

The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage

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Abstract. The fish assemblage from the Eocene deposits of Monte Bolca, Northern Italy, are compared with those of Recent coral reefs. A family-level taxonomic definition of a Recent coral reef fish assemblage is formulated to permit direct comparisons. On this basis, the Monte Bolca fishes represent the earliest clearly defined coral reef fish assemblage. Quantitative analyses of the relative abundance of fish families revealed significant differences between the two assemblages. The Bolca assemblage has Mesozoic links (Pycnodontiformes) and non-perciform taxa are relatively abundant, particularly the Beryciformes (Holo-centridae). However, Bolca represents the earliest record of a perciform-dominated benthic fish assemblage (68.4% of all non-clupeid taxa). Within the Perciformes, the abundance of the major reef fish lineages (higher squamipinnes and Labroidae) differs markedly between the two assemblages. The numerical dominance of labroid fishes on coral reefs appears to have been a relatively recent occurrence.

If indeed this is a coral reef fish assemblage, then the Bolca fishes will be of paramount importance in our understanding of the evolution of coral reef fishes. However, it is critically important to establish the status of the Bolca fishes and the relationship between the Bolca fish assemblage and those of Recent coral reefs. At present this relationship is unclear. What we lack is a rigorous definition of what constitutes a coral reef fish assemblage to act as a basis for a direct comparison between the two assemblages.

The key question is: do the Eocene fishes of Monte Bolca represent a coral reef fish assemblage?

This study addresses this question in three stages. Firstly, a definition of a Recent coral reef fish assemblage is established in terms of the taxa present and their numerical abundance. Secondly, the composition of the Bolca assemblage is established based on the same taxonomic criteria. And finally, using the taxonomic and numerical data, the status of the Bolca fish assemblage is appraised.

Introduction

Fossils form the basis of our understanding of the evolution of marine organisms and the environments in which they lived. They document how communities have developed and changed through time and how individual taxa have endured these changes. In studies of coral reef fishes, however, the evidence from the fossil record has been largely overlooked. Only recently have reef fish biologists recognized the need to consider historical factors in the interpretation of Recent reef systems (Choat and Bellwood 1991).

The oldest putative reef fish fossils come from the slopes of Monte Bolca in the foothills of the Italian Alps. Here Eocene marine deposits have yielded what is perhaps the finest fossil record of a Tertiary marine fish assemblage. It has been suggested that the sediments were deposited in the vicinity of a coral reef and that the fish assemblage had reefal links (Blot 1980; Sorbini 1983).

Background: the Eocene deposits of Monte Bolca

The fossil deposits of Monte Bolca are outstanding in terms of the number and quality of the specimens. The deposits have yielded over 247 species of fish in 82 families from 17 orders (modified after Blot 1980). These specimens represent the first record of numerous marine fish families (Patterson 1993a). They are preserved in excellent condition. Most are fully articulated, with some soft tissue preservation, revealing the details of the skeleton, fins and scales (Fig. 1), in some cases even pigmentation patterns are retained.

This diversity is combined with a remarkable lack of preservation bias. The deposits have yielded a vast range of fish types from 1 cm long larval fish to 1 m batoid rays, all preserved with comparable clarity. The result is a unique collection of early fishes. The detailed preservation permits specimens to be clearly identified and placed with some confidence in a classification scheme based on Recent taxa. It also permits a quantitative analysis of the composition of the assemblage.

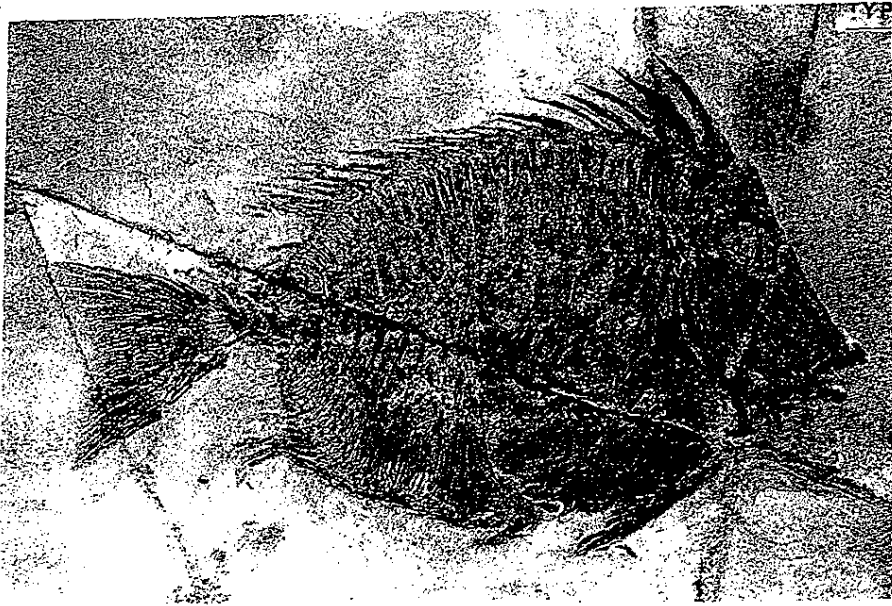


Fig. 1. The acanthurid *Eorandallius rectifrons* (Agassiz), MNHN Paris 10909 Holotype 189 mm standard length, showing the typical preservation quality of the Bolca fishes

