OCCASIONAL PAPERS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

No. 138, 58 pages, 44 figures, 10 tables. January 17, 1984

Systematics and Distribution of Cottid Fishes of the Genera *Rastrinus* and *Icelus*

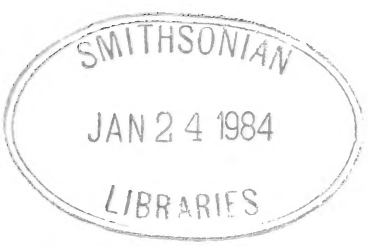
By

Douglas W. Nelson

School of Fisheries, College of Ocean and Fishery Sciences, University of Washington, Seattle, Washington 98195

SAN FRANCISCO

PUBLISHED BY THE ACADEMY



US ISSN 0068-5461

The California Academy of Sciences
Golden Gate Park
San Francisco, California 94118

PRINTED IN THE UNITED STATES OF AMERICA
BY ALLEN PRESS INC., LAWRENCE, KANSAS

TABLE OF CONTENTS

ABSTRACT

NELSON, DOUGLAS W. Systematics and distribution of cottid fishes of the genera *Rastrinus* and *Icelus*. *Occasional Papers of the California Academy of Sciences*, No. 138, 58 pages, 44 figures, 10 tables, 1983.—The cold-water cottid genera *Rastrinus* and *Icelus* are revised on the basis of approximately 1400 specimens collected in the North Pacific, North Atlantic, and Arctic oceans. The genus *Rastrinus* contains a single species restricted to the northern Gulf of Alaska and the southern Bering Sea. The genus *Icelus* contains 13 species widely distributed throughout the North Pacific, North Atlantic, and Arctic oceans in depths of 20–800 m.

Three species groups are recognized within the genus *Icelus* (the *I. spiniger* group, *I. euryops* group, and *I. bicornis* group) based primarily on morphology of the platelike scales of the dorsal scale row and of the lateral line scales, and by the presence or absence of parietal spines and of spines on the suborbital stay. Two species (*Icelus gilberti* and *I. armatus*) exhibit mosaics of character states that make present placement into any of these species groups impossible.

The osteology of *Icelus spiniger* is described and figured, and compared with those of other species of *Icelus* and *Rastrinus*. The species constituting the two genera are diagnosed, described, and their geographic distributions are plotted and discussed. Complete annotated synonymies and a key to *Icelus* species are provided.

Systematics and Distribution of Cottid Fishes of the Genera *Rastrinus* and *Icelus*[1]

Douglas W. Nelson

Introduction

The genus *Icelus* was established by Krøyer (1845) to accommodate *Cottus uncinatus* (=*Artediellus uncinatus*) and a new species of sculpin (*Icelus hamatus*) from Belsund, Spitzbergen. Jensen (1904) determined that the latter species was *Cottus bicornis*, described earlier by Reinhardt (1840a), and reestablished the priority of Reinhardt's description and nomenclature. A period of species descriptions followed Krøyer's work, based largely on Albatross collections made in the North Pacific (Bean 1890; Gilbert 1895; Gilbert and Burke 1912) and Russian expeditions in the Sea of Okhotsk and Sea of Japan (Schmidt 1915, 1927; Taranetz 1936). Some material collected by these expeditions resulted in descriptions of new genera closely allied with, and sometimes synonymized with *Icelus*: *Agonocottus* Pavlenko (1910) and *Ochotskia* Schmidt (1915).

Jordan and Evermann (1896) placed *Icelus scutiger* Bean (1890) into a new monotypic genus, *Rastrinus*, and subsequently provided a generic diagnosis (Jordan and Evermann 1898). Most subsequent authors have placed *Rastrinus scutiger* back into the genus *Icelus* (Taranetz 1935, 1936, 1937, 1941; Wilimovsky 1958; Howe and Richardson 1978), but were largely unable to diagnose the genus once expanded. Schmidt (1927, 1935), in his revisions of the genus *Icelus*, did not include *I. scutiger*; he was apparently satisfied with the new genus of Jordan and Evermann (1898).

Four major revisionary works have been published on the genus *Icelus*, two dealing with regional faunas and two dealing with the genus as then understood. Schmidt (1927) presented a worldwide revision of *Icelus*, concentrating on the North Pacific region and recognizing eight species (*Rastrinus scutiger* excluded). Schmidt (1935) subsequently recognized 10 species (again excluding *R. scutiger*) and suggested relationships among *Icelus* species based on development and adult morphology of the platelike scales of the dorsal scale row. He also erected several subspecies for *Icelus bicornis* based largely on differences in the urogenital papillae of males. Andriashev (1937a) partially revised the genus, dealing only with *I. spatula* and *I. uncinalis*, and further complicated the taxonomy of these species by recognizing several subspecies, based largely on differences in the development of the parietal and nuchal spines. Andriashev's (1937a) work was most instrumental in illustrating the ranges of variation in *Icelus* species. Jensen and Volsoe (1949) reviewed the North Atlantic species and suggested aids to identification of the North Atlantic and Arctic species. McAllister (1963) presented similar identification aids to the Canadian Arctic species *I. spatula* and *I. bicornis*; however, these aids are of limited usefulness in other geographic regions.

Several provisional classifications of teleosts have recognized Jordan's (1923) family Icelidae. Most recent classifications that recognize this family include three genera in it: *Icelus* Krøyer, *Marukawichthys* Sakamoto, and *Ereunias* Jordan and Snyder (the last two are monotypic Japanese endemics) (Schmidt 1950; Greenwood et al. 1966; Nelson 1976). Characters that have been used to diagnose the family include: presence of one or more rows of enlarged, platelike scales; opisthotic large, vagus nerve passing through foramen in opisthotic; and vomer and mesethmoid unossified (Jordan 1923; Schmidt 1950; Quast 1965; Nelson 1976; Yabe 1981). Taranetz (1941) proposed subfamilial status for the Icelinae, based largely on the characters used by others in arguments for familial status. Watanabe (1960) confusingly divided *Icelus* into two cottid subfamilies: Triglopsinae and Hemilepidotinae. Howe and Richardson (1978), following Matsubara (1936), recognized *Icelus* as a genus of the family Cottidae and advanced some hypotheses regarding interrelationships among eastern Pa-

[1] Contribution no. 609 from the School of Fisheries, College of Ocean and Fishery Sciences, University of Washington, Seattle, Washington 98195.

cific cottid genera. Richardson (1981) proposed several cottid groups based on larval characters, placing *Icelus* with *Icelinus, Paricelinus, Triglops,* and *Chitonotus.* More recently, Yabe (1981) placed *Icelus* back into the Cottidae based on morphological comparisons with *Hemilepidotus, Ereunias,* and *Marukawichthys*; and following Jordan (1923) and Berg (1940), placed *Ereunias* and *Marukawichthys* back into the family Ereuniidae.

Taranetz (1935), as noted above, synonymized the genus *Rastrinus* with *Icelus,* believing that the scales above the lateral line in *Rastrinus scutiger* were simply variations of the "bony plates" found in *Icelus* species, and that the state of this character alone did not warrant separate generic status for this species. The condition of these scales in *R. scutiger* may represent a primitive state in a transformation series leading to the character states observed in *Icelus* species, but these scales do not exhibit the enlarged, embedded bases observed in the platelike scales of *Icelus* species. In addition, the absence of nuchal spines (present in all species of *Icelus*) further distinguishes *Rastrinus* from *Icelus.* To attempt to incorporate these character states into the generic diagnosis for *Icelus* so broadens the diagnosis as to render it necessary to synonymize a number of other cottid genera (e.g., *Icelinus, Chitonotus, Ricuzenias,* and *Radulinus*) with *Icelus.* To more precisely diagnose the genera *Rastrinus* and *Icelus,* and to avoid the attendant loss of information which would result from "lumping" many cottid genera with *Icelus,* it has been necessary to herein resurrect the genus *Rastrinus.*

The purposes of this study are to delimit and describe the genera *Rastrinus* and *Icelus,* to diagnose and describe the several species which constitute the two genera, to describe the variation within and between these species, and to describe the geographic and bathymetric distributions of these species.

Materials and Methods

Measurements follow those described and figured by Miller and Lea (1972) with the following additions: lacrimal length is the distance between anterior edge of orbit and anteriormost edge of lacrimal; least interorbital width is measured between lateral margins of frontals at their narrowest widths; greatest body depth is measured from base of pelvic fin rays to base of second dorsal fin spine; pectoral fin base length is measured from ventral margin of base of lowermost pectoral fin ray to dorsal margin of uppermost pectoral fin ray.

Standard lengths are used throughout unless otherwise specified. Dorsal scale row counts include all scales with enlarged, platelike embedded portions (bases). Lateral line scale counts include scales posterior to the hypural plate (i.e., extending onto caudal rays). Axillary scales are those found on the side of the body immediately beneath the pectoral fin; total number of axillary scales and the number in the uppermost row are generally given. Dorsal caudal peduncle scales are defined as those found on the lateral aspect of the caudal peduncle posterior to the posteriormost platelike scale of the dorsal scale row. Ventral caudal peduncle scales are those on the lateral aspect of the caudal peduncle below the lateral line; or, when the lateral line does not extend onto the caudal peduncle, below the midline of the caudal peduncle. Methods of counting other scale rows are defined in the appropriate species accounts.

Bone terminology follows Weitzman (1974), with the exception of the vertebral column nomenclature which follows Nybelin (1963). Nomenclature for circumorbital bones is as follows: the first circumorbital is referred to as the lacrimal; the third circumorbital as the suborbital stay; the remaining circumorbital bones as circumorbitals 2, 4, 5, 6, counting the lacrimal as circumorbital 1 and numbering posteriorly and counterclockwise. Terminology for the head spines follows Eschmeyer (1969), with the exception of the lacrimal spine (=preorbital of Eschmeyer 1969), which retains the name "lacrimal" to maintain consistency with the osteological nomenclature. Nomenclature for the head cirri is derived from the head spine nomenclature with some exceptions (see Fig. 21).

The osteological study is based on cleared and stained specimens (Table 1) prepared by the trypsin digestion method of Taylor (1967). Only the detailed osteology of *I. spiniger* is figured and discussed. Comparative osteological discussions are presented for other *Icelus* species and *R. scutiger* where differences exist.

Drawings were prepared with the aid of a Wild M5 stereomicroscope equipped with a camera lucida. In the osteological figures, bone is rendered in white, cartilage in open stipple, and

(where necessary for clarity) foramina and open spaces in dense stipple.

The suites of characters used in the generic diagnoses of *Rastrinus* and *Icelus,* and those used in the specific diagnoses within the genus *Icelus,* are fully comparable.

Depositories of specimens examined in this study are as follows: Academy of Natural Sciences, Philadelphia (ANSP); British Columbia Provincial Museum, Victoria, B.C. (BCPM); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Natural History Museum, Stanford University (now deposited in the California Academy of Sciences) (CAS-SU); Field Museum of Natural History, Chicago (FMNH); Laboratory of Marine Zoology, Hokkaido University, Japan (HUMZ); Natural History Museum of Los Angeles County, Los Angeles (LACM); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of Canada, Ottawa, Ontario (NMC); Naturhistoriska Riksmuseet, Stockholm, Sweden (NRMS); National Science Museum, Tokyo, Japan (NSMJ); Department of Fisheries and Wildlife, Oregon State University (OSU); Royal Ontario Museum, Toronto, Ontario (ROM); Scripps Institution of Oceanography, La Jolla (SIO); Smithsonian Oceanographic Sorting Center, Smithsonian Institution, Washington, D.C. (SOSC); Department of Biology, University of British Columbia (UBC); University Museum, University of Tokyo, Japan (UMUT); National Museum of Natural History, Washington, D.C. (USNM); School of Fisheries, University of Washington (UW); Zoological Institute, Academy of Sciences, Leningrad, U.S.S.R. (IZL); Zoological Museum, University of Copenhagen (ZMUC). Additional material, unavailable for this study, is deposited in universities and museums in the U.S.S.R.

Table 1. List of Osteological Material Examined.

Rastrinus

Rastrinus scutiger: OSU 7874 (1:64.0 mm); Aleutian Is., 51°46′N, 177°23′E, 194–205 m; 21 July 1980.

Icelus

Icelus spiniger: UW 20802 (2:79.0–90.0 mm); Bering Sea, near Pribilof Is.; Aug. 1979.

Icelus cataphractus: UW 20827, 29833 (2:76.0–92.0 mm); Sea of Japan, 42°32′N, 143°51′E, no depth; 6 Sep. 1975.

Icelus euryops: UW 20801 (1:115.0 mm); Bering Sea, 60°59′N, 179°11′W, 300 m, Discovery Bay 79-2, haul 39; 18 July 1979.

Icelus canaliculatus: UW 20798 (1:109.0 mm); Bering Sea, 60°15′N, 178°52′W, 455 m, Discovery Bay 79-2, haul 49; 18 July 1979. UW 20842 (4:87.0–101.0 mm); Bering Sea, 59°19.65′N, 178°06.70′W, Yakushi Maru 21, sta. 44; 28 June 1979.

Icelus bicornis: NMC 70-277 (2:60.0–82.0 mm); N.W.T., Frobisher Bay betw. Mair I. and Cairn I., 5 mi. [8 km] SSE of Frobisher Settlement, 63°40′N, 68°26′W; 7 Aug. 1970.

Icelus spatula: NMC 77-1455D (2:52.0 mm); Darnley Bay, 70°11′24″N, 124°16′42″W; 7 Aug. 1963. UW 20774, 20777 (2:65.0–66.0 mm); Bering Sea, 60°50′N, 176°36′W, 125 m, Discovery Bay 79-2, haul 35; 15 July 1979. UW 20834 (1: 57.0 mm); Bering Sea, 62°37.8′N, 173°29.0′W, 67 m; 20 July 1979.

Icelinus

Icelinus borealis: UW 2272 (2:50.0–53.0 mm); Washington, Lopez I., Flat Pt.; 9 Aug. 1932.

Icelinus tenuis: UW 4176 (1:83.0 mm); Washington, Puget Sound, Saratoga Pass.; Mar. 1937.

Chitonotus

Chitonotus pugetensis: UW 20905 (2:90.0–94.0 mm); Washington, Puget Sound, West Pt.; 6 Oct. 1978.

Triglops

Triglops pingeli: UW 20906 (1:85.0 mm); Bering Sea, 60°40′N, 172°49′W, 45 m; 21 July 1979.

Artedius

Artedius harringtoni: UW 18020 (1:67.0 mm); Washington, San Juan I., Hannah Hts.; 3 Aug. 1963.

Hemilepidotus

Hemilepidotus hemilepidotus: UW 4242 (1:42.0 mm); Washington, Puget Sound, Alki Pt.; 8 Sep. 1937.

Osteology of *Icelus spiniger*

Neurocranium

(Figures 1, 2)

Ethmoid cartilage large, broad, extending to anterior and lateral margins of vomer; bounded posteriorly and laterally by lateral ethmoids (Figs. 1, 2); dorsally rounded, domelike. Mesethmoid well ossified (contrary to Quast 1965); oval in shape; covering posterodorsal surface of ethmoid cartilage (Neyelov 1979; Yabe 1981). Long, posteriorly directed median process of mesethmoid underlying anterior portion of frontals; anteriorly this process diverging into two anterolaterally directed ridges; each ridge terminating in a short, sharp spine (Fig. 1). Lateral ethmoids covering posterior and lateral surfaces of ethmoid cartilage; a wide lateral expansion of each lateral ethmoid forming anterior margin of orbit; attached by stout connective tissue to lateral edges of fron-

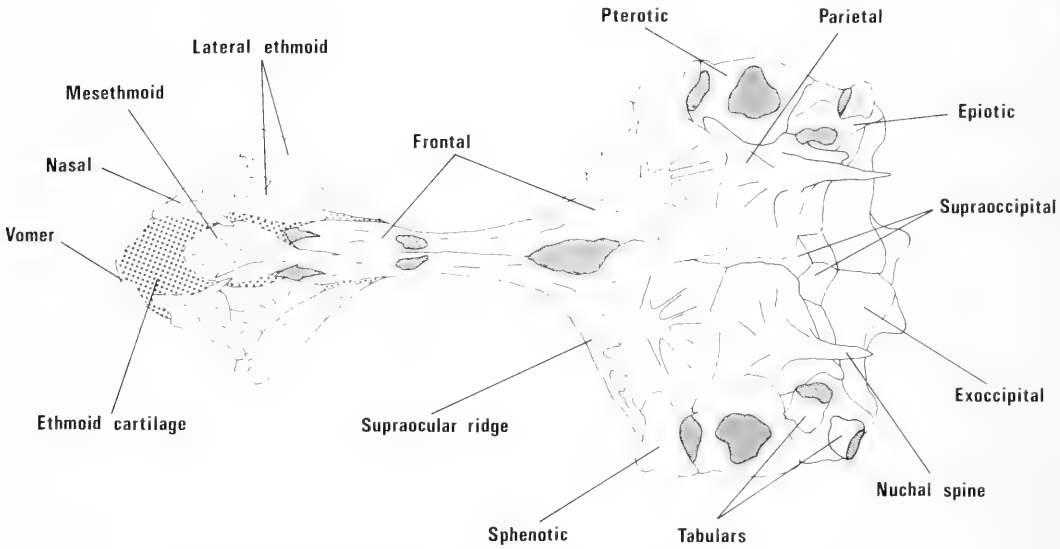


FIGURE 1. Neurocranium of *Icelus spiniger*, dorsal view, UW 20802, 90.0 mm SL.

tals above anterior portion of orbit; ventral portions expanded into large, rounded surfaces for articulation of palatines and lacrimals (Fig. 2).

Frontals narrow anteriorly, mid-orbital widths narrowest; posteriorly widening to occupy widest part of posterodorsal surface of neurocranium (Fig. 1); posterodorsal rim of orbit (formed by frontal) strongly developed into ridge (supraocular ridge) provided with two or three strong spines (Figs. 1, 2); branch of cephalic lateral line canal passing through this ridge, provided with three lateral line pores; this branch of cephalic lateral line continuing through canal in frontal; canal provided with a dorsal pore approximately mid-orbit and another pore at anterior end of frontal. Parietal large, occupying much of posterodorsal surface (that part not covered by frontals) of neurocranium; parietal spine absent; nuchal spine well developed, straight, sharp, posterodorsally directed (Figs. 1, 2); parietals overlying supraoccipital, almost meeting on midline of dorsal surface of head. Supraoccipital small, roughly trapezoidal in posterior view, with poorly developed median ridge on posterior surface; almost entirely overlain by parietals.

Nasals roughly pyramid-shaped, with medial edge projecting dorsally into long, sharp spine; cephalic lateral line canal passing anteroposteriorly through basal portion.

Vomer well ossified (contrary to Quast 1965); expanded anteriorly; tapering to narrow shaft posteriorly; anteroventral surface bearing a crescent-shaped band of villiform teeth (not shown in Fig. 2). Neyelov (1979) and Yabe (1981) also note the ossified condition of this element.

Parasphenoid (Fig. 2) long, shaftlike, with a dorsally projecting medial ridge running longitudinally from vomer to otic region of skull; broadening posteriorly into two dorsally projecting "wings" that overlie the anterolateral portions of prootics and abut ventral edges of pterosphenoids (Yabe 1981); posteriormost portions of shaft tapering into two rami which overlie ventral portion of basioccipital.

Pterosphenoid (Fig. 2) small, leaf-shaped, forming mid-portion of posterior rim of orbit; dorsally overlain by lateral expansion of frontal.

Sphenotic (Figs. 1, 2) broad and thin dorsally, overlain by lateral expansion of frontal; thickening ventrally; expanded ventral surface with a well-defined depression into which anterior head of hyomandibular fits; dorsolaterally overlain by pterotic.

Pterotic (Figs. 1, 2) narrow and thin dorsally, slightly overlying lateral margin of parietal; broad and thicker ventrally; large anteroposteriorly directed cephalic lateral line canal in ventrolateral portion of pterotic; posterolateral surface shallowly depressed; into this depression fit two tabulars (scalebones); ventral surface expanded, with

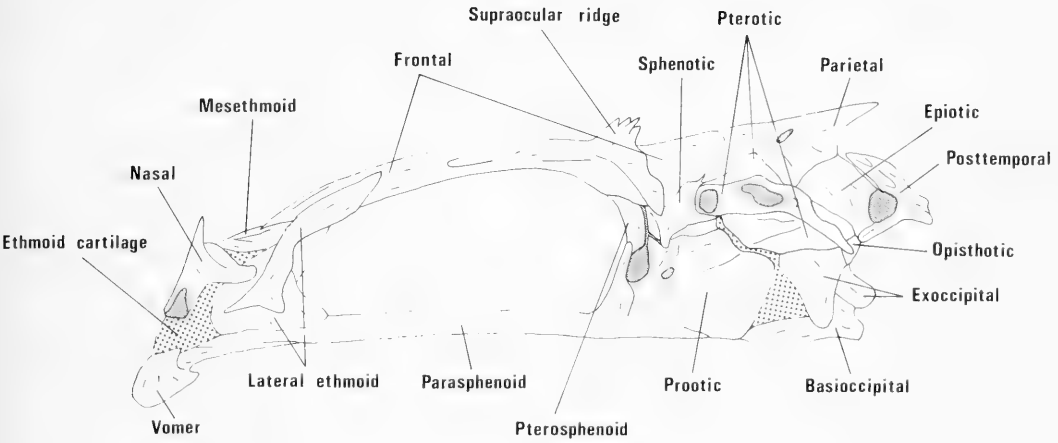


FIGURE 2. Neurocranium of *Icelus spiniger*, lateral view, UW 20802, 90.0 mm SL.

a depression into which fits posterior head of hyomandibular.

Tabulars (Fig. 1) two, one slightly anterodorsal to the other; thin, tubular; forming a Y-connection for a dorsolateral and an anterolateral branch of cephalic lateral line; dorsolateral branch passing dorsally through a foramen in base of nuchal spine (Fig. 2) and traversing posterodorsal surface of head, meeting its counterpart from other side on dorsal midline; anterolateral canal passing anteriorly through pterotic and giving off a dorsal branch that passes dorsally through supraocular ridge of frontal and a ventral branch that passes ventrally through posterior circumorbitals.

Epiotic (Fig. 2) large, roughly triangular in posterior view; forming posterior dorsolateral part of otic capsule; bounded medially by supraoccipital, posteroventrally by opisthotic and exoccipital, anteroventrally by prootic; nearly completely overlain dorsally by parietal.

Prootic (Fig. 2) large, ventrolateral portion convex (bulla acoustica); forming anterolateral portion of otic capsule; dorsolateral portion concave, abutting pterotic and sphenotic dorsally; facialis foramen (Allis 1909) in anterior face of prootic, where anterior portion bends medially to abut pterosphenoid and winglike dorsal process of parasphenoid; junction of these three bones incomplete, forming a notch through which passes the trigeminal nerve (Allis 1909); prootic bordered posteriorly by exoccipital and ventrally by basioccipital; a triangular cartilaginous area bounded by these three bones forming part of lateral surface of otic capsule.

Opisthotic (Fig. 2) small, "limpet"-shaped bone (Wilson 1973); overlying dorsolateral portion on exoccipital; dorsally just touching ventral surface of posteriormost process of pterotic (contrary to Quast [1965] the opisthotics do not meet on the posterior midline of the skull; nor do they form any portion of the borders of the foramen magnum; nor does the foramen for the vagus nerve penetrate the opisthotic) (Neyelov 1979; Yabe 1981).

Exoccipital (Figs. 1, 2) large, saddle-shaped anteriorly; bounded dorsally by supraoccipital, dorsolaterally by epiotic, and anterolaterally by prootic; ventrally and ventrolaterally abutting and slightly overlying basioccipital; posterior condyle (against which abuts the 40th preural centrum) small, about one-third diameter of basioccipital condyle; small, stout strut projecting medially from anterior portion of medial surface of exoccipital pedicel (the necklike portion just anterior to exoccipital condyle); this strut attaching to dorsal surface of basioccipital; exoccipitals meeting on posterior midline below supraoccipital, forming ventrolateral borders of foramen magnum; foramen for vagus nerve in exoccipital.

Basioccipital (Fig. 2) thin and broad anteriorly; lateral borders of anterior portion rounded; narrowing posteriorly to short pedicel which terminates in a large condyle against which abuts the 40th preural centrum; dorsally forming (on

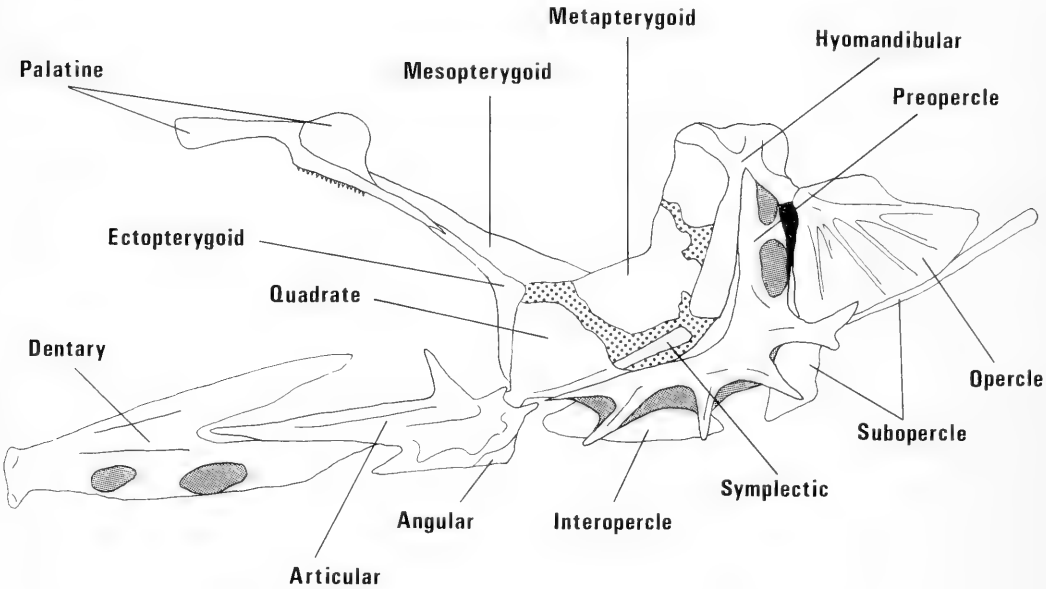


FIGURE 3. Suspensorium of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL.

posterior neurocranium) ventral border of foramen magnum.

Posttemporal (Fig. 2) forked; upper fork large and bladelike, dorsally directed to articulate with posterodorsal surface of epiotic; lower fork short, stout, ventrally directed to articulate with posterior surface of neurocranium at opisthotic–epiotic junction; central body of posttemporal cylindrical, with anteroposteriorly directed canal through which passes the lateral line.

Suspensorium

(Figure 3)

Palatine long; anterior process well developed; posterolateral ridge overlying (laterally) mesopterygoid and ectopterygoid; ventrolateral edge bearing many small conical teeth; dorsal surface articulating with ventral surface of lateral ethmoid; small, laterally directed process articulating with medial surface of lacrimal.

Mesopterygoid elongate, thin, roughly triangular; forming a medially directed shelf below eye.

Ectopterygoid elongate, narrow, posterior portion directed ventrally; anteriorly projecting portion about twice as long as ventrally directed portion; overlain anterolaterally by palatine; abutting mesopterygoid medially and anterior edge of quadrate posteriorly.

Metapterygoid large, flat, irregularly shaped; ossified portion just touching (anteriorly) mesopterygoid; posterior edge meeting anterior edge of ventrally directed shaft of hyomandibular; wide, unossified borders separate ossified portion and: mesopterygoid, ectopterygoid, ventral part of dorsal enlargement of hyomandibular, anterior edge of preopercle, symplectic, and dorsal edge of quadrate.

Symplectic long, rodlike, tapering anteriorly; widening posteriorly to become more flattened; lying alongside and attached to dorsomedial part of posteroventral ridge of quadrate.

Quadrate roughly triangular; vertex of triangle anteroventrally directed; thickened ridge running down anterior edge, around vertex and along entire length of ventral edge; vertex bearing spool-shaped condyle with which articulates the articular.

Hyomandibular t-shaped, with vertices of t interconnected by thin sheets of bone; vertices of t also connected to ventrally directed shaft by similar sheets of bone; anterior and dorsal vertices articulating with neurocranium at junctions of sphenotic and prootic and in ventrolateral depression of pterotic, respectively; posterior vertex of t forming articulating surface for opercle; ventral tip of ventrally directed shaft providing attachment surface for interhyal and symplectic.

Preopercle crescent-shaped; bearing four large

spines, the uppermost bifurcated at distal tip; preopercle housing preopercular-mandibular branch of cephalic lateral line; cephalic lateral line with five pores in preopercular region, one between each pair of preopercular spines, one above dorsalmost spine and one below ventralmost spine; preopercle bound (anteriorly) to ventral edge of quadrate and (dorsally) to posterolateral surface of hyomandibular.

Mandibular Arch

(Figures 3, 4)

Premaxilla (Fig. 4) narrow at proximal end; widening abruptly midbone to form postmaxillary process; tapering to slender distal tip; articular process massive, about two-thirds length of ascending process; small conical teeth (not shown in Fig. 4) in a broad band along anterior ventral surface.

Maxilla (Fig. 4) slender and rodlike proximally; widening to a broad blade distally; distal edge straight; elaborately developed condyle at proximal end, articulating posteriorly with anterior surface of palatine and anteriorly with articular process of premaxilla.

Articular (Fig. 3) comprising about one-half length of mandible; long dorsal part attaching to dorsal surface of lower arm of dentary; Meckel's cartilage fitting into deep medial groove in articular and extending almost to tip of dentary; posteriormost dorsal surface broad and deeply depressed to form surface articulating with ventrally directed spool-shaped condyle of quadrate; anterior portion of this articulating surface strengthened by a stout ridge and projecting anterodorsally as a long, sharp process; mandibular branch of cephalic lateral line entering posterior end of articular at junction of articular and angular, passing anteriorly through articular and dentary; large lateral pore between articular and dentary.

Dentary (Fig. 3) forked posteriorly; upper fork almost meeting dorsally projecting process of articular; lower fork overlain by articular; small, ventrally directed symphyseal knob at anterior tip of dentary; wide band of small conical teeth (not shown on Fig. 3) along dorsal side; cephalic lateral line passing anteriorly through ventral part of dentary, giving rise to three pores which communicate with skin surface through foramina in dentary; posterior two foramina in lateral surface of dentary; anterior one medial, just posterior to symphyseal knob.

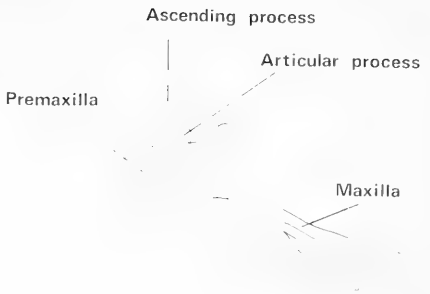


FIGURE 4. Maxilla and premaxilla of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL.

Angular (Fig. 3) roughly boot-shaped; heel of boot forming posteroventral edge of mandible; shank of angular forming medial wall of mandibular branch of cephalic lateral line (where it enters posterior mandible); laterally, shank of angular overlain by articular; large foramen present in articular where it overlies angular (providing entry for cephalic lateral line canal).

Opercular Series

(Figure 3)

Opercle large, fan-shaped; well-developed lateral ridge, giving off several smaller, posteroventrally directed ridges; well-developed, ventrally directed ridge strengthening anterior edge of opercle.

Subopercle forked; dorsally directed fork short, sharp, paralleling anterior edge of opercle; dorsoposteriorly directed fork very long, three times length of dorsal fork, paralleling ventral edge of opercle, extending past posterior vertex of opercle; anterior head of subopercle coming to an acute point anteriorly; lateral surface of anterior head strengthened by a ridge.

Interopercle flat, thin, roughly elliptical, but truncated posteriorly; posterior margin slightly concave; interopercle about one-third length of subopercle.

Hyoid Arch

(Figure 5)

Ossified basihyal absent (nor could such an ossification be found in other *Icelus* species or in *Rastrinus scutiger*).

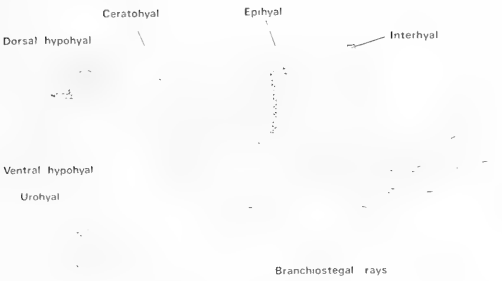


FIGURE 5. Elements of hyoid arch of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL.

Dorsal hypohyal oval, occupying a position anterior and dorsomedial to narrow, shaftlike portion of ceratohyal, dorsal and posterior to ventral hypohyal; ossified portion giving appearance of folded oval sheet; lateral portion and central portion unossified.

Ventral hypohyal caplike, occupying a position at anterior end of ceratohyal; dorsal portion slightly overlying (dorsally) anterior end of ceratohyal; a narrow, posteriorly directed shaft overlapping lateral surface of anterior end of ceratohyal; posterior ventral portion abutting anterior end of ceratohyal; meeting on midline, tightly bound together by ligamentous connective tissue.

Ceratohyal bladelike; anterior portion narrow; posterior one-third abruptly widening to broad, almost rectangular surface.

Epihyal triangular; base of triangle abutting posterior edge of ceratohyal; posterior vertex with dorsal depression for articulation with ventral end of interhyal.

Interhyal rodlike; interconnecting posterodorsal vertex of epihyal and anteroventral end of hyomandibular.

Urohyal roughly oval, with truncated, deeply notched posterior edge; thickened anteriorly to form surface which fits tightly against posteroventral portion of junction of ventral hypohyals.

Branchiostegals six; two articulating on ventral edge of narrow, anterior portion of ceratohyal, two on ventrolateral surface of wide, posterior portion of ceratohyal, and two on ventrolateral surface of anterior portion of epihyal; anterior two narrow, bladelike along entire length; middle three broad, bladelike, with enlarged proximal bases; posteriormost largest, bladelike, proximal base not enlarged.

Branchial Arches

(Figure 6)

Basibranchials 1–3 short, rodlike, flattened; well ossified, but surrounded by much unossified material; basibranchial 4 unossified, providing median support for ceratobranchials 4 and 5.

Hypobranchial 1 elongate, flattened; hypobranchial 2 about three-quarters length of hypobranchial 1, more broad and flattened than hypobranchial 1; hypobranchial 3 about one-half length of hypobranchial 1, almost as broad as long, with short anteromedially directed process; hypobranchial gill rakers absent.

Ceratobranchials 1–4 rodlike; ceratobranchial 4 with an anteroventrally oriented Y-shaped proximal head articulating with basibranchial 4; ceratobranchial 5 about one-half length of ceratobranchial 4, much broader than other ceratobranchials, bearing a large, roughly oval patch of conical teeth; dorsal (distal) end of ceratobranchial 5 rodlike, attached to ceratobranchial 4 (about mid-length) by connective tissue; ceratobranchials 1–3 bearing anterior and posterior rows of modified gill rakers (gill arch teeth; Weitzman 1974); ceratobranchial 4 bearing anterior row only; ceratobranchial 5 without gill rakers.

Epibranchials 1–4 rodlike, about equal in length, approximately one-third ceratobranchial length; somewhat flattened near articulations with pharyngobranchials; bearing one or two modified gill rakers.

Pharyngobranchials 1 and 2 absent (Yabe 1981); ventral surface of pharyngobranchial 3 covered by roughly oval tooth plate.

Gill rakers modified; stumplike or flattened, with broad bases, distally bearing toothlike structures.

Circumorbital Series

(Figure 7)

Lacrimal roughly triangular; provided with a dorsomedial articular surface that meets lateral process of palatine and ventral surface of lateral ethmoid; raised ridge on dorsolateral surface forming canal for cephalic lateral line; one large lateral line pore about mid-bone; large lateral line pore between lacrimal and circumorbital 2.

Circumorbital 2 elongate, with anteriorly projecting dorsal ridge that dorsally overlies medial ridge of lacrimal; posteriorly directed ridge overlain by suborbital stay; in addition to cephalic

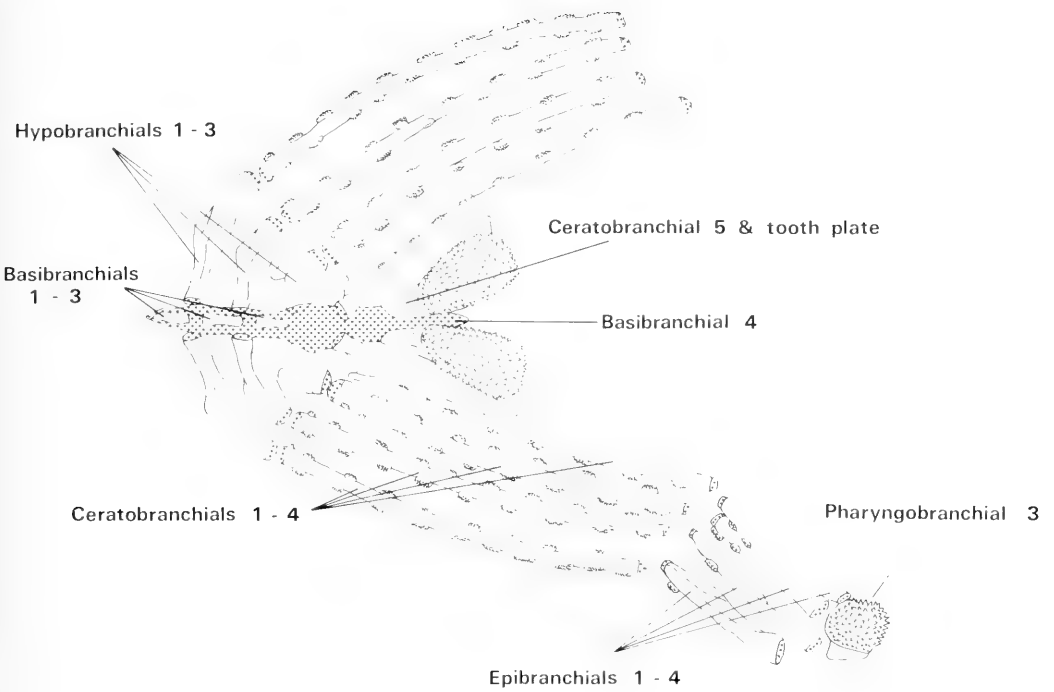


FIGURE 6. Branchial arches of *Icelus spiniger*, ventral portion, dorsal view; dorsal portion (left side only) folded back, ventral view; UW 20802, 90.0 mm SL.

lateral line pore shared with lacrimal, one pore communicating to surface of skin about midway down length; a ventrally directed branch of cephalic lateral line canal passing between circumorbital 2 and suborbital stay.

