Taxonomy and Distribution of the

Bull Trout, *Salvelinus confluentus* (Suckley),

from the American Northwest

by

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Museum of Zoology

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Abstract

Morphological and distributional evidence is presented favoring the specific distinction of the bull trout, a currently unrecognized form of *Salvelinus*, native to western North America. This species has been confused with the Dolly Varden, *Salvelinus malma* (Walbaum). Separation of the two is most easily seen in the characters of the head and cranial skeleton. Diagnosis and description are given for the bull trout along with a history of its early taxonomy. Information is provided on past and present distribution of the bull trout which ranges between 41° and 60° N. latitude. North of the 49° parallel it is found in most of the major drainages east and west of the Continental Divide. The bull trout is or at one time was sympatric with the Dolly Varden in at least three major river systems, in addition to the salt waters of Puget Sound.

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The salmonid fishes belonging to the genus Salvelinus have long been recognized as a difficult taxonomic group. Without exaggeration, Vladykov (1954) has referred to the taxonomy of Salvelinus (along with other salmonid genera) as "extremely involved and time-consuming". This is particularly true for members which are native to land areas bordering the North Pacific Ocean Basin. Some writers (see McPhail, 1961, p 293) have referred to these populations as part of the Salvelinus alpinus complex because of the unsatisfactory state of their taxonomy and incompleteness of representative material.

The existence of more than one kind of Salvelinus in the American Northwest has been a controversial subject since the days of the Pacific Railroad Survey. Morton (1970) last dealt with the subject and concluded only one species, Salvelinus malma (Walbaum) was recognizable, while none of the proposed subspecies were valid.

The findings reported here were prompted by an initial examination in 1968 of skeletal material of Salvelinus, some of which was prepared by Norden (1961). Morphometric, meristic, osteological and distributional evidence is presented to show that there are two widely distributed forms of Salvelinus native to the western United States and Canada. For years these two taxa, here considered specifically distinct, have been submerged under one name, the Dolly Varden, Salvelinus malma ~~(Walbaum)~~. The latter name is correctly applied to the form which is generally characterized as anadromous. As now understood, its range spans the netire island and mainland arc of the North Pacific from the Sea of Japan and Kuril Islands, across the Aleutian chain to Alaska and south along the North American Pacific coast to the northwest region of the United States.

bull trout is not strictly an interior, non-anadromous form, but combines coastal and inland, as well as northern and southern aspects to its distribution. Because of the taxonomic difficulties with this species, the bull trout has lacked uniform scientific recognition even though it is a well-known sport fish. The scientific literature, especially sources that compile information on regional faunas, has lumped information about the

Because of its international usage, the common name, Dolly Varden, is better reserved for this species although it may originally have applied to the other. The second species ranges well inland in the United States and Canada and is generally non-anadromous. Where individuals often reach an adult size of several pounds or more, such as in the Kootenay River of British Columbia and the Flathead River drainage of Montana, fishermen refer to this species as the bull trout (see Dymond, 1932; Brown, 1971: 61), probably because of its large, broad head, ugly appearance of its jaws, and strong predaceous behavior toward other fishes. The original name for the bull trout, *Salmo spectabilis* Girard is a secondary homonym (Suckley, 1861 ; Morton, 1970), but there are four other scientific names available for the bull trout, all proposed by Suckley (1858, 1861 ~~, 186~~): *Salmo confluentus*, *Salmo bairdii*, *Salmo parkei*, and *Salmo campbelli*. The first binomial, *Salvelinus confluentus* (Suckley), is selected for use because it has precedence over the other three in date of publication (Suckley, 1858); also, fewer nomenclatorial problems, including spelling are anticipated for the name, *confluentus*, and the type, a dried head and skin (USNM 1135), is still ~~in existence~~ extant. Jordan et al (1930) placed *Salmo confluentus* Suckley in synonomy with *Oncorhynchus tschawytscha* (Walbaum), probably because Suckley's description (1858, 1860) reads, in part, like a Pacific salmon (*Oncorhynchus*). Careful comparison of the head of the type specimen (USNM 1135) and its labelling with Suckley's description of the holotype has led me to conclude that without any doubt ~~that~~ they are the same. The names *S. bairdii* and *S. parkei* lack type specimens. Although char rather than trout may be better applied to members of the genus *Salvelinus* (Morton, 1955), trout is used in combination ~~with~~ common names for species of *Salvelinus* (e.g. brook trout) in accordance with the American Fisheries Society's (Bailey, 1970) attempts to stabilize fish nomenclature.

Although primarily an inland species, collection records show that the ecology, morphology and life history for so long that the two distinct forms, malma and confluentus, have been largely confused. If there are morphological characters and aspects of their biology that consistently separate malma and confluentus over their distributional ranges, then why has there been a taxonomic problem? A large part of the explanation must lie in the lack of adequate comparative material available to any one investigator.

The findings in this paper are part of a more extensive systematic treatment of the genus Salvelinus begun at the University of Michigan in 1968. Conclusions on the specific distinction of the bull trout reached here are essentially those presented in a preliminary report at the 1969 Annual Meeting of the American Society of Ichthyologists and Herpetologists in New York City (Cavender, 1969).

Materials and Methods

Specimens of Salvelinus studied are principally those in the collections of the University of Michigan Museum of Zoology (UMMZ), the National Museum of Natural Sciences, Canada (NMC) and the United States National Museum of Natural History (USNM). These are listed under specimens examined. Locations given on the distributional map (Fig. 9) follow only this list. Specimens from which morphometric data were taken are those that have the standard length recorded.

The specimens of S. malma used for morphometric comparison with S. confluentus (Tables 1-8) were taken from the Pacific drainages of the United States, including Alaska, and Canada. They represent a population which McPhail (1961) has termed the southern form of the Dolly Varden. The National Museum of Natural Sciences, Canada possesses excellent series of Salvelinus confluentus and Salvelinus malma. A large part of this material came from the collections at the University of British Columbia, Vancouver. A number of old and valuable specimens of Salvelinus are at the United States National Museum, including ~~Girard's~~ the types of "Salmo spectabilis" and "Salmo confluentus," Livingston Stone's collections made from the McCloud River in the 1870's, and specimens taken in the early 1880's from Puget Sound and coastal waters of British Columbia. In 1974 a small collection of bull trout was made by the author for the Ohio State University Museum of Zoology (OSUM). Field observations of Salvelinus confluentus were also made in the Flathead River drainage of Montana. Osteological information came from study of both dry skeletal and cleared and stained preparations. These are located both at the Ohio State University and the University of Michigan.

Methods used in counting are as follows: the number of gill rakers was determined by removing the first arch on the right side and counting under a dissecting microscope the individual rakers, including all rudimentary ones; ~~when the total number of rakers on an arch was divided between the upper and lower limbs, the single raker consistently seated at the joint of the two limbs was included with the count for the lower limb~~; branchiostegal rays were counted after determining the smallest, most anterior rays by dissection; mandibular pores were counted by exposing the openings of the mandibular sensory canal with a fine jet of compressed air; all pores were included in the count, but not the opening that exits the canal from the rear of the lower jaw; pyloric caeca were cleaned of connecting tissue and fat deposits but were not damaged; a count was made and then repeated until the result was the same; all vertebral counts were made from radiographs. These are deposited at the University of Michigan Museum of Zoology.

(the arch was then replaced)?

In studying gill-raker morphology, the anterior right arch was removed, stained in alizarin red-s and cleared in glycerin. The most posterior gill raker on the lower limb was then drawn using a Wild-M5 Stereoscope with integral camera lucida attachment. Photographs and line drawings are those of the author except Fig. 3 , which was taken by Gus Spreitzer, Ohio State University.

Osteological abbreviations: AO - antorbital; ART - articularangular ATL - atlas vertebra; BOC - basioccipital; BR - branchiostegal ray; BS - basisphenoid; DE - dentary; ECPT - ectopterygoid; ENPT - endopterygoid; EOC - exoccipital; EPO - epiotic; FR - frontal; HYO - hyomandibular; INT - intercalar; IO - infraorbital; IOP - interopercular; LE - lateral ethmoid; MPT - metapterygoid; MX - maxilla; NA - nasal; ORS - orbitosphenoid; OP - opercle; P - parasphenoid; PA - parietal; PMX - premaxilla; POP - preopercle; PRO - prootic; PTF - posttemporal fossa; PTO - pterotic; QU - quadrate; SE - supraethmoid; SO - supraorbital; SOC - supraoccipital; SOP - subopercle; SPO - sphenotic; SPOP - suprapreopercle; SY - symplectic; V - vomer.

Specimens Examined

Salvelinus confluentus (Suckley)

Sacramento R. Basin, McCloud R., Calif.: CAS 25691, one, 110mm, Shasta Co.; CAS ✓ , one, 136mm, near Nasoni Creek, Shasta Co.; CAS 19889, one, 147mm, near Bullibokka Mt., Chasta Co.; CAS ✓ , one, 173mm, Shasta Hatchery near Mt. Shasta, Shasta Co.; USNM 26196, one, skeleton; USNM 10547, one, 175mm; USNM 27820, three, 211-284mm; USNM 15549, two, 101mm, 163mm, Livingston Stone, 2 July 1874; USNM, one, 339mm; USNM 22452, one, 301mm; USNM 20816-20818, three.

Klamath R. Basin: UMMZ 188849, five (two cleared and stained), 140-168mm, Long Cr., Lake Co., Ore.; UMMZ 188851, one skeleton, 169mm, Long Cr., Lake Co., Ore.; USNM 16793, one skin and skeleton, Lin Creek, Ft. Klamath, Ore.

Columbia R. Basin, Snake Drainage: USNM 125309, two , 142mm, 154mm, Meadow Cr. near Sawtooth, Ida.; UMMZ 117879, one, 216mm, Stanley Lake, a tributary to the Salmon R., Custer Co., Ida.; UMMZ 162298, one, 166mm, Dave Cr., Elko Co., Nev., a tributary of the Jarbridge R.; Univ. Utah No. 1, one, 103mm, Dave Cr., Elko Co., Nev.; CAS ✓ , six, (one cleared and stained), 90-155mm, West Fork Jarbridge R., Elko Co., Nev.; UMMZ 127607, one, 134mm, Little Lost R. on Custer-Butte Co. line, Ida.

Columbia R. Basin: USNM 7078, one (type specimen), Columbia R. at The Dalles, Oregon; USNM 25273-25276, four, 279-313mm, Walla Walla, Wash.; NMC 66-61, one, Columbia River at Arrowhead, Brit. Col.; NMC 66-63, twenty-two, Mars Cr., trib. of Columbia R. at Big Bend Highway, Brit. Col.; NMC 66-64, five, Kinbasket Lake at Tsar Cr., trib. of Columbia R., Brit. Col.; NMC 66-70, three (includes one head), Lower Arrow Lake off Deer Cr., trib of Columbia R., Brit. Col.; NMC 59-169, twenty, Luthead Lake, Banff National Park, Brit. Col.; UMMZ 164591, one, 252mm, Emerald Lake, Yoho National Park, Brit. Col.

Columbia R. Basin, Clark Fork Drainage: USNM 38028, one, 310mm, Clark

Fork River; USNM 44002, one, 158mm, Rattlesnake Cr. at Missoula, Montana; NMC 59-148, eleven, Shepp Cr., trib. of Flathead R., Brit. Col.; NMC 66-72, seventy-seven, Pollock Cr., trib. of Flathead R., Brit. Col.; NMC 66-77, seventeen, Gumbo Flats Cr., trib. of Flathead R., Brit. Col.; UMMZ 161871, three, 134-166mm, Flathead Lake, Lake Co., Mont.; UMMZ 172458, seven, including three cranial skeletons), 212-423mm, Flathead Lake, Lake Co., Mont.; UMMZ 161866, one, 350mm, Flathead Lake, Lake Co., Mont.; UMMZ 188857, three (including one cleared and stained), 130-145mm, Morrell Cr. near Seeley Lake, trib. of Clearwater R.; UMMZ 188856, four, 47-90mm, Big Creek, trib. of North Fork Flathead R. on western boundary of Glacier National Park; OSUM 25212, two (one cleared and stained) , 208mm, 235mm, Hungry Horse Cr., trib. to Hungry Horse Reservoir on South Fork Flathead R., Mont.; OSUM 25213-5, one skeleton, mm, Flathead R. at Coram below the confluence of North and Middle Forks, Flathead Co., Mont.; UMMZ 102948, one 257mm, Pend d'Oreille Lake, Banner Co., Ida.

Columbia R. Basin, Kootenay Drainage: NMC 66-52, two, Slocan Lake, trib. of Kootenay R., Brit. Col.; NMC 66-57, four, Duncan Lake near Howser, trib. of Kootenay R., Brit. Col.; NMC 66-59, one, Kootenay Lake at the mouth of the Duncan R., Brit. Col.; NMC 66-68, six, Kootenay R. at Canal Flats, Brit. Col.; NMC 66-74, one, mouth of Wolf Creek at Skookumchuck, trib. of Kootenay R., Brit. Col.; NMC 66-78, two, mouth of Gold Cr. near Newgate, trib. of Kootenay R., Brit. Col.; NMC (no number), twelve, Lardeau R., trib. to Duncan R., Brit. Col.

Puget Sound, Washington: USNM 1135, one, 733mm, Pullayup R. at Steilacoom, G. Suckley, about 1 Feb. 1857, type of Salmo confluentus; USNM 27264, two, 295, 568mm, D.S. Jordan, 1880; USNM 42044, one, 297mm, Elliot Bay, O.B. Johnson, 21 May 1889.

Fraser R. Basin: NMC 55-130, two, 184, 185mm, Salmon River at Hart Hwy., north of Prince George, Brit. Col.

Skeena R. Basin, British Columbia: UMMZ 159357, three, 223-358mm, Lakelse Lake; UMMZ 159345, two, 181-195mm, Damshilgwit (Cabin) Lake; UMMZ 159333, one, 230mm, Morrison Lake; UMMZ 159337, two, 188-203mm, Morice Lake; UMMZ 159352, one, 368mm, Slamgeesh Lake; UMMZ 159351, one, 341mm, Sustut Lake; USNM 86207, one, 265mm, Bear Lake, Brit. Col.

