Morphologically distinct populations of the shorthead sculpin, *Cottus confusus*, and mottled sculpin, *Cottus bairdi* (Pisces, Cottidae), near the western border of Canada and the United States

ALEX E. PEDEN AND GRANT W. HUGHES
Royal British Columbia Museum, Victoria, B.C., Canada V8V 1X4

AND

W. E. ROBERTS
Department of Zoology, University of Alberta, Edmonton, Alta., Canada T6G 2E9

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Previously known within Canada from the Flathead River, nominal *Cottus confusus* also occur in the Kettle, Columbia, and Slocan rivers of British Columbia. The latter populations are similar to those from Washington, and possess a postmaxillary pore, lower numbers of pectoral rays, prickles behind the pectoral fin, and a smooth head. They are sympatric with nominal *Cottus bairdi*, with some individuals morphologically intermediate between the two species. Flathead River samples of nominal *C. confusus* differ from Columbia River populations in absence of the pore and prickles, higher fin ray counts, and larger head papillae. Specimens of nominal *C. bairdi* previously reported from the St. Mary River (Saskatchewan and Nelson drainages) and Milk River (Missouri River drainage) of Alberta are similar to Flathead River *C. confusus*, with others intermediate between Flathead River *C. confusus* and Columbia River populations of *C. bairdi* and *C. confusus*. Differences between Flathead River and Columbia River samples suggest that these populations require separate status in Canada. Similkameen River samples of *C. bairdi* are morphologically variable, individuals from upstream populations having some characters similar to those of *C. confusus*. A thorough study of *C. bairdi* and *C. confusus* in the United States is needed to redefine species limits.

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Déjà connue au Canada dans la rivière Flathead, l'espèce nominale *Cottus confusus* vit égalcment dans les cours d'eau Kettle, Columbia et Slocan en Colombie-Britannique. Les poissons de ces dernières populations sont semblables à ceux du Washington et possèdent un pore postmaxillaire, un nombre réduit de rayons pectoraux, des épines derrière la nageoire pectorale et leur tête est lisse. Ces populations vivent en sympatrie avec des poissons reconnus comme *Cottus bairdi* et certains individus sont de morphologie intermédiaire entre les deux espèces. Les populations de *C. confusus* de la rivière Flathead diffèrent des populations du Columbia car elles ne possèdent ni pore, ni épines, le nombre de leurs rayons est plus élevé et leurs papilles céphaliques sont plus grandes. Certains des spécimens appelés *C. bairdi* au cours d'études antérieures dans la rivière St. Mary (bassins de la Saskatchewan et de la Nelson) et dans la rivière Milk (bassin du Missouri) en Alberta sont semblables aux *C. confusus* de la Flathead et d'autres sont intermédiaires entre les *C. confusus* de la Flathead et les populations des *C. bairdi* et *C. confusus* du Columbia. Les différences entre les échantillons de la Flathead et ceux du Columbia semblent indiquer que ces populations requièrent des statuts différents au Canada. Les *C. bairdi* de la rivière Similkameen sont variables morphologiquement : les individus des populations des eaux d'amont ont certaines caractéristiques communes avec *C. confusus*. Une étude approfondie des *C. bairdi* et des *C. confusus* des populations américaines s'impose, car il faut redéfinir les limites entre les deux taxons.

[Traduit par la revue]

Introduction

The shorthead sculpin, *Cottus confusus* (Bailey and Bond 1963), was previously recognized in Canada only from the Flathead River (Carl et al. 1959; McAllister and Lindsey 1961; Scott and Crossman 1973; Hughes and Peden 1984), and its Canadian status was further considered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (see Peden and Hughes 1984) to be threatened by proposed coal mining. Another species, *Cottus bairdi*, was also recorded from the Similkameen and Kettle rivers (Carl et al. 1959; McAllister and Lindsey 1961; Scott and Crossman 1973). However, this form, originally described as *Cottus hubbsi* (Bailey and Dimick 1949), was later thought by Bailey and Bond (1963) to be conspecific with eastern populations of *C. bairdi*, with a wide geographic gap through central North America separating eastern and western *bairdi*. Bond (1963) further recognized *C. b. punctulata* as representing populations from the northern Rocky Mountains of the United States and *C. b. semiscaber* those from the Great Basin and Columbia River of the northwestern United States. More recently, one of us (W.E.R.) identified *C. confusus* from specimens caught in the Canadian segment of the Columbia River (Fig. 1) by R. L. and L. Environmental Services Ltd. of Edmonton, Alberta. They were later recorded by Ash et al. (1982, pp. 3 and 110). Because these new specimens were difficult to separate from specimens of sympatric *C. bairdi* (= *C. hubbsi*?), and might affect previously published conclusions on geographic distribution, systematic relationships (Bailey and Bond 1963; Hughes and Peden 1984), and perceived rarity of the species in Canada (Peden and Hughes 1984), we gathered as many specimens as we could to assess the relationships of these taxa.

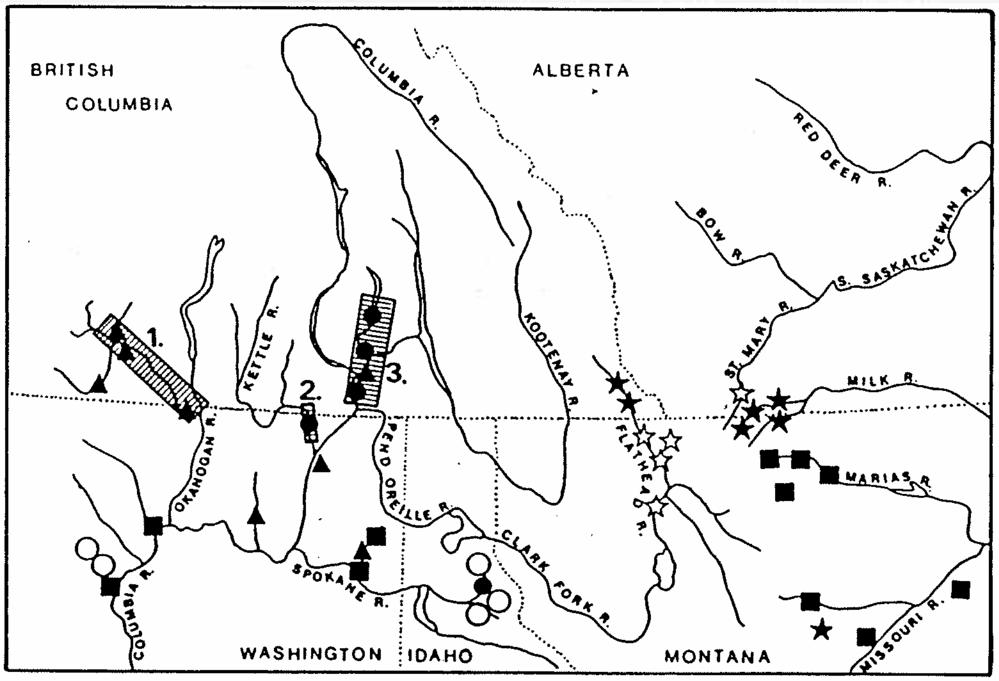

FIG. 1. Distribution of nominal *Cottus bairdi* and nominal *C. confusus* in western Canada and northwestern United States. Enlargements of areas 1, 2, and 3 can be seen in Figs. 16, 7, and 13, respectively. ●, ○, our samples and literature records, respectively, of western form of *Cottus confusus*. ★, ☆, our samples and literature records, respectively, of either eastern nominal *C. confusus* or *C. bairdi* of Flathead River and Missouri River drainages; ▲, ■, samples and literature records, respectively, of nominal *C. bairdi* and (or) *C. hubbsi* (records from the Missouri River drainage must be reexamined to determine whether they represent the eastern form of *C. confusus*).