Suborbital stay spatulate; median ridge running longitudinally down anterior two-thirds length of lateral surface; this ridge bearing two laterally directed spines; posteriorly tightly bound to preopercle by connective tissue; cephalic lateral line entering dorsal edge of bone, branching into two canals, one anteriorly directed and one ventrally directed.

Circumorbitals 4–6 much smaller than other elements of circumorbital series; tubular; interconnecting dorsal edge of suborbital stay and ventralmost portion of frontal (supraocular ridge); housing a postorbital branch of cephalic lateral line.

FIGURE 7. Circumorbital series of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL. (P = dorsomedial articular surface of lacrimal; S = spines of suborbital stay)

Vertebral Column

(Figures 8, 9, 10)

In the specimen of *Icelus spiniger* on which the osteological discussion is based, there are 41 total vertebrae, including the ural centrum.

Fortieth preural centrum (Fig. 8) with anterior face bearing three concave facets which articulate with posterior neurocranium; large central facet placed close to posterior condyle of basioccipital; two smaller facets dorsolateral to this large central facet placed very close to posterior condyles of exoccipitals; these facets tightly bound (ligamentously) to basioccipital and exoccipitals;

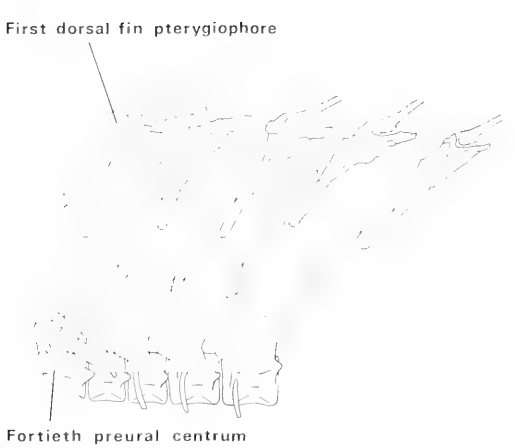


FIGURE 8. Fortieth through 36th preural centra and anteriormost dorsal fin pterygiophores of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL.

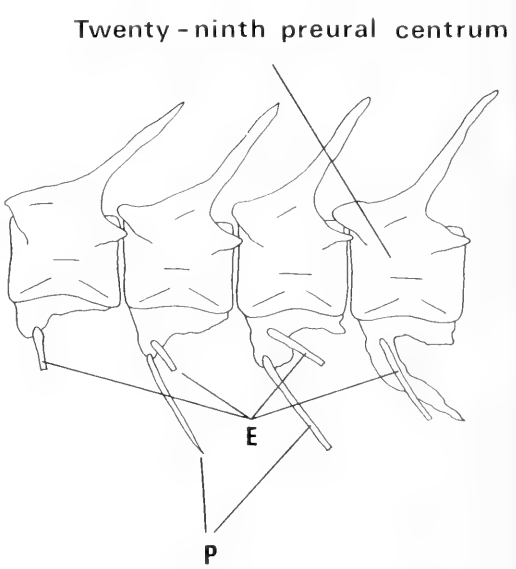


FIGURE 9. Thirty-second through 29th preural centra of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL. (E = epipleural ribs; P = pleural ribs)

neurapophyses not ankylosed dorsally, shallowly depressed laterally; epipleural rib articulating on shallowly depressed lateral surface of neurapophysis; no parapophysis evident; well-developed postzygapophysis on middle of posterior margin of centrum.

Preural centra 39–37 with well-developed neurapophyses (Fig. 8), ankylosed dorsally (as are neurapophyses of all vertebrae posterior to these), bearing very long neural spines which interdigitate with pterygiophores 1–4 of spinous dorsal fin; epipleural ribs articulating on bases of neurapophyses; well-developed postzygapophyses, becoming more dorsal in position posteriorly (especially evident in 37th preural centrum); no parapophyses or haemapophyses evident.

Preural centra 36 and 35 with greatly reduced neural spines; epipleural ribs articulating on small depressions just posterior to small, anterolaterally directed prominences; no haemapophyses evident; postzygapophyses at dorsal margins of centra (as in all vertebrae posterior to these).

Preural centra 34–30 similar to each other (with the below-mentioned exceptions); neural spines shorter than in 35th preural centrum; haemapophyses present, with shallow anterolateral depressions on which epipleural ribs articulate; haemapophyses more strongly developed in 31st and 30th preural centra, bearing pleural ribs (only on these two vertebrae) just ventral to epipleural ribs (Fig. 9); pleural ribs on 30th preural centrum very long, almost touching dorsal tip of first anal fin pterygiophore.

Preural centra 29–10 similar to each other (with the below-mentioned exceptions); neural spines becoming smaller and shorter posteriorly; haemal spines becoming longer on preural centra 26–15, interdigitating with pterygiophores of anal fin; haemal spines of preural centra 14–10 shorter and more flattened; neural spines of preural centra 14–10 shorter and more flattened than in preceding centra.

Preural centra 9–2 with broad, flattened neural and haemal spines, especially marked in preural centra 5–2 (Fig. 10); preural centra 7–2 with well-developed bony ridge (keel) on lateral aspect of centrum.

Caudal Complex

(Figure 10)

First preural centrum with broad, flat neural spine, irregularly toothed along anterior and dorsal margins; haemal spine broad, flat, roughly triangular, with ventral border longest side of triangle; posterior apex of triangle ventral to hypural plate; parhypural fused to posterior margin of haemal spine of first preural centrum.

Ural centrum (half centrum) short, slightly curved dorsally, with large, fanlike hypural plate

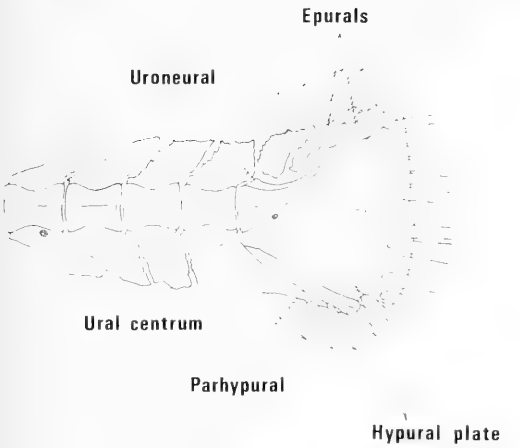


FIGURE 10. Caudal skeleton of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL.

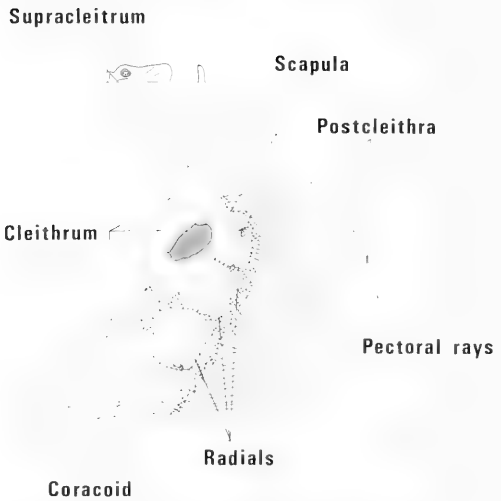


FIGURE 11. Pectoral girdle and fin of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL.

fused to posterior and posteroventral borders; deep notch in hypural plate about midway down posterior edge.

Uroneural stout and thick anteriorly, elongate and tapering posteriorly, forming a strengthening ridge for dorsal margin of hypural plate. Yabe (1981), however, indicates that this element ("stegural") is absent in *Icelus spiniger*.

Epurals three; anteriormost wing-shaped, broad, irregularly toothed along anterior and dorsal edges; posterior two elongate, flat, narrow, not toothed along edges.

Principal caudal rays (those that articulate with hypural plate) 11; 6 articulating with upper portion of hypural plate, 5 with lower portion; dorsalmost and ventralmost principal caudal rays unbranched, remainder branched. Dorsal procurrent caudal rays eight; ventral procurrent caudal rays six; posteriormost ventral procurrent caudal ray large, appearing almost to articulate with hypural plate.

Dorsal and Anal Fins

Dorsal fin of two distinct portions: an anterior spinous part with 9 unsegmented, uniserial spines, and a posterior part with 21 biserial, segmented, unbranched soft rays. First two dorsal spines articulating on large, broad first dorsal pterygiophore (Fig. 8), the dorsal edge of which bears two shallow depressions for these articulations; each of the remaining spines and soft rays articulating with an elongate, somewhat leaf-shaped pterygiophore; first dorsal pterygiophore positioned almost directly dorsal to 40th preural centrum; proximal end of last dorsal pterygiophore just posterior to distal tip of neural spine of 12th preural centrum.

Anal fin of 16 biserial, segmented, unbranched soft rays, each articulating with an elongate, leaf-shaped pterygiophore; proximal end of first anal pterygiophore just posterior and ventral to distal end of haemal spine of 29th preural centrum; proximal end of last anal pterygiophore almost touching tip of haemal spine of 15th preural centrum.

Pectoral Girdle and Fin

(Figure 11)

Supracleithrum broad, bladelike, with thickened anterior and dorsal ridges; well-developed anterodorsal process articulating with shallow depression in medial surface of posttemporal; lateral line canal passing through short tubular foramen in dorsal ridge.

Cleithrum gently curved; broadened dorsally, anteroventrally and ventrolaterally; anterodorsal ridge developed into elongate, pointed shaft; posterior dorsal portion produced into short, wide blade; anterior surface of ventral portion forming posterior walls and posterior floor of branchial chamber; ventrally, cleithra bound tightly together by connective tissue.

Postcleithra two; elongate, slender; dorsalmost (postcleithrum 1) laterally overlapping ventral-

FIGURE 12. Pelvic girdle and fin of *Icelus spiniger*, ventral view, UW 20802, 90.0 mm SL.

most (postcleithrum 2) for about one-half its length; proximal end of postcleithrum 1 articulating on medial surface of broad, flat dorsal portion of cleithrum (disarticulated in Fig. 11).

Scapula flat, thin, roughly rectangular; dorsal portion wide, with thickened dorsal margin; tapering ventrally to more narrow ventral margin; anterior margin shallowly concave; posterior margin slightly convex; large scapular foramen, almost mid-bone; ossified portion of scapula separated by cartilage from coracoid.

Coracoid thin, roughly L-shaped; dorsal arm of L broad, bladelike; dorsal and posterior margins rounded; anteriorly directed arm of L narrow, shaftlike, thickened anteriorly, abutting lateral surface of ventral portion of cleithrum; outer (posterior) angle of L projected posteriorly to form triangular posteroventral margin.

Radials four, platelike; dorsalmost (first) roughly triangular; second roughly rectangular; ventral two irregularly rectangular; interradial foramina present between dorsalmost radial and scapula, between first and second radials, and between third and ventralmost radials; foramen between second and third radials absent (Quast [1965] stated that cottids have no interradial foramina, but these foramina are present in all species of *Icelus* examined, in *Rastrinus scutiger,* and in several other cottid genera examined, e.g., *Icelinus, Chitonotus,* and *Triglops*). Yabe (1981) corroborates these findings in *I. spiniger* and *Hemilepidotus.*

FIGURE 13. (A) Scales of dorsal scale row of *Icelus spiniger*; (B) scales of lateral line of *Icelus spiniger*; left lateral view, UW 20802, 90.0 mm SL.

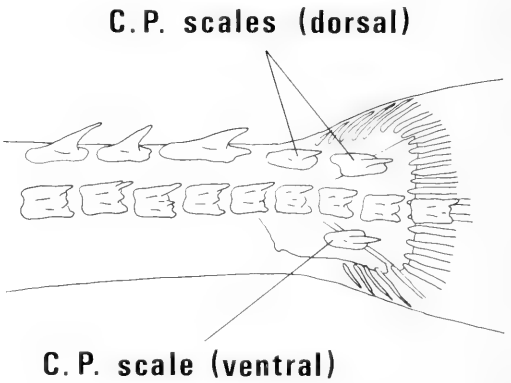


FIGURE 14. Scales of caudal peduncle of *Icelus spiniger*, left lateral view, UW 20802, 90.0 mm SL.

Pectoral rays 18; biserial, segmented, unbranched; middle rays elongated; all rays interconnected by pectoral fin membrane.

Pelvic Girdle and Fin

(Figure 12)

Basipterygia paired, tightly bound together along midline; elongate; prominent lateral ridge on ventral side; lateral borders rounded posteriorly, tapering to dorsally projected, slender, acutely pointed posterior apex; slender medial processes arising from posteromedial ventral surface, fusing near distal tips; pelvic fin spine articulating on posterolateral edge of basipterygium; three biserial, segmented, unbranched rays articulating on posteromedial edge of basipterygium.

Scales

(Figures 13, 14)

Single row of enlarged, platelike scales, each bearing a single strong spine (Fig. 13*A*), along dorsolateral body surface just below dorsal fins; scale row extending from just posterior to nuchal spine to dorsal surface of caudal peduncle; embedded bases of scales slightly overlapping,

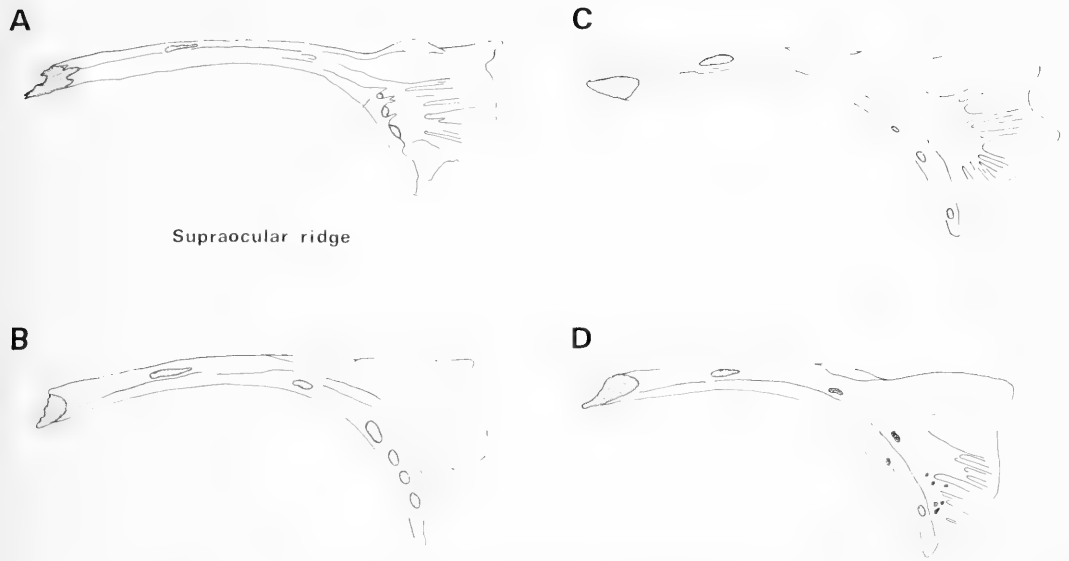


FIGURE 15. Frontal bones of *Rastrinus* and *Icelus*: (A) *Icelus spiniger*, UW 20802, 90.0 mm SL; (B) *Rastrinus scutiger*, OSU 7874, 64.0 mm SL; (C) *Icelus canaliculatus*, UW 20798, 109.0 mm SL; (D) *Icelus spatula*, UW 20774, 66.0 mm SL; left dorsolateral view.

anterior edge slightly overlain by posterior edge of preceding scale; three similar scales on lateral surface of caudal peduncle (caudal peduncle scales), two above lateral line and one below (Fig. 14).

Similar, smaller scales scattered among scales of dorsal row, on top and sides of head, and on opercular region; scales irregularly arranged in rows on sides of body in axil of pectoral fin (axillary scales), each with an enlarged, embedded base and bearing an oblique ridge of spinules.

Lateral line scales tubular (Fig. 13*B*); lateral surface expanded; dorsal and ventral edges partially embedded; dorsal edge rounded; ventral edge elongated posteriorly and rounded; laterally directed ridge of spinules along midline of lateral scale surface; lateral line pore at posterior end of tube formed by scale.

COMPARATIVE OSTEOLOGY

In this section comparisons of the character states of several osteological features are presented for the genera *Rastrinus* and *Icelus*, and also for species and species groups within the genus *Icelus*. Three species groups (diagnoses presented in Systematics section) are recognized within the genus *Icelus*: the *I. spiniger* group, the *I. euryops* group, and the *I. bicornis* group. Two other species (*Icelus gilberti* and *I. armatus*) exhibit mosaics of character states that make present placement of these species into any of these species groups impossible.

Neurocranium

In almost all respects, the neurocranium of *Icelus spiniger* (Figs. 1, 2) is representative of all species of *Icelus* and *Rastrinus scutiger*. Some differences, however, exist in the morphology of the frontals and the parietals among these species. In *Icelus spiniger* the posterolateral expansion of the frontal (the supraocular ridge) is pronounced and provided with one to four dorsally directed, sharp spines (Figs. 2, 15*A*). This condition is also observed in *I. cataphractus*. In *Rastrinus scutiger* (Fig. 15*B*) the supraocular ridge is weakly developed, spines are absent, and three or four cephalic lateral line pores are present. These pores, while present in all species of *Icelus* examined, are most well developed in the genus *Rastrinus*. The supraocular ridge is weakly developed in the *I. euryops* group, as observed in *I. canaliculatus* (Fig. 15*C*). This ridge is often prominent in members of the *I. bicornis* group, but may be moderately or weakly developed, as observed in *I. spatula* from the eastern Bering Sea (Fig. 15*D*).

The morphology of the parietals in members

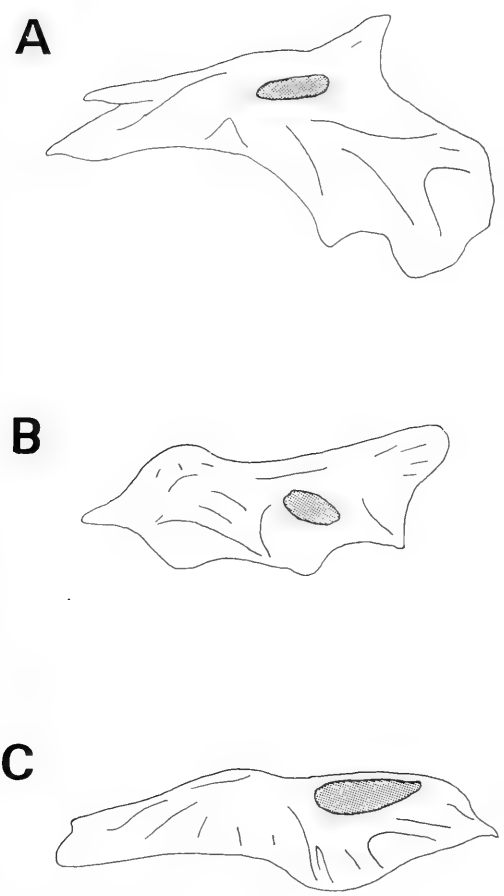


FIGURE 16. Parietal bones of *Rastrinus* and *Icelus*: (A) *Icelus canaliculatus*, UW 20798, 109.0 mm SL; (B) *Icelus spatula*, UW 20774, 66.0 mm SL; (C) *Rastrinus scutiger*, OSU 7874, 64.0 mm SL; left lateral view.

of the *I. euryops* group, as is observed in *I. canaliculatus* (Fig. 16*A*), is similar to that in *I. spiniger* (Figs. 1, 2), except the nuchal spine is much more weakly developed in members of the *I. euryops* group. In members of the *I. bicornis* group, as a general rule, both the parietal and nuchal spines are well developed, as in *I. spatula* from the eastern Bering Sea (Fig. 16*B*). The parietal spine is absent, however, in two species belonging to this group: *I. ochotensis* and *I. stenosomus*. In *R. scutiger* (Fig. 16*C*) a canal is present in the dorsal part of the parietal, but the dorsal roof of this canal is not produced into a nuchal spine, as is the case for all species of *Icelus*.

Circumorbital Series

The character states exhibited by the elements of the circumorbital series of *Icelus spiniger* (Fig. 17*A*), with a few exceptions, are representative of other *Icelus* species and *R. scutiger*. The lacrimal of *I. cataphractus* (Fig. 17*B*) bears one (rarely two) strong, laterally directed spines; these spines are absent in *I. spiniger* and in all other species of *Icelus* and *Rastrinus*. In the *I. euryops* group the broad, bladelike suborbital stay bears one or two strong, laterally directed spines, as in *I. canaliculatus* (Fig. 17*E*). These spines are occasionally absent in *I. rastrinoides*, but present in both members of the *I. spiniger* group: *I. spiniger* and *I. cataphractus*. Suborbital stay spines are also present in *I. armatus*; but in the *I. bicornis* group, as observed in *I. spatula* from the Bering Sea (Fig. 17*C*), *I. gilberti*, and *R. scutiger* (Fig. 17*D*), the broad suborbital stay lacks spines. In *I. canaliculatus* (Fig. 17*E*) circumorbital 2 is more tightly bound to the posterior edge of the lacrimal than in other *Icelus* species, and this bone tapers more rapidly posteriorly. This tapering of circumorbital 2 greatly enlarges the lateral line pore located between circumorbital 2 and the suborbital stay. In small specimens of all species of *Icelus* and *R. scutiger* (and also in some large specimens), the tube formed by circumorbital 6 is incompletely closed; examples of this phenomenon are observed in *I. spatula* (Fig. 17*C*) and in *R. scutiger* (Fig. 17*D*).

Scales of Dorsal Scale Rows

In *Rastrinus scutiger* the body is completely covered with small scales, each of which bears an oblique ridge of small spinules (Pattern A, Fig. 18*A*). In all species of the genus *Icelus*, the embedded bases of the scales of one or more dorsal scale rows (and sometimes ventral scale rows) are enlarged, platelike, and generally overlap. In the *I. bicornis* group and in *I. gilberti*, the enlarged base is roughly circular, and an oblique ridge of spinules traverses the lateral scale surface (Pattern B, Fig. 18*B*). In the *I. euryops* group and in *I. armatus*, the embedded base of each scale is expanded dorsoventrally, so the scale base is elongated and the oblique ridge of spinules is displaced ventrally (Pattern C, Fig. 18*C*). In the *I. spiniger* group, the embedded bases are roughly oval or circular and very much enlarged, and the dorsal body surface is almost completely covered by overlapping platelike scales. Instead of

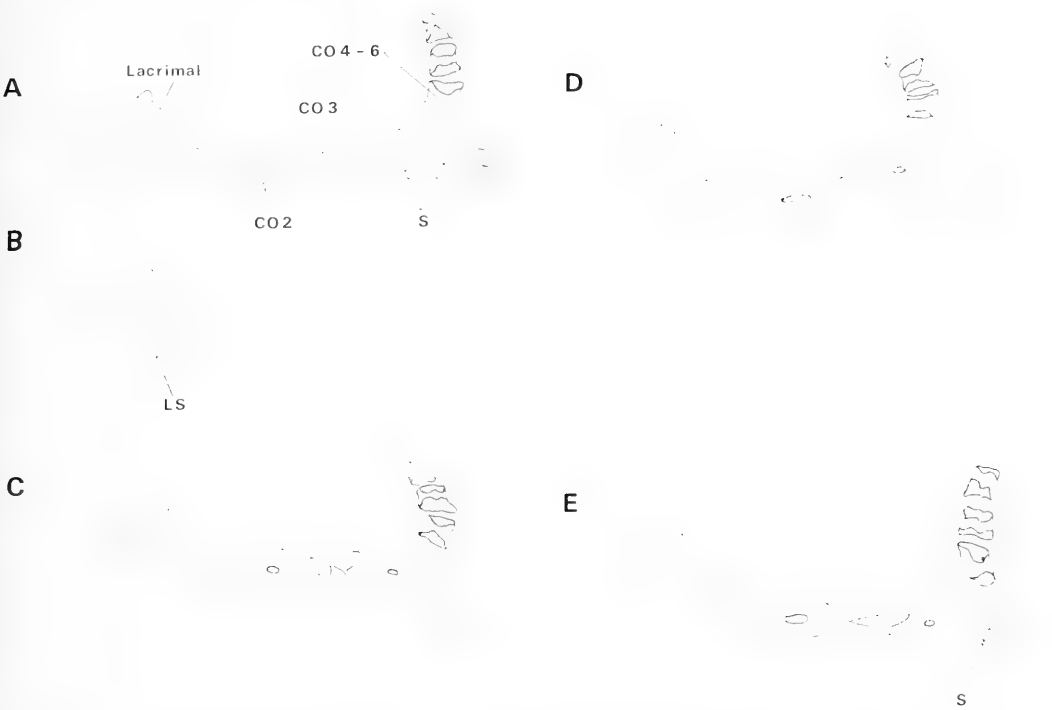


FIGURE 17. Circumorbital series of *Rastrinus* and *Icelus*: (A) *Icelus spiniger*, UW 20802, 90.0 mm SL; (B) *Icelus cataphractus*, UW 20827, 92.0 mm SL (lacrimal only); (C) *Icelus spatula*, UW 20774, 66.0 mm SL; (D) *Rastrinus scutiger*, OSU 7874, 64.0 mm SL; (E) *Icelus canaliculatus*, UW 20798, 109.0 mm SL; left lateral view. (LS = lacrimal spine; S = suborbital stay spines)

an oblique ridge of spinules, each of these scales bears a single strong spine on the lateral scale surface (Pattern D, Fig. 18*D*).

Lateral Line Scales

The lateral line scales of *Rastrinus scutiger* and all species of *Icelus* are tubular; spinules are present in some form on the lateral surfaces of these scales. The shapes assumed by these scales and the number and placement of the spinules vary considerably among *Icelus* species. In *R. scutiger* and in members of the *I. bicornis* group, the scales of the lateral line bear spinules along a weakly developed dorsal ridge on the lateral surface of the scale and also bear posteriorly directed spinules on the lateral surface of the scale above and below the lateral line pore (Pattern A, Fig. 19*A*). Occasionally, the posteriorly directed spinules below the lateral line pore are absent in *I. spatula*, particularly in specimens collected in Arctic Canadian waters. In *I. bicornis* the lateral line scales do not extend onto the caudal peduncle, and spinules below the lateral line pore are invariably present. In the *I. euryops* group, the lateral surface of the scale is expanded dorsally to form a ridge (Pattern B, Fig. 19*B*). Numerous spinules are present along this ridge, and numerous posteriorly directed spinules are present above and below the lateral line pore. Lateral surfaces of the lateral line scales of the *I. spiniger* group (Pattern C, Fig. 19*C*) are greatly expanded, and a laterally directed ridge of spinules or serrations replaces the dorsal spinule ridge of other *Icelus* species groups. In *I. spiniger* these spinules are simple or serrated (Fig. 20*A*), whereas in *I. cataphractus* the laterally directed spinules are produced into anteriorly and posteriorly directed processes (Fig. 20*B*). In *I. spiniger* the edges of the lateral line scales do not overlap, but in *I. cataphractus* the anterior edge of each scale is overlapped laterally by the posterior edge of the preceding scale.

Caudal Peduncle Scales

Caudal peduncle scales are present in the *I. euryops* group, the *I. spiniger* group, and in some

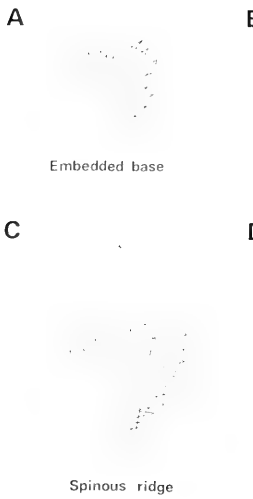


FIGURE 18. Scales of dorsal scale row(s): (A) Pattern A, *Rastrinus scutiger*; (B) Pattern B, *Icelus bicornis* group and *Icelus gilberti*; (C) Pattern C, *Icelus euryops* group and *Icelus armatus*; (D) Pattern D, *Icelus spiniger* group; left lateral view.

FIGURE 19. Lateral line scales: (A) Pattern A, *Rastrinus scutiger*, *Icelus bicornis* group and *I. armatus*; (B) Pattern B, *Icelus euryops* group; (C) *Icelus spiniger* group; left lateral view.

members of the *I. bicornis* group. These scales are also present in *I. armatus* and *I. gilberti*, but are represented by elements of the dorsal (and, in *I. armatus*, ventral) scale rows, rather than being represented by isolated scales. Caudal peduncle scales are morphologically similar to scales of the dorsal scale row in most *Icelus* species. In the *I. spiniger* group, each of these scales bears a single, strong, posteriorly directed spine on the lateral scale surface. In the *I. euryops* group, the lateral scale surface bears a posteriorly directed ridge of small spinules. In members of the *I. bicornis* group, dorsal and ventral caudal peduncle scales are usually present in *I. bicornis* and *I. stenosomus*, while only dorsal caudal peduncle scales are present in *I. ochotensis* and (rarely) in *I. spatula*. In the *I. bicornis* group, these scales may bear a single, posteriorly directed spine on the lateral scale surface (*I. bicornis*) or a posteriorly directed ridge of small spinules (*I. ochotensis*, *I. stenosomus*, *I. spatula*). Caudal peduncle scales are absent in *I. uncinalis*.

SYSTEMATICS

The following list of taxa summarizes the taxonomic conclusions presented in this article:

Genus *Rastrinus* Jordan and Evermann, 1896
Rastrinus scutiger (Bean, 1890)
Genus *Icelus* Krøyer, 1845
Icelus gilberti Taranetz, in Schmidt, 1935
Icelus armatus (Schmidt, 1915)
Icelus spiniger Group
Icelus spiniger Gilbert, 1895
Icelus cataphractus (Pavlenko, 1910)
Icelus euryops Group
Icelus rastrinoides Taranetz, in Schmidt, 1935
Icelus euryops Bean, 1890
Icelus canaliculatus Gilbert, 1895
Icelus perminovi Taranetz, 1936
Icelus bicornis Group
Icelus bicornis (Reinhardt, 1840)
Icelus spatula Gilbert and Burke, 1912
Icelus ochotensis Schmidt, 1927
Icelus uncinalis Gilbert and Burke, 1912
Icelus stenosomus Andriashev, 1937

Genus **Rastrinus** Jordan and Evermann

Icelus: BEAN 1890:41 (in part).
Rastrinus JORDAN AND EVERMANN, 1896:437 (type-species *Icelus scutiger* Bean, 1890, by monotypy); 1898:1909, fig. 692 (diagnosis of *Rastrinus*).

DIAGNOSIS.—A genus of the family Cottidae (as characterized by Taranetz 1941; Bolin 1944, 1947) distinguished in having the following combination of characters. Branchiostegal rays six. Pelvic fins with one spine, three soft rays. Small conical teeth on premaxillae, dentaries, vomer, and palatines. Parietal and nuchal spines absent (Fig. 21 illustrates head spine and head cirri terminology). Preopercular spines four, uppermost

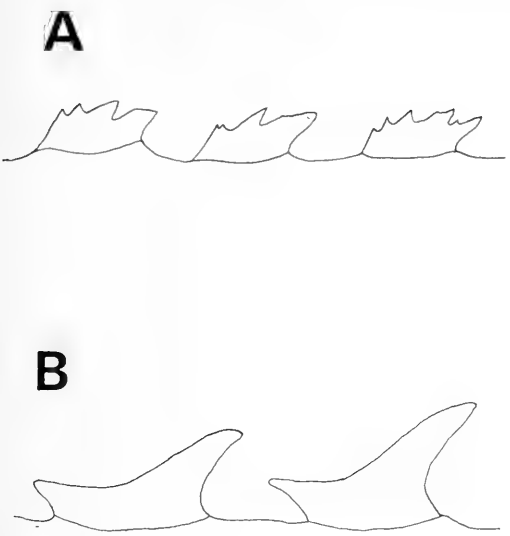


FIGURE 20. Laterally directed spinules on lateral line scales in *Icelus spiniger* group: (A) *Icelus spiniger*; (B) *Icelus cataphractus*; right dorsal view.

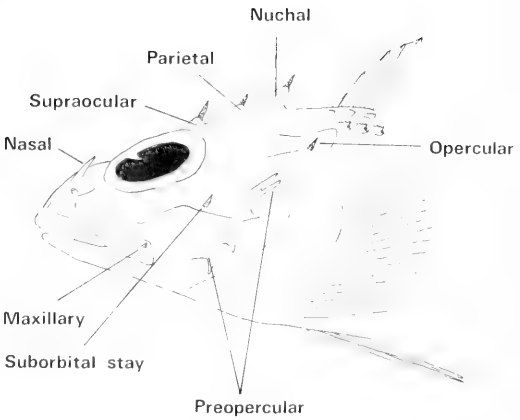


FIGURE 21. Head spine and head cirri terminology. Terminology for head spines follows Eschmeyer (1969); that for head cirri derived from osteological discussion.

curved or bifurcated. Suborbital stay without spines. Dorsal rows of enlarged, platelike scales absent. Sides of body above and below lateral line completely invested with small, spiny scales (Pattern A, Fig. 18*A*). Axillary scales present. Lateral line scales tubular, flattened on lateral and medial surfaces, bearing spinules on dorsal and posterior margins of lateral scale surface (Pattern A, Fig. 19*A*). Scales, tending to be arranged in rows, on upper portion of eye. Head cirri darkly pigmented, present on head as follows: supraocular, parietal, nuchal, suborbital stay, and opercular. Male urogenital organ (urogenital papilla of Jensen and Volsoe [1949]) cylindrical, dorsoventrally flattened, with distal hooklike terminal appendage (Fig. 23*A*).

REMARKS.—Jordan and Evermann (1896) erected the genus *Rastrinus* to accommodate a single species, *Rastrinus scutiger*, and provided a diagnosis in a subsequent publication (Jordan and Evermann 1898). Taranetz (1935) placed *Rastrinus scutiger* back into the genus *Icelus*, believing that the scales above the lateral line in *R. scutiger* were simply variations of the "bony plates" found in *Icelus* species and that the state of this character alone did not warrant separate generic status for this species.

The condition of the small, spiny scales in *R. scutiger* may represent a primitive condition in a transformation series leading to the more well developed, platelike scales in *Icelus* species, but these scales do not exhibit the same enlarged, embedded (basal) plate found in *Icelus* species. In addition, the absence of parietal and nuchal spines (nuchal spines are present in all species of *Icelus*) further distinguishes *Rastrinus* from *Icelus* (Table 2).

To incorporate the character states described above for the genus *Rastrinus* into the generic diagnosis for the genus *Icelus* broadens the diagnosis so as to render it necessary to synonymize a number of other cottid genera (e.g., *Icelinus, Chitonotus,* and *Ricuzenias*) with *Icelus*. To more precisely diagnose the genera *Rastrinus* and *Icelus*, and to avoid the attendant loss of information which would result from "lumping" many cottid genera with *Icelus*, the genus *Rastrinus* is hereby resurrected.

Rastrinus scutiger (Bean, 1890)

(Figure 22)

Icelus scutiger BEAN, 1890:41 (orig. descr.; Gulf of Alaska, near Trinity Is., 56°00′N, 154°20′W, 290 m, ALBATROSS sta. 2853; holotype, male, 70.5 mm, USNM 45368); GILBERT 1895: 415 (expanded descr.); TARANETZ 1936:150 (compar. with *I. rastrinoides*); 1937:106, 108 (key to *Icelus* spp.; distr.); WILIMOVSKY 1958:67 (key; distr.); QUAST AND HALL 1972: 22 (compiled distr: Bering Sea; Gulf of Alaska; Aleutian Is.; lit.); HOWE AND RICHARDSON 1978:48, 138 (diag.; lit.; key).

Rastrinus scutiger JORDAN AND EVERMANN, 1896:437 (*I. scutiger* referred to new genus); 1898:1909, fig. 692 (descr. after Bean [1890] and Gilbert [1895]; N. Pacific, Alaska); EVERMANN AND GOLDSBOROUGH 1907:300, fig. 51 (fig. from Jor-

TABLE 2. DIAGNOSTIC FEATURES DISTINGUISHING THE GENERA *RASTRINUS* AND *ICELUS*.

Character	*Rastrinus*	*Icelus*
1. Parietal spines	Absent	Present or absent
2. Nuchal spines	Absent	Present
3. Suborbital stay spines	Absent	Present or absent
4. Dorsal row of enlarged, platelike scales	Absent	Present
5. Body scales	Body completely scaled	Body with rows of scales not completely covering body
6. Body scale type (dorsal scale type)	A (Fig. 19*A*)	B, C, D (Figs. 19*B, C, D*)
7. Lateral line scale type	A (Fig. 20*A*)	A, B, C (Figs. 20*A, B, C*)

dan and Evermann 1898; compiled distr.); GILBERT AND BURKE 1912:38 (range extended w to Attu and Bering Is., ALBATROSS sta. 4784 and 4790, respectively; compar. with Gulf of Alaska spec.); JORDAN, EVERMANN, AND CLARK 1930: 378 (compiled distr.).

DIAGNOSIS.—As for genus.

DESCRIPTION.—General body shape shown in Figure 22. Body elongate, laterally compressed posterior to opercular openings. Body depth greatest at anterior portion of spinous dorsal fin. Head large; head depth about equal to head width. Profile (from snout to supraocular region) gently rounded. Eye large, about 1.5 to 2 times snout length. Interorbital space narrow, shallowly depressed. Mouth moderately large, maxilla extending to below middle of orbit. Nasal spines short and sharp. Spinous portion of dorsal fin taller than soft-rayed portion. Pectoral fin fanlike, longest rays reaching to anal opening. Longest rays of pelvic fin reaching to anal opening. Posterior border of caudal fin gently rounded.