Taku R. Basin: NMC 68-896, five, 150-246mm, Flannigan Slough, Taku R. at International boundary between British Columbia and Alaska.

Upper Yukon River Basin: NMC 68-1231, seven of fifteen, 97-198mm, Partridge Cr., trib. to the Swift R. near Yukon-British Columbia boundary.

MacKenzie R. Basin, Liard Drainage: NMC 62-234, one, 313mm, Tatsho Cr. near Dense Lake, trib. to Liard R., Brit. Col.; NMC 62-235, two, 340mm, 344mm, Letain Lake near King Mt., Brit. Col.; NMC 68-1230, four, 129-176mm, outlet to Little Lake, mile 450, Alaskan Highway.

MacKenzie R. Basin, Peace Drainage: NMC 66-435, one, 375mm, Chuchi Lake on Nation R., trib. of Parsnip R.; NMC 66-436, one of two, 113mm, Germanson Lake on Omineca R., Brit. Col.; NMC 66-437, one, 510mm, Finley R., about 4 miles upstream from Ft. Grahame, Brit. Col.; NMC 66-438, seven, 172-333mm, mouth of Manson R., where it joins the Finlay at Finlay Forks, Brit. Col.; NMC 66-440, one, 206mm, Peace R., 25 miles downstream from Hudson-Hope, Brit. Col.; NMC 68-802, one 171mm, Peace R., 11 miles west of Hudson-Hope, Brit. Col.;

MacKenzie R. Basin, Athabaska Drainage, Alberta: UMMZ 80837, one, 253mm, Jacques Lake, trib. to Rocky R., Jasper National Park; UMMZ 159930, five, 225-324mm, Jacques Lake, Jasper National Park; NMC 59-48, four (including two heads), Jacques Lake, Jasper National Park, Alberta.

Saskatchewan R. Basin: USNM 64326, one, 715mm, headwaters of Brazeau R., trib. to North Saskatchewan R., Alberta; UMMZ 164943, one, 164mm, Banff National Park, Spray R., trib. to Bow R. of South Saskatchewan drainage, Alberta; UMMZ 164928, one, 190mm, Bow Lake, Banff National Park, Alberta; UMMZ 164930, one, 215mm, Bow R., Alberta; NMC 60-343, one, ~~mm~~, Red Deer R. drainage at Morrin, 65 miles northeast of Calgary, Alberta; USNM 44444, one, 231mm, Oldman R., trib. of S. Saskatchewan R., Alberta; UMMZ 188900, eight, 190-267mm, Cracker Lake, trib. to St. Mary's R., of S. Saskatchewan R. drainage, Glacier National Park, Montana.

<u>Salvelinus</u> <u>malma</u> (Walbaum)

Sacramento R. Basin, McCloud River, Calif.: USNM 20819, two, 235, 241mm, coll. by Livingston Stone, Nov. 1872.

Soleduck R., Washington: UMMZ 93829, fourteen (three cleared and stained), 100-134mm, above Soleduck Falls, Olympic Peninsula.

Puget Sound, Washington: USNM 34301-34305, five, 252-274mm, Port Townsend, James G. Swan, coll. in 1884 or earlier.

Skagit R. Drainage, British Columbia: UMMZ 179422, two, 50-65mm, Skagit R. near Hope.

Skeena R. Basin, British Columbia: UMMZ 159323, one, ~~(a possible hybrid between S. malma and S. confluentus),~~ 200mm, Alastair Lake; UMMZ 159344, two, 140-144mm, Johanson Lake.

British Columbia: NMC 59-150, two of six, 126, 130mm, East Fork Seltat Cr. at Haines Rd. and about 1 mile below Snowater Lake, trib. of Klehin R.; NMC 65-213, one head, Nass Harbour, Iceberg Bay near mouth of Nass R.; NMC 65-212, three, 146-159mm, Nass Harbour just north of Jacques Point, Iceberg Bay; NMC 65-225, five, 189-242mm, mouth of stream, cove on south shore steamer passage about 3/4 mile west of Khutzeymaten Inlet; NMC 65-159, two, 197mm, 293mm, cove on west side of Refuge Bay and at north end of Porcher I., S of Prince Rupert; USNM 31979, one, 285mm, Port Simpson, Capt. H.E. Nichols, June 1882; USNM 37610, one, 98mm, taken in fresh water at Port Simpson.

Taku R. Basin, Alaska: NMC 58-402, two, Twin Glacier Lake, trib. Taku R.; NMC (BC 58-388), five (part of large series), Canyon Is., Taku R., Alaska.

Alaska, Aleutian Islands: UMMZ 106266, thirteen (two cleared and stained), 52-127mm, small stream on Atka I.; UMMZ 106529, three, 383-497mm, Unalaska I.

Alaska: UMMZ 128983, four, 257-310mm, vicinity of King Cove, Belkofski Bay, Alaska Peninsula; UMMZ 106260, one, 288mm, freshwater stream trib. to Three Saints Bay, Kodiak I.; UMMZ 126507, two, 286-289mm, Karluk R., Kodiak I.; UMMZ 126476, eleven (two cleared and stained), 71-151mm, Upper Thumb R., trib. to Karluk L., Kodiak I.; UMMZ 159395, two, 100mm, 125mm, North Fork of Upper Thumb R. above falls, Kodiak I.; UMMZ 159393, one, 53mm, Falls Cr., above falls, trib. to Karluk L., Kodiak I.; OSUM 25213, five, 98-138mm, mouth of trib. entering Karluk L., Kodiak I.; UMMZ 106267, one, 174mm, Lake at north end of Sitkalijak I.; UMMZ 182299, one, 134mm, Baranof I., stream on north shore of Port Lucy at west end of Island.

Copper River Drainage, Alaska: UMMZ 162600, one, 173mm, Chitina R.; NMC (BC 58-227), five, 205-327mm, South L. of Chenan Lakes, trib. to Copper R.

Yukon R. Basin: UMMZ 144581, one, 85mm, Grant Cr. about 30 mi W of Tanana; UMMZ 133553, two, 186,194mm, Riley Cr., McKinley National Park; NMC (BC 58-271), four, 152-190mm, Dry Cr. near Alaska Highway, Tanana R. drainage.

MacKenzie R. Basin, British Columbia: USNM 147661, one, 102mm, Hot Springs, 3 miles WNW of junction Trout River and Liard River, July 6-8, 1948, J.R. Alcorn.

Korea: UMMZ 188698, four, 70-187mm, Upper Tuman River, Mozan; UMMZ 188712, one, 429mm, Joshin Bay near Seishin.

U.S.S.R.: UMMZ 145814, one, 123mm, Pogarna R., Kamchatka.

Copper River Drainage, Alaska: UMMZ 162600, (1), 173mm, Chitina R.; NMC (BC 58-227), (5), 205-327mm, South L. of Chenan Lakes, trib. to Copper R.

Yukon R. Basin: UMMZ 144581*, (1), 85mm, Grant Cr. about 30 mi. W of Tanana; UMMZ 133553*, (2), 186, 194mm, Riley Cr., McKinley National Park; NMC (BC 58-271), (4), 152-190mm, Dry Cr. near Alaska Highway, Tanana R. drainage.

MacKenzie R. Basin, British Columbia: USNM 147661, (1), 102mm, Hot Springs, 3 miles WNW of junction Trout River and Liard River, July 6-8, 1948, J. R. Alcorn.

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U.S.S.R.: UMMZ 145814, (1), 123mm, Pogarna R., Kamchatka.

Japan and Kuril Islands: NMC 60-154, (6), Shokotsu R., Soya Province, Hokkaido; UMMZ 186872, (6), one cleared and stained, 130-135mm, Pon-mataochi R., Nemuro Province, Hokkaido; UMMZ 188710, (9), one cleared and stained, 79-168mm, Ishikari R. at Sounkei, Ishikari Province, Hokkaido; UMMZ 188711, (9), 65-180mm, Kuzira Bay, Paramusiro I., Northern Kuril Islands.

* specimens that represent the northern form of Salvelinus malma (McPhail, 1961)

Bull Trout

Salvelinus confluentus (Suckley)

(Figs. 1 - 9)

Salmo spectabilis - Girard, 1856: 218 (orig. descr.)

Salmo spectabilis - Girard, 1858: 307-308 (amended descr.)

Salmo confluentus - Suckley, 1858: 8-9 (orig. descr.)

Salmo spectabilis - Suckley, 1860: 342-343 (correct locality given)

Salmo confluentus - Suckley, 1860: 334-335 (amended descr.)

Salmo bairdii - Suckley, 1861: 309 (orig. descr.)

Salmo parkei - Suckley, 1861: 309-310 (orig. descr.)

Salmo campbelli - Suckley, 1861: 313 (orig. descr.)

Salvelinus spectabilis - Jordan, 1879: 79-81 (amended diag.)

Salvelinus malma - (in part) Jordan and Gilbert, 1882: 319-320 (synonymy given)

Taxonomic History

The bull trout was first described by Girard (1856) as Salmo spectabilis. The holotype of spectabilis, USNM 7078, does not become the holotype of the revised species Salvelinus confluentus (Suckley) described in 1858, since this function is taken by USNM 1135.

Girard gave the locality of USNM 7078 as St. Mary's Mission on the Clark Fork of the Columbia River, Montana, but George Suckley (1860) who collected the specimen in 1854 redescribed spectabilis and corrected Girard's locality information stating that the holotype came from Ft. Dalles on the lower Columbia River. This specimen (USNM 7078) is a mutilated, half-rotted individual estimated at 200mm standard length. In still another paper Suckley (1861) realized that the name spectabilis was preoccupied and substituted Salmo campbelli (after Archibald Campbell, Chief of the N.W. Boundary Commission). Morton (1970) has given a detailed account of this name change and the rules that pertain to it. In the same paper, Suckley (1861) also described Salmo bairdii and Salmo parkei which are both conspecific with spectabilis. S. bairdii was based on a specimen from the Clark Fork of the Columbia and S. parkei, on a specimen from the Kootenay River. A search of the USNM collections failed to turn up the types of bairdii and parkei. However, the holotype of Suckley's Salmo confluentus, USNM 1135, was found (Fig. 1). This specimen consists of a dried head and skin now preserved in alcohol. The head is that of a bull trout, but the description by Suckley (1858) states that the dorsal, adipose and caudal fins were spotted profusely with dark brown or black (unlike Salvelinus). This could not be confirmed, for on examination of USNM 1135, no dark spots were found. It is still possible that the description of Salmo confluentus was based on the remains or observations of two different individuals, one of which was a bull trout and the other a Pacific salmon. The locality for Salmo confluentus was given as the Puyallup River near Ft. Steilacoom, Washington Territory. The type was procured 27 Sept. 1856 by Suckley. Apparently, Indians had captured the fish--a large male in spawning condition. It possesses a kype that fits into a deep notch between the premaxillae. The notch is accented because of the dried condition of the specimen. Its standard length is estimated at close to 700mm.

Thus, it is evident that Suckley not only collected the holotype of S. spectabilis and later redescribed it, but within a few years described the same species three more times under different names, using specimens he himself had collected.

Jordan (1879), in his key to the species of Salvelinus found within the United States, included characters of the bull trout - "head large, stout, broad and flattened above" - in his diagnosis of Salvelinus spectabilis (Girard). He apparently based his key characters on a study of specimens taken from the Clackamas River, Oregon, by Livingston Stone. He also examined Girard's type of Salmo spectabilis, noting that the holotype was still preserved in the U. S. National Museum, while that of parkei was lost. He added that the species (parkei) was unquestionably the same as S. spectabilis. In the same paper, Jordan recognized the bull trout from the McCloud River as S. bairdii (Suckley), believing it differed from S. spectabilis by lacking basibranchial teeth. He did not list S. malma (Walbaum) in his key.

Jordan and Gilbert (1882) were responsible for placing of the bull trout in synonymy with Salvelinus malma (Walbaum). Jordan and Evermann (1896) followed this precedent, which has been continued to the present. Jordan never correctly distinguished the bull trout from coastal Dolly Varden where they occurred together in Puget Sound. Under his use of the name, "spectabilis," he lumped the bull trout with the Dolly Varden of coastal areas as far north as Alaska. In later papers (Jordan, 1923, Jordan and Hubbs, 1925), the name Salvelinus spectabilis was used for a supposed "southern form" which ranged from northern California northward to Alaska and the name Salvelinus malma applied to a "northern form" known from Unalaska to Kamchatka.

The earlier descriptions of "Salmo spectabilis" mentioned a number of distinctive characteristics of the bull trout. Girard (1856, 1858) emphasized the curved maxilla in the type specimen and its elongate head which entered the standard length 3.5 times. Under his description of Salmo confluentus, Suckley (1858) was the first to mention the "projection of the chin anterior to the front teeth;" in fact, he confused this character with the hooked lower jaw of spawning male Oncorhynchus. He also added that the type of confluentus had 13 or 14 branchiostegals. Again, in listing characters for Salmo bairdii, Suckley (1861) described the "snout having a deep notch between the extremities of the premaxillaries receiving a conical fleshy protuberance, projecting upwards from the chin." In the same paper under Salmo parkei, Suckley noted the large head "about four and a half times in the total length; its top flat; muzzle pointed" and "branchiostegals 13-14." Also in parkei, Suckley mentioned "a disposition toward the formation of a fleshy "tit" projecting upwards at the point of lower jaws with a corresponding notch between the premaxillaries." Despite what Morton (1970) has published to the contrary, there is little doubt, that in his description of Salmo bairdii and Salmo parkei, Suckley (1961) was writing about the bull trout and not Salvelinus malma (Walbaum).

To conclude this discussion of taxonomic history, it is emphasized that ~~although~~ the name confluentus must be substituted for spectabilis in accordance with the rules of zoological nomenclature, the holotype of the revised species becomes USNM 1135.