Materials and methods

Features either known from the literature or thought to be possibly diagnostic were chosen for principal component factor analysis (Nie et al. 1975). In preliminary sorting, specimens were provisionally identified as *C. confusus* or *C. bairdi*. The following characters were then recorded:

Head length (HL) was measured from posterior end of soft tissue on operculum to anterior tip of snout (including premaxillae in the retracted position).

Fin ray count (and *standard length* (SL)) followed the methods of Hubbs and Lagler (1964).

Lateral line pore count included each opening between ossified lateral line elements plus the pore posterior to the most posterior element. When specimens were observed under a binocular microscope, a weak jet of compressed air was used to remove liquid. Anteriorly, the pores were well formed and oriented slightly downward between ossified elements. Posteriorly, the lateral line was degenerate in most specimens although a few had the lateral line complete to the base of the caudal skeleton. In many specimens, the lateral line was interrupted, without pores under the posterior part of the dorsal fin but having one or more ossified canal elements, with associated pores occurring near the caudal peduncle. Specimens from the Flathead River were usually devoid of such posterior pores. If the ossified elements and associated tissue formed a groove there were no pores to count, but if they formed a tube, the pore consequently formed posteriorly was counted. If the tubular elements were widely separated there was the appearance of two pores forming between adjoining elements, but only one pore was used to account for each lateral line element. These counts not only describe the relative size and spacing of lateral line elements within the standard length of specimens, but also indicate the degree of degeneracy of the lateral line.

There was an apparent increase in lateral line elements with growth (Fig. 2), but the size and age at which the number of pores is fixed were not determined in this study. As a rule of thumb we accepted 40 mm SL as the minimum size for which to include counts, but where sample sizes were small (i.e., Slocan and Columbia rivers), specimens down to 35 mm were included.

The *postmaxillary pore* represents a single pore immediately above the preoperculo-mandibular series and behind the maxilla. Bailey and Bond (1963) report variation in other head pores which should be analyzed in future studies.

The *third preopercular spine* (Fig. 3) is absent or reduced in most *C. confusus* (Bailey and Bond 1963). When present, it varies in size and degree of development. As a preopercular fossa occurs between each pair of spines, a spine was determined to be absent if it was missing between the third and fourth fossae down the preopercular margin. A value of 1 was given if the spine had an acute angle of less than 90°, 1/2 if blunt and greater than 90°, and 0 if the preopercular margin had little or no protuberance.

Papillae on top of head, if present, covered the entire occiput between the eyes and back of the skull and were judged in the context of comparison with sympatric congeners within the same river system (i.e., *C. cognatus* and *C. confusus* in the Flathead River, and *C. bairdi* and *C. confusus* in the Columbia, Slocan and Kettle rivers). Those with papillae had much looser skin over the occiput, whereas those with smooth heads had tauter skin. Although fish under 40 mm SL may have less development of papillae, these structures were obvious when present in larger specimens. If a thick film of preserved mucus covered the head, this was scraped off for easier observation.

Presence or absence of prickles behind the axil of the pectoral fin was a subjective character because some may be partly embedded and difficult to see. One of us (W.E.R.) found that some prickles may be lost with age in Alberta populations; however, our comparisons of populations with relatively similar sized specimens should minimize this source of variation. We recorded prickles as present if they were obvious without dissection or special treatment (a needle was scraped over surface, if required) and partly present if only 6–10 were visible.

Specimens from the following collections were used for analysis: UAMZ, collections housed at the University of Alberta Museum of

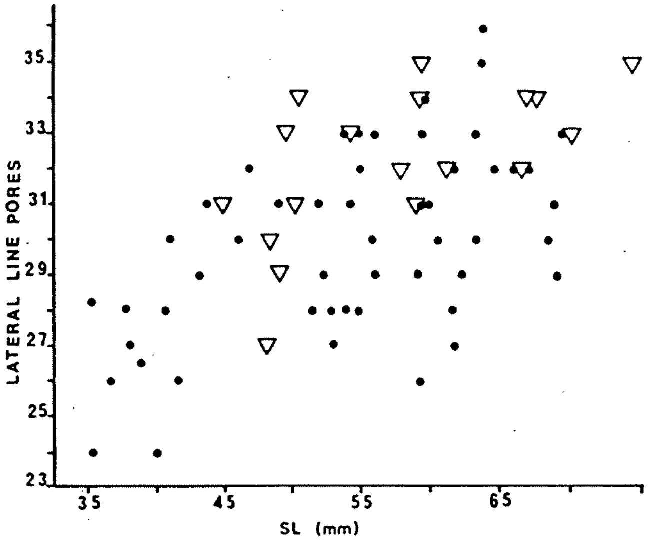

FIG. 2. Relationship of lateral line pore number and standard length (SL) in nominal *Cottus bairdi* of the Similkameen River. ●, upstream samples from Wolfe, Hayes, and Otter creeks, plus Tulameen River; Δ, downstream samples at or below the Canadian – United States international border (see Fig. 16 for sample localities).

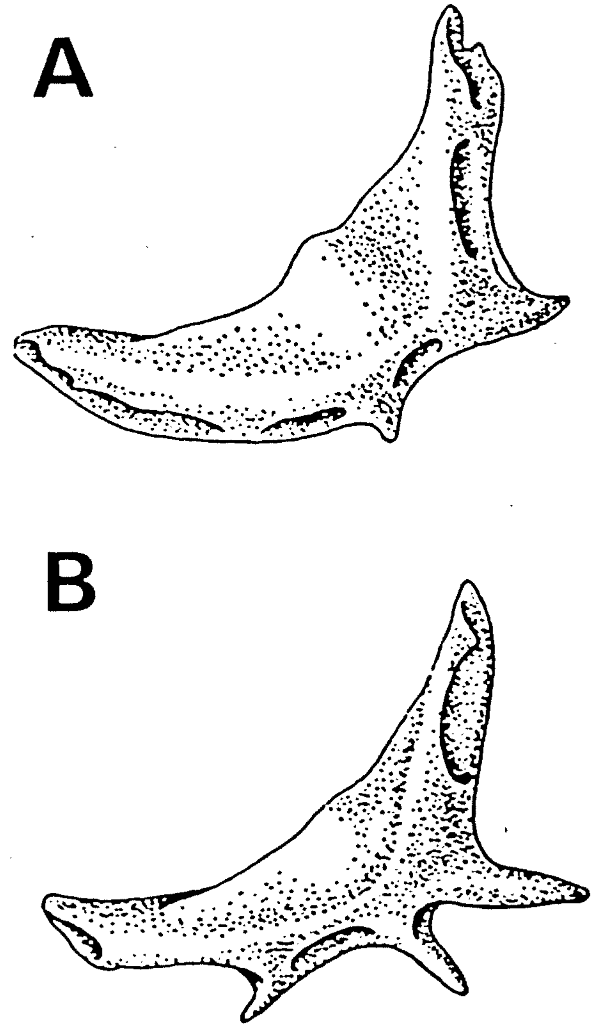

FIG. 3. Left preopercular bone of *Cottus*. (A) Typical *C. confusus*. (B) *Cottus extensus* (similar to that of *C. bairdi*). Reconstructed from Bailey and Bond (1963).

