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CLASSIFICATION, VARIATION, AND DISTRIBUTION OF THE SCULPINS, GENUS *COTTUS*, INHABITING PACIFIC SLOPE WATERS IN CALIFORNIA AND SOUTHERN OREGON, WITH A KEY TO THE SPECIES¹

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INTRODUCTION

The sculpins of the genus *Cottus* comprise one of the most perplexing groups of North American freshwater fishes. Variation is so marked and often so haphazard that interpretation of the species limits is frequently difficult. Moreover, many of the numerous nominal forms are based on a few poorly preserved specimens and inadequate descriptions. Perhaps for these reasons, few systematic contributions on *Cottus* have been made in recent years. That by Bailey and Dimick (1949) added substantially to our knowledge of western sculpins when they separated

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their new species, *C. hubbsi*, from *C. rhotheus* and discussed briefly other western forms.

Sculpins form an important component of the stream fauna through much of the West. They are particularly common in colder waters and are often reported in conjunction with studies on trout and salmon.

The acquisition of new material and a review of type specimens at the United States National Museum and at Stanford University now permit a more complete discussion of the several species from the upper parts of the Klamath and Pit rivers of Oregon and California. In addition, we present a key to the species of *Cottus* now known from the Pacific drainage of California and southern Oregon and discuss their nomenclature.

The existing difficulty in identifying the numerous species has led to considerable confusion in the literature and so our primary purpose at this time is to provide an acceptable classification at the species level. The delineation of subspecies awaits more exhaustive studies, both in the field and laboratory.

Leonard P. Schultz, Ernest A. Lachner, and Robert H. Kanazawa have kindly made available material and working space at the United States National Museum. George S. Myers, Margaret Storey, and Norman J. Wilimovsky similarly aided us at the Stanford Natural History Museum. Edward C. Raney loaned specimens from Cornell University. To Reeve M. Bailey and Carl L. Hubbs appreciation is expressed for permission to use field notes. Joseph H. Wales obtained the excellent series of *C. asperrimus* from Hat Creek. We are indebted to Vladimir Walters for notes on the types of *C. aleuticus* and *C. shasta* at Stanford University.

The following museum abbreviations are employed: CU, Cornell University; UMMZ, University of Michigan Museum of Zoology; SNHM, Stanford Natural History Museum; and USNM, United States National Museum. The number of specimens and their range in standard length is given in parentheses after each museum number.

METHODS

Counts and measurements have been taken by the methods described by Hubbs and Lagler (1947, p. 8-15) except as noted below.

Dorsal and Anal Soft Rays. Hubbs and Lagler (1947, p. 10) recommend that the last two elements of the dorsal and anal fins be treated as one ray. Upon dissection it is found that in many groups of fishes the last two rays stem from a single interspinal series, whereas each preceding series supports only one ray. This method of counting is well founded in such groups. In the genus *Cottus*, the dorsal and anal rays are unbranched in most species and, as described above, the last two rays are often close together and stem from a single interspinal series (Figure 1, B). Occasionally, however, this last interspinal bears three very closely approximated rays, the first well developed and the last two splint-like (Figure 1, C). In each instance the rays which arise from the last interspinal are considered one. An important variation occurs when the last ray is well developed, well separated from the preceding ray, and stems from its own interspinal (Figure 1, A). Were this a rarity or of equally probable occurrence in all populations, then

the arbitrary rule of counting the last two rays as one would introduce only a negligible and random error. Unfortunately, this is not the situation, for when this variant occurs it is likely to involve the entire sample. Moreover, it is the prevalent condition in such forms as *C. tenuis* (Figure 1, A; also Evermann and Meek, 1898, p. 83, fig. 6) and *C. cognatus* (Greeley, 1928, pl. 7), and is unusual in most other species (Figure 1, B and C), as exemplified by *C. hubbsi* (Bailey and Dimick, 1949, pl. 1). Careful dissection reveals that a very small and completely imbedded splint ray is often present in the variants; sometimes the last ray is truly single. To count the last two rays as one under these circumstances leads to apparent population differences of one ray, a large variation in this feature, when no such differences actually exist. To count every ray, no matter how small, leads to an equally biased result. In this study the last two (or three) rays are counted as one only when they stem from a single interspinal. With experience, the true situation is easily seen by noting the degree of separation of the rays: they are very close together when they stem from a common interspinal and equally far apart when they arise from separate interspinals. If there is uncertainty, an incision is made along the bases of the last several rays to expose the interspinals. In this manner unbiased counts may be made with little chance of error.

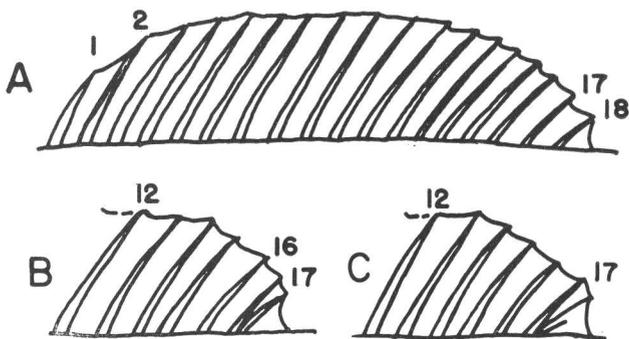


FIGURE 1. Second dorsal fin of *Cottus*, showing the variation in enumeration of rays (for clarity, segmentation is omitted). A, every element is counted; B, last two elements counted as 1; C, last three elements counted as 1.

Pelvic Rays. Every ray is counted no matter how rudimentary. Since a hidden spine is closely appressed to the first soft ray in all forms of *Cottus*, this element is not enumerated.

Branching of Soft Rays. In those species in which the pectoral and pelvic rays are branched, the branching occurs typically at or near the tips. The lower rays of the pectoral fin are never branched and the first ray of the pelvic fin often is simple. Branching is correlated with growth of the fins; thus, young individuals may have simple rays (though flattened and frayed at the tips), whereas branched rays are characteristic of the adult. Usually only a few elements are involved in the branching of dorsal and anal rays.