Diagnosis

A large species of North American Salvelinus reaching a greater size (to 18.3 Kg, about 40 lbs.) than S. malma (Walbaum). Distinguished from the latter by its long, broad head which is flat above and sharply tapered through the snout with the eye positioned near the dorsal margin; head measures 3.7 in standard length (averaging 3.6 in juveniles and 3.9 in large adults); anadromous malma measures about 4.3 (3.9-4.7); jaws and teeth well-developed, with cleft of mouth terminal; maxilla constantly curved downward; branchiostegal rays typically 13 or 14 on the right side, 24-31 with both sides combined; mandibular pore count is usually 7 to 9 on a side, 16 combined, while malma typically has 6 on a side; gill rakers are robust with strong teeth projecting from their mesial edges toward the branchial cavity, whereas S. malma has relatively long, finely tapered, and flexible gill rakers that are much compressed dorsoventrally and without teeth projecting from the mesial edge; gill rakers 14-19, pyloric caeca 21-36 and vertebrae 62-67; basibranchial teeth 0 to 11 averaging 4, consistently arranged in a single longitudinal row; in all specimens examined, there is a pronounced gap on each side between the palatine and vomerine tooth rows; in anterior view, there so.

In anterior view, there is a notch at the lower terminus of the snout (between the premaxillae) that receives a fleshy protuberance on the symphysis of the mandibles. This is a character best developed in the adult (both male and female), but also seen in larger juveniles. It is not to be confused with the kype of spawning male salmonines, although the same area is somewhat modified in large breeding males of S. **confluentus**.

A noticeable pigmentation characteristic is the round, light spots usually somewhat smaller than the pupil of the eye that cover the upper flanks and extend over the back of the fish. Those on the back stand out vividly on both live and preserved specimens, especially in front, to each side and behind the dorsal fin. However, malma may also show a similar spot pattern on the back and very dark individuals of the bull trout have been examined that have very faint spots or no spots at all dorsally.

The body of S. **confluentus** is long and slender, somewhat rounded and without much lateral compression. There is very little elevation at the dorsal-fin origin. S. malma has a more compressed body and head and often with more depth to the trunk.

Description - Some of the characters which have been employed for many years in Salvelinus taxonomy, such as numbers of gill rakers and pyloric caeca, will not separate S. malma and S. **confluentus** (Tables 7 and 8). This is one reason why the bull trout has not been recognized as a distinct form.

The characters of S. confluentus, described below, were found to be consistent in samples taken from localities throughout its known distributional range. These samples comprise a total of 332 individuals from eight major river basins draining to the Pacific and Arctic Oceans and Hudson Bay: Sacramento, Klamath, Columbia, Skeena, Taku, Yukon, MacKenzie and the Saskatchewan.

Most useful in separating **confluentus** from malma are the form and size of the head. In addition, characteristics of the jaws, teeth and gill rakers, number of mandibular pores, number of branchiostegal rays, arrangement of basibranchial teeth, neurocranium profile and configuration of certain bones of the cranium, such as the supraethmoid, frontal, preopercle and opercle are very useful. Number of gill rakers, pyloric caeca and vertebrae show considerable overlap between the two taxa.

In dorsal view (Fig. 2A), the head appears very broad and flat on top and is hard to the touch. The frontals slope only slightly in a lateral direction away from the midline. In *malma* (Fig. 2B) the head is more compressed and the frontals usually peak at the midline. Unlike the hard-head quality of *confluentus*, *S. malma* has the frontals usually covered with thick fatty tissue underlying the skin. The latter is best observed in anadromous *malma*.

In lateral view (Fig. 2A), the head of *confluentus* is low and sharply conical (also see Paetz and Nelson, 1970: Fig. on p. 83). The terminal cleft of the mouth evenly divides the anterior profile of the head region, while in *malma* the snout tends to be shorter and deeper and often overhangs the tip of the lower jaw, especially in the juvenile (Fig. 3B). The eye in *confluentus* is more dorsal in position than in *malma*. The vertical distance from the center of the eye to the dorsal margin of the head falls well short of the distance from the center of the eye to the posterior narial opening, while in *malma*, this distance reaches the nares or nearly so. In anterior view, the greater breadth of the head is again noticeable in *confluentus*. A major characteristic is found in the notch dividing the premaxillae which receive a fleshy elevation at the terminus of the lower jaw (Fig. 2A). This character is best developed in adults of both sexes and reaches maximum development in spawning males (Fig. 1A, B). Juveniles more than two years old also may have this feature.

Salvelinus malma may have a well-developed kype in spawning males of anadromous populations as shown by Morton (1965, Fig. 5), but the kype is barely evident in many spawning males of the non-anadromous *S. confluentus* (Morton 1965, Fig. 6). On specimens examined for this study, the kype was found best developed on the largest spawning males (over 500mm SL) and its existence is probably a function of size. The kype in *malma* is directed dorsally, whereas in *confluentus*, it has a slightly more anterodorsal orientation.

The upper jaw of the bull trout in lateral view (Fig. 2A) always possesses a pronounced curve downward as seen in the concavity of the toothed margin and convexity of the dorsal margin, particularly where the supermaxillary is seated. Typically, the maxilla in *malma* is more slender with the toothed shaft straight or only slightly curved downward.

Head size in *confluentus* (Table 1), measured by calipers from the tip of the snout to the most posterior limit of the gill cover, typically enters the standard length less than four times, whereas in *malma*, it enters the standard length about four and one-fourth times. The difference is greater when data from dwarf landlocked populations of *malma* are excluded.

The data given in Table 2 show that the proportion of head length to standard length changes with the size of the fish in both *malma* and *confluentus*. Individuals under 100mm would be difficult to separate using this character. Those over 250mm show a high degree of separation. No difference was found in proportionate head size of adult male and female *confluentus*, although it is suspected that males over 500mm will have longer heads. In *malma* males over 200mm tended to have larger heads than of the same size females.

Among the populations of *confluentus* studied in the southern half of its range, proportionate head size was quite uniform. The Snake River and Klamath Basin populations tended to have smaller heads. In the northern half of its range, *confluentus* from the Taku River Basin may be smaller-headed, although the sample size measured was not adequate to determine this.

Branchiostegal rays (Tables 3 and 4) - Salvelinus confluentus has the highest branchiostegal ray count of all the Salvelinus investigated (including S. alpinus, S. leucomaenis and S. namaycush). It averages 14 rays on the left side and 13 on the right in 120 specimens with a range from 12 to 16. The range for both sides combined was found to be 24 to 31 with a mean of 27. Among the species of Salvelinus, namaycush is closest to confluentus in number of branchiostegals. Vladykov (1954) reported S. namaycush to average 13 on the left side with a mean of 25.3 for both sides combined. This character is important in separating confluentus from malma. Among 88 specimens of S. malma, the average was 12 on the left side, 11 on the right, with a range of 9-13. For both sides combined, malma has a range from 19 to 25 with a mean of 22.6. Counting branchiostegal rays on the right side separated 90% of the confluentus. By combining both sides, the separation was not increased significantly.

repeats data in tables

Fig 4

Mandibular pores - There are usually eight pores of the mandibular sensory canal in S. confluentus with a range of 6-10 (Table 5). Out of 118 individuals examined, 89 (76 percent) had eight or more pores on at least one side. In S. malma there are six or seven pores on a side. Only one individual had as many as eight pores on one side. Elsewhere among the species of Salvelinus, only S. namaycush has a higher mandibular pore count. Morton and Miller (1954) found the lake trout usually has nine or 10 pores on a side with a range from 8-11.

but table shows not one but both sides combined

Basibranchial teeth - S. confluentus characteristically has the basibranchial teeth (usually three to five in number) arranged in a single longitudinal row. Out of 40 individuals, six had no basibranchial teeth. In malma basibranchial teeth are usually more numerous and arranged in one to three rows on the basibranchial plate. A few (three of 35) individuals were found with no teeth. Morton and Miller (1954) found that four out of 20 specimens examined had no basibranchial teeth.

Gill Raker Morphology - After examining large numbers of gill ~~rakers~~ arches from S. confluentus and S. malma, it was found that the form of the raker and the characteristics of its dentition were more important in separating confluentus from malma than actual gill-raker counts, which have been employed so extensively in salmonid taxonomy. Gill raker morphology provided a very high degree of separation of confluentus from malma. Features of the raker that worked best in comparison are the proportions of the rakers and amount of dorso-ventral compression; also, the relative size of the teeth and their presence or absence along the mesial edges of the rakers (that edge that faces the branchial cavity).

The gill rakers of S. confluentus are heavily constructed and oval in cross section. They have strong teeth projecting well out from the mesial edge (Fig. 4C) as well as having smaller teeth on dorsal and ventral surfaces. The raker is ornamented with strong ridges along its lateral margin. S. malma (Fig. 4D) shows a sharp contrast to this type since it has rakers that are strongly compressed dorsoventrally so that the broad surfaces of the rakers are flat and weakly ridged. Usually the rakers possess long tapered tips that are quite delicate. Although there are usually small teeth on these surfaces in malma, the mesial edge lacks the strong projecting teeth entirely.

Body form - The trunk of S. confluentus tends to be slender and rounded with only slight lateral compression (Fig. 5). In S. malma the trunk, like the head, is more laterally compressed. A proportional difference that can serve to separate the two species is found in stepping the head length into the distance from the vent to the base of the tail. The head length nearly always equals or exceeds this distance in S. confluentus, ~~while~~ whereas in S. malma it falls short.

Spotting pattern - The size and distribution of spots are weak characters, although they have been used on North American Salvelinus, especially by early taxonomists. The light spots of S. confluentus are normally smaller than the pupil diameter of the eye, yet large enough to be seen on a fish in clear water. Typically, they cover most of the back and are best developed just in front, to the sides and behind the dorsal fin. Early descriptions of the bull trout by Suckley (1860) and Campbell (1882) made note of these light spots on the back.

Meristic characters - Variation in numbers of vertebrae, gill rakers and pyloric caeca are shown in Tables 6 -8. S. confluentus consistently showed about the same range of variation in these counts as did S. malma, with almost a complete overlap between the two species. The mean numbers of pyloric caeca for confluentus and malma differed by less than two (27.8 and 26.0, respectively). S. confluentus has a high number of vertebrae (mean of 64.8) for the Salvelinus taxa from the Pacific basin . Southern S. malma has a mean of 62.9. The increase in number occurs in the precaudal series (36 vs 39) and probably is correlated with the piscivorous habits of S. confluentus. Other fish-eaters such as species of Esox have a long abdominal cavity to accommodate large prey. The bull trout is characterized by a slightly lower number of gill rakers among North American Salvelinus. The number was found to range between 14 and 20 in S. confluentus with a mean of 17. These figures for the malma studied are 14-21 (23) with a mean of 18.

Osteology - The skeleton of Salvelinus confluentus offers an impressive set of characters that fully separate this species from S. malma. It was an examination ~~in 1968~~ of an osteocranium of a specimen from Flathead Lake that first led me to suspect that the bull trout was different from the coastal Dolly Varden.

The external morphological characters of the head described previously are paralleled by the features of the cranial skeleton. Distinctive differences found are consistent in samples taken from the various drainages where the bull trout occurs. The osteological characters have been carefully checked using dissection methods on preserved material, radiographs of nearly 100 alcohol specimens, cleared and stained material, as well as dry skeletal preparations. The latter have been used for purposes of illustration. A comparative osteological study of the head skeleton in certain *Salvelinus*, including *malma* from the western Pacific basin, has been published by Shaposhnikova (1971, Figs. 10,11). This should be referred to in comparing *confluentus* with *malma*.

The articulated cranium (Fig. 6A) shows the flattened skull roof, elliptical orbit with longitudinal axis much longer than the vertical, the large cavity behind the orbit which was occupied by the adductor muscle of the lower jaw and the massive jaws with strong teeth. The jaw teeth are best developed on the premaxilla, dentary and anterior end of the maxillary alveolar shaft. The latter is curved with its dorsal margin covered posteriorly by a sigmoid-shaped supramaxilla.

Fig 6

The large area for attachment of the adductor mandibulae muscle is made possible by expansion of the lateral hyomandibular surface (Fig. 4A). Because of this expansion, the hyomandibular is one of the most diagnostic of all the cranial elements. Among the *Salvelinus* investigated, the lake trout, *Salvelinus namaycush*, has a similar hyomandibular. The opercle is deep and relatively narrow. Its anterior and posterior borders converge slightly toward the top of the bone and the dorsal margin is rounded. The posterior margin is characteristically crenulated in the adult. Similar crenulations are often found on the posterior subopercular margin. The laminar parts of the preopercle, especially in the vertical limb, are weakly developed; thus, this bone has a rather slender, sickle shape. Often an emargination can be found on the lower posterior border of the preopercle. This may also occur in *S. malma*.

The frontal bones are without much ornamentation and with scarcely an elevation of the midline. In *Salvelinus malma* the frontals are typically gabled as in a barn roof. The heavy covering of fatty tissue over the frontals in this species has given rise to many ridges, pits and cavities as well as causing the pores of the supraorbital canal to be elevated in bony tubes above the surface.

As with the hyomandibular, the supraethmoid (Fig. 7) is also highly diagnostic for the bull trout. Instead of ~~the bone~~ being sharply divided into two parts (head and posterior extension) by a pronounced constriction as in S. malma, the lateral margins of the bone are nearly parallel posteriorly and then taper gradually toward the anterior end. The head is marked by just a slight lateral expansion about halfway along the lateral margin. Both the head and posterior extension of the supraethmoid in S. confluentus are more elongated than in malma and in this respect they approach the condition in S. namaycush. The anterior margins of the ascending processess of the premaxillaries attach along the supraethmoid head and are correspondingly lengthened in S. confluentus. Again, this is a character also found in the lake trout.

The neurocranium (Fig. 6B) is depressed in comparison to that of other Salvelinus, with the parasphenoid only slightly flexed. S. malma possesses a well-developed flexure in the parasphenoid which is consistent with its deeper neurocranium. The lateral profile of the neurocranium showing these characteristics can usually be seen in radiographs taken with the specimens lying flat on their sides.

When observing the palate in S. confluentus, this species like S. malma (Morton and Miller, 1954) does not show a well-developed toothed platform on the vomer. The outline of vomerine teeth usually trace a shallow V. Sometimes these teeth are arranged in a single transverse row. There is always a well-developed gap between the palatine and vomerine tooth rows. This is a consistent feature of S. confluentus while in malma it is variable.