Zoology; BCPM, Royal British Columbia Museum, formerly British Columbia Provincial Museum; NMC, National Museum of Natural Sciences, formerly part of the National Museums of Canada; UBC, University of British Columbia. The number of specimens is indicated in parentheses; an asterisk indicates a specimen used in the analysis).

Milk River, Alberta: NMC 66-421 (5), 2 mi (1 mi = 1.609 km) W of Del Bonita, North Fork of Milk River; NMC 67-662 (1), 8 mi W of Del Bonita, Milk River; *NMC 67-664 (17), 9 mi W of Del Bonita, north fork of Milk River; NMC 79-905 (16), 13 km W of Del Bonita, north fork of Milk River.

Milk River, Montana: NMC 66-429 (2), 20 mi E of Babb, north fork of Milk River; NMC 67-667 (1), near Del Bonita, but 5 mi S of Port of Entry, south fork of Milk River.

Flathead River, British Columbia: *BCPM 981-163 (38) (see Hughes and Peden (1984) for other material observed).

Columbia River area, British Columbia: nominal *C. confusus* from lower Columbia River drainages: *UAMZ-6328 (4), Pass Creek (= Norns Creek?); BCPM 988-864 (33), BCPM 988-883 (10), above normal flood level of Columbia River in Norns Creek; *UAMZ-6601 (1), Creek P285; *UAMZ-6602 (2) and 6603 (3), Blueberry Creek; *BCPM 983-1691 (1), Columbia River, 4 mi N of U.S. border; *BCPM 983-1694 (2), mouth of Beaver Creek; BCPM 988-885 (65), BCPM 988-888 (24), above normal flood level of Columbia River in Beaver Creek. Slocan River area: *BCPM 987-334 (3), at Slocan; *BCPM 985-220 (3), near Passmore; *BCPM 986-16 (7), second bridge upstream on road to Slocan; *BCPM 986-15 (8), mouth of Slocan River. Nominal *C. bairdi* from Columbia River: *BCPM 986-14 (1), 1st Avenue in Castlegar; *BCPM 987-358 (11), near Beaver Creek; *BCPM 983-1691 (1), 4 mi N of U.S. border; Kootenay River: *BCPM 987-349 (1), opposite mouth of Slocan River; *BCPM 987-349 (8), in reservoir at bridge on main road above South Slocan Dam.

Columbia River drainage, Washington: BCPM 988-900 (38), nominal *C. confusus* from first riffle and pools in Sheep Creek, above Columbia River, opposite Northport.

Kettle River, British Columbia, below Cascade Falls: nominal *C. confusus* from *BCPM 979-11275 (1); nominal *C. bairdi* from *BCPM 979-11275 (1); *BCPM 979-11295 (14); *BCPM 979-11276 (3); *BCPM 980-619 (10); plus *BCPM 977-124 (1), at mouth of outlet from Christina Lake.

Kettle River, Washington: nominal *C. confusus* from *BCPM 983-1689 (8), *BCPM 984-454 (2), downstream from northern bridge to Pierre Lake; *BCPM 980-617 (4), downstream of Rock Cut Bridge (48°54.8'N, 118°11.7'W); *BCPM 980-616 (1), 5 mi S of Laurier; *BCPM 984-456, 1 km upstream from Barstow; nominal *C. bairdi* from *BCPM 984-455 (1), downstream from Boulder Creek; *BCPM 980-615 (2), near Avey Field, Laurier; *BCPM 980-616 (5), 5 mi S of Laurier; *BCPM 980-618 (1) 6½ mi S of Laurier.

Similkameen River (upstream): nominal *C. bairdi* from BCPM 988-770 (1), BCPM 988-851 (10), below mouth of Copper Creek, E of Similkameen Falls; *BCPM 983-1665 (2), Tulameen River, 2 km up from Tulameen; *BCPM 983-1668 (1), Hayes Creek, just above Trehearne Creek; BCPM 988-771, Hayes Creek, just upstream from Grant Creek; BCPM 988-772, Hayes Creek, at bridge on road to Red Creek (between Collett and Trehearne creeks); *BCPM 983-1680 (1), mouth of Wolfe Creek: UBC 54-338 (36), Borgeson (Round) Lake, Allison Creek area (label indicates identification by Bailey and Bond; UBC 54-193 (41), Dry Lake, Allison Creek area (label indicates identification by Bailey and Bond); UBC 56-127 (4), Liard Lake, Allison Creek area (label indicates identification by Bailey and Bond); *BCPM 983-1676 (19), Otter Creek, 800 m S of outlet from Goose Lake; *BCPM 983-1661 (17), Otter Creek, 1.5 km N of Frembd Lake; *BCPM 983-1675 (12), Otter Creek, between Frembd Lake and Otter Lake.

Similkameen River (downstream): nominal *C. bairdi* from *BCPM 983-1687 (1), 1.2 km N of international border; *BCPM 983-1696 (5), 2.5 km upstream from Nighthawk, WA; *BCPM 985-222 (6), upstream from Nighthawk, WA.

Other reference material: nominal *Cottus bairdi* from NMC 68-171 (16), Prickly Pear Creek, Lewis and Clark County, MT; BCPM 984-457 (7), Colville River, WA; BCPM 984-452 (12), Sanpoil River at McMann Creek, WA; BCPM 986-247 (6), Sanpoil River below Cash Creek Road; BCPM 986-249 (2), Sanpoil River N of Keller; BCPM 986-214 (1), Little Spokane River at Elk–Camden Road, WA; BCPM 986-211 (5), Little Spokane River at road to Tum Tum, WA; BCPM 986-238 (1), Chamokane Creek, Little Spokane drainage, WA; BCPM 986-218, Spokane River at Spokane, WA; BCPM 986-225 (8), Palouse River at Liard Park, ID; nominal *C. confusus* from BCPM 986-227 (5), Coeur d'Alene River, ID.

Results

Factors differentiating Flathead River from Columbia River populations of nominal *C. confusus* (i.e., presence or absence of head papillae, prickles behind pectoral base, and presence of a postmaxillary pore) were plotted for all specimens (Fig. 4) against the factor best differentiating sympatric nominal *C. bairdi* from *C. confusus* (i.e., number of lateral line pores, number of pectoral fin rays, relative head length, presence or absence of a third preopercular spine). This factor analysis (Nie et al. 1975) indicated three groups (1, *C. bairdi* from Columbia, Kettle, and Similkameen rivers; 2, *C. confusus* from Slocan, Columbia and Kettle rivers; and 3, *C. confusus* from Flathead River) plus intermediates (Fig. 5). Most notably, *C. confusus* from the Flathead River was more differentiated from its presumed conspecific form in the Columbia–Kettle rivers than sympatric *C. confusus* and *C. bairdi* were within the latter two rivers (Fig. 5). When presumed *C. bairdi* populations from the Milk River (east of the Rocky Mountains) were included (Fig. 4), they were more similar to Flathead River *C. confusus* than to either congener in the Columbia River system. On the other hand, intermediate individuals masked this distinction. Because such comparisons of allopatric populations revealed a complex situation in which different environments might exaggerate phenotypic differences, we compared specimens of sympatric populations within single river systems.

Kettle River

Samples from the Kettle River best differentiated sympatric populations of nominal *C. bairdi* and *C. confusus* (Fig. 6), and our preliminary sorting to species was confirmed. Both species were generally distributed along the lower Kettle River, but as observed for *Rhinichthys umatilla* (Peden and Hughes 1988), upstream dispersal is apparently blocked by waterfalls near Cascade, British Columbia (Fig. 7). *Cottus cognatus* occurs abundantly above the falls but has not been found in any of our samples below the falls. Although *C. confusus* is reputed to typically occur farther upstream than *C. bairdi* in other river systems (Bailey and Bond 1963), our limited collecting did not indicate similar ecological segregation. The outlet from Christina Lake (at Cascade) is the only possible associated Canadian tributary that might provide habitat, although it nearly dries up in summer. In the American section of the Kettle River, creeks such as Toulou Creek may permit upstream segregation of *C. confusus*, although we did not sample here. *Cottus rhotheus*, being very abundant, is the chief potential congeneric competitor in the Kettle River.

