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Revision of the Cottid Genus *Gymnocanthus*, with a Description of their Osteology.

by

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We accept this thesis as conforming to the required standard

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ABSTRACT

<u>Gymnocanthus</u> is a cottid genus containing six species which inhabit the North Pacific, Arctic, and North Atlantic Oceans. The genus is characterized by edentulous palatines and prevomer, granulations on the nape, scales restricted to axillary prickles, and an elongate, multicusped preopercular spine. Six species (<u>Gymnocanthus detrisus</u>, <u>galeatus</u>, <u>herzensteini</u>, <u>intermedius</u>, <u>pistilliger</u>, and <u>tricuspis</u>) are recognized. These are identified by their different meristic characters, interorbital width, cleithral spine development, presence or absence of subpectoral dermal pistillae in males, and other features. No subspecies are recognized. Synonymies, descriptions, colour, maximum size, etymology, and range are given for each species. The key, used in conjunction with diagrams showing several diagnostic characters is useful for identifying specimens to at least 60 mm. Though some morphometric characters (head length, interorbital width and others) are significantly different between some species because of their great variability they are seldom taxonomically useful. Superimposed on this variability is strongly developed sexual dimorphism, males possessing significantly longer dorsal and pelvic fins than females. Other sexually dimorphic characters include the roughening of the inner edge of the pectoral rays, the brighter colours, and the penis in males of all species, and the axillary pistils in males of <u>Gymnocanthus pistilliger</u> and <u>G. intermedius</u>.

Though its systematic position is obscure, <u>Gymnocanthus</u> probably arose in the Aleutian Islands, dispersing westward by planktonic larvae, and eastward by migration along the shallow Aleutian shelf. *Gymnocanthus* evolved in two directions, one forming a group of three smaller species (*G. tricuspis*, *pistilliger*, and *intermedius*) showing great sexual dimorphism and low meristic characters, the other, a group of larger species (*G. galeatus*, *detrisus*, and *herzensteini*) with lesser developed dimorphism and high meristic characters. Possible origins for the two lines are discussed.

For lack of comparative information, the systematic position of *Gymnocanthus* within the family Cottidae is not examined in the present paper. To facilitate future intergeneric comparative studies, the osteology and cephalic lateral line system is described for the genus. No profound osteological differences between species exist; superficial differences between species reflect those diagnostic specific differences (i.e. interorbital width, head length) previously noted. Pore number and distribution in the cephalic lateral line system tend to differ between species, but are too variable to be of taxonomic use.

Breeding seasons are inferred from presence of young and from gonad maturity. *G. herzensteini* is a winter breeder, *G. galeatus* and *G. pistilliger* breed in spring, while *G. tricuspis* breeds in late summer. Data are not available for *G. detrisus* and *G. intermedius*. In three species examined (*G. tricuspis*, *galeatus*, and *pistilliger*) fish live to four years or more. Females grow more quickly than males, especially after two years.

G. tricuspis has a wider salinity range and lower temperature tolerance than have the other species, permitting it to survive in

Arctic waters. Ecological separation of the remaining species is not so clear, though *G. pistilliger* and *G. intermedius* seem to inhabit shallower water as adults than do *G. galeatus* and *G. herzenstein*.

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Introduction

In terms of numbers of species and individuals the scorpaeniform fishes are one of the dominant groups in the North Pacific Ocean. One family, the Cottidae, as defined by Bolin (1947), contains many genera indigenous to the North Pacific. Among these genera is the genus *Gymnocanthus*, in which this author recognizes at least six valid species: *Gymnocanthus detrisus*, *G. tricuspis*, *G. galeatus*, *G. herzensteini*, *G. pistilliger*, and *G. intermedius*. These species share the following characteristics: edentulous palatines and prevomer; bony granulations on the nape; four strong, straight preopercular spines, the first long and cusped; scales reduced to a patch of subpectoral prickles; pelvics with one spine and three rays; gill membranes free from isthmus; and lateral line of bony cylindrical ossicles.

Species definitions range from the typological species concept of early taxonomists (such as those from Linnaeus to Darwin) in which the species is defined morphologically to the "biological species" concept (Mayr, 1963) in which species are considered reproductively isolated and ecologically distinct. In practice, the two examples cited are usually synonymous in that morphological modifications distinguishing species reflect ecological adaptations. As for many other experimentally inaccessible animals, a typological species approach has been adopted in this revision. Where sympatry and morphological distinctness are observed for species pairs within *Gymnocanthus* reproductive isolation is implied.

The taxonomy of *Gymnocanthus* has long been confused due to the wide geographic range and morphological variability of species in the genus.

The taxonomic history of Gymnocanthus began in 1811 when Pallas described Cottus pistilliger (= Gymnocanthus pistilliger) from Kamchatka. In 1838 Reinhardt described Cottus tricuspis (= G. tricuspis). These two species have been identified with each other since that time, and with various of the other four species as they were subsequently described. Gymnocanthus tricuspis has probably contributed more to the uncertainty than any other species in the genus. This species is circumpolar, extending into the north Bering Sea and northwest Atlantic. While several characters such as relative head length and meristic formula for this species remain constant, other features like the granulation distribution and interorbital width vary tremendously (though clinally) over this range. Other species originally characterized by wide interorbitals and a peculiar distribution of granulations (G. detrisus and G. galeatus respectively) may resemble G. tricuspis in these features in some parts of its range and have, as a consequence frequently been identified with it, as well as with each other. Contributing to this confusion were the limited facilities in the 1800's for exchange and comparative study of ichthyological collections. For example, G. tricuspis was identified with G. pistilliger as early as 1865 (Malmgren, 1865), a mistake which was perpetuated by later authors who evidently never saw true G. pistilliger and depended too heavily on erroneous earlier literature. G. pistilliger closely resembles G. intermedius and has been continually confused with that species as well. Consequently, even very recent literature (McAllister, 1960) sometimes lists the Pacific species as coming from the Arctic Ocean.

The first serious attempt to revise the genus was made by Schmidt (1929) who worked with inadequate numbers of specimens and was unable to describe the extent of variation which may be encountered. *G. galeatus* was keyed but not described at all. Since then no further revisions have been attempted, old errors of identification remain uncorrected, and new errors are made. Most keys to the genus (Schmidt, 1950; Soldatov and Lindberg, 1930) have likewise suffered from a lack of appreciation of variation within species and diagnostic characters between species. *Gymnocanthus pistilliger* and *G. intermedius* have typically been distinguished from other species by the presence of subpectoral pistillae in males only. Secondly, morphometric differences used in keys have allowed neither for allometric growth nor the variation in adults. These two factors have severely limited the usefulness of existing keys. Lately, with the increasing accumulation and availability of specimens from various research collections taken over the range of the genus (e.g., the Japanese collections of the Albatross expeditions, the 1961-1962 International Pacific Halibut Commission collections in the Alaskan Gulf, and a host of Arctic collections) a comparative study of *Gymnocanthus* over its entire range has become possible.

The purpose of this paper is to demonstrate the validity of the six species recognized and to assign proper latin names to them. In addition, an attempt is made to describe the morphology, variation and geographic distribution of the six species, and to discuss the phylogeny and origin of the genus. This is accomplished by examining large numbers of specimens over the entire range of Gymnocanthus, finding natural morphological groupings within these collections, then referring to type material, original descriptions, and collection records for identification and distribution. Phylogeny is postulated by grouping species according to the presence of characters unlikely to have arisen independently in the different species. To aid future comparative research within the family Cottidae, the osteology and cephalic lateral line system of the genus are described.

MATERIALS AND METHODS

Measurements were made using either a 17 cm. or 33 cm. dial caliper to .1 mm. precision. Fin counts of specimens were made while teasing the fins with a dissecting needle. Small specimens were bent dorsoventrally to splay the dorsal and anal fins to aid counting rays and spines. Specimens were examined either with the unaided eye or a binocular dissecting microscope.

Counts and measurements are according to Hubbs and Lagler (1947) with the following additions and exceptions:

Suborbital stay length: refers to the distance from the posteriormost part of the orbit to the posterior end of the 3rd suborbital (=suborbital stay)

Interpostorbital: refers to the distance between the bony orbit rims behind the postorbital tubercles.

Snout-postorbital length: refers to the distance between the anteriormost tip of the premaxillary to the posterior margin of the postorbital tubercle.

Orbit depth: refers to the greatest vertical distance between the frontals and the suborbitals.

Preopercular spine length: refers to the distance from the tip of the second preopercular spine (after Sandercock and Wilimovsky, 1968). No broken spines were measured.

Head width: refers to the width taken just anterior to the point of emergence of the first preopercular spine, which corresponds to the maximum head width.

Head depth: refers to the vertical distance between the nape and the pelvic fin base, which corresponds also to the maximum body depth.

Preopercular spine cusps: a cusp is defined as a pointed prominence on the uppermost preopercular spine. Cusps are counted only on unbroken spines.

Cusp height: refers to the distance from the tip of the highest cusp to the ventral side of the spine below that cusp.

Pectoral base: refers to the distance between the dorsal side of first pectoral ray origin to the ventral side of the last ray origin.

Penis: refers to the distance from the penis base to its tip.

First predorsal distance: refers to the distance between the anteriormost premaxillary margin to the origin of the first dorsal spine.

Second predorsal distance: refers to the distance between the anteriormost premaxillary margin to the origin of the first dorsal ray.

Prepelvic distance: refers to the distance from the anteriormost margin of the premaxillary to the origin of the pelvic fins.

Preanal distance: refers to the distance from the anteriormost margin of the premaxillary to the origin of the first anal ray.

SL: abbreviation for standard length.

The cephalic sensory canal system was prepared by washing a preserved, fixed specimen in running water, then bleaching briefly in 3-5% hydrogen peroxide under strong incandescent light. A small (5 ml) hypodermic needle filled with India ink was slipped through one of the pores anteriorly into the thoracic lateral line. The ink was then injected into the lateral line system. Dermal staining from ink escaping through the pores may be avoided by running water over the specimen while injecting. The ink will begin to penetrate various canals in the head. Head canals resistant to ink penetration may more easily be demonstrated by reinserting the needle through pores into ink-filled canals close to the empty canals. Care must be taken not to press the needle through the canal wall subdermally, since the effect is to broadly, permanently stain beneath the skin.

Diagrams of the basic sensory canal system were drawn from injected specimens. When injecting, small pores and canals appear only transitorily, and were drawn as ink was being injected.

Clearing and staining followed Taylor (1967) with the following modifications. In most specimens, flesh from the left side was removed by making vertical slits along the neural and haemal spines from the hypural plate to the neurocranium. Epipleural and pleural rib integrity are maintained by sagittally cutting below and above them (anteriorly stopping short of the postcleithra). Cutting along the ventral midline of the abdomen. Viscera were removed before bleaching, clearing, and staining to permit greater penetration of the stain in the occipital-vertebral region. Bleaching was performed with about 3% hydrogen peroxide in water, sometimes under a strong incandescent light. Glycerine solutions used were 35%, 50%, and 100%. The specimen was left in each solution until it sunk, or while in 35 % glycerine, until the alizarin stopped leaching out of the specimen. While most of the skeleton was clearly defined in the undissected cleared and stained specimen, the branchial apparatus was obscured by other bones..This structure was dissected out of a <u>Gymnocanthus</u> <u>galeatus</u> and stained separately.

Disarticulated skeletons were prepared from both frozen and preserved fish. In the latter case, only specimens that are well preserved (i.e., the skeleton is not softened by acidic preservative) may be successfully used. Specimens to be reduced were eviscerated. To hasten reduction, large specimens were sometimes defleshed like those being cleared and stained. Fresh specimens were placed in 10 to 40 times their volume of weak (about .1 % or less) KOH solution to which 1-2 cc. trypsin (BDH, trypsin from beef pancreas, 7.5 Anson units/g.) was added. Preserved specimens were first washed in running water to remove all alcohol or formalin, then placed in the solution which was incubated at 35-40°C. When the solution became cloudy (two days for fresh material, around 7 days for preserved) the supernatant was drained, and the remaining sludge was mixed with hot (50°C.) water. The cloudy solution and digestant-laden froth are discarded and the remaining sludge washed again. This last process is repeated until the hot water does not become cloudy. If any sludge remains or if tissue is still attached to the bones, the entire process may be repeated with fresh enzyme and KOH solution.

Otoliths were taken from fresh specimens caught east of Kodiak

Island, Alaska. A large blade was placed on the postorbital tubercles and drawn through the skull towards the first preopercular spine, opening the recessus sacculi and revealing the sacculiths, both of which were removed with forceps and placed in individually labelled glass vials. The otoliths were initially stored dry, but later had a small amount of water and trypsin added to them. After 48 hours, this solution was replaced by a 50 % solution of glycerine in water. After soaking in the glycerine-water for at least 7 days, the otoliths were placed in a bowl of 50 % glycerine and were obliquely illuminated from below by a high intensity lamp. Following Jessop (1972), hyaline zones were taken to be equivalent to annuli (for further discussion, see Van Oosten, 1929, and Hile, 1941), and the age the number of hyaline zones. The otoliths were read through a Bausch and Lomb binocular dissection microscope at .7x power.

All radiographs were made with a GE Model D-1 X-ray machine, using 11" X 14" Kodak type M-54 Industrial X-ray film. X-ray operation, exposure times, developing and fixing follow Wilson (MS). Vertebrae were counted from and including the atlas to but excluding the hypural plate. Two fused central are counted as two rather than one vertebra.

Most of the Gymnocanthus collections examined were borrowed from the Institute of Fisheries Ichthyology Museum (BC). Additional material was borrowed from the University of Washington (UW), California Academy of Sciences (CAS, IU, SU), and the National Museum of Canada (NMC).

The Institute of Fisheries collection is rich in Aleutian and western American Arctic material. The majority of deepwater Aleutian specimens were collected during the International Pacific Halibut Commission cruises of 1961-63 (International Pacific Halibut Commission, 1964) while the shallow water collections were made in 1961-63 by Garry I. McT. Cowan, A. Laurie, Alex Peden, F. Keith Sandercock, Norman J. Wilimovsky, and others. Arctic collections housed in the Institute were caught largely by Norman J. Wilimovsky on the MV William E. Ripley and Norman J. Wilimovsky and Dayton L. Alverson on the MV John N. Cobb in the cruises of 1954 and 1959 respectively.

The University of Washington material is comprised mainly of *Gymnocanthus tricuspis* from the St. Lawrence Island - Norton Sound region which were collected in 1949 by J. G. Ellson, Donald E. Powell, and Henry H. Hildebrand on the MV Deep Sea (Ellson *et al.*, 1950).

The California Academy of Sciences museum is the repository of much Albatross material, and consequently is rich in Asian material from the 1889-1891 and 1906 expeditions (Tanner, 1893; U. S. Bureau of Fisheries, 1907).

The National Museum of Canada specimens borrowed were almost entirely from Canadian Arctic Archipelago, Hudson Bay, Labrador, and Gulf of St. Laurence waters. These were collected by the MV Salvelinus, MV Calanus, and others.

In all, the author was able to examine 515 *Gymnocanthus galeatus*, 1984 *G. tricuspis*, 196 *G. pistilliger*, 43 *G. detrisus*, 28 *G. ventralis*, and 11 *G. herzensteini*.

Graphs

Meristic data are given both in histograms for visual comparison of specific meristic differences, and in a diagrammatic fashion (after Hubbs and Hubbs, 1953) to present a statistical comparison of the data. The center vertical line in the bar graph indicates the mean; the width of the black bar is four standard error units; the width of the open bar

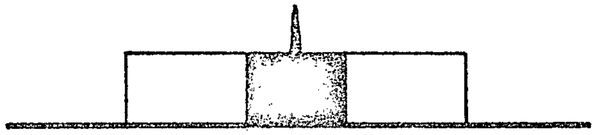

Figure 1
Hubbs and Hubbs (1953) method of graphical analysis.

is four standard deviation units, and the horizontal line shows the range of the values. The bars encompass 95.46 % of the specimens and samples respectively (Figure 1).

Several morphometric characters varying between species or between sexes within species have been plotted. Non-sexually dimorphic characters are plotted on linear axes, while sexually dimorphic characters are plotted as logarithms to eliminate the effect of allometry.

Descriptions of Gymnocanthus species

This revision recognizes six species in the genus Gymnocathus. Neither subgenera nor subspecies are recognized. Reasons for rejecting subspecies and synonymizing some species are given in the text for each species. A generic description including synonymy, morphology, osteology, and cephalic lateral line pattern is presented first, followed by descriptions of the individual species. All specific descriptions include a synonymy, morphometric, meristic, and colour (preserved, and where possible, live) descriptions, maximum size, etymology, range, and systematic notes. For each species, the specimens actually described, their size, collection data, and reference number are listed. Large collections (*G. galeatus*, up to 149 specimens; *G. tricuspis*, to 131; *G. pistilliger*, to 99; *G. detrisus*, to 43; *G. intermedius*, to 27; *G. herzensteini*, to 11) were measured to provide morphometric data. The figure given first is the mean of these values, followed by the range in parentheses. Where sexual dimorphism occurs, the data are presented separately for males and females. The mode, range, and mean are given for meristic data. A list of specimens examined, literature records and a map with representative collection localities indicating the range for each species follow the systematic notes. Numbers at the collection points refer to the literature records or list of specimens examined for that species. The taxonomic section begins with a synonymy for the genus *Gymnocanthus*.

Genus Gymnocanthus Swainson

Cottus: - Reinhardt, 1838: 117 (type species Cottus gobio of Fabricius in Fabricius, 1780:159; Cottus tricuspis by subsequent designation, Reinhardt, 1838.)

Gymnocanthus: - Swainson, 1839:271 (type-species Cottus ventralis Cuvier and Valenciennes in Cuvier and Valenciennes, 1829: 194.)

Phobetor: - Kroyer, 1844:263 (type-species Cottus gobio of Fabricius in Fabricius, 1780:159; Cottus tricuspis by subsequent designation of Reinhardt, 1838; Phobetor tricuspis by subsequent designation of Kroyer, 1780.)

Acanthocottus: - Girard, 1851:186 (type-species Acanthocottus pistilliger Girard (lapsus calami) by monotypy.)

Elaphocottus: - Sauvage, 1878:142 (type-species Cottus pistilliger Pallas in Pallas, 1811:143.)

Sclerocottus: - Fischer, 1885:58 (type-species Sclerocottus schraderi Fischer.)

Gymnacanthus: - Gill, 1861: (emendation of Gymnocanthus)

Gymnocenthus: - Andriashev, 1937:311 (lapsus calami)

Gymacanthus: - Huntsman, Bailey and Hachey, 1953:248 (lapsus calami)

Comnocanthus: - Chyung and Kim, 1959:10 (lapsus calami)

Diagnosis

No palatine or prevomerine teeth; nape with flat, bony granulations; first preopercular spine long, with 1-6 cusps; 6 infraorbitals (counting lachrymal); gill membrane attached to isthmus, with broad fold; body naked except for a patch of subpectoral scales; lateral line complete, with bony ossicles; pelvics I,3; males with penis.

Generic Description

Body robust anteriorly, oval to subcircular in cross-section; peduncle weakly laterally compressed. Head moderate, moderately compressed. Mouth terminal, moderate. Small viliform teeth randomly placed on premaxillary and dentary tooth pads; prevomer and palatines edentulous. Orbits longer than deep, dorsolateral; in fresh specimens, dorsal eye margin elevated above interorbital. Nasal spines moderate to strong, usually emergent. Six infraorbital bones. Frontals usually forming tubercle at orbit posterodorsal margin; frontal-parietal ridges extending from this postorbital tubercle to supratemporal sensory canal, arching laterally to become confluent with lateral line; these ridges with tubercle development on frontal immediately behind postorbital tubercle and on either side of supratemporal canal. Nape with flat, platelike bony granulations, these granulations in some species extending onto opercle, infraorbitals, interorbital. Preopercle with four spines, the uppermost long, with several (2-6) sharp cusps dorsally, smooth ventrally; all other preopercular spines smooth. Gill membranes joined to isthmus, forming broad fold across it; pore behind last gill arch small or wanting; gill arches with spinous bony plates in place of rakers. Lateral line above middle of body, dropping abruptly to body midline above last anal ray; lateral line composed of a series of small, tubular, bony (not cartilaginous) ossicles with slightly flared margins anteriorly and constricted margins posteriorly; ossicles subcylindrical, compressed towards trunk; broad U shaped notch anteriorly on lateral side, narrower V shaped notch posteriorly on medial side; pore to exterior forming at posterior end. Skin mostly naked; patch of modified scales present, restricted to pectoral axil; scales T shaped, with several cusps on crossbar directed away from shaft; shaft imbedded in skin, cusps emergent. Dorsal fins separate; base of spinous dorsal shorter than soft dorsal base; spinous dorsal from semicircular to elongate, convex; soft dorsal convex; anal margin weakly convex to flat; caudal weakly rounded or truncate; pectorals convex. Sexual dimorphism in fin length; in males, pelvics, spinous dorsal especially long. All fins connected for the most part by membrane, except for ends of elongate pelvics of males. Pelvic formula always I,3. 6 branchiostegals. Anal papilla present; anus immediately in advance of anal fin. Male with moderate conical penis.

Range

Gymnocanthus presently contains six species ranging in the North Pacific from southwest Alaska to Korea, north through the Bering Straits, on all Arctic polar coasts to Northern Norway, Spitzbergen, south to Maine on the American coast.

