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Phylogeny of the Pacific Trouts and Salmon (*Oncorhynchus*) and Genera of the Family Salmonidae

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Abstract.—Seven genera—*Brachymystax*, *Acantholingua*, *Salmothymus*, *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus*—make up the living Salmoninae. Relationships of 33 extant and 4 fossil salmonid species and subspecies were studied on the basis of 119 characters analyzed by parsimony algorithms. Twelve equally parsimonious trees each requiring 253 steps were calculated. Monophyly of recognized genera is consistent with all 12 estimates. The earliest branch of the family Salmonidae is the subfamily Coregoninae. Its sister group is the clade including the Thymallinae and Salmoninae. Within the Salmoninae, *Eosalmo*, from the Eocene of British Columbia, is the sister group of all living genera, as previously shown by Mark Wilson. The living Asian species *Brachymystax lenok* is the sister species of all other living Salmoninae, as documented by Carroll Norden. Three species of archaic trouts from the Mediterranean area—*Acantholingua ohridana*, *Salmothymus obtusirostris*, and *Salmothymus (Platysalmo) platycephalus*—branch off after *Brachymystax* but before diversification of all other salmonines. *Platysalmo platycephalus* Behnke is the sister species of *Salmothymus obtusirostris* and is placed in *Salmothymus*. The clade beyond the archaic trouts includes four genera in two clades: (1) *Hucho* plus *Salvelinus* and (2) *Salmo* plus *Oncorhynchus*. The Atlantic trouts and salmon are a monophyletic group, *Salmo*, and the Pacific trouts and salmon are a monophyletic group, *Oncorhynchus*. The terms “trout” and “salmon” refer roughly to life history modes, not to phylogenetic relationships. Morphological and mitochondrial DNA data disagree regarding the relationship of *Oncorhynchus clarki* (cutthroat trout) to *Oncorhynchus mykiss* (rainbow, California golden, and redband trouts) and the relationship of *Oncorhynchus gorbuscha* (pink salmon) to *Oncorhynchus keta* (chum salmon). Parsimony analysis suggests that *Oncorhynchus mykiss* is the sister of the Pacific salmon, not of *O. clarki*, though *O. clarki* and *O. mykiss* hybridize. *Oncorhynchus gorbuscha* is the sister species of *O. nerka* (sockeye salmon), not of *keta*, though *O. gorbuscha* and *O. keta* hybridize. Mitochondrial DNA is interpreted as having been transferred by introgression between *O. gorbuscha* and *O. keta*, providing misleading evidence of relationship. Fossil species of *Oncorhynchus* document a minimum age of 6 million years for the modern species of Pacific trouts and salmon.

The family Salmonidae includes three subfamilies—Coregoninae (whitefishes), Thymallinae (graylings), and Salmoninae (lenok, mekous, bel-

vica, huchen, taimen, chars, trouts, and salmon)—widely distributed in the northern hemisphere (Norden 1961). There is strong evidence that each of these is a monophyletic clade, a natural group that contains all of the descendants of its most recent common ancestor. The Salmonidae are basal Euteleostei related to the Esocidae,

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Ostariophysi, Argentinoidei, and Osmeroidei (Lauder and Liem 1983; Fink 1984; Begle 1991). Previous salmonid phylogenies (e.g., Norden 1961; Wilson 1974; Kendall and Behnke 1984; Sanford 1990) have interpreted the Salmoninae and Thymallinae as sister groups of each other and the Coregoninae as the sister group of the clade including those two (Figure 1a, b, c).

The subfamily Salmoninae comprises between five and nine extant genera (Figure 1) containing approximately 30 species (Norden 1961; Behnke 1968; Kendall and Behnke 1984). The best known genera are *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus*, which are relatively advanced salmonid fishes. Four other taxa—*Brachymystax*, *Platysalmo*, *Salmothymus*, and *Acantholingua*—are morphologically primitive and their relationships have been problematic. The last three are often included in *Salmo*. In addition, four fossil genera and several fossil species belonging to extant genera have been recognized. Without a phylogeny based on broad evidence from all species, the direction of evolution and the positions of the fossils and problematic taxa relative to the more advanced genera cannot be known. The relationships of chars (*Salvelinus*) to other salmonines are also crucial to the classification of trouts and salmon. Some systematists (e.g., Norden 1961) have considered *Salvelinus* as the sister lineage of a clade including *Salmo* and *Oncorhynchus*, whereas others (e.g., Kendall and Behnke 1984) have placed *Salvelinus* closer to *Hucho* and *Brachymystax*.

Although salmonid biologists agree that Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* are closely related to Pacific trouts and salmon, they have disagreed about the classification of Pacific trouts. Regan (1914) and Vladykov (1963) drew attention to the closer relationship of Pacific trouts to Pacific salmon (*Oncorhynchus*) than to Atlantic trout and salmon (*Salmo*). Traditionally, however, Pacific trouts have been classified in *Salmo*, thus making *Salmo* an unnatural group—paraphyletic—because it does not include all of its descendants (Smith and Stearley 1989). In the present paper, the relationships of the species of Pacific trouts and salmon to each other are treated in the context of the phylogeny of all fossil and Recent genera of salmonines.

History of Salmon and Trout Classification

Salmo, as proposed by Linnaeus in 1758, included all salmonines then known, as well as thymallines and coregonines (and some groups of

fishes, such as osmerids, now placed outside the family Salmonidae). During the two centuries since Linnaeus's classification, ichthyologists have thoroughly documented and classified salmonine diversity. Following is a brief summary of the taxonomic histories of three salmonine assemblages: (1) the four genera of morphologically plesiomorphic "archaic trouts," (2) the huchen (*Hucho*) and chars (*Salvelinus*), and (3) the more derived salmonines and trouts in *Salmo* and *Oncorhynchus*.

Archaic Trouts

At least four species of archaic trouts in *Brachymystax*, *Salmothymus*, *Acantholingua*, and *Platysalmo* are native to Siberia, China, Korea, Armenia, and drainages on the northeast periphery of the Mediterranean Sea from Dalmatia to Turkey. They possess short, broad maxillae and short dentaries with high coronoid processes, and they have small teeth. The phylogenetic relationships of these archaic trouts have been a problem because they share primitive characters with the genus *Salmo*. Norden (1961) recognized that *Brachymystax* is morphologically and phylogenetically intermediate between *Thymallus* and more derived salmonines, based on several features. However, other systematists have placed *Brachymystax* as the sister group of *Hucho*, because they share a unique vomerine tooth pattern (discussed below).

Salmothymus is sometimes considered to include two species, *S. obtusirostris* (Heckel), the Dalmatian trout or "mekous," and *S. (Acantholingua) ohridanus* (Steindachner), the "belvica," endemic to Lake Ohrid in Yugoslavia. Behnke (1968:10) noted: "although vital to any comprehensive phylogenetic study of salmonid fishes, the status of *Salmothymus* has never been firmly established." Steindachner's classifications of *Salmothymus obtusirostris* demonstrate the ambiguity indicated by its morphology: he first classified the mekous as a grayling, *Thymallus microlepis* (1874), but later placed it in *Salmo* (Steindachner 1882). Berg (1908:505) called it *Salmothymus obtusirostris*, remarking that its features were intermediate between *Brachymystax* and *Salmo*: "Sie bildet eine besondere Gattung, welche ein Bindeglied zwischen den eben genannten Gattungen [i.e., *Salmo* and *Brachymystax*] darstellt." Hadzisce (1961) first recognized the fundamental differences between *obtusirostris* and *ohridanus* and allocated the two species to two monotypic genera—*Salmothymus obtusirostris* and *Acantholingua ohridana*. Behnke (1968) considered *Sal-*

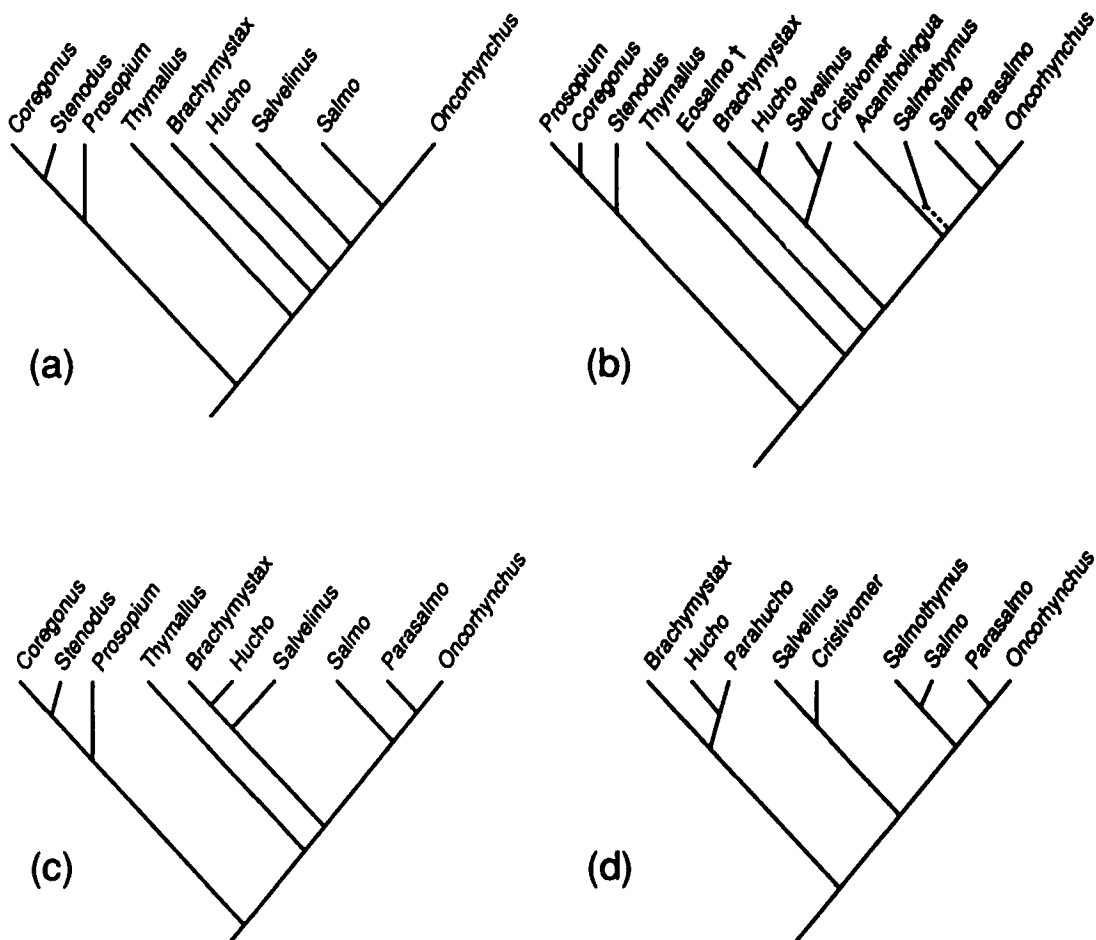


FIGURE 1.—The major phylogenetic hypotheses regarding the Salmonidae (rearranged to comparable format): (a) Norden (1961), (b) Wilson (1974), (c) Kendall and Behnke (1984), (d) Dorofeyeva (1989). The dagger indicates a fossil taxon; dotted lines indicate uncertainty.

mothymus and *Acantholingua* to be subgenera of *Salmo*. Svetovidov (1975) placed *Acantholingua ohridana* in *Salmothymus*, a classification that has been widely followed.

Behnke (1968) described another species of archaic trout, *Salmo* (*Platysalmo*) *platycephalus*, from Turkey. He saw evidence that *Platysalmo*, like *Salmothymus* and *Acantholingua*, had diverged from European *Salmo* long before differentiation of modern *Salmo salar* and *S. trutta* had occurred, but he classified them in *Salmo*. Similarly, "*Salmo*" *ischan* from Armenia and "*Salmo*" *carpio* from Italy may be Archaic trouts related to *Salmothymus obtusirostris* and *S. platycephalus*. Such a broad concept of *Salmo* makes a genus containing relatively unrelated species—a polyphyletic assemblage.

Huchen and Chars

The huchen was described by Linnaeus (1758) as *Salmo hucho* and placed in the subgenus *Hucho* by Günther (1866). Jordan and Snyder (1902) elevated *Hucho* to generic rank and described a second species, *H. perryi*. Vladikov (1963) created the subgenus *Parahucho* for *Hucho perryi*. Lindsey (1964) called attention to broad similarities between *Hucho* and *Salvelinus*. But huchen were regarded as close relatives of *Brachymystax* by Shaposhnikova (1968, 1975), Holčík (1982a, 1982b), and Holčík et al. (1988). Kendall and Behnke (1984) treated *Brachymystax* plus *Hucho* as a clade related to *Salvelinus*.

Chars, *Salvelinus*, are a monophyletic group with many holarctic species (see Behnke 1972; Balon

1980, 1984). Diverse proposals have been made for recognizing taxonomic structure within the genus (Vladykov 1963; Cavender 1978, 1980, 1984; Cavender and Kimura 1989; Phillips et al. 1989; Kendall and Behnke 1984; Grewe et al. 1990). Recently a new genus of char has been described from Lake El'gytgyn in Siberia and given the name *Salvethymus* (Chereshnev and Skopets 1990).

Trouts and Salmon

Trouts and salmon occur in northern Atlantic and northern Pacific drainages. Formal classification of the Atlantic *Salmo trutta* (brown trout) and *Salmo salar*, (Atlantic salmon) date from Linnaeus (1758). Pacific basin trouts and salmon had already been discussed in an unpublished manuscript on fishes of Kamchatka by Georg Wilhelm Steller; after Linnaeus's work, Johann Walbaum (1792) formally named Steller's species in *Salmo*: *Salmo mykiss* (rainbow trout), *S. kisutch* (coho salmon), *S. tshawytscha* (chinook salmon), *S. keta* (chum salmon), *S. nerka* (sockeye salmon), and *S. gorbuscha* (pink salmon). Walbaum apparently worked from Pallas' translation of Steller's manuscripts, as published in Pennant's "Arctic Zoology" (Briggs 1965). Richardson (1836) rediscovered and named these same taxa *Salmo gairdnerii* (rainbow trout), *S. tsuppitch* (coho salmon), *S. quinnat* (chinook salmon), *S. consuetus* (chum salmon), *S. paucidens* (sockeye salmon), and *S. scouleri* (pink salmon) on the basis of specimens from northwestern North America. Among Richardson's other discoveries was *Salmo clarki* (cutthroat trout), which occurs only on the east side of the Pacific.

In 1861, Suckley renamed several of the Pacific trout and salmon again and proposed the subgenus *Oncorhynchus* (type species, *S. gorbuscha*) for those anadromous *Salmo* with a "permanently hooked snout" and enlarged teeth (Suckley 1861). His suggestion was amplified in a posthumous work (Suckley 1874). In the latter paper, it is clear that his conception of *Oncorhynchus* was based primarily on breeding males. Mature males were usually included under the subgenus *Oncorhynchus* while immature and female individuals of the same species were not; for example, the chinook salmon was artificially divided into *Oncorhynchus cooperi* and *Salmo richardi*. Suckley considered steelhead, coastal cutthroat trout, and female chinook salmon, coho salmon, chum salmon, pink salmon, and sockeye salmon to be "salmon," but not in *Oncorhynchus*.

Günther (1866) elevated *Oncorhynchus* to generic rank, rejected Suckley's characters, redefined *Oncorhynchus* to be based on a longer anal fin (with more than 14 rays; he was unaware of *Oncorhynchus masou*, which has 11–13 anal rays) so that it applied to Pacific salmon but not trout, and classified males and females of the same species together. He continued to classify Pacific trouts, huchen, and chars in *Salmo*. Jordan and Gilbert (1883) sorted out some of the confusion resulting from Walbaum's, Richardson's, and Suckley's synonymous species names, but the diagnosis of *Oncorhynchus* remained ambiguous even to Jordan. In 1892 he described the Kamloops rainbow trout as an *Oncorhynchus* related to *O. tshawytscha* (Jordan 1892), but assigned it to *Salmo* a year later. The identity of the east and west Pacific rainbow trout remained confused until the work of Behnke (1966) and especially Okazaki (1984).

The cause of the generic ambiguity was discerned in the early decades of this century by C. T. Regan of the British Museum. Regan (1914: 406) noted that "examination of the skeletons leaves no doubt that the Pacific species (Steelhead, Rainbow Trout, Quinnat Salmon, etc.) form a natural group that differs in several characters from the Salmon and Trout of the Atlantic." However, Americans (e.g., Jordan and Evermann 1920) ignored Regan and continued to group Pacific trouts with Atlantic trouts and salmon in *Salmo* on the basis of the difference in number of anal rays. From Jordan and Evermann (1896) to Jordan et al. (1930) and through four editions of the American Fisheries Society's "List of Common and Scientific Names of Fishes from the United States and Canada," American ichthyologists grouped the Pacific trouts with the brown trout and Atlantic salmon in the genus *Salmo*, although workers such as Neave (1958), Behnke et al. (1962), Rounsefell (1962), and Behnke (1972) recognized the close relationship between Pacific trout and Pacific salmon.