Lateral-line Pores. The first pore counted is the first one behind the union of the opercular membrane to the body. When the lateral line is

developed onto the tail, the last pore counted is the one directly over or immediately in front of the posterior edge of the hypural plate. The lateral line is termed complete when it reaches this point. When it is incomplete, every pore is counted. This count is reliable on adult fish only; in the present study no fish smaller than 40 mm. in standard length was used.

Head-pore Arrangement. Useful and important differences (unpublished) have been noted by the writers in their studies of this group. Although we are most concerned with the infraorbital and preoperculo-mandibular canals, in this study we present in Figure 2 a schematic

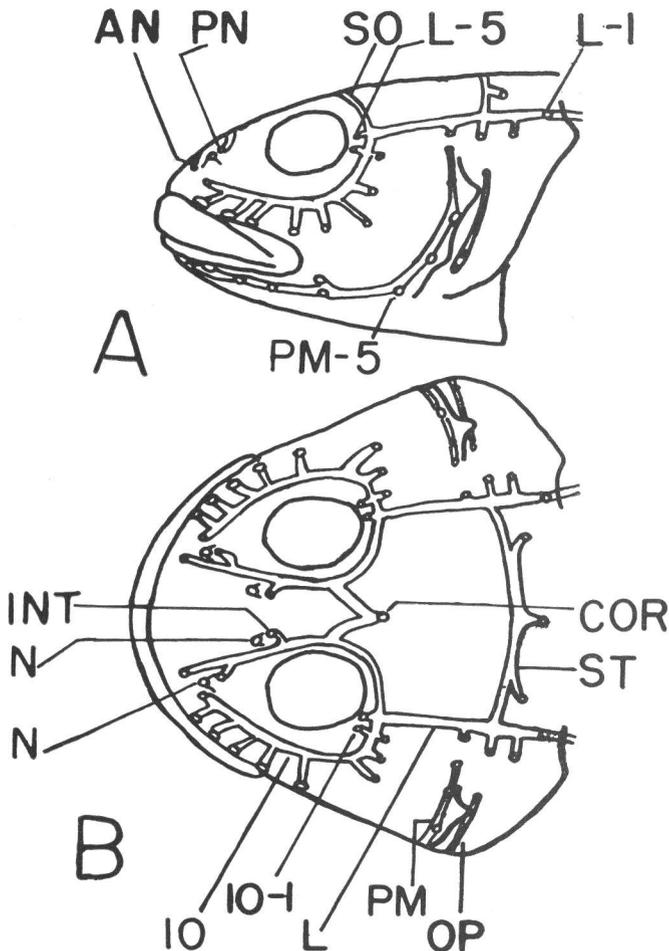


FIGURE 2. Schematic drawing of the head-pore arrangement in a hypothetical species of *Cottus*. A, lateral view. AN, anterior nasal pore; PN, posterior nasal pore; SO, supraorbital canal; L-1, L-5, lateral canal pores 1 and 5; PM-5, pore 5 of preoperculo-mandibular canal. B, dorsal view. N, nasal openings; IO, infraorbital canal (IO-1 = pore 1); L, lateral canal; PM, preoperculo-mandibular canal; OP, opercular canal (often lacking); ST, supratemporal canal; COR, coronal pore; INT, interorbital pore.

outline of the entire cephalic canal system of a hypothetical species of sculpin. It is hoped that these features will be investigated by other workers and that this outline will serve as a basis for comparison. The terminology is after Hubbs and Cannon (1935) as modified by Illick (1956). In contrast with Illick (*op. cit.*, p. 206, fig. 1) we enumerate the pores of the lateral canal from the attachment of the gill membrane forward (the more anterior pores are absent in many species) and distinguish between the pores of the lateral and infraorbital canals. For a critical review of this topic the reader is referred to Illick (*op. cit.*) and the references cited therein.

Infraorbital Pores. The pore which often is present on the lateral canal at its junction with the infraorbital canal is not counted.

Preoperculo-mandibular Pores. Every pore below the lateral canal is counted. In most species the two preoperculo-mandibular canals do not unite on the chin and each has 11 pores, as indicated by the formula 11-11. In some species these canals are united on the chin and share a median chin pore (pore count = 10-1-10, Figure 3, A). In others the uppermost of the two post-maxillary pores, behind the corner of the mouth (Figure 3, B; also pl. 1 in Bailey and Dimick, 1949), is absent (pore count = 10-10). When both conditions exist the pore count is expressed as 9-1-9.

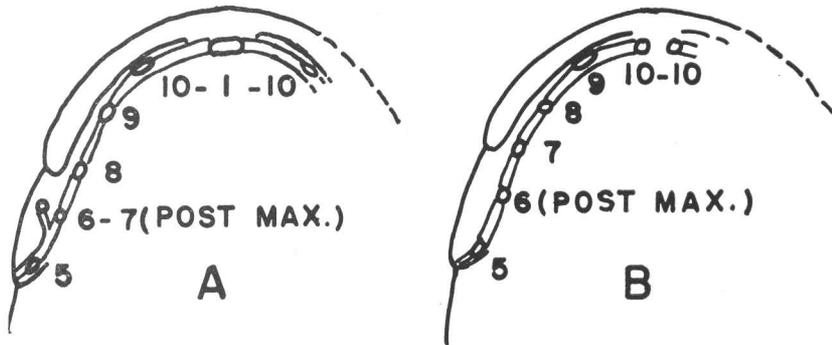


FIGURE 3. Ventral view of chin of *Cottus*. A, postmaxillary pore double, chin pore single, count = 10-1-10. B, postmaxillary pore single, chin pore double, count = 10-10. Combinations of these conditions yield counts of 9-1-9 and 11-11.

Prickles on the Body. The presence or absence of prickles on the body, and their distribution, has been used to characterize almost every species of *Cottus*. The considerable constancy which this feature exhibits within most populations undoubtedly led to its employment as a systematic tool. So much variation occurs between populations of most species, however, that its geographic constancy in one or two forms, such as *C. princeps*, is difficult to evaluate. A correlation with habitat has been noted. Within a given species, samples from mountain brooks are naked or have many fewer prickles, whereas lake populations exhibit the most extensive prickles. The first prickles to appear and the ones lost last are those mesial to the pectoral fin.

