An Historical Review of *Sebastes* Taxonomy and Systematics

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ABSTRACT—Following the initial description of a species of Sebastes *from the Atlantic in the late 1700's, in the late 1800's the incredible taxonomic diversity of the genus began to be recognized as more species were discovered in northeast Pacific waters. With over 100 species, most of them from the North Pacific, the genus* Sebastes *(rockfishes) now presents taxonomic problems at every level. For example, although early efforts to understand relationships among the species resulted in the erection of several subgenera, those and more recent efforts remain largely unsuccessful. Also, the position of the genus within the order Scorpaeniformes, as well as the limits of the genus and the validity of some species are all unresolved. This paper examines the worldwide history and status of taxonomic studies on* Sebastes, *and reviews the 23 subgenera that have been erected over the years. This review of research, which includes morphological and genetic studies, provides a framework against which to evaluate studies using new genetic techniques.*

Discovery: The Late 1700's

The systematics of the speciose genus *Sebastes*[1], rockfishes, particularly in the North Pacific, have challenged ichthyologists and others even casually interested in these fishes for well over a century. Fernholm and Wheeler (1983) detailed problems associated with the early descriptions of *Sebastes*. The first scholarly reference to a rockfish was by Linnaeus (1761) who included Norway and Italy as the range of a fish he described in 1758 and named *Perca marina*. In his former publication (Linnaeus, 1758), he also described *Perca scriba*, a Mediterranean serranid. Reiterating his description of *Perca marina*, Linnaeus (1761) cited the common Norwegian name (uer or rödfisk) for the fish from Norway, making it clear that he was including a rockfish, as well as a fish from the Mediterranean region in his description.

Cuvier (1829) was the first to use the generic name *Sebastes*, and in his second, and much more thorough description of the genus (Cuvier and Valenciennes, 1829) he included descriptions of species from the North Atlantic (*Sebastes norvegicus*), the Mediterranean Sea (*S. imperialis* = *Helicolenus dactylopterus*), and the Southern Hemisphere (*S. capensis*).[2] Cuvier and Valenciennes (1829) recognized the confusion between the northern fish and *Perca marina*, which he said was "hardly believable"; nevertheless, the name *Sebastes marinus* (Linnaeus) was used until recently for this fish from the North Atlantic. However, Fernholm and Wheeler (1983) found that the specimen Linnaeus used as the basis of his description was in fact the Mediterranean serranid *Serranus scriba*, so *Sebastes (Perca) marina* became a synonym of *Serranus scriba*, and the rockfish was left without a type species for reference. This made way for recognizing Ascanius (1772) as the author of *Perca norvegica* (i.e. *Sebastes norvegicus*), the most common rockfish of the northeastern Atlantic.

Proliferation of Subgenera: 1861–1898

By 1845, similar fish had been described as species of *Sebastes* from both the eastern and western North Pacific. In 1854, Ayres discovered *Sebastes paucispinis* from off California (Ayres, 1854a). Since *Sebastes paucispinis* is very different from *Sebastes norvegicus*, but clearly related to it, its discovery prompted Gill (1861) to erect another genus for it: *Sebastodes*. This began a trend by Gill and others to establish generic or subgeneric groupings as more and more similar species were described on both sides of the North Pacific during the 1860's–1880's (Fig. 1, 2). By 1898, Jordan and Evermann grouped the 55 northeast Pacific species that they recognized into 13 subgenera (Jordan and Evermann, 1898). They also mentioned 13 species from Japan and 3 species from the Southern Hemisphere. Generally the characters of a proposed subgenus were only those of the type species for the subgenus. In most cases the definitions of the subgenera were inferred rather than explicitly stated (Appendix I).

Confusion: 1863–1900

There was considerable disagreement among ichthyologists of the late 1800's concerning these subgenera of northeast Pacific rockfishes and the importance of the characters used to distinguish them. Reading the papers of Ayres (1854a, b, 1855, 1859, 1863a, b, c, d), Gill (1861,

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[1] *Sebastiscus* and *Hozukius* have been considered subgenera of *Sebastes* by some and separate but closely related genera by others. This paper will consider each a separate genus and will focus primarily on the taxonomic history of *Sebastes*. *Sebastes* is by far the most species-rich and widely distributed genus; *Sebastiscus* and *Hozukius* have three and two species, respectively, and occur only in the northwest Pacific. As will be discussed later, *Sebastes* and these other two genera form an unresolved trichotomy within the Sebastidae of the suborder Scorpaenoidei (Ishida, 1994). These three genera could be given the subfamily name Sebastinae, following Matsubara (1943).

[2] See Simpson, A. J., A. W. Kendall, Jr., and J. W. Orr. 2000. Translations of the original descriptions of *Sebastes* by Georges Cuvier. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle WA 98115. Proc. Rep. 2000-09, 24 p.

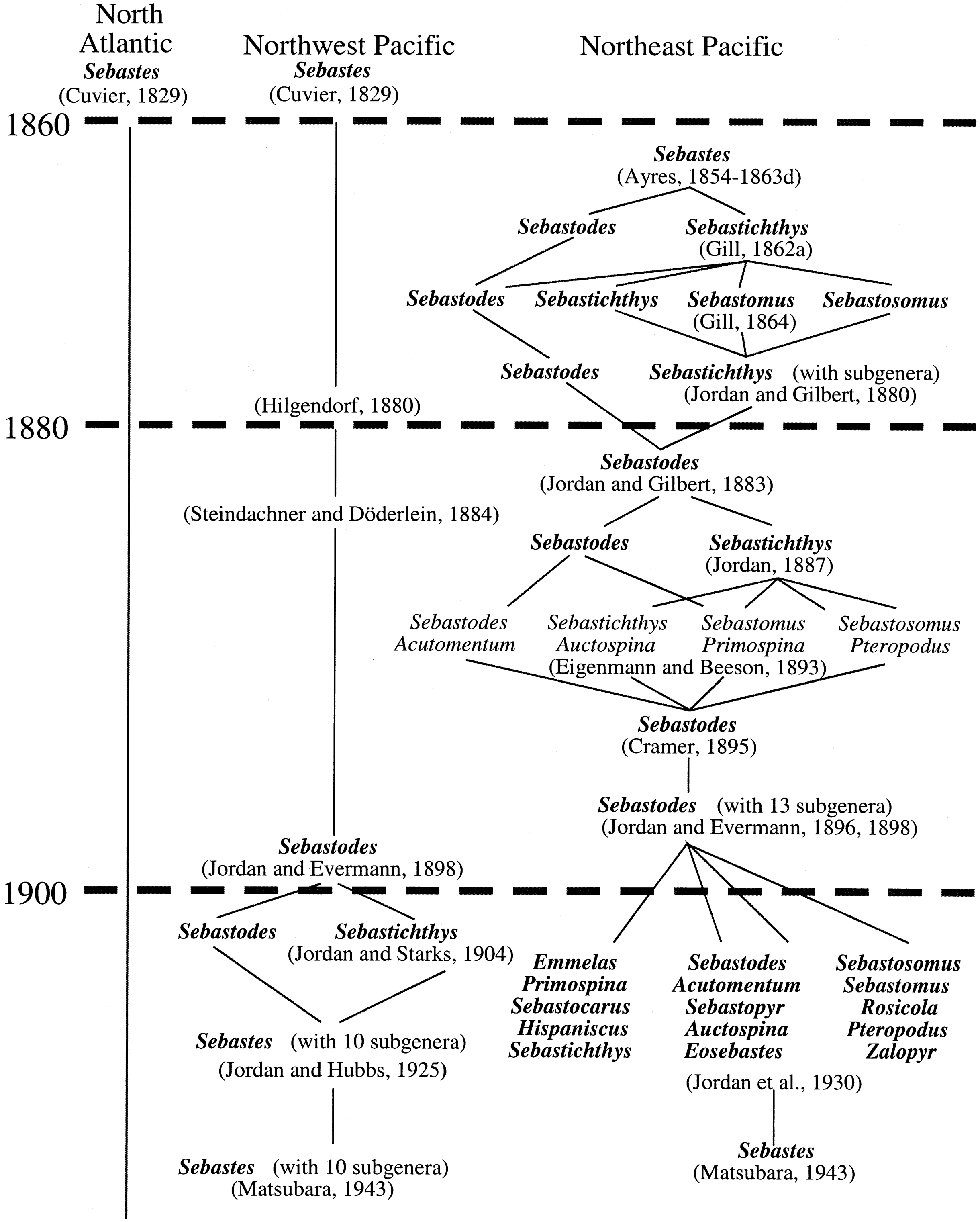


Figure 1.—Chronology of generic and subgeneric names for *Sebastes*. Based on Ishida (1984). Generic names are in bold. References below the names propose or support all the names on the line above them.

1862a, b, 1864), Jordan and Evermann (1896, 1898), Eigenmann and Beeson (1893, 1894), and Cramer (1895) on the subject indicates that more heat than light was generated. For example, by 1862 Gill had erected two genera (*Sebastodes* for *Sebastes paucispinis*, and *Sebastichthys* for all other species) for northeast Pacific rockfishes. He based these subgenera on a few morphological characters. Ayres (1863a, d) rejected the characters of Gill, but placed the 11 species known to him in two genera: one with smooth heads, for which he used the name *Sebastodes*, and the other with spiny heads, which he suggested be included with the North Atlantic species in *Sebastes*. In Gill's 1864 paper "Critical remarks on the genera *Sebastes* and *Sebastodes* of Ayres" he stated: "The value of the characters used to distinguish the genera *Sebastes*, *Sebastichthys* and *Sebastodes* are now indeed so generally conceded by scientific men, that it is unnecessary to further argue in their favor. I shall only remark that the combinations and distinction of forms by Dr. Ayres are alike unnatural and violate all natural affinities . . ." In discussing Ayres' ideas on affinities of flatfishes, Gill (1864) stated: "Dr. Ayres . . . ideas of affinity are extremely crude and unreliable, nothing can be learned from them." However, in discussing this paper Günther (1865) commented: "Dr. Gill would advance ichthyology by giving us serviceable descriptions, instead of limiting himself to synoptical tables with minute sub-generic subdivisions. As regards his frequent critical remarks on synonyms, it would be very useful if he would state whether he arrived at his conclusions from an examination of typical specimens, but it is not even evident whether he has known the species from autopsy." Ayres (Fig. 3) was not the only naturalist from San Francisco to receive severe criticism from Gill (Fig. 4): "Of course, Gill had an agenda for this criticism for he objected to the intrusion of these Californian upstarts, amateurs in his opinion, in what he had carved out as his personal fiefdom, the fishes of the North Pacific" (Leviton and Aldrich, 1997, footnote 16.3, p. 196).

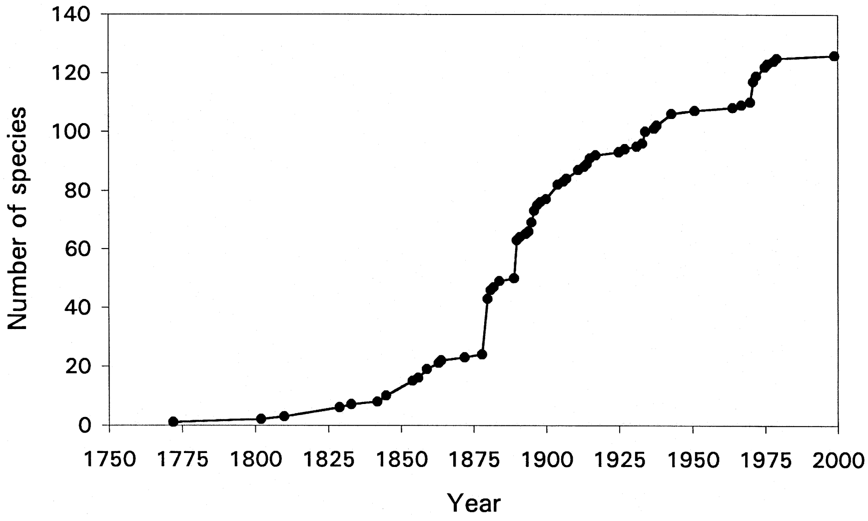


Figure 2.—Cumulative number of described and currently recognized species of *Sebastes*.

In 1880, Jordan and Gilbert (1880) described 7 new species from California, and after trying to place them in the four genera then recognized by Gill, they left *paucispinis* in *Sebastodes* and stated that: "the groups *Sebastosomus* and *Sebastomus* cannot be maintained as genera distinct from *Sebastichthys*, and that, in order to recognize them as subgenera even, a different distribution of species must be adopted."

