraoccipital crest posteriorly (**6.2**). Secondly, the posterior extension of the epioccipital. This extension is absent in the outgroups but present in all scarids (**8.1-3**), where the epioccipital is extended posteriorly to form a curved flange. Dorsally, the flange is confluent with the top of the neurocranium. Medially, it curves ventrally fusing with an exoccipital flange which tapers off as it extends towards the exoccipital condyle. In *Cryptotomus* and *Nicholsina* the epioccipital flange is relatively short (**8.1**; not reaching the exoccipital condyle). In all other genera, with the exception of *Calotomus*, the epioccipital flange is well developed and extends posteriorly to or beyond the level of the exoccipital condyle (**8.2**). In *Calotomus* the flange extends anteromedially and fuses with the laterally expanded flanges of the trifid supraoccipital crest (**8.3**). A slight anteromedial twisting of the flange may be seen in *Sparisoma*. In all genera, the epioccipital flange represents the site of origin of posterior portion of the levator posterior. This site of origin is bordered posteromedially by the exoccipital flange. The exoccipital flange is long (ie, extending beyond exoccipital condyle) in all scarid genera except *Hipposcarus* and *Scarus*, where it terminates well short of the exoccipital condyle (**7.1**). This flange is not present in any of the outgroups.

It is in the ventral aspect that the most striking features of the neurocranium of scarids may be seen: A) the presence of deep subtemporal fossae and B) the articulatory facets of the pharyngeal articulation.

A pair of large, deep subtemporal fossae are present in all scarid genera (**9.1-2**), with an additional smaller pair posteriorly in some genera (**9.1**). These fossae are unique to the Scaridae. In some labrids the neurocranium may have depressions in this region (eg, in *Semicossyphus* and some *Bodianus* species), but only in scarids are deep shaft-like fossae present. The anterior fossae are subtriangular when viewed ventrally and are bordered by the prootic, pterotic, exoccipital and intercalar, with the supraoccipital, parietal and epioccipital forming the roof. The posterior pair of fossae, when present, are invariably smaller and are usually a more elongate triangular shape with a posteriorly directed apex. The anterior fossae are parallel sided or slightly wider dorsally. The posterior pair taper dorsally and appear to be bordered by the epioccipital, intercalar, parietal and pterotic. The posterior margins of the posterior fossae are reduced in *Bolbometopon* and are

present only as a vestige in *Chlorurus, Hipposcarus* and *Scarus* (9.2) where they are marked by a protrusion of the intercalar.

The anterior subtemporal fossae are the site of origin of the medial fibres of the large fourth levator externus muscle. Posterior fossae are the site of origin of the posterior fibres of the fourth levator externus, although some of the anterior fibres of the levator posterior may
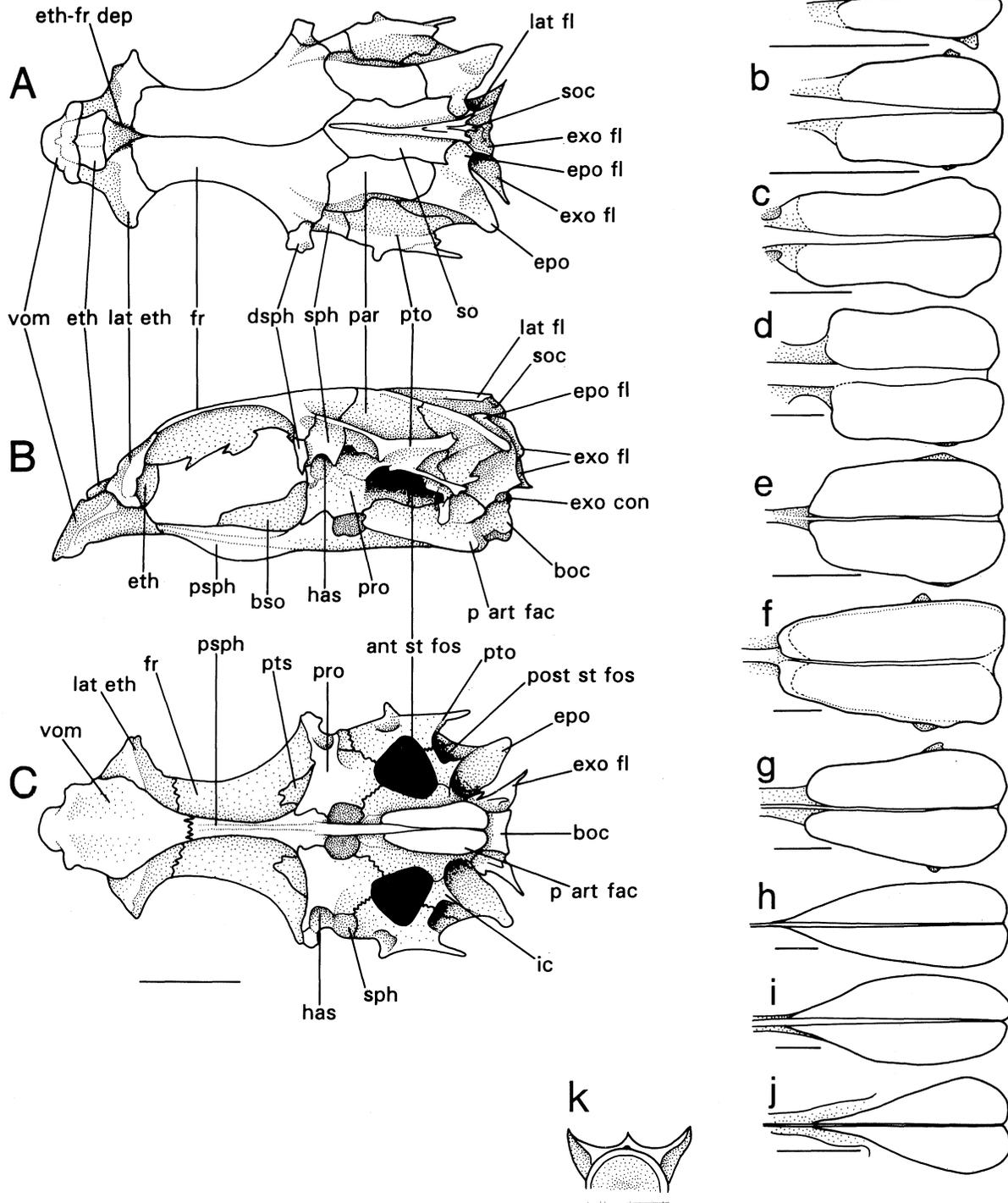
Fig. 1. The neurocranium of *Cryptotomus roseus*: A, dorsal view, B, lateral view, C, ventral view, scale bar equals 5 mm; a-k, pharyngeal articulation facets, anterior to left, scale bars equal 5 mm, a-j, ventral view: a – *Cryptotomus roseus*; b – *Nicholsina usta*; c – *Calotomus carolinus*; d – *Leptoscarus vaigiensis*; e – *Sparisoma viride*; f – *Cetoscarus bicolor*; g – *Bolbometopon muricatum*; h – *Chlorurus gibbus*; i – *Hipposcarus longiceps*; j – *Scarus psittacus*; k – *Scarus psittacus*, posterior view (ventral surfaces uppermost). Abbreviations given in Appendix III).

encroach upon the fossa. The presence of these fossae represents a major change in the structure of the neurocranium and probably also in the mechanics of the pharyngeal apparatus. Bellwood (1986) suggested that this change may be correlated with an increase in the role of the anterior pharyngeal muscles, increasing mobility for grinding rather than simple crushing power.

In most labroids and in all the outgroups examined, the facets of the neurocranial-pharyngeal articulation are short and convex. In scarids, however, these facets are represented by a pair of large, elongate (length greater than 2.5 times width) anteroposteriorly oriented grooves on the posterior part of the parasphenoid (**10.1**). These elongate, concave (**12.1**) articulation facets differ markedly from those of all other members of the Labroidei and represent a unique derived feature of the Scaridae. These facets point to a change in the function of the upper pharyngeal jaws, from a rotational movement (as in labrids) to a sliding movement, or a rotation around a much larger circumference. Within the Scaridae the form of the facets vary considerably in shape, having either straight edges and a bluntly rounded anterior margin or tapering to a point anteriorly as in *Chlorurus*, *Hipposcarus* and *Scarus* (**11.1**; Fig. 1).

Oral jaws

The oral jaws (mandibular arch) of parrotfishes have been described on numerous occasions and have been recognised as one of the few external characters to be of taxonomic value at supraspecific levels. Descriptions of the tooth plates are almost invariably included in species descriptions (eg, Randall, 1983a; Randall & Bruce, 1983; Bruce & Randall, 1985; Choat & Randall, 1986). Descriptions of the osteology of the oral jaws are provided in Gregory (1933), Tedman (1984a), Clements & Bellwood (1988), and Bellwood & Choat (1990).

Premaxilla (characters 13 – 31)

Fig. 2

There is a great deal of variability in the structure of the premaxilla between scarid genera. The basic shape, with a relatively thick, blunt ascending process and a shorter alveolar process at 45 to 90° to it, is relatively uniform. Most variability is found in the form of the dental plates, the teeth and the articulation facets.

The paired premaxillae are joined medially by cruciate ligaments which connect the anterodorsal regions of the ascending processes. The ascending process may be pointed terminally, but is usually blunt. Some genera have a depression on the posteroventral surface of the ascending process (**23.1**) (the region occupied by the rostral cartilage), whilst on the lateral surface, there may be an elongate indentation (**22.1**), corresponding with the location of the palatine dorsal process. Neither of these depressions/indentations were recorded in the outgroups examined. On the ventral

surface, a shelf or groove marks the location of the insertion of the posterior maxillary-premaxillary ligament. In *Pseudodax* and all scarids, the ventrally facing maxillary facet is located immediately lateral to this shelf or groove, at the base of the alveolar and ascending processes (**29.1**). This facet represents the dorsal surface of the main maxillary-premaxillary joint and corresponds with the premaxillary condyle of the maxilla. In all remaining outgroups, the maxillary facet is located part way along the ascending process.

A maxillary fossa was not recorded in any outgroup, but was present in all scarid genera with the exception of *Scarus*. This fossa is indistinct in *Cryptotomus* and *Nicholsina* (**15.1**) and distinct in the remaining scarid genera (**15.2**). The maxillary fossa may be located at the angle of the ascending process and the alveolar process, either at the base of the ascending process facing laterally, or at the base of the alveolar process facing posteriorly, or intermediate between these two. This fossa may be represented by a flat facet, a deep concave facet or a raised crater-shaped concave facet. It is into this fossa that the protrusion on the anterior face of the maxillary head inserts. In *Sparisoma*, there is a unique flat facet immediately above the maxillary fossa (**31.1**). This is an anterior extension of the palatine-maxillary articulation.

In scarids, the alveolar process is bifid distally (**24.1**). In labrids the alveolar process is usually rounded or pointed distally (some odacids may have a slight indentation distally). In most scarid genera, there is a small concave/flat facet between the two processes (**30.1**). This facet is absent in *Hipposcarus* and *Scarus*, whilst in *Leptoscarus* the facet is convex (**30.2**).

The dental plates display a wide variety of tooth forms and configurations. There are three basic individual tooth forms: caniniform, conical and incisiform. There are two basic tooth forms when fused: a) small flattened incisiform/conical or b) large incisiform. In addition, there are three main toothed regions: anterior, lateral and posterior.

Teeth in the anterior region are relatively large. They may be caniniform (*Cryptotomus*, *Nicholsina*), pointed but flattened (*Calotomus*, some *Sparisoma*) or thickened with a blunt cutting margin (all genera with coalesced teeth except *Leptoscarus*). These teeth all develop in a dorsal alveolar region and migrate anteroventrally before erupting on or near the cutting edge. It is these teeth which typically fuse to form the characteristic fused dental plates. The presence of coalesced teeth was only recorded in *Odax* and some scarid genera (**13.1**). In the remaining outgroups and scarid genera, teeth were either isolated or in rows with no evidence of coalescence. The plates are usually covered with a layer of cement (**19.3**), although the occurrence of cement is highly variable between taxa. This cement appears to be similar to the osteodentine described in tetraodontids by Andreuci *et al.* (1982). The cement is usually white but in TP *Chlorurus* and *Scarus* it is often blue or blue-green.

The presence of anterior caniniform teeth in most
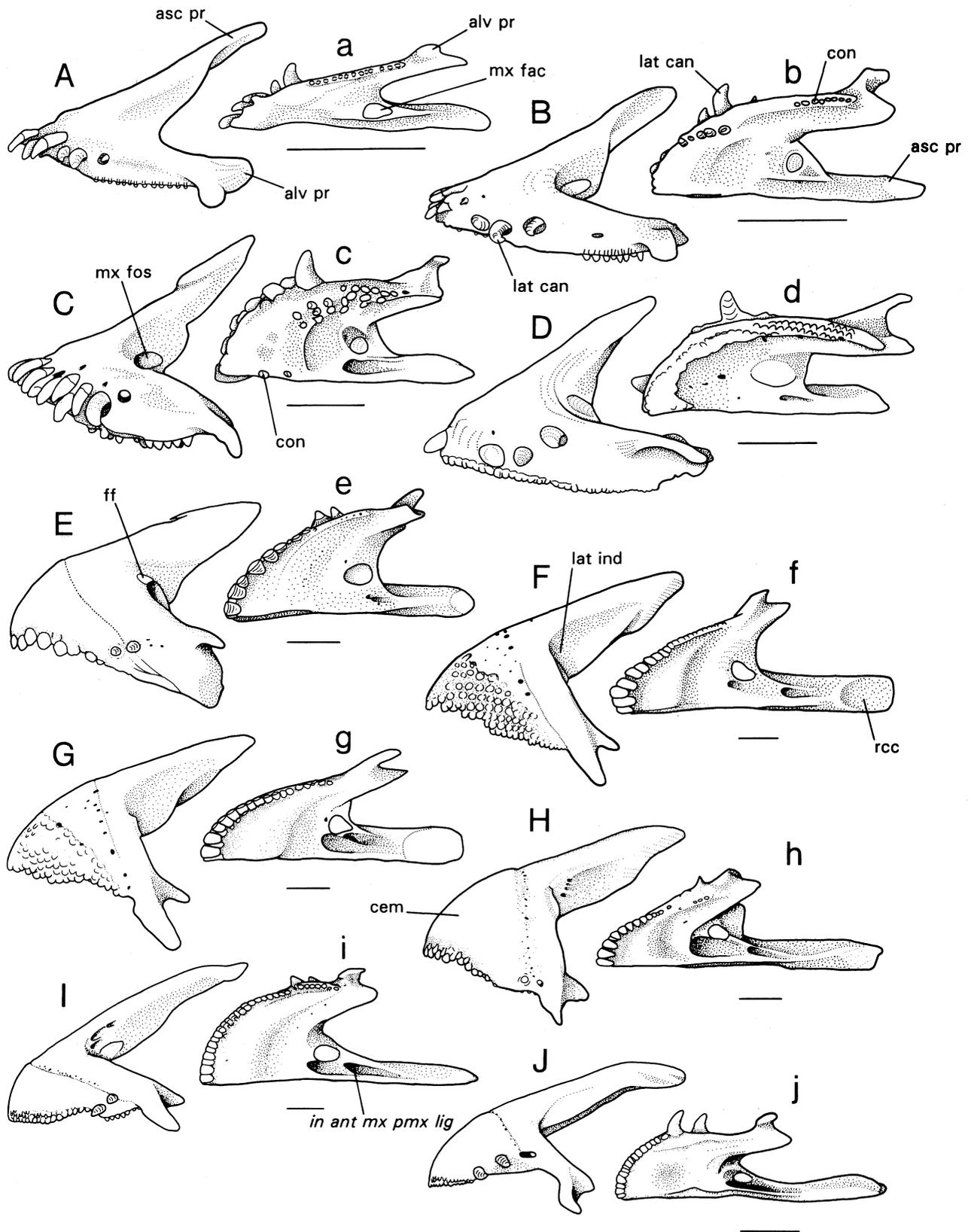
Fig. 2. Premaxillae: A-J, lateral view; a-j, ventral view; anterior to left; scale bars equal 5 mm; A-a – *Cryptotomus roseus*; B-b – *Nicholsina usta*; C-c – *Calotomus carolinus*; D-d – *Leptoscarus vaigiensis*; E-e – *Sparisoma viride*; F-f – *Cetoscarus bicolor*; G-g – *Bolbometopon muricatum*; H-h – *Chlorurus gibbus*; I-i – *Hipposcarus longiceps*; J-j – *Scarus psittacus*.

outgroups suggests that the loss in several scarid taxa is a derived feature (**16.1**). The condition in *Pseudodax* is unusual with highly modified flattened incisiform teeth anteriorly. Within *Calotomus* and *Sparisoma* the presence of caniniform teeth varies both within and between species.

On the lateral face of the premaxillae, immediately posterior to the anterior teeth, are the lateral canines. These arise at the posterior or posteroventral extremity of the main alveolar region, and migrate anteroventrally before erupting. Although the lateral canines may be short and blunt, they are usually long and pointed and curve posteriorly. Lateral canines may be present in the initial phase, but their presence is often associated with sexual maturity or the sexual transition to the male, terminal phase. Although present in *Halichoeres*, lateral canines are absent in most labrid taxa and their presence is considered to be derived (**17.1**). It appears that they may have arisen as a result of a lateral rotation of the large caniniform teeth found in many labrid genera (eg, *Pseudolabrus* and *Bodianus*).

In species without fused dental plates, a bony ridge runs inside the anterior teeth and extends along the alveolar process. Along the posterior portion of this ridge are the posterior teeth. These teeth are usually small and conical. Some or all of the teeth may be found in a row along the ridge. In *Nicholsina*, there is an additional row anteriorly, in *Calotomus* the teeth extend medially, and in *Leptoscarus* they appear to be fused in rows which extend forward along the bony ridge. Posterior teeth develop at the posterior extremity of the toothed area and migrate anteriorly or anterolaterally before erupting on the cutting edge. In *Nicholsina* and *Calotomus* there is some degree of cement deposition at the base of the teeth in the lateral row. In *Leptoscarus*, the teeth are short and even, and are fused in tight rows which progress anterolaterally along the cutting edge.

Small conical teeth are occasionally visible in species in genera with fused dental plates. In these species, these teeth are present at the posterior extremity of the cutting edge (eg, *Hipposcarus*, Fig. 1I,i).

The form of the dental plates varies greatly within and between genera. In the analyses, several characters which relate to the form of the dental plates were used: 1) the form of the cutting edge, which may be a single entire edge, extending from the symphysis to the angle of the jaws (**14.1**), or incomplete/broken as in all outgroups except *Odax*; 2) the number of tooth rows, in which genera with three to six rows (some scarids; all outgroups except *Odax*) are clearly distinguished from the remaining genera which have approximately 12 to 22 (**20.1**); 3) the presence of conical teeth medial to the cutting edge (**25.1**); 4) the presence of a conical tooth or teeth on the medial face adjacent to the medial symphysis, found only in *Calotomus* (**26.1**); 5) the origin of the teeth in the lateral tooth rows, which is indeterminate in most outgroups, but lateral in *Pseudodax* and all scarid genera except *Leptoscarus* where the teeth erupt on the medial surface of the jaw (**27.1**); 6) the presence of clearly visible diagonal rows

of large developing teeth (**28.1**), which are absent or small in all outgroups and some scarid genera. The presence of oblique tooth rows is a distinct feature of all scarid species, including *Leptoscarus*. In *Leptoscarus*, the dental plates are shallow with strongly oblique tooth rows. In the other genera, the dental plates are deep and the tooth rows are more acute, although a *Leptoscarus*-like condition is found in *Sparisoma radians*.

Only one character of the oral jaw apparatus as a whole was used in the phylogenetic analyses, namely, the nature of the jaw overlap. Previously, this feature was one of the key characters used to divide the two subfamilies within the Scaridae: Sparisomatinae (upper jaw included within lower jaw when mouth closed) and Scarinae (edge of lower jaw included in that of upper jaw when mouth closed) *sensu* Schultz (1958). The functional implications of this difference are not known. In most outgroups the jaws oppose with interdigitating teeth. In scarids, the extent to which the dentary protrudes (**21.1**) may vary (being indistinct in *Cryptotomus*, *Nicholsina* and *Calotomus*), but is clearly distinguished from the overshot condition with a protruding premaxilla (**21.2**) in *Cetoscarus*, *Bolbometopon*, *Chlorurus*, *Hipposcarus* and *Scarus*.

Although the development of coalesced teeth in scarids and other labroids awaits a more detailed investigation, it appears that there may be two separate types of fusion. The first, posterior type, being a flattening and fusion by cement connection of the small conical teeth at the angle of the jaws, with several adjacent oblique rows forming the cutting edge. In this scheme, new teeth erupt at the posterior end of each row, from here, they migrate anteriorly to take a place on the cutting edge, replacing worn teeth. This pattern of fusion is typified by *Leptoscarus*. A similar pattern may be found in *Sparisoma radians*, whilst several *Calotomus* species show some degree of flattening and fusion by cement of the small conical teeth at the angle of the jaws.

The second, anterior type of fusion is characterised by a mosaic formed by rows of large teeth on the front of the dental plates. In this pattern, new teeth develop in the alveolar region of the dental plate, they progress towards the cutting edge, where they erupt through the anterior/lateral face of the dental plates. From here, they migrate to the cutting edge where they wear and are lost, to be replaced by the teeth immediately above them. It appears that the teeth in this scheme are modified anterior caniniform teeth.

Within the Scaridae there appears to be a range of intermediate stages in the development of the anterior type of fusion. The proposed sequence, and that supported by the cladogram, is: 1) the plesiomorphic condition with caniniform teeth on the anterior face of premaxilla as in *Cryptotomus*; 2) a flattening of these teeth as in *Calotomus*; 3) an increase in the depth of the dental plates, with more rows of teeth and a greater number of exposed teeth per row as in *Sparisoma rubripinne* and *S. chrysopterum*; 4) individual teeth

increase in strength and expand posteriorly, producing solid dental plates as in large *Sparisoma viride*; 5) individual teeth enlarge further as in *Cetoscarus* and *Bolbometopon*, whilst the whole dental plate may be covered in cement as in *Chlorurus*; 6) individual teeth decrease in size but retain the cement and growth pattern (*Hipposcarus* or *Scarus*).

Whilst the two patterns are not mutually exclusive (*Calotomus* has traces of both patterns and *S. radians* appears to have an intermediate form or a fusion of both anterior and posterior types), the presence of small conical teeth in some *Scarus*, *Hipposcarus* and *Chlorurus* species suggests that the dental plates in these genera are a result of anterior fusion rather than an anterior progression of a posterior fusion.

The hypothesis that the form of the dental plates of *Chlorurus* and *Scarus* species is a result of fusion of the anterior teeth is supported by observations of the ontogeny of the oral jaws in these two genera (Bellwood, 1986). In both genera, recently settled specimens 7 to 9 mm SL (ie, within days of leaving the plankton) have caniniform teeth on the anterior edge of the jaws. Developing teeth on the anterior face of the dental plates are also caniniform. At 10 to 12 mm SL, the caniniform anterior teeth are lost, although small conical teeth are present at the angle of the jaws. The new anterior teeth are scale-shaped with a flattened overall appearance and a broadly curved leading edge. During the early juvenile phase, 14 to 50 mm SL, the anterior teeth become progressively stronger, and become more pear-shaped, with the broad margin on the cutting edge, the number of tooth rows and number of teeth per row slowly increases. The small conical teeth at the angle of the jaws are usually lost between 19 to 27 mm SL. Above 25 mm SL, the developing teeth are clearly visible within the dental plates, and the overall appearance is similar to that of some *Sparisoma* species. In progressively larger specimens, individual teeth become thicker, the material covering the plates become increasingly opaque and the plates are eventually covered in cement.

Maxilla (characters 32 – 36)

Fig. 3

In scarids, the maxilla is more robust than in labrids. This difference probably reflects the greater force applied to the jaws during feeding in scarids. The three main regions of the maxilla are A) the maxillary arm, a large flattened lateral limb; B) the maxillary head, at the dorsal end of the maxillary arm and surrounding the facet of the palatine-maxillary articulation (the principal articulation point of the upper jaw); and C) the premaxillary process, which lies medial to the maxillary head.

The maxillary arm is usually broad and laterally flattened with a bony flange or process on the posterodorsal margin. The size of this process varies greatly, and in some genera, is greatly expanded posterodorsally. Distally, the maxillary arm may be straight or curved anteriorly. In most genera, a small facet may be located on the anterior face of the maxillary arm, corresponding to the facet between the bifid processes of the premaxillary alveolar process. On the mid-anterior margin of *Sparisoma* there is an unusual grooved process (**32.1**), where the maxillary arm abuts the premaxillary alveolar process. This process is absent in the outgroups and all other scarid genera. It may represent an extraordinary enlargement of the facet found in this position in other scarid genera.

The maxillary head varies considerably in its relative size. The medial face is often enlarged with a posteriorly expanded bony flange. The maxillary facet of the palatine-maxillary articulation lies in the middle of the maxillary head facing posterodorsally. This facet is lacking in labrids. In scarids it may be concave, convex, or concave with a posteroventral groove (**33.1-3**). The medial face of the maxillary head bears the neurocranial condyle posteriorly and extends anteriorly to form the premaxillary process. The premaxillary condyle is located on the anterodorsal extremity of the premaxillary process. This condyle may extend on to the lateral and/ or medial faces. In *Leptoscarus* the condyle is only present on the lateral face as the flange on the maxillary head extends along the premaxillary process. On the medial face, immediately below this condyle is a small groove (in some scarids and all outgroups), cavity (**35.2**) or deep fossa (**35.1**), marking the insertion site of the anterior maxillary-premaxillary ligament.

In labrids and some scarids, the A1t inserts anteriorly on the ventral face of the premaxillary process. In *Cryptotomus*, *Calotomus* and *Sparisoma*, this origin is from a small rod in this position (no rod in *Nicholsina* and *Leptoscarus*). The insertion of the A1t in *Chlorurus*, *Hipposcarus* and *Scarus* is at base of the maxillary head. In *Cetoscarus* and *Bolbometopon* a stout ridge extends from the ventral surface of the premaxillary process to the medial surface of the maxillary arm, terminating in the A1t insertion scar. The presence of this ridge is considered derived (**36.1**).

A premaxillary facet is present on the anterior face of the maxillary head in all scarid genera except *Scarus* This facet inserts into the maxillary fossa on the premaxilla. The premaxillary facet may be on the medial (**34.1**) or anterior (**34.2**) face of the maxillary head. This structure has been recorded only in scarids.

In *Hipposcarus*, a large palatine facet is present posteriorly on the lateral face of the medial flange of the maxillary head. This facet corresponds with a large flat facet on the medial face of the palatine (*cf.* character 53).

Dentary (characters 37 – 44)

Fig. 4

The form of the dentary varies widely between scarid genera, from the labrid-like condition found in

Fig. 3. Maxillae: A-J, lateral view, anterior to left; a-j, medial view, anterior to right; scale bars equal 5 mm; A-a – *Cryptotomus roseus*; B-b – *Nicholsina usta*; C-c – *Calotomus carolinus*; D-d – *Leptoscarus vaigiensis*; E-e – *Sparisoma viride*; F-f – *Cetoscarus bicolor*; G-g – *Bolbometopon muricatum*; H-h – *Chlorurus gibbus*; I-i – *Hipposcarus longiceps*; J-j – *Scarus psittacus*.

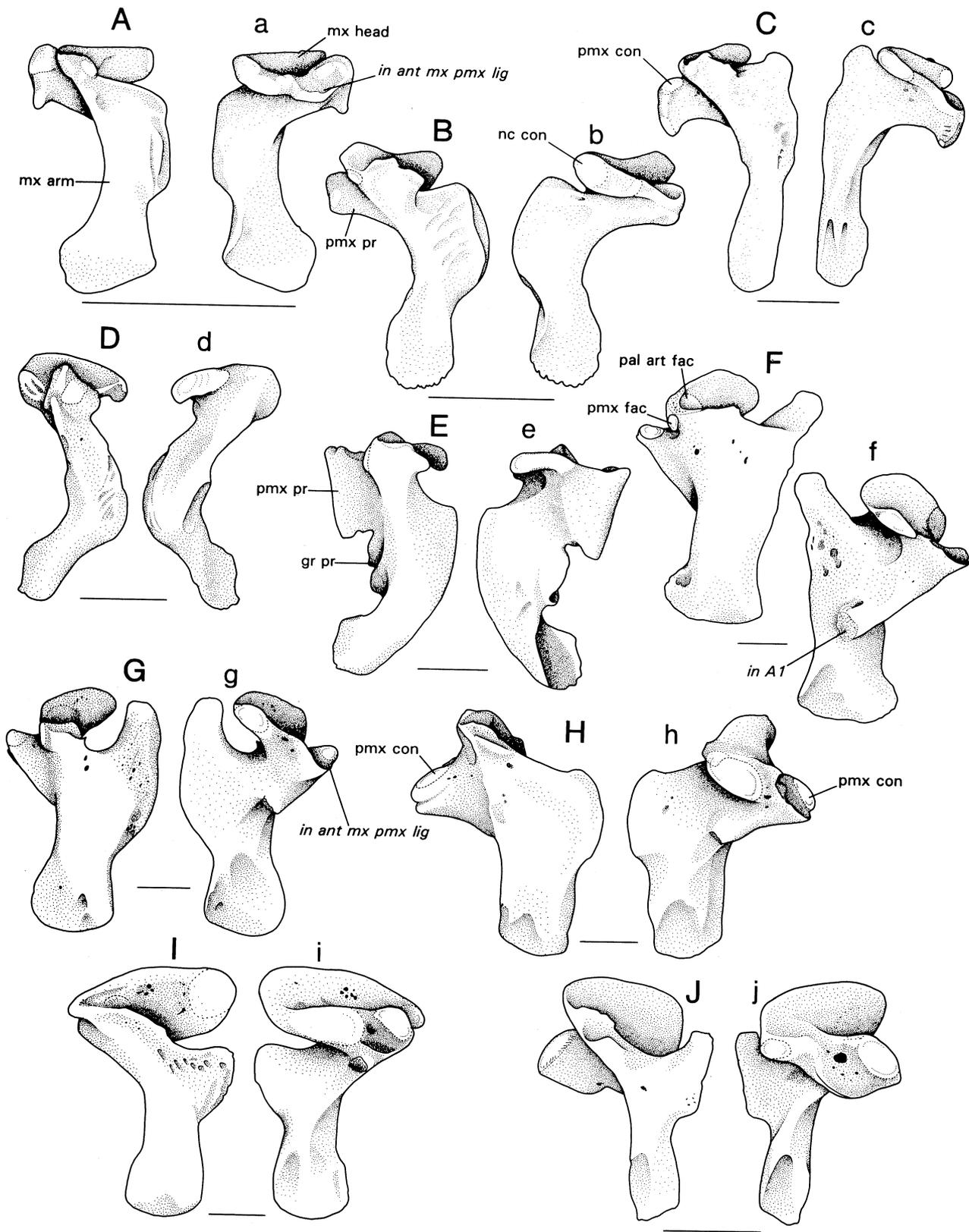**Fig. 4.** Dentaries: A-J, lateral view, anterior to left; a-j, medial view, anterior to right; scale bars equal 5 mm; A-a – *Cryptotomus roseus*; B-b – *Nicholsina usta*; C-c – *Calotomus carolinus*; D-d – *Leptoscarus vaigiensis*; E-e – *Sparisoma viride*; F-f – *Cetoscarus bicolor*; G-g – *Bolbometopon muricatum*; H-h – *Chlorurus gibbus*; I-i – *Hipposcarus longiceps*; J-j – *Scarus psittacus*.
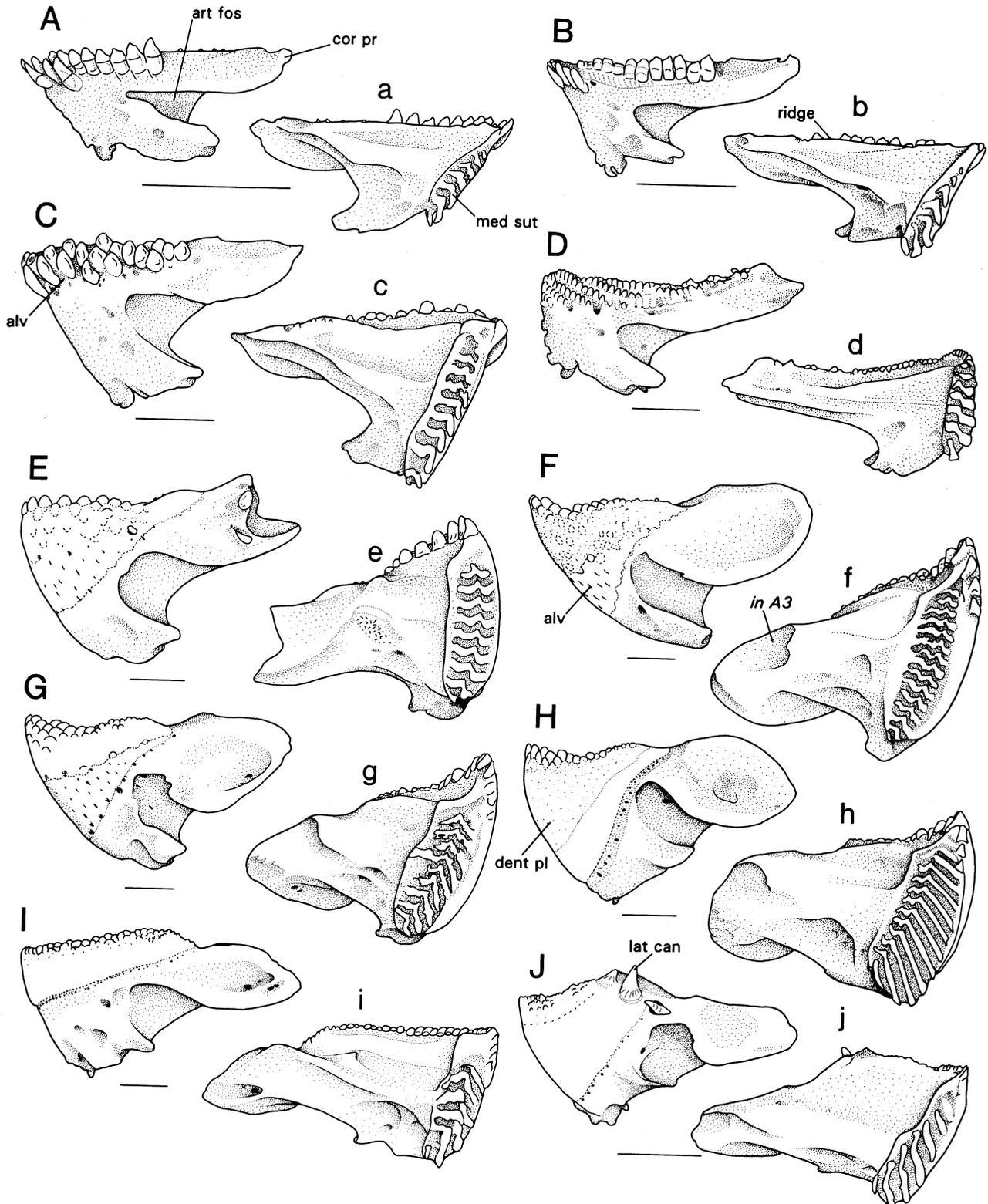
Cryptotomus which is characterised by discrete rows of caniniform teeth, to highly modified forms as in *Chlorurus* which has deep dental plates, a greatly expanded coronoid process and a deep articular fossa.

In terms of the overall shape of the dentary, the greatest departures from the labrid-like form of *Cryptotomus* are: 1) the expansion of the coronoid process (deep rounded form Fig. 4; **43.1**), from the narrow pointed form found in all outgroups and some scarids. In *Sparisoma* this process has a distinctive notch posteriorly (**44.1**). This notch is a unique derived feature of the genus; 2) the form of the articular fossa. This may be represented by either a broad flat tapering groove, where the anterior ascending process of the articular is bound to the dentary (as in most scarids and all outgroups), or a deep rounded fossa (**42.1**), which represents the articulation socket of the articulatory articular-dentary joint (as in *Chlorurus*, *Hipposcarus* and *Scarus*). Some foreshortening of the groove is apparent in *Bolbometopon* but this does not represent an articulatory fossa.

On the medial face, differences are marked by: 1) the presence of a large insertion scar marking the insertion of the A3t on the posterodorsal region of the medial face of the dentary coronoid process (corresponding with **120.2**); 2) an anterior extension of the coronoid process as a bone ridge passing medial to the main cutting edge (**38.1**), which is absent in some outgroups and most scarid genera; 3) modified medial sutures.

In all scarids, the paired dentaries are sutured along the medial symphysis. Comparable medial sutures are present in several labrid taxa and appear to be correlated with a strengthening of the jaw during occlusion (Gomon, 1979). A similar correlation has been suggested for the presence of sutures in some cichlids (Stiassny, personal communication). In labrids and cichlids, the sutures are represented by a series of straight diagonal ridges, as in *Scarus* (and juveniles of other scarid genera), and are usually small and few in number. In scarids, the sutures usually have an irregular or zig-zag form (**40.2**), with their margins becoming increasingly uneven in large individuals. There are two notable exceptions, in *Chlorurus* the sutures are straight with a small inflected or zig-zag portion posteriorly (**40.3**) whilst in *Scarus* the sutures are straight (the plesiomorphic condition). Within a species the number of sutures increases with increasing size (Bruce, 1979). In scarids, and if present in labrids, the medial sutures usually extend to the anterior edge of the dentary, excluding the cement. In *Cetoscarus* and *Bolbometopon*, however, the sutures do not reach the anterior margin (**41.1**).

In general, the form of the teeth and dental plates mirror those of the premaxilla, however, there is less differentiation of teeth into anterior, lateral and posterior fields. The teeth on the dentary appear to be dominated by teeth from the anterior tooth field. Posterior teeth are usually greatly reduced, as in *Cryptotomus*, *Sparisoma* and *Hipposcarus*, or absent as

in *Nicholsina* and most *Scarus* species. Lateral canine teeth on the dentary appear to be an unusual development restricted to a few *Scarus* species. The extent of coalescence and cement deposition on the teeth or dental plates follows that found on the premaxilla.

In all scarid genera, the tooth rows on the dentary are characterised by new teeth erupting on the lateral surface of the jaw at the posterior end of each tooth row. Erupted teeth progress anterodorsally towards the cutting edge, where they become functionally active and replace worn teeth.

In *Cryptotomus* and *Nicholsina* there are three and three to five tooth rows, respectively, the anterior two rows consist of flattened caniniform teeth. Teeth in the lateral row(s) are incisiform (occasionally pointed). In some *Cryptotomus* there are also few small conical teeth in a short row posteriorly. In all genera except *Cryptotomus*, *Nicholsina* and *Calotomus*, the number of diagonal tooth rows is greater than five (usually 6-10; **37.1**). In the outgroups there is usually only one row of teeth, tooth rows as in scarids are not present. *Pseudodax* is unusual, with a row of numerous small teeth. In this genus, the developing teeth alternate in their position and may be interpreted as rows, although these 'rows' of two to three teeth are not as clear as those of scarids, and are not considered homologous. In the Scaridae, the angle of the tooth rows with respect to the cutting edge may be either oblique (less than 45° eg, *Cryptotomus*), approximately 45° forming a mosaic (**39.1**, eg, *Cetoscarus*), or perpendicular (**39.2**, eg, *Scarus*).

Articular (characters 45 – 47)

Fig. 5

In most scarid genera, the articular closely resembles that of labrids, with well-developed anterior and posterior ascending processes and a broad descending process, incorporating the angular on the posteroventral corner. In scarids, the anterior ascending process may taper to a point as in labrids, be short and broad with a terminal notch (**45.1**), or moderately broad and rounded distally (**45.2**). In most labrids and scarids, the articular descending process has a medial bony flange which may extend onto the anterior ascending process. In some scarid genera, however, this flange is reduced with only the vertical portion remaining as an articular medial spine (**47.1**). In some genera, the articular is highly modified, with the loss of the posterior ascending process (**46.1**). Within the family, there is a progressive reduction in the size of Meckel's fossa, from a large labrid-like fossa in *Cryptotomus* to its absence in *Scarus*. Meckel's cartilage is lost in *Chlorurus* and *Scarus*.