The age and location of the assemblage is also of critical importance. It is of early Middle Eocene age (ca. 50 Ma, Patterson 1993b), and has yielded the earliest record of numerous perciform fish families, including many fish taxa found on Recent coral reefs. The age of the deposits also coincides with the early proliferation and dominance of scleractinian coral reefs, the first appearance of coral reefs as we know them today.

Biogeographically, the Monte Bolca deposits are located in what was the center of the Tethys sea. Although provinciality of tropical faunas was evident at this time, the central Tethys would almost certainly have contained many cosmopolitan marine taxa (Rosen 1988; Rosen and Smith 1988). Material from this location therefore is likely to provide a clear picture of the familial composition of the widespread shallow tropical marine fish assemblages of the Tethys, prior to its fragmentation and the final closure with the terminal Tethyan event.

This study represents the first of a series on the Bolca fish assemblage. The composition of the Monte Bolca fossil fish assemblage is examined in terms of its taxonomic and numerical composition and is directly compared with that of Recent coral reefs.

Materials and methods

Recent reef fish assemblages

Definition

One of the key questions in addressing the evolution of coral reef fishes is to define what constitutes a coral reef fish and consequently a 'coral reef fish assemblage'. It is relatively easy to recognize a collection of fishes from a coral reef. Most coral reef fish are brightly colored and such a collection would contain many species found only on reefs.

However, such distinctions are of little help in examining the fossil record, where colors are lost and few, if any, species still live on reefs today. Many species are regional and few are pan-tropical. A broader definition of a coral reef fish is therefore needed. In this study, a new family-level definition of a coral reef fish assemblage is provided as a basis for assessing the fossil record. The family level was selected for the following reasons:

1. The taxonomy is relatively stable, with several families being defined based on cladistic criteria.
2. Families are often defined based on osteology, the primary data source available when examining fossils.
3. Families are less susceptible to biases resulting from inadequate samples than species or genera.
4. Families are the lowest taxonomic level at which perciform fish taxa span the whole of the Tertiary period, offering potential continuity and a basis for comparisons.
5. Families often have clear trophic or life-history traits.

To provide a definition of a Recent reef fish assemblage, the presence or absence (and number of genera and species) of all fish families were surveyed based on 21 published faunal lists or regional texts (listed in Table 1). These sources were from coral reef regions (16 primary; 5 marginal), with representatives from all the oceans of the world. The results give a working definition of what constitutes a Recent coral reef fish assemblage in terms of families. Families which were present at 21 locations are taken as a minimum consensus list of coral reef fish families and, in combination, define a coral reef fish assemblage. A Recent coral reef fish assemblage therefore, can be assumed to contain all of the families listed, irrespective of its biogeographic location.

Relative abundances

Quantitative estimates of the abundances of Recent coral reef fish families are based on three separate techniques: visual censuses, rotenone and explosive samples. Each technique has distinct biases which will be addressed but, in combination, they provide a clear overview of the relative abundance of reef fish taxa. The surveys were

Table 1. Consensus list of Recent coral reef fish families: families present at all 16 reef locations

	No. genera mean \pm SE	No. species mean \pm SE
Acanthuridae	4.4 \pm 0.4	22.4 \pm 3.0
Apogonidae	7.3 \pm 0.9	31.4 \pm 5.9
Blenniidae	12.9 \pm 2.0	26.9 \pm 4.8
Carangidae ^a	10.3 \pm 1.7	21.8 \pm 4.4
Chaetodontidae	4.7 \pm 0.4	22.7 \pm 3.5
Holocentridae ^a	4.1 \pm 0.6	17.3 \pm 2.4
Labridae	22.0 \pm 2.1	61.0 \pm 8.7
Mullidae	2.7 \pm 0.2	11.3 \pm 1.5
Pomacentridae	10.8 \pm 1.3	45.7 \pm 8.3
Scaridae	4.2 \pm 0.4	17.0 \pm 2.3