Etymology

The generic name Gymnocanthus is from the Greek γυμνός (naked) and ακανθα (spine) in reference to the naked preopercular spine and cusps.

Osteology

The description of the osteology of Gymnocanthus is divided into six subheadings, neurocranium, branchiocranium, orbital series, pectoral and pelvic girdle, suspensorium, and axial skeleton. Terminology follows Harrington (1955) and Allis (1909) for the cranium, and Weitzman (1962) and Liem (1963) for the non-cranial skeleton.

Neurocranium

Nasal bone consisting of vertical shaft, the upper end sharp and emergent, the lower end blunt; off middle of this shaft extend two prongs perpendicular with dorsoventral shaft and each other; lateral prong twice the length of medial prong; lateral prong abuts onto anteroventral edge of lateral ethmoid, medial prong abutting to the medial border of ethmoid lateral wings.

Ethmoid broad, sloping down anteriorly, spike-like posteriorly; anterior plate with paired, anterior-extending processes (articulating with nasals) separated from lateral ethmoid wing by shallow fossa; anterior of ethmoid with longitudinal ridge dorsally, groove ventrally. Ethmoid cartilage extending ventrally from ethmoid, attaching to parasphenoid dorsal ridge.

Prevomer edentulous, tapering to point posteriorly, broad anteriorly; ventrally with narrow, low ridge running length of prevomer; anterior margin thickened weakly dorsally, moderately ventrally; dorsal and ventral ridges divided laterally by a deep V-shaped notch; dorsal ridge divided medially by broad V-shaped notch; prevomer articulationg by long, tapered point to base of parasphenoid, abutting medially onto lateral ethmoid.

Prefrontal-lateral ethmoids (= prefrontals) paired, each side widely separated from the other by forward extensions of frontals, ethmoid; prefrontal-lateral ethmoid of two distinct regions, one region a broad, thick bone (= prefrontal) forming anterior margin of orbit, abutting ventrally in a ligamentous joint with the lachrymal, anteriorly articulating via a bony prominence with the nasal spine lateral process, and medially with frontals; second region a complex medial bone (= lateral ethmoid) with several faces, the basal face abutting against prevomer lateral margin, the dorsal face abutting against ethmoid wings, and the posterior face resting on the anterior parasphenoid; olfactory foramen passing through junction of prefrontal and lateral ethmoid components.

Frontals paired, narrow anteriorly, broadened posteriorly; in most species, forming tubercle followed by notch (= postorbital tubercle, postorbital notch) at posterodorsal orbit margin; postorbital notch may be followed by second tubercle; posteriorly, where frontals broaden to cover anterior half of braincase the two bones suturally unite in superficially crenate fashion, but actually by broadly overlapping lobes; sometimes a narrow fontanel present posteriorly, usually covered by granulations; ridge (= nape ridge) running longitudinally along middle of each frontal, confluent with that on parietal bone; laterally, frontal forming narrow blade over sphenoid.

Posteriorly, the frontals overlap the paired parietals; parietals sutured along midline, each side carrying longitudinal ridge from frontal, this ridge leading onto epiotic; parietals bound by frontals, pterotics, epiotics, supraoccipital, plus a series of small cephalic lateral line enclosing tubular bones.

Pterosphenoid a small bone forming anterodorsal border of myodome, overlaid dorsally by a triangular ventral process of frontals, antero-ventrally by an ascending central wing of parasphenoid; posteriorly, forming triradiate suture with prootic, sphenotic; ventrally, jugular canal passing from 5th cranial nerve foramen which opens exteriorly to the internal jugular recess in the pterosphenoid, into and through the trigemino-facialis recess in the prootic.

Prootic large, platelike, approximately pentangular, bounded by basioccipital, exoccipital, pterotic in triradiate suture, pterosphenoid, sphenotic in triradiate suture and parasphenoid; apparently only one foramen for profundus, facialis, trigeminus nerves in trigeminofacialis recess of prootic; recess protected laterally by bony strut passing from ventral margin of recess to anterior surface of dilatator fossa for reception of hyomandibular; this fossa deep, of two bones, the ventral half of prootic, the dorsal half of sphenotic; internally, prootic with shelf meeting fellow along midline, separated from cranium base by a gap.

Sphenotic small, overlaid by frontals; ventrally flat, in triradiate suture with pterosphenoid and prootic; dorsally forming part of dilatator fossa.

Parasphenoid long, overlapping prevomer anteriorly, pterosphenoid, prootic, basioccipital (respectively) posteriorly; anteriorly slender, with single thin dorsal blade and equally thin lateral blades; dorsal blade greatest development anteriorly, diminishing posteriorly, becoming obsolete by myodome; anteriorly, ventrally developed groove where parasphenoid overlies prevomer, this groove becoming more shallow posteriorly; centrally, parasphenoid with dorsolateral wings, these forming ventral margins of myodome, covering anterior margin of prootic ventrally, anteroventral corner of pterosphenoid dorsally; posteriorly, parasphenoid tapering from broad U-shaped bone (narrowly separate from wings) to a point or narrow fork under basioccipital.

Basioccipital fan-shaped anteriorly, forming floor of rear half of basicranium; meeting prootic above parasphenoid; suturally joined to exoccipital dorsally. Basioccipital narrow-waisted just before expanding posteriorly to form oval condylar surface; this surface narrower dorsally, slightly posteriorly produced ventrally.

Opisthotic small, flattened limpet-like bone closely applied to posterior exoccipital-pterotic suture, possibly just touching epiotic strut.

Exocciptial large, bounded by basioccipital, prootic, pterotic, epiotic, supraoccipital, in triradiate suture with latter two; exoccipital meeting fellow below supraoccipital; exoccipitals forming floor of supratemporal fossae; posteriorly, developing conic condylar surfaces which originate above basiocciptial condyle but point down towards it; these three cones forming walls and base of foramen length separating them anteriorly, becoming adjacent posteriorly; ossicles extending onto caudal rays. Pistillae usually in the pectoral axil of males only (may fall off in preservative); pistillae long, slender, length equalling width of pupil, end often bifid. Scales large, sparse, at least as long as ossicles below the spinous-soft dorsal interspace; dorsally, scales separated from each other by a distance often exceeding their own length; scale patch extending 4/5 of the distance to the end of the pectoral fins. Snout narrow, length 4.17 (3.88-4.80) times in head length, 11.82 (10.72-12.53) times in SL; lateral ethmoid-nasal spine distance short, making snout abrupt, blunt in lateral profile. Teeth villiform, small, posteriorly recurved, randomly placed on jaws; tooth band up to four teeth wide on dentary near symphysis, up to six teeth wide on premaxillary near symphysis; in both, tooth band narrowing posteriorly; tissue in mouth may be papillose directly ahead of or behind tooth pads; single row of papilla ahead of dentary and premaxillary teeth, several (2-3) rows of papillae posterior to these teeth; mouth moderate, upper jaw 2.49 (2.38-2.58) times in head; maxillary extending to or past vertical through center of pupil. Single pair moderate, often emergent, weakly posteriorly recurved nasal spines; two pair of nostrils, first pair on vertical plane through nasal spines, length of nasal tube subequal to nasal spine length, constricted terminally such that terminal pore opens anteriorly; posterior nares posterolateral to nasal spines, distance from nasal spine tip 1/2-2/3 distance from orbit rim; posterior nostril tube always much lower than nasal spine or anterior nasal tube; posterior tube produced such that terminal pore opens upward or posterolaterally; distance of posterior nares base 1/2 to magnum; cones fused to basioccipital medially for almost entire length; each exoccipital with thin, lateral, posteriorly extended blade separated from condylar cone by gap, roofing foramen magnum; supratemporal fossa face with broad V-shaped groove running from the dondyle base medial to medial to epiotic-supraoccitital-exoccipital suture; lateral exoccipital groove extending from condylar base to just ventral to prootic-pterotic-exoccipital suture; small posterolateral spine in groove at condyle base; single or double foramen (for passage of fagus and occipital nerves?) at apex of lateral groove close to condylar base; glossopharyngeal foramen on anteroventral exoccipital corner; large foramen at prootic-basioccipital-exoccipital junction, possibly filled with investing cartilage in life.

Pterotic forming dorsoposterolateral border of cranium; bordered by exoccipital, prootic, epiotic, sphenoid, parietal; acute, postero-lateral spine well separated from epiotic spine; pterotic relatively broad ventrally, much less so dorsally; long, shallow fossa for reception of posterodorsal arm of hyomandibular composed of pterotic posteriorly, sphenotic anteriorly, with a corner of the prootic ventrally.

Pterotic overlaid anterodorsally by long, tubular lateral extrascapular (Allis, 1909) enclosing the posterior part of the lateral cephalic sensory canal; from here, this canal passes anteriorly through another tubular bone closely fused to frontal at postorbital notch (=postfrontal of Allis, 1909 ?); posteriorly, canal passes into posterior extrascapular bone where the canal bifurcates into the posttemporal and supratemporal sections; a third tubular bone, the parietoextrascapular (Allis, 1909) receiving the supratemporal sensory canal medial fork, conducting it to supraoccipital. Parietoextrascapular restricted to parietals; posterior, lateral extrascapulars overlay pterotic, part of sphenotic; postfrontal (?) overlaying sphenotic, frontal bone.

Epiotic pyramidal, apex with posteriorly directed dorsoventral plate roofed by sagittal plate[1]; this plate sloping abruptly ventromedially into posttemporal fossa, forming third plate.

Supraoccipital with long, broad horizontal blade anteriorly, with two lateral wings extending out from centre; anterior blade overlaid by posterior margin of frontal and anterior margin of parietal, wings overlaid by posterior margin of parietals; posterolateral area of exoccipital forming anterior extremity of supratemporal fossa; vertical, posteriorly directed blade roofed by narrow horizontal plate medial in supratemporal fossa.

Branchiocranium

Basibranchial single, with posterior fan-shaped lobe; lobe longest dorsally; anterior margin thickened to form slenderly triangular, ventrally pointed cap; cap constricted slightly in the middle; in lateral

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1. Allis (1909) calls this plate "suprascapular spine". It is not possible to tell whether this bone is part of the epiotic or just fused to it.

profile, cap posteriorly recurved both dorsally and ventrally.

Hypohyal paired, double; anterior bone medially flattened pyramid anteriorly, with small condylar-like process at apex articulating with fellow; cap dorsomedially synchondrally sutured with fellow; posteriorly directed spine off medial side; pyramidal cap fitting over anterior tip of ceratohyal, spine running along medial border; posterior bone tubular, inserting into posterodorsal fossa of anterior bone, anterodorsal border of ceratohyal. It is uncertain which of the hypohyals represents the dorsal and which the ventral one (Weitzman, 1962; Liem, 1963). Although they are on about the same vertical level, the anterior pyramidal bone articulates with the ceratohyal more ventrally, and therefore probably represents the ventral hypohyal.

Ceratohyal large, broad and triangular posteriorly, narrow and shaft-like anteriorly; oblique, slender strut given off anteriorly from central dorsal margin, this strut connected to anterior shaft by thin web of bone for its entire length; small anteroposterior foramen through this web; anterior hypohyal fitting onto end of shaft; posterior hypohyal fitting into medial groove between ceratohyal strut and shaft.

Epihyal triangular, articulating across its broad anterior border with equally broad ceratohyal; posteriorly, with small, dorsally directed articular surface for reception of interhyal.

Interhyal small, cylindrical, articulating dorsally with posterior border of anteroventral hyomandibular leg.

Six branchiostegals, rarely seven; if six, two articulating with epihyal, two with triangular portion of ceratohyal, two with shaftlike portion of ceratohyal; if seventh present, it is short, slender, anterior to branchiostegals on ceratohyal shaft.

Material for the branchial arch osteological description is not entirely adequate. Consequently, the description may be incomplete. Four unmodified gill arches, first three with ossified basibranchials, fourth apparently with unossified basibranchial; first three arches with broad hypobrachials, fourth apparently lacking that bone; first four gill arches with long, slender ceratobranchials, lined on either side with dome-like tooth bearing placodes, teeth perpendicular to placode or weakly recurved into buccal cavity; all four arches with shorter epibranchials (half ceratobranchial length); at least first epibranchial may have tooth placode ventrally, others lacking placodes; first epibranchial forked. Fifth arch consisting of tooth bearing ceratohyal, pharygobranchial; no apparent ossified hypobranchial, basibranchial; ceratobranchial elongate, somewhat arrowhead shaped, broad medial end articulating with fellow, cartilaginous basibranchial; shaftlike lateral end ligamentously attached to middle of fourth ceratobranchial; dorsally forming tear-shaped tooth pad. Pharygobranchial structure uncertain; first epibranchial appears to lack pharyngobranchial; second with small lobate tooth-bearing pharyngobranchial closely applied to large tooth bearing pharyngobranchial abutting against third and fourth arches; this pharyngobranchial an oval tooth pad with small wing from its dorsal side extending anteriorly beneath the smaller pharyngobranchial tooth pad.

Orbital Series

Lachrymal broadly triangular, with double condylar surface at apex; anteromedial surface fitting against anterior wall of palatine cup; dorsal surface fitting against condyle on ventrolateral margin of prefrontal; medially, lachrymal extending down as a deep, thin blade; laterally, extending down parallel to the medial blade, forming an open space between the blades; this space divided into two chambers by an oblique dorsoventral septem; these chambers continuous dorsally, emerging anteriorly as small foramen; chambers carry anterior infraorbital cephalic sensory canal; posteriorly, lateral wall developing small spike, this spike fitting in complementary groove in second infraorbital.

Lachrymal and second infraorbital fitting closely together. Second infraorbital broadly triangular; pointed anterior end resting on lachrymal, entering very small fossa below condyle of that bone; medial blade of second infraorbital deep, closely applied medially to lachrymal, lateral blade shallow, these blades again enclosing infraorbital sensory system in a bony chamber; chamber opens anteriorly, posteriorly, small foramen in midventral wall of chamber.

Third infraorbital (suborbital stay) strong, laterally considerably flattened, pointed at either end; posterior blade with concave upper margin, convex lower margin; anterior spike straight edged; anterior spike resting on posterior end of second infraorbital; infraorbital canal passing into suborbital stay below this spike, emerging as foramen middorsally; stay thickened along its midline posteriorly; infraorbital canal passing into posterior blade, giving off pores above and below thickening posteriorly beyond dorsal foramen; stay extending back, ligamentously attached to preopercular just above first spine.

Fourth, fifth, sixth infraorbitals[1] laterally compressed, extending from middorsal stay to anterior end of sphenoid.

Pectoral, pelvic girdle

Posttemporal with long, wide anteromedial blade overlapping epiotic and slender, cylindrical anteroventral strut resting at opisthotic-epiotic-exoccipital junction; psttemporal canal enters through foramen in horizontal shelf-like bone above strut, emerging above strut origin.

Supracleithrum with thickened dorsal edge, long bladelike process extending down and back; thickened dorsal edge receiving posttemporal canal on its anterolateral surface; canal reemerging 2/3 of the way along the flat dorsal margin; posteroventral blade thicker on leading than trailing edge; blade extending across, ligamentously (?) uniting with dorsal end of cleithrum; supracleithrum anterior end condylar, articulating with small surface below posterior end of posttemporal blade.

Cleithrum spatulate, ligamentously meeting its fellow under myodome ventrally; arching laterally dorsally, terminating anterodorsally in long, thin spine reaching first or second lateral line ossicles; leading edge of cleithrum develops a strong ridge running perpendicular to basal spatulate plate; ridge facing laterally at its basal origin,

1. Sixth infraorbital equivalent to Harrington's (1955) dermosphenotic.

twisting 45° posteriorly, terminating in lobe across which supracleithrum lies; this lobe separated from dorsal spine by deep cleft; lobe considerably thickened on trailing edge; thickening may terminate in long, strong spine emerging through the skin (eg. G. intermedius) or may terminate in dull point barely discernible on bone (eg. G. galeatus); second smaller ridge originating posteriorly on the cleithrum just above spatulate plate; ridge extends along this edge of the cleithrum, subtending a grouve eventually meeting dorsal spine.

Postcleithra double, long, rib-like; first postcleithrum applied to medial side of dorsal cleithral lobe, extending down and back, terminating in pectoral axil; beneath 4th-6th pectoral ray, first postcleithrum synchondrally sutures to second postcleithrum which curves anteriorly, still restricted to pectoral axil.

Scapula U-shaped, with superior branch wide, closely applied for over half its length to upper cleithral lobe; inferior branch just short of reaching cleithrum, but connected by cartilage; between branches, scapula widely separated from cleithrum; inferior branch synchondrally sutures to the first of a series of four large platelike radials.

First and last radial tending towards triangularity, smaller, about half the size of second and third; second, third radials rectangular; small foramina between scapula, first radial, first and second, second and third; radials separated from cleithrum by strip of cartilage, this strip most narrow under third radial; radials closely synchondrally sutured to each other.

Ventrally, fourth radial broadly synchondrally sutured to coracoid; coracoid synchondrally sutured to cleithrum medial to fourth radial; anteriorly, coracoid forming tubular strut abutting against cleithral palte; between cleithral-coracoid contacts, coracoid subtends large foramen.

Pelvic girdle composed of right, left basipterygia (Liem, 1963); basipterygia diamond shaped with large convex sided anterior triangle, small, concave sided posterior triangle; larger triangle has along its lateral perimeter a strongly produced dorsolateral ridge and weakly produced ventromedial ridge; ventral, small keel along central midline; at lateral junction of two pelvic girdle triangles are strong condyles with two articular surfaces, lateral surface for articulation with pelvic spine, posterior surface for articulation with pelvic rays; on midline between condyles originates anterior extending finde forklike processus medialis (Liem, 1963); between condyles and basipterygial keel, bone very thin. Basipterygia fit closely between cleithral basal plates.

Suspensorium

Hyomandibular distinctly cross-shaped, four pronged, the dorsal two arms short, articulating with the deep anterior dilatator fossa and shallower posterior sphenoid-prootic-pterotic fossa; posteroventral arm longer, articulating with condylar surface of opercular; anteroventral arm very long, broad distally, terminally articulating through broad synchondral joint to symplectic; broad, thin blade connecting anterior arms; narrow, thin blade connecting posterior arms; strong blade originating at arm junction, extending down posterolateral border of longest arm, this blade terminating ventrally in a short spine separated from anteroventral arm by small foramen.

Matapterygoid composed of papery thin blade, dorsally synchondrally butured broadly to anterior hyomandibular blade; ventrally, matapterygoid narrow waisted, then widening into equilateral triangular bone whose entire base synchondrally sutures to equally wide triangular anterodorsal wing of quadrate.

Quadrate anteroventral margin modified into condyle for articulation with articular; long spike with shallow-grooved ventral side extending posteriorly from condyle, widely sutured to ventral border of quadrate "triangle", this spike resting on end of preopercular descending arm.

Symplectic elongate, very slender ventrally where it passes medial to quadrate, (articulating with that bone near condyle), broadening somewhat dorsally where it synchondrally articulates with base of hyomandibular anteroventral arm; symplectic weakly arced dorsally.

Endopterygoid composed of long, slender anterior spine, short, ventrally oblique posterior spine; posterior spine slanting down, broadly synchondrally sutured to leading edge of quadrate triangle; anterior spine with blade superiorly, this blade high, serrated posteriorly, low anteriorly; anterior spine sutured over its entire length to ectopterygoid dorsally, over much of its length to posterior spine of palantine ventrally; ectopterygoid long, somewhat broader than endopterygoid, anteriorly sutured to palatine fan at its point of contact with palatine spine.

Palatine complex, formed of a posterior spine, anteriorly with downwardly oblique cylindrical shaft half the length of spine; with high, laterally concave fan above junction of shaft and cylinder, the rim of this fan reaching toward but not meeting parasphenoid; anterior end of cylinder distally meeting anterior tip of lachrymal, articulating with notch on maxillary anterior end; medial condylar surface of lachrymal resting on base of palatine fan concavity; narrow, horizontal medial ridge below fan; posterior spine with sharp ventrolateral ridge narrowing toward spine terminus; palatine edentulous.

Preoperculum an inverted T, the descending process and first spine forming the crossbar, the perpendicular ascending process forming the shaft; ascending and descending processes connected medially by a broad, thin web of bone; this web narrowly separated from ascending process by a small gap, forming a small spine dorsally on the web; small foramen at base of gap; first spine long, cusped, located at base of ascending process; terminus of descending process forked, lower branch forming fourth preopercular spine; spines two and three approximately evenly spaced between first and fourth spine; spine length decreasing from first to fourth; large foramen on midlateral aspect of ascending arm, spines with foramina immediately anterior to them; preopercular ascending process closely applied to groove posterior to strong lateral hyomandibular ridge; small hyomandibular spine fits into preopercular web notch.

Operculum V-shaped, with condylar process on medial side of apex; outer edges of "V" strong, thick, thinner towards inner edges; laterally, "V" reinforced with ridges of bone radiating from condyle; dorsal arm twice width of ventral arm, with twice as many ridges; arms of operculum connected centrally by cartilage, never ossified.

Subopercular anteriorly with long, anteriorly arched, dorsoventral spine, more attenuated dorsally than ventrally; lower posterior margin giving off broad, thin triangular blade which in turn gives off thin process from tis posterodorsal margin; small, thick triangular knob on spine opposite blade; ascending spine and posterior blade closely medially applied to anterior and ventral margins respectively of opercular ventral arm.

Interopercular long, triangular, with thickened dorsal border, thin ventral blade; posteriorly, with thickened ridge running obliquely to lower posterior corner, forming small point; interopercular broadly separated from but ligamentously connected to subopercular below triangular knob; anteriorly, interopercular running between preopercular descending limb, epihyal.