Preopercular Armature. This feature behaves much like the body prickles. In species which inhabit mountain brooks as well as lakes, the lake samples have the longer, sharper, and generally better-developed spines. The armature is totally absent in some populations of several mountain forms. Armature, like body prickles, may greatly assist in the identification of species at any one locality, but is often unreliable for relating or distinguishing allopatric forms.

In order to facilitate the identification of the species of *Cottus* in southern Oregon and California (Pacific slope), we present the following key. The data are based on studies of material from throughout the known ranges of all the species.

KEY TO SPECIES OF *COTTUS* OF THE PACIFIC SLOPE OF CALIFORNIA AND SOUTHERN OREGON ²

1. Pelvic rays 3-3; palatine teeth absent; some pectoral rays branched; lateral line incomplete ----- 2
1. Pelvic rays 4-4 (if 3-3 then lateral line complete); palatine teeth present or absent; pectoral rays branched or not; lateral line variable ----- 3
2. Two or 3 (usually) preopercular spines, the uppermost relatively long and pointed, the next lower typically recurved at tip; lateral line more complete, usually extending to or beyond base of last dorsal ray (see text for variability); ventral surface of head and abdomen nearly immaculate ----- *C. tenuis*
2. One or 2 (at most) preopercular spines, the uppermost comparatively short and blunt, the next lower not recurved at tip and usually weak; lateral line less complete, not extending beyond base of third from last dorsal ray; ventral surface of head liberally sprinkled with melanophores ----- *C. asperrimus*
3. Lateral line usually complete, with 28 or more pores (if fewer, palatine teeth present); palatine teeth variable; pectoral rays unbranched; dorsal spines 8-9 ----- 5
3. Lateral line incomplete (usually with 15-25 pores but higher in *klamathensis* below Klamath Falls); palatine teeth absent; some pectoral rays branched; dorsal spines 5-7 (rarely 8) ----- 4
4. Preoperculo-mandibular pores 10-1-10; infraorbital pores 7-7; preopercular armature much reduced or absent; dorsal soft rays usually 20-21; head pores much enlarged (larger than nasal openings) ----- *C. princeps*
4. Preoperculo-mandibular pores 10-10; infraorbital pores 8-8; upper preopercular spine well developed (2 accessory spines often present below it); dorsal soft rays usually 18-19; head pores small (smaller than nasal openings) ----- *C. klamathensis* ³
5. Anal rays usually 17-18, pectoral rays modally 16 (often 17), dorsal rays 19-22; palatine teeth present and well developed ----- *C. asper*
5. Anal rays 12-15, pectoral rays modally 15, dorsal rays 16-18 (if more, palatine teeth absent); palatine teeth variable ----- 6
6. Pelvic fins long (when depressed, reach anus); palatine teeth absent; dorsal soft rays 17-20, total dorsal elements usually 27-29; caudal vertebrae 24-27 ----- *C. aleuticus* ⁴
6. Pelvic fins short (when depressed, usually fall far short of anus); palatine teeth variable; dorsal rays 16-18 (rarely 19), total dorsal elements usually 26 or fewer; caudal vertebrae 21-24 ----- *C. gulosus* ⁵

² *C. beldingi* has been reported only once from the Sacramento River basin (Rutter, 1908, p. 147), based on a collection taken prior to 1900. To our knowledge, the species does not now occur in this drainage.

³ Including *C. macrops*, see text.

⁴ Including *C. protrusus*, see text.

⁵ Including *C. shasta*, see text.

SYSTEMATIC ACCOUNT

Cottus tenuis

(Tables 1 and 2)

Uranidea tenuis. Evermann and Meek, 1898, p. 83-84, fig. 6 (original description; type locality: lower end of Upper Klamath Lake, near Klamath Falls, Oregon).

Cottus tenuis. Rutter, 1908, p. 145 (comparison with *C. asperrima* [sic]). Hubbs and Schultz, 1932, p. 50 (compared with *tubulatus*). Hubbs and Miller, 1948, p. 69 (relationship to *asperrimus* indicated). Bailey and Dimick, 1949, p. 15 (comparison with *C. hubbsi*).

The drawing of the type (Evermann and Meek, 1898, p. 83, fig. 6) does not accurately depict the body form since the figure represents a recently spawned and much emaciated individual. The undivided last dorsal and anal ray, the profuse branching of the upper pectoral rays, the long lateral line and the preopercular armature are correctly figured. The short spinous dorsal fin is contiguous with the soft dorsal but the two are never broadly joined. In most specimens several of the dorsal and anal soft rays are branched. The pelvic rays are branched distally in all but a few of our specimens, mostly young (see material examined), a condition noted by us in only one other species (*C. asperrimus*).

Frequency distributions of fin-ray counts and numbers of lateral-line pores are presented in Table 2.

The lateral line is never complete and generally terminates under the last few rays of the second dorsal fin. Specimens from Sprague River have a less well developed lateral line than the other populations studied (see Table 1). The head pores have seldom been used in studies on this genus although they are useful in separating many species. In *tenuis* there are 10-10 pores in the preoperculo-mandibular canals (61 specimens), rarely 9-1-9 (6 specimens). The infraorbital canal has 8-8 pores in 61 specimens, with very little variation (8-9 in one and 9-9 in two).

The body prickling is quite variable. Lake specimens usually have the entire upper half of the body covered with fine prickles, while creek specimens have a patch of prickles mesial to the pectoral fin or are entirely naked. The dorsal surface of the head is never prickled. Similarly the preopercular armature is best developed in lake examples. Three sharp spines are noted in those from Upper Klamath Lake. Specimens from Sprague River retain the three spines but they are shorter and more blunt.

Vomerine teeth are present but palatine teeth are lacking in all material examined by us. Caudal vertebrae (including hypural) number 23 (3 specimens), 24 (7), or 25 (1).