Description of hybrids - Two of nine specimens of bull trout (UMMZ 188852) taken from Long Creek, Lake Co., Oregon, in the upper Klamath basin were identified as hybrids with brook trout, Salvelinus fontinalis (Fig. 8). The hybrids had much darker pigmentation over the head, body and fins than the other seven specimens and the lower fins were tri-colored. Light spots on the flanks were uniformly smaller than those on the flanks of the bull trout. The maxillary bones of the upper jaw were long and straight, a characteristic of the brook trout. Vertebral counts for the hybrids were ~~low~~ intermediate (both with 62) ~~while~~ whereas the Long Creek bull trout ranged from 64 to 66 with a mean of 65. According to Vladykov (1954) brook trout have 58-62 vertebrae with a mean of 59.5. The branchiostegal ray count was high, 13 and 14 on the left side like that of the bull trout, while whereas brook trout usually have 11 on the left side (Vladykov, 1954). All four specimens possessed basibranchial teeth.

Elsewhere hybridization between the bull trout and the brook trout has been mentioned by Paetz and Nelson (1970) in the Clearwater River drainage of Alberta.

Two possible hybrids between S. malma and S. confluentus were identified from lakes in the Skeena River basin, British Columbia. The first individual (UMMZ 159328, 203mm, female) was taken from Swan Lake. It resembles confluentus in the number of branchiostegals (27), and vertebrae (66) and agrees more with malma in number of gill rakers (20) and mandibular pores (13). Gill raker characteristics are intermediate between malma and confluentus. In head form and maxillary shape, the hybrid resembles malma. The second specimen (UMMZ 159333, 188mm, female) from Morrison Lake is very similar in appearance to the Swan Lake individual, especially in its head morphology. It has 24 branchiostegals, 67 vertebrae, 20 gill rakers and 15 mandibular pores. Like the first specimen, the gill rakers are also intermediate in shape and tooth characters between those of malma and those of confluentus. The specimens were collected a year apart, 1945 and 1946.

DISTRIBUTION

Salvelinus confluentus is distributed in a north-south belt along the Rocky Mountain and Cascade ranges of the northwestern part of the continent (Fig. 9). The area stretches from 41°N latitude to 60°N latitude or slightly beyond. Localities plotted are about equally distributed on both sides of the Continental Divide between 50° and 60°N latitude. Major drainages involved in the distribution pattern on the Pacific slope are: The McCloud in the upper Sacramento River basin of California, the upper Klamath in Oregon, the Snake in Oregon, Idaho and Nevada and the upper Snake above Shoshone Falls, the Columbia River throughout its length, the Pend d'Oreille, the Clark Fork of Idaho and Montana, including the Flathead and the Kootenay Rivers of British Columbia; the Fraser River of British Columbia plus Puget Sound in Washington and the Skeena and Taku Rivers of British Columbia. In the Bering Sea drainage, the headwaters of the Yukon at the boundary between British Columbia and the Yukon Territory. On the east side of the Continental Divide, *Salvelinus confluentus* is found in the headwaters of the South and North Saskatchewan Rivers of the Hudson Bay drainage in Alberta and in headwater areas of the Athabaska, Peace and Liard Rivers of the MacKenzie System in Alberta and British Columbia, the latter draining to the Arctic Ocean. No specimens were examined from the Nass, Stikine or Alsek drainages of the Pacific slope of Canada. McPhail's (1961, Fig. 4) data indicate bull trout are in Bowser Lake of the Nass drainage.

The distributional pattern of *Salvelinus confluentus* has been developed principally by headwater migration and drainage crossover. In the northern half of its range this has occurred following the retreat of the last continental ice sheet. Stream capture of the upper Columbia tributaries by those of the Saskatchewan enabled the bull trout to cross to the east side of the Continental Divide along with other salmonids, *Salmo clarki*, *Salmo gairdneri* and *Proscpium williamsoni*. Lindsey (1964) has explained transfer of fishes from the upper Fraser to the Peace River by a drainage block at the time of the continental ice sheet was retreating from northern British Columbia. It is possible that Salvelinus confluentus entered the Taku River by means of migration along the coastal waters, but other species (see McPhail and Lindsey, 1970) entered the Taku from the east through the Liard tributaries or the from the Liard via the Yukon headwaters without any coastal connections. Salvelinus confluentus is known to have entered coastal waters in Puget Sound, Washington, as indicated by ~~from~~ old records made prior to 1900.

Because the bull trout is so thoroughly distributed throughout the Columbia River basin and the fact that this basin borders on others where the bull trout is found, it is likely that this species originated there. Transfer to drainage basins in the southern part of its range, such as the Klamath and Sacramento, may have occurred during ~~or~~ following the last glaciation, but it is possible this distribution follows an older pattern. The isolated records of Salvelinus confluentus in the upper reaches of the Sacramento, Klamath and Snake Rivers do suggest such a pattern. Fossil evidence (Miller, 1965; Miller and Smith, 1967) shows that fish had transferred between the Snake and both the Klamath and Sacramento basins by Early Pleistocene time. These drainage areas lie well south of the boundary for continental glaciation. The Snake or its antecedent is believed to have flowed west during part of its history, connecting with waters of the Klamath (Miller, 1959) and/or the Sacramento (Miller and Smith, 1967; Miller, 1965).

The distribution of the bull trout corresponds in many ways to that of the mountain whitefish, Prosopium williamsoni. The latter species differs in having achieved the headwaters of the Missouri drainage in northwestern Wyoming and western Montana. It also has crossed into the Bonneville and Lahontan basins, ~~as well as into the upper reaches of the Colorado River system in northwestern Colorado~~. The mountain whitefish is not known from

refer to Smith, 1975

reached?

the headwater tributaries of the Yukon drainage (Scott and Crossman, 1973), where the bull trout is present.

There is a possibility that Salvelinus confluentus was at an earlier time in the Bear River of the Bonneville basin as there is testimony of a species of Salvelinus being known in these waters before 1850 (Rostlund, 1951). If this is true it may also have reached the Lahontan basin as did Prosopium williamsoni and has since disappeared. The retreat of Salvelinus confluentus from the southern extremes of its range is occurring today as it probably has in the past. The gradual change in the climate since the Late Pleistocene with the subsequent loss of water once supplied from mountain glaciers and snowfields has been a major factor in eliminating habitats where the bull trout can survive. Once a prominent species in the McCloud River of the Sacramento system in California, the bull trout has gradually declined in number since the late 1800's and is now close to extirpation. Modifications of the watershed environment by man has speeded up the process of population decline many times over.

During all the years since Livingston Stone first called attention to the bull trout of the McCloud River in 1872, very few specimens from the McCloud have been deposited in museums. Fifteen are known to me, including three probably taken on Stone's initial tour of the McCloud. These three specimens, USNM 20816-20818, are in such poor state of preservation that they cannot be removed from their glass container. Another specimen (USNM 15549) labelled Wye-dai-deck-it, the original Indian name for the bull trout in the McCloud Valley was collected by Stone in 1874. Six more (including one skeleton) were sent by Stone to the USNM in 1878 and 1880. The remaining four specimens were taken singly between 1938-1950, one came from the Shasta Hatchery at Mt. Shasta in 1956. These specimens, all small individuals, are housed in the California Academy of Science. The exact locations of capture of Stone's bull trout are not known, although they were probably taken in the vicinity of the trout hatchery on Green's Creek (Wales, 1939) where set lines were placed to catch rainbow trout.

Wales (1939) presented testimony that the bull trout formerly occurred in the upper Sacramento River in the vicintiy of Dunsmuir, Siskiyou Co., and in the Pit River near the mouth of Squaw Creek, Shasta Co. Jordan (1907) listed Upper Soda Springs on the Sacramento River as a locality, but Evermann and Bryant (1919) stated the McCloud River is the only stream in California in which the bull trout is known to be native.

Campbell (1882) reported bull trout from the junction of the McCloud with the Pit River upstream to Big Springs. The latter is a source of melt water from snowfields on Mt. Shasta which yields a nearly constant flow of cold water at 45°F (Wales, 1939). Although Campbell had fished the entire stream extensively, he never took bull trout above the lower falls where he reported the water temperature as being warm, from 60°F to 70°F, on the hottest days. Downstream at the fish hatchery on Green Creek, the river water was stated by Campbell to be 55°F to 60°F at midday in the hottest weather and from the hatchery up to the Big Spring the river gets "one degree colder about every 10 or 12 miles for the distance of 65 or 70 miles".

Several early records from Oregon and Washington indicate the bull trout was once more widely distributed on the Pacific side of the Cascade and Coast ranges than it appears to be today. Jordan (1879) examined Livingston Stone's collections from the Clackamas River, Oregon, which contained the bull trout based on Jordan's description. Specimens taken from Puget Sound by Jordan and others in the 1880's are assignable to either Salvelinus confluentus or S. malma. The head of Suckley's (1858) type of Salmo confluentus is a bull trout taken from a Coast Range drainage (Pullayup River) that empties into Puget Sound. Cope (1879) reported one of the earliest records for "Salvelinus spectabilis" from the Klamath basin. The USNM skeleton and skin (No. 15793) collected at Linn Creek, Ft. Klamath in 1876 may be Cope's specimen. The earliest confirmed record for _S. confluentus_ is the holotype collected in 1854 from The Dalles on the lower Columbia River, where impoundments and undesireable habitat for the bull trout exist today.

DISCUSSION

The main objective of this paper is to provide evidence for the separation of Salvelinus confluentus from Salvelinus malma, in particular, that part of malma that ranges south from southern Alaska on the eastern side of the Pacific basin in North America. The systematics of S. malma throughout its range in Alaska and the North Pacific basin are too lengthy and complicated a subject to be included here and will be treated elsewhere.

Are there valid reasons for considering the bull trout a full biological species? This is the most important question regarding the taxonomy of this form. The evidence presented here in favor of full species recognition is as follows: 1) The character states investigated that separate confluentus from malma are constant throughout a broad geographical area occupied by confluentus indicating one relatively stable population with a homogeneous gene pool; 2) stability is further indicated by the fact that variation of all characters investigated is minimal when compared to other recognized species of Salvelinus; 3) even though the ranges of malma and confluentus overlap in the Pacific slope drainages from northern California to southern Alaska, there is no evidence of introgression in the material studied. Sympatry of malma and confluentus is indicated by specimens examined of both species from the Sacramento Basin of California, Puget Sound, Washington, Skeena Basin of British Columbia and Taku Basin of southern Alaska and northern British Columbia. Both malma and confluentus were identified from the Yukon Basin; however, the malma came from the Tanana drainage of central Alaska and the confluentus from the extreme headwaters in British Columbia of Canada. A full case for sympatry and a complete understanding of how confluentus and malma exist together will probably come from a study of these forms in the Skeena Basin of British Columbia. Both appear to be disseminated throughout these waters where considerable study of the "Dolly Varden" has already taken place.

In the Skeena drainage (Fig. 9, insert), specimens of S. confluentus were studied from the following lakes: Lakelse, Damschilgwit (Cabin), Morrison, Morice, Slamgeesh, Bear and Sustat. Specimens of S. malma came from Johanson and Alastair Lakes. Two hybrid suspects between malma and confluentus came from Swan and Morrison Lakes. Although the hybrids indicate both species probably occur in some lakes, it is possible that certain of the lakes may contain only one of the species pair. Larger samples from the lakes may be helpful in determining to what extent hybridization is taking place. In the Taku River S. malma was taken fourteen miles upstream from the mouth at Canyon Island where Meehand and Siniff (1962) reported downstream migration of juvenile Dolly Varden in 1961. S. confluentus was taken at a further distance inland in a small tributary of the Taku River (Flannigan Slough). The Taku River collections suggest the malma and confluentus may be ecologically separated with anadromous malma occupying most of the lower drainage, especially Twin Lakes, the lower main channel and the river mouth and confluentus being restricted to certain small tributaries, such as Flannigan Slough and perhaps the headwaters.

Of nine Puget Sound specimens examined, five were S. malma taken in the Sound at Port Townsend, Washington, 1884. Labelling, as well as their silvery pigmentation, indicated they were sea run individuals. The other four specimens are S. confluentus. Two of these were taken by D.S. Jordan, 1880, and labelled Puget Sound. The third was taken in Elliot Bay at Seattle in 1889 and the fourth was captured in a freshwater tributary to Puget Sound at Ft. Steilacoom in 1856. Jordan's specimens are two of an original ten sent to the United States National Museum and may have originated from his work on the fishes of Puget Sound (Jordan and Starks, 1895).

S. confluentus appears to be distributed throughout the MacKenzie basin in British Columbia and Alberta. No material was available from the Nahanni

River, part of the Liard drainage in the Northwest Territories. Unfortunately, only one specimen of *S. malma* was found in samples from the MacKenzie. This specimen had characteristics of *malma* and the possibility of it belonging to *S. alpinus* does not seem likely.

McPhail (1961) demonstrated the existence of northern and southern forms of *S. malma* in North America. The northern form occurs in the coastal drainages of the Bering Sea north to Seward Peninsula. Specimens corresponding to the northern form have been examined for this study from the Yukon basin of central Alaska. These specimens also resemble the *malma*-like char described as *Salvelinus anaktuvukensis* by Morrow (1973) from the north slope of the Brooks Range, Alaska. Data taken from these *Salvelinus* were not used in making comparisons with *confluentus*. McPhail (1961) stated that head size would not distinguish the form which Jordan et al (1930) called *Salvelinus malma spectabilis*. However, if McPhail's data (1961, Fig. 4) on head size are reexamined in light of the present work, it can be seen that the samples shown to have the longest heads (~~Bowser Lake~~, Cottonwood River, Sage Creek, ~~and~~ Glacier National Park and probably also Bowser Lake in the Nass drainage) are from localities where *S. confluentus* is found. Except for the Taku River where *confluentus* and *malma* may have been mixed, the other samples represent *S. malma* and show an average smaller head size. Much of McPhail's material was reexamined for this study. The samples of *confluentus* from the Taku River drainage were found to be smaller headed with respect to samples of *confluentus* from other localities, including the adjacent Yukon basin. Taku River basin *confluentus* live at the extreme end of the northern dispersal route as transfer to this basin probably took place from the Liard via the Yukon headwaters or directly from the western reaches of the Liard. At the end of the southern dispersal route in the Sacramento basin, the McCloud River population of *confluentus* possessed the largest head size and were also distinguished in having a greater percentage of individuals (50% of those examined) lacking basibranchial teeth. These teeth are nearly always present in other confluentus Only one specimen outside of the McCloud River was found to lack basibranchial teeth. Jordan (1879) at one time recognized the McCloud River population as a separate species (*Salvelinus bairdii* (Suckley)) on the basis of this character.