Palatine arch (characters 48 – 56)

Fig. 6

The palatine arch has not been used previously as a
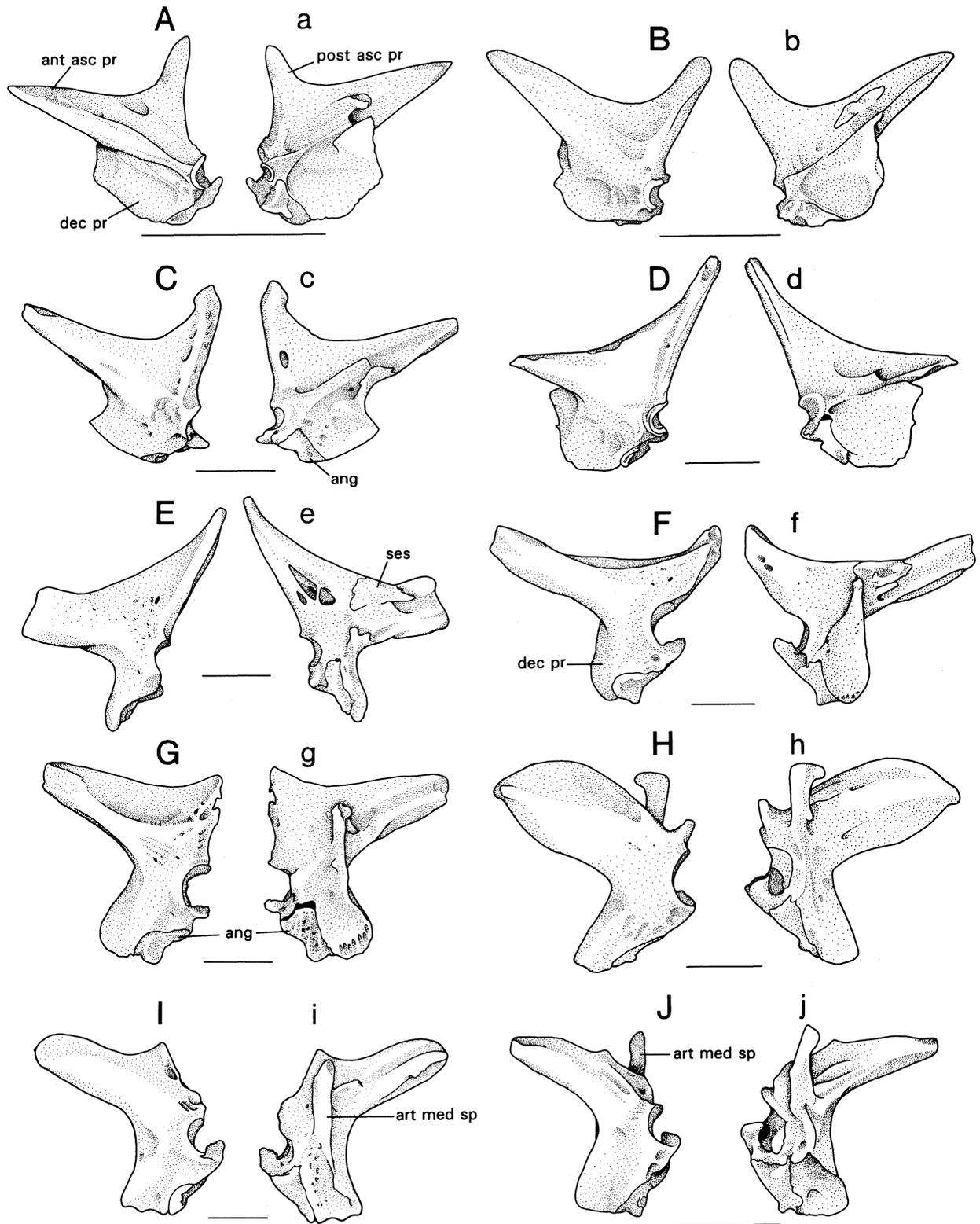
Fig. 5. Articulars: A-J, lateral view, anterior to left; a-j, medial view, anterior to right; scale bars equal 5 mm; A-a – *Cryptotomus roseus*; B-b – *Nicholsina usta*; C-c – *Calotomus carolinus*; D-d – *Leptoscarus vaigiensis*; E-e – *Sparisoma viride*; F-f – *Cetoscarus bicolor*; G-g – *Bolbometopon muricatum*; H-h – *Chlorurus gibbus*; I-i – *Hipposcarus longiceps*; J-j – *Scarus psittacus*.

source of characters in systematic studies of the Scaridae. The overall form differs little from that of the Labridae and other labroids, with the exception of the form of the palatine and the palatine-maxillary articulation. In the Labridae, the palatine dorsal process is a thin bone with an elongate palatine dorsal process. Anteriorly, it articulates with the maxilla via ligaments that attach the two bones (Gomon, 1979; Russell, 1988). There is no terminal condyle. In scarids, the palatine dorsal process is relatively robust and bears

a distinct maxillary condyle terminally (**51.1**). Basally, the palatine is strongly ankylosed to the entopterygoid and ectopterygoid (**56.1**), in contrast to the loose association found in labrids. These features appear to reflect an increase in the overall strength of the palatine-maxillary articulation.

Within the Scaridae the form of the palatine varies considerably. In *Cetoscarus*, *Bolbometopon* and *Chlorurus*, unlike other scarids and the outgroups, the palatine dorsal process is short and robust (**50.1**; Fig.
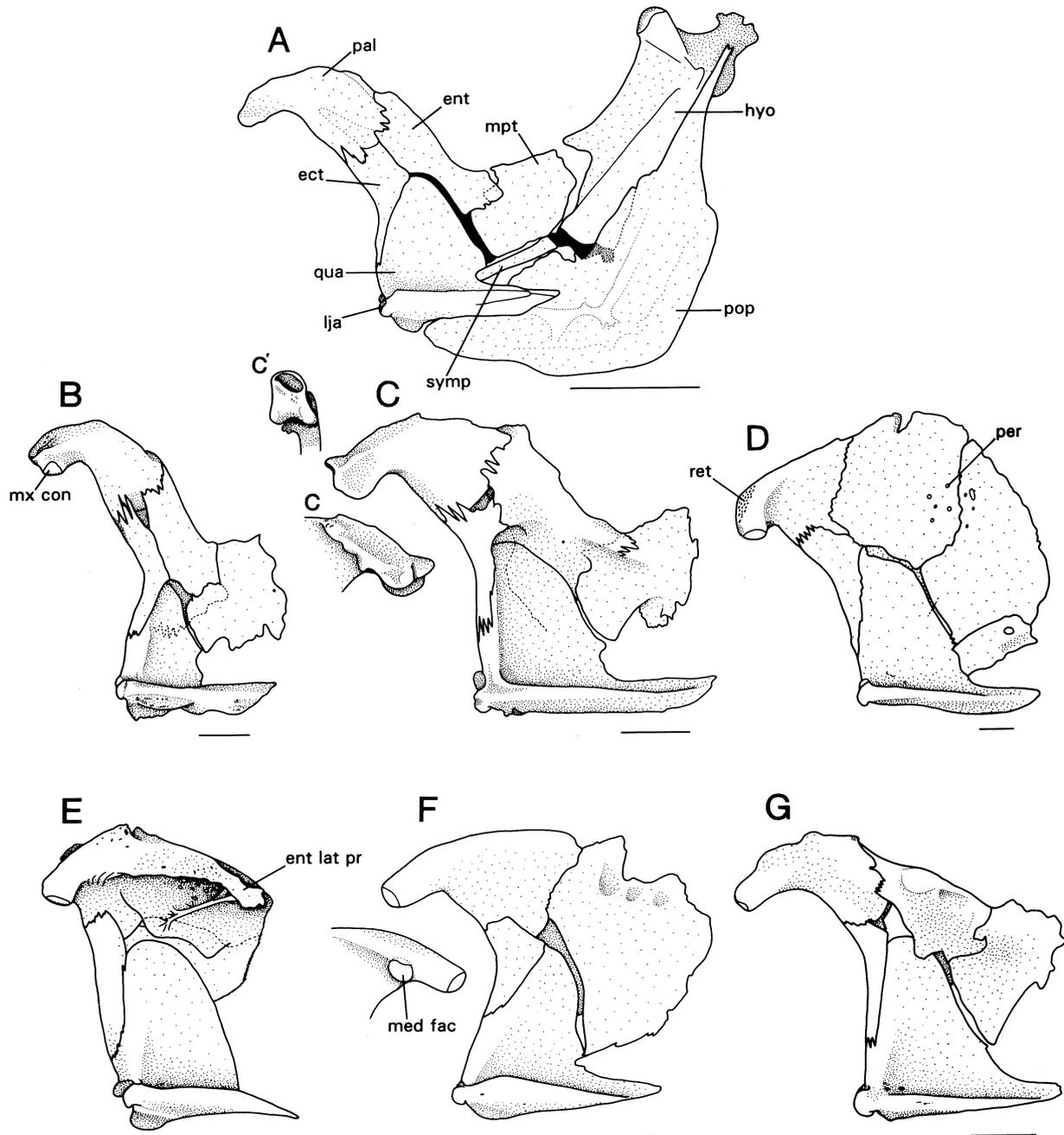
Fig. 6. The palatine arch: lateral view; anterior to left; scale bars equal 5 mm; A, whole suspensorium, B-G, anterior elements of the palatine arch; A – *Cryptotomus roseus*; B – *Calotomus carolinus*; C – *Leptoscarus vaigiensis*, c – medial view of the palatine, c' – anterior view of the palatine; D – *Bolbometopon muricatum*; E – *Chlorurus gibbus*; F – *Hipposcarus longiceps*, inset – medial view of the palatine; G – *Scarus psittacus*.

6D,E). The form of the condyle also varies, with marked differences in its orientation. A move to a more ventral orientation (**52.1**) appears to be correlated with an overall increase in the strength of the jaws, whilst an anteroventral orientation reflects greater mobility (Bellwood & Choat, 1990). In *Leptoscarus* the condyle is concave rather than convex (Fig. 6c'). In *Bolbometopon*, reticulate bone may be found on the dorsal surface of the palatine dorsal process (**54.1**), whilst in *Hipposcarus,* a large flat facet is present on the medial surface (**53.1**). This facet articulates with a corresponding facet located posteriorly on the lateral face of the medial flange of the maxillary head. A superficially similar flange is present on the medial face of the palatine in odacids (Gomon & Paxton, 1985), and articulates with the vomer.

The other bone in the palatine arch which shows considerable variation within the Scaridae, and which may be of phylogenetic significance, is the entopterygoid. In *Cryptotomus, Nicholsina, Calotomus* and *Leptoscarus*, the entopterygoid is relatively elongate extending anterodorsally towards the palatine (**55.1**). In the remaining scarid genera and in all outgroups, the entopterygoid is shorter. In most scarids and all outgroups, the entopterygoid is entire. In *Cetoscarus, Bolbometopon* and *Chlorurus*, the medial region of the entopterygoid is perforated with a series of holes (**49.1**). The most unusual feature of the entopterygoid is the presence of an entopterygoid lateral process found only in *Chlorurus* (**48.1**). This process is characterised by a lateral expansion of the dorsal margin of the entopterygoid. This expansion forms a narrow strut, which is buttressed by one or two flanges perpendicular to it. At the base of the entopterygoid lateral process, a small hole marks the site at which the mandibular branch of the trigeminal nerve (ramus mandibularis V) passes through the lateral process. A small lateral flange may be present in some *Scarus* species (eg, *S. globiceps* and *S. spinus*). These are not regarded as entopterygoid lateral processes, as there are no traces of buttresses and the trigeminal nerve invariably passes posterior to these flanges and not through them.

The leading edge of the lateral process forms part of a superficial tendinous connection of the adductor mandibulae section A1. The buttresses form two to three deep triangular fossae. The anterior fossa is the site of origin of the deep portion of the A1 muscle, whilst the posterior fossa(ae) is the site of origin of the dorsomedial fibres of the A3 (Bellwood & Choat, 1990).

Hyoid arch (character 57 – 64)

Figs 7, 8

Overall, the hyoid arch is relatively generalised (Fig. 7) and differs little from outgroup taxa. It also possesses features which are generally regarded as primitive in labrids eg, traces of a beryciform foramen and the lack

of epihyal-ceratohyal sutures (*cf.* Gomon, 1979). In contrast to most of the outgroups, except *Pseudodax,* the ceratohyal and epihyal of all scarids are joined by cartilage (**57.1**). In *Chlorurus, Hipposcarus* and *Scarus,* a faint hint of a suture may be detected on the dorsolateral margin of the joint, but the degree if interdigitation is minimal. In all genera, there are five branchiostegal rays (**60.1**). The outgroups had either five or six branchiostegal rays. In all scarids, curved dorsal projections on the ceratohyal and hypohyal form an incomplete foramen (**58.1**), this appears to be a remnant of the beryciform foramen as found in the ceratohyal and hypohyal of some (basal) labrids (Gomon, 1979; Gomon & Paxton, 1985), but found in none of the outgroups. In all scarids and *Pseudodax,* the ventral hypohyal is expanded posteroventrally to or beyond the point of attachment of the anteriormost branchiostegal ray (**59.1**). In other labrids the ventral hypohyal is usually short, and does not reach the point of attachment of the anteriormost branchiostegal ray (Russell, 1988, figures an expanded ventral hypohyal in *Pseudolabrus luculentus* although *P. miles* (personal observation) and allied genera have the shorter condition).

In all scarids and some outgroup labrids, the urohyal is a low, elongate triangular shaped bone (**61.1**; depth less than 35% of length; Fig. 8) (deep in most outgroups), with dorsal and ventral processes projecting posteriorly. The curtain of bone connecting these two processes is concave in the outgroups, but deeply notched in *Pseudodax* and all scarids (**64.1**). Both the dorsal and ventral processes are expanded laterally. The dorsal process is narrowly spatulate or rounded, whilst the ventral process in scarids may be pointed posteriorly narrowly spatulate (**63.2**), broadly spatulate (**63.1**) or tapering posteriorly with an expanded posterior extremity (**63.3**). In all instances it is broadly rounded posteriorly in contrast to labrids in which it is almost always pointed (*Cheilio* and odacids have a flared ventral process; **63.4**). Anteriorly there are a pair of lateral processes which mark the site of the
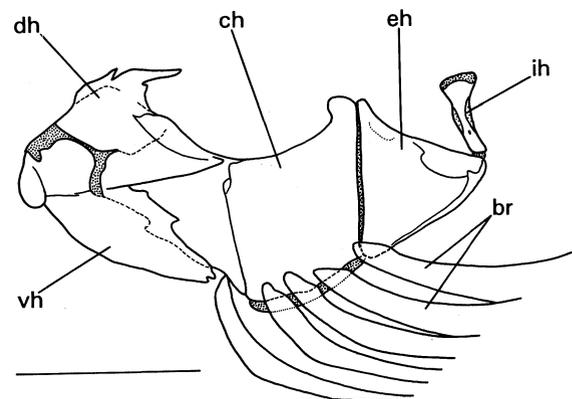
Fig. 7. Hyoid arch of *Cryptotomus roseus*, lateral view, anterior to left, scale bar equals 5 mm, cartilage indicated by heavy stipple.

connection with the ventral hypohyals. On the dorsal surface, between these two processes is a single ascending process which articulates with a ventrally expanded keel on the first basibranchial (Fig. 11). In labrids, this process is usually represented by an elongate flange with a medial thickening leading to a rounded depression on the dorsal margin (Rognes, 1973; Stiassny & Jensen, 1987; Russell, 1988; personal observations). In scarids, there is no flange, the ascending process has a narrow neck with a trumpet-shaped end and a small depression in the dorsal surface (**62.1**).

Branchial arches (characters 65 – 92)

Figs 9-12

The branchial arches and the pharyngeal apparatus of scarids and other labroids have received a great deal of attention and are widely accepted as structures of considerable phylogenetic significance (Stiassny & Jensen, 1987). There are numerous published descriptions of the branchial and pharyngeal structures of scarids (Gregory, 1933; Al-Hussaini, 1945; Monod, 1951; Board, 1956; Gohar & Latif, 1959;
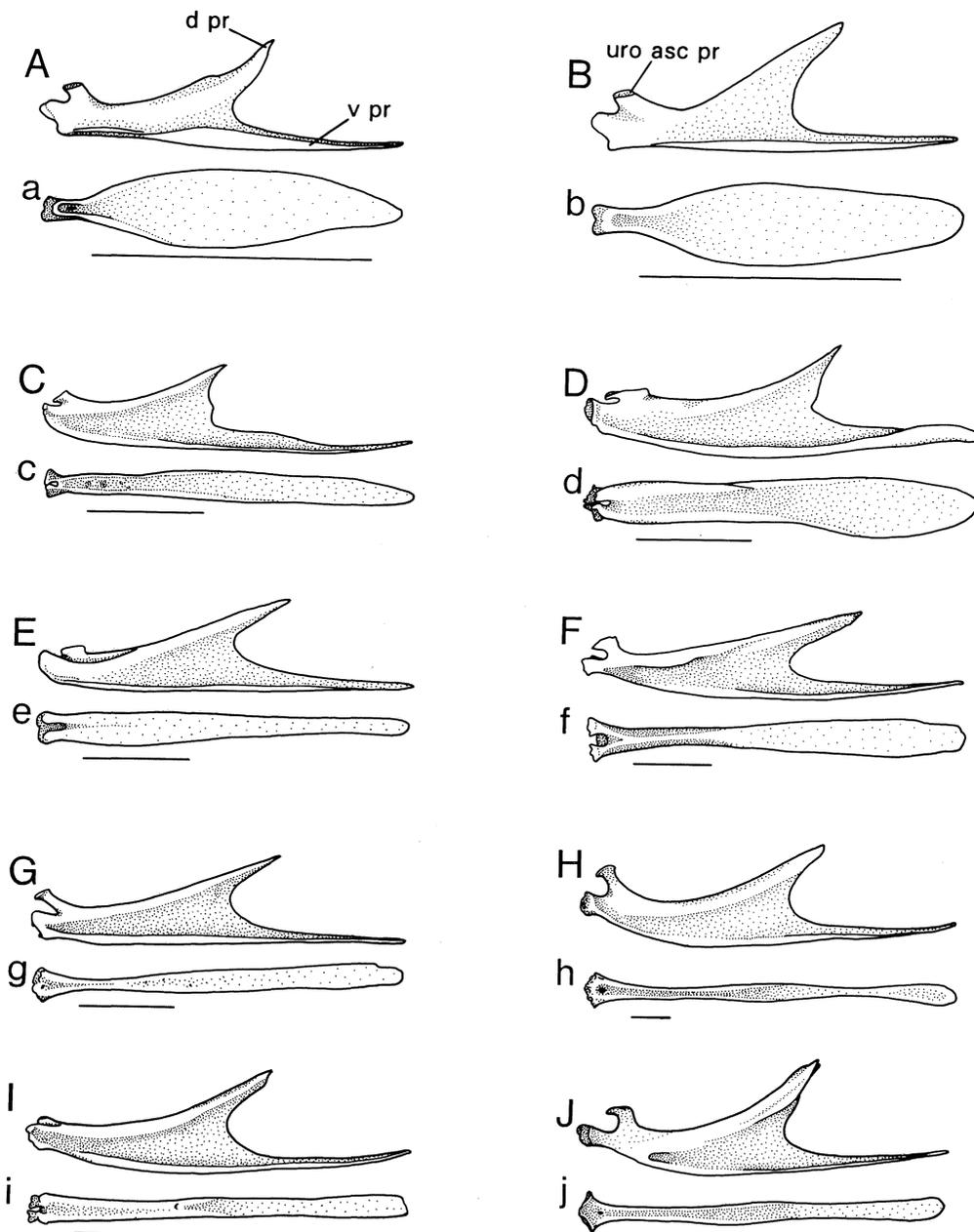
Fig. 8. Urohyal: A-J, lateral view; a-j, ventral view; anterior to left; scale bars equal 10 mm; A-a – *Cryptotomus roseus*; B-b – *Nicholsina usta*; C-c – *Calotomus carolinus*; D-d – *Leptoscarus vaigiensis*; E-e – *Sparisoma viride*; F-f – *Cetoscarus bicolor*; G-g – *Bolbometopon muricatum*; H-h – *Chlorurus gibbus*; I-i – *Hipposcarus longiceps*; J-j – *Scarus psittacus*.

Nelson, 1967; Yamaoka, 1980; Liem & Greenwood, 1981; Kaufman & Liem, 1982, Clements & Bellwood, 1989; Gobalet, 1989). Comparative studies primarily compare scarids with other pharyngognath families (eg, Nelson, 1967; Liem & Greenwood, 1981; Kaufman & Liem, 1982), whilst the form of pharyngeal bones has been widely used in taxonomic and systematic studies of the family (eg, Hattori, 1976, 1984; Masuda, *et al.*, 1984; Schultz, 1958, 1969).

Within the Scaridae, gill raker counts show considerable inter- and intra-specific variability and are therefore of limited use for taxonomic purposes at the species level (Choat & Randall, 1986). However, they are of considerable use in distinguishing genera (Randall & Bruce, 1983; Bruce & Randall, 1985) and appear to be of phylogenetic significance. Gill raker counts of the ten scarid genera, based on values given in Smith (1959), Schultz (1969), Randall (1983a), Randall & Bruce (1983), Masuda *et al.* (1984) and Bruce & Randall (1985), are as follows: *Cryptotomus* – 10-11; *Nicholsina* – 12-13; *Calotomus* – 8-14; *Leptoscarus* – 10-14; *Sparisoma* – 10-21; *Cetoscarus* – 20-26; *Bolbometopon* – 16-18; *Chlorurus* – 39-75; *Hipposcarus* – 45-65; *Scarus* – 38-84.

In the outgroups, gill raker counts are relatively low (12-23 in *Bodianus*, Gomon, 1979; 16-22 in *Labrus*, Quignard & Pras, 1986). The distinct jump to raker counts of over 35 appears to be a derived condition (**65.1**). In addition to gill raker numbers, the form of the posterior gill rakers also appears to be of significance. Within the Scaridae, most scarid genera possess branched posterior gill rakers, with straight gill rakers being the derived condition (**66.1**). The widespread occurrence of straight gill rakers in the Labroidei, however, suggests that this condition is secondarily derived.

As in other labroids, the branchial arches of scarids are highly modified. However, their structure differs markedly from the typical labroid morphology. The anterior epibranchials are reduced and serve to support the pharyngeal valve, the fourth epibranchial is greatly expanded, and the pharyngeal jaws display a unique shape and mode of tooth replacement.

Despite these differences, the branchial structure are relatively uniform within the Scaridae, with most intrafamilial variation being in the form of the pharyngeal dentition.

DORSAL BRANCHIAL ELEMENTS. The dorsal branchial elements comprise the epibranchials, infrapharyngobranchials and upper pharyngeal bones (Fig. 9). Gobalet (1989) provides a detailed description of the bones, their associations and related musculature in *Scarus*.

In scarids the form of the first three pairs of epibranchials differ markedly from the typical labrid condition, where they are much more robust. These differences are not interpreted as a series of character changes, rather, all are regarded as the result of a single character change, namely the possession of a
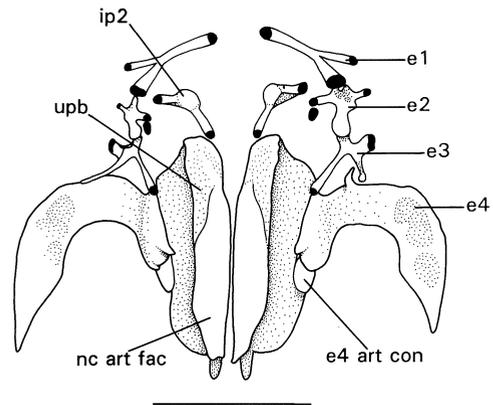
**Fig. 9.** Dorsal branchial elements of *Cryptotomus roseus*, dorsal view, anterior to top, scale bar equals 5 mm, cartilage is shaded in black.

pharyngeal valve in the Scaridae (**78.1**).

The first epibranchial is a thin "Y"-shaped element. The medial stalk supports the leading lip of the pharyngeal valve. The second and third epibranchials are also modified when compared to those of labrids. In scarids, they have elongate processes and lack the flattened laminae found in most labrids (*cf.* Yamaoka, 1978; Gomon, 1979; Russell, 1988). The form of the elements described in Gobalet (1989) are typical of the scarid condition.

The fourth epibranchials are not associated with the pharyngeal valve but do display unique modifications. In some labrids the fourth epibranchials may be laterally expanded, but this expansion is restricted to a broadening of the lateral portion. None display the hypertrophy characteristic of the scarid fourth epibranchial. In all scarids, the fourth epibranchial is greatly expanded laterally to form a large flat wing which curves posterolaterally (**77.1**; Fig. 9). The margin of the wing is bordered by a vertical flange. The lateral wing is convex on the dorsal surface and deeply concave ventrally. The wing is usually rounded posteriorly but may be pointed as in *Cryptotomus*. In *Leptoscarus*, the posterior portion is inflected ventrally. Basally, the fourth epibranchial has an elongate condylar section bearing a large elongate concave groove on the medial surface which articulates with the upper pharyngeal.

Muscular associations are relatively uniform throughout the family and follow the pattern described by Gobalet (1989).

In scarids, the first infrapharyngobranchials are absent. The paired second infrapharyngobranchials are represented by small rod-like bones with a slight swelling and inflection mid-way along their length. There is no associated tooth plate. The second infrapharyngo- branchials are located medial to the second epibranchials and lie in the posterior portion of the main pad of the pharyngeal valve.

The largest of the dorsal elements are the paired upper pharyngeal bones (third infrapharyngobranchials and associated tooth plates; Nelson, 1967). It is in the

form of the upper pharyngeal bones that the major differences between scarid genera are apparent (Fig. 10). Some of these differences were recognised by Smith (1956, 1959) and Schultz (1958, 1969) as taxonomically useful characters for distinguishing genera. Differences in the morphology of these bones also appear to be of phylogenetic significance. The morphology of the upper pharyngeal bones of scarids is unique. Within the Labroidei, only the upper pharyngeals of *Pseudodax* bear any resemblance to those of scarids.

When compared to the upper pharyngeals of most labrids, the upper pharyngeals of scarids are strongly
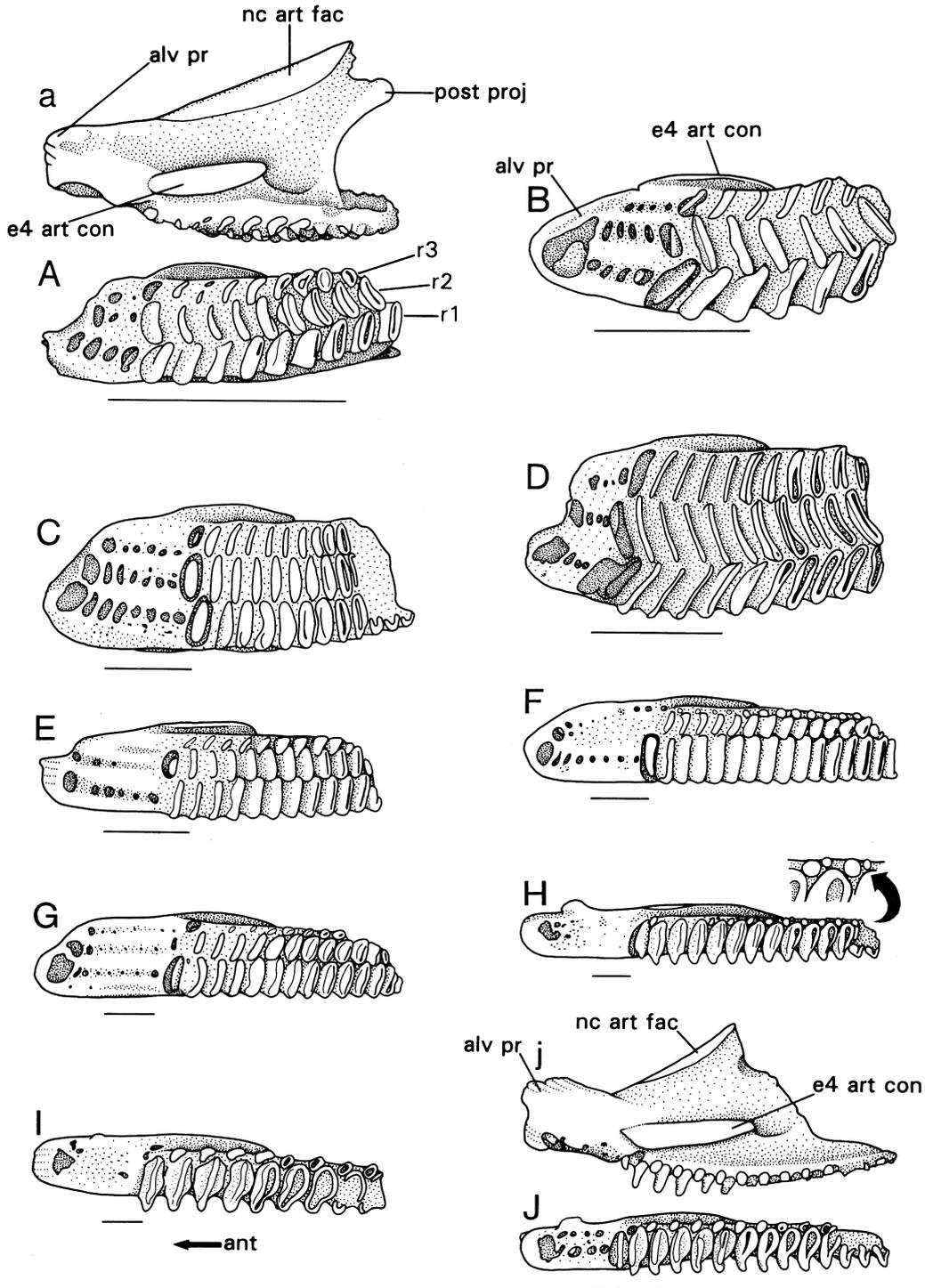
Fig. 10. Upper pharyngeal bones: A-J, ventral view; a, j, lateral view; anterior to left; scale bars equal 5 mm; A-a – *Cryptotomus roseus*; B – *Nicholsina usta*; C – *Calotomus carolinus*; D – *Leptoscarus vaigiensis*; E – *Sparisoma viride*; F – *Cetoscarus bicolor*; G – *Bolbometopon muricatum*; H – *Chlorurus gibbus*; I – *Hipposcarus longiceps*; J-j – *Scarus psittacus*.

compressed laterally. The cladogram suggests that the extent of this lateral compression increases within the family. In labrids the paired upper pharyngeals are more than twice as broad as high. In scarids they vary from 1 to 1.9 times as wide as high (**69.1**) to less than 0.8 times as wide as high (**69.2**). In lateral view, the bones are triangular with an anteriorly oriented apex, which may be bordered laterally by the alveolar process (**68.1**, Fig. 10j). The posterior margin is a thin sheet of bone which bears a small posterior projection (the insertion site of the retractor dorsalis). This projection is well developed *Cryptotomus* but reduced in all other scarid genera (**76.1**). Among the outgroup taxa, a comparable process is present only in *Pseudodax*. A large elongate condyle on the midlateral surface represents the articulation site of the fourth epibranchial. On the dorsal surface each upper pharyngeal bone bears an elongate facet which articulates with the neurocranium. In labrids, this articulatory facet is short and strongly rounded. In all scarids it is elongate, being either slightly curved (**67.1**) or straight (**67.2**).

In labrids, teeth may erupt in the dental plates of the upper pharyngeal bones. In all scarid genera, the upper pharyngeal teeth erupt only from an anterior germinative alveolar region and migrate posteriorly, wearing progressively with use. Teeth erupt in rows and maintain their relative position as they progress posteriorly, like conveyor-belts (**71.2**). Tooth rows are absent in the outgroups and their presence in scarids is considered derived. There may be one to three tooth rows in each bone (**70.1-2**). A single row has only been recorded from adult individuals of *Scarus rubroviolaceus*, *S. perrico* and *S. compressus*. Schultz (1958) erected a separate genus *Scarops* for the former two species based on this character. As these species have two rows as juveniles and occasionally as adults (Rosenblatt & Hobson, 1969; Schultz, 1969; personal observation), the value of this character is questionable, and is not considered sufficient to warrant recognition of a separate genus or subgenus. *Scarops* is therefore placed in synonymy with *Scarus*, following Rosenblatt & Hobson (1969), Randall & Bruce (1983) and Choat & Randall (1986). Ontogenetic observations (Bellwood, 1986) indicate that there is a progressive reduction in the relative size of the teeth in the outermost tooth rows. These changes are reflected in the adult conditions (**72.1-2**; state 0, near equal tooth sizes in each row; state 1, row 3 less than half row 2, row 1 and 2 subequal; state 2, row 3 less than half row 2 and row 2 less than half row 1). In addition to changes in the relative sizes of the teeth the shape of the teeth may differ markedly, particularly the medial tooth rows (1 on each bone). Reduction in the size of the teeth in the outer tooth row results in small rounded teeth. The teeth in the medial row are usually an elongate ovoid shape (**74.1**; rounded in most outgroups except *Pseudodax*). In *Chlorurus*, *Hipposcarus* and *Scarus*, however, these teeth are curved and produced medially, with the

alternating teeth on the two bones interdigitating down the midline (**74.2**). The extent of interdigitation varies considerably and is generally reduced in large individuals. In most scarid genera, the two medial teeth rows run parallel to each other (**75.1**), in contrast to *Cryptotomus*, *Nicholsina*, *Calotomus* and *Leptoscarus* where the rows are curved and diverge posteriorly.

The dentigerous area of the upper pharyngeal bones of labrids is broad. In scarids, it is relatively narrow, with an apparent reduction within the family (**73.1-3**; broad, length/total width of both bones less than 0.6, state 0; 0.6-0.9, state 1; 1.0-2.0, state 2; length greater than 2.1 times width, state 3). In large individuals the dentigerous area of the tooth plates is parallel sided. In smaller individuals, it often narrows posteriorly. It has been suggested that this may be a result of rapid growth in small individuals with new, larger teeth erupting faster than the old teeth are worn (G. Nelson, personal communication). In larger individuals growth is reduced, with no significant change in size over the time period between tooth eruption and loss.

VENTRAL BRANCHIAL ELEMENTS. Six unpaired elements lie along the ventral midline (Fig. 11). The basihyal is laterally compressed anteriorly and may bear a ventral flange. In some *Scarus* species the basihyal is greatly reduced (Gobalet, 1989; also in *Sparisoma*). The first basibranchial is a short, thin bone but is greatly expanded ventrally. The ventral margin of this bone is
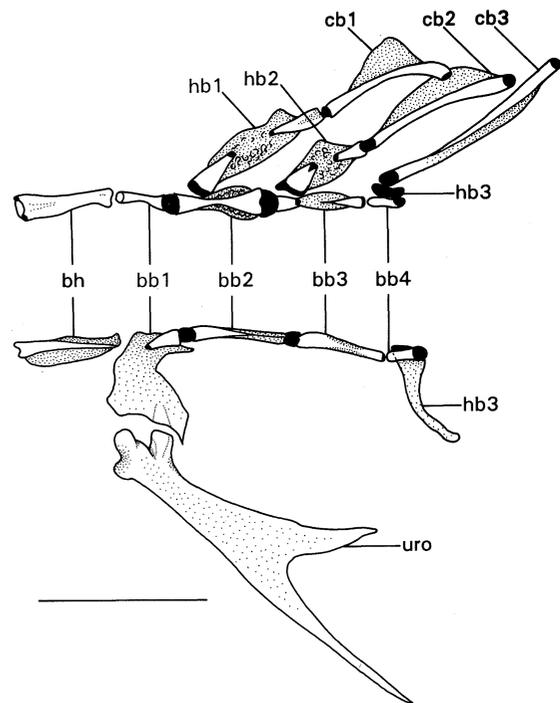

Fig. 11. Anterior ventral branchial elements of *Cryptotomus roseus*, dorsal view – above, lateral view – below, anterior to left, scale bar equals 5 mm, cartilage is shaded black.
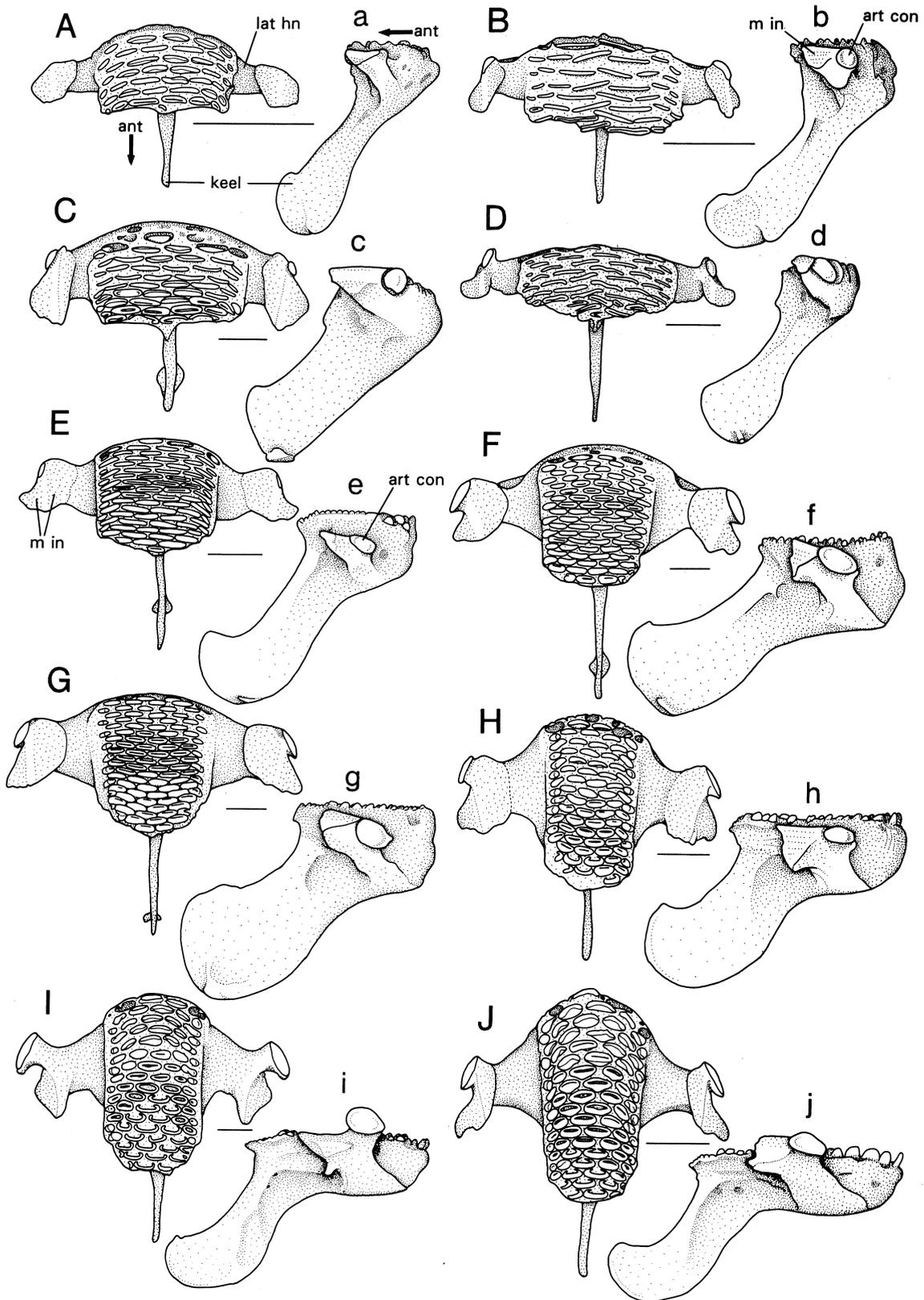
Fig. 12. Lower pharyngeal bones: A-J, dorsal view, anterior to bottom; a-j, lateral view, anterior to left; scale bars equal 5 mm; A-a – *Cryptotomus roseus*; B-b – *Nicholsina usta*; C-c – *Calotomus carolinus*; D-d – *Leptoscarus vaigiensis*; E-e – *Sparisoma viride*; F-f – *Cetoscarus bicolor*; G-g – *Bolbometopon muricatum*; H-h – *Chlorurus gibbus*; I-i – *Hipposcarus longiceps*; J-j – *Scarus psittacus*.

tightly bound by a ligament to the anterodorsal process of the urohyal. The second basibranchial is an elongate hour-glass shaped rod, which may possess lateral laminae. The third basibranchial is either a more elongate hour-glass shape or tapers posteriorly. It may occasionally have small lateral laminae. The fourth basibranchial is represented in most genera by a small cylindrical cartilaginous rod. In *Cryptotomus*, this element is lightly ossified.

The paired first and second hypobranchials, attach to the lateral margins of the second and third basibranchials respectively. Basibranchial 4 receives the dorsal portion of the third hypobranchial and the anterior portion of ceratobranchials 3 and 4.

The paired elements of the gill arches are relatively light. The paired first and second hypobranchials are flattened rods which taper towards the middle. Often with laminae along the anterior and posterior margins. The third hypobranchial is a thin ventrolaterally projecting rod or flattened element which tapers distally.

Ceratobranchials 1, 2 and 3 are elongate rods. All may have anterior and/or ventrally directed laminae. Ceratobranchial 4 is a thin bone with a small posterior flange anteriorly. Posteriorly, it attaches to the ventral edge of the anteriormost part of the lateral expansion of the fourth epibranchial. The fourth ceratobranchial supports a hemibranch (there is no gill slit behind the fourth arch). The fifth ceratobranchials are fused and form the lower pharyngeal bone. This is described in detail below.

LOWER PHARYNGEAL BONE. All scarids share a common pharyngeal morphology which differs markedly from that of all other labroids (Fig. 12). In scarids, new lower pharyngeal teeth erupt only along the posterior margin of the dentigerous area and progress anteriorly (**90.2**). In other labroids the teeth usually arise either in stacks (phyllodont *sensu* Bellwood, 1990) or individually over the whole dentigerous area. Unlike all the outgroups, where teeth are either scattered or in non-linear patterns, the lower pharyngeal teeth of scarids form distinct transverse rows of five (**79.2**) to six teeth (**79.1**). The teeth migrate anteriorly in rows, which results in a straight-sided dentigerous area. This is in stark contrast to the triangular form in labrids. The dentigerous areas may be broadly rectangular (**81.1**; length/width ratio of less than 0.7), square (**81.2**; l/w 0.7-1.3) or an elongate rectangle (**81.3**; l/w greater than 1.5). The number of tooth rows present at any given time varies from 5-25, with a sharp discontinuity between those genera with 10 or less and those with 11 or more (usually greater than 16; **80.1**). The number of rows does not increase simply as a result of an elongation of the dentigerous area, the largest numbers were recorded from *Cetoscarus* and *Bolbometopon* which have relatively short dentigerous areas. As the teeth progress anteriorly they wear, resulting in an elongate pair of ridges (most scarids) or a broad spindle-shaped

ridge of enamel, with a central depression (**82.1**)). In most outgroups the dentigerous area has rounded lateral margins. In *Pseudodax* and some scarids, the whole dentigerous area is worn forming a concave or slightly biconcave groove, the lateral margins of which may be distinctly raised (**83.1**). The condition in the scarids and *Pseudodax*, however, appears to be homoplaseous.

Either side of the dentigerous area are lateral horns, which bear insertion scars of the fifth adductor, levator posterior and fourth levator externus muscles on the dorsolateral extremities (scarring regions indistinct in *Cryptotomus*, *Nicholsina* and the outgroups). There are two main regions of scarring, with the inner area usually being the largest (**84.1**). The two regions may be separated by a straight anteroposteriorly oriented ridge (**85.1**) (curved in *Hipposcarus*, **85.2**). On the posterolateral extremity each horn bears a distinct round facet/condyle. This represents the pharyngeal facet of the pharyngocleithral joint. In *Hipposcarus* only, the lower pharyngeal jaw articulation facet is expanded laterally and extends beyond the site of the insertion scars (**86.1**). The main shaft of the lateral horn is usually broader (anteroposteriorly) than deep (**87.1**). In labrids, the shaft is deeper than broad and is taken to represent the plesiomorphic state.