There are limited statistical differences between *C. confusus*

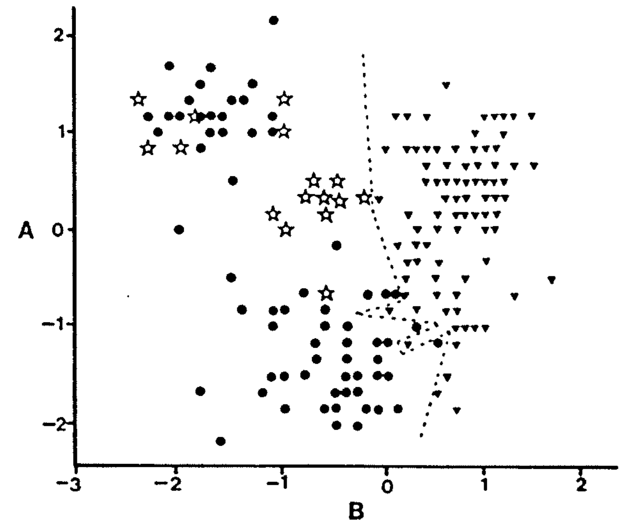

FIG. 4. Plots of principal components (Nie et al. 1975) for factor A (presence of head papillae, absence of premaxillary pore, and absence of prickles) against factor B (number of lateral line pores, presence of third preopercular spine, number of pectoral fin rays, presence of postmaxillary pore, presence of prickles, and head length ratio). ●, nominal *Cottus confusus* (eastern and western forms); ▼, nominal *C. bairdi* of the Columbia River drainage; ☆, specimens from Milk River previously identified in literature as *C. bairdi*. Broken line separates specimens sorted to species before analysis.

and *C. bairdi* in anal, dorsal, and lateral line counts for samples from the Kettle River (Figs. 8, 9, 10). Despite the common name "shorthead" for *C. confusus*, relative head length proved to be of limited value in separating species (Fig. 11). On the other hand, pectoral fin ray counts (Fig. 12), presence of absence of third preopercular spines, and development of head papillae separated *confusus* and *bairdi* best.

Columbia, Kootenay, and Slocan rivers

Our samples from the Columbia, Kootenay, and Slocan rivers (Fig. 13) separated into two groups supporting our initial sorting to species. However, there were intermediate specimens, and our line separating the two species (Fig. 14) may need to be shifted to include some presumed *bairdi* as *confusus*, or possibly the existence of hybrids should be tested. Differences in lateral line and fin counts were less distinct than those for the Kettle River (Figs. 8, 9, and 10), although there still appeared to be a strong separation of pectoral counts and a difference in the third preopercular spine (Fig. 12).

Our samples suggested that *C. confusus* occurs without *bairdi* in the Slocan River, thus supporting previous observations by Bailey and Bond (1963) that *confusus* preferred upstream habitats (Fig. 13). This river draining the mountainous region of Slocan Lake is smaller and apparently cooler than nearby sections of the Kootenay and Columbia rivers (as evidenced by ice cover during our winter sampling). Although *C. confusus* was found in the Columbia River, most individuals were taken in or near Norns, Blueberry, and Beaver creeks in British Columbia, and Sheep Creek, Washington. Perhaps river-dwelling *C. confusus* originate from these tributaries. We recently located very large populations of *C. confusus* during early fall in or near the first riffles above normal flood levels of the Columbia River at Norns, Beaver, and Sheep creeks. Although they were not available at the time of

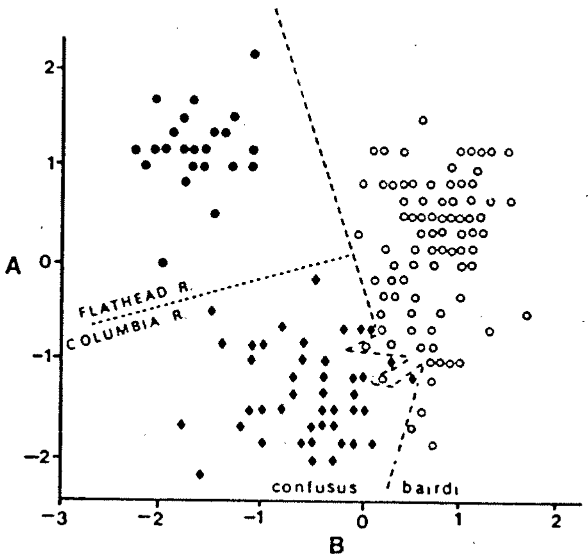

FIG. 5. Plots of principal components for factor A against factor B (see Fig. 4) but without Milk River (Missouri River drainage) samples. ○, nominal *Cottus bairdi*; ●, nominal *C. confusus* of the Flathead River; ♦, nominal *C. confusus* of Kettle and Columbia rivers. Broken lines separate specimens sorted to species before analysis.

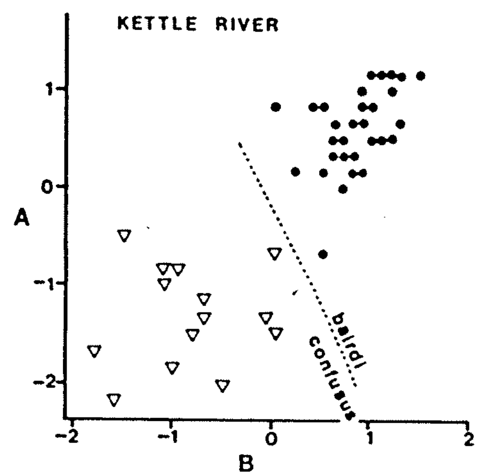

FIG. 6. Plots of Kettle River samples used in the principal components analysis illustrated in Figs. 4 and 5. ●, nominal *Cottus bairdi*; Δ, nominal *C. confusus*. Broken line separates specimens sorted to species before analysis.

