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Multiple Recurrent Evolution of Trophic Types in Northeastern Atlantic and Mediterranean Seabreams (Sparidae, Percoidei)

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Abstract. Seabreams are among the most valuable fish, not only for small-scale and semiindustrial fisheries but also for aquaculture throughout the Mediterranean. Nevertheless, their phylogenetic relationships are not at all clear. The current taxonomy is based solely on trophic morphology and rests on the assumption that each trophic type evolved only once from a less specialized ancestral condition. We analyzed a 486-bp segment of the mitochondrial 16S rDNA of all 24 seabream species described for the northeastern Atlantic and the Mediterranean to elucidate their generic and subfamily-level relationships. Three major mitochondrial lineages, each comprising species of different feeding strategy and dentition, were found that do not agree with the present taxonomic assignments. Most of the investigated genera were resolved paraphyletically, indicating that the structure and arrangement of oral teeth must have repeatedly evolved from a less specialized ancestral condition. Further, the genus *Sparus* was resolved as distantly related to the genus *Pagrus*, in that it was assigned to a different major mitochondrial lineage. *Oblada melanura* was consistently placed within the *Diplodus* radiation as sister group to *Diplodus puntazzo.* Our phylogenetic hypothesis thus suggests multiple independent origins of similar trophic specializations within the Sparidae and indicates that the currently recognized three or four subfamilies need to be redefined.

Key words: mtDNA — 16S rDNA — Sparidae — Molecular phylogeny — Trophic morphology — Taxonomy

Introduction

The Sparidae comprise a total of about 100 species which are found predominantly in coastal waters of tropical and temperate zones. While most of their closely related families (Lethrinidae, Nemipteridae, Haemulidae, Lutjanidae) are more or less restricted to the Indo-Pacific region, the Sparidae have their center of diversity in the Atlantic Ocean. Twenty-four species are described from the northeastern Atlantic and Mediterranean coasts (Bauchot and Hureau 1986). As major targets for small-scale and semiindustrial fisheries, they are of considerable economic importance. Some species such as the gilthead bream (*Sparus aurata*) and the red seabream (*Pagrus major*) have become important aquaculture subjects (Hempel 1993). Their aquacultural value has resulted in a series of genome manipulation programs focusing on higher productivity such as transgenesis (Cavari et al. 1993), gynogenesis (Sugama et al. 1990), triploidization (Garrido-Ramos et al. 1996), and interspecific hybridization (Dujacovic and Glamuzina 1990). Cultivation of additional Mediterranean species such as *Pagrus pagrus, Diplodus sargus,* and *Diplodus puntazzo* is presently being attempted (Reina et al. 1994). Despite their economic importance, the systematics of the family Sparidae still remain unclear. Their classification is so far based solely on morphological grounds, in particular, defined by the number of hard and soft fin rays and dentition (Bauchot and Hureau 1986; Smith and Smith 1986). Fiedler (1991)

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Table 1. Characterization of the investigated species of the family Sparidae: Species names follow the nomenclature of Bauchot and Hureau (1986)