In scarids, the ventral keel of the lower pharyngeal bone extends along the midline and is greatly expanded anteroventrally with a broad rounded portion anteriorly (**89.1**; Fig. 12). In all outgroups, the keel is relatively short and tapers anteriorly. The base of the keel may arise anterior (as in the outgroups), on (**88.2**) or posterior (**88.1**) to the broad ventral bar that connects the lateral horns. In most labrids, the keel is thickened near the anterior margin forming a stout ridge. In *Pseudodax* and scarids, this thick ridge is not developed (**91.1**). Thickening is restricted to the proximal portion, with the remainder of the keel being represented by a thin bony sheet. In *Pseudodax* and scarids, the ventral edge of the keel may bear small lateral projections (**92.1**), or a laterally expanded flat margin (**92.2**). Neither structure is present in the other outgroups.

Opercular series

The four elements of the opercular series are relatively uniform throughout the family and have a typical labroid appearance (*cf.* Russell, 1988). The preoperculum bears no spines or serrations and has an entire posterior margin.

Pectoral girdle (characters 93 – 97)

Figs 13, 14

The pectoral girdle of scarids is relatively robust, with a typical labroid morphology (Fig. 13). In all

scarids, the first pectoral ray is rudimentary, the second ray is well developed and unbranched, the remaining 11 to 15 rays are all branched. The number of pectoral rays is highly variable in the outgroups, however, relatively high counts (greater than 14) appear to be the plesiomorphic condition (*Pseudodax* 15, *Bodianus* 15-18, *Pseudolabrus* 12-15, *Odax* 11-18). Within the family, there is a distinct discontinuity between taxa encompassing species with 13 (**97.1**) pectoral rays and

Fig. 13. Pectoral girdle of *Cryptotomus roseus*, lateral view, anterior to left; A – posttemporal, scale bar equals 2 mm; B – pectoral girdle, scale bar equals 5 mm.

Fig. 14. Cleithra: anterior view; scale bars equal 5 mm; A – *Cryptotomus roseus*; B – *Leptoscarus vaigiensis*; C – *Scarus psittacus*.

those with 14 or more rays (modal values). This character was used by Schultz (1958) to separate the Scaridae into two subfamilies. This character is included in the present analyses and appears to be of phylogenetic significance, but a subfamilial division is no longer supported.

In most scarid taxa there is a distinct round facet on the anterior face of the cleithrum (Fig. 14). This facet marks the articulation point of the synovial pharyngocleithral joint. A contact between the lower pharyngeal and the cleithrum is a characteristic of all labroids (*sensu* Greenwood *et al.*, 1966; Kaufman & Liem, 1982). In *Cryptotomus* it is represented by an elongate indistinct facet on the cleithrum as in labrids. However, in most scarids this contact is marked by a distinct facet (**93.1**). This suggests that the basic mechanics of the labroid pharyngeal apparatus have been modified in the Scaridae. In some scarid genera, there is a medial indentation beneath the pharyngocleithral facet (**94.1**) or a perforate region above it (**95.1**). Both features are absent in the outgroups. The functional implications of these changes are unknown. The postcleithra have a typical labrid form.

Scarids differ markedly from the labroid condition in the form of the posttemporal. In scarids, the posttemporal has an elongate posteroventral flange which lies along the dorsal margin of the supracleithrum (**96.1**; Fig. 13A). This flange is lacking in the labrids and in all other labroid families, and therefore appears to be an unique unreversed synapomorphy of the Scaridae.

Pelvic girdle (characters 98 – 99)

Fig. 15

The pelvic girdle consists of two laterally paired basipterygia which support the pelvic fins posteriorly. The basic form of the basipterygia is uniform within the family, with the bones tapering anteriorly. However, unlike those of labrids where the bones are pointed anteriorly, in scarids they may be either broadly rounded (**99.2**) or bear short lateral flanges (**99.1**; Fig. 15). At the posterior margin of the medial symphysis the bones are often protruded, and in *Chlorurus* and *Scarus* bear distinct horns (**98.1**; Fig. 15).

Fig. 15. Pelvic girdle of *Scarus psittacus*, dorsal view, anterior to left, scale bar equals 5 mm.

Axial skeleton (characters 100 – 105)

Figs 16-19

All scarids have 25 vertebrae, including the urostyle (**105.2**). This vertebral count is common among the Labridae (Leis & Rennis, 1983) and may represent the plesiomorphic condition for the Labroidei (*sensu* Greenwood *et al.*, 1966) as a whole. However, the cladogram infers a close relationship between the Hypsigenyini, *Pseudodax* and the Scaridae and suggests that the presence of 25 vertebrae in the Scaridae is a reduction from the ancestral condition (27+) and therefore represents a synapomorphy uniting the family.

Within the Scaridae the number of precaudal vertebrae typically varies from 9 to 11, with *Bolbometopon* being the sole exception with 12 (**101.1**). Variability in this character in the outgroups makes polarity assignment difficult, however, the cladogram suggests that within the Scaridae 9 precaudal vertebrae is the plesiomorphic condition, with an increase to 10 to 11 being a derived state (**101.2**). A precaudal count of 10 to 11 was one of the characters used by Schultz (1958) to define the subfamily Scarinae. This character appears to be of phylogenetic significance, but a subfamilial division is not supported by the data in the present study.

In all outgroups examined, the first neural spine is autogenous. In the Scaridae this spine is fused with the centrum (**100.1**), and is of a comparable length to subsequent spines (Fig. 16). The size of the anterior neural prezygopophyses is highly variable. They are usually small and simple but may be expanded anterodorsally almost reaching the neural spine of the preceding vertebra.

All scarids are characterised by a unique posterolateral expansion of the haemal postzygopophyses on the first 1 to 2 vertebrae (**102.1-2**; Figs 16, 17). These expanded postzygopophyses usually have a strong central ridge. On vertebrae 3 and 4 (and occasionally 5) the haemal postzygopophyses are expanded to a lesser extent, and are connected to the posterior margins of the parapophyses by a bony curtain which extends along the lateral edge of the centrum (**103.1**; Fig. 17). This connection is most pronounced on vertebra 3, but differs in extent between genera.

The paired parapophyses of the posterior 4 to 6 precaudal vertebrae are connected by a transverse bony bridge, forming a small (primary) haemal arch. Parapophyses thus connected, may be termed

Fig. 17. Anterior vertebrae: ventral view, anterior to left, scale bars equal 5 mm; A – *Cryptotomus roseus*; B – *Calotomus carolinus*; C – *Leptoscarus vaigiensis*; D – *Bolbometopon muricatum*; E – *Scarus psittacus*.

Fig. 16. Anterior vertebrae and dorsal spines of *Cryptotomus roseus*, lateral view, anterior to left, scale bar equals 2 mm.

haemapophyses (Clothier, 1950; Russell, 1988). The posterior part of the vertebral column comprises 14 to 16 caudal vertebrae. These vertebrae, with the exception of the highly modified urostyle and penultimate vertebra, are characterised by the possession of a haemal spine. The structure of the first haemal spine (character 104; Figs 18, 19) appears to be of considerable phylogenetic significance.

In most labrids the first haemal spine is relatively robust (see range in Russell, 1988). However, *Pseudodax*, *Bodianus* and all scarids share a modified first haemal spine (**104.1**). In scarid genera with nine precaudal vertebrae, the first haemal spine arises from the middle of the bone bridge joining a pair of haemapophyses. The first haemal spine is usually exceedingly thin and projects posteriorly, curving posteroventrally. The next vertebra has either a more robust haemal spine arising from a pair of haemapophyses, or an almost completely fused haemal spine, the fusion been marked only by a slight inflection in the spine when viewed laterally. Subsequent vertebrae have completely fused haemal spines. In genera with ten to 12 precaudal vertebrae, the first haemal spine is usually robust, arising from the middle of the bridge joining a pair of haemapophyses. The next haemal spine occasionally possess a slight inflection, all subsequent spines are completely fused. In these genera, the first haemal spine is often preceded by a small thin rudimentary haemal spine which arises from a pair of haemapophyses on the last precaudal vertebra.

A thin first haemal spine which arises from the middle of a bridge joining the last pair of parapophyses (haemapophyses) appears to be one of the key character states which links the Scaridae and Hypsigenyini (and *Pseudodax* and *Lachnolaimus*). This shared character state supports the proposal that the Scaridae, *Pseudodax* and the hypsigenyine labrids form a monophyletic assemblage that diverged early from the rest of the Labridae (Gomon, 1979).
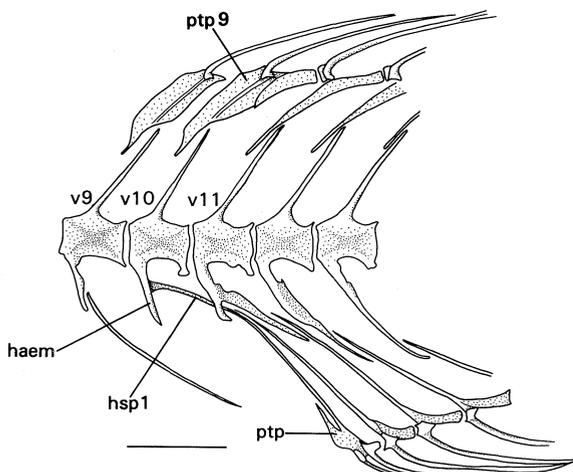
Dorsal fin (characters 106 – 109)

Figs 16, 18

In most labrid and scarid genera, a single supraneural (predorsal) bone is present anterior to the first neural spine. It is a relatively narrow curved rod-shaped bone with a slight expansion distally. The loss of this bone in *Odax*, *Chlorurus* and *Scarus* is considered derived (**106.1**).

In all scarids, there are 18 dorsal pterygiophores supporting nine spinous and ten branched segmented rays (the last 2 rays are closely apposed and are counted as 1). The nine anterior pterygiophores are broad, with a narrow central shaft which expands and thickens dorsally, at this point each dorsal spine is attached by a ring joint. The dorsal spines may be pungent (as in most labrids) or flexible (**108.1**). A small posterodorsal projection present on the first eight pterygiophores appears to be expanded on the ninth pterygiophore and serves as the site of attachment of the first branched ray. The remaining nine pterygiophores have a thin shaft bearing a narrow blade posteriorly, each supports a single branched ray with the exception of the last pterygiophore which supports two small rays. The base of the first pterygiophore is located between the neural spines of the first and second vertebrae (**107.1**), this represents a departure from the typical labrid condition where the first pterygiophore lies between the neural spines of vertebrae 2 and 3 (Gomon, 1979; Russell, 1988). The remaining pterygiophores are each located between successive pairs of spines, the last two pterygiophores, however, are both located between the neural spines of the 17th and 18th vertebrae. The dorsal fin membrane may be either deeply incised or continuous (**109.1**), the cladogram suggests that the latter condition is derived.

Anal fin (character 110)

Fig. 18

All scarids possess ten anal pterygiophores which support three spines and ten branched segmented

Fig. 18. Middle axial skeleton of *Cryptotomus roseus*, lateral view, anterior to left, scale bar equals 5 mm.
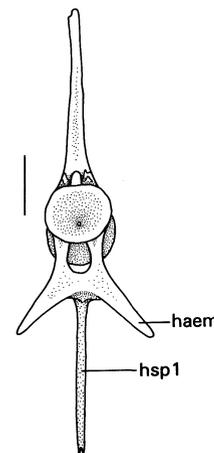

Fig. 19. First caudal vertebra of *Chlorurus gibbus*, anterior view, scale bar equals 10 mm.

rays. The last two rays are closely apposed and are counted as one. The first pterygiophore has a bony crest along the distal anterior margin. Separation of the crest anteriorly, as in *Cryptotomus* (Fig. 18), is atypical. The remaining pterygiophores typically possess only a small posterior bony crest at the ventral inflection. The first pterygiophore supports two spines, the second pterygiophore supports the third spine and the first branched ray. All spines are attached by ring joints. The spines may be pungent or flexible. Pterygiophores 3 to 9 each bear one branched ray, the two small rays on the last (10th) pterygiophore are counted as one.

In scarids, as in labrids, there are usually two to three (exceptionally 0) pterygiophores anterior to the first haemal spine, the presence of four pterygiophores in *Bolbometopon* is considered derived (**110.2**). The remaining pterygiophores are each located between successive pairs of haemal spines, with the exception of the last two pterygiophores which are located between the spines of the 17th and 18th vertebrae.

Caudal skeleton (characters 111 – 114)

Fig. 20

The caudal skeleton bears a close resemblance to that of labrids (*cf.* Gomon, 1979; Stiassny & Jensen, 1987; Russell, 1988). There are two epural bones, hypurals 1 and 2 are fused forming a ventral hypural plate, hypurals 3 and 4 fuse to form the dorsal hypural plate. Basally, hypurals 3 and 4 are fused with a fused uroneural/urostyle block. No sutures are visible between any of these elements. Hypural 5 is a short bone lying close to the dorsal margin of the dorsal hypural plate. Basally, the ventral hypural plate is closely associated with the urostyle but remains autogenous.
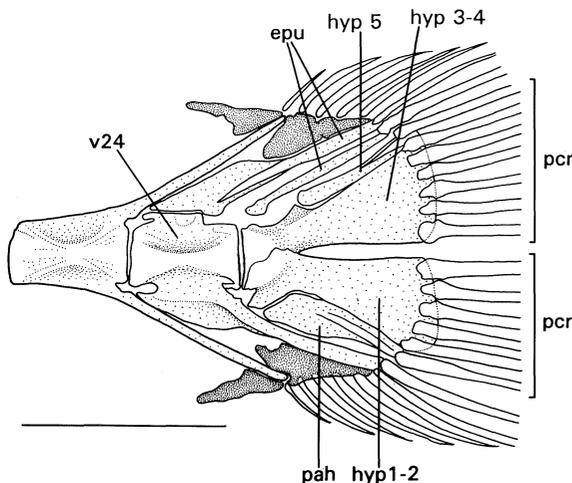

Fig. 20. Caudal skeleton of *Cryptotomus roseus*, lateral view, anterior to left, scale bar equals 5 mm.

Unlike labrids, the parhypural is foreshortened (**111.1**). It has no attachment to the urostyle or ventral hypural plate, it lacks a hypurapophysis, and is usually preceded by a laterally compressed process on the anterior margin of the ventral hypural plate. A foreshortening of the parhypural was not recorded in any other labroid family and appears to be a unique synapomorphy uniting the Scaridae. A laterally compressed process on the anterior face of the ventral hypural plate is found in all scarid genera, although the size of the protrusion varies considerably, from a trace in *Cetoscarus* (**112.2**) to almost complete closure across the space left by the short parhypural (**112.1**) as in *Cryptotomus* and *Nicholsina*. This structure is usually absent in labrids but has been recorded in *Choerodon* by Gomon (1979).

The haemal spine of the penultimate (24th) centrum is autogenous, but closely associated with the centrum. The neural process of the penultimate vertebra is represented by a short protrusion (**113.1**). A short neural process is present in some labrid genera eg, *Halichoeres* and *Pseudolabrus*, but a long process in *Bodianus* and *Pseudodax* suggest that the foreshortening in the Scaridae represents a derived condition and therefore a synapomorphy of the Scaridae. The haemal spine of the antepenultimate (23rd) vertebra is fused with the centrum.

The caudal rays usually comprise, starting dorsally: five to seven procurrent unsegmented, unbranched rays; one unbranched ray approximately half length of segmented rays, from tip of posterior epural, often segmented, especially in small individuals; one segmented unbranched ray from hypural 5; six branched segmented rays, from dorsal hypural plate; five branched segmented rays, from entral hypural plate; one unbranched segmented ray from parhypural; one ray from tip of haemal spine of penultimate vertebra, unbranched, half length of segmented rays, often segmented in small individuals; five to six unbranched unsegmented procurrent rays. The number of principal caudal rays (7+6; ie, the rays supported by the hypurals and parhypural; **114.1**) represents a significant departure from the counts recorded in labrids (7+7, 7+8, Leis & Rennis, 1983; 8+8, Russell, 1988).

Lipid in bones (character 115)

The presence or absence of lipid in the bones when prepared by either maceration in hot water or defleshing in a dermestid beetle colony, may reflect basic differences in the lipid metabolism of scarids versus labrids and other labroids. In all labrid, odacid, pomacentrid, embiotocid and cichlid material examined that had been prepared in this manner, the bones had an oily property when dried. With time, the bones turned brown, presumably as the lipid oxidises. In contrast, the bones of scarids were invariably white with no evidence of lipid (**115.1**).

Soft anatomy

Jaw muscles (characters 116 – 125)

Figs 21-25

Considerable variation is displayed in the form of the jaw muscles between scarid genera. Within the Scaridae there are five basic configurations of the jaw muscles. To facilitate descriptions, the five basic types will be described separately. The genera may be grouped according to their muscle configurations as follows: 1. *Cryptotomus*, *Nicholsina*, *Calotomus*, *Leptoscarus*; 2. *Sparisoma*; 3. *Cetoscarus*, *Bolbometopon*; 4. *Chlorurus*; 5. *Hipposcarus*, *Scarus*.

1. *Cryptotomus* (Fig. 21), *Nicholsina* (Fig. 22A), *Calotomus* (Fig. 22B), *Leptoscarus* (Fig. 23A). Adductor mandibulae sub divisions A1, A2 and A3 are all well developed in these genera. All are weakly pinnate.

The A1 is a single superficial muscle, occupying a mid-lateral position, it arises from the vertical limb and angular region of the preoperculum and the posterior edge of the hyomandibula. It inserts via a long tendon (A1t) which passes medial to the maxillary shaft before inserting on the anteroventral extremity of the premaxillary process of the maxilla. In *Cryptotomus* and *Calotomus* this insertion is onto a small ventrally protruding rod. A small tendon connects the A1t to the articular; another small tendon connects A1t and A2t (2 tendons in *Cryptotomus*).
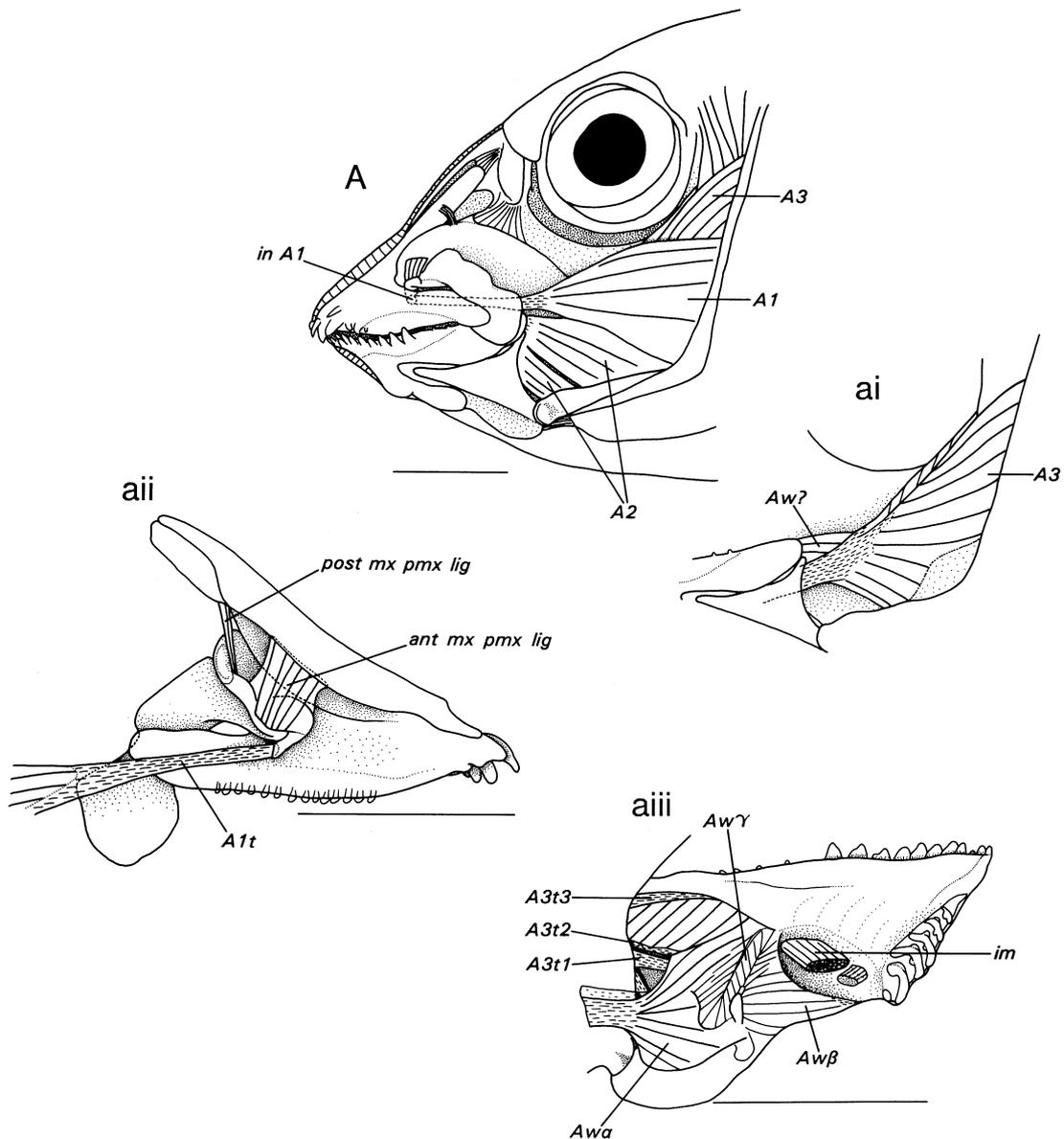
Fig. 21. Myology of the oral jaws of *Cryptotomus roseus*: A – integument and infraorbital bones removed, scale bar equals 5 mm; ai – as A, except adductor mandibulae sections *A1* and *A2* removed; aii – details of upper jaw, medial view, anterior to right, scale bar equals 5 mm; aiii – details of lower jaw, medial view, anterior to right, scale bar equals 5 mm.

The A2 occupies the ventral part of the suspensorium. Its origin occupies the whole of the ventral part of the quadrate, and may extend posteriorly to include the part of the angular portion of the preoperculum. In *Cryptotomus* and *Nicholsina* it has two distinct portions, in *Calotomus* and *Leptoscarus* it is a single muscle mass. The lower portion or part of the A2 invariably inserts muscularly on the posterior margin of the articular. The dorsal part or portion inserts wholly or partially on the articular posterior ascending process. The dorsal fibres may converge on a broad thin tendon (A2t) which passes medial to this
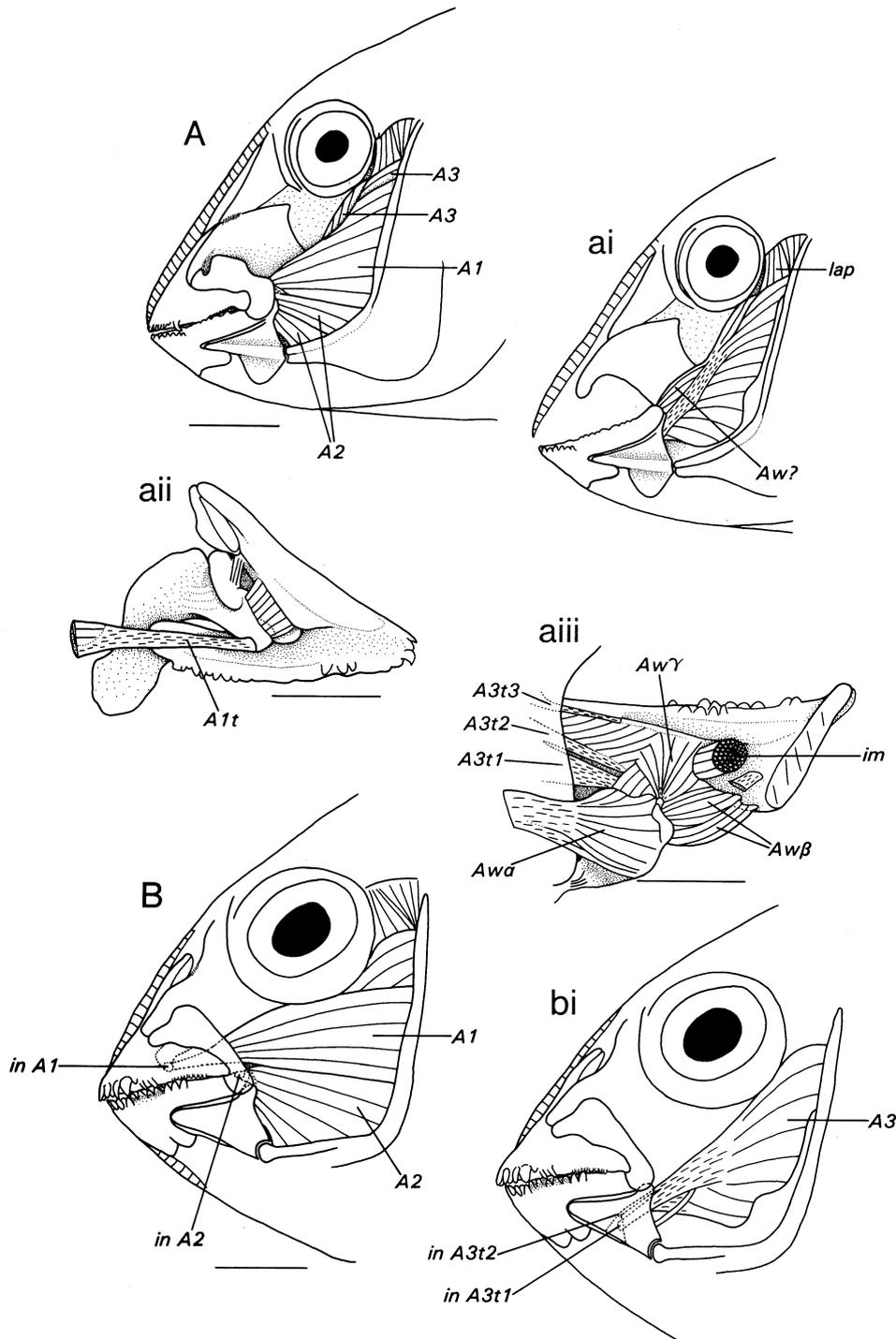
Fig. 22. Myology of the oral jaws: A-aiii, *Nicholsina ustus*; A – integument and infraorbital bones removed, scale bar equals 10 mm; ai – as A, except adductor mandibulae sections *A1* and *A2* removed; aii – details of upper jaw, medial view, anterior to right, scale bar equals 5 mm; aiii – details of lower jaw, medial view, anterior to right, scale bar equals 3 mm. B-bi, *Calotomus carolinus*; B – integument and infraorbital bones removed, scale bar equals 10 mm; bi – as B, except adductor mandibulae sections *A1* and *A2* removed.

process and inserts on the posterior part of the ridge on the medial face of the dentary coronoid process. In *Cryptotomus* and *Nicholsina* this tendon is small, in *Calotomus* it is well developed and in *Leptoscarus* it is absent.

The A3 is a large muscle which lies medial to the superficial A1 and A2 portions. Sites of origin include the hyomandibula, preoperculum, symplectic, quadrate, and metapterygoid. The only portion visible laterally is the posterodorsal extremity. The origin of the muscle in this region is often divided by levator arcus palatini. The fibres converge dorsally onto a large tendon which runs along the anterodorsal edge of the muscle. A broad bundle of fibres arising from the anterodorsal edge of this tendon insert on the medial surface of the dentary coronoid process (occasionally also connecting with the A2t). These fibres are clearly visible in *Cryptotomus* and *Nicholsina* (Aw?; Figs 21ai, 22ai) but are reduced in *Calotomus* and *Leptoscarus*. They correspond with the "A3β" of Dietz (1914) and Stiassny (1981). Winterbottom (1974) considers these fibres to be part of the Aw section. The A3 tendon may split prior to insertion. The larger, ventral portion (A3t1) inserts on the midmedial surface of the articular onto the coronomeckelian. The smaller, dorsal portion (A3t2) passes medial to the ventral portion and inserts on the anterodorsal extremity of the flange on the ventral edge of the anterior ascending process. This dorsal division is extremely small or absent in *Leptoscarus*. In *Cryptotomus* and *Nicholsina* the fibres on the dorsal margin of the A3 have a thin tendinous insertion (A3t3) along a ridge on the medial face of the dentary coronoid process. This insertion is immediately anterior to the dentary insertion of the A2t.

In all four genera, the main Aw division (Awα) has a posterior tendinous attachment to the medial face of the quadrate. Anteriorly, the muscle fibres arise broadly within the Meckelian fossa, extending over the flange which joins the descending and anterior ascending processes. A few dorsal fibres insert on the medial face of the dentary. Immediately anterior to the main Aw (Awα) is a complex collection of short muscle fibres which comprise the sub-divisions Awβ and Awα.

In *Leptoscarus* and to a lesser extent *Calotomus*, the posterior tendon of Awα is expanded and has a covering of muscle fibres. This structure was described as separate muscle, the M. adductor mandibulae medialis, by Lubosch (1923) and later (Lubosch, 1929) the M. quadrato mandibularis internus.

The clear homology of the main Aw muscle division (Awα) in scarids and the Aw of other labroids necessitates a revision of the terminology applied to the smaller Aw subdivisions within the Scaridae. In this study, the main Aw subdivision is designated Awα and the smaller anterior subdivisions Awβ and Awγ.

In all four genera the Awβ and Awγ are closely associated. The Aw comprises a series of parallel muscle fibres which connect the leading face of the articular medial flange and the posteroventral edge of the dentary, in the region ventral to the insertion site of the intermandibularis. The Awβ has been variously referred to as the adduktor-symphysialier (Lubosch, 1923), the Aw (Lubosch, 1929), the abductor portion of the Aw (Gobalet, 1980), and Awα (Bellwood & Choat, 1990).

The Awγ comprises a series of fibres which connect the anterodorsal extremity of the medial flange on the articular anterior ascending process and the medial face of the dentary, at the base of the coronoid process. The muscle fibres either radiate from a single point on the tip of the articular medial spine or arise from a small tendon which inserts on this point. The Awγ has been referred to as the M. articulari-dentalis by Lubosch (1923), the adductor portion of the Aw by Gobalet (1980) and Awβ by Bellwood & Choat (1990).

In all species a short intermandibularis is present connecting the two dentaries.

2. *Sparisoma* (Fig. 23B). In *Sparisoma*, the form of the adductor muscles differs significantly from the genera described above, but displays considerable variability within the genus.

The A1 is a single muscle mass which is multipinnate in larger specimens. The superficial fibres of A1 converge on a short round tendon (A1t) which passes medial to the maxillary arm before inserting on a raised process on the ventromedial base of the premaxillary process of the maxilla. There is a small tendon connecting A1t and the dorsal tendon of A2 (A2t1).

The degree of association between A1 and A2 varies greatly. In most species the muscle fibres of these two sections are closely associated basally. In the larger species *S. cretensis*, *S. strigatus* and *S. viride*, the deeper fibres of the A1 representing about 30% of the total muscle volume, converge on to the A2t1.

The A2 is a large superficial muscle occupying the whole of the ventromedial area of the suspensorium. It has two distinct divisions, although this may be obscured superficially by the tendinous sheet which covers the outer surface of the whole of the adductor muscle mass. The dorsal division of A2 (A2α) is usually the largest division, except in small specimens or in small species such as *S. radians*. The A2α arises from the quadrate, angular region of the preoperculum, the symplectic and the ventral region of the hyomandibula. Fibres in this subdivision are strongly pinnate in large specimens. The A2α has two insertion sites. Superficial ventral fibres converge on a short tendon (A2t2) which inserts on the medial face of the dentary coronoid process near to the posteroventral edge. The bulk of the A2α comprising the dorsal and medial fibres, converge anteriorly on a large tendon (A2t1) which inserts on the medial or lateral face of the posterior extremity of the alveolar process of the premaxilla.

In the larger species, *S. cretensis*, *S. strigatus* and *S. viride*, and to a lesser extent in *S. aurofrenatum*, *S. chrysopterum* and *S. rubripinne*, the A2t1 is associated with fibres from all three major adductor muscle divisions, sections A1, A2 and A3.

The anterior region of A2α is tightly connected by connective tissue to the dorsal part of the articular posterior ascending process. Basally the A2α is usually closely associated with the A1 and A2β.

The small subdivision A2β is restricted to the anteroventral region of the suspensorium. It arises from the anterior region of the quadrate and inserts along the posterior edge of the articular ascending process.
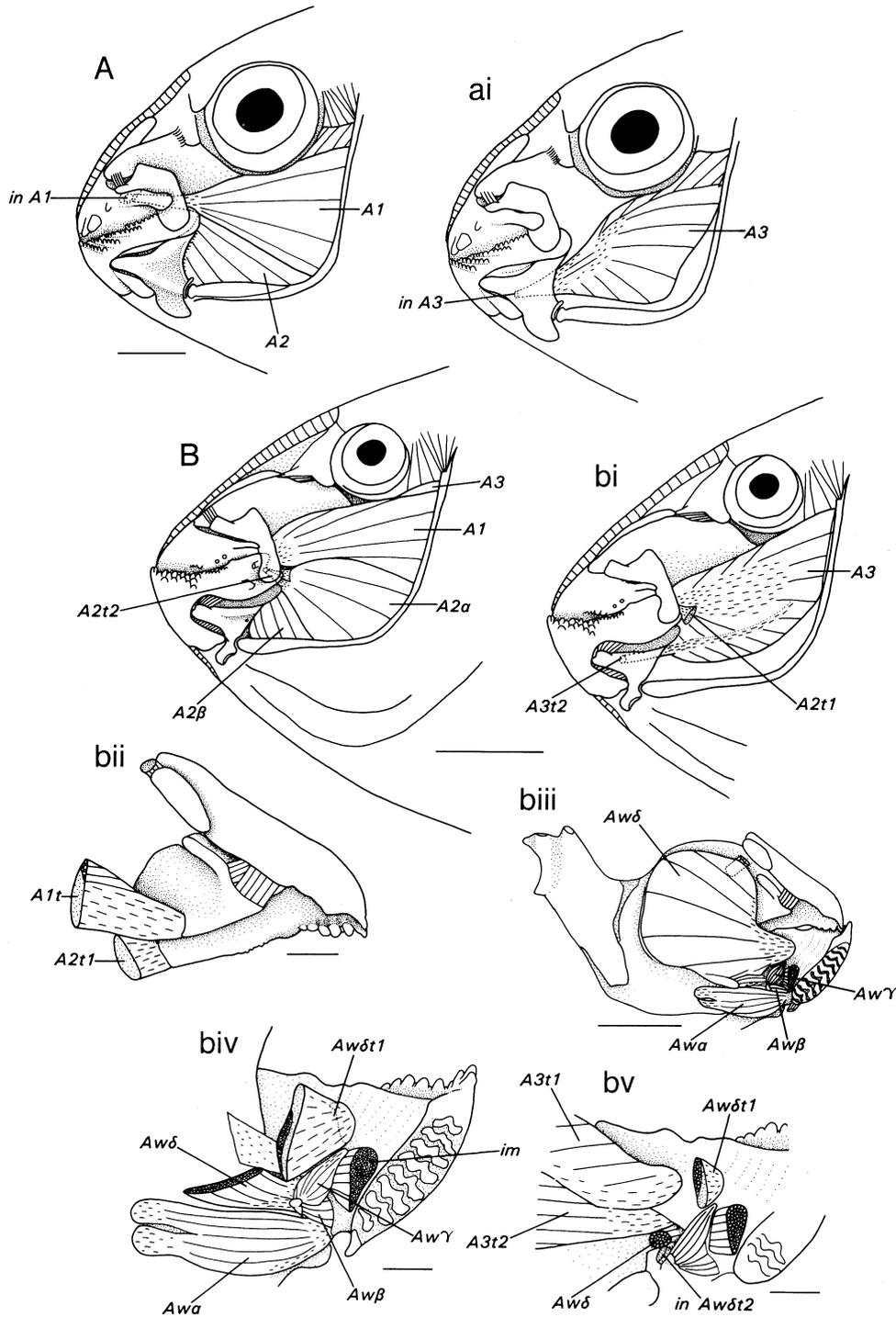
Fig. 23. Myology of the oral jaws: A-ai, *Leptoscarus vaigiensis*; A – integument and infraorbital bones removed, scale bar equals 5 mm; ai – as A, except adductor mandibulae sections *A1* and *A2* removed. B-bv, *Sparisoma viridis*; B – integument and infraorbital bones removed, scale bar equals 20 mm; bi – as B, except adductor mandibulae sections *A1* and *A2* removed; bii – details of upper jaw, medial view, anterior to right, scale bar equals 5 mm; biii – details of lower jaw, medial view, anterior to right, scale bar equals 20 mm; biv – details of lower jaw, medial view, anterior to right, scale bar equals 5 mm, with the bulk of *Aw* removed; bv – as biv, except for the removal of *Aw* and the quadrate.

Dorsally, it is closely associated with A2α.

The A3 is a large muscle lying medial to A1 and A2. It arises from the hyomandibular, metapterygoid, symplectic and quadrate, the site of origin often being divided dorsally by the site of origin of the levator arcus palatini. The A3 division has three possible insertion sites. In larger species (eg, *S. cretensis*, *S. strigatus* and *S. viride*), the superficial fibres converge on a small tendon which fuses with the medial surface of the common tendon A2t1. In all species, the bulk of the fibres, from the central region of the muscle, converge on a short broad tendon (A3t1) which inserts on the medial face of the dentary, at the base of the coronoid process. On the medial surface some fibres insert muscularly with the whole muscle being covered by a thin tendinous sheet. The remaining portion of the A3, comprising the anteromedial fibres, converge on a more elongate tendon (A3t2) which passes under the ventral edge of the coronoid process and insert on the medial surface of the articular anterior ascending process half way along its length near to the dorsal margin (**120.1**). In most labrids and scarids the insertion of the A3 is on the articular. A few fibres arising on the lateral face of A3t2 insert on the ventral medial surface of the dentary coronoid process. A small tendon connects the ventral margin of A3t1 to the dorsal margin of A3t2.

On the medial face of the jaws, the Aw section in *Sparisoma* is well developed. The main posterior portion (Awα) has two tendinous sheets attaching to the quadrate and a large body of muscle fibres crossing the lower jaw articulation. Anteriorly, the Awα inserts tendinously on the posteroventral edge of the dentary immediately lateral to the insertion of the protractor hyoideus. The lateral surface of the Aw is closely attached by tendons and connective tissue to the medial surface of the articular descending process.

Anteriorly, the Awβ and Awγ are distinct subdivisions. The Awβ connects the anterior edge of the articular flange/spine to the posteroventral margin of the dentary immediately above the insertion of the main Awα. The Awγ connects the tip of the flange/spine on the articular descending process to the medial face of the dentary.

In addition to these subdivisions, the adductor muscles of *Sparisoma* are unique in that they include a large subdivision arising on the medial face of the suspensorium (**125.1**). The sites of origin and insertions of this muscle strongly suggest that it arose as a dorsal expansion of the Aw division of the adductor mandibulae. It is therefore regarded herein as a dorsal division of the Aw, and named Awδ. This muscle was figured and described in *Sparisoma cretense* by Board (1956) but was not named.

The Awδ is a large muscle covering a large proportion of the medial surface of the suspensorium. Its site of origin includes the medial surface of the quadrate, metapterygoid, entopterygoid and pterygoid and may be bordered posteriorly by a ridge on the entopterygoid and metapterygoid. It may displace the anterior portion of the adductor arcus palatini. A thin tendinous sheet which covers the surface of the

muscle is attached to this ridge. The Awδ has three insertions. These are most clearly seen in the larger species. The tendinous sheet covering the muscle consolidates anteriorly forming a broad tendon (Awδt1) which inserts on the medial surface of the dentary. A few fibres along the ventral edge of the Awδ insert muscularly directly onto the medial surface of the articular at the base of the anterior ascending process, medial to the insertion of A3t2. A few of the most ventral fibres converge on a small tendon (Awδt2) that inserts on the posterodorsal margin of the articular medial spine. A short sheet of tendon connects a ridge on the medial face of the quadrate to the lateral surface of the Awδ just prior to its dorsal insertion (Fig. 23biv). In small species the ventral margin of Awδ is almost confluent with the dorsal margin of Awα.

3. *Cetoscarus, Bolbometopon* (Fig. 24A,B). When compared to *Sparisoma* the adductor mandibulae of *Cetoscarus* and *Bolbometopon* are relatively simple. The three main sections are well developed and strongly pinnate (bi- or multi-pinnate; **122.1**). In most scarids and all outgroups the fibres are weakly pinnate.

The A1 arises from the ascending arm of the preoperculum, the posterior margin of the hyomandibula, the metapterygoid and the symplectic. Superficial fibres also arise from the tendinous sheet which covers the whole adductor muscle mass. The A1 inserts *via* a short thick tendon on the middle of the medial face of the maxillary arm (**116.1**), at the end of a ridge which extends from the base of the maxillary medial process (*cf.* Fig. 2F,G). In all outgroups and most other scarids, the insertion of the A1 is onto the premaxillary process of the maxilla.

The origin of the A2 include the preoperculum, symplectic, and quadrate. It inserts *via* a short thick tendon on the medial face of the dentary coronoid process near to the posterodorsal edge. In *Cetoscarus* a few fibres insert on the posterior margin of the posterior ascending process of the articular. In *Bolbometopon* there is a second small tendinous insertion on the distal medial surface of the posterior ascending process of the articular.

The A3 arises from the entopterygoid, metapterygoid, hyomandibula and quadrate. It has two tendinous insertions. The largest insertion (A3t1) is on the dorsal part of the medial face of the dentary coronoid process. The second, smaller, insertion is on the medial face of the articular near the base of the posterior ascending process.

The Awα is present, but is only represented by a small muscle connecting the medial surface of the anterior part of the quadrate to the flange on the descending process of the articular. Anteriorly, the Awβ and Awγ are present as in *Sparisoma*.

4. *Chlorurus* (Fig. 24C). In *Chlorurus* the adductor muscles are all well developed. The major divisions, A1α, A2, and A3 all have strongly multipinnate fibres (**122.1**).