Articular with posterior dorsomedial condylar surface, long, strong anterior spike, short spike projecting upward and forward from anterior border of articular surface and connected by a broad web of bone to the anterior spike, this web attenuating anteriorly; wide, flat-based blade originating broadly below condylar surface, separated from shaft by U-shaped gap; foramen penetrating gap emerging below small upturned knob which forms posterormost border of condyle. Angular small knob-like bone at articular posteroventral border.

Dentary Y-shaped, bearing ventral knob at symphysis followed by three increasingly long foramina; lower branch terminates with foramen; upper branch bearing tooth pad dorsally; base of tooth pad thin, sockets almost penetrating through; ventral side of dorsal branch concave; long shaft of angular resting on, broadly synchondrally attached to dorsal surface of lower dentary branch, reaching almost to dentary fork.

Maxillary long, spatulate posteriorly, narrowing anteriorly; anteriorly, with several articular surfaces; dorsally, an oval condylar surface articulating with prevomer; ventrally, a condylar surface articulating with secondary premaxillary ascending process; these two condylar surfaces connected by bony wall continuing ventrolaterally, enclosing and anteriorly directed fossa; condylar surfaces separated from maxillary shaft by a deep, broad groove which receives the palatine and lachrymal.

Premaxillary with two high ascending processes arranged such that they enclose an anteriorly facing groove, leaving small V-shaped notch at symphysis between tooth pads; lateral, secondary ascending processes broad, thick, short, about half as high as primary ascending processes, situated at right angles to primary ascending processes; posteriorly, premaxillary narrows, anteriorly produced dorsally into a high ridge, tapering to pointed or weakly rounded end; tooth pad at 45° to primary ascending process.

Axial Skeleton

Two obliquely upward directed lateral processes from atlas articulating with skull exoccipital condyles, apparently permitting limited dorsoventral movement, no lateral movement. Haemal spines absent from atlas. Atlas neural spines short, not meeting as arch. Neural spines with deep midlateral fossa. Neural postzygapophyses especially strong on atlas, weakening (but never disappearing) posteriorly, concomitantly shifting dorsally; neural prezygapophyses not appreciably developed on atlas, knoblike on abdominal vertebrae, slender on caudal vertebrae, obsolete on peduncle (except ural and preural) vertebrae. Caudal vertebrae with long, oblique haemal spines with small prezygapophyses, these becoming obsolete towards atlas and peduncle, strengthening on last 4-5 vertebrae. Atlas and first 4-5 vertebrae totally lacking haemal postzygapophyses; haemal postzygapopheses strongest on first few caudal vertebrae, weaking anteriorly and posteriorly, becoming obsolete on last 6-7 vertebrae. All vertebrae with neural arches; caudal vertebrae with haemal arches; some precaudal vertebrae[1] with partially developed haemal arches. Neural and haemal arches becoming blade-like towards end of caudal vertebrae. All vertebrae opisthocoelous, decreasing in size from atlas to ural-preural vertebrae. All centra except those of first 5-7 abdominal vertebrae, last 6-7 caudal vertebrae strongly laterally compressed.

Two types of ribs present, epaxial and hypaxial. In Gymnocanthus, epipleural ribs by far the more numerous. On atlas, ribs originating on midmesial aspect of neural spine in fossa; posteriorly, origin descends, moving away from neural spine to haemal spine prezygapophyses; epaxial ribs occurring as far back as first few caudal vertebrae. Pleural ribs not numerous, developing first on vertebrae towards posterior end of

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1. Definition following Schultz, 1958.

coelomic cavity where vertebrae are becoming buried in hypaxial musculature. Pleural ribs originate on haemal prezygapophyses immediately below epipleural origin, terminating short of epipleural termination.

Two vertebrae involved in support of caudal fin. Penultimate vertebrae with strong haemal spine almost reaching hypural posterior margin. Two hypural plates, anteriorly fused for 1/2 - 2/3 of their lengths, ventral plate of hypurals 1-3, dorsal plate of hypurals 4-6; hypural plates fused to urostyle (Quast, 1965); lower plate not as firmly ankylosed, penetrated by small foramen at base. 12 primary caudal rays, 6 per hypural; up to 12 secondary rays both above, below hypurals.

One pterygiophore per neural, haemal spine. Spinous dorsal first pteryiophore with broad, thin, medially thickened blade descending between neural spines; dorsally, pterygiophore thickened, angled back where it forms dorsoventrally compressed fan-like process. First pterygiophore largest, these bones becoming smaller posteriorly. Anal, soft dorsal pteryophores similar to spinous dorsal pterygiophores except posterior fan becomes conelike, and blade medial thickening broadens laterally towards the fins. Unlike the characid pterygiophore (Weitzman, 1962), the distal, proximal, and medial radials are fused into a single pterygiophore.

Internal Anatomy

Thick walled esophagus leading into anterior of thick-walled (when empty) stomach; right anterior margin of stomach giving off small intestine; intestine giving off 4-10 pyloric caeca ventrally, then running down right side of body cavity to anal region, usually doubling back to stomach; in some specimens, a short extra anteriorly directed loop may be given off from small intestine posterior extremity; at stomach, small intestine giving off large intestine which ventrally overlaps caeca with medial loop, then posteriorly extends along ventral body wall to anus. Pancreas diffuse, in intestinal mesentery. Liver unilobate, filling anterior left of coelom; processes off liver filling space dorsal, ventral, and anterior to stomach. Spleen large, unilobate situated above and to the right of the stomach. Gall bladder large, above and to the right of spleen. Gonads bilobed, joining posteriorly, lying against coelom roof anteriorly; in males, whitish testes long, tubular; in females, yellowish ovaries short, lobate. Large urinary bladder applied to right of cloaca, bladder between ovaries and body cavity roof.

Cephalic Lateral Line System

The cephalic sensory system in *Gymnocanthus* shows a basic structure common to all six species. Specific variation was examined in bleached and injected specimens of all six species. The passage of the lateral line system through head bones was described in the osteology section. Nomenclature for the most part follows Cowan (1968) and Reno (1969).

The supraorbital canal begins far forward on the snout as medionasal (MN) canal, this canal originating as pore anteromedial to nasal spine, extending posteriorly; postnasal (PN) canal originating as pore posterolateral to nasal spine, canal running medially to meet MN, forming supraorbital (SO) canal posteromedially to nasal spine; MN, PN, anterior end of SO imbedded in dermis, all following canals imbedded in bone; SO running along interorbital, entering frontal bone medial to prefrontal;

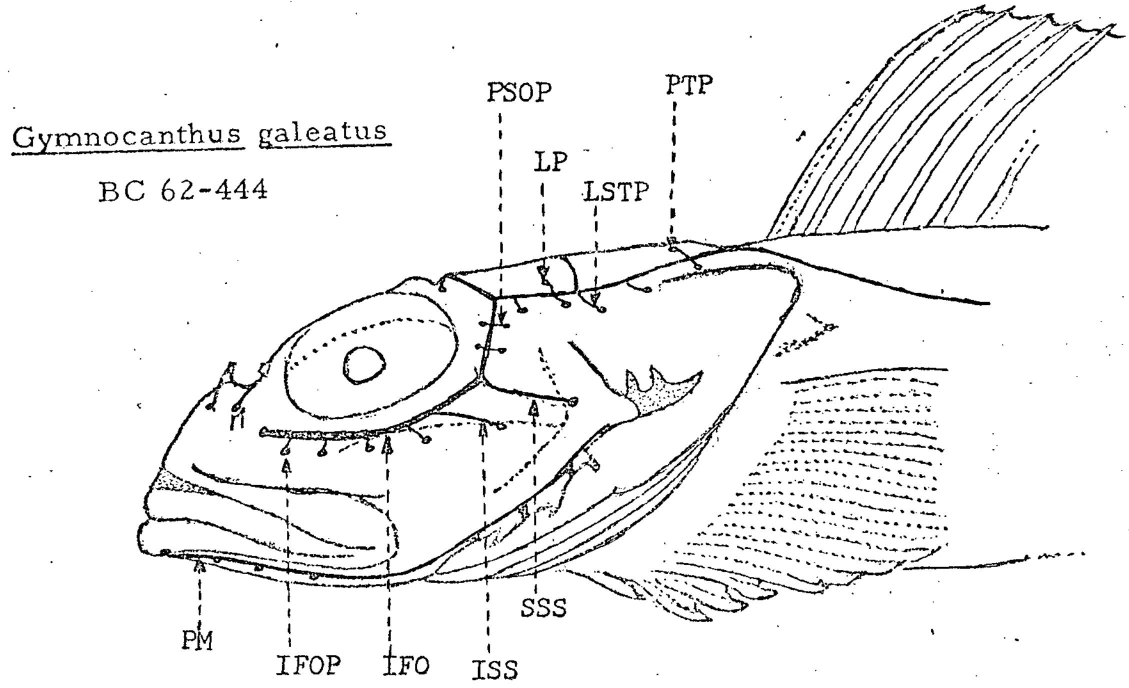
SO forming pore slightly anterior to interorbital narrowest width, SO joining fellow just behind postorbital tubercle by the interorbital (IO); IO usually developing short, medial, posteriorly directed interorbital process (IOP); IO extending laterally behind eye forming posterior supraorbital (PSO) canal; PSO giving off cross canal, the posterior supraorbital process (PSOP), one branch emerging in postorbital notch, the other medial to frontal spine; infraorbital canal (IFO) beginning as pore below and just anterior to orbit, running beneath the orbit to suborbital stay, giving at least four short infraorbital processes (IFOP), the first and second from the lachrymal, the third and fourth from the second infraorbital; short canal, infrasuborbital stay (ISS) given off along ventral side of suborbital stay; longer suprasuborbital stay (SSS) canal extending from IFO along dorsal side of suborbital stay; PSO and IFO connected behind the eye by postorbital (PO) canal; PO canal giving off two short cross-canals, the postorbital processes (POP), these canals emerging between each of the 4th, 5th and 6th (dermosphenotic) infraorbital bones; lateral canal (L) running back from PSO and PO canals at frontal-dermosphenotic junction along lateral frontal bone margin, through a series of extascapulars; usually at least two cross branches, the lateral extrascapular capping pterotic giving off supratemporal (ST) canal medially, this canal joining its counterpart; ST giving off medial cross branch, the supraoccipital (SOC) canal; SOC shorter anterior to ST than posterior to ST; second posteriorly directed supratemporal process (STP) lateral to parietal tubercle; ST largely within supratemporal (LSTP) from ST and L junction; from this junction, posttemporal (PT) canal passing

Figure 2.

Cephalic lateral line system

The canal and pore pattern shown is the basic system common to all species of *Gymnocanthus*. The extra pores and accessory canals found in most *G. galeatus* have been deleted.

Abbreviations: IFO, infraorbital; IFOP, infraorbital process; IO, interorbital; IOP, interorbital process; ISS, infrasuborbital stay; L, lateral canal; LL, lateral line; LP, lateral canal process; LSTP, lateral supratemporal process; MN, medionasal; PM, preoperculomandibular; PN, postnasal; PO, postorbital; PSO, posterior supraorbital; PSOP, posterior supraorbital process; PT, posttemporal; PTP, posttemporal process; SO, supraorbital; SOC, supraoccipital; SSS, suprasuborbital stay; ST, supratemporal; STP, supratemporal process.



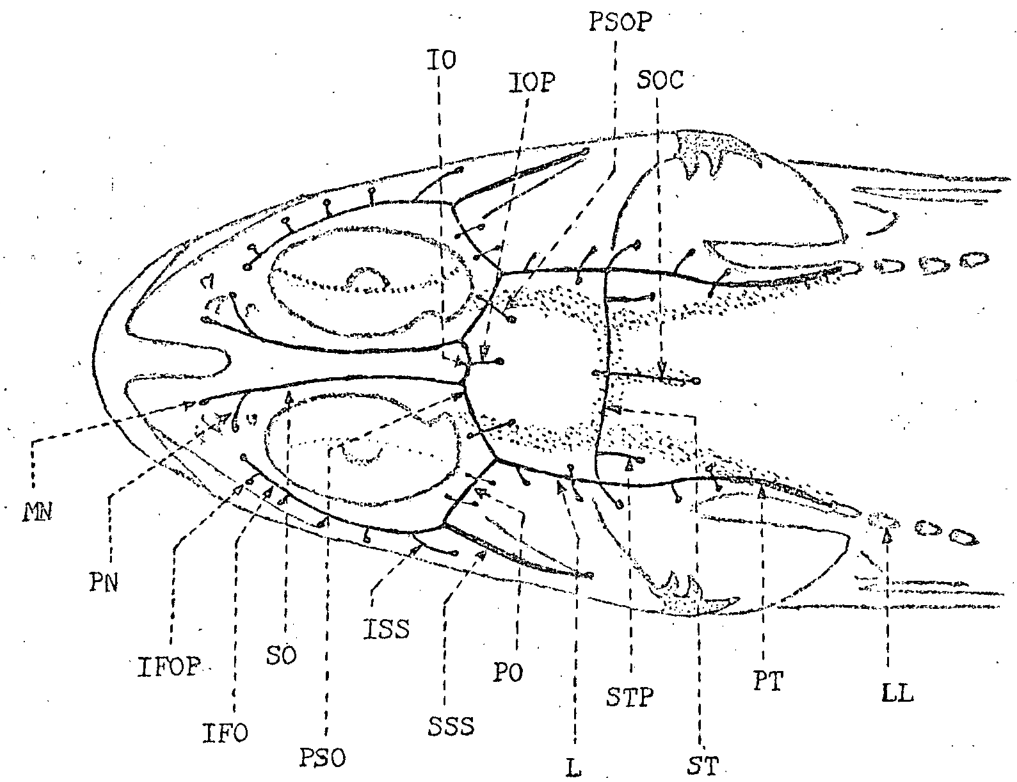


Figure 2

Cephalic Lateral Line System.

back through posttemporal bone, supracleithrum, thence into lateral line ossicles; PT giving off two small posttemporal processes (PTP), one from between lateral extrascapular and posttemporal bone and one from between posttemporal bone and supracleithrum; all processes, dead-ending canals terminating in pores.

Preoperculomandibular (PM) canal evidently not connected with rest of cephalic sensory system; mandibular portion beginning as pore lateral to dentary symphyseal knob; canal runs within dentary, giving off two more pores through foramina; fourth pore at articular-dentary junction; PM passing through articular, entering preopercular descending limb, giving off single pore immediately beneath each of the preopercular spines.

The basic system described is that possessed by most *G. tricuspis*. Other species, especially *G. galeatus* may have many extra pores and small accessory canals along the major canals, especially IFO, SSS, PO, PO, and SO. Porosity tends to be variable within a species and becomes better developed in larger fish. It is therefore impractical to quantify pore counts for comparative purposes.

Gymnocanthus herzensteini Jordan and Starks

Synonymy

Gymnocanthus galeatus (non Bean): - ?Schmidt, 1904:97 (description, counts, measurements, colour, cf. with *G. pistilliger*, *G. tricuspis*); ?Popov, 1933b:139-155; ?Dogel; 1948:17-66 (parasites on "*G. galeatus*").

Gymnocanthus herzensteini: - Jordan and Starks, 1904:294 (type description, figure, counts, measurements, colour); ?Popta, 1911:333-353 (locality); Tanaka, and Snyder, 1913 (figure, listed); Rendahl, 1931a:73 (counts, cf. with G. intermedius, tricuspis, pistilliger); Taranetz, 1937:118 (distribution, key); Okada, 1938:230 (listed); Lindberg, 1947:188 (distribution); Khlupova, 1950:135:154 (vitamin A in liver); Gusev, 1951:394-463 (copepod parasites); ?Kizevetter and Lagovskaya, 1951:128-138 (vitamin A in liver); Mori, 1952:163 (listed, locality data); Kizevetter, 154:273-293 (vitamin A in livers); Okada, 1955:336 (counts, description, fishery); Legeza, 1956:122-131 (distribution); Mori, 1956:28 (listed); ?Sato and Kobayashi, 1956:7 (locality; possibly G. intermedius; specimens small); Abe, 1958: 57 (description, range, counts, figure); Abe, 1971:217 (counts, description, range, figure); Watanabe, 1960:5 (counts, description, measurements, colour, figure plate).

Gymnocanthus merzensteini: - Jordan and Starks, 1904:290 (lapsus calami).

Gymnacanthus herzensteini: - Schmidt, 1927:30 (key, counts, measurements, distribution, cf. with G. detrisus).

Gymnocanthus galeatus herzensteini: - Soldatov and Lindberg, 1930:248 (synonymy, counts, distribution, key).

? Comnocanthus pistilliger: - Chyung and Kim, 1959:10 (figure; lapsus calami).

? Gymnocanthus pistilliger: - Chyung and Kim, 1959:6 (description, locality).

Description

Specimens described are SU 18652, 1 male, 16.52cm. (Kamoi Mizaki, Japan); SU 22291, 1 male, 16.86cm., 1 female, 12.75cm. (Kamoi Mizaki, Japan); SU 7572, 1 female, 19.83cm. (Hakodate); BC63-153, 1 male, 24.84cm. (Oshyuro Bay, Otary, Japan); BC72-112, 1 female, 24.90cm. (Shikabe, Hakodate, Japan).

Body moderate, robust anteriorly, tapering posteriorly to a narrow peduncle, depth 23.39 (21.32-25.50) times in SL; peduncle weakly laterally compressed, oval in cross section; trunk egg-shaped in cross section, dorsum slightly elevated, moderately to strongly convex such that dorsum pointed; greatest depth usually on vertical through pelvic girdle, depth at this vertical 4.92 (4.51-5.46) times in SL. Head long, length 2.77 (2.57-2.87) times in SL; head equally wide as deep, laterally compressed anteriorly, depth 1.02 (.93-1.12) times in width; in frontal profile, nape broadly, weakly concave or flat, ventrum flat, Lateral line ossicles small, anteriorly with ossicle-length separating them, remaining slightly separated caudally; ossicles extend onto caudal rays. Never any pectoral pistillae. Axillary scales small, half the length of lateral line ossicle at spinous-soft dorsal interspace; scale patch very dense. Snout laterally flattened, moderately pointed, long, 3.74 (3.48-3.98) times in head, 10.36 (8.83-11.32) times in SL; lateral ethmoid-nasal spine distance short such that dorsal profile of snout does not jut out appreciably. Teeth small, villiform randomly arranged, weakly posteriorly recurved; on dentary, tooth pad up to 3-4 teeth wide at symphysis; on premaxillary, tooth band up to 6 teeth wide at symphysis; tooth pads narrow posteriroly.

Mouth tissue papillose behind, ahead of tooth pads, up to 3 rows wide behind premaxillary, dentary, up to 3 rows wide ahead of premaxillary, 2 rows wide ahead of dentary. Upper jaw long, length 2.26 (2.17-2.38) times in head; maxillary long, extending past vertical through pupil center, often past vertical through posterior edge of pupil. Single pair small, strongly posteriorly recurved nasal spines, spines often emergent. Two pairs of nostrils, first pair on vertical through nasal spines; nasal tubule equally as high as nasal spine; nasal tubule produced such that terminal pore opening anterolaterally. Posterior nares posterolateral to nasal spines, distance from nasal spine tip 1/5 the distance to edge of lateral ethmoid; posterior nasal tubules lower than anterior tubules; distance from posterior nare base from nasal spine tip 1/4-1/5 distance of tip from anterior nare base from nasal spine tip. Orbits moderate, longer than deep, length 4.04 (3.27-4.55) times in head, length .82 (.79-.89) times in depth. Interorbital broad, from flat to weakly concave, width 12.61 (10.53-18.92)[1] times in head. Posterodorsal margin of orbit forming a postorbital tubercle which is strongly produced laterally, weakly vertically produced, setting off distinct postorbital notch, width 5.48 (4.96-5.93) times in head. No postorbital cirri. Nape with weak ridge extending back from postorbital notch, spreading laterally at supratemporal cephalic sensory canal, becoming confluent with lateral line; very weak tubercle on ridge directly behind notch; no other distinct

1. Watanabe (1960) reports a range in 45 specimens from 8.6 to 14.3, mean 11.1.

tubercles. Granulations heavily investing nape; may extend posteriorly, laterally and medially to a line 2-3 dorsal spine widths anterior to spinous dorsal; may extend anteriorly across interorbital (but not on interorbital rims) to a line joining posterior nares; laterally, largely contained by lateral canals; several granulations may occur on upper branch of opercular, 4th, 5th infraorbitals, upper border of suborbital stay; lateral cephalic sensory canal often protected by investing granulations. Suborbital stay strong, length 4.29 (3.67-4.99) times in head; preopercular with four spines; uppermost spine moderately strong, extending back beyond vertical throgh opercular notch anterior border, but not opercular edge; spine bearing 2-5 cusps, modally 3-4 (mean 3.26); dorsal margin of opercle straight to gently rounded; ventrally directed subopercular spine small, seldom emergent. Cleithral spine weak, never emergent. Dorsal spines separate, interdorsal distance up to 3 times dorsal spines width; first predorsal length 3.02 (2.84-3.11); first dorsal sexually dimorphic; in females, spinous dorsal convex throughout, increasingly convex posteriorly, longest spine 3rd-5th, height 6.29 (5.59-6.73) times in SL; in males, spinous dorsal margin convex posteriorly, almost straight anteriorly, reaching and surpassing soft dorsal when folded, 4th-6th spines longest, length 4.81 (4.34-5.29) times in SL; spinous dorsal longer than soft dorsal, spinous dorsal height .89 (.80-1.03) times in soft dorsal height; base of spinous dorsal shorter than soft dorsal base, spinous dorsal base 1.28 (1.16-1.43) times in soft dorsal base, 4.19 (3.99-4.79) times in SL; second predorsal 1.77 (1.73-1.82) in SL; height of soft dorsal sexually dimorphic; longest ray 4th-6th; margin flat anteriorly, convex posteriorly; in males, longest ray 5.75 (5.21-6.44) times in SL, in females, 6.84 (6.54-7.26) times in SL; spinous dorsal originates on vertical through pelvic fin base, soft dorsal originating on vertical between 1st and 3rd anal ray, terminating on vertical between penultimate and antepenultimate anal rays. Preanal 1.86 (1.76-1.98) in SL; anal base long, 2.98 (2.77-3.22) times in SL; margin convex, shortest rays at either end. Pelvics originating halfway between anal origin, snout; pelvic fin length sexually dimorphic, in females, middle ray longest, length 4.93 (4.39-5.37) times in SL, not reaching anus; in males, inner or middle ray longest, length 4.40 (3.91-4.88) times in SL, reaching as far as anal origin; pectorals broad based, base 6.67 (6.32-7.04) times in SL; base about 45° off vertical; longest rays 3rd-5th, length 2.91 (2.52-3.08) times in SL; pectoral strongly convex; no specimen with serrations on pectoral rays. Caudal truncate. Anus on small, rugose papilla slightly in advance of anus; male with small, conical penis, length 33.11 (26.31-49.04) times in SL.