Eigenmann and Beeson (1893, 1894) tried to bring some order to the argument

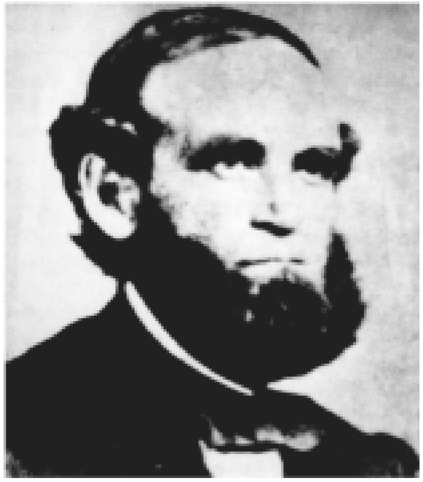


Figure 3.—Photograph of W. O. Ayres, reproduced through courtesy of California Academy of Sciences Archives. William Orville Ayres (1805–1887) was born in Connecticut and educated at Yale University to be a medical doctor (Hawkes, 1887). An early interest in natural history caught the attention, and fostered the friendship of J. J. Audubon, who named a woodpecker (*Picus ayresii*) in Ayres' honor stating "I have named this handsome bird after my young and learned friend W. O. Ayres, Esq. who is well known to science as an excellent ichthyologist; and who is well conversant with the birds of our country" (as seen in 1967 republication of Audubon, 1840–1844 [the bird is now considered a hybrid of the yellow- and red-shafted flicker]). In 1844, coincident with Audubon's death, convinced that "no field had been ungleaned in ornithology, [Ayres] turned to the water, teeming with attractive life and pregnant with interest for him" (Hawkes, 1887). Ayres migrated to San Francisco in 1854 and became a leading member and officer in the California Academy of Sciences, which met every, or every-other Monday evening in the 1850–1870 period, to hear of new natural history discoveries of the area. Besides maintaining a highly-regarded medical practice, Ayres often presented descriptions of fishes he came across at the fish markets, and even presented information on birds at some of the meetings. However ". . . Gill's ruthless criticism of Ayres, finally caused Ayres to give up research in ichthyology in 1864. Ayres left San Francisco in 1871 and returned East, first to Chicago, Ill., where he suffered serious financial reversals and then in 1878 to New Haven, Conn., where he re-established his medical practice and taught at Yale's medical school" (Leviton and Aldrich, 1997: footnote 3.2, p. 43).

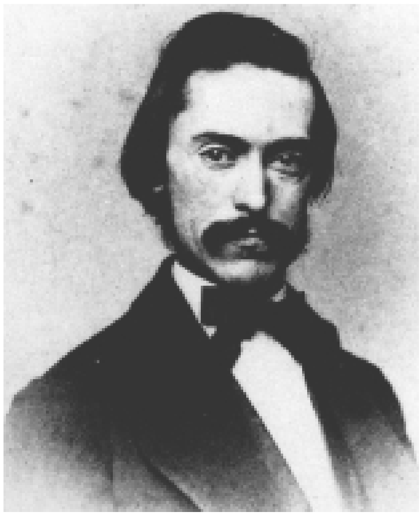


Figure 4.—Photograph of T. N. Gill, reproduced with permission (Neg. #SA602. Theodore N. Gill. Smithsonian Institution Archives. Record Unit 95, Photograph Collection, 1850s-). Theodore Nicholas Gill (1837–1914) grew up in New York City where early visits to the Fulton Fish Market spurred his interest in ichthyology (Dall, 1916). Early on Gill was schooled in the classical languages, with his father intending him to study theology, but this, as well as a job in a law firm, did not suit him, and his inclination in natural history prevailed. He was granted a scholarship to study science in Philadelphia, and from there he went to Washington, D.C., where he found a mentor and supporter in S. F. Baird at the Smithsonian Institution. Baird published one of Gill's first papers, on the fishes of New York, when Gill was only 19 years old (Gill, 1856). Shortly thereafter Gill made his only extensive field trip in which he studied the marine and freshwater fishes of the Antilles Islands. Upon returning to Washington he settled at the Smithsonian and, through Baird's influence, was appointed to work on fishes collected during the Northwest Boundary Survey. During this work he encountered many of the newly described and undescribed species of *Sebastes* from the northeast Pacific and the work of W. O. Ayres on them. As a result of his studies he published several descriptions of new species and erected several new genera to contain Pacific *Sebastes*. In these publications he frequently questioned Ayres' work, and eventually published (Gill, 1864) a criticism of Ayres (Ayres, 1863a) who had taken Gill to task for his classification of rockfishes. Ayres took this criticism so hard that he ceased to publish ichthyological papers. Gill remained in Washington, D.C., for the rest of his life, working on fishes, mollusks, mammals, and birds. Gill's strength was in higher order classification rather than in species descriptions ("In matters of classification [taxonomy] he was easily first in the world" Jordan (1931)). He had a reputation of being very helpful to up-coming students of natural history, but this did not seem to extend to Ayres.

by publishing a key and diagram of relationships for the eight subgenera they recognized (with *mystinus* as the sole member of *Primospina* representing the base from which all other species radiate) (Fig. 5). However, a footnote by the editor (R. Edward Earll) to the title of the 1894 paper which appeared in the Proceedings of the U.S. National Museum stated: "The classification adopted by the authors of this paper is based on their own peculiar interpretation of the importance of certain structural characters. The arrangement and nomenclature proposed here will not be, at present at least, followed by the National Museum." Further, Cramer (1895), in his detailed study of the cranial osteology of these fishes, took strong exception with the importance of the first dichotomy (union or nonunion of the parietals) in the key of Eigenmann and Beeson (1893). Since Cramer's work was in essence a rebuttal of the work of Eigenmann and Beeson, he included their entire article as an appendix to his paper. Cramer (1895) did not explicitly recognize any subgenera for the 32 species of *Sebastes* he examined, but his key to species based on cranial characters exactly groups the species into the subgenera eventually used by Jordan and Evermann (1898) in their classic "The Fishes of North and Middle America." In the introduction to their species accounts of *Sebastes*, Jordan and Evermann (1898) included from Cramer (1895) extensive quotations from his text, and his entire key to species, which they amended slightly by adding a few species Cramer did not consider, and from Eigenmann and Beeson (1893) their key to subgenera. Jordan and Evermann (1898) commented on Eigenmann and Beeson's (1894) work saying: "Messrs. Eigenmann & Beeson have attempted to subdivide this genus into several subgenera on the basis of cranial characters. Mr. Cramer has given in detail...his reasons for rejecting these proposed genera and for reverting to the sequence of species in Jordan & Gilbert's Synopsis [1883]. The character especially put forward by Eigenmann & Beeson, that of the contact (not union) of the parietals, seems to us of very slight value, even at a specific distinction."

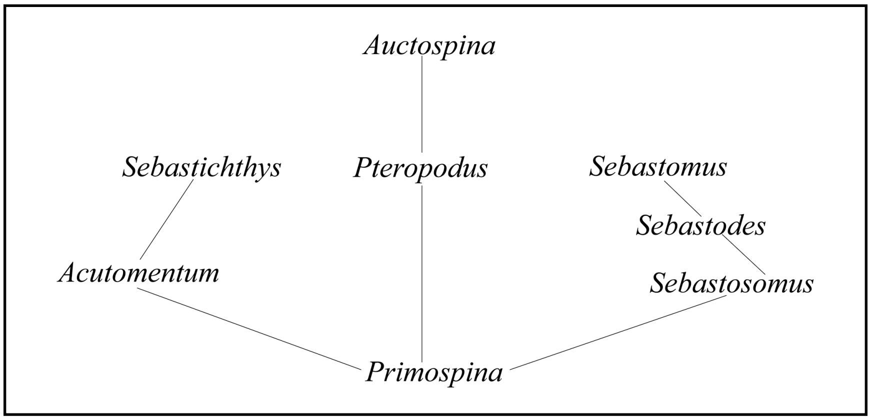


Figure 5.—Relationships among subgenera of *Sebastes* proposed by Eigenmann and Beeson (1893).

Consolidation: the Early 1900's

The proliferation of subgeneric names for rockfishes of the Northeast Pacific slowed after the turn of the 20th century. One more was proposed by Jordan and Hubbs (1925), two more by Jordan and Evermann (1927), and one by Hubbs (1951). Through the first half of the

20th century, authors variously lumped, split, or ignored subgenera completely. Although in their “Checklist of Fishes of North and Middle America,” Jordan et al. (1930) placed 66 species of rockfishes they recognized in 16 genera (that is, they elevated the subgeneric names to generic status), most American researchers used only two genera: *Sebastes* for Atlantic species and *Sebastodes* for Pacific species, disregarding the subgenera.

Matsubara (1943) (Fig. 6) presented a very detailed analysis of the Scorpaenidae of the Northwest Pacific. He subdivided the family into 14 subfamilies, and in the Sebastinae he included four genera, one of which was *Sebastes*. He grouped the 30 species of *Sebastes* he considered into 10 subgenera, 5 of which were newly erected. The five previously established subgenera he used had representative species in the Northeast Pacific also. Matsubara (1943) provided a key to the subgenera he used, and descriptions based on a number of osteological, meristic, and morphometric characters. He also concluded that there was no validity in grouping the Atlantic species of *Sebastes* separately from the Pacific species (then considered in *Sebastodes*), and since *Sebastes* is the older name it takes precedence.

The early-described Pacific species have fewer dorsal spines and vertebrae than the Atlantic species, characters thought important enough to justify placing the species from the two oceans in separate genera. However, species were later found in the northern Pacific Ocean and Bering Sea that have vertebral and dorsal spine counts approaching those of the Atlantic species, calling into question the rationale for maintaining the generic distinction. This change in thinking is reflected in successive editions of the American Fisheries Society’s “List of Common and Scientific Names of Fishes from the United States and Canada.” The first two editions (AFS, 1948; Bailey et al., 1960) recommended *Sebastes* for Atlantic species and *Sebastodes* for Pacific species; however, later editions (Bailey et al., 1970; Robbins et al., 1980; 1991) recommended using *Sebastes* for rockfishes from both the Atlantic and Pacific waters of North America.

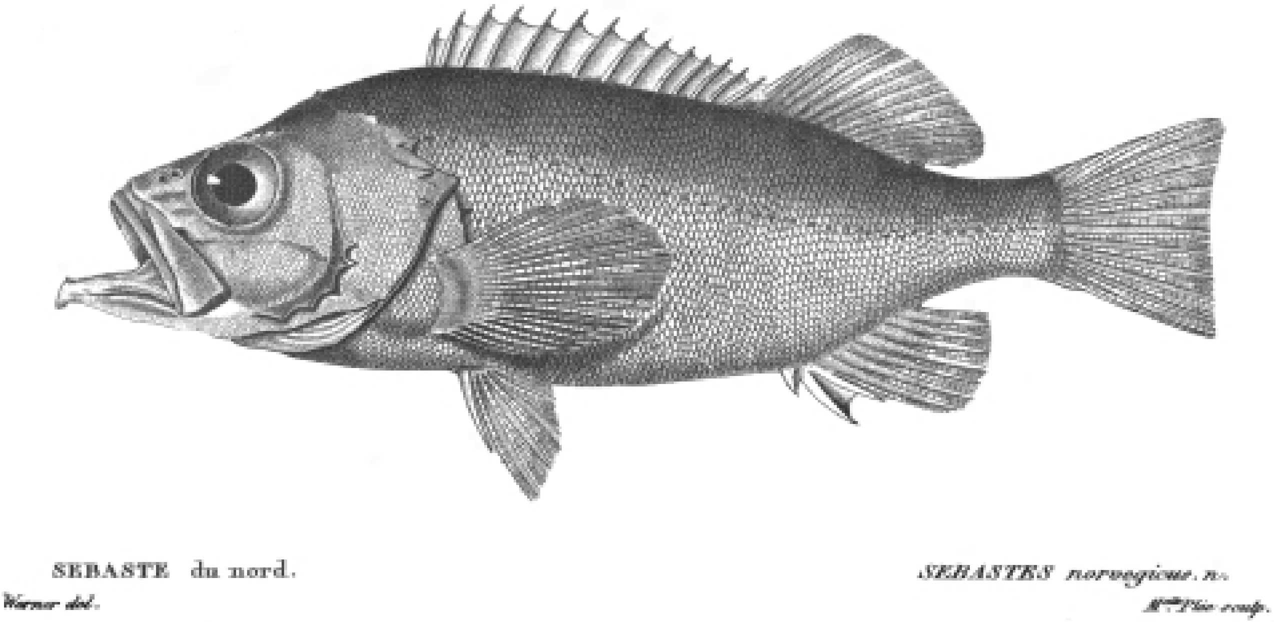
Limited Morphological Studies: the 1970’s

Chen (1971) reviewed *Sebastomus*, the most distinctive subgenus of *Sebastes*. Occurring in the northeast Pacific and in the Southern Hemisphere, *Sebastomus* contains 16 species, which are all characterized by having strong head spines, the second anal spine longer than the third, and a series of six large white blotches (one at the tip of the opercle and five between the dorsal fin and lateral line [not all are present in all species]). Chen (1971) gave detailed accounts of the species and constructed a diagram of relationships among the 13 then-known species based on a subjective analysis of about 15 characters. He considered phenetic similarity among the species in constructing his diagram. The characters he used were color patterns, body configuration (morphometrics and head spines), and meristics. He did not specify the outgroup for his analysis, or what he considered to be the primitive states of the characters he used. Without this information and with the informal discussion of relationships he offered, it is difficult to evaluate his conclusions. Thus, even within this relatively well-known and cohesive species group, considerable additional work is needed.