Tchernavin (1937, 1938a) also rejected Regan's classification and offered a notable logic in support of his argument. Tchernavin (1937:236) used shared primitive characters for diagnosing genera: "Some of these [skeletal] elements seem to retain old ancestral characters and thus afford a guide to the natural arrangement of families and genera; while other elements of the skeleton, mostly those belonging to the investing bones, change with the development of the species and present clear distinctions for determining species." Although Tchernavin was trying to discover natural groups,

his criteria were inconsistent with Regan's phylogenetic criteria. The distinction is that Tchernavin sought genealogical evidence in the unchanged anatomy, whereas Regan used shared specializations as evidence of relationship, as later formalized by Hennig (1966). The former method results in a subjective classification based on grades of advancement; the latter leads to a classification of monophyletic groups of sequentially related clades. Character evidence documented by Tchernavin included an unforked rostral cartilage and the lack of dorsal fontanelles in the Pacific salmon chondrocranium.

Norden's (1961) review of the osteology of the grayling (*Thymallus*) summarized all the character evidence for sequestering Pacific salmon in *Oncorhynchus*: "widely separated palatine and vomerine teeth; postorbitals contacting preopercle; no ascending process of premaxilla; opisthotic touches prootic; in adult no dorsal fontanelles" (Norden 1961:753). These characters were subsequently used to diagnose *Oncorhynchus* (see Kendall and Behnke 1984). They will be examined in detail below because they also apply to some large Pacific trouts and so the group thus diagnosed makes Pacific trouts paraphyletic (Smith and Stearley 1989), that is, an assemblage that does not include all of its descendants.

Most data accumulated since Tchernavin's time—meristic (Rounsefell 1962), osteological (Vladykov 1963; Behnke 1972; Cavender and Miller 1972, 1982; Smith and Stearley 1989; Sanford 1990), and molecular (Berg and Ferris 1984; Grewe et al. 1990)—support Regan. They indicate that the Pacific trouts and Pacific salmon form a unified clade separate from Atlantic salmon and trout. But most workers have been reluctant to upset the established nomenclature, sacrificing historical accuracy and potential predictability for stability (Smith and Stearley 1989).

Vladykov (1963), however, proposed a compromise solution—a new genus or subgenus (the original designation is ambiguous), *Parasalmo*, for the Pacific trouts. Vladykov and Gruchy (1972) designated *S. clarki* as the type species of the subgenus *Parasalmo* in *Salmo*. This solution received recent support (e.g., Cavender and Miller 1982; Kendall and Behnke 1984:figure 1; Dorofeyeva 1989). However, placing Pacific trouts in a new subgenus of *Salmo* does not solve the problem, which is that Pacific trouts are related to *Oncorhynchus*, not *Salmo*. Balon's (1984) analysis is consistent with the Vladykov classification, but

his phylogeny of the salmonine fishes differs from those of other workers.

Vladykov (1963:496) regarded *Parasalmo* (type species *clarki*) to be the same as the group containing the fossil trout *Rhabdofario lacustris*. But perhaps because the latter is a fossil, he missed the nomenclatural priority (Cope 1870) of the name *Rhabdofario* Cope 1870 over *Parasalmo* Vladykov 1963, if the clade is taken to include both the rainbow trout (*mykiss*) and cutthroat trout (*clarki*). Relationship of *Rhabdofario lacustris* to extant Pacific trouts had been established by Uyeno and Miller (1963), who also placed the species with Pacific trouts in the genus *Salmo* (and changed the species name to *copei* because the combination *Salmo lacustris* had been used by Linnaeus). Vladykov and Gruchy (1972) gave separate diagnoses for *Parasalmo* and *Rhabdofario*. Cavender and Miller (1972) compared their new fossil genus *Smilodonichthys* to *Oncorhynchus*, *Salmo* (including Pacific trouts), and *Rhabdofario*, and in 1982 recognized *Parasalmo* as a subgenus of *Salmo*. Smith (1975) used *Rhabdofario* to emphasize differences between the fossil species, *lacustris*, and the recent trouts in western North America. Kendall and Behnke (1984) regarded *Rhabdofario* as a fossil clade apart from *Parasalmo* but confused the species each contains. The current study attempts to diagnose monophyletic lineages of trouts and salmon, while resolving the nomenclatural conflicts among *Salmo*, *Oncorhynchus*, *Parasalmo*, *Smilodonichthys*, and *Rhabdofario*.

Methods

Our approach to the classification problem is founded on the principle that biological classification should reflect, if possible, phylogenies (Darwin 1859:486); named groups should correspond to monophyletic clades, which include all of the descendants of a common ancestor. Unnatural groups, which exclude derived relatives or include nonrelatives (paraphyletic and polyphyletic assemblages, respectively), are not admissible in such a classification. If *Salmo* is made polyphyletic or paraphyletic by the inclusion of species (e.g., *obtusirostris* or *clarki*) more closely related to other lineages, than such species must be removed from *Salmo* and classified with their relatives.

Monophyletic groups are discovered and diagnosed by the presence of shared, derived character states—synapomorphies (Hennig 1966). Shared

primitive characters—symplesiomorphies—such as used by Tchernavin (1937) carry no information about the phylogenetic (i.e., branching) relationships of the evolving lineages in the group. Homoplasies (convergently or introgressively acquired shared character states and states acquired by character reversal) are understood to be false evidence regarding branching sequence and are identified by their noncongruence (disagreement) with other characters in the study. (Nonindependent homoplasies, such as might arise from parallel reduction in size or introgressive hybridization, are possible sources of error; note the discussion of apparently paedomorphic *Acantholingua ohridana* and introgressed *Oncorhynchus gorbuscha* below.) In the parsimony methods we employ, diverse homoplasies are expected to be outweighed, as evidence, by characters whose congruence is a result of their shared evolutionary history. The choice between alternative phylogenetic trees is therefore made by calculating the branching sequence that accounts for the observed pattern of character evolution with the fewest reversals or convergences—or in terms of the parsimony hypothesis, the branching sequence that requires the fewest ad hoc assumptions to explain the observed character state distributions.

One hundred nineteen characters were assessed on representatives of 33 extant and 4 fossil taxonomic units (Table 1; Appendix). Algorithms programmed by David Swofford (PAUP 2.4—Phylogenetic Analysis Using Parsimony) and James S. Farris (HENNIG86) were used to estimate the most parsimonious trees (Swofford 1985; Farris 1988). Branch-swapping algorithms were employed, with Farris optimization procedures, to identify the shortest trees. Nelson consensus trees were calculated when several most parsimonious trees (found by both programs) were of equal length.

Skeletonized, cleared-and-stained, dissected and fossil specimens were examined. Many characters used herein have been identified in prior studies, but all relevant anatomical material was reexamined and new characters were discovered. We acknowledge a large debt to prior character discovery by Svetovidov (1936, 1975), Tchernavin (1938a, 1938b), Miller (1950, 1972), Norden (1961), Behnke et al. (1962), Hikita (1962), Vladikov (1962, 1963), Needham and Gard (1964), Behnke (1968), Shapozhnikova (1968), Cavender (1970, 1980), Cavender and Miller (1972, 1982), Scott and Crossman (1973), Wilson (1977), Dorofeyeva (1978, 1989), Holčík (1982a, 1982b),

Jollie (1984, 1986), Sanford (1990), and Begle (1991).

Character states were polarized by including three taxa outside the Salmonidae, but related to it, as reference points (outgroups) to indicate primitive character states. Although general relationships of basal euteleost families are understood (Gosline 1960; Rosen 1974, 1985; Fink and Weitzman 1982; Fink 1984; Howes and Sanford 1987; Begle 1991) no single closest sister group of the Salmonidae has been identified. Primitive outgroups are the extant osmerid genus *Thaleichthys*, the extant umbrid *Novumbra hubbsi*, and plesiomorphic ostariophysan genus *Chanos*. The Osmeridae and Ostariophysi are two of the closest extant sister groups to the Salmonidae (Gosline 1960; Fink 1984; Rosen 1985). Within the osmerid fishes, *Thaleichthys* is considered to be plesiomorphic (Weitzman 1967; Howes and Sanford 1987; Begle 1991) and hence was chosen as the source of osmerid character information. Similarly, the gonorhynchid *Chanos* represents a plesiomorphic member of the Ostariophysi (Fink and Fink 1981). The genus *Novumbra* was considered the plesiomorphic sister group of other umbrids by Wilson and Veilleux (1982). Use of three outgroups provides the algorithms with the information necessary to polarize the character states regardless of initial code assignments, but other basal euteleosts provided perspective on character state codes and are used to assign 0 to represent possible primitive states, and 1, etc., to represent more advanced states in Table 1 and Appendix 1. Cretaceous euteleosts *Gaudryella* and *Humbertina* (Patterson 1970) and *Leptolepis* (Cavender 1970) are additional sources of information about primitiveness. The Coregoninae and Thymallinae are morphologically plesiomorphic salmonids. The plesiomorphic coregonines *Prosopium coulteri*, *Coregonus huntsmani*, and *Stenodus leucichthys* and the thymalline *Thymallus arcticus* are included as outgroups nearest to the Salmoninae. Character states and polarizations are listed in Table 1. Code values are assigned to character states in a simplified scheme, with 0 usually referring to the primitive state and with 1 (sometimes 1 and 2) representing the derived state(s). Evolution in two opposite directions from an ancestor was coded as 0 and 2 derived from 1. Directional information in multistate characters was included in the coding (additive coding) when we had evidence that intermediacy in morphology required intermediacy in history. Character data are presented in tabular form in the Appendix.

TABLE 1.—Description of 119 salmonid character states. Assignments of numerical character states (bold digits) are tabulated in the Appendix. Generally, 0 denotes the primitive state, and 1 and 2 denote derived states.

1. Dorsal chondrocranium. Temporal fontanelles remain open throughout life (0) or close during late ontogeny (1) (Figure 2; see Tchernavin 1937)
2. Dermethmoid. Paired (0), single and median with posterior separation (notch) (1), or single and median with no posterior separation (2)
3. Dermethmoid. Short to moderately long (0) or extremely long, up to four times width (1) (Figure 3; see also Norden 1961)
4. Dermethmoid. Overlapping frontals and lying between nasals (0) or contacting frontals but without broad overlap (1)
5. Dermethmoid. Without prominent midlength constriction (0) or with constriction, spearhead-shaped (1)
6. Dermethmoid. Not broad and blunt (0) or very broad, in shape of blunt diamond (1) (*Salmo*, Figure 3)
7. Dermethmoid. Not "A-shaped" (0). "A-shaped" with narrow taper (1), or with widely (greater than 40°) divergent, posterior wings (2) (Figure 3)
8. Dermethmoid. Without anterior extension in breeding individuals (0) or with anterior extension in breeding individuals (1) (Vladykov 1962)
9. Ethmoid. Present (0) or absent (1). (This median chondral ossification, underlying the dermethmoid, is often termed the "hypethmoid" by salmonid systematists [e.g., Norden 1961], but this name is not in general use. We adopt the term advocated by Harrington 1955 rather than the "supraethmoid" of Patterson 1975, because the latter name has often been used synonymously with "dermethmoid.")
10. Lateral ethmoids. Deeper dorsoventrally than wide (0) or width approximately equal to maximal depth (1)
11. Posttemporal fossae roofed (0) or open (1)
12. Frontals. Not included as part of the floor of the posttemporal fossae (0) or included as part of the floor of these (1)
13. Frontals. Not widely expanded above the autosphenotics (0) or expanded laterally, covering the autosphenotics (1)
14. Frontals and parietals. Parietals not flanking frontals (0) or flanking frontals that are extended posteriorly along the midline (1) (Norden 1961)
15. Frontals. Without depression at posterior midline (0) or with depression (1)
16. Frontals. Without anterior shelf-like expansion above orbit (0) or with shelf above orbit (1) (Figure 4)
17. Frontals. Not in contact with epiotics (0) or contacting epiotics in large individuals (1)
18. Sphenotic. Anterior ramus thin and directed laterally (0) or stout and directed anteriorly (1) (Figure 5)
19. Pterotic. With short hyomandibula fossa, extending half the length of the pterotic (0), or fossa extending the entire length of the pterotic (1) (Figure 5)
20. Epiotics. With flat posterior surface (0) or surface with sulcus (1)
21. Epiotics. Without stout conical dorsoposterior processes (0) or with processes (1)
22. Supraoccipital. Crest short, not as long as anterior-posterior dimension of supraoccipital (0), or as long as anterior-posterior dimension of supraoccipital (1)
23. Intercalar. With small otic ramus (0) or with long otic ramus, typically contacting the prootic (1) (Figure 5)
24. Prootic. Narrow anteroposteriorly and anterior branch of trigeminofacial nerve exiting through foramen on anteromesial margin (0) or expanded anteroposteriorly and nerve exiting through foramen on lateral margin (1) (Figure 5)
25. Orbitosphenoid. Absent (0) or present (1)
26. Orbitosphenoid. With anterior emargination (0) or without emargination (1)
27. Orbitosphenoid. Left and right halves fused ventrally, forming a Y-shaped cross section (0), or unfused, broadly oval in cross section (1)
28. Orbitosphenoid. Not in form of spongy ball (0) or in form of spongy ball (1)
29. Parasphenoid. In sagittal profile, flexed (0) or straight (1)
30. Parasphenoid. Not extending posteriorly to the posterior edge of the basioccipital (0) or extending to posterior edge of basioccipital (1)
31. Posterior parasphenoid. Flat in cross section (0) or with high vertical walls flanking the posterior myodome (1) (Figure 5)
32. Parasphenoid. Basisphenoid process of parasphenoid not ossified (0) or stout and ossified (1)
33. Occipital condyle. Simple and involving only the basioccipital (0), tripartite and involving the basioccipital and processes from the two exoccipitals (1), or secondarily fused (2) (Cavender and Miller 1972)
34. Vomer. Dentition present (0) or teeth absent or vestigial in adults (1)
35. Vomer. Short (0) or long, extending posteriorly to the lateral ethmoids, and with teeth on shaft (1)
36. Vomerine longitudinal tooth row. Not extending to posterior edge of vomer (0) or long, extending to posterior edge of vomer (1)
37. Vomer. Without prominent anterior transverse tooth row (0) or with such row (1) (Figure 6)
38. Vomer. Without teeth on posterior extension (crest) of the vomerine capitulum (0) or with such teeth (1) (Figure 6)
39. Vomer. Without anterior extension in breeding males (0) or with such extension (1)
40. Vomer. Teeth not deciduous (0) or deciduous and typically lost during breeding migration (1)

TABLE 1.—Continued.