Species	*n*/*n*^{a}	Subfamily^a	Habitat	Lifestyle	Dentition	Main food type	Genbank accession no.(s.)
Boops boops	3/1	Boopsinae	Ubiquitous	Semipelagic	I	Zooplankton	AJ247268
Sarpa salpa	3/1	Boopsinae	Rocky/sea grass	Gregarious	I	Benthic algae	AJ247269
Spondyliosoma cantharus	3/1	Boopsinae	Rocky/sandy	Gregarious	CO	Crustaceans	AJ247280
Oblada melanura	3/2	Boopsinae	Rocky/sea grass	Semipelagic	I/CO(r)	Benthic invertebrates	AJ247296, AJ247297
Dentex (Cheimerius) canariensis	1/1	Denticinae	Ubiquitous	Demersal	CA	Fish	AJ247270
Dentex (Dentex) dentex	3/1	Denticinae	Rocky	Demersal	CA	Fish	AJ247271
Dentex (Cheimerius) gibbosus	1/1	Denticinae	Rocky/sandy	Demersal	CA	Fish, crustaceans	AJ247272
Dentex (Polysteganus) macrophthalmus	3/1	Denticinae	Rocky/muddy	Demersal	CA	Fish, crustaceans	AJ247273
Dentex (Polysteganus) maroccanus	3/1	Denticinae	Ubiquitous	Demersal	CA	Fish, crustaceans	AJ247274
Pagrus auriga	3/1	Sparinae	Hard bottoms	Demersal	CA/M	Bivalve mollusks	AJ247275
Pagrus coeruleostictus	3/1	Sparinae	Hard bottoms	Demersal	CA/M	Bivalve mollusks	AJ247276
Pagrus pagrus	3/2	Sparinae	Rocky/sandy	Demersal	CA/M	Crustaceans, mollusks	AJ247277, AJ247278
Pagellus bellottii bellottii	3/1	Sparinae	Rocky/sandy	Demersal	CO/M	Benthic invertebrates	AJ247282
Pagellus erythrinus	4/1	Sparinae	Ubiquitous	Demersal	CO/M	Benthic invertebrates	AJ247284
Pagellus acarne	3/1	Sparinae	Ubiquitous	Demersal	CO/M	Benthic invertebrates	AJ247281
Pagellus bogaraveo	3/1	Sparinae	Ubiquitous	Gregarious	CO/M	Pelagic invertebrates	AJ247283
Lithognathus mormyrus	2/1	Sparinae	Sandy/muddy	Demersal	CO/M	Crustaceans, mollusks	AJ247285
Sparus aurata	3/1	Sparinae	Ubiquitous	Demersal	CA/M	Bivalve mollusks	AJ247279
Diplodus annularis	3/2	Sparinae	Rocky/sea grass	Gregarious	I/M	Benthic invertebrates	AJ247286, AJ247287
Diplodus bellottii	3/2	Sparinae	Ubiquitous	Gregarious	I/M	Mollusks, crustaceans	AJ247288, AJ247289
Diplodus cervinus cervinus	3/1	Sparinae	Rocky/muddy	Gregarious	I/M	Benthic invertebrates, algae	AJ247290
Diplodus puntazzo	3/2	Sparinae	Rocky	Gregarious	I/M(r)	Benthic invertebrates, algae	AJ247291, AJ247292
Diplodus sargus	5/1	Sparinae	Rocky	Gregarious	I/M	Benthic invertebrates	AJ247293
Diplodus vulgaris	4/2	Sparinae	Rocky/sandy	Gregarious	I/M	Invertebrates	AJ247294, AJ247295

n, number of individuals sequenced; *n*^{a}, number of individuals in the phylogenetic tree. CA, caniniform; CO, conical; I, incisiform; M, molariform; (r), rudimentary.

[a] According to Fiedler (1991).

distinguished three subfamilies, the Sparinae, the Denticinae, and the Boopsinae, based mainly on their dentition and diet. Smith and Smith (1986) named the Pagellinae as a fourth subfamily, also according to their trophic specialization. The relationships within these subfamilies remain unresolved, due to overall similarities and the lack of clear diagnostic characters. Remarkably little variation in external morphology between *Sparus aurata* and *Pagrus pagrus* led to long-lasting uncertainty upon their phylogenetic relationships, in that they were classified in a single genus (Bauchot et al. 1981; Basaglia 1992) or in separate genera (Bianchi 1984; Bauchot and Hureau 1986; Vitturi et al. 1992). First attempts to answer these questions through cytogenetics (Cataudella et al. 1980) or on the basis of isozyme electrophoresis (Basalia 1991) failed, while more recent isozyme data (Reina et al. 1994), as well as studies on satellite DNA (Garrido-Ramos et al. 1995, 1998, 1999), point to the existence of considerable incongruences to the present taxonomic assignments. Our study not only attempts to resolve these taxonomic problems by means of molecular genetic methods, but also aims to reconstruct the pathways of ecological and morphological adaptations during the radiation of this group.

Materials and Methods

Seventy-one individuals belonging to the 24 species of the Sparidae recorded for the northeastern Atlantic and the Mediterranean have been analyzed (Table 1). In addition, three individuals of *Spicara maena* of the family Centracanthidae were defined as an outgroup. Most of the littoral species (*Boops boops, Diplodus annularis, Diplodus puntazzo, Diplodus sargus sargus, Diplodus vulgaris, Lithognathus mormyrus, Oblada melanura, Sarpa salpa, Sparus aurata, Spondyliosoma cantharus, Spicara maena*) were selectively captured by use of a speer gun along the Revellata peninsula near Calvi, Corsica, in September 1996. Samples of *Pagellus acarne, Pagellus erythrinus,* and *Pagellus bogaraveo* were obtained in December 1997 from a fish market in Barcelona (Spain), *Diplodus cervinus cervinus* specimens were caught in April 1996 at Cabo La Nao (Spain), *Pagrus pagrus* and additional *Boops boops* specimens in December 1997 near Barcelona, and *Dentex dentex* specimens in April 1997 near Alicante (Spain). Samples of the predominantly Atlantic species (*Dentex canariensis, Dentex gibbosus, Dentex macrophthalmus, Dentex maroccanus, Diplodus bellottii, Diplodus sargus cadenati, Pagellus bellottii bellottii, Pagrus auriga,* and *Pagrus coeruleostictus*) were taken from a fish market in Agadir (Morocco) during March 1998.