Hallacher (1974) characterized the structure and points of attachment of swimbladder muscles for 82 species of *Sebastes*, and found two major types and seven patterns within these types. In general, he found little correspondence between species sharing the same muscle patterns and their placement in the proposed subgenera (including *Sebastomus*). For example, two similar appearing members of *Sebastodes* (*S. brevispinis* and *S. paucispinis*) had major differences in structure. However, all but one species of *Pteropodus* shared the same swimbladder muscle pattern.

During this period several new species were described or reviewed (e.g. Barsukov (1970), Chen (1975), Tsuyuki and Westrheim (1970)), and some studies dealt with the component species of some subgenera (e.g. the *Sebastes*

Figure 6.—Photograph of K. Matsubara, reproduced with permission of the American Society of Ichthyologists and Herpetologists. Kiyomatsu Matsubara (1907–1968) was a prominent ichthyologist and teacher of ichthyology in Japan, who credited his interest in fishes to Carl Hubbs (Hubbs, 1969). Matsubara published several papers on scorpaenoid fishes of Japan, capped by his seminal monograph revising the Japanese fishes in this suborder and providing significant insight into the systematics of the group worldwide (Matsubara, 1943). Considering the world situation at the time, besides the remarkable ichthyological endeavor this monograph represents, it is amazing that it was published in perfect English, in Tokyo. Although a species of *Sebastes* from Japan is named *S. matsubarae*, it was not named after this renowned ichthyologist; rather it was described by Hilgendorf in1880, who named it after Shinnosuke Matsubara, director of the Imperial Fisheries Institute in Tokyo (Jordan and Starks, 1904). Besides his work on scorpaenoid fishes, Matsubara also published several more general volumes on systematic ichthyology and papers on various other fish groups of Japan. Although he worked at a time when limited access to foreign collections and literature forced many Japanese scientists to consider only local material in their work, Matsubara framed his work on scorpaenoids in a larger worldwide context. He was the first to suggest that the genera *Sebastes*, representing Atlantic species, and *Sebastodes*, representing Pacific species, be synonymized.



Sebastes norvegicus from Cuvier (1829): Plate 23, figure 3 (reproduced by permission of ASHER Rare Books, the Netherlands). This illustration accompanied the original description of the genus *Sebastes*.

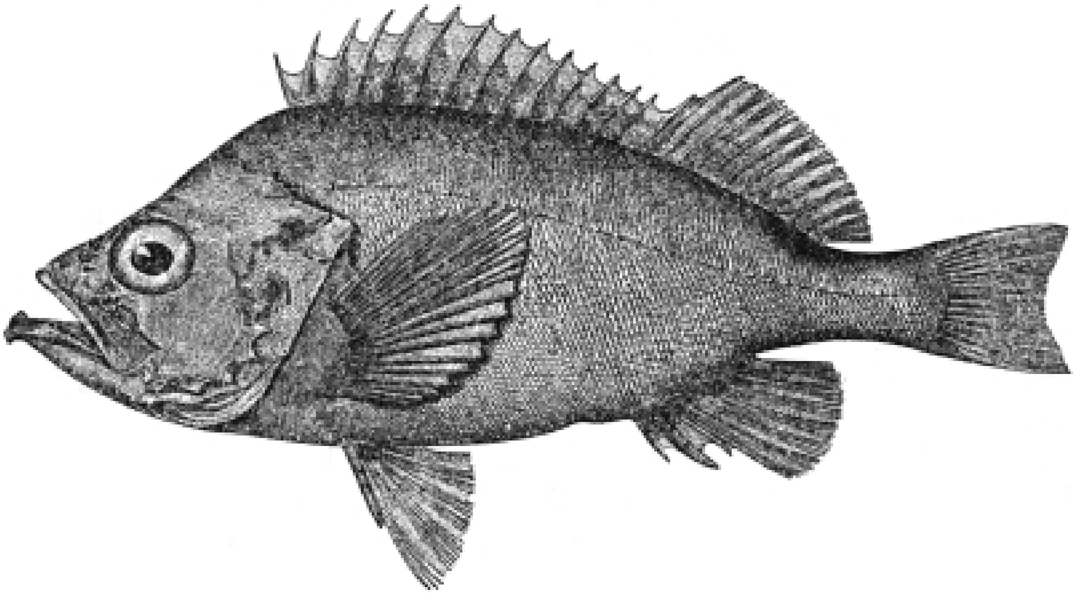
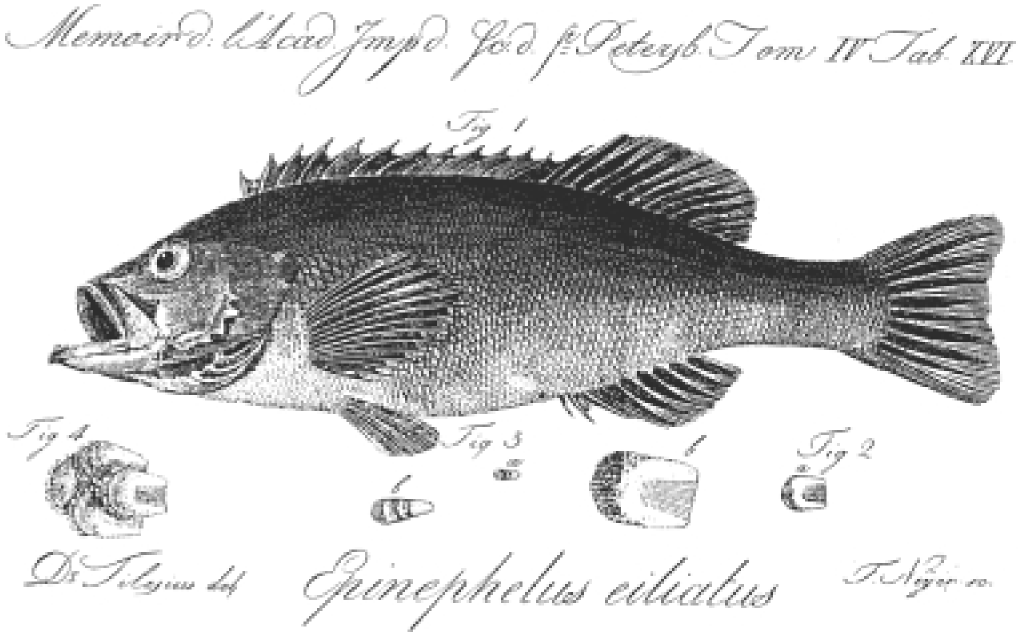
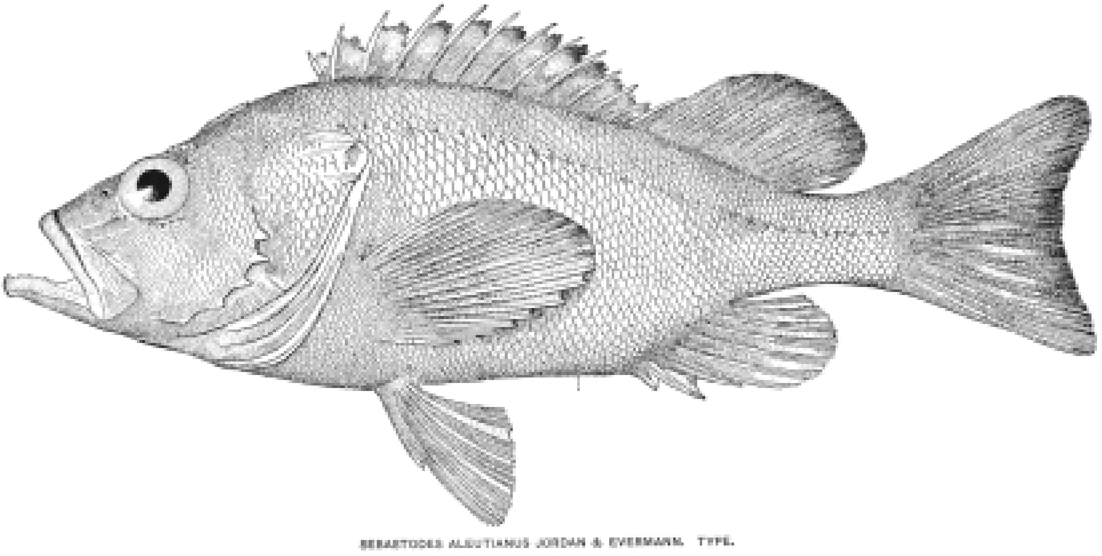


FIG. 141.—Rosefish (*Sebastes marinus*).

Sebastes marinus (probably *S. fasciatus*); drawn by H. L. Todd and originally published in Goode and Associates (1884). At the time of this publication only one species of *Sebastes* was recognized in the northwest Atlantic; however, three species are now known to occur there.



Sebastes ciliatus from the original description of the species by Tilesius (1813). This was the first species of *Sebastes* to be described from the Northeast Pacific Ocean.



Sebastes aleutianus from Evermann, and Goldsborough (1907). This is one of several fine illustrations of species of *Sebastes* from Alaska in this early publication.

vulpes “complex”: Chen and Barsukov (1976), *Sebastiscus*: Barsukov and Chen (1978), and *Mebarus*: Chen (1985)).

Systematic morphological analysis of the entire genus during this period was limited to Barsukov (1981), who published a complex diagram of interspecific relationships of the Sebastinae based on a dubious speciation hypothesis (Kendall, 1991). Barsukov (1981) proposed that there were seven cycles in the evolutionary history of the Sebastinae. “In each one no more than three descendant species originated sympatrically from one ancestral species. Such a triad is characteristic of speciation with incomplete (mainly biotopic) isolation. A species, once established at intermediate depths, emerges into the extreme position of another dimension, i.e., it develops ecological and morphological features unique for the trio, and usually associated with adaptations to life in open water” (Barsukov, 1981:1). Based on this premise he reviewed the sequence of geological events that led to the divergence found in some lineages of these fishes, and related the morphology of living forms to their history, ecology, and zoogeography. For example, in the first cycle he considered the subfamily Sebastinae to be composed of three genera: the shallow water *Helicolenus* with 13 species, the intermediate depth *Sebastes* with 102 species, and the deep-water *Hozukius* with 2 species. In the second cycle he felt that the genus *Sebastes* split into three subgenera: the shallow water *Sebastiscus* with 3 species, the intermediate depth *Sebastodes* with 88 species, and the deep-water *Sebastes* with 14 species. More divergence occurred in the intermediate-depth branch than in the other two during each cycle, and some branching was not successful (incipient species became extinct). Using these questionable evolutionary principles Barsukov (1981) diagramed the relationships of all known species of the Sebastinae.

Genetics Enters the Picture: the Late 1900’s

Starting in the 1960’s, newly developed genetic techniques were applied to systematic studies of rockfishes. Barrett et al. (1966) examined electrophoretic patterns of hemoglobin in 27 species of *Sebastes* from off California and found that each species, including some morphologically similar species pairs (e.g. *Sebastes caurinus*-*S. vexillaris*, *S. eos*-*S. chlorostictus*), had a distinctive pattern. They also found shared patterns among species in some subgenera (e.g. *Pteropodus*, *Sebastomus*), but distinct differences among some members of other subgenera (e.g. *Sebastosomus*). This work was closely followed by a study (Tsuyuki et al., 1968) examining hemoglobin, eye lens, and muscle protein electrophoretic patterns in numerous species of *Sebastes* from both the Atlantic and Pacific, as well as representatives of other scorpaeniform genera. As in Barrett et al. (1966), species-specific patterns were found in hemoglobins, and they interpreted within-species variation as evidence of additional undescribed species. Muscle proteins were not all species-specific, but they separated the 27 species of Pacific *Sebastes* they examined into four subgroups. Comparing these subgroups with the subgenera, little correspondence is seen. Among the 27 species, 11 subgenera are represented. *Sebastes aurora*, the sole member of *Eosebastes*, had a distinct pattern. As in Barrett et al. (1966), there was some coherence among the species of *Pteropodus*; two species (*S. caurinus* and *S. nebulosus*) grouped together as distinct from the other species. However, another species of *Pteropodus* (*S. maliger*) was in a group of 12 species, representing 8 subgenera in which there were no relationships among the species. The muscle and eye lens proteins were distinct at the generic level.