The A1 is expanded and covers the greater part of the superficial area of the adductor muscle mass. The A1 has two major subdivisions, the main A1α and a dorsal division A1β. A1α arises from the preoperculum, hyomandibula, metapterygoid and symplectic, and from the tendinous sheet which covers the adductor muscle mass. It inserts *via* a thick round tendon on the medial face of the maxillary arm, at the base of the medial
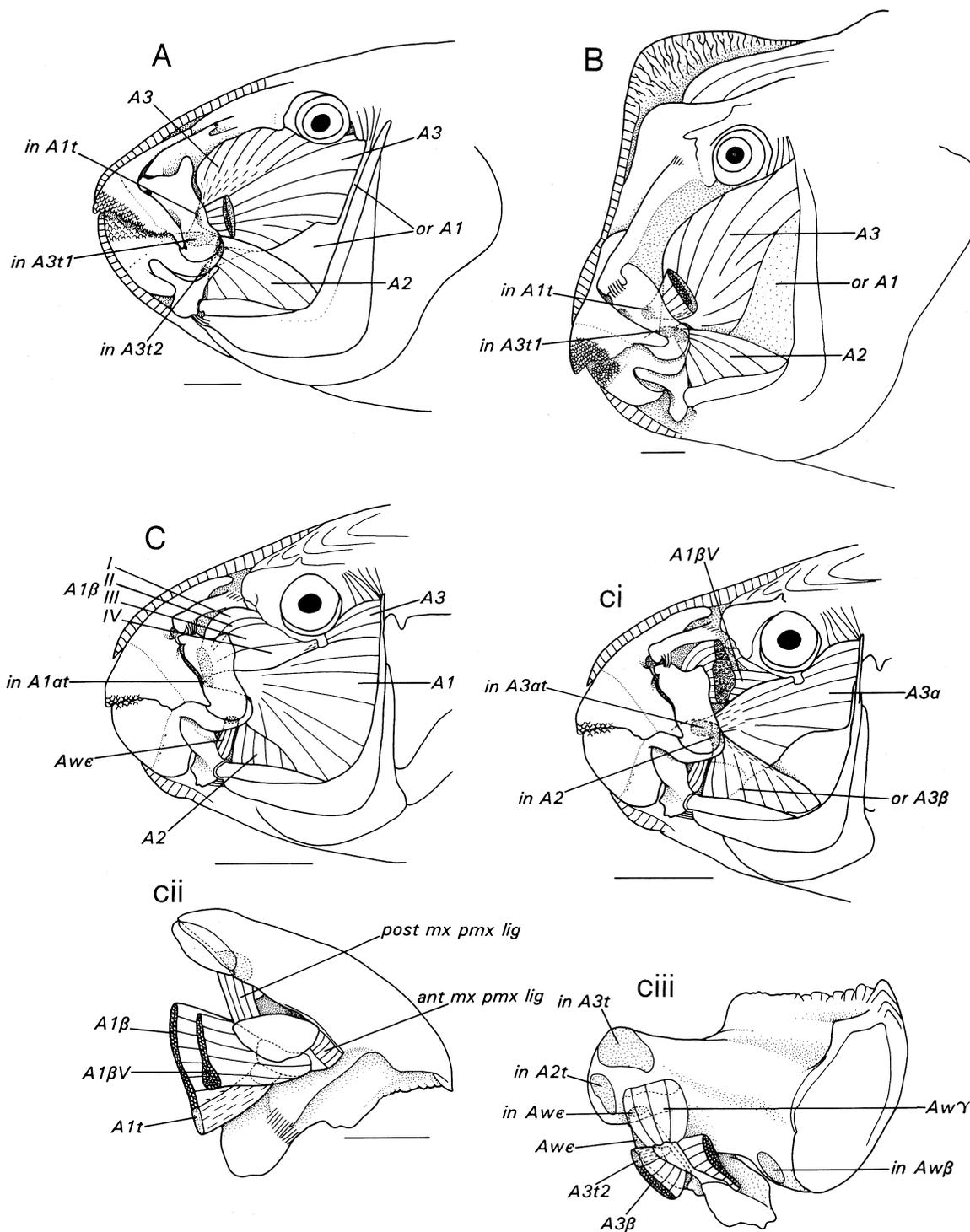
Fig. 24. Myology of the oral jaws: A – *Cetoscarus bicolor*, integument, infraorbital bones and adductor mandibulae section *A1* removed, scale bar equals 20 mm; B – *Bolbometopon muricatum*, integument, infraorbital bones and adductor mandibulae section *A1* removed, scale bar equals 20 mm; C-ciii, *Chlorurus sordidus*: C – integument and infraorbital bones removed, scale bar equals 20 mm; ci – as C, except adductor mandibulae section *A1* removed; cii – details of upper jaw, medial view, anterior to right, scale bar equals 10 mm; ciii – details of lower jaw, medial view, anterior to right, scale bar equals 10 mm.

process. An extremely small tendon connecting the medial surface of A1α to the base of the articular ascending process is present as in the genera described above.

The A1β arises from the palatine and entopterygoid and inserts muscularly on the medial face of the maxilla, dorsal to the insertion of A1αt. The lower fibres of A1β may insert on the dorsal margin of A1αt. In large individuals the anterior region of A1β has a tendinous sheath. Within the A1β there are often five subdivisions visible. The four superficial divisions arise from the palatine. The deeper portion arises from a deep anterior cavity which is formed by the buttressed entopterygoid lateral process. An A1β was not recorded in the outgroups, and in the Scaridae has only been recorded from *Chlorurus* and *Scarus* (118.1).

The A2 arises from the quadrate, symplectic, preoperculum and the superficial tendinous sheet which covers the adductor muscle mass. A dorsal aponeurosis converges with a tendinous medial septum to form a short round tendon which inserts on the medial face of the dentary coronoid process (Fig. 24ci).

The A3 arises from the quadrate, entopterygoid (including the main deep cavity at the base of the entopterygoid lateral process), metapterygoid and hyomandibula, and posterodorsally from the superficial tendinous sheet. The large medial/posterodorsal portion of the A3, designated A3α, contains tendinous septa which converge anteriorly to form a single large round tendon which inserts on the medial surface of the dentary coronoid process near to its dorsal margin. The anteroventral fibres of A3, designated A3β, arise from the anterior region of the quadrate and are covered by a thin tendinous sheet which consolidates anteriorly to form a small strap-like tendon which inserts on the medial surface of the articular near to the base of the articular medial spine. A few fibres of A3β insert muscularly below this tendinous insertion.

Section Aw differs markedly from all the genera described above (and all outgroups). The posterior portion (Awα) connecting the quadrate and articular is lost (124.2), although the two anterior portions Awβ and Awγ, are distinct and well developed. There is also a unique additional muscle present in *Chlorurus*, the Awε (123.1; = Awγ of Bellwood, 1986 and Bellwood & Choat, 1990). This portion connects the ventromedial edge of the dentary coronoid process to the dorsal surface of the articular ascending process, immediately above the lower jaw articulation. The insertion sites of Awε and its proximity to Awγ, suggest that Awε developed as a lateral expansion of Awγ.

5. *Hipposcarus* and *Scarus* – *Hipposcarus* (Fig. 25A). In *Hipposcarus*, the adductors are only moderately developed, with the largest sections A1 and A2 having weakly pinnate fibres.

The A1 is the largest division and has no dorsal subdivision. It arises from the hyomandibula, preoperculum, metapterygoid and symplectic, and to a limited extent, from the superficial tendinous sheet covering the adductors. Anteriorly it converges on a thin round tendon which inserts on the medial surface of the maxillary arm, at the base of the medial process. A few of the anteroventral fibres converge on a small tendon which inserts on the medial posterodorsal extremity of the dentary coronoid process.

The A2 arises from the quadrate and inserts *via* a short tendon on the posterior edge of the medial face of the dentary coronoid process.

In comparison with other scarids and most outgroups, the A3 is greatly reduced (121.1). It is represented merely by a thin multipinnate muscle, with origins on the hyomandibula, entopterygoid, metapterygoid and quadrate. It has two equally sized insertions. The dorsal fibres converge on a narrow round tendon which inserts on the dorsomedial surface of the dentary coronoid process. The ventral fibres converge on a broad tendon which inserts on the medial face of the articular ascending process and on the distal end of the articular medial spine.

In *Hipposcarus*, the Awα is represented by a small thin sheet of fibrous muscle connecting the anterior medial face of the quadrate and a mass of connective tissue which is associated with the anterior portions of Aw, Awβ and Awγ. These subdivisions are comparable to those of *Chlorurus*, but there is no Awε.

There is a tendinous attachment between the ventral margin of the A1t and the dorsal margin of the A2t. This connection approaches the condition found in *Scarus* species and, although not complete, is regarded as a functional coupling of the A1 and A2 sections in *Hipposcarus*. Fusion of these sections was only found in these two genera and is therefore considered derived (117.1).

Hipposcarus and *Scarus* – *Scarus* (Fig. 25B). The condition in *Scarus* most closely resembles that of *Hipposcarus*. The adductors are generally only moderately well developed and all are weakly pinnate.

The A1 is a relatively large muscle with a small dorsal division, the A1β. The larger ventral portion of A1, A1α and the A2 are fused to form a single muscle complex, the A1α/A2 (117.1). In some species, a superficial division may be visible between the two muscles, but in all cases the two sections are tightly bound anteriorly. The A1α/A2 arises from the hyomandibula, preoperculum, metapterygoid, entopterygoid, quadrate, and the fibrous sheet covering the medial portion of section A3. Fibres in the dorsal region converge on a thick tendon A1α/A2t1 which inserts on the medial face of the maxillary arm, at the base of the medial process. Fibres in the anteroventral region converge on a strong round tendon the A1α/A2t2 which inserts on the medial face of the dentary coronoid process, near its dorsal margin. The remaining fibres in the mid region of the A1α/A2 complex converge on a strong tendinous belt which connects the ventral surface of the A1α/A2t1 and the dorsal surface of the A1α/A2t2.

The small dorsal portion A1β, arises from the entopterygoid. The ventral fibres of A1β converge with

the dorsal surface of the tendon A1α/A2t1, the dorsal fibres insert muscularly at the base of the medial process of the maxilla, above the insertion of A1α/A2t1.

Section A3 in *Scarus* is represented by an exceedingly thin narrow muscle which lies beneath the larger A1α/A2 complex. The A3 arises from the hyomandibula, metapterygoid, symplectic and quadrate. The weakly pinnate fibres fuse with an elongate dorsal aponeurosis which consolidates to form a thin strap-like tendon A3t which inserts on the medial face of the articular, immediately above the base of the articular medial spine. Anteriorly, a few muscle fibres connect the dorsal margin of the A3t with the medial surface of the dentary coronoid process. Comparable fibres in the Labridae were labelled "A3β" by Stiassny (1981) and A3α? by Bellwood & Choat (1990). Winterbottom (1974) considered them to be a posterior extension of the Aw.

The posterior portion of the Aw, the Awα, is not present. The anterior portions Awβ and Awγ are both well developed and distinct. In the Awγ, in addition to the usual insertion site on the tip of the articular medial spine, some fibres may insert on the medial face of the articular, dorsal to the insertion of the A3t. There is no Awε.

Summary of derived characters of jaw muscles: insertion of A1 moved from the premaxillary process of maxilla to the maxillary arm (**116.1**); fusion of A1 and A2 (**117.1**); presence of an A1β (**118.1**); insertion of the A2 restricted to the dentary (loss of the articular insertion, **119.1**); inclusion of the dentary in the insertion of A3 (**120.1-2**); A3 greatly reduced (**121.1**); multipinnate fibres (**122.1**); presence of an Awε (**123.1**); presence of an Awδ (**125.1**); enlargement (**124.1**) or loss (**124.2**) of the Awα.

Pharyngeal muscles (characters 126, 127)

The pharyngeal apparatus of scarids follows the typical labroid pattern (*cf.* Liem & Greenwood, 1981; Kaufman & Liem, 1982). The myology of the pharyngeal apparatus of *Scarus* has been described by Liem & Greenwood (1981), Clements & Bellwood (1988) and in detail by Gobalet (1989). The pharyngeal myology of *Calotomus* has been described by Yamaoka (1980).

The pharyngeal myology of the Scaridae differs from the labrid condition primarily in:

1. The origin of the levator posterior, which is restricted dorsally by the posteriorly expanded exoccipital (**126.1**). There is no origin from the supraoccipital crest. In *Odax*, *Bodianus* and *Pseudodax*

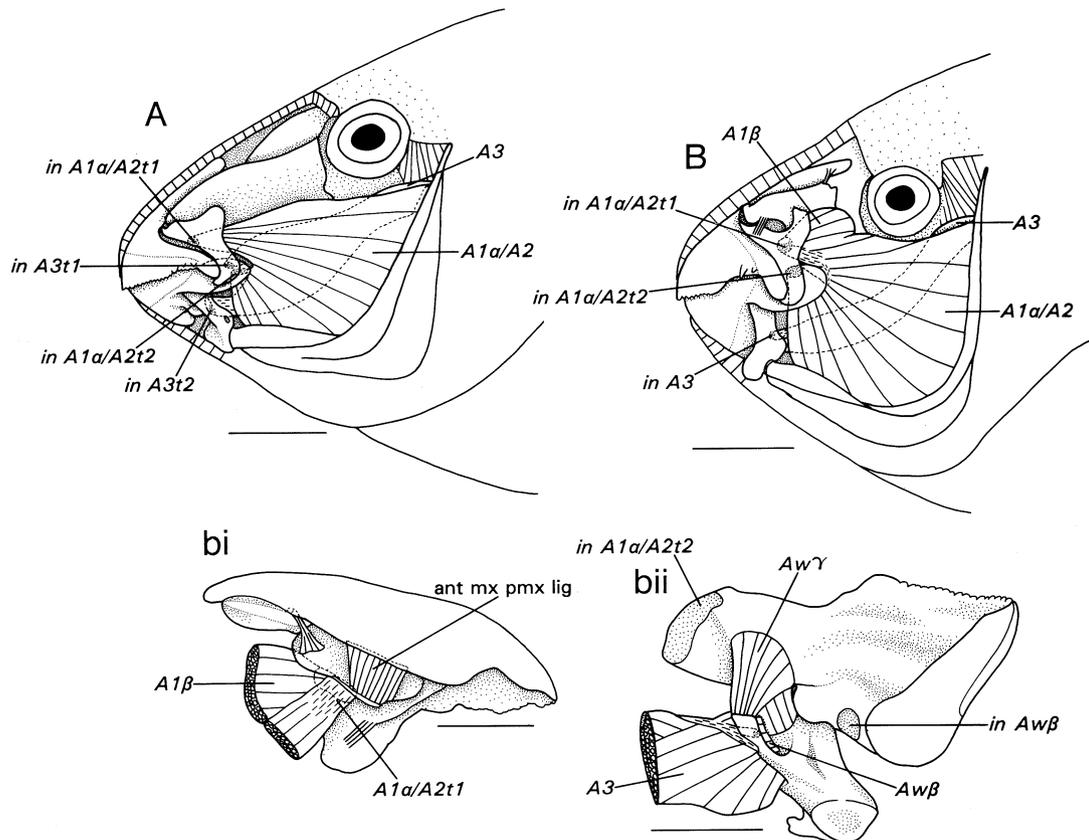**Fig. 25.** Myology of the oral jaws: A – *Hipposcarus longiceps*, integument and infraorbital bones removed, scale bar equals 20 mm; B-bii, *Scarus frenatus*: B – integument and infraorbital bones removed, scale bar equals 20 mm; bi – details of upper jaw, medial view, anterior to right, scale bar equals 10 mm; bii – details of lower jaw, medial view, anterior to right, scale bar equals 10 mm.

the origin of the levator posterior includes the supraoccipital crest. In other labrids the origin may not extend this far dorsally, but it is not restricted by the exoccipital (cf. Yamaoka, 1978). Contrary to Yamaoka (1980), the condition in *Calotomus* is not regarded as an origin from the supraoccipital crest. In *Calotomus*, the muscle arises from flanges on the exoccipital, epioccipital and possibly part of the supraoccipital, but not from the supraoccipital crest *per se* as in some labrids (Yamaoka, 1978) and *Odax* (Clements & Bellwood, 1988).

2. The presence of a pharyngeal valve (**78.1**). All scarid genera possess an unusual pharyngeal valve. This has been described in *Hipposcarus* and *Scarus* (Gohar & Latif, 1959; Gobalet, 1989), *Chlorurus* (as *Scarus*; Al Hussaini, 1945) and *Sparisoma* (Board, 1956), and is present in *Nicholsina* (Gobalet, 1989), *Cryptotomus*, *Calotomus*, *Leptoscarus*, *Cetoscarus* and *Bolbometopon* (personal observation). Such a structure is lacking in labrids, and appears to be a unique feature of the Scaridae. Detailed analyses of the pharyngeal valve and the associated osteology and myology will probably reveal a suite of unusual morphological characters associated with the presence of this structure (see the description of the branchial arches; character 78).

3. The form of the transversus dorsalis posterior. In most labrids and odacids, the transversus dorsalis posterior crosses the midline (Liem & Greenwood, 1981, Liem & Sanderson, 1986). In scarids, the transversus dorsalis posterior does not cross the midline (Liem & Greenwood, 1981; Gobalet, 1989; personal observation). In both scarids and *Pseudodax*, it connects the posterior portion of the lateral surface of the upper pharyngeal bone to the posterodorsal margin of the condylar region of the fourth epibranchial (and is thus, technically, an obliquus dorsalis IV). This division was recorded only in scarids and the monotypic labrid genus *Pseudodax* and is considered derived (**127.1**). It appears to be functionally related to the elongation of the upper pharyngeal bones.

Ligaments (characters 128, 129)

The loss, in some scarid genera, of a post-pharyngeal ligament connecting the lower pharyngeal jaw and the cleithrum (**128.1**) is regarded as a derived condition. This ligament is present in some labrids (Yamaoka, 1978; personal observation), the odacid *Odax pullus* (Clements & Bellwood, 1988) and several scarid genera.

In many labrid genera, there is a broad thin ligament connecting the dorsal part of the lateral face of the maxilla (arising from a small cleft) to the suspensorium in the region of the palatine-entopterygoid-pterygoid junction (Stiassny, 1980, in Lauder & Liem, 1983; personal observation). The loss of this ligament in all scarid genera appears to be a synapomorphy of the Scaridae (**129.1**).

Viscera (characters 130 – 132)

Fig. 26

The viscera include the liver, intestine, and swim bladder. The structure of the former two organs have been described in detail by Gohar & Latif (1959, 1961) (in *Scarus* and *Hipposcarus*). Brief descriptions of the intestine are provided by Suyehiro (1942) (in *Calotomus*), Al Hussaini (1945, 1947) (in *Chlorurus* and *Cetoscarus*), and Clements & Bellwood (1988) (in *Scarus*). Visceral characters have not been used previously in systematic studies of the Scaridae or Labridae.

The liver has two major lobes, a small dextral (right) lobe and a greatly enlarged sinistral (left) lobe. The liver of scarids is large and oily (Al Hussaini, 1945, 1947; Gohar & Latif, 1959). It typically has a yellow-tan colour, in contrast to the deep red of most labrids. In scarids, the liver size and colour vary greatly within and between species (1.5 - 7.4% of total body weight; Gohar & Latif, 1959). Scarids lack the fat bodies which are characteristic of other reef herbivores, which are represented either by distinct fat bodies, as in the Acanthuridae (Fishelson *et al.*, 1985, 1987), or as deposits around the intestines, as in some members of the Siganidae and Pomacanthidae (Bellwood, 1986). The unusually large oily liver in scarids suggests that this organ may serve as the primary lipid storage site. It is interesting to note that scarids lack the characteristic oily bones found in all other labroid groups (cf. character 115). These differences suggest that the Scaridae may have a novel form of lipid metabolism.

The intestines of scarids differ markedly from the typical labrid pattern. As in labrids, all scarids lack a gastric stomach. However, unlike labrids, some scarid genera possess a lateral intestinal bulb (**132.1**), ie, a blind sac-shaped bulb on the dorsal/sinistral surface of the duodenum immediately behind the oesophageal/
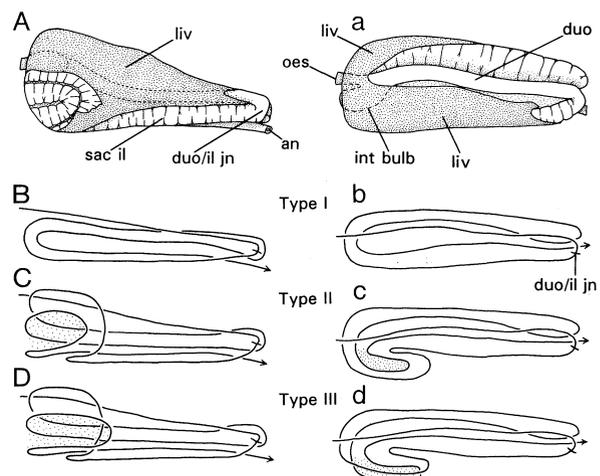

Fig. 26. Viscera and gut coiling patterns in the Scaridae: A-D – lateral view; a-d – dorsal view. See text for explanations of coiling types; figures A-a, based on a Type II coiling pattern in *Scarus frenatus*.

duodenal junction. In some species, a small additional bulb may be present dextrally. The duodenum is a straight smooth tube which extends to the back of the body cavity, where it joins the ilial section of the intestine. The ilium of some scarids is unique among fishes, with the ilial wall constricted at short intervals, forming irregular internally imperfect pouches (**131.1**). Overall, the ilium has a sacculated appearance which closely resembles that of the mammalian colon. The extent of sacculation varies between genera. The intestine may be either a simple tube, a tube with slight constrictions, or fully sacculated. Bellwood (1986) suggested that the degree of sacculation may be correlated with the amount of carbonate ingested. There is a distinct rectum marked by a constriction at the ilio-rectal valve. The rectum is not sacculated.

The coiling of the intestine in scarids is distinctive and usually follows one of three basic patterns (Fig. 26). The simple coiling pattern, Type I (**130.1**), has no sinistral loops. Additional sinistral loops are only found in Type II and Type III patterns (**130.2**). Type III differs from Type II in that the smaller sinistral loop (finely stippled in Fig. 26) lies lateral to the larger sinistral loop. In Type II, the smaller loop lies within the larger loop. The length of the sinistral loops varies widely, from a small loop (sometimes with only the larger loop apparent) to both loops extending to the posterior region of the abdominal cavity.

A Type I pattern may be found in some labrid species (*cf.* Gohar & Latif, 1959) which approximates the type B pattern of Mok (1980), who describes it as the dominant labroid intestinal pattern, although most labrids examined in the present study, including the outgroups, had a type LA pattern *sensu* Mok (1980). Type LA is therefore considered plesiomorphic and Type I derived. Type II and III intestinal coiling patterns, as found in the Scaridae, do not correspond with any of the patterns described by Mok (1980) in his survey of actinopterygian intestinal patterns, and may represent unique coiling patterns.

During ontogeny, the intestinal pattern of *Chlorurus* and *Scarus* changes from linear to a single left-hand loop (at or near notochord flexion; Leis & Rennis, 1983). In post-settlement individuals, the loop expands and a second loop develops anteriorly, passing down the right hand side of the peritoneal cavity. A Type I pattern is present at 11 mm SL. An anterior extension of the intestine which curves to the left, results in a Type II or III pattern which is complete at approximately 60 mm SL (Bellwood, 1986). The transformation series for character 130, therefore, is: linear/single loop - Type I - Type II/III.

Reproductive system (characters 133, 134)

The reproductive patterns of scarids has been described in the introduction. Two aspects of the reproductive system were used in the analyses:

reproductive mode and egg shape. The reproductive mode of scarids is predominantly protogynous hermaphroditism. This has been determined based on gonad examination in *Cryptotomus* (Robertson & Warner, 1978), *Calotomus* (Robertson *et al.*, 1982), *Sparisoma* (Robertson & Warner, 1978), *Bolbometopon* (Bruce, 1979; Randall & Bruce, 1983), *Chlorurus* (as *Scarus*; Choat & Robertson, 1975), *Hipposcarus* (Choat & Robertson, 1975; Bruce, 1979; Randall & Bruce, 1983) and numerous *Scarus* species (Choat & Robertson, 1975; Bruce, 1979; Robertson & Warner, 1978).

There is no published evidence of hermaphroditism in *Nicholsina* or *Cetoscarus*, however, in *Cetoscarus* at least, the presence of small female IPs and only large TP males (Randall & Bruce, 1983; Choat & Randall, 1986) strongly suggest that the single species in this genus is also a protogynous hermaphrodite.

Protogynous hermaphroditism is the common pattern in the Labridae (Warner & Robertson, 1978; Robertson & Choat, 1974) and represents the plesiomorphic condition within the Scaridae. The only variant to the common pattern of protogynous hermaphroditism is *Leptoscarus*, the sole species of which, based on gonad examinations, appears to be gonochoristic (**134.1**; Robertson *et al.*, 1982).

All scarid species spawn pelagic eggs. The eggs of *Calotomus* (Kamiya, 1925), *Sparisoma* (Wynn & Bardach, 1960; Randall & Randall, 1963), *Cetoscarus* (Colin & Bell, 1991), and *Bolbometopon* (R.W. Bruce, personal communication) are spherical. As the eggs of labrids are invariably spherical (Leis & Rennis, 1983), this state is considered to be plesiomorphic. In *Chlorurus*, *Hipposcarus* (Colin & Bell, 1991) and *Scarus*, the eggs are distinctly spindle-shaped, about one third as long as wide (Wynn & Bardach 1960; personal observation). This represents a uniquely derived feature (**133.1**).

Juvenile colour patterns (characters 135, 136)

Adult colour patterns are of limited value in distinguishing supraspecific groups within the Scaridae. Most species have highly variable and complex adult colour patterns. This intrageneric variability precludes their use in the analyses of generic relationships. However, the colour patterns of juveniles are relatively conservative and show little variation outside a limited range of colour patterns (Bellwood & Choat, 1989). There are two striking exceptions: A) the large ocellus on the anterior part of the dorsal fin found only in *Cetoscarus* (**135.1**) and B) the presence of a single line on the body terminating with a single dark dot at the base of the caudal fin found only in juvenile *Hipposcarus* (**136.1**). Juvenile scarids are figured in Smith (1959), Randall & Bruce (1983), Bruce & Randall (1985), Bellwood (1989), Bellwood & Choat (1989).

External morphology (characters 137 – 143)

External morphological features have been widely employed in the determination of supraspecific scarid taxa (Smith, 1956, 1959; Schultz, 1958, 1969). However, few appear to be of phylogenetic significance. Those characters which were variable, but displayed consistent patterns within genera are outlined below. Meristic values are based on the values given in Smith (1959), Schultz (1969), Randall (1983a), Randall & Bruce (1983), Masuda *et al.* (1984), Bruce & Randall (1985) and Choat & Randall (1986).

In overall shape, only *Cryptotomus* displays a labrid-like appearance with a elongate body and distinctly pointed snout (**143.1**; Figs 21-25). Most scarids have a relatively deep body and a sloping, blunt or rounded snout. The two extremes being *Hipposcarus* which has an elongate snout and *Bolbometopon* which has an almost vertical profile.

All scarids have large cycloid scales with 22 to 24 pored scales in the lateral line. In all the outgroups, the lateral line was continuous, whilst in scarids it is broken posteriorly by one or two scale rows (**141.1**). There are one to four cheek scale rows (**140.1-2**) (numerous in most outgroup taxa), two rows on the interoperculum (with the exception of one in *Cetoscarus*), and three to seven (usually 4 to 6) median predorsal scales (**139.1**; numerous in most outgroup taxa).

The branchiostegal membranes may be free (as in all outgroups) or broadly attached to the isthmus, with (**142.1**) or without (**142.2**) a free-fold membrane.

In scarids, the form of the nostrils is often distinct. The anterior nostril is usually small with a fleshy rim, with or without a small fleshy flap posterodorsally (without in outgroups). In some genera this flap extends over half way to, or beyond, the posterior nostril (**138.1**). These flaps are usually simple but in *Sparisoma* they bear multifid cirri (**138.2**).

In most scarid genera and outgroups, the two nostrils are of comparable size and are widely spaced. In *Cetoscarus* and *Bolbometopon*, however, the nostrils are in close proximity and the posterior nostril is more than twice the area of the anterior nostril (**137.1**).

Phylogenetic Analyses

Methods

The method of cladistic analysis involves three stages: selection of taxa and outgroups, the choice of characters and their coding into character states, and lastly the analysis of the data and the construction of the cladogram.

Selection of taxa and outgroups. As described earlier, the analyses in this study were based on the external examination of 65 scarid species, with dissections and/ or examinations of osteological preparations of 63

species (Appendix I). This represents approximately 81% and 79%, respectively, of the 80 extant scarid species recognised in this study (given in the revised classification of genera of Scaridae). These species included representatives of all genera and sub-genera of previous authors (*Scaridea* excepted). The species examined were classified into ten groups. Each group comprised those species for which the available character state distributions were either identical or differed only marginally. For the characters used, variability within a species or species group was minimal, occurring in only eight out of the possible 1430 ingroup character state designations (Table 2, Appendix IV). All groups corresponded with previously recognised genera. The species examined included the type species from each of these genera.

A number of recent studies have presented evidence which indicates that the Labridae, Odacidae and Scaridae represent a monophyletic assemblage (Liem & Greenwood, 1981; Stiassny & Jensen, 1987). If the Scaridae represents a monophyletic group, then the immediate sister group of the Scaridae must be contained within the Labridae or Odacidae. However, despite the widespread suggestion that the Labridae is the closest family to the Scaridae, the Labridae is almost certainly paraphyletic and intrarelationships within the group are currently unclear. The immediate sister group of the Scaridae therefore, can not be determined with any certainty. The apparent paraphyletic nature of the Labridae prompted Russell (1988) in his analyses of *Pseudolabrus* and allied genera to select the Embiotocidae as a sister group to the Labridae *sensu lato*, based on the proposed phylogeny of Kaufman & Liem (1982). In a re-analysis of labroid interrelationships however, Stiassny & Jensen (1987) suggest that the Pomacentridae may be the sister-group of the Labridae *sensu lato* (including Scaridae and Odacidae) but emphasised the tentative nature of hypotheses regarding labroid relationships.

In a recent review of the Odacidae, Gomon & Paxton (1985) presented evidence which suggests that the Odacidae is monophyletic, but they did not discuss its relationships with other labroid groups other than to refer to Gomon & Russell (1981, unpublished). Gomon & Russell (unpublished, 1981), represents an oral paper presented at the International Conference on the Systematics and Evolution of Indo-Pacific Fishes held in Sydney, Australia, September 1981. At this meeting, they presented a proposed outline of interrelationships among groups within the Labridae (*sensu* Kaufman & Liem, 1982) based on osteological evidence. In this scheme, it was suggested that the Odacidae and the monotypic genus *Cheilio* should be recognised as a tribe, the Odacini, within the Labridae. It was proposed that the Scaridae along with the monotypic genus *Pseudodax* be recognised as distinct line which, with the genus *Lachnolaimus*, forms the tribe Scarini; the tribes Scarini and Hypsigenyini forming the subfamily Scarinae.

The similarity and inferred close relationship between the Scaridae and *Pseudodax* has been noted by other

workers (Kner, 1860; Kaufman & Liem, 1982). Gomon (1979) argued that *Pseudodax* was the immediate sister group of the Scaridae based on their shared unique modification of the first haemal spine and unusual modifications of the pharyngeal apparatus.

Whilst *Pseudodax* may represent the immediate sister group of the Scaridae it is a highly modified monotypic genus. Selection of *Pseudodax* as the sole outgroup could restrict the number of characters that can be polarised and may lead to spurious character state polarities. To overcome this problem, a number of labrid genera, including *Pseudodax*, were selected as outgroups.

The second outgroup chosen was *Bodianus*, the largest and most widespread genus in the tribe Hypsigenyini. This tribe was proposed by Gomon & Russell (1981, unpublished) as the sister group of the tribe Scarini which comprises the Scaridae, *Pseudodax* and *Lachnolaimus*.

In addition to *Pseudodax* and *Bodianus*, one genus was selected from each of three tribes from the four remaining labrid tribes proposed by Gomon & Russell (1981, unpublished): *Labrus* from the Labrini, *Odax* from the Odacini, and *Pseudolabrus* from the Julidini. The above three outgroup genera were selected to include a broad range of labrid types. These particular genera were selected as: A) detailed published descriptions of anatomical characters were available, B) each had recently been reviewed and the phyletic status of the group and associated genera resolved (*Labrus* excepted), and C) comparative material was readily available. No taxa within the tribe Chelinini fulfilled all these criteria and although chelinine material was examined, it was not represented in the analyses.

The inclusion of several outgroups including those groups reportedly close to the ingroup was necessary i) because of poorly resolved outgroup associations and ii) to facilitate a robust ancestral state assessment. In the analyses, a global parsimony criterion was used to assess outgroup and ingroup relationships simultaneously following Maddison *et al.* (1984). Analyses of several outgroups in this manner enabled the character states for the 'outgroup node' to be determined. This represents a hypothetical taxonomic unit that is directly ancestral to the ingroup.

The use of the global parsimony criterion alleviates the problems faced when working with poorly resolved or highly derived outgroups, where the arbitrary choice of a particular outgroup may markedly affect ingroup polarities, as it allows the program (PAUP) to select the 'best', ie, most parsimonious, outgroup-ingroup relationship. It also acts as a type of 'test' of the proposed monophyly of the ingroup.

Published descriptions of the following genera were used in the compilation of the outgroup data matrix: *Bodianus* (Yamaoka, 1978; Gomon, 1979), *Labrus* (Rognes, 1973; Stiassny & Jensen, 1987), *Odax* (Gomon & Paxton, 1985; Clements & Bellwood, 1988), *Pseudodax* (Gomon, 1979), *Pseudolabrus* (Russell, 1988).

Additional labrid, cichlid, pomacentrid and embiotocid material was examined but was not required to resolve character states, and was not included in the analyses. A list of outgroup material examined is given in Appendix II.

Character selection and coding. Particular attention was paid to the selection of characters to be used in the analyses. Characters were excluded if they exhibited a clear functional correlation with other established characters (eg, the fossa on the premaxilla and the corresponding process on the maxilla). To minimise the effects of functional or developmental interdependence of characters, characters were obtained from as wide a range of structures and functional systems as possible.

In cases where it follows a logical precedent that character 'A' must be present prior to character 'B', (if B inserts on A for example) then taxa lacking 'A' must also lack 'B'. In such cases, the status of character B in taxa which lack A are coded as '?' ie, all possible states.

In the analyses, all character states were based on the adult condition. However, the inevitable problem of heterochrony was apparent. Where possible, especially in large species, both adult and juvenile specimens were examined to ensure that character states were not directly linked to size or developmental stage. Characters which were clearly linked to sexual status were not included in the analyses, although it is recognised that such characters may be extremely useful for analyses at the species level.

The characters chosen for inclusion in the analyses were those known or found to be of high taxonomic value. That is, characters with clearly defined character states, which were consistent within a species, relatively uniform within species groups, and useful for distinguishing such groups. The choice of characters and the identification of character states are described in the Comparative Morphology section and character analysis section below. In all cases, characters with two or more clearly defined character states were preferred. In the analyses, characters which were invariant within the Scaridae but differed between outgroups were included to facilitate the determination of ingroup-outgroup associations and reliable ingroup character polarities. Character polarities were determined by direct outgroup analyses based on a simultaneous resolution of in- and out-groups, using a global parsimony criterion following Maddison *et al.* (1984). If characters are only found in the ingroup, outgroup comparisons are not possible. In such cases, character polarity was determined during the global parsimony procedure. The low number of such characters (10 out of 143 characters) would have a minimal effect on the ingroup cladogram.

ONTOGENY CRITERION. Insufficient data was available to determine the polarity of most characters based on the ontogeny criterion (see Wiley, 1981; Nelson, 1978). However, this rule was applied to resolve the transformation sequence of some multistate characters

(these characters are marked O in column 3 of Table 1, Appendix IV). The morphological changes during ontogeny from settlement to sexual maturity in two species in the genera *Chlorurus* and *Scarus* are described briefly in Bellwood (1986). Additional observations were made during the present study.

CRITERION OF GEOLOGICAL PRECEDENCE. As part of this study, fossil scarids and labrids were examined, but these data were not used to determine character states. This criterion was not used in the present study on both theoretical and practical grounds. The criticisms of the technique by Schaeffer *et al.* (1972) and Nelson (1978) are accepted, whilst the paucity and nature of scarid fossils (Bellwood & Schultz, 1991) makes fossils and geological precedence a poor source of information with which to determine character polarities in the Scaridae.

Phylogenetic analyses. A total of 143 characters, coded as 334 character states, were selected for inclusion in the analyses. A list of the characters and character states is given in Table 1 (Appendix IV). The character numbers given in Table 1 (Appendix IV) are used throughout the text and in the figure captions pertaining to the cladograms presented in figures 27 and 28. Characters and their respective character states were described in the previous section on the comparative morphology of the Scaridae.

The complete matrix of character states used in the analyses for the ten ingroup taxa and five outgroup taxa is given in Table 2 (Appendix IV). This table includes autapomorphic character states. These characters or character states (if terminal autapomorphies in multistate characters) were removed prior to analysis to prevent an artificial increase in the consistency index of the cladogram, whilst providing no information on relationships. Where character states are polymorphic within a genus, the condition is coded as 'P' in Table 2 (Appendix IV), but was coded as '?' in the analyses (ie, all possible states). Multi-state characters were all specified as unordered unless the probable transformation series could be inferred based on ontogenetic evidence (marked O in column 3 of Table 3, Appendix IV). In addition to the main analysis, the data set was analysed with all unordered characters removed (characters 6 and 30 were retained as removal of the terminal autapomorphic state resulted in a binary character). All characters were unweighted.

The phylogenetic analyses followed the cladistic method of Hennig (1966), using the principle of maximum parsimony for inferring phylogenies. Computational procedures were carried out using PAUP version 4.2.1 (Phylogenetic Analysis Using Parsimony; Swofford, 1985).

In all analyses the branch and bound option (BANDB) was used, an exact algorithm which guarantees to find the shortest (most parsimonious) tree or trees. To root the ingroup tree the ROOT = OUTGROUP option was used, permitting inclusion of several outgroups and enabling the program to polarise the character states in a manner ensuring global parsimony (Maddison *et al.*, 1984; Swofford, 1985). Initial analyses with no specified outgroups confirmed the monophyly of the Scaridae. Default options of HOLD = 1 and ADDSEQ = CLOSEST were used in the analyses.

Results

The analyses produced two equally parsimonious trees each 238 steps long with a consistency index of 0.697 (Fig. 27). The two trees differed only in the arrangement of the three outgroups furthest from the ingroup. In both trees, the ingroup and the two closest outgroups always formed a monophyletic assemblage with identical topologies, branch lengths and character state distributions. The cladogram of the ingroup (the Scaridae) is given in Figure 28. Analyses based on binary data only produced a single tree (topology as in Tree 2, Fig. 27) with a consistency index of 0.680.

Interpretation

This section will be presented in two parts. Firstly, the distribution of character states on the cladogram will be examined by considering each character in turn. This part of the analyses will address character polarity decisions and will assess evidence of homoplasy as a result of convergence, parallelism or reversal, in terms of the hypothesised evolutionary sequence of character state changes. These changes are considered with respect to characters in other labroid taxa. Secondly, individual clades within the ingroup cladogram will be examined, with an appraisal of the evidence supporting the monophyly of each clade. In this study the term 'monophyletic' is used following Hennig (1966), ie, referring to a group containing a single ancestral species and all descendant species or taxa, equivalent to 'holophyletic' (*cf.* Ashlock, 1971, 1972).

Character analysis. In the analyses, character states are considered **unique** if they were not recorded elsewhere in the in the Labroidei. This includes the outgroup taxa examined, additional material examined and published descriptions of additional labrid taxa, including members of the Cichlidae, Embiotocidae and Pomacentridae. Character states were considered **unreversed** if the character was retained, even if it was subject to subsequent modification. In the analyses, the use of several outgroups prevents the application of the DELTRANS option which maximises the occurrence of parallel events rather than reversals. In instances where the former may be preferred, the alternative interpretations are noted. The consistency (c) of each character (calculated after the

exclusion of terminal autapomorphies) is given in parentheses after the name of the character.

NEUROCRANIUM. 1. *Ethmoid-vomerine process* (*c* = 0.500). The cladogram indicates that an elongate ethmoid-vomerine process arose independently in *Hipposcarus* and as a synapomorphy of clade 16.

2. *Ethmoid-frontal depression* (*c* = 0.500). The loss of the ethmoid-frontal depression is a synapomorphy of clade 20, with a reversal in *Scarus*. The loss appears to be associated with an overall structural strengthening of the neurocranium, which may be related to the power of the bite (*cf.* Bellwood & Choat, 1990).

3. *Ethmoid-frontal fusion* (*c* = 0.333). The cladogram indicates that fusion of the ethmoid-frontals is the plesiomorphic condition with separation representing a synapomorphy of the Scaridae (clade 24). A reversal to

the fused condition occurs in clade 20, with separation again in *Scarus*.

4. *Reticulate ethmoid.* Autapomorphy of *Bolbometopon.*

5. *Maxillary facets on vomer* (*c* = 1.000). The cladogram indicates that anterodorsolaterally oriented facets on the vomer represent the plesiomorphic condition. A shift to a lateral or dorsolateral orientation is a synapomorphy of clade 20.