41. Hyomandibula. Dorsolateral surface narrow with adductor ridge (0) or broad and dish-shaped without trace of adductor ridge (1) (Figure 7)
42. Metapterygoid. Positioned between quadrate and symplectic and in broad contact with symplectic (0) or positioned more dorsally with minimal contact with symplectic (1) (Figure 7)
43. Metapterygoid. Extending dorsally to middle of hyomandibula (0) or extending nearly to the pterotic (1) (Figure 7)
44. Mesopterygoids. Bearing teeth (0) or toothless (1)
45. Mesopterygoid. In marginal contact with metapterygoid and quadrate (0) or extended posteriorly, broadly overlapping metapterygoid and overlapping quadrate (1) (Figure 7)
46. Palatine. Well-toothed (0) or teeth vestigial or absent (1)
47. Palatine. Premaxillary process with no or small posterior crest (0) or with long blade-like crest (1) (Figure 7; also see Smith and Stearley 1989, figure 1)
48. Quadrate. Angle between anterior and posterior margins 90° or greater (0) or acute (1) (Figure 7)
49. Maxilla. Bearing teeth (0) or teeth absent in adults (1) (Norden 1961).
50. Maxilla. Short, not extending posterior to orbit (0), or long, extending posterior to orbit (1)
51. Maxilla. Bladelike and ventral edge convex (0), straight or slightly concave (1), or strongly arched (2)
52. Maxilla. Flat in cross section (0), ovate in cross section (1), or round in cross section (2)
53. Maxilla. Premaxillary process extending dorsally less than 10° from the main axis of the maxilla (0) or extending dorsally at angle of 10° or more from the main axis of the maxilla (1) (see Smith and Stearley 1989)
54. Maxilla. Premaxillary process not projecting below axis of maxilla (0) or palmate and extending below the axis of the maxilla (1) (see Smith and Stearley 1989)
55. Premaxilla. Toothed (0) or vestigial teeth in adults (1) (Norden 1961)
56. Premaxilla. Without enlarged breeding tusks (0) or with enlarged breeding tusks (1) (Vladykov 1962)
57. Premaxilla. With rudimentary ascending process (0) or with broad ascending process (1)
58. Premaxilla. Ascending process not deflected posteriorly (0) or deflected posteriorly and typically arched in breeding males (1)
59. Premaxilla. Without "thin crest" (sensu Vladykov 1962) (0) or with thin crest (1)
60. Premaxilla. Teeth without dark enamel (0) or with dark enamel (1) (Cavender and Miller 1972)
61. Premaxilla. Without substantial mesial pocket for rostral cartilage (0) or with pocket (1) (see Smith and Stearley 1989)
62. Premaxilla. Without strong process mesial to the rostral cartilage pocket (0) or with process (1) (see Smith and Stearley 1989)
63. Supramaxilla. Broad and ovate (0), thin and lanceolate (1), or long and inflected (2)
64. Dentary. Without stout and deep body anterior to the Meckelian groove (0) or deep anterior to the Meckelian groove (1)
65. Coronoid process of dentary. Rising steeply from the symphysis at an angle greater than 45° such that the highest portion of the mandible is positioned close to the symphysis (0), rising less steeply such that the highest portion of the mandible is positioned midway (1), or rising at a very shallow angle such that the highest portion of the mandible is positioned posteriorly (2) (Cavender and Miller 1972)
66. Dentary and angular-articular. Coronoid process of dentary and coronoid ramus of angular-articular in close fit (0) or gap between these (1) (Smith and Todd, in press)
67. Dentary. Without anterior cartilaginous expansion (kype) in breeding males (0) or with kype (1). (Although the term "kype" is used in salmonid literature to refer to the hooking of either upper or lower jaw accompanying breeding status, Morton 1965 demonstrated that this word historically refers to the strong hook on the mandible.)
68. Dentary. Without extreme development of kype (0) or with extreme development of kype (1)
69. Dentary. Teeth well socketed (0) or not well socketed, deciduous in breeding individuals (1)
70. Dentary and maxilla. Without dark enameloid on interior of teeth (0) or with dark enameloid (1) (see Vladykov 1962:52)
71. Angular-articular. Posterior process extending horizontally (0) or at an angle to the horizontal (1)
72. Retroarticular. Ventral and suture with angular-articular at low angle (0), suture at angle higher than 45° (1), or suture at high angle and retroarticular mesial to angular-articular (2)
73. Supraorbital. Long and bordering most of the dorsal surface of the orbit (0) or short and bordering the anterior third of the dorsal surface of the orbit (1)
74. Supraorbital. Not contacting the dermosphenotic (0) or contacting the dermosphenotic (1)
75. Supraorbital(s). Single supraorbital (0) or multiple (1)
76. Postorbitals. Long and covering hyomandibula (0) or short and covering less than half the hyomandibula (1) (Smith and Stearley 1989)
77. Infraorbitals. Typically 6 (0) or restricted to 5 (1) (i.e., circumorbitals typically 8 [0] or restricted to 7 [1])
78. Second infraorbitals. Second infraorbital blade-like (0) or thin and tubular (1) (Smith and Stearley 1989)
79. Postorbitals. Not divided into two series (0) or divided into anterior and posterior series (1)
80. Suprapreopercle. Absent (0) or present (1)

TABLE 1.—Continued.

81. Preopercle. Ventral limb long, two-thirds the length of dorsal limb (0), reduced, half the length of dorsal limb (1), or greatly reduced, less than half the length of dorsal limb (2) (Figure 8)
82. Preopercle. Dorsal limb not deep, approximately 20% of its length (0), or expanded posteriorly, ranging up to 30% or more of its length (1) (Figure 8)
83. Subopercle. Deep, two-thirds as deep as wide (0), or shallow, similar in shape to branchiostegal (1)
84. Extrascapulars. Tabular (0) or tubular (1)
85. Median basihyal denticles. Present (0) or absent (1)
86. Basihyal. Without teeth on perimeter (0) or with stout teeth around perimeter (1)
87. Basihyal. Blunt anteriorly (0) or thin and pointed anteriorly (1) (Vladykov 1962)
88. Basibranchial plate. Present (0) or absent (1) (Norden 1961)
89. Basibranchial plate. With teeth (0) or without (1) (Norden 1961; Behnke 1972)
90. Anterior ceratohyal. Imperforate (0) or perforate (1)
91. Anterior ceratohyal. Slender and slightly constricted (0), or rectangular, length : depth ratio 2.5 or less (1) (Figure 9)
92. Branchiostegals. Fewer than 10 (0), 10–13 (1), or more than 13 (2)
93. Vertebral number. Mean number less than 61 (0), 62–65 (1), or more than 65 (2)
94. Caudal skeleton. Posterior hemal spines, parahypural, and first hypural lacking peg-and-socket connections (0) or with peg-and-socket connections (1)
95. Caudal skeleton. With ossifications ("tendon bones") in the urostyle (0) or without urostyle ossifications (1)
96. Caudal skeleton. First uroneural not amplified into a large fan-shaped stegural (0) or amplified into a fan-shaped stegural (1)
97. Caudal skeleton. With complete neural arch and spine on preural centrum 2 (PU2) (0) or with spine detached from arch (1)
98. Caudal skeleton. With three epurals (0) or two epurals (1) (Norden 1961; Vladykov 1962)
99. Dorsal fin rays. Fewer than 17 (0) or more than 17 (1)
100. Number of gill rakers on first arch. More than 16 (0) or fewer than 16 (1)
101. Gill rakers. Mean count below 25 (0) or very high, above 25 (1)
102. Lateral line scales. Roughly circular (0) or very elliptical, reduced to little more than the nerve tube (1)
103. Karyotype. Diploid (0) or tetraploid (1)
104. Nostril flaps. One flap per narial opening (0) or two flaps (1) (Hubbs and Lagler 1947)
105. Pyloric caecae. Fewer than 20 (0), 20–70 (1), or more than 70 (2)
106. Dorsal trunk. Without pronounced hump in breeding males (0) or with hump (1)
107. Dorsal trunk. Without extreme development of hump (0) or with extreme development of hump (1)
108. Nuptial tubercles. Present (0) or absent (1)
109. Egg size. Less than 3.0 mm (0), 3.5–4.5 mm (1), or greater than 4.5 mm in diameter (2) (Norden 1961)
110. Coloration. Without vertical bars ("parr marks") in juveniles (0) or with vertical bars (1)
111. Coloration. Without pale spots (0) or with pale spots (1)
112. Coloration. Without cutthroat mark (0) or with cutthroat mark (1)
113. Coloration. Without yellow cutthroat mark (0) or with yellow cutthroat mark (1)
114. Coloration. Without dark patch on border of adipose fin (0) or with dark patch on border of adipose fin (1)
115. Coloration. Without vermiculated spots on back (0) or with vermiculations (1)
116. Coloration. Without X-shaped spots (0) or with X-shaped spots (1)
117. Coloration. Dorsal, anal, and pelvic fins without white tips (0) or with white tips (1)
118. Coloration. Caudal fin without red anterior edge (0) or with red anterior edge (1)
119. Nostrils. Without minute papillae around margins (0) or with papillae around margins (1) (Stanford 1990)

Results

Twelve equally parsimonious trees, requiring 253 steps, resulted from the computer-assisted analyses by PAUP and HENNIG86. The consistency index for each was 0.54. The low consistency index is a consequence of the large number of taxa and inclusion of many homoplastic but potentially informative characters, such as meristic characters. The 12 trees are similar at most points. The generic relationships chosen by us are based on monophyletic groups that are consistent with the topology of the 12 trees. Figures 10–12 depict

the consensus tree of the 12 equally parsimonious trees, calculated with the CONTREE program (Swofford 1985) and the Nelson consensus tree option in HENNIG86. The polytomies in Figures 10–12 are consistent with the equally parsimonious solutions in three areas. (1) The relationships of *Acantholingua ohridana* are either to the other archaic trouts or to all salmonines above *Brachymystax* (Figure 10). (2) Two species of *Salvelinus*, *leucomaenus* and *fontinalis*, have equally parsimonious alignments to another node (Figure 11). (3) Four fossil and recent relatives of *Oncorhynchus*

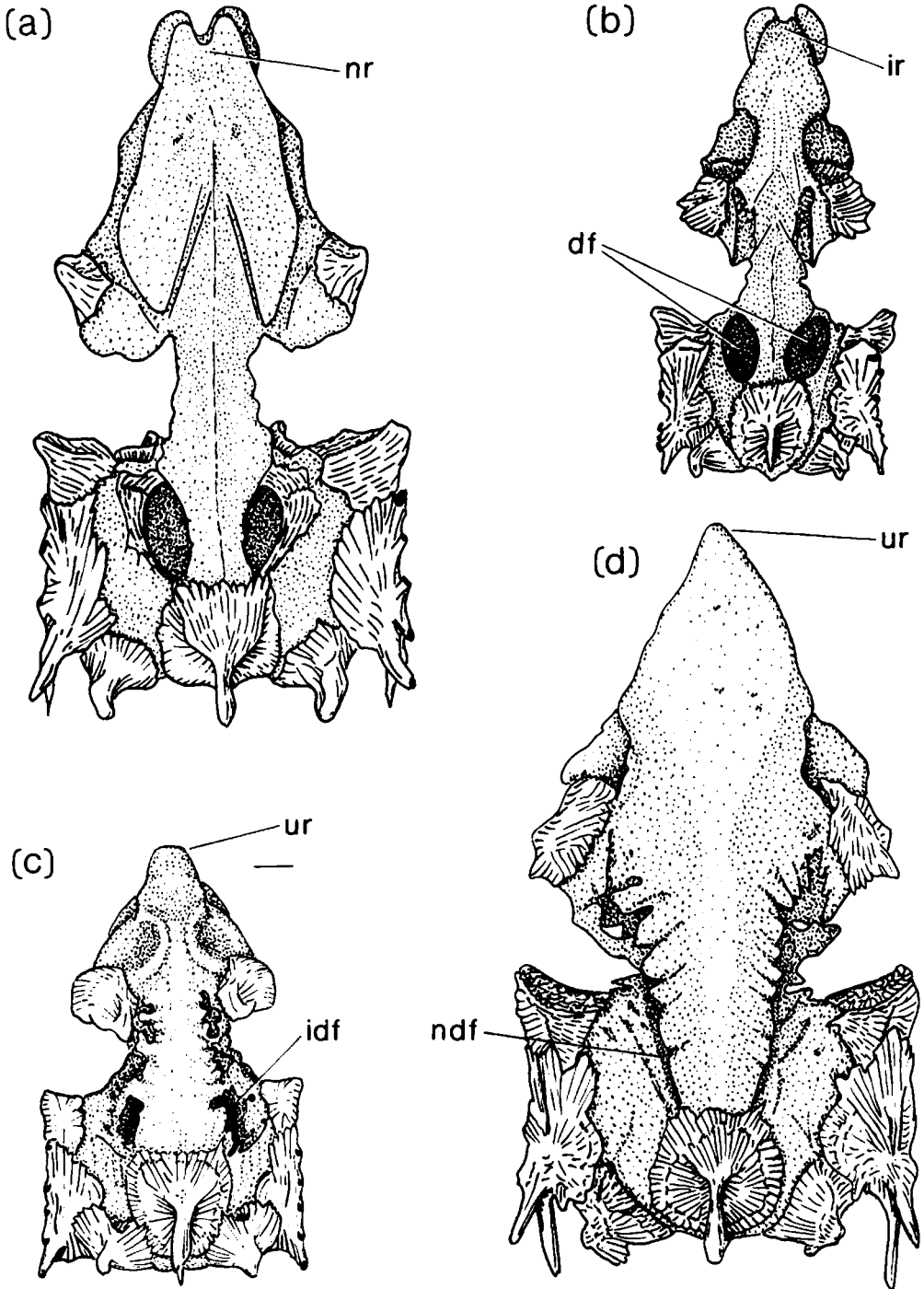


FIGURE 2.—Neurocranium, dorsal bones removed to show fontanelles in cartilage, anterior up. (a) *Salmo salar*, after Tchernavin (1937: figure 1); (b) *Oncorhynchus mykiss*, after Tchernavin (1937: figure 4); (c) *Oncorhynchus masou*, Oregon State University Collection 8087; (d) *Oncorhynchus tshawytscha*, after Tchernavin (1937: figure 2). Abbreviations: df, dorsal fontanelles; idf, incomplete dorsal fontanelle; ir, intermediate rostrum; ndf, no dorsal fontanelle in adults; nr, notched or divided rostrum; ur, undivided rostrum.

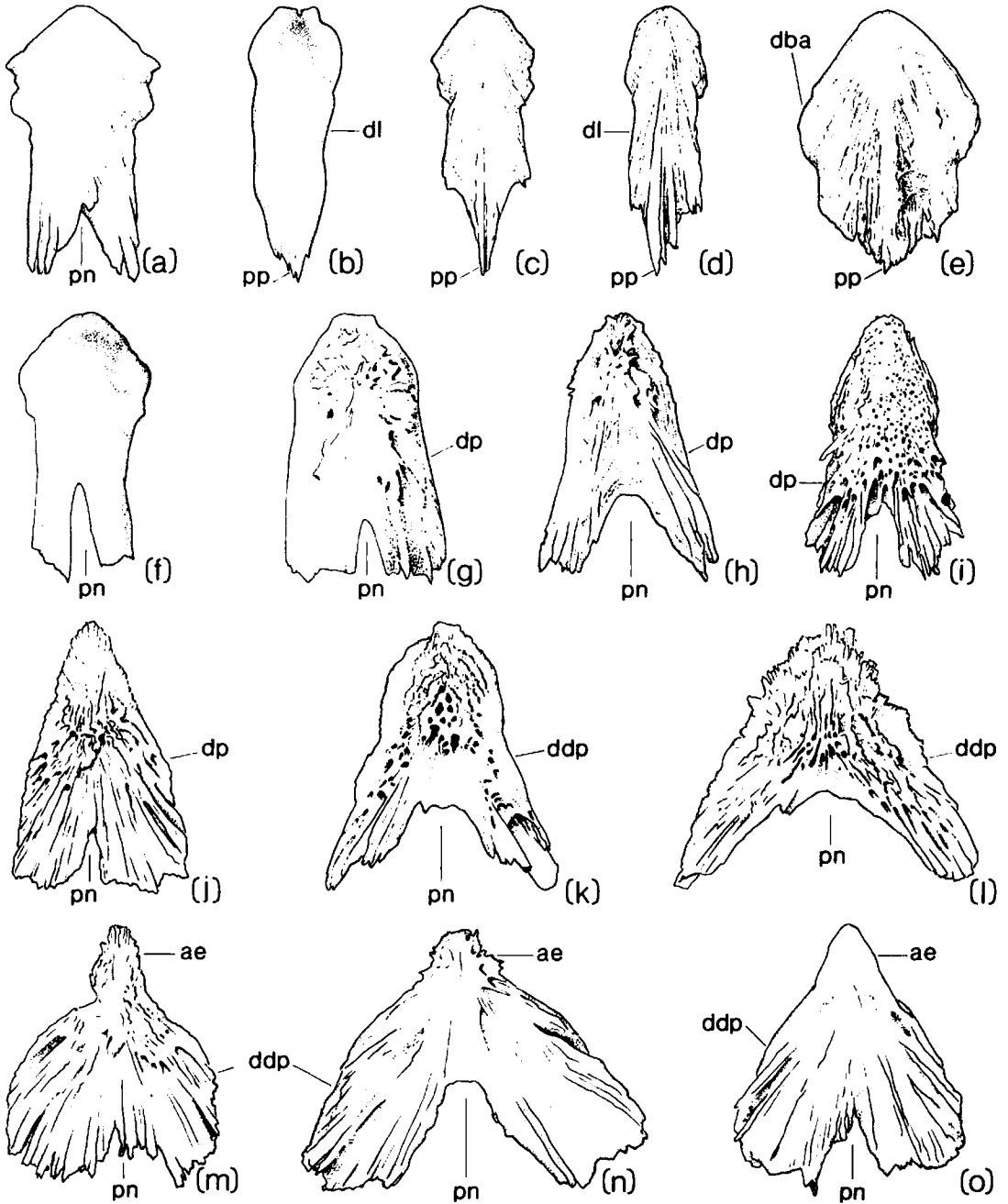


FIGURE 3.—Dermethmoids, dorsal view, anterior up. (a) *Thymallus arcticus*, UMMZ (University of Michigan Museum of Zoology) 186233S; (b) *Brachymystax lenok*, UMMZ 172491; (c) *Hucho perryi*, UMMZ 187613S; (d) *Salvelinus namaycush*, UMMZ 203837S; (e) *Salmo trutta*, UMMZ 183694S; (f) *Oncorhynchus clarki*, UMMZ 181728S; (g) *Oncorhynchus mykiss*, UMMZ 213375S; (h) *Oncorhynchus mykiss* (redband), UMMZ 219575S; (i) *Oncorhynchus rhodurus*, UMMZ 208141S; (j) *Oncorhynchus kisutch*, UMMZ 186653S; (k) *Oncorhynchus ishawytscha*, UMMZ 212765S; (l) *Oncorhynchus ishawytscha*, UMMZ 178987S; (m) *Oncorhynchus keta*, UMMZ 175915S; (n) *Oncorhynchus nerka*, UMMZ 172454S; (o) *Oncorhynchus gorbuscha*, UMMZ 201722S. Abbreviations: ae, anterior extension; dba, broad anterior; ddp, strongly divergent posterior wings; dl, long dermethmoid; dp, divergent posterior wings; pn, posterior notched; pp, posterior pointed.