^aLists from an additional 5 peripheral reef areas agreed with the above list with the exclusion of the Carangidae and Holocentridae. Literature sources: *Reefs*: Allen and Steene (1979), Brock (1982), Tinker (1982), Randall (1983a, b, 1985), Masuda et al. (1984), Allen (1985), Randall et al. (1985), Myers (1988, 1991), Winterbottom et al. (1989), Randall et al. (1990), Aizawa and Senou (1991), Kulbicki et al. (in press), Rivaton et al. (in press). *Marginal reefs*: Allen et al. (1976), Thomson et al. (1979), Lubbock (1980), Allen and Russell (1986), Francis et al. (1989)

based on the Great Barrier Reef region. This region was selected because (1) it is close to the middle of the Indo-Pacific region and is representative of a broad Indo-West Pacific biogeographic realm, (2) it has been extensively surveyed, (3) it is broadly comparable to the location of the Bolca deposits, i.e. a coastal system with an associated barrier reef approximately in the middle of a broad tropical biogeographic region, and (4) it has been subject to minimal anthropogenic disturbance.

Visual censuses. Available evidence suggests that the Bolca sediments were deposited in a sheltered marine environment close to the mainland and probably enclosed by a coral reef (Sorbini 1983). To provide a comparison of numerical abundance of Recent reef fish taxa from a comparable environment, a series of visual censuses were undertaken in sheltered waters around Lizard Island (14°40' S, 145°28' E), a mid-shelf reef in the northern region of the Great Barrier Reef.

In these censuses, all fish families were included. Three locations were chosen (Mermaid Cove, Lagoon Entrance and the Lagoon). At each location 2 to 3 sites were censused at two habitats per site: the reef edge (marking the boundary between the reef and the sand) and the reef top (5–25 m from the reef edge). A total of 14 censuses were undertaken.

Each census was based on three superimposed 20 m tape transects. Firstly, the number of large (> 10 cm) or highly mobile individuals were recorded. Individuals were counted within 2.5 m either side of the tape, from the reef to the surface of the water (1–4 m above). The observer then swam back along the tape recording all small (< 10 cm) individuals in a 1 m wide transect. Finally, the observer swam back along the transect looking under corals and boulders to search for cryptic species. In each transect, care was taken to avoid recounting the same individuals. This was relatively easy as there was little taxonomic overlap between the three transects. Counts were all standardized to individuals per 100 m² and pooled. The data are presented as the mean number of individuals in each family per 100 m² (\pm SE) based on a mean of all 14 censuses.

Destructive censuses. Quantitative estimates of reef fish abundances were based on collection records in the Australian Museum.

Rotenone: a total of 43 samples were included in the analyses. Only those samples with a reefal location and a clear kill were included (i.e. no note of strong currents dispersing the mixture). Samples covered the length of the Great Barrier Reef from the Torres Straits (10° S) to One Tree Island, in the Capricorn Bunker Group (23° S). At each station the total number of species and specimens in each family were analyzed. The results are expressed as the percent of individuals in each family as a proportion of all individuals at that site.

Explosive samples: a total of 14 samples were included in the analyses, from the northern (Lizard Island) region and southern (Capricorn Bunker) regions of the Great Barrier Reef. As in the rotenone samples, the number of specimens in each family are expressed as a proportion of the specimens at that site.

The Monte Bolca fish assemblage

The fossils of Monte Bolca are early Mid-Eocene age, approximately 50 Ma. They have been excavated from two small sites which lie a few hundred metres apart on the slopes of Monte Bolca, in northern Italy (11°13' E, 45°35' N).

Taxonomic structure. This taxonomic survey follows Blot (1980) with additions or deletions based on more recent findings. Several taxa are currently under investigation. In these cases the identifications of Blot (1980) are provisionally followed. Where possible, reef fish taxa were included in families based on Recent forms if they shared a number of the synapomorphies which define these families. Relevant taxonomic/systematic works include Tyler et al. (1989), Blot and Tyler (1990), Sorbini et al. (1990), Tyler and Sorbini (1990), Guiasu and Winterbottom (1993) and Winterbottom (1993) for the Acanthuroidei and Bannikov and Sorbini (1990), Bellwood (1990: 1994; in press), Bellwood and Schultz (1991), and Bellwood and Sorbini (in press) for the Labroidei.

In this study, all families recorded from Monte Bolca are considered, although only those which are characteristic of Recent coral reefs were examined in detail. This included the Pomacanthidae, Siganidae, Zanclidae and Ehippididae, in addition to those families on the consensus list, described above.

Numerical abundances. The fishes of Monte Bolca offer an unparalleled opportunity to examine the numerical composition of an early Tertiary marine fish assemblage. In many museum fossil collections only spectacular, rare or well-preserved material is retained. In Monte Bolca this has also happened to some extent, especially with older collections, e.g. the Baja collections (Sorbini 1983), which contain many spectacular specimens. These are not representative of the deposits as a whole.