Coloration in preservative. Overall body color light brown. Four darker grayish-brown bands on upper half of body, sometimes extending below lateral line: below spinous dorsal fin, below anterior portion of soft-rayed dorsal fin, below posterior part of soft-rayed part of dorsal fin, at posterior margin of caudal peduncle. Similarly colored band at posterior margin of caudal fin. Spinous dorsal fin with dark brown or black patch (not shown on Fig. 22). Similar patches of color often present on soft-rayed portion of dorsal fin, anal fin, and pectoral fins. Dark brown or black splotch below (occasionally through) eye (not shown on Fig. 22). Underside of body much lighter brown or whitish. Urogenital papilla of male whitish.

MEASUREMENTS (from 33 spec., 34.5–85.0 mm; except where indicated).—The following are expressed as thousandths of SL [value for holotype] range (mean; standard deviation): head length [355] 298–373 (339; 16.2); lacrimal length [52] 18–57 (31; 9.3); snout length (19 spec.) [66] 42–71 (52; 7.2); least interorbital width [18] 10–20 (13; 2.4); orbit diameter [142] 107–157 (130; 10.3); greatest body depth [184] 149–211 (183; 12.3); least caudal peduncle depth (32 spec.) [45] 45–82 (55; 7.8); upper jaw length (15 spec.) [177] 157–179 (170; 6.3).

COUNTS (from 25 spec.; except where indicated).—Values given, [value for holotype] range (mode; mean): dorsal fin spines [9] 9–10 (9; 9.3); dorsal fin soft rays [19] 18–21 (19; 19.4); anal fin rays (24 spec.) [18] 17–19 (18; 18.1); pectoral fin rays (26 spec.) [17] 17–19 (18; 17.7); lateral line scales (26 spec.) [43] 43–44 (44; 43.6).

DISTRIBUTION.—*Rastrinus scutiger* occurs in the northern Gulf of Alaska (around the Trinity Islands), in the southern Bering Sea, and along the Aleutian Islands westward to Bering Island (167°11′E) (Fig. 25). This species inhabits waters of the continental shelf and upper continental slope at depths of 120–512 m.

Table 3 presents a summary of geographic and bathymetric distributional information for *R. scutiger* and the recognized 13 species of *Icelus*.

ETYMOLOGY.—The generic name, *Rastrinus*, is derived from the Latin *rastrum*, meaning a scraper; and the specific name from the Latin roots *scut-* and *ger-*, meaning shield-bearing (Jordan and Evermann 1898).

MATERIAL EXAMINED (45 spec., 34.5—85.0 mm).—**Holotype:** USNM 45368, male, 70.5 mm; Gulf of Alaska, off Trinity Is., 56°00′N, 154°20′W, 290 m, ALBATROSS sta. 2853; 9 Aug. 1888.

Paratypes: USNM 227362 (2: both 55.0 mm); same data as for holotype.

Nontype-material. GULF OF ALASKA: BMNH 1900.9.29:192 (1); Alaska, no date. CAS-SU 2293 (12); 54°46′N, 157°43′30″W, 512 m; 28 Aug. 1890. USNM 59357 (6); same data as for CAS-

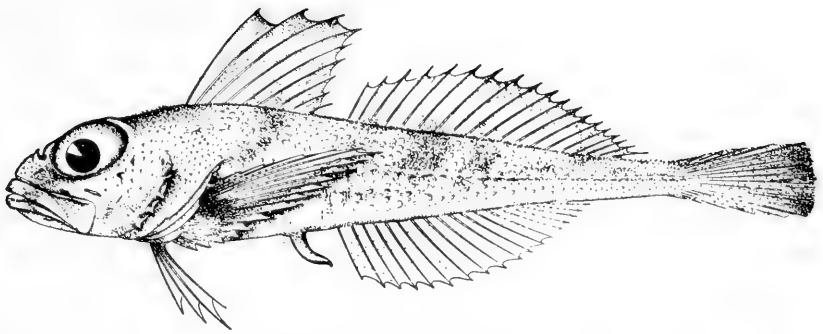


FIGURE 22. *Rastrinus scutiger* (Bean, 1890), male, approximately 73.0 mm TL; after Jordan and Evermann (1898).

SU 2293. BERING SEA: CAS-SU 2279 (12); 52°55'40"N, 173°26'E, 247 m; 11 June 1906. OSU 7874 (4); 51°46.4'N, 177°23.0'E, 194–205 m; 21 July 1980. OSU 7875 (7); 51°34.8'N, 176°37.3'W, 294–296 m; 8 July 1980. OSU 7876 (1); 52°30.1'N, 173°34.1'W, 201–212 m; 15 July 1980. OSU 7877 (2); 51°31.8'N, 176°38.7'W, 377–379 m; 8 July 1980. OSU 7878 (1); 51°14.7'N, 179°10.6'E, 364–375 m; 18 July 1980.

Genus **Icelus** Krøyer, 1845

Cottus: REINHARDT 1840a:9 (in part).
Icelus KRØYER, 1845:253, 261 (in part; type-species *Icelus hamatus* Krøyer, 1845, by orig. design.).
Centridermichthys: GÜNTHER 1860:172 (in part).
Agonocottus PAVLENKO, 1910:23 (type-species *Agonocottus cataphractus* Pavlenko, 1910, by monotypy).
Ochotskia SCHMIDT, 1915:612 (type-species *Ochotskia armata* Schmidt, 1915, by monotypy).
Icelichthys SCHMIDT, 1935:416 (subgenus; type-species *Icelus gilberti* Taranetz, in Schmidt, 1935, by monotypy).
Icelopsis TARANETZ, 1936:149 (subgenus; erroneous amendation of *Icelichthys* Schmidt, 1935, therefore taking same type-species *Icelus gilberti* Taranetz, in Schmidt, 1935).

DIAGNOSIS.—A genus of the family Cottidae (as characterized by Taranetz 1941; Bolin 1944, 1947) distinguished in having the following combination of characters. Branchiostegal rays six. Pelvic fins with one spine, three soft rays. Small conical teeth present on premaxillae, dentaries, vomer, and palatines. Parietal spines present or absent. Nuchal spines present. Preopercular spines four; uppermost spine simple, bifurcated or trifurcated. Suborbital stay spines present or absent. Sides of body not completely invested with small, spiny scales. One or more rows of enlarged, platelike scales above (and sometimes below) lateral line. Axillary scales present or absent. Lateral line scales tubular, flattened on lateral and medial surfaces, bearing spinules on dorsal and posterior margins of lateral scale surface or on central part of lateral scale surface. Scales,

TABLE 3. GEOGRAPHIC AND DEPTH DISTRIBUTIONS OF THE SPECIES OF *RASTRINUS* AND *ICELUS*.

Species	Geographic distribution	Depth (m)
Rastrinus scutiger	Gulf of Alaska; s Bering Sea w to Attu I.	120–512
Icelus gilberti	Sea of Japan; Sea of Okhotsk	56–180
Icelus spiniger	Coast of British Columbia; Gulf of Alaska; Bering Sea; Sea of Okhotsk	55–350
Icelus cataphractus	Sea of Japan; s Sea of Okhotsk; N. Pacific s of Hokkaido	79–454
Icelus armatus	Sea of Okhotsk	150–350
Icelus euryops	Gulf of Alaska; E Bering Sea	200–740
Icelus canaliculatus	Bering Sea; Sea of Okhotsk	20–800
Icelus rastrinoides	Sea of Japan	230–411
Icelus perminovi	Sea of Okhotsk	250–450
Icelus bicornis	E Beaufort Sea E to w Greenland and N Labrador; E Greenland E to Barents Sea; Kara, White, and Laptev seas	shallow–560
Icelus spatula	Sea of Okhotsk; Bering Sea; N Gulf of Alaska; Chukchi Sea; Beaufort Sea E to w Greenland and Labrador; Siberian, Laptev and Kara seas	shallow–293
Icelus ochotensis	Sea of Japan; Sea of Okhotsk; w Bering Sea	55–125
Icelus uncinalis	w Bering Sea	79–247
Icelus stenosomus	Sea of Japan	71–171

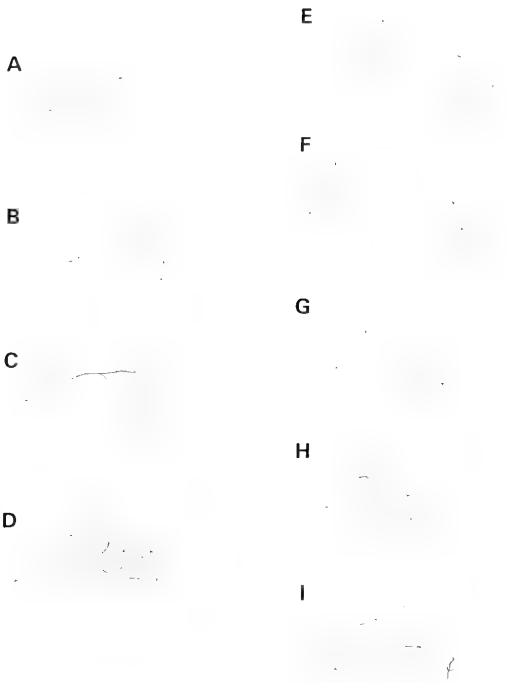


FIGURE 23. Urogenital papillae of males of species of *Rastrinus* and *Icelus*: (A) *Rastrinus scutiger*, OSU 7874, 72.0 mm SL; (B) *Icelus rastrinoides*, UMUT 32022, 90.0 mm SL; (C) *Icelus euryops*, UW 20808, 101.0 mm SL; (D) *Icelus canaliculatus*, UW 20806, 138.0 mm SL; (E) *Icelus uncinalis*, holotype, USNM 74366, 81.0 mm SL; (F) *Icelus ochotensis*, USNM 119861, 104.0 mm SL; (G) *Icelus spatula*, holotype, USNM 74367, 55.0 mm SL; (H) *Icelus bicornis*, NMC 70-277, 55.0 mm SL; (I) *Icelus spiniger*, UW 20781, 110.0 mm SL; left lateral view.

tending to be arranged in rows, on upper portion of eye. Supraocular cirri present. Parietal, nuchal, opercular, suborbital stay, maxillary, upper jaw, preopercular, and lateral line cirri present or absent. Male urogenital papilla with basal portion and terminal appendage variously developed (Fig. 23).

ETYMOLOGY.—The generic name is taken from the Greek *Hicelos*, son of Hypnos (god of sleep), and probably refers to a "quiescent lurking fish" (Hart 1973).

Key to the Species of the Genus *Icelus*

1a. Each scale of dorsal row of platelike scales bearing a single, strong spine (Fig. 18*D*) 2

1b. Each scale of dorsal row of platelike scales bearing an oblique ridge of small spinules (Figs. 18*B*, 18*C*) 3

2a. Strong, laterally directed spine on lacrimal (Fig. 17*B*); laterally directed spinules on lateral line scales with anteriorly and posteriorly directed processes (Fig. 20*B*) ..... *Icelus cataphractus* (Pavlenko, 1910) (p. 27)
Sea of Japan; southern Sea of Okhotsk

2b. Lacrimal spine absent (Fig. 17*A*); laterally directed spinules on lateral line scales simple or serrated (Fig. 20*A*) ..... *Icelus spiniger* Gilbert, 1895 (p. 24)
Bering Sea; Gulf of Alaska; eastern Sea of Okhotsk

3a. Cirri on preopercle, above upper jaw, on lateral line scales ..... *Icelus gilberti* Taranetz, in Schmidt, 1935 (p. 21)
Sea of Japan

3b. Cirri on preopercle, above upper jaw, on lateral line scales absent 4

4a. Two to four rows of platelike scales below lateral line 5

4b. Rows of platelike scales below lateral line absent, or only one row of such scales just above anal fin, or only one to four such scales confined to caudal peduncle 6

5a. Nuchal spine reduced, short; nuchal cirri present; uppermost preopercular spine simple ..... *Icelus rastrinoides* Taranetz, in Schmidt, 1935 (p. 29)
Sea of Japan

5b. Nuchal spine large, straight; nuchal cirri absent; uppermost preopercular spine bifurcated or trifurcated ..... *Icelus armatus* (Schmidt, 1915) (p. 22)
Sea of Okhotsk

6a. Nasal tubes black 7

6b. Nasal tubes lightly pigmented 8

7a. Suborbital stay spines present ..... *Icelus canaliculatus* Gilbert, 1895 (p. 32)
Bering Sea; Sea of Okhotsk

7b. Suborbital stay spines absent ..... *Icelus perminovi* Taranetz, 1936 (p. 34)
Sea of Okhotsk

8a. Suborbital stay spines present ..... *Icelus euryops* Bean, 1890 (p. 30)

Bering Sea; northern Gulf of Alaska

8b. Suborbital stay spines absent 9

9a. Parietal spine absent 10

9b. Parietal spine present 11

10a. Greatest body depth less than 200 thousandths SL; nuchal spines short, sharp, posteriorly directed ..... *Icelus stenosomus* Andriashev, 1937 (p. 53)

Sea of Japan; Tartar Strait

10b. Greatest body depth greater than 250 thousandths SL; nuchal spines large, blunt, conical, directed upward ..... *Icelus ochotensis* Schmidt, 1927 (p. 50)

Sea of Japan; Sea of Okhotsk; eastern coast of Kamchatka

11a. Lateral line scales extending past posterior edge of hypural plate, one lateral line scale on caudal rays; dorsal and ventral caudal peduncle scales absent; supraocular cirri narrow at base, broad and multifid distally, not darkly pigmented ..... *Icelus uncinalis* Gilbert and Burke, 1912 (p. 52)

Western Bering Sea

11b. Lateral line scales not extending past posterior edge of hypural plate, no lateral line scales on caudal rays; dorsal and ventral caudal peduncle scales present or absent; supraocular cirri usually simple, slender, gently tapering distally, if broad and multifid, then darkly pigmented 12

12a. Lateral line scales extending to posterior edge of hypural plate; caudal peduncle scales absent or present only above lateral line; axillary scales 2–14; rows of scales between dorsal scale row and lateral line absent; row of scales just above anal fin absent; male urogenital papilla flattened or spatulate, with a short, curved or hooklike terminal appendage (Fig. 23*G*) ..... *Icelus spatula* Gilbert and Burke, 1912 (p. 41)

Sea of Okhotsk; Bering Sea; northern Gulf of Alaska; Chukchi Sea eastward to western Greenland and Labrador and westward to Laptev and Kara seas.

12b. Lateral line scales incomplete posteriorly, terminating on or before anterior portion of caudal peduncle (rarely extending to posterior edge of hypural plate); caudal peduncle scales generally present above and below midline of caudal peduncle; axillary scales 9–30; row of small scales often present between dorsal scale row and lateral line; row of small scales often present just above anal fin; urogenital papilla of male cylindrical, with an elongate, tapering terminal appendage (Fig. 23*H*) ..... *Icelus bicornis* (Reinhardt, 1840) (p. 35)

Beaufort Sea eastward to western Greenland and Labrador; eastern Greenland eastward to northern Iceland; Faeroe Islands; Spitzbergen; seas of northern Arctic Europe eastward to Kara and Laptev seas.

Icelus gilberti Taranetz, in Schmidt, 1935

(Figure 24)

Icelus gilberti Taranetz, in Schmidt, 1935:414, 416 (orig. descr.; key to *Icelus* species; Sea of Japan); Taranetz 1936: 149 (descr.; fig.; Sea of Japan at Vladimir Bay, Olga Bay, Southern Cape; Sea of Okhotsk at Aniva Bay; 56–180 m, on pebble ground; no type-specimens indicated); 1937:106, 107 (key to spp.; Sea of Japan and Tartar Str.); Schmidt 1950:125 (doubtfully listed as occurring in Sea of Okhotsk; Aniva Bay spec. apparently lost); Ueno 1972:91 (w Sea of Japan; off sw Sakhalin, in Tartar Str.).

Diagnosis.—Parietal spine reduced or absent. Nuchal spine short, blunt, covered by skin. Suborbital stay spines and lacrimal spines absent. Uppermost preopercular spine simple, straight or curved. Two to five rows of enlarged, platelike scales (Pattern B, Fig. 18*B*) between dorsal fins and lateral line. Rows of scales below lateral line absent. Axillary scales absent. Lateral line scales each with a continuous arc of small spinules along dorsal and posterior margins of lateral scale surface; lateral line scales extending to posterior margin of hypural plate. Dorsal caudal peduncle scales present, represented by numerous scales of dorsal scale rows; ventral caudal peduncle scales absent. Cirri present as follows: supraocular, parietal, nuchal, opercular, suborbital stay, preopercular, maxillary, above upper jaw, and

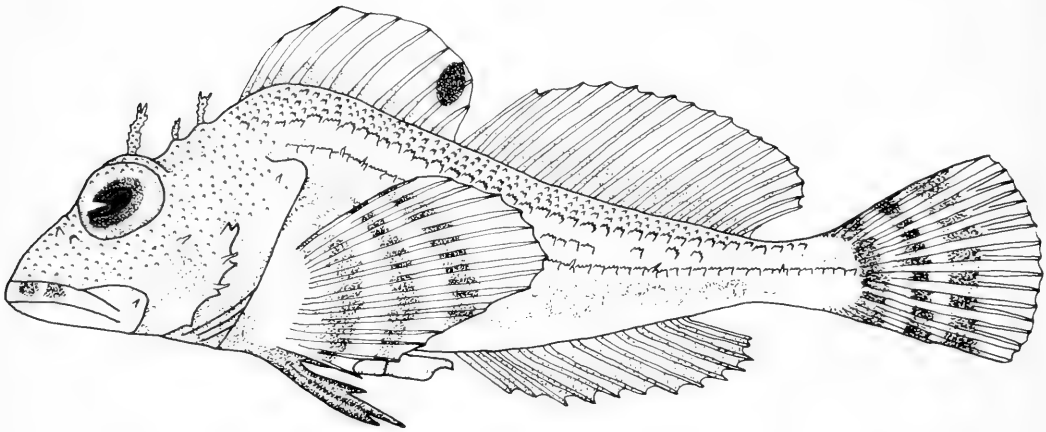


FIGURE 24. *Icelus gilberti* Taranetz, in Schmidt, 1935, male, unknown length; after Taranetz, 1936.

on several lateral line scales. Head cirri lightly pigmented. Nasal tubes lightly pigmented (similar to skin of snout). Urogenital papilla of male cylindrical, slightly dorsoventrally flattened, gently tapering to a rounded tip.

DESCRIPTION.—General body shape shown in Figure 24. Body short, deep; greatest body depth at spinous dorsal fin. Head deeper than wide; entire body laterally compressed. Eye large; orbit diameter about equal to snout length. Mouth large; posterior edge of maxilla nearly reaching posterior rim of orbit. Top and sides of head, including opercles, densely scaled. Supraocular, parietal, nuchal cirri bearing small, spiny scales along their entire lengths.

Coloration in preservative. Overall body color light yellowish-brown. Indistinct, slightly darker brown saddles on sides of body below dorsal fins. Underside whitish. Dark spot on posterior part of spinous dorsal fin.

MEASUREMENTS (from 3 spec., 42.5–71.0 mm).—The following expressed as thousandths of SL (ranges only are given): head length 408–420; lacrimal length 68–78; snout length 96–130; least interorbital width 40–49; orbit diameter 111–130; greatest body depth 260–310; least caudal peduncle depth 63–66; pectoral fin base length 140–165; upper jaw length 146–201.

COUNTS (from 3 spec., except where indicated).—Ranges of values only are given. Dorsal fin spines 9; dorsal fin soft rays (2 spec.) 18–19; anal fin rays 12–13; pectoral fin rays 16; dorsal scale row (in *I. gilberti* dorsal scale row counts are made along the row of largest platelike scales, the second row above the lateral line) 34; lateral line scales 38–39; axillary scales absent.

REMARKS.—The specimens upon which Taranetz (Schmidt 1935; Taranetz 1936) based his original description (deposited in IZL) were unavailable for examination; hence, no lectotype is herein designated.

DISTRIBUTION.—All three specimens examined are from the Sea of Japan (Fig. 25). Only one specimen has precise capture data: 45°33′40″N, 140°54′E, 157 m. Taranetz (1936, 1937) reported that the species ranges northward to Aniva Bay, Sea of Okhotsk; and Ueno (1972) listed the southernmost limit of its range as about 42°N in the Sea of Japan. The depth distribution is 56–180 m (Taranetz 1936). It appears to be rare in, and possibly endemic to, the Sea of Japan, but it may range northward into the southern Sea of Okhotsk.

ETYMOLOGY.—The species is named after Charles H. Gilbert, ichthyologist of many North Pacific ALBATROSS expeditions.

MATERIAL EXAMINED (3 spec., 42.5–71.0 mm; nontype-material).—MCZ 34077 (2:42.5–71.0 mm); Vladimir Bay, Sea of Japan, 95 m; 31 May 1931. USNM 119853 (1:50.0 mm); Bomashiri Shima, Sea of Japan, 45°33′40″N, 140°54′E, 157 m, ALBATROSS sta. 4995; 22 Sep. 1906.

Icelus armatus (Schmidt 1915)

(Figure 26)

Ochotskia armata SCHMIDT 1915:612, fig. 1 (orig. descr.; type-locality St. Jonas I., Sea of Okhotsk, 56°18′N, 145°04′E, 320 m); SOLDATOV AND LINDBERG 1930:180, fig. 29 (summary

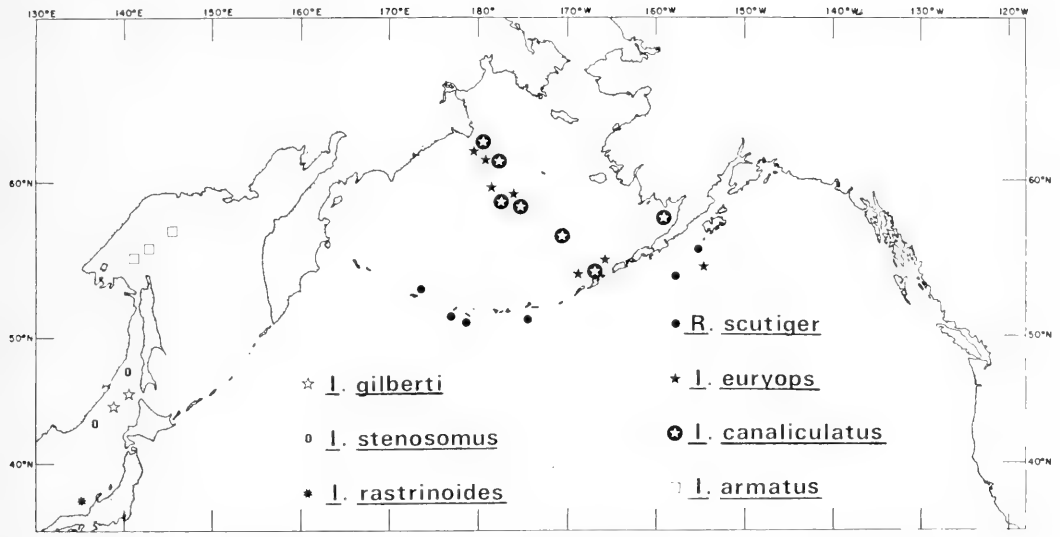


FIGURE 25. Known distributions of *Rastrinus scutiger* and six species of *Icelus* in the North Pacific Ocean.

of Schmidt 1915; distr.); POPOV 1931:130 (brief descr.; distr.); OKADA AND MATSUBARA 1938:321 (compiled distr. in Sea of Japan).

Icelus vicinalis: SCHMIDT (non Gilbert) 1927:3 (these spec. later det. by Taranetz [1935] to be *I. armatus*; Sea of Okhotsk).

Icelus armatus TARANETZ 1935:91 (*Ochotskia* a synon. of *Icelus*; Schmidt's [1927] misident. of *I. vicinalis* corrected); SCHMIDT 1935:413 (*I. armatus* placed with *I. canaliculatus* and *I. rastrinoides* into subgen. *Ochotskia*; key; distr.); TARANETZ 1936:152 (key; *I. armatus* placed close to *I. vicinalis*, *I. euryops*, *I. canaliculatus*, *I. rastrinoides*, and *I. perminovi*); 1937:107, 108 (key; distr.); SCHMIDT 1950:123 (follows Taranetz [1936] in placing *I. armatus* with other *Icelus* spp. into subgen. *Ochotskia*; distr.).

DIAGNOSIS.—Parietal spines absent. Nuchal spines long, straight, sharp. Laterally directed spine on suborbital stay. Lacrimal spine absent. Uppermost preopercular spine bifurcated or trifurcated. Two to three rows of enlarged, platelike scales (Pattern C, Fig. 18*C*) between dorsal fins and lateral line. Three to five rows of similar scales between lateral line and anal fin. Axillary scales numerous, confluent with scale rows below lateral line; five to seven scales in uppermost axillary row. Lateral line scales extending past posterior edge of hypural plate; one scale on caudal rays. Lateral line scales Pattern A (Fig. 19*A*). Caudal peduncle scales present, represented by scales of dorsal and ventral scale rows. Superocular, parietal, maxillary cirri present; other cirri absent. Head cirri not darkly pigmented. Nasal tubes lightly pigmented (similar to skin of snout). Urogenital papilla of male with cylindrical basal portion and gently curved terminal appendage (Schmidt 1950).

DESCRIPTION.—General body shape shown in Figure 26. Body elongate, slender, depth greatest at anterior portion of spinous dorsal fin. Head large, as deep as wide. Eye large; orbit diameter about 1.5 times snout length. Mouth large; posterior edge of maxilla nearly reaching posterior rim of orbit. Sides of body, above and below lateral line, almost completely covered by rows of enlarged, platelike (Pattern C) scales. Top and sides of head, including opercles, covered with small, spiny scales.

Coloration in preservative. Overall body color yellowish brown. Indistinct darker markings on upper portion of body. Top of head darker brown. Underside whitish.

MEASUREMENTS (from 3 spec., all females, 71.0–118.0 mm).—The following expressed as thousandths SL (ranges only are given): head length 300–352; lacrimal length 51–59; snout length 73–90; least interorbital width 21–27; orbit diameter 119–141; greatest body depth 161–190; least caudal peduncle depth 34–45; pectoral fin base length 120–136; upper jaw length 169–189.

COUNTS (from 3 spec.).—Values for holotype are taken from Schmidt (1915); values given, [value for holotype (where available)] range (for 3 spec. examined): dorsal fin spines [9] 9; dorsal

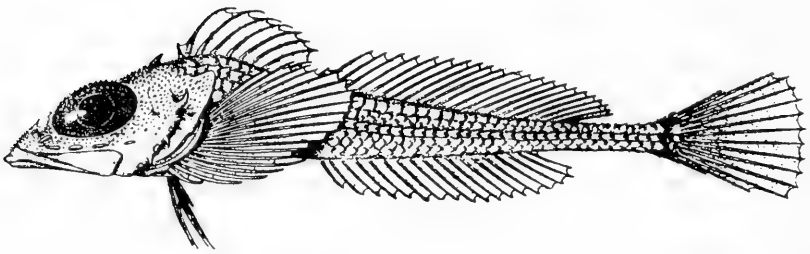


FIGURE 26. *Icelus armatus* (Schmidt, 1915), female, approximately 72.0 mm TL; after Schmidt (1915).

fin soft rays [23] 23–24; anal fin rays [18 (Schmidt lists anal fin as 1 spine, 17 soft rays)] 18–19; pectoral fin rays [19] 17–18; scales in dorsalmost scale row 38–41; number of scale rows between lateral line and anterior portion of anal fin 3; lateral line scales [46] 45–46; axillary scales, uppermost row 5–7.

DISTRIBUTION.—The three specimens examined were collected in the western Sea of Okhotsk. The type-locality was near St. Jonas Island, Sea of Okhotsk. Schmidt's (1927) specimens of *I. vicinalis,* later referred to *I. armatus* by Taranetz (1935), were taken at 55°41′N, 141°25.5′E, 275 m. Schmidt (1950) described the distribution of this species as around St. Jonas Island and off the eastern coast of North Sakhalin Island, in depths of 150–350 m. The species appears to be rare and endemic to the Sea of Okhotsk (Fig. 25).

ETYMOLOGY.—The specific name *armatus,* from Latin, refers to the several rows of strong, spiny, platelike scales which almost completely cover the body.

MATERIAL EXAMINED (3 spec., 71.0–118.0 mm; nontype-material).—BMNH 1964.4.18:1 (1:71.0 mm); Sea of Okhotsk, 55°41′N, 141°25.5′E; 31 July 1918. HUMZ 60411 (1:118.0 mm); Sea of Okhotsk, 56°37′N, 143°35′E, 240 m; 22 Sep. 1976. USNM 105117 (1:110.0 mm); W Sea of Okhotsk; no date given.

Icelus spiniger Group

DIAGNOSIS.—Scales of dorsal scale row enlarged, platelike, Pattern D (Fig. 18*D*). Lateral line scales Pattern C (Fig. 19*C*). Suborbital stay spine present. Parietal spines absent. Nuchal spines long, straight, sharp.

Icelus spiniger Gilbert, 1895

(Figure 27)

Icelus spiniger GILBERT, 1895:412, pl. 24 (orig. descr.; type-locality Bering Sea, 56°48′30″N, 165°49′W, 156 m, ALBATROSS sta. 3225 [LECTOTYPE: USNM 164258, male, 74.0 mm, hereby designated]); JORDAN AND EVERMANN 1896:437 (Unalaska I. and Bristol Bay, Alaska); 1898:1914, fig. 693 (compiled descr.; fig. from Gilbert 1895; Bristol Bay, Alaska); SCHMIDT 1904:107 (in part; descr.; Peter the Great Bay spec. are *I. cataphractus*); JORDAN AND STARKS 1904:246, fig. 6 (in part; descr.; Vladivostok spec. are *I. cataphractus*); EVERMANN AND GOLDSBOROUGH 1907:300, fig. 52 (range extended S to N Gulf of Alaska); JORDAN, TANAKA, AND SNYDER 1913:258 (in part; descr.; distr.); SCHMIDT 1927:3 (in part; descr.; S Sakhalin spec. are *I. cataphractus*); JORDAN, EVERMANN, AND CLARK 1930:378 (compiled); SOLDATOV AND LINDBERG 1930:175 (in part; descr.; Bering Sea; S Sea of Okhotsk and Sea of Japan spec. are *I. cataphractus*); SCHMIDT 1935:413 (in part; placed into subgen. *Agonocottus*; key to spp. of *Icelus*); TARANETZ 1935:91 (in part; *I. spiniger* placed into its own species group; compar. with other *Icelus* species); 1936:151 (key); ANDRIASHEV 1937b:301 (in part; subsp. diag.; descr.; distr.); TARANETZ 1937:108 (in part; key; distr.); OKADA 1938:226 (in part; distr.); LINDBERG AND ANDRIASHEV 1938:515 figs. 1–4 (in part; subspp.; aids to ident.; key; distr.); ANDRIASHEV 1939:42 (in part; distr. of *I. spiniger spiniger* and *I. spiniger intermedius*); SCHMIDT 1950:127 (in part; descr. of subspp. in Sea of Okhotsk; distr.); WILIMOVSKY 1958:66 (key; Bering Sea, SE Alaska); LINDBERG 1959:252 (in part; compiled distr. in Soviet Far East); WATANABE 1960: 42, fig. 15, pl. II, fig. 2 (in part; descr.; distr.; Sea of Japan spec. are *I. cataphractus*); SKALKIN 1963:179 (descr. of otoliths); SHUNTOV 1965:1681 (depth distr. in Sea of Okhotsk: 150–350 m, most common at 150–200 m); BARRACLOUGH 1971:1922, fig. 1 (descr.; range extended S to British Columbia, Canada); UENO 1972:91 (in part; compiled distr.); QUAST AND HALL 1972:23 (distr.; lit.); FEDOROV 1973:15 (depth distr. in Bering Sea); HART 1973:515 (in part; descr.; fig.; distr.); HOWE AND RICHARDSON 1978:49, 138 (in part; diag.; distr.; lit.; key); YABE 1981:293, figs. 2B, 7D, 8C, 9B, 12B, 13B, 14 (comp. osteol.; removed *Icelus* from Icelidae, placing genus back into Cottidae).

Icelus spiniger intermedius LINDBERG AND ANDRIASHEV, in ANDRIASHEV 1937b:301 (orig. descr.; Sea of Okhotsk); TARANETZ 1937:108 (key; distr.); LINDBERG AND ANDRIASHEV 1938:517, figs. 1, 2 (descr.; Sea of Okhotsk, off SW Kamchatka, 185–195 m); ANDRIASHEV 1939:42 (W Bering Sea; Sea of Okhotsk); SCHMIDT 1950:127 (descr.; synon.; distr.); LINDBERG 1959:252 (E coast Sakhalin; Pacific coast Iturup I.); FEDOROV 1973:15 (depth distr.).

Icelus spiniger spiniger TARANETZ 1937:108 (key; distr.); ANDRIASHEV 1937b:301 (compar. notes on subspp.; E Bering Sea; Aleutian Is.); LINDBERG AND ANDRIASHEV 1938:516

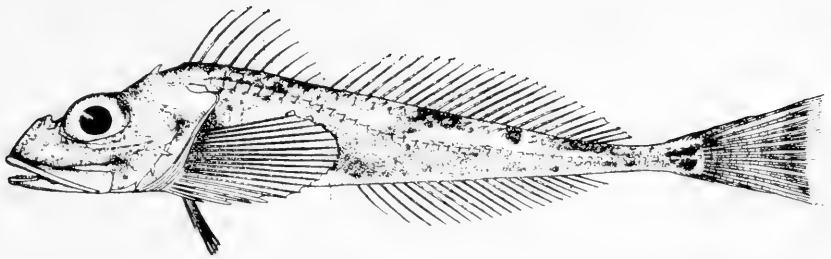


FIGURE 27. *Icelus spiniger* Gilbert, 1895, female, approximately 118.0 mm TL; after Gilbert (1895).

(descr.; key; distr.); ANDRIASHEV 1939:42 (E Bering Sea); WILIMOVSKY 1958:66 (key; Bering Sea; SE Alaska); FEDOROV 1973:15 (depth distr.; Bering Sea).

DIAGNOSIS.—Parietal spines absent. Nuchal spines long, straight, sharp. One or two laterally directed spines on suborbital stay. Lacrimal spines absent. Uppermost preopercular spine bifurcated. Single dorsal row of enlarged, platelike scales, each bearing a single strong spine (Pattern D, Fig. 18*D*), between dorsal fins and lateral line. Rows of scales between dorsal scale row and lateral line absent; rows of scales between lateral line and anal fin absent. Axillary scales 2–17. Lateral line scales Pattern C (Fig. 19*C*), bearing a laterally directed ridge of spinules on lateral scale surface (Fig. 20*A*); lateral line scales extending past posterior edge of hypural plate onto caudal rays. Dorsal and ventral caudal peduncle scales present. Supraocular cirri present; parietal cirri present or absent; other cirri absent. Head cirri lightly pigmented. Nasal tubes lightly pigmented (similar to snout). Urogenital papilla of male with spatulate basal portion; terminal appendage curved or hooklike (Fig. 23*I*).

DESCRIPTION.—General body shape shown in Figure 27. Body elongate, slender, laterally compressed posterior to opercular openings. Greatest body depth at spinous dorsal fin. Head large, as deep as wide. Eye large, about 1.5 times snout length. Mouth large; posterior edge of maxilla nearly reaching posterior rim of orbit. Supraocular ridge with 1–4 sharp, dorsally directed spines (Figs. 1, 2; not shown in Fig. 27). Nasal spine short, sharp. Small, spiny scales scattered about enlarged, platelike scales of dorsal scale row. Similar scales on top and sides of head, including opercles. Edges of embedded portions of lateral line scales not overlapping.

Coloration in preservative. Overall body color light pinkish tan, with darker brown splotches scattered over sides of body. Darker brown patches on pectoral fins tending to be arranged in vertical bars. Soft-rayed dorsal fin with two or three dark brown bars. Spinous dorsal fin with a prominent dark brown or black spot near posterior dorsal edge (not shown in Fig. 27). Underside whitish. Specimens collected in deeper water (200–300 m) tend to be darker overall with more dark splotches on sides of body.

MEASUREMENTS (from 56 spec., 73.0–192.0 mm, except where indicated).—The following expressed in thousandths SL, [value for lectotype] range (mean; standard deviation): head length [358] 321–366 (346; 11.9); lacrimal length [58] 47–77 (63; 4.7); snout length (from 32 spec.) [101] 87–108 (99; 4.9); orbit diameter [149] 100–154 (114; 9.7); least interorbital width [20] 18–33 (25; 3.0); greatest body depth [202] 170–232 (199; 12.8); least caudal peduncle depth [39] 34–51 (43; 3.7); pectoral fin base length [128] 105–131 (119; 6.4); upper jaw length (32 spec.) [176] 157–204 (187; 6.2).

COUNTS (from 111 spec., except where indicated).—Values expressed, [value for lectotype] range (mode; mean): dorsal fin spines [9] 8–10 (9; 8.9); dorsal fin soft rays [21] 19–23 (21; 21.4); anal fin rays [16] 15–19 (17; 17.3); pectoral fin rays [18] 17–20 (18; 18.3); dorsal scale row (142 spec.) [28] 22–34 (27; 27.6); lateral line scale row (127 spec.) [44] 42–45 (44; 44.1); axillary scales (118 spec.) [9] 2–17 (8; 9.2).

REMARKS.—Examination of material from the Sea of Okhotsk (17 spec.) does not substantiate the subspecific diagnosis for *Icelus spiniger intermedius* (sensu Lindberg and Andriashev, in Andriashev 1937b). The character states of the supraorbital (=supraocular ridge) spines and the suborbital stay spines, described as differentiating *I. spiniger intermedius* from *I. spiniger spiniger*, are present in both of these nominal taxa.