In the early 1970’s, Johnson et al. (1970a, b, 1971, 1972) and Johnson (1972) conducted a series of investigations on intraspecific variation in *Sebastes alutus* and other species of *Sebastes*, interspecific variation among *Sebastes*, and intergeneric variation within the Scorpaenidae, using electrophoresis of muscle proteins and several enzymatic systems. Polymorphisms were found in 11 of the 31 species studied. Three patterns were seen in *S. alutus* using two enzyme systems, however these patterns were not related to the geographic distribution of the samples. Among 27 species of *Sebastes* from the Pacific, 10 had unique patterns that allowed them to be identified based on the muscle protein and enzyme systems used in these studies. Several species demonstrated differences in only one enzyme system and thus appeared to be closely related to each other (e.g. *S. reedi* and *S. crameri* and *S. caurinus, S. auriculatus* and *S. maliger*). There was little variation between Atlantic and Pacific *Sebastes*, which were clearly distinct from *Sebastolobus* and *Helicolenus*.

Wishard et al. (1980) used protein electrophoresis to examine within-species relationships among five species of *Sebastes* from the northeast Pacific. Based on allele frequencies at 21 loci, they found evidence of three populations of *S. alutus*, two of *S. pinniger*, and one each of *S. flavidus*, *S. goodei*, and *S. paucispinis*.

At about the same time, genetic methods were being used in studies on the morphologically similar North Atlantic species of *Sebastes* (Nefyodov, 1971; Naevdal, 1978; Payne and Ni, 1982). A major focus of these studies using electrophoresis of hemoglobin and various enzyme systems was to confirm the presence of more than one sympatric species (*S. mentella*, *S. fasciatus*, and *S. norvegicus*). More recent work on Atlantic rockfish has employed genetic techniques to identify specimens, particularly juveniles, where more than one species occurs (Nedreaas and Naevdal, 1991; Rubec et al., 1991), and to examine population structure within *S. norvegicus* (Nedreaas et al., 1994).

Electrophoretic studies on Pacific *Sebastes* reached a plateau with the work of Seeb (1986). She analyzed electrophoretic variations of 28 enzymes in 48 species of *Sebastes* and was able to identify all but a few closely related species pairs on the basis of this analysis. She produced phenograms based on genetic distances among the species. As in previous studies (see above), species in some subgenera grouped closely together in these diagrams, while some of the branches contained members of several subgenera. For example, all the members of *Zalopyr*, *Sebastes*, and *Se*-

bastomus that she considered grouped together, as did most species of *Pteropodus*, and *Sebastodes*. However, species in *Acutomentum*, *Allosebastes*, and *Sebastosomus* were scattered among several lineages within her diagrams. Further work with allozymes of Pacific rockfish investigated population structure within *S. alutus* (Seeb and Gunderson, 1988: little structure was found), and the applicability of allozymes in identifying larval and juvenile specimens (Seeb and Kendall, 1991: allozyme activity and resolution decreased with decreasing size of the fish, but was adequate to aid in identification of juveniles and larvae).

In the 1990's, newer, more powerful genetic techniques were applied to rockfish taxonomic studies in both the Atlantic and northeast Pacific. McGauley and Mulligan (1995) amplified the mitochondrial rRNA (mtDNA) genes of *Sebastes flavidus* using polymerase chain reaction (PCR) and then used restriction fragment length polymorphism (RFLP) analysis to examine population structure. They found essentially no variation in haplotype frequencies among fish collected from Vancouver Island (British Columbia), Westport (Washington), and Cordell Bank (California), indicating that gene flow may be unrestricted within this species throughout its range. They attributed this to long-range dispersal of larvae. However, analysis of a more variable region of the mtDNA may have shown differences that their analysis failed to find. Seeb (1998) investigated gene flow among *S. auriculatus*[3], *S. caurinus*, and *S. maliger* using both allozymes and restriction analysis of mtDNA and found evidence of introgression between all three species in fish from Puget Sound, indicating some level of hybridization.

A major step forward in genetic studies occurred as Rocha-Olivares with others (Rocha-Olivares, 1998a; Rocha-Olivares et al., 1999a, b) began determining the sequence of nucleotides in the cytochrome *b* gene and part of the control region of the mtDNA molecule (a total of 1,633 bases) in Pacific *Sebastes*, particularly with members of the subgenus *Sebastomus*. These data were then used to address a number of taxonomic and systematic questions. An examination of 14 species of *Sebastomus*, and 40 other species of *Sebastes*, showed that the subgenus was monophyletic. Low levels of divergence in the genetic data indicated recent rapid radiation of the subgenus within the last million years (Fig. 7). Among *Sebastomus*, *S. rosaceus* appeared to represent the oldest lineage, and the rest of the species belonged to one of two clades: a northern clade and a southern clade. Generally, the species pairs produced by the molecular data were the same ones that Chen (1971) found based on morphological data.

Rocha-Olivares (1998b) used multiplex haplotype-specific PCR primers to create subgenus and species-specific assays for portions of the cytochrome-*b* gene in four species in the subgenus *Sebastomus*. He then screened 250 adults representing 31 species of *Sebastes* that had been identified morphologically, and found that with few exceptions, specimens were correctly assigned to species using the primers. Larvae were correctly assigned to the subgenus *Sebastomus*, although none was identified as a species from which the primers were developed. Rocha-Olivares and Vetter (1999) also used sequence data to examine intraspecific variation within *Sebastes helvomaculatus* collected at five sites from Fairweather Bank in the Gulf of Alaska to Cordell Bank off California. They found a high degree of population genetic diversity which could be related to their life history and zoogeography.

The application of genetic techniques is well demonstrated by their resolution of taxonomic problems associated with *Sebastes* from the Southern Hemisphere. *Sebastes* of the Southern Hemisphere has proven to be an exceptional challenge ever since *S. capensis* was placed in the genus by Cuvier and Valenciennes (1829). By the time of Chen's review of *Sebastomus* (Chen, 1971), 11 nominal species of *Sebastes* had been described from the Southern Hemisphere, all apparently in *Sebastomus*. After reviewing the literature (e.g. De Buen, 1960), and specimens from the west coast of South America and from South Africa, Chen (1971) concluded that more work was needed, but that he would consider all nominal species to be forms of *S. capensis*, as have others (Norman, 1937; Kong Urbina, 1985).

However, Eschmeyer and Hureau (1971) considered the *Sebastes* off the west coast of South America (*S. oculatus*) different from those around south central Atlantic islands and off South Africa (*S. capensis*), and suggested that more than one species occurs off the Pacific coast of South America. Chen (1971) and Eschmeyer and Hureau (1971) both pointed to the limited differentiation of *Sebastes* below the equator as evidence of the difficulty for this Northern Hemisphere, temperate and subarctic genus to cross the tropics.

Based on genetic sequence data, Rocha-Olivares et al. (1999b) found that within the southern clade of *Sebastomus*, *S. constellatus* represented the stock that gave rise to the Southern Hemisphere species: *S. oculatus* off South America and *S. capensis* off Africa. Further genetic studies (Rocha-Olivares et al., 1999c) on Southern Hemisphere *Sebastes* demonstrated that the tropical barrier was crossed successfully only once, and that three lineages (cryptic species?) now exist. The ancestral species is represented by *S. capensis* which occurs off Tristan da Cuhna and South Africa; this lineage is also present in the southwest Atlantic. There are two lineages of *S. oculatus* off the coasts of South America: one off the Pacific coast and the other off the Atlantic coast.

Recent work on the Atlantic species of *Sebastes* has used advanced genetic techniques to investigate relationships among the three morphologically similar sympatric species (e.g. Bentzen et al., 1998; Roques et al., 1999). Bentzen et al. (1998) found an unusual number of tandemly repeated copies of a section of the mtDNA molecule in all three species. The number of tandem repeats (9–17, mean 12.43) was similar in all

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[3] *Sebastes auriculatus* is in the subgenus *Auctospina* with *S. dalli*. However, this study and others (e.g. Johnson et al., 1972) indicated it is closely related to other shallow-water deep-bodied spiny rockfishes (e.g. *S. caurinus*) that are in *Pteropodus*.

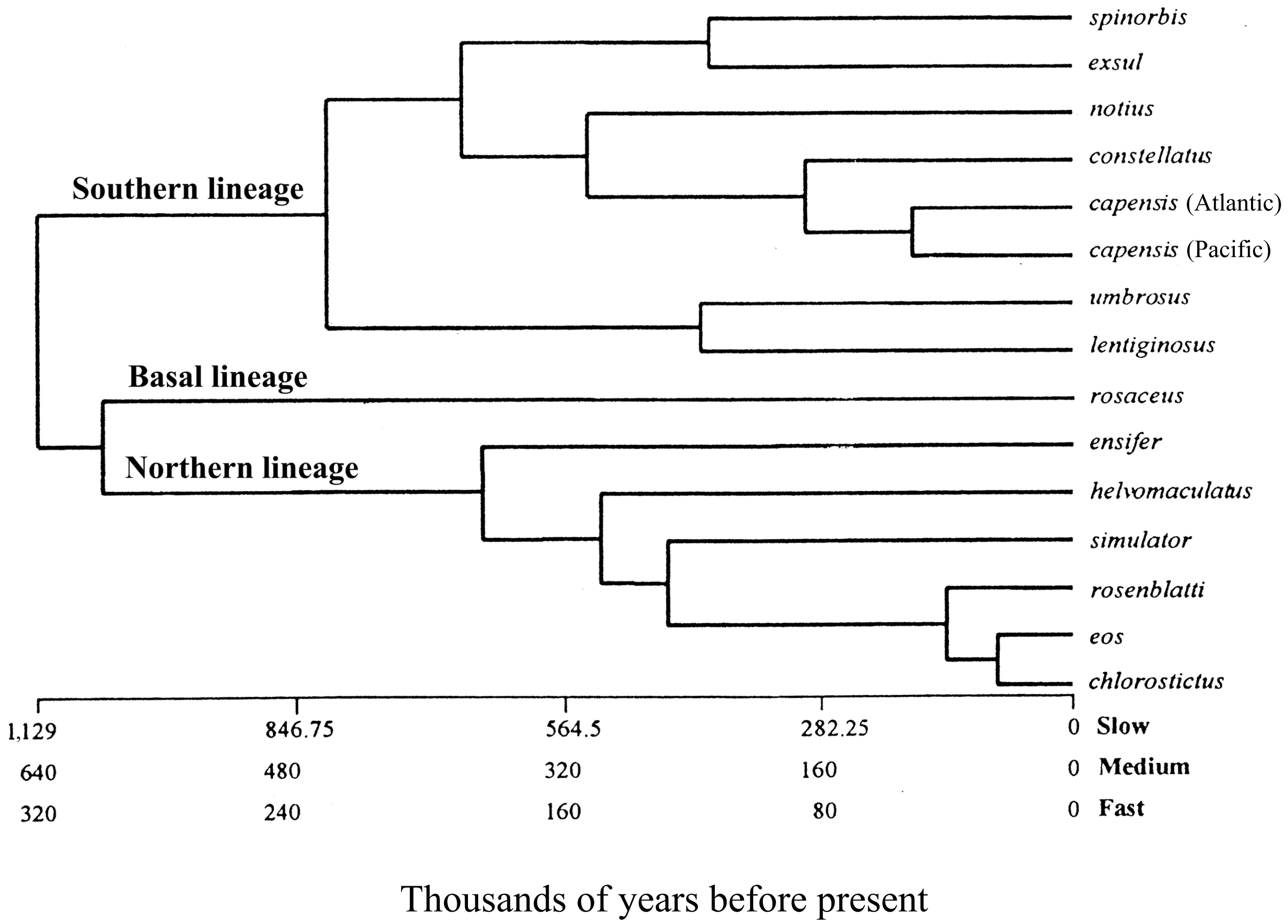

Figure 7.—Relationships among the species in the subgenus *Sebastomus* based on genetic data (from Rocha-Olivares et al., 1999b). Time scales represent different assumed rates of evolution.

three species, suggesting that the duplication might have preceded the divergence of the species. They speculated that the Pacific sister species of the Atlantic species might have homologous repeats. They investigated this hypothesis with *S. aleutianus*, which is another member of the subgenus *Sebastes* according to Barsukov (1981), but did not find the tandem repeats. They suggested that other Pacific species could be examined to determine if they had the tandem repeats and thus might represent the lineage from which the Atlantic species arose. Roques et al. (1999) found that microsatellite data from eight loci could be used to assign individual fish to the correct species more precisely than with other genetic techniques. It was less likely to assign individuals to the correct population within species. They also concluded, on the basis of shared alleles, that *S. norvegicus* represents the lineage from which the other Atlantic species arose, and that *S. fasciatus* and *S. viviparus* are more closely related to each other than to the other Atlantic species.