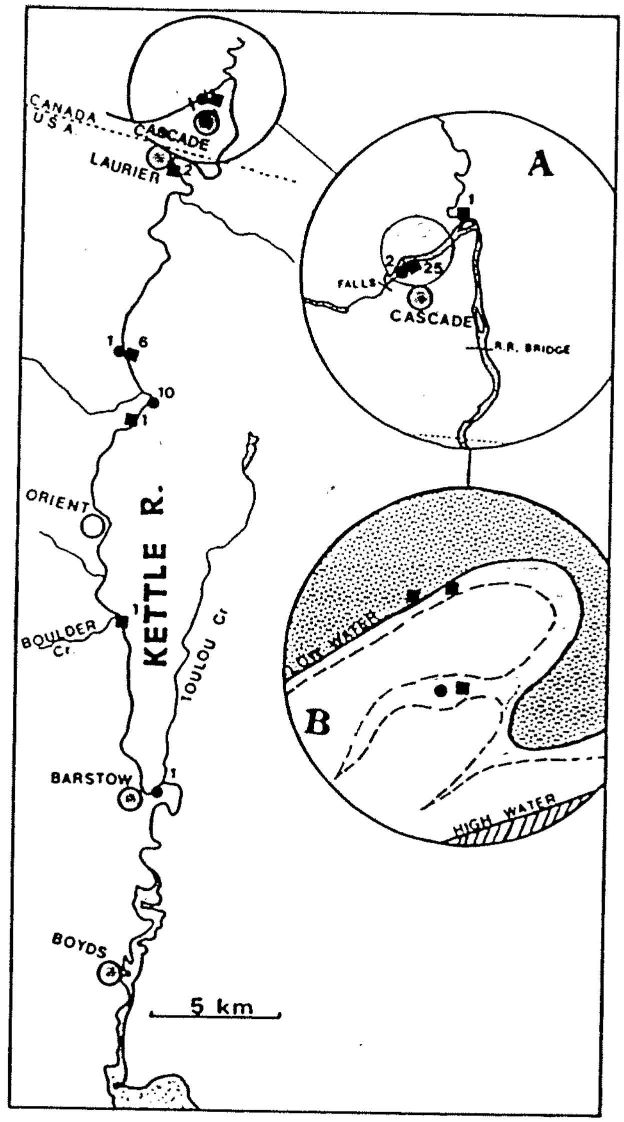

FIG. 7. Kettle River drainage between Cascade, British Columbia, and Roosevelt Reservoir on the Columbia River in Washington, showing sites where *Cottus confusus* (●) and *C. bairdi* (■) were captured. Inset A: enlargement of the Cascade area, showing collection sites in relation to presumably impassable falls. Inset B: area of gravel bars with some subsurface flow and side channels at higher water levels where *Cottus* and juvenile *Rhinichthys umatilla* (Peden and Hughes 1988) were taken. Numbers indicate size of sample at each site.

our analysis, they confirm our contention that *C. confusus* prefers tributaries, whereas *C. bairdi* tends to occur in the main rivers of the area. In each instance, the creeks were more brown-stained than the nearby Columbia River, and had a lush film of brown and (or) dark-coloured algae covering all stones along the bottom. The inshore area of the swift Columbia River had cleaner stones, possibly caused by manipulation of water levels by upstream hydroelectric dams which daily exposed the shallowest waters. Depths of 2 ft (1 ft = 0.305 m) or more had lush green algae on the stones, and the water was very clear and unstained. Waterfalls ¼ mi upstream on Beaver Creek and ½ mi up Norns Creek probably prevent upstream dispersal, although populations of naked-skinned *Cottus rhotheus* seem to have surmounted these falls in the past.

Cottus bairdi were taken in the main part of the Columbia River near the American border, at the boat ramp on the Columbia River near Beaver Creek, at Castlegar, and in reservoirs of the Kootenay River, including that above South Slocan Dam. The latter collection suggests *bairdi* (if not *confusus*) was at least this far upstream at the time that the Kootenay River was impounded. We suspect waterfalls now flooded by South Slocan Dam and Bonnington Falls Dam probably blocked upstream dispersal of *C. confusus* and *C. bairdi*, as was suggested for *Rhinichthys umatilla* by Peden and Hughes (1988). As in the Kettle River, *C. cognatus* was abundant above the falls but absent below, and might be competitively displaced upriver by *C. confusus* and *C. bairdi* if the latter could disperse over these river barriers. Like *Rhinichthys*

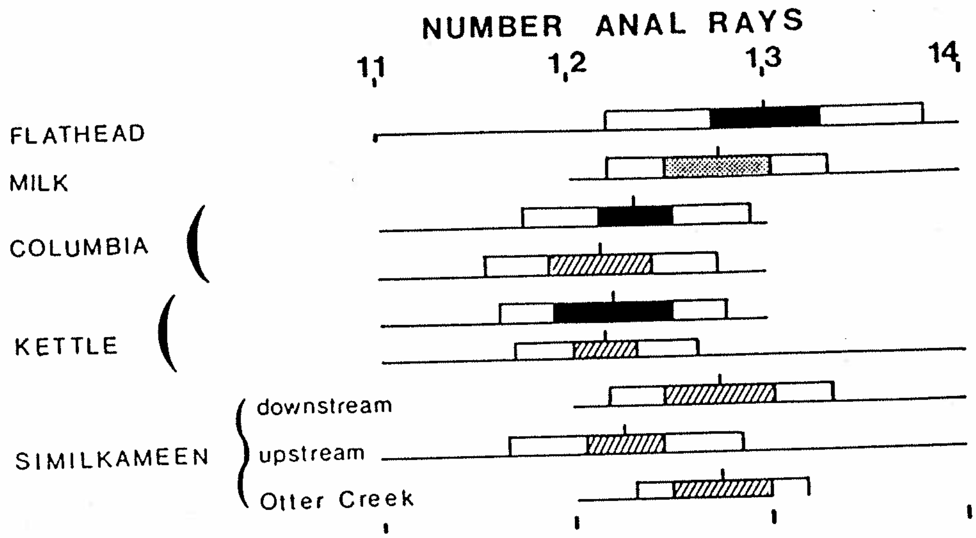

FIG. 8. Distribution of numbers of anal fin rays of nominal *Cottus bairdi* and *C. confusus*, graphed according to method of Hubbs and Hubbs (1953). Horizontal lines represent range of counts; a shaded bar plus a hollow bar indicates one standard deviation either side of the mean; a shaded bar indicates two standard errors either side of the mean; a solid bar indicates samples currently recognized as *C. confusus*; a cross-hatched bar indicates *C. bairdi*; a shaded bar indicates Milk River *Cottus*. Otter Creek sample refers to a single sample between Otter and Frembd lakes. Other Otter Creek samples are grouped with upstream samples.

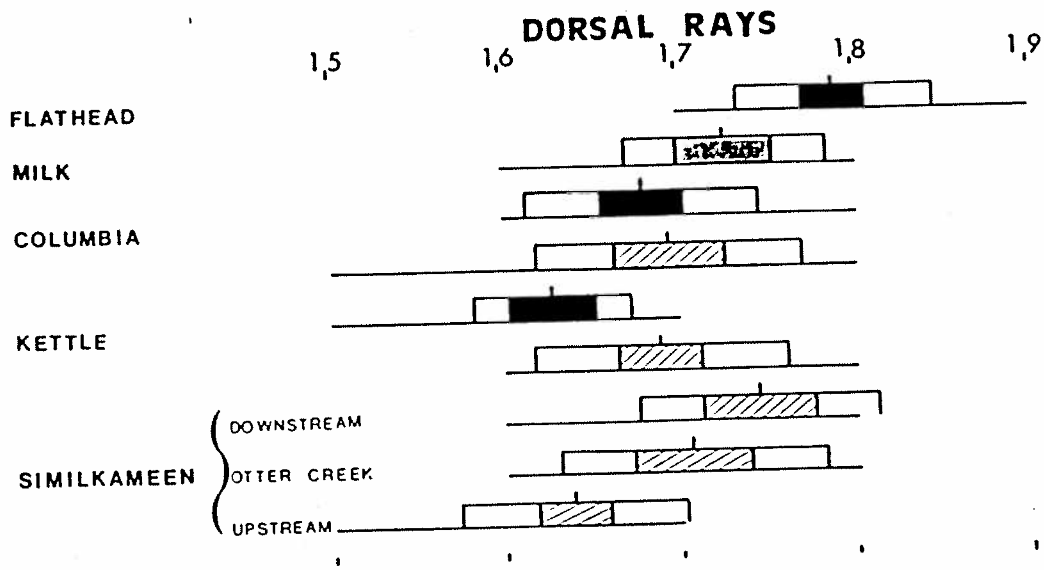

FIG. 9. Distribution of numbers of dorsal fin rays of nominal *Cottus bairdi* and *C. confusus*. See Fig. 8 for explanation.

umatilla, whose distribution was described by Peden and Hughes (1988), these species are not known to have penetrated the Columbia River proper beyond the Castlegar area, and perhaps the highly impounded Arrow Lakes provide a barrier to dispersal. Throughout the lower Kootenay, Columbia, and Slocan areas of British Columbia, *C. asper* and *C. rhotheus* are abundant and sympatric, and represent potential competitors.