6. *Supraoccipital crest* (*c* = 1.000). In labrids and other labroid taxa, the supraoccipital crest is a simple crest with a smooth margin. The lateral flanges on the posterodorsal margin of the supraoccipital crest of scarids appear to be a unique, unreversed synapomorphy of the Scaridae, with the highly extended flanges of *Calotomus* (state 2) being a secondary modification.
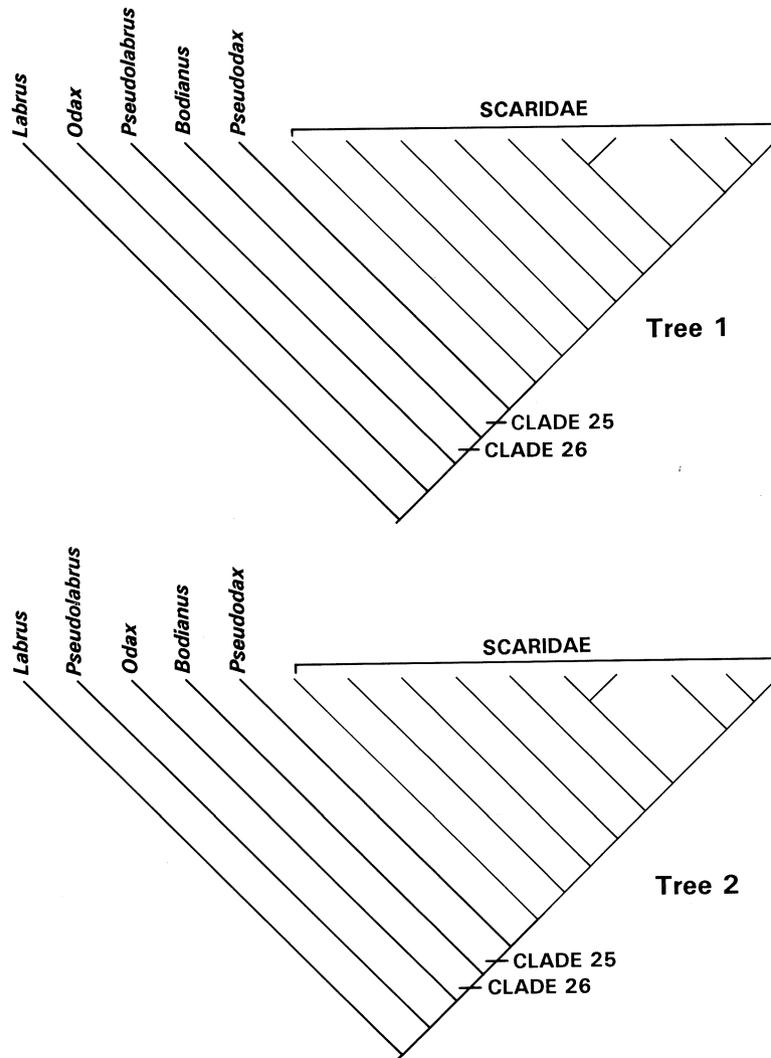
Fig. 27. Cladograms showing the relationship of the Scaridae with the outgroup taxa. Both trees have a length of 238 steps and a consistency index of 0.697. Clades are numbered arbitrarily following the analyses. Character state distributions are as follows (character numbers and character states (in parentheses) follow Table 3; synapomorphies which are unique and unreversed are in bold). *Clade 25*: 29(1), 40(2), **59(1)**, 64(1), 69(2), 73(3), **74(1)**, 81(3), **91(1)**, **92(1)**, **127(1)**. *Clade 26*: **19(1)**, 57(1), **71(1)**, **90(1)**, **104(1)**, 105(1).

7. *Exoccipital flange* (c = 1.000). A shortening of the posterior exoccipital flange, which terminates before the exoccipital condyle is a synapomorphy of clade 17.

8. *Posterior extension of epioccipital* (c = 1.000). The presence of a posterior extension (flange) of the epioccipital which forms an arch-like site of origin for the levator posterior is a unique, unreversed synapomorphy of the Scaridae (clade 24). Within the Scaridae a short posterior extension (state 1) represents the plesiomorphic condition, with a long extension being derived (state 2). An anterodorsal curving of the extension and a close association with the lateral processes of the supraoccipital crest is an autapomorphy of *Calotomus* (state 3).

9. *Deep subtemporal fossae* (c = 1.000). The possession of deep subtemporal fossae, which forms the site of origin for the 4th levator externus muscles, is a unique, unreversed synapomorphy of the Scaridae (clade 24). The cladogram indicates that the loss of the posterior

pair of fossae (state 2) is a synapomorphy of clade 18.

10. *Size of pharyngeal articulation facets* (c = 1.000). The possession of elongate pharyngeal articulation facets (length greater than 2.5 width), is a unique, unreversed synapomorphy of the Scaridae (clade 24).

11. *Shape of pharyngeal articulation facets* (c = 1.000). Facets which taper to a point anteriorly are a synapomorphy of clade 18. This condition is found in some labrids and cichlids.

12. *Curvature of pharyngeal articulation facets* (c = 1.000). Strongly concave articulation facets on either side of a sharp medial ridge represent a unique, unreversed synapomorphy of the Scaridae (clade 24).

MANDIBULAR ARCH – PREMAXILLA. 13. *Coalescence of jaw teeth* (c = 0.500). Coalescence of the teeth, representing the apomorphic state, is found in *Odax* and in clade 21. This is regarded as homoplasy. Despite a superficial similarity, the nature of the coalesced teeth
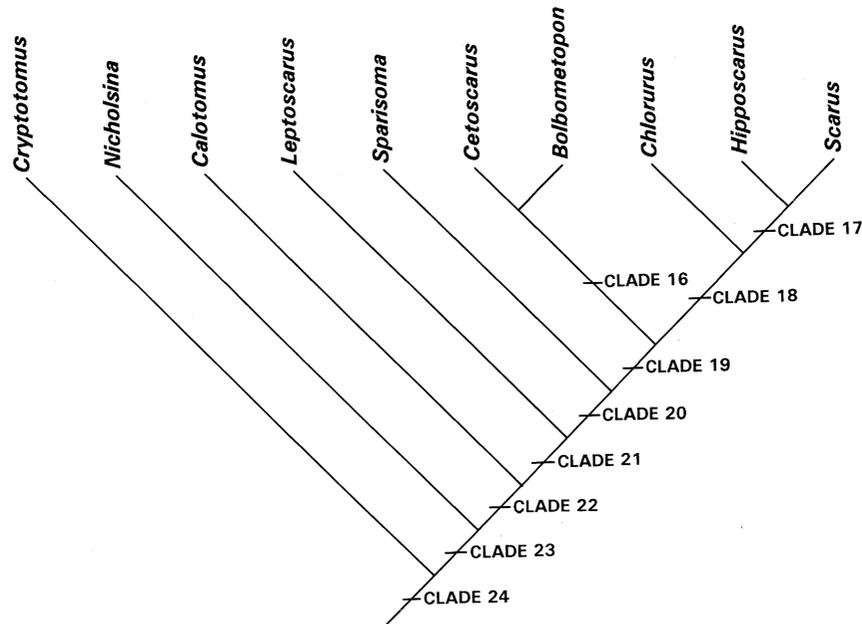
Fig. 28. Cladogram of genera within the Scaridae. Clades are numbered arbitrarily for reference following the analyses. Character state distributions are as follows (character numbers and character states (in parentheses) follow Table 3; synapomorphies which are unique and unreversed are in bold; terminal autapomorphic character states are underlined). *Clade 24*: the Scaridae, 3(1), **6(1)**, **8(1)**, **9(1)**, **10(1)**, **12(1)**, 15(1), 17(1), 21(1), 24(1), 30(1), 33(1), 34(1), 38(1), 55(1), 56(1), 58(1), 60(1), **62(1)**, 63(1), 67(2), 69(1), **70(1)**, **71(2)**, 73(1), **77(1)**, **78(1)**, **79(1)**, 81(1), 88(1), **89(1)**, 90(2), **96(1)**, 97(1), 98(0), **99(1)**, 100(1), **102(1)**, **103(1)**, 105(2), **107(1)**, 108(1), **111(1)**, 112(2), 113(1), 114(1), 115(1), 126(1), 129(1), **130(1)**, 139(1), 140(1), 141(1), 142(1). *Cryptotomus*: 19(0), 95(1). *Clade 23*: 51(1), 67(1), 76(1), 93(1), 143(1). *Nicholsina*: No synapomorphies. *Clade 22*: 8(2), 15(2), 37(1), 52(1), 63(2), **85(1)**, 87(1), 138(1), 142(2). *Calotomus*: 6(2), 8(3), 25(1), 26(1), 35(1), 95(1), 109(1). *Clade 21*: 13(1), 14(1), 19(3), 22(1), 38(0), 124(1). *Leptoscarus*: 27(1), 30(2), 33(3), 87(0), 102(2), 134(1). *Clade 20*: 2(1), 3(0), 5(1), 16(1), **20(1)**, 23(1), **28(1)**, 39(1), **45(1)**, 55(0), 69(2), 72(1), 73(2), 75(1), 79(2), 80(1), 81(2), 83(1), 84(1), 88(2), 120(2), 122(1), 128(0), **130(2)**, **131(1)**, **132(1)**. *Sparisoma*: 22(0), 31(1), 32(1), 44(1), 108(0), 120(1), 125(1), 138(2). *Clade 19*: 21(2), 34(2), 35(1), **43(1)**, **47(1)**, 49(1), 50(1), 95(1), 97(0), 101(2), 109(1), 112(1), 116(1), 140(2), 142(0). *Clade 16*: 1(1), 17(0), 19(2), **36(1)**, **41(1)**, 99(2), 110(1), **137(1)**. *Cetoscarus*: 34(1), 95(0), 135(1). *Bolbometopon*: 4(1), 18(1), 54(1), 101(1), 110(2). *Clade 18*: 9(2), 11(1), **42(1)**, 45(2), **46(1)**, 65(1), 66(1), 67(2), **68(1)**, 72(2), 73(3), **74(2)**, 81(3), **82(1)**, 92(2), **94(1)**, 98(1), 106(1), 118(1), **119(1)**, 124(2), **133(1)**, 138(0). *Chlorurus*: 40(3), 48(1), 63(3), 123(1). *Clade 17*: 7(1), 22(0), 23(0), 30(0), **33(2)**, 35(2), **39(2)**, 49(0), 50(0), 52(0), **70(2)**, 88(0), 117(1), 120(1), 121(1), 122(0). *Hipposcarus*: 1(1), 53(1), 85(2), 86(1), 98(0), 106(0), 118(0), 124(1), 136(1). *Scarus*: 2(0), 3(1), 15(0), 34(0), 40(1), 110(1), 120(0).

differs markedly. In odacids, the teeth are small and coalescence is primarily a result of fusion by the cement covering. In the scarids, the teeth are much larger and form a clear coalesced beak with or without a cement covering.

14. *Cutting edge* ($c = 0.500$). The cladogram suggests that the presence of a single entire cutting edge has arisen independently in *Odax* and clade 21.

15. *Maxillary fossa* ($c = 0.500$). Absent in all outgroups studied, the presence of this fossa appears to be a synapomorphy of the Scaridae. The cladogram indicates a change from the indistinct condition (state 1) to a relatively robust form (state 2) in clade 22. This parallels the ontogenetic sequence described in *Chlorurus* (Bellwood, 1986). The fossa is lost in *Scarus*.

16. *Conical/caniniform teeth anteriorly* ($c = 0.500$). The cladogram indicates that the presence of anterior canines is the plesiomorphic condition with an independent loss in *Pseudodax* and clade 20. The loss in *Pseudodax* is a result of flattening of the anterior teeth which are broad and incisiform. In clade 20 the teeth are lost or fused to form a dental plate.

17. *Lateral canines* ($c = 0.500$). In some labrid genera a ventrolaterally oriented canine is present at the angle of the jaws (eg, *Halichoeres, Bodianus, Stethojulis*). However, the orientation of these teeth is markedly different from the large recurved lateral canines of scarids. The cladogram suggests that the presence of lateral canines is a synapomorphy uniting the Scaridae, with a reversal to the plesiomorphic condition in clade 16.

18. *Nodules on teeth*. An autapomorphy of *Bolbometopon*, which has distinct nodules at the base of each tooth. Small, indistinct nodules are visible in large *Scarus guacamaia* and *S. coelestinus*, but were not recorded in other *Scarus* species.

19. *Cement* ($c = 0.600$). Cement (dermadentine) may be present either as a thin layer at the base of teeth (state 1), in a thin layer at the base of the dental plates (state 2) or thick layer covering the dental plates (state 3). The cladogram suggests that a thick cement layer is a synapomorphy of clade 21, with a reduction in the extent of the cement being a synapomorphy of clade 16. The absence of cement in *Cryptotomus* is considered to be a secondary loss. It is not considered to be the result of heterochrony as cement is clearly visible in specimens of a comparable size in other taxa.

20. *Tooth rows* ($c = 1.000$). The presence of six or more distinct diagonal or vertical tooth rows is a unique unreversed synapomorphy of clade 20.

21. *Jaw overlap* ($c = 0.667$). The cladogram indicates that the labroid condition with no distinct overlap and interdigitating teeth is the plesiomorphic condition. The condition in *Pseudodax* is considered to be a modified labroid condition with no distinct overlap, with interdigitation of the teeth being prevented by their great lateral flattening. In *Cryptotomus, Nicholsina, Calotomus* and *Leptoscarus* the anterior caniniform teeth overlap the teeth in the dentary although the remainder of the alveolar process and

any associated tooth ridges lie medial to the teeth on the dentary. This condition is classified as being an underslung dentary (state 1) which is exemplified by *Sparisoma* which lacks the anterior caniniform teeth. An overshot premaxilla (state 2) is a synapomorphy of clade 19 and independently derived in *Odax*. The division between overslung (state 2) versus underslung (state 1) was regarded by Schultz (1958, 1969) as a key character in the division of the Scaridae into two subfamilies, the Sparisomatinae (underslung) and the Scarinae (overslung). Whilst this subfamilial division is not supported by other characters, the nature of jaw overlap does appear to be of phylogenetic significance.

22. *Lateral depression in the premaxillary ascending process* ($c = 0.333$). A lateral depression in the ascending process of the premaxilla marking the position of the palatine dorsal process appears to have arisen in clade 21, with a subsequent reversal in *Sparisoma* and clade 17.

23. *Concave rostral cartilage site* ($c = 0.500$). A concavity in the posteroventral extremity of the ascending process, marking the location of the rostral cartilage is a synapomorphy uniting clade 20, with a reversal in clade 17.

24. *Alveolar process* ($c = 1.000$). A distal bifurcation of the alveolar process of the premaxilla is an unreversed synapomorphy of the Scaridae (clade 24).

25. *Conical teeth medial to cutting edge* ($c = 1.000$). The cladogram suggests that the presence of conical teeth medial to the cutting edge is an autapomorphy of *Calotomus*. The presence of comparable teeth in *Nicholsina* precludes this however, the teeth may have different origins. In *Nicholsina*, they form a single row anteriorly, whilst in *Calotomus* they are represented by a more diffuse patch of teeth posteriorly. More detailed analyses of the development of teeth in the oral jaws of scarids is required.

26. *Conical teeth on the ventral surface near the medial symphysis*. Autapomorphy of *Calotomus*.

27. *Origin of teeth in lateral tooth rows*. A medial origin of teeth in the lateral tooth rows is an autapomorphy of *Leptoscarus*. In all other genera, the origin is lateral.

28. *Developing tooth rows* ($c = 1.000$). The presence of large teeth in distinct diagonal or vertical tooth rows is a unique unreversed synapomorphy of clade 20.

29. *Maxillary facet* ($c = 1.000$). In the plesiomorphic condition, the maxillary facet of the premaxilla lies on the ventral surface of the premaxillary ascending process. A move to the base of the ascending process, at the angle of the ascending and alveolar processes is a synapomorphy of clade 25.

30. *Facet on distal end of alveolar process* ($c = 0.500$). The presence of a facet is a synapomorphy of the Scaridae (clade 24). The facet is often faint in *Chlorurus*, and is lost in clade 17. A convex facet (state 2) is an autapomorphy of *Leptoscarus*.

31. *Articulation facet of palatine-maxilla extending onto premaxilla*. Autapomorphy of *Sparisoma*.

MAXILLA. 32. *Grooved anterior process on maxillary arm.* Autapomorphy of *Sparisoma*.

33. *Facet of palatine articulation* (c = 1.000). The presence of a distinct concave maxillary facet (state 1) at the articulation point of the maxillary-palatine is a synapomorphy of the Scaridae (clade 24). A convex facet (state 3) is a unique autapomorphy of *Leptoscarus*, whilst a modified facet with a ventral groove (state 2) is a unique unreversed synapomorphy of clade 17.

34. *Premaxillary facet* (c = 0.500). The presence of a premaxillary facet is a synapomorphy of the Scaridae (clade 24). The cladogram suggests that a facet on the medial face of the medial process (state 1) arose first, with a subsequent movement to an anterior position (state 2) in clade 19, with a reversal to the plesiomorphic condition in *Scarus*, and from state 2 to 1 in *Cetoscarus*.

35. *Anterior maxillary-premaxillary ligament insertion* (c = 0.667). In the plesiomorphic condition, the maxillary insertion site is indistinct or marked by a shallow narrow groove. A relatively deep groove/hole (state 1) arose independently in *Calotomus* and clade 19. Subsequent modification in clade 17 resulted in an insertion site marked by a shallow concavity (state 2).

36. *Medial ridge for A1 insertion* (c = 1.000). The presence of a stout ridge on the medial face of the maxilla terminating in the insertion scar of the A1t, is a unique unreversed synapomorphy of clade 16.

DENTARY. 37. *Number of diagonal tooth rows* (c = 1.000). The cladogram indicates that within the Scaridae the plesiomorphic condition is five or less diagonal tooth rows. The presence of six or more diagonal tooth rows (usually 6 to 10) is a synapomorphy uniting clade 22. In the analyses, *Scarus* is coded '1', as although most rows are vertical, a diagonal component may be seen during ontogeny and in the adult stages of some species. In all such cases at least six rows were indicated. *Calotomus* is coded 'P' as most species have three to six rows (exceptionally up to 8).

38. *Bone ridge inside cutting edge* (c = 0.500). An anterior extension of the dorsal margin of the coronoid process is present as a bony ridge which passes medial to the posterior region of the cutting edge in *Cryptotomus*, *Nicholsina* and *Calotomus*. This is interpreted as a synapomorphy of clade 24 with a reversal in clade 21.

39. *Tooth row orientation* (c = 1.000). The cladogram indicates that in the Scaridae oblique tooth rows are the plesiomorphic condition (state 1) with a mosaic composed of both diagonal and vertical components (state 2) being a synapomorphy of clade 20. A pattern dominated by vertical rows (state 3) is a synapomorphy of clade 17.

40. *Medial suture form* (c = 0.500). The presence of medial sutures appears to be correlated with bite strength, and may be found in many labroid taxa. When present, the sutures are usually represented by a series of simple oblique ridges which interdigitate at the symphysis. The cladogram suggests that this represents the plesiomorphic condition (state 1), with irregular ridges (state 2) a synapomorphy of clade 25 (lost in *Pseudodax*). The presence of straight ridges with a distinct zig-zag posteriorly (state 3) is an autapomorphy of *Chlorurus* (this pattern is distinct in all species with the exception of *C. perspicillatus* where only a single inflection is visible). A reversal to the plesiomorphic state (state 1) is recorded in *Scarus* (a slight hint of an inflection may be seen in exceptionally large individuals).

41. *Medial suture location* (c = 1.000). In the plesiomorphic condition, the medial sutures extend to the edge of the dentary. An anterior foreshortening is a unique, unreversed synapomorphy of clade 16.

42. *Articular fossa* (c = 1.000). A deep rounded articular fossa is a unique unreversed synapomorphy of clade 18. This reflects the presence of an articulating articular-dentary joint in the three taxa in clade 18: *Chlorurus*, *Hipposcarus* and *Scarus*.

43. *Coronoid process* (c = 1.000). A greatly enlarged, deep coronoid process is a unique unreversed synapomorphy of clade 19.

44. *Notch in posterior margin of coronoid process.* Autapomorphy of *Sparisoma*.

ARTICULAR. 45. *Anterior articular ascending process* (c = 1.000). The cladogram indicates that a broad anterior ascending process is a unique unreversed synapomorphy of clade 20. Within the clade, the possession of a slight terminal notch (state 1) is the more plesiomorphic state, with a rounded end (state 2) being a synapomorphy of clade 18.

46. *Posterior ascending process* (c = 1.000). A loss of the posterior ascending process is a unique unreversed synapomorphy of clade 18.

47. *Articular medial spine* (c = 1.000). The presence of an articular medial spine is a unique unreversed synapomorphy of clade 19.

PALATINE ARCH. 48. *Entopterygoid lateral process.* Autapomorphy of *Chlorurus*.

49. *Latticework of holes in entopterygoid* (c = 0.500). The presence of holes is a synapomorphy of clade 19 with a reversal in clade 17.

50. *Palatine dorsal process* (c = 0.500). A short palatine dorsal process is a synapomorphy of clade 19 with a reversal in clade 17.

51. *Condyle on palatine* (c = 1.000). A distinct maxillary condyle on the palatine dorsal process is an unreversed synapomorphy of clade 23. Although not found in the outgroup taxa examined, a condyle is occasionally visible in other labrid taxa.

52. *Direction of maxillary condyle* (c = 0.500). The cladogram indicates that an anteroventrally facing condyle is plesiomorphic (state 0). A shift to a ventral/posteroventral orientation (state 1) is a synapomorphy of clade 22, and is followed by a reversal to the plesiomorphic condition in clade 17.

53. *Facet on medial face of palatine* (c = 0.500). A flat facet on the medial face of the palatine dorsal process appears to have arisen independently in *Odax* and *Hipposcarus* (see notes in Comparative Morphology section).

54. *Reticulate bone on palatine dorsal process*. Autapomorphy of *Bolbometopon*. A distinct reticulate matrix of bone on the dorsal surface of the palatine dorsal surface was only found in *Bolbometopon*. The slight reticulation in some *Calotomus* species was not considered to be homologous.

55. *Entopterygoid* (c = 0.500). An elongate entopterygoid that extends onto the posterodorsal margin of the palatine is a synapomorphy of the Scaridae (clade 24) with a reversal in clade 20.

56. *Palatine-entopterygoid joint* (c = 1.000). A strong ankylosed fusion of the palatine and entopterygoid is an unreversed synapomorphy of the Scaridae (clade 24).

HYOID ARCH. 57. *Ceratohyal-epihyal joint* (c = 1.000). The loss of distinct suturing of the ceratohyal-epihyal joint is a synapomorphy of clade 26.

58. *Trace of beryciform foramen* (c = 1.000). Although the presence of a beryciform foramen is regarded as a plesiomorphic condition in percoid fishes (Gomon, 1979), the cladogram indicates that the presence of traces of the beryciform foramen represent a synapomorphy of the Scaridae (clade 24).

59. *Ventral hypohyal* (c = 1.000). An elongate ventral hypohyal is a synapomorphy of clade 25.

60. *Number of branchiostegal rays* (c = 0.333). The number of branchiostegal rays is of limited value as a phylogenetic character as a result of variability in the outgroups. Gomon (1979) and Russell (1988) suggest that the general perciform number is 6-7; Russel regarded 5 as a derived condition in *Notolabrus*. Although the cladogram suggests that five rays is a synapomorphy of the Scaridae (clade 24), the Scaridae appears to be merely one of a number of labroid groups possessing five rays (*cf.* Gomon, 1979).

61. *Urohyal* (c = 0.500). An elongate urohyal is a synapomorphy of clade 27, with a reversal in *Pseudodax*.

62. *Urohyal anterodorsal process* (c = 1.000). The presence of a narrow anterodorsal process which lacks anteroposterior flanges, is a unique unreversed synapomorphy of the Scaridae (clade 24).

63. *Urohyal ventral aspect* (c = 1.000). The cladogram indicates that a narrow ventral process which tapers posteriorly to a point is the plesiomorphic condition (state 0). Lateral wings which flare posteriorly (state 4) are found only in *Odax* (flared wings and a low lateral profile are a unique feature of odacids; Gomon & Paxton, 1985). A spatulate ventral aspect (state 1) is a synapomorphy of the Scaridae (clade 24) and a narrow ventral aspect (state 2) a synapomorphy of clade 22. A posterior expansion (state 3) is an autapomorphy of *Chlorurus*.

64. *Urohyal posterior margin* (c = 1.000). A deeply notched urohyal is a synapomorphy of clade 25. This condition is marginal in *Pseudodax* but clear in all scarids.

BRANCHIAL ARCHES. 65. *Number of gill rakers* (c = 1.000). Gill raker counts vary widely both within and between species (Munro, 1967; Choat & Randall, 1986; Randall, 1983a). However, some divisions are apparent; a count of 35 or greater is an unreversed synapomorphy of clade 18.

66. *Form of posterior gill rakers* (c = 1.000). The presence of simple (unbranched) gill rakers is an unreversed synapomorphy of clade 18.

BRANCHIAL ARCHES – DORSAL ELEMENTS. 67. *Form of neurocranial facets* (c = 0.667). An anteroposterior curvature of the neurocranial facets is pronounced in the outgroup taxa and represents the plesiomorphic condition. In most scarids a slight curvature is retained (state 1), with straight facets (state 2) arising independently in *Cryptotomus* and clade 18.

68. *Alveolar process* (c = 1.000). A distinct anterodorsal projection of the alveolar process represents a synapomorphy of clade 18.

69. *Width/Height* (c = 0.667). The cladogram indicates that broad upper pharyngeals (W/H greater than 2.0) are plesiomorphic. A reduction in width (W/H 1-1.9; state 1) is a synapomorphy of the Scaridae (clade 24) with a marked further reduction uniting clade 20 (W/H less than 0.8; state 2). This condition appears to have arisen independently in *Pseudodax*.

70. *Number of tooth rows* (c = 1.000). Absent in all outgroup taxa examined, the presence of regular tooth rows is a unique unreversed synapomorphy of the Scaridae (clade 24). Within the family, three rows (state 1) is the plesiomorphic condition. A loss of the outer row (state 2) is a unique unreversed synapomorphy of clade 17. In some adult *Scarus* species both outer rows may be lost. The transformation series 3-2-1 is supported by ontogenetic evidence. Several taxa show a progressive reduction in size and occasional loss of the outer row during ontogeny (Bellwood, 1986).

71. *Tooth replacement pattern* (c = 1.000). The addition of cardinal teeth at the posterior margin or in fields within the dentigerous area represents the plesiomorphic condition (state 0), and was found in all the outgroup taxa examined (including Pomacentridae, Embiotocidae, Cichlidae and most labrids). Phyllodont development (state 1; described by Bellwood, 1990) was only recorded in *Bodianus* and other hypsigenyine genera (including the oblique phyllodont development of *Pseudodax*). A conveyor-like progression (state 2) is a unique, unreversed synapomorphy of the Scaridae (clade 24). This condition is interpreted as a highly modified type of phyllodont development where development has a dominant linear component with numerous functional teeth (see section on Comparative Morphology).

72. *Tooth sizes* (c = 1.000). The cladogram indicates that within the Scaridae near equal tooth sizes in each row is the plesiomorphic condition. A reduction in the

size of teeth in row 3 (state 1: row 3 less than half row 2, row 1 and 2 subequal) is a synapomorphy of clade 20, with a further reduction of both outer rows (state 2: row 3 less than half row 2 and row 2 less than half row 1) a synapomorphy of clade 18. In the analyses these character states were ordered based on the ontogenetic sequences observed in *Chlorurus* and *Scarus* (Bellwood, 1986).

73. *Dentigerous area* (c = 0.750). The cladogram suggests that the dentigerous area becomes progressively more elongate within the Scaridae. Most outgroup taxa have a broad dentigerous area (length/total width of both bones less than 0.6). An increase to 0.6 to 0.9 (state 1) is a synapomorphy of clade 24, with a further elongation to 1.0 to 2.0 (state 2) a synapomorphy of clade 20. The most elongate condition with the length more than 2.1 times the width (state 3) is a synapomorphy of clade 18. This condition appears to have arisen independently in *Pseudodax*.

74. *Shape of medial tooth* (c = 1.000). The possession of a broad, laterally expanded tooth (state 1) is a synapomorphy of clade 25. A modified tooth which is curved, narrowing medially, with all the teeth in the opposing medial rows of each upper pharyngeal bone strongly interdigitating (state 2) is a unique unreversed synapomorphy of clade 18. Character states were coded as ordered following changes observed in ontogenetic sequences (Bellwood, 1986).

75. *Medial margins of dentigerous areas* (c = 0.500). A parallel orientation of the medial margins of the upper pharyngeal dentigerous areas has arisen independently in *Pseudodax* and clade 20.

76. *Horn on posterior margin of upper pharyngeal* (c = 1.000). The cladogram suggests that the presence of a distinct horn as found in *Pseudodax* and *Cryptotomus* is the plesiomorphic condition (state 0), with a reduction (state 1) uniting clade 23. Outgroup taxa were coded as '?' as the presence or absence of a horn could not be determined with confidence in taxa with short broad upper pharyngeal bones.

77. *Epibranchial 4* (c = 1.000). A greatly expanded lateral flange on the fourth epibranchial is a unique unreversed synapomorphy of the Scaridae (clade 24).

78. *Pharyngeal valve* (c = 1.000). The presence of a pharyngeal valve is a unique unreversed synapomorphy of the Scaridae.

BRANCHIAL ARCHES – VENTRAL ELEMENTS.
79. *Number of teeth per row* (c = 1.000). The presence of teeth in even rows across the lower pharyngeal is a unique unreversed synapomorphy of the Scaridae (clade 24), with six teeth being the more plesiomorphic condition (state 1). The subsequent reduction to five teeth per row (state 2) is a synapomorphy of clade 20. In *Hipposcarus longipinnis* rows may alternate regularly between five and six teeth but in the type species *H. harid* five teeth are typical. The condition in *H. longiceps* is regarded as a modification of the 5 condition.

80. *Number of tooth rows* (c = 1.000). The presence of 11 or more tooth rows is a synapomorphy of clade 20.

81. *Shape of dentigerous area* (c = 0.750). The cladogram suggests that following the appearance of a broad rectangular dentigerous area in the Scaridae (clade 24) there has been a progressive increase in the relative length of the dentigerous area, from a length/width ratio of less than 0.7 (state 1) in clade 24, to 0.7 to 1.3 (state 2) in clade 20 and greater than 1.5 (state 3) in clade 18. This latter condition appears to have arisen independently in *Pseudodax*.

82. *Tooth shape when worn* (c = 1.000). The presence of worn teeth which result in ovoid enamel ridges is a unique unreversed synapomorphy of clade 18.

83. *Raised sides on dentigerous area* (c = 0.500). This condition has arisen independently in some odacids, *Pseudodax* and clade 20, and appears to be a result of convergence. In *Pseudodax* the raised sides are represented by an unusual series of incisiform teeth on a bone ridge around the anterior and anterolateral margins and a series of phyllodont teeth posteriorly. In scarids the ridge appears to be primarily the result of differential wearing, which is highest medially and lowest along the lateral margins.

84. *Lateral horn muscle insertion scars* (c = 1.000). A medial insertion scar (primarily of the 4th levator externus and levator posterior) which is larger than the lateral insertion scar (primarily of the 5th adductor) represents a synapomorphy of clade 20. The exact location and size of the insertion scars are not visible in *Cryptotomus*, *Nicholsina* and the outgroup taxa examined.

85. *Ridge separating insertion scars* (c = 1.000). In the plesiomorphic condition there is no ridge visible. A distinct straight ridge (state 1) is a unique unreversed synapomorphy of clade 22, with a curved ridge (state 2) an autapomorphy of *Hipposcarus*.

86. *Lateral projection of the pharyngocleithral condyle.* A lateral protrusion of the pharyngocleithral condyle beyond the insertion scars on the lateral horn is an autapomorphy of *Hipposcarus*.

87. *Lateral horn shaft* (c = 0.500). A flattened shaft which is broader than deep is a synapomorphy of clade 22, with a reversal in *Leptoscarus*.

88. *Location of keel base* (c = 0.667). In the plesiomorphic condition the keel arises anterior to the bar which crosses between the two lateral horns (state 0). The cladogram suggests that a movement of the keel base to the posterior edge of the crossbar (state 1) is a synapomorphy of the Scaridae (clade 24), with subsequent movement to the middle of the crossbar (state 2) a synapomorphy of clade 20. A reversal to the plesiomorphic condition is found in clade 17.

89. *Keel form* (c = 1.000). An elongate keel which is deep, rounded and flattened distally is a unique unreversed synapomorphy of the Scaridae (clade 24).

90. *Tooth development* (c = 1.000). Developmental patterns are complex. In the cladogram, the simple labroid pattern is plesiomorphic, with phyllodont

development (state 1) representing a derived feature of *Bodianus* and *Pseudodax* (the tooth development patterns of *Pseudodax* are complex but include phyllodont series; coded as state 1). Sequential eruption of several teeth in a transverse row (state 2) is a unique unreversed synapomorphy of the Scaridae (clade 24).

91. *Ridge on keel* (c = 1.000). The presence of a stout ridge along the anterior edge of the keel represents the plesiomorphic condition. The absence of a distinct ridge is a synapomorphy of clade 25.

92. *Keel margin* (c = 1.000). The plesiomorphic condition is represented by a simple even narrow margin. The presence of a pair of lateral flanges ventrally is a synapomorphy of clade 25. The presence of a flange which extends along the margin is a synapomorphy of clade 18.

PECTORAL GIRDLE. 93. *Articular facet on cleithrum* (c = 1.000). The presence of a distinct round facet of the pharyngocleithral joint on the cleithrum is a synapomorphy of clade 23.

94. *Medial indentation of cleithrum* (c = 1.000). An indentation immediately beneath the pharyngocleithral articulation facet is a unique unreversed synapomorphy of clade 18.

95. *Holes above cleithral facet* (c = 0.250). A lattice-work series of holes above the pharyngocleithral articulation facet appears to have arisen independently in *Cryptotomus*, *Calotomus* and clade 19, with a reversal in *Cetoscarus*.

96. *Posterior flange on posttemporal* (c = 1.000). A long posterior extension of the posttemporal which extends along the dorsal margin of the supracleithrum is a unique unreversed synapomorphy of the Scaridae (clade 24).

97. *Pectoral rays* (c = 0.500). The cladogram indicates that a decrease in the modal number of pectoral rays to 13 or less is a synapomorphy of the Scaridae (clade 24). This reduction is reversed in clade 19 with a return to the plesiomorphic condition of 14 or more rays.

PELVIC GIRDLE. 98. *Horns on symphysis of basipterygum* (c = 0.250). It is difficult to determine the polarity of this character. Distinct posterior extensions or horns on the symphysis of the basipterygum appear in several labrid genera including *Chelinus*, *Bodianus* and *Pseudodax*. The cladogram suggests that the presence of horns is a synapomorphy of clade 18 with a reversal (loss) in *Hipposcarus*.

99. *Basipterygum anterior extremities* (c = 1.000). The presence of lateral flanges (state 1) is a unique unreversed synapomorphy of the Scaridae (clade 24). In clade 16 these flanges are reduced and the extremities are broadly rounded (state 2).

AXIAL SKELETON. 100. *First neural spine* (c = 0.500). The cladogram suggests that fusion of the first neural spine to the centrum arose independently in *Odax* and the Scaridae (clade 24).

101. *Precaudal vertebrae* (c = 0.600). Variability in the number of precaudal vertebrae in the outgroups makes polarity decisions difficult. However, the cladogram suggests that an increase to ten to 11 (state 2) is a synapomorphy of clade 19, with 12 (state 1) independently derived in *Pseudodax* and *Bolbometopon*.

102. *Expanded postzygopophyses* (c = 1.000). A marked posterolateral expansion of the haemal postzygopophyses on the first two vertebrae (state 1) is a unique, unreversed synapomorphy of the Scaridae (clade 24), the flattening of the protrusion on the second vertebra (state 2) is a autapomorphy of *Leptoscarus*.

103. *Expanded flanges on parapophyses* (c = 1.000). Expanded flanges on the parapophyses of the anterior three to five vertebrae are a unique unreversed synapomorphy of the Scaridae (clade 24).

104. *Form of the first haemal spine* (c = 1.000). The presence of a relatively thin curved first haemal spine that arises from a distinct secondary haemal arch which spans across the haemapophyses of the first caudal vertebra, appears to be a synapomorphy uniting the Scaridae and the hypsigenyine labrids (*sensu* Gomon, 1979).

In other labrids the first haemal spine is usually formed by an extension of the haemapophyses which join ventrally resulting in a secondary haemal arch. The size of this arch varies greatly, and in some species, may be absent (Russell, 1988). In species where remnants of the parapophyses remain, the haemal spine is bifid proximally (as in *Notolabrus*; Russell, 1988) arising laterally from the medial surface of the parapophyses, rather than from the middle of a bridge joining the parapophyses as in hypsigenyines and scarids. The only possible reversal is the straightening of the spine in *Cetoscarus*.

105. *Number of vertebrae* (c = 0.667). Variability in the outgroups make character polarity difficult. The cladogram indicates that the possession of 25 vertebrae is a synapomorphy of the Scaridae (clade 24). However, this number is found in many labroid groups, and may be the plesiomorphic condition within the Labroidei.

DORSAL FIN. 106. *Number of predorsal bones* (c = 0.333). The plesiomorphic condition is one predorsal. Stiassny & Jensen (1987) suggest that the reduction of the number of predorsal bones from the general percoid condition of three (Smith & Bailey, 1961; Johnson, 1984) to two in the Labridae and two or fewer in the Cichlidae represents a synapomorphy uniting these two groups. Whilst it is accepted that a reduction may represent the derived condition, in this study all labrids examined had only one predorsal bone (see also Gomon, 1979; Russell, 1988). In the analyses, the loss of the predorsal bone in odacids, *Chlorurus* and *Scarus* are interpreted as an independent loss in *Odax* and clade 18, with a reversal in *Hipposcarus*. However the alternative interpretation of independent loss in *Chlorurus* and *Scarus* may be preferred.

107. *Neural spines before first dorsal pterygiophore* (c = 1.000). A reduction to one, from the plesiomorphic condition of two, appears to be a unique unreversed synapomorphy of the Scaridae (clade 24).

108. *Dorsal spines* (c = 0.333). Soft dorsal spines are a synapomorphy of the Scaridae (clade 24). A reversal to the plesiomorphic condition, ie, with pungent spines is found in *Sparisoma* and in *Calotomus zonarchus* (Bruce & Randall, 1985).

109. *Dorsal fin membrane* (c = 0.333). A continuous (as opposed to deeply incised) dorsal fin margin appears to have arisen independently in *Calotomus* and clade 19.

ANAL FIN. 110. *Pterygiophores before first haemal spine* (c = 0.333). The cladogram suggests that in the plesiomorphic condition one to two pterygiophores are present before the first haemal spine, with three pyerygiophores arising independently in *Odax*, clade 16 and *Scarus*, with a subsequent change to four being an autapomorphy of *Bolbometopon*.

CAUDAL SKELETON. 111. *Parhypural length* (c = 1.000). A foreshortened parhypural is a unique unreversed synapomorphy of the Scaridae (clade 24).

112. *Anterior protrusion on hypurals 1/2* (c = 1.000). A distinct protrusion which fully or partially closes the gap between hypurals 1+2 and the haemal spine of the penultimate vertebra (state 1) is a synapomorphy of the Scaridae (clade 24). A marked reduction of the protrusion (state 2) is a synapomorphy of clade 19. A small protrusion is present in some *Bodianus* specimens.

113. *Neural flange on penultimate vertebra* (c = 0.500). Although outgroup variability makes character polarity difficult, a short neural protrusion without a distinct flange appears to be a synapomorphy of the Scaridae (clade 24). Both large and reduced states are found in a range of other outgroup taxa, although a reduction does appear to be the derived condition (*cf.* Stiassny & Jensen, 1987).

114. *Principal caudal rays* (c = 1.000). A reduction to 7+6 principal rays (ie, rays supported by the hypurals and parhypural; as opposed to 7+7, 8+7 or 8+8 in labrids, Leis & Rennis, 1983; Russell, 1988) is a synapomorphy of the Scaridae.

LIPID IN BONES. 115. *Bone colour* (c = 1.000). When prepared by controlled maceration in boiling water or in beetle cultures, the bones of all outgroups examined contained lipid which turns brown within weeks of preparation (oxidisation?). Although there was no *Cryptotomus* material available prepared in this manner, the lack of lipid in the bones of all other scarid genera, as evidenced by pure white bones (target bone = maxilla), suggests that this condition is a unique unreversed synapomorphy of the Scaridae (clade 24).

MYOLOGY – ORAL JAWS. 116. *A1 insertion* (c = 0.500). An insertion of the tendon of the adductor mandibulae muscle section 1 (A1t) onto the premaxillary process of the maxilla, as found in most labrids, represents the plesiomorphic condition. Stiassny (1981) considered it a synapomorphy of the Labridae although this was later refuted by Stiassny & Jensen (1987). A movement of the A1t insertion to the base of the premaxillary process appears to have arisen independently in *Odax* and clade 19. This condition is similar to that in several other labroid groups (*cf.* Stiassny & Jensen, 1987).

117. *Fusion of A1 and A2* (c = 1.000). A synapomorphy of clade 17.

118. *Presence of an A1β* (c = 0.333). The analyses suggest that the presence of an A1β is a synapomorphy of clade 18 with a reversal in *Hipposcarus*. The alternative interpretation of an independent origin in *Chlorurus* and *Scarus* is equally parsimonious and may be preferred.

119. *A2 insertion* (c = 1.000). The cladogram indicates that an insertion restricted to the dentary is a unique unreversed synapomorphy of clade 18.

120. *A3 insertion* (c = 0.500). In the plesiomorphic condition the A3 inserts on the articular. The cladogram suggests that the loss of the articular insertion (state 2) is a synapomorphy of clade 20, with a shift to include the dentary (state 1) being independently derived in *Sparisoma* and clade 17. This is followed by a loss of the dentary insertion in *Scarus* which again displays the plesiomorphic condition. However, it must be noted that, because of the changes in the mechanics of the lower jaw, the functional role of the A3 in *Scarus* may differ markedly from that of the A3 in the outgroups.

121. *A3 size* (c = 0.500). A great reduction in the relative size of section A3 is a synapomorphy of clade 17.

122. *Degree of fibre pinnation* (c = 0.500). The presence of strongly pinnate fibres in the adductor muscles is a synapomorphy of clade 20. This condition is reversed in clade 17.