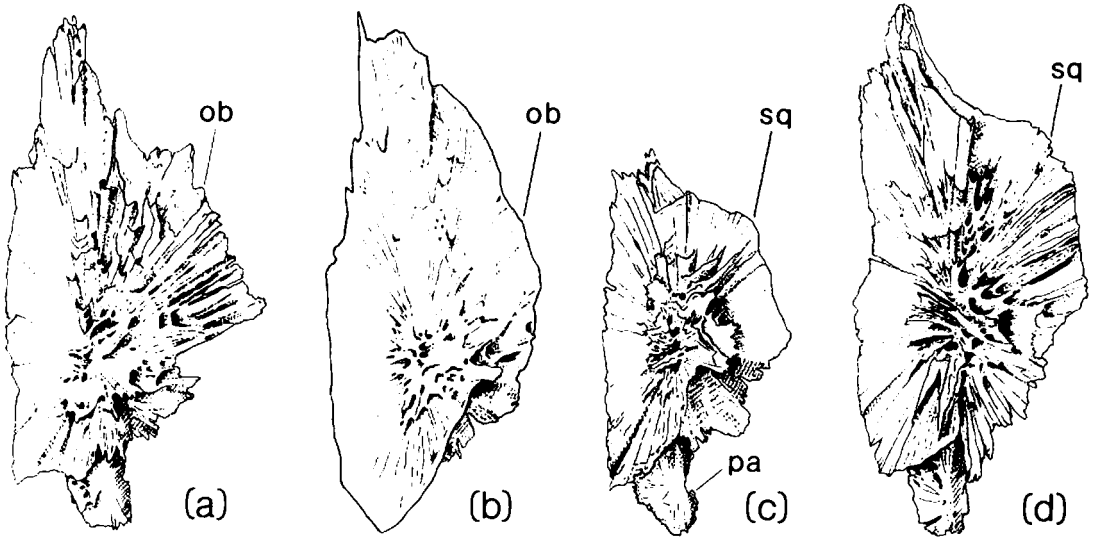


FIGURE 4.—Frontals, right, dorsal view, anterior up (parietals attached except in b). (a) *Salmo trutta*, UMMZ 175169S; (b) *Oncorhynchus clarki*, UMMZ 181728S; (c) *Oncorhynchus mykiss*, UMMZ 198677S; (d) *Oncorhynchus kisutch*, UMMZ 187925S. Abbreviations: ob, anterolateral margin oblique; pa, parietal; sq, anterolateral margin squared.

chus mykiss can be variously aligned with each other (Figure 12).

Several diagnosable nodes were discovered (Figure 10). Of particular interest are the major monophyletic groups substantiated by previous work: the family Salmonidae (node 1 in Figure 10 and Table 2), the subfamily Coregoninae (node 2), and the unnamed group (node 7) composed of the subfamily Thymallinae plus the subfamily Salmoninae. Within the Salmoninae, the Eocene *Eosalmo* is the sister group of all living salmonines (node 9) as described by Wilson (1977). The living Asian species, *Brachymystax lenok*, is the sister of all other living salmonines (node 11) as documented previously by Norden (1961).

Above the level of *Brachymystax*, some new relationships are diagnosed by our characters (Figure 10). Three species of Mediterranean archaic trouts—*Acantholingua ohridana*, *Salmothymus obtusirostris*, and *Platysalmo platycephalus*—are next, sister groups of other salmonines (nodes 13–18 in Figure 10 and Table 2). *Platysalmo platycephalus* Behnke is shown to be the sister group of *Salmothymus obtusirostris*. *Acantholingua ohridana* has several plesiomorphic states that prevent it from joining the *Salmothymus* clade and, in one of two equally parsimonious solutions, that exclude it from the *Salmothymus* plus Eusalmonina clade: characters 2 (notched dermethmoid), 15 (flat posterior frontal contact), 29 (flexed para-

sphenoid), 37 (transverse row of vomerine teeth present), and 81 (long ventral limb of preopercle) (Table 2). Some of these may be paedogenic characters. In the equally parsimonious solution, *Acantholingua ohridana* joins *Salmothymus*. The consensus solution has a trichotomy at node 13.

The clade above the archaic trouts includes *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus*. These four genera form a morphologically and cladistically advanced clade here named the Eusalmonina (node 18)—the modern salmonines. Within the Eusalmonina, *Hucho* plus *Salvelinus* form a clade, the Salvelini (node 19), which is the sister group of the clade *Salmo* plus *Oncorhynchus*, the Salmonini (node 22). Within the Salmonini, the Atlantic trouts and salmonines are a monophyletic group, *Salmo* (node 23), and the Pacific trouts and salmonines are a monophyletic group, *Oncorhynchus* (node 24). *Oncorhynchus* unambiguously includes the Pacific trouts formerly classified as part of *Salmo*. Among the Pacific trouts, the rainbow trout and its close relatives (Behnke 1992: golden trout, redband trout, and the fossil trout “*Rhabdofario*”) are closest to Pacific salmon; the Gila and Apache trouts (see Behnke 1992), cutthroat trout, and Mexican golden trout are outside the Pacific salmon–rainbow trout group. Table 2 lists the monophyletic groups supported by our data and details all apomorphies (shown below nodes in Figure 10) as optimized by PAUP, as well as autapomorphies

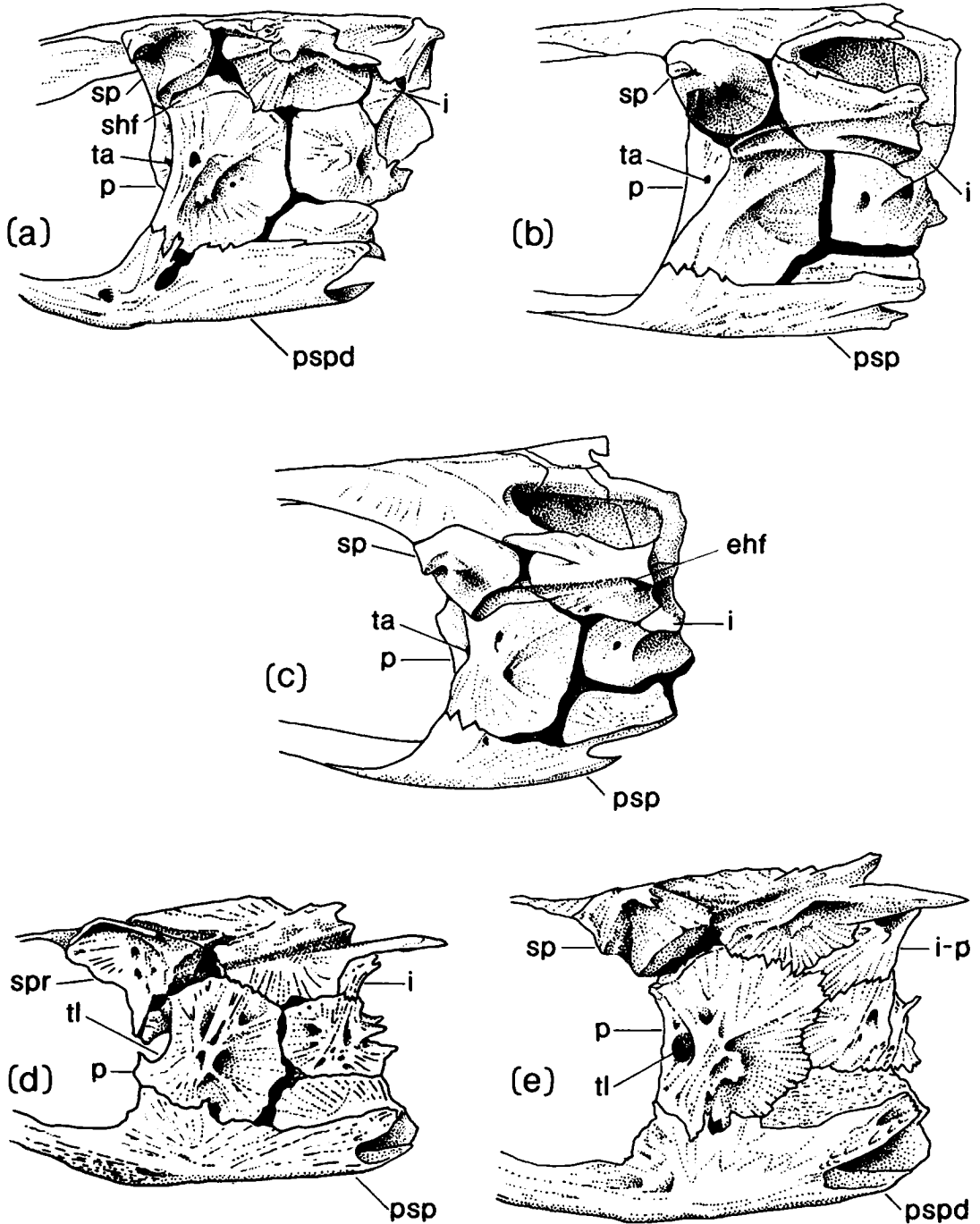


FIGURE 5.—Otic region of neurocranium, left lateral view. (a) *Thymallus arcticus*, UMMZ 172465S; (b) *Brachymystax lenok*, UMMZ 172491S; (c) *Acantholingua ohridana*, UMMZ 177293S; (d) *Salvelinus namaycush*, UMMZ 172464S; (e) *Oncorhynchus mykiss*, UMMZ 198677S. Abbreviations: ehf, elongate hyomandibular fossa; i, intercalar not contacting prootic; i-p, intercalar contacting prootic; p, prootic; psp, parasphenoid not deep posteriorly; pspd, parasphenoid deep posteriorly; shf, short hyomandibular fossa; sp, sphenotic without expanded anterior ramus; spr, sphenotic ramus expanded; ta, trigemino-facial foramen anterior; tl, trigemino-facial foramen lateral and expanded.

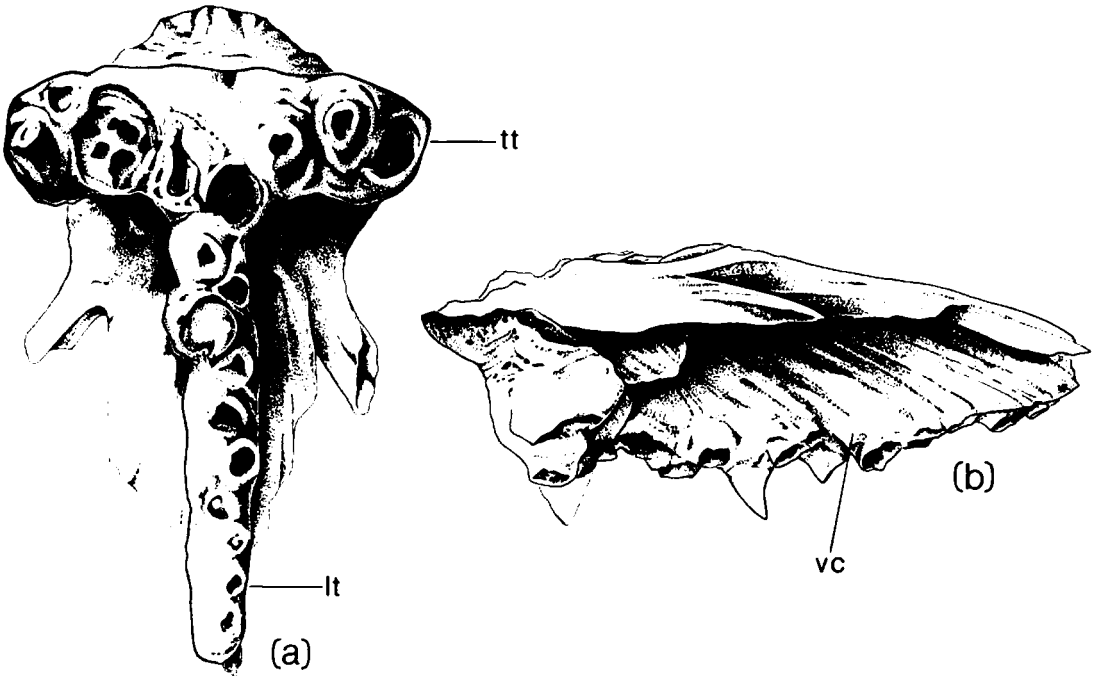


FIGURE 6.—Vomer, *Salvelinus larsoni*, UMMP (University of Michigan Museum of Paleontology) V69018. (a) ventral view, anterior up; (b) left lateral view. Abbreviations: lt, longitudinal tooth row; tt, transverse tooth row; vc, vomerine crest supporting longitudinal tooth row.

(species-specific advanced traits, which were not included in the search for the most parsimonious tree) that diagnose terminal branches.

Discussion

The goals of this study were to understand the phylogeny of the Salmoninae, especially the Pacific trouts and salmons, the Salmonini. Some of the results are new and potentially controversial and require further discussion.

Archaic Trouts

The classification of the archaic trouts and the resulting polarity of characters of morphologically advanced salmonines is strengthened by the addition of the fossil trout, *Eosalmo*, to the analysis. *Eosalmo* possesses some, but not all, of the synapomorphies that have traditionally been used to diagnose Salmoninae (noted by Wilson 1974). It possesses a large, fan-shaped process on the stegural, a complete arch and spine on preural centrum 2, and a hyomandibula situated high on the neurocranium (Figure 10, node 9), as in extant Salmoninae. However, the frontals do not extend posteriorly to separate the parietals, and the extrascapulars are broad (Figure 10, node 10), as in

Thymallus. *Eosalmo* is also the earliest known salmonine (Middle Eocene). Consilience between the stratigraphic record and the phylogenetic tree is evidence that the phylogeny may be consistent with the history of the group.

The parsimony analysis presented above (Figure 10) strongly supports Norden's and Berg's position that the archaic trouts *Brachymystax*, *Acantholingua*, and *Salmothymus* form a series of cladistic intermediates between *Thymallus* and more derived salmonines (*Hucho*, *Salvelinus*, *Salmo*, *Oncorhynchus*). Because *Platysalmo platycephalus* Behnke 1968 is diagnosable as the sister species to *Salmothymus obtusirostris*, it is classified here in the genus *Salmothymus* Berg 1908 as *Salmothymus platycephalus* (Behnke). Preliminary observations on published descriptions of *Salmo ishchan* of Armenia (Dorofeyeva 1978: figures 1, 2, 3) indicate that it, too, and perhaps *Salmo carpio* of Italy, belong to this clade. It is also possible that *Acantholingua ohridana* should be classified in this clade, as suggested by Svetovidov (1975) and one of two equally parsimonious solutions in the present analysis; the character states that hold it out of *Salmothymus* may be reductive losses of synapomorphic states.