However, some of the material removed from the Monte Bolca deposits has been collected more systematically, with most specimens of interest being retained in a single repository: the Museo Civico di Storia Naturale, Verona. This includes fishes of all sizes and preservation quality. The material that is not retained is overwhelmingly dominated by clupeids. Although the numerically dominant taxa in the assemblage, the clupeids are not retained in the collections in numbers which reflect this abundance. For this reason, and their limited association with coral reefs, they are excluded from the analyses.

Material retained in the museum has been photographed, provisionally identified (primarily by L. Sorbini, with some additions by J. C. Tyler and A. Bannikov) and catalogued. As a result, the collections contain over 1500 catalogued specimens, of which approximately 1250 are provisionally identified. The remainder, which includes many incomplete specimens, await designation.

It is this relatively non-selective 25 year catalogued collection (as of June, 1992) that was used in the numerical survey. With the exception of time averaging, i.e. the assemblage is composed of specimens from several non-contemporaneous populations or communities, the assemblage displays minimal preservation bias. There is

little evidence of scavenging or disturbance. Most specimens are intact, frequently including even the most delicate parts of the fins. There is no evidence of sorting prior to burial or other preservation bias. All specimens from 12 mm (*Scatophagus*) to 100 cm (battoid rays) are preserved with comparable clarity. Evidence of advanced decomposition (disarticulation and loss of scales) is found only in exceptional cases. This lack of preservation bias provides for a sound quantitative analysis and permits direct comparisons between living and fossil assemblages.

The numerical survey of the fishes of Monte Bolca is based solely on the identified catalogued material in the Museo Civico di Storia di Verona, with minor recent additions. All reef associated groups were re-examined and identifications checked. The number of specimens in each family were counted. Where possible, part and counterpart were linked and scored as one individual. Families in non-perciform orders were pooled. Total numbers are based on all non-clupeid taxa.

Results

Recent coral reef fish assemblages

A consensus list of reef fish families

Of the 92 families recorded in the 16 reef checklists, only 10 were present at all 16 primary locations. These are listed in Table 1. This table also provides an indication of their relative generic and species diversity. In addition to the 16 coral reef locations, five marginal reef locations were also examined. The consensus list for coral reefs and marginal reefs ($n = 21$) was the same as for the 16 primary reefs except for the loss of the Holocentridae and Carangidae. Both consensus lists are dominated by three lineages: the Labroidei, higher squamipinnes and Apogonidae. This is particularly clear when both diversity and abundance are considered.

This consensus list provides the following bases for constructing a definition of a Recent coral reef fish assemblage:

1. The following eight reef fish families are present – Acanthuridae, Apogonidae, Blenniidae, Chaetodontidae, Labridae, Mullidae, Pomacentridae, Scaridae.
2. The following characteristic reef associated families may be present – Holocentridae, Siganidae, Ehippidae, Serranidae, Pomacanthidae, Carangidae, Zanclidae.

Abundance of Recent reef fish taxa

The relative abundances of Recent coral reef fish taxa are summarized in Fig. 2. The three collecting techniques indicate that Pomacentridae, Apogonidae and Gobiidae are the three most abundant families. However, the three methods give quite different results in terms of the relative abundance of the three families. This reflects the biases in the methodologies.

Rotenone is an asphyxiating ichthyocide and is widely used in ichthyological surveys. It is toxic to all fishes and in this respect is relatively non-selective. The total number of families recorded (74) was much higher than for the other techniques (26 visual, 43 explosive). However, in terms of relative abundance, it probably overestimates the number