Comparisons and Relationships

C. tenuis is most closely allied to *C. asperrimus*, which inhabits several tributaries of the Pit River of the Sacramento River system. A comparison of these forms is given under the treatment of *asperrimus*. No very close relationship is noted with any other species. *C. tenuis* and *C. asperrimus* are unique in having branched pelvic rays. *C. princeps*

differs from *tenuis* in having the dorsal fins fused, 4-4 pelvic rays, 7 dorsal spines, 20-21 dorsal soft rays, a less complete lateral line, much enlarged head pores, 7-7 infraorbital pores, 10-1-10 preoperculo-mandibular pores, and in numerous other ways. *C. klamathensis* shares with *tenuis* an absence of palatine teeth and similar head-pore counts. It differs in having more numerous dorsal spines (usually 7) 4-4 pelvic rays, a less complete lateral line (15-22 pores), and a broad union of the dorsal fins (Gilbert, 1898, fig. on p. 10). Limited material of *klamathensis* from below Klamath Falls shows a better-developed lateral line.

As discussed below, we treat *macrops* and *klamathensis* as conspecific. *C. gulosus*, an extremely variable form, has 4-4 pelvic rays, 8-9 dorsal spines, unbranched rays in all fins and a more complete lateral line (usually 32-36 pores). Evermann and Meek (1898, p. 83) ally *tenuis* and *C. marginatus*, probably on the basis of two features which they share: 3-3 pelvic rays and a lack of palatine teeth. The pelvic rays of *marginatus* are not branched, however, and it has 10-1-10 preoperculo-mandibular pores and 7-9 dorsal spines. In its general physiognomy *marginatus* appears more closely allied to *perplexus* and *klamathensis* than to *tenuis* and *asperrimus*.

There is presented in Table 1 a color comparison of *princeps*, *tenuis*, *asperrimus*, *klamathensis*, and "*macrops*", drawn by C. L. Hubbs from freshly collected specimens; that for the first three species is based on material taken in Upper Klamath Lake (Pelican Bay) on August 14, 1934 (field sta. M34-130), and the notes on *asperrimus* and "*macrops*" are based on specimens from the Fall River system near Dana, California, taken on August 17, 1934 (field sta. M34-135). Statements in parentheses under *asperrimus* are our observations where no specific reference to these items appears in Dr. Hubbs' notebook.

Geographic Variation

Populations from Upper Klamath Lake, Agency Lake-Crooked Creek, and Sprague River—all in the Klamath basin—exhibit some degree of differentiation. We do not feel that these differences are sufficient to merit nomenclatural recognition. Specimens from Agency Lake and Crooked Creek are most similar to the Klamath Lake population but differ in having somewhat fewer dorsal soft rays and pectoral rays. The Sprague River material has a distinctly lower pectoral-ray count and somewhat fewer pores in the lateral line.

Habits

An examination of the abundant type material of *tenuis*, collected on November 3, 1896, reveals many females with enlarged eggs and others which have obviously spawned. This evidence, coupled with Evermann and Meek's (1898, p. 84) reference to a ripe female, definitely shows that *tenuis* is a fall spawner in Klamath Lake.

Geographic Range

C. tenuis is restricted to Upper Klamath Lake and its tributaries, Oregon.

TABLE 1
Life Colors of Four Species of *Cottus* *

Feature	<i>princeps</i>	<i>tenuis</i>	<i>asperimus</i>	<i>kiamathensis</i>	" <i>macrops</i> "
General tone	Olive to purplish	A grayish olive to brown	Olive brown to purplish brown	More yellow-olive, with or without reddish in lighter reticulations	Yellow to olive-green to very dark slaty olive; light areas greener than ground color
Belly	White to gray	More metallic, silvery to brassy	(with scattered melanophores; see Rutter, 1908, fig. 3)	Duller, creamy gray to blue-gray	Dark
Bicolored contrast	Moderate	Strong	Variable, generally moderate to weak, strong in some, especially in young	Weak	Little
Lateral blotching	Coarse, rather faint	Most disrupted and intense	Reticulated, intense, with tendency for irregular light splashes	Rather faint and reticulated	Indistinct, the blotches much disrupted
Chin	Whitish to gray, more or less marbled with slaty	White to yellow, not marbled	(dusted with melanophores, marbled in some)	Olive to yellowish, with faint marbling or none	Somewhat marbled or uniform
Pelvic fins	White	White	Clear white or brassy	Yellowish or olive, with trace of bars	Brown to red, with greenish-gray cross markings
Anal fin	White to faintly barred	As in <i>princeps</i>	Brown to reddish, lighter than dorsal, crossed by light gray streaks	Rather strongly barred	Like pelvics
Dorsal fin	Light, with faint to definite dark bars	Light, with dark bars or intense dashes	Brown to reddish, crossed by light gray streaks	Reddish, with narrow olive bars	Brown to red, with greenish-gray or darker cross markings
Caudal fin	Light olive, with pale to dark reddish or brownish bars	Light gray, cream or yellow, with blackish bars	Like dorsal	Dark reddish or brownish, with narrow olive bars	Brown to red

* Taken from field notes by C. L. Hubbs (see text), except for statements in parentheses.

Cottus asperrimus
(Tables 1 and 2)

Cottus asperrima. Rutter, 1908, p. 144-145, fig. 3 (original description; type locality: Fall River at Dana, California). Snyder, 1917, p. 82 (synonym of *gulosus*).

Cottus asperrimus. Hubbs and Schultz, 1932, p. 5 (compared to *tubulatus*). Hubbs and Miller, 1948, p. 69 (relationship with *tenuis*). Bailey and Dimick, 1949, p. 16 (removed from synonymy of *C. gulosus*).