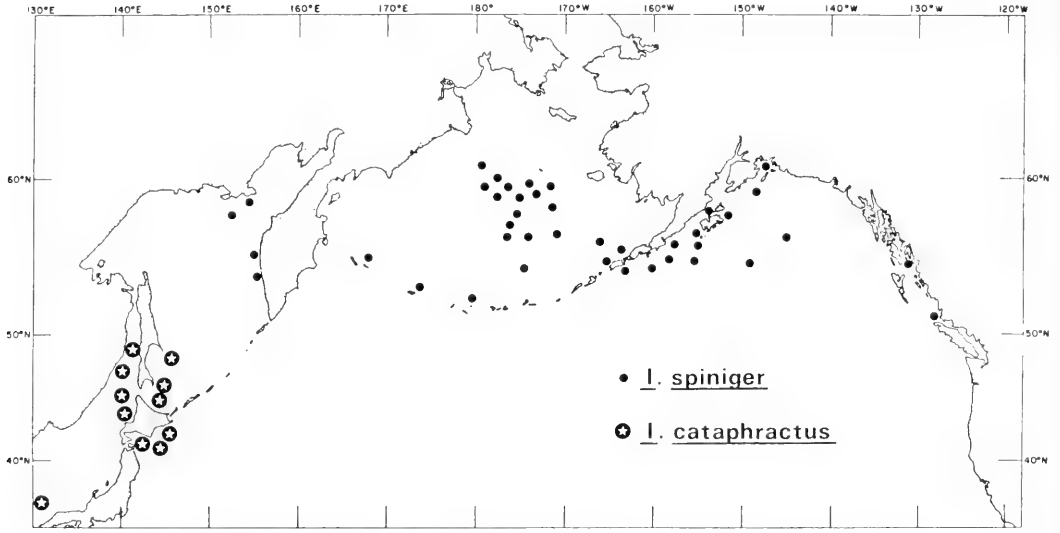


FIGURE 28. Known distributions of *Icelus spiniger* and *I. cataphractus* in the North Pacific Ocean.

The pectoral fins are distinctly notched in larger specimens collected in the eastern Bering Sea, and the lowermost 6–8 fin rays are slightly exserted and somewhat elongated; these conditions are also cited by Lindberg and Andriashev (1938) as diagnostic for *I. spiniger intermedius*. Analyses of measurements and counts similarly do not substantiate subspecific differences.

Icelus spiniger, throughout its geographic range, is readily distinguishable from *I. cataphractus* based on characters listed in the diagnoses of these two species.

DISTRIBUTION.—*Icelus spiniger* is widely distributed throughout the Bering Sea and the Gulf of Alaska, and also found along the Aleutian Islands, the eastern coast of Kamchatka, and in the eastern part of the Sea of Okhotsk (Fig. 28). The species appears to be most common in depths of 100–200 m, but (based on material examined in this study) may be found between 55 and 320 m (Jordan and Evermann 1898; Lindberg and Andriashev 1938; Shuntov 1965; Howe and Richardson 1978). The southernmost record along the Pacific coast of North America is off Vancouver Island, British Columbia, 50°28′N, 127°29′20″W, 104–113 m (Barraclough 1971). The species ranges north in the Bering Sea to at least 59°28′N, 178°16′W, 280 m. In the Sea of Okhotsk *I. spiniger* is found to at least 58°29′N in the north and to southeastern Kamchatka (Lindberg and Andriashev 1938) in the south, with a depth range of 100–350 m (Lindberg and Andriashev 1938; Schmidt 1950; Shuntov 1965).

ETYMOLOGY.—The specific name *spiniger*, from the Latin roots *spin-* and *ger-* (to bear), refers to the spiny armor of the dorsal row of platelike scales and on the supraocular ridge, which give the fish its common name, thorny sculpin.

MATERIAL EXAMINED (324 spec., 29.0–192.0 mm).—**Lectotype:** USNM 164258, male, 74.0 mm; Bering Sea, 54°48′30″N, 165°49′W, 156 m, ALBATROSS sta. 3225; 22 May 1890.

Paralectotypes (all ALBATROSS sta. from Bering Sea): CAS-SU 2266 (2:63.0–104.0 mm); 55°01′N, 167°25′W, 234 m, sta. 3226; 23 May 1890. CAS-SU 2231 (40:29.0–92.5 mm); 54°48′30″N, 165°49′W, 156 m, sta. 3225; 22 May 1890. CAS-SU 2269 (16:51.0–118.0 mm); 56°56′N, 172°55′W, 130 m, sta. 3309; 4 Aug. 1890. MCZ 29270 (1 [of 3]:84.5 mm); 54°24′30″N, 163°37′W, 112 m, sta. 3216; 21 May 1890.

Nontype-material. GULF OF ALASKA: FMNH 55954 (1); Alaska; no date given. LACM 33296-1 (1); offshore Johnstone Bay, approx. 40 mi. NE of Seward; 19 July 1963. LACM 33294-1 (1); Marmot Bay, SE of Afagnak I., NE of Kodiak I.; 21 June 1964. LACM 35752-1 (3); 54°57′N, 166°02′W, 140 m; 14 June 1975. UBC BC62-447 (3); 54°26′30″N, 149°48′W; 4 July 1961. UBC BC65-96 (1); 53°44.5′N, 164°11.5′W; 11 Aug. 1964. UBC BC65-133 (1); Canada, British Columbia, head of Alice Arm; 26 Sep. 1954. UBC BC65-67 (1); 55°08′N, 156°57′W; 4 Aug. 1964. UBC BC62-509 (1); 55°18′N, 158°00′W. UBC BC62-669 (2); 54°39′N, 158°44′W; 22 July 1961. UBC BC65-68 (5); 54°26′N, 159°52′W; 7 Aug. 1964. UBC BC62-659 (1); Alaska, M/V ARTHUR H. sta. 31H; 20 Sep. 1961. UBC BC65-148 (1); 55°39′N, 155°52′W; 3 Aug. 1964. UBC BC65-475 (3); 54°26′30″N, 144°48′W; 4 July 1961. UBC BC62-527 (1); 54°27′40″N, 160°15′W; 30 June 1961. UBC BC62-760 (1); Alaska; 27 June 1962. UBC BC62-682 (1); 54°27′N, 159°45′W;

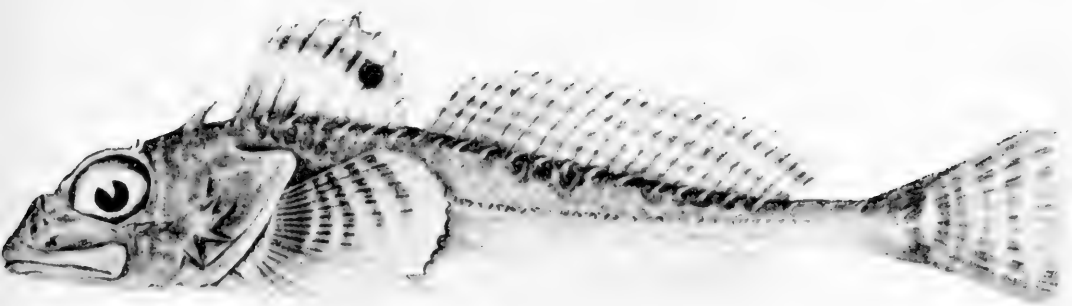


FIGURE 29. *Icelus cataphractus* (Pavlenko, 1910), female, length unknown, after Watanabe (1960).

6 Apr. 1962. UBC BC65-145 (1); Alaska, Kodiak area; 1961. UBC BC61-442 (2); 55°42′N, 157°30′W; 13 July 1961. UBC BC65-149 (1); 54°17′N, 160°54′W; 7 Aug. 1964. UBC BC63-138 (2); Alaska; 17 Aug. 1958. USNM 119401 (4); Olga Bay, 70–175 m; 4 Nov. 1940. USNM 60493 (6); Shelikof Str., 170–190 m; 15 Aug. 1903. USNM 60494 (3); Shelikof Str., 90–120 m; 15 Aug. 1903. USNM 60496 (1, 1 removed to *Icelus spatula*); Chignik Bay, 55–75 m; 10 Aug. 1903. USNM 60497 (1); Alaska, near Naha Bay, Behm Canal, 113–120 m; 7 July 1903. USNM 60500 (2); Alitak Bay, Kodiak I., 66–75 m; 6 Aug. 1903. USNM 60495 (1); Uyak Bay, Kodiak I.; 14 Aug. 1903. BERING SEA: BCPM 979-11032 (3); 56°19′N, 170°07′W; 25 June 1978. BCPM BC71-43 (1); 56°56′N, 172°55′W, 130 m; 4 Aug. 1890. CAS-SU 22260 (9); 52°46′50″N, 158°44′30″E, 88–126 m; 20 June 1906. CAS-SU 5651 (3); 51°16′N, 158°03′E, 183 m; 20 Aug. 1895. MCZ 28239 (8); 56°56′N, 172°55′W, 130 m; 4 Aug. 1890. SIO 76-392 (2); Alaska; 9 May 1976. SIO 76-299 (33, 1 removed to *Icelus spatula*, 1 removed to *Icelinus borealis*); 56°43′N, 153°22′W; no date given. UBC BC62-531 (1); 57°01′N, 154°59′W; 13 July 1961. UBC BC62-526 (3); 56°54′N, 155°00′W; 6 Oct. 1961. UBC BC62-564 (2); 25 miles (ca. 40 km) s of Akutan I., Aleutian Is.; 21 July 1960. USNM 74745 (9); 54°50′N, 167°13′E; 14 June 1906. USNM 74744 (4); 54°49′45″N, 167°12′30″E, 102 m; 14 June 1906. USNM 231803 (2); 59°12.59′N, 178°26.35′W, 305–317 m; 26 June 1979. USNM 231807 (8); 59°28.30′N, 178°15.87′W, 274–280 m; 28 June 1979. USNM 231808 (1); 58°46.10′N, 177°38.02′W, 233 m; 26 June 1979. USNM 231804 (1); 58°26.22′N, 175°35.24′W, 280–330 m; 25 June 1979. USNM 231800 (11); 58°31.32′N, 175°16.15′W, 302–310 m; 24 June 1979. USNM 231802 (3); 58°02.8′N, 174°05.66′W, 245–250 m; 22 June 1979. USNM 231797 (2); 57°43.2′N, 173°00.72′W, 121–122 m; 21 June 1979. USNM 231796 (1); 56°59.41′N, 173°00.65′W, 127 m; 21 June 1979. USNM 231794 (3); 55°09.01′N, 169°39.37′W, 260 m; 16 June 1979. USNM 231801 (4); 54°57.95′N, 167°19.25′W, 236–260 m; 13 June 1979. USNM 231799 (4); 54°50.61′N, 166°58.40′W, 280–315 m; 13 June 1979. USNM 231806 (3); 54°49.16′N, 166°40.85′W, 200–230 m; 13 June 1979. USNM 231805 (1); 57°28.02′N, 173°00.52′W, 122–124 m; 21 June 1979. USNM 231795 (1); 57°00′N, 172°02′W, 117 m; 27 June 1978. USNM 231809 (2); 58°21′N, 172°55′W, 106 m; 25 July 1977. UW 20780, 20781, 20782, 20783, 20784, 20785 (22 [total]); 57°20.2′N, 171°28.2′W, 106 m; 23 Aug. 1979. UW 20786 (8); 57°39.9′N, 171°31.9′W, 104 m; 23 Aug. 1979. UW 20787, 20788, 20789 (20 [total]); 57°00.2′N, 171°33.6′W, 116 m; 24 Aug. 1979. UW 20790 (1); 59°N, 176°W; Aug. 1978. UW 20791 (1); 60°50′N, 176°36′W, 117 m; 15 July 1979. UW 20792 (1); 60°59′N, 179°11′W, 300 m; 16 July 1979. UW 20793 (2); 58°20′N, 174°19′W; 4 Aug. 1978. UW 20794 (1); 56°39′N, 171°21′W; 26 June 1978. UW 20795 (2); 58°48.1′N, 174°00′W; 14 July 1979. UW 20796 (6); 59°30.3′N, 172°58.9′W, 87–96 m; 14 July 1979. UW 20797 (4); 59°01.9′N, 172°21.6′W, 99 m; 14 July 1979. UW 20802 (2); near Pribilof Is.; Aug. 1979. SEA OF OKHOTSK: HUMZ 45057 (1); 54°05′N, 154°40′E, 170 m; 8 May 1975. HUMZ 46384 (1); 57°59′N, 152°00′E, 207 m; 9 June 1976. HUMZ 58209 (1); 58°29′N, 153°58′E, 176 m; 13 Sep. 1976. UBC BC63-675 (13); 52°43′N, 155°42′E; 10 Sep. 1961. USNM 105144 (1); 9 June 1932.

Icelus cataphractus (Pavlenko, 1910)

(Figure 29)

Icelus spiniger: SCHMIDT 1903:15 (in part; Sea of Japan, near Vladivostok); JORDAN AND STARKS 1904:246, fig. 6 (in part; Sea of Japan); SCHMIDT 1904:107 (in part; Peter the Great Bay); JORDAN, TANAKA, AND SNYDER 1913:258 (in part; descr.; distr.); SCHMIDT 1927:3 (in part; descr.; key; Aniva Bay, s Sakhalin, Tartar Str.); SOLDATOV AND LINDBERG 1930:175 (in part; descr.; synon.; distr.); SCHMIDT 1935:413 (in part; placed into subgen. *Agonocottus*; key); TARANETZ 1936:151 (in part; key to sp. groups); ANDRIASHEV 1937b:301 (in part; descr. of subspp.; synon.; distr.); TARANETZ 1937:107, 108 (in part; key to spp. and subspp. of *Icelus*; distr.); LINDBERG AND ANDRIASHEV 1938:520, figs. 3, 4 (in part; descr. of subspp.; distr.); OKADA 1938:226 (in part; N Sea of Japan); ANDRIASHEV 1939:42 (in part; Sea of Japan); SCHMIDT 1950:127 (in part; subspp. descr.; distr.; synon.); HONMA 1957:111 (in part; range extended s to Niigata Pref., Sea of Japan); LINDBERG 1959:252 (in part; subspp.; s Sakhalin and Aniva Bay); WATANABE 1960:42, fig. 15, pl. II, fig. 2 (in part; descr.;

morph. and meristic char.; distr.; all Sea of Japan material is *I. cataphractus*); Ueno 1972:91 (in part; Sea of Japan and s Sakhalin).

Agonocottus cataphractus Pavlenko 1910:23, figs. 2, 3 (orig. descr.; type-locality Cape Povorotnye, Peter the Great Bay, w Sea of Japan).

Icelus omodakae Tanaka 1915:616 (orig. descr.; type-locality off Hinomi Saki, s Sea of Japan, 120 fm; compar. with descr. [Schmidt 1904] of *I. spiniger* off Vladivostok).

Icelus spiniger cataphractus Andriashev 1937b:301 (descr. of subspp.; Sea of Japan; synon.); Taranetz 1937:107, 108 (key; distr.); Lindberg and Andriashev 1938:520, 524, figs. 3, 4 (subspp. descr.; neotype designated for *Agonocottus cataphractus* Pavlenko, 1910, IZL 25189; neotype locality near Petrov I., Sea of Japan, 150 m; key; synon.; Sea of Japan and Aniva Bay); Schmidt 1959:127 (synon.; Sea of Japan, Peter the Great Bay, Tartar Str., s Sea of Okhotsk); Legeza 1956:128 (ecol. notes; s Sea of Okhotsk and Tartar Str.); Lindberg 1959:252 (s Sakhalin).

Icelus cataphract Ueno 1972:91 (misspelling of specific name; s Sakhalin, s Sea of Okhotsk).

Diagnosis.—Parietal spines absent. Nuchal spines long, straight, sharp. One or two laterally directed spines on suborbital stay. One (rarely two) laterally directed spines on lacrimal (Fig. 17*B*). Uppermost preopercular spine bifurcated. Single row of enlarged, platelike scales, each bearing a single strong spine, between dorsal fins and lateral line (Pattern D, Fig. 18*D*). Rows of scales between dorsal scale row and lateral line absent. Rows of scales between lateral line and anal fin absent. Axillary scales 9–21. Lateral line scales (Pattern C, Fig. 19*C*) extending past posterior edge of hypural plate onto caudal rays; bearing anteriorly and posteriorly directed processes on lateral scale surface (Fig. 20*B*). Dorsal and ventral caudal peduncle scales present. Supraocular cirri present; parietal cirri present or absent; other cirri absent. Head cirri lightly pigmented. Nasal tubes lightly pigmented (similar to snout). Urogenital papilla of male with spatulate basal portion; terminal appendage curved or hooklike.

Description.—General body shape shown in Figure 29. Body elongate, slender, laterally compressed posterior to opercular openings. Greatest body depth at spinous dorsal fin. Head large, as deep as wide. Eye large, about 1.5 times snout length. Mouth large; posterior edge of maxilla nearly reaching posterior rim of orbit. Supraocular ridge with 1–4 sharp, dorsally directed spines. Small spiny scales scattered among platelike scales of dorsal scale row. Similar scales on top and sides of head, including opercles. Edges of embedded portions of lateral line scales overlapping.

Coloration in preservative. Overall body color light pinkish tan, with darker splotches scattered over sides of body. Dark brown vertical bars on pectoral fins. Dark brown, somewhat oblique bars on soft-rayed dorsal fin. Spinous dorsal fin with a small dark brown or black spot near the anterior margin and a large dark brown or black spot near posterior dorsal margin. Caudal fin with vertical dark brown bars. Underside whitish.

Measurements (from 32 spec., 71.0–217.0 mm, except where indicated).—The following expressed in thousandths SL, range (mean; standard deviation): head length 311–363 (332; 11.7); lacrimal length 45–70 (60; 5.6); snouth length (25 spec.) 80–103 (92; 6.3); least interorbital width 18–32 (23; 3.6); orbit diameter 103–132 (115; 8.1); greatest body depth (30 spec.) 158–253 (181; 19.5); least caudal peduncle depth 35–47 (41; 2.8); pectoral fin base length (19 spec.) 103–120 (109; 4.5); upper jaw length 149–182 (164; 8.9).

Counts (from 32 spec., except where indicated).—Values expressed, [value for holotype, where available; taken from Pavlenko (1910)] range (mode; mean): dorsal fin spines [10] 9–10 (9; 9.2); dorsal fin soft rays [21] 20–24 (22; 22.1); anal fin rays [18] 16–20 (18; 18.6); pectoral fin rays [16] 17–19 (18; 17.9); dorsal scale row 23–32 (29; 26.4); lateral line scale row [44] 43–46 (44; 44.3); axillary scales [17] 9–21 (11; 13.5).

Remarks.—The neotype designated by Lindberg and Andriashev (1938) and deposited in IZL was unavailable for examination.

Throughout its geographic range, *Icelus cataphractus* is readily distinguishable from *I. spiniger* by the presence of one (rarely two) laterally directed lacrimal spine (Fig. 17*B*) and by the distinctive laterally directed spinules on the lateral line scales (Fig. 20*B*).

Distribution.—*Icelus cataphractus* occurs throughout the Sea of Japan to about 36°N (just north of the Korea Strait) at depths of 79–454 m. It ranges northward into the Tartar Strait and southern Sea of Okhotsk. The northernmost extent of its range is about 48°43′N (along the eastern coast of Sakhalin Island). The species also occurs off the southern and southeastern coasts of Hokkaido in depths of 82–320 m. It appears that all the records of *I. spiniger* in the Sea of Japan (e.g., Schmidt 1903, 1904; Jordan and

Starks 1904; Jordan, Tanaka, and Snyder 1913; Lindberg and Andriashev 1938; Watanabe 1960; Ueno 1972) are attributable to *I. cataphractus*. Figure 28 summarizes the distribution of this species based on material examined.

ETYMOLOGY.—The specific name, *cataphractus*, is derived from the Greek *kataphractos*, meaning mailed, and refers to the large, spiny scales of the dorsal scale row and the lateral line.

MATERIAL EXAMINED (66 spec., 71.0–217.0 mm).—Nontype-material. SEA OF JAPAN: CAS-SU 22375 (2); 36°01′30″N, 129°42′E, 128 m; 30 July 1906. CAS-SU 22304 (5); 36°17′N, 129°40′E, 123 m; 31 July 1906. CAS-SU 28695 (1); Hokkaido, Otaru; 3 Oct. 1906. CAS-SU 18650 (1); 43°01′N, 140°22′E, 315 m; 19 Sep. 1906. CAS-SU 18651 (1); 43°04′N, 140°12′E, 454 m; 19 Sep. 1906. HUMZ 56095, 56101 (2); 42°27′N, 140°19′E, 340 m; 12 June 1979. UBC BC64-14 (1); Japan, off Cape Ofuyu; 27 Oct. 1961. UMUT 31533 (1); Japan, off Matsue City; Feb. 1936. UMUT 32894, 32898 (2); Japan, Notown, Niigata Pref.; Sep. 1938. UMUT 32991 (1); Japan, near Hagi City, Yamaguchi Pref.; no date given. USNM 74569 (5); 36°18′N, 129°44′E, 223 m; 31 July 1906. USNM 74573 (7); 36°17′N, 129°41′E, 170 m; 31 July 1906. USNM 120110, 144246, 74542 (5 [total]); 43°04′20″N, 140°12′10″E, 454 m; 19 Sep. 1906. NORTH PACIFIC, SOUTH OF HOKKAIDO: CAS-SU 22363 (1); 42°02′40″N, 142°36′E, 320 m; 30 Sep. 1906. HUMZ 45503, 45504 (2); 42°32′N, 143°48′E, 87 m; 6 Sep. 1975. HUMZ 45571, 53408, 53411 (3); 42°32′N, 143°51′E, 110 m; 6 Sep. 1975. HUMZ 45651 (1); 42°53′N, 144°18.2′E, 180 m; 15 July 1975. HUMZ 45665, 45679 (2); 42°51′N, 144°35.9′E, 82 m; 16 July 1975. UBC BC59-166 (2); North Pacific, off Hokkaido; 24 May 1957. UMUT 39271 (1); Japan, Kesengun, Iwate Pref.; no date given. USNM 120111 (1); 42°02′40″N, 142°36′E, 320 m; 2 Oct. 1906. TARTAR STRAIT: BMNH 1964.4.18:14–15 (2); 48°08′30″N, 140°08′30″E, 115 m; 9 Sep. 1913. HUMZ 53153, 53160 (2); 46°48′N, 141°33′E, 370 m; 30 May 1976. HUMZ 54162 (1); 45°15′N, 143°05′E; 2 June 1976. SEA OF OKHOTSK: HUMZ 54729 (1); 44°43′N, 144°05′E, 195 m; 17 June 1976. USNM 74564 (1); 48°33′30″N, 144°59′30″E, 123 m; 27 Sep. 1906. USNM 74562 (1); 48°33′30″N, 144°56′45″E, 95 m; 27 Sep. 1906. USNM 74560 (8); 46°17′N, 143°09′E, 79 m; 25 Sep. 1906.

Icelus euryops Group

DIAGNOSIS.—Scales of dorsal row enlarged, platelike, Pattern C (Fig. 18*C*). Lateral line scales Pattern B (Fig. 19*B*). Suborbital stay spines present or absent. Parietal spines absent. Nuchal spines short (often very reduced), sharp, posteriorly directed.

Icelus rastrinoides Taranetz, in Schmidt, 1935

Icelus rastrinoides TARANETZ, in SCHMIDT, 1935:414 (orig. descr.; placed *I. rastrinoides* into subgen. *Ochotskia* with *I. armatus* and *I. canaliculatus*; key; distr.); TARANETZ 1936: 150 (descr.; N Sea of Japan and S Sea of Okhotsk; compar. with *I. scutiger*); 1937:106 (key; distr.); SCHMIDT 1950:123 (*I. rastrinoides* placed into subgen. *Ochotskia* with *I. armatus*, *I. canaliculatus*, *I. euryops*, *I. vicinalis*, and *I. perminovi*); LINDBERG 1959:252 (Sea of Japan); UENO 1972:91 (Sea of Japan).

DIAGNOSIS.—Parietal spines absent. Nuchal spines short, sharp, posteriorly directed. Laterally directed spine on suborbital stay present or absent. Lacrimal spine absent. Uppermost preopercular spine simple, curved. Two to three rows of enlarged, platelike scales (Pattern C, Fig. 18*C*) between dorsal fins and lateral line. Smaller, similar scales above these rows and scattered among these rows. Three to four rows of enlarged, platelike scales similar to scales of dorsal scale rows (Pattern C, Fig. 18*C*) between lateral line and anal fin. Axillary scales numerous, confluent with rows of scales below lateral line; 5–9 scales in uppermost row. Dorsal and ventral caudal peduncle scales present, represented by scales of dorsal and ventral scale rows. Lateral line scales Pattern B (Fig. 19*B*), extending past posterior edge of hypural plate onto caudal rays. Supraocular, parietal, nuchal cirri present; other cirri absent. Head cirri lightly pigmented (similar to dorsal surface of head). Nasal tubes lightly pigmented (similar to snout). Urogenital papilla of male with cylindrical, slightly dorsoventrally flattened basal portion and gently curved terminal appendage (Fig. 23*B*).

DESCRIPTION.—Body elongate, slender, tapering; greatest depth at spinous dorsal fin. Head large, about as deep as wide. Eye large, about 1.5 times snout length. Mouth moderately large; posterior end of maxilla reaching to below middle of orbit. Rows of enlarged, platelike scales almost completely covering sides of body above and below lateral line; smaller, similar scales scattered about dorsal scale rows. Narrow space devoid of scales just above and below lateral line. Small, spiny scales on top and sides of head, including opercles.

Coloration in preservative. Overall body color uniform light brown on dorsal surface and sides. Light tan or whitish on underside. Three faint darker brown saddles on dorsal surface: under spinous dorsal fin, under anterior portion of soft-rayed dorsal fin, and under posterior portion of soft-rayed dorsal fin. Caudal fin with a dark brown vertical bar near posterior margin. Pectoral fins dark brown; dorsal and anal fins (although dam-

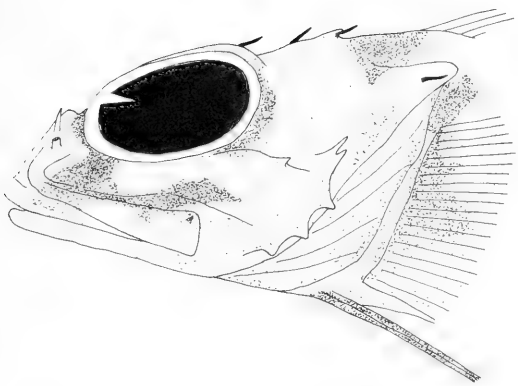


FIGURE 30. Head of *Icelus euryops* (UW 20808, male, 101.5 mm SL) showing black pigmentation of head cirri, short snout, and large eye.

aged in all specimens examined) exhibit some dark brown or black markings.

MEASUREMENTS (from 3 spec., 88.0–90.0 mm).—Values expressed as thousandths SL; ranges only are given: head length 313–330; lacrimal length 44–46; snout length 80–84; least interorbital width 21–24; orbit diameter 119–123; greatest body depth 170–183; least caudal peduncle depth 52–57; pectoral fin base length 119–134; upper jaw length 153–156.

COUNTS (from 3 spec.).—Values given, [range of values for type-specimens (from Taranetz 1936)] range of values for specimens examined: dorsal fin spines [9] 8–9; dorsal fin soft rays [21–22] 20; anal fin rays [19–20] 17–18; pectoral fin rays [18] 17–18; number of dorsal scale rows [no values] 3; number of ventral scale rows [no values] 2; number of axillary scale rows [2–3] 6–7; axillary scales, uppermost row [no values] 5–9; lateral line scales [43–44] 42–43.

REMARKS.—The type-specimens of *I. rastrinoides* are deposited in IZL and were unavailable for examination; hence, no lectotype is herein designated.

Taranetz's (1936) description leaves little room for doubt regarding the identity of the specimens I examined. Dorsal and anal fin counts are lower in my specimens, and scale row counts in the axillary region are higher, but meristic and possibly geographic variation account for these differences. In all other respects, the specimens are identical with the descriptions of the types.

DISTRIBUTION.—The three specimens I examined were taken in the Sea of Japan, off Fukui Prefecture (Fig. 25). Taranetz (1936) stated that the species ranged to 45°N in the Sea of Japan and that depths of capture ranged between 230 and 411 m. Lindberg (1959) and Ueno (1972) recorded the species from southern Sakhalin Island and the northern Sea of Japan. The UMUT specimens represent a southward range extension in the Sea of Japan. *Icelus rastrinoides* is apparently endemic to the Sea of Japan.

ETYMOLOGY.—The specific name is derived from the Latin *rastrum* (a scraper) and the Greek *eidos* (resemblance); a reference to the many rows of spiny, platelike scales.

MATERIAL EXAMINED (3 spec., 88.0–90.0 mm).—Nontype-material: UMUT 32015, 32022, 32025 (3); Japan, off Fukui Pref. (about 38°N, 136°E), no depth or capture date specified.

Icelus euryops Bean, 1890

(Figure 30)

Icelus euryops BEAN, 1890:41 (orig. descr.; type-locality Gulf of Alaska, near Trinity Is., 56°00′N, 154°20′W, 290 m, ALBATROSS sta. 2853 [LECTOTYPE, male, 59.5 mm, USNM 45367 hereby designated]); GILBERT 1895:414 (descr.; compar. with *I. vicinalis*); JORDAN AND EVERMANN 1896:437 (compiled record; erroneously referred to Bering Sea); 1898:1915 (descr. after Bean 1890); EVERMANN AND GOLDSBOROUGH 1907:300 (compiled); SCHMIDT 1927:2 (key; *I. euryops* not seen by Schmidt); JORDAN, EVERMANN, AND CLARK 1930:378 (compiled); SCHMIDT 1935:414 (key; *I. euryops* placed in subgen. *Icelus* with *I. bicornis, I. spatula, I. uncinalis,* and *I. vicinalis*); TARANETZ 1936:151 (key to spp. groups; compar. with *I. rastrinoides*); 1937:106, 108 (key); SCHMIDT 1950:123 (*I. euryops* placed in subgen. *Ochotskia* with *I. armatus, I. vicinalis, I. canaliculatus, I. rastrinoides,* and *I. perminovi*); WILIMOVSKY 1958:67 (key); QUAST AND HALL 1972:22 (list); HOWE AND RICHARDSON 1978:47, 138 (diagnostic features; lit.; key).

Icelus vicinalis GILBERT, 1895:413 (orig. descr.; type-locality Bristol Bay, Alaska, 53°33′50″N, 167°46′50″W, 200 m, ALBATROSS sta. 3324; lectotype, USNM 48737, by sub. desig. of Jordan and Evermann [1898]); JORDAN AND EVERMANN 1896:437 (Bristol Bay); 1898:1916 (descr. after Gilbert 1895); EVERMANN AND GOLDSBOROUGH 1907:300 (listed); SCHMIDT 1927:2 (in part; descr.; Sea of Okhotsk spec. later det. by Taranetz [1935] to be *I. armatus*); TARANETZ 1935:91 (*I. vicinalis* from Sea of Okhotsk referred to *I. armatus*); SCHMIDT 1935:414 (key; *I. vicinalis* placed into subgen. *Icelus*; E Bering Sea); TARANETZ 1936:151 (key; comp. with *I. rastrinoides*); 1937:106 (key; Bering Sea; Bristol Bay, Alaska); WILIMOVSKY 1958:67 (key); QUAST AND HALL 1972:23 (list).

DIAGNOSIS.—Parietal spines absent. Nuchal spines short, straight, sharp, posteriorly directed. Laterally directed spine on suborbital stay. Lacrimal spine absent. Uppermost preopercular spine bifurcated. Dorsal row of enlarged, platelike scales (Pattern C, Fig. 18*C*) between dorsal fins and lateral line. Smaller, similar scales scattered

among these scales (Fig. 31*A*); one to three rows of similar scales between dorsal scale row and lateral line. Scale rows between lateral line and anal fin absent. Axillary scales 10–27; 5–7 in uppermost row. Dorsal and ventral caudal peduncle scales present. Lateral line scales Pattern B (Fig. 19*B*); extending past posterior edge of hypural plate onto caudal rays. Supraocular, parietal, nuchal, opercular cirri present; darkly pigmented; other cirri absent. Nasal tubes lightly pigmented (similar to snout). Urogenital papilla of male cylindrical, dorsoventrally flattened, with large, curved terminal appendage (Fig. 23*C*).

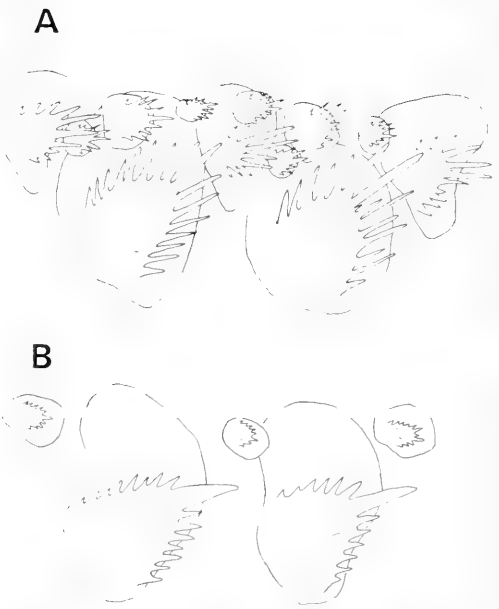


FIGURE 31. Scales of dorsal scale rows: (A) *Icelus euryops*, UW 20808, female, 115.0 mm SL; (B) *Icelus canaliculatus*, UW 20798, female, 109.0 mm SL; left lateral view.

DESCRIPTION.—General features of head shown in Figure 30. Body elongate, slender, tapering; laterally compressed posterior to opercular openings. Greatest body depth at spinous dorsal fin. Head large, depressed; wider than deep. Eye large, about twice snout length. Mouth large; posterior end of maxilla extending past middle of orbit. One to three small black papillae (not shown on Fig. 30) usually present on lateral surface of head just above upper jaw. Suborbital pores of cephalic lateral line large, conspicuous, but without smaller pores densely clustered about them (as in *I. canaliculatus*).

Coloration in preservative. Overall body color light brown, with irregularly shaped darker brown or gray saddles on dorsal body surface. Dorsal, anal, caudal fins dark brown. Pectoral and pelvic fins dark brown or black. Sides of head and opercles with irregularly shaped blotches of dark brown. Posterior portion of mouth and underside of head whitish. Branchiostegal membranes dusky brown; not black as in *I. canaliculatus*. Head cirri black. Urogenital papilla of male whitish.

MEASUREMENTS (from 34 spec., 56.0–141.0 mm, except where indicated).—The following expressed as thousandths SL, [value for lectotype] range (mean; standard deviation): head length [328] 292–354 (326; 13.7); lacrimal length (21 spec.) [35] 35–52 (44; 5.3); snout length (18 spec.) [61] 48–65 (57; 4.9); least interorbital width [25] 17–30 (22; 3.0); orbit diameter [143] 97–155 (128; 16.1); greatest body depth [168] 147–191 (168; 10.9); least caudal peduncle depth (33 spec.) [41] 41–54 (46; 6.0); pectoral fin base length (14 spec.) [lectotype damaged, no measurement taken] 104–129 (116; 7.9); upper jaw length (19 spec.) [151] 146–180 (156; 7.6).

COUNTS (from 35 spec., except where indicated).—Values given, [value for lectotype, where available] range (mode; mean): dorsal fin spines [9] 8–10 (9; 8.7); dorsal fin soft rays [23] 20–23 (22; 20.9); anal fin rays [18] 15–19 (19; 18.2); pectoral fin rays [17] 16–18 (18; 17.6); dorsal scale row (33 spec.) [38] 34–43 (39; 40.1); dorsal-lateral scales (number of enlarged, platelike scales arranged in one to three rows between dorsal scale row and lateral line) (33 spec.) [lectotype damaged] 5–51 (17; 21.3); axillary scales (29 spec.) [lectotype damaged] 10–27 (21; 19.4); lateral line scales [45] 43–45 (45; 44.5); ventral caudal peduncle scales [1] 1–3 (1; 1.5).

REMARKS.—Orbit diameter (Fig. 32) and least interorbital width measurements (Fig. 33) for type-material of *Icelus euryops* and *I. vicinalis*, as well as additional nontype-material indicate that the separation of these two species by Gilbert (1895) on the basis of these two characters is not warranted. Based on similarities in these and other characters, the two species are hereby synonymized under the first name, *Icelus euryops* Bean, 1890.

Icelus euryops is readily distinguishable from *I. canaliculatus* (with which it commonly occurs) by the presence of three pairs of black cirri on

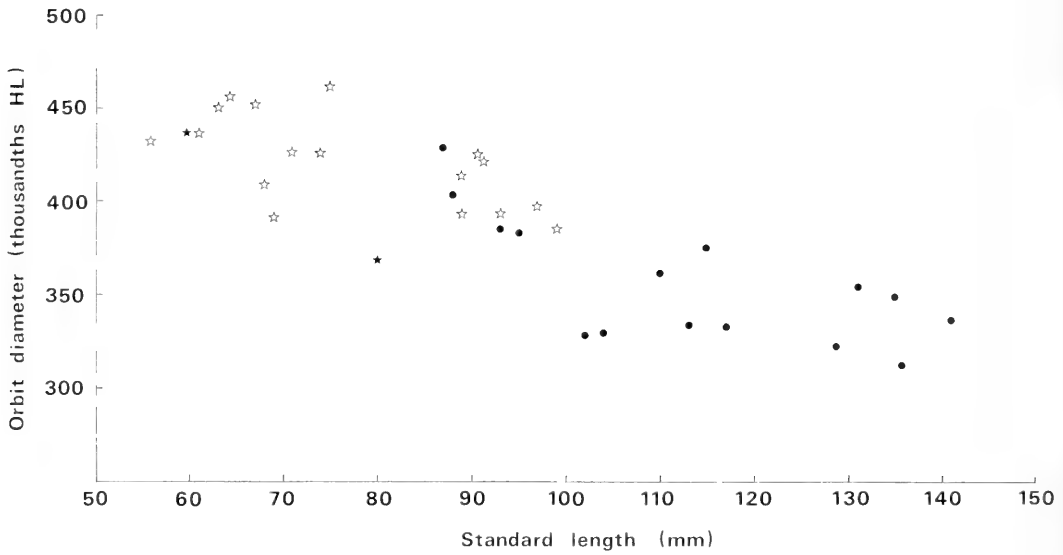


FIGURE 32. Plot of orbit diameter (thousandths of head length) versus standard length in *Icelus euryops*. *Icelus euryops* type-material (solid stars). *Icelus vicinalis* type-material (open stars). *Icelus euryops* nontype-material (solid circles).

the top of the head, rows of spiny scales between the dorsal scale row and the lateral line, and by the absence of black pigmentation on the nasal tubes.