Meristic formulae

Spinous dorsal 11 (10-11) (10.82); soft dorsal 17 (16-17) (16.64); pectoral 20 (19-21) (19.95); anal 19 (18-19) (18.73); pelvics I, 3; lateral line pores[1] 46 (43-48); vertebrae 38 (37-39) (37.73); branchiostegals 6.

Colour in alcohol

Ground colour on dorsum to hypaxial-epaxial body division light

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1. after Watanabe, 1960.

brown to gray, dipping ahead of anal fin, intensifying on nape, snout, cheek, opercle; body punctulations usually not present; if present, vague; four large blotches on dorsum, one under spinous dorsal, two under soft dorsal, one on peduncle, these blotches, when present, very vague, belly, branchiostegals, dentary, posterior 2/3 of premaxillary, posterior tip of maxillary, broad region between preopercular spines, maxillary wedge on peduncle, ground colour of fins white to yellow; spinous, soft dorsals with 3-4 oblique bands; pectorals with 3-4 transverse bands; caudal with 3 transverse bands, width about that of interband width. Buccal cavity, peritoneum pale.

Maximum size

Male, 25.5 cm. SL, female 28.1 cm. SL.

Colour in Life

"...the body is largely cherry-red, pectorals golden, with whitish tips and black bands bordered with bright orange; maxillary orange; chin and belly white; orange bars on back; a brick-red band across top of head." (Jordan and Starks, 1904:295)

Etymology

The specific name herzensteini is patrinymic, and is named for Dr. Solomon Herzenstein, in recognition of his excellent work on the fishes of Hokkaido (Jordan and Starks, 1904).

Range

Gymnocanthus herzensteini ranges around Hokkaido, mainland side of Japan Sea south to Korea.

Specimens Examined

	Reference	Locality	No.	Coordinates	Depth in meters
1.	BC63-153	Oshyoro Bay near Otaru, Hokkaido	2	140°59'E, 43°14'N	
2.	BC72-118	Off Shikabe, east of Hakodate	4	140°49'E, 42°03'N	50
3.	SU 7572	Hakodate	1	140°44'E, 41°46'N	
4.	SU 18652	Hakodate?	1	147°17'E, 43°14'N	
5.	SU 22291	Albatross Stn. 4988	3	140°21'E, 43°23'N	117
			11		

Literature Records

No.	Location	Coordinates	Depth in meters	Reference
6.	Hakodate, Hokkaido	41°36'N, 140°44'E		Jordan and Starks, 1904
7.	Tyosen (Korea)			Okada, 1938
8.	Gulf of Aniva (Zaliv Aniva)	49°00'N, 143°40'E		Taranetz, 1937
9.	Hakodate, Hokkaido	41°36'N, 140°44'E		Schmidt, 1950
10.	Gensan (Wonsan), Korea	39°07'N, 127°26'E		"
11.	Peter the Great Bay (Zaliv Petra Velikogo)	43°00'N, 132°00'E		"
12.	Chongjin, Korea	41°50'N, 129°50'E		Mori, 152
13.	Tohoku (North Honshu)			Okada, 1955
14.	Toyama Bay	36°42'N, 137°14'E		"
15.	Wonsan, Korea	39°07'N, 127°26'E		Abe, 1958
16.	Wakkanai, Hokkaido	45°26'N, 141°43'E	153	Watanabe, 1960
17.	Yoichi, Hokkaido	43°14'N, 140°47'E	66	"
18.	Abashiri, Hokkaido	44°02'N, 144°17'E	77	"
19.	Nemuro, Hokkaido	43°22'N, 145°36'E	66	"
20.	Akkeshi Bay, Hokkaido	43°02'N, 144°52'E	77	"

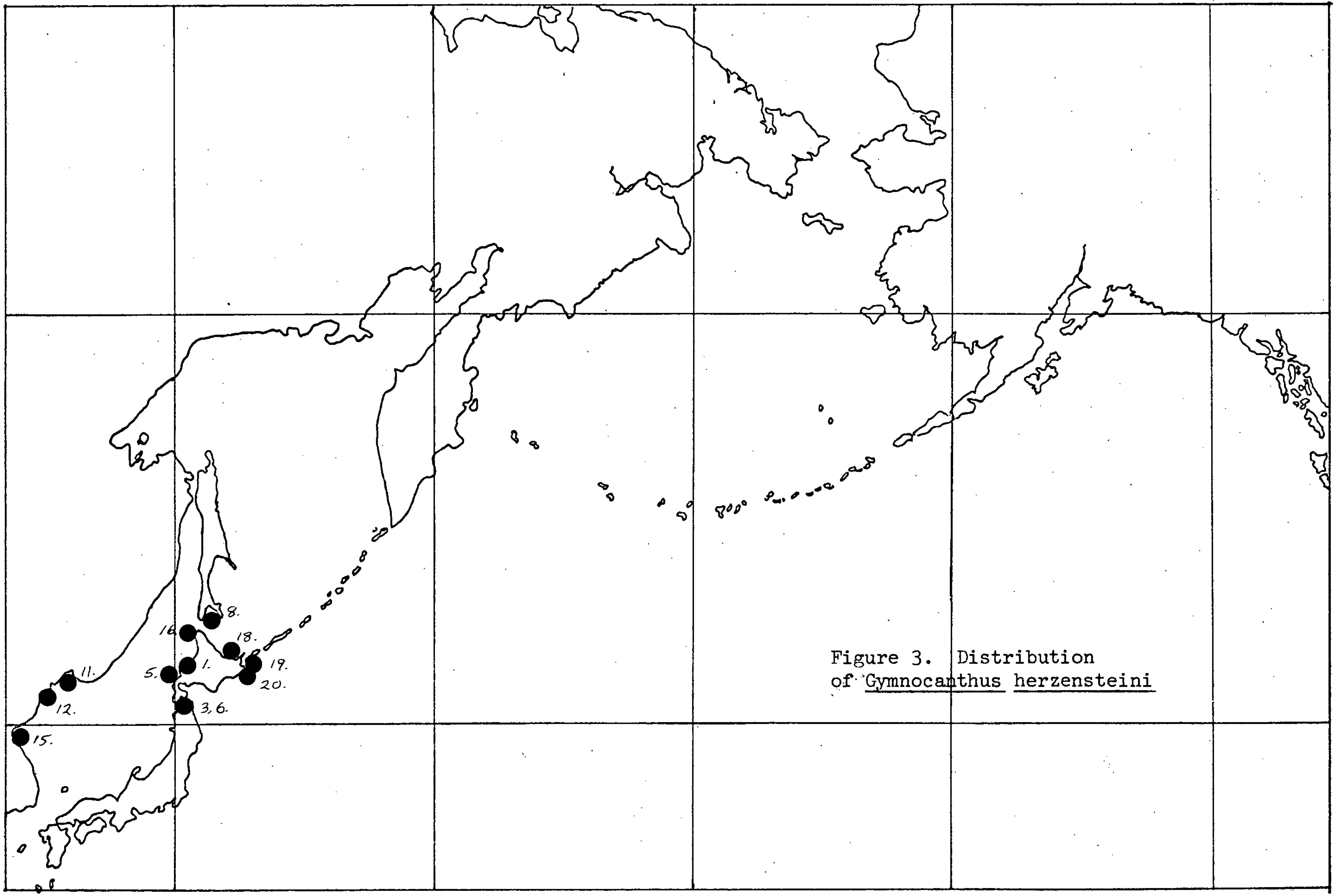

Figure 3. Distribution of *Gymnocanthus herzensteini*

Gymnocanthus detrisus Gilbert and Burke

Synonymy

Gymnocanthus detrisus: - Gilbert and Burke, 1912:61 (description, counts, measurements, colour, figure, distribution); Popov, 1933a:61 (description, ecology); ?Taranetz, 1933:67-68; Taranetz, 1937: 118 (key, measurements, distribution); Okada, 1938:230 (listed); Andriashev, 1939b:1-187 (ecology, zoogeography); Kuronuma, 1943: 110 (counts, locality, data); Lindberg, 1947:188 (distribution); Vinogradov, 1949:575 (habitat); Schmidt, 1950:163 (synonymy, description, distribution); Kizevetter, 1954:273-293 (vitamin A in livers); Legeza, 1956:122-131 (distribution); Watanabe, 1960: 61 (description, counts, measurements, colour, figure, plate).

?Gymnacanthus galeatus (non Bean): - Schmidt, 1903:97 (description, counts, measurements, colour, cf. with G. pistilliger, G. tricuspis).

Gymnacanthus detrisus: - Schmidt, 1927:30 (measurements, cf. with G. herzensteini, distribution); Andriashev, 1937:28 (cf. with G. galeatus, counts, measurements, figure).

Gymnocanthus galeatus detrisus: - Lindberg and Soldatov, 1930:249 (synonymy, counts, description, distribution, key).

Description

Gymnocanthus detrisus Gilbert and Burke is a large northwestern Pacific form. Variation is slight, and descriptions of a small number of specimens is adequate to express this variation. Specimens described were BC56-344A, 2 females, 16.90, 16.93cm., 1 male, 19.60cm. ("Japan");

BC63-675, 2 females, 23.95, 24.00cm. (Sea of Okhotsk); SU 22283, 1 female, 8.18cm., 1 male, 13.64cm. (Sakhalin Is.); F-810, F-811, 1 female, 22.55cm., 1 male, 27.61cm. (Japan).

Body elongate, robust anteriorly, tapering posteriorly to a narrow peduncle, depth 23.21 (20.72-26.78) times in SL; peduncle rectangular, weakly laterally compressed. Greatest depth on vertical through pelvic girdle, depth at pelvic girdle 5.66 (4.92-6.48); trunk generally ovate, weakly flattened ventrally, gently rounded dorsally. Head moderate, length 2.84 (2.76-3.10) times in SL; head tending to broader than deep, depth 1.23 (1.09-1.40) times in width; in frontal profile, head almost flat ventrally, flat or broadly weakly concave dorsally. Lateral line ossicles large, half an ossicle length or less separating ossicles anteriorly, becoming adjacent posteriorly; ossicles extend onto caudal rays. Never any pistillae in pectoral axil. Scales about 1/3 the length of the ossicles below the spinous-soft dorsal interspace; dorsally, scales separated by distance equal to or exceeding their own length; scale patch extending practically to the end of the pectoral fins: scales sparse. Snout broad, blunt, length 4.21 (3.75-4.63) times in head, 11.95 (10.89-13.01) times in SL; orbit-nasal spine distance moderate, making snout jut out slightly. Teeth villiform, small, posteriorly recurved, randomly situated on jaws; tooth band up to 5 teeth wide on premaxillary near symphysis; tooth band narrowing posteriorly; tissue in mouth may be papillose directly ahead of or behind tooth pads; 1-2 rows of papillae on lips anterior to dentary and premaxillary; 2-3 rows posterior to these teeth; mouth moderate, upper jaw length 2.51 (2.19-2.68) times in head; maxillary extending to or past vertical through pupil center in fish larger than 10cm. not reaching this line in smaller fish. Single pair strong, frequently emergent, moderately posteriorly recurved nasal spines; two pairs of nostrils, first pair on vertical plane through nasal spines, length of nasal tube subequal to nasal spine length; tube constricted terminally such that oval terminal pore opens anteriorly; posterior nares posterolateral to nasal spines, 2/3 distance from orbit rim; tube always much lower than nasal spine, anterior nostrils; nasal tube produced such that pore opens upward or posterolaterally. Orbits moderate, longer than deep, length 3.53 (3.23-3.91) in head, depth 1.35 (1.25-1.44) into length; never any orbital cirri; interorbital very broad, flat or weakly concave; if concave, broadly U-shaped in large specimens (over 10cm.) and broadly V-shaped in smaller specimens (under 10cm.); width of interorbital 6.42 (5.25-10.0) times in head, larger specimens with disproportionately wider interorbitals, smaller specimens (under 8cm.) with the narrower interorbitals. Tubercle development on head not particularly variable; posterodorsal orbit margin forming strong tubercle which is produced more laterally than vertically, setting off a distinct postorbital notch; postorbital notch width 3.86 (3.47-4.33) times in head; strong nape ridges extending back from postorbital, curving outward at supratemporal cephalic sensory canal becoming confluent with lateral line; moderate tubercle development just behind postorbital tubercle; small ridge-like tubercle behind supratemporal cephalic sensory canal; tubercle development in fish 6cm. or greater size independent. Nape heavily invested in granulations especially in specimens over 8cm. long; granulations often extending posteromedially to a point 1-2 dorsal spines distance in front of spinous dorsal, posterolaterally to the vertical through 2nd-4th dorsal spines; granulations extending anteriorly across interorbital often past line between posterior nostrils; granulations may be found on leading face of prefrontals, along interorbital margin, ascending preopercular shaft, upper branch of opercular, 4th and 5th infraorbitals, upper side of suborbital stay, although are largely contained by lateral cephalic sensory canals; lateral canals protected by distinct ridge of granulations. Suborbital stay strong, 4.76 (4.10-5.18) times in head. Four preopercular spines, the uppermost strong with 2-6 cusps, modally 4 (mean 3.70); first preopercular spine occasionally reaching posterior opercular margin, invariably reaching well past vertical through opercular notch anterior margin; ventrally directed subopercular spine often sharp, exposed; dorsal border of opercle straight or weakly concave. Cleithral spine very weak, almost never emergent. Dorsal fins separate, interdorsal distance variable, width of up to 3 dorsal spines; first predorsal length 2.95 (2.74-3.17) times in SL; spinous dorsal moderately convex; longest spine 3rd-4th, height 5.77 (4.66-7.35) times in SL; base of spinous dorsal shorter than soft dorsal base, spinous dorsal base 4.68 (4.28-5.14) times in SL, 1.41 (1.28-1.59) times in soft dorsal base; soft dorsal base 3.33 (2.95-3.56) times in SL; second predorsal 1.80 (1.71-1.93) times in SL; margin convex anteriorly and posteriorly, flat between; longest dorsal ray 3rd-4th, height 5.83 (4.70-7.15) times in SL; spinous and soft dorsals about equally long, spinous dorsal height 1.03 (.87-1.15) times in soft dorsal height; first dorsal origin on vertical through first pectoral ray origin; origin of soft dorsal on vertical through 2nd-3rd anal ray, terminating on vertical between last and antepenultimate anal rays. Preanal 1.85 (1.69-2.00) times in SL; anal base long, 3.12 (2.88-3.46) times in SL; margin flat, all rays except first and last about equally long. Pelvics originating halfway between snout and anus, length moderately sexually dimorphic; middle or inner ray longest; in males, extending past anus, often as far as anal fin origin, length 3.42 (2.80-4.05) times in SL; in females, pelvics not reaching anus, length 5.14 (4.70-5.98) times in SL. Pectoral broad based, base 6.74 (5.97-7.52) times in SL; base about 45° off vertical; pectoral margin strongly convex, most posteriorly extending ray 5th-7th; inner face of pectoral rays entirely lacking serrated edge in both sexes. Caudal truncate. Anus on small rugose papilla slightly in advance of anal fin; male with small, conical penis immediately behind anus, penis length 28.96 (20.37-52.46) times in SL.

Meristic Formulae

Spinous dorsal 10 (9-11) (10.02); soft dorsal 16 (15-18) (16.28); pectoral 20 (19-20) (19.80); anal 18 (15-19) (17.91); pelvis I, 3, vertebrae 38 (37-39) (38.05); branchiostegals 6.

Colour in Alcohol

Body ground colour brown to tan on dorsum to epaxial-hypaxial body division; ahead of anal fin, dark colouration dropping below that line; ground colour intensifying on snout, cheek, occiput, upper branch of opercular; upper half of body with many punctulations; in addition, four large blotches on dorsum, first under spinous dorsal center, second and third under soft dorsal, last on peduncle; series of small, vague blotches along midlateral aspect tending to coalesce with dorsal blotches; spinous dorsal slightly dusky in males, clear in females; spinous dorsal with about 3 oblique bands; soft dorsal with 4-6 vertical or oblique bands; pectoral with 3-4 transverse moderate (often as wide as pupil) bands; caudal with 3-4 tranverse bands, interband width exceeding band width; ventrum, posterior tip of maxillary, posterior half of dentary and premaxillary, branchiostegals, ground colour of fins (except spinous dorsal), wedge on peduncle extending to upper margin of caudal fin, margin around lower three preopercular spines yellowish to white; males without distinct pectoral axillary white spots or white-striped pelvics; buccal cavity pale; peritoneum pale. Juvenile colour essentially that of adult except spinous dorsal not dusky in males.

Maximum size

Males and females 27cm.

Etymology

The origin of the specific name, detrisus is unknown; Gilbert and Burke (1912) do not offer any derivation.

Range

Gymnocanthus detrisus ranges along both the southwestern and south-eastern Kamchatkan coasts, the northern Kurile Islands, northern Hokkaido, Tatar Strait, along the western coast of the Sea of Japan to Vladivostok.

Systematic notes

As observed previously, this species has sometimes been regarded as a subspecies of *G. galeatus*. However, *G. detrisus* has been found to be distinguishable from that form at all times on the basis of its very wide interorbital, its slightly but consistently different tubercle pattern, its different colour pattern, long preopercular spine, and different range. In Gilbert and Burke's (1912) original description they stated that *G. detrisus* was most closely related to *G. herzensteini*, with which I disagree. *G. detrisus* shares with that species a wide interorbital, but differs in its much broader head and entirely different granulation tubercle and axillary scale development. Instead, I suggest it is very close to *G. galeatus* which it more closely resembles in these latter characters.