Similkameen river drainages

We found *C. bairdi* but no *C. confusus* in the Similkameen River and associated drainages. They were identified by the strong third preopercular spine, mottled appearance, and other features reputed to identify the species (Bailey and Bond 1963). There were also morphological differences between samples from the lowest portion of the river in the United States and those upstream, indicating a shift in some features toward *C. confusus* (Fig. 15). In particular, a higher frequency of 14 pectoral fin rays in upstream populations (Fig. 12) reduces the utility of many published keys for identifying *C. bairdi* from *C. confusus* (e.g., Scott and Crossman 1973). Although shifts in number of lateral line pores are also apparent (Fig. 10), a reduction of head papillae similar to that in *C. confusus* was most conspicuous and caused us to reexamine species identity.

Downstream samples of *C. bairdi* are from a relatively arid area of Washington State where the river is wide, there are few tributaries, and, judging by reduced winter ice, the river is warmer. Upstream samples were known from Wolfe, Hayes, Allison and Otter creeks (Fig. 16). The Allison Creek samples

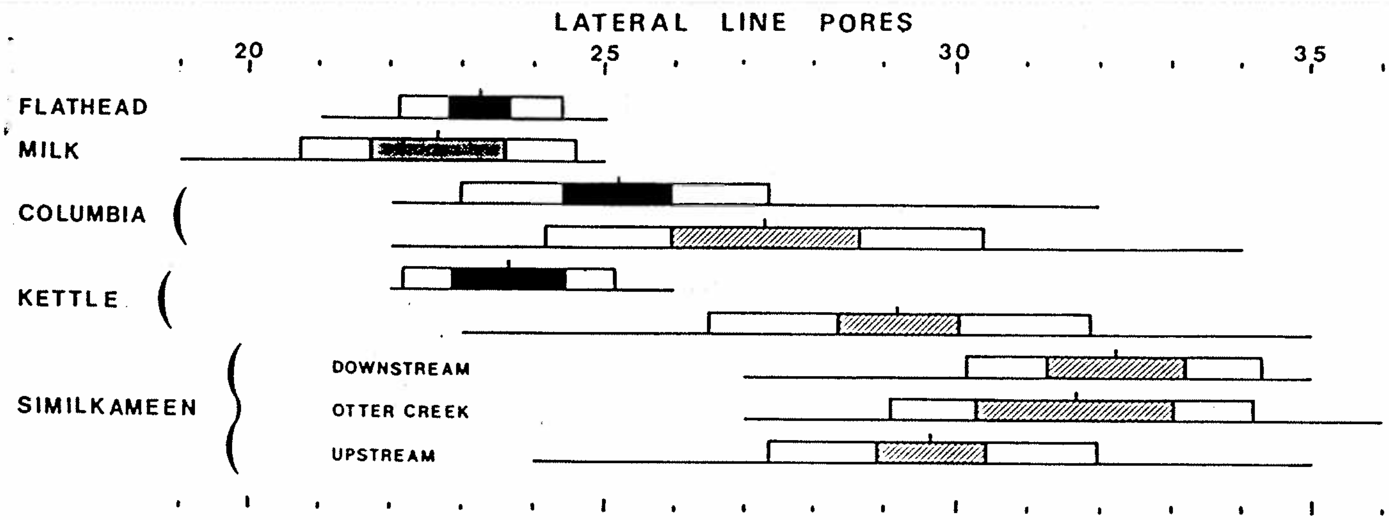

FIG. 10. Distribution of numbers of lateral line pores of nominal *C. bairdi* and *C. confusus*. See Fig. 8 for explanation.

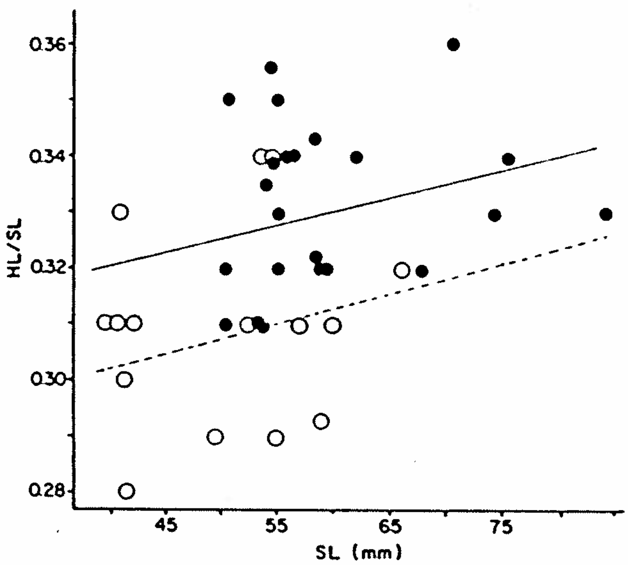

FIG. 11. Relation of head length:standard length (HL/SL) ratio to SL of nominal *Cottus bairdi* (●) and *C. confusus* (○) inhabiting the Kettle River. Solid line indicates regression for *C. bairdi* ($Y = 0.30572 + (403 \times 10^{-6}) \times X$) and broken line regression for *C. confusus* ($Y = 0.28466 + (531 \times 10^{-6}) \times X$).

(not used in this analysis) represent old collections from lakes and ponds where the species continued presence needs verification. Otter Creek, which is small and passes through a low, forested valley leading toward the Fraser River drainage, was described by McPhail and Lindsey (1986) as a possible post-glacial dispersal route for fishes. They further noted *Rhinichthys umatilla* and *C. bairdi* as later immigrants which did not disperse beyond this valley. The nearby Tulameen River is swift, large, and cold, with fewer fishes, although a few *C. bairdi* were found here as well. Very recently, we obtained *C. bairdi* on the Similkameen River at Copper Creek, and suspect that nearby Similkameen Falls provides the barrier to upstream dispersal. Throughout the Similkameen drainage, *C. rhotheus* is an extremely abundant potential congeneric competitor; however, we encountered *Cottus asper* only in the Otter Lake area.

Flathead and Milk rivers

The Flathead River population of nominal *C. confusus* (Pacific drainage) was thoroughly described by Hughes and Peden (1984) and Peden and Hughes (1984). Milk River populations originally identified as *C. bairdi* by Willock (1968, 1969) and Paetz and Nelson (1970) were described in detail and reidentified as *C. confusus* by Roberts (1988). In addition to differences between Flathead River and western populations in meristics and the presence of a postmaxillary pore (Figs. 4, 5, 8, 9, 10), the presence of head papillae (also found in nominal *C. bairdi*) differentiated Flathead River *C. confusus* from its previously presumed conspecific populations of the Columbia and Kettle rivers. These features, plus the absence of the prickles found in all other populations studied here, indicated affinity between Flathead River and Milk River populations. Despite a high proportion (70%) of our Milk River specimens having a postmaxillary pore (Roberts (1988) found 90% with the pore and significantly more with an interrupted lateral line), analysis of our material (Fig. 4) emphasizes the overall similarity between populations of *Cottus* in the Milk and Flathead rivers.