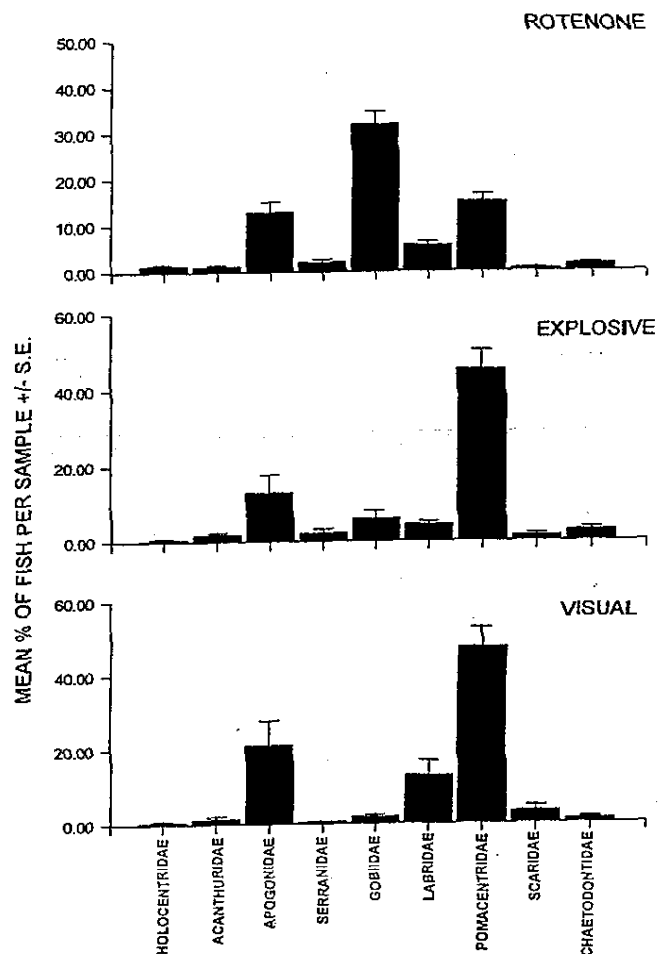


Fig. 2. The relative abundance of Recent reef fishes in the Great Barrier Reef region. Results are expressed as the mean percent of fishes in each family as a proportion of all fishes in each sample (rotenone $n = 43$; explosive $n = 14$; visual census $n = 14$)

of small sedentary taxa while underestimating the number of larger more mobile taxa.

Rotenone is released onto the reef by divers where it spreads in a thick brown cloud. It takes several minutes before fish react to exposure to the rotenone cloud. Larger fish are able to swim away from the diver-induced disturbance and the rotenone cloud and are able to survive swimming through the rotenone cloud. Small fish which cannot escape from the cloud and sedentary taxa which remain within the cloud for a prolonged period are usually killed. Thus, although all fish are susceptible to rotenone, it is probably positively biased towards smaller, less mobile taxa.

Explosives appear to be more selective than rotenone in that they have a limited effect on taxa that lack swim bladders (e.g. the Blenniidae). They are also likely to yield underestimates of taxa in holes or close to the substratum because, unlike rotenone, explosives do not drive fish out of hiding. However, explosives will effectively kill fish in the water column irrespective of size, taxon or

behaviour. They therefore provide a good quantitative estimate of the relative abundance of taxa in the water column.

Visual censuses can, by definition, only record visually apparent taxa. They may miss small or cryptic taxa (Brock 1982) and underestimate mobile taxa (particularly in areas where fishing activity is common). For estimating relative abundances there are also problems of fish size (Bellwood and Alcalá 1988) and mobility. The census technique used in the present study was designed to minimize these inherent biases and to provide a relatively sound estimate of visually apparent taxa.

The three methods used in conjunction provide a robust overview of the relative abundance of fish taxa on a Recent coral reef. Each technique on its own has limitations but, in combination, they ensure that all taxa are represented and enable the relative impact of census bias to be taken into account.

Despite the differences, the dominant patterns are relatively consistent. In all cases, the Pomacentridae, Gobiidae and Apogonidae are numerically dominant, with the Holocentridae having limited numbers. This is in sharp contrast to the Bolca fish assemblage.

The Monte Bolca fish assemblage

A total of 1271 fish fossils were included in the analyses. All clupeid and indeterminate specimens were excluded. The composition of the Monte Bolca fish assemblage in terms of the orders present and their relative abundance is summarized in Table 2. This is compared with the relative abundance of the orders on Recent reefs. Recent reef data are based on rotenone samples which yielded the highest diversity of families. In both assemblages, the Perciformes is the numerically dominant order. However, in comparison with Recent coral reef fish assemblages, the Bolca assemblage has relatively high numbers of individuals in non-perciform taxa, with large numbers of beryciform fishes. The Bolca assemblage also differs in the presence of representatives of the extinct Mesozoic order, the Pycnodontiformes. The relative abundance of major reef fish families is shown in Fig. 3. This figure includes most of

Table 2. The relative abundance of major fish orders in the Bolca assemblage and in a Recent coral reef assemblage. Recent data are based on 43 pooled rotenone stations from the Great Barrier Reef

Order	Eocene % of total (Bolca)	Recent % of total (GBR)
Perciformes	68.4	89.3
Beryciformes	8.0	1.6
Anguilliformes	6.7	2.7
Gasterosteiformes	4.3	1.0
Scorpaeniformes	3.4	1.4
Tetraodontiformes	3.3	0.7
Pycnodontiformes	1.8	—
Other	3.9	3.1