To test the phylogenetic relationships, we sequenced a 486-base pair segment of the mitochondrial 16S rDNA. Total DNA was extracted by placing small amounts of epaxonic white muscle tissue in 500 μl of 5% Chelex 100 (BIO RAD) suspended in sterile H_2O, by incubation at 56°C for at least 4 h under permanent shaking. Extracts were finally incubated at 94°C for 15 min and then stored at −20°C.

Aliquots (1.7 μl) of the DNA extracts were directly used for PCR after centrifugation at 13,000 rpm (10.000 g) for 5 min.

For PCR amplification two universal primers for the 16S rDNA gene were used [16-sar and 16-sbr (Kessing et al. 1989)]. One double-stranded amplification (17-μl total volume) was conducted. The amplification products were purified with a commercial PCR purification kit prior to direct sequencing (Sanger et al. 1977). Both strands were sequenced for at least two specimens per species, while only one strand was sequenced for the remaining individuals (using the 16-sbr primer). The DNA sequences were determined by automatic sequencing on an ABI 373A DNA Sequencer (Perkin Elmer) through 8% polyacrylamide–urea gels in Tris–borate–ethylenediamine tetraacetate buffer (27 m*M*, pH 8.0) for 14 h at a constant power of 28 W.

Phylogenetic Analysis

The sequences were individually controlled and aligned using the Sequence Navigator program (version 1.0.1; ABI-Perkin Elmer). The Clustal alignments were then further improved by eye. To ensure that all analyzed taxa had comparable rates of base substitutions, we conducted a relative rate test by means of the computer program LINTRE (Takezaki et al. 1995). To examine the degree of variation within the sequence data set, we performed a sliding window analysis (Pesole et al. 1992; Sturmbauer and Meyer 1992). The percentage of variation within windows of nine bases was determined with three bases of overlap. The genetic variation is expressed as a percentage of the 27 possible base substitutions in a window of 9 bases. Three classes of variation were defined: <20% as regions of low variation, 20–40% as regions of high variation, and >40% as regions of very high variation. Then transition–transversion ratios were calculated for each of these regions separately and translated into appropriate weights for parsimony analysis, depending on the phylogenetic age addressed by our analyses.

Data were analyzed by applying the parsimony, neighbor-joining (Saitou and Nei 1987), and quartet puzzling (Strimmer and Haeseler 1996) methods in parallel, using the computer program PAUP* [test version 4.0d65 (Swofford 1999)], to test for the influence of the algorithm used on the resulting phylogenetic hypothesis. Parsimony analysis was done using heuristic search with random addition of taxa and 100 replications and the ACCTRAN option in PAUP. Phylogenies were subjected to bootstrap analysis (Felsenstein 1985) in parsimony and neighbor joining. Likelihood values were calculated in PUZZLE for all internal branches.

Due to the presence of both phylogenetically ancient and much younger branching events, we performed the analysis in two steps. In the first step a representative of the Centracanthidae (*Spicara maena*) was designated as an outgroup. Our selection is supported by Johnson (1993), who suggested the Centracanthidae to be the sister group of the Sparidae, based upon similarities of their maxillary–premaxillary articulation. In parsimony, transversion mutations were weighted three times over transitions in regions of low variation and five times over transitions in regions of high variation. In regions of more that 40% variation, transitions were completely excluded from analysis. Parallel neighbor-joining analyses were performed using Kimura (1980) distances. The maximum-likelihood analysis was performed by the quartet puzzling algorithm using the PUZZLE program which is implemented in the PAUP* package. In PUZZLE the ratio of transition to transversion mutations was set to 2, according to the observed average relative frequencies in our data set. The second step in the analysis focused on the most recent branching events within each clade found in the first analysis. To reduce the implementation of unnecessary homoplasies, two new outgroups were chosen, each representing the nearest possible sister group identified in the first analysis. Due to the generally small genetic differences observed among the taxa in question, transition and transversion mutations, as well as indels, were weighted equally. Accordingly, neighbor-joining analysis was performed using Jukes–Cantor distances and PUZZLE was run with a one-parameter substitution model.