DISTRIBUTION.—*Icelus euryops* is widespread in the eastern Bering Sea and northern Gulf of Alaska (Fig. 25). In the Bering Sea it is found between 54°–60°N and 166°–179°W, in 200–740 m. The single record in the Gulf of Alaska (type-material of *I. euryops*) is from near the Trinity Islands in 290 m.

ETYMOLOGY.—The specific name, *euryops,* is derived from the Greek *eurus,* meaning wide, and *ops,* or eye, and refers to the large eye which characterizes this species.

MATERIAL EXAMINED (49 spec., 56.0–141.0 mm).—**Lectotype** of *Icelus euryops*: USNM 54637, male, 59.5 mm; Gulf of Alaska, off Trinity Is., 56°00′N, 154°20′W, 290 m, ALBATROSS sta. 2853; 9 Aug. 1888.

Paralectotypes of *Icelus euryops*: USNM 227262 (2: one damaged [no length taken], one 80.0 mm); same data as for lectotype.

Lectotype of *Icelus vicinalis*: USNM 48737, male, 57.0 mm; Bering Sea, 54°00′45″N, 166°53′50″W, 700 m, ALBATROSS sta. 3330; 21 Aug. 1890.

Paralectotypes of *Icelus vicinalis* (all from Bering Sea): BMNH 1896.7.23:91 (2:56.0–64.5 mm); 54°01′40″N, 166°48′50″W, 640 m, ALBATROSS sta. 3331; 21 Aug. 1890. BMNH 1900.7.11: 8(1:73.0 mm); Alaska, ALBATROSS [no sta. data given]. CAS-SU 3484 (1:69.0 mm); 54°01′40″N, 166°48′50″W, 640 m, ALBATROSS sta. 3331; 21 Aug. 1890. CAS-SU 3018 (12:56.0–99.0 mm); 53°33′50″N, 167°46′50″W, 200 m, ALBATROSS sta. 3324; 20 Aug. 1890. CAS-SU 45714 (2:35.0–72.0 mm); 54°01′40″N, 166°48′50″W, 640 m, ALBATROSS sta. 3331; 21 Aug. 1890. MCZ 28344 (1:75.0 mm); 54°01′40″N, 166°48′50″W, 640 m, ALBATROSS sta. 3331; 21 Aug. 1890. USNM 53038 (1[of 2]: 74.0 mm); 54°01′40″N, 166°48′50″W, 640 m, ALBATROSS sta. 3331; 21 Aug. 1890. USNM 233758 (1); 54°00′45″N, 166°53′50″W, 700 m, ALBATROSS sta. 3330; 21 Aug. 1890. USNM 233759 (2:60.0–62.0 mm); 54°01′40″N, 166°48′50″W, 640 m, ALBATROSS sta. 3331; 21 Aug. 1890. USNM 48597 (1); 54°02′50″N, 166°45′W, 740 m, ALBATROSS sta. 3332; 21 Aug. 1890.

Nontype-material. BERING SEA: BCPM 980-18 (5); 60°59′N, 179°11′W, 290 m; 16 July 1979. CAS 49895 (3); 59°19′N, 178°06.7′W; 27 June 1979. HUMZ 84554 (1); 58°30.2′N, 175°12.4′W, 450 m; 23 June 1979. HUMZ 84834 (1); 59°37.3′N, 178°27.7′W, 470 m; 27 June 1979. UW 20844 (4); 59°19.65′N, 178°06.70′W; 28 June 1979. UW 20801 (5); 60°59′N, 179°11′W, 290 m; 16 July 1979. UW 20808 (7); 60°20′N, 179°50′W, 340 m; 29 July 1980.

Icelus canaliculatus Gilbert, 1895

(Figure 34)

Icelus canaliculatus GILBERT, 1895:412, pl. 24 (orig. descr.; type-locality Bering Sea, N of Unalaska I., 53°56′50″N, 167°08′15″W, 730 m, ALBATROSS sta. 3329; [LECTOTYPE: male, damaged (no length taken), CAS-SU 2182 hereby designated]); JORDAN AND EVERMANN 1896:438 (list); 1898:1917, fig. 694 (descr. after Gilbert 1895); EVERMANN AND GOLDSBOROUGH 1907:301, fig. 53 (compiled); SCHMIDT 1927:2 (key to *Icelus* spp.); JORDAN, EVERMANN, AND CLARK 1930:378 (compiled distr.); SCHMIDT 1935:414 (*I. canaliculatus* placed in subgen. *Ochotskia* with *I. armatus* and *I.*

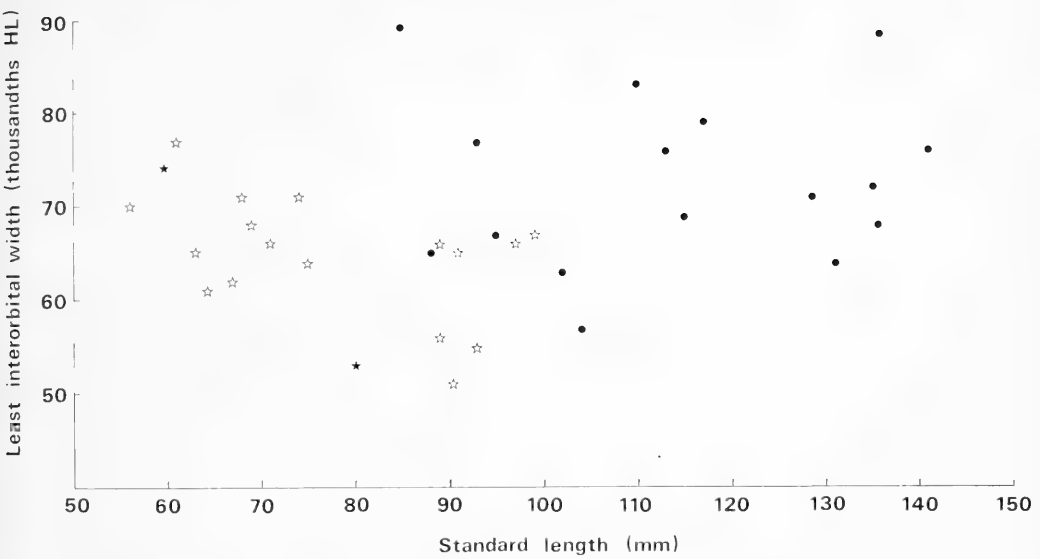


FIGURE 33. Plot of least interorbital width (thousandths of head length) versus standard length in *Icelus euryops*. *Icelus euryops* type-material (solid stars). *Icelus vicinalis* type-material (open stars). *Icelus euryops* nontype-material (solid circles).

rastrinoides; key); TARANETZ 1936:151 (key; comp. with *I. rastrinoides*); 1937:106, 108 (key; compiled distr.); SCHMIDT 1950:124 (descr. of a 92 mm [total length] male from Sea of Okhotsk, 525 m); WILIMOVSKY 1958:66 (key); SHUNTOV 1965:1681 (depth distr. in Sea of Okhotsk 250–800 m, most common at 800 m); QUAST AND HALL 1972:22 (list); HOWE AND RICHARDSON 1978:47, 138 (diag. feat.; depth distr.; key).

DIAGNOSIS.—Parietal spines absent. Nuchal spines short, straight, sharp, posteriorly directed. Laterally directed spine on suborbital stay. Lacrimal spine absent. Uppermost preopercular spine simple, bifurcated or trifurcated. Dorsal row of enlarged, platelike scales (Pattern C, Fig. 18*C*) between dorsal fins and lateral line, with smaller, similar scales interspersed (Fig. 31*B*). Rows of scales between dorsal scale row and lateral line absent. Row of small, spiny scales between lateral line and anal fin, just above anal fin base, present or absent. Axillary scales 14–39. Dorsal and ventral caudal peduncle scales present. Lateral line scales Pattern B (Fig. 19*B*); extending past posterior edge of hypural plate onto caudal rays. Supraocular, parietal, opercular, maxillary cirri present; darkly pigmented; other cirri absent. Nasal tubes black. Urogenital papilla of male with darkly pigmented, cylindrical basal portion; terminal appendage large, curved (Fig. 23*D*).

DESCRIPTION.—General body shape shown in Figure 34. Body elongate, slender, tapering; laterally compressed posterior to opercular openings; greatest depth at spinous dorsal fin. Head large, depressed; wider than deep. Eye moderately large; about 1.5 times snout length. Mouth large; posterior end of maxilla reaching middle of orbit. Top and sides of head sparsely scaled. Suborbital cephalic lateral line pores large; smaller pores thickly clustered about these large pores.

Coloration in preservative. Overall body color light yellowish brown. Irregularly shaped darker brown saddles on dorsal body surface. Suborbital region and mouth region with irregularly shaped darker brown blotches. Dorsal, anal, caudal, pectoral, and pelvic fins dark brown to almost black. Opercles dark brown; branchiostegal membrane black. Nasal tubes black. Urogenital papilla of male with dark brown basal portion; terminal appendage whitish (Fig. 23*D*).

MEASUREMENTS (from 48 spec., 45.0–137.0 mm, except where indicated).—The following expressed as thousandths SL, [value for BMNH paralectotype] range (mean; standard deviation): head length [331] 305–351 (326; 11.8); lacrimal length [46] 38–60 (50; 6.1); snout length (24 spec.) [67] 67–100 (84; 7.1); least interorbital width [28] 21–35 (28; 3.1); orbit diameter [140] 108–140 (121; 8.8); greatest body depth (44 spec.) [169] 149–185 (167; 9.0); least caudal peduncle

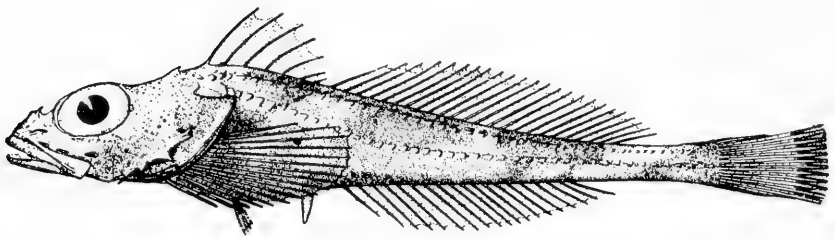


FIGURE 34. *Icelus canaliculatus* Gilbert, 1895, male, approximately 94.0 mm TL; after Gilbert (1895).

depth [46] 34–50 (45; 3.7); pectoral fin base length (41 spec.) [116] 98–125 (113; 6.9); upper jaw length (24 spec.) [158] 137–158 (146; 5.1).

COUNTS (from 47 spec., except where indicated).—Values expressed, [range of values for type-specimens (from Gilbert 1895)] range (mode; mean): dorsal fin spines [7–8] 7–8 (8; 8.0); dorsal fin soft rays [23–24] 22–25 (23; 23.2); anal fin rays [19] 18–20 (19; 19.2); pectoral fin rays [16] 15–19 (17; 16.7); scales in dorsal scale row (46 spec.) [45] 35–45 (38; 38.5); scales in anal scale row (46 spec.) [2–3] 0–10 (0; 3.2); axillary scales [20–26] 14–39 (26; 27.4); lateral line scales (46 spec.) [43–46] 43–46 (44; 44.2).

DISTRIBUTION.—*Icelus canaliculatus* occurs over a large portion of the Bering Sea between 53°–60°N and 157°–179°W, in depths of 20 (ALBATROSS sta. 3232) to 730 m (Fig. 25). The species is most commonly collected in 200–600 m, where it is often taken with *I. euryops*. I did not examine the specimen Schmidt (1950) recorded from the Sea of Okhotsk at a depth of 525 m. His description of meristic, morphometric, and most morphological characters (especially coloration) of the specimen fits the diagnosis of *I. canaliculatus* quite well. However, he makes no mention of black pigmentation on the nasal tubes, a character perhaps subject to geographic variation, but present in all Bering Sea *I. canaliculatus* I examined. Shuntov (1965) examined several Sea of Okhotsk specimens and recorded the most commonly inhabited depth as near 800 m. I have not examined these specimens.

ETYMOLOGY.—The specific name, *canaliculatus*, of Latin derivation, refers to the many small canals associated with the larger canals of the cephalic lateral line.

MATERIAL EXAMINED (104 spec., 44.5–137.0 mm).—**Lectotype:** CAS-SU 2182, male, damaged (no length taken); Bering Sea, N of Unalaska I., 53°56′50″N, 167°08′15″W, 730 m, ALBATROSS sta. 3329; 21 Aug. 1890.

Paralectotypes: BMNH 1896.7.23:80 (1:45.0 mm); same data as for lectotype. CAS-SU 68828 (3: damaged [no lengths taken]); same data as for lectotype.

Nontype-material. BERING SEA: BCPM 980-23 (5); 60°14′N, 178°46′W, 322 m; 18 July 1979. BCPM 980-25 (3); 59°23′N, 177°54′W, 436 m; 19 July 1979. CAS-SU 3720 (1); 58°31′30″N, 157°34′15″W, 20 m; 2 June 1890. CAS 45672 (1); 58°32′N, 176°06.3′W; 24 June 1979. CAS 45680 (7 [3 removed to *Icelus euryops*]); 59°19′N, 178°06.7′W, 24 June 1979. CAS 45691 (1); 59°52′N, 178°51′W, 26 June 1979. HUMZ 84551, 84552, 84556 (3); 58°30.2′N, 175°12.4′W, 460 m; 23 June 1979. HUMZ 84630, 84631 (2); 59°19.6′N, 178°06.7′W, 610 m; 28 June 1979. UW 20840 (1); 58°32.04′N, 176°06.35′W, 497–539 m; 25 June 1979. UW 20841 (2); 59°53.83′N, 178°57.12′W, 564–580 m; 27 June 1979. UW 20843 (63 [4 removed to *I. euryops*]); 59°19.65′N, 178°06.70′W, 603–610 m; 28 June 1979. UW 20798, 20799 (9 [total]); 60°15′N, 178°52′W, 455 m; 18 July 1979. UW 20800 (1); 55°59′N, 170°02′W, 225 m; 29 Nov. 1979. UW 20806 (4); 59°22′N, 177°46′W, 465 m; 28 July 1980.

Icelus perminovi Taranetz, 1936

Icelus perminovi TARANETZ, 1936:151 (orig. descr.; type-locality Sea of Okhotsk, 56°12′N, 143°49′E, no depth specified; a single specimen, female, 85.0 mm total length); 1937:107, 108 (key); SCHMIDT 1950:125 (not seen by Schmidt; distr. from Taranetz [1936]); SHUNTOV 1965:1680 (depth distr. in Sea of Okhotsk 250–450 m; most common at 300 m).

DIAGNOSIS.—Parietal spines absent. Nuchal spines very reduced, short, sharp. Laterally directed spine on suborbital stay absent. Lacrimal spine absent. Uppermost preopercular spine simple or bifurcated. Dorsal row of enlarged, platelike scales (Pattern C, Fig. 18*C*) between dorsal fins and lateral line, with smaller, similar scales interspersed. Rows of scales between dorsal scale row and lateral line absent. One small, spiny scale just dorsal to anterior part of anal fin base. Axillary scales 53; 7 in uppermost row. Dorsal and ventral caudal peduncle scales present. Lateral line scales Pattern B (Fig. 19*B*); extending past posterior edge of hypural plate onto caudal rays. Supraocular, parietal, nuchal, opercular, and suborbital stay cirri present; darkly pigmented; other cirri absent. Nasal tubes black. Shape, size, and coloration of urogenital papilla of male unknown.

DESCRIPTION.—General body shape elongate,

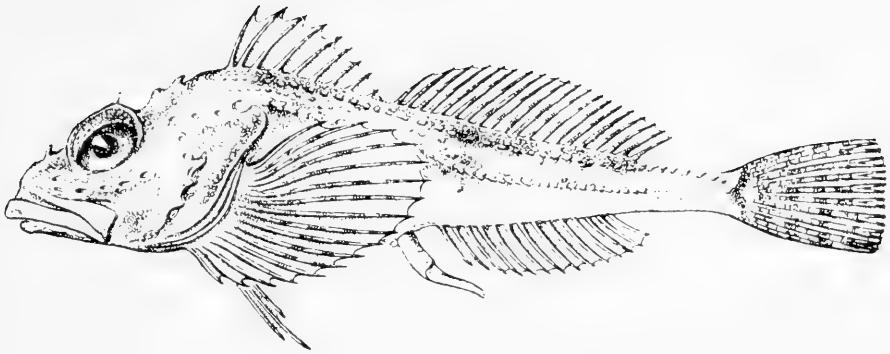


FIGURE 35. *Icelus bicornis* (Reinhardt, 1840), male, 61.0 mm TL; after Andriashev (1954).

slender, tapering; somewhat more robust than *I. canaliculatus*; greatest depth at anterior part of spinous dorsal fin. Head large, depressed; wider than deep. Eye 1.5 times snout length. Mouth large; posterior end of maxilla reaching middle of orbit. Head densely scaled (compared with *I. canaliculatus*). Suborbital cephalic lateral line pores large; smaller pores scattered about these pores (but not as densely clustered as in *I. canaliculatus*).

Coloration in preservative. Overall color moderately dark yellowish brown. Five dark brown saddles on back and sides: under anterior part of spinous dorsal fin, under posterior part of spinous dorsal fin, two near posterior part of soft-rayed dorsal fin, and on posterior part of caudal peduncle. Top and sides of head dark brown. Underside of head and branchiostegal membranes with dark brown mottling; not uniformly dark brown or black as in *I. canaliculatus*. Nasal tubes black. Black markings on dorsal, anal, and caudal fins (especially on edges). Dark brown bars on pectoral fins. Pelvic fins brown with some black markings.

MEASUREMENTS (from 1 spec., 114.0 mm).—The following expressed as thousandths SL: head length 325; lacrimal length 54; snout length 79; least interorbital width 24; orbit diameter 111; greatest body depth 186; least caudal peduncle depth 53; upper jaw length 149.

COUNTS (from 1 spec.).—Values expressed, [value for holotype (from Taranetz 1936); where available] value for specimen examined: dorsal fin spines [8] 8; dorsal fin soft rays [23] 22; anal fin rays [19–20] 19; pectoral fin rays [17–18] 17; scales in dorsal scale row 41; scales in anal scale row 1; axillary scales 53; axillary scales, uppermost row 7; lateral line scales 44.

REMARKS.—This species closely resembles *Icelus canaliculatus*, from which it is distinguished by the absence of suborbital stay spines, by the very weakly developed nuchal spines, and by the lighter overall coloration (especially the lighter coloration of the underside of the head and the branchiostegal membranes).

DISTRIBUTION.—*Icelus perminovi* occurs in the Sea of Okhotsk in depths of 250–450 m (Taranetz 1936; Shuntov 1965). It co-occurs with *I. canaliculatus*, but is generally found in shallower depths (Shuntov 1965).

MATERIAL EXAMINED (1 spec., female, 114.0 mm).—Non-type-material: IZL 39206 (1); N Kurile Is., RT ADLER; 23 July 1967.

Icelus bicornis Group

DIAGNOSIS.—Scales of dorsal row enlarged, platelike, Pattern B (Fig. 18*B*): lateral line scales Pattern A (Fig. 19*A*); suborbital stay spines absent; parietal spines present or absent; nuchal spines variously developed (see species descriptions below).

Icelus bicornis (Reinhardt, 1840)

(Figure 35)

Cottus bicornis REINHARDT, 1840a:9 (orig. descr.; type-locality East Greenland; compar. with *Cottus uncinatus*); 1840b:75 (second publication of orig. descr.); 1841:226 (third publication of orig. descr.).

Icelus hamatus KRØYER, 1845:253, 261 (orig. descr.; type-locality Bell Sound, Spitzbergen, 18 m; [LECTOTYPE, female, 43.0 mm, ZMUC P81.1869, hereby designated]); GÜNTHER 1860: 172 (descr.; distr.; confusingly, Günther cited Greenland and Spitzbergen for *Icelus*, in which he included only *I. hamatus*, but he gave only Spitzbergen for *I. hamatus*); MALMGREN 1864:507 (descr.; Spitzbergen; compar. with Greenland spec.); ESMARK 1868:518 (descr.; Finland); COLLETT 1874:35 (descr.; distr.); LÜTKEN 1876:380 (descr.; distr.); GÜNTHER 1877:293 (in part; distr. extended to Arctic

Canada; common betw. 78° and 82°N); COLLETT 1879:14 (descr.; distr.); BEAN 1879:128 (in part; confirmation of Günther's [1877] range extension); COLLETT 1880:34, pl. I, fig. 8 (in part; descr.; E and W Greenland, Jan Mayen, Spitzbergen, Bohuslan; fig. of *I. hamatus*; synon.); JORDAN AND GILBERT 1882:691 (in part; descr.; Arctic seas, Alaska to Spitzbergen); COLLETT 1884:56 (descr.; distr.); LILLJEBORG 1884: 164 (descr.; Sweden); STORM 1884:8 (descr.; distr.); DRESEL 1884:252 (in part; excellent descr. of *Icelus spatula,* which at this time was not differentiated from *I. bicornis* [=*I. hamatus*]; measurements; Davis Str., Arctic Canada); STEINDACHNER 1886:105 (descr.; meristic char.; Jan Mayen); LÜTKEN 1887:9 (in part; descr.; range extended to Kara Sea); GÜNTHER 1887:63 (in part; distr.; synon.); LÜTKEN 1898:36 (in part; SW Greenland and N Iceland); COLLETT 1905:88 (distr., length to 103 mm); LE DANOIS 1914:5, figs. 1, 2, 5, pl. I, figs. 3, 4 (in part; descr.; distr., synon.); BERTELSEN 1937:48 (Uttental Sound, NE Greenland; misspelling of specific name [*I. haematus*]).

Centridermichthys bicornis: GÜNTHER, 1860:172 (in part; *Cottus bicornis* placed into *Centridermichthys*; descr.; Greenland; synon.); PIETSCHMANN 1932:36, fig. 15 (in part; spec. from W Greenland partly *I. spatula* based on lateral line scale counts).

Icelus bicornis: GILL, 1861:42 (lists *Cottus bicornis* and *C. uncinatus* in *Icelus*); JORDAN AND GILBERT 1882:693 (in part; species recognized, questionably, along with *I. hamatus*; descr.; Greenland; synon.); GILBERT 1895:411 (in part; recorded incorrectly from Bristol Bay, Alaska; these spec. are *I. spatula*); GOODE AND BEAN 1896:267 (in part; compiled descr., distr., synon.); JORDAN AND EVERMANN 1896:437 (in part; compiled; circumpolar in Arctic seas); KNIPOVICH 1897: 144 (White Sea; rare); JORDAN AND EVERMANN 1898:1911 (in part; compiled descr., synon.; Arctic seas, circumpolar ". . . if all specimens named *bicornis* and *hamatus* belong to one species, which is doubtful."); KNIPOVICH 1901:62 (Spitzbergen; meristic char.); 1903:146 (Spitzbergen; ecol.); JENSEN 1904:245, pl. XI, fig. 5 (in part; descr.; meristic char. of E Greenland specs.; argued against Lütken's [1876] synon.; reestablished priority of Reinhardt's nomenclature based on spec. [non-type] identified by Reinhardt as *Cottus bicornis*; Greenland to Kara Sea); KNIPOVICH 1907:29 (in part; descr.; distr. in Russian Arctic seas); EVERMANN AND GOLDSBOROUGH 1907:300 (in part; recognized, incorrectly, from Chignik and Alitak bays, Kodiak, Alaska; these specs. are *I. spatula*); KOEFOED 1907:485, 487 (descr.; Spitzbergen); JENSEN 1910: 8 (descr. of awl-shaped urogenital papilla of male; distr. extended to Arctic Canada); KENDALL 1911:508 (in part; collection of juvs.; Labrador, 5 fm, rocky bottom); JOHANSEN 1912:654, pl. XLV, fig. 8 (in part; descr.; meristic var.; bathymetric distr. of life history stages; NE Greenland); HALKETT 1913:99 (in part; Arctic Canada); HOFSTEN 1919:17, fig. 4 (ecol.; bibliog.); THIELEMANN 1921:199 (descr.; temp. regime; Barents Sea); SOLDATOV 1923:29 (descr.; E Barents Sea; although Knipovich [1926] cited this paper as containing the orig. descr. of subsp. *I. bicornis derjugini,* Soldatov never mentioned this subsp.); POPOV 1923:39 (S coast of Novaya Zemlya, 6–78 m); KNIPOVICH 1926:123, fig. 86 (descr.; distr.); SAEMUNDSSON 1926:108, fig. 73 (descr.; Iceland; not found along S Iceland); SCHMIDT 1927:2, 6 (in part; descr. of subspp. based on morphol. of urogenital papillae of males; distr.); RASS 1929:12 (*I. bicornis derjugini* compared with other subspp.); JORDAN, EVERMANN, AND CLARK 1930:378 (in part; distr.); ESIPOV 1931:157 (Franz Josef Land; meristic char.); 1933:172 (common in Kara Sea); POPOV 1933:158 (in part; *I. bicornis* and an undescr. sp. of *Icelus* off Taimyr Pen., Laptev Sea); VLADYKOV 1933:14 (in part; descr.; size of females; Hudson Bay); SCHMIDT 1935:413 (in part; key; subgen. *Icelus* containing *I. bicornis, I. spatula, I. uncinalis, I. euryops, I. vicinalis,* and *I. canaliculatus*); EHRENBAUM 1936: 182, fig. 162 (in part; descr.; distr.); TARANETZ 1936:151 (in part; key); ANDRIASHEV 1937a:254 (descr.; *I. spatula* co-occurring with *I. bicornis* from Arctic Alaska to Greenland; compar. with *I. spatula* and *I. uncinalis*); PFAFF 1937:12 (in part; Chesterfield Inlet, NW Greenland); JOUBIN 1938:18 (in part; generic and specific diag.; figs. of male and female; distr.; synon.); BRISKINA 1939:878 (diet; Russian Arctic seas); HILDEBRAND 1939:8 (in part; Greenland); ESIPOV 1939:878 (in part; Spitzbergen, Kara Sea); 1940:140 (Laptev Sea); RASS 1949:10 (eggs, larvae); JENSEN AND VOLSOE 1949:10, 18; figs. 1, 2, 5, 6, 10a, 11; maps 1, 2 (descr.; synon.; distr.; aids to ident.; anatomy of urogenital organs); SAEMUNDSSON 1949: 12 (in part; descr.; distr.); SCHMIDT 1950:122 (subgen. *Icelus* redefined to include only *I. bicornis, I. spatula,* and *I. uncinalis*); DUNBAR AND HILDEBRAND 1952:119 (aids to ident.; Ungava Bay, Canada); WALTERS 1953:6 (descr.; meristic char.; Ellesmere I.); ANDRIASHEV 1954:388, fig. 202 (descr.; synon.; compar. with *I. spatula*; distr.; ecol.; life history); WALTERS 1955:314, 337 (zoogeogr.); BACKUS 1957:309, table 28 (*I. bicornis* from Labrador referred to *I. spatula spatula*; Kendall's [1911] descr. of *I. bicornis* also referred to *I. spatula spatula*; meristic char.; distr.); MCALLISTER 1960:15 (Arctic Canada); ROLLEFSEN 1960:57, pl. 133 (descr.; complementary iconography; Atlantic); MCALLISTER 1962:30 (descr.; meristic char.; Herschel I., Canada); HOGNESTAD 1962:32 (ecol.; depth distr.; Spitzbergen); MCALLISTER 1963:53, table 2 (descr.; aids to ident. of Canadian spp. of *Icelus*; distr.); LEIM AND SCOTT 1966:351 (descr.; fig.; distr.); QUAST AND HALL 1972:22 (in part; Alaska, E of Pt. Barrow in Beaufort Sea; Bristol Bay incorrectly listed); HOWE AND RICHARDSON 1978:46 (distr. notes; lit.); RICHARDSON 1981:109, fig. 3C (*Icelus* placed with *Icelinus, Paricelinus, Chitonotus,* and *Triglops* based on larval char.; Ehrenbaum's [1905] fig. of 25-mm larval *Centridermichthys hamatus* reproduced).

Icelus furciger MALM, 1865:410 (orig. descr.; type-locality Bohuslan, S Sweden; specific difference in presence of row of scales just above anal fin).

Centridermichthys hamatus: FRIES, EKSTRÖM, AND SUNDEVALL, 1893–1895:165, fig. 50 (descr.; synon.; E Greenland E to Kara Sea); EHRENBAUM 1901:79 (descr.; meristic char.; synon.; Spitzbergen); 1905:63, fig. 26 (larva of *C. hamatus* descr. and fig.; this larva seems unusually large [25 mm] considering its undeveloped state; it possibly is not *I. bicornis*).

Icelus bicornis derjugini SOLDATOV, in KNIPOVICH, 1926:124 (orig. descr. [Knipovich attributed the descr. to Soldatov]; no type-specimens designated, type-locality White Sea; distr.); DERJUGIN 1928:343 (descr.; distr.; temp. regime); ANDRIASHEV 1937a:253 (White Sea); 1954:388, 391 (indicates Knipovich [1926] as orig. describer of subsp.; synon.).

Icelus bicornis spitzbergensis SCHMIDT 1927:7 (orig. descr.; no type-specimens designated; type-locality should be Spitzbergen; subsp. diff. in shape of male urogenital papilla and presence of a row of scales between dorsal scale row and lateral line); ANDRIASHEV 1937b:18 (synon.; Spitzbergen); 1954:389 (comp. notes on subspp.; distr.; synon.).

Icelus bicornis furciger NYBELIN, 1941:221 (descr.; meristic char.; *Icelus furciger* Malm, 1865 reduced to subsp. status; synon.;

coasts of Sweden and Norway); JENSEN AND VOLSOE 1949: 10, 13 (discussion of confluence of distr. of *I. bicornis spitzbergensis* and *I. bicornis furciger*; synon.); ANDRIASHEV 1954: 389 (comp. notes on *I. bicornis* subspp.; sw Sweden and coasts of Norway).

DIAGNOSIS.—Parietal spines short, blunt. Nuchal spines blunt or pointed. Spines on suborbital stay absent. Lacrimal spines absent. Platelike scales of dorsal scale row Pattern B (Fig. 18*B*). One or more rows of small, spiny scales between dorsal scale row and lateral line present or absent. Row of small, spiny scales between lateral line and anal fin (just above anal fin base) present or absent. Axillary scales 9–30; 3–9 in uppermost row. Dorsal and ventral caudal peduncle scales present (occasionally absent). Lateral line scales Pattern A (Fig. 19*A*); generally interrupted posteriorly, not extending onto caudal peduncle. Supraocular cirri present. Parietal, opercular, suborbital stay cirri present or absent. Cirri lightly pigmented (similar to dorsal surface of head). Nasal tubes lightly pigmented (similar to snout). Urogenital papilla of male with cylindrical basal portion and long, tapering terminal appendage (Fig. 23*H*).

DESCRIPTION.—General body shape shown in Figure 35. Body elongate, laterally compressed posterior to opercular openings; depth greatest at anterior portion of spinous dorsal fin. Head large; profile (from snout to occipital region) steeper than in *I. spatula*. Eye large, about 1.5 to 2 times snout length. Mouth large; posterior end of maxilla reaching posterior rim of orbit. Supraocular ridge generally much more prominent than in *I. spatula*. Interorbital space narrow, shallowly concave. Deep, roughly diamond-shaped depression, bounded by supraocular ridges anteriorly and by parietal ridges posterolaterally, in posterior dorsal surface of head (occipital pit of Gilbert 1895). Parietal and nuchal spines well developed: the former short and blunt, the latter large and either blunt or pointed (seldom sharply pointed as usual in *I. spatula* from Arctic Canada). Small, spiny scales on top and sides of head, including opercles. Head much more densely scaled than in *I. spatula*.

Coloration in preservative. Overall body color light brown, with whitish underside. Irregularly spaced darker brown, greenish-brown or black splotches on dorsal surface, sides, and unpaired fins. Dark spot on base of pectoral fin. Dark vertical bars on caudal fin. Dark, almost vertical bar on side of head through eye (not shown in Fig.

TABLE 4. GEOGRAPHIC VARIATION IN SELECTED MEASUREMENTS FOR *ICELUS BICORNIS*. Class intervals of values in thousandths of standard length. CAN = Arctic Canada and Labrador; EGR = eastern Greenland, Denmark Strait, and Faeroe Islands; SPZ = Spitzbergen; BKS = Barents and Kara seas.

		Head length									Greatest body depth								Upper jaw length					
Growth stage	Locality	300–319	320–339	340–359	360–379	380–399	400–419	420–439	440–459	$\bar{x}$	180–199	200–219	220–239	240–259	260–279	280–299	300–319	$\bar{x}$	120–139	140–159	160–179	180–199	200–219	$\bar{x}$
Young (23.0–50.0 mm SL)	CAN	3	6	7	10	7	3	–	2	366	–	2	13	10	8	4	1	252	–	4	4	–	1	163
	EGR	–	–	–	–	2	–	–	–	394	–	1	–	1	–	–	–	235	–	–	–	2	–	192
	SPZ	–	–	1	2	2	–	–	–	376	–	–	2	3	–	–	–	240	1	2	2	–	–	152
	BKS	–	–	2	3	–	–	–	–	361	–	4	–	–	–	–	–	204	–	–	1	3	–	180
Adult (>50.0 mm SL)	CAN	–	–	3	6	3	–	–	–	372	–	1	6	4	–	–	–	240	–	–	3	9	4	190
	EGR	–	–	–	1	–	–	–	–	377	–	–	1	–	–	–	–	236	–	–	1	–	–	179
	SPZ	1	–	1	2	1	–	–	–	359	1	–	–	3	1	–	–	241	1	1	1	2	–	162
	BKS	–	–	1	5	3	–	–	–	375	–	2	3	3	–	1	–	236	–	–	1	6	1	189

TABLE 5. GEOGRAPHIC VARIATION IN SELECTED COUNTS FOR *ICELUS BICORNIS*. CAN = Arctic Canada and Labrador; EGR = eastern Greenland, Denmark Strait, and Faeroe Islands; SPZ = Spitzbergen; BKS = Barents and Kara seas. (C.P. scales = caudal peduncle scales)

	Dorsal fin spines				Dorsal fin soft rays					Anal fin rays						Pectoral fin rays				Axillary scales (upper row)							
Locality	8	9	10	$\bar{x}$	18	19	20	21	$\bar{x}$	12	13	14	15	16	$\bar{x}$	16	17	18	$\bar{x}$	3	4	5	6	7	8	9	$\bar{x}$
CAN	6	39	1	8.9	2	21	13	7	19.6	—	5	15	20	4	14.5	3	34	8	17.1	2	2	5	9	9	4	1	6.2
EGR	2	6	—	8.8	2	1	4	—	19.3	1	1	2	4	—	14.1	2	5	1	16.9	—	1	4	2	2	—	—	5.7
SPZ	3	5	1	8.8	3	—	3	2	19.5	—	1	3	4	—	14.4	3	4	1	16.8	—	1	2	4	3	—	—	5.5
BKS	4	7	1	8.8	—	4	7	1	19.8	—	—	5	7	—	14.6	—	10	1	17.1	—	—	2	3	5	2	2	7.0

	Axillary scales (L)																									
Locality	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	$\bar{x}$
CAN	1	2	4	3	6	3	6	3	3	1	3	1	1	—	1	—	—	—	—	—	—	—	—	13.7
EGR	—	—	—	—	1	—	1	4	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	15.4
SPZ	—	1	—	—	—	—	1	1	1	2	1	1	1	—	1	—	—	—	—	—	—	—	—	16.7
BKS	—	—	—	—	—	1	—	2	1	1	1	—	3	2	—	1	4	—	—	1	—	—	1	20.7

	Lateral line scales (L)[1]														C.P. scales (dorsal)					C.P. scales (ventral)					
Locality	31	32	33	34	35	36	37	38	39	40	41	42	43	$\bar{x}$	0	1	2	3	$\bar{x}$	0	1	2	3	4	$\bar{x}$
CAN	—	—	—	1	1	4	1	1	3	—	1	—	1	37.6	6	42	2	—	0.9	14	26	6	2	1	0.9
EGR	—	—	—	—	—	1	—	—	—	—	—	—	—	36.0	—	2	4	3	2.1	4	—	3	1	1	1.4
SPZ	1	—	—	—	—	1	—	1	1	1	—	—	—	36.8	—	9	—	—	1.0	3	3	1	2	—	1.2
BKS	1	1	1	—	1	2	2	—	—	—	—	—	—	34.6	—	11	3	—	1.2	1	8	5	—	—	1.3

[1] Growth stage: Adult (>50.0 mm standard length).

35). Excellent descriptions of coloration in *I. bicornis* in specific geographic regions have been presented by Collett (1880) [Jan Mayen, Spitzbergen], Jensen (1904) and Johansen (1912) [Greenland], Joubin (1938) [North Atlantic], Andriashev (1954) [northern seas of U.S.S.R.], and Leim and Scott (1966) [Arctic Canada and Labrador].

MEASUREMENTS (from 77 spec., 25.0–91.0 mm, except where indicated).—The following expressed as thousandths SL; ranges only given; variations (ontogenetic and geographic) in selected measurements are presented in Table 4: head length 300–452; lacrimal length (73 spec.) 42–75; snout length (21 spec.) 54–107; least interorbital width (76 spec.) 16–48; orbit diameter 101–157; greatest body depth (72 spec.) 194–307; least caudal peduncle depth (60 spec.) 41–70; pectoral fin base length (48 spec.) 108–165; upper jaw length (25 spec.) 122–206.