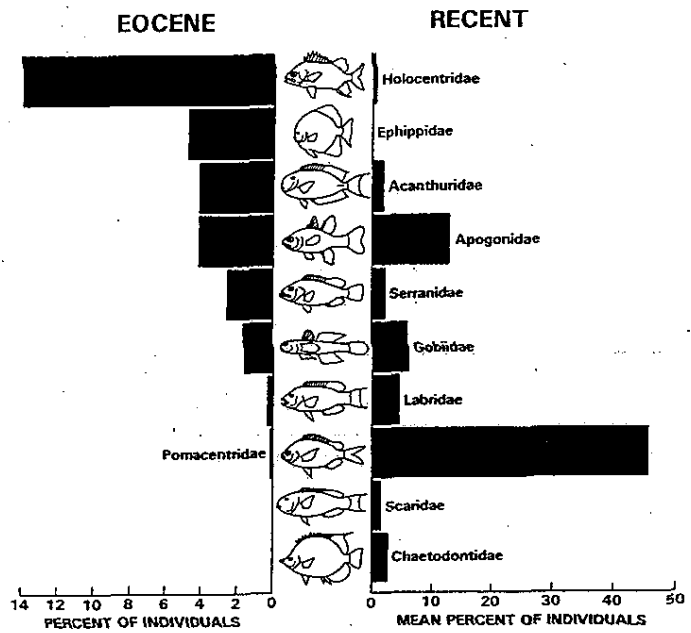


Fig. 3. The relative abundance of coral reef fish families during the Eocene (Monte Bolca) and on Recent coral reefs (Great Barrier Reef, GBR). Bolca data are expressed as the proportion of all identified non-clupeid taxa in the collections examined. Recent data are the mean proportion of individuals present in 14 explosive samples from the GBR. The Blenniidae and Mullidae were minor components in both samples (0.2% and 0.1% in Bolca, and 0.8% and 0.04% on the GBR, respectively)

Table 3. The major reef fish lineages in Eocene and Recent fish assemblages. The Recent data refer to the mean number of individuals/genera in 12 explosion samples. No Pomacanthidae were recorded in either sample

	% Individuals		Number of genera	
	Eocene	Recent	Eocene	Recent
Labroidei	1.5	51.4 ± 5.1	5	14.5 ± 0.9
Labridae	0.2	4.5 ± 0.7	2	6.9 ± 0.8
Scaridae	—	1.4 ± 0.5	—	1.1 ± 0.2
Pomacentridae	0.1	45.5 ± 5.0	1	6.5 ± 0.5
Tortonesidae	0.9	—	1	—
<i>Sorbinia inc. ced.</i>	0.2	—	1	—
Higher squamipinnes	9.8	5.2 ± 0.6	14	5.9 ± 0.5
Chaetodontidae	—	2.9 ± 0.6	—	3.3 ± 0.4
Scatophagidae	1.7	0.0	1	0
Ephippidae	4.7	0.02	2	0.01 ± 0.01
Acanthuridae	4.0	1.9 ± 0.5	8	2.2 ± 0.4
Siganidae	0.7	0.4 ± 0.2	1	0.4 ± 0.1
Zanclidae	0.4	0.0	1	0

the families in the Recent coral reef fish consensus lists (including marginal reefs) and some characteristic Recent coral reef families. Of these, all can be placed with some confidence in families included in Recent taxa with the notable exception of the Gobiidae. The identification of

this material is provisionally accepted following Blot (1980) although there is an urgent need for re-evaluation of this material. Summaries of the two main perciform lineages, the Labroidei and higher squamipinnes, are provided in Table 3.

There is a striking contrast between the two assemblages. In the Bolca assemblage the Holocentridae and Ehippidae are particularly well represented. Today, they represent only a minor component of coral reef fish assemblages, even though they often reach their greatest numbers on coral reefs.

Care is needed in assessing holocentrid abundances on Recent reefs, where they are nocturnal and hard to census. However, they are very susceptible to rotenone and in none of the samples on Recent reefs did they approach the numbers found in Bolca. Therefore, a lower numerical abundance on Recent reefs appears likely.

In terms of presence or absence of reef fish families, the Bolca assemblage shows a strong similarity to Recent coral reef fish assemblages. The Bolca assemblage possesses 8 of the 10 families on the primary consensus list (only the Scaridae and Chaetodontidae are not recorded). In this respect the assemblage may be considered to have a strong coral reef association. Several other families commonly found on coral reefs are also present, including the Serranidae, Sparidae, Priacanthidae, Sphyracidae and Zanclidae (the families covered in the survey are listed in Appendix 1). Today, the Zanclidae is found exclusively on coral reefs.

In all taxa, the link between Monte Bolca and Recent assemblages is similar. They share families but not genera or species. Most reef fish families are present in Bolca but they are represented by few species, apparently irrespective of the number of specimens recovered. Only three holocentrid species have been found even though this family represents 8% of the total non-clupeid collections and in total probably represents over 200 specimens.

Despite the strong similarities, there are striking differences between the two assemblages. This is particularly clear in the relative abundance of the dominant reef fish lineages, the Labroidei and the higher squamipinnes, in terms of both the patterns of relative abundance and taxonomic diversity (Table 3).

In the Bolca assemblage the labroids are relatively scarce when compared to the number of higher squamipinnes. The latter is dominated by the Ehippidae and Acanthuridae, and to a lesser extent the Scatophagidae. This is the opposite of Recent coral reef assemblages, where the Labroidei is the numerically dominant lineage.