123. *Awε.* An autapomorphy of *Chlorurus*

124. *Posterior section of Aw (Awα)* (c = 0.400). A simple labrid-like tendinous posterior connection to the quadrate is the plesiomorphic condition. A posterior expansion of muscle fibres to form a distinct muscular bundle (state 1) is a synapomorphy of clade 21. The analyses suggest that the complete loss of the posterior connection (state 2) is a synapomorphy of clade 18, with a reversal in *Hipposcarus*. However, the alternative interpretation of an independent loss in *Chlorurus* and *Scarus* may be preferred.

125. *Awδ.* Autapomorphy of *Sparisoma*.

PHARYNGEAL APPARATUS. 126. *Origin levator posterior* (c = 1.000). A site of origin of the levator posterior which is restricted posteriorly to the epioccipital region, with no extension to the supraoccipital crest, is a synapomorphy of the Scaridae (clade 24). It must be noted, however, that there is considerable variability within the Labridae (Yamaoka 1978), and that the scarid pattern is not unique.

127. *Transversus posterior dorsalis* (*c* = 1.000). In most labrids, as in the Odacidae, Cichlidae, Embiotocidae and Pomacentridae, the transversus posterior dorsalis crosses the midline posterior to the upper pharyngeal bones (*cf.* Liem & Greenwood, 1981; Kaufman & Liem, 1982). In *Pseudodax* and all scarids, the transversus posterior dorsalis does not cross the midline. This modification is regarded as a unique unreversed synapomorphy uniting clade 25.

LIGAMENTS. 128. *Post pharyngeal ligament* (*c* = 0.500). The loss of the postpharyngeal ligament is a synapomorphy of clade 20. Although inconsistency in the outgroup makes polarity decisions difficult, the presence of a postpharyngeal ligament in several labroid groups (Yamaoka, 1978) supports the polarity decision in the analyses.

129. *Maxillary-Palatine ligament* (*c* = 1.000). A thin ligament connecting the lateral face of the maxilla to the suspensorium, near to the palatine-entopterygoid junction (a modified primordial ligament?) is present in the Labridae, Embiotocidae, Cichlidae and Pomacentridae (Anker, 1987; Stiassny & Jensen, 1987). The loss of this ligament is an unreversed synapomorphy of the Scaridae.

VISCERA. 130. *Intestinal coiling pattern* (*c* = 1.000). The presence of a distinct dextral loop (state 1; Type I) is a unreversed synapomorphy of the Scaridae and is probably unique (*cf.* Mok, 1980). A modified pattern with an additional pair of short anterior loops extending along the left side (state 2; Type II+III) is a unique unreversed synapomorphy of clade 20. Considerable individual variability is observed, with ontogenetic changes from Type I to II or III. Characters are coded based on the modal pattern of large mature specimens. In the analyses, character states were coded as ordered based on observations on the ontogenetic development of gut coiling patterns in *Chlorurus* and *Scarus* (Bellwood, 1986).

131. *Sacculation of the intestine* (*c* = 1.000). Sacculation of the intestine is a unique unreversed synapomorphy of clade 20. The slight invaginations or creases occasionally found in the intestines of *Calotomus* and *Leptoscarus* do not represent sacs. These intestines, therefore, are not considered to be sacculated.

132. *Lateral intestinal bulb* (*c* = 1.000). The presence of a lateral bulb is a unique unreversed synapomorphy of clade 20.

REPRODUCTIVE SYSTEM. 133. *Egg shape* (*c* = 1.000). A spindle-shaped egg appears to be a unique unreversed synapomorphy of clade 18.

134. *Gonochorism.* Autapomorphy of *Leptoscarus.*

JUVENILE COLOUR PATTERNS. 135. *Dorsal fin with distinct anterior ocellus.* An ocellus in the dorsal fin of the juvenile is an autapomorphy of *Cetoscarus.*

136. *Juvenile with single body stripe.* A single body stripe terminating in a dark dot posteriorly is an autapomorphy of *Hipposcarus.*

EXTERNAL MORPHOLOGY. 137. *Posterior nostrils* (*c* = 1.000). A posterior nostril more than twice the size of the anterior nostril (with the nostrils separated by a small gap) is a unique unreversed synapomorphy of clade 16.

138. *Fleshy flap on anterior nostril* (*c* = 0.500). In te plesiomorphic condition the flap is either absent or simple and less than half the distance to the posterior nostril. An elongate flap almost touching or extending beyond the posterior nostril (state 1) is a synapomorphy of clade 22, with a reversal to the plesiomorphic condition in clade 18. A long branched flap (state 2) is an autapomorphy of *Sparisoma.*

139. *Median predorsal scales* (*c* = 1.000). A reduction in the number of median predorsal scales to seven or less is a synapomorphy of the Scaridae (clade 24).

140. *Cheek scale rows* (*c* = 1.000). The plesiomorphic condition is represented by numerous rows of small scales. The presence of a single row of five to seven large scales (state 1) is a synapomorphy of the Scaridae (clade 24), the presence of two to four rows of large scales is a synapomorphy of clade 19.

141. *Lateral line* (*c* = 1.000). In the cladogram, the plesiomorphic condition is represented by a continuous lateral line, with an interruption of one/two scale row(s) representing a synapomorphy of the Scaridae (clade 24). However, it must be noted that several labrid taxa also have an interrupted lateral line (Webb, 1990).

142. *Gill membranes* (*c* = 0.667). In the plesiomorphic condition the gill membranes are not attached to the isthmus and form a deep free fold posteriorly. A broad attachment to the isthmus with no free fold (state 1) is a synapomorphy of the Scaridae (clade 24), whilst a broad attachment with a free fold (state 2) is a synapomorphy of clade 22. In clade 19 there is a reversal to the plesiomorphic condition.

143. *Head profile* (*c* = 1.000). A sloping or rounded profile is a synapomorphy of clade 23.

Clade Analysis

In the following section, the clades that comprise the cladogram given in Figure 28 and their respective synapomorphies are discussed. Each clade is numbered as in Figure 28, this is followed by its name or included taxa, and by a list of its synapomorphies, giving the character number (following Table 1, Appendix IV) and character state in parentheses. Synapomorphies which are unique and unreversed are listed in bold. Character states are considered unique if they are not recorded elsewhere in the Labroidei (*sensu* Kaufman & Liem, 1982). Unreversed characters are only referred to in clades with two or more taxa. Terminal autapomorphic character states are underlined. The correspondence between the cladogram and the formal classification of the family is addressed in the following discussion.

Clade 24. The Scaridae [3(1), **6(1)**, **8(1)**, **9(1)**, **10(1)**, **12(1)**, 15(1), 17(1), 21(1), 24(1), 30(1), 33(1), 34(1), 38(1), 55(1), 56(1), 58(1), 60(1), **62(1)**, 63(1), 67(2), 69(1), **70(1)**, **71(2)**, 73(1), **77(1)**, **78(1)**, **79(1)**, 81(1), 88(1), **89(1)**, 90(2), **96(1)**, 97(1), 98(0), **99(1)**, 100(1), **102(1)**, **103(1)**, 105(2), **107(1)**, 108(1), **111(1)**, 112(2), 113(1), 114(1), 115(1), 126(1), 129(1), **130(1)**, 139(1), 140(1), 141(1), 142(1)]. The family is defined by 54 synapomorphies, of which 19 are unique and unreversed. These latter characters are related to the structure of the pharyngeal apparatus (8, 9, 10, 12, 70, 71, 77, 78, 79, 89, 102, 103), the dorsal fin (107), the caudal skeleton (111), the neurocranium (6), the urohyal (62), the posttemporal (96), the basipterygum (99) and the intestinal coiling pattern (130). Although dominated by pharyngeal characters there is a wide range of characters from other functional systems. The pharyngeal characters include associated articulation sites on the neurocranium and insertion sites of pharyngeal muscles on the neurocranium and vertebral column.

Cryptotomus [19(0), 95(1)]. Both synapomorphies are weak, 19(0) appears to be a reversal whilst 95(1) appears to have been independently derived in *Cryptotomus*, *Calotomus* and clade 19.

Clade 23. *Nicholsina, Calotomus, Leptoscarus, Sparisoma, Cetoscarus, Bolbometopon, Chlorurus, Hipposcarus, Scarus* [51(1), 67(1), 76(1), 93(1), 143(1)]. The five synapomorphies uniting this clade are relatively weak with no unique character states.

Nicholsina There are no synapomorphies defining this taxon. Further analyses are required to determine the phyletic status of this genus.

Clade 22. *Calotomus, Leptoscarus, Sparisoma, Cetoscarus, Bolbometopon, Chlorurus, Hipposcarus, Scarus* [8(2), 15(2), 37(1), 52(1), 63(2), **85(1)**, 87(1), 138(1), 142(2)]. The monophyly of this clade is supported by nine synapomorphies including one unique unreversed synapomorphy: a ridge separating insertion scars on the lateral horn of the lower pharyngeal bone [85(1)]. These synapomorphies include pharyngeal (8, 85, 87), oral jaw (15, 37), urohyal (63) and external (138, 142) characters.

Calotomus [6(2), 8(3), 25(1), 26(1), 35(1), 95(1), 109(1)]. This genus is clearly defined by three autapomorphic character states, two of the neurocranium (6, 8) and one in the oral jaws (26). The four remaining synapomorphies are weak. All the synapomorphic character states appear to have arisen independently in other scarid taxa.

Clade 21. *Leptoscarus, Sparisoma, Cetoscarus, Bolbometopon, Chlorurus, Hipposcarus, Scarus* [13(1), 14(1), 19(3), 22(1), 38(0), 124(1)]. This is a relatively weakly defined clade. Of the six synapomorphies, not one is unique, two are subsequently reversed (19, 22), one

is a reversal (38) and one is a loss (124). Another weakness appears to be the affinities of *Leptoscarus*. Whilst *Leptoscarus* may share character states with the other members of clade 21 the exact nature of these character states often differs and homology may be questioned (particularly the oral jaw characters: 14, 19, 22). The monophyly of the other genera within the clade is strongly supported (clade 20), with the cladogram suggesting that *Leptoscarus* is the sister-group. *Leptoscarus* appears to be an anomalous monotypic genus with only loose affinities to the other taxa in clade 20.

Leptoscarus [27(1), 30(2), 33(3), 87(0), 102(2), 134(1)]. This is an unusual monotypic genus which is clearly defined by five distinct autapomorphies. Its affinity to other taxa, however, is unclear as noted above.

Clade 20. *Sparisoma, Cetoscarus, Bolbometopon, Chlorurus, Hipposcarus, Scarus* [2(1), 3(0), 5(1), 16(1), **20(1)**, 23(1), **28(1)**, 39(1), **45(1)**, 55(0), 69(2), 72(1), 73(2), 75(1), 79(2), 80(1), 81(2), 83(1), 84(1), 88(2), 120(2), 122(1), 128(0), **130(2)**, **131(1)**, **132(1)**]. This is a clearly defined clade with six unique unreversed synapomorphies associated with the oral jaws (20, 28, 45) and intestine (130, 131, 132). In addition, the monophyly of this clade is supported by 20 other synapomorphies with characters from the neurocranium (2, 3, 5), oral jaws (16, 23, 39), palatine arch (55), pharyngeal apparatus (69, 72, 73, 75, 79, 80, 81, 83, 84, 88), myology (120, 122) and ligaments (128). The number and nature of the synapomorphies defining this clade suggest that clade 20 represents a distinct phyletic lineage, characterised by significant changes in a number of functional systems, which in turn may reflect a major ecological shift in the biology of the component taxa.

Sparisoma [22(0), 31(1), 32(1), 44(1), 108(0), 120(1), 125(1), 138(2)]. A distinctive genus clearly defined by five autapomorphies based on characters from the oral jaws (31, 32, 44), myology (125) and external morphology (138). The presence of the adductor mandibulae subsection Aw (125) is a particularly unusual feature and has not been recorded previously in the Teleostei (*cf.* Winterbottom, 1974).

Clade 19. *Cetoscarus, Bolbometopon, Chlorurus, Hipposcarus, Scarus* [21(2), 34(2), 35(1), **43(1)**, **47(1)**, 49(1), 50(1), 95(1), 97(0), 101(2), 109(1), 112(1), 116(1), 140(2), 142(0)]. This is a well-defined clade with two unique unreversed synapomorphies: the presence of a deep coronoid process (43) and an articular spine (47). The 13 other synapomorphies are based on characters of the oral jaws (21, 34, 35), palatine arch (49, 50), pectoral girdle (95, 97), axial skeleton (101), dorsal fin (109), caudal skeleton (112), oral jaw myology (116), and external morphology (140, 142).

Clade 16. *Cetoscarus, Bolbometopon* [1(1), 17(0),

19(2), **36(1)**, **41(1)**, 99(2), 110(1), **137(1)**]. This is a small but well-defined clade comprising two monotypic genera. There are three unique unreversed synapomorphies: insertion of A1 on raised ridge (36), a foreshortening of the dentary medial sutures (41), and a large posterior nostril (137). Of the five remaining synapomorphies, four are unreversed within the clade (1, 17, 19, 99).

Cetoscarus [34(1), 95(0), 135(1)]. This monotypic genus is defined by one autapomorphy (135) based on the juvenile colour pattern.

Bolbometopon [4(1), 18(1), 54(1), 101(1), 110(2)]. This distinctive monotypic genus is defined by four autapomorphies based on characters from the neurocranium (4), oral jaws (18), palatine arch (54) and anal fin (110).

Clade 18. *Chlorurus, Hipposcarus, Scarus* [9(2), 11(1), **42(1)**, 45(2), **46(1)**, 65(1), 66(1), 67(2), **68(1)**, 72(2), 73(3), **74(2)**, 81(3), **82(1)**, 92(2), **94(1)**, 98(1), 106(1), 118(1), **119(1)**, 124(2), **133(1)**, 138(0)]. This is a well-defined clade with eight unique unreversed synapomorphies. These are associated with the oral jaws (42, 46), pharyngeal apparatus (74, 82), pectoral girdle (94), oral jaw myology (119) and reproductive system (133). Perhaps the most significant feature of this clade is the presence of a unique second articulation in the lower jaw, between the articular and dentary (42). This represents a major morphological innovation with no comparison within the Labroidei. The monophyly of this clade is supported by a further 15 synapomorphies.

Chlorurus [40(3), 48(1), 63(3), 123(1)]. A distinctive genus defined by four autapomorphies based on characters from the oral jaws (40), palatine arch (48), urohyal (63) and myology (123). The presence of an adductor mandibulae subsection Aw (123) is particularly distinctive and has not been recorded previously in the Teleostei (*cf.* Winterbottom, 1974).

Clade 17. *Hipposcarus, Scarus* [7(1), 22(0), 23(0), 30(0), **33(2)**, 35(2), **39(2)**, 49(0), 50(0), 52(0), **70(2)**, 88(0), 117(1), 120(1), 121(1), 122(0)]. This is a clearly defined clade, with three unique unreversed synapomorphies: a modified palatine articulation facet on the maxilla (33), dental plates with dominant vertical tooth rows (39) and the loss of the outer tooth row on the upper pharyngeals (70). There are an 13 additional synapomorphies which unite this clade. However, a large proportion of these represent reversals of character states which are synapomorphies defining clades 19 (49, 50), 20 (23, 88, 122), 21 (22, 52) and 24 (30). Many of the character states displayed in clade 17 are comparable to those found in juveniles of other taxa in the family (especially characters 30, 50, 52, 122). Clade 17 appears to be distinguished, at least in part, by paedomorphic development (ie, the retention of juvenile

characters of ancestral forms by adults of their descendants).

Hipposcarus [1(1), 53(1), 85(2), 86(1), 98(0), 106(0), 118(0), 124(1), 136(1)]. *Hipposcarus* is marked by a number of characters interpreted in the cladogram as reversals of character states which were synapomorphic in clade 18 (ie, characters 98, 106, 118, and 124). However, the alternative interpretation of parallel changes in *Chlorurus* and *Scarus* is noted, and may be preferred.

Scarus [2(0), 3(1), 15(0), 34(0), 40(1), 110(1), 120(0)]. Most of the character states synapomorphic for *Scarus* are reversals of states which are synapomorphic in clades 24 (15, 34, 40) and 20 (2, 3, 120). The paedomorphic trend seen in clade 17 is continued in *Scarus* with further evidence of paedomorphosis, the state of characters 15, 34, 40 in *Scarus* being characteristic of juvenile specimens of other scarid taxa.

Discussion

Relationships of the Scaridae with other labroid taxa. The findings of this study overwhelmingly support the monophyly of the Scaridae. There is little doubt that the Scaridae represents a distinct natural group (defined by 54 synapomorphies, 19 of which are unique and unreversed). Their relationships with other labroid taxa, however, remain unclear. Nevertheless two points may be made.

Firstly, the analyses support the widespread suggestion that *Pseudodax* is closely related to the Scaridae. Furthermore the cladogram is consistent with the suggestion of Gomon (1979) that the Scaridae, *Pseudodax* and other hypsigenyine genera form a monophyletic assemblage, with the component taxa sharing a modified first haemal spine, phyllodont tooth development (*cf.* Bellwood, 1990) and the loss of the hypurapophysis.

Secondly, there remains a striking degree of homoplasy between some scarids and odacids, raising the question of the nature of their evolution. The possibility of convergence correlated with the functional constraints of a herbivorous diet and fused oral teeth may be worth investigating, despite marked differences in their feeding modes (*cf.* Clements & Bellwood, 1988).

Phylogeny and classification of the Scaridae. The Scaridae has long been recognised as a distinctive and clearly defined family of fishes, traditionally characterised by coalesced teeth in the oral jaws and a highly modified pharyngeal apparatus (eg, Nelson, 1984; Myers, 1991; Randall *et al.*, 1990). However, in a cladistic analysis few of the traditional characters would support the monophyly of the family. Few, if any, are unique and many are not shared by all members of the family. Indeed, based on traditional characters it is

difficult to define the limits of the Scaridae. This has led some authors to question the status of the family (Kaufman & Liem, 1982).

The results of the present study strongly support the monophyly of the Scaridae but also indicate that the traditional characters are inadequate. The family lacks diagnostic external characters. The study has revealed a new suite of characters which provide diagnostic features of the family (unique unreversed synapomorphies), only a small proportion of which represent traditional characters. All are internal characters and of these, the majority are osteological.

The character states that define the family are drawn from a wide range of functional systems. This points to a major divergence from the labrid condition. It is also interesting to note that, as in other labroid taxa, the pharyngeal apparatus possesses many characters which are of phylogenetic significance. This structure appears to have been intimately associated with the evolution of the Scaridae and its component taxa.

The only previous attempt at a cladistic analysis of scarid taxa was by Bellwood (1986) who examined the phylogeny of genera in the subfamily Scarinae (sensu Schultz, 1958), using data which arose from functional analyses of species of Chlorurus and Scarus (all previously placed in the genus Scarus). This study considered 60 characters and 13 scarid taxa but was limited by the extent of missing data. Only 28 characters were employed in the analyses and in the construction of a cladogram. Despite the paucity of characters, these initial observations cast doubt upon two established taxonomic groups: the Sparisomatinae and the genus Scarus. The validity of the two scarid subfamilies, the Sparisomatinae and the Scarinae, was questioned and it was inferred that the Sparisomatinae was paraphyletic. The need for more detailed observations on sparisomatine genera was emphasised.

The genus Scarus also appeared to be paraphyletic, and it was suggested that the genus was comprised of two distinct phyletic lineages. These two groups were identified as separate functional groups by Bellwood (1986) and, subsequently, by Bellwood & Choat (1990). This distinction also appeared to have a phylogenetic basis.

These observations are supported by the data in the present study. These data indicate that the sparisomatine genera Cryptotomus, Nicholsina, Calotomus, Leptoscarus and Sparisoma represent a paraphyletic assemblage. A division of the family into two subfamilies is not supported by the data and is therefore rejected.

With regards to the familial status of the Scaridae, the results do not change my position as outlined in the introduction. That is, that fusion of the Labridae, Scaridae and Odacidae into a single family is premature. Monophyly may be a prerequisite to the recognition of the group as a family but it is not a justification. Consideration of the familial status of the Scaridae must await a detailed study of all the labroid fishes (sensu Greenwood et al., 1966) and a resolution of their

interrelationships. For now, the current familial divisions are retained in an endeavour to maintain taxonomic stability. It is nevertheless recognised that, in view of the paraphyletic nature of the Labridae sensu stricto, an appraisal of the higher classification of the labroid fishes is urgently required and that a change in the taxonomic rank of the Scaridae may be warranted.

Previous appraisals of the generic classification of the Scaridae have likewise been severely hampered by the lack of suitable external characters. The number of characters used in the present study and the nature of their distribution has resulted in a well defined cladogram. Again, the analysis is dominated by internal characters.

The cladogram presented in Figure 28, summarises the relationships between species groups within the Scaridae. Most of these groups correspond with existing genera. The data support the monophyly of Calotomus, Leptoscarus, Sparisoma, Cetoscarus, Bolbometopon and Hipposcarus. As in most cladograms, the basal taxa are relatively poorly defined, with few synapomorphies/ autapomorphies. This is the case with Cryptotomus and Nicholsina, and more detailed investigations are required to further resolve their relationships. Only one genus, Scarus, has been substantially modified from current usage. The genus Scarus sensu lato as currently used comprises two distinct phyletic lineages. In the revised classification, the vast majority of the species remain in the genus Scarus sensu stricto, with the remaining species being placed in the genus Chlorurus.

Unless the cladogram suggests otherwise, existing taxa have been retained in their current usage, to preserve taxonomic utility and nomenclatural stability. Although a cladogram may be converted into a hierarchical Linnaean classification, the results are almost invariably unwieldy. I believe that the best means of expressing relationships is by using a cladogram, where taxonomic rank is of little significance. However, taxonomic ranks do help to classify forms into readily identifiable groups in practical applications. In this study, existing taxonomic groups and their ranks have been retained if the data support their monophyly. Groups which were clearly paraphyletic have not been retained. Where the monophyly of a group could not be established, but, if at the same time, no alternative grouping was indicated by the data then the taxonomic status of that group has been retained and the need for further study noted. The revised generic classification of the Scaridae is given below. Details of this

Family	Genus	No. spp.
Scaridae	Cryptotomus	1
	Nicholsina	2
	Calotomus	5
	Leptoscarus	1
	Sparisoma	8
	Cetoscarus	1
	Bolbometopon	1
	Chlorurus	14
	Hipposcarus	2
	Scarus	45

classification, including taxonomic diagnoses, a key to genera and a list of extant species are given in the revised classification of genera of Scaridae.

Fossil record and historical biogeography. The construction of a cladogram of scarid genera provides a basis for examining biogeographic patterns in the Scaridae. By substituting areas for terminal taxa one is able to construct a hypothesis of area relationships. The examination of such area cladograms (*sensu* Humphreys & Parenti, 1986) enables one to evaluate the role that vicariance, dispersal and differential speciation/ extinction may have played in determining current distribution patterns. An area cladogram for the Scaridae is given in Figure 29.

The two main patterns that can be identified from the area cladogram are: 1) A distinct division between Indo-Pacific and Atlantic genera. Seven of the ten genera are present in only one of the two regions; 2) Only three genera have representatives in both regions, and of these, only one genus, *Scarus*, has a pantropical distribution. This genus is one of the most recent taxa, yet it is also the most abundant and widespread.

Any explanation of these patterns must account for the marked difference between Atlantic/Caribbean and Indo-Pacific faunas and the presence of the most derived genus *Scarus* in both provinces.

The major differences between the Indo-Pacific and the Caribbean scarid faunas are interpreted as a consequence of early faunal differentiation and vicariance events, followed by major differences in the history of reefs and other tropical marine habitats in the two regions during the succeeding 13 million years. The available evidence suggests that there were two major vicariance events in the historical biogeography of the Scaridae: the closure of the eastern Tethys and the closure of the Isthmus of Panama, with the

subsequent fate of the isolated scarid populations being determined by habitat associations and the patterns of habitat availability through time. These events are summarised in Table 3 (Appendix IV). The evidence which supports this series of events will be discussed below in three sections: i) differentiation of eastern and western populations prior to the closure of the eastern Tethys; ii) differential development of Caribbean/Atlantic and Indo-Pacific populations; iii) the pantropical distribution of *Scarus*.

i) DIFFERENTIATION OF EASTERN AND WESTERN POPULATIONS PRIOR TO THE CLOSURE OF THE EASTERN TETHYS. Differentiation of eastern (Indian and Pacific Ocean) and western (Atlantic, Caribbean and east Pacific) populations prior to the closure of the eastern Tethys is supported by two pieces of evidence.

A. The fossil record shows that at least one clearly differentiated scarid genus was present in the Paratethys (southern Europe) at approximately the time of the closure of the eastern Tethys.

B. There are no basal taxa present in both areas.

The oldest recorded fossil scarid is a *Calotomus* species (*C. preisli*) from the Mid-Miocene (14 Myr BP) of Europe (Bellwood & Schultz, 1991). This is the first unequivocal fossil representative of the family and clearly establishes the presence of scarids at approximately the time of the closure of the eastern Tethys (12-14 Myr BP; *cf.* Rögl & Steininger, 1983), and in the key central region of the Tethys. This supports the contention that the basal taxa were present at this time, that they had differentiated sufficiently to be placed within groups based on Recent taxa, and that scarids were present in the central Tethys and were therefore likely to be influenced by the closure of the eastern Tethys.

The lack of any pantropical basal taxa suggests that the eastern and western areas were already
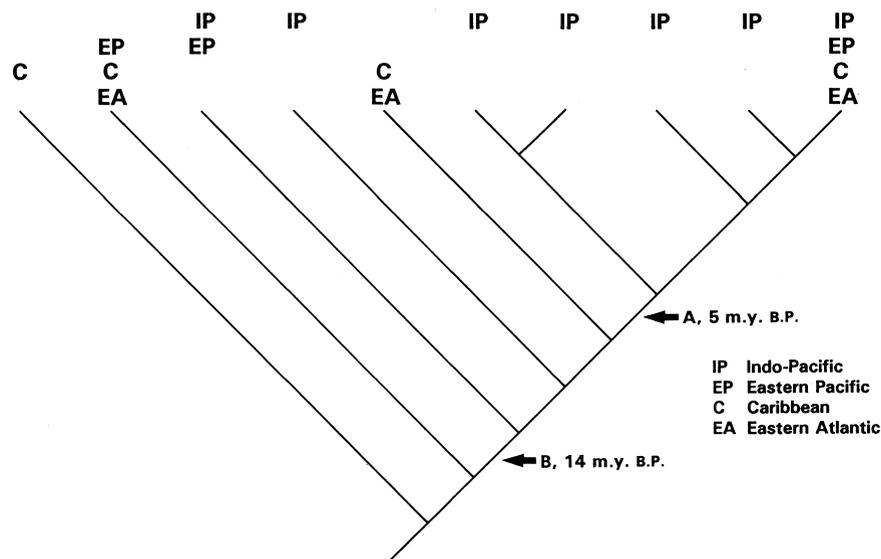

Fig. 29. Area cladogram of scarids (based on the cladogram of genera of Scaridae given in Figure 28). A and B indicate minimum ages of divergence based on fossil evidence. Details are provided in the text.

distinct at this time, each with a clearly identifiable scarid fauna: *Cryptotomus*, *Nicholsina* and *Sparisoma* in the western (Atlantic) region; *Calotomus*, *Leptoscarus*, and the ancestor of clade 19 in the eastern (Indo-Pacific) region.

The above hypothesis is proposed as the most parsimonious explanation for present day distribution patterns. The only alternative explanation would require the complete and reciprocal loss of basal taxa in the two regions (ie, the complete loss of any taxon in one region that remains in the other).

ii) DIFFERENTIAL DEVELOPMENT OF CARIBBEAN/ ATLANTIC AND INDO-PACIFIC POPULATIONS. During the 13 to 15 Myr following the closure of the eastern Tethys, the Caribbean/Atlantic/Eastern Pacific and Indo-Pacific regions have had a distinctly different history, with periods of global sea level changes and other climatic factors markedly affecting tropical faunas. This appears to have held true for the scarid populations as well.

Eastern Province: Indian and Pacific Oceans. Although the Indo-Pacific encountered numerous sea level changes throughout the late Neogene and especially in the Pleistocene it appears to have had continuity of coral reef development. Thus, although on a regional basis reefs may have disappeared, the Indo-Pacific province as a whole probably retained considerable reef habitat (*cf.* Newell, 1971; Rosen, 1988).

For reef fish taxa with a relatively long pelagic larval phase (30-50 days, Brothers, *et al.*, 1983) such regional losses would be of only minor significance and the province as a whole would have continuous availability of coral reef habitats.

The presence of a fossil fragment ascribed to the genus *Bolbometopon* in the Miocene of Sri Lanka (Bellwood & Schultz, 1991) points to the presence of the more derived reef-associated scarid taxa in the Indian Ocean during this period.

It is suggested that it is the combination of a large area and continuity of habitat availability that permitted the speciation and survival of reef associated scarid taxa in the Indo-Pacific.

Western Province: Atlantic, Caribbean and eastern Pacific. The history of the western province is in stark contrast to that of the eastern (Indo-Pacific) province. Although both provinces underwent periods of sea level change their effects in the western province were much more severe and resulted in a considerable faunal loss. There is extensive evidence of regional extinctions in the Caribbean and Eastern Pacific (Vermeij & Petuch, 1986) with reef corals being particularly susceptible to changes during the Pleistocene glaciations (Frost, 1977; Jackson *et al.*, 1985).

Given widespread faunal losses, depletion of coral taxa, marked sea level and surface temperature changes, limited geographical extent and close proximity to major land masses (and concomitant freshwater

runoff) the fate of coral reefs in the Caribbean especially during the Pleistocene glaciations was a tenuous one (Newell, 1971; Frost, 1977). These factors point to a possible cessation of coral reef growth and loss of shallow-water coral reefs over extensive areas.

However, other marine habitats may not have been equally susceptible. Seagrasses, in particular, probably fared better. Today, seagrasses are a dominant and widespread shallow water marine habitat in the Caribbean. They extend into temperate areas and thrive in coastal areas with terrigenous runoff (*cf.* Larkum & Hartog, 1989). They also represent a key habitat for three of the four Caribbean scarid genera.

The role of seagrasses as refuges for reef taxa with seagrass-dwelling representatives may have been critical during this period. The ability of seagrasses to withstand low temperatures, and to survive in areas with a relatively high sediment load and nutrient input suggest that the effects of the Pleistocene glaciations on Caribbean seagrass communities may have been much less than their impact on coral reefs.

As a significant shallow-water habitat, Caribbean coral reefs may not have had the continuity of availability as seen in the Indo-Pacific. The role of seagrasses and other off-reef habitats as refuges for reef fish taxa during the Pleistocene glaciations may have been critical in the shaping of the present-day Caribbean reef fish fauna. Indeed it may be that the modern Caribbean coral reef fish fauna is dominated by taxa which were recently seagrass and rocky-reef dwelling forms. This suggestion may, in part, explain why seagrasses in the Caribbean serve as initial habitats for reef fishes at settlement to an extent that is not seen in the Indo-Pacific (*cf.* Shulman, 1985; Shulman & Ogden, 1987; Parrish, 1989).

The Eastern Pacific seems to have suffered a similar fate to the Caribbean during the Pleistocene, but with an even greater loss of corals (Heck & McCoy, 1978) and lacking extensive seagrasses, it may have lost even more scarid species. It is interesting to note that the only scarid species with Caribbean affinities present in the Eastern Pacific is a rocky reef dwelling species, *Nicholsina denticulata*.

iii) THE PANTROPICAL DISTRIBUTION OF *SCARUS*. One of the most problematical aspects of the distribution patterns of scarid genera is the pantropical presence of *Scarus*, which is in stark contrast to all other scarid genera. The question arises of whether *Scarus* was present in the Caribbean prior to the closure eastern Tethys or if it appeared after, either arising in the Caribbean or migrating in from the Indo-Pacific prior to the closure of the Isthmus of Panama.

It is not possible, at this stage, to distinguish between these alternatives, however, the available evidence offers some support for the suggestion that *Scarus* arose in the Indo-Pacific and has repeatedly crossed the eastern Pacific barrier, both before and after the formation of the Isthmus of Panama.

Fossil evidence of the Scaridae from the Americas is

equivocal as all records appear to be misidentifications, most being oplegnathid material (Bellwood & Schultz, 1991; personal observation).

Only two genera occur on both sides of the Isthmus of Panama, *Nicholsina* and *Scarus*. *Nicholsina* is represented by two species, one in the Caribbean and Atlantic, the other in the eastern Pacific. As noted above, *Nicholsina* is one of the most basal taxa and has probably been represented in the western (Atlantic, Caribbean, east Pacific) province since at least the Mid-Miocene. The two species were presumably isolated by the formation of the Isthmus of Panama, which is a widely recognised vicariance event separating Atlantic and Pacific marine populations (Vermeij & Petuch, 1986).

The distribution patterns of *Scarus* differ markedly from all other scarid genera. There are 39 *Scarus* species in the Indian and Pacific Oceans. This includes the eastern Pacific scarid fauna, which comprises two endemics and two widespread species (*S. ghobban*, *S. rubroviolaceus*). None of these species are present in the Caribbean. There are only six *Scarus* species in the Caribbean and one in the Atlantic. All are endemic to these regions.

The presence of two widespread Indo-Pacific species in the eastern Pacific, along with sightings of a widespread *Calotomus* species, are regarded as evidence of recent dispersal events (*cf.* Rosenblatt & Hobson, 1969). This is supported by electrophoretic data on other fish taxa (Rosenblatt & Waples, 1986), which shows strong genetic links between east-Pacific and Indo-Pacific fish populations.

It is interesting to note that the two endemic Eastern Pacific *Scarus* species are similar in terms of counts and meristic values to the widespread *Scarus ghobban*. Perhaps they represent previous colonisations by a common ancestor, rather than remnants of a more widely distributed scarid fauna as suggested by Rosenblatt & Hobson (1969).

The fact that the three immediate primitive sister-groups of *Scarus* are all restricted to the Indo-Pacific suggests that *Scarus* had Indo-Pacific origins. This, combined with the presence of widespread Indo-Pacific species in the eastern Pacific and the lack of genetic isolation in some east Pacific fishes suggest that *Scarus* arose in the Indo-Pacific and was able to cross the east Pacific Barrier both prior to, and after, the final closure of the Isthmus of Panama.

The present data can not establish the origins of Caribbean *Scarus* species. However, biochemical analyses (*cf.* Rosenblatt & Waples, 1986) may provide a means of evaluating the various alternatives, whilst a cladogram of species would undoubtably offer some insight into the factors that may have determined present distribution patterns.

Overall, the patterns observed today appear to be the result of a series of vicariance events during the Cenozoic, with subsequent developments depending on habitat associations, possibly with the superimposition of relatively recent extinctions/dispersal events

following the closure of the Isthmus of Panama.

The advantage of the above explanation is that it is based on a relatively robust cladogram, incorporating taxa which have well documented distributions. In most cases the component hypotheses are refutable and therefore potentially testable. Most have a distinct time frame which makes them particularly amenable to refutation or testing by further examination of the fossil record, comparisons with molecular data sets, and comparisons with cladograms from other taxa.

The above hypotheses are specific. They refer only to the biogeography of the Scaridae. Whether the patterns observed and the explanations proposed are specific to the Scaridae or have a more general basis remains to be determined. This requires comparisons with other groups. Some comparative data on corals, echinoderms and fish are available (Rosen & Smith, 1988; Blum, 1989) which suggest that some of the patterns observed may be general ones prompting a general explanation. However, such conclusions must await a detailed appraisal of these comparative data sets. Nevertheless, these data offer exciting possibilities in the investigation of the biogeography of reef organisms.

Phylogenetic perspectives on ecology and life history. Several aspects of the ecology of scarids may be assessed in an evolutionary framework based on an examination of the cladogram.

HABITAT ASSOCIATIONS. The above observations contrasting the evolutionary history of the Scaridae in the Indo-Pacific and Caribbean, identify habitat-associations and the availability of seagrasses and off-reef habitats as key elements in the evolution of the scarid faunas in these regions. This raises several questions with regards to scarid habitat associations: in which habitat did scarids evolve? Are they a predominantly reef-associated group as generally considered? And what is their association with seagrasses?

These questions were addressed by examining the habitat associations of extant taxa in a phylogenetic framework. If the habitat associations of extant taxa are substituted for terminal taxa in the cladogram in Figure 28, the distribution of habitat use is quite striking (Fig. 30). It appears that reef associated taxa arose from seagrass dwelling forms, with the common ancestor of all scarids being a seagrass dwelling species.

The earlier suggestion of differentiation of eastern and western scarid populations prior to the terminal Tethyian event was referring predominantly to seagrass-dwelling taxa. Thus, when considering distribution patterns of the Scaridae, it is imperative to consider both seagrasses and reefs as potential habitats. The early biogeography of the family may owe more to distributions of seagrasses than to coral reefs. Indeed reef dwelling taxa may have only arisen very recently. There is, for example, no reliable evidence to suggest that reef-dwelling scarid taxa are more than 15 Myr old.

Although these observations are based on present

habitat associations, the fossil record does offer some support for inferences on past habitat associations. The earliest fossil scarid, *Calotomus preisli* Bellwood & Schultz (1991), was found in deposits bearing seagrasses. Today, this represents the dominant habitat of species in this genus.

The role of seagrass dwelling species in the evolution of marine herbivory in the Labroidei as a whole may be of considerable importance. In the Odacidae, a family of temperate water labroids, it appears that the herbivorous representatives (*Odax pullus, O. cyanomelas, O. cyanoallix*) may also have arisen from seagrass dwelling taxa. Today, most odacids, including the basal taxa, are frequently associated with seagrasses, with some including seagrasses in their omnivorous diets (Gomon & Paxton, 1985).

Seagrass dwelling scarids also include seagrasses in their diet. The possible role of seagrasses as a first step in the evolution of herbivory in the Labroidei may be worthy of further investigation.

FEEDING MODES. The cladogram in Figure 28, also gives a valuable insight into the possible evolution of feeding modes in the Scaridae. In an analysis of the feeding biology of scarids, Bellwood & Choat (1990) described two basic feeding modes: scraping and excavating. A third mode which was not described may be classified as browsing, where the teeth of the oral jaws are used to remove pieces of epilithic algae, or fragments of macroalgae or seagrasses, without scarring or scraping the substratum.

If the taxa in the cladogram in Figure 28 are replaced by adult feeding modes, a clear pattern arises, with a transition from a browsing mode to an excavating mode, and finally to a scraping mode (Figure 31). It appears that species with an excavating feeding mode arose from taxa which fed by browsing. Scraping is a relatively recent feeding mode.
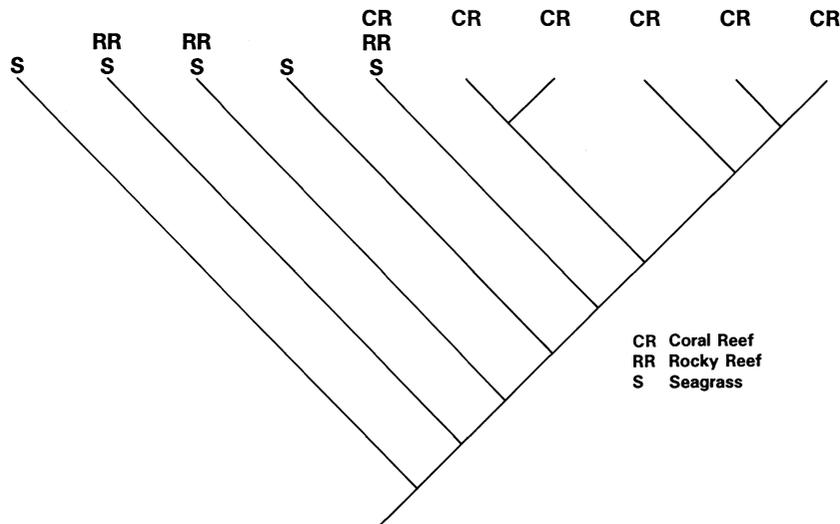

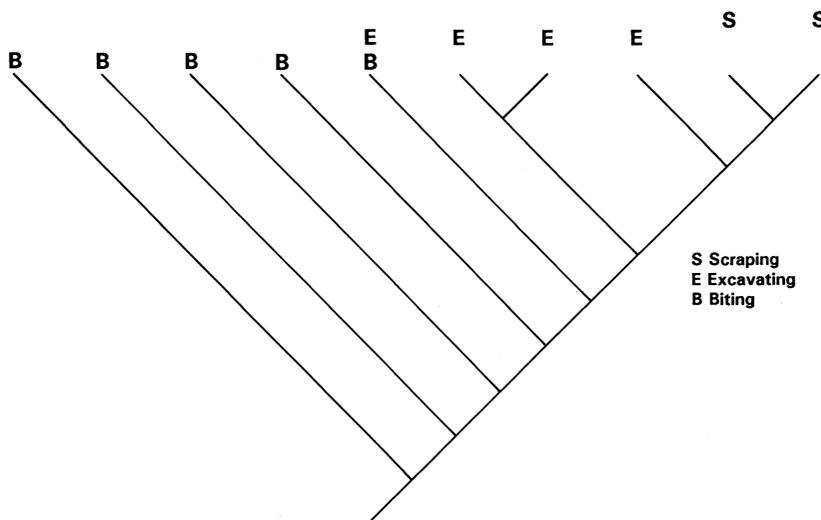**Fig. 30.** Cladogram of habitat associations of scarids (based on Figure 28).

Fig. 31. Cladogram of feeding modes of scarids (based on Figure 28).

It is interesting to note that both feeding modes are only recorded in one genus (*Sparisoma*) and that within this genus there is a clear division between species feeding in either way (an excavating feeding mode appears to have arisen independently in this genus and in clade 19). These patterns also reflect habitat utilisation patterns, with the browsers living predominantly in seagrasses and excavators predominantly on reefs. *Sparisoma* is unusual in that within the genus there is a gradation of morphological characters that mirror changes in the family as a whole, from browsing seagrass-dwelling species to excavating reef-dwelling forms. It is hypothesised that this diversity may have arisen as a result of the long isolation of *Sparisoma*, the history of environmental disturbances in the Caribbean, and the possible role of seagrasses as a refuge during these times.