Results

Phylogenetic Distances

Spicara maena, the outgroup species, turned out to be closely related to the Sparidae, with an average Kimura distance of 9.2% (SD, 1.3%). The 24 analyzed species were grouped in three major lineages as described in more detail below (Fig. 1). The average observed corrected sequence divergence (Kimura 1980) among the three major lineages comprising 24 species of the Sparidae amounted to 9.4% (SD, 1.6%). The genera *Spondyliosoma, Boops,* and *Sarpa,* comprising the first lineage, had an average Kimura distance of 8.8% (SD, 2.6%); the members of the second lineage, containing all *Dentex* and *Pagrus* species as well as *Pagellus erythrinus* and *Pagellus bellottii bellottii,* were all closely related, with an average Kimura distance of 3.2% (SD, 1.4%). The third lineage, containing the genera *Lithognathus, Sparus, Diplodus,* and *Oblada,* as well as *Pagellus acarne* and *Pagellus bogaraveo,* had an average Kimura distance of 5.0% (SD, 2.4%). The relative rate test identified *Lithognathus mormyrus* to have a slightly faster rate of base substitutions ($z = 3.36$), while all remaining taxa had similar rates. Thus, we tested the influence of the inclusion of *Lithognathus* on the resulting topologies by analyzing the data set with and without the taxon and by comparing the resulting topologies in parsimony, neighbor joining, and maximum likelihood to each other. It turned out that *Lithognathus* was invariably placed at the very base of the third lineage and that the resulting topologies remained unaffected by the presence or absence of *Lithognathus.*

Phylogenetic Relationships

In the first step in the analysis, focusing on the identification of more ancient splits, parsimony analysis resulted in three most parsimonious trees of an unweighted tree length of 324 mutations (weighted tree length, 1991 steps; consistency index excluding uninformative sites, 0.54; retention index, 0.80). Three major lineages were consistently found by parsimony, neighbor joining, and quartet puzzling as shown in Fig. 1. In parsimony, the first and most basal lineage, represented by *Spondyliosoma cantharus, Sarpa salpa,* and *Boops boops,* was followed by a second lineage containing all *Dentex* and *Pagrus* species, *Pagellus bellottii bellottii,* and *Pagellus erythrinus.* The third lineage comprised *Lithognathus mormyrus* as the most basal branch, followed by *Sparus aurata, Pagellus bogaraveo, Pagellus acarne,* and all members of the genus *Diplodus,* but also including