Small head size distinguished the two specimens collected in 1872 from the McCloud River that are identified as *S. malma*. In other characters, such as the 18 gill rakers, compressed body, straight maxilla and supraethmoid type, they resemble *S. malma*. Silver pigment on their sides indicated they may have been anadromous individuals. In the shape of their gill rakers and head form they are not typical of *S. malma* but the rotted condition of these specimens prevented further study. Of the coastal collections, *S. malma* from Puget Sound, Washington and the Soleduck River of Washington's Olympic Peninsula were geographically closest to the McCloud River specimens. Those taken from Puget Sound in the 1880's were anadromous and compared closely with *malma* from further north along the coast of British Columbia. The Soleduck River specimens represent a population isolated above a high falls. The largest individual measured 135 mm. They differed from anadromous *malma* in their larger heads and low vertebral and gill raker numbers. It appears likely that prior to 1900, *S. malma* ranged south along the Pacific Coast to California and may have been fairly common in Washington's coastal waters of Puget Sound (Jordan and Starks, 1895; Dymond, 1942).

Radiographs of 112 *Salvelinus confluentus* showed about 13% with whole fish in their stomachs. These probably had been ingested not too long before capture. Sculpins made up the majority of these stomach contents, but at least two bull trout had eaten other salmonids. Fewer *S. malma* had stomach contents containing fish. Some *malma* had eaten gastropods, a food not seen in the stomachs of *S. confluentus*. One 380mm *S. confluentus* examined from the Finlay River near Ft. Grahame, British Columbia (NMC 66-437), had completely swallowed a 215mm individual of its own species. Two bull trout from northern British Columbia had eaten small mammals (one a shrew and the other a rodent). Fish eating habits of the bull trout have been noted by Jeppson and Platts (1959), Godfrey (1955), Bjornn (1961), Ricker (1941) and Thompson and Tufts (1967). See also Armstrong and Morton (1969) for summaries of other food studies of the bull trout which follow these names: Bjornn ~~(1957)~~, ~~Ricker (1941)~~, Webb ~~(1965)~~ and Withler ~~(1948)~~. Scott and Crossman (1973) have recently reviewed the food habits of the bull trout under their section on the Dolly Varden. According to Brown (1971) the principal food of the adult bull trout is fish, although it will utilize other vertebrates of suitable size, such as frogs, snakes, mice and ducklings.

Characters of the jaws, teeth and head of S. confluentus which differ from those of S. malma are best explained as adaptations to a piscivorous habit. The larger area for jaw muscle insertion, more powerful jaws and teeth, the curved maxilla, the elongate hyoid bar with higher branchiostegal counts, the high number of mandibular sensory pores and the longer head of the supraethmoid for articulation of the extended premaxillary ascending processes are features paralleled in the lake trout, S. namaycush - a species well-known for its piscivorous diet.

The direction of evolution in S. confluentus has been away from a diverse predator, such as anadromous malma toward a more specialized fish-eating mode of existence entirely in freshwater. The changes in the head and component bones are the easiest to document but there are probably marked behavioral and ecological differences between confluentus and malma that have not as yet been studied. Most of the similarities pointed out above between the bull trout and the lake trout are considered as parallel developments and do not provide evidence of a close relationship.

CONCLUSIONS

The bull trout was first described in 1856 by C.F. Girard from a specimen collected at The Dalles, Oregon on the lower Columbia River. Girard's specific name "spectabilis" does not stand because of the rules of zoological nomenclature pertaining to homonyms. The name campbelli was substituted by Suckley, who described the bull trout three more times under the names, "confluentus","bairdii"and"parkei". In 1882 Jordan and Gilbert included the above names except confluentus in the synonomy of Salvelinus malma ~~(Walbaum)~~ where they have remained to the present time. In the event of formal species recognition for the bull trout, its scientific name becomes Salvelinus confluentus (Suckley) and the common name, Dolly Varden, applies to Salvelinus malma (Walbaum).

Evidence for specific distinction of the bull trout is found in a series of osteological, morphometric and meristic characters that remain relatively constant throughout its distributional range including areas that overlap with the range of Salvelinus malma. The appearance of the head and jaws, head length, number of branchiostegal rays and the morphology of the gill rakers are the easiest characters to use in separating the bull trout from Salvelinus malma. The shape of the supraethmoid bone is highly diagnostic for the bull trout but it must first be exposed through removal of overlying tissue. The shape of the neurocranium and hyomandibular are also distinctive. Additional osteological characters are found in the maxilla, premaxilla, ceratohyal, opercle and frontal bones of the skull.

The cranial structures in the bull trout that differ from those of malma are interpreted as modifications toward a more piscivorous mode of existence in freshwater. The changes are genetic and have occurred through the long process of selection and adaptation. By no means can they be construed as environmentally-induced somatic changes.

The life history of the bull trout differs significantly from that of malma in being almost completely non-anadromous throughout its known range. Ecological and behavioral differences between the two are expected but as yet have not been studied.

The bull trout is widely distributed in montane lake and stream habitats on both sides of the Continental Divide between 50° and 60° N latitude. It appears to have an affinity for cold waters fed by mountain glaciers and snowfields. In the deglaciated part of its range in western Canada the bull trout has dispersed from the Columbia River basin through headwater transfer and crossover following the retreat of the Cordilleran ice sheet in Late Wisconsin time. The distribution pattern to the south of the ice sheet may be much older. Populations of bull trout in the Sacramento, Klamath and southern Snake River drainages all show signs of depletion. Their failure to maintain recruitment may in part be due to hybridization and introgression with the introduced eastern brook trout, *Salvelinus fontinalis*.

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Legends to Tables

Table 1. Distribution and variation of head size shown as a ratio of standard length to head length in Salvelinus confluentus and Salvelinus malma.

Table 2. Comparison of head size in Salvelinus confluentus and Salvelinus malma in relation to body size and sex. Head size shown as ratio of standard length to head length.

Table 3. Distribution and variation of branchiostegal ray number for left and right sides in Salvelinus confluentus and Salvelinus malma.

Table 4. Distribution and variation of branchiostegal ray number with left and right sides combined in Salvelinus confluentus and Salvelinus malma.

Table 5. Distribution and variation of mandibular pore number in Salvelinus confluentus and Salvelinus malma.

Table 6. Distribution and variation of vertebral number in Salvelinus confluentus and Salvelinus malma.

Table 7. Distribution and variation of gill raker number in Salvelinus confluentus and Salvelinus malma.

Table 8. Distribution and variation in number of pyloric caeca in Salvelinus confluentus and Salvelinus malma.

TABLE 1: Variation in Head Size
Shown as Proportion of Standard Length

Salvelinus confluentus

DRAINAGE	NUMBER	RANGE	MEAN
McCloud River, California	12	3.2-3.9	3.6
Klamath River Basin, Oregon	5	3.5-4.1	3.8
Columbia River Basin Snake River drainage	11	3.6-4.7	3.8
Columbia River Basin (excluding Snake drainage) Puget Sound, Fraser River Basin	23	3.3-4.1	3.7
Skeena River Basin	10	3.5-4.0	3.7
Taku River Basin	5	3.7-4.1	3.9
Yukon River Basin	7	3.6-4.0	3.7
MacKenzie River Basin	25	3.5-4.1	3.7
Saskatchewan River Basin	13	3.5-4.0	3.7
TOTAL	111	3.2-4.1 (4.7)	3.73

Salvelinus malma

DRAINAGE	NUMBER	RANGE	MEAN
McCloud River, California	2	4.5-4.7	4.6
Soleduck River, Washington	5	3.8-3.9	3.9
Puget Sound, Washington	4	4.2-4.6	4.35
Skeena River Basin	3	3.9-4.5	4.1
Coastal British Columbia	14	3.5-4.5	4.2
Taku River Basin	7	3.5-4.6	4.1
Gulf of Alaska, Kodiak Island, Coastal Streams and Islands	20	3.6-4.7	4.3
TOTAL	55	3.5-4.7	4.23

TABLE 2 : Head Size in Relation to Body Size and Sex.
Shown as a proportion of Standard Length

Salvelinus confluentus

STANDARD LENGTH	NUMBER	RANGE	MEAN
50 - 100 mm	5	3.3-3.8	3.63
101 - 150 mm	20	3.4-3.9	3.62
151 - 200 mm	27	3.2-4.0	3.67
201 - 250 mm	24	3.5-4.1	3.74
251 - 300 mm	15	3.6-4.1	3.82
301 - 350 mm	11	3.5-3.9	3.70
351 - 568 mm	10	3.6-4.1	3.86
♀ (200-568 mm)	20	3.5-4.0	3.73
♂ (200-423 mm)	18	3.5-4.0	3.73

Salvelinus malma

STANDARD LENGTH	NUMBER	RANGE	MEAN
50 - 100 mm	10	3.3-4.1	3.63
101 - 150 mm	10	3.8-4.3	4.00
151 - 200 mm	10	3.6-4.5	4.16
201 - 250 mm	9	3.9-4.7	4.36
251 - 300 mm	14	4.0-4.7	4.38
301 - 445 mm	8	3.8-4.7	4.40
♀ (200-380 mm)	12	4.1-4.7	4.46
♂ (200-445 mm)	10	3.8-4.4	4.10

TABLE 3 : NUMBER OF BRANCHIOSTEGAL RAYS

Salvelinus confluentus

		LEFT									RIGHT								
DRAINAGE BASIN	N	10	11	12	13	14	15	16	MEAN	S.D.	9	10	11	12	13	14	15	MEAN	S.D.
McCloud River, California	10				2	4	4		14.20	0.74				1	1	7	1	13.80	0.74
Klamath Basin, Oregon	7				3	4			13.57	0.49					5	2		13.29	0.45
Columbia Basin, Snake River	12				5	3	4		13.91	0.86				1	7	4		13.25	0.59
Columbia Basin, Fraser River, Puget Sound	30			1	3	16	9	1	14.23	0.80				1	12	14	3	13.63	0.70
Skeena Basin	10				3	6	1		13.80	0.60					6	4		13.40	0.48
Taku Basin	5				4	1			13.20	0.40					4	1		13.20	0.40
Yukon Basin	7					4	3		14.43	0.49						5	2	14.29	0.45
MacKenzie Basin	26				12	8	6		13.77	0.79				1	12	12	1	13.50	0.63
Saskatchewan Basin	13			2	6	3	2		13.38	0.92				5	4	4		12.92	0.82
TOTAL	120			3	38	49	29	1	13.89	0.82				9	51	53	7	13.48	0.71

Salvelinus malma

		LEFT									RIGHT								
DRAINAGE BASIN	N	10	11	12	13	14	15	16	MEAN	S.D.	9	10	11	12	13	14	15	MEAN	S.D.
Soleduck River, Washington	11	1	3	7					11.54	0.65		2	9					10.82	0.38
Puget Sound, Skagit River	7	2	3	1	1				11.14	0.98		3	2	2				10.86	0.83
Skeena River Basin	3			2	1				12.33	0.47			3					11.00	0.00
Coastal British Columbia	15	1	3	9	2				11.80	0.74		1	8	6				11.33	0.59
Taku River	7		5	1	1				11.43	0.72		2	4	1				10.86	0.63
Gulf of Alaska , Coastal Drainages and Islands	32	1	10	17	4				11.75	0.70		7	18	7				11.00	0.66
Aleutians	13	3	4	5	1				11.31	0.91	1	5	5	2				10.62	0.83
TOTAL	88	8	28	42	10				11.61	0.80	1	20	49	18				10.95	0.68

TABLE 4 : NUMBER OF BRANCHIOSTEGAL RAYS

Salvelinus confluentus

DRAINAGE BASIN	N	19	20	21	22	23	24	25	26	27	28	29	30	31	MEAN	STANDARD DEVIATION
		BOTH SIDES COMBINED														
McCloud River, California	10								2	1	2	5			28.00	
Klamath Basin, Oregon	7								3	2	2				26.86	0.83
Columbia Basin, Snake River	12							1	4	3		4			27.17	1.40
Columbia Basin, Fraser River, Puget Sound	30							2	1	10	7	8	1	1	27.83	1.31
Skeena Basin	10								2	5	2	1			27.20	0.87
Taku Basin	5								3	2					26.40	0.48
Yukon Basin	7										3	3	1		28.71	0.69
MacKenzie Basin	26								10	6	4	5	1		27.27	1.25
Saskatchewan Basin	13						2	3	3	1	2	2			26.31	1.68
TOTAL	120						2	6	28	30	22	28	3	1	27.37	1.38

Salvelinus malma

DRAINAGE BASIN	N	19	20	21	22	23	24	25	26	27	28	29	30	31	MEAN	STANDARD DEVIATION
		BOTH SIDES COMBINED														
Soleduck River, Washington	11			2	3	6									22.36	0.77
Puget Sound, Skagit River	7		2	1	1	2		1							22.00	1.69
Skeena River Basin	3					2	1								23.33	0.47
Coastal British Columbia	15			2		9	2	2							23.13	1.08
Taku River	7			2	3	1		1							22.28	1.27
Gulf of Alaska, Coastal Drainages and Islands	32		1	6	4	14	3	4							22.75	1.29
Aleutians	13	1	2	3	1	4	1	1							21.92	1.68
TOTAL	88	1	5	16	12	38	7	9							22.57	1.36