Discussion

Our data amply demonstrate that nominal *C. bairdi* and *C. confusus* represent two sympatric species inhabiting the Kettle and lower Columbia rivers of British Columbia. The *C. confusus* represent a 250-km extension of the species' known geographic range from the Wenatchee River of Washington, and a 200-km extension northwest from the Coeur d'Alene and St. Mary's rivers of Idaho (Bailey and Bond 1963; Lee et al. 1980; R. L. Wallace, personal communication). The meristics and head pores in our samples are also similar to those described by Bailey and Bond for western *C. confusus*; however, detailed comparisons of such Washington populations should still be made. Even though the Coeur d'Alene River (Spokane drainage) is geographically closer to the Flathead River, the meandering Pend d'Oreille and Clark Fork rivers provide the closest water connection (500 km) between our Columbia River samples of *C. confusus* and the morphologically distinct Flathead River populations of Montana and British Columbia. Nominal *C. bairdi* (= *C. hubbsi*

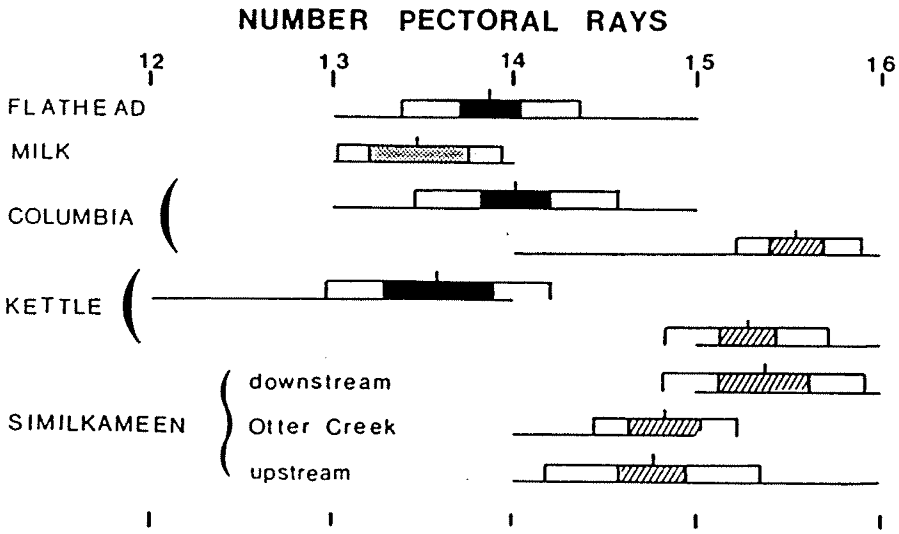

FIG. 12. Distribution of numbers of pectoral fin rays of nominal *Cottus bairdi* and *C. confusus*. See Fig. 8 for explanation.

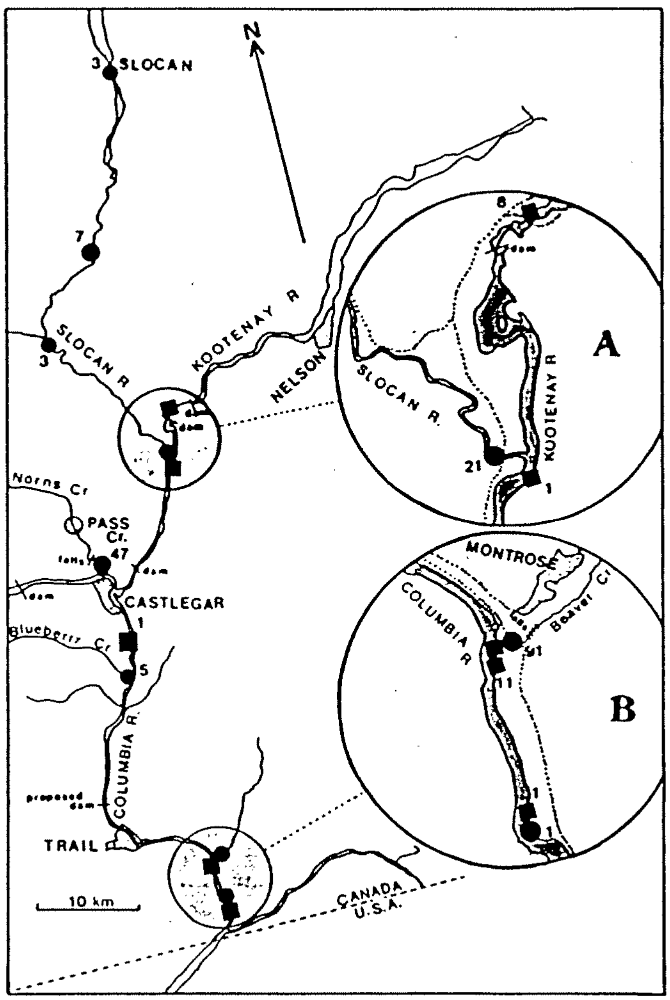

FIG. 13. Columbia River area, showing collection sites of nominal *Cottus bairdi* (■) and *C. confusus* (●). Numbers beside each symbol indicates number of specimens. Insets A and B: mouths of Slocan River and Beaver Creek, respectively, with locations of each species in tributary compared with Columbia and Kootenay rivers.

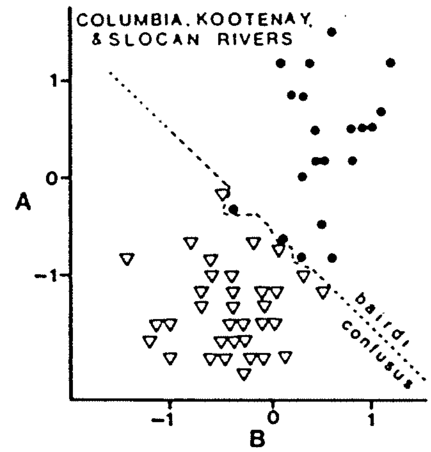

FIG. 14. Plots of samples from the Columbia, Kootenay, and Slocan rivers, used in the principal components analysis shown in Figs. 4 and 5. ●, nominal *Cottus bairdi*; △, nominal *C. confusus*. Broken line separates samples previously sorted to species before analysis.

Hubbs & Dimick?) is present in nearby American segments of the Columbia River (Colville, Spokane, Sanpoil, and Entiat rivers); however, this species is similarly not recorded in the same intervening waters of the highly impounded Pend d'Oreille and Clark Fork rivers of Idaho (Simpson and Wallace 1978) or Montana (Brown 1971). Our limited collecting did locate some *C. cognatus* in the lower Pend d'Oreille River, which may suggest exclusion of *C. confusus* and *C. bairdi* in these interconnecting water ways now flooded by the Wanita, Seven Mile, and Boundary dams near the border between Canada and the United States. Waterfalls now flooded by these artificial impoundments may have also prevented postglacial dispersal of *C. confusus* and *C. bairdi*. However, though early surveys (Gilbert and Evermann 1895) indicate that relatively mobile salmon may have surmounted these barriers, especially the now-flooded Metaline Falls in Washington, provided they could bypass Kettle Falls downstream on the Columbia River, such evidence is lacking. *Rhinichthys fal-*