COUNTS (from 75 spec., except where indicated).—Ranges only are presented; variations (ontogenetic and geographic) for selected counts are presented in Tables 5 and 6: dorsal fin spines 8–10; dorsal fin soft rays (70 spec.) 18–21; anal fin rays (71 spec.) 12–16; pectoral fin rays (73 spec.) 16–18; scales in dorsal scale row (72 spec.) 27–41; axillary scales (78 spec.) 9–30; axillary scales, uppermost row (44 spec.) 3–9; scales in anal scale row (59 spec.) 0–20; dorsal caudal peduncle scales 0–3; ventral caudal peduncle scales 0–4; lateral line scales (67 spec.) 24–43.

REMARKS.—For a large part of its taxonomic history, *Icelus bicornis* (and its several synonyms) was not distinguished from *I. spatula*. Jordan and Evermann (1898) seem to have been the first to question whether the names *I. bicornis* and *I. hamatus* were attributed to more than one species. Jensen and Volsoe (1949), Andriashev (1954), and McAllister (1963) provided aids to identification that adequately distinguish *I. bicornis* and *I. spatula* where they co-occur.

Throughout its geographic range (see distributional comments below) *I. bicornis* displays much less geographic variation than does *I. spatula*. The number of scales in the lateral line is greatly (but not exclusively) dependent on body size. Andriashev (1954) noted that specimens from the White Sea generally have more lateral line scales than the Greenland specimens; but, I found the number of lateral line scales to be less in specimens from the Barents, White, Kara, and Laptev seas than in specimens from other areas (Table 5). The few specimens I examined from

TABLE 6. GEOGRAPHIC AND ONTOGENETIC VARIATION IN NUMBER OF SCALES IN THE DORSAL SCALE ROW IN *ICELUS BICORNIS*. CAN = Arctic Canada and Labrador; EGR = eastern Greenland, Denmark Strait, and Faeroe Islands; SPZ = Spitzbergen; BKS = Barents and Kara seas.

		Dorsal scale row (L)															
Growth stage	Locality	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	$\bar{x}$
Young	CAN	1	—	3	2	5	5	2	1	9	2	—	—	1	—	1	33.0
(23.0–50.0	EGR	—	—	—	3	1	1	—	—	—	—	—	—	—	—	—	30.6
mm SL)	SPZ	—	—	—	1	—	—	—	1	—	1	—	1	—	—	—	34.5
	BKS	—	1	—	1	—	—	—	1	—	—	—	—	1	—	—	32.8
Adult	CAN	—	1	1	1	4	1	3	1	1	—	—	—	—	—	—	31.6
(>50.0 mm SL)	EGR	—	—	—	1	—	1	1	—	—	—	—	—	—	—	—	31.7
	SPZ	—	1	—	1	—	—	—	2	—	—	—	1	—	—	—	32.8
	BKS	—	1	1	1	1	1	1	2	—	—	—	—	—	—	—	31.4

near the Faeroe Islands (about 65°N, 11°W) had fin ray counts at the lower range of variation observed in the species (12–14 anal rays, 18 dorsal soft rays) and caudal peduncle scale counts near the upper limit of variation (1–3 dorsal, 2–4 ventral). Coloration of Faeroe Island specimens is also somewhat unusual for the species: light yellowish tan with many large olive-drab splotches over the dorsal surface and sides of the body.

The presence of scale rows between the dorsal scale row and the lateral line, and of a scale row just dorsal to the anal fin base occur in specimens from throughout the geographic range of *Icelus bicornis*. An anal scale row is uncommon in specimens from all geographic areas examined except around the Faeroe Islands, where the specimens had 6, 18, 20 (left-side counts) scales. McAllister (1963) noted the presence of an anal scale row ("scale above anal origin") in 17 of 39 Arctic Canada specimens. Based on the present study, however, this frequency appears to be rather high. Malm (1865) described *I. furciger* from southern Sweden based on the presence of these scale rows, but Nybelin (1941) suggested subspecific status for Malm's species based on similar characters. Neither of these taxa can be supported by the present study. *Icelus bicornis furciger* is therefore placed in the synonymy of *I. bicornis*.

Arguments for the recognition of *I. bicornis spitzbergensis* (Schmidt, 1927) and *I. bicornis derjugini* (Knipovich, 1926) involve similar overlaps (with specimens from other geographic areas) of character states: morphology and measurements of the urogenital papillae of males; the presence of scale rows between the dorsal scale row and the lateral line; and the presence of an anal scale row. Andriashev (1954) suggested that *I. bicornis derjugini* be suppressed because of the presence of these scale rows in specimens from other geographic areas. My data indicate that similar arguments have merit regarding other subspecies of *I. bicornis*. *Icelus bicornis* is readily identifiable over its entire geographic range (which appears to be interrupted by major discontinuities, Fig. 36); the recognition of numerous subspecies complicates the taxonomy of the group without providing useful biological information.

DISTRIBUTION.—*Icelus bicornis* co-occurs with *I. spatula* between approximately Point Barrow in the eastern Beaufort Sea and western Greenland and Labrador (Fig. 36). In eastern Greenland, northern Iceland, the Faeroe Islands, Spitzbergen, and the Barents Sea, *I. bicornis* is the only species of *Icelus* represented. In the Kara and Laptev seas, *I. bicornis* again co-occurs with *I. spatula*.

Andriashev (1954) cited a wide bathymetric distribution for this species: from shallow depths to 560 m. Esipov (1933) recorded the greatest depth range for a single body of water (Kara Sea): 17–560 m. In the Barents Sea the depth range is 17–111 m (Andriashev 1954), along the coasts of Norway (Goode and Bean 1896) 92–458 m. Along northeastern Greenland juvenile specimens were found in nearshore littoral and sublittoral zones, while adults were in depths to 50 m (Johansen 1912). Across Arctic Canada the species has been collected between 48 m and 142 m (Dunbar and Hildebrand 1952; McAllister 1963) and probably also occurs in much shallower and deeper waters.

Andriashev (1954) and Walters (1955) observed that *Icelus bicornis* seems to prefer ex-

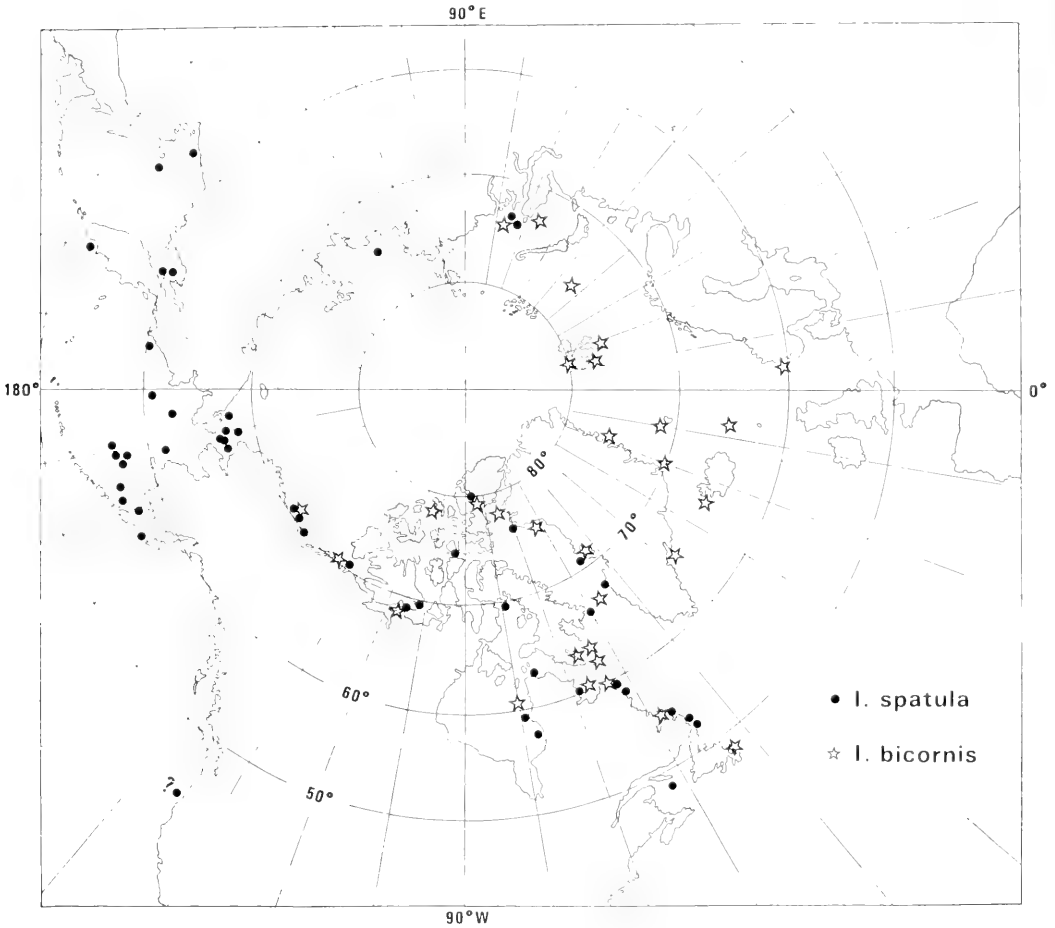


FIGURE 36. Known distributions of *Icelus bicornis* and *I. spatula*.

tremely cold water—hence its distribution to 82°N along the northeastern coast of Greenland. It is apparently relatively eurythermal and euryhaline, occurring in water temperatures between −1.8°C and 8.8°C and in salinities of 25.4‰ to 35‰ (in the Barents and Kara seas) (Andriashev 1954). The species has not been collected from the western Beaufort Sea, the Chukchi Sea, or the Siberian Sea.

ETYMOLOGY.—The name *bicornis* is derived from the Latin *bi-* (two) and *cornus* (horn), and refers to the two pairs of spines, parietal and nuchal, present on the parietal bone (occipital region).

MATERIAL EXAMINED (289 spec., 22.0–91.0 mm).—**Lectotype** of *Icelus hamatus*: ZMUC P81.1869; female, 43.0 mm; Belsund, Spitzbergen, about 18 m; July 1844.

Nontype-material. ARCTIC CANADA, WEST GREENLAND, LABRADOR: CAS-SU 5281 (1); Eglington Harbor, Davis Str.; no date. NMC 77-975 (1); 70°37′42″N, 127°20′W; 28 July 1977. NMC 77-1460 (4); 67°41′48″N, 107°54′30″W; 13 Aug. 1977. NMC 74-281 (7); 70°33′N, 145°45′W; 9 Aug. 1972. NMC 79-509 (7); 70°50′N, 145°31′W; 29 Aug. 1979. NMC 59-469 (1); 62°39′N, 65°47′30″W; 24 Aug. 1951. NMC 72-155 (1); 71°58′N, 125°12′W; 30 July 1972. NMC 59-13B (1); 80°08′N, 86°20′W; 20 Aug. 1955. NMC 77-1346 (1); 59°10′06″N, 106°25′42″W; 28 July 1966. NMC 63-155 (1); 48°51′30″N, 53°04′W; 2 June 1963. NMC 60-445 (8); 78°47′N, 103°32′W; 27 July 1954. NMC 60-446 (7); 80°08′N, 86°20′W; 7 Aug. 1955. NMC 70-277 (45); 63°40′N, 68°26′W; 7 Aug. 1970. NMC 77-1350 (6); 69°09′30″N, 105°52′42″W; 3 Aug. 1966. ROM 23264 (1); Cockburn Pt., Dolphin and Union Str.; 14 Sep. 1915. ROM 12512 (2); Pangnirtung, 15–36 m; 13 Sep. 1939. ROM 12514 (1); Baffin I., mouth of Lake Harbourfield, 55 m; 4 Aug. 1939. ROM 12510 (1); Baffin I., mouth of Lake Harbourfield, 48–55 m; 2 Aug. 1939. USNM 121918 (1, one removed to *I. spatula*); w shore Frobisher Bay, chart #5380; 26 Aug. 1942. USNM 121919 (1); Daniels Harbor, Frobisher Bay, Baffin Land, 110 m; 16 Sep. 1942. USNM 165296 (1); N side Hamilton Inlet; 24 Aug. 1951. USNM 221345 (5); Kangalak-

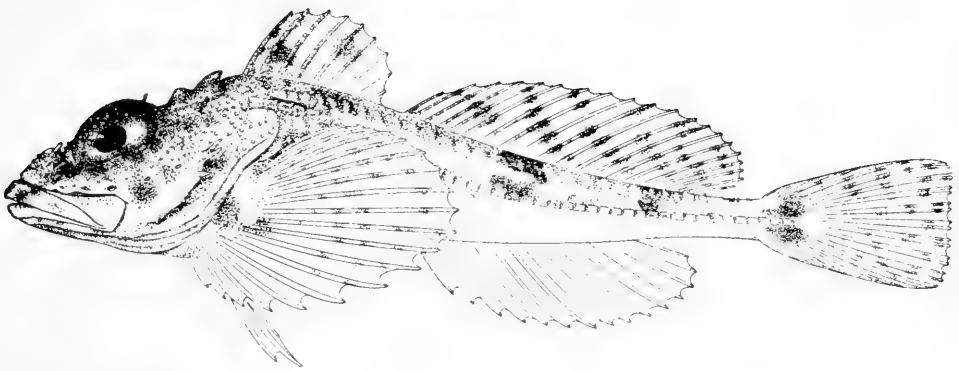


FIGURE 37. *Icelus spatula* Gilbert and Burke, 1912, male, 55.0 mm SL; after Gilbert and Burke (1912).

scorvsk Fjord; 8 Aug. 1950. USNM 108244 (1); NW Greenland, Belricks Bay; 6 Aug. 1937. USNM 118171 (2); NW Greenland, off T-Bone I., Melville Bay; 19 July 1942. USNM 107802 (11); NW Murchison Sound, 77°45′N, otter trawl on walrus grounds; 7 Aug. 1939. ZMUC P81.1018–1042 (25); Davis Str., INGOLF sta. 31, 33, 34; 1896. ZMUC P81.1118–1128 (11, 6 removed to *I. spatula*); 77°17′N, 69°59′W; 8 May 1928. ZMUC P81.1080a–c (3); Uttental Sound, 30–40 m; 21 Aug. 1933. ZMUC P81.1875 (1); Greenland; 26 Aug. 1841. ZMUC P81.1877 (1); Greenland; 15 July 1862. ZMUC P81.1878 (1); Greenland, Lichtenau; 26 Aug. 1841. EAST GREENLAND: ZMUC P81.1870 (1); Heklas Havn, 18 m; 18 Aug. 1891. ZMUC P81.1872 (1); Ryders Exp.; 7 Sep. 1897. ZMUC P81.1881–1882 (2); Denmarks Havn, 6–12 m; 8 Aug. 1907. ZMUC P81.1887 (6); Denmarks Havn, 6–10 m; 20 Sep. 1906. ZMUC P81.1871 (1); Heklas Havn, 20 m; 13 May 1892. ZMUC P81.1880 (24); Angmakssalik; 14–16 Sep. 1900. ZMUC P81.1879 (1); Denmark Str., 66°20′N, 25°12′W; 1891. JAN MAYEN: ZMUC P81.1885 (8); 100 m, slik. scraber; 28 June 1900. FAEROE ISLANDS: ZMUC P81.1183 (2); Mellem I., 64°16′N, 11°15′W; 1891. SPITZBERGEN: CAS-SU 8088 (4); Isfjorden, Green Harbor, 10–80 m; 25 June 1900. NRMS SPN 3007 (1); Mussel Bay, Wijdefjorden, 9–18 m; 3 Aug. 1868. NRMS SPN/3003 (7); Treunenberg Bay, 22 m; 1861. NRMS SPN/3004 (1); Norsköarne, 27–36 m; 12 Aug. 1872. NRMS SPN/3015 (1); 80°N, 13°E, 127–246 m; 1 June 1861. NRMS SPN/3005 (1); Norsköarne, 27 m; 14 Aug. 1872. NRMS SPN/3013 (1); Liefde Bay, 9 m; 3 Sep. 1868. NRMS SPN/3010 (2); Brandywine Bay, 27 m; 5 Sep. 1868. NRMS SPN/3009 (3); Liefde Bay, 9 m; 3 Sep. 1868. NRMS SPN/3014 (1); Danes-Gat, 13–18 m; 21 Aug. 1868. NRMS SPN/3006 (1); Mossel Bay, Wijdefjorden, 31 m; 19 Nov. 1872. NRMS SPN/3008 (1); Liefde Bay, 9–27 m; 3 Sep. 1868. NRMS SPN/1204 (1); Isfjorden; 1908. BARENTS AND KARA SEAS: BMNH 1964.4.18: 2–3 (2); 75°07′N, 54°51′E, 181 m; 10 Aug. 1902. BMNH 1891.1.15:6–8 (4); Kara Sea; no date. ZMUC P81.1888 (1); Norway, off Bergen; Aug. 1904. ZMUC P81.1874 (6); Kara Sea, 110 m; 1 June 1885. ZMUC P81.1003–1016 (14); Kara Sea; 1 June 1885. ZMUC P81.1873 (2); Kara Sea, 140 m; 1 June 1885.

Icelus spatula Gilbert and Burke, 1912

(Figure 37)

Centridermichthys bicornis: GÜNTHER 1860:172 (non *Cottus bicornis* Reinhardt, 1839; in part; Greenland); PIETSCHMANN 1932:36 (in part; based on high lateral line scale counts, some W Greenland material is *I. spatula*).

Icelus hamatus: GÜNTHER 1860:172 (in part; descr.; W Greenland material contains *I. spatula*); LÜTKEN 1876:380 (in part; descr.; Kara Sea); GÜNTHER 1877:293 (in part; distr. extended to Arctic Canada); BEAN 1879:128 (in part; confirmation of Günther's [1877] range extension); COLLETT 1880: 34 (in part; W Greenland); JORDAN AND GILBERT 1882:691 (in part; Alaska and W Greenland); DRESEL 1884: 252 (descr.; measurements; Davis Str., Canada); LÜTKEN 1887:123 (in part; distr.); 1898:36 (in part; SW Greenland); LE DANOIS 1917:5 (in part; distr.).

Icelus bicornis: JORDAN AND GILBERT 1882:693 (in part; recognized, questionably, along with *I. hamatus*; Greenland); GILBERT 1895:411 (Bristol Bay, Alaska; Gilbert stated that ". . . the Pacific form may prove specifically separable"); GOODE AND BEAN 1896:267 (in part; descr.; distr.; Kara Sea material contains *I. spatula*); JORDAN AND EVERMANN 1896: 437 (in part; compiled distr.); 1898:1911 (compiled descr.; synon.; Alaska and W Greenland); JENSEN 1904: 245 (in part; compiled synon., distr.); KNIPOVICH 1907:29 (in part; Kara Sea); EVERMANN AND GOLDSBOROUGH 1907:300 (compiled; Chignik and Alitak bays, Kodiak, Alaska); JENSEN 1910:8 (in part; Arctic Canada); KENDALL 1911:508 (collection of juvs.; Labrador; referred to *I. spatula* by Backus [1957]); JOHANSEN 1912:654 (in part; W Greenland); HALKETT 1913: 99 (in part; Arctic Canada); SCHMIDT 1927:8 (in part; Siberia and Alaska); JORDAN, EVERMANN, AND CLARK 1930:378 (in part; compiled; Alaska, W Greenland, Labrador); POPOV 1933: 158 (in part; Laptev Sea); VLADYKOV 1933:14 (in part; Hudson Bay); SCHMIDT 1935:415, 418 (in part; Canada); EHRENBAUM 1936:182 (in part; distr.); TARANETZ 1936:151 (in part; key; Arctic Canada); PFAFF 1937:12 (in part; NW Greenland); JOUBIN 1938:18 (in part; compiled; Arctic Alaska, W Greenland, Labrador); HILDEBRAND 1939:8 (in part; Alaska, Labrador); ESIPOV 1939:878 (in part; Kara Sea); 1940:140 (in part; Laptev Sea); SAEMUNDSSON 1949:12 (in part; distr.); QUAST AND HALL 1972:22 (in part; compiled; Bristol Bay, Alaska).

Icelus spatula GILBERT AND BURKE, 1912:41, figs. 3, 3a (orig. descr.; type-locality Avatcha Bay, Kamchatka, 52°47′20″N, 158°44′30″E, 106–126 m, ALBATROSS sta. 4794); SCHMIDT 1927:4 (descr.; males to 84.2 mm; distr.); SOLDATOV AND LINDBERG 1930:177 (in part; descr.; E coast of Kamchatka); JORDAN, EVERMANN, AND CLARK 1930:379 (compiled; E coast

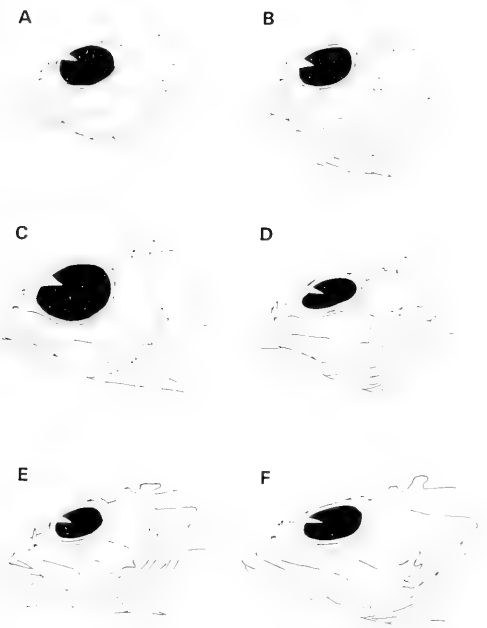


FIGURE 38. Variations in development of supraocular ridge and in parietal and nuchal spines in *Icelus spatula*: (A) western Bering Sea (USNM 74367, holotype of *Icelus spatula*, 55.0 mm SL); (B) Sea of Okhotsk (*I. spatula ochotensis* Andriashev, 1937) (CAS-SU 40927, 56.0 mm SL); (C) Sea of Okhotsk (*I. spatula bispinis* Andriashev, 1937) (HUMZ 58941, 89.5 mm SL); (D) Labrador (USNM 165184, 72.0 mm SL); (E) Kodiak (USNM 60503, 66.5 mm SL); (F) Eastern Bering Sea (UW 20778, 101.0 mm SL).

of Kamchatka); ESIPOV 1933:173 (compar. with *I. bicornis* and *I. karaensis* in the Kara Sea); SCHMIDT 1935:414 (comments on subspp.; synon.; distr.; key); TARANETZ 1936:151 (key to sp. groups); ANDRIASHEV 1937a:268, figs. 1, 3, pl. 6 (descriptions of subspp.; synon.; distr.; key); 1937b:302 (synon.; distr.; habitat); TARANETZ 1937:107, 108 (key; distr.); OKADA 1938:226 (Avatcha Bay, Sea of Okhotsk); ANDRIASHEV 1939:42 (zoogeog. in N Pacific Ocean); BRISKINA 1939: 345 (Kara Sea; diet); ESIPOV 1940:140 (Laptev Sea); JENSEN AND VOLSOE 1949:15, 19, figs. 3, 4, 7, 8, 10B, 12A–E, map 2 (descr.; synon.; distr.; anatomy of male and female urogenital organs); SCHMIDT 1950:123, 125 (descr. of subspp. in Sea of Okhotsk; distr.); DUNBAR AND HILDEBRAND 1952: 119 (descr.; Ungava Bay, Canada); WALTERS 1953:7 (descr.; meristic char.; NE Arctic Canada); ANDRIASHEV 1954:385, figs. 200, 201 (descr.; synon.; Arctic seas; ecol. and life history notes); WALTERS 1955:314, 337 (Arctic zoogeog.; lit.); BACKUS 1957:309 (descr.; Labrador); WILIMOVSKY 1958:67 (key; distr.); MCALLISTER 1960:15 (Arctic Canada); 1962:30 (descr.; W Arctic Canada); 1963:53, table 2 (descr.; compar. with *I. bicornis*; aids to ident.); LEIM AND SCOTT 1966:352 (descr.; fig.; compar. with *I. bicornis*; distr.); QUAST AND HALL 1972:23 (distr.; lit.); FEDOROV 1973:15, 60 (Bering Sea); HOWE AND RICHARDSON 1978:48, 138 (diag.; lit.; key).

Icelus karaensis SOLDATOV, 1923:31, fig. 1 (orig. descr.; type-locality Kara Sea; meristic char.; compar. with *I. bicornis*, *I. spatula*, and *I. uncinalis*); KNIPOVICH 1926:124 (descr.; Kara Sea, E Barents Sea around Novaya Zemlya; Siberian Sea); ESIPOV 1933:173 (compar. with *I. bicornis*; Kara Sea); POPOV 1933:158 (E Siberian Sea); ANDRIASHEV 1937a:254, 272 (synon. with *I. spatula spatula*).

Icelus ochotensis SCHMIDT 1927:4 (in part; orig. descr.; type-locality N Sea of Okhotsk); SOLDATOV AND LINDBERG 1930: 178 (in part; Sea of Okhotsk); ANDRIASHEV 1937a:268, pl. 6, fig. 4 (in part; descr.; Sea of Okhotsk); OKADA 1938:226 (in part; Sea of Okhotsk).

Icelus uncinalis: SCHMIDT 1927:3 (in part; distr. extended [incorrectly] to N Sea of Okhotsk); SOLDATOV AND LINDBERG 1930:176 (in part; Sea of Okhotsk spec. are referred to *I. spatula ochotensis* by Andriashev [1937a]); YABE 1981:293, fig. 3B (compar. osteol.; fig. is *Icelus spatula*).

Icelus bicornis beringianus SCHMIDT, 1927:7 (orig. descr.; type-locality Providence Bay, N Bering Sea, 63°27′ to 64°25′N, 168°48′ to 176°27′E, 15–80 m); ANDRIASHEV 1937a:272 (synon. with *I. spatula spatula*).

Icelus uncinalis ochotensis: SCHMIDT 1935:414, 417 (in part; descr.; Sea of Okhotsk).

Icelus spatula spatula: SCHMIDT 1935:414, 417 (recognition of subspp.; Bering Sea); ANDRIASHEV 1937a:272, pl. 6, fig. 6 (descr.; synon.; Bering Sea, Chukchi Sea W to Kara Sea and E to W Greenland); ANDRIASHEV 1937b:302 (distr.); TARANETZ 1937:107, 108 (key; distr.); ANDRIASHEV 1939:42 (distr. in North Pacific); ESIPOV 1940:140 (Laptev Sea); BACKUS 1957:309 (descr.; Labrador); WILIMOVSKY 1958:67 (key; Bering Sea).

Icelus uncinalis crassus ANDRIASHEV, 1937a:265 (in part; orig. descr.; type-locality N Sea of Okhotsk; some N Sea of Okhotsk spec. are *I. spatula*); TARANETZ 1937:107, 108 (in part; key; Sea of Okhotsk); SCHMIDT 1950:125 (in part; descr.; synon.; Sea of Okhotsk).

Icelus spatula bispinis ANDRIASHEV, 1937a:270, pl. 6, fig. 5 (orig. descr.; type-locality NE Sea of Okhotsk; synon.); ANDRIASHEV 1937b:302 (distr.); TARANETZ 1937:107, 108 (key; Sea of Okhotsk); SCHMIDT 1950:126 (disting. char.; synon.; N Sea of Okhotsk and E coast of Sakhalin).

Icelus spatula ochotensis ANDRIASHEV, 1937a:268, pl. 6, fig. 4 (orig. descr.; type-locality N Sea of Okhotsk); TARANETZ 1937: 107, 108 (key; distr.); SCHMIDT 1950:125 (NW Sea of Okhotsk, 55–110 m).

DIAGNOSIS.—Parietal and nuchal spines present, the shapes of these spines variable (Fig. 38). Suborbital stay spines absent. Lacrimal spines absent. Uppermost preopercular spine simple or bifurcated. Platelike scales of dorsal scale row Pattern B (Fig. 18*B*). Rows of scales between dorsal scale row and lateral line absent. Rows of scales between lateral line and anal fin absent. Axillary scales 1–14; 0–5 in uppermost row. Lateral line scales Pattern A (Fig. 19*A*), extending to posterior edge of hypural plate. Supraocular cirri present; parietal, opercular, suborbital stay cirri present or absent; other cirri absent. Head cirri lightly pigmented (similar to top of head) or darkly pigmented (black). Nasal tubes lightly

TABLE 7. GEOGRAPHIC AND ONTOGENETIC VARIATION IN SELECTED MEASUREMENTS FOR *ICELUS SPATULA*. Class intervals of values in thousandths of standard length. OKH 1 = Sea of Okhotsk: *I. spatula ochotensis*; OKH 2 = Sea of Okhotsk: *I. spatula bispinis*; WBS = western Bering Sea; EBS = eastern Bering Sea; KOD = Kodiak, Alaska; CHU = Chukchi Sea; BEA = Beaufort Sea; ARC = Arctic Canada and Labrador; KLS = Kara and Laptev seas.

		Orbit diameter							Upper jaw length						
Growth stage	Locality	80–99	100–119	120–139	140–159	160–179	180–199	$\bar{x}$	120–139	140–159	160–179	180–199	200–219	220–239	$\bar{x}$
Young	OKH 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(23.0–50.0	OKH 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
mm SL)	WBS	—	1	—	—	—	—	117	—	—	—	1	—	—	182
	EBS	—	7	15	12	—	—	131	—	6	4	1	—	—	161
	KOD	—	2	1	—	—	—	118	—	1	1	—	—	—	153
	CHU	—	2	8	2	—	—	128	1	2	1	2	3	—	176
	BEA	—	2	3	2	2	—	137	—	—	—	—	—	—	—
	ARC	—	3	21	5	1	1	131	1	3	5	3	3	—	174
	KLS	—	—	1	2	—	—	139	1	—	—	2	—	—	170
Small adult	OKH 1	—	—	5	1	—	—	133	—	—	2	2	2	—	197
(50.5–75.0	OKH 2	—	—	1	1	—	—	140	—	—	1	1	—	—	186
mm SL)	WBS	—	2	4	—	—	—	125	—	—	—	5	1	—	193
	EBS	1	8	10	3	—	—	124	—	—	4	19	1	—	186
	KOD	—	1	1	—	—	—	127	—	—	1	—	1	—	187
	CHU	—	1	2	4	—	—	135	—	—	1	2	3	—	200
	BEA	—	—	2	1	—	—	135	—	—	—	—	—	—	—
	ARC	—	—	9	16	—	—	144	—	—	—	2	10	2	210
	KLS	—	—	2	4	—	—	144	—	—	1	5	—	—	202
Large adult	OKH 1	—	—	2	—	—	—	130	—	—	1	1	—	—	188
(>75.0 mm SL)	OKH 2	—	2	3	1	—	—	131	—	—	—	4	2	—	196
	WBS	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	EBS	—	16	7	—	—	—	115	—	—	2	11	8	—	197
	KOD	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	CHU	—	—	6	—	—	—	128	—	—	—	—	3	2	216
	BEA	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	ARC	—	—	10	5	—	—	138	—	—	—	—	7	2	215
	KLS	—	—	—	—	—	—	—	—	—	—	—	—	—	—

pigmented (similar to snout). Urogenital papilla of male with spatulate or dorsoventrally flattened basal portion and curved or hooklike terminal appendage (Fig. 24*G*).

DESCRIPTION.—General body shape shown in Figure 37. Body elongate, laterally compressed posterior to opercular openings; greatest depth at anterior of spinous dorsal fin. Head large, about as deep as wide. Eye large, about 1.5 to 2 times snout length. Mouth large; posterior edge of maxilla reaching to middle of orbit (occasionally to posterior rim of orbit).

Coloration in preservative. Overall body color light brown, with several darker brown or black saddles marking dorsal surface of body and dorsal and anal fins. Underside whitish. Pectoral and caudal fins marked with dark brown vertical bars. Eastern Bering Sea specimens with much lighter overall coloration and with many small dark "freckles" scattered over sides of body. Specimens collected in the Chukchi Sea, Arctic Canada, and Labrador with a much darker overall coloration and less distinguishable dorsal saddle markings. For more comprehensive coloration discussions, the reader is referred to the following regional descriptions of *I. spatula*: Bering Sea (Gilbert and Burke 1912); Sea of Okhotsk (Schmidt 1927; Andriashev 1937a); Arctic Canada (Dresel 1884; McAllister 1963; Leim and Scott 1966); and Arctic seas of the U.S.S.R. (Andriashev 1954).

MEASUREMENTS (from 194 spec., 27.0–116.5 mm, except where indicated).—The following expressed as thousandths SL, [value for holotype] range; variations (ontogenetic and geographic) in selected measurements are presented in Tables 7 and 8: head length [373] 289–414; lacrimal length (188 spec.) [65] 27–80; snout

length (98 spec.) [87] 41–127; least interorbital width [27] 13–44; orbit diameter [116] 94–185; greatest body depth [236] 157–306; least caudal peduncle depth (172 spec.) [55] 36–68; pectoral fin base length (127 spec.) [118] 109–159; upper jaw length (77 spec.) [182] 128–239.

COUNTS (from 175 spec.).—Values expressed, [value for holotype] range; variations in selected counts are presented in Tables 9 and 10: dorsal fin spines [9] 7–11; dorsal fin soft rays [20] 18–22; anal fin rays [16] 14–18; pectoral fin rays [18] 16–20; scales in dorsal scale row [30] 19–37; axillary scales [6] 1–14; axillary scales, uppermost row [2] 0–5; lateral line scales [41] 33–43.

REMARKS.—The shapes of the parietal and nuchal spines, on which the subspecific diagnoses established by Andriashev (1937a) were based, vary considerably both within and between geographic areas (Fig. 38). The absence of spinules below the pore on the lateral line scales (Jensen and Volsoe 1949) is an unreliable character, as both "spinous" and "non-spinous" conditions occur within most geographic areas sampled. The lateral line scales extend to the posterior margin of hypural plate (in specimens greater than 40.0 mm), but the scales do not extend onto the caudal rays (as is generally the case in *I. uncinalis*). The posteriormost scale of the dorsal scale row is embedded in the dorsolateral surface of the caudal peduncle, and the base (embedded portion) is much larger than the bases of the preceding scales. This scale generally bears one or two simple spines similar to those observed in *I. spiniger*. The axillary scales are generally much fewer than in *I. bicornis* and *I. uncinalis*.

The supraocular cirrus is invariably present, but is developed to a different extent and is variably pigmented in different geographic regions (see discussion below). The parietal cirrus is generally present in specimens smaller than about 60.0 mm, but this cirrus is often damaged or obliterated in larger specimens by the eruption of the parietal spine through the surface of the skin. Gilbert and Burke (1912) described this cirrus, but their material consisted only of small specimens (49.5–59.0 mm). Opercular and suborbital stay cirri are present irregularly (opercular cirri are frequently present in specimens collected in the Sea of Okhotsk) in material from all areas sampled.

The base of the urogenital papilla of the male is spatulate or dorsoventrally flattened throughout the geographic range of the species, but the shape of the germinal appendage is variable. Populations inhabiting the western Bering Sea (including the type-specimens of *I. spatula*), the Sea of Okhotsk, and the Arctic seas of Canada and the U.S.S.R. exhibit a claw-shaped terminal appendage (Fig. 23*G*), while eastern Bering Sea specimens exhibit a conical or slightly curved terminal appendage. Both of these conditions are observed in specimens from the Chukchi Sea.

GEOGRAPHIC VARIATION.—Geographic variation in several characters observed in this species are dramatic and often have resulted in the descriptions of species and subspecies. For this reason, and in order to provide additional aids to identification of the geographic variants of *Icelus spatula,* the following notes dealing with variation in selected character states are presented by geographic region.

Sea of Okhotsk: Extremes of variation with respect to several characters are observed in specimens from the Sea of Okhotsk. These variations tend to be clustered into two groups which were described as subspecies by Andriashev (1937a). However, intermediate character states complicate and largely obfuscate these groupings.

Icelus spatula ochotensis Andriashev, 1937, constitutes one of these groups. Specimens belonging to this nominal subspecies are supposedly characterized by the following features: well-developed, tuberclelike parietal and nuchal spines (Fig. 38*B*); supraocular ridge prominent (Fig. 38*B*); occipital pit deep; body deep and robust (Table 8); caudal peduncle relatively deep compared to *I. spatula bispinis* (Fig. 39); caudal peduncle scale present above lateral line (rarely absent), rarely present below lateral line; axillary scales 6–14, 2–4 in uppermost row; top and sides of head, including opercles, much more densely scaled than in *I. spatula bispinis*; supraocular cirrus slender, darkly pigmented along entire length (rarely only darkly pigmented for a portion of its length); parietal, opercular, suborbital stay cirri generally present; lateral line scales 40–42 (38–40 [Schmidt 1927]). The largest male examined was 79.0 mm, the largest female 95.0 mm. The urogenital papilla of the male has a flattened, elongate basal portion with an incised groove at the distal end; the terminal appendage is short and hooklike.

Specimens belonging to the other nominal sub-

TABLE 8. GEOGRAPHIC AND ONTOGENETIC VARIATION IN SELECTED MEASUREMENTS FOR *ICELUS SPATULA*. Class intervals of values in thousandths of standard length. OKH 1 = Sea of Okhotsk: *I. spatula ochotensis*; OKH 2 = Sea of Okhotsk: *I. spatula bispinis*; WBS = western Bering Sea; EBS = eastern Bering Sea; KOD = Kodiak, Alaska; CHU = Chukchi Sea; BEA = Beaufort Sea; ARC = Arctic Canada and Labrador; KLS = Kara and Laptev seas.