TABLE 5 : NUMBER OF MANDIBULAR PORES

Salvelinus confluentus

DRAINAGE	N	BOTH SIDES COMBINED 10	11	12	13	14	15	16	17	18	19	20	MEAN	STANDARD DEVIATION
Mc Cloud River, California	5					1	1	2	1				15.60	1.01
Klamath Basin, Oregon	7			1	1	4	1						13.71	0.88
Columbia Basin, Snake River Drainage	12				1	1	6	2	2				15.25	1.08
Columbia Basin, Fraser Basin, Puget Sound	33					4	4	12	4	6	3		16.39	1.45
Skeena Basin	11							6	3	2			16.64	0.77
Taku Basin	5					1		3	1				15.80	0.97
Yukon Basin	7					1	4	1	1				15.29	0.88
MacKenzie Basin	25				2	4	8	7	4				15.28	1.14
Saskatchewan Basin	13			2	1	5	2	2			1		14.46	1.78
TOTAL	118			3	5	21	26	35	16	8	4		15.57	1.49

Salvelinus malma

DRAINAGE	N	BOTH SIDES COMBINED 10	11	12	13	14	15	16	17	18	19	20	MEAN	STANDARD DEVIATION
Soleduck River, Washington	11		1	7	3								12.18	0.57
Puget Sound, Skagit River	7		2	4		1							12.00	0.92
Skeena River Basin	3			3									12.00	0.00
Coastal British Columbia	15		1	11	2	1							12.20	0.65
Taku River Basin	7			7									12.00	0.00
Gulf of Alaska, Coastal Drainages and Islands	32	1	5	18	5	2	1						12.16	0.97
Aleutians	12	1	2	6	3								11.91	0.86
TOTAL	87	2	11	56	13	4	1						12.10	0.80

TABLE 6 : NUMBER OF VERTEBRAE

Salvelinus confluentus

DRAINAGE	N	58	59	60	61	62	63	64	65	66	67	68	69	70	MEAN	S.D.
McCloud River, California	4					1	2	1							63.00	0.70
Klamath Basin, Oregon	7							1	4	2					65.14	0.63
Columbia Basin, Snake River	10							2	4	4					65.17	0.70
Columbia Basin, Fraser River, Puget Sound	17						2	4	9	2					64.64	0.83
Skeena Basin	11							3	5	2	1				65.09	0.89
Taku Basin	5								5						65.00	0.00
Yukon Basin	7								3	4					65.67	0.49
MacKenzie Basin	25						1	9	14	1					64.60	0.63
Saskatchewan Basin	12							4	7	1					64.75	0.59
TOTAL	98					1	5	24	51	16	1				64.81	0.84

Salvelinus malma

DRAINAGE	N	58	59	60	61	62	63	64	65	66	67	68	69	70	MEAN	S.D.
Soleduck River, Washington	11				4	4	3								61.91	0.79
Puget Sound, Skagit River	2						1	1							63.50	0.50
Skeena River Basin	3				1	1	1								62.00	0.81
Coastal British Columbia	14				2	6	3	2	1						62.57	1.11
Taku River	4					1	1	2							63.25	0.82
Gulf of Alaska, Coastal Drainages, and Islands	28					5	8	11	2	2					63.57	1.19
Aleutians	16			2	2	2	3	4	2	1					62.94	1.74
TOTAL	78			2	9	19	20	20	5	3					62.94	1.71

TABLE 7 : NUMBER OF GILL RAKERS

Salvelinus confluentus

DRAINAGE	N	13	14	15	16	17	18	19	20	21	22	23	24	25	MEAN	S.D.
McCloud River, California	12				4	6	2								16.83	0.68
Klamath River Basin	7				2	1	2	2							17.57	1.17
Columbia Basin, Snake River Drainage	12		1	1	3	5	2								16.50	1.11
Columbia Basin, Fraser Basin	28		1	3	13	6	3	1	1						16.50	1.23
Skeena River Basin	10		1	2	4	3									15.90	0.94
Taku River Basin	5					1	3	1							18.00	0.63
Yukon River Basin	7		1		3	2	1								16.28	1.16
MacKenzie Basin	26			2	10	8	4	1	1						16.81	1.14
Saskatchewan Basin	13		1	2	4	4	2								16.31	1.14
TOTAL	120		5	10	43	36	19	5	2						16.64	1.19

Salvelinus malma

DRAINAGE	N	13	14	15	16	17	18	19	20	21	22	23	24	25	MEAN	S.D.
McCloud River, California	1						1								18.00	0.00
Soleduck River, Washington	11				1	5	4	1							17.45	0.78
Puget Sound, Skagit River, Washington	7				1	1	4	1							17.71	0.88
Skeena River Basin	3						2		1						18.67	0.94
British Columbia, Coast	15			1	1	3	5	3	1	1					18.00	1.46
Taku River Basin	7				1		3	1	1	1					18.57	1.50
Gulf of Alaska, Coastal Islands and Drainages	30				1	4	7	10	3	4		1			18.90	1.57
Aleutians	13		2	3	3	1	1	2	1						16.46	1.91
TOTAL	92		2	4	8	14	30	20	7	6		1			18.08	1.58

TABLE 8 : NUMBER OF PYLORIC CAECA

Salvelinus confluentus

DRAINAGE	N	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	MEAN	S.D.
McCloud River, California	6				1		1	2	1		1										25.00	1.82
Klamath Basin	1				1																22.00	0.00
Columbia Basin, Snake River	9				1	1	1	1		2	1						2				27.11	4.12
Columbia Basin, Fraser River, Puget Sound	20				1	1		1	2	2	2	2	7	1				1			28.30	2.88
Skeena Basin	7							1			1	1	1	1				2			30.43	3.37
Taku Basin	5					1		1	1	1	1										25.80	1.72
Yukon Basin	6							1	1		1	1	1				1				28.67	2.92
MacKenzie Basin	24			1		1		2	5	4	4	1	3	1	2						27.42	2.59
Saskatchewan Basin	12				1			3		1	2					2	2		1		29.17	4.41
TOTAL	90			1	5	4	2	12	10	10	13	5	12	3	2	2	5	3	1		27.82	3.44

Salvelinus malma

DRAINAGE	N	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	MEAN	S.D.
Soleduck River, Washington	11	3		3	1			3	1												22.09	2.57
Puget Sound, Skagit River	8			1	1					2	1	1	1	1							26.88	3.37
Skeena River Basin	1											1									29.00	0.00
Coastal British Columbia	12			1				3	3	1	1	1		2							26.67	2.68
Taku River	7						1		1	3	1						1				27.57	2.87
Gulf of Alaska, Coastal Drainages and Islands	28					1	2	4	4	2	5	2	3	1	2	1	1				27.82	2.91
Aleutians	11			1	2		2	1	2	1	1					1					25.27	3.22
TOTAL	79	3		6	4	1	5	11	11	9	9	5	4	4	2	2	2				26.04	4.56

Legends to Figures

Figure 1. (A) Type of "Salmo confluentus" Suckley 1858, USNM 1135, head length 173mm, Pullayup R. near Steilacoom, Washington; (B) head (lateral and ventral view) of spawning male Salvelinus confluentus, NMC 66-70, estimated 550mm standard length, Deer Cr., Brit. Col.; (C) lateral and ventral view of head, spawning male Salvelinus malma, UMMZ 126507, 295mm, Karluk R., Kodiak I., Alaska.

Figure 2. Comparison of head form (lateral, dorsal, ventral and frontal views) in the adult female of (A) Salvelinus confluentus, NMC 66-437, 580mm, Finlay R. trib., Brit. Col.; (B) Salvelinus malma, UMMZ 126507, 289mm, Karluk R., Kodiak I., Alaska.

Figure 3. Comparison of head form (frontal, lateral, dorsal views) in (A) Salvelinus confluentus, OSUM 25212, 235mm, female, trib. of S. Fork Flathead R., Montana; (C) Salvelinus confluentus, UMMZ 188857, 134mm, male, trib. of Clearwater R., Montana; (B) Salvelinus malma, OSUM 25213, 138mm, female, trib. Karluk R., Kodiak I., Alaska.

Figure 4. Comparison of skeletal elements (A) right hyomandibular from Salvelinus confluentus, UMMZ 188857, 130mm, trib. Clearwater R., Montana; (B) right hyomandibular from Salvelinus malma, UMMZ 93829, 140mm, Soleduck R., Washington; (C) most posterior gill raker of first arch, right side (ventral view, left; dorsal view, right) from Salvelinus confluentus, UMMZ 17248, 285mm, Flathead L., Montana; (D) comparable gill raker from Salvelinus malma, UMMZ 128983, 312mm, King Cove, Alaska.

Figure 5. Body form and pigmentation in Salvelinus confluentus (A) UMMZ 188857, 134mm, juvenile, trib. Clearwater R., Montana; (B) OSUM 25212, 235mm, juvenile, trib. S. Fork Flathead R., Montana.

Figure 6. (A) Osteocranium of Salvelinus confluentus, UMMZ 172458, head length 112mm, Flathead L., Montana; (B) neurocranium of same individual, dorsal, ventral and lateral views.

Figure 7. Comparison of supraethmoids in Salvelinus malma (A-C) and Salvelinus confluentus (D-F). Not drawn to same scale; (A) UMMZ 126507, 286mm, female, Karluk R., Kodiak I., Alaska; (B) UMMZ 106259, 383mm, female, Unalaska I., Alaska; (C) UMMZ 106259, 485mm, female, Unalaska I., Alaska; (D) UMMZ 159333, 227mm, male, Morrison L., Brit. Col.; (E) UMMZ 172458, est. 490mm, Flathead L., Montana; (F) UMMZ 172458, est. 420mm, Flathead L., Montana.

Figure 8. Two hybrid individuals, below (Salvelinus confluentus X S. fontinalis) compared with two S. confluentus, above; all from same catch, Long Cr., Lake Co., Oregon.

Figure 9. Distribution of Salvelinus confluentus and Salvelinus malma over same latitudinal range in North America; plotted from localities of specimens examined.