Finally, the scraping mode appears to be a clear example of paedomorphosis. This type of development was suggested based on individual character state distributions but it also appears to apply to the feeding mode in general. The early juvenile stages of *Chlorurus*, *Cetoscarus* and *Bolbometopon* all feed as scrapers (*sensu* Bellwood & Choat, 1990). The excavating mode only appears in specimens above 90 mm SL (Bellwood, 1986). Morphological and field observations suggest that this also applies to those juvenile *Sparisoma* species which feed as excavators as adults (eg, *S. viride*; personal observation). The retention of a scraping feeding mode in adult *Hipposcarus* and *Scarus* species is interpreted as an example of paedomorphosis (ie, the retention of juvenile characters of ancestral forms by adults of their descendants).

Summary

The above discussion has brought to light a number of misconceptions about the Scaridae. Based on the abundance of *Scarus* species and their numerical dominance on reefs, scarids are generally regarded as reef dwelling forms that scrape the coral substratum with fused beaks-like jaws. However, inferences based on cladistic analyses indicate that although this may be the dominant view based on the numerical abundance of extant species, historically scarids may have much closer affinities with seagrasses than with coral reefs. Scarids probably arose in seagrasses as browsing herbivores which lacked fused teeth, characteristics that are retained in five of the ten extant scarid genera. The 'typical' reef dwelling scarid therefore, although numerous, may be a relatively recent form.

Revised Classification of Genera of Scaridae

One of the primary aims of this study was to provide a supra-specific classification of the Scaridae which reflects their probable phylogeny.

In the preceding sections, the major groups of species within the family have been identified and a hypothesis of their phylogenetic relationships presented. All recognised groups may be referred to previously described genera. With the exception of *Cryptotomus* and *Nicholsina*, all genera are believed to be monophyletic.

In this section a revised classification of genera of Scaridae is provided. For each genus a synonymy is given, followed by the etymology of the generic name, a short diagnosis, a definition based on external character states, a list of Recent species in the genus, notes on the geographic distribution, a short list of principal taxonomic references and a remarks section, covering taxonomic comments and notes on the biology of species in the genus.

In the definitions, external characters include apomorphic and plesiomorphic character states, internal characters refer to unique derived character states only. All genera can be assumed to possess the characters listed in the family definition.

Of the references given in this section, only original descriptions of valid genera and principal taxonomic references are provided in the list of references cited. For details of the references in the synonymies see Eschmeyer (1990).

A key to genera based on external characters is provided before the generic descriptions. A list of material examined is provided in Appendix II.

Scaridae Rafinesque, 1810

Diagnosis. Distinguished from all other labroid fishes by a wide range of derived characters (internal characters listed below), of these, the form of the pharyngeal dentition is particularly distinctive. The Scaridae is unique among perciform fishes in the possession of deep subtemporal fossae.

Definition. External – dorsal fin continuous with 9 spines and 10 rays, anal fin with 3 spines and 9 rays, dorsal and anal fins naked except for basal sheath of 1 scale row; pelvic fins I,5; pectoral fins with 2 unbranched rays (the first always rudimentary) and 11-15 branched rays; gills broadly joined to isthmus, with or without freefold. Body scales large and cycloid; lateral line interrupted, with 22-24 scales. Cheek scale rows 1-4, median predorsal scales 2-8. Oral jaw teeth may be caniniform, incisiform or coalesced to form dental plates.

Internal – neurocranium with trifid supraoccipital crest, posterior extension on epioccipital, 1-2 pairs of deep subtemporal fossae in ventral surface, elongate concave pharyngeal articulation facets; pharyngeal bones well developed, upper pharyngeal bones with teeth in 1-3 longitudinal rows, lower pharyngeal bone with series of transverse tooth rows each

comprising 5-6 teeth, teeth progress like a conveyor-belt, lower pharyngeal with greatly extended ventral keel; fourth epibranchial greatly expanded; pharyngeal valve present; posterior flange on posttemporal; anterior extremities of basipteryigium with lateral flanges; expanded postzygopophyses on first 2 vertebrae and flanges on parapophyses of anterior 3-4 vertebrae; 2 neural spines present before first dorsal pterygiophore; foreshortened parhypural; Type I-III intestinal coiling pattern.

A Key to Genera of Scaridae

This key is based on external characters and refers to adult specimens. It is based on all available characters not just derived character states. It is provided primarily as an aid to the identification of scarid genera both in the field and in museum collections. Notes on colour patterns have been excluded as patterns are often lost during fixation and preservation, and are subject to possible misinterpretation. For species identifications users are directed to the taxonomic references given under that genus in the descriptions provided below.

1. Gill membranes broadly joined to isthmus; jaws meet or upper jaw edge enclosed by lower when mouth closed; 1 cheek scale row; pectoral rays 13 (rarely 12 or 14) 2

—— Gill membranes narrowly joined to isthmus; lower jaw edge enclosed by upper when mouth closed; 2-4 cheek scale rows; pectoral rays 14-16 (rarely 13 or 17) 6

2. Individual teeth in oral jaws distinct, without cement covering; cutting edge broken or irregular 3

—— Individual teeth in oral jaws coalesced to form dental plates, with thin covering of cement (dental plates may be very narrow, on premaxilla especially); single entire cutting edge on jaws 5

3. Narrow free fold present at junction of gill membranes and isthmus 4

—— No free fold present at junction of gill membranes and isthmus (with the exception of occasional *Calotomus japonicus* specimens) (Indo-Pacific) .... *Calotomus*

4. Elongate body (depth greater than 4.0 in SL) and pointed snout; adult size 30-90 mm SL, probably does not exceed 105 mm SL; lateral tooth row of dentary not extending to angle of jaws (single row of small conical teeth may be present posteriorly) (Caribbean) .... *Cryptotomus*

—— Relatively deep body (depth less than 3.5 in SL) and snout rounded or steeply sloping; adult size greater than 100 mm SL, maximum greater than 200 mm SL; lateral tooth row of dentary not extending to angle of jaws (single row of small conical teeth may be present posteriorly) (east Pacific, Caribbean, Atlantic) .... *Nicholsina*

5. Cutting edges of jaws formed by rows of small incisiform teeth, with those on the premaxilla arising from the medial face of the jaws; stout anterior canines above cutting edge present in adults; dental plates very narrow (Indo-Pacific) .... *Leptoscarus*

—— Cutting edges of jaws formed by rows of medium-large incisiform teeth, with those on the premaxilla arising from the lateral face of the jaws; no stout anterior canines above cutting edge (occasionally small caniniform teeth near symphysis); dental plates moderately deep (Caribbean, Atlantic, Mediterranean) .... *Sparisoma*

6.   Dental plates covered with thin layer of cement basally; individual teeth visible in dental plates; no lateral canines present; posterior nostril large (more than twice size of anterior nostril); gill rakers less than 33 7

—— Dental plates covered with thick layer of cement; individual teeth visible only near cutting edge; lateral canines often present; posterior nostril small (usually of similar size to anterior nostril); gill rakers greater than 35 8

7.   Individual teeth smoothly rounded; 2 rows of scales on interoperculum; head profile evenly convex; median predorsal scales 5-7; pectoral rays 14 (occasionally 15) (Indo-Pacific) .... *Cetoscarus*

—— Individual teeth with distinct nodule basally (in specimens greater than 350 mm SL); 1 row of scales on interoperculum; head profile steep with distinct hump (greater than 200 mm SL), profile almost vertical in large individuals (greater than 600 mm SL); median predorsal scales 2-5 (usually 4); pectoral rays 15-16 (Indo-Pacific) .... *Bolbometopon*

8.   Head profile pointed with distinctly angular snout; eye near dorsal profile; dental plates relatively narrow with white cement; cheek scales small, in an isolated patch, in indistinct rows (Indo-Pacific) .... *Hipposcarus*

—— Head profile not pointed, snout blunt or rounded; eye not near dorsal profile; dental plates relatively deep with white, blue or blue-green cement; cheek scales large, in distinct rows, not in an isolated patch 9

9.   Head profile blunt; dental plates broadly exposed; vertical tooth rows alternate in possessing a tooth on the cutting edge; cutting edge crenate; pectoral fin rays 15 or more (exceptionally 14); median predorsal scales 4 (rarely 3) with no anterior pair (Indo-Pacific) .... *Chlorurus*

—— Head profile rounded; dental plates usually covered by lips; each vertical tooth row possesses a tooth on the cutting edge; cutting edge even; pectoral fin rays usually 15 or less; median predorsal scales 3-8, usually 4-6, some species with an anterior pair (circumtropical) .... *Scarus*

Cryptotomus Cope, 1870

Cryptotomus Cope 1870: 462-463. Type species *Cryptotomus roseus* Cope, 1870, by monotypy.

Etymology. Cope (1870) did not explain the etymology of the name, although it appears to be derived from the Greek terms *kripto* – hide and *tomos* – a volume or book, or a piece of a larger item, the term being akin to the term referring to the cutting or shearing action which forms the piece (Greek *tomi* – cut). The name *Cryptotomus* presumably refers to the hidden cutting teeth in this genus. In most scarids, the cutting teeth are clearly visible.

Diagnosis. Distinguished from other scarid genera by an elongate body and pointed snout, small adult size (30-90 mm SL; maximum approximately 103 mm SL), and dentary bearing pointed, flattened teeth anteriorly, but only small conical teeth at the angle of the jaws.

Definition. Body elongate with distinctly pointed snout; lips covering or almost covering teeth in both jaws; pectoral rays 13, dorsal spines flexible; median predorsal scales 4, 1 row of scales on the cheek; gill rakers 10-11; anterior nostril with raised rim but no fleshy flap; gill membranes broadly attached to isthmus with small free fold across isthmus; premaxilla with stout caniniform teeth anteriorly, a single row of small conical teeth posteriorly and in adults 1-3 recurved lateral canines, dentary with 3 rows of teeth, anterior 2 rows with flattened caniniform teeth, posterior row flat incisiform teeth (pointed prior to wear), additional row of small conical teeth present posteriorly in some specimens.

Composition. Monotypic: *roseus* Cope, 1870.

Distribution. Western Atlantic, Caribbean.

References. Randall, 1983a; Schultz, 1958, 1969.

Remarks. An unusual monotypic genus. The type species, *C. roseus*, is the smallest member of the family, growing to a maximum adult size of approximately 103 mm SL (120 mm TL). Found at depths ranging from 8 to 60 m, it is most frequently recorded in relatively shallow seagrass beds. Randall (personal communication) reports that a second species or subspecies has been collected from the northern Caribbean.

Nicholsina Fowler, 1915

Nicholsina Fowler, 1915: 3, as subgenus. Type species *Cryptotomus beryllinus* Jordan & Swain, 1884: 101 [= *Nicholsina usta* (Valenciennes) in Cuvier & Valenciennes 1840: 286], by original designation.

Xenoscarus Evermann & Radcliffe 1917: 129. Type species *X. denticulatus* Evermann & Radcliffe, 1917: 129-130, by original designation (also monotypic).

Etymology. Named after Mr John T. Nichols, an ichthyologist at the American Museum of Natural History.

Diagnosis. Distinguished from other scarid genera by the combination of 1) gill membranes broadly attached to the isthmus with a narrow free fold posteriorly and 2) the dentary bearing flattened pointed teeth with the posterior row extending to the angle of jaws.

Definition. Body moderately deep, head slopes steeply; lips covering or almost covering teeth in both jaws; pectoral rays 13, dorsal spines flexible; median predorsal scales 4 (occasionally 5), 1 row of scales on the cheek; gill rakers 12-13; short simple fleshy flap on anterior nostril; gill membranes broadly attached to isthmus with small free fold across isthmus; premaxilla with 2-4 rows of caniniform teeth anteriorly, a single row of small conical teeth posteriorly (*N. usta* only, single row of small conical teeth medial to the anterior cutting edge and in adults 1-3 recurved lateral canines), dentary with 3-5 rows of row flat incisiform teeth (pointed prior to wear; anterior 2 rows flattened caniniform in *N. usta*).

Composition. Two species: *usta* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840; *denticulata* (Evermann & Radcliffe, 1917)

Distribution. Eastern Atlantic, western Atlantic, Caribbean and eastern Pacific.

References. Randall 1983a; Schultz 1958, 1968, 1969.

Remarks. This genus is very similar to *Cryptotomus*, however, neither genus can be defined based on derived features. The status of *Nicholsina* therefore remains uncertain. A more detailed analysis of the relationships of the more basal scarid taxa is clearly needed. At this stage, the cladogram suggests that *Nicholsina* is more closely related to other scarids than it is to *Cryptotomus*. This observation, and the fact that both taxa can be distinguished by a number of features is taken as an indication that the two groups are distinct. At this stage therefore, the present generic distinctions are tentatively retained. However, further investigations are strongly recommended.

Species of *Nicholsina* may be found in rocky coastal areas, seagrass beds and deep reefs, from 0 to 80 m. Schultz (1968) recognised two subspecies, *N. usta usta* (Valenciennes) from the western Atlantic, and *N. usta collettei* Schultz from the east Atlantic. *Nicholsina denticulata* is restricted to the eastern Pacific.

Calotomus Gilbert, 1890

Calotomus Gilbert 1890: 70. Type species *Calotomus xenodon* Gilbert, 1890: 70 [= *Calotomus carolinus* (Valenciennes), in Cuvier & Valenciennes, 1840], by original designation (also monotypic).

Scaridea Jenkins 1903: 468. Type species *Scaridea zonarcha* Jenkins, 1903: 468, by original designation (also monotypic).

Etymology. Gilbert (1890) did not explain the etymology of the name *Calotomus*. However, it appears to be a combination of the Greek terms *kalloyi* − beauty and *tomos* − a volume or book, or a piece of a larger item, a term akin to that for the cutting or shearing action which forms the piece (Greek *tomi* − cut). The name *Calotomus* presumably refers to the beautiful cutting teeth of the type species.

Diagnosis. Distinguished from other scarids by 3 derived character states: extended lateral projections on the supraoccipital crest, an anterior expansion of the posterior extension of the epioccipital connecting with the lateral projections on the supraoccipital crest, and small conical teeth on the medial face of the premaxilla adjacent to the medial symphysis.

Definition. Body moderately deep, head rounded; lips covering or almost covering teeth in both jaws; pectoral rays 13, dorsal spines usually flexible; median predorsal scales 4 (occasionally 3), 1 row of scales on the cheek; gill rakers 8-14; anterior nostril with fleshy rim and simple flap which extends to or beyond posterior nostril; gill membranes broadly attached to isthmus, usually without a free fold across isthmus; premaxilla with flattened pointed teeth anteriorly, a broad group of small conical teeth posteriorly and in adults 1-4 recurved lateral canines and 1-2 conical teeth on the medial surface of the jaws close to the medial symphysis, dentary with 3-8 imbricate rows of rounded incisiform teeth, additional row of small conical teeth present posteriorly in some specimens.

Composition. Five species: *carolinus* (Valenciennes,

1840) in Cuvier & Valenciennes, 1840; *japonicus* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840; *spinidens* (Quoy & Gaimard, 1824); *viridescens* (Rüppell, 1835); *zonarchus* (Jenkins, 1903).

Distribution. Red Sea, Indian Ocean, west, central and eastern Pacific.

References. Bruce & Randall, 1985.

Remarks. Found in rocky coastal areas, seagrass beds and deep reefs, from 1 to 180 m, usually most abundant in seagrass beds. They appear to feed primarily on seagrasses, macroalgae or associated epiphytes.

Leptoscarus Swainson, 1839

Leptoscarus Swainson 1839: 172, 226. Type species *Scarus vaigiensis* Quoy & Gaimard, 1824: 288, by monotypy; misspelled *vargiensis* by Swainson 1839: 226.

Scarichthys Bleeker 1859a: 334.–Bleeker, 1859b: 17, 106-107. Type species, *Scarus naevius* Valenciennes, in Cuvier & Valenciennes, 1840: 253 (= *Scarus vaigiensis* Quoy & Gaimard, 1824: 288) designated by subsequent monotypy (Jordan, 1919: 287).

Etymology. Swainson (1839) did not explain the derivation of the name *Leptoscarus*, but is almost certainly derived from the Greek *leptos* – thin, slender and *Scarus* the ancient Greek term for parrotfish, in reference to the unusually slender body of the type species.

Diagnosis. Distinguished from all other scarids by 5 derived character states: teeth in lateral tooth rows of premaxilla arise from medial surface of the jaw, convex facet on premaxillary alveolar process, convex palatine articulation facet on maxilla, expanded and raised postzygopophyses only on first vertebra, gonochoristic.

Definition. Body elongate, head rounded; lips covering teeth in both jaws; pectoral rays 13, dorsal spines usually flexible; median predorsal scales 4 (occasionally 3), 1 row of scales on the cheek; gill rakers 8-10; anterior nostril with fleshy rim and simple fleshy flap which extends to or beyond posterior nostril; gill membranes broadly attached to isthmus without a free fold across isthmus; cutting edge of lower jaw closes over upper jaw when mouth closed; premaxilla with oblique fused rows of short even incisiform teeth along the cutting edge forming shallow dental plates, teeth arise medially, adults with stout caniniform teeth anteriorly above fused teeth on cutting edge, lateral canines present, dentary with shallow dental plates formed by oblique rows of short fused even incisiform teeth along the cutting edge.

Composition. Monotypic: *vaigiensis* (Quoy &

Gaimard, 1824).

Distribution. Red Sea, Indian Ocean, west and southern Pacific.

References. Bruce & Randall, 1985

Remarks. This is a widespread monotypic genus. The type species *L. vaigiensis*, is unusual in many ways. It is the only gonochorist in the family and it has an unusual distribution, which extends from the Red Sea throughout the Indian Ocean and the south-west Pacific Ocean as far as Easter Island. It is one of the few scarid species to extend into sub-tropical regions, yet it is absent from all central and northern Pacific Reefs. *Leptoscarus vaigiensis* is abundant in seagrass beds feeding upon the seagrasses. In areas where seagrasses are lacking, it may be found in shallow water in areas with a heavy cover of macroalgae. It may occasionally be found in dislodged algae floating near the reef.

Sparisoma Swainson, 1839

Sparisoma Swainson 1839: 172, 227. Type species *Scarus abildgaardii* Bloch 1791: 22 [= *Sparisoma viride* (Bonnaterre, 1788)], by monotypy.

Callyodontichthys Bleeker 1861: 230. No type species designated.

Euscarus Jordan and Evermann 1896: 416, as subgenus. Type species *Labrus cretensis* Linnaeus 1766: 474, by original designation.

Etymology. Swainson (1839) did not allude to the etymology of the name *Sparisoma*. Zeiller (1975) suggests that it is derived from the Greek terms *Sparus* – "I gasp", referring to the ancient Greek term for a sparoid fish, and *soma* – body. The name *Sparisoma* referring therefore, to a fish with a sparoid-like body.

Diagnosis. Distinguished from other scarids by five derived character states: palatine-maxilla articulation facet extending onto premaxilla, grooved anterior process on maxilla, distinct notch in posterior margin of coronoid process, presence of an Awδ, branched fleshy flap on anterior nostril.

Definition. Body moderately deep, head rounded; lips covering the teeth in both jaws; pectoral rays 13, dorsal spines pungent; median predorsal scales 4, 1 row of scales on the cheek; gill rakers 11-21; anterior nostril with fleshy rim and long fleshy flap, with 2-20 cirri, which extends to or beyond posterior nostril; gill membranes broadly attached to isthmus without a free fold across isthmus; teeth of lower jaw close over upper jaw; premaxilla with broadly flattened teeth, with thin cement covering, in larger specimens teeth coalesced into dental plates, lateral canines present in adults, caniform teeth present along anterior symphysis of

some species, dentary with numerous rows of broadly flattened teeth, covered with thin cement and forming dental plates in larger specimens.

Composition. Eight species: *atomarium* (Poey, 1861); *aurofrenatum* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840; *chrysopterum* (Bloch & Schneider, 1801); *cretensis* (Linnaeus, 1766); *radians* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840; *rubripinne* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840; *strigatus* (Günther, 1862); *viride* (Bonnaterre, 1788).

Distribution. Western Atlantic, Caribbean, central and eastern Atlantic, Mediterranean.

References. Randall, 1965, 1983a; Schultz, 1958, 1969.

Remarks. Found from 1 to 80 m, on reefs, in rocky coastal areas and in seagrass beds. They feed either directly on seagrasses and macroalgae or by scraping turf algae from the reef substratum. Some species may excavate the substratum when feeding.

Cetoscarus Smith, 1956

Cetoscarus Smith 1956: 16 (4). Type species *Scarus pulchellus* Rüppell, 1835: 25 [= *Scarus bicolor* Rüppell, 1829], by original designation.

Etymology. Smith (1956) did not explain the etymology of the name *Cetoscarus*. It appears to have been derived from the Greek terms *cetos* – whale or sea monster and *Scarus* the ancient Grecian word for parrotfish, possibly referring to the unusually large size attained by the type species.

Diagnosis. Distinguishes from other scarids by one derived character state: juvenile with distinct dorsal ocellus. Also distinguished by 2 rows of scales on interoperculum.

Definition. Body moderately deep, head rounded; lips largely covering dental plates; pectoral rays 14-15, dorsal spines flexible; median predorsal scales 4-7, 3 rows of scales on the cheek, interoperculum with 2 longitudinal rows (1 in all other scarid genera); gill rakers 20-24; anterior nostril with fleshy rim, posterior nostril large and oval in adults; teeth of upper jaw close over lower jaw; gill membranes broadly attached to isthmus with continuous freefold membrane; teeth in both jaws coalesced to form dental plates, plates with thin white cement covering basally, teeth stout, cutting edge crenate, exposed teeth forming a mosaic and broadly rounded on the cutting edge, no lateral canines.

Composition. Monotypic: *bicolor* (Rüppell, 1829).

Distribution. Red Sea, Indian Ocean, western, central and southern Pacific, but not Hawaii.

References. Smith, 1956; Randall & Bruce, 1983; Choat & Randall, 1986.

Remarks. A distinctive monotypic genus, found only on coral reefs. Rosenblatt & Hobson (1969) and Schultz (1969) did not recognise *Cetoscarus* as a valid genus. In both studies, it was regarded as a junior synonym of *Bolbometopon*. Randall & Bruce (1983) questioned this action and presented evidence to support the retention of the two genera.

In the present study, the phylogenetic analyses support the contention that the two genera are closely related. However, sufficient differences remain to warrant the recognition of two separate genera. Both genera possess autapomorphic character states, and additional characters which provide a practical means of distinguishing the two genera. The number and nature of the character states that distinguish these two genera are comparable to those used elsewhere within the family to recognise monophyletic polytypic taxa as genera. *Cetoscarus* and *Bolbometopon* are therefore recognised herein as full genera.

Bolbometopon Smith, 1956

Bolbometopon Smith, 1956: 8. Type species *Scarus muricatus* Valenciennes, in Cuvier & Valenciennes 1840, by original designation (also monotypic).

Etymology. Smith (1956) does not explain the etymology of the name *Bolbometopon*, which is almost certainly derived from the Greek terms *bulbus* – bulbous or swollen and *metopon* – forehead, in reference to the large hump on the forehead of adult specimens.

Diagnosis. Distinguished from all other scarids by 4 derived character states: a large mass of reticulate bone on the anterodorsal region of the ethmoid, which supports the large gibbosity on the forehead of adult specimens, distinct nodules at the base of each exposed oral jaw tooth, reticulate bone on the palatine, 4 anal pterygiophores before the first haemal spine. In addition *Bolbometopon* is characterised by a deep body, with a steep profile and a large maximum adult size.

Definition. Body deep, head with steep profile and large hump; dental plates largely exposed; pectoral rays 15-16, dorsal spines flexible; median predorsal scales 2-5, 3 rows of scales on the cheek, interoperculum with 1 longitudinal row; gill rakers 16-19; anterior nostril with fleshy rim, posterior nostril large and slit-like in adults; teeth of upper jaw close over lower jaw; teeth in both jaws coalesced to form dental plates, plates with thin white cement covering basally, teeth stout, cutting edge crenate, exposed teeth forming a mosaic each with distinct nodule basally, no lateral canines.

Composition. Monotypic: *muricatum* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840.

Distribution. Red Sea, Indian Ocean, western, central and southern Pacific, but not Hawaii.

References. Smith, 1956; Randall & Bruce, 1983; Choat & Randall, 1986.

Remarks. A very distinct monotypic genus, found only on coral reefs. *Bolbometopon muricatum* is the largest member of the family growing up to 1000 mm SL and is the only species in which live corals form a significant proportion of the diet.

Chlorurus Swainson 1839

Chlorurus Swainson 1839: 227. Type species *Scarus gibbus* Rüppell 1828: 81, by monotypy.

Pseudoscarus Bleeker 1861: 230. Type species *Scarus microrrhinos* Bleeker 1854, by subsequent designation (Jordan & Evermann 1898: 1655).

Xanothon Smith 1956: 4 (3). Type species *Callyodon bipallidus* Smith 1955, by original designation.

Ypsiscarus Schultz 1958: 33, 47, as subgenus. Type species *Callyodon oedema* Snyder 1909: 603, by original designation (also monotypic), full generic status by Schultz 1969: 4.

Etymology. Swainson (1839) did not describe the etymology of the name *Chlorurus*, although it is probably derived from the Greek prefix *chloros* – green, in reference to the brilliant green colour of the type species *C. gibbus* (Forsskål).

Diagnosis. Distinguished from other scarids by 4 unique derived character states: dentary medial sutures straight with zig-zag posteriorly, an entopterygoid lateral process, a urohyal ventral aspect which is swollen posteriorly, and the presence of an Awϵ subsection of the adductor mandibulae.

Definition. Body moderately deep, head bluntly rounded or with large hump; dental plates broadly exposed; pectoral rays 15-16 (occasionally 14), dorsal spines flexible; median predorsal scales 3-4, 2-3 rows of scales on the cheek, interoperculum with one longitudinal row; gill rakers 42-75; nostrils small and subequal; teeth of upper jaw close over lower jaw; teeth in both jaws coalesced to form dental plates, thick cement covering plates coloured white, green or blue-green, teeth stout, cutting edge crenate, lateral canines present on premaxilla.

Composition. Fourteen species: *atrilunula* (Randall & Bruce, 1983); *bleekeri* (de Beaufort, 1940) in Weber & de Beaufort, 1940; *bowersi* (Snyder, 1909); *capistratoides* (Bleeker, 1849); *cyanescens* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840; *enneacanthus* (Lacepède,

1802); *frontalis* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840; *genazonatus* (Randall & Bruce, 1983); *gibbus* (Rüppell, 1828) *; *oedema* (Snyder, 1909); *perspicillatus* (Steindachner, 1879); *japanensis* (Bloch, 1789); *sordidus* (Forsskål, 1775); *troschelii* (Bleeker, 1853).

Distribution. Red Sea, Persian Gulf, Indian Ocean, western, central and southern Pacific Ocean, and Hawaii.

References. Schultz (1958, 1969); Randall & Nelson (1979); Randall & Choat (1980); Randall (1981, 1983b); Randall & Bruce (1983); Choat & Randall (1986).

Remarks. A widespread genus found only on coral reefs. Species in this genus excavate the substratum when feeding and may play an important role in bioerosion on reefs (Bellwood & Choat, 1990).

It appears that Swainson (1839) may have confused *Chlorogaster* (p. 172) and *Chlorurus* (p. 173), as the description of *Chlorogaster* on page 172 fits the later description of *Chlorurus* on page 227. The description of *Chlorurus* on page 173 is at variance with the subsequent description (p. 227). The description of *Chlorogaster* on page 172 lacks a type species designation and contains insufficient information to refer it to any other taxon. It is therefore regarded as a *nomen nudum*. Likewise, the description of *Chlorurus* on page 173 is considered a *nomem nudum*. The genus *Chlorurus* therefore, is based on the account given on page 227, which includes a description, a figure and a nominated type species. Eschmeyer (1990: 92) regards *Chlorogaster* (p. 172; cited as p. 173) as a misspelling of *Chlorurus* (see also Eschmeyer, 1990 p. 653).

Hipposcarus Smith, 1956

Hipposcarus Smith 1956: 17 (4). Type species *Scarus harid* Forsskål, 1775: 30, by original designation (also monotypic).

Etymology. Smith (1956) did not refer to the etymology of the generic name, however, it is almost certainly derived from the Latin *hippo* – horse (Greek *ippos*), in reference to the elongate snout of the type species which Smith (1956) describes as a "typical horse-like snout".

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* Some authors regard *C. gibbus* as a species complex comprising *C. gibbus* in the Red Sea, *C. strongylocephalus* (Bleeker, 1854) in the Indian Ocean and *C. microrhinos* (Bleeker, 1854) in the western and central Pacific (see Smith, 1959; Randall & Choat, 1980; Randall & Bruce, 1983; Choat & Randall, 1986; Randall *et al.*, 1990). Colour varieties are also reported from the north-west Pacific (Masuda *et al.*, 1984) and the south Pacific (Randall & Choat, 1980). There is clearly a need for a comprehensive study of this species, or species complex, to determine the taxonomic status of the various forms.

Diagnosis. Distinguished from other scarids by 4 derived character states: articular facet on medial face of palatine, lower pharyngeal bone with a curved ridge separating the insertion scars on the lateral horns and a protruded pharyngocleithral condyle; juvenile colour pattern with a single body stripe terminating in a dark dot posteriorly.

Definition. Body moderately deep, head angular with elongate snout; lips largely cover dental plates; pectoral rays 15, dorsal spines flexible; median predorsal scales 3-4 (usually 4), 3-4 rows of scales on the cheek, rows often irregular; gill rakers 45-65; nostrils extremely small and subequal; teeth of upper jaw close over lower jaw; teeth in both jaws coalesced to form dental plates, plates narrow, covered with white cement, teeth relatively weak, cutting edge even, lateral canines present on premaxilla.

Composition. Two species: *harid* (Forsskål, 1775); *longiceps* (Valenciennes, 1840) in Cuvier & Valenciennes, 1840.

Distribution. Red Sea, Indian Ocean, western, central and southern Pacific Ocean.

References. Smith, 1956, 1959; Schultz, 1958, 1969; Randall & Bruce, 1983; Choat & Randall, 1986.

Remarks. A distinctive genus, found in the vicinity of coral reefs, often in sheltered sandy areas near to the reef. Although only two species are recognised herein, detailed analyses of the Red Sea and Indian Ocean populations may result in a subdivision following Smith (1959).

Scarus Forsskål, 1775

Scarus Forsskål 1775: 25. Type species *Scarus psittacus* Forsskål 1775: 29, by subsequent designation (Jordan & Gilbert 1882: 938); status of type species determined by Randall & Ormond, 1978.
Callyodon Gronow 1763: 72. Non-binomial, inadmissible.
Novacula Catesby 1771: 18. Unavailable, rejected work.
Callyodon Scopoli 1777: 449 (on *Callyodon* Gronow 1763, preoccupied by *Scarus* Forsskål). Type species *Scarus croicensis* Bloch 1790, by subsequent designation (Jordan & Gilbert 1882: 606).
Callyodon Bloch 1788: 242. Type presumably *Scarus croicencis* Bloch 1790, listed in Jordan 1917: 45.
Mormyra Browne 1789: 446. Unavailable, rejected work.
Calliodon Walbaum, 1792: 649. On *Callyodon* Gronow, no type species designated.
Hemistoma Swainson 1839: (172) 226. Type species *H. reticulata* Swainson 1839: 226, based on *Scarus pepo* Bennett 1834, by monotypy.
Petronason Swainson 1839: (172) 226. Type species *Scarus psittacus* Forsskål 1775: 29, by subsequent designation (Swain 1883: 274).
Erychthys Swainson 1839: (172) 226. Type species *Scarus croicensis* Bloch 1790, by subsequent designation (Swain,

1883: 274).
Loro Jordan & Evermann 1896: 418. Type species *Scarus guacamaia* (not Parra) Cuvier, 1829, by original designation.
Margaritodon Smith 1956: 15 (4). Type species *Callyodon verweyi* Weber & de Beaufort, 1940: 15, by original designation.
Scarops Schultz 1958: 18 (16). Type species *Scarus rubroviolaceus* Bleeker 1849: 52, by original designation.
Xenoscarops Schultz 1958: 23 (16), as subgenus. Type species *Scarus perrico* Jordan & Gilbert, 1881: 357, by original designation (also monotypic).

Etymology. Forsskål (1775) did not describe the etymology of the name *Scarus*. However, *Scarus* is the ancient Greek word for parrotfish. The Greeks were familiar with the parrotfish species found along the Mediterranean shores (*Sparisoma cretense*) and were aware of its biology, the name *Scarus* most likely being derived from the Grecian term *scarizo* − to go/take to pasture, presumably referring to the grazing habits of parrotfishes.

Diagnosis. Distinguished from other scarids by the loss of the maxillary fossa on the premaxilla and straight dentary medial sutures. Also characterised by a greatly reduced A3 which inserts only on the articular.

Definition. Body moderately deep, head rounded; lips largely cover dental plates; pectoral rays 13-16 (usually 14-15), dorsal spines flexible; median predorsal scales 3-8 (usually 4-7), 2-4 rows of scales on the cheek; gill rakers 39-61; nostrils very small and subequal; teeth of upper jaw close over lower jaw; teeth in both jaws coalesced to form dental plates, cement white, green, blue-green or blue, teeth relatively weak wearing on the cutting edge, cutting edge even, most species with lateral canines on premaxilla as adults, few species also with lateral canines on dentary.

Composition. Forty five species: *altipinnis* (Steindachner, 1879); *arabicus* (Steindachner, 1902); *atropectoralis* Schultz, 1958; *caudofasciatus* (Günther, 1862); *chameleon* Choat & Randall, 1986; *coelestinus* Valenciennes, 1840, in Cuvier & Valenciennes, 1840; *coeruleus* (Bloch, 1786); *collana* Rüppell, 1835; *compressus* (Osburn & Nichols, 1916); *dimidiatus* Bleeker, 1859; *dubius* Bennett, 1828; *falcipinnis* (Playfair, 1867); *ferrugineus* Forsskål, 1775; *festivus* Valenciennes, 1840, in Cuvier & Valenciennes, 1840; *flavipectoralis* Schultz, 1958; *forsteni* (Bleeker, 1861); *frenatus* Lacepède, 1802; *fuscopurpureus* (Klunzinger, 1871); *ghobban* Forsskål, 1775; *globiceps* Valenciennes, 1840, in Cuvier & Valenciennes, 1840; *guacamaia* Cuvier, 1829; *hoefleri* (Steindachner, 1881); *iserti* (Bloch, 1789); *longipinnis* Randall & Choat, 1980; *javanicus* Bleeker, 1854*; *koputea* Randall & Choat, 1980; *niger* Forsskål, 1775; *obishime* Randall & Earle, 1993; *oviceps* Valenciennes,

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* Some authors regard *S. hypselopterus* (Bleeker, 1953) as a senior synonym of *S. javanicus* Bleeker, 1854 (eg, Myers, 1991).

1840, in Cuvier & Valenciennes, 1840; *?ovifrons* Temminck & Schlegel, 1846; *perrico* Jordan & Gilbert, 1882; *persicus* Randall & Bruce, 1983; *prasiognathos* Valenciennes, 1840, in Cuvier & Valenciennes, 1840; *psittacus* Forsskål, 1775; *quoyi* Valenciennes, 1840, in Cuvier & Valenciennes, 1840; *rivulatus* Valenciennes, 1840, in Cuvier & Valenciennes, 1840; *rubroviolaceus* Bleeker, 1849; *russelii* Valenciennes, 1840, in Cuvier & Valenciennes, 1840; *schlegeli* (Bleeker, 1861); *scaber* Valenciennes, 1840, in Cuvier & Valenciennes, 1840; *spinus* (Kner, 1868); *taeniopterus* Desmarest, 1831; *tricolor* Bleeker, 1849; *vetula* Bloch & Schneider, 1801; *viridifucatus* (Smith, 1956).

There is at least one additional species which may be referred to this genus (Randall & Myers, in preparation; *cf.* Myers, 1991). Several other forms currently placed in synonymy with species in the above list may represent distinct species and require further examination (personal observation).

Distribution. Pantropical, with representatives in the Red Sea, Persian Gulf, Indian Ocean, central and western Pacific, eastern Pacific, Caribbean and Atlantic Ocean, including the west coast of Africa. Throughout most of this range, it is numerically the dominant scarid genus.

References. Smith, 1956, 1959; Schultz, 1958, 1969; Randall, 1963, 1981, 1983a,b; Rosenblatt & Hobson, 1969; Randall & Ormond, 1978; Randall & Nelson, 1979; Randall & Choat, 1980; Randall & Bruce, 1983; Choat & Randall, 1986; Randall *et al.*, 1990.

Remarks. This is the most widespread scarid genus. The vast majority of species are found only on coral reefs with only adult *S. ghobban* being regularly reported in off-reef locations. Species in this genus form the numerically dominant scarid component in most localities. The highest diversity is in the Indo-Pacific where there are 26 widespread species and 12 regional endemics. There are six species in the Caribbean and one endemic from the west coast of Africa. Species in this genus are an important component of the herbivorous reef fish community but, unlike *Chlorurus*, they rarely excavate the substratum when feeding (Bellwood & Choat, 1990).

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APPENDIX I

Species and numbers of specimens of Scaridae examined.

(Key: *, type species; L, information taken from published literature cited in the text)

Genus	species	External	Osteology	Myology	Viscera	Reproduction
Cryptotomus	roseus *	16	6	1	1	L
Nicholsina	usta *	11	5	1	2	-
	denticulatus	6	1	1	1	.
Calotomus	carolinus *	8	4	4	5	L
	japonicus	L	1	.	.	.
	spinidens	11	5	3	5	L
	viridescens	L	.	.	.	.
	zonarchus	3	1	.	.	.
Leptoscarus	vaigiensis *	24	5	5	6	L
Sparisoma	atomarium	1	1	.	.	L
	aurofrenatum	6	6	1	1	L
	chrysopterum	6	4	1	1	L
	cretensis	20	2	1+L	3	.
	radians	8	2	1	1	L
	rubripinne	8	4	1	1	L
	strigatus	11	1	1	1	.
	viride *	7	4	1	2	L
Cetoscarus	bicolor *	9	6	6	7	3L
Bolbometopon	muricatum *	14	6	4	4	1L
Chlorurus	atrilunula	1	1	.	.	.
	bleekeri	24	6	6	8	.
	bowersi	4	3	3	3	.
	capistratoides	1	2	.	.	.
	cyanescens	L	.	.	.	.
	enneacanthus	L	.	.	.	.
	frontalis	4	4	1	1	.
	genazonatus	2	.	.	.	.
	gibbus *	22	7	5	5	L
	japanensis	5	2	2	2	.
	oedema	8	2	1	1	.
	perspicillatus	3	3	1	.	.
	sordidus	30	21	21	21	L
	troschelii	1	.	.	.	.
Hipposcarus	harid *	L	8	.	.	L
	longiceps	8	5	5	4	L
Scarus	altipinnis	5	3	3	3	L
	arabicus	L	.	.	.	.
	atropectoralis	1	.	.	.	.
	caudofasciatus	L	.	.	.	.
	chameleon	15	5	5	5	L
	coelestinus	3	4	1	1	.
	coeruleus	2	5	1	1	.
	collana	L	.	.	.	.
	compressus	L	2L	L	.	.
	dimidiatus	25	5	5	5	L
	dubius	5	2	2	2	.
	falcipinnis	L	.	.	.	.
	ferrugineus	L	.	.	.	.
	festivus	3	1	1	1	.
	flavipectoralis	23	6	6	6	L

Genus	species	External	Osteology	Myology	Viscera	Reproduction
Scarus	*forsteni*	8	3	3	5	.
	frenatus	25	11	11	11	L
	fuscopurpureus	1	.	.	.	.
	ghobban	15	6	5	5	L
	globiceps	30	21	21	21	L
	guacamaia	3	9	1	1	.
	hoefleri	6	1	.	.	.
	iserti	5	4	1	.	L
	javanicus	2	1	.	.	.
	koputea	2	.	.	.	.
	longipinnis	3	1	1	1	.
	niger	25	8	8	8	L
	obishime	L	.	.	.	.
	oviceps	10	8	8	4	L
	ovifrons	?1	L	.	.	.
	perrico	1	2L	L	.	.
	persicus	1	.	.	1	.
	prasiognathos	11	4	4	4	.
	psittacus *	25	6	6	6	L
	quoyi	15	5	5	5	.
	rivulatus	25	6	6	6	L
	rubroviolaceus	14	6	6	4	L
	russellii	L	.	.	.	.
	schlegeli	25	5	5	5	L
	scaber	2	9	.	.	.
	spinus	9	3	3	3	L
	taeniopterus	L	1	.	.	.
	tricolor	12	4	8	4	.
	vetula	3	5	1	1	L
	viridifucatus	L	6	.	.	.

APPENDIX II

Material held in Museum collections

The following lists provide details of specimens examined in museum collections and voucher material deposited in these collections. Material is listed as follows: institutional abbreviation, registration number(s), number of specimens and standard length(s) in mm. The nature of the material is designated as follows: CS - cleared and stained; X - radiograph; AS - articulated skeleton; O - disarticulated osteological preparation; DF - material dissected when fresh (only osteological material retained); DP - material dissected when preserved; P - material preserved in alcohol; * - type species (collection location of specimens given); p - partial specimen or isolated elements. Institutional abbreviations: AMNH – American Museum of Natural History, New York; AMS – Australian Museum, Sydney; BMNH – British Museum (Natural History), London; BPBM – Bernice P Bishop Museum, Honolulu, Hawai'i; CAS – California Academy of Sciences, San Francisco; USNM – National Museum of Natural History, Washington, DC.