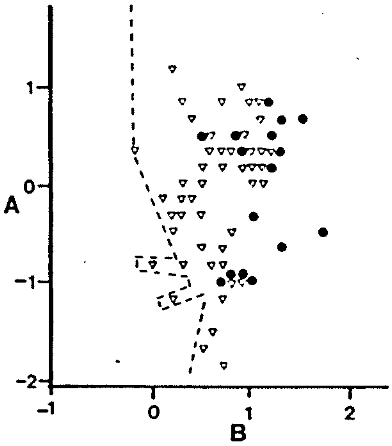

FIG. 15. Plots of principal components of nominal *Cottus bairdi* from the Similkameen River, as shown in Figs. 4 and 5. ●, downriver samples at or below the Canadian – United States border; △, upriver samples from Wolfe, Hayes, and Otter creeks, plus Tulameen River. Broken line separates specimens of *C. bairdi* from nominal *C. confusus* presorted before analysis.

catus and *R. umatilla* did penetrate the lower Pend d'Oreille River (Peden and Hughes 1988), but modern dams now prevent assessment of original habitats. McPhail and Lindsey (1986) suggest that much of the upper (northern) Columbia Basin, including the Pend d'Oreille River, was glaciated, and the presence of species such as *C. cognatus* is indicative of a cooler habitat. The Flathead River Basin of British Columbia in the foothills of the Rocky Mountains, inhabited by *C. confusus* (and *C. cognatus*), lies above 1200 m elevation, whereas *C. confusus* and *C. bairdi* of the Columbia, Slocan, and Kettle rivers live at elevations near 450 m, and *C. bairdi* of the Similkameen River occurs generally below 920 m. Environmental differences such as temperature are correlated and extensively discussed by Peden and Clermont.[1] We were at first concerned that the flooding of Roosevelt Reservoir on the Columbia River of Washington during the 1940s could have allowed flooding of populations over Kettle Falls because *R. umatilla*, *C. bairdi*, and *C. confusus* could then have been artificially dispersed upstream into Canada. Although the Brilliant Dam on the Kootenay River was built afterward, the South Slocan and Bonnington Falls dams, built as early as 1928, were constructed early enough to trap *C. bairdi* and *R. umatilla* before the influence of the Roosevelt Reservoir was felt, thus suggesting that the dace and sculpin distributions are natural.

The geographic gap (Fig. 1) and morphological divergence (Fig. 5) between Flathead River and Columbia River *C. confusus* indicate that eastern and western populations are different and deserve separate status. On the other hand, the interrelationships of Flathead River with other *C. confusus* and *C. bairdi* populations (i.e., *C. b. punctulata* (Bailey, 1952) Bond, 1963) need special study because of the nature of their allopatry and possible phenotypic variation. The similarity of nominal Atlantic drainage (Milk River) *C. bairdi* to Flathead

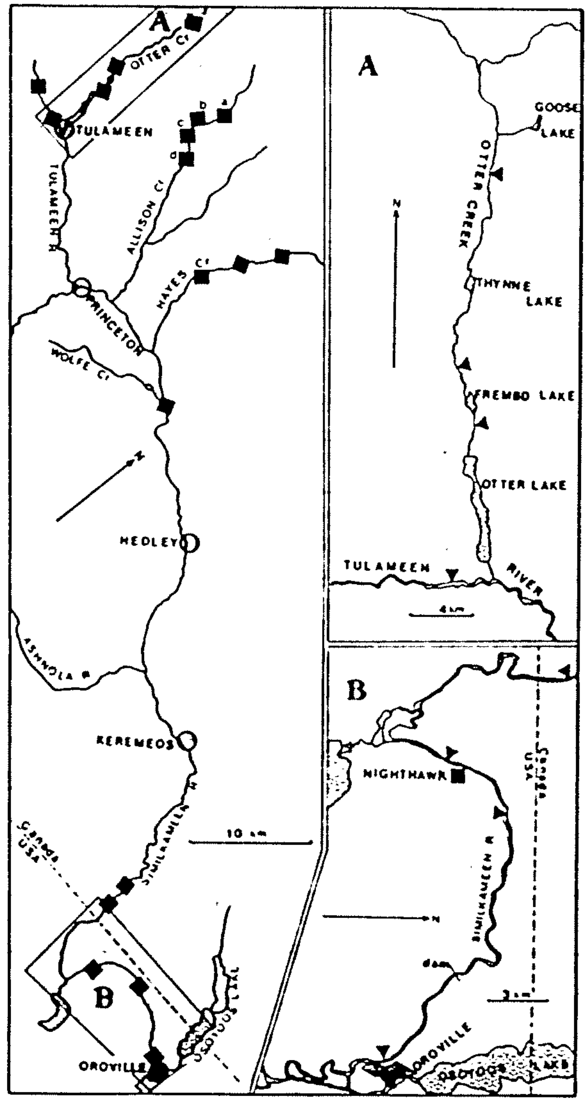

FIG. 16. Map of Similkameen River, showing distribution of nominal *Cottus bairdi* (■, ▲) used or observed in this study. Insets A and B: Otter Creek and lower Similkameen River, respectively; tips of triangles point to collecting sites along the water courses. Sample between Otter and Frembd lakes (inset A) was plotted separately in Figs. 8, 9, 10, and 12. *a*, Allison lake; *b*, Borgeson Lake; *c*, Dry Lake; *d*, Liard Lake. The uppermost sample on the Similkameen River, below Similkameen Falls, is shown in Fig. 1.

River *C. confusus* demonstrates a need to reassess the status of these closely related populations, but such decisions are premature without data from other nominal *C. bairdi* populations from the Missouri River drainages of Montana (Brown 1971) and the Snake River of Idaho (Simpson and Wallace 1978). The fact that some Milk River specimens are somewhat intermediate between Flathead River *confusus* and Columbia River *confusus* and *bairdi* further complicates the issue. Most importantly, we believe our data throw open the question of whether the name *C. hubbsi* Hubbs & Dimick (1949) should be resurrected for *C. bairdi* of western North America. Or, in light of the relatively similar Flathead River and Milk River populations being referred to different species by current literature (Scott and Crossman 1973), which of the western

[1]A. E. Peden and T. Clermont. Updated report on the status of shorthead sculpin (*Cottus confusus*) in Canada. Submitted for publication.

populations of *bairdi*, *confusus*, or *hubbsi* are most similar to the *C. bairdi* of eastern North America?

Variation within river drainages between upstream and downstream *C. bairdi*, as well as some apparent breakdown of reported diagnostic characters to separate species described by Bailey and Bond (1963), point out a need to study interspecific relationships between *confusus* and *bairdi* in all river drainages. In particular, the shift in number of pectoral rays and size of head papillae of *C. bairdi* in upstream Similkameen populations toward those found in *C. confusus*, a species also known to typically occur farther upriver than *C. bairdi*, opens questions as to whether (*i*) each species was derived in isolation, with later reinvasion of *bairdi* (*hubbsi*?) to replace *confusus* in downstream segments of river systems, or (*ii*) populations of *confusus* and *bairdi* were independently derived in different tributaries, some populations achieving greater differentiation and even biological species status in some rivers compared with other rivers. Similar questions can be asked with respect to the Snake River, where Bond (1963) indicated that *C. b. semiscaber* have shorter lateral lines in upstream waters than they do in downstream waters. Do intergrading specimens suggest that some populations hybridize, with breakdown of isolating mechanisms, while other populations do not, are there better diagnostic features to identify distinct populations, or do intergrading specimens indicate populations or hybrids in the process of diverging?

Although our study was originally intended just to differentiate the morphological forms inhabiting the Columbia and Kettle rivers, it is now apparent that more comprehensive work is required over a much wider geographic area to resolve species limits throughout the species' geographic range. To this end, better quantification of other characters should be pursued, such as the diagnostically different dentition described by Bailey and Bond (1963). On the other hand, researchers using biochemical or other refined techniques for analysis may resolve the issue more directly.

Acknowledgments

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