Fig. 1

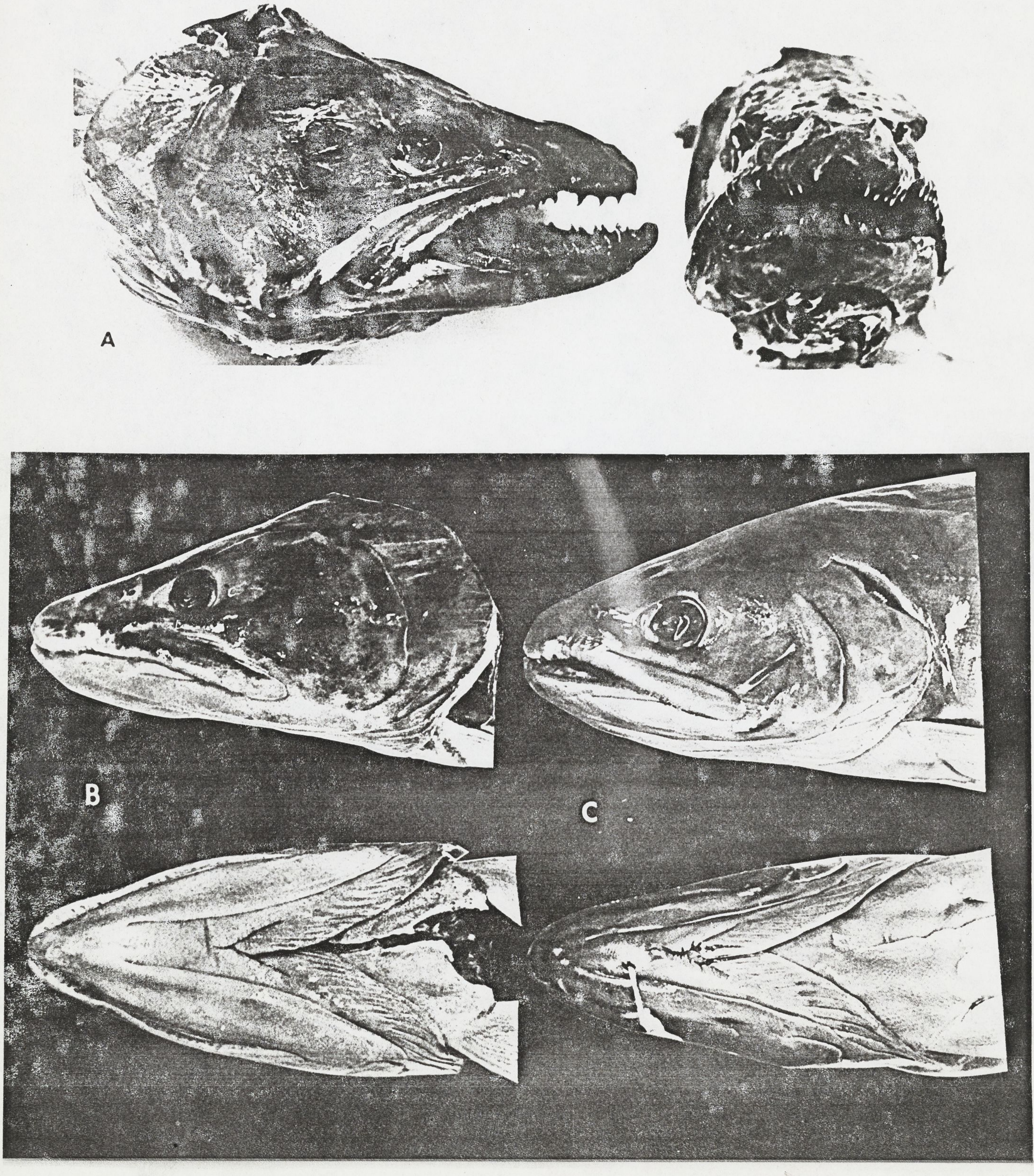


Fig 2

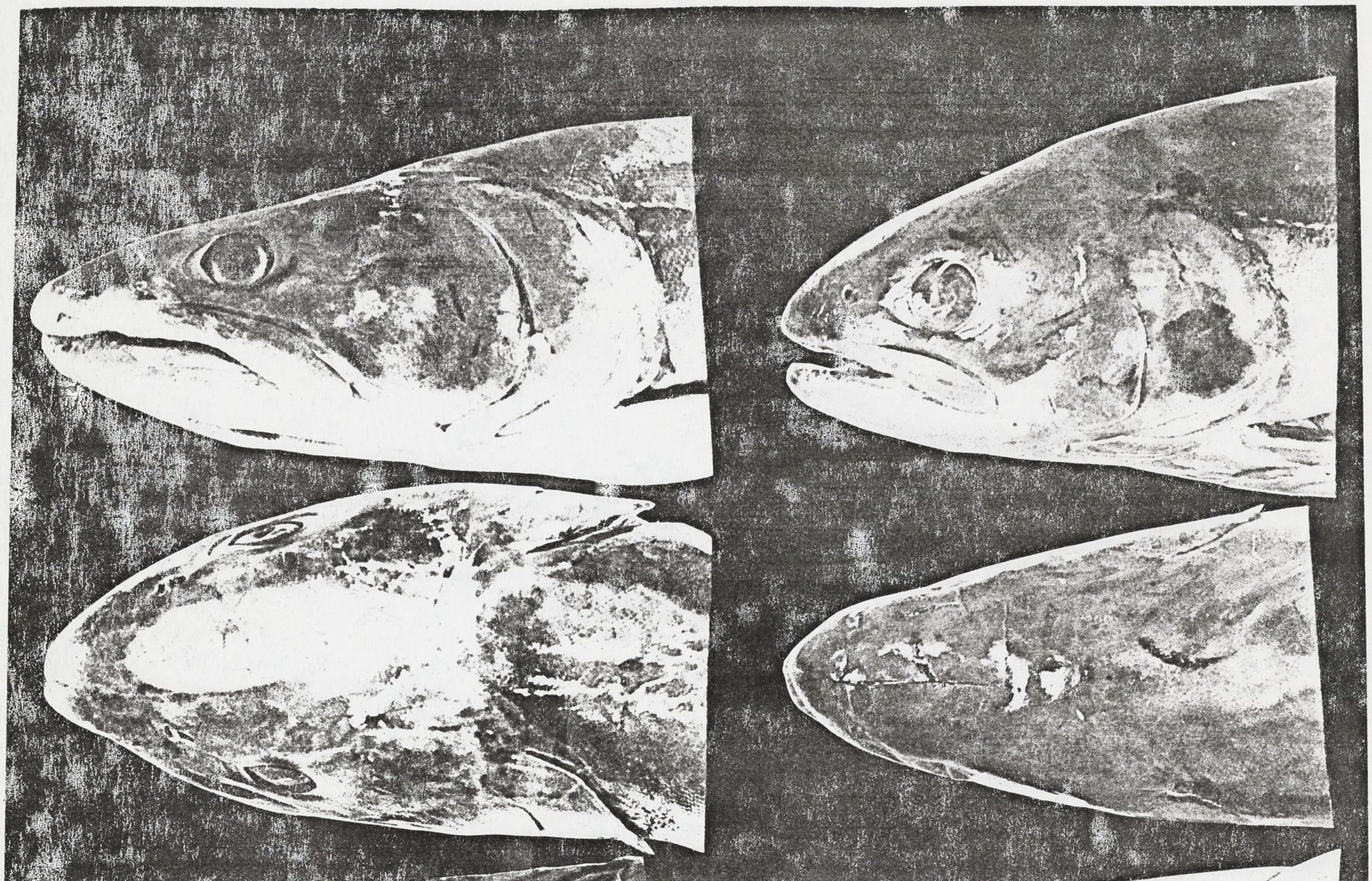
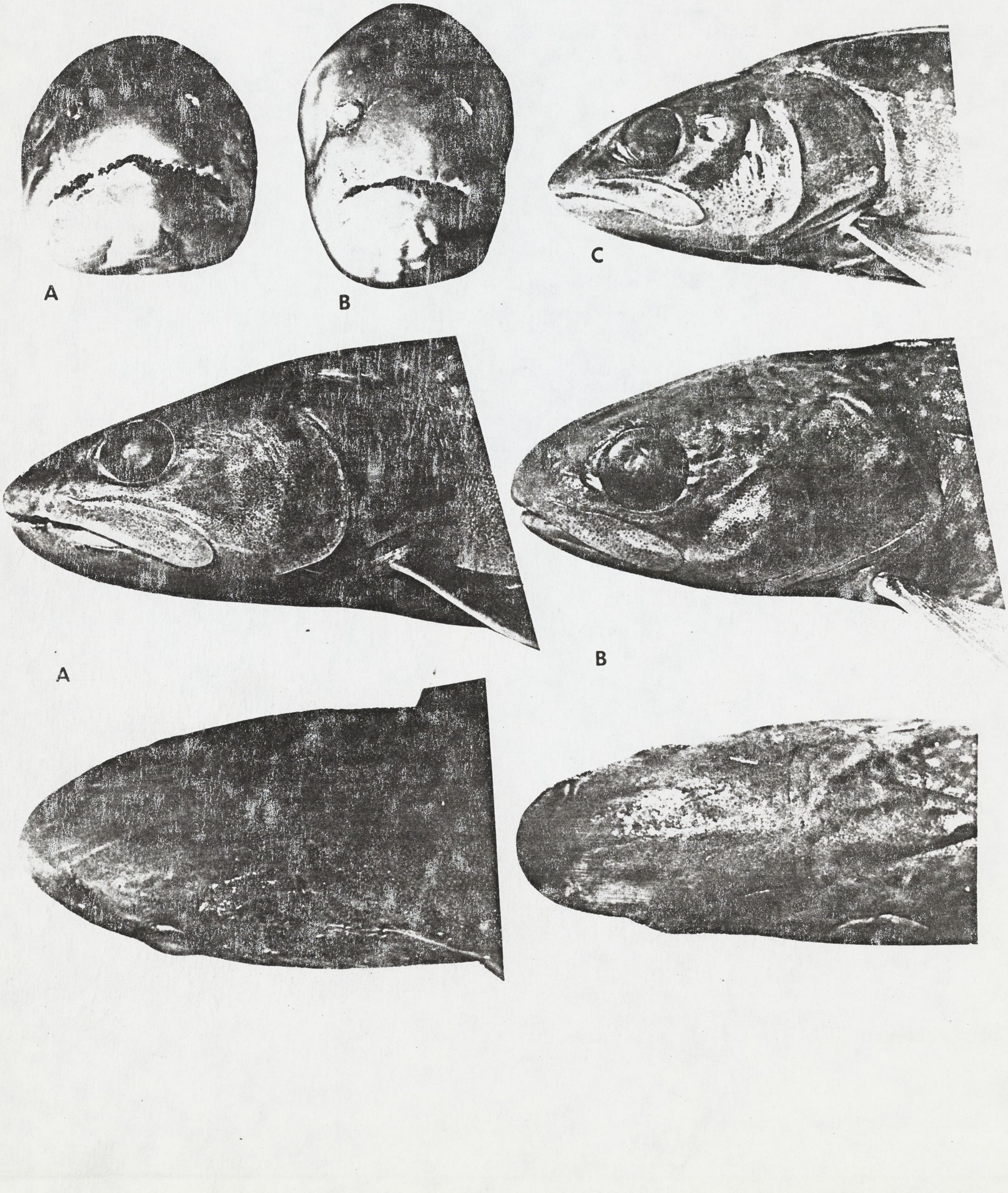


Fig 3



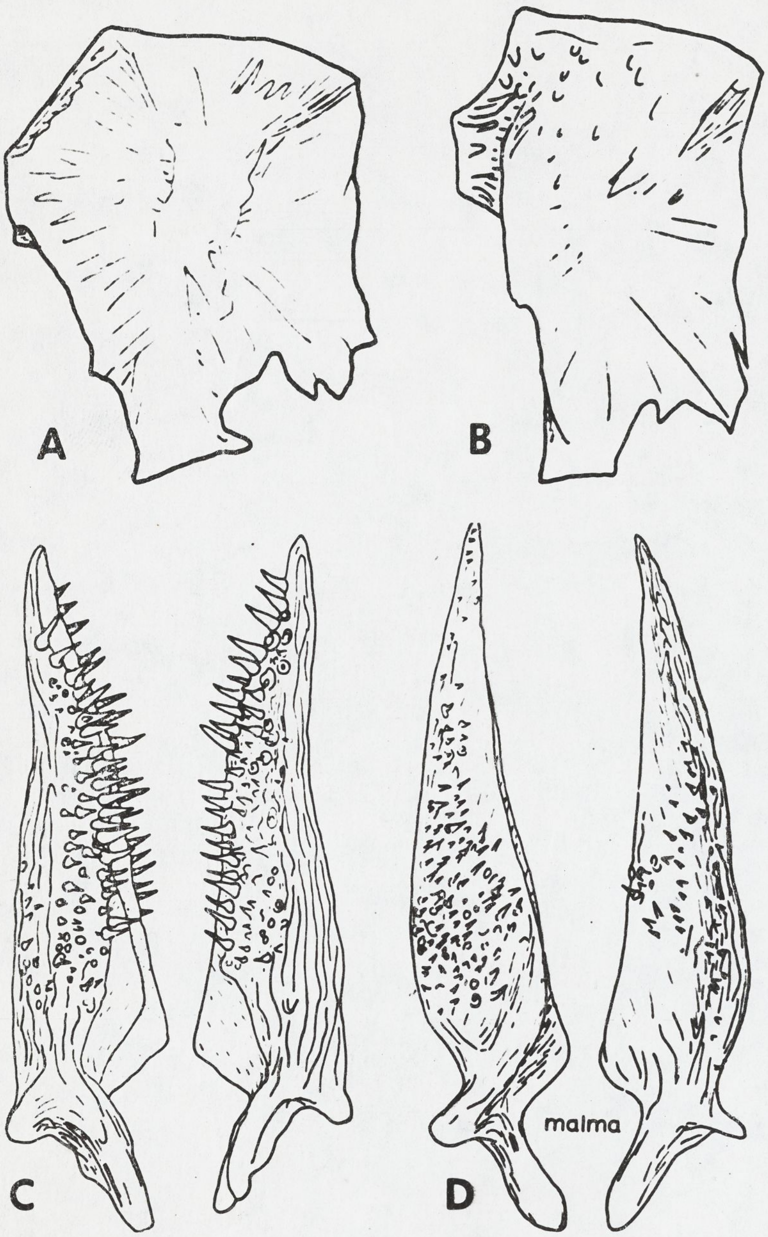
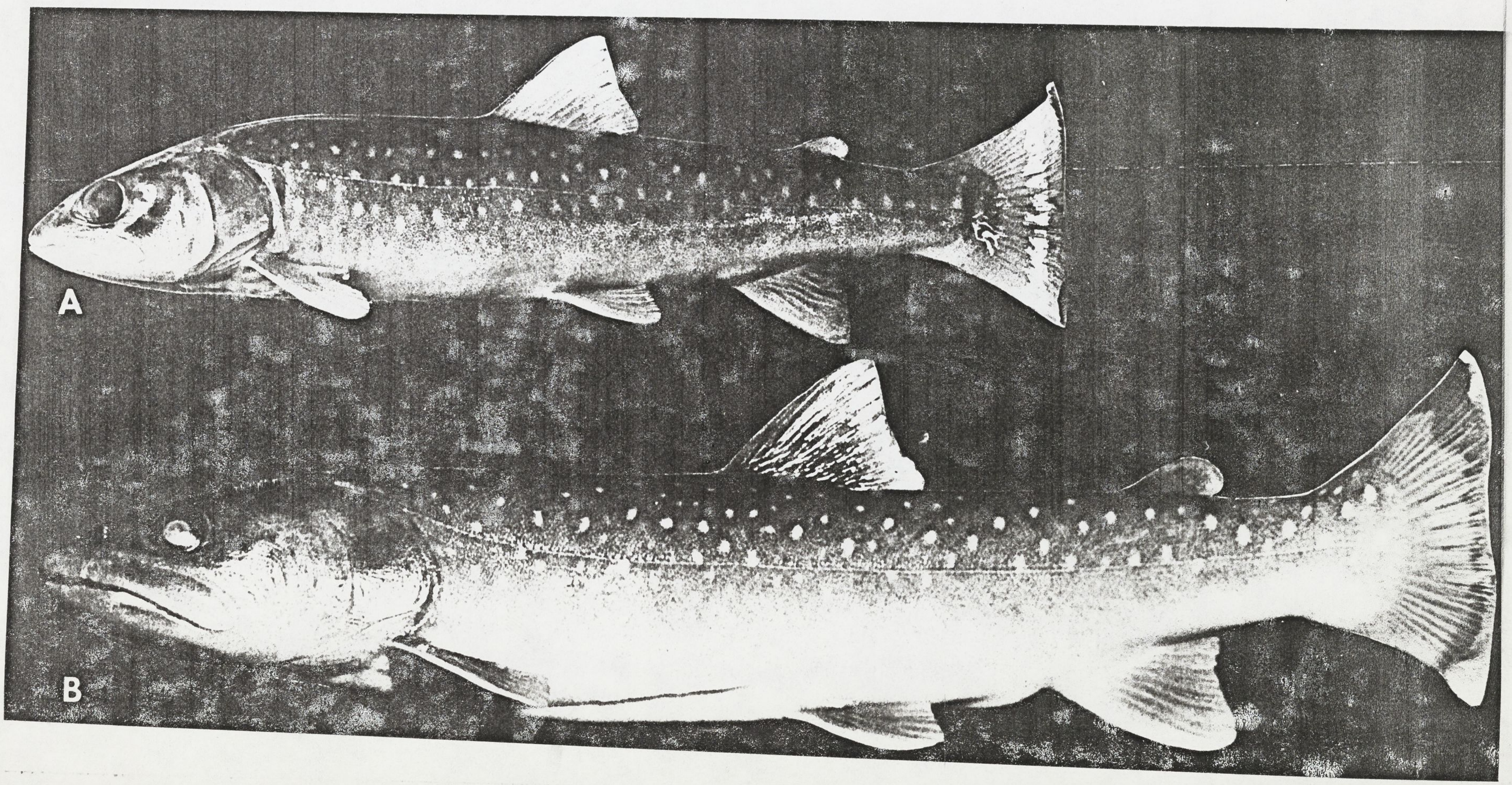