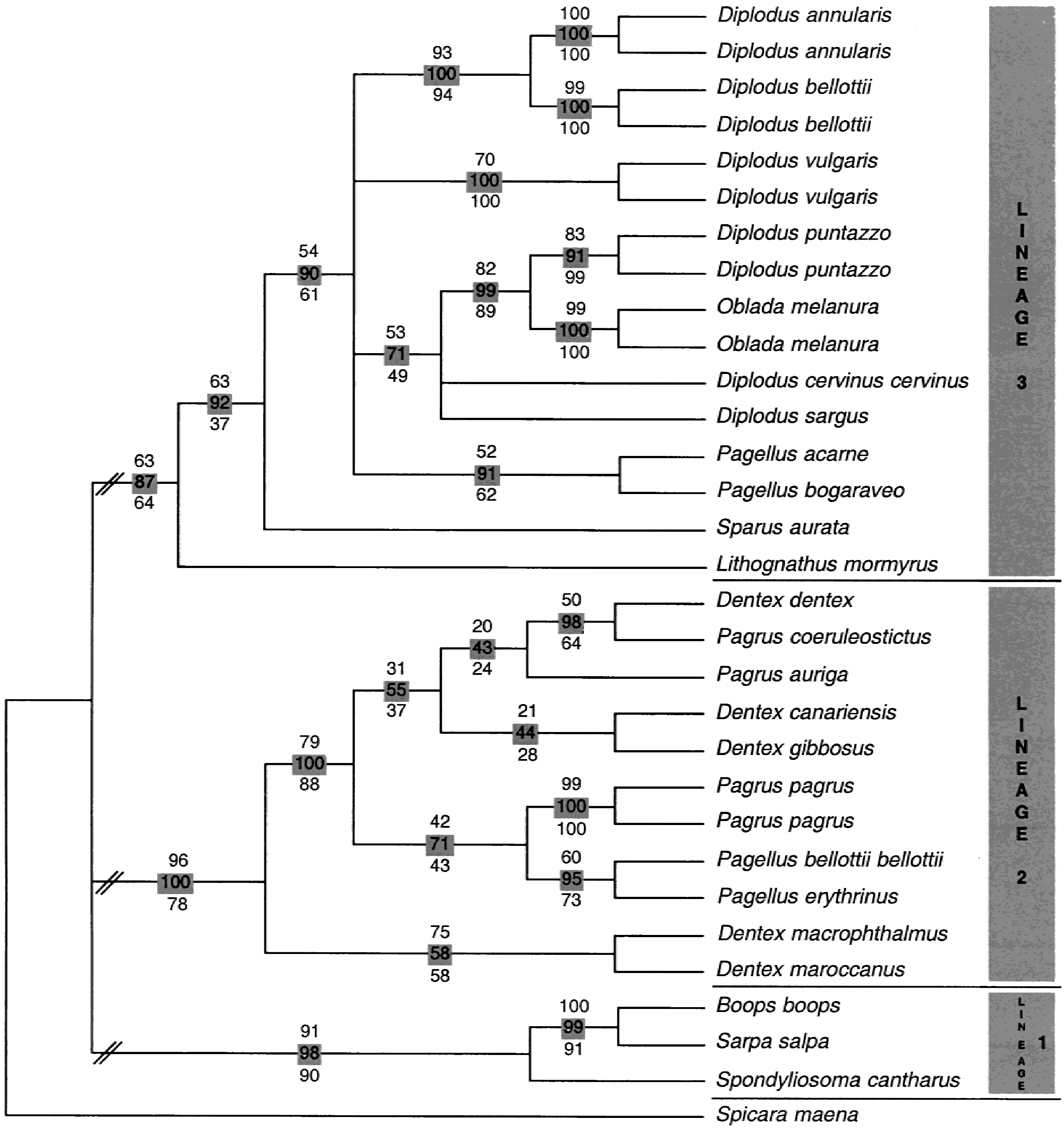

Fig. 1. Phylogenetic analysis of 31 taxa of the 16S rDNA region (486 bp) representing all seabream species distributed in the northeastern Atlantic and the Mediterranean Sea. *Spicara maena,* a member of the family Centracanthidae, was declared as the outgroup. The tree shows the strict consensus topology obtained by the three algorithms (parsimony, neighbor joining, and quartet puzzling) applied in parallel and summarizes the results of the two steps in the analysis. The resulting phylogenetic trees, weights used in parsimony, tree lengths, and consistency indices are described in the text. In neighbor joining the Kimura two parameter model was used in the first step in the analysis and Jukes–Cantor distances were used in the second step. The *numbers above the branches* are bootstrap values for parsimony, *those on the branches* are likelihood values obtained by quartet puzzling, and *those below the branches* are bootstrap values for neighbor joining.

Oblada melanura. The parallel neighbor-joining analysis using Kimura two-parameter distances, as well as the PUZZLE analysis, differed from the topology obtained by parsimony in that the clade comprising *Spondyliosoma cantharus, Sarpa salpa,* and *Boops boops* was resolved on the very base of the tree, followed by a clade containing all *Dentex* and *Pagrus* species as well as *Pagellus bellottii bellottii* and *Pagellus erythrinus.* Within this second lineage the topology varied with respect to the algorithm used and agreed only in that *Dentex macrophthalmus* and *Dentex maroccanus* were placed on the base (not shown). The third lineage again comprised *Lithognathus mormyrus*, *Sparus aurata*, *Pagellus bogaraveo*, *Pagellus acarne,* and all members of the genus *Diplodus,* as well as *Oblada melanura,* in agreement with parsimony. Two clades comprising *Lithognathus* and *Sparus* were consistently placed on the base of lineage three. The further branching order within the second and third lineage varied with respect to the algorithm chosen (not shown), but the relationships within each of the lineages were addressed in a second step of analysis.

In the second step in the analysis, focusing on the relationships within each lineage, we declared the clade containing *Spondyliosoma cantharus, Sarpa salpa,* and *Boops boops* as the outgroup and analyzed the relationships among the genera *Dentex* and *Pagrus* as well as *Pagellus bellottii bellottii* and *Pagellus erythrinus.* Parsimony analysis resulted in four most parsimonious trees of an unweighted tree length of 152 mutations (consistency index excluding uninformative sites, 0.64; retention index, 0.69). One of these four trees was identical to that found by neighbor joining and PUZZLE. In the parsimony analysis focusing on the relationships among the species comprising the third lineage, its most basal taxon, *Lithognathus mormyrus,* was declared as an outgroup, according to the first step in the analysis. A single most parsimonious tree was found, with a length of 125 mutations (consistency index excluding uninformative sites, 0.55; retention index, 0.71). *Sparus aurata* branched next to the outgroup, followed by a clade comprising *Diplodus bellottii* and *Diplodus annularis,* then by a branch containing *Diplodus vulgaris,* followed by a clade containing *Pagellus acarne* and *Pagellus bogaraveo,* then *Diplodus sargus,* then *Diplodus cervinus cervinus,* and, finally, a clade comprising *Diplodus puntazzo* and *Oblada melanura.* The resulting phylogenies obtained by neighbor joining and PUZZLE were identical and differed from the most parsimonious tree, in that the clade of *Pagellus acarne* and *Pagellus bogaraveo* branched after *Sparus aurata,* followed by a clade comprising *Diplodus cervinus cervinus* and *Diplodus sargus* at its base, followed by *Diplodus puntazzo* and *Oblada melanura,* and a clade with *Diplodus vulgaris* at its base, followed by *Diplodus bellottii* and *Diplodus annularis.* The phylogenetic tree shown in Fig. 1 is a summary of the two steps in the analysis, based on strict consensus trees of all alternative topologies obtained by the three algorithms applied.