Material Examined

	Collection Number	Locality data or original collector	No.	Coordinates	Depth in metres
1.	BC56-344A	Japan	5	?	
2.	BC60-153	Oshyoro Bay, Otaro, Hokkaido, Japan	1	140°59'E, 43°14'N	
3.	BC63-671		11	155°24'E, 52°49'N	84
4.	BC63-675	Okhotsk Sea	19	155°42'E, 52°43'N	54
5.	SU 18648	Albatross Stn. 5006	1	142°29'E, 46°04'N	78.7
6.	SU 22283	Albatross Stn. 5008, Sakhalin Is.	2	142°37'E, 46°07'N	73.2
7.	SU 22361	Albatross Stn. 4798	2	156°21'E, 51°37'N	54.9
8.	F 810, F 811		2	150°16'E, 45°56'N?	64.0
			43		

Literature Records

No.	Location	Coordinates	Depth in meters	Reference
9	Albatross Stn. 4798	51°37'N, 156°21'E	55	Gilbert and Burke, 1912
10	Tatar Strait (Tatarskiy Proliv)	50°00'N, 141°00'E		Schmidt, 1927
11	Avacha, U.S.S.R.	53°07'N, 158°33'E		"
12	Western Kamchatka	52°38'N, 155°40'E		"
13	Akhemten?	?		"
14	Peter the Great Bay (Zaliv Petra Valikogo)	43°00'N, 132°00'E		Tatanetz, 1937
15	Paramushir Is. (Kurile Islands)	50°30'N, 156°00'E		Kuronuma, 1943
16	Wakkanai, Hokkaido	45°26'N, 141°43'E	77	Watanabe, 1960
17	Nemuro, Hokkaido	43°22'N, 145°36'E	61	"
18	Mombetsu, Hokkaido	44°20'N, 143°20'E	153	"
19	Akkeshi Bay, Hokkaido	43°02'N, 144°52'E	77	"

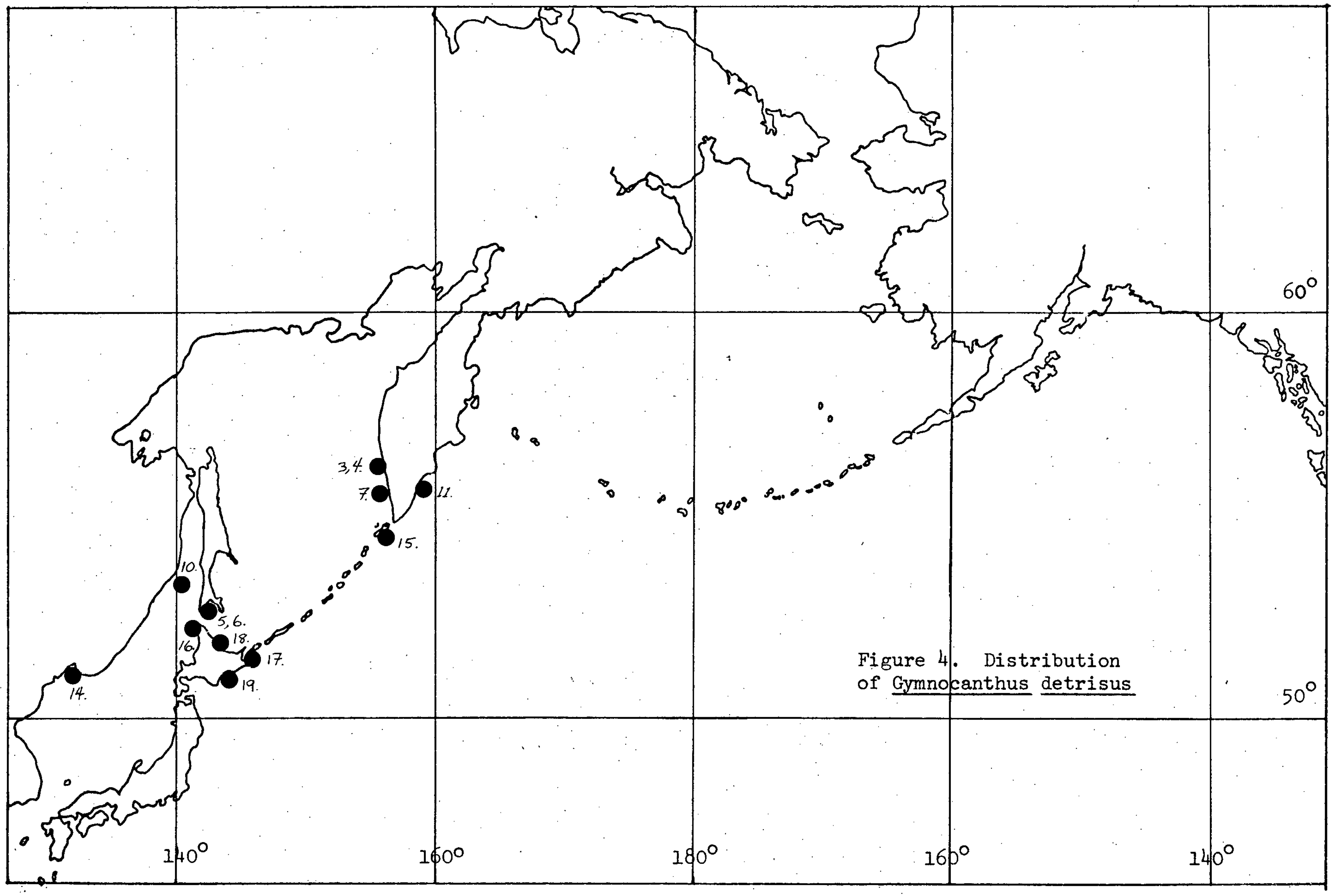

Figure 4. Distribution of Gymnocanthus detrisus

Gymnocanthus intermedius (Temminck and Schlegel)

Cottus intermedius: - Temminck and Schlegel, 1843:88 (type description, colour, counts).

?Cottus filamentosus: - Sauvage, 1875:279 (description, locality data Hawaii, likely erroneous, probably Japanese).

Gymnacanthus intermedius: - Gilbert, 1893:424 (counts, description, measurements, granulation pattern, distribution, cf. with G. tricuspis).

Gymnocanthus intermedius: - Jordan and Starks, 1904:282 (synonymy, description, counts, measurements, colour, distribution, cf. with G. pistilliger, Cottus filamentosus); Gratsianov, 1907:303 (key, synonymy, distribution); Jordan, Tanaka, and Snyder, 1913: 272 (listed); Soldatov and Lindberg, 1930:247 (synonymy, counts, description, distribution, key); Rendahl, 1931a:73 (counts, cf. with G. pistilliger, herzensteini, tricuspis); Mori and Uchida, 1934:18 (listed); Taranetz, 1937:118 (distribution, key); Taranetz, 1941:8 (figure of neurocranium); Lindberg, 1947:188 (distribution); Katayama, 1956 (locality, measurements, figure); Legeza, 1956:122-131 (distribution); Sato and Kobayashi, 1956:7 (locality, ecology); Watanabe, 1960:54 (descriptions, counts, measurements, colour, figure, plate).

Gymnocanthus ventralis (non Cuvier and Valenciennes): - Gratsianov, 1907: 303 (key, synonymy, distribution); Okada, 1938:230 (listed); Mori, 1952:162 (listed, locality); Mori, 1956:28 (listed).

Gymnacanthus pistilliger ventralis (non Cuvier and Valenciennes): - Schmidt, 1927:27 (synonymy, description, cf. with G. pistilliger, distribution).

Gymnocanthus pistilliger ventralis (non Cuvier and Valenciennes): - Schmidt, 1950:162 (key, distribution, cf. with G. pistilliger).

?Gymnocanthus galeatus (non Bean): - Watanabe, 1960:59 (description, counts, measurements, colour; apparently not that species, probably G. intermedius).

Description

Gymnocanthus intermedius (Temminck and Schlegel) is a small, distinctive northwest Pacific form showing only slight variation within the species. Specimens described were UW 2817, 1 male, 10.64 cm., 1 female, 10.62 cm. (Mitsu Bay, Japan); IU 10686, 2 females, 8.43, 6.71 cm. (Aonori, Kikuoku, Japan); IU 7571, 2 males, 17.33, 13.33 cm., 2 females, 17.99, 16.78 cm. (Hakodate, Japan); BC56-340, 1 male, 14.14 cm. ("Japan"); SU 17172, 1 female, 13.58 cm. (Korea).

Body moderate, robust anteriorly, tapering to a narrow peduncle, depth 19.57 (17.17-20.63) times in SL; in cross section, peduncle rectangular, weakly laterally compressed. Greatest depth on vertical through pelvic girdle, depth at pelvic girdle 5.05 (4.00-5.90) times in SL; trunk generally ovate in cross section, weakly rounded ventrally, moderately rounded dorsally. Head moderate, length 2.84 (1.68-2.94) times in SL; head tending to be as broad as deep, depth 1.04 (.92-1.25) times in width; in frontal profile, nape broadly, weakly concave, ventrum flat to broadly rounded. Lateral line ossicles large, less than half an ossicle

2/3 the distance of the anterior nares base from the nasal spine tip. Orbits moderate, longer than deep, length 3.52 (3.24-3.90) times in head, depth 1.20 (1.10-1.35) times in length; single, strong, unifid cirrus originating immediately below postorbital tubercle in both juveniles and adults; interorbital moderate, flat to weakly, broadly concave, width 13.56 (11.20-16.05) in head. Tubercle development on head not particularly variable; posterodorsal orbit margin forming strong postorbital tubercle which is more strongly produced laterally than vertically, setting off a distinct postorbital notch, width 5.45 (5.01-6.12) times in head; weak nape ridges extending back from postorbital tubercle, curving laterally at supratemporal cephalic sensory canal, becoming confluent with lateral line; in larger specimens (over 10cm.) long ridgelike tubercle on ridge at supratemporal canal, but no appreciable tubecle development immediately behind notch. Nape heavily invested in granulations, especially in specimens over 8cm. long; granulations often extending posteromedially to a point 2-3 dorsal spines distance in front of spinous dorsal, posterolaterally to the same line; granulations extending anteriorly at least to postorbital tubercles and in larger specimens, across the interorbital, short of posterior nares; granulations largely contained by lateral cephalic sensory canals; 5th infraorbital occasionally with a granulation; no granulations on operculum, preoperculum, or suborbital stay; lateral canal usually, supratemporal, supraoccipital canals occasionally protected by distinct ridge of granulations. Suborbital stay strong, length 4.33 (3.93-4.80) times in SL. Four preopercular spines, the uppermost strong with 1-5 cusps, modally 3 (mean 2.91); first preopercular spine usually reaching past opercle border; ventrally directed subopercular spine sharp, exposed; superior border of opercular flap straight to weakly convex. Cleithral spine broad, very strong, usually exposed; spine forms distinct lump under skin where not exposed. Dorsal fins separate, interdorsal distance variable, width up to 3 dorsal spines; first predorsal lenth 2.97 (2.81-3.13) times in SL; spinous dorsal margin convex, longest spine 2nd-3rd; spinous dorsal length sexually dimorphic, in males 5.19 (4.27-5.72) times in SL, in females 5.60 (4.83-6.27) times in SL; base of spinous dorsal shorter than soft dorsal base, spinous dorsal base 1.33 (1.16-1.47) times in soft dorsal base, 4.49 (4.00-4.79) times in SL; soft dorsal base 3.36 (3.10-3.87) times in SL, second predorsal 3.56 (3.10-3.87) times in SL; soft dorsal margin flat anteriorly, convex posteriorly; longest dorsal ray 3rd-5th- height 6.22 (5.13-7.30) times in SL; spinous dorsal longer than soft dorsal, spinous dorsal length .85 (.74-.99) times in soft dorsal length; first dorsal origin on vertical through origin of first pectoral ray; origin of second dorsal over first or second anal ray, ending on vertical between last and antepenultimate anal ray. Preanal 1.82 (1.73-1.88) times in SL; anal base long, 3.14 (2.30-3.32) times in SL; anal margin flat, all rays (except for shorts first and last rays) approximately equally long. Pelvics originating halfway between cloaca and snout; inner ray usually longest; in males, extending past 4th anal ray, length 2.84 (2.52-3.35) times in SL; in females, pelvics shorter, rarely reaching anus, length 4.73 (4.40-4.90) times in SL. Pectoral broad-based, base 6.75 (5.87-7.58) times in SL; base 40-45° off vertical; pectoral margin strongly convex, posterormost extending ray 5th-7th, often reaching past 2nd dorsal ray; some males with well-developed serrations on inner face of pectoral rays, all females lacking these serrations. Caudal truncate. Anus on moderate, rugose papilla slightly in advance of anus; male with small, conical penis immediately behind anus, length 30.82 (19.93-56.56) times in SL.

Meristic formulae

Spinous dorsal 9 (9-10) (9.48); soft dorsal 15 (14-15) (14.67); pectoral 19 (16-20) (19.22); anal 15 (14-16) (15.07); pelvics I, 3; vertebrae 34 (33-35) (34.0); branchiostegals 6.

Colour in Alcohol

Body ground colour brown to tan on dorsum to epaxial-hypaxial body division; ahead of anal fin, dark colouration dipping below that line; ground colour intensifying on entire cheek, much of nape; body with many tightly arranged punctulations, these punctulations sometimes tending to coalesce into four dorsal blotches, one under the spinous dorsal, two under the soft dorsal, and on the peduncle; also, tending to coalesce into small blotches along midlateral aspect; spinous dorsal with dark spots sometimes arranged in broad bands; rayed dorsal with 3-4 oblique dark bands; pectoral with 3-4 dark, narrow (narrow than pupil) transverse bands; caudal with 3-4 transverse bands, interband width much greater than band width; belly, branchiostegals, dentary, posterior tip of maxillary, posterior half of premaxillary, ground colour of fins, wedge on peduncle extending to upper margin of caudal fin, lower margin of opercle yellowish to white; males with white pistillae, white spots in pectoral axil, white band across interorbital, wide spots on nape, upper opercular; postorbital cirrus dark; buccal cavity pale; peritonium pale.

Colour in Life

"Olive, finely mottled with brown, salmon red shades on sides; fins barred; the dorsal, anal, caudal, pectoral washed with salmon red, brightest on pectoral and caudal; ventral white, faintly barred with salmon; lower side of head more or less yellow" (Jordan and Starks, 1904:293)

Maximum size

Females 17.7 cm., males 14.7 cm. SL.

Etymology

The species name, intermedius is from the latin "intermedius", and is a reference to its supposed intermediate position between Enophrys diceraus and Gymnocanthus pistilliger (Temminck and Schlegel, 1842).

Range

The species is found on both the north and south ends of Hokkaido, in the Strait of Tatar, along the west side of the Japan Sea to Korea.

Systematic Notes

This small Japan Sea species is very similar to G. pistilliger in several features such as the size range, form of sexual dimorphism, development of cleithral spine, and fin counts. It is apparently a distinct species and not a subspecies of G. pistilliger (Schmidt, 1950) since it geographically overlaps with that form. Secondly, the cleithral spine development and sexual dimorphism which show this species to be closely related to G. pistilliger are subtly, but consistantly different enough to distinguish the forms at all times.

Gymnocanthus intermedius has been called G. ventralis on occasion (Gratsianov, 1907; Schmidt, 1927). According to Cuvier and Valenciennes, (1829:194) Gymnocanthus ventralis possesses a preopercular spine which "n'atteint pas le bord de l'opercule....Il y a une petite épine en avant de l'oeil, une pointe mousse, ou plutôt une tubérosité, de chaque côté de l'occiput." In most G. pistilliger examined, the preopercular spine almost reaches, but does not quite reach the edge of the operculum. Secondly, that species possesses distinct occipital tubercles. In G. intermedius, the first preopercular spine does frequently pass the opercular margin, while its occipital "tubercles" are little more than very poorly developed ridges. In all likelihood, G. ventralis is identifiable with G. pistilliger.

Material Examined

	Reference	Locality	No.	Coordinates	Depth in meters
1.	BC56-340	"Japan"	2	?	
2.	IU 10686	Aonori (Aomori?), Kikuoku	3	140°43'E, 40°50'N	
3.	SU 7570	"Japan"	2	?	
4.	SU 7571	Hakodate, Japan	12	140°40'E, 41°40'N	
5.	SU 7907	"Japan"	1	?	
6.	SU 17172	"Korea"	1	?	
7.	UW 2817	Mitsu Bay, Japan	6	132°50'E, 34°20'N?	
			27		

Literature Records

No.	Location	Coordinates	Depth in metres	Reference
8	Jezo (-Hokkaido)	?		Schlegel, 1843
9	Hakodate, Hokkaido	41 46'N, 140 44'E		Gilbert, 1893
10	Same (-Sameminato?), Hokkaido	40 32'N, 141 32'E		"
11	Otaru, Hokkaido	43 14'N, 140 59'E		"
12	Ishikara, Hokkaido	43 30'N, 140 40'E		"
13	Peter the Great Bay (-Zaliv Petra Velikoyo)	43 00'N, 132 00'E		Taranetz, 1937
14	Vladimir Bay (-Zaliv Vladimira)	43 54'N, 135 30'E		"
15	Tyosen (-Korea)			Okada, 1938
16	Pos'et Bay, U.S.S.R.	42 38'N, 130 47'E		Schmidt, 1950
17	Sakhalin, west coast			"
19	Fusan (-Pusan), Korea	35 05'N, 128 02'E		Jordan and Metz, 1913
20	Chongjin, Korea	41 50'N, 129 55'E		Mori and Uchida, 1934
21	Volcan Bay (-Ichiura Wan), Hokkaido	42 21'N, 140 59'E		Sato and Kobayashi, 1956
22	Wakkanai, Hokkaido	45 26'N, 141 36'E	66	Watanabe, 1960
23	Abashiri, Hokkaido	44 02'N, 144 17'E	59	"
24	Abashiri, Hokkaido	44 02'N, 144 17'E	153	"
25	Nemuro, Hokkaido	43 22'N, 145 36'E	59	"
26	Akkeshi Bay, Hokkaido	43 02'N, 144 52'E	55	"
27.	Mashike, Hokkaido	43 52'N, 141 32'E	66	"
28	Usu, Hokkaido	42 34'N, 140 27'E	77	"

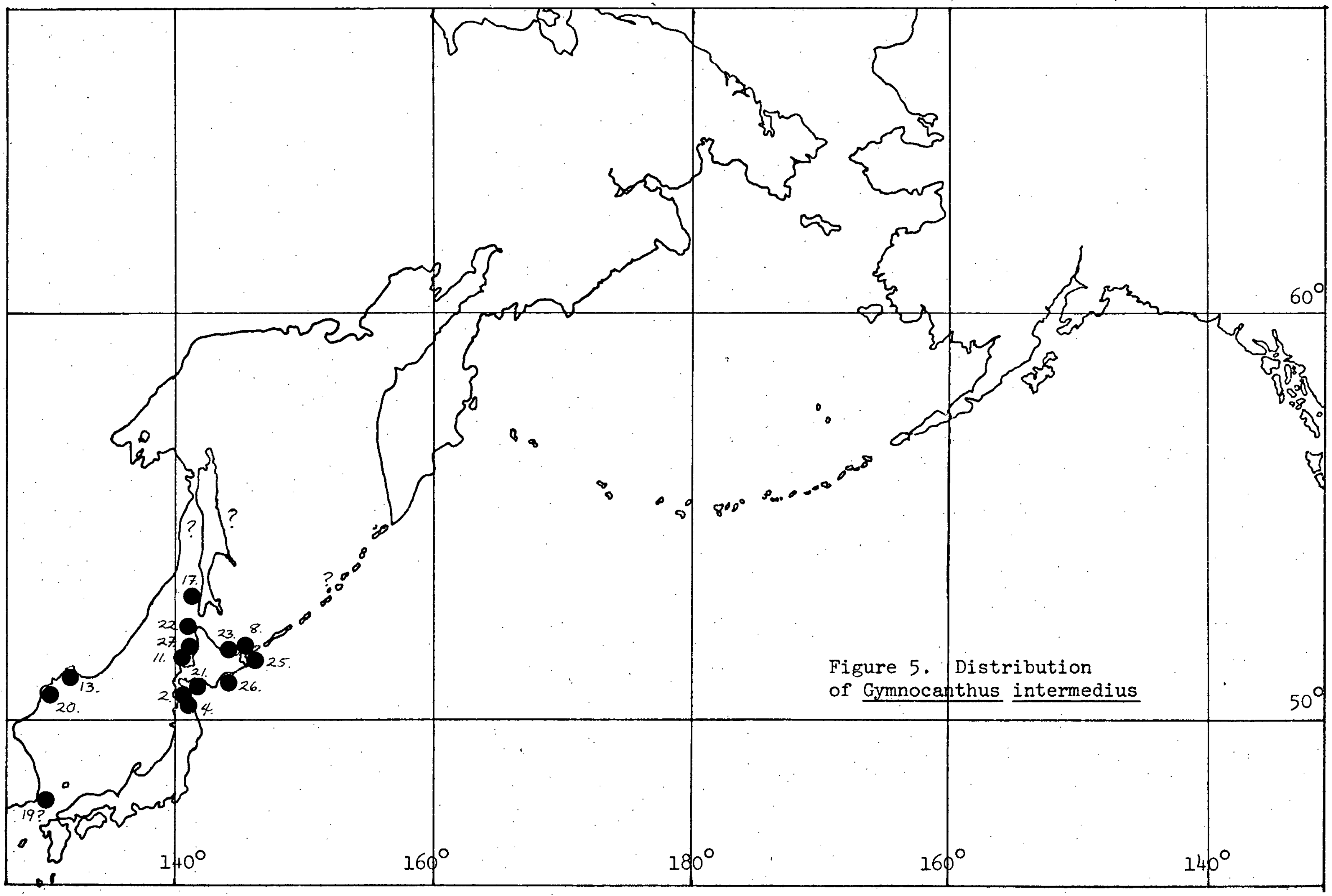

Figure 5. Distribution of Gymnocanthus intermedius

<u>Gymnocanthus pistilliger</u> (Pallas)

<u>Cottus pistilliger</u>: - Pallas, 1811:143 (type-description, counts, colour); Cuvier and Valenciennes, 1829:193 (description, counts, colour); Lay and Bennett, 1829:58 (description after Cuvier and Valenciennes); Günther, 1860:167 (description).

<u>Cottus cephaloides</u>: - Grey, in Cuvier and Valenciennes, 1829:194 (description colabeled under <u>Cottus ventralis</u>, <u>Cottus cephaloides</u>; type of <u>Cottus ventralis</u>).

<u>Cottus ventralis</u>: - Cuvier and Valenciennes, 1829:194 (description, counts, colour); Gunther, 1860:168 (partly non Cuvier and Valenciennes; description, counts).

<u>Gymnocanthus ventralis</u>: - Swainson, 1839:271 (description; type <u>Cottus ventralis</u> Cuvier and Valenciennes by monotypy).

<u>Acanthocottus psittiliger</u>: - Girard, 1851:186 (listed; lapsus calami)

<u>Elaphocottus pistilliger</u>: - Sauvage, 1878:109-158 (description, cf. with other subgenera of the archaic "<u>Cottus</u>").

<u>Gymnacanthus pistilliger</u>: - Collett, 1880:26 (partly non-Pallas; description, counts, colour, distribution); Bean, 1882:249 (partly non Pallas; distribution); Smitt, 1893:161 (description, figure of male, female, dimorphism, measurements, cf. with <u>G. tricuspis</u>); Bean and Bean, 1896:42 (locality) Gilbert, 1896: 424 (description, counts, measurements, colour, cf. with <u>G. tricuspis</u>); Knipovich, 1903:9 (counts, measurements, description, cf. with <u>G. tricuspis</u>); Schmidt, 1904:94 (synonymy); ?Andriashev, 1939b:1-187 (ecology); Andriashev, 1954:400 (description, counts,

figure, distribution).