OUTGROUPS

EMBIOTOCIDAE

Damalichthys vacca (1 specimen): CAS 26197, (1) O
Amphistichus rhodoterus (1 specimen): CAS 25832 (as *Holconotus rhodoterus*, 1)(O)

POMACENTRIDAE

Chromis punctipinnis (1 specimen): CAS 62851 (1:213)(O)

ODACIDAE

Odax pullus (1 specimen: 285 mm SL): BMNH 1893-12-13:14 (1:285)(AS)

LABRIDAE

Anampses caerulopunctatus (1 specimen: 158 mm SL): AMS I. 31428-001 (1:158)(O)
A. geographicus (2 specimens: 187 - 210 mm SL): AMS I. 31194-001 (1:210)(O, DF); I. 31429-002 (1:187)(O)
Bodianus bilunulatus (1 specimen: 305 mm SL): AMS I. 31429-003 (1:305)(O, DF)
B. diana (1 specimen: 148 mm SL): AMS I. 31430-001 (1:148)(O, DF)
B. luteopunctatus (1 specimen: 128 mm SL): AMS I. 31430-002 (1:128)(O, DF)
B. mesothorax (1 specimen: 129 mm SL): AMS I. 31430-003 (1:129)(O, DF)
Chelinus diagrammus (1 specimen: 230 mm SL): AMS I. 31430-004 (1:230)(O, DF)
C. fasciatus (1 specimen: 237 mm SL): AMS I. 31431-001 (1:237)(O, DF)
C. trilobatus (2 specimens: 140 - 267 mm SL): AMS I. 31430-005 (1:267)(O); I. 31432-001 (1:140)(O, DF)
Cheilio inermis (3 specimens: 223 - 316 mm SL): AMS I. 31430-006 to 008 (3:223-316)(O, DF)
Choerodon anchorago (2 specimens: 112 - 203 mm SL): AMS I. 31430-009 (1:203)(O); I. 31431-002 (1:112)(O, DF)
C. fasciata (1 specimen: 164 mm SL): AMS I. 31433-001 (1:164)(O, DF)
C. zamboangae (1 specimen: 220 mm SL): AMS I. 31430-010 (1:220)(O, DF)
Cirrhilabrus cyanopleura (1 specimen: 91 mm SL): AMS I. 31430-011 (1:91)(O)
Coris gaimardi (1 specimen: 224 mm SL): AMS I. 31429-004 (1:224)(O, DF)
Halichoeres argus (1 specimen: 84 mm SL): AMS I. 31434-001 (1:84)(O)
Hemigymnus fasciatus (1 specimen: 195 mm SL): AMS I. 31429-005 (1:195)(O, DF)
H. melapterus (2 specimens: 230 - 260 mm SL): AMS I. 31429-006 (2:230-260)(O, DF)
Hologymnus doliatus (2 specimens: 239 - 253 mm SL): AMS I. 31430-012, 013 (2:239-253)(O, DF)
Labrus bimaculatus (1 specimen: 243 mm SL): AMS I. 31435-001 (1:243)(O, DF)
Macropharyngodon melagris (1 specimen: 120 mm SL): AMS I. 31430-014 (1:120)(O)
Novaculichthys taeniurus (1 specimen: 225 mm SL): AMS I. 31429-007 (1:225)(O, DF)
Pseudodax moluccanus (2 specimens: 157 - 185 mm SL): AMS I. 31430-015 (1:157)(O, DF). USNM 111891 (1:185)(P)
Pseudolabrus miles (1 specimen: 234 mm SL): AMS I. 31436-001 (1:234)(O, DF)
Stethojulis trilineata (1 specimen: 93 mm SL): AMS I. 31430-016 (1:93)(O)
Xyrichthys pentadactylus (1 specimen: 163 mm SL): AMS I. 31430-017 (1:163)(O, DF)

APPENDIX II (cont'd)

Species and numbers of specimens of Scaridae examined. (* - type species)

Cryptotomus roseus * (15 specimens: 36- 101 mm SL): AMNH 28712 (1)(Op). BMNH 1939.4.19:32 (Bahamas, 1:64)(DP, CS); 1879.5.22:108 (1:97)(P); 1933-10-12:73-6 (Dry Tortugas, 3:53-56)(P, CS); 1976-6-3:35 (Grand Cayman, 1:36)(P). USNM 293163 (Gulf of Mexico, Florida, 1:101)(DP); 293164 (Cuba, 1:99)(P); 178004 (Nonsuch Island, 1:95)(P); 117120 (Dry Tortugas, 2:86-87)(P); uncat. Silver Bay 2361 (2)(X); uncat. Oregon 2631 (1)(X)

Nicholsina usta * (12 specimens: 111 - 149 mm SL): BMNH 1890.2.25:30, Rio Janeiro, (1:140)(AS); 1933-10-12:69-72 (Dry Tortugas, Florida; 3:111-140)(P); 1961.9.4.:8-13 (British Guiana; 4:128-149)(P, DP). USNM 293204 (Brazil, 1:147)(DP); uncat. (3)(X)

N. denticulatus (5 specimens: 142 - 183 mm SL): USNM 202348 (3:142-160)(P); 293205 (1:183)(DP); 128112 (1)(Op)

Calotomus carolinus * (6 specimens: 192 - 256 mm SL): AMS I. 31429-008 to 010 (Apo Island, Philippines, 3:200-220)(DF, O). BMNH 1980-2-15:68, 74, 77 (Aldabra, 3:192-256)(Op)

C. japonicus (1 specimen): AMNH 57668 (1)(Op)

C. spinidens (6 specimens: 103 - 140 mm SL): AMS I. 31430-018, 019 (3:110-140)(O, DF). BMNH 1980-2-15:96 (1:103)(Op). CAS 20232 (1:131)(P), 20835 (1:114)(P)

C. zonarchus (3 specimens: 156 - 210 mm SL): AMNH uncat. (1)(Op). CAS 7099 (1:156)(P); 7441 (1:210)(P)

Leptoscarus vaigiensis * (4 specimens: 133 - 235 mm SL): AMS I. 31450-001 (Philippines, 2:133-199)(O, DF); I. 31451-001 (Philippines, 1:235)(O, DF); I. 31430-020 (Philippines, 1:235)(O, DF)

Sparisoma atomarium (1 specimen): AMNH 28221 (1)(Op)

S. aurofrenatum (9 specimens: 145 - 240 mm SL): AMNH 56947SD, 56760SD, 56888SD, 56402SD, 30831SD, 56790SD (6:180-240)(AS). BMNH 1922-2-3:60 (1:145)(P); 1931.12.5: 221-225 (1)(DP). USNM 175793, (1:211)(DP)

S. chrysopterum (6 specimens: 67 - 175 mm SL): AMNH 30747 (1)(Op). USNM uncat. (3: 67 - 97)(X); 117111 (2:160-175)(P, DP)

S. cretensis (19 specimens: 119 - 380 mm SL): AMNH 16869, 3507 (2)(Op). BMNH 1960-6-10:36-7 (2:119-185)(P); 1976-11-22:4-5 (2:235-240)(DP); 1981.2.2: 201-202 (2:353-380)(DP, P); 1976.11.22: 4-5 (DP); 1983-9-8-:188-9 (2:292-352)(P); 1983-10-11:88-90 (3:125-215)(P); 1864.6.6:21 (1)(O); 1984.3.6: 64-67 (4:155-185)(P, DP). USNM 94518 (1)(Op)

S. radians (8 specimens: 82 - 137 mm SL): BMNH 1904-6-24:24 (1:82)(P); 1923.7.30:277-278 (2:135-137)(P, DP). USNM 038676 (2:105-110)(P, DP); 163565 (1:112)(P); uncat. (2)(X)

S. rubripinne (11 specimens: 122 - 158 mm SL): BMNH 1924.7.22: 64-67, 1922-6-22:96 (5:122-158)(P,DP); 1923.7.30: 274-276 (2:143)(P, DP). USNM 293203 (1:156)(DP); 175804 (1)(Op); uncat. (2)(X)

S. strigatus (7 specimens: 225 - 380 mm SL): BMNH, 1953.8.10:10 (holotype, 1)(P); 1908.8.28:1-2 (2:225-260)(P); 1959.12.30:21 (1: 275)(P); 1985.12.6:32 (1:285)(P); 1979.1.5:146 (1:380)(DP). USNM 163446 (1)(Op)

S. viride * (10 specimens: 159 - 385 SL): AMNH 56746SD (Puerto Rico; 1:230)(AS); 22226SD (1)(Op); 56789SD, 56799SD (Puerto Rico; 2:approx. 215)(AS). BMNH 1874-10-31:10 (Bermuda, 1:approx 385)(P); 1931.12.5: 214-218 (St James, Antigua, 4:159-262)(DP, P). USNM uncat. (1)(X)

Cetoscarus bicolor * (11 specimens: 326 - 410 mm SL): AMS I. 31438-001 (Myrmidon Reef, Great Barrier Reef, 1:388)(O, DF); I. 31439-001 (Lizard Island, Great Barrier Reef, 1:486)(O); I. 31447-001 (Negros, Philippines, 1:326)(O, DF). USNM 157086, 160094, 113688, 157305, 147268, 113687, 160095 (as *Chlorurus pulchellus*) (7)(X), 157085 (1:410)(P, X)

Bolbometopon muricatum * (9 specimens: 171 - 900 mm SL): AMS I. 31437-001 (Yonge Reef, GBR, 1:613)(O, DF). BMNH 1874-11-16:5 (Palau, 1:171)(P), 1893-8-10:6 (1)(Op), 1894-10-10:10 (Solomon Island; 1:approx. 900)(AS), 1980-2-15:78 (1:927)(Op). CAS 62585, 1:205 (P). USNM 160314, 157253, 160315 (as *Chlorurus gibbus*, 3)(X)

Chlorurus atrilunula (2 specimens: 214 mm SL): BMNH 1980-2-15:181 (paratype, 1:214)(Op). USNM 226362 (paratype, 1)(P)

C. bleekeri (3 specimens: 193 - 268 mm SL): AMS I. 31430-030 (1:268)(O, DF); I. 31449-004 (1:240)(O, DF); I. 31455-007 (1:193)(O)

C. bowersi (4 specimens: 194 - 234 mm SL): AMS I. 31460-002 (1:194)(O, DF); I. 31449-002 (1:234)(O, DF). CAS 30557 (1:205)(P). USNM 062950 (holotype, 1)(X)

C. capistratoides (2 specimens): BMNH 1862-2-287 (holotype, 1)(P); BPBM 16013 (1)(Op)

C. frontalis (6 specimens: 186 - 240 mm SL): BMNH 1955-11-4:1 (1:186)(P). USNM 113671-8 (4:191-240)(P, DP); 181939 (1)(Op)

C. genazonatus (2 specimens: 199 - 255 mm SL): BMNH 1980-6-13:1 (paratype, 1:199)(P). USNM 223879 (paratype, 1:255)(P)

C. gibbus * (7 specimens: 194 - 410 mm SL): AMS I. 31448-002 (Sharm el Sheikh, Red Sea, 1:>200)(O); I. 31451-002 (Cebu, Philippines, 1:194)(O, DF); I. 31460-001, 003 (Dumaguete, Philippines, 2:410)(O, DF); I. 31463-001 (Osprey Reef, Coral Sea, 1:340)(O, DF); I. 31464-001 (Flinders Reef, Coral Sea, 1:219)(O, DF). USNM 202414 (Red Sea, 1)(Op)

C. japanensis (3 specimens: 153 - 235 mm SL): AMS I. 31449-005 (1:235)(O, DF); I. 31465-001 (1:153)(O). USNM 051754 (as *Callyodon abacurus*, holotype)(X)

C. oedema (10 specimens: 235 - 370 mm SL): USNM 062951 (holotype, 1:370)(P, X); 157033 (4:241-351)(P, DP, X); 147305 (1:240)(P); 112224 (1:235)(P); 112232 (1:352)(P); 160088 (1:325)(P); 147305 (1)(Op)

C. perspicillatus (3 specimens: 165 mm SL): AMNH 7451 (1:approx. 165)(Op); uncat. (1)(Op). USNM 08417 (as *Scarus kraussi*, holotype, 1)(X)

C. sordidus (3 specimens: 161 - 234 mm SL): AMS I. 31193-001 (1:161)(O, DF); I. 31457-002 (1:234)(O, DF); I. 31464-002 (1:219)(O)

C. troschelii (1 specimen: 288 mm SL): BMNH 1864-5-15:19 (holotype; 1:288)(P)

Hipposcarus harid * (8 specimens: >200 - 419 mm SL): AMS I. 31448-001 (Sharm el Sheik, Red Sea, 1:>200)(O). BMNH 1980-2-15:87-92 (Aldabra Island; 5:to 419)(Op).

USNM 202289 (Red Sea; 1)(Op); 202294 (Farquhar Island; 1)(Op)

H. longiceps (6 specimens: 59 - 405 mm SL): AMS I. 31194-002 (1:367)(O, DF); I. 31449-001 (2:375-400). CAS 62594 (1: 59)(CS). USNM 147269 (1:405)(P); 147412 (1:410)(P)

Scarus altipinnis (1 specimen: 340 mm SL): AMS I. 31452-001 (1:340)(O, DF)

S. atropectoralis (1 specimen: 220 mm SL): USNM 147217 (holotype, 1:220)(P)

S. chameleon (2 specimens: 254 mm SL): AMS I. 31453-001 (1)(O); I. 31454-001 (1:245)(O)

S. coelestinus (3 specimens: 178 - 365 mm SL): AMNH 35448SD, 30840SD (2:approx. 365)(AS). USNM 164283 (1:178)(DP)

S. coeruleus (5 specimens: 252 - 440 mm SL): AMNH 27954SD, 35478SD, 27957SD, 27958SD, (4:325-440)(AS). USNM 088980 (1:252)(DP)

S. compressus (2 specimens): AMNH uncat. (1)(Op). USNM 087549 (holotype, 1)(X)

S. dimidiatus (4 specimens: 198 - 247 mm SL): AMS I. 31429-011 (1:198)(O, DF); I. 31430-021 (1:247)(O, DF); I. 31455-001 (1:214)(O, DF). USNM 061170 (as *Callyodon fumifrons*, paratype, 1)(X)

S. festivus (1 specimen: 210 mm SL): AMS I. 31430-022 (1:210)(O, DF)

S. flavipectoralis (4 specimens: 186 - 234 mm SL): AMS I. 31430-023, 024 (2:208-234)(O, DF); I. 31455-002 (1:186)(O, DF); I. 31456-001 (1:222)(O, DF)

S. forsteni (3 specimens: 138 - 299 mm SL): AMS I. 31430-025 (1:138)(O, DF); I. 31449-003 (1:299)(O, DF); I. 31450-002 (1:229)(O, DF)

S. frenatus (4 specimens: 214 - 291 mm SL): AMS I. 31456-002 (1:291)(O, DF); I. 31457-001 (1:214)(O, DF). BMNH 1980-2-15:173 (1)(Op). USNM 163414 (1)(Op)

S. fuscopurpureus (1 specimen): BMHN 1871-7-15:13 (holotype; 1)(P)

S. ghobban (7 specimens: 266 - 370 mm SL): AMS I. 31454-002 (1)(O); I. 31455-003 (1:226)(O, DF); I. 31458-001 (1:370)(O, DF); I. 31459-001 (1:293)(O, DF); I. 31456-003 (1:360)(O, DF). USNM 050084 (as *Scarus noyesi*, paratype, 1)(X); 065439 (as *Chlorurus azureus*, 1)(X)

S. globiceps (1 specimens: 175 mm SL): AMS I. 31461-001 (1:175)(O, DF)

S. guacamaia (10 specimens: 189 - 700 mm SL): AMNH 56726SD (1)(AS); uncat. (1)(Op); 30826SD, 22224SD, 30862SD, 35440SD, 56501SD, 35455SD, 27956 (7:300-approx. 700)(AS). USNM 125658 (1:189)(DP)

S. hoefleri (7 specimens: 68 - 255 mm SL): BMNH 1938-12-15:21 (1:255)(P); 1951-3-12:7 (1:approx. 220)(P); 1962-9-18:142 (1:203)(P); 1977-3-21:148-151 (2:68-97)(P). USNM 164275-6 (2:131)(P,Op)

S. iserti (6 specimens: 50 - 235 mm SL): AMNH 21757SD (1:235)(AS). BMNH 1976-7-15:12-18 (1:approx. 50)(CS). USNM uncat. (as *S. croicensis*) (3)(X); 175761 (1)(Op)

S. javanicus (1 specimen: 204 mm SL): BMNH 1864-5-15:21 (holotype, 1:204)(P)

S. koputea (2 specimens: 300 mm SL): USNM 175272-3 (paratypes, 2:300)(P)

S. longipinnis (1 specimen: 75 mm SL): AMS I. 25789-001 (1:75)(DP)

S. niger (7 specimens: 185 - 282 mm SL): AMS I. 31432-002 (1:260)(O, DF); I. 31455-004 (1:240)(O, DF). BMNH 1858-4-20:210 (1:207)(AS); 1978-9-14:8 (1:185)(P), 1980-2-15:28, 30 (2:271-282)(Op). USNM 202347 (1)(Op)

S. oviceps (1 specimen: 304 mm SL): AMS I. 31456-004 (1:304)(O, DF)

S. perrico (3 specimens: 380 mm SL): AMNH uncat. (1)(Op). USNM 65440 (1:380)(P); 087548 (as *Callyodon microps*, holotype, 1)(X)

S. persicus (1 specimen: 195 mm SL): USNM 224474 (paratype, 1:195)(P)

S. prasiognathos (1 specimen: 320 mm SL): AMS I. 31430-026 (1:320)(O, DF)

S. psittacus * (4 specimens: 127 - 196 mm SL): AMS I. 31192-001 (Sharm el Sheikh, Red Sea, 1)(O); I. 31432-003 (Balicasag Island, Philippines, 1:180)(O, DF); I. 31455-005 (Lizard Island, 1:196)(O, DF). BMNH 1980-2-15:99 (1:127)(Op)

S. quoyi (2 specimens: 235 - 240 mm SL): AMS I. 31430-027 (2:235-240)(O, DF)

S. rubroviolaceus (12 specimens: 146 - 477 mm SL): AMS I. 31429-012 (1:380)(O, DF); I. 31430-028 (1:350)(O, DF). BMNH 1980-2-15:1-6, 8 (7:146-477)(Op). USNM 051749 (as *Callyodon ruberrimus*, holotype, 1)(X); 055500 (as *Chlorurus jordani*, 1)(X); 055499 (as *Scarops jordani*, 1)(X)

S. schlegeli (2 specimens: 253 - 258 mm SL): AMS I. 31429-013 (1:258)(O, DF); I. 31456-005 (1:253)(O, DF)

S. scaber (9 specimens): BMNH 1980-2-15:31-39 (9)(Op)

S. spinus (3 specimens: 185 - 197 mm SL): AMS I. 31429-014 (1:185)(O, DF); I.31454-003 (1:196)(O, DF); I. 31455-006 (1:197)(O, DF)

S. taeniopterus (1 specimen: 188 mm SL): AMNH 56404SD (1:188)(AS)

S. tricolor (3 specimens: 221 - 244 mm SL): AMS I. 31429-001 (1:221)(O, DF); I. 31430-029 (2:240-244)(O, DF)

S. vetula (6 specimens: 180 - 320 mm SL): AMNH 56745SD, 56758SD, 22538SD, 30844SD (4:approx. 245-320)(AS). BMNH 1863.8.7:96 (1:180)(AS). USNM 175803, (1:241)(DP)

S. viridifucatus (6 specimens: 183 - 239 mm SL): BMNH 1980-2-15:159, 163-7 (6:183-239)(Op)

APPENDIX III

Abbreviations used in the text figures

A1, A2, A3	Adductor mandibulae muscles divisions 1-3
A1α, A1β	Adductor mandibulae subdivisions
A3α, A3β	Adductor mandibulae subdivisions
A1t, A2t, A3t	Tendons of the adductor mandibulae (subdivisions abbreviated as A1t1, A1t2 etc.)
Aw	Adductor mandibulae muscle division Aw
Awα, Awβ, Awγ, Awδ, Awε	Adductor mandibulae muscle subdivisions
alv	Alveolar region
alv pr	Alveolar process
an	Anus
ang	Angular
ant	Anterior
ant asc pr	Anterior ascending process
ant mx pmx lig	Anterior maxillary-premaxillary ligament
ant st fos	Anterior subtemporal fossa
art med sp	Articular medial spine
art con	Articulation condyle of the pharyngeo-cleithral joint
art fos	Articulation fossa of the dentary
art fac	Articulation facet
asc pr	Ascending process of the premaxilla
bb1-4	1st to 4th basibranchial elements
bh	Basihyal
boc	Basioccipital
br	Branchiostegal rays
bso	Basisphenoid/basisphenotic
cb1, cb2, cb3	1st to 3rd ceratobranchials
cem	Cement covering of dental plates
ch	Ceratohyal
cl	Cleithrum
con	Conical tooth
cor	Coracoid
cor pr	Coronoid process of the dentary
dec pr	Articular descending process
dec pr fl	Bone flange on the articular descending process
dent pl	Dental plate
dh	Dorsal hypohyal
d pr	Dorsal process
dsph	Dermosphenotic
duo	Duodenum
duo/il jn	Duodenal/ilial junction
e1-4	1st to 4th epibranchial bones
e4 art con	Articular condyle of upper pharyngeal-4th epibranchial joint
ect	Ectopterygoid
eh	Epihyal
ent lat pr	Entopterygoid lateral process
ent	Entopterygoid
ep	Epihyal
epo	Epioccipital
epo fl	Epioccipital flange
epl	Epipleural rib
epu	Epural
eth	Ethmoid (mesethmoid)
eth-fr dep	Ethmoid-frontal depression
exo con	Exoccipital condyle
exo fl	Exoccipital flange
ff	Flat facet of the maxillary fossa
fr	Frontal
gr pr	Grooved process of the maxilla
1°ha, 2°ha	Primary/secondary haemal arch
haem	Haemapophyses (parapophyses)
has	Hyomandibula articulation socket
hb1-3	1st to 3rd hypobranchials

ho	Holes
h postz	Haemal postzygopophyses
hsp1	First haemal spine
hyo	Hyomandibula
hyp1-2, 3-4, 5	Hypural plates
ic	Intercalar
ih	Interhyal
im	Intermandibularis muscle
in	Insertion site (eg, in A3t = insertion site of adductor mandibulae section A3
int bulb	Intestinal bulb
ip2	Second infrapharyngeobranchial
keel	Keel of lower pharyngeal bone
lap	Levator arcus palatini
lat can	Lateral canine
lat fl	Lateral flange
lat ind	Lateral indentation of the premaxillary ascending process
lat eth	Lateral ethmoid
lat hn	Lateral horn
liv	Liver
lja	Lower jaw articulation
m in	Muscle insertion scars
med sut	Medial sutures of dentary
med horns	Medial horns
med fac	Medial facent of the palatine
med indent	Medial indentation
meth	Mesethmoid (or ethmoid)
mpt	Metapterygoid
mx fos	Maxillary fossa of the premaxilla
mx fac	Maxillary facet of the premaxilla
mx arm	Maxillary arm
mx head	Maxillary head
mx con	Maxillary condyle
n sp	Neural spine
n prez	Neural prezygopophyses
nc con	Neurocranial condyle of the maxilla
nc art fac	Articulation facet of the upper pharyngeal
oes	Oesophagus
or	Site of origin of adductor muscles (eg, *or* A1)
p art fac	Pharyngeal articulation facents of the neurocranium
pal	Palatine
pal art fac	Palatine articulation facet of the neurocranium
pah	Parhypural
par	Parietal
parap	Parapophyses
pc	Postcleithrum
pcr	Principal caudal rays
pd	Predorsal bone (supraneural)
per	Perforate bone
pl	Pleural ribs
pmx pr	Premaxillary process of maxilla
pmx con	Premaxillary condyle of maxilla
pmx fac	Premaxillary facet of the maxilla
pop	Preoperculum
post mx pmx lig	Posterior maxillary-premaxillary ligament
post asc pr	Posterior ascending process of the articular
post proj	Posterior projection
post st fos	Posterior subtemporal fossa
pr	Pectoral fin rays
pro	Prootic
psph	Parasphenoid
pt	Posttemporal
ptf	Posttemporal flange
ptp	Pterygiophore
pto	Pterotic
pts	Pterosphenotic

qua	Quadrate
r1-3	Upper pharyngeal tooth rows (row 1 is medial)
rcc	Concavity marking the position of the rostral cartilage
ret	Reticulate bone
sac il	Sacculated ilium
sc	Scapula
scl	Supracleithrum
ses	Sesamoid articular
so	Supraoccipital
soc	Supraoccipital crest
sph	Sphenotic
symp	Symplectic
upb	Upper pharyngeal bone
uro	Urohyal
uro asc pr	Ascending process of the urohyal
v pr	Ventral process
v1-24	Vertebrae 1 - 24
vh	Ventral hypohyal
vom	Vomer

APPENDIX IV

Table 1. List of characters and character states used in the cladistic analysis of the genera of Scaridae.

(All character states are ordered except those marked U in column 3; a O in column 3 indicates thet the characters are ordered based on ontogenetic evidence. Asterisks indicate terminal autapomorphic character states. The plesiomorphic character state is given in column 8, states given in parentheses refer to plesiomorphic character states within the ingroup).

No.	Character	Unordered	Character state 0	1	2	3	Plesio-morphic
Neurocranium:							
1	Ethmoid-vomerine process	-	Short	Elongate	-	-	0
2	Ethmoid-frontal depression	-	Present	Absent	-	-	0
3	Ethmoid-frontal fusion	-	Fused	Separate	-	-	0
4	Reticulate ethmoid	-	None	Present*	-	-	0
5	Maxillary facets on vomer	-	Ant.dors.lat.	Lateral/dorso-lat.	-	-	0
6	Supraoccipital crest	-	Simple	Trifid	Extended*	-	0
7	Exoccipital flange	-	Long	Short	-	-	(0)
8	Posterior extension of epioccipital	U	Absent	Present, short	Present, long	To crest on * supraoccipital	0
9	Deep subtemporal fossae	U	Absent	2 pairs	1 pair	-	0
10	Size pharyngeal articulation facets	-	Short	Elongate	-	-	0
11	Shape pharyngeal articulation facets	-	Straight edges	Tapers to a point	-	-	0
12	Curvature of pharyngeal facets	-	Convex	Concave	-	-	0
Mandibular arch – Premaxilla:							
13	Coalescence of jaw teeth	-	Absent	Present	-	-	0
14	Cutting edge	-	Broken	Entire	-	-	0
15	Maxillary fossa	O	None	Trace	Distinct	-	0
16	Anterior canines	-	Present	Absent	-	-	0
17	Lateral canines	-	Absent	Present	-	-	0
18	Nodules on teeth	-	Absent	Present*	-	-	0
19	Cement	U	Absent	Thin on tooth base	Thin on plates	Covering plates	0
20	Tooth rows	-	6 or less	>6	-	-	0
21	Jaw overlap	U	None protrudes	Dentary protrudes	Premaxilla protrudes	-	0
22	Lateral depression in premaxilla ascending process	-	Absent	Present	-	-	0
23	Concave rostral cartilage site	-	Absent	Present	-	-	0
24	Alveolar process	-	Simple	Bifid	-	-	0
25	Conical teeth mesial to cutting edge	-	Absent	Present	-	-	0
26	Conical teeth nr. medial symphysis	-	Absent	Present*	-	-	0
27	Origin of teeth in lateral tooth rows	-	Lateral	Medial*	-	-	0
28	Developing tooth rows	-	None or small teeth	Large diagonal	-	-	0
29	Maxillary facet	-	On ascending process	At angle of processes	-	-	0
30	Facet on alveolar process	-	Absent	Concave-flat	Convex*	-	0
31	Palatine-maxilla articulation facet extending onto premaxilla	-	Absent	Present*	-	-	0
Mandibular Arch – Maxilla:							
32	Grooved process on maxillary arm	-	Absent	Present*	-	-	0
33	Facet of palatine articulation	U	Absent	Concave	Concave + groove	Convex*	0
34	Premaxillary facet	U	Absent	Medial	Anterior	-	0
35	Anterior maxillary-premaxillary ligament insertion site	U	Indistinct/thin groove	Deep groove/hole	Shallow concavity		0
36	Medial ridge for A1 insertion	-	Absent	Present	-	-	0

Table 1 (cont'd).

No.	Character	Unordered	0	Character state 1	2	3	Plesio-morphic

Dentary:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
37	Number of diagonal tooth rows	-	5 or less	>5	-	-	(0)
38	Anterior extension of coronoid pr.	-	Absent	Present	-	-	0
39	Tooth row orientation	U	Oblique	Mosaic	Vertical	-	(0)
40	Medial sutures	U	Absent	Simple	Irregular	Zig-zag*	1
41	Medial suture location	-	To edge	Foreshortened	-	-	0
42	Articular fossa	-	Shallow	Deep hole	-	-	0
43	Coronoid process	-	Narrow	Expanded	-	-	0
44	Notch in coronoid process	-	Absent	Present*	-	-	0

Articular:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
45	Anterior ascending process	U	Pointed	Notched	Rounded	-	0
46	Posterior ascending process	-	Present	Absent	-	-	0
47	Articular medial spine	-	Absent	Present	-	-	0

Palatine arch:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
48	Entopterygoid lateral process	-	Absent	Present*	-	-	0
49	Holes in entopterygoid	-	Absent	Present	-	-	0
50	Palatine dorsal process	-	Elongate	Short	-	-	0
51	Condyle on palatine	-	Indistinct	Distinct	-	-	0
52	Direction of maxillary condyle	-	Ant.ventral	Ventral/ post. ventral	-	-	(0)
53	Facet on medial face of palatine	-	Absent	Present	-	-	0
54	Reticulate bone on palatine	-	Absent	Present*	-	-	0
55	Entopterygoid	-	Short	Elongate	-	-	0
56	Palatine-entopterygoid joint	-	Simple	Ankylosed	-	-	0

Hyoid arch:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
57	Ceratohyal-epihyal joint	-	Sutured	No suture	-	-	0
58	Trace beryciform foramen	-	Absent	Present	-	-	0
59	Ventral hypohyal	-	Short	Elongate	-	-	0
60	Number of branchiostegal rays	-	Six	Five	-	-	0
61	Urohyal	-	Deep	Elongate	-	-	0
62	Urohyal anterodorsal process	-	Broad	Narrow	-	-	0
63	Urohyal ventral aspect	U	Pointed posteriorly	Broadly spatulate	Spatulate	Swollen posteriorly*	0
64	Urohyal posterior margin	-	Slight curve	Deep notch	-	-	0

Branchial arches:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
65	Number of gill rakers	-	10-33	35-60	-	-	0
66	Form of posterior gill rakers	-	Branched	Simple	-	-	(0)

Dorsal elements:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
67	Neurocranial facets of UPJ	U	Strongly	Slight curved	Straight curve	-	0
68	Alveolar process	-	Small	Projects	-	-	(0)
69	Width/height	U	>2.0	1-1.9	<0.8	-	0
70	Number of tooth rows	U	Zero	Three	Two	-	0
71	Tooth replacement pattern	U	Labroid	Phyllodont	Conveyor-belt	-	0
72	Tooth sizes	O	Equal	Row 3 reduced	Rows 2 & 3 reduced	-	(0)
73	Dentigerous area	U	Broad	Reduced	Narrow	Elongate	0
74	Shape of medial tooth	O	Round	Elongate ovoid	Curved & interdigitating	-	0
75	Medial margins of dentigerous areas	-	Curved	Parallel	-	-	0
76	Horn on posterior margin of UPJ	-	Distinct	Trace	-	-	0
77	Epibranchial 4	-	Small	Expanded	-	-	0
78	Pharyngeal valve	-	Absent	Present	-	-	0

Table 1 (cont'd).

No.	Character	Unordered	Character state				Plesio-morphic
			0	1	2	3	

Ventral elements:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
79	LPJ, tooth rows (No. per row)	U	Zero	Six	Five	-	0
80	Number of tooth rows	-	<10	>11	-	-	(0)
81	Shape of dentigerous area	U	Triangular	Broad	Square	Elongate	0
82	Tooth shape when worn	-	Elongate	Ovoid	-	-	0
83	Raised sides on dentigerous area	-	Absent	Present	-	-	0
84	Lateral horn muscle insertion scars	-	Lateral large	Medial large	-	-	(0)
85	Ridge separating insertion scars	-	Absent	Straight	Curved*	-	0
86	Pharyngocleithral condyle/facet	-	Short	Protruded*	-	-	(0)
87	Lateral horn shaft	-	Deep	Broad	-	-	0
88	Location of keel base	U	Anterior	Posterior	Medial	-	0
89	Keel form	-	Short-tapering	Long-expanded	-	-	0
90	Tooth development	U	Labroid	Phyllodont	Sequential	-	0
91	Ridge on keel	-	Stout	Absent	-	-	0
92	Keel margin	U	Simple	Lateral flanges	Marginal flange	-	0

Pectoral girdle:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
93	Articular facet on cleithrum	-	Absent	Present	-	-	0
94	Medial indentation of cleithrum	-	Absent	Present	-	-	0
95	Holes above cleithral facet	-	Absent	Present	-	-	0
96	Posterior flange on posttemporal	-	Absent	Present	-	-	0
97	Pectoral rays	-	14 or more	13	-	-	0

Pelvic girdle:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
98	Horns on symphysis of basipterygium	-	Absent	Present	-	-	0?
99	Basipteryigium anterior extremities	U	Pointed	Lateral flanges	Rounded	-	0

Axial skeleton:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
100	First neural spine	-	Autogenous	Fused	-	-	0
101	Precaudal vertebrae	U	13	12	10-11	9	0?
102	Expanded/raised postzygopophyses	-	Absent	Two	One*	-	0
103	Expanded flanges on parapophyses	-	Absent	Present	-	-	0
104	Form first haemal spine	-	'Labrid'	Hypsigenyine	-	-	0
105	Number of vertebrae	U	29+	27-28	25	-	0/1

Dorsal fin:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
106	Number of supraneural bones	-	One	Zero	-	-	0
107	Spines before first pterygiophore	-	Two	One	-	-	0
108	Dorsal spines	-	Pungent	Flexible	-	-	0
109	Dorsal fin membrane	-	Incised	Continuous	-	-	0

Anal fin:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
110	Pterygiophores before haemal spine	U	1-2	3	4*	-	0

Caudal skeleton:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
111	Parhypural	-	Long	Short	-	-	0
112	Anterior protrusion of hypurals 1+2	U	Absent	Large	Small	-	0
113	Flange on penultimate vertebra	-	Large	Reduced	-	-	0
114	Principal caudal rays	-	7+7, 8+7	7+6	-	-	0

Lipid in bones:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
115	Bone colour	-	Brown	White	-	-	0

Oral jaw muscles:

No.	Character	Unordered	0	1	2	3	Plesio-morphic
116	A1 insertion site	-	Premaxillary process	Maxilla arm	-	-	0
117	Fusion of A1 and A2	-	Divided	Fused	-	-	0

Table 1 (cont'd).

No.	Character	Unordered	0	1	2	3	Plesio-morphic
				Character state			

Oral Jaw Muscles (cont'd):

No.	Character	Unordered	0	1	2	3	Plesio-morphic
118	Presence of A1ß	-	Absent	Present	-	-	0
119	A2 insertion site	-	Includes articular	Dentary only	-	-	0
120	A3 insertion site	U	Articular	Articular + dentary	Dentary	-	0
121	Size of A3	-	Large	Small	-	-	0
122	Degree of fibre pinnation	-	Weak	Strong (multipinnate)	-	-	0
123	Awε	-	Absent	Present*	-	-	0
124	Awα	U	Simple	Enlarged	Absent	-	0
125	Awδ	-	Absent	Present*	-	-	0

Pharyngeal musculature:

| 126 | Origin of levator posterior from supraoccipoital crest (SOC) | - | Includes SOC | Excludes SOC | - | - | 0 |
| 127 | Travsversus posterior dorsalis | - | Crosses midline | Divided | - | - | 0 |

Ligaments:

| 128 | Postpharyngeal ligament | - | Present | Absent | - | - | 0 |
| 129 | Maxillary-Palatine ligament | - | Present | Absent | - | - | 0 |

Viscera:

130	Intestinal pattern	O	'Labrid'	Type I	Type II/III	-	0
131	Sacculation of the intestine	-	Absent	Present	-	-	0
132	Lateral intestinal bulb	-	Absent	Present	-	-	0

Reproductive system:

| 133 | Egg shape | - | Spherical | Spindle | - | - | 0 |
| 134 | Reproductive pattern | - | Protogynous | Gonochoristic* | - | - | 0 |

Juvenile colour patterns:

| 135 | Juvenile with dorsal ocellus | - | Absent | Present* | - | - | 0 |
| 136 | Juvenile with single body stripe with dark dot posteriorly | - | Absent | Present* | - | - | 0 |

External morphology:

137	Posterior nostril	-	Small	Large	-	-	0
138	Fleshy flap on anterior nostril	-	Small	Large	Branched*	-	0
139	Median predorsal scales	-	Numerous (>8)	7 or less	-	-	0
140	Cheek scale rows	U	Numerous (>4)	One	2-4	Naked	0
141	Lateral line	-	Continuous	Interrupted	-	-	0
142	Gill membranes, joint to isthmus	U	Free	Broadly joint free fold	Broadly joint no free fold	-	0
143	Head profile	-	Pointed	Steep or rounded	-	-	0

APPENDIX IV (cont'd)

Table 2. The character state matrix used in the cladistic analyses of genera of Scaridae.

(See Table 1 for a list of characters and character states, ? = missing value, P = variable/polymorphic; *Labrus*, *Pseudolabrus*, *Odax*, *Bodianus* and *Pseudodax* are outgroups)

Character number

Region	Neurocranium 1	Premaxilla 2 3	Mx	Dent 4	Art	Pal 5
Labrus	000000?000?0	000000000000?0?0000	00000	???0?000	000	0000?0000
Pseudolabrus	000000?000?0	000000000000?0?0000	000?0	???P0000	00?	0000??000
Odax	P0?0?0?000?0	1100003?2000?0?0000	00000	???10000	000	0000?100P
Bodianus	000000?000?0	000000100000P0?0000	00000	?0?1?000	000	0000?0000
Pseudodax	000000?00000	0001001000000000100	00000	?0?0?000	000	0000?0000
Cryptotomus	001001011101	0010100010010000110	01100	01020000	000	000000011
Nicholsina	001001011101	001010P01001P000110	01100	01020000	000	000100011
Calotomus	001002031101	002P101010011100110	01110	P1020000	000	000110011
Leptoscarus	001001021101	1120103011010010120	03100	10020000	000	000110011
Sparisoma	010011021101	112P103?10110001111	11100	10120001	100	000110001
Cetoscarus	110011021101	1121002121110001110	01111	10121010	101	011110001
Bolbometopon	110111021101	1121012121110001110	01211	10121010	101	011110101
Chlorurus	010011022111	1121103121110001110	01210	10130110	211	111110001
Hipposcarus	110011122111	1121103120010001100	02220	10220110	211	000101001
Scarus	001011122111	1101P03120010001100	02020	10210110	211	000100001

	Hyo 6	Uro	BA	UPJ 7	LPJ 8 9	Pect	Pel	Axial 0
Labrus	P001	0000	0?	0?000?000?00	0?0?0?0?000000	0?000	??	000000
Pseudolabrus	00P0	0000	??	0?000?000?00	0?0?0?0?000000	0000P	00	030002
Odax	0001	1040	??	0?000?000?00	0?0?P?0?000000	0?00P	??	100000
Bodianus	P000	1000	0?	0?001?000?00	0?0?0?0?000100	00000	10	0P0011
Pseudodax	1010	0001	??	0?201?311000	0?301?0?000111	00000	10	010011
Cryptotomus	1111	1111	00	201120110011	10100?0?011211	0?111	01	131112
Nicholsina	1111	1111	00	101120110111	10100?00011211	10011	01	131112
Calotomus	1111	1121	0?	101120110111	10100010111211	10111	01	131112
Leptoscarus	1111	1121	0?	101120110111	10100010011211	10011	01	132112
Sparisoma	1111	1121	00	102121211111	21201110121211	10011	01	131112
Cetoscarus	1111	1121	00	102121211111	21201110121211	10010	02	1211?2
Bolbometopon	1111	1121	00	102121211111	21201110121211	10110	02	111112
Chlorurus	1111	1131	11	212122321111	21311110121212	11110	11	121112
Hipposcarus	1111	1121	11	212222321111	21311121101212	11110	01	121112
Scarus	1111	1121	11	212222321111	?1311110101212	11110	11	121112

	Dors	A 1	Cau		Myol 2	Ph	L	Int 3	R J	Ext 4
Labrus	0?00	0	00P?	0	0000010000	?0	00	000	0? 00	0000000
Pseudolabrus	000?	0	0010	0	0000000000	?0	0?	000	00 00	00?P000
Odax	101P	1	00?0	0	1010000010	00	1?	000	00 00	00PP000
Bodianus	0000	0	0P00	0	0P00000000	00	?0	000	00 00	??00000
Pseudodax	0001	0	0000	0	0000000010	01	10	000	?? 00	0000000
Cryptotomus	0110	0	1211	?	0000000000	11	11	100	?0 00	0011110
Nicholsina	0110	0	1P11	1	0000000000	?1	11	100	?? 00	0011111
Calotomus	01P1	0	1211	1	0000000000	11	?1	100	00 00	0111121
Leptoscarus	0110	0	1211	1	0000000010	11	11	100	?1 00	0111121
Sparisoma	0100	0	1211	1	0000101011	?1	01	211	00 00	0211121
Cetoscarus	0111	1	1P11	1	1000201010	11	01	211	00 10	1112101
Bolbometopon	0111	2	1111	1	1000201010	11	01	211	00 00	1112101
Chlorurus	1111	0	1111	1	1011201120	11	01	211	10 00	0012101
Hipposcarus	0111	0	1111	1	1101110010	11	01	211	10 01	0012101
Scarus	1111	1	1111	1	1111010020	11	01	211	10 00	0012101

Table 3. Summary of hypothesised events in the historical biogeography of the Scaridae.

Tectonic events	Age Myr BP	Scarid biogeography
	15+	Differentiation of eastern (Indian Ocean) and western (Atlantic) populations
	14	*Calotomus* present in Paratethys (first fossil record of the family)
Closure of the eastern Tethys	13	Physical isolation of eastern & western populations
	13-0	Indo-Pacific: proliferation of reef associated taxa
	5+	*Bolbometopon* present in Indo-Pacific
	13-0	Caribbean: proliferation of rocky reef and seagrass associated taxa
	5+	Dispersal of *Scarus* from Indo-Pacific across Eastern Pacific into Caribbean?
Closure of Isthmus of Panama	5	Physical isolation of Atlantic/Caribbean faunas from Indo-Pacific fauna
	5-0	Colonisation of Eastern Pacific by Indo-Pacific taxa