Frequency distributions of fin-ray counts and numbers of lateral-line pores are given in Table 2. *C. asperrimus* is so similar to *tenuis* that only the differences between them need to be noted. This similarity must have been suspected by Rutter (1908, p. 145) since he presented a tabular comparison between these two species, but the characters listed by him are slight and do not hold when comparable specimens are examined. We note several diagnostic features. Typically, *asperrimus* has only one well-developed preopercular spine and a blunt knob below it, often absent, whereas *tenuis* has three preopercular spines. The lateral line is less well developed in *asperrimus*, generally extending to the base of the second to fifth ray from the last, but reaching to or beyond the last dorsal ray in *tenuis*. The latter species spawns in the fall, whereas *asperrimus* evidently spawns earlier (see Habits, below.) The life coloration (Table 1) appears to be distinctive and the pigmentation also differs, *asperrimus* showing profuse chromatophores on the venter, whereas *tenuis* is nearly immaculate. Although the pelvic, soft dorsal, and anal rays of *asperrimus* are branched, as in *tenuis*, the degree of branching seems to be weaker, particularly on the smaller topotypes (UMMZ 130650), than it is in *tenuis*. The number of preoperculo-mandibular pores is variable. In 19 specimens (including the holotype) the formula is 9-1-9, whereas in 41 specimens (including 2 paratopotypes, SNHM 9968) it is 10-10, as in *tenuis*. The two forms perhaps warrant only subspecific status, but our material is insufficient to decide this point with assurance.

An extensive patch of prickles is present mesial to the pectoral fin, and in most specimens the prickling extends caudad along the body above the lateral line to a point under the middle of the second dorsal fin. Few specimens exhibit such extensive prickling as the holotype (Rutter, 1908, p. 144, fig. 3). The figure of the type errs in showing unbranched pectoral rays and a peculiar head profile. Actually, the ventral contour is flat to the tip of the chin, as in other sculpins, and the dorsal profile turns abruptly downward in front of the eyes.

Comparisons

C. asperrimus differs from other sculpins in most of the characters which separate them from *C. tenuis* (see above). The 3 soft rays of the pelvic fins readily distinguish it from *klamathensis*, which occurs with *asperrimus* and has 4 pelvic rays.

The origin of *asperrimus* is considered in the zoogeographical discussion.

Geographic Variation

Available material of this species is inadequate to determine the range of variability but does show that the number of pectoral rays in samples from above the Pit River falls is significantly greater than it is in the one sample from below these falls (15 versus 14, Table 2).

Habits

Specimens of *asperrimus* from Hat Creek (below Pit River falls) taken on May 6, 1949, include females with large eggs, suggesting that this species, in contrast with *tenuis*, is a spring spawner.

Geographic Range

C. asperrimus is probably restricted to the Pit River portion of the Sacramento River system, for a short distance above and below the falls at Fall River Mills, California.

Cottus princeps (Tables 1 and 2)

Cottus princeps Gilbert, 1898, p. 12-13, fig. on p. 12 (original description; type locality: Upper Klamath Lake, Oregon). Evermann and Meek, 1898, p. 83 (specimens from Pelican Bay, Upper Klamath Lake). Hubbs and Schultz, 1932, p. 4-5 (comparison with *tubulatus*). Hubbs and Miller, 1948, p. 68 (adaptation to lake life). Bailey and Dimick, 1949, p. 15-16 (compared with *hubbsi*; characters).

Cottus evermanni Gilbert, 1898, p. 11-12, fig. on p. 11 (original description; type locality: Lost River near Klamath Falls, Oregon). Hubbs and Schultz, 1932, p. 4-5 (comparison with *tubulatus*). Bailey and Dimick, 1949, p. 15-16 (synonymized with *princeps*, rule of first reviser).

C. princeps is one of the most distinctive species in the genus. There are generally 7 dorsal spines, 20-21 soft dorsal rays, 16 anal rays, 4 pelvic rays, 15-16 pectoral rays, and 15-25 lateral-line pores (Table 2). The lateral line is incomplete and ends under the posterior half of the second dorsal fin. The dorsal fins are entirely fused. A few specimens show some branched dorsal and anal rays, but this is unusual. The pelvic rays are never branched, whereas the upper pectoral rays are usually, but not always, branched.

The pelvic fins are long, reaching the anus when depressed. The body is extensively prickled. Below the lateral line the prickling usually extends caudad to a point about under the center of the second dorsal fin. Above the lateral line the entire body is prickled, except on the caudal peduncle and head.

The figures of the types of *princeps* and *evermanni* accurately depict the body form and color pattern. The anterior nasal tubes are very well developed. The head pores are much enlarged; those of the infra-orbital and preoperculo-mandibular canals are larger than the nasal openings. The canals are very prominent and cause cavernous openings in the bones through which they pass. All 34 specimens examined have 10-1-10 preoperculo-mandibular pores. Infraorbital pores number 7-7 (12 specimens) or 6-7 (2 specimens).

The palatine teeth are absent. The preopercular armature is reduced to one blunt spine. The lower jaw usually projects slightly beyond the upper jaw. We note 24 caudal vertebrae in two specimens and Bailey and Dimick (1949, p. 16) recorded 26.

Comparisons and Relationships

The combination of characters listed above imparts to *princeps* a distinctiveness that renders it unmistakable. *C. klamathensis* has the dorsal fins partly or completely fused, lacks palatine teeth, and has 4-4 pelvic rays. It differs trenchantly in its lower ray counts (second dorsal rays usually 18-19 instead of 20-21; anal rays 13-14 instead of 15-17), its higher number of infraorbital pores (8-8 instead of 7-7), its separate preoperculo-mandibular canals (pores number 10-10 instead of 10-1-10), its more robust body form, and in many other ways. Distinguishable features for *tenuis* and *aperrimus* have already been explained. *C. gulosus* has separate dorsal fins, 13-15 anal rays, 8-9 dorsal spines, 16-18 soft dorsal rays, and a much more complete lateral line (usually 32-36 pores).

The relationships of *princeps* are uncertain. The high number of caudal vertebrae (24-26) places it with *aleuticus* and *asper*. It shares with those species a preoperculo-mandibular pore count of 10-1-10. *C. aleuticus* apparently never develops palatine teeth, while *asper* has well developed palatine tooth patches. Like *princeps*, *asper* has a long second dorsal (19-22 rays) and anal fin (15-19 rays). *C. aleuticus* similarly has a long dorsal fin but has fewer anal rays (12-15, usually 13-14). Both generally have complete lateral lines, although *aleuticus* is more variable in this respect. The color pattern of *asper* is suggestive of *princeps*. The long pelvic fins of *aleuticus* reach the anus when depressed, a feature seldom noted in other American species of *Cottus* but characteristic of *princeps* and several Asiatic species. *C. asper* is more prone to move inland than is *aleuticus*, a form common in coastal streams. If *princeps* is derived from either an *asper* or *aleuticus* type, the two have long been differentiated. Its relationships to other American species appear to be even more distant.