Gymnocanthus pistilliger: - Jordan and Evermann, 1896:2006 (description, counts, measurements, plate, cf. with G. tricuspis); Jordan and Gilbert, 1899:460 (description. locality data); Scofield, 1899:503 (counts); Ehrenbaum, 1901:85 (synonymy, cf. with G. tricuspis); Jordan and Starks, 1904:290 (synonymy, description, colour, counts, figure); Gratsianov, 1907:303 (key, synonymy, distribution); Evermann and Goldsborough, 1909:319 (figure, distribution); Gilbert and Burke, 1912:61 (description, counts); Le Danois, 1913:425 (cf. with G. tricuspis); Jordan, Tanaka, and Snyder, 1913:271 (listed, figure); Jordan, Evermann, and Clark, 1930:389 (synonymy, distribution); Soldatov and Lindberg, 1930: 245 (synonymy, counts, description, distribution, key); Krivobok 1931:107-115 (locality); Popov, 1933a:61a (locality, ecology, description); Popov, 1933b:139-155: Popov, 1935:353-355; Andriashev, 1937:27 (cf. with G. tricuspis; counts); ?Taranetz, 1937:118 (figure, distribution); Okada, 1938:230 (listed); Andriashev, 1939b (zoogeography); Lindberg, 1947:188 (distribution); Vinogradov, 1949:575 (locality); Kobayashi and Ueno, 1956:252 (locality, measurements, counts, colour); Legeza, 1956:121-131 (distribution); Abe, 1958:57 (description, counts, distribution, figure); McAllister, 1960:16 (key); Watanabe, 1960:56 (description, counts, measurements, colour, figure, plate); Quast and Hall, 1972:21 (references).

Gymnocanthus pistilliger pistilliger: - Schmidt, 1927:26 (key, distribution cf. with _G. intermedius_); Rendahl, 1931b:55 (counts, description, measurements, cf. with _G. galeatus, intermedius, herzensteini_); Schmidt, 1950:161 (description, distribution, cf. with G. _ventralis, G. intermedius_).

Gymnocanthus pistilliger meridionalis: - Rendahl, 1931b:68 (cf. with _G. pistilliger_).

Description

Gymnocanthus pistilliger has a very broad distribution, reaching from Southeast Alaska to Vladivostok and north almost to the Bering Straits. The variation encountered over this range is not great, and a description of the following species was adequate to express this variation. Specimens described were UW 7325, 1 male, 1109cm., 1 female, 10.20cm. (Norton Sound, Alaska); SU 3003, 1 male, 10.07cm., 1 female, 11.18cm. (Bristol Bay, Alaska); BC63-1026, 1 male, 13.41cm., 1 female, 14.34cm. (Region Island, Alaska); BC56-340, 1 male, 15.35cm., 1 female, 18.34cm. ("Japan").

Body moderate, robust anteriorly, tapering posteriorly to a narrow peduncle, depth 23.82 (19.56-29.95) times in SL; peduncle generally rectangular, weakly laterally compressed; greatest depth of body on vertical through pelvic girdle, depth at pelvic girdle 5.11 (4.54-5.87) times in SL; trunk oval, weakly laterally compressed from peduncle to vertical through anal origin. Head moderate, length 2.96 (2.74-3.15) into SL; head broad, flattened, depth 1.12 (.73-1.29) in width; in frontal profile, head weakly, broadly concave ventrally, moderately, narrowly concave dorsally. Lateral line ossicles moderate, half an ossicle-length separating them anteriorly, becoming virtually adjacent caudally; ossicles extend to peduncle, onto caudal rays; males with pistillae in pectoral axil; pistils 1-2 ossicles long, spatulate at tip, 3-5 times as broad at tip as at base; 1-3 pistillae arising from common origin. Axillary scales moderate, about half the size of lateral line ossicles at spinous soft dorsal interspace; dorsally, scales density moderate. Snout blunt, length moderate, 4.18 (3.63-4.94) times in head, 12.44 (10.70-14.56) times in SL. Lateral ethmoidnasal spine distance short to moderate, making lateral orbit-snout profile moderately to weakly abrupt. Teeth randomly placed, small, villiform, weakly posteriorly recurved; dentary tooth pad up to 3 teeth wide at symphysis, premaxillary pad up to 4 teeth wide at symphysis; tooth band width narrows posteriorly. Tissue in mouth papillose directly ahead of or behind tooth pads; up to 2 rows posterior to premaxillary teeth, about 1 row behind dentary ahead of dentary, premaxillary teeth. Mouth moderate, upper jaw 2.64 (2.48-2.91) times in head; maxillary may reach vertical through pupil center, usually only to anterior pupil margin. Single pair moderate, moderately recurved nasal spines. Two pairs of nostrils, first pair just anterior to vertical plane through nasal spines; first pair tubular, tubes about 1/2 as high as nasal spines; anterior nostrils constricted distally such that terminal pore is directed anterolaterally; posterior nasal tubule, posterolateral to nasal spine base; this tubule almost as high as anterior tubule; posterior tubule equidistant from prefrontal base of nasal spine; posterior tubule produced such that it is directed straight up or posterolaterally; posterior and anterior nasal tube bases equidistant from nasal spine base. Orbits moderate, longer than deep, length 3.53 (3.13-4.16) times in head, .76 (.68-1.04) times in depth. Interorbital narrow, 19.11 (13.71-28.08) times in head V-shaped. Tubercle development consistant; posterodorsal margin of orbit forming postorbital tubercle; this tubercle developed strongly laterally and vertically, setting of distinct postorbital notch, width 3.53 (3.13-4.16) times in SL; young fish (under 6cm.) may have small, unifid cirrus originating immediately under postorbital tubercle. Nape ridges extending back from notch, angling laterally at supratemporal, cephalic sensory canals becoming confluent with lateral line; moderate to strong tubercle on ridge directly behind postorbital notch; second moderate tubercle just ahead of supratemporal canal; third strong tubercle directly over or just behind that canal. Nape usually, but not always, covered by bony granulations; these, when present, may extend posteromedially to a point 2-3 dorsal spines width ahead of spinous dorsal; laterally, extending back to origin of spinous dorsal; anteriorly, reaching interorbital but not completely crossing it; laterally, reaching lateral canals, and are largely confined to within these canals; occasionally, granulations on upper branch of operculum, on preopercular ascending limb; granulations not found on either infraorbitals or suborbital stay; when granulations present, tending to thinly invest sensory canals. Suborbital stay strong, 4.24 (3.74-4.88) in head. Preopercular with four spines, the upper strong, bearing 1-4 cusps, modally 2 (mean 2.24); this spine usually reaching past vertical through opercular notch anterior margin, but not reaching posterior margin of opercular; suboperculum with sharp, ventrally directed, generally exposed point; opercle with flat to gently convex dorsal margin. Cleithral spine moderate to strong, point usually emergent, imbedded shaft forming visible lump. Dorsal fins separate, interdorsal distance variable, up to 3 times width dorsal spine; first predorsal length 3.06 (2.90-3.[illegible]7) times in SL; first dorsal margin strongly convex; height strongly sexually dimorphic; in males, longest spine 3rd-4th, length 4.67 (3.87-5.97) times in SL, in females, longest spine 2nd or 3rd, length 6.05 (5.10-7.97) times in SL; spinous and soft dorsals almost equally high, spinous dorsal height .98 (.75-1.25) times in soft dorsal; spinous dorsal base shorter than soft dorsal base, length of spinous dorsal base 4.56 (4.06-5.28) times in SL, 1.30 (1.15-1.54) times in soft dorsal base; soft dorsal base 3.49 (3.10-3.76) times in SL, second predorsal 1.80 (1.56-1.92) times in SL; soft dorsal flat anteriorly, convex posteriorly; height sexually dimorphic; in males, longest ray 6th-8th, height 5.04 (4.00-7.02) times in SL, in females, longest ray 4th-6th, height 5.93 (5.13-7.37) times in SL; spinous dorsal originates on vertical through first pectoral ray, soft dorsal originates on vertical between 1st-2nd anal rays, terminates on vertical between last and antepenultimate anal ray. Anal fin long, base 3.11 (2.86-3.34) times in SL; anal low, margin straight, all rays (except for short last ray) approximately similar lengths; preanal 1.89 (1.78-1.99) times in SL. Pelvics originating halfway between snout, anal origin; length very sexually dimorphic; in males, middle ray usually longest, inner ray sometimes longest, sometimes reaching past anal fin center, length 2.71 (1.94-3.22) times in SL; in females, inner ray longest, reaches only to anus; length 4.63 (4.23-5.11) times in SL. Pectorals broad based, base 6.50 (5.97-7.45) times in SL, length 2.55 (2.16-2.98) times in SL; longest ray 4th-6th; pectoral margins strongly convex; in males, inner face of pectoral rays raised as serrated edge. Caudal truncate. Anus on moderate anal papilla slightly in advance of anal fin; male with large penis, length 21.01 (12.28-38.44) times in SL.

Meristic formulae

Spinous dorsal 10 (9-11) (9.74); soft dorsal 14 (13-16) (14.41); pectoral 19 (15-20) (18.53); anal 16 (14-18) (16.08); pelvic I, 3; lateral line pores 34-42, usually 37-40[1], vertebrae 36 (34-37) (35.62); branchiostegals 6.

Colour in Alcohol

Ground colour of dorsum to epaxial-hypaxial body division light grey to brown, dipping ahead of anal fin; ground colour intensifying on cheek forward to anterior nostrils, on occiput; dorsum with many dark punctulations, these coalescing to form four large blotches on dorsum, one under spinous dorsal, two under soft dorsal, and one on peduncle; also coalescing to form smaller, vague blotches along midlateral aspect of body; belly, branchiostegals, rear half of premaxillary and dentary, posterior tip of maxillary, preoperculum below first spine, ground colour of fins, wedge on peduncle white to pale yellow; males with large, bright white spots as well as white pistillae in pectoral axillae; males with small melanophores around axillary spots; females with 3-4 very irregular narrow bands on spinous dorsal, ground colour clear-yellowish; males with 3-4 broader, equally irregular bands on spinous dorsal, ground colour dusky, spinous dorsal with white spots; 3-4 narrow oblique bands on soft dorsal; pectoral

1. Soldatov and Lindberg, 1930.

with 3-5 narrow transverse bands, caudal with 3-4 narrow transverse bands, interband width much greater than band width males with white bands on the yellowish pelvics, females lacking these bands. Buccal cavity, peritoneum pale.

Colour of juveniles dissimilar in that the dorsal four blotches are much intensified; sexual dimorphism not present.

Maximum size

Females 18.7cm., males, 15.5cm. SL.

Etymology

The specific name pistilliger is from the latin "pistillum" (pestle), and the latin "gero" (to bear), in reference to the subpectoral dermal appendages born by the male.

Range

Known from Southeast Alaska, south Alaska, Aleutians to Amchitka, Bristol Bay, Pribilof Islands, north to Port Clarence, northern Hokkaido, both east and west coast of Kamchatka, Gulf of Sakhalin, mainland coast of Sea of Japan south at least to Vladivostok.

Systematic Notes

Although Gymnocanthus pistilliger was the first species of the genus Gymnocanthus described, the characteristic pistillae of the males, restricted variation, and more restricted distribution have saved it from the nomenclatorial fate endured by G. tricuspis. G. pistilliger has often been confused with that species (see synonymy for G. tricuspis) but may always be distinguished by certain features (see synopsis). As pointed out previously (see G. intermedius) the controversial synonym G. ventralis may be identified with G. pistilliger. Several authors (Schmidt, 1927, 1950; Rendahl, 1931) have seen fit to make G. tricuspis, G. intermedius, and G. pistilliger subspecies of G. pistilliger, a decision with which I cannot agree. They are clearly closely related, but have practically separate distributions with some overlap, and so far as this author can ascertain, show no hybridization or intergradation of characters.

Material Examined

	Reference	Locality	No.	Coordinates	Depth in metres
1.	BC56-340	"Japan"	2		--
2.	BC60-153	Oshyoro Bay, Otaru, Hokkaido	1	140 /, 43 13'N	--
3.	BC61-515	Kenai Peninsula, Alaska	1	151 52'W, 59 35'N	--
4.	BC61-520	"	3	151 52'W, 59 35'N	--
5.	BC62-441	Shumagin Is., Alaska	4	160 59'W, 55 25'N	32.9
6.	BC62-455	"	1	159 45'W, 55 03'N	69.5
7.	BC62-484	Kodiak Is., Alaska	2	151 40'W, 56 31'N	100.7
8.	BC62-488	Shumagin Is., Alaska	4	160 33'W, 55 24'N	93.3
9.	BC62-489	Alaska Peninsula, Alaska	4	161 28'W, 55 36'N	27.5
10.	BC62-490	"	2	161 45'W, 55 19'N	42.1
11.	BC62-719	"	1	161 47'W, 55 19'N	109.8
12.	BC62-756	Afognak Is., Alaska	1	152 04'W, 58 20'N	--
13.	BC62-792	Lynn Channel, Alaska	2	134 20'W, 58 08'N	9.2
14.	BC63-1026	Region Is., Alaska	76	152 20'W, 57 47'N	--
15.	BC63-1438	Shumagin Islands, Alaska	8	162 32'W, 55 06'N	1.2-1.5
16.	BC65-40	Izembak Bay, Alaska	2	162 48'W, 55 20'N	0-3.1
17.	BC65-83	Shumagin Is., Alaska	1	160 58'W, 55 18'N	55.8
18.	BC65-708	Bristol Bay, Alaska	3	161 30'W, 57 30'N	49.4
19.	BC65-711	"	22	162 15'W, 58 15'N	43.9
20.	BC65-712	"	5	162 15'W, 58 15'N	32.0
21.	BC65-729	Shumagin Is., Alaska	2	162 45'W, 55 45'N	54.9
22.	IU 6866	Albatross Stn. 3244	2	161 05'W, 58 37'N	8.2

	Reference	Locality	No.	Coordinates	Depth in metres
23.	IU 6884	Albatross Stn. 3230	1	157 13'W, 58 31'N	5.9
24.	IU 6886	" 3296	1	158 46'W, 57 26'N	43.9
25.	IU 6896	" 3289	1	159 16'W, 56 44'N	29.3
26.	IU 6902	" 3246	2	161 36'W, 58 26'N	32.0
27.	SU 3001	" 3240	5	159 36'W, 58 30'N	26.5
28.	SU 3002	" 3232	2	157 34'W, 58 32'N	19.2
29.	SU 3003	" 3239	8	159 23'W, 58 22'N	21.6
30.	SU 5613	Port Clarence	3	166 30'W, 65 15'N	--
31.	SU 5755	Petropaulski Harbour (Petropavlovsk), Kamchatka	4	158 30'E, 53 N	--
32.	SU 22398	Petropavlovsk, Kamchatka	3	158 30'E, 53 N	--
33.	SU 60226	Dry Spruce Bay, Alaska	1	153 02'W, 57 56'N	--
34.	SU 60246	Kodiak Is., Alaska	1	153 52'W, 58 22'N	--
35.	UW 5046	Chiniak Bay, Alaska	4	152 20'W, 57 42'N	--
36.	UW 7345	Deep Sea, 19	6	163 25'W, 63 55'N	18.3
37.	UW 10175	Albatross Stn.	4	160 28'W, 58 45'N	20.1
38.	UW 15576	Kachemak Bay, Alaska	1	151 30'W, 59 30'N	--
			196		

Literature records

No.	Location	Coordinates	Depth in metres	Reference
39	"Sea of Kamchatka" (?-Kamchatskiy Zaliv) U.S.S.R.	56 00'N, 162 30'E		Cuvier and Valenciennes, 1829
40	Unalaska, Alaska	53 40'N, 166 40'W		Pallas, 1831
41	Avachinskaya Guba, U.S.S.R.	57 03'n, 158 50'E		"
42	Kyska (-Kiska Harbour) Alaska	51 58'N, 177 34'E		Bean, 1882b
44	? Cape Tchaplin (-Chaplino) U.S.S.R.	64 25'N, 172 16'E		"
45	Bering Island (-Ostrova Beringa) U.S.S.R.	55 00'N, 166 00'E		"
46	Petropaulski (-Petropavlovsk) U.S.S.R.	53 03'N, 158 43'E		"
47	Najtschkaj (-Nakhtakhe) Lagoon, U.S.S.R.	46 50'N, 138 22'E		Smitt, 1893
48	Bristol Bay, Alaska Albatross Stations 3231, 3233, 3237-38, 3241-45, 3291, 3300	58 30'N, 159 00'W	8-48	Gilbert, 1896
49	Avachinskaya	53 07'N, 158 33'E		Schmidt, 1904
50	Amyrsh (-Amurskiy Zaliv)	43 10'N, 131 50'E		Gratsianov, 1907
51	Vladivostok	43 0('N, 131 53'E		"
52	Port Szestakov (-Shestakova Bukhta)	59 15'N, 148 50'E		"
53	Tareinski Harbour, Kamchatka (-Tar'ya Bukhta)	52 55'N,		Evermann and Goldsborough, 1909

No.	Location	Coordinates	Depth in metres	Reference
54	Petropavlovsk	53 03'N, 148 43'E		Rendahl, 1931b
55	Avatscha (-Avachinska) Bay	53 07'N, 158 33'E	10	"
56	? Solevarka Bay	? ?		Popov, 1933
57	Tarynsky Bay (-Tar'ya Bukhta)	52 55'N, 158 28'E	6-10	"
58	Avatcha (-Avachinska)	53 07'N, 158 33'E		"
59	Rakovaja Bay (-Rakovaya Bay)	52 58'N, 158 40'E		Popov, 1933
60	Near Mishennaya Mt. (-Mishennyy)	53 02'N, 158 39'E		
61	Kasak Cape (-Myskazak)	52 58'N, 158 28'E	4-6	"
62	Peter the Great Bay (-Zaliv Petra Veli-kogo)	53 00'N, 132 00'E		Taranetz, 1937
63	Avanchinskii Bay (-Avachinska)	53 07'N, 158 33'E		Vinogradov, 1949
64	Terpenie Bay (-Terpeniya Zaliv)	49 00'N, 143 30'E		Schmidt, 1950
65	Amur Liman (-Amurskiy Liman)	52 50'N, 141 30'E		"
66	Gulf of Sakhalin (-Sakhalinskiy Zaliv)	53 45'N, 141 30'E		"
67	Udskaya Bay	54 50'N, 136 00'E		"
68	Yavinskaya Bank	? ?		"
69	Karaginskii Island (-Ostrov Karaginskiy)	58 50'N, 164 00'E		"
70	Tyulenii Island (-Ostrov Tyuleniy)	48 30'N, 144 38'E		"

No.	Location	Coordinates	Depth in metres	Reference
71	Aniva Bay (-Zaliv Aniva)	46 16'N, 142 48'E		Schmidt, 1950
73?	Chukot Peninsula (-Chukotskiy Poluostrov)	67 04'N, 173 50'E		Andriashev, 1954
74	Wakkanai, Hokkaido	54 26'N, 141 23'E	77	Watanabe, 1960
75	Mashike, Hokkaido	43,52'N, 141 32'E	66	"
76	Monbetsu (-Mombetsu) Hokkaido	44 20'N, 143 20'E	153	"
77	Nemuro, Hokkaido	43 22'N, 145 36'E	66	"
78	Akkeshi Bay, Hokkaido	43 02'N, 144 52'E	77	"

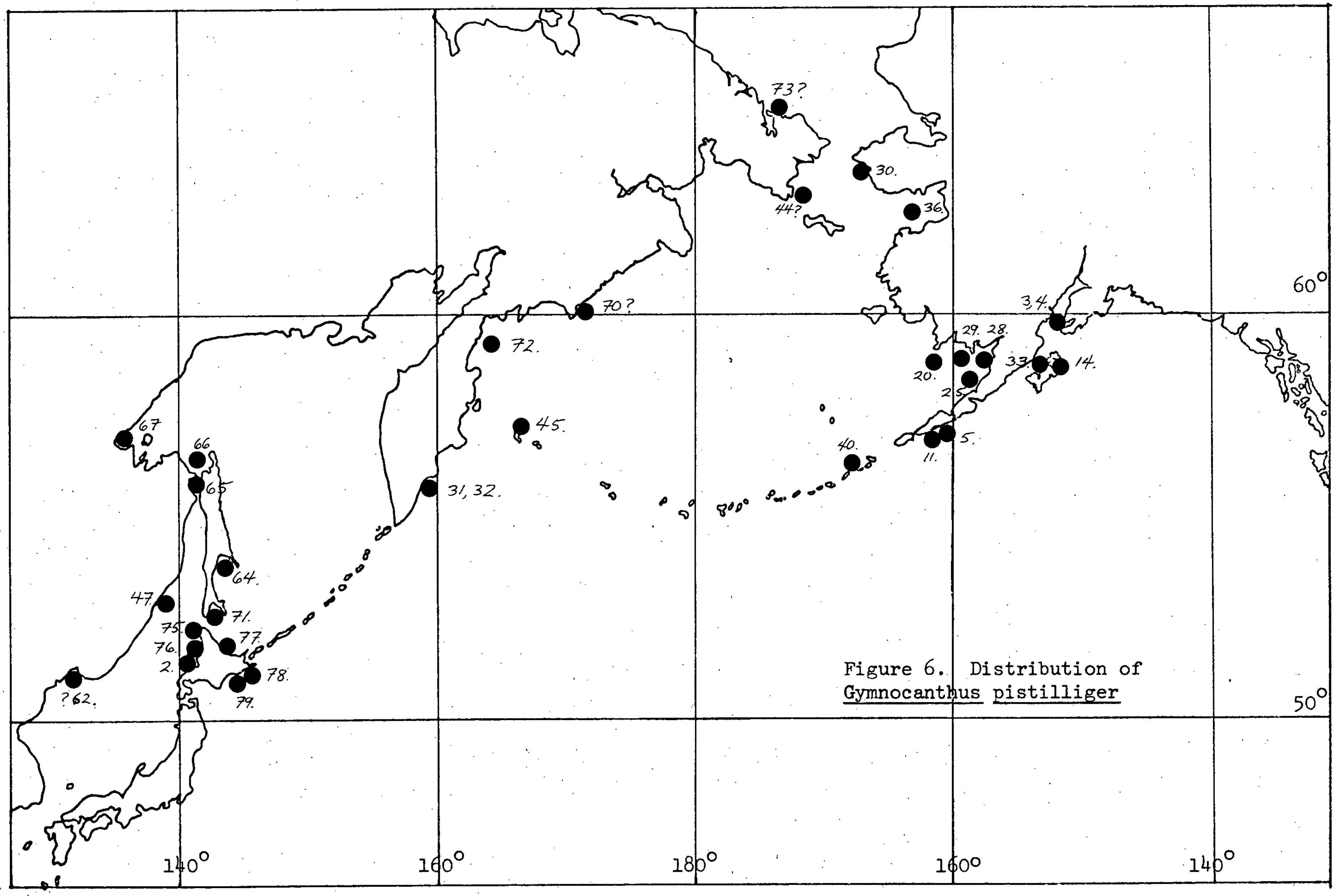

Figure 6. Distribution of Gymnocanthus pistilliger

Gymnocanthus gäleatus (Bean)

Gymnacanthus galeatus: - Bean, 1882a:153 (description, counts, cf. with G. pistilliger, G. tricuspis, distribution); Jordan and Gilbert, 1882:709 (description); Gilbert, 1896-425 (cf. with G. tricuspis, G. pistilliger, description, counts); Andriashev, 1954:401 (descriptions, counts, distribution, cf. with G. tricuspis, figure).