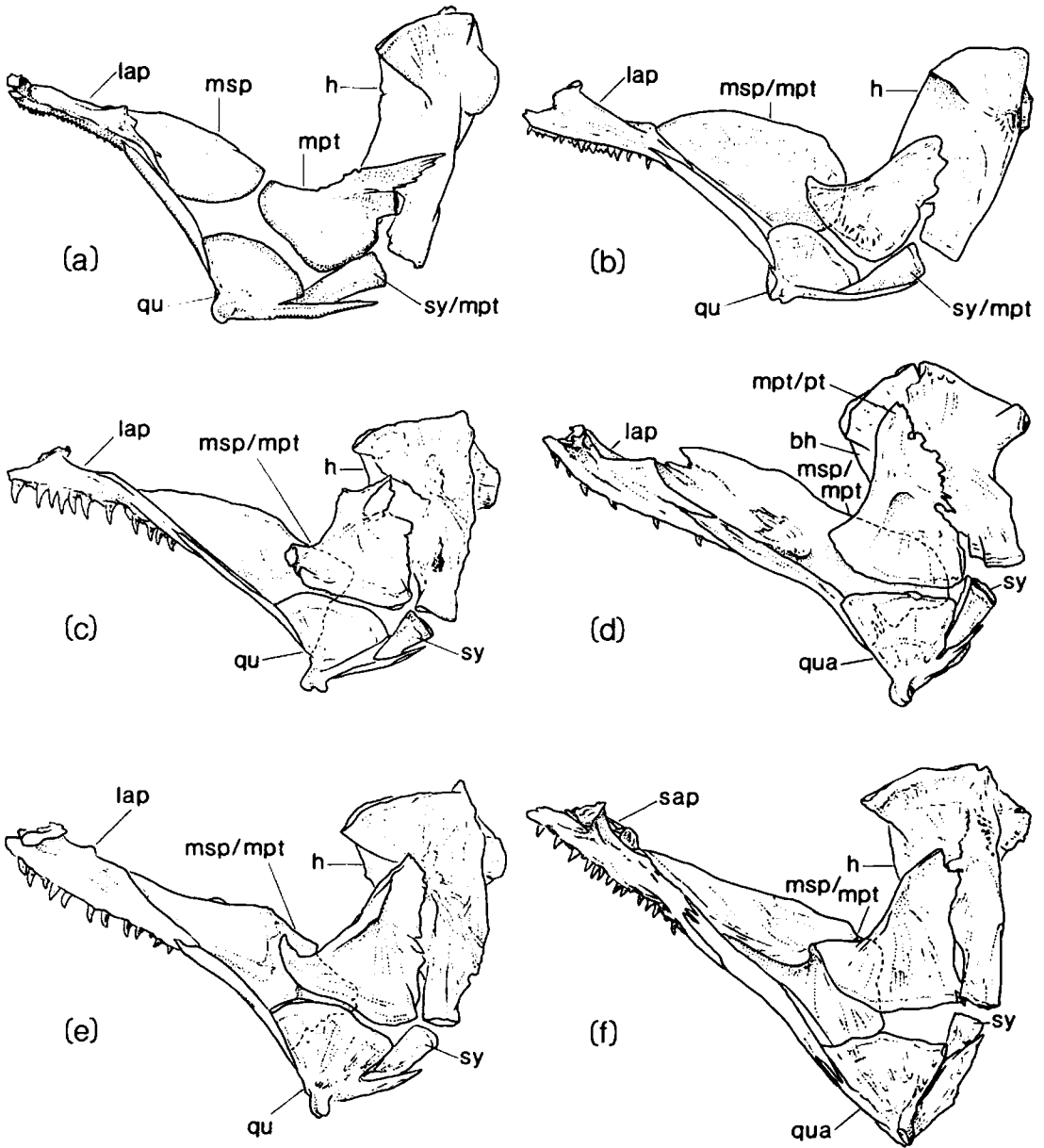


FIGURE 7.—Suspensorium and palatoquadrate, left side, lateral view. (a) *Thymallus arcticus*, UMMZ 186233S; (b) *Brachymystax lenok*, UMMZ 172491S; (c) *Hucho perryi*, UMMZ 187613S; (d) *Salvelinus namaycush*, UMMZ 177542S; (e) *Salmo trutta*, UMMZ 183694S; (f) *Oncorhynchus mykiss*, UMMZ 198677S. Abbreviations: bh, anteriorly broadened hyomandibula; h, narrow hyomandibula; lap, long autopalatine crest; msp mpt, no overlap of mesopterygoid and metapterygoid; msp/mpt, mesopterygoid-metapterygoid overlap; mpt/pt, metapterygoid-pterygoid overlap; qu, obtuse quadrate angle; qua, acute quadrate angle; sap, short autopalatine crest; sy, symplectic; sy/mpt, broad contact of symplectic and metapterygoid.

Salvelinus and *Salvethymus*

The hypothetical arrangement of species of *Salvelinus* in our study is not supported by other estimates of relationship in this genus (Cavender

1978, 1980, 1984; Balon 1980, 1984; Kendall and Behnke 1984; Cavender and Kimura 1989; Phillips et al. 1989; Grewe et al. 1990). Resolution of the conflicting estimates awaits a study that uses the total evidence.

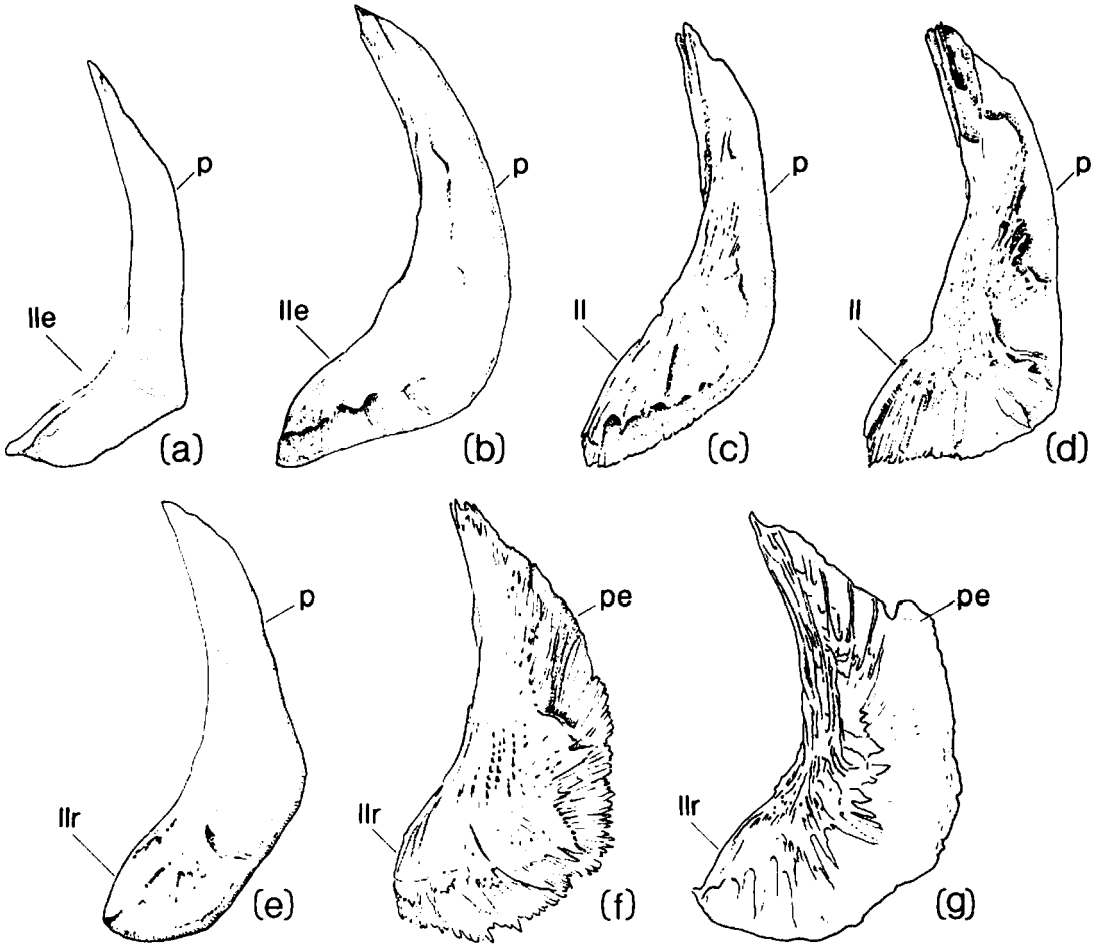


FIGURE 8.—Preopercles, left lateral view. (a) *Brachymystax lenok*, UMMZ 172491; (b) *Hucho perryi*, UMMZ 187612S; (c) *Salvelinus confluentis*, UMMZ 189196S; (d) *Salmo salar*, UMMZ 209263S; (e) *Oncorhynchus clarki*, UMMZ 181728S; (f) *Oncorhynchus tshawytscha*, UMMZ 209844S; (g) *Oncorhynchus nerka*, UMMZ 182453S. Abbreviations: ll, lower limb of preopercle intermediate; lle, lower limb elongate; llr, lower limb reduced; p, preopercle without posterior extension; pe, posterior extension of preopercle.

Salvethymus was described by Chereshev and Skopets (1990) from Lake El'gygytyn in Siberia. The preponderance of reductive characters cited in the diagnosis of *Salvethymus svetovidovi* suggests that either the genus derived from *Salvelinus* by reductive evolution or it is plesiomorphic. Chereshev and Skopets (1990) favored the latter explanation. Their description of this distinctive new species documents slow growth, small size, and several reductive characters—reduction of predorsals, supraorbitals, orbitosphenoid, basi-sphenoid, pelvic axillary processes, vomerine teeth, and breeding colors. These stand in contrast to its specialized characters such as straight maxilla, large teeth, and increased gill raker number. Possibly

S. svetovidovi is an advanced species of *Salvelinus* related to *malma* and *alpinus*, as indicated by the teeth, maxilla, vomer, metapterygoid, and the hyomandibular. The alternative interpretation—that it is an earlier branch, older than any of the species of *Salvelinus*—is indicated by the plesiomorphic (unreduced) basibranchial and glossohyal teeth.

Vomerine Tooth Pattern

The relationships of the archaic trouts described by the parsimony analysis (Figure 10) disagree with those put forth by classification schemes relying on vomerine tooth pattern (e.g., Kendall and Behnke 1984). Vladykov (1963) cautioned against

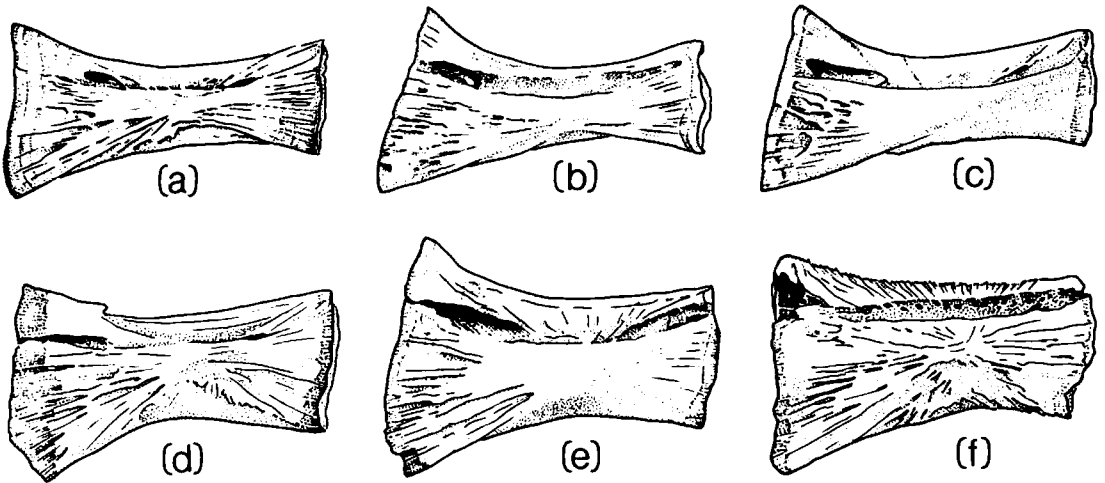


FIGURE 9.—Ceratohyals, right lateral view. (a) *Salvelinus namaycush*, UMMZ 203837S; (b) *Salmo trutta*, UMMZ 172470S; (c) *Oncorhynchus clarki*, UMMZ 203892; (d) *Oncorhynchus gilae*, 182405S; (e) *Oncorhynchus mykiss*, 203835S; (f) *Oncorhynchus kisutch*, UMMZ 205431S. Examples a, b, and c are elongate; d, e, and f are short relative to depth.

overly weighting this character. Five basic patterns of vomerine tooth arrangement can be identified in extant salmonids. *Thymallus* possesses a short vomer with a small, anterior patch of teeth. In the extant coregonine genera *Prosopium* and (most) *Coregonus*, teeth are also small and restricted to the anterior end of the vomer. By contrast, *Salmo*, *Oncorhynchus*, *Salmothymus* (including *Platysalmo*) all possess a long, often zig-zag longitudinal row of substantial teeth on a

long vomeral shaft. *Hucho* and *Brachymystax* are unusual in having a broad transverse row of teeth on a laterally expanded anterior end (head) of a short vomer. Finally, *Salvelinus* species all possess teeth in a patch on the head of the vomer, and in most *Salvelinus* species, this patch is followed by a zig-zag column of teeth supported not by the shaft of the vomer but by a crest ventral to the shaft and anchored to the head of the vomer.

(Text resumes on page 22.)

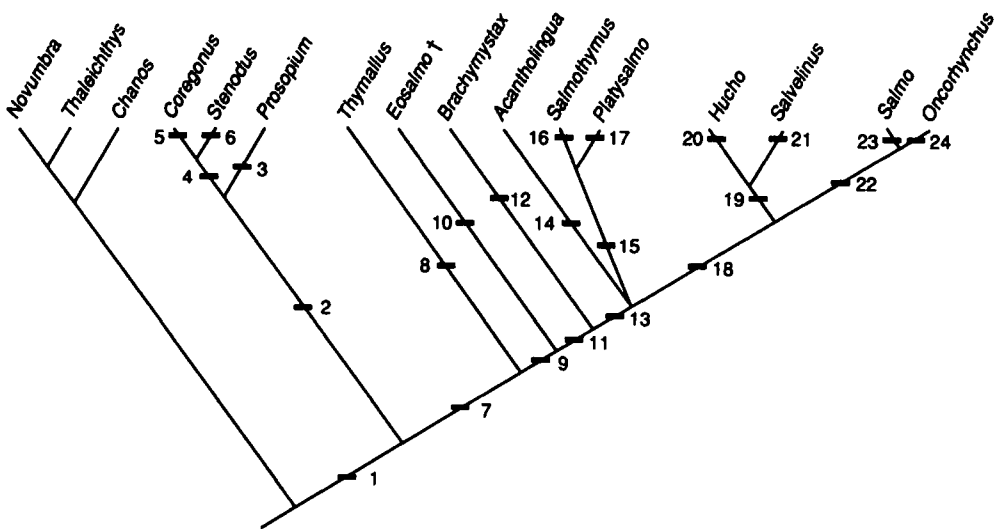


FIGURE 10.—Cladogram of relationships of salmonid genera. Character suites supporting nodes 1–24 are described in Table 2. The taxon known only as fossils is indicated by a dagger.

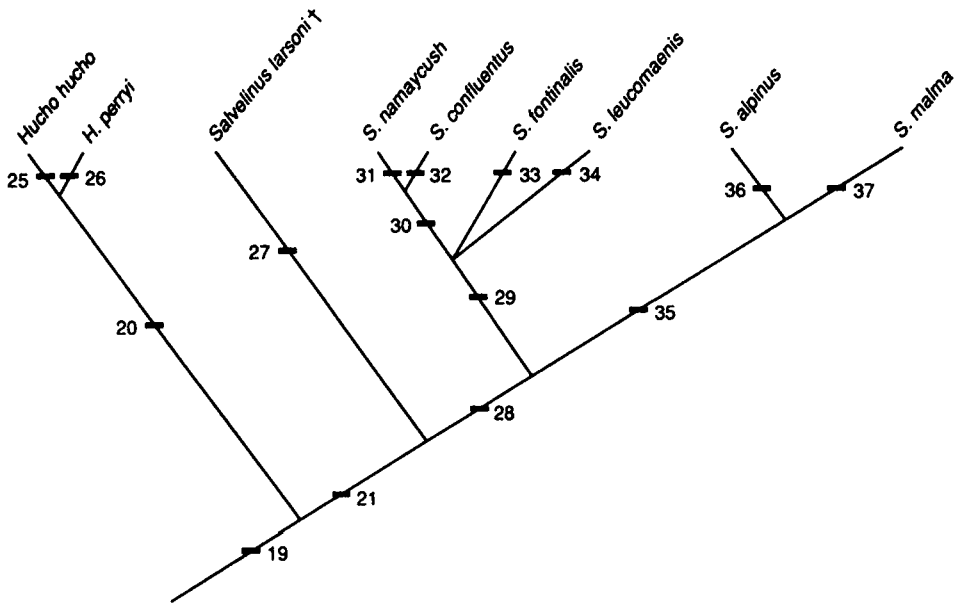


FIGURE 11.—Consensus cladogram of relationships of *Hucho* and *Salvelinus*. Character suites supporting nodes 19–37 are described in Table 2. The taxon known only as fossils is indicated by a dagger.