Habits

All females in a series of specimens collected on November 3-5, 1896, by Meek and Alexander (USNM 124952), have the ovaries bulging with mature eggs.

Geographic Range

C. princeps is known only from Upper Klamath Lake and from Lost River (near Klamath Falls), Oregon.

MATERIAL EXAMINED

Cottus princeps. USNM 48227 (1, 41) holotype; USNM 48228 (1, 47), holotype of *C. evermanni*. The following are all from Upper Klamath Lake, Ore.: USNM 124952 (18, 30-68); UMMZ 130627 (14, 30-44); UMMZ 138574 (7, 47-64); SNHM 38029 (29, 45-60); and SNHM 40744 (2, 42-63).

Cottus tenuis. USNM 48229 (1, 74), holotype. All others are paratopotypes: USNM 48230 (38, 25-62); USNM 124958 (38, 23-70); USNM 48780 (13, 22-71); and SNHM 5705 (20, 20-44).

Additional material examined from Upper Klamath Lake, Ore.: UMMZ 130603 (2, 38-51); UMMZ 130626 (6, 32-49); UMMZ 172293 (4, 26-38); and SNHM 9333 (1, 86).

Other material: Klamath County, Ore.: UMMZ 130610 (149, 24-80) Crooked Creek; UMMZ 130581 (9, 20-56) Sprague River; UMMZ 130617 (27, 21-44) Agency Lake, mouth of Wood River; and SNHM 24185 (11, 36-48) Spring Creek, Shasta County, Calif.

Cottus asperrimus. USNM 58500 (1, 50), holotype; USNM 126463 (1, 48), paratopotype; SNHM 9968 (2, 41-49), paratopotypes; UMMZ 130647 (1, 39) Rush Creek, Modoc County, Calif.; UMMZ 130650 (7, 14-64) Fall River system, Shasta County, Calif.; and UMMZ 158416 (28, 41-89) reservoir on Hat Creek, about 4 miles above its junction with Pit River, Shasta County, Calif.

NOTES ON THE CLASSIFICATION OF OTHER SPECIES

Cottus klamathensis

Cottus macrops, described from Fall River, California (Rutter, 1908, p. 146-147, fig. 4), has generally been maintained as a valid species (Hubbs and Miller, 1948, p. 69; Bailey and Dimick, 1949, p. 15; and others), although these writers noted its similarity to *klamathensis*. Snyder (1917, p. 82) failed to observe the intimate relationship of *macrops* and *klamathensis* and combined both *macrops* and *asperrimus* with *gulosus*.

A careful comparison of the type material of *klamathensis* and *macrops* and of fresh collections of the two nominal forms fails to reveal differences that we judge to be of specific value. Rutter recognized the very close relationship between the two but indicated that *macrops* had a heavier build, a larger eye, the head less pointed, and the dorsal fin somewhat more posterior in position. Our material fails to confirm some of these distinctions (e.g., the larger eye), and we regard other features to be too variable or indicative of ranking below the species level. Like *klamathensis*, the body prickles in *macrops* occur on smaller individuals only (up to about 55 mm. standard length), the large adults having the skin entirely smooth. Generally, *macrops* has only one well developed preopercular spine, with the two accessory spines reduced to blunt knobs or absent. In many samples of *klamathensis* there are individuals that have all three spines developed, others that have only two, but populations from below Klamath Falls are somewhat intermediate between *klamathensis* (above the Falls) and *macrops* in this feature, having one or two developed spines. Life colors (Table 1) of the two nominal forms indicate no marked differences. The most consistent difference we have noted between the two involves the width of the mouth. In *macrops*, the snout is blunter and the mouth wider (its greatest width enters the anal base 1.2-1.6 times). In *klamathensis* (above the Falls) the snout is more pointed and the mouth narrower (its greatest width enters the anal base 1.6-2.0 times; in one collection (15 specimens) below the falls, the ratios vary from 1.3-1.8 times). The reliability of this feature is uncertain, and we feel it can be used

for subspecific separation at most. The two share a preoperculo-mandibular pore count of 10-10, lack palatine teeth, have broadly connected dorsal fins, have the vertical fins similarly marbled and with a black blotch on the posterior membranes of the first dorsal, and have similar fin-ray counts, which may be summarized as follows: dorsal spines, 6 (1), 7 (25), 8 (6); dorsal soft rays, 18 (10), 19 (21), 20 (1); anal rays, 13 (6), 14 (25), 15 (1); pelvic rays, 4-4 (26 fins); pectoral rays, 14 (9 fins), 15 (49 fins), 16 (3 fins). The lateral-line pores range from 14-22. These data are based on the following material: USNM 58499 (14, 23-57) syntypes of *macrops*; USNM 126464 (4, 22-51) syntypes of *macrops*; SNHM 24186 (4, 31-57) syntypes of *macrops*; USNM 88464 (2, 40-44) Fall River, Calif.; USNM 48266 (1, 118) type of *klamathensis*; and CU 21612 (7, 24-76) Shasta River, Calif.

We synonymize *macrops* with *klamathensis* but note that study of additional features may show them worthy of subspecific rank. Comparison of populations from above and below Klamath Falls shows that those from the lower river (excluding one sample from Shasta River) have a more complete lateral line (this was also noted by Gilbert, 1898, p. 11), and these may represent a third form worthy of naming. Gilbert believed *klamathensis* to be most nearly related to *perplexus*, a view which we share. *C. klamathensis* affords another example of fishes shared by the upper Klamath and Pit rivers (see discussion of zoogeography).