Discussion

Our phylogenetic analyses clearly indicate that the northeastern Atlantic and Mediterranean seabreams can be assigned to three major lineages (Fig. 1). Our genetically based species assignment, however, is not in agreement with the subdivision of the Sparidae into three subfamilies according to Fiedler (1991) on the basis of trophic morphology and diet. The mitochondrial phylogeny refutes the monophyly of the Boopsinae (as defined by Fiedler 1991) in that *Oblada melaura* was unequivocally placed in a different major lineage (Lineage 3 in Fig. 1), within a clade comprising all members of the genus *Diplodus.* A revision of the northeastern Atlantic Boopsinae could be achieved, in that they should comprise only *Boops boops, Sarpa salpa,* and *Spondyliosoma cantharus,* with *Boops* and *Sarpa* forming a closely related assemblage (Kimura distance, 5.9%) and *Sponyliosoma* being more distantly related to them (Kimura distances, 9.8 to 10.8%). Since *Sarpa* was previously assigned to the genus *Boops* (Riedl 1983), it is questionable whether a placement in two genera should be maintained.

The second major lineage comprises all species of the genera *Dentex* and *Pagrus* as well as *Pagellus erythrinus* and *Pagellus bellottii bellottii.* The generic assignments within this clade, however, point to the paraphyly of all involved genera. It should be noted here that the present taxonomic assignments within the genus *Dentex* and its closely related genera are inconsistent in that the splitting into three genera, namely, *Dentex, Cheimerius,* and *Polysteganus,* is maintained for the South Atlantic (Smith and Smith 1986) and western Indian Ocean species (Bauchot et al. 1984), while all northeastern Atlantic and Mediterranean species were merged into the single genus *Dentex* (Bauchot and Hureau 1986). In our analysis the species *Dentex maroccanus* and *Dentex macrophthalmus* form the most basal branch within this clade. They are clearly separated from all remaining *Dentex* species, indicating the paraphyly of the genus *Dentex* (Fig. 2). Their former assignment to the genus *Polysteganus* could thus be maintained in a revision of the genus, once their relationships to the South Atlantic and western Indian Ocean allies are investigated. *Dentex canariensis* and *Dentex gibbosus,* formerly placed in the genus *Cheimerius,* are resolved as sister taxa, while *Dentex dentex* forms a distinct clade together with *Pagrus auriga* and *Pagrus coeruleostictus.* The genus *Pagellus* was resolved paraphyletically in two major lineages: two species, *Pagellus erythrinus* and *Pagellus bellottii bellottii,* form a clade together with *Pagrus pagrus.* The two remaining representatives of *Pagellus* were resolved within the species complex comprising *Diplodus* and *Oblada.* The observed paraphyly of the genus *Pagrus* further underlines the widespread inconsistencies to the current taxonomic assignments, as also suggested by a recently published phylogeny including a smaller number of taxa based upon centromeric satellite DNA (Garrido-Ramos et al. 1999).

Within the third major lineage, comprising *Lithognathus mormyrus, Sparus aurata, Pagellus acarne, Pagellus bogaraveo, Oblada melanura,* and all *Diplodus* species, the exact phylogenetic relationships could not be resolved by our 16S rDNA-based analysis, due to the young evolutionary age of this group and the relatively slow rate of evolution in this gene. Even a phylogenetic study based upon centromeric satellite DNA could not resolve the relationships of these taxa (Garrido-Ramos 1999). A more exact resolution has to be left for a future analysis using a more rapidly evolving DNA region, such as the mitochondrial control region. What can be con-