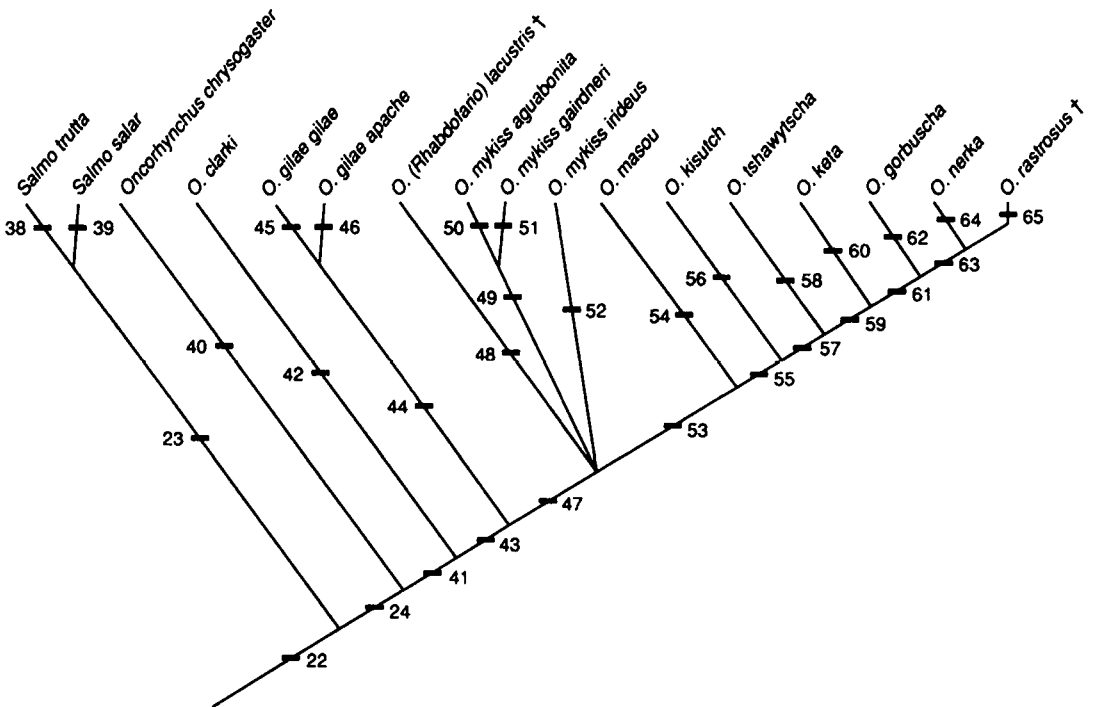


FIGURE 12.—Consensus cladogram of relationships of *Salmo* and *Oncorhynchus*. Character suites supporting nodes 22–65 are described in Table 2. The taxa known only as fossils are indicated by a dagger.

TABLE 2.—Character support for monophyletic groups discovered in this analysis. Character states are those listed in Table 1 and illustrated in Figures 10–12. To help assess the evidence for each node, suffixes are added to character descriptions. Unique and unreversed character states are followed by an asterisk (*). Unambiguous character state transitions (as opposed to states that could be parsimoniously optimized otherwise) are followed by "unam." Several characters undergo reversals in various clades. Reversed characters are indicated by symbols showing the transition; for example, "1>0." Reversals are frequently unambiguous as well. Autapomorphies that were not included in the computer analysis are indicated by "aut."

Char-acter	Description and state
Node 1: Salmonidae	
20	Epiotics with posterior sulcus (1) (*)
25	Orbitosphenoid present (1)
30	Parasphenoid extends to posterior of basioccipital (1) (*)
31	Posterior parasphenoid with high walls flanking myodome (1)
33	Occipital condyle tripartite (0)
73	Supraorbital short (1)
94	Caudal arches with peg-and-socket arrangement (Rosen 1974) (1) (*)
97	Neural spine detached from arch on preural centrum 2 (1) (unam.)
103	Tetraploid karyotype (1) (*)
110	Parr marks present (1)
Node 2: Coregoninae	
4	Dermethmoid contacts but does not overlap frontals; frontals separate nasals (1) (*)
55	Premaxillary teeth vestigial in adults (1) (*)
90	Broad, typically perforate ceratohyal (1)
95	Urostyle ossifications ("tendon bones") present (1>0) (*)
Node 3: Prosopium	
2	Dermethmoid without posterior notch (1>2) (unam.)
3	Long dermethmoid (unam.)
66	Gap between coronoid of dentary and angular-articular (aut.)
Node 4: Coregonus plus Stenodus	
33	Occipital condyle secondarily fused (2) (unam.)
73	Long supraorbital (1>0)
88	Basibranchial plate absent (1)
104	Two nostril flaps (1) (*)
105	Pyloric caecae more than 70 (2) (unam.)
110	Without parr marks (1>0)
Node 5: Coregonus	
No unique characters	
Node 6: Stenodus	
18	Sphenotic with stout anterior ramus (1) (unam.)
29	Parasphenoid with straight sagittal profile (1)
31	Posterior parasphenoid flat in cross section (unam.) (1>0)

TABLE 2.—Continued.

Char-acter	Description and state
34	Toothed vomer (1>0)
74	Supraorbital contacts dermosphenotic (aut.)
92	Branchiostegals between 10 and 13 (1)
Node 7: Thymallus plus Salmoninae	
9	Ethmoid (hypethmoid) absent (1) (unam.)
34	Toothed vomer (1>0)
46	Well-toothed palatines (1>0) (*)
49	Toothed maxillae (1>0) (*)
57	Premaxilla with ascending process (1) (*)
63	Long, lanceolate supramaxilla (1) (unam.)
65	Coronoid process of dentary lower, rising at angle of 45° or less (1) (*)
71	Posterior process of angulo-articular at angle to horizontal (1) (*)
108	Nuptial tubercles absent (1) (unam.)
Node 8: Thymallinae, Thymallus	
25	Orbitosphenoid absent (1>0) (*)
88	Basibranchial plate absent (1)
99	17 or more dorsal fin rays (1) (aut.)
119	Sensory papillae surrounding nares (1) (aut.)
Node 9: Salmoninae	
12	Frontals form anterior floor of posttemporal fossae (1) (unam.)
13	Frontals expanded above sphenotics (1) (*)
19	Pterotic with long hyomandibula fossa (1) (*)
31	Posterior parasphenoid flat in cross section (1>0) (unam.)
37	Vomerine teeth in expanded anterior transverse row (1)
45	Mesopterygoid overlapping quadrate (1) (*)
80	Suprapreopercle present (1) (*)
85	Median basihyal denticles absent (1)
86	Strong teeth on perimeter of basihyal (1) (*)
96	Large fan-shaped plate on stegural (1) (*)
97	Complete arch and spine on preural centrum 2 (0) (unam.)
Node 10: Eosalmo	
No unique characters	
Node 11	
2	Dermethmoid without posterior notch (1>2)
14	Frontals extend between parietals (1) (*)
47	Palatine crest long (1)
53	Premaxillary process of maxilla angled dorsally (1)
76	Postorbitals do not cover hyomandibula (0>1)
84	Extrascapulars tubular (1) (*)
105	Pyloric caecae between 20 and 70 (1)
109	Egg size greater than 3.5 mm (1) (*)
Node 12: Brachymystax	
3	Dermethmoid long (1) (unam.)
102	Lateral line scales elliptical (1)
105	Pyloric caecae more than 70 (1>2) (unam.)
Node 13	
35	Vomerine shaft bears teeth and extends posterior to lateral ethmoids (1) (unam.)

TABLE 2.—Continued.

Char-acter	Description and state
61	Premaxilla with cartilage pocket (1) (unam.)
83	Subopercle shallow (1 > 0)
92	Branchiostegals more than 10 (1) (unam.)
98	Two epurals (1)
Node 14: <i>Acantholingua ohridanus</i>	
2	Dermethmoid with posterior notch (2 > 1)
36	Vomer teeth extending to posteriormost end of vomeral shaft (aut.)
75	Multiple supraorbitals (aut.)
85	Median basihyal denticles present (1 > 0)
Node 15: <i>Salmothymus plus Platysalmo</i>	
9	Ethmoid present (1 > 0) (unam.)
15	Posterior midline depression in frontals (1) (*)
29	Parasphenoid straight in sagittal profile (0 > 1)
37	Transverse row of vomerine dentition reduced (1 > 0)
Node 16: <i>Salmothymus</i>	
31	Posterior myodome with high walls (0 > 1)
101	Gill rakers more than 25 (0 > 1) (unam.)
102	Lateral line scales elliptical (1)
Node 17: <i>Platysalmo</i>	
105	Pyloric caecae fewer than 20 (1 > 0) (unam.)
Node 18: <i>Eusalmonina</i>	
24	Prootic foramina displaced posteromedially (1) (*)
26	Orbitosphenoid without anterior emargination (1) (unam.)
42	Metapterygoid not in broad contact with symplectic (1) (*)
50	Maxilla extends posterior to orbit (1) (*)
51	Maxilla straight to arched, without convex ventral edge (1) (*)
65	Coronoid process of dentary shallow (1) (unam.)
109	Egg size greater than 4.5 mm (1 > 2) (*)
Node 19: <i>Salvelinus plus Hucho</i>	
18	Sphenotic with stout anterior ramus (1) (unam.)
35	Vomer short (1 > 0) (unam.)
63	Supramaxilla long, inflected (1 > 2) (*)
89	Basibranchial teeth present (1 > 0)
93	Vertebral count greater than 60 (1)
102	Lateral line scales elliptical (1)
Node 20: <i>Hucho</i>	
29	Parasphenoid straight in sagittal profile (1)
64	Dentary deep anterior to Meckelian groove (1) (unam.)
100	Gill raker count low, fewer than 16 (1) (*)
105	Pyloric caecae count high, more than 70 (1 > 2)
Node 21: <i>Salvelinus</i>	
27	Orbitosphenoid oval in cross section (1) (*)
38	Vomer teeth on a raised crest (1) (*)

TABLE 2.—Continued.

Char-acter	Description and state
Node 22: <i>Salmo plus Onchornynchus</i>	
37	Anterior transverse tooth row on vomer reduced (1 > 0)
39	Vomer with anterior extension in breeding males (1) (*)
51	Maxillae arched (1 > 2) (unam.)
52	Maxillae ovate to round in cross section (1) (*)
58	Ascending process of premaxilla posterolaterally deflected (1) (*)
67	Kype on dentary (1)
Node 23: <i>Salmo</i>	
6	Dermethmoid broad, blunt, diamond-shaped (1) (*)
62	Mesial process present on premaxilla (1) (*)
68	Extreme development of kype on dentary (Morton 1965) (1) (*)
83	Subopercle shallow (1 > 0)
Node 24: <i>Oncorhynchus</i>	
2	Dermethmoid with posterior notch (2 > 1) (unam.)
23	Intercalar contacts prootic (1) (unam.)
47	Palatine crest short (1 > 0) (unam.)
48	Margins of quadrate form acute angle (unam.)
53	Premaxillary process of maxilla not dorsal (1 > 0) (unam.)
64	Dentary deep anterior to Meckelian groove (1)
72	Retroarticular suture at high angle (1)
76	Postorbitals cover hyomandibula (1 > 0) (unam.)
78	Second infraorbital tubular (1) (*)
81	Lower limb of preopercle greatly reduced (1 > 2) (unam.)
98	Three epurals (1 > 0)
112	Red or orange cutthroat mark (1)
114	Dark border of adipose fin (1) (unam.)
Node 25: <i>Hucho hucho</i>	
88	Basibranchial plate absent (10) (unam.)
89	Basibranchial teeth absent (1)
Node 26: <i>Hucho perryi</i>	
9	Ethmoid present (1 > 0) (unam.)
85	Median basihyal denticles present (1 > 0)
93	Vertebrae 60 or fewer (1 > 0)
98	Three epurals (1 > 0)
Node 27: <i>Salvelinus larsoni</i>	
85	Median basihyal denticles present (1 > 0)
Node 28: Extant <i>Salvelinus</i>	
37	Anterior vomeral transverse tooth row reduced (1 > 0)
67	Kype present on dentary (1)
77	Infraorbitals restricted to 5 (0 > 1) (*)
111	White spots on dark background (1) (*)

TABLE 2.—Continued.

Char-acter	Description and state
Node 29	
41	Hyomandibula broad, "dish-shaped" sensu Cavender 1980 (1) (*)
48	Margins of quadrate form acute angle (1) (unam.)
115	Vermiculations present (1)
Node 30	
43	Metapterygoid extends dorsally almost to pterotic (1) (*)
93	Vertebral number 61 or greater (1)
Node 31: <i>Salvelinus namaycush</i>	
105	Pyloric caecae more than 70 (1 > 2)
108	Nuptial tubercles present (1 > 0) (unam.)
Node 32: <i>Salvelinus confluentus</i>	
29	Parasphenoid straight in sagittal profile (1)
51	Maxilla arched (1 > 2) (unam.)
72	Retroarticular suture at high angle (1)
115	Vermiculations absent (1 > 0)
Node 33: <i>Salvelinus fontinalis</i>	
81	Extreme reduction of lower limb of preopercle (1 > 2) (unam.)
Node 34: <i>Salvelinus leucomaenis</i>	
23	Intercalar contacts prootic (1) (unam.)
Node 35	
5	Dermethmoid with prominent midlength constriction (1) (*)
12	Frontals do not form part of floor of post-temporal fossae (1 > 0) (unam.)
72	Retroarticular suture at high angle (1)
93	Vertebral count high, 61 or greater (1)
Node 36: <i>Salvelinus alpinus</i>	
No unique characters	
Node 37: <i>Salvelinus malma</i>	
37	Anterior transverse vomeral dentition present (0 > 1)
101	Gill raker count high, greater than 25 (1) (unam.)
Node 38: <i>Salmo trutta</i>	
92	Branchiostegals fewer than 10 (1 > 0)
Node 39: <i>Salmo salar</i>	
40	Vomeral teeth deciduous (0 > 1) (unam.)
116	X-shaped spots (aut.)
Node 40: <i>Oncorhynchus chrysogaster</i>	
29	Parasphenoid straight in sagittal section (1)
72	Retroarticular eclipsed (1 > 2) (unam.)
79	Postorbitals divided into two series (aut.)
92	Branchiostegals fewer than 10 (1 > 0)
Node 41	
31	Posterior myodome with high walls (1) (unam.)
32	Basisphenoid process of parasphenoid well ossified (1) (*)
93	Vertebral count greater than 60 (1)

TABLE 2.—Continued.

Char-acter	Description and state
Node 42: <i>Oncorhynchus clarki</i>	
89	Basibranchial teeth present (1 > 0)
Node 43	
91	Ceratohyal square, stubby (1) (unam.)
Node 44: <i>Oncorhynchus gilae</i>	
76	Postorbitals not covering hyomandibula (1)
113	Yellow cutthroat mark (1) (*)
Node 45: <i>Oncorhynchus gilae gilae</i>	
No unique characters	
Node 46: <i>Oncorhynchus gilae apache</i>	
No unique characters	
Node 47	
7	Dermethmoid "A-shaped" (1) (*)
10	Lateral ethmoids square (1) (*)
16	Frontals with expanded shelf above orbit (1) (*)
Node 48: <i>Oncorhynchus lacustris</i>	
21	Epiotics with large conical processes (1) (aut.)
Node 49: <i>Oncorhynchus mykiss aguabonita</i> plus "redband"	
26	Orbitosphenoid with anterior emargination (1 > 0) (unam.)
Node 50: <i>Oncorhynchus mykiss aguabonita</i>	
91	Slender ceratohyal (1 > 0)
117	Dorsal, anal, and pelvic fins with white tips (1) (aut.)
Node 51: <i>Oncorhynchus mykiss gairdneri</i> ("redband" trout, Oregon)	
No unique characters	
Node 52: <i>Oncorhynchus mykiss irideus</i> (North America) and <i>O. m. mykiss</i> (Asia)	
No unique characters	
Node 53: Subgenus <i>Oncorhynchus</i> (Pacific salmon)	
40	Vomeral teeth deciduous (1) (unam.)
54	Premaxillary process of maxilla palmate (1) (*)
56	Premaxilla with enlarged breeding tusks (1) (*)
61	Premaxillary cartilage pocket absent (1 > 0) (unam.)
63	Supramaxilla broadly ovate (1 > 0) (unam.)
64	Dentary not deep anterior to Meckelian groove (1 > 0)
69	Dentary teeth deciduous (1) (*)
72	Retroarticular suture high; retroarticular eclipsed (1 > 2) (unam.)
82	Dorsal limb of preopercle expanded posteriorly (1) (*)
92	Branchiostegals more than 13 (1 > 2) (unam.)
Node 54: <i>Oncorhynchus masou</i>	
98	Two epurals (1)
118	Anterior margin of caudal fin red (1) (aut.)