Cottus aleuticus

This species is widespread in coastal streams from central California (northern San Luis Obispo County) to Alaska. As noted by Hubbs and Schultz (1932, p. 6, table 1) it belongs to those species of *Cottus* which have many (24-27) caudal vertebrae. In other features it is distinguished by having 10-1-10 preoperculo-mandibular pores, 8-9 dorsal spines, 17-20 dorsal rays (usually 18-19), 12-14 anal rays, 4 pelvic rays, 14-16 pectoral rays, long pelvic fins, no palatine teeth, and few if any prickles. Schultz and Spoor (1933) described *C. protrusus* from Unalaska Island. They noted its similarity to *aleuticus* in several features but contrasted *protrusus* only with *chamberlaini*, a very different form doubtfully distinct from *C. cognatus*. The holotype (USNM 104496) and a paratopotype (UMMZ 64234) of *protrusus* were compared with the syntypes of *aleuticus* (SNHM 2610) from Iliuliuk, Unalaska, and with other specimens from Alaska to California (variously labelled as *protrusus*, *aleuticus*, or *Uranidea microstoma*). No differences signifying other than individual variation were noted. Specimens which exhibit protruding eyes (the basis of *protrusus*) are known from widely scattered localities and appear even in the syntypic series of *aleuticus*. Whether this is a response to temperature (improbable) or one induced by disease or parasitism is not known. We regard the condition as an anomaly and, in the absence of any other difference, consider *protrusus* synonymous with *aleuticus*. *Uranidea microstoma* Lockington is preoccupied in *Cottus*, a fact long known, and was placed in the synonymy of *aleuticus* when that species was described. In the course of this study we re-examined the holotype (USNM 26922) and take this opportunity to confirm its identity with *aleuticus*.

In summarizing the distribution of this species in California, Evermann and Clark (1931, p. 57) overlooked the southernmost record given by Hubbs (1921, p. 7-8). The presence of *aleuticus* in northern San Luis Obispo County is confirmed by a recent collection (UMMZ 141194) of 74 specimens from San Carpoforo Lagoon, just south of the Monterey County line.

Shapovalov and Taft (1954, p. 26) record this species from Waddell Creek and (*in litt.*) note that their extensive collections are deposited in the California Academy of Sciences.

Cottus gulosus

It is unfortunate that this variable species, known widely in the Sacramento-San Joaquin drainage and several lesser coastal streams of California, has been considered a subspecies in the *bairdi* complex by recent writers (Hubbs and Wallis, 1948, p. 141-142; Shapovalov and Dill, 1950, p. 387, as *C. b. shasta*). There is little positive evidence to support this relationship and many reasons for doubting it. We feel that this subspecific allocation has caused considerable confusion and, pending more thorough study, consider *gulosus* a valid species very closely allied to *hubbsi*. For the present, we feel that the only western forms of *Cottus* that should be aligned specifically with *bairdi* are *C. b. semiscaber* and *C. b. punctulatus* of the upper Columbia and Colorado rivers, respectively.

We agree with Synder (1905, p. 337) that *C. shasta* and *C. gulosus* are synonymous. A re-examination of the types (SNHM 4193, 3 syntypes of *shasta*; USNM 291, 2 syntypes⁶ of *gulosus*) and other material, including topotypes, from the range of both forms, fails to reveal any basis for specific separation. The preoperculo-mandibular pore count is quite variable (10-1-10, 10-10, 11-11) but shows no geographic consistency. A study of fin-ray counts and numbers of lateral-line pores indicates no differences between *shasta* and *gulosus* but suggests that populations in coastal streams from Monterey Bay northward have a much less complete lateral line.

Uranidea semiscabra centropleura Eigenmann and Eigenmann has never been adequately discussed. Jordan and Evermann (1898, p. 1945) and Evermann and Clark (1931, p. 57) identified it with *gulosus*. Rutter (1908, p. 145) placed it in the synonymy of *asper*. Re-examination of the type (USNM 41919, 63 mm. standard length) shows conclusively that this form belongs to the *gulosus* series. The two dorsals are separate but contiguous. Fin-ray counts are as follows: 8 dorsal spines, 17 dorsal soft rays, 13 anal rays, 13 rays in each pectoral, and 4 rays in each pelvic fin. There are 35 lateral-line pores and 10-1-10 preoperculo-mandibular pores. Palatine teeth are present but not strongly developed. These features are all characteristic of *gulosus* except the few pectoral rays; should this low count be typical then subspecific recognition might be warranted for *centropleurus*.

Most of the records of *gulosus* from Washington and northern Oregon are based on *C. perplexus* Gilbert and Evermann, a species synonymized with *gulosus* by Schultz (1930, p. 14). None of these records represents *gulosus* as we define that species. Counts of the holotype of *perplexus*,

⁶Jordan and Evermann (1898, p. 1945) erred in listing USNM 290 as types.

USNM 43387 (1, 71), and of 14 of the paratopotypes, USNM 45388 (24, 18-55), are summarized as follows: dorsal spines, 7 (13 specimens)⁷, 8 (2); dorsal soft rays, 18 (4), 19 (5), 20 (2)⁷; anal rays, 13 (2), 14 (4), 15 (6)⁷, 16 (3); pelvic rays (both fins), 4 (30)⁷; pectoral rays, 14 (3), 15 (18), 16 (9)⁷; lateral-line pores, 20 (2); 21 (1), 22 (1), 23 (1), 24 (3), 26 (1)⁷; preoperculo-mandibular pores, 10-10 (8)⁷, 11-11 (1). Two other specimens in the series of paratopotypes are *C. rhotheus*. In its robust body form, strongly marbled vertical fins, and the joined dorsal fins, *C. perplexus* seems more closely allied to *klamathensis* than to *gulosus*. The type material lacks palatine teeth but in 39 subtopotypes (UMMZ 93437) these teeth are present or absent.