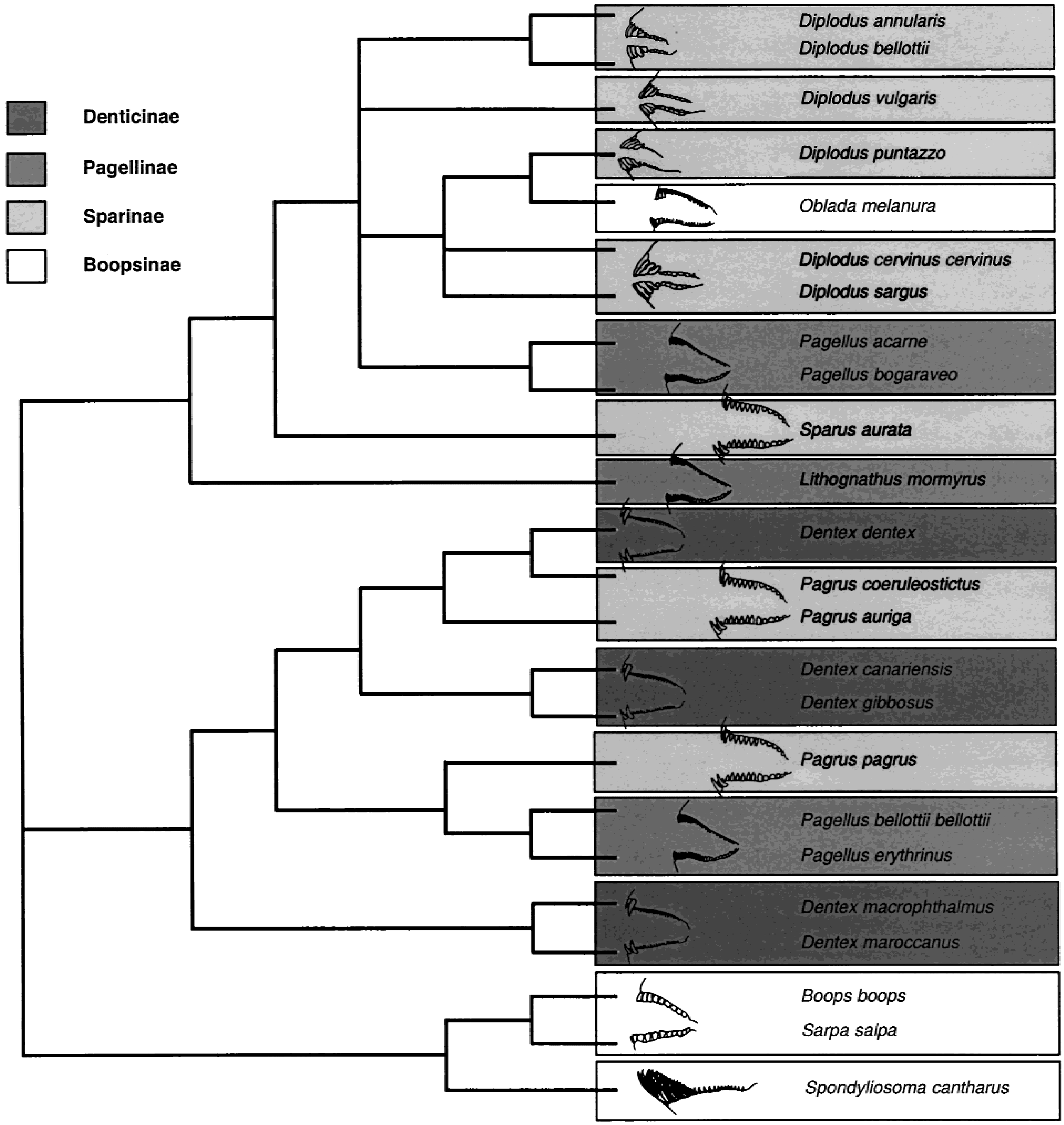

Fig. 2. Phylogenetic hypothesis including all recognized northeastern Atlantic and Mediterranean seabream species and their present assignment to subfamilies according to Smith and Smith (1986) based upon their dental morphologies, as depicted by *shaded boxes*. The scattered placement of similar dental morphologies points to a high probability of multiple recurrent evolution of corresponding tooth patterns and trophic specializations in the Sparidae and questions the usefulness of trophic morphology as a diagnostic trait for taxonomy.

cluded from the present analysis is that *Lithognathus mormyrus* was consistently placed as the most basal branch within this major lineage, followed by *Sparus aurata.* The remaining taxa form four subclades of uncertain branching order. Perhaps the most interesting aspect is the inclusion of *Oblada melanura* in the *Diplodus* species complex, considering its overall similarity to *Diplodus* with respect to its color pattern, despite its morphological distinctness; all three algorithms applied in our analysis resolved *Oblada melanura* as the sister taxon of *Diplodus puntazzo.*