As new genetic techniques are developed, they continue to be applied to systematic and taxonomic studies of rockfishes at a variety of levels. For example, Johns and Avise (1998) sequenced the mitochondrial cytochrome-*b* gene from 28 species of rockfish and used these data, as well as the allozyme data of Seeb (1986), to construct molecular phylogenies. They then compared these phylogenies with those of other groups of fishes (Lake Victoria cichlids and icefishes) in which “species flocks” occur. They found that many of the speciation events in *Sebastes* occurred in clusters in time, and that these events were far more ancient than similar events in African cichlids. They concluded that rockfishes are an ancient species flock, with significant radiation occurring about 5 million years ago (3.6–18 million years ago depending on assumptions concerning rates of evolution).

With the rapid advances in genetic techniques that are now occurring, it is difficult to predict the limits of what will be known of rockfish taxonomy and systematics just a few years from now. However, as more genomic data are accumulated from these phylogenetically interesting fishes, further ad-

Table 1.—*Sebastiscus*, and *Hozukius*, and *Sebastes* subgenera: type species, ranges, numbers of species, and authors.

Subgenus	Type species	Range	No. of species	Authors	Reference
Acutomentum	*ovalis*	NE-NW Pac.	11	Eigenmann and Beeson, 1893	Am. Nat. 27:669
Allosebastes	*sinensis*	NE Pac.-Gulf Calif.	14	Hubbs, 1951	Proc. Biol. Soc. Wash. 64:129-130
Auctospina	*auriculatus*	NE Pac.	2	Eigenmann and Beeson, 1893	Am. Nat. 27:670
Emmelas	*glaucus*	NW Pac.	1	Jordan and Evermann, 1898	Bull. U.S. Natl. Mus. 47:1773
Eosebastes	*aurora*	NE Pac.	3	Jordan and Evermann, 1896	Rep. U.S. Comm. Fish Fish. 1895, pt. 21:430
Hatumeus	*owstoni*	NW Pac.	1	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo
Hispaniscus	*rubrivinctus*	NE Pac.	3	Jordan and Evermann, 1896	Rep. U.S. Comm. Fish Fish. 1895, pt. 21:431
Hozukius	*emblemarius*[1]	NW Pac.	2	Matsubara, 1934	J. Imp. Fish. Inst. Tokyo 30:199-210.
Mebarus	*inermis*	NE-NW Pac.	7	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo:194
Murasoius	*pachycephalus*	NW Pac.	1	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo:235
Neohispaniscus	*schlegeli*	NW Pac.	2	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo:226
Primospina	*mystinus*	NE Pac.	1	Eigenmann and Beeson, 1893	Am. Nat. 27:669
Pteropodus	*maliger*	NE-NW Pac.	10	Eigenmann and Beeson, 1893	Am. Nat. 27:670
Rosicola	*pinniger*	NE Pac.	3	Jordan and Evermann, 1896	Rep. U.S. Comm. Fish Fish. 1895, pt. 21:429
Sebastes	*norvegicus*	N Atl.	4	Ascanius, 1772	Claude Philibert, pt. 2
Sebastichthys	*nigrocinctus*	NE Pac.	1	Gill, 1862	Proc. Acad. Nat. Sci. Phila. 14:278, 329
Sebastiscus	*marmoratus*	NW Pac.	2	Jordan and Starks, 1904	Proc. U.S. Nat. Mus. 27:91-175
Sebastocarus	*serriceps*	NE Pac.	1	Jordan and Evermann, 1927	Proc. Calif. Acad. Sci., Ser. 4, 16:507
Sebastocles	*hubbsi*	NW Pac.	1	Jordan and Hubbs, 1925	Mem. Carnegie Mus. 10:260.
Sebastodes	*paucispinis*	NE-NW Pac.	5	Gill, 1861	Proc. Acad. Nat. Sci. Phila. 13:165
Sebastomus	*rosaceus*	NE Pac.-S Hemis.	16	Gill, 1864	Proc. Acad. Nat. Sci. Phila. 16:147
Sebastopyr	*rubberimus*	NE Pac.	1	Jordan and Evermann, 1927	Proc. Calif. Acad. Sci., Ser. 4, 16:506
Sebastosomus	*melanops*	NE Pac.	5	Gill, 1864	Proc. Acad. Nat. Sci. Phila. 16:147
Takenokius	*oblongus*	NW Pac.	1	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo:233
Zalopyr	*aleutianus*	NE-NW Pac.	3	Jordan and Evermann, 1898	Bull. U.S. Natl. Mus. 47:1795

[1] The species name *emblemarius* has been misspelled *embremarius* in several publications including Matsubara (1934, 1943).

vances in our understanding of relationships among them and their evolution are assured.

Present Views on the Subgenera

Although the subgeneric names are mentioned occasionally in recent literature, all but *Sebastomus* still lack rigorous definitions. There is also a lack of agreement concerning the appropriate subgenus for some species (Appendix II). Some species have been assigned to several different subgenera by various authors through the years. For example, *Allosebastes* was erected for *Sebastes sinensis* alone by Hubbs (1951); however, Chen (1986) placed 11 other species in the subgenus, without giving a reason for his action.

Based on the literature, subgeneric names have been assigned to 96 of the currently recognized species of *Sebastes* (Table 1). There are 23 subgenera containing from 1 to 16 species. Nine subgenera contain only one species. Five subgenera have species in both the northwest and northeast Pacific Ocean, six have species only in the northwest Pacific, and ten are exclusively in the northeast Pacific. The North Atlantic contains a subgenus, *Sebastes*, that occurs only there, while the species in the Southern Hemisphere are in *Sebastomus*, which also occurs in the northeast Pacific. Some of the subgenera have been proposed as genera, and some groups of subgenera have been considered as genera. No rigorous analysis of the validity of the subgenera has yet been attempted, except for *Sebastomus* (Rocha-Olivares, 1999a).

Several field guides and keys for northeast Pacific *Sebastes* have been published (Phillips, 1957; Hitz, 1965; Miller and Lea, 1972; Kramer and O'Connell, 1988; Orr et al., 2000) which assist greatly in identifying the sometimes bewildering array of rockfishes caught even at a single location (Table 2). These guides generally rely on head spine, meristic, morphometric, and color characters that are probably not indicative of systematic relationships among species. The subgenera are usually not mentioned in field guides, although *Sebastomus* is occasionally noted since the species are quite distinctive externally.

Ishida (1984) reviewed what he considered to be the Japanese Sebastinae (*Sebastes*, 26 species; *Helicolenus*, 3 species; *Hozukius*, 2 species; and *Sebastiscus*, 2 species). He included a careful evaluation of all species in these genera that occur around Japan. He summarized his views on the relationships within *Sebastes*, saying ". . . *Sebastes* and *Sebastiscus* of Matsubara (1943) are adopted provisionally and subgenera are not used until world-wide review of these fishes is carried out."

Challenges

Where Does *Sebastes* Belong?

Sebastes is very provisionally placed in the order Scorpaeniformes, suborder Scorpaenoidei, family Sebastidae, subfamily Sebastinae (Nelson, 1994). Much work is yet to be done on the systematics of *Sebastes*, beginning at the ordinal level (is the Scorpaeniformes monophyletic? How does it relate to the Perciformes?). The placement of *Sebastes* within the Scorpaeniformes is presently uncertain. For example, if the Perciformes and Scorpaeniformes had a common ancestor, could it have been similar to *Sebastes*? *Sebastes* and basal perciforms share many characteristics. The hallmark of the scorpaeniforms, the suborbital stay is much reduced in *Sebastes*, and, except for the suborbital stay, *Sebastes* is more similar to basal perciforms than are other scorpaeniforms. In other ways, *Sebastes* is the least specialized of the scorpaeniforms: e.g. head spination is minimal,

Table 2.—Major field guides to identify species of Northeast Pacific *Sebastes*.

Reference	Geographic area	No. of species	Presentation
Clemens and Wilby (1946)	British Columbia.	20	Extended individual species accounts including airbrush monochrome drawings.
Phillips (1957)	California, but ranges of some species extend to Baja California and Alaska.	49	Key to the species and individual species accounts with monochrome photographs.
Clemens and Wilby (1961)	British Columbia.	23	Revision of Clemens and Wilby (1946).
Hitz (1965)[1]	Baja California to the Bering Sea.	53	Species pages arranged by body color and relative length of 2nd and 3rd anal spines. Brief species accounts with black-and-white line sketches and head spine diagrams.
Miller and Lea (1972)	California, but ranges of some species extend to Baja California and Alaska.	58	Brief individual species accounts and a key illustrated with monochrome sketches showing important characters.
Hart (1973)	British Columbia.	33	Key to the species and extended individual species accounts with monochrome drawings.
Eschmeyer et al. (1983)	Coastal waters from the Gulf of Alaska to Baja California.	58	Individual species accounts and color plates annotated with important characters.
Kramer and O'Connell (1988)	Species that occur off Alaska, includes most species from British Columbia, Washington, and Oregon also.	35	Brief individual species accounts including head spine diagrams, sketches of important characters, and color photographs.
Orr et al. (2000)	Northeast Pacific Ocean north of Mexico, including the eastern Bering Sea.	66	Format follows Hitz (1965). Includes individual species accounts and color photographs of most species.

[1] Hitz (1965) was updated, expanded and reprinted three times in informal editions: in 1977, 1981, and 1991.

Table 3.—Characters used to evaluate genera of Sebastidae, following Ishida, 1994.

Characters		States and coding			
Number	Description	Primitive (0)	Intermediate (1)	Derived (2)	Distribution of derived states outside Sebastidae
3	A1 fibers	long		short	Congiopodidae
17	insertion of transversus dorsalis anterior	branched		unbranched	Congiopodidae and occasional elsewhere
41	swimbladder	present		absent	Widespread, especially Scorpaenidae
56	infraorbitals 4 & 5	both present	one present	both absent	Very widespread
64	pharyngobranchials 2 & 3, upper pharyngeal	all separate	pharyngobranchials fused	all fused	Intermediate rare, derived Aploactinidae and Pataecidae
70	number of vertebrae	24		more than 24	Widespread except Setarchidae and Scorpaenidae
80	number of hypurals	2+3	1+3	1+2	Derived states widespread
83	scapula and upper radial	autogenous		fused	Widespread
88	supraneural	1 present		absent	Very widespread

squamation is normal. Is this due to convergence or a common ancestor? Basic unresolved questions regarding the origin and relationships of *Sebastes* and its close relatives include: was their ancestor tropical or boreal, and was it demersal or pelagic? Does *Sebastes* represent the point of divergence that led the demersal-boreal scorpaeniforms away from the pelagic-tropical perciforms, or does the genus represent an end point in scorpaeniform evolution (Washington et al., 1984a)? Although these questions may eventually be resolved using cladistic methodology, the diversity and numbers of species in both the perciforms and scorpaeniforms may continue to deter their resolution.

Within the suborder Scorpaenoidei, Ishida (1994) considered the Sebastidae to contain eight genera. Some members of the Sebastidae have derived states of 9 of the 95 characters that he used to examine the Scorpaenoidei (Tables 3, 4). All members of the family have derived states of two characters relative to their states in lower percoids, the presumed outgroup of scorpaenoids: the shortening of a1 fibers with the lengthening of the associated maxillary tendon (character 3), and an increase in the number of vertebrae from 24 (character 70) (Table 3).

Within the Sebastidae, the genera *Sebastes*, *Sebastiscus*, and *Hozukius* share identical character states, resulting in an unresolved trichotomy, which can be given the subfamilial name Sebastinae. This subfamily has the derived states of four characters and shares the derived states of two of these characters with all of the other genera in Sebastidae. However, they do not possess uniquely derived states of any characters. They are united in possessing swimbladders, which is a character reversal (in that the rest of the family lacks them, which is the presumed derived state). If *Hozukius* is found to be viviparous like *Sebastes* and *Sebastiscus*, then viviparity would be another derived character to support this subfamily. If *Hozukius* is found to be oviparous, it may be considered the primitive sister genus of *Sebastes* and *Sebastiscus* within the subfamily.

Table 4.—Characters and character states for analysis of Sebastidae, following Ishida, 1994.

	Characters[1]								
Genus	3	17	41	56	64	70	80	83	88
Sebastes	1	0	0	0	0	1	2	1	0
Sebastiscus	1	0	0	0	0	1	2	1	0
Hozukius	1	0	0	0	0	1	2	1	0
Helicolenus	1	0	1	0	0	1	2	1	0
Adelosebastes	1	0	1	0	0	1	2	1	0
Sebastolobus	1	0	1	0	0	1	2	0	0
Trachyscorpia	1	0	1	1	0	1	0	0	0
Plectrogenium	1	1	1	1	1	1	0	0	1

[1] 0=primitive, 1=intermediate, 2=derived.