		Head length								Greatest body depth									
		280–	300–	320–	340–	360–	380–	400–		140–	160–	180–	200–	220–	240–	260–	280–	300–	
Growth stage	Locality	299	319	339	359	379	399	419	$\bar{x}$	159	179	199	219	239	259	279	299	319	$\bar{x}$
Young	OKH 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(23.0–50.0	OKH 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
mm SL)	WBS	—	—	—	1	—	—	—	354	—	—	—	—	—	1	—	—	—	242
	EBS	—	2	1	13	14	—	1	357	—	—	13	14	3	1	—	—	—	205
	KOD	—	1	—	1	1	—	—	341	—	—	1	1	1	—	—	—	—	200
	CHU	—	—	3	5	4	—	—	350	—	—	—	2	8	1	—	—	1	236
	BEA	—	—	—	2	3	4	—	373	—	—	—	1	5	3	—	—	—	234
	ARC	1	1	2	9	8	8	2	363	—	—	—	5	10	9	6	1	—	241
	KLS	—	—	1	1	1	—	—	347	—	—	1	—	1	1	—	—	—	226
Small adult	OKH 1	—	—	—	2	2	—	2	372	—	—	—	—	—	3	3	—	—	260
(50.5–75.0	OKH 2	—	1	—	1	—	—	—	337	—	—	—	1	1	—	—	—	—	220
mm SL)	WBS	—	—	—	2	3	1	—	371	—	—	—	1	4	1	—	—	—	230
	EBS	—	1	5	8	6	—	—	350	—	—	6	10	2	1	—	—	—	205
	KOD	—	—	—	—	—	1	1	394	—	—	1	—	1	—	—	—	—	211
	CHU	—	—	—	2	4	1	—	368	—	—	—	1	1	3	2	—	—	242
	BEA	—	—	—	—	1	1	1	385	—	—	—	1	—	1	1	—	—	241
	ARC	—	—	—	2	12	9	2	378	—	—	—	6	5	8	6	—	—	243
	KLS	—	—	—	1	2	1	2	381	—	—	—	—	6	—	—	—	—	233
Large adult	OKH 1	—	—	—	1	1	—	—	366	—	—	—	—	1	1	—	—	—	240
(>75.0 mm	OKH 2	—	—	1	1	1	2	1	372	—	—	1	1	1	2	1	—	—	233
SL)	WBS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	EBS	—	—	5	10	8	—	—	351	1	4	10	4	3	—	—	—	—	195
	KOD	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	CHU	—	—	—	2	1	3	—	370	—	—	—	—	—	3	2	1	—	262
	BEA	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	ARC	—	—	—	—	4	8	3	386	—	—	—	—	—	7	7	1	—	261
	KLS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

species, *Icelus spatula bispinis* Andriashev, 1937, are supposedly distinguished by the following suite of characters: parietal and nuchal spines long, sharp (Fig. 38*C*); supraocular ridge not prominent (Fig. 38*C*); occipital pit shallow; body deep and robust under spinous dorsal fin, more elongate and tapering than in *I. spatula ochotensis* (Table 8); caudal peduncle more slender than in *I. spatula ochotensis* (Fig. 39); caudal peduncle scales absent; axillary scales 3–7, 0–2 in uppermost row; top and sides of head, including opercles, much less densely scaled than in *I. spatula ochotensis*; supraocular cirrus not darkly pigmented; other cirri absent; lateral line scales 41–43 (Table 9). The largest male examined was 89.5 mm long and was extremely elongate and slender (greatest body depth 184 thousandths SL). The largest female examined was 116.5 mm long and had a deep and robust (possibly gravid?) body shape (greatest body depth 266 thousandths SL). The urogenital papilla of the male is morphologically similar to that of *I. spatula ochotensis*.

Complicating the polarities of the character states differentiating these two nominal subspecies are intermediate states of the above-described features. The shapes of the parietal and nuchal spines vary considerably between the extremes described by Andriashev (1937a) as diagnostic for the subspecies (Figs. 38*B, C*). In one specimen of *I. spatula ochotensis*, the supraocular ridge (usually prominent) is almost flat; and in one specimen of *I. spatula bispinis*, this ridge is elevated and prominent. The top and sides of the head are invariably densely scaled in *I. spatula ochotensis*, but this condition is also observed (albeit rarely) in specimens of *I. spatula bispinis*. The development of the occipital pit is highly variable in each of these groups. This character

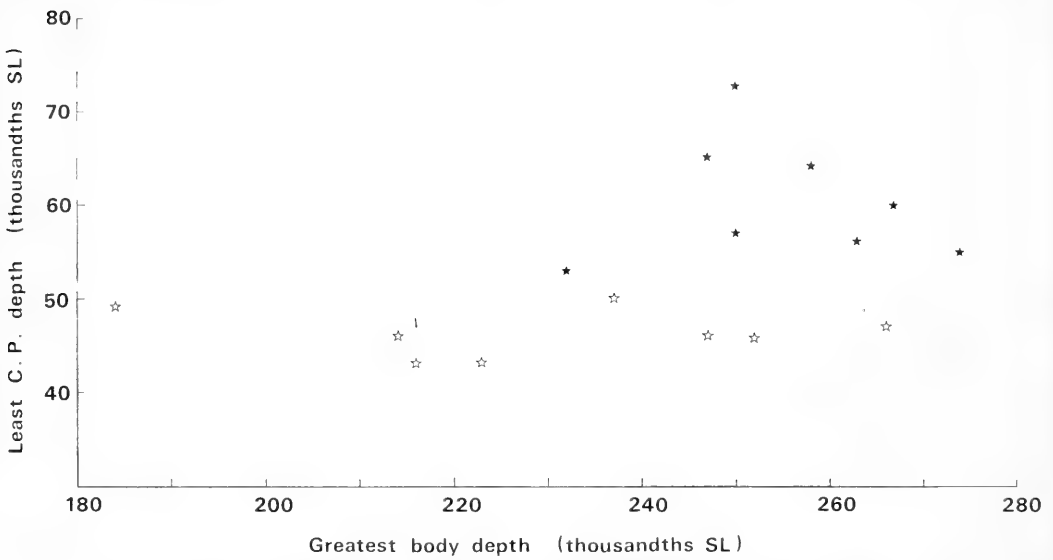


FIGURE 39. Plot of least caudal peduncle (C.P.) depth versus greatest body depth in two nominal subspecies of *Icelus spatula* from the Sea of Okhotsk: *I. spatula ochotensis* (solid stars); *I. spatula bispinis* (open stars).

is difficult to quantify, and consistent differences are difficult to detect. Specimens of *I. spatula bispinis* rarely exhibit an elongate, slender body shape (similar to specimens of *I. spatula* from the eastern Bering Sea); this condition was not observed in *I. spatula ochotensis*. The presence of caudal peduncle scales is diagnostic for *I. spatula ochotensis*, but absence of these scales occurs in both groups. Similarly, the presence of an opercular cirrus is characteristic of *I. spatula ochotensis*, but is sometimes absent in both groups. Frequency distributions of meristic characters (Tables 9, 10) reveal some differences between these two nominal subspecies, but regions of overlap make clear-cut distinctions between the two groups difficult. Differences in least caudal peduncle depth (Fig. 39) are consistent, but alone are insufficient criteria for specific or subspecific separation.

Andriashev's (1937a) subspecies must be rejected based on their distributions—they are apparently sympatric in the northern Sea of Okhotsk (Schmidt 1927, 1935, 1950; Andriashev 1937a; and the 16 specimens examined in this study). Mayr (1969) argued for rejection of subspecies for which sympatry may be demonstrated. On that argument the two must be regarded either as members of a single, highly variable species, or as members of two reproductively isolated units, each a biological species. The present material is insufficient to resolve this question; the data suggest, however, a single, remarkably variable species (*Icelus spatula*) in the Sea of Okhotsk.

Bering Sea: Icelus spatula occurs throughout the shallower depths of the western and eastern Bering Sea, where it is remarkably constant in its character states. When compared with representatives from other geographic areas, however, these specimens exhibit several distinguishing features.

The parietal and nuchal spines are well developed, but blunt and tuberclelike (Fig. 38*F*); occasionally, the nuchal spine may be bluntly pointed, as in the small adult specimens composing the type-material (Fig. 38*A*). This condition is more common in smaller specimens and may reflect ontogenetic, rather than geographic, differences. The supraocular ridge is nearly flat, resulting in a less-interrupted profile of the dorsal part of the head (Figs. 38*A*, 38*F*). The body shape in eastern Bering Sea *I. spatula* (adult specimens greater than 75.0 mm) is extremely elongate and slender compared with populations elsewhere (Fig. 40, Table 8). Caudal peduncle scales are invariably absent, and males apparently achieve

TABLE 9. GEOGRAPHIC VARIATION IN SELECTED COUNTS IN *ICELUS SPATULA*. OKH 1 = Sea of Okhotsk: *I. spatula ochotensis*; OKH 2 = *I. spatula bispinis*; WBS = western Bering Sea; EBS = eastern Bering Sea; KOD = Kodiak, Alaska; CHU = Chukchi Sea; BEA = Beaufort Sea; ARC = Arctic Canada and Labrador; KLS = Kara and Laptev seas.

	Dorsal fin spines						Dorsal fin soft rays							Anal fin rays							Pectoral fin rays					
Locality	7	8	9	10	11	$\bar{x}$	17	18	19	20	21	22	$\bar{x}$	13	14	15	16	17	18	$\bar{x}$	16	17	18	19	20	$\bar{x}$
OKH 1	—	3	5	—	—	8.6	2	2	3	1	—	—	18.4	1	4	3	—	—	—	14.3	1	3	4	—	—	17.4
OKH 2	—	3	5	—	—	8.6	—	—	1	6	1	—	20.0	—	—	1	6	1	—	16.0	—	—	5	3	—	18.4
WBS	—	1	7	—	—	8.9	—	—	1	5	—	—	19.8	—	—	—	7	—	—	16.0	—	4	4	—	—	17.5
EBS	—	—	91	6	—	9.0	—	4	33	49	10	—	19.7	—	2	10	65	28	2	16.2	1	8	70	28	—	18.3
KOD	—	1	4	—	—	8.8	—	—	4	1	—	—	19.2	—	—	4	—	—	—	15.0	—	—	4	1	—	18.2
CHU	1	5	12	—	—	8.6	—	1	5	9	3	—	19.8	—	3	7	6	2	—	15.4	1	3	8	4	—	17.9
BEA	—	1	8	2	—	9.1	—	1	2	7	1	—	19.7	—	1	4	5	1	—	15.5	—	1	8	2	—	18.1
ARC	—	10	78	8	1	8.7	—	6	37	43	10	—	19.6	—	8	41	38	10	—	15.4	—	8	68	20	1	18.1
KLS	—	3	4	—	—	8.6	—	—	2	4	—	1	20.0	—	—	4	2	1	—	15.6	—	—	—	7	—	19.0

	Dorsal scale row (L)																				Lateral line scales (L)					
Locality	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	$\bar{x}$	40	41	42	43	44	$\bar{x}$
OKH 1	—	—	—	—	—	—	—	—	—	1	—	4	1	1	—	—	—	—	—	—	30.1	6	1	1	—	—	40.4
OKH 2	—	—	—	—	—	—	—	—	—	—	—	2	2	1	3	—	—	—	—	—	31.6	—	2	3	3	—	42.1
WBS	—	—	—	—	—	—	1	—	—	2	1	3	—	—	—	—	—	—	—	—	28.6	—	2	3	1	—	41.8
EBS	—	—	—	—	—	—	—	—	—	2	1	8	7	15	24	20	13	9	2	—	33.1	4	30	52	13	—	41.7
KOD	—	—	—	—	—	—	—	—	—	—	—	2	2	1	—	—	—	—	—	—	30.8	4	1	—	—	—	40.2
CHU	—	—	—	—	—	2	1	2	2	4	2	2	—	1	—	1	1	—	—	—	28.3	—	7	9	2	—	41.7
BEA	—	—	—	—	3	—	1	3	—	—	3	1	—	1	—	—	—	—	—	—	26.8	1	3	3	2	—	41.7
ARC	1	1	—	1	2	—	—	7	4	5	6	7	19	15	21	6	5	2	—	—	30.7	—	19	37	22	1	42.1
KLS	—	—	—	—	—	—	—	—	1	—	2	1	4	1	1	—	—	—	—	1	31.1	—	3	6	1	—	41.8

only a small size. Of 122 specimens examined from Bering Sea, 34 were males. The largest female examined was 110.0 mm, the largest male 59.0 mm (CAS-SU 40931, paratype of *Icelus spatula*). In other geographic areas (for which adequate sample sizes were available), males attained almost the same maximum size as females. The shape of the male urogenital papillae differs somewhat between eastern and western Bering Sea specimens. The basal portion is flattened or spatulate in males from both areas, but the terminal appendage may be conical or curved (eastern Bering Sea), or clawlike (western Bering Sea) (Fig. 23*G*).

Kodiak: Five specimens collected by the ALBATROSS in Chignik and Alitak bays near Kodiak Island, Alaska, exhibit several unusual character states. The nuchal spines are well developed, blunt, bent posteriorly, and somewhat laterally flattened (Fig. 38*E*). The supraocular cirrus is

TABLE 10. GEOGRAPHIC VARIATION IN AXILLARY SCALE COUNTS IN *ICELUS SPATULA*. OKH 1 = Sea of Okhotsk: *I. spatula ochotensis*; OKH 2 = *I. spatula bispinis*; WBS = western Bering Sea; EBS = eastern Bering Sea; KOD = Kodiak, Alaska; CHU = Chukchi Sea; BEA = Beaufort Sea; ARC = Arctic Canada and Labrador; KLS = Kara and Laptev seas.

	Axillary scales (L)															Axillary scales (upper row)						
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	$\bar{x}$	0	1	2	3	4	5	$\bar{x}$
OKH 1	—	—	—	—	—	2	1	2	—	1	—	1	—	1	8.9	—	—	3	4	1	—	2.8
OKH 2	—	—	2	2	1	1	2	—	—	—	—	—	—	—	4.8	1	3	4	—	—	—	1.4
WBS	—	—	—	—	—	2	1	—	1	—	—	—	—	—	7.0	—	1	3	2	1	—	2.4
EBS	—	3	7	32	31	5	3	4	—	—	—	—	—	—	4.6	1	12	44	22	1	—	2.1
KOD	—	—	—	—	—	—	3	—	—	—	—	—	—	—	7.0	3	1	—	—	—	—	0.25
CHU	1	1	6	10	7	7	1	2	3	—	—	—	—	—	4.9	1	10	21	3	3	—	1.9
BEA	—	—	1	2	1	1	4	2	—	1	—	—	—	—	5.8	—	2	5	3	1	1	2.5
ARC	4	8	10	19	18	15	13	5	3	1	—	1	—	—	5.0	10	21	40	23	3	—	1.9
KLS	—	—	—	2	—	—	—	5	1	1	1	3	—	1	9.1	—	2	2	6	4	—	2.9

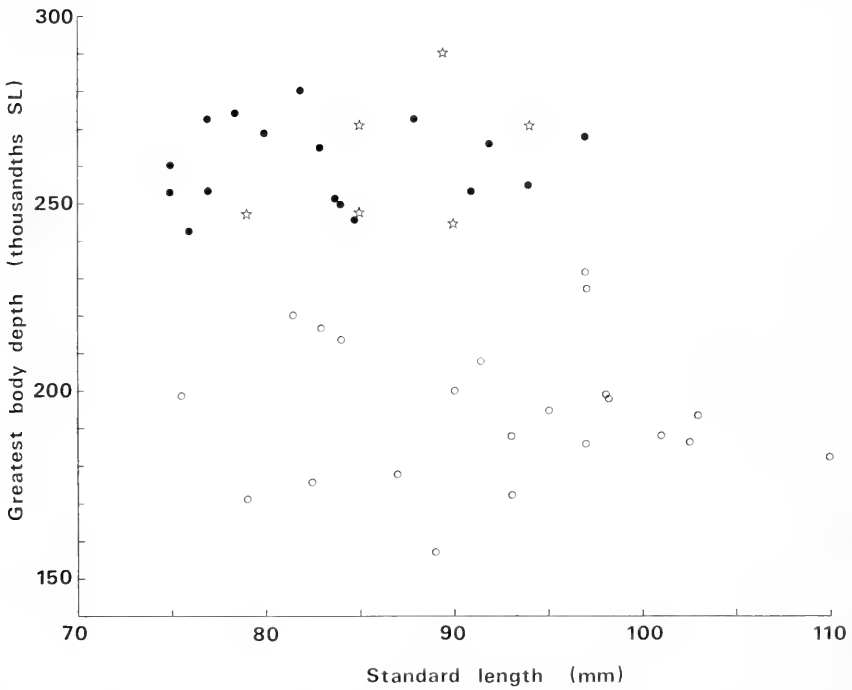


FIGURE 40. Plot of greatest body depth versus standard length in *Icelus spatula* from three geographic regions: eastern Bering Sea (open circles); Chukchi Sea (stars); Arctic Canada and Labrador (solid circles).

very large, multifid, and darkly pigmented along most or all of its length, unlike *I. spatula* collected in other geographic areas. In addition, the head length of these specimens is much greater than in eastern Bering Sea specimens of equal length; and the lateral line scales are fewer than for eastern Bering Sea specimens (Tables 8, 9).

Chukchi Sea, Arctic Canada, Kara Sea: The various character states exhibited within the Arctic (almost circumpolar) geographic variants of *I. spatula* are remarkably constant, with a few exceptions. In large adults (greater than 75.0 mm), the parietal spines are usually bluntly pointed, the nuchal spines very acutely pointed (Fig. 38*C*), and the greatest body depth is much greater than in specimens from the eastern Bering Sea (Fig. 40), giving the body a more robust appearance. Head and upper jaw lengths are somewhat greater than in specimens from other geographic areas (Tables 7, 8). Dorsal fin spine counts are generally higher than for Bering Sea specimens (Table 9). Caudal peduncle scales are invariably absent. The urogenital papillae of the males from these regions have spatulate basal portions, with short, hooklike terminal appendages. A few Chukchi Sea males exhibit slightly curved terminal appendages.

DISTRIBUTION.—*Icelus spatula* occupies the widest geographic distribution of any *Icelus* species (Figs. 36, 41). In the North Pacific Ocean, the species occurs in the northern Sea of Okhotsk in depths of 10–150 m and temperatures of −1.6°–1.8°C (Schmidt 1950); in the Bering Sea it occurs from the eastern coast of Kamchatka northward to Providence Bay (Schmidt 1927) and throughout the shallower areas of the eastern Bering Sea in 30–293 m and in waters −1.7°–7.8°C (Andriashev 1954). Around Kodiak Island *I. spatula* has been collected in depths of 55–110 m (ALBATROSS stations 4278, 4281, 4285). In the Arctic seas of Alaska, Canada, western Greenland southward to Labrador and the Gulf of Saint Lawrence, and in the Arctic seas of the U.S.S.R., the species occurs in shallow depths to 360 m (Leim and Scott 1966; Andriashev 1954); and in the shallower parts of the Chukchi, Siberian, Laptev, Kara, and eastern Barents seas in depths of 20–50 m (Andriashev 1954). Throughout the

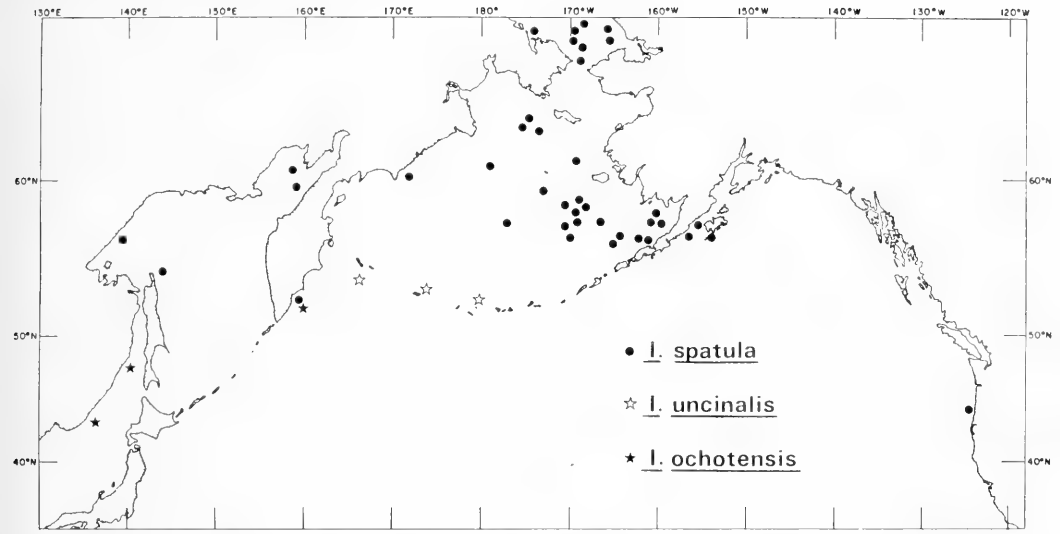


FIGURE 41. Known distributions of three species of *Icelus* in the North Pacific Ocean.

Arctic seas the species tolerates extremely cold water (to −1.85°C) and wide salinity ranges (25–34.2‰) (Andriashev 1954; Walters 1955; Backus 1957).

ETYMOLOGY.—The specific name, *spatula*, of Latin derivation, refers to the spatulate basal portion of the male urogenital papilla.

MATERIAL EXAMINED (510 spec., 27.0–116.5 mm).—**Holotype:** USNM 74367, male, 55.0 mm; Bering Sea, Kamchatka, Avatcha Bay off Staritschkof I., 52°47′20″N, 158°44′30″E, 58–69 m, ALBATROSS sta. 4794; 20 June 1906.

Paratypes: CAS-SU 40931 (5:49.5–59.0 mm); same data as for holotype.

Nontype-material. SEA OF OKHOTSK: BMNH 1964.4.18: 8–9 (2); no date. BMNH 1964.4.18:6–7 (2); 59°21′N, 158°35′E; 3 July 1915. CAS-SU 40930 (2); 60°18′N, 158°13′E; 29 July 1915. CAS-SU 40927 (1); 56°21′N, 138°17′E; 2 May 1913. CAS-SU 40933 (1); 54°14′N, 143°45′E; 1918. HUMZ 58941 (1); 55°02′N, 141°54′E, 138 m; 6 Sep. 1979. HUMZ 55223 (1); 60°01′N, 159°19′E, 120 m; 6 June 1976. MCZ 34055 (1); Sep. 1932. USNM 88345 (2); 59°21.2′N, 158°35′E, 128 m; 3 July 1915. USNM 88346 (2); 56°21′N, 138°17.5′E, 78 m; 3 Aug. 1916. BERING SEA: BMNH 1964.4.18:12–13 (2); Natalya Bay, Kamchatka, 74 m; 25 July 1932. BCPM BC71-38 (8); 56°25′40″N, 162°39′15″W, 75 m; 28 June 1890. BCPM 980-13 (6); 60°59′N, 179°11′W, 293 m; 16 July 1979. CAS-SU 68829 (1); 52°47′N, 158°44′E; 18–19 June 1906. CAS-SU 2429 (15); 56°14′N, 161°41′15″W, 66 m; 28 June 1890. CAS-SU 2265 (23); 57°16′45″N, 159°03′30″W, 55 m; 18 July 1890. FMNH 2656 (3), 57°22′20″N, 164°24′40″W, 55 m; 14 June 1890. HUMZ 76255, 76257 (2); 57°06′N, 166°46′W, 74 m; 30 May 1978. HUMZ 76736 (1); 58°37.5′N, 172°47.5′W, 110 m; 15 June 1978. HUMZ 76834,76837 (2); 56°33.5′N, 163°47′W, 78 m; 21 May 1978. LACM 36000-1 (1); Alaska, Bering Sea; 12 Sep. 1975. LACM 35751-1 (2); 56°17′N, 163°16′W, 90 m; 9 June 1975. NMC 79-809 (2); 62°42′54″N, 174°58′54″W; 26 Apr. 1979. USNM 135654 (5); 57°32′N, 169°38′W, 71 m; 1 Aug. 1893. USNM 119866 (2); 58°27′N, 169°01′W, 64 m; 1 Aug. 1893. USNM 119854 (2); North Pacific, ALBATROSS [no station data given]. USNM 53726 (4); 57°39′N, 170°02′W, 71 m; 1 Aug. 1893. USNM 53731 (2); 56°45′N, 170°18′W, 104 m; 2 Sep. 1893. USNM 144268 (1); 56°14′N, 164°08′W, 90 m; 10 Aug. 1893. USNM 48659 (1); 57°06′N, 170°35′W, 75 m; 3 Aug. 1893. UW 20774, 20776, 20777 (5 [total]); 60°50′N, 176°36′W, 119 m; 15 July 1979. UW 20775 (2); 61°29′N, 176°50′W, 71 m; 15 July 1979. UW 20778 (1); 57°40′N, 168°25′W, 68 m; 1 Aug. 1978. UW 20779 (1); 57°21′N, 159°40′W, 55 m; 6 June 1977. GULF OF ALASKA: SIO 76-299 (1); 56°43′N, 153°22′W; no date. USNM 60505 (1); Alitak Bay, Kodiak I.; 6 Aug. 1903. USNM 60503 (1); Chignik Bay, Kodiak I., 104–115 m; 10 Aug. 1903. USNM 60504 (1); Chignik Bay, Kodiak I., 57–108 m; 10 Aug. 1903. USNM 60502 (2); Chignik Bay, Kodiak I., 76–79 m; 10 Aug. 1903. CHUKCHI SEA: BCPM BC71-177 (1); 67°57′N, 168°34′W; 20 Aug. 1959. OSU 7081 (5); 67°30′N, 173°45′W; 23 Oct. 1962. UBC BC61-418 (7); 67°53.3′N, 166°42′W; 20 Aug. 1959. UBC BC61-104 (1); 67°47.5′N, 168°11′W; 14 Aug. 1959. UBC BC61-416 (1); 67°57′N, 168°02′W; 20 Aug. 1959. UBC BC61-103 (4); 68°32′N, 168°52′W; 14 Aug. 1959. UBC BC61-106 (3); 68°25′N, 167°55′W; 16 Aug. 1959. UBC BC61-417 (5); 67°55′N, 167°22′W; Aug. 1959. UBC BC61-440 (5); 66°43′N, 166°22′W; 25 Aug. 1959. UBC BC61-409 (1); 67°43.8′N, 167°55′W; 19 Aug. 1959. UW 15272 (1); 67°37′N, 168°50′W; 12 Aug. 1959. UW 15273 (1); 67°13′N, 167°30′W; 10 Aug. 1959. UW 15271 (1); 67°31.5′N, 165°55′W; 19 Aug. 1959. UW 15274 (1); 67°52′N, 168°12′W; 13 Aug. 1959. UW 15276 (1); 67°43.8′N,

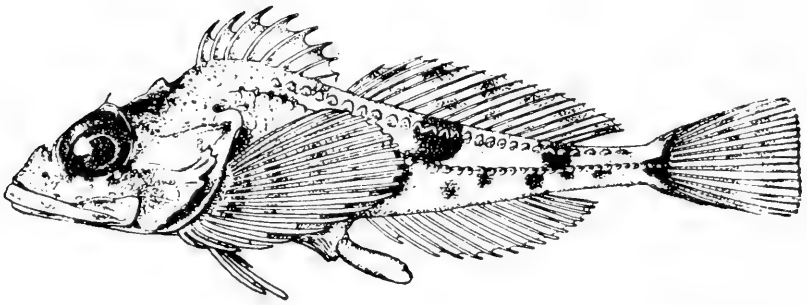


FIGURE 42. *Icelus ochotensis* Schmidt, 1927, male, approximately 90.0 mm TL; after Schmidt (1927).

168°35′W; 19 Aug. 1959. ARCTIC CANADA, LABRADOR, WEST GREENLAND: NMC 77-1463D (3); 69°09′48″N, 106°37′W; 30 Aug. 1965. NMC 77-1455D (12); 70°11′24″N, 124°16′42″W; 7 Aug. 1963. NMC 74-280 (2); 70°18′N, 143°13′W; 8 Aug. 1972. NMC 74-285 (2); 70°19′48″N, 146°26′30″W; 14 Aug. 1972. NMC 60-492 (4); 69°32′N, 138°57′W; 25 Aug. 1960. NMC 60-476 (3); 69°38′N, 138°38′W; 6 Aug. 1960. NMC 60-447 (6); 80°08′N, 86°20′W; 20 Aug. 1955. NMC 62-402 (1); 80°00′N, 86°00′W; 27 July 1962. NMC 62-385 (21); 74°39′06″N, 94°15′42″W; 17 July 1962. NMC 61-210 (1); 48°27′N, 63°47′W; 4 Oct. 1961. NMC 60-87 (3); 69°34′N, 80°17′W; 19 Sep. 1955. NMC 70-286 (2); 63°28′N, 67°21′W; 15 Aug. 1970. NMC 77-1351 (18); 69°09′30″N, 105°52′42″W; 3 Aug. 1966. ROM 28889 (1); 74°40′N, 94°50′W; 10 July 1972. ROM 28894 (1); 74°40′N, 94°50′W; 22 July 1972. ROM 23249 (2); Temple Bay; Belle I. Str.; 13 Aug. 1923. ROM 23164 (4); New Brunswick, Charlotte Cove, Temple Bay; 18 Aug. 1923. ROM 24094 (8); Nova Scotia, Temple Bay; 17 Aug. 1925. USNM 165179 (10); 59°23′N, 64°03′W; 10 Aug. 1950. USNM 165182 (3); 58°08′N, 62°55.6′W; 11 Aug. 1949. USNM 165178 (1); Labrador, Kangalaksiorvik Fjord; 10 Aug. 1950. USNM 165180 (1); 52°21′N, 55°56′W; 30 Aug. 1950. USNM 165181 (1); 54°15′45″N, 58°01′30″W; 22 July 1951. USNM 165177 (1); 59°25′N, 63°47′W; 10 Aug. 1950. USNM 165183 (7); Labrador, Lake Melville, off Lawland Pt.; 25 July 1950. USNM 165184 (11); 55°01.5′N, 59°33.3′W; 29 July 1949. USNM 165174 (7); 58°11.4′N, 62°34.2′W; 9 Aug. 1949. USNM 165376 (10); 56°37′N, 61°58′W; 7 Aug. 1951. USNM 165421 (6); Labrador, NE of Goose Bay Bar, Lake Melville; 28 Aug. 1951. USNM 165176 (49); 59°24′N, 63°51′W; 8 Aug. 1950. USNM 177595 (5); Labrador, Hebron Fjord, 3 miles (ca. 5 km) E of Freytag Inlet, 180 m; 31 July 1952. USNM 221344 (1); N.W.T., W shore Frobisher Bay; 26 Aug. 1942. USNM 165175 (4); 58°09′N, 63°34.2′W; 8 Aug. 1949. USNM 165185 (2); 58°09′N, 62°45.7′W; 9 Aug. 1949. USNM 165186 (3); 52°22.3′N, 55°56.7′W; 12 July 1949. USNM 177628 (3); Labrador, Hebron Fjord; 9 July 1954. USNM 165188 (7); Labrador, Kangalaksiorvik Fjord; 8 Aug. 1950. USNM 177621 (11); Labrador, Hebron Fjord; 10 July 1954. USNM 165391 (14); 56°37′N, 62°04′W; 7 Aug. 1951. USNM 165187 (7); 55°05′N, 59°30′W; 1 Aug. 1949. USNM 177641 (11); Labrador, Hebron Fjord; 11 July 1954. USNM 165297 (35); 58°08.6′N, 62°55.6′W; 18 Aug. 1949. ZMUC P81.1110–1112 (3); Totnesrroad, Exeter Sound, Baffinland, 75–200 m; 17 Sep. 1928. ZMUC P81.1891 (1); Greenland, Nordre Stromfjord; 24 July 1911. ZMUC P81.1069 (1); 71°21′N, 54°27′W; 6 Sep. 1928. ZMUC P81.1129–1134 (6); 77°17′N, 69°59′W; 5 Aug. 1928. ZMUC P81.1889 (1); Lichtenau, W Greenland; 26 Aug. 1841. KARA, LAPTEV SEAS: BMNH 1964.4.18:10–11 (2); 74°53′N, 122°20′E, 20 m; 24 Aug. 1932. CAS-SU 40928 (1); 73°50′N, 75°52′E, 27 m; 1936. CAS-SU 40929 (1); 74°27′N, 73°12′E, 29 m; 1936. ZMUC P81.1890 (4); Kara Sea, 180 m; 1 June 1885. ZMUC P81.998–1002 (4); Kara Sea, Dijmphna-Togtets Exped.; 1 June 1885. ZMUC P81.1016 (1); Kara Sea, Dijmphna-Togtets Exped.; 1 June 1885.

Icelus ochotensis Schmidt, 1927

(Figure 42)

Icelus ochotensis SCHMIDT, 1927:4, figs. 1, 2 (in part; orig. descr.; type-locality N Sea of Okhotsk, between 58°48.5′–53°56′N and 151°18.5′–137°32′E, 60–105 m; some of these spec. are *I. spatula*; illus. of male and male urogenital papilla; key).

Icelus uncinalis: SCHMIDT 1927:3 (in part; Andriashev [1937a] cited these spec., in part, as synon. of *I. uncinalis crassus* [see below]; these spec. were not available to me); SOLDATOV AND LINDBERG 1930:176 (in part; Sea of Okhotsk, Sea of Japan).

Icelus uncinalis ochotensis: SCHMIDT 1935:414, 417 (in part; Sea of Okhotsk; key).

Icelus uncinalis crassus ANDRIASHEV 1937a:265, pl. 5, fig. 2 (in part; orig. descr. of subsp.; Sea of Okhotsk, Shantar Is.); TARANETZ 1937:107 (key; Sea of Okhotsk); SCHMIDT 1950: 125, fig. 11 (descr.; Sea of Okhotsk, 10–115 m).

DIAGNOSIS.—Parietal spines absent; nuchal spines large, blunt, conical, directed dorsally. Suborbital stay spines absent; lacrimal spines absent. Uppermost preopercular spine bifurcated. Platelike scales of dorsal scale row Pattern B (Fig. 18*B*). Rows of scales between dorsal scale row and lateral line absent. Rows of scales between lateral line and anal fin absent. Axillary scales 10–14; 3–5 in uppermost row. Dorsal caudal peduncle scales present; ventral caudal peduncle scales present or absent. Lateral line scales Pat-

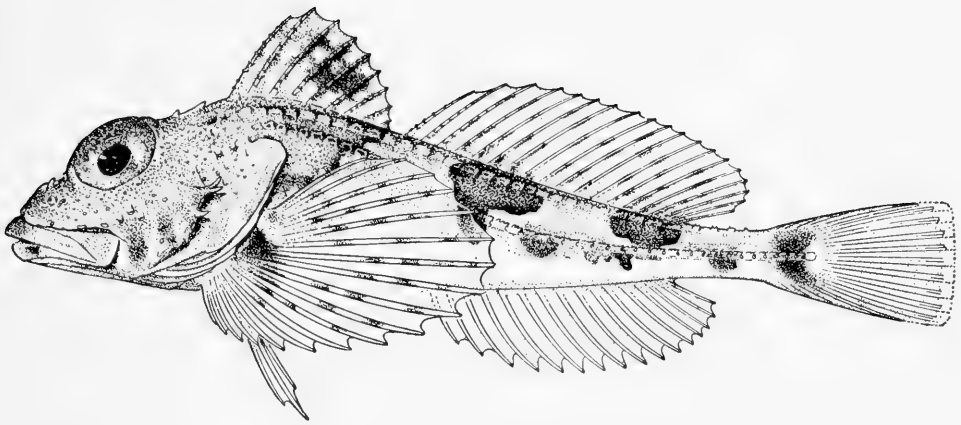


FIGURE 43. *Icelus uncinalis* Gilbert and Burke, 1912, male, 81.0 mm SL; after Gilbert and Burke (1912).

tern A (Fig. 19*A*), extending past posterior edge of hypural plate onto caudal rays. Supraocular cirrus lightly pigmented (darkly pigmented in one specimen examined), other cirri absent. Nasal tubes lightly pigmented (similar to snout). Urogenital papilla of male with dorsoventrally flattened basal portion and hooklike terminal appendage (Fig. 23*E*).

DESCRIPTION.—General body shape shown in Figure 42. Body elongate, deep, robust anteriorly; greatest depth at anterior part of spinous dorsal fin. Head large, deeper than wide. Eye moderately large, 1.0–1.5 times snout length. Mouth large; posterior edge of maxilla reaching (or nearly reaching) posterior rim of orbit. Top and sides of head sparsely to moderately densely scaled.

Coloration in preservative. Overall body color light brown. Irregularly shaped darker brown or black blotches on dorsal body surface and top of head. Scattered darker brown blotches on sides of body and dorsal fins. Pectoral fins and caudal fin marked with dark brown vertical bars. Underside much lighter brown or whitish.

MEASUREMENTS (from 3 spec., 104.0—140.5 mm).—Ranges of values only are given; the following expressed as thousandths of SL: head length 384–394; lacrimal length 72–81; snout length 114–130; least interorbital width 28–31; orbit diameter 110–130; greatest body depth 252–274; least caudal peduncle depth 53–57; pectoral fin base length 135–152; upper jaw length 196–220.

COUNTS (from 4 spec., except where indicated).—Ranges only: dorsal fin spines 8–9; dorsal fin soft rays (3 spec.) 18–20; anal fin rays 14–16; pectoral fin rays 17–18; scales in dorsal scale row (3 spec.) 34–35; axillary scales 10–14; axillary scales, uppermost row 3–5; lateral line scales (3 spec.) 42.

REMARKS.—Schmidt's (1927) type-specimens, deposited in IZL, were unavailable for this study; hence, no lectotype is herein designated.

DISTRIBUTION.—The specimens I examined were from the southern Sea of Okhotsk (ALBATROSS sta. 5016 and 5017) at depths of about 125 m; off the eastern coast of Kamchatka; and in the Sea of Japan in about 169–210 m (Fig. 41). Distributional records for unexamined material are not included because many of the specimens determined by Andriashev (1937a) to be *Icelus uncinalis crassus* are most likely *I. spatula*. However, Schmidt's (1927) material, among which are the types, included specimens from the northern Sea of Okhotsk: "It is found there between 58°48.5′ and 53°56′N and 151°18.5′ and 137°32′E Gr. in the depths of 30–53 fathoms" (Schmidt 1927:6).

ETYMOLOGY.—The specific name, *ochotensis*, is derived from the site of the collection of the type-material, the Sea of Okhotsk.