Taxonomic diversity in the Bolca assemblage shows a similar pattern. Bolca has more than twice as many higher squamipinnes genera as labroid genera. Recent reef fish assemblages, in contrast, have numerous labroid genera and few higher squamipinnes genera. However, care is needed in these comparisons, as the taxonomy of both groups requires further analysis.

Overall, the two assemblages are broadly similar in their familial composition. They differ, however, in the numerical abundance of the various families and in their taxonomic diversity at a generic/species level.

Discussion

Bolca as a coral reef fish assemblage

The consensus list of reef fish families used in the present study provides a conservative definition of a Recent coral reef fish assemblage, that is, a fish assemblage in which the following eight reef fish families are present – Acanthuridae, Apogonidae, Blenniidae, Chaetodontidae, Labridae, Mullidae, Pomacentridae, Scaridae – characteristic reef associated families may be present – Holocentridae, Siganidae, Ehippidae, Serranidae, Pomacanthidae, Carangidae, Zanclidae.

Unlike previous definitions, it is taxon-based reflecting presence or absence of taxa rather than ecological criteria assessing their association with coral reefs (cf. Bellwood 1988; Choat and Bellwood 1991).

All Recent coral reefs and marginal reefal areas will almost certainly include the minimum 8 families listed. This list is not exclusive. None of the families listed are found exclusively on coral reefs. However, most have strong affinities with coral reefs, and with the possible exception of the Mullidae, all achieve their greatest species diversity and numerical abundance on coral reefs.

In comparison, the Monte Bolca assemblage contains 6 of the 8 families listed in group 1 and all from group 2. Given the almost complete overlap in both lists it is concluded that the Monte Bolca assemblage may be regarded as a coral reef fish assemblage or, at the very least, to contain a significant coral reef fish component.

The absence of the Chaetodontidae and Scaridae from the Bolca assemblage does not change this basic conclusion. Recent phylogenetic studies suggest that Chaetodontidae is closely related to the Acanthuroidei, with the chaetodontid lineage arising from one of the basal divisions within the higher squamipinnes (Blum 1988; Tyler et al. 1989). The presence of acanthuroid taxa in the Bolca assemblage suggests that the chaetodontid lineage was present at this time. The absence of the Chaetodontidae possibly reflects low abundance. The first record of the Chaetodontidae is unclear (all *Pygaeus* species examined were not chaetodontids). However, there is a strong possibility of clearly defined specimens of Oligocene age (Patterson 1993b; DRB personal observation).

The Scaridae, although not recorded from Bolca, is regarded by some workers as a highly derived labrid which should be placed within the Labridae (cf. Kaufman and Liem 1982; Bellwood 1994). The absence of the Scaridae may therefore be a taxonomic artefact, reflecting taxonomic inconsistencies. The oldest substantiated record of the Scaridae is from the Middle Miocene (Bellwood and Schultz 1991). It is interesting to note, however, that the labroid lineage that is believed to have given rise to the Scaridae is already present in Bolca (*Phyllopharyngodon*: Bellwood 1990, cf. Bellwood 1994).

Additional indirect evidence of reefal links comes from the absence or low numbers of coastal marine taxa which are characteristic of Recent soft sediment areas e.g. the Leiognathidae, Ambassidae, Sciaenidae, Mugilidae, Hae-

mulidae, Gerreidae, Teraponidae, etc. Although the absence of evidence is not evidence of absence, it is striking that so few soft sediment taxa/individuals are represented in the assemblage.

Taxonomic diversity and numerical abundance of reef fish families

The Eocene deposits of Monte Bolca contain numerous perciform fish families and offer an insight into the early evolution of coral reef fishes. There are currently approximately 247 described species in 194 genera, 82 families and 17 orders in the assemblage (modified after Blot 1980). This includes the first record of almost all coral reef fish families and numerous other perciform fish families. This taxonomic diversity is matched by numerical abundance. From these analyses three major features of the assemblage are immediately apparent:

1. The Bolca assemblage has a clear link with Mesozoic fish assemblages, i.e. the presence of pycnodontids. This is one of the youngest records of the order Pycnodontiforms and marks the final transition from the 'lower' neopterygian-dominated assemblages which were characteristic of shallow marine habitats throughout the Mesozoic to the perciform-dominated assemblages which have been a distinctive feature of marine fish assemblages throughout the Tertiary.

2. In Bolca, non-perciform taxa are relatively abundant, with the Beryciformes being the most noteworthy. Represented by only three species, all in the family Holocentridae, they comprise 8% of the specimens identified. Recent holocentrids are strongly associated with reefs and their abundance in Bolca suggests an early coral reef association.