TABLE 2.—Continued.

Character	Description and state
Node 55	
1	Dorsal fontanelles close during ontogeny (1) (*)
93	Vertebral count greater than 65 (1 > 2) (*)
105	Pyloric caecae more than 70 (1 > 2)
114	Dark border of adipose fin absent (1 > 0) (unam.)
Node 56: <i>Oncorhynchus kisutch</i>	
22	Supraoccipital crest extremely long (1) (aut.)
Node 57	
7	Dermethmoid with widely divergent posterior wings (1 > 2) (*)
Node 58: <i>Oncorhynchus tshawytscha</i>	
28	Orbitosphenoid in form of spongy ball (1) (aut.)
Node 59: "Type A" Pacific salmon (Hikita 1962)	
8	Dermethmoid with anterior constricted extension (Vladykov 1962) (1)
51	Maxilla straight (2 > 1) (unam.)
59	Thin crest of premaxilla (sensu Vladykov 1962) (1) (*)
87	Pointed basihyal (0 > 1) (*)
Node 60: <i>Oncorhynchus keta</i>	
98	Two epurals (1)
Node 61	
17	Frontals contact epiotics in large individuals (1) (*)
101	Gill raker count high, greater than 25 (1) (unam.)
106	Dorsal hump in breeding males (condition in <i>O. rastrosus</i> unknown)
Node 62: <i>Oncorhynchus gorbuscha</i>	
72	Retroarticular suture high but retroarticular not eclipsed (2 > 1)
107	Extreme development of dorsal hump (1) (aut.)
Node 63: <i>Oncorhynchus nerka</i> plus <i>O. rastrosus</i>	
81	Ventral limb of preopercle only moderately reduced (2 > 1) (unam.)
Node 64: <i>Oncorhynchus nerka</i>	
70	Dark enameloid on interior of teeth (Vladykov 1962) (1) (aut.)
Node 65: <i>Oncorhynchus rastrosus</i>	
8	Dermethmoid without anterior constricted extension (1 > 0)
33	Occipital condyle simple (0 > 1) (unam.)
60	Dark enamel on premaxillary tusk (1) (aut.)
64	Dentary deep anterior to Meckelian groove (1)
65	Coronid process of dentary only moderately low, approximately 45° (2 > 1) (unam.)

However, morphologically intermediate species that exhibit combinations of the above states exist (or formerly existed). *Acantholingua* possesses a strong transverse row of anterior vomerine teeth, as well as the longitudinal row of teeth on a long shaft (i.e., a "T-shaped" pattern). The extinct salmonine *Salvelinus larsoni* (Kimmel 1975) is remarkable for the possession of a strong transverse row of teeth on the head of the vomer as in *Hucho*, but with a longitudinal column of teeth on a raised crest behind the head of the vomer as in *Salvelinus* (Figure 6).

Thus, the parsimony analysis (Figures 10, 11, 12; Table 2) yields the following hypothetical transformation series of vomerine tooth patterns within the Salmoninae. At node 7, the ancestral state is a transverse patch or a pair of small patches of teeth on the anterior end of short vomer as in *Thymallus*. The patch became a transverse tooth row on the head of a short vomer at node 9, as in *Brachymystax*. Extension of the vomerine shaft and addition of a longitudinal tooth row to the transverse tooth row formed a "T-shaped" pattern at node 13; the longitudinal row was further extended in *Acantholingua*, node 14. The condition at node 13 transformed three separate times at nodes 15, 21, and 22: reduction of the "T" to an "I" pattern by loss of the transverse row, retention of teeth on the vomerine shaft (independently acquired in two clades, *Salmothymus obtusirostris* plus *platycephalus* [node 15] and *Salmo* plus *Oncorhynchus* [node 22]), and elevation of the "T" pattern onto transverse and longitudinal crests at node 21, as seen in *Salvelinus larsoni* (Figure 6). This left the plesiomorphic presence of a transverse row of teeth on the head of the vomer in *Hucho* (node 20), which has no longitudinal row. Reduction of the "T" pattern to an elevated "I" pattern on the vomerine crest, by (variable) loss of the transverse row on the head of the vomer, occurred in extant species of *Salvelinus* (node 28). This transformation series of vomerine states emerges in the most parsimonious trees resulting from the cladistic analysis.

Characters Uniting Salmo and Oncorhynchus

Several characters are common to Pacific and Atlantic salmon and trouts (Figures 10, 12; node 22, Table 2). The diagnostic characters are the more elongate vomer with a reduced transverse tooth row (character 37), which becomes extended anteriorly in breeding males (character 39); a long maxilla that is arched (character 51, individuals of larger size generally exhibiting greater arch) and

ovate in cross section (character 52; the definitive round maxillary shaft of *Rhabdofario* eventually appears in about 1-m-long specimens of this clade as an allometric terminal addition, but the arch is later lost in *Oncorhynchus nerka*, *keta*, and *gorbuscha* at node 53); a long premaxilla with posteriorly deflected ascending processes (character 58; the ascending processes are associated with the rostral cartilage and typically become arched in breeding males); and a dentary with a well-developed kype in breeding males (character 67, documented by Morton 1965). Although character 39, the anterior extension of the vomer, was used by Cavender and Miller (1982) to diagnose the clade of Pacific trouts and salmon only, examination of more specimens leads to agreement with Tchernavin (1938b) that all trouts and salmon possess this feature to some extent, so it appears at node 22. Strong kypes are also found in *Salvelinus malma*; weakly developed kypes are found in *Salvelinus fontinalis* and *Salvelinus confluentus* (Morton 1965; R. J. Behnke, Colorado State University, personal communication).

Synapomorphies of Pacific trouts and salmon.—Thirteen morphological features unite Pacific trouts and Pacific salmon (Figures 10 and 12, node 24). The most diagnostic characters are the following: prominent posterior notch in the dermethmoid (character 2); intercalary contacting prootic (23); shorter palatine crest (47); anterior and posterior borders of the quadrate forming an acute angle (48); premaxillary process of the maxilla not angled strongly dorsad (53); longer postorbitals (76); tubular second infraorbital (78); and three epurals (*O. masou* and *O. keta* excepted; 98). The prominent posterior notch in the supraethmoid was first noted by Regan (1914) when he suggested placing Pacific salmon and Pacific trouts in one genus. The long postorbitals and number of epurals were noted by Vladykov (1963). These features, as well as the contact between the intercalary and prootic, were cited by Sanford (1990) in an independent suggestion to place the Pacific salmon and trouts in *Oncorhynchus*. Characters 2, 47, 53, 76, and 78 were figured by Smith and Stearley (1989) in support of the relationship of Pacific trouts and salmon. In Norden's (1961) detailed discussion of the chondrocranium, he noted that the zygous rostrum (Figure 2d), said to be diagnostic of *Oncorhynchus* by Tchernavin (1937) and Kendall and Behnke (1984), was secondary, typical of Pacific salmon coming into breeding condition. We find it to be present in large, migratory *O. mykiss* (steelhead), as well.

Several morphological features are common to only some of the more derived Pacific trouts and to Pacific salmon. All Pacific trouts and salmon, except the Mexican golden trout (*Oncorhynchus chrysogaster* Needham and Gard 1964), possess a deep posterior parasphenoid with an accompanying ossified basisphenoid process of the parasphenoid. The keel on the parasphenoid at its flexure, noted by Cavender and Miller (1982) in Pacific salmon, is present on large specimens of Pacific trout as well. All Pacific trouts and salmon, except *O. chrysogaster* and *O. clarki*, possess rectangular ceratohyals. Three features, an "A"-shaped dermethmoid, frontals with a wide anterior shelf expanded over the orbits, and wide lateral ethmoids, are possessed by the rainbow, redband, and California golden trouts and Pacific salmon.

Several fossil forms—*Oncorhynchus* "*Rhabdofario*" *lacustris* from the Miocene and Pliocene of Idaho and Oregon (Kimmel 1975; Smith 1975; Smith et al. 1982), and *Oncorhynchus australis* (Cavender and Miller 1982) of the Pleistocene of Mexico—are related to the *O. mykiss* lineage, based on the shape of their frontals, jaw bones, ceratohyals, and dermethmoids. The lineage of *Oncorhynchus clarki* is represented from Miocene and Pliocene specimens from the Great Basin as "*Salmo cyniclope*" from the Miocene of Nevada (LaRivers 1964), "*Rhabdofario*" sp. from Pliocene sediments at Honey Lake, California (Taylor and Smith 1981), and "*Salmo* sp." from the Pliocene Mopung Hills locality in Nevada (Taylor and Smith 1981). These records imply that species of Pacific trout originated in the Miocene, probably before 6 million years ago (see also Behnke 1992). More than 6 million years of history for some modern lineages of Pacific salmon is further supported by *Oncorhynchus* "*Smilodonichthys*" *rastrousus* from the Miocene of California and Oregon (Cavender and Miller 1972; Barnes et al. 1985); an interior form of "*Smilodonichthys*," *Oncorhynchus* sp., from the Miocene of Idaho (Smith et al. 1982); *Oncorhynchus salax*, a sister species of *O. nerka* from the Miocene of Idaho and Oregon (Smith 1975; Smith et al. 1982); and *Oncorhynchus keta* from the Miocene of Oregon and Idaho (Smith 1992). In contrast to the frequently cited conclusion (Clemens 1953; Neave 1958) that salmon species evolved in the Pleistocene or even in the past 1 million years, these fossils of *Oncorhynchus* document abundant evidence for a minimum age of 6 million years for the modern species of Pacific trout and salmon (Smith 1992).

Molecular and Biochemical Evidence

Berg and Ferris (1984) studied the amount of divergence of mitochondrial DNA (mtDNA) among four species: brook trout, brown trout, rainbow trout, and chinook salmon. Their discovery that rainbow trout and chinook salmon had diverged from each other less than either had diverged from brown trout or brook trout provided support for close genealogical relationship between rainbow trout and Pacific salmon, not between rainbow trout and brown trout (see also Grewe et al. 1990). The convincing cladistic evidence in Berg and Ferris' (1984) data set is the similarity of two mtDNA fragments created by the endonuclease *Xba*I and four fragments created by *HIND*III that are unique to rainbow trout and chinook salmon and not found in the brown trout or the outgroup brook trout. It is probable that at least some of the unique fragments were produced by homologous, derived restriction sites and that they offer good cladistic evidence.

The study of mtDNA of Pacific salmon by Thomas et al. (1986) provided valuable maps of restriction sites for rainbow trout and five species of Pacific salmon. Their data, which they analyzed as phenetic distances, indicate genetic similarity between rainbow trout and coho and chinook salmon and some genetic distance of these species from chum, pink, and sockeye salmon (Figure 13a; see also Grewe et al. 1990). Without inclusion of an outgroup, however, the distances provide no evidence of cladistic relationships and, in fact, give a misleading impression of relationships. We have reanalyzed this data set cladistically, after designating the rainbow trout as the outgroup and thus specifying its characters as primitive for the species included in this study. We base the choice of outgroup on the conclusions of Behnke (1968) and our cladistic analysis of morphological data, on the protein evidence of Tsuyuki and Roberts (1966) and Utter et al. (1973), and on the molecular evidence that rainbow trout have diverged less than Pacific salmon from brown trout and brook trout (Berg and Ferris 1984; Grewe et al. 1990). The restriction site data of Thomas et al. (1986) are coded as discrete characters in Table 3 and arranged to show the directions of derived character state transitions from the states shown by *Oncorhynchus mykiss*—the best indication of the primitive state for each character. The diagnoses of groups are apparent in the left-to-right character state transitions in Table 3. The resulting cladistic estimate is shown in Figure 13b. If *Oncorhynchus*

mykiss is the outgroup, the successive branches of the tree are coho, chinook, sockeye, chum, and pink salmon.

Two major unsolved problems remain in *Oncorhynchus* after this analysis of molecular data sets. The first is the placement of the cutthroat trout; the second is resolution of the relationships of pink, chum, and sockeye salmon. The cutthroat trout has always been regarded as the sister group of the rainbow, Gila, Apache, golden, and redband trouts (Behnke 1992). Cladistic analysis of the data set presented in this paper supports that view, with a crucial qualification: the cutthroat trout descended from a basal lineage (node 41) near the Mexican golden trout: that is, from the ancestor to all other Pacific trout and salmon (Figure 12). It was not anticipated that the Pacific salmon, not the cutthroat trout, are the *closest* sister group of the rainbow trout (Figure 12, node 47).

Evidence for our phylogeny lies in the discovery that there are no morphological synapomorphies linking cutthroat trout to rainbow trout separate from the other trouts and salmon. On the other hand, Wilson et al. (1985), in their study of relationships among steelhead, rainbow trout, and cutthroat trout, had shown three restriction sites—*Eco*R I (3rd site), *Bgl* II (3rd site), and *Kpn* I (3rd site)—linking cutthroat trout to rainbow trout populations (Wilson et al. 1985: table 1). Furthermore, Gyllensten and Wilson (1987) showed 19 mtDNA fragments, cut by 10 restriction enzymes, unique to rainbow and cutthroat trout. However, none of these sites or fragments can be demonstrated to be a synapomorphy for *clarki* plus *mykiss*. The three sites shown by Wilson et al. (1985) all appear to be shared by Pacific salmon, as shown by Thomas et al. (1986: figure 3), and therefore provide no evidence for a separate sister group relationship for rainbow and cutthroat trout. Comparison of the fragment lengths shown by Gyllensten and Wilson (1987: appendix 12.1) with the sites mapped by Thomas et al. (1986) for the eight enzymes in common between these two studies reveals that of the 13 fragments common to rainbow and cutthroat trout, only one (*Pst* I, 10.5 kilobases long) may involve a unique synapomorphy; the others are common to many Pacific salmon and are therefore not evidence for separate shared ancestry for *O. mykiss* and *O. clarki*. It remains to be seen (by a cladistic study of molecular evidence) whether the other six fragments are evidence of plesiomorphic or synapomorphic sites. In conclusion, there is almost no mtDNA evidence for shared ancestry between

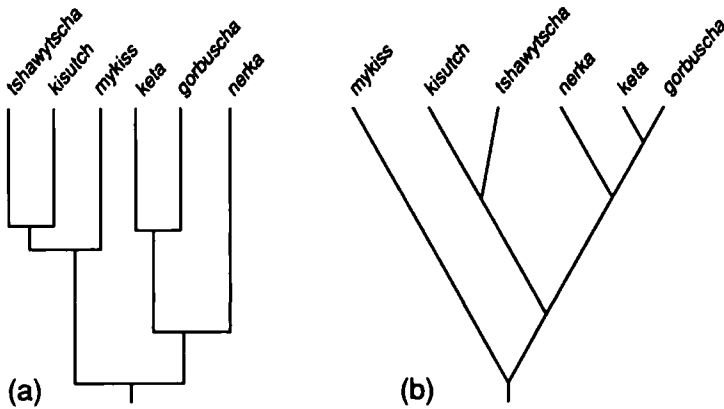


FIGURE 13.—Comparison of (a) phenogram and (b) cladogram of mitochondrial DNA (mtDNA) data (from Thomas et al. 1986) bearing on the relationships of certain species of *Oncorhynchus* for which mtDNA data are available. The phenogram developed with the unweighted pair-group method with arithmetic averages (a) estimates genetic similarity without respect to branching order in time. The cladogram (b) estimates branching order in time and phylogenetic relationships, assuming *Oncorhynchus mykiss* to be the outgroup for the other taxa (Pacific salmon).

rainbow and cutthroat trout, separate from Pacific salmon.

The molecular and biochemical data contribute to a remarkable contrast in the evidence for relationships among chum, pink, and sockeye salmon. In a study of more than 19 gene loci, Utter et al. (1973) found pink and sockeye salmon to be similar (index of similarity, 0.71), contrasting with chum salmon similarities of 0.47 and 0.54 with pink and sockeye salmon, respectively. Tsuyuki and Roberts (1966) also found protein evidence for a relationship between pink and sockeye salmon. Cladistic reanalysis of the data of Utter et al. as discrete character states shows four protein synapomorphies shared by pink and sockeye salmon, compared to no clear support for other pairs. Our morphological data, especially characters involving the gill rakers and teeth, agree with the protein data in indicating that *gorbuscha* is the sister species of *nerka*.

But pink salmon are similar to chum salmon in their mtDNA, showing sequence divergence of only 2.7% (compared to 4.6% and 5.2% sequence divergence between pink and sockeye salmon and chum and sockeye salmon, respectively). Cladistic analysis of the mtDNA data shows four synapomorphies shared by pink and chum salmon, compared to no clear support for other combinations (Table 3). The mtDNA data are consistent with interpretations based on life history (Hoar 1958).