Gymnocanthus galeatus: - Jordan and Evermann, 1896:2010 (partly non Bean; description, counts, measurements, cf. with G. pistilliger, G. tricuspis, plate); Evermann and Goldsborough, 1907:319 (partly non Bean; measurements, counts, distribution); Ehrenbaum, 1901: 86 (range, synonymy); Gratsianov, 1907:304 (key, synonymy, distribution); Jordan, Tanaka, and Snyder, 1913:273 (listed); Jordan, Evermann, and Clark, 1930:389 (synonymy, distribution); ?Deryugin, 1933:5-35 (locality); Taranetz, 1937:118 (key, distribution); Andriashev, 1937:28 (synonymy, cf. with G. detrisus, figure); Andriashev, 1939b:1-187 (ecology, zoogeography); Kobayashi and Ueno, 1956:253 (counts, measurements, description, colour, locality); McAllister, 1960:16 (key); Hubbard and Reeder, 1965:507 (locality); Isakson, Simenstad, and Burgner, 1971:21 (ecology); Quast and Hall, 1972:21 (locality references).

Gymnocanthus galeatus herzensteini: - Soldatov and Lindberg, 1930:248 (key, synonymy, counts, distribution).

Gymnocanthus detrisus (non Gilbert and Burke): - Vladykov, 1933:16 (cf.

with *G. galeatus*).

Gymnocathus herzensteini (non Jordan and Starks): - Vladykov, 1933:16 (cf. with *G. galeatus*).

Gymnocenthus galeatus: - Andriashev, 1937:28 (description, synonymy, cf. with *G. detrisus*).

Description

Gymnocanthus galeatus (Bean) is a large subarctic Pacific species, distributed from southeastern Alaska to the end of the Aleutians but apparently excluded from the Arctic and Japanese waters. Variation across their range is slight, and descriptions of a small number of specimens is adequate to express this variation. Specimens described were BC62-651, 1 male, 20.78 cm., 1 female, 22.24cm. (Kodiak); BC62-444, 2 females, 22.28cm., 23.30cm. (Unalaska); BC63-170, 1 male, 18.15cm. (Southeast Alaska); UW 1644, 1 female, 20.34 cm. (Southeast Alaska); BC63-282, 1 male, 11.60cm. (Southeast Alaska); SU 3004 and 5938, 2 males, 15.91, 10.11 cm., 1 female, 10.51cm. (Anette Island); BC63-917, 2 females, 6.28, 6.63cm. (Semisopochnoi Island).

Body elongate, robust anteriorly, tapering posteriorly to a narrow peduncle, dpeth 22.23 (17.98-27.84) times in SL; peduncle rectangular, weakly laterally compressed. Greatest depth on vertical through pelvic girdle, dpeth at pelvic girdle 5.81 (4.88-6.63) times in SL; trunk generally ovate, weakly flattened ventrally, either gently rounded or weakly flattened dorsally. Head moderate, length 3.01 (2.76-3.30) times in SL; head tending to be broader than deep, depth 1.18 (.98-1.46) times in width; in frontal profile, head broadly, weakly concave ventarally, narrowly weakly concave dorsally. Lateral line ossicles large, about half an ossicle length separating them anteriorly, becoming virtually adjacent towards the peduncle; ossicles extend to peduncle, frequently onto caudal rays. Never any pistillae in pectoral axil. Axillary scales moderate, in triangular patch, base forward under pectoral; scales about 1/3 the length of the ossicles below the spinous soft dorsal fin interspace; scales separated by distance usually equal to or greater than their own length; scale patch extending practically to the pectoral fin end. Snout somewhat elongate, weakly pointed, length 4.11 (3.43-4.82) times in head, 12.30 (9.75-14.98) times in SL; orbit-nasal spine distance moderate, making snout lateral profile from premaxillary to nasal spines jut out slightly. Teeth villiform, small, posteriorly recurved; teeth randomly placed on tooth pads, up to two teeth wide on dentary at symphysis, up to four teeth wide at symphysis on premaxillary, tooth band narrowing posteriorly; tissue in mouth may be papillose directly ahead of or behind tooth pads, up to two rows of papilla posterior to dentary and premaxillary teeth, one row of papilla anterior to premaxillary teeth; moth moderate, upper jaw length 2.48 (2.20-3.01) times in head; maxillary extending past leading edge of pupil, frequently past center of pupil. Single pair strong, frequently emergent, moderately posteriorly recurved nasal spines. Two pairs of nostrils, first pair on vertical plane through base of nasal spines, length of tube subequal to nasal spine height; nostril constricted distally such that the oval terminal pore points anterolaterally; posterior nostrils directly behind nasal spines, about equidistant from nasal spine and orbit rim; tube always much lower than nasal spine, produced such that pore tend to point posterolaterally; posterior nasal tube about half the height of anterior tube. Orbits moderate, length 3.68 (3.24-4.07) in head, produced equally vertically and laterally, forming a distinct postorbital notch, postorbital notch width 5.33 (4.65-6.18) times in head; strong nape ridges extending back from postorbital, curving outward at the supratemporal cephalic sensory canal, becoming confluent with the lateral line; ridge developing small tubercle behind postorbital notch, but no particular tubercle development around supratemporal canal; tubercle development only weakly size dependent. Nape heavily invested in granulations, especially in specimens over 8cm. long; granulations extending posteromedially to a point about two dorsal spines distance ahead of spinous dorsal; wings of granulation extending back on either side of dorsal sometimes to a vertical through the third dorsal spine; anteriorly, usually extending across the interorbital to the posterior nares, usually some granulations lining inter-orbital margin; prefrontals frequently invested in granulations; laterally, granulations primarily contained by lateral cephalic sensory canals; a few granulations on ascending preopercular shaft, dorsal branch of opercular, 2nd, 4th, 5th infraorbitals, along upper and lower margins (but not middle) of suborbital stay; lateral, supratemporal, supraoccipital, suprapostorbital cephalic sensory canals often protected by a ridge of granulations. Sub-orbital stay strong, 4.66 (4.07-6.31) times in head. Four preopercular spines, the uppermost strong with 1-3 cusps, modally 2 (mean 1.90), this spine rarely reaching posterior opercle margin, but reaching well past vertical through opercular notch anterior margin; ventrally directed subopercular spine obsolete, not emergent; dorsal border of opercle straight, rarely gently rounded. Cleithral spine very weak, almost never emergent. Dorsal fins separate, interdorsal distance up to 2 dorsal spines; first predorsal length 3.11 (2.71-3.33) times in SL; spinous dorsal more or less flat along anterodorsal margin, becoming increasingly convex posteriorly; spinous dorsal more strongly convex in males than females; spinous dorsal length weakly dimorphic, longest spine 2nd or 3rd, length in males 6.37 (5.27-7.92), females 7.65 (6.65-8.78) times in SL; base of spinous dorsal shorter than soft dorsal base, spinous dorsal base 1.37 (1.19-1.57) in SL, soft dorsal base 3.27 (2.98-3.60) times in SL; second predorsal 1.83 (1.74-1.93) times in SL; margin gently convex, more so anteriorly and posteriorly than in the middle; longest ray 3rd to 5th, height 7.01 (5.21-8.51) in SL; spinous and soft dorsals about equally long, length of spinous dorsal .99 (.84-1.22) times in soft dorsal length; spinous dorsal originating on vertical through first pectoral ray origin; origin of soft dorsal on vertical through 2nd-3rd anal ray, terminating on vertical through penultimate-antepenultimate anal ray. Preanal 1.92 (1.78-2.06) times in SL, anal base long, 2.90 (2.69-3.20) times in SL; anal margin straight in the center, weakly convex at either end. Pelvics originating halfway between snout and anus, length strongly sexually dimorphic; in females, inner ray longest, not reaching anus, length 5.26 (4.75-6.38) times in SL; in males, middle or inner ray longest, usually reaching past anus, often past anal origin, in some, as far as 5th anal ray, length 3.47 (2.48-5.01) times in SL. Pectoral broad-based, base 6.89 (6.28-7.37) times in SL; base about 45° off vertical; pectoral margin strongly convex, most posteriorly extending ray 5th-7th, length 2.81 (2.41-3.16) times in SL; inner face of pectoral rays entirely lacking serrated edge in both sexes. Caudal truncate, anus on small, generally rugose papilla slightly in advance of anal fin; male with conical penis immediately behind anus, length 17.9-61.4 times in SL.

Meristic Formulae

Spinous dorsal 11 (10-12) (11.0); soft dorsal 16 (14-17) (16.1); pectoral 20 (18.21) (20.0); anal 19 (17-20) (18.73); pelvics I,3; vertebrae 39 (36-40) (38.6); branchiostegals 6.

Colour in Alcohol

Body ground colour tan on dorsum to just below epaxial-hypaxial body division (indicated by midlateral groove); ahead of anal fin, dark colouration tending to drop well below that line; ground colour intensifying on cheek, snout, suborbital, interorbital, nape in region bounded by lateral and supratemporal cephalic sensory canals; weak development of small punctulations of body; four large, clear spots of dorsum, the first under the spinous dorsal center, the second and third under the soft dorsal, and the fourth on the peduncle; series of small, vague dark blotches along midlateral aspect, largely separate from dorsal blotches; spinous dorsal slightly dusky in males, clear in females, both with 3-4 oblique bands; soft dorsal clear, with 6-8 oblique bands; pectoral with 4-6 tranverse narrow (narrower than pupil) bands; pectoral base often with broad, diffuse band; caudal with 4-5 transverse bands, the interband width equalling or exceeding the band width; ventrum, posterior tip of maxillary, posterior half of dentary, premaxillary, branchiostegals, ground colour of, fins (except spinous dorsal), wedge on peduncle extending to upper margins of caudal fin, margin around lower three preopercular spines yellowish to white; males without distinct pectoral axillary white spots or white-striped pelvics; buccal cavity pale;

peritoneum pale. Juvenile colour essentially that of adults except spinous dorsal not dusky in males.

Maximum size

Males 25.9cm., of females 29.2cm. SL.

Etymology

The species name galeatus, from the latin "galea" (a helmet) is in reference to the granulation-invested occiput.

Range

This species is definitely recorded as coming from Southeast Alaska, South Alaska, the Aleutians west to Amchitka, Pribilov Islands, and Bristol Bay. It has been recorded by Andriashev (1954) as having come from the east Kamchatkan coast. By its fin formula, Scofield's (1898) specimens from Point Barrow is almost certainly G. tricuspis, not G. galeatus.

Systematic Notes

This large Alaskan species, being the first of the three large Gymnocanthus species to be described has been recorded as coming from Southeast Alaska to the Sea of Japan, south to Korea (Schmidt, 1904). Although the records from the east Kamchatka coast appear reliable, those from the Sea of Japan do not, and by the descriptions given are almost certainly records of G. herzensteini. Various authors (Schmidt, 1927; Lindberg and Soldatov, 1930; Vladykov, 1933) have synonymized G. herzensteini, G. detrisus, and G. galeatus. However, these species are distinct in many characters, and in my experience are entirely separable.

Material Examined

	Reference	Locality	No.	Coordinates	Depth in metres
1.	BC61-520	Kachemak Bay, Alaska	1	151° 30'W, 59° 30'N	
2.	BC62-431	Unimak Is., Alaska	3	164° 44'W, 54° 08'N	80.5
3.	BC62-438	--	1	154° 55'W, 57° 54'N	62.3
4.	BC62-439	Shumagin Is., Alaska	1	159° 48'W, 55° 44'N	128.0
5.	BC62-444	Unimak Is., Alaska	6	164° 30'W, 54° 13'N	101.7
6.	BC62-451	Shumagin Is., Alaska	1	160° 18'W, 52° 02'N	104.0
7.	BC62-455	"	2	159° 45'W, 55° 03'N	69.5
8.	BC62-484	--	1	157° 40'W, 56° 31'N	101.7
9.	BC62-488	Shumagin Is., Alaska	1	160° 33'W, 55° 24'N	93.3
10.	BC62-498	Unimak Is., Alaska	1	163° 00'W, 54° 54'N	100.0
11.	BC62-499	--	2	159° 43'W, 55° 34'N	93.0
12.	BC62-503	Kodiak Is., Alaska	2	154° 31'W, 57° 36'N	129.9
13.	BC62-504	Unimak Is., Alaska	3	163° 30'W, 54° 12'N	91.5
14.	BC62-526	Kodiak Is., Alaska	1	155° 00'W, 56° 42'N	32.9
15.	BC62-530	"	3	154° 30'W, 56° 42'N	32.9
16.	BC62-537	"	1	155° 10'W, 55° 46'N	131.8
17.	BC62-557	Port Armstrong, Alaska	1	134° 23'W, 56° 43'N	--
18.	BC62-579	"	1	134° 40'W, 56° 18'N	--
19.	BC62-591	"	3	134° 40'W, 56° 18'N	--
20.	BC62-643	Shumagin Is., Alaska	12	159° 33'W, 54° 53'N	43.9
21.	BC62-645	Kodiak Is., Alaska	5	152° 30'W, 57° 06'N	129.1
22.	BC62-651	"	6	155° 00'W, 56° 48'N	98.8
23.	BC62-655	Unimak Is., Alaska	1	163° 00'W, 54° 54'N	98.8

	Reference	Locality	No.	Coordinates	Depth in metres
24.	BC62-657	Shumagin Is., Alaska	5	160°00'W, 54°48'N	106.1
25.	BC62-659	--	1	157°36'W, 55°51'N	109.8
26.	BC62-663	--	2	154°33'W, 54°11'N	100.7
27.	BC62-665	Unimak Is., Alaska	3	164°33'W, 54°14'N	109.8
28.	BC62-668	Kenai Peninsula, Alaska	1	151°00'W, 57°42'N	80.5
29.	BC62-673	Afognak Is., Alaska	2	151°44'W, 58°04'N	166.5
30.	BC62-676	Kodiak Is., Alaska	5	154°30'W, 57°36'N	129.9
31.	BC62-680	"	18	154°30'W, 56°48'N	58.6
32.	BC62-709	"	7	154°30'W, 56°42'N	32.9
33.	BC62-709	Shumagin Is., Alaska	18	159°29'W, 54°48'N	43.9
34.	BC62-772	Afognak Is., Alaska	2	151°25'W, 58°N(?)	--
35.	BC63-120	Kenai Peninsula, Alaska	2	151°34'W, 59°29'N	73-110
36.	BC63-170	Lynn Canal, Alaska	1	134°47'W, 58°27'N	128.1
37.	BC63-282	Chatham Strait, Alaska	1	134°38'W, 56°22'N	9.2
38.	BC63-297	Amchitka Is., Alaska	1	179°19'E, 51°24'N	5.5-183
39.	BC63-309	"	1	179°19'E, 51°24'N	--
40.	BC63-349	--	1	165°00'W, 54°45'N	--
41.	BC63-917	--	7	179°48'E, 52°08'N	36.6-54.9
42.	BC63-983	"Oceanographic Station 24"	1	?	73.2
43.	BC63-1015	Amchitka Is., Alaska	12	179°19'E, 51°24'N	109.8
44.	BC63-1026	Region Is., Alaska	12	152°20'W, 57°47'N	
45.	BC63-1423	Atka Is., Alaska	20	174°12'W, 52°12'N	1.2-3.1
46.	BC63-1443	Pribilof Is., Alaska	6	170°10'W, 57°10'N	0-1.0
47.	BC63-1456	"	1	170°15'W, 57°10'N	.5-1.4

Reference	Locality	No.	Coordinates	Depth in metres
48. BC65-1	--	23	173°15'E, 52°56'N	6.1
49. BC65-17	Agatu Is., Alaska	9	173°42'E, 52°25'N	0-2.7
50. BC65-21	"	1	173°30'E, 52°27'N	0-2.7
51. BC65-24	"	200	173°15'E, 51°56'N	0-5.4
52. BC65-30	Adak Is., Alaska	3	176°26'W, 51°47'N	1.2-3.1
53. BC65-40	--	2	162°48'W, 55°20'N	0-2.7
54. BC65-110	Unimak Is., Alaska	1	164°04'W, 54°35'N	60.4
55. BC65-112	Unimak Is., Alaska	1	163°20'W, 54°22'N	65.9
56. BC65-154	Kachemak Bay, Alaska	6	151°58'W, 59°30'N	71.4-78.7
57. BC65-390	Adak Is., Alaska	3	176°25'W, 51°45'N	
58. BC65-717	Pribilof Is., Alaska	1	167°45'W, 56°45'N	78.7
59. BC65-718	Pribilof Is., Alaska	3	167°45'W, 56°45'N	95.2
60. BC65-719	Trinity Is., Alaska	1	155°30'W, 56°30'N	137.2
61. BC65-729	--	5	162°45'W, 55°45'N	54.9
62. BC65-733	Pribilof Is., Alaska	10	168°45'W, 56°45'N	
63. BC65-800	Amchitka Is., Alaska	46	179°13'E, 51°25'N	
64. SU 3004	Chernofski Harbour, Alaska	3	167°33'E, 54°24'N	
65. SU 5938	Anette Is., Alaska	1	131°30'W, 55°00'N	
66. SU 5720	St. Paul's Is., Alaska	3	170°15'W, 57°10'N	
67. UW 1644	Wrangell, Alaska	1	132°23'W, 56°28'N	
68. UW 5457	Amak Is., Alaska	2	163°10'W, 55°25'N	
69. UW 14322	Washington Bay, Kuiu Is., Alaska	1	134°23'W, 56°43'N	

Literature Records

No.	Location	Coordinates	Depth in meters	Reference
70.	Unalaska, Alaska	53°40'N, 166°40'W		Bean, 1882
71.	Captains Harbour, Alaska	55°10'N, 162°05'W		Gilbert, 1896
72.	Atka Island, Alaska	51°50'N, 176°40'W		Evermann & Goldsborough, 1907
74.	Akutan Bay, Alaska	54°10'N, 166°00'W		"
75.	Bering Sea, Albatross #3598	56°28'N, 172°39'W		"
76.	Stephens Passage, Albatross #4253	57°30'N, 134°00'W		"
77.	Shakan Bay, U.S.S.R.	56°08'N, 133°30'W		"
78.	Olyutorskii Bay, U.S.S.R.	60°30'N, 168°00'E		Andriashev, 1954
79.	Koryakskaya Zemlya, U.S.S.R.	60°30'N, 169°00'E		"
80.	Natal'ya Bay, U.S.S.R.	61°10'N, 172°25'E		"
81.	Burling Bay, Kodiak Island, Alaska	57°12'N, 153°21'W		Hubbard and Reeder 1965