Cottus asper

Jordan and Evermann (1898, p. 1945) and Jordan, Evermann and Clark (1930, p. 383) listed *Cottopsis parvus* Girard in the synonymy of *gulosus*. Of the four series of specimens recorded by Girard in his summary account (Girard, 1858, p. 54-55), we have located one of the 12 from Petaluma (UMMZ 171133) and three of the four from Fort Reading (USNM 295; 3, 88-103). Since Girard considered only the material from Presidio in his original description (1854, p. 144-145), the specimens listed above are not types. Nevertheless, study of this material and of Girard's description leaves no doubt in our minds that *Cottopsis parvus* is identical with *Cottus asper*. Particularly diagnostic are the numerous dorsal and anal rays and the body prickles. A variational study of this widespread species is much needed. Its role as an important predator on juvenile trout and salmon is discussed by Shapovalov and Taft (1954, p. 293). Their abundant material is included in the collections of the California Academy of Sciences.

ZOOGEOGRAPHICAL IMPLICATIONS

The mutual occurrence of *Cottus klamathensis* and the allopatric forms *C. tennisi* and *C. asperrimus* in the upper Pit and Klamath rivers poses an interesting problem in distribution and origin. A consideration of the fish faunas of the Klamath and Sacramento basins as a whole is necessary to an understanding of the hypothesis proposed below to explain the distribution of the species of *Cottus*.

Despite its geographic position between the Sacramento and Columbia drainages, the fauna of the Klamath basin surprisingly lacks the characteristic endemic genera of either of those great river systems (Miller, 1946, table 1). Even *Ptychocheilus*, ubiquitous in both the Sacramento and Columbia and with a representative species in streams between the Klamath and Columbia rivers, is absent in the Klamath system. Yet the latter basin has a comparatively rich, highly endemic fauna that is suggestive of long isolation (Hubbs and Miller, 1948, p. 68-69, and references cited). Close relationships are shown, however, between certain fishes of the Klamath Lakes and the Great Basin; for example, the peculiar suckers of the genus *Chasmistes* and the distinctive chubs assigned to the genus *Siphateles*.

⁷ Holotype.

In addition to the common bond between the upper Pit and Klamath rivers exemplified by the species of *Cottus*, there is a dwarf non-parasitic lamprey (genus *Entosphenus*) known only from these two regions, and the stream representatives of *Siphateles bicolor* also show intimate relationship.

These similarities call for some kind of past connection between the Klamath system above Klamath Falls and what is now the upper segment of Pit River, including Goose Lake. It is reasonable to assume that the connection was by way of interconnecting streams through a chain of lakes (see Cope, 1883, map opposite p. 166) on the northern part of the Modoc Plateau and that the evidence for the waterway lies buried beneath the extensive Modoc lava flows (Anderson, 1941). That none of the endemic Sacramento forms reported from the upper Pit drainage (e.g., *Hesperoleucus*, *Mylopharodon*, *Ptychocheilus*, and *Hysterocarpus*) occurs in the Klamath suggests that the connection between these two basins was severed prior to the invasion of the upper Pit region (through headward erosion by Pit River) by these Sacramento types.

With this picture in mind, we may envision the origin and differentiation of two species of *Cottus* in the upper Pit as follows. After penetrating the Klamath basin prior to the formation of Klamath Falls, the ancestors of *C. klamathensis* and *C. tenuis* subsequently crossed the Modoc Plateau to reach what is now the upper Pit basin and thus attained a wide distribution in these presently disrupted waters. When the connection between the Klamath and Pit rivers was severed, the isolated stocks underwent differentiation, weaker for *C. klamathensis* than for *C. tenuis*, resulting in the evolution of the allpatric form *C. asperrimus*. With the development of the Pit River falls, the Hat Creek population of *asperrimus* below the barrier further differentiated. Although by this hypothesis we regard the Hat Creek population as a downstream derivative of *asperrimus*, an alternate idea may be considered. This is to regard *tenuis* and the Hat Creek population as peripheral remnants of a single form which has somewhat diverged and that the form occupying the old center area has diverged most into what is now called *asperrimus*. Perhaps future work will show that there are three subspecies of *tenuis*, one in the upper Klamath, one in the upper Pit, and one in Pit river below the falls. Our material, however, does not permit us to adopt this arrangement but it makes clear the intimate relationship between *asperrimus* and *tenuis*.

The clear indication of close relationship between the fishes of these two regions with those in the adjacent Great Basin finds support amongst other vertebrate groups, as in birds. The northeastern corner of California, including the upper part of Pit River (mostly above the falls), is ascribed wholly or largely to the Modoc faunal district (of the Great Basin faunal division) by Grinnell (1915, p. 12, pl. III) and by Miller (1951, p. 591, fig. 4), a district which obviously extends into the Klamath Lake region.

SUMMARY

The characters, distribution and geographic variation of *C. tenuis*, *asperrimus*, and *princeps* are treated and nomenclatural notes are given for *klamathensis*, *aleuticus*, *gulosus*, and *asper*.

Emphasis in this paper has been directed toward working out relationships at the species level. Detailed studies need to be made in order to determine differentiation of subspecific value.

C. asperrimus, of Pit River, California, is regarded to be a very close relative of *tenuis*, limited to the upper Klamath drainage of Oregon and California; further studies may show them to be conspecific.

The placement of *evermanni* in the synonymy of *princeps* is confirmed and the possible relationship of this species to *aleuticus* and *asper* is discussed.

C. macrops is considered to be conspecific with *klamathensis*, *protusus* is placed in the synonymy of *aleuticus*, *shasta* is regarded as identical with *gulosus*, and *parvus* is synonymized with *asper*.

It is urged that the name *bairdi* not be used for any western forms other than *punctulatus*, and *semiscaber*. The application of this name to *gulosus* has been particularly confusing and does not seem warranted in the light of our present knowledge.

Uranidea semiscabra centropleura is aligned with *gulosus* and may prove to be a valid subspecies.

C. perplexus is removed from the synonymy of *gulosus* and is considered a valid species, but its relationships with *klamathensis* need to be clarified.

The relationships of the fish fauna of the upper Klamath and Pit rivers is emphasized in a section on zoogeography, with a discussion of the origin and dispersal of the species of *Cottus* common to these two regions.

A key to the species of *Cottus* in the Sacramento and Klamath drainages is presented.

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