3. The assemblage is dominated by perciform fishes. While this may be no surprise when compared with Recent reef fish assemblages, this is a particularly significant factor given the pre-Eocene fossil record. Although reported from the late Cretaceous (*Nardoichthys* Sorbini and Bannikov 1991), only a few pre-Eocene perciform taxa have been described and most are questionable (Patterson 1993a). The Bolca assemblage clearly establishes the earliest known date for not only great taxonomic radiation of perciform fishes, but also their numerical dominance in shallow tropical marine benthic communities.

The high diversity of perciform fishes reported in the Bolca assemblage applies equally well to reef fish taxa. However, there are two striking differences between the Bolca assemblage and those of Recent coral reefs: (a) the nature of the diversity recorded and (b) the relative status of the two main reef fish lineages, the Labroidei and higher squamipinnes.

First in terms of diversity, it appears that the Bolca assemblage is characterized by a high diversity of families, and in some cases genera, but with low species diversity. Recent reefs have a higher species diversity but possibly a lower family or genus-level diversity.

The second main difference between Bolca and Recent coral reef fish assemblages is the relative status of the two

main reef fish lineages, the Labroidei and higher squamipinnes. On Recent reefs the Labroidei is the dominant taxon in terms of both numerical abundance and species/generic diversity. The higher squamipinnes are less diverse and numerically a much smaller component. In contrast, in the Bolca assemblage, the higher squamipinnes are more diverse and more abundant than the Labroidei.

This contrast between the two assemblages in most striking in terms of the Pomacentridae. On Recent reefs, the Pomacentridae is the first or second most abundant family comprising approximately 15–48% of all individuals (Fig. 1), with over 107 spp on the Great Barrier Reef spp in 10 genera. To date, only two specimens of one species have been recorded from Monte Bolca, representing less than 0.15% of all individuals. This probably represents the major difference between the reef fish component of the Bolca fish assemblages and those of Recent reefs. In Bolca, most families are present but their relative abundance differs.

Overview of the evolution of reef fishes

We see in Monte Bolca the first complete reef fish assemblage. Within a few million years of the first perciform fishes, a complete reef fish assemblage is already in place. It is dominated by the Perciformes and contains almost all modern reef fish families. The familial diversity of the assemblage rivals that found on reefs today.

Reef fishes did not slowly accumulate during the Tertiary. The diversity seen on coral reefs today is, in some ways, illusionary. It is predominantly species diversity based primarily on differences in color patterns. The basic body plans and phylogenetic lineages are the same or a subset of those present 50 million years ago. The earliest record of almost every reef fish family is in the Eocene – based on Monte Bolca. By the late lower Eocene all major reef fish lineages were represented and most already possessed the derived morphological structures which are characteristic of Recent representatives. The two most striking aspects are (a) the completeness of the assemblage and (b) the extent of subsequent stasis. In terms of the familial composition and the basic body plan of component taxa, change since the Eocene appears to have been small.

The results of this study suggest that the evolution of coral reef fishes has been characterized by rapid early proliferation of families followed by stasis. Coral reefs are extremely dynamic, with whole reef regions such as the Great Barrier Reef being lost and re-established on a frequent basis (Davies 1988). However, the presence of reefs, if not their position, is highly predictable. In the Indo-Pacific, coral reefs have been present throughout the Tertiary and, as such, offer continuity of habitat (Rosen and Smith 1988). This period was also marked by the appearance and success of Recent scleractinian coral genera (Veron 1986). The form of coral reefs therefore, as fish habitats throughout this period was presumably broadly comparable to that of Recent reefs. The basic reef regions and structural features, at least, remained consistent

throughout the period (Rosen personal communication). This temporal if not spatial continuity of coral reef habitat may in part account for the conservative nature of reef fish evolution.

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Appendix 1

These perciform families and orders (n specimens) from Monte Bolca were included in the analyses:

Families in the Perciformes: Acanthonemidae (7), Acanthuridae (32), Acropomatidae (32), Amphistiidae (8), Apogonidae (32), Blenniidae (2), Blochiidae (36), Carangidae (71), Centropomidae (142), Ductoridae (35), Enoplosidae (2), Ehippididae (38), Excellidae (14), Gobiidae (12), incertae sedis (66), Labridae (2), Lutjanidae (1), Menidae (47), Monodactylidae (9), Mullidae (1), Mugilidae (4), Percidae (3), Potamidae (27), Priacanthidae (1), Scatophagidae (14), Scombridae (22), Serranidae (19), Siganidae (6), Sparidae (87), Sphyrnidae (23), Tortonesidae (7), Trachinidae (3), Zanclidae (3).

Orders: Pycnodontiformes (25), Anguilliformes (94), Elopiformes (11), Clupeiformes (166+), Myctophiformes (2), Gadiformes (4), Lophiiformes (24), Atheriniformes (19), Lampriformes (3), Beryciformes (112), Gasterosteiformes (60), Scorpaeniformes (52), Perciformes (962), Tetraodontiformes (46), Pleuronectiformes (11).

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