MATERIAL EXAMINED (4 spec., 104.0–140.5 mm).—Non-type-material. CAS-SU 68830 (1); Petropavlovsk, Avatcha Bay, E coast of Kamchatka, 52°47′N, 158°44′E; 18–19 June 1906. HUMZ 65664 (1); Sea of Japan, 37°14′N, 136°27′E, 169–210

m; 7 June 1977. USNM 119856 (1); 46°43′30″N, 143°45′E, 125 m, Albatross sta. 5017; 26 Sep. 1906. USNM 119861 (1); 46°44′30″N, 143°45′E, 125 m, Albatross sta. 5016; 26 Sep. 1906.

Icelus uncinalis Gilbert and Burke, 1912

(Figure 43)

Icelus uncinalis Gilbert and Burke, 1912:39, figs. 2, 2a (orig. descr.; type-locality Attu I., 52°55′40″N, 173°26′E, 247 m, Albatross sta. 4784; compar. with *I. spatula*); Schmidt 1927:3 (in part; se Bering Sea and around Commander Is.); Jordan, Evermann, and Clark 1930:379 (compiled distr.); Schmidt 1935:414, 417 (in part; key to *Icelus* spp.); Taranetz 1937:107, 108 (in part; key; distr.); Andriashev 1937a:259, pl. 5, fig. 1 (in part; descr. of subspp.; key; distr.); Wilimovsky 1958:67 (in part; key; compiled distr.); Quast and Hall 1972:23 (in part; compiled; e Bering Sea records are most likely *I. spatula*); Howe and Richardson 1978: 49, 138 (diag.; key; lit.).

Icelus uncinalis uncinalis: Schmidt 1935:414, 417 (desig. of subsp.; w Bering Sea; key); Taranetz 1937:107, 108 (key; Bering Sea); Andriashev 1937a:259, pl. 5, fig. 1 (descr. of subspp. based on morphol. of parietal and nuchal spines, shape of head, and length of dorsal scale row; w Bering Sea); Wilimovsky 1958:67 (in part; compiled).

Diagnosis.—Parietal and nuchal spines present, short, sharp. Suborbital stay spines absent; lacrimal spines absent. Uppermost preopercular spine simple or bifurcated. Platelike scales of dorsal scale row Pattern B (Fig. 18*B*). Scales between dorsal scale row and lateral line absent. Scales between lateral line and anal fin absent. Axillary scales 12–20, 4–7 in uppermost row. Dorsal and ventral caudal peduncle scales absent. Lateral line scales Pattern A (Fig. 19*A*), extending past posterior edge of hypural plate onto caudal rays (one scale on caudal rays). Supraocular cirrus present; narrow at base, widening distally, usually branched or multifid at tip. Parietal, opercular, suborbital stay cirri present or absent; other cirri absent. Head cirri lightly pigmented (similar to dorsal surface of head). Nasal tubes lightly pigmented (similar to snout). Urogenital papilla of male with cylindrical, slightly dorsoventrally flattened basal portion and short, curved terminal appendage (Fig. 23*E*).

Description.—General body shape shown in Figure 43. Body elongate, robust anteriorly; greatest depth at anterior portion of spinous dorsal fin. Head large, deeper than wide, "cheeks vertical" (Gilbert and Burke 1912). Eye large, about 1.5 times snout length. Mouth moderately large; posterior end of maxilla reaching to below middle of orbit. Top and sides of head, including opercles, with scattered small scales or prickles (occasionally densely scaled).

Coloration in preservative. Overall body color light yellowish brown. Four distinct darker grayish-brown saddle markings on dorsal body surface and sides (above lateral line): a large one under spinous dorsal fin, two smaller ones under soft-rayed dorsal fin, and one marking the posterior edge of the caudal peduncle. Spinous dorsal fin with a faint darker brown spot. Pectoral fins with faint brown vertical bars. Scattered dusky spots on sides of body above and below lateral line. Underside lighter yellowish tan or whitish.

Measurements (from 14 spec., 38.5–81.0 mm, except where indicated).—The following expressed as thousandths SL, [value for holotype] range (mean; standard deviation): head length (13 spec.) [370] 359–400 (377; 12.1); lacrimal length (13 spec.) [80] 52–80 (61; 8.1); snout length (11 spec.) [117] 77–117 (93; 12.7); least interorbital width [20] 20–29 (23; 2.5); orbit diameter [123] 115–148 (131; 9.8); greatest body depth (12 spec.) [247] 217–270 (237; 14.4); least caudal peduncle depth (11 spec.) [58] 43–60 (55; 5.0); pectoral fin base length (6 spec.) [123] 116–133 (123; 5.7); upper jaw length (13 spec.) [173] 130–204 (163; 22.1).

Counts (from 8 spec., except where indicated).—Values expressed, [value for holotype] range (mode; mean): dorsal fin spines [9] 9 (9; 9.0); dorsal fin soft rays [19] 19–20 (19; 19.5); anal fin rays [16] 14–16 (15; 15.0); pectoral fin rays [18] 17–18 (18; 17.8); scales in dorsal scale row (13 spec.) [35] 30–35 (31; 32.4); axillary scales (14 spec.) [20] 12–20 (16; 16.4); axillary scales, uppermost row (14 spec.) [7] 4–7 (5; 5.0); lateral line scales (11 spec.) [42] 41–42 (41; 41.5).

Distribution.—*Icelus uncinalis* has only been collected in the western Bering Sea—off Petrel Bank, Bering Island, Commander Islands, and western Aleutian Islands (Fig. 41)—between about 52°–55°N, and 167°E–179°W, in depths of 79–247 m. Numerous accounts of the species in the Sea of Japan, Sea of Okhotsk, and the eastern Bering Sea are attributable to *I. spatula* (and likely other *Icelus* species as well).

Etymology.—The specific name, *uncinalis,* is derived from the Latin *uncinus,* meaning a small hook, and refers to the short, curved terminal appendage of the male urogenital papilla.

Material Examined (14 spec., 38.5–81.0 mm).—**Holotype:** USNM 74366, male, 81.0 mm; near Attu I., 52°55′40″N, 173°26′E, 247 m, Albatross sta. 4784; 11 June 1906.

Paratypes: CAS-SU 25237 (2:46.0–54.0 mm); Cape Monati, Bering I., 54°36′15″N, 166°57′15″E, 132 m, Albatross sta. 4792; 14 June 1906. USNM 70855 (1:79.0 mm); Semiso-

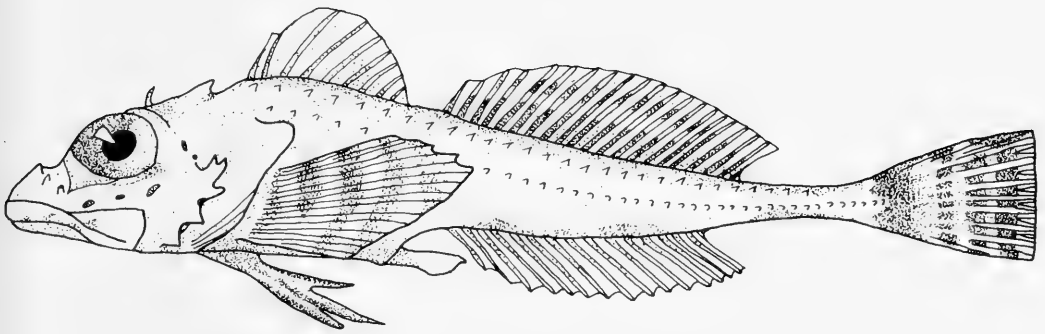


FIGURE 44. *Icelus stenosomus* Andriashev, 1937, male, approximately 52.0 mm TL; after Andriashev (1937a).

pochnoi I., 52°11′N, 179°49′E, 79–95 m, ALBATROSS sta. 4777; 5 June 1906. USNM 70885 (2:38.5–41.0 mm); near Attu I., 52°55′40″N, 173°26′E, 247 m, ALBATROSS sta. 4784; 11 June 1906. USNM 70912 (3:43.5–47.0 mm); Semisopochnoi I., 52°11′N, 179°57′W, 99–112 m, ALBATROSS sta. 4779; 5 June 1906. USNM 70892 (1:73.0 mm); Cape Monati, Bering I., 54°38′45″N, 167°11′45″E, 117 m, ALBATROSS sta. 4790; 14 June 1906. USNM 70897 (2:51.5–53.5 mm); Cape Monati, Bering I., 54°36′15″N, 166°58′15″E, 139 m, ALBATROSS sta. 4791; 14 June 1906.

Nontype-material: BMNH 1964.4.18:16–17 (2:54.0–58.5 mm); W side Bering I., 126 m, VITIAZ sta. 526; 18 Aug. 1950.

Icelus stenosomus Andriashev, 1937

(Figure 44)

Icelus uncinalis: SCHMIDT 1927:3 (in part; Sea of Japan; placed in synonymy by Andriashev [1937a]); SOLDATOV AND LINDBERG 1930:176 (in part; Sea of Japan); POPOV 1931:145 (in part; compiled).

Icelus uncinalis stenosomus ANDRIASHEV 1937a:266, pl. 5, fig. 3 (orig. descr.; no type-specimens designated; Sea of Japan, Peter the Great Bay N to Tartar Str.); TARANETZ 1937:107, 108, fig. 60 (key to spp. and subspp. of *Icelus*; Sea of Japan); HONMA 1957:111 (meristic char.; Sea of Japan).

Icelus uninalis UENO 1972:91 (in part; name misspelled; compiled distr.).

DIAGNOSIS.—Parietal spines absent; nuchal spines short, sharp, posteriorly directed. Suborbital stay spines absent; lacrimal spines absent. Uppermost preopercular spine bifurcated. Platelike scales of dorsal scale row Pattern B (Fig. 18*B*). Rows of scales between dorsal scale row and lateral line absent. Rows of scales between lateral line and anal fin absent. Axillary scales 8–10, 4 in uppermost row. Dorsal and ventral caudal peduncle scales present. Lateral line scales Pattern A (Fig. 19*A*), extending past posterior edge of hypural plate onto caudal rays (one scale on caudal rays). Supraocular cirrus present, lightly pigmented (similar to dorsal surface of head); other cirri absent. Nasal tubes lightly pigmented (similar to snout). Urogenital papilla of male with cylindrical, slightly dorsoventrally flattened basal portion and a short, curved terminal appendage.

DESCRIPTION.—General body shape shown in Figure 44. Body elongate, slender; laterally compressed posterior to opercular openings. Greatest body depth at spinous dorsal fin. Head large, depressed; wider than deep. Eye large, about twice snout length. Mouth large; posterior end of maxilla nearly reaching posterior rim of orbit. Scattered scales or prickles on top and sides of head. Narrow band of small scales or prickles just dorsal to dorsal scale row.

Coloration in preservative. Overall body color light brown. Three indistinct darker brown bars on dorsal body surface: one beneath spinous dorsal fin, one beneath anterior portion of soft-rayed dorsal fin, and one beneath posterior portion of soft-rayed dorsal fin. Dark brown or black splotch on cheek beneath eye (not shown in Fig. 44). Underside whitish; urogenital papilla of male whitish.

MEASUREMENTS (2 spec., 55.0—55.5 mm).—Ranges of values only given; the following expressed as thousandths SL: head length 327–342; lacrimal length 45–47; snout length 60–65; least interorbital width 20–25; orbit diameter 126–127; greatest body depth 182–198; least caudal peduncle depth 45–49; upper jaw length 171–182.

COUNTS (from 2 spec.).—Values expressed, [range of values from Andriashev's (1937a) description] range of values for 2 specimens examined: dorsal fin spines [8–9] 9; dorsal fin soft

rays [18–19] 19; anal fin rays [13–16] 16; pectoral fin rays [16–18] 17–18; scales in dorsal scale row [32–36] 35–38; axillary scales [no values] 8–10; axillary scales, uppermost row [no values] 4; lateral line scales [40–43] 41–42.

COMMENTS.—Andriashev's (1937a) specimens of *Icelus uncinalis stenosomus,* deposited in IZL (nos. 17645, 17641–42, 17646–47, 21906–907), were unavailable for examination; hence, no lectotype is herein designated.

DISTRIBUTION.—The two specimens I examined were collected in the Sea of Japan and Tartar Strait (Fig. 25). Andriashev (1937a) listed *I. stenosomus* as occurring in the Sea of Japan southward to Peter the Great Bay and northward to the Tartar Strait in depths of 71–171 m.

ETYMOLOGY.—The specific name, *stenosomus,* is derived from the Latin *sten-*, meaning narrow, and *somus,* or body, and refers to the very slender, elongate body form.

MATERIAL EXAMINED (2 spec., 55.0–55.5 mm).—Nontype-material: BMNH 1964.4.18:18–19 (1); Tartar Str., 48°08′30″N, 140°08′30″E, 115 m; 2 Sep. 1913. CAS-SU 40932 (1); Sea of Japan, 42°51′N, 133°56′E; 2 May 1913.

Icelus sp.

COMMENTS.—This odd female exhibits a mosaic of character states which makes its present specific identification impossible. The presence of Pattern B (Fig. 18*B*) scales in the dorsal scale row, of parietal spines, and the short, stout, rather robust body identifies this specimen as a member of the *I. bicornis* group. The presence of dorsal and ventral caudal peduncle scales, and the posteriormost lateral line scale on the caudal rays is similar to *I. stenosomus.* However, the presence of parietal spines is dissimilar to *I. stenosomus,* and many of the body proportions (see measurements below) are well outside the ranges established for this species.

MEASUREMENTS.—Length 64.0 mm; the following expressed as thousandths SL: head length 398; lacrimal length 89; snout length 113; least interorbital width 27; orbit diameter 148; greatest body depth 242; least caudal peduncle depth 55; pectoral fin base length 148; upper jaw length 208.

COUNTS.—Dorsal fin spines 9; dorsal fin soft rays 18; anal fin rays 18; pectoral fin rays 17; scales in dorsal scale row 35; axillary scales 12; axillary scales, uppermost row 4; dorsal caudal peduncle scales 1; ventral caudal peduncle scales 2; lateral line scales 42.

MATERIAL EXAMINED.—USNM 119862, female, 64.0 mm; Sea of Japan, Bomasiri Shima, 45°27′50″N, 140°54′E, ALBATROSS sta. 4994; 22 Sep. 1906.

ACKNOWLEDGMENTS

I express my deepest appreciation for the advice, encouragement, and support provided by my major professor, Theodore W. Pietsch, without whose guidance this study would not have been possible. I also acknowledge the support provided by the other members of my supervisory committee, Bruce S. Miller and T. Saunders English.

The following persons and institutions provided material in the way of loans and gifts: W. F. Smith-Vaniz (ANSP); A. Peden (BCPM); A. Wheeler and M. L. Holloway (BMNH); W. N. Eschmeyer, T. Iwamoto, and P. Sonoda (CAS); R. K. Johnson (FMNH); K. Amaoka and M. Yabe (HUMZ); W. L. Fink and K. Hartel (MCZ); D. E. McAllister (NMC); E. Ahlander (NRMS); K. Matsuura (NSMJ); J. Long (OSU); E. J. Crossman and E. Peck (ROM); J. Pulsifer (SIO); L. Knapp (SOSC); N. J. Wilimovsky and R. Carveth (UBC); T. Abe (UMUT); S. Weitzman and S. Karnella (USNM); T. W. Pietsch (UW); and E. Bertelsen (ZMUC). Special thanks go to W. N. Eschmeyer, T. Iwamoto, P. Sonoda, and the collection technicians of the California Academy of Sciences and to R. Carveth and J. D. McPhail of the University of British Columbia for their assistance and hospitality during visits to their respective institutions.

The assistance of Kevin M. Howe in the compilation of literature records, in providing partial funding to the author, and for providing many hours of stimulating discussion about cottoid systematics is gratefully acknowledged. Daniel M. Cohen and an anonymous reviewer provided helpful comments on the manuscript. Many thanks also to fellow graduate students D. B. Grobecker, G. S. Glodek, and S. Leipertz for their helpful comments during the course of this study.

Lastly, a very special "thank you" goes to my wife, Joanna, and to my son, Anthony, for their patience, devotion, and support, which greatly aided me in the completion of this work.

This study was supported by a grant to T. W. Pietsch from the Cooperative Systematics and Analyses of Polar Biological Materials (National Science Foundation Grant DPP-76-23979A01), B. Landrum, principal investigator. An earlier

version was submitted to the Graduate School, University of Washington in partial fulfillment of the requirements for the degree of Master of Science.

Literature Cited

Allis, E. P. 1909. The cranial anatomy of the mail-cheeked fishes. Zoologica (Stuttgart) 22:1–219.

Andriashev, A. P. 1937a. Neue Angaben über die Systematik und Geographische der zweihörnigen pazifischen *Icelus* Arten. Zool. Jahrb. 69:253–276.

———. 1937b. On the ichthyofauna of the Bering and Chukchi seas. Issled. Morei 25:292–335.

———. 1939. A survey of zoogeography and the origin of the fish fauna of the Bering Sea and adjacent waters. Leningrad Univ. 187 p.

———. 1954. Fishes of the northern seas of the USSR. Moscow-Leningrad Izd. AN SSSR. 567 p. (Translated from Russian by the Israel Program for Scientific Translations [1964], 617 p.)

Backus, R. H. 1957. The fishes of Labrador. Bull. Am. Mus. Nat. Hist. 113:273–338.

Barraclough, W. E. 1971. A sculpin (*Icelus spiniger*) new to the coastal waters of British Columbia. J. Fish. Res. Bd. Can. 28:1922–1924.

Bean, T. 1879. Fishes collected in Cumberland Gulf and Disko Bay. Bull. U.S. Natl. Mus. 15:107–140.

———. 1890. New fishes collected off the coast of Alaska and the adjacent region southward. Proc. U.S. Natl. Mus. 13:37–45.

Berg, L. S. 1940. A classification of fishes, both recent and fossil. Tr. Zool. Inst. SSSR 5:87–517.

Bertelsen, E. 1937. Contributions to the animal ecology of the fjords of Angmakssalik and Kangerdlugssuaq in East Greenland. Meddel. Grønland 108:1–58.

Bolin, R. L. 1944. A review of the marine cottid fishes of California. Stanford Ichthyol. Bull. 3:1–135.

———. 1947. The evolution of the marine Cottidae of California, with a discussion of the genus as a systematic category. Stanford Ichthyol. Bull. 3:153–168.

Briskina, M. 1939. Feeding in non-commercial fishes of the Barents Sea. Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okean. 4:339–354.

Collett, R. 1874. Norges fiske, med bemaerkninger om deres Udbredelse. Forh. Vidensk. Selsk. Krist. 1874 (1875): 1–240.

———. 1879. Fiske fra Nordhavs-Expeditionens sidst togt, sommeren, 1878. Forh. Vidensk. Selsk. Krist. 1878 (1879), 14:1–106.

———. 1880. Fiske, Zoologi, Norske Nordhavs-Expedition, 1876–1878. Christiana. 165 p.

———. 1884. Meddelelser om Norges fiske i aarene 1879–1883. Nyt Mag. Naturvid. Christiana 29:47–123.

———. 1905. Meddelelser om Norges fiske i aarene 1884–1901. III. Forh. Vidensk. Selsk. Krist. 7:1–173.

Derjugin, K. M. 1928. Fauna of the White Sea and its life conditions. Issled. Morei SSSR 7:1–511.

Dresel, H. G. 1884. Notes on some Greenland fishes. Proc. U.S. Natl. Mus. 7:244–258.

Dunbar, M. J., and H. H. Hildebrand. 1952. Contributions to the study of the fishes of Ungava Bay. J. Fish. Res. Bd. Can. 9:83–128.

Ehrenbaum, E. 1901. Die Fische der Arctis. Fauna Arctica 2:65–168.

———. 1905. Eier und Larven von Fische. Nordisches Plankton 1:1–216.

———. 1936. Naturgeschichte und Wirschaffliche der Seefische Nordeuropas. Handbuch der Seefischerei Nordeuropas 2:1–337.

Eschmeyer, W. N. 1969. A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpaenidae). Occas. Pap. Calif. Acad. Sci. 79. 143 p.

Esipov, V. 1931. Fishes collected by the expedition to Franz Josef Land in summer, 1929. Tr. Inst. Izuch. Severa 49:156–165.

———. 1933. Brief review of the ichthyofauna of the Kara Sea. Arktika 1:169–185.

———. 1939. Fishes collected by the expedition on the icebreaker "SADKO" in 1935. Zool. Zh. 18:877–887.

———. 1940. Fishes of the Laptev Sea. Zool. Zh. 19:139–142.

Esmark, L. 1868. Bidrag til Finmarkens fiskefauna. Skand. Naturforsk. Forh. 10:516–529.

Evermann, B. W., and E. L. Goldsborough. 1907. The fishes of Alaska. Bull. U.S. Bur. Fish. 26:219–360.

Fedorov, V. V. 1973. A listing of Bering Sea fish. Izv. Tikh. Nauchno-issled. Inst. Rybn. Khoz. Okean. 87:2–71.

Fries, B. F., C. U. Ekström, and C. J. Sundevall. 1893–1895. A history of Scandinavian fishes, rev. and compl. by F. A. Smitt, Stockholm and Paris, I. 1893:1–566+viii, figs. 1–134.

Gaimard, P. 1842–1856. Voyage en Scandinavie, en Laponie, au Spitzberg et aux Ferge sur la corvette "Recherche." Poissons, Section VII. Zoologie. Plates.

Gilbert, C. H. 1895. The ichthyological collections of the steamer Albatross during the years 1890 and 1891. Rep. U.S. Comm. Fish. 19:393–476.

———, and C. V. Burke. 1912. Fishes from Bering Sea and Kamchatka. Bull. U.S. Bur. Fish. 30:31–96.

Gill, T. 1861. Catalogue of the fishes of the eastern coast of North America from Greenland to Georgia. Proc. Phila. Acad. Sci. (2)13:1–63.

Goode, G. B., and T. Bean. 1896. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers Blake, Albatross, and Fish Hawk, with an atlas containing 417 figures. U.S. Natl. Mus. Spec. Bull. 2. 553 p.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:341–455.

Günther, A. 1860. Catalogue of the acanthopterygian fishes in the collection of the British Museum 2. London. 548 p.

———. 1877. Account of the fishes collected by Capt. Feilden between 78° and 83° N Lat. during the Arctic Expedition 1875–6. Proc. Zool. Soc. London 1877:293–295.

———. 1887. Report on the deep-sea fishes procured during the voyage of H.M.S. Challenger during the years 1873–1876. Rep. Sci. Results H.M.S. Challenger, Zool. 22(57): 1–335, pls. 1–73.

Halkett, A. 1913. Checklist of the fishes of the Dominion of Canada and Newfoundland. King's Printer. Ottawa. 138 p.

Hart, J. L. 1973. Pacific fishes of Canada. Fish. Res. Bd. Can. Bull. 180. 740 p.

Hildebrand, S. F. 1939. An annotated list of the fishes col-

lected on the several expeditions to Greenland, the Fox Basin region, and the coast of Labrador by Capt. R. A. Bartlett, from 1925 to 1935. Meddel. Grønland 125:1–12.

Hofsten, N. 1919. Die fische des eisfjords. K. Svensk. Akad. Handl. 54:1–129.

Hognestad, P. T. 1962. Contributions to the fish fauna of Spitzbergen. 1. The fish fauna of Isfjorden. Acta Boreal. (A) 18:1–36.

Honma, Y. 1957. Further additions to "A list of fishes collected in the province of Echigo, including Sado Island." Japan. J. Ichthyol. 6:109–112.

Howe, K. M., and S. L. Richardson. 1978. Taxonomic review and meristic variation in marine sculpins (Osteichthyes: Cottidae) of the northeast Pacific Ocean. Unpubl. report, NOAA-NMFS Contract No. 03-78-M02-120, 30 Sep. 1978. 142 p.

Jensen, A. S. 1904. The fishes of East-Greenland. Meddel. Grønland 29:211–276.

———. 1910. Fishes. Report of the Second Norwegian Arctic Expedition in the "Fram," 1898–1902, no. 25. 15 p.

———, and H. Volsoe. 1949. A revision of the genus *Icelus* (Cottidae) with remarks on the structure of its urogenital papilla. Danske Vidensk. Selsk. Biol. Meddel. 21:1–26.

Johansen, F. 1912. The fishes of the Danmark Expedition. Meddel. Grønland 45:633–675.

Jordan, D. S. 1923. A classification of fishes, including families and genera as far as known. Stanford Univ. Publ. Biol. Sci. 3:77–243.

———, and B. W. Evermann. 1896. A check-list of the fishes and the fish-like vertebrates of North and Middle America. Rep. U.S. Fish. Comm. 21:207–584.

———, and ———. 1898. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47 (Pt. 2):1241–2188.

———, ———, and H. W. Clark. 1930. Checklist of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rep. U.S. Fish. Comm. (1900). Appendix 10. 670 p.

———, and C. H. Gilbert. 1882. Synopsis of the fishes of North America. Bull. U.S. Natl. Mus. 16:1–1074.

———, and E. C. Starks. 1904. A review of the Cottidae or sculpins found in the waters of Japan. Proc. U.S. Natl. Mus. 27:231–335.

———, S. Tanaka, and J. O. Snyder. 1913. A catalogue of the fishes of Japan. J. Coll. Sci. Imp. Univ. Tokyo 33:1–497.

Joubin, M. 1938. Faune ichthyologique de l'Atlantique Nord. Cons. Int. l'Explor. Mer. Köbenhavn. No. 18.

Kendall, W. 1911. Report on the fishes collected by Mr. Owen Bryant on a trip to Labrador in the summer of 1908. Proc. U.S. Natl. Mus. 38:503–510.

Knipovich, N. 1897. Verzeichniss der Fische des Weissen und Murmanschen Meeres. Ann. Mus. St. Pétersbourg 1897, 2:144–158.

———. 1901. Zoologische Ergebnisse der russischen Expeditionen nach Spitzbergen—Ueber die in den Jahren 1899–1900 in Gebiete von Spitzbergen gesammelten Fische. Ann. Mus. Zool. Acad. Sci. St. Pétersbourg 6:56–83.

———. 1903. Zoologische Ergebnisse der russischen Expeditionen nach Spitzbergen. Fische. Nachtrag. Ann. Mus. Zool. Acad. Sci. St. Pétersbourg 8:144–156.

———. 1907. Zur Ichthyologie des Eismeeres. Die von der russischen Polar-Expedition im Eismeer gesammelten Fische. Mém. Acad. Sci. St. Pétersbourg (8)18(5):1–53.

———. 1926. A key to fishes from the Barents, White and Kara seas. Tr. Inst. Izuch. Severa 27:1–183.

Koefoed, M. 1907. Poissons. Pages 485–499 *in* Croisière oceanographique accomplie a bond de la Belgica dans la Mer du Grönland, 1905. Brussels.

Krøyer, H. N. 1845. Ichthyolgiske bidrag. 7. *Icelus hamatus*. Naturhist. Tidsskr. 1:253–263.

Le Danois, E. 1914. Etudes sur quelques poissons des océans arctique et atlantique. Ann. Inst. Océanogr. Monaco 7:1–75.

Legeza, M. 1956. Ecology and distribution of the sculpins of the waters of southern Sakhalin and the southern Kurile Islands. Tr. Probl. Temat. Cob. Zin. 6:122–131.

Leim, A. H., and W. B. Scott. 1966. Fishes of the Atlantic Coast of Canada. Fish. Res. Bd. Can. Bull. 155. 485 p.

Lilljeborg, W. 1884. Sveriges och Norges fiskar 1. Uppsala. 728 p.

Lindberg, G. U. 1959. A list of the fauna of southern Sakhalin and the southern Kurile Islands. Issled. Dal'nevost. Morei SSSR 6:173–256.

———, and A. P. Andriashev. 1938. Survey of the geographical forms of the Far Eastern goby (*Icelus spiniger* Gilb.). Tr. Hydrobiol. Exped. Zool. Inst. AN SSSR, Sea of Japan. Pp. 515–525.

Linnaeus, C. 1758. Systema naturae per regna tria secundum classes, ordinum, genera, species cum characteribus, differentiis, synonymis, locis. Laurentii Salvii, Holmiae. Tenth edition, Vol. I, 824 p.

Lütken, C. F. 1876. Korte bidrag til nordiske ichthyographi. Vidensk. Meddel. Naturh. Forh. Kjøbenhavn 1876:355–388.

———. 1887. Et bidrag til kundskab om Kara-Havets fiske. Pages 1–40 *in:* Dijmphna-Togtets Zoologisk-botaniske Udbytte, Kjøbenhavn.

———. 1898. The ichthyological results of the expeditions of the "Ingolf." Danish Ingolf Exped. 2(1):1–39.

McAllister, D. E. 1960. Keys to the marine fishes of Arctic Canada. Nat. Hist. Pap. Natl. Mus. Can. 5:1–21.

———. 1962. Fishes of the 1960 "Salvelinus" program from western Arctic Canada. Bull. Natl. Mus. Can. 185:17–39.

———. 1963. Systematic notes on the sculpin genera *Artediellus*, *Icelus* and *Triglops* on Arctic and Atlantic coasts of Canada. Bull. Natl. Mus. Can. 185:50–59.

Malm, A. W. 1865. Ichthyologiska bidrag till Skandinaviens fauna. Förhandl. Skand. Natur. 9:405–414.

Malmgren, A. J. 1865. Om Spetsbergens fisk-fauna. Oefvers. Avens. Vet. Akad. Förhandl. 1864:489–539.

Matsubara, K. 1836. A review of two genera of Japanese sculpins, *Ereunias* and *Marukawichthys*, with special reference to their systematic positions. J. Imp. Fish. Inst. (Japan) 31:97–114.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Co., New York. 428 p.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game Fish Bull. 157. 235 p.

Nelson, J. S. 1976. Fishes of the world. Wiley-Interscience, New York. 416 p.

Neyelov, A. V. 1979. Seismosensory systems and the classification of kerchaki fishes (Cottidae: Myoxocephalinae, Artediellinae). Leningrad "Nauka." Leningrad Otdel. 208 p.

Nybelin, O. 1941. Cottiden-Studien. Zool. Anz. Leipzig 133: 215–224.

———. 1963. Zur Morphologie und Terminologie des Schwanzskelettes der Actinopterygier. Ark. Zool. 15:485–516.

Okada, Y. 1938. A catalogue of vertebrates of Japan. Maruzen Co. Ltd., Tokyo. 412 p.

———, and K. Matsubara. 1938. Keys to the fishes and fish-like animals of Japan. Tokyo-Osaka. 584 p.

Pavlenko, M. N. 1910. Fishes of Peter the Great Bay. Tr. Kazan. Obshch. 42:1–95.

Pfaff, J. R. 1937. Fishes collected on the Fifth Thule Expedition. Report of the Fifth Thule Expedition, 1921–1924, Zoology (Fishes) 2:1–19.

Pietschmann, V. 1932. Ichthyologische Ergebnisse einer Fischdampferreise nach Grönland. Meddel. Grønland 92: 1–59.

Popov, A. M. 1926. On fishes of the Kara Sea and adjacent regions of the Barents Sea. Tr. Leningrad Obshch. Estest. 6:27–58.

———. 1931. Study of the fish fauna in the Sea of Okhotsk. Issled. Morei SSSR 14:121–154.

———. 1933. On the fishes of the Siberian Sea. Artika 1: 157–167.

Quast, J. C. 1965. Osteological characteristics and affinities of the hexagrammid fishes, with a synopsis. Proc. Calif. Acad. Sci., Ser. 4, 31:563–600.

———, and E. L. Hall. 1972. List of fishes of Alaska and adjacent waters, with a guide to some of their literature. NOAA Tech. Rep. NMFS Spec. Sci. Rep. Fish. 658. 47 p.

Rass, T. S. 1929. A survey of fishes collected by the Murmansk Biological Station in summer, 1926. Rab. Murman. Biol. Sta. 3:1–30.

———. 1949. Composition of the ichthyofauna of the Barents Sea and taxonomic characters of the eggs and larvae of fishes from this water body. Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okean. 17:7–65.

Reinhardt, J. C. H. 1840a. Om nye Grönlandske fiske (*Microstomus Grönlandicus, Cottus bicornis*). Overs. Danske Vidensk. Selsk. Forh. Kjøbenhavn 7:8–10.

———. 1840b. Bidrag til vor kundskab om Grönlandske fishe. Danske Vidensk. Selsk. Naturvid. Math. Afhandl. 8: 74–76.

———. 1841. Om nye Grönlandske fiske (*Microstomus Grönlandicus, Cottus bicornis*). Naturhist. Tidsskr. 3:225–227.

Richardson, J. 1844. Ichthyology. Pages 51–150 *in* J. R. B. Hinds (ed.), The zoology of the voyage of H.M.S. "Sulphur," under the command of Captain Sir Edward Belcher, during the years 1836–1842, vol. 2.

Richardson, S. L. 1981. Current knowledge of larvae of sculpins (Pisces: Cottidae and allies) in northeast Pacific genera, with notes on intergeneric relationships. Fish. Bull. (U.S.) 79:103–121.

Rollefsen, G. 1960. Havet og Vare Fisker. J. W. Eides Forlag. Bergen. 156 p., 223 pls. (with 111 p. of complementary text).

Saemundsson, B. 1926. Fiskarnir (Pisces Islandiae). Islensk dyr I. Reykjavik.

———. 1949. Marine Pisces. Zoology of Iceland IV (Pt. 72): 1–150.

Schmidt, P. 1903. Sur les conditions physico-geographique et la faune de la mer du Japan et de la mer d'Okhotsk. Bull. Imper. Russ. Geogr. Soc. (St. Petersburg) 38:503–532.

———. 1904. Fishes of the eastern seas of the Russian Empire. Izd. Russ. Geogr. Obshch. 466 p.

———. 1915. Ichthyological notes. I. On some new and little known Cottidae of the North Pacific. Ann. Mus. Zool. Acad. Sci. St. Petersburg 20:611–627.

———. 1927. A revision of the genus *Icelus* Kröyer (Pisces: Cottidae) with the description of a new species from the Okhotsk Sea. Ann. Mus. Zool. Acad. Sci. USSR 28:1–8.

———. 1935. On the genus *Icelus* Kröyer (Cottidae). Izv. AN SSSR, Otdei Matematiki i Estest Nauk. Pp. 413–418.

———. 1950. Fishes of the Sea of Okhotsk. Moscow-Leningrad Izd. 370 p. (Translated from Russian by the Israel Program for Scientific Translations, Jerusalem [1963], 392 p.)

Shuntov, V. P. 1965. Vertical zonality in fish distribution in the upper bathial of the Okhotsk Sea. Zool. Zh. 44:1678–1688.

Skalkin, V. A. 1963. Otoliths of some fishes of the far eastern seas. Izv. Tikh. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 49:159–199.

Soldatov, V. K. 1923. Data on some fishes from the Kara Sea and eastern part of the Barents Sea from the collections by the Institute's expedition of 1921. With an appendix of a list of fishes collected by zoologist I. D. Strel'nikov in the Kara Sea in 1921. Tr. Plov. Morsk. Nauch. Inst. 3:1–80.

———, and G. U. Lindberg. 1930. A survey of the fishes of the Far Eastern seas. Izv. Tikh. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 5:47–576.

Steindachner, F. 1886. Fische von Jan Mayen gesammelt von Dr. F. Fischer. Pages 105–108 *in* Die Internationale Polarforschung, 1882–83. Osterreichische Polarstation Jan Mayen . . . Beobachtungs-Ergebnisse 3.

Storm, V. J. 1884. Bidrag til kundskab om throndhjemsfjordens. Pt. 5. Om de i fjorden forekomne fiske. Norske Vid. Selsk. Skrift. 1884:1–48.

Tanaka, S. 1915. Two new species of fish from Japan. Zool. Mag. Tokyo 27:615–616.

Taranetz, A. 1935. Some changes in the classification of fishes of the Soviet Far East, with notes on their distribution. Vestnik DVNAR SSSR 13:89–101.

———. 1936. Description of three new species of the genus *Icelus* Kröyer (Pisces: Cottidae) from the Sea of Japan and from Okhotsk Sea. Dokl. AN SSSR 4 (13) No. 3 (107):149–152.

———. 1937. Handbook for identification of fishes of the Soviet Far East and adjacent waters. Izv. Tikh. Nauchno-issled. Rybn. Khoz. Okeanogr. 11:1–200.

———. 1941. On the classification and origin of the family Cottidae. Isues. AN SSSR Otd. Biol. 1943:427–447. (Translated from Russian by N. J. Wilimovsky and E. Lanz, Univ. British Columbia Mus. Contr. 5:1–28.)

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122:1–17.

Thielemann, M. 1921. Die Fische. Arbeiten der deutschen wissenshaftlichen Kommison für die internationale Meeresforschung B. Aus der Biologischen Anstalt auf Helgoland no. 28:187–228.

Ueno, T. 1972. List of marine fishes from the waters of Hokkaido and its adjacent regions. Sci. Rep. Hokkaido Fish. Exp. Sta. 13:61–102.

Vladykov, V. D. 1933. Biological and oceanographic conditions in Hudson Bay, 9. Fishes from the Hudson Bay region (except the Coregonidae). Contr. Can. Biol. Fish. 8:13–61.

Walters, V. 1953. Notes on fishes from Prince Patrick and Ellesmere islands, Canada. Am. Mus. Novit. 1648:1–17.

———. 1955. Fishes of the western Arctic America and the eastern Arctic Siberia, taxonomy and zoogeography. Bull. Am. Mus. Nat. Hist. 106:255–368.

Watanabe, M. 1960. Fauna Japonica. Cottidae (Pisces). Tokyo News Serv. Ltd. Tokyo. 218 p.

Weitzman, S. H. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. Bull. Am. Mus. Nat. Hist. 153:327–478.

Wilimovsky, N. J. 1958. Provisional keys to the fishes of Alaska. U.S. Fish and Wildlife Service, Fish. Res. Lab., Juneau, Alaska. 113 p.

Wilson, D. E. 1973. Revision of the cottid genus *Gymnocanthus*, with a description of their osteology. M.S. Thesis, Univ. British Columbia. 223 p.

Wollebaek, A. 1924. Norges Fisker. Kristiana. 239 p.

Yabe, M. 1981. Osteological review of the family Icelidae Berg, 1940, (Pisces: Scorpaeniformes), with comment on the validity of this family. Bull. Fac. Fish. Hokkaido Univ. 32: 293–315.