Table 5.—Ecological correlates of characters of *Sebastes*.

Character	Demersal state	Pelagic state
Head spines strength	Strong	Weak
Head spine numbers	Many	Few
Jaw length	Lower > upper	Equal
Interorbital shape	Concave	Convex
Lower pectoral rays	Thick	Not thick
Gill raker length	Short	Long
Jaws scaled	Yes	No
Base of skull	Curved	Flat
Mesethmoid process	Strong	Weak
Color	Red	Black
	Low latitude state	High latitude state
Vertebrae	<29	>28
Dorsal spines	<14	14–15
Dorsal rays	<14	15–16
Anal rays	5	9
Principal caudal rays	13	15
Pectoral rays	17–18	>18

What Morphological Characters Can Be Used for Cladistic Analysis of *Sebastes*?

To be used in a cladistic analysis, morphological characters must be independent of each other and nonadaptive. However, many of the characters used to identify *Sebastes* and used in early attempts to establish relationships among the species are correlated with each other and are adaptive for either pelagic or demersal existence (Table 5).

There is a basic dichotomy in *Sebastes* ecology: species either live in the water column or on the bottom. This is not an absolute; there is a cline between these two basic conditions. Bottom-dwelling species have the lower jaw protruding, eyes close together with a concave interorbital area, heavy armature, thickened pectoral rays, short gill rakers, scaled jaws, and a curved skull base, while pelagic species have opposite states for all of these characters. Convergence toward these character states is expected in species occupying these niches regardless of their ancestry.

Another factor to consider when interpreting characters is that meristic characters tend to show a latitudinal cline: the closer the species lives to the pole, the higher the value (Jordan's Rule: see Lindsey, 1988). This basic pattern is seen in medial fin ray and vertebral counts among species of rockfishes (Table 5). For example, *Sebastiscus*, which lives farther south than most other taxa, has low counts for all these characters and *Emmelas*, which lives in the northern part of the range, has higher counts. The species of *Sebastomus*, which live primarily in the southern part of the range of *Sebastes* in the northeast Pacific, including the Gulf of California, and the Southern Hemisphere, have lower medial fin ray counts than most other *Sebastes*. The Atlantic species of *Sebastes* have the highest vertebral counts in the genus, and presumably they originated from species that traversed the Arctic Ocean from the Pacific.

Can Early Life History Information Be Applied to the Problem?

Scorpaenoids display a variety of reproductive patterns, but the use of information on reproduction in systematic studies is limited, since the patterns are unknown in several genera (Washington et al., 1984b). While most scorpaenoids share ovoviviparity with most other teleosts, *Sebastes*, *Sebastiscus*, and possibly *Helicolenus* share the unique pattern of internal fertilization, intraovarian embryological development with maternal contribution to nutrition, and production of many (~10^5) newly hatched, undeveloped larvae. The reproductive pattern of *Hozukius* is unknown, although the anal anatomy is that of a live-bearer (Ida[4]). As opposed to the widespread pattern of producing individual planktonic eggs, several scorpaenid genera (*Sebastolobus*, *Pterois*, *Scorpaena*) extrude eggs in a floating bilobed gelatinous egg mass. A single oil globule is present in eggs of *Pterois* and *Sebastolobus*, while none is present in the eggs of *Scorpaena* or *Dendrochirus*.

The larvae of many scorpaeniforms, including the scorpaenoids, have parietal and other head spines, which are not seen in larvae of other fishes. In *Sebastolobus* and *Scorpaenodes* the parietal ridge is enlarged and ends in a bifid spine, with the posterior part (the nuchal spine) being predominant, whereas in *Sebastes, Sebastiscus* (Okiyama, 1988), and *Helicolenus* the parietal spine is larger and slightly separate from the nuchal spine (Moser et al., 1977; Moser, 1996). There is a tendency for early development of pectoral fins in scorpaeniforms, and in some groups the pectoral fins are quite pronounced in the larvae. Pronounced pectoral fins are seen in *Sebastolobus*, *Scorpaenodes*, *Ectreposebastes* and some species of *Sebastes* (e.g. *S. levis*). Larvae of *Helicolenus* develop a spongy mass of tissue anteriorly along the dorsal midline. Once the larvae of more scorpaenoids become known, such characters will prove invaluable in systematic studies of the group.

Within the genus *Sebastes*, the preflexion-extrusion larvae of most species are known (Matarese et al., 1989; Moser, 1996). These can be obtained fairly easily, and their identity known, by collecting pregnant females and extruding the larvae. Aside from some shared characteristics among preflexion larvae of species of *Sebastomus*, the appearance of these larvae seems to offer little taxonomic or systematic promise. There is considerable overlap in characters among species in these larvae and considerable within-species variation.

Later-stage larvae of *Sebastes* are distinctive from larvae of other fishes, but many share characters with each other that prevent identifying them to species in all but a few cases. Larval characters that may be useful in taxonomy and systematics include body shape, pigment patterns, and the development and subsequent reduction or loss of head spines (Kendall, 1991). As with early larvae, the later larvae of *Sebastomus* share some characters that distinguish them from other *Sebastes* larvae, but within the subgenus, the larvae of many species are quite similar. It appears that larvae of *Pteropodus* may also share some characters, but the larvae of several species are still unknown. A few other species have distinctive larvae (e.g. *Sebastes paucispinis*, *S. jordani*, *S. melanostomus*, and *S. levis*), but their morphology does not seem to be related to their subgeneric placement. There are some intriguing similarities among the larvae of some species of *Sebastes* that may indicate

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[4] Ida, Hitoshi, Kitasato Univ., Sanriku, Jpn., personal commun., 20 January 1999.

relationships not otherwise suggested (e.g. the larvae of *S. jordani*, *S. alutus*, and *S. polyspinis* from the Pacific all look quite similar to the larvae of the Atlantic species of *Sebastes*).

As juveniles, *Sebastes* are morphologically quite different from the larvae and the adults. Some species reside in the water column, some associate with flotsam or school, and some take up a demersal existence (Moser and Boehlert, 1991). The observed pigment patterns of juveniles may be adaptive for these various modes of existence, so caution is advised when using them in systematic analysis.

Clearly the early life history of scorpaenoids in general and *Sebastes* in particular offers a large number of characters to apply to systematic studies. However, until the reproductive patterns and early life history series of more species are described, this potential cannot be realized.

Conclusions

After a period of discovering the incredible diversity of *Sebastes* in the middle 1800's, the history of the systematics of the genus was marked by bitter debate in the late 1800's over relationships among the species. With few exceptions (e.g. *S. carnatus*-*S. chrysomelas*-*S. atrovirens*, and *S. ciliatus*) the species of *Sebastes* are now well-defined, and few new ones are being described (Kim and Lee, 1994; Eitner et al., 1999). However, little recent work has been done on the genus as a unit, and its systematics remain in a confused state, with over 100 species, and very little obvious structure within the genus. What other fish genus contains so many species, but with such little indication of structure within it? Beyond the fairly cohesive group *Sebastomus* and a few species pairs (e.g. *Sebastes fasciatus*/*S. mentella*, *S. babcocki*/*S. rubrivinctus*, *S. serranoides*/*S. flavidus*), practically any two species look as similar to each other as to any other species.

In order to progress in our understanding of the relationships within this interesting, and ecologically and economically important group of fishes, traditional gross morphological as well as novel characters, such as those available through genetics, need to be evaluated more rigorously. With the incredible size of the genus and its wide distributional range, this will be an enormous task.

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Appendix I

Original Definitions of *Sebastes, Hozukius,* and *Sebastiscus,* and the Subgenera of *Sebastes*

Sebastes Cuvier (1829), type species: *S. norvegicus*: “Have all the characters of the *Scorpaena* except that they lack cutaneous filaments, and that their head, less covered with bristles, is scaly.

“There is a large species of them in the North Sea, called ‘marulke,’ and in some places ‘carp’ (*Sebastes norvegicus*, Nob., *Perca marina*, Pennt., *Perca norvegica*, Müll.), Bonnat. Encycl. Meth., plate on ichthyology, fig. 210. It is red, and is often more than two feet long. It is dried to make food provisions. Its dorsal spines are used as needles by Eskimos.

“The Mediterranean has a species very similar, but its dorsal rays are less numerous (*Sebastes imperialis*, Nob., *Scorpaena dactyloptera*, Laroche, Annales Mus., 13, plate 22, fig. 9). Its palate is black; it lacks a swim bladder, although the preceding species has one.”[2]

Sebastodes Gill (1861), type species: *S. paucispinis*: “A very different facies from *Sebastes*, and is readily distinguished by the longer body, the very protuberant lower jaw, which has a symphyseal swelling beneath, the very minute scales, the form and armature of the head, the deep emargination of the dorsal fin and the emarginated caudal.”

Sebastichthys Gill (1862b), type species: *S. nigrocinctus*: “Species referred to the genus *Sebastes*, which has eleven to twelve (XI.+1.–XII.+1.) spines in its first dorsal fin, palatine teeth, and the physiognomy of *Sebastes* (*norvegicus*).”

Sebastomus Gill (1864), type species: *S. rosaceus*: “Distinguished by the texture of the bones of the skull, armed orbital ridges, prefrontals &c.”

Sebastosomus Gill (1864), type species: *S. melanops*: “. . . the genus *Sebastichthys* includes at least three genera. The *Sebastichthys nigrocinctus* is somewhat related to *Scorpaena*, and distinguished by elevated, serrated coronal crests. The other California species represented by the *Sebastes melanops*, seen by me, differ so much that they may be separated and combined under the genus *Sebastosomus* . . .”

Acutomentum Eigenmann and Beeson (1893), type species: *S. ovalis*: Taken from their key: “Parietals meeting above the supra-occipital. Lower jaw much projecting; head broad, the skull usually convex; cranial ridges, when present, low; gill rakers very long and slender; scales usually smooth, few if any accessory scales. Parietal ridges ending in spines; preocular, supraocular and tympanic spines well developed. Peritoneum black. Postocular spine present. Second anal spine usually stronger and longer than third. Symphyseal knob strong, projecting forward. Dorsal low. (Peritoneum black, mandibles and maxillary scaled).”

Primospina Eigenmann and Beeson (1893), type species: *S. mystinus*: Taken from their key: Parietals meeting above the supra-occipital. Lower jaw much projecting; head broad, the skull usually convex; cranial ridges, when present, low; gill rakers very long and slender; scales usually smooth, few if any accessory scales. Postocular spine not developed. Parietal ridges not ending in spines. Preocular spines well developed. Supraocular and tympanic spines sometimes present. Interorbital wide, convex. Peritoneum black. Approximated edges of sub-opercle, and interopercle frequently ending in spines.

Pteropodus Eigenmann and Beeson (1893), type species: *S. maliger*: Taken from their key: Parietals separated by the supra-occipital. Cranium with many ridges, all ending in spines. Postocular spines wanting. Coronal spines none.

Auctospina Eigenmann and Beeson (1893), type species: *S. auriculatus*: Taken from their key: Parietals separated by the supra-occipital. Cranium with many ridges, all ending in spines. Postocular spines wanting. Coronal spines present.

Eosebastes Jordan and Evermann (1896), type species: *S. aurora*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Hispaniscus Jordan and Evermann (1896), type species: *S. rubrivinctus*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Rosicola Jordan and Evermann (1896), type species: *S. pinniger*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Emmelas Jordan and Evermann (1898), type species: *S. glaucus*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Zalopyr Jordan and Evermann (1898), type species: *S. aleutianus*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Sebastiscus Jordan and Starks (1904), type species: *Sebastiscus marmoratus*: “This genus is based on species having the external appearance of *Sebastodes* and much resemblance to the subgeneric group called *Pteropodus*, but having 12 spines in the dorsal fin and the vertebrae 10+14=24, agreeing in these regards with *Scorpaena*. From *Helicolenus*, *Sebastiscus* differs, solely, perhaps, in the presence of a well-developed air-bladder. Peritoneum pale.”

Sebastocles Jordan and Hubbs (1925), type species: *S. elegans* (=*S. hubbsi*): “Dorsal spines low, normally fourteen; interorbital deeply concave, size small.”

Sebastocarus Jordan and Evermann (1927), type species: *S. serriceps*: “This genus is closely allied to *Sebastichthys* from which it differs in the more compressed body and especially in the strict and high ridges on the head, all of them being free from serrations or accessory tubercles.”

Sebastopyr Jordan and Evermann (1927), type species: *S. ruberrimus*: “This genus is allied to *Sebastomus*, but of much coarser build, the cranial spines in the adult being rough with blunt spinules.”