The current phylogeny of the Sparidae is based solely on trophic morphology, suggesting that each trophic type evolved only once from a less specialized ancestral condition. Our results allow us to reject the traditional hypothesis, that species with identical or similar trophic specializations are always derived from a single ancestor. In seabreams trophic specialization is encompassed predominantly by modifications in shape and arrangement of oral teeth, so that the three or four currently distinguished subfamilies reflect the three or four major feeding types. Our data indicate that lineages with identical trophic morphology have evolved by multiple recurrent evolution (Fig. 2). This seems to be the case for *Sparus aurata* and *Pagrus pagrus* due to corresponding selective constraints connected to their lifestyle as demersal carnivores feeding mainly on hard-shelled benthos invertebrates. Since species of the genus *Pagrus* were repeatedly placed in paraphyly with several members of the genus *Dentex*, heterodontous dentition patterns must have repeatedly evolved from homodontous ancestors, or vice versa (Fig. 2). So are *Dentex dentex* and *Pagrus coeruleostictus* separated by morphology-based taxonomy on the basis of their different dentition only, while they share a variety of other characters, such as body shape, the presence of blue spots on their body sides, and their yellow color patterns at maturity. They were resolved as closely related sister taxa. A third case of recurrent evolution of dental morphology must be assumed for the presently assigned *Pagellus* species, which were placed in two major mitochondrial lineages (Fig. 1). Our findings are in striking agreement to evolutionary patterns found in East African cichlid fish. Kocher et al. (1995) demonstrated parallel evolution of corresponding feeding types of Lake Malawi and Lake Tanganyika cichlids; and Rueber et al. (1999) demonstrated the same pattern within a single lineage of rock-dwelling cichlids in Lake Tanganyika.

The mitochondrial phylogeny further indicates that banding patterns seem to be more evolutionarily conserved than expected. All taxa assigned to the third major lineage show distinct banding patterns in form of transverse stripes or dark marks in the postopercular region and/or on the caudal peduncle. *Oblada melanura*, which was resolved as part of the *Diplodus* radiation, also shows a banding pattern characteristic for all *Diplodus* species. Even if *Oblada* changed from a gregarious to a more semipelagic lifestyle, as reflected in its body shape and dentition, its color pattern remained more or less unchanged. The maintenance of color patterns is also striking in the case of *Pagellus acarne* and *Pagellus bogaraveo*, which seem likely to be closely related to *Sparus aurata*. All three species have a distinct color pattern in the postopercular region. Further, all species assigned to lineage 1 (i.e., *Spondyliosoma*, *Boops*, and *Sarpa*) have gold-colored longitudinal lines. Among the members of lineage 2, *Pagellus erythrinus*, *Pagellus bellottii bellottii*, *Pagrus coeruleostictus*, *Pagrus pagrus*, and *Dentex dentex* have blue spots along their flanks that never occur in species assigned to one of the other two major lineages.

Our results point to the urgent need for a revision of the Sparidae by a careful re-evaluation of anatomical traits. Such a taxonomic revision may be achieved, in that the three major lineages should be reflected in the formation of three subfamilies (Boopsinae, Sparinae, and Denticinae). The generic assignments within each subfamily may be revised in two ways. The first alternative would be to reduce the number of genera by deletion of the genus names *Sarpa*, *Pagellus*, *Pagrus*, and *Oblada*, in that *Sarpa* is renamed *Boops* and the polyphyletic genus *Pagellus* is renamed according to their most closely related sister taxa in each of the two major lineages, i.e., *Dentex* in lineage 2 and *Diplodus* in lineage 3. The paraphyletic genus *Pagrus* would therefore also have to be renamed *Dentex*. Finally, *Oblada* would have to be changed to *Diplodus*. The second alternative would be to increase substantially the number of genera by renaming all taxa that are placed in para- or polyphyly. To us, the first alternative seems preferable.

The adaptive radiation of seabreams may be driven by similar evolutionary forces as in East African cichlid fish. The evolutionary success of cichlids was explained to a great extent by their potential quickly to modify their feeding apparatus by relatively small but efficient allometric changes, while their overall body morphology remained more or less unchanged (Liem 1973; Greenwood 1984; Stiassny 1991). While cichlids have two sets of jaws, one oral and a second on their pharyngeal apophysis, only oral jaws are found in seabreams. The key to their evolutionary success might thus be the evolutionary plasticity of their oral teeth to exploit a variety of resources effectively without much further change in other body parts.

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