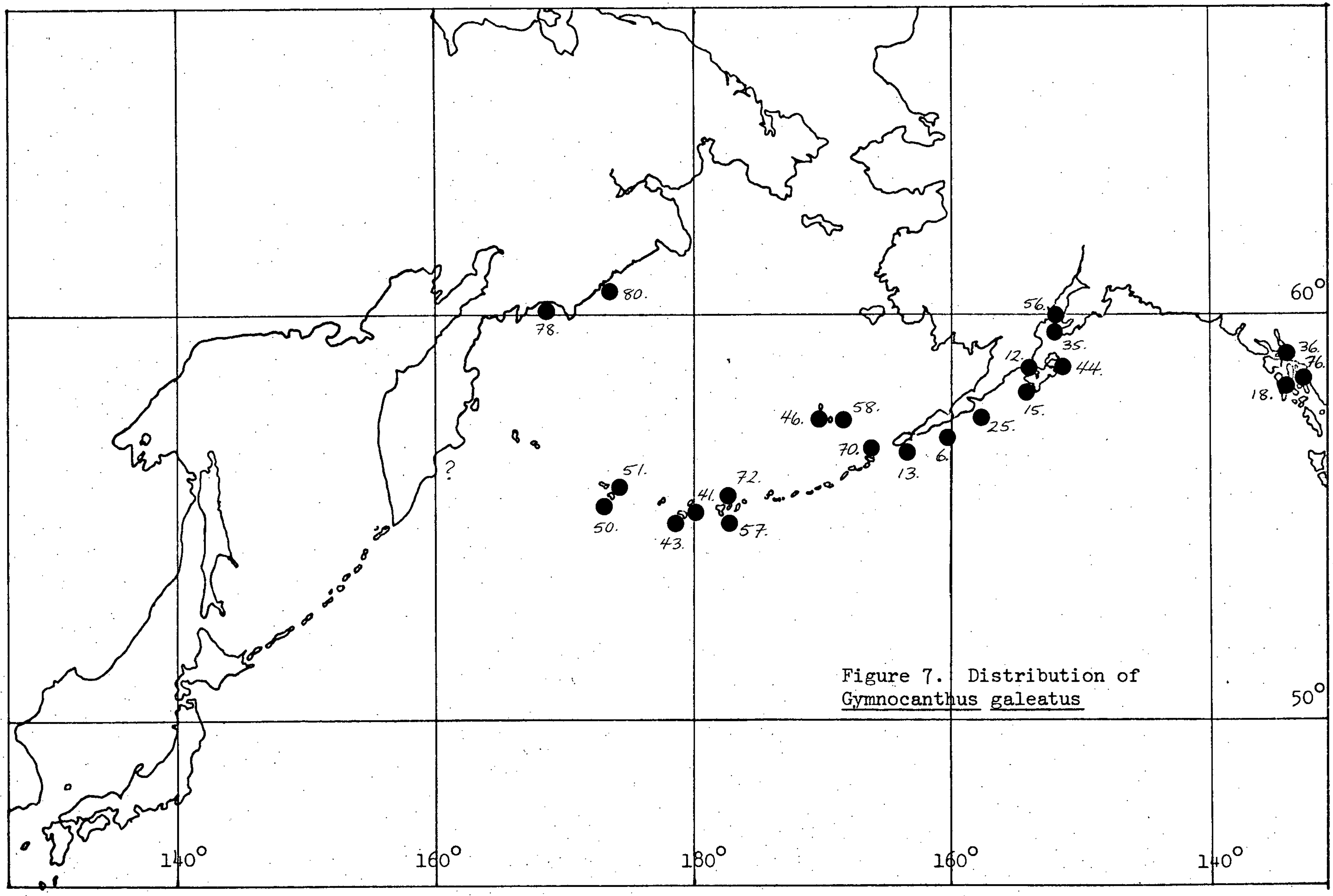

Figure 7. Distribution of <u>Gymnocanthus galeatus</u>

Gymnocanthus tricuspis (Reinhardt)

Cottus gobio (non Linnaeus): - Fabricius 1780:159 (description, colour, ecology).

Cottus tricuspis: - Reinhardt, 1838:117 (redescription of Fabricius' "Cottus gobio", cf. with G. gobio); ? Gaimard, 1842; Lilljeborg, 1850: 233-242; Gunther, 1860:168 (counts, description, measurements); Gill, 1861:42 (list); Eaton, 1874:3821 (locality); Lilljeborg, 1891:118; Heuglin, 1874:209 (distribution).

Phobetor tricuspis: - Kroyer, 1844:263 (redescription of Fabricius' "Cottus gobio"); Gaimard, 1845 (Plate 4, figure 1); Richardson, 1855:6 (synonymy, cf. with Cottus gobio, figure, description, measurements); Malmgren, 1863:11 (locality); Malmgren, 1865:504 (cf. with Cottus ventralis, Acanthocottus patris, ecology); Lutken, 1876:364 (single unconfirmed report from Iceland; reference to axillary scales as "pistillae").

Cottus fabricii: - Girard, 1851a:59 (redescription, identification of Fabricius' Cottus gobio).

Acanthocottus psittiliger: - Girard, 1851b: 186 (lapsus calami).

Acanthocottus patris: - Storer, 1857:250 (type description, counts, colour, plate).

Gymnacanthus patris: - Gill, 1861:42 (list); Gill, 1865:251 (counts, listed); Weiz and Packard, 1866:273 (locality).

Cottus ventralis (non Cuvier and Valenciennes): - Malmgren, 1865:504 (cf. with Acanthocottus patris); Steindachner, 1875:613.

Phobetor ventralis (non Cuvier and Valenciennes): - Frisch, 1865:35 (locality); Malmgren, 1867:259 (range, synonymy); Collett, 1879:15 (distribution, counts, measurements); Holmqvist, 1899: 217 (synonymy, distribution); Johansen, 1912:649 (habitat, dimorphism, colour, figure).

Gymnacanthus tricuspis: - Gill, 1873:800; Dresel, 1884:251 (synonymy, locality data, cf. with Gymnacanthus pistilliger, description, colour, counts); Knipovich, 1903:14 (description, measurements, counts, distribution, cf. with Gymnacanthus pistilliger); Jensen, 1904:227 (distribution, figure, synonymy); Collett, 1905:84 (locality); Knipovich, 1907:14 (counts, measurements, distribution); Jensen, 1910:4 (counts, measurements); Thielemann, 1921:128 (description, counts); Soldatov, 1928:20 (distribution, ecology, description); Soldatov, 1928:1-320; Briskina, 1939:340-354 (food); Pertseva, 1939:417-470 (fry); Gordon and Backus, 1957:19 (locality); Scholander et al., 1957:5 (freezing resistance); Barsukov, 1958:143 (synonymy, depth); Ellis, 1960:41 (locality).

Gymnacanthus pistilliger (non Pallas): - Bean, 1879:127 (locality data, nomenclature); Collett, 1880:26 (description, counts, measurements, distribution); Bean, 1882a:153 (cf. with Gymnacanthus galeatus); Bean, 1882b:249 (locality); Jordan and Gilbert, 1883:708 (description, counts, range); Stearns, 1884:125 (locality); Van Hoffen, 1897:89 (synonymy with Cottus tricuspis); Walters, 1853:13 (locality, counts).

Sclerocottus schraderi: - Fischer, 1885:58 (type description, erroneously reported from Antarctica).

Phobetor pistilliger (non Pallas): - Klinkowstrom, 1892.

Gymnocanthus ventralis (non Cuvier and Valenciennes): - Smitt, 1893:160 (description, measurements, counts, synonymy, figure, cf. with G. pistilliger); Lonnberg, 1899:4 (distribution, description, measurements, cf. with G. pistilliger); Ehrenbaum, 1901:84 (synonymy, distribution, counts); Le Danois, 1913:425 (cf. with G. pistilliger); Le Danois, 1914:31 (synonymy, counts, colour, sexual differences, distribution); Johansen, 1925:204 (locality).

Gymnocanthus galeatus (partly non Bean): - Jordan and Evermann, 1896: 2010 (distribution); Scofield, 1898:504 (description, counts); Jordan and Gilbert, 1899:460 (distribution); Vladykov, 1933: 16 (counts, measurements, description, range, colour).

Gymnocanthus tricuspis: - Jordan and Evermann, 1896:2008 (counts, description, colour, key, synonymy); Hjort, 1902:1-251 (locality); Ehrenbaum, 1905:51 (locality); Koefoed, 1907 (locality); Kendall, 1910:509 (locality); Fowler, 1914:360 (locality); Hofsten, 1919:4 (range, habitat); Bigelow and Welsh, 1925:328 (description, counts, colour, distribution); Breder, 1929:244 (range); Jordan, Evermann, and Clark, 1930:289 (synonymy, distribution); Jeffers, 1932:6 (locality, counts); Popov, 1933c:157-167; Prefontaine, 1933:258 (locality); Norman, 1935: 141 (synonymy with Sclerocottus schraderi); Vladykov and Tremblay, 1935:78 (locality); Pfaff, 1937:16 (locality); Taranetz, 1937:

118 (distribution, key); Norman, 1938:32 (synonymy with Sclerocottus schraderi); Andriashev, 1939a:731 (habitat); Hildebrand, 1939:9 (range, sexual dimorphism); Vladykov, 1946:57 (G. tricuspis as food of white whales); Dunbar, 1947:3 (fry counts, description); Dunbar and Hildebrand, 1952:117 (description, counts, granulation patterns of various "sub-species"); Jensen, 1952:17 (synonymy, distribution, ecology, cf. with G. pistilliger, description); Bigelow and Schroeder, 1953:452 (description, colour, range); Walters, 1953:13 (locality, counts); Walters, 1955:313 (range, cf. with G. galeatus, extent of nape granulations); McKenzie, 1959:826 (locality); McAllister, 1960:16 (key); Hognestad, 1961:26 (measurements, distribution, depth); Ellis, 1962:187 (distribution, depth); McAllister, 1962:29 (locality, measurements, description, counts, variation, colour); Andersson, 1964:71 (description, distribution); McAllister, 1964:174 (live colour, habitat); Muus, 1964:164 (key); Leim and Scott, 1966:348 (counts, description, colour, distribution, biology, figure); Ellis, 1968:2729 (records, depth); Bergeron and Legendre, 1970:45 (locality data of Musee de la Station Biologique marine de Grande-Riviere specimens in St. Lawrence River); Drainville, 1970:640 (ecology, habitat in Saguenay River).

Gymnocanthus pistilliger (non Pallas): - Jordan and Gilbert, 1899:460 (partly non Pallas, distribution); Hofsten, 1919:8 (cf. with G. tricuspis, distribution); Pietschmann, 1932:13 (counts, measurements, figure of granulations, sexual dimorphism, preopercular cusps, scales, pectoral serrations, figure erroneously labelled *Myoxocephalus scorpius*).

Gymnacanthus ventralis (non Cuvier and Valenciennes): - Knipovich, 1898: 1-11 (locality); Knipovich, 1901:58 (description, counts, measurements, distribution, cf. with *G. pistilliger*); Knipovich, 1903:146 (locality); Stappers, 1909:39 (food).

Gymnacanthus tricuspis groenlandicus: - Schmidt, 1927:28 (description, distribution, measurements).

Gymnacanthus tricuspis occidentalis: - Schmidt, 1927:29 (description, distribution, measurements).

Gymnacanthus tricuspis orientalis: - Schmidt, 1927:29 (description, distribution, measurements).

Gymnocanthus pistilliger tricuspis: - Rendahl, 1931a:76 (counts, cf. with *G. pistilliger pistilliger*); Rendahl, 1931b:50 (cf. with *G. p. pistilliger*); Popov, 1933:158.

Gymnocanthus tricuspis hudsonius: - Vladykov, 1933:17 (counts, description, range, measurements, colour).

Gymnocanthus tricuspis tricuspis: - Vladykov, 1933:17 (counts, description, distribution); Bachus, 1957:31 (locality data, cf. with *G. t. hudsonius*).

Gymnocanthus tricuspis orientalis: - Andriashev, 1937:26 (ecology, cf. with other subspecies); Andriashev, 1939b:1-187 (zoogeography, ecology); Alverson and Wilimovsky, 1966:854-856 (locality data).

Gymnocanthus vandesandei: - Poll, 1949:234 (figure, description, counts, measurements, colour, locality mistakenly listed as Africa).

Gym acanthus tricuspis: - Huntsman, Bailey, and Hachey, 1953:248 (locality data; lapsus calami:).

Description

Gymnocanthus tricuspis (Reinhardt) is a widely distributed form with many local variations in such features as head tubercle development and granulation frequency and distribution. It has therefore been necessary to examine a large number of specimens encompassing as much range and variation as possible. Specimens described were UW 7297, 4 females, 10.05, 10,48, 10.77, 10.37cm. (St. Lawrence Island, Alaska); UW 7300, 1 male, 8.61 cm. (St. Lawrence Island, Alaska); BC/61-102, 3 females, 11.07, 11.29, 12.70cm., 1 male, 10.12cm. (Chukchi Sea, Alaska); BC/63-106 2 males, 9.65, 9.65, 9.30cm. (Chukchi Sea, Alska); NMC 60-466, 3 females, 7.22, 7.34, 7.21cm., 3 males, 6.35, 5.48, 6.03cm. (Herschel Island, Yukon terr.); NMC 62-336, 2 females, 15.79, 16.09cm. (Liverpool Bay, NWT); NMC 62-428, 4 females, 10.58, 8.33, 7.22, 6.55cm. (Franklin Bay, NWT); NMC 63-385, 1 female, 6.50cm., 1 male, 7.40cm. (Cornwallis Island, NWT); NMC 62-402, 1 male, 7.13cm. (Ellesmere Island, NWT); NMC 65-358, 1 male, 7.17cm. (Cornwallis Island, NWT); NMC 62-555, 1 female, 19.4 cm. (Belcher Islands, Que.); NMC 62-342, 1 male, 18.40cm. (Chesterfield Inlet, NWT); NMC 62-296, 1 male, 12-79cm. (Foxe Channel); NMC 63-233, 1 male, 10.18cm. (Gulf Hazzard); NMC 62-248, 1 female, 16.20cm. (Ungava Bay); NMC 59-444, 2 females, 7.57, 7.47cm. (Ungava Bay); NMC 67-757, 1 male, 10.35cm.

(Saguenay Fjord); NMC 70-47, 1 female, 13.35cm. (Saguenay Fjord); SU 8090, 1 male, 6.86cm., (E. Greenland); SU 7921, 1 female, 6.04cm. (Spitzbergen).

Reference to "Western" collections include those specimens taken from the Bering Sea to Mackenzie Bay; "eastern" collections include specimens taken from Ungava Bay to the Gulf of St. Lawrence while "archipelago" collections refer to those fish taken in the Canadian Archipelago.

Body moderate, robust anteriorly; in some females, bulbous between pelvics and cloaca; tapering posteriorly to a narrow peduncle, depth 22.26 (15.87-26.22) times in standard length; peduncle roughly rectangular, generally weakly laterally compressed. Greatest depth in both males and females generally behind vertical through pelvic girdle, as far back as vertical through 3rd-5th dorsal spine. Trunk rectangular to oval, weakly elevated dorsally, weakly flattered ventrally, depth at pelvic girdle 4.68 (3.77-5.42) times in SL. Head length moderate, 3.10 (2.88-3.40) times in SL.; head about as broad as deep, maximum depth 1.03 (.88-1.29) times in width. Frontal profile reveals head to be weakly concave ventrally; dorsal of head variable, in western specimens weakly convex to weakly concave; in eastern specimens, weakly to moderately concave. Lateral line ossicles small, almost an ossicle-length separating them anteriorly, becoming virtually adjacent towards the peduncle; ossicles extend to peduncle, but rarely onto caudal ray. Never any pistillae in pectoral axil. Axillary scales large, usually almost as large as lateral line ossicles below spinous-soft dorsal fin interspace; scales usually separated by a distance equal to their own length; scale patch extending almost to the pectoral fin end. Snout moderate, tending to be rounded, length 4.39 (3.73-5.41) times in head, 13.62 (10.87-17.47) times in SL; orbit- nasal spine distance short, making snout lateral profile appear rounded. Snout from dorsal view moderately to broadly rounded. Teeth villiform, small, weakly posteriorly recurved; teeth randomly placed, up to four teeth wide at symphysis on premaxillary, fewer posteriorly; tooth pad up to two teeth wide at dentary symphysis, fewer posteriorly. Tissue in mouth may be papillose directly ahead of or behind tooth pads, up to 2 rows of papilla posterior to dentary and premaxillary teeth, one row of papilla anteriror to premaxillary teeth in large specimens. Mouth moderated, upper jaw 2.44 (2.14-2.84) times in head; maxillary usually extending to or past vertical through pupil center. Single pair moderately posteriorly recurved nasal spines, moderate in eastern collections weakening in western and in European specimens; spines seldom emergent. Two pairs of nostrils, first pair just anterior to vertical plane through nasal spines, usually as high as or higher than nasal spines except in some eastern collections in which they may be equal to or shorter than nasal spines; anterior nostril constricted distally expecially in archipelago and western collections; oval to round terminal pore opens anteriorly; posterior nostrils directly behind nasal spines; always lower than nasal spines, though tending to elongate slightly in western collections; produced such that they open weakly posterolaterally or directly upwards. Posterior nasal tubule half the height of anterior tubule; distance from posterior nostril base to nasal spine tip about 2/3 that from the tip to the anterior nostril base. Orbits moderate, length 3.62 (3.26-4.05) in head, orbit longer than deep, depth 1.3. (1.14-1.47) in length. Interorbital variable, generally concave, rarely flat; if concave, V-shaped especially at narrowest part; width 17.90 (10.74-26.50) in head, western collections tending to have much more narrow interorbitals than eastern collections. Tubercle pattern development on head variable; posteordorsal edge of orbit forming tubercle; in Bering-Chukchi Sea specimens ("G. tricuspis orientalis"), this tubercle very weak, not developed enough laterally to set off a distinct postorbital notch; Franklin-Liverpool Bay collections still without lateral components to postorbital tubercles; almost all northern Canadian archipelago collections with distinct postorbital tubercle, some lateral tubercle development, but postorbital notch still not present; Hudson Bay and Foxe Channel specimens with lateral tubercle development such that postorbital notch usually present; Ungava Bay to Gulf of St. Lawrence specimens with postorbital tubercle well developed in dorsal and lateral plane; Gulf of St. Lawrence specimens with post-orbital tubercles produced well above eyes; postorbital notch width 5.49 (4.53-6.98) times in head. Nape ridges extending back from postorbital notches, angling laterally at the supratemporal cephalic sensory canal, becoming confluent with lateral line. In some specimens, a tubercle may develop on ridge immediately behind postorbital notch; this tubercle virtually or totally obsolete in western collections; tubercle moderate in eastern collections; development pattern follows that of postorbital tubercle. Some specimens with ridge tubercle development on either side of supratemporal canal, the anteriormost tubercle, if present, being about half the size of the posterior tubercle. Tubercle development from west to east follows the pattern of the postorbital tubercle; European collections similar to western American collections; tubercle development size dependent, tubercles disproportionately larger in larger specimens. Granulation development variable, from no granulations to complete granulation of nape; when present, situated primarily between lateral cephalic sensory canals extending in some specimens across the interorbital to posterior nares; granulations seldom, if ever, coating prefrontals or margin of interorbital; in others, not reaching past postorbital tubercles; may extend posteromedially to a point about two dorsal spines distance ahead of spinous dorsal; wings of granulation tending to follow lateral line may extend past this point, may reach vertical through third dorsal spine origin; past supratemporal canal, granulations tend to be larger than those ahead of canal. Specimens occasionally with 1-2 granulations on postorbitals, usually confined to upper border; sometimes 1-2 (rarely more) granulations on upper lobe of opercular; no granulations on suborbital stay or preoperculum. Supratemporal and supraoccipital cephalic sensory canals not protected by any orderly pattern of granulations. Suborbital stay strong, length 4.67 (3.51-6.03) times in head. Preopercular with four spines, the uppermost strong with 1-4 cusps, modally 2-3 (mean 2.51); this spine not reaching posterior opercular margin, but just passing vertical through anterior margin of opercular notch. Opercle with ventrally directed occasionally weakly emergent spine at base of subopercular; dorsal border of opercle gently rounded, rarely straight. Cleithral spine weak to moderate, weak in western collections, moderate in eastern collections. Dorsal fins separate, interdorsal distance variable, width up to 3 dorsal spines; first predorsal length 3.11 (2.90-3.88) times in SL. Spinous dorsal outer margin convex, moderately in females, strongly in males; spinous dorsal length simorphic; in males, longest spine 3rd-4th, length 5.86 (4.60-7.74) in SL.; in females, longest spine 3rd-4th, length 7.51 (5.47-9.15) in SL; in females, spinous dorsal never reaches soft dorsal origin when folded back; in males, folded spinous dorsal often extends past soft dorsal origin; base of spinous dorsal shorter than soft dorsal base, spinous dorsal base, 1.19 (.96-1.56) times into soft dorsal base; spinous dorsal base 4.23 (3.66-5.20) times into SL, soft dorsal base 3.55 (3.11-4.74) times into SL. Second predorsal length 1.77 (1.47-1.93) into SL; soft dorsal moderately convex anteriorly and posteriorly, weakly convex between; longest ray 4th to 6th, length moderately sexually dimorphic, in males, length 5.94 (4.19-7.46) times into SL, in females, length 7.18 (5.52-9.27) times in SL; spinous and soft dorsal almost equally long, length of spinous dorsal 1.02 (.76-1.28) in soft dorsal length; spinous dorsal origin on vertical through origin of first pectoral ray, origin of soft dorsal on vertical through 2nd-3rd anal ray ending on vertical between last and antepenultimate anal ray. Preanal 1.87 (1.73-2.00) in SL; anal base long, 3.01 (2.70-3.79) times in SL; margin weakly convex, middle rays the longest, first ray about half as long, last ray about 3/4 as long, grading from either end to the middle. Pelvics originating halfway between snout and anus, length strongly sexually dimorphic; in females, middle ray the longest, rarely reaching anus, length 4.