Hozukius Matsubara (1934), type species: *H. emblemarius*: “External: Body rather robust and somewhat compressed. Maxillary, and mandible covered with small ctenoid scales but not on branchiostegals. Teeth in villiform bands on vomer and palatines. Head much spinous; nasal, preocular, supraocular, postocular, tympanic, coronal, parietal, and nuchal spines present; upper and posterior margins of orbit provided with many accessory spines; parietal ridge not conspicuous. Orbital margins of preorbital and second suborbital bones armed with a sharp spine which is directed backward; first suborbital margined with several small spines; lower border of preorbital with two very strong, sharp bifid spines. Lower three preopercular spines much larger than upper two; subopercle and interopercle each with a small, sharp spine at their approximation. Symphyseal knob very large. Dorsal with 12 spines and about 12 rays; anal with 3 spines and about 6 rays. Auxillary flap absent.

"Internal: Skull thick and heavy. Base of skull (paraspheniod) moderately curved. Frontal, parietal, pterotic and supratemporal much cavernous resembling a bee-hive in general appearance. Parietals entirely meeting; upper margin of orbit and frontal ridges somewhat raised. Mesethmoid processes directed upward and forward. Nodule on the front of prefrontal for the articulation with palatine well developed. Ventral process of basisphenoid rudimentary, not reaching to paraspheniod; basisphenoid with a small pore between it and basis crania. Myodome well developed, with a rather large posterior opening. Second suborbital bone very broad and long entirely touching to the upper ridge of preopercle; third and fourth suborbital bones present. Gill-rakers long and stout, the longest one much longer than the longest gill-lamella. Vertebrae 9 + 16 + hypural = 26; parapophysis developed from the sixth vertebra, its processes widely diverging, directed outward and downward. Air bladder absent. Peritoneum jet black."

Hatumeus Matsubara (1943), type species: *S. owstoni*: "Cranium thin and papery; interorbital space and occiput flat, the former about 3.3 times in base of the cranium; preocular, postocular, tympanic and parietal spines present, but small and weak; nuchal spines sometimes present; supraocular and coronal spines absent; cranial ridges absent except for the parietal ridges which are low but never scaled over; parietals separated; mesethmoid processes never directed upward; base of cranium markedly curved; ventral process of basisphenoid feeble, never attached to the parasphenoid; nasal spines low, but strong; preorbital lobes without spines; second suborbital bone much wider than long. Vertebrae usually 30 including the hypural. Peritoneum jet black. Gill-rakers long and slender. Dorsal mostly XIV, 14; anal usually III, 9 to 10. Lower jaw strongly produced beyond the upper when the mouth is closed; symphyseal knob evident; jaws thickly covered by small scales."

Mebarus Matsubara (1943), type species: *S. inermis*: "Cranium rather thin; interorbital space and occiput plain or very slightly convex, the former about 3.0 times in base of the cranium; preocular spines always present; supraocular and parietal spines small or absent; postocular, tympanic and nuchal spines entirely absent; cranial ridges absent except for the parietal which is very low and sometimes scaled over; parietals widely separated; mesethmoid processes depressed or slightly directed upward; base of cranium strongly curved; ventral process of basisphenoid feeble; nasal spines low, but strong. Vertebrae usually 26 or 27 including the hypural. Peritoneum black or pale. Gill-rakers long and slender. Dorsal spines 13. Lower jaw projecting far beyond the upper, provided with a prominent symphyseal knob; maxillary at least scaly; preorbital lobes with or without spines.

"The present new subgenus is closely related to the subgenus *Rosicola*, but differs from it in having weak parietal ridges and flattish interorbital space and lacking the postocular and tympanic spines. The subgenus is also separable from *Sebastosomus* in having usually the strong preocular spine, flattish interorbital space and parietals widely separated."

Murasoius Matsubara (1943), type species: *S. pachycephalus*: "Cranium very thick and heavy; interorbital space deeply concave, about $3^1/_2$ in base of cranium; cranial spines broad and stout, the pointed tips directed backward; preocular, postocular, tympanic and parietal spines present; supraocular, coronal and nuchal spines absent; supraocular ridges exceedingly high and stout, forming a narrow flat area between them; frontal ridges barely evident, can not be seen without elimination of the skin; parietal ridges broad and high, but a little lower than the supraocular ridges; nasal spines stout, directed upward and slightly backward; mesethmoid processes strongly compressed, directed forward and upward; parietal bones separated; base of cranium straight; ventral process of basisphenoid entirely meeting the parasphenoid. Vertebrae 26 including hypural. Peritoneum white. Air-bladder entirely free from the layer of connective tissue lying outside the peritoneum, the bladder being easily detached from the coelom; the extrinsic muscle band of the bladder gives rise posteriorly to a single short ligament; the anterior part of the muscle band not pierced through by a ligament. Gill-rakers very short and blunt. Dorsal spines 13. Jaws, snout and branchiostegals mostly naked; upper jaw projecting beyond the lower when mouth is closed; symphyseal knob at the tip of lower jaw absent or barely evident."

Neohispaniscus Matsubara (1943), type species: *S. schlegelii*: "Skull thick and heavy; interorbital space flat or slightly convex, its width about 2.6 to 3.3 times in base of the cranium; cranial spines well developed, directed straightly backward; preocular, postocular, tympanic and parietal spines always present supraocular, corneal and nuchal spines absent; parietal ridges high and naked; frontal ridges low but distinct, the space between them shallowly concave; supraocular edges low or depressed. as high as or lower than the frontal ridges; mesethmoid processes slightly elevated upward; base of cranium some-what curved; parietals separated or partly meeting; ventral process of the basisphenoid well developed, entirely meeting the parasphenoid. Vertebrae 26 including hypural. Peritoneum usually white. Gill-rakers, comparatively long and slender with pointed tips. Lower jaw generally projecting beyond the upper when the mouth is closed, with a rather small symphyseal knob. Jaws usually naked.

"The present subgenus is closely related to *Hispaniscus*, but differs from it in having a much longer and wider interorbital space, elevated mesethmoid processes and shallowly depressed area between the frontal ridges."

Takenokius Matsubara (1943), type species: *S. oblongus*: "Cranium thick and heavy; interorbital space and occiput flat or slightly convex, the former about 3.7 times in base of cranium; postocular, tympanic and parietal spines present, directed backward and downward; preocular supraocular, coronal and nuchal spines entirely absent; parietal ridges low but broad; supraocular edges depressed, never higher than the frontal ridges; frontal ridges low, the space between them flattish, never deeply concave; mesethmoid processes directed forward and upward; parietals meeting or narrowly separated; the patch of vomerine teeth triangular; base of cranium straight; ventral process of basisphenoid meeting the parasphenoid. Vertebrae 26 including hypural. Peritoneum pale. Gill-rakers very short, tubercular. Jaws equal in length and entirely scaleless; symphyseal knob inconspicuous."

Allosebastes Hubbs (1951), type species: *S. sinensis*: "… reduction of the anal soft-rays to 5. … smooth, mostly cycloid scales; the unswollen lower pectoral rays; the excessively long anal spines (the second extends well beyond the longest soft-ray); the closely clumped subparallel upper 3 preopercular spines (the lower 2 are well separated and divergent); the protuberant posterior end of the mandible, almost resembling a flat spine; and, especially, the very firm well-exposed suborbital stay (second suborbital), with the bone widened about the unusually large pore, which has a somewhat raised and roughened rim."

Appendix II

Summary of Nomenclature of *Sebastes* Listed Alphabetically by Subgenus

Original species[1]	Authors	Date	Present species[2]	Common name	Eigenmann and Beeson, 1894
	(Fitch)	1964	*phillipsi*	chameleon rockfish	
	Lea and Fitch	1979	*melanosema*	semaphore rockfish	
	(Westrheim and Tsuyuki)	1967	*reedi*	yellowmouth rockfish	
	Barsukov	1988	*cheni*		
	(Taranetz and Moiseev)	1933	*polyspinis*	northern rockfish	
	Kim and Lee	1994	*koreanus*	hwanghee-bolnak	
	Eitner et al.	1999	*moseri*	whitespeckled rockfish	
alutum	(Gilbert)	1890	*alutus*	Pacific ocean perch	*Acutomentum*
brevispine	(Bean)	1884	*brevispinis*	silvergray rockfish	*Pteropodus*
clavilatum	Starks	1911	*(?)*		
eigenmanni	Cramer	1896	*(?)*		
entomelas	(Jordan and Gilbert)	1880	*entomelas*	widow rockfish	*Primospina*
	(Cramer)	1895	*hopkinsi*	squarespot rockfish	
	(Eigenmann and Beeson)	1893	*macdonaldi*	Mexican rockfish	*Acutomentum*
ovale	(Ayres)	1863	*ovalis*	speckled rockfish	*Acutomentum*
rufum	(Eigenmann and Eigenmann)	1890	*rufus*	bank rockfish	*Sebastomus*
	(Jordan and Starks)	1904	*flammeus*	sankou-menuke	
	(Jordan and Starks)	1904	*iracundus*	oo-saga	
	(Jordan and Snyder)	1900	*scythropus*	ukeguchi-mebaru	
	(Wakiya)	1917	*baramenuke*	bara-menuke	
paucispinosus	Matsubara	1943	*(alutus)*		
	Chen	1975	*varispinis*		
	Chen	1975	*peduncularis*		
	(Beebe and Tee-Van)	1938	*cortezi*		
	(Gilbert)	1890	*sinensis*		*Pteropodus*
	Quast	1971	*variegatus*	harlequin rockfish	
	Lea and Fitch	1972	*rufinanus*	dwarf-red rockfish	
	(Gilbert)	1890	*diploproa*	splitnose rockfish	*Sebastichthys*
	(Starks)	1911	*emphaeus*	Puget Sound rockfish	
prorigerum	(Jordan and Gilbert)	1880	*proriger*	redstripe rockfish	*Pteropodus*
	(Gilbert)	1890	*saxicola*	stripetail rockfish	*Pteropodus*
	(Gilbert)	1897	*semicinctus*	halfbanded rockfish	
	(Gilbert)	1915	*wilsoni*	pygmy rockfish	
	(Gilbert)	1890	*zacentrus*	sharpchin rockfish	*Pteropodus*
dallii	(Eigenmann and Beeson)	1894	*dalli*	calico rockfish	*Pteropodus*
auriculata	Girard	1854	*auriculatus*	brown rockfish	*Auctospina*
	Hilgendorf	1880	*glaucus*	kuro-menuke	
	(Gilbert)	1890	*aurora*	aurora rockfish	*Auctospina*
	(Jordan)	1897	*crameri*	darkblotched rockfish	
deani	Starks	1911	*(?)*		
introniger	(Gilbert)	1890	*(melanostomus)*		*Acutomentum*
	(Eigenmann and Eigenmann)	1890	*melanostomus*	blackgill rockfish	*Acutomentum*
rupestris	(Gilbert)	1890	*(melanostomus)*		*Sebastomus*
	(Jordan and Thompson)	1914	*owstoni*	hatsume	
	Ayres	1859	*elongatus*	greenstriped rockfish	
	(Eigenmann and Eigenmann)	1889	*levis*	cowcod	*Sebastomus*
	(Jordan and Gilbert)	1880	*rubivinctus*	flag rockfish	*Sebastichthys*
atrorubens	(Gilbert)	1898	*(atrovirens)*		
	(Jordan and Gilbert)	1880	*atrovirens*	kelp rockfish	*Pteropodus*
	(Jordan and Hubbs)	1925	*thompsoni*	usu-mebaru	
	(Matsubara)	1934	*wakiyai*	gaya-modoki	
	Cuvier and Valenciennes	1829	*inermis*	mebaru	
	Gunther	1878	*joyneri*	togotto-mebaru	
taczanowskii	(Steindachner)	1880	*taczanowski*	ezo-mebaru	
	Barsukov	1972	*minor*	aka-gaya	
guentheri	(Jordan and Starks)	1904	*(inermis)*		
paradoxus	Matsubara	1943	*(wakiyai)*		
tokionis	(Jordan and Starks)	1904	*(inermis)*		
	Matsubara	1943	**nudus*		
	Temminck and Schlegel	1843	*pachycephalus*	mura-soi	
	(Schmidt)	1931	**nigricans*		
	Matsubara	1943	**chalcogrammus*		
	Hilgendorf	1880	*schlegeli*	kuro-soi	
	Steindachner and Doderlein	1884	*vulpes*	kitsune-mebaru	