However, because of the lack of recombination, the several mtDNA characters are not independent evidence; if introgression has occurred, all of

the shared mtDNA characters might have been transferred as a block, countable as one cladistic step no matter how many site or fragment characters are present (Smith 1992). Ferris et al. (1983)

TABLE 3.—Species of Pacific salmon *Oncorhynchus* spp. and their nearest relative (*O. mykiss*) arranged to show the sequential acquisition (from left to right) of derived mitochondrial DNA restriction sites (1+) and loss of primitive sites (1-). Primitive states are coded 0. Mitochondrial DNA data are from Thomas et al. (1986). *Oncorhynchus gorbuscha* shares four unique sites with *O. keta*, but only one unique site, P64, with its sister species, *O. nerka*.

Restriction site	<i>O. mykiss</i> rainbow trout	<i>O. kisutch</i> coho salmon	<i>O. tshawytscha</i> chinook salmon	<i>O. nerka</i> sockeye salmon	<i>O. gorbuscha</i> pink salmon	<i>O. keta</i> chum salmon
S10	0	0	0	0	1-	1-
H150	0	0	0	0	1+	1+
X46	0	0	0	0	1-	1-
H87	0	0	0	0	1-	1-
K10	0	0	0	1+	1+	1+
B78	0	0	0	1-	1-	1-
P58	0	0	0	1-	1-	1-
H140	0	0	0	1+	1+	1+
BII42	0	0	0	1-	1-	1-
P64	0	0	0	1-	1-	0
X50	0	0	0	1-	0	1-
BII95	0	0	1+	1+	1+	1+
BI26	0	0	1-	0	1-	1-
H133	0	1+	1+	0	1+	1+
X64	0	1-	0	0	1-	1-
K81	0	1-	1-	0	0	1-
K91	0	1-	1-	0	0	0

demonstrated introgressive transfer of mtDNA through populations of European species of mice. Smith (1992) documented evidence of introgressive transfer of characters in fishes.

The conflict between the biochemical evidence for relationship between *nerka* and *gorbuscha* versus the molecular evidence for relationship between *nerka* and *keta* may be tested by comparisons with independent data sets. The karyotype evidence is an important, independent source of information. The 2N chromosome numbers are 74 in *keta* (26 metacentric and 48 acrocentric), 56 in *nerka* (44 metacentric and 12 acrocentric), 52 in *gorbuscha* (48 metacentric and 4 acrocentric), and 68 (32 metacentric and 36 acrocentric) in the outgroup species, *tshawytscha* (Simon 1963; R. B. Phillips, University of Wisconsin, Milwaukee, personal communication). A parsimony analysis of fission and fusion steps among metacentrics and acrocentrics of the above four taxa indicates that 22 steps (6 fissions and 16 fusions) would yield numbers required to be consistent with the tree based on the protein data; at least 34 steps (18 fissions and 16 fusions) would be necessary to be congruent with the tree based on the mtDNA data. Thus the chromosome data are congruent with the protein and morphological data in indicating that *nerka* and *gorbuscha* are sister species, and that the ancestor of those two was the sister species to *keta*.

This reanalysis leads to three important conclusions. (1) *Oncorhynchus gorbuscha* is more closely related to *O. nerka* than to *O. keta*. (2) Mitochondrial DNA estimates of historical relationship are often in error because the data are analyzed as phenetic distances, not in cladistic branching order. (3) Estimates of relationships are sometimes in error because evolutionary history has been lost through introgression. Introgressive loss of evolutionary history may also lead to flawed estimation of rates of evolution; an example is seriously overestimated rates of evolution of Pacific salmon (Smith 1992).

Summary

The phylogenetic analysis demonstrates that the extant "archaic trouts" *Brachymystax*, *Acantholingua*, and *Salmothymus* (including *Platysalmo*) are cladistically intermediate between graylings, *Thymallus*, and the advanced salmonines *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus*. *Eosalmo*, the oldest fossil salmonine, is confirmed to be the most archaic trout—the sister group of all other salmonines, as documented by Wilson (1977).

Advanced salmonines form two lineages: (1) the clade of chars, *Salvelinus*, and huchen, *Hucho*; and (2) the clade of Atlantic and Pacific salmon and trouts, *Salmo* and *Oncorhynchus*. The Pacific trouts are not a monophyletic group but rather represent several ancient branches, one of which produced Pacific salmon. *Oncorhynchus mykiss*, the rainbow trout, California golden trout, and redband trout, is in a natural group with Pacific salmon. Cutthroat trout and the Mexican golden trout are outside the Pacific salmon—rainbow trout group. Recognition of Pacific trouts as a clade "*Parasalmo*" is not supported because that name is applicable only to the cutthroat trout. It cannot be broadened to include rainbow trouts because *Rhabdofario* is a prior name for that group. Pacific trouts are not a natural group because they are paraphyletic in that the taxon so formed does not include all of its descendants.

The terms "trout" and "salmon" do not refer to natural phylogenetic groups. These names originally referred to life history attributes: trout usually complete their life cycle in freshwater streams and lakes, while salmon usually migrate to sea (according to English usage, but in Nineteenth Century French, the appellations signified the opposite; see Dumeril 1856). Interesting exceptions to common English usage include members of trout species that migrate to the sea—"salmon trouts" (sea-run *S. trutta*), coastal *O. clarki*, and steelhead (*O. mykiss*)—and members of salmon species that are lake-locked (kokanee, sebago, ouananiche, etc). The common names based on these life history attributes need not match phyletic groupings. Both the Atlantic clade, *Salmo*, and the Pacific clade, *Oncorhynchus*, include trouts as well as salmon. The Pacific salmon clade is a well-defined, cladistically advanced, monophyletic subgroup of six species, most of whose members die after spawning. These six species (Figure 12) of the genus *Oncorhynchus* can be diagnosed and recognized as the subgenus *Oncorhynchus*. Some modern species in the subgenus *Oncorhynchus* have a fossil record that goes back to the late Miocene.

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Appendix: Data Matrix for Salmonid Character States

TABLE A.1.—Numerical character state codes assigned to 119 salmonid characters as described in Table 1. Primitive states are coded as 0, derived states as 1 or 2. Missing or unavailable data are represented by “?”.

Taxon	Character							
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40
<i>Novumbra</i>	00000	00010	11000	00000	00000	??000	00100	00000
<i>Thaleichthys</i>	00010	00000	10000	00000	00000	??000	00100	01000
<i>Chanos</i>	01000	00000	00000	00000	01000	??000	00110	00000
<i>Prosopium</i>	02100	00000	10000	00001	00001	00001	10010	00000
<i>Coregonus</i>	01010	00000	10000	00001	00001	00001	10110	00000
<i>Stenodus</i>	01010	00000	10000	00101	00001	00011	00100	00000
<i>Thymallus</i>	01000	00010	10000	00001	00000	??001	10000	00000
<i>Eosalmo</i>	?1000	000??	1??00	00011	000?1	??001	00000	?????
<i>Brachymystax</i>	02100	00010	11110	00011	00001	00001	00000	01000
<i>Acantholingua</i>	01000	00010	11110	00011	00001	00001	00001	11000
<i>Salmothymus</i>	02000	00000	11111	00011	00001	00011	10001	00000
<i>Platysalmo</i>	02000	00000	11111	00011	00001	00011	00001	00000
<i>Hucho hucho</i>	02000	00010	11110	00111	00011	10011	00000	01000
<i>Hucho perryi</i>	02000	00000	11110	00111	00011	10011	00000	01000
<i>Salvelinus</i>								
<i>larsoni</i>	?2000	00010	11110	00111	00011	11001	00000	01100
<i>malma</i>	02001	00010	10110	00111	00011	11001	00000	01100
<i>alpinus</i>	02001	00010	10110	00111	00011	11001	00000	00100
<i>namaycush</i>	02100	00010	11110	00111	00011	11001	00000	00100
<i>fontinalis</i>	02100	00010	11110	00111	00011	11001	00000	00100
<i>confluentis</i>	02100	00010	11110	00111	00011	11011	00000	00100
<i>leucomaenis</i>	02000	00010	11110	00111	00111	11001	00000	00100
<i>Salmo trutta</i>	02000	10010	11110	00011	00011	10001	00001	00010
<i>Salmo salar</i>	02000	10010	11110	00011	00011	10001	00001	00011
<i>Oncorhynchus</i>								
<i>chrysogaster</i>	01000	00010	11110	00011	00111	10011	00001	00010
<i>clarki</i>	01000	00010	11110	00011	00111	10001	11001	00010
<i>gilae</i>	01000	00010	11110	00011	00111	10001	11001	00010
<i>apache</i>	01000	00010	11110	00011	00111	10001	11001	00010
<i>lacustris</i>	?1000	01011	11110	10011	10111	10001	11001	00010
<i>mykiss</i>	01000	01011	11110	10011	00111	10001	11001	00010
<i>aguabonita</i>	01000	01011	11110	10011	00111	00001	11001	00010
<i>(redband)</i>	01000	01011	11110	10011	00111	00001	11001	00010
<i>masou</i>	01000	01011	11110	10011	00111	10001	11001	10011
<i>kisutch</i>	11000	01011	11110	10011	01111	10001	11001	10011
<i>tshawytscha</i>	11000	02011	11110	10011	00111	10101	11001	10011
<i>rastronus</i>	?1000	020?1	11110	11011	0011?	???01	111?1	00011
<i>keta</i>	11000	02111	11110	10011	00111	10001	11001	00011
<i>nerka</i>	11000	02111	11110	11011	00111	10001	11001	00011
<i>gorbuscha</i>	11000	02111	11110	11011	00111	10001	11001	00011

TABLE A.1.—Extended.

Taxon	Character							
	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80
<i>Novumbra</i>	00001	01010	10000	00000	00001	00000	01??0	1???0
<i>Thaleichthys</i>	00000	01000	00000	00000	00002	00000	00000	10100
<i>Chanos</i>	00010	10010	0010?	?0000	00?00	000??	00000	01001
<i>Prosopium</i>	00010	10010	00001	00000	00000	10000	00100	00000
<i>Coregonus</i>	00010	10010	00001	00000	00000	00000	00000	00000
<i>Stenodus</i>	00010	10010	00001	00000	00000	00000	00010	00000
<i>Thymallus</i>	00010	00000	00000	01000	00101	00000	10100	00000
<i>Eosalmo</i>	0001?	00000	00000	01000	00101	0000?	1?100	0000?
<i>Brachymystax</i>	00011	01000	00100	01000	00101	00000	10100	10001
<i>Acantholingua</i>	00011	01000	00100	01000	10101	00000	10101	10001
<i>Salmothymus</i>	00011	01000	00100	01000	10101	00000	10100	10001
<i>Platysalmo</i>	00011	01000	00100	01000	10101	00000	10100	10001
<i>Hucho hucho</i>	01011	01001	10100	01000	10212	00000	10100	10001
<i>Hucho perryi</i>	01011	01001	10100	01000	10212	00000	10100	10001
<i>Salvelinus</i>								
<i>larsoni</i>	01011	01001	10100	01000	10202	00000	10100	10001
<i>malma</i>	01011	01001	10100	01000	10202	01000	11100	11001
<i>alpinus</i>	01011	01001	10100	01000	10202	01000	11100	11001
<i>namaycush</i>	11111	01101	10100	01000	10202	00000	10100	11001
<i>fontinalis</i>	11011	01101	10100	01000	10202	01000	10100	11001
<i>confluentis</i>	11111	01101	20100	01000	10202	01000	11100	11001
<i>leucomaenis</i>	11011	01101	10100	01000	10202	00000	10100	11001
<i>Salmo trutta</i>	01011	01001	21100	01100	11102	01100	10100	10001
<i>Salmo salar</i>	01011	01001	21100	01100	11102	01100	10100	10001
<i>Oncorhynchus</i>								
<i>chrysogaster</i>	01011	00101	21000	01100	10112	0?000	12100	01111
<i>clarki</i>	01011	00101	21000	01100	10112	01000	11100	00101
<i>gilae</i>	01011	00101	21000	01100	10112	0?000	11100	10101
<i>apache</i>	01011	00101	21000	01100	10112	01000	11100	10101
<i>lacustris</i>	01011	00101	21000	01100	10112	01000	11100	00101
<i>mykiss</i>	01011	00101	21000	01100	10112	01000	11100	00101
<i>aguabonita</i>	01011	00101	21000	01100	10112	01000	11100	00101
<i>(redband)</i>	01011	00101	21000	01100	10112	01000	11100	00101
<i>masou</i>	01011	00101	21010	11100	00002	01010	12100	00101
<i>kisutch</i>	01011	00101	21010	11100	00002	01010	12100	00101
<i>tshawytscha</i>	01011	00101	21010	11100	00002	01010	12100	00101
<i>rastronus</i>	01011	00101	11010	11111	00011	01010	1?100	00101
<i>keta</i>	01011	00101	11010	11110	00002	01010	12100	00101
<i>nerka</i>	01011	00101	11010	11110	00002	01011	12100	00101
<i>gorbuscha</i>	01011	00101	11010	11110	00002	01010	11100	00101

TABLE A.1.—Extended.

Taxon	Character							
	81-85	86-90	91-100	101-110		111-119		
<i>Novumbra</i>	001?0	00000	00001	00100	00000	00100	00000	0000
<i>Thaleichthys</i>	00010	00000	00200	00000	00000	00000	00000	0000
<i>Chanos</i>	00101	00010	00001	00100	10000	00000	00000	0000
<i>Prosopium</i>	00100	00011	00010	01000	00100	00001	00000	0000
<i>Coregonus</i>	00100	00111	00110	01000	00112	00000	00000	0000
<i>Stenodus</i>	00100	00111	01110	01000	00112	00000	00000	0000
<i>Thymallus</i>	00100	00110	00011	01010	00100	00101	00000	0001
<i>Eosalmo</i>	00101	????0	00011	1000?	?????	?????	?????	????
<i>Brachymystax</i>	00111	10010	00011	10000	01102	00111	00000	0000
<i>Acantholingua</i>	00010	10010	01011	10100	00101	001?1	00000	0000
<i>Salmothymus</i>	10011	10010	01011	10100	11101	001?1	00000	0000
<i>Platysalmo</i>	10011	10010	01011	10100	00100	00111	00000	0000
<i>Hucho hucho</i>	10111	10110	01111	10101	01102	00121	00000	0000
<i>Hucho perryi</i>	10110	10000	01011	10001	01102	00121	00000	0000
<i>Salvelinus</i>								
<i>larsoni</i>	10110	10000	0????	?????	?1???	?????	?????	????
<i>malma</i>	10111	10000	01111	10100	11101	00121	10000	0000
<i>alpinus</i>	10111	10000	01111	10100	01101	00121	10000	0000
<i>namaycush</i>	10111	10000	02111	10100	01102	00021	10001	0000
<i>fontinalis</i>	20111	10000	01011	10100	01101	00121	10001	0000
<i>confluentis</i>	10111	10000	02111	10100	01101	00121	10000	0000
<i>leucomaenis</i>	10111	10000	02011	10100	01101	00121	10001	0000
<i>Salmo trutta</i>	10011	10010	00011	10100	00101	00121	00000	0000
<i>Salmo salar</i>	10011	10010	01011	10100	00101	00121	00000	1000
<i>Oncorhynchus</i>								
<i>chrysogaster</i>	20111	10010	00011	10000	00101	00121	01010	0000
<i>clarki</i>	20111	10000	01111	10000	00101	00121	01010	0000
<i>gilae</i>	20111	10010	11111	10000	00101	00121	01110	0000
<i>apache</i>	20111	10010	11111	10000	00101	00121	01110	0000
<i>lacustris</i>	20111	10??0	11???	????0	0????	?????	?????	????
<i>mykiss</i>	20111	10010	11111	10000	00101	00121	00010	0000
<i>aguabonita</i>	20111	10010	01111	10000	00101	00121	01010	0100
<i>(redband)</i>	20111	10010	11111	10000	00101	00121	01010	0000
<i>masou</i>	21111	10010	12111	10100	00101	00121	00010	0010
<i>kisutch</i>	21111	10010	12211	10000	00102	00121	00000	0000
<i>tshawytscha</i>	21111	10010	12211	10000	00102	00121	00000	0000
<i>rastronus</i>	11111	????0	12???	????0	1????	?????	?????	????
<i>keta</i>	21111	11010	12211	10100	00102	00121	00000	0000
<i>nerka</i>	11111	11010	12211	10000	10102	10121	00000	0000
<i>gorbuscha</i>	21111	11010	12211	10000	10102	11121	00000	0000