Fig. 4

Fig 5



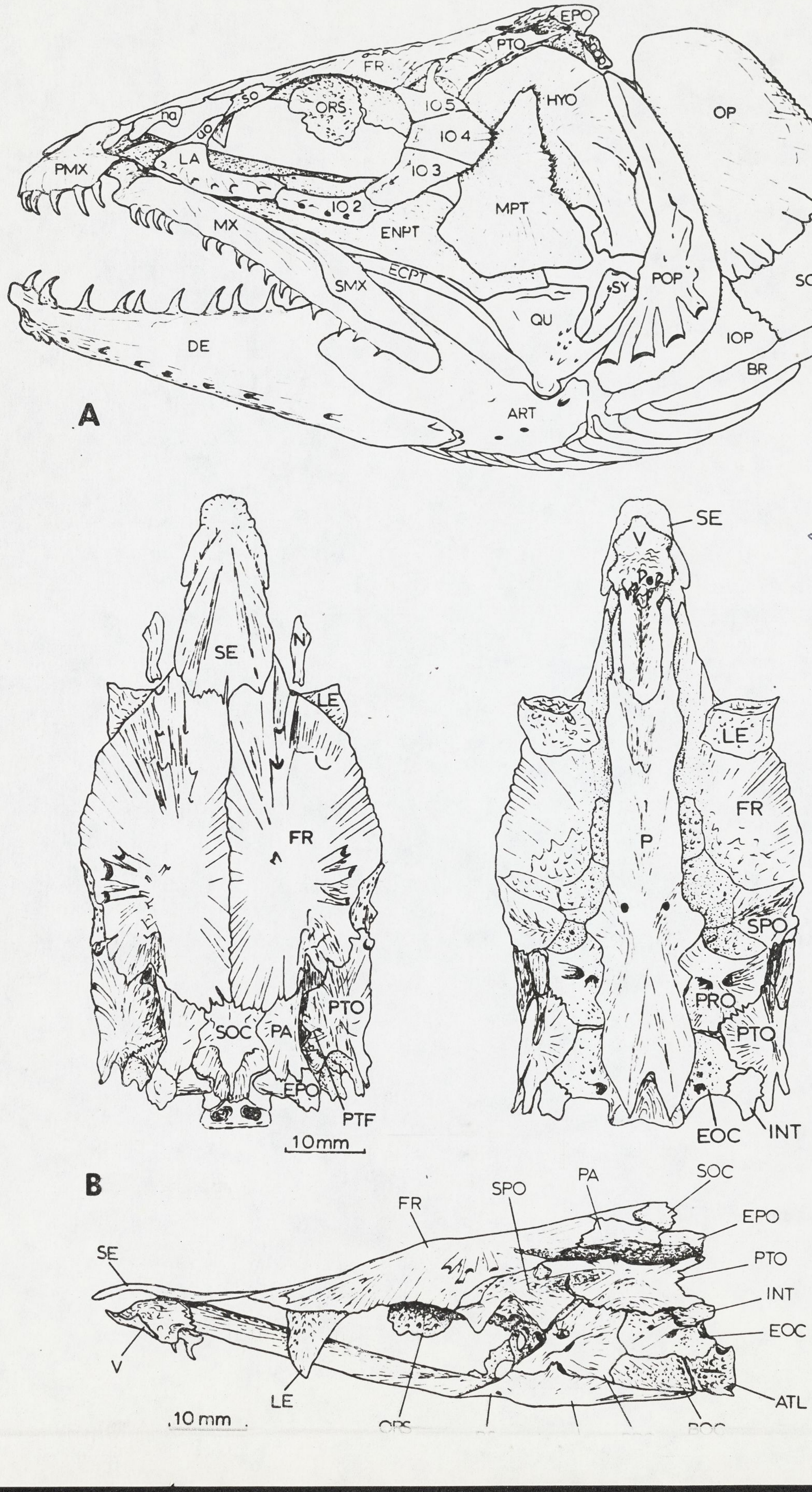

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Fig. 6

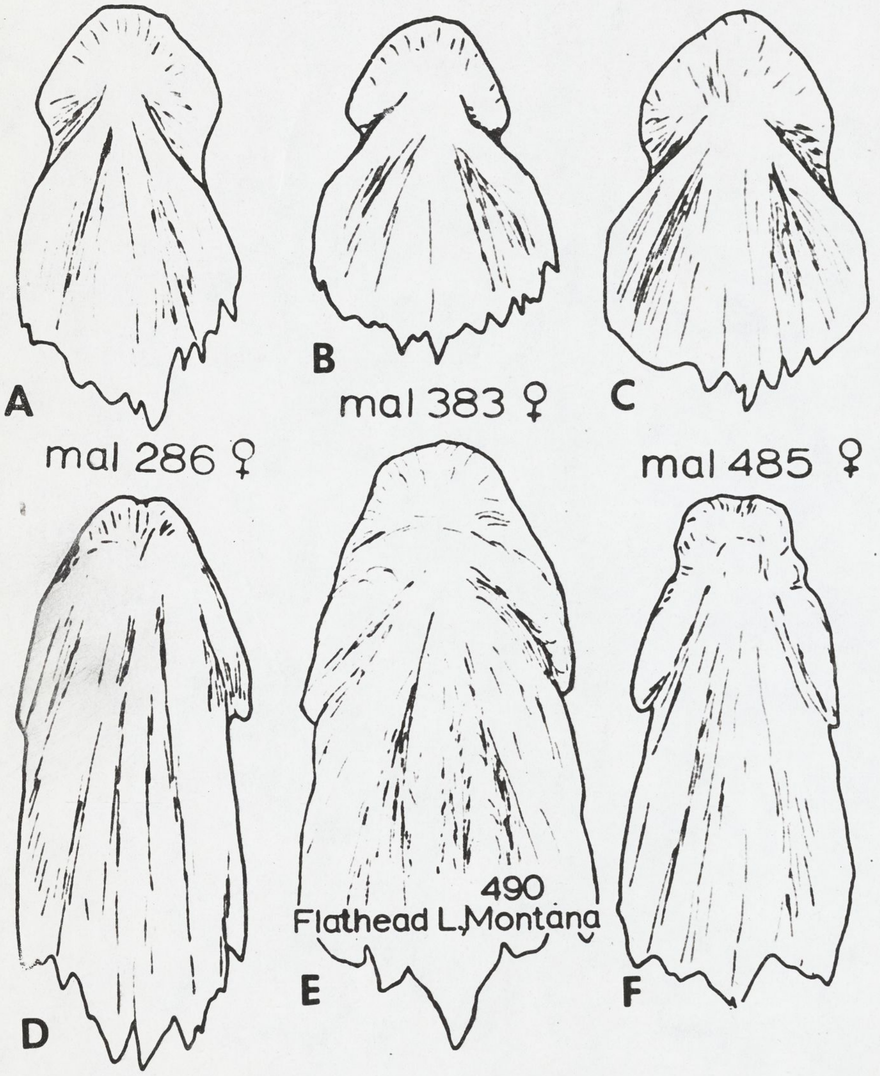


Fig 7

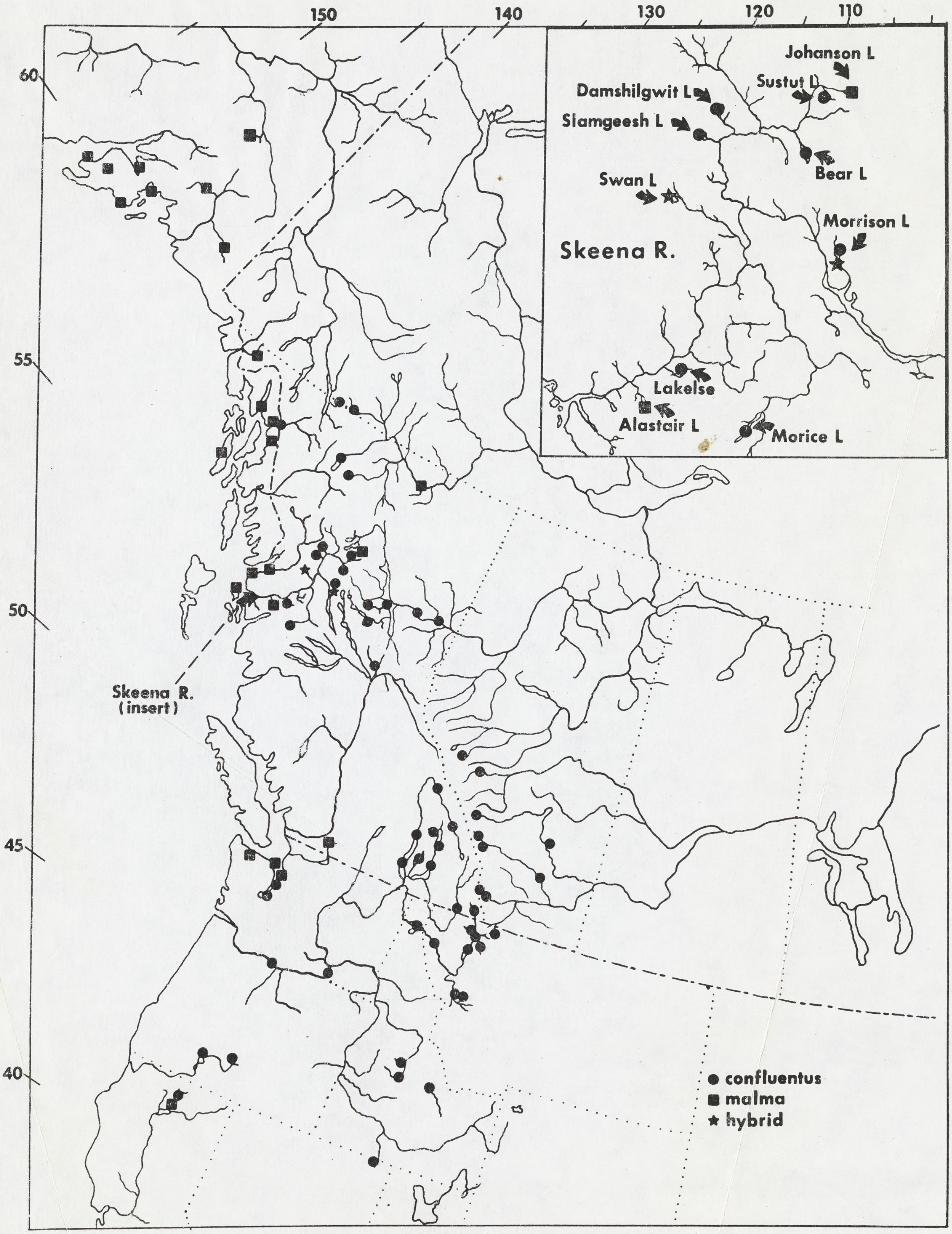
Fig. 7

[illegible]

Fig. 8

Fig. 8

Fig. 9



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Johanson L
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Slamgeesh L
Bear L
Swan L
Morrison L
Skeena R.
Lakelse
Alastair L
Morice L
Skeena R.
(insert)
confluentus
malma
hybrid

THE OHIO STATE UNIVERSITY

18 November 1976

Dr. Robert Behnke
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, Colorado 80521

Dear Bob,

I'd like to thank you for your time and help during my visit to Colorado State University. Your trout collection and research results have provided me with a much better understanding of the Salmo taxa now present in the western United States.

The x-rays and specimens arrived here in good shape. Enclosed is a list of the specimens from your collection that I brought back to Ohio State. Some of the labels may not have been copied correctly. If there are individuals you would like returned or don't want me to skeletonize, please let me know.

Mailed separately is a copy of the first draft of my Salvelinus manuscript. Difficult parts, like the Taxonomic History, have been rewritten and the second draft is now at the California Academy of Sciences. I'm working on a second paper dealing with just the McCloud River Salvelinus. My notes taken at the USNM indicate the S. malma were collected Nov., 1872 when Stone collected both in the San Francisco Bay area and on the McCloud River. Do you know what species is referred to by Stone's designation "Silver Trout"?

I will be sending you some osteological character descriptions and illustrations that seem to work in western Salmo. Hybridization creates intermediate conditions in skeletal characters. Subtle distinctions are easily done away with. Some of the morphological similarities among the different taxa may be independent adaptations to headwater environments. I find a range of variation within Salmo clarki that includes the ranges of S. gilae and S. apache for most characters.

If I understand your latest papers correctly, you believe the redband is close to the ancestral Salmo that gave rise to the rainbow. Could you clarify the phylogenetic position of the golden, cutthroat, apache and Gila trouts in relation to the above two species?

Sincerely,

Ted

Ted M. Cavender

College of Biological Sciences / Museum of Zoology / 1813 North High Street / Columbus, Ohio 43210 / Phone (614) 422-8560

Specimens from Dr. Robert Behnke

<u>Salmo</u> <u>aguabonita</u> 2 specimens

WYOMING: Deep Creda Lake or Deep Creel Lake ?
electroshock
August (?)

<u>Salmo</u> <u>clarki</u> <u>pleuriticus</u> 4 specimens

WYOMING: Sublette Co., Little Sandy Cr. above L. Sandy Lake, Green River basin.
Dunning
1971

<u>Salmo</u> <u>clarki</u> ssp. 2 specimens

OREGON: Malheur Co., Whitehorse Cr. in Whitehorse Canyon, Alvord Basin, Hasford, Oregon.
22 July 1972

<u>Salmo</u> <u>clarki</u> <u>stomias</u> 1 specimen

COLORADO: Boulder Co., Island Lake, head of North Boulder Creek.
Turnbull
6 July 1970

<u>Salmo</u> <u>clarki</u> <u>stomias</u> 4 specimens 2 taken from each of 2 jars

COLORADO: Boulder Co., (North Boulder Creek?) downstream section
1975 or 1976 ?

<u>Salmo</u> <u>clarki</u> <u>virginalis</u> 4 specimens

NEW MEXICO: Rio Chiquito, tributary to Rio Taos, Rio Grande Basin, south of Taos, New Mexico, Sangre de Cristo Mtns., Carson National Forest.
Dean
4 May 1966

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Bull Trout

First Class

~~Manuscript~~

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MWC

brook trout hybrids ~ Long Cabs

rainbow → Col → Missouri

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