Major generic or subgeneric assignments			Other subgeneric assignments		
Jordan and Evermann, 1898	Jordan, Evermann, and Clark, 1930	Matsubara, 1943	Reference	Subgenus	Current subgenus
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
Acutomentum	*Acutomentum*	*Acutomentum*			*Acutomentum*
Acutomentum	*Acutomentum*				*Acutomentum*
	Acutomentum				*Acutomentum*
Acutomentum	*Acutomentum*				*Acutomentum*
Acutomentum	*Acutomentum*		Chen, 1986	*Acutomentum*	*Acutomentum*
Acutomentum	*Acutomentum*		Chen, 1986	*Acutomentum*	*Acutomentum*
Acutomentum	*Acutomentum*				*Acutomentum*
Acutomentum	*Acutomentum*		Chen, 1986	*Acutomentum*	*Acutomentum*
Acutomentum	*Acutomentum*		Chen, 1986	*Acutomentum*	*Acutomentum*
		Acutomentum			*Acutomentum*
		Acutomentum			*Acutomentum*
		Acutomentum			*Acutomentum*
		Acutomentum			*Acutomentum*
		Acutomentum			*Acutomentum*
			Chen, 1986	*Allosebastes*	*Allosebastes*
			Chen, 1986	*Allosebastes*	*Allosebastes*
			Chen, 1986	*Allosebastes*	*Allosebastes*
Hispaniscus	*Hispaniscus*		Hubbs, 1951; Chen, 1986	*Allosebastes*	*Allosebastes*
			Chen, 1986	*Allosebastes*	*Allosebastes*
					Allosebastes
Eosebastes	*Eosebastes*		Chen, 1986	*Allosebastes*	*Allosebastes*
	Eosebastes		Chen, 1986	*Allosebastes*	*Allosebastes*
Acutomentum	*Acutomentum*		Chen, 1986	*Allosebastes*	*Allosebastes*
Eosebastes	*Eosebastes*		Chen, 1986	*Allosebastes*	*Allosebastes*
Eosebastes	*Eosebastes*		Chen, 1986	*Allosebastes*	*Allosebastes*
	Acutomentum		Chen, 1986	*Allosebastes*	*Allosebastes*
Hispaniscus	*Hispaniscus*		Chen, 1986	*Allosebastes*	*Allosebastes*
	Auctospina				*Auctospina*
Auctospina	*Auctospina*				*Auctospina*
Emmelas	*Emmelas*	*Emmelas*			*Emmelas*
Eosebastes	*Eosebastes*				*Eosebastes*
Eosebastes	*Eosebastes*				*Eosebastes*
	Eosebastes				*Eosebastes*
Eosebastes	*Eosebastes*				*Eosebastes*
Eosebastes	*Eosebastes*				*Eosebastes*
Sebastomus	*Sebastomus*				*Eosebastes*
		Hatumeus			*Hatumeus*
Hispaniscus	*Hispaniscus*				*Hispaniscus*
Hispaniscus	*Hispaniscus*				*Hispaniscus*
Hispaniscus	*Hispaniscus*				*Hispaniscus*
Zalopyr	*Zalopyr*				*Mebarus*
Zalopyr	*Zalopyr*		Chen, 1985; 1986	*Mebarus*	*Mebarus*
		Mebarus	Chen, 1985; 1986	*Mebarus*	*Mebarus*
		Mebarus	Chen, 1985	not *Mebarus*	*Mebarus*
		Mebarus	Chen, 1985; 1986	*Mebarus*	*Mebarus*
		Mebarus	Chen, 1985; 1986	*Mebarus*	*Mebarus*
		Mebarus	Chen, 1985	not *Mebarus*	*Mebarus*
					Mebarus
		Mebarus			*Mebarus*
		Mebarus			*Mebarus*
		Mebarus			*Mebarus*
		Murasoius			*Murasoius*
		Murasoius			*Murasoius*
		Murasoius			*Murasoius*
		Murasoius			*Murasoius*
		Neohispaniscus			*Neohispaniscus*
		Neohispaniscus	Chen, 1986	*Takenokius*	*Neohispaniscus*

continued

Appendix II (continued)

Original species[1]	Authors	Date	Present species[2]	Common name	Eigenmann and Beeson, 1894
ijimae	(Jordan and Metz)	1913	*(vulpes)*		
zonatus	Chen and Barsukov	1976	*(vulpes)*		
	(Jordan and Gilbert)	1880	*carnatus*	gopher rockfish	*Pteropodus*
	Richardson	1844	*caurinus*	copper rockfish	*Pteropodus*
	(Jordan and Gilbert)	1881	*chrysomelas*	black-and-yellow rockfish	*Pteropodus*
gilberti	Cramer	1896	*(dalli)*		
	(Jordan and Gilbert)	1880	*maliger*	quillback rockfish	*Pteropodus*
	Ayres	1854	*nebulosus*	China rockfish	*Pteropodus*
	(Jordan and Gilbert)	1880	*rastrelliger*	grass rockfish	*Pteropodus*
vexillaris	(Jordan and Gilbert)	1880	*(caurinus)*		*Pteropodus*
	Hilgendorf	1880	*nivosus*	goma-soi	
	Hilgendorf	1880	*trivittatus*	shima-zoi	
	(Matsubara)	1937	*hubbsi*	yoroi-mebaru	
	(Matsubara)	1934	*longispinis*	kourai-yoroi mebaru	
alexandri	(Evermann and Goldsborough)	1907	*(auriculatus)*		
	(Thompson)	1915	*babcocki*	redbanded rockfish	
	(Jordan and Gilbert)	1880	*miniatus*	vermilion rockfish	*Sebastomus*
	(Gill)	1864	*pinniger*	canary rockfish	*Sebastomus*
	(Travin)	1951	*mentella*	deepwater redfish	
	Storer	1854	*fasciatus*	Acadian redfish	
norvegica	(Ascanius)	1772	*norvegicus*	golden redfish	
	Kroyer	1845	*viviparus*	Norway haddock	
	Ayres	1859	*nigrocinctus*	tiger rockfish	*Sebastichthys*
albo-fasciatus •	(Lacepede)	1802	*albofasciatus*	ayame-kasago	
	(Cuvier and Valenciennes)	1829	*marmoratus*	kasago	
tertius	(Barsukov and Chen)	1978	*(marmoratus)*		
	(Jordan and Gilbert)	1880	*serriceps*	treefish	*Sebastichthys*
	(Eigenmann and Eigenmann)	1890	*goodei*	chilipepper	*Sebastodes*
	(Gilbert)	1896	*jordani*	shortbelly rockfish	
	Ayres	1854	*paucispinis*	bocaccio	*Sebastodes*
	(Jordan and Starks)	1904	*itinus*	yanagi-mebaru	
	Hilgendorf	1880	*steindachneri*	yanagi-no-mai	
	Chen	1975	*spinorbis*		
	Chen	1971	*exsul*		
	Chen	1971	*simulator*	pinkrose rockfish	
	Chen	1971	*rosenblatti*	greenblotched rockfish	
	Chen	1971	*ensifer*	swordspine rockfish	
	Chen	1971	*notius*		
	Ayres	1859	*helvomaculatus*	rosethorn rockfish	*Sebastomus*
	Chen	1971	*lentiginosus*	freckled rockfish	
ayresii	(Gilbert and Cramer)	1897	*(rosaceus)*		
	(Jordan and Gilbert)	1880	*chlorostictus*	greenspotted rockfish	*Sebastomus*
	(Jordan and Gilbert)	1880	*constellatus*	starry rockfish	*Sebastomus*
	(Eigenmann and Eigenmann)	1890	*eos*	pink rockfish	*Sebastomus*
gillii	(Eigenmann)	1891	*gilli*	bronzespotted rockfish	*Sebastomus*
rhodochloris	(Jordan and Gilbert)	1880	*(helvomaculatus)*		*Sebastomus*
	Girard	1854	*rosaceus*	rosy rockfish	*Sebastomus*
	(Jordan and Gilbert)	1882	*umbrosus*	honeycomb rockfish	*Sebastomus*
	Valenciennes	1833	*oculatus*		
	(Gmelin)	1789	*capensis*		
chamaco	(Evermann and Radcliffe)	1917	*(capensis)*		
	(Tilesius)	1813	*ciliatus*	dusky rockfish	*Sebastosomus*
	(Ayres)	1862	*flavidus*	yellowtail rockfish	*Sebastosomus*
	Girard	1856	*melanops*	black rockfish	*Sebastosomus*
	(Jordan and Gilbert)	1881	*mystinus*	blue rockfish	*Primospina*
	(Eigenmann and Eigenmann)	1890	*serranoides*	olive rockfish	*Sebastosomus*
	(Jordan and Gilbert)	1883	*ruberrimus*	yelloweye rockfish	
	Gunther	1877	*oblongus*	takenoko-mebaru	
	Barsukov	1970	*borealis*	shortraker rockfish	
	(Jordan and Evermann)	1898	*aleutianus*	rougheye rockfish	
kawaradai	(Matsubara)	1934	*(aleutianus)*		
melanostictus	(Matsubara)	1934	*(aleutianus)*		
swifti	(Evermann and Goldsborough)	1906	*(aleutianus)*		
	Hilgendorf	1880	*matsubarae*	akou-dai	

[1] Listed when different from present species name.

[2] ( )=synonomyzed with; *=form of *pachycephalus*.

Major generic or subgeneric assignments			Other subgeneric assignments		
Jordan and Evermann, 1898	Jordan, Evermann, and Clark, 1930	Matsubara, 1943	Reference	Subgenus	Current subgenus
		Neohispaniscus	Chen, 1986	*Takenokius*	*Neohispaniscus*
			Chen, 1986	*Takenokius*	*Neohispaniscus*
Pteropodus	*Pteropodus*				*Pteropodus*
Pteropodus	*Pteropodus*				*Pteropodus*
Pteropodus	*Pteropodus*				*Pteropodus*
Pteropodus	*Pteropodus*				*Pteropodus*
Pteropodus	*Pteropodus*				*Pteropodus*
Pteropodus	*Pteropodus*				*Pteropodus*
Pteropodus	*Pteropodus*				*Pteropodus*
Pteropodus	*Pteropodus*				*Pteropodus*
		Pteropodus	Chen, 1986	*Takenokius*	*Pteropodus*
		Pteropodus	Chen, 1986	*Takenokius*	*Pteropodus*
		Pteropodus	Jordan and Hubbs, 1925	*Sebastocles*	*Pteropodus*
		Pteropodus			*Pteropodus*
	Rosicola				*Rosicola*
	Rosicola				*Rosicola*
Rosicola	*Rosicola*				*Rosicola*
Rosicola	*Rosicola*				*Rosicola*
					Sebastes
					Sebastes
	Sebastes				*Sebastes*
	Sebastes				*Sebastes*
Sebastichthys	*Sebastichthys*				*Sebastichthys*
			Matsubara, 1943	*Sebastiscus*	*Sebastiscus*
			Matsubara, 1943	*Sebastiscus*	*Sebastiscus*
			Chen, 1986	*Sebastiscus*	*Sebastiscus*
Sebastichthys	*Sebastocarus*				*Sebastocarus*
Sebastodes	*Sebastodes*				*Sebastodes*
Sebastodes	*Sebastodes*				*Sebastodes*
Sebastodes	*Sebastodes*				*Sebastodes*
		Sebastodes			*Sebastodes*
		Sebastodes			*Sebastodes*
			Chen, 1975	*Sebastomus*	*Sebastomus*
			Chen, 1971	*Sebastomus*	*Sebastomus*
			Chen, 1971	*Sebastomus*	*Sebastomus*
			Chen, 1971	*Sebastomus*	*Sebastomus*
			Chen, 1971	*Sebastomus*	*Sebastomus*
			Chen, 1971	*Sebastomus*	*Sebastomus*
					Sebastomus
			Chen, 1971	*Sebastomus*	*Sebastomus*
Sebastomus	*Sebastomus*				*Sebastomus*
Sebastomus	*Sebastomus*				*Sebastomus*
Sebastomus	*Sebastomus*				*Sebastomus*
Sebastomus	*Sebastomus*				*Sebastomus*
Sebastomus	*Sebastomus*				*Sebastomus*
Sebastomus	*Sebastomus*				*Sebastomus*
Sebastomus	*Sebastomus*				*Sebastomus*
Sebastomus	*Sebastomus*				*Sebastomus*
			Chen, 1971	*Sebastomus*	*Sebastomus*
			Chen, 1971	*Sebastomus*	*Sebastomus*
			Chen, 1971	*Sebastomus*	*Sebastomus*
Primospina	*Sebastosomus*				*Sebastosomus*
Sebastosomus	*Sebastosomus*				*Sebastosomus*
Sebastosomus	*Sebastosomus*				*Sebastosomus*
Primospina	*Sebastosomus*				*Sebastosomus*
Sebastosomus	*Sebastosomus*				*Sebastosomus*
Sebastomus	*Sebastopyr*				*Sebastropyr*
		Takenokius	Chen, 1986	*Takenokius*	*Takenokius*
					Zalopyr
Zalopyr	*Zalopyr*				*Zalopyr*
		Zalopyr			*Zalopyr*
		Zalopyr			*Zalopyr*
	Eosebastes				*Zalopyr*
		Zalopyr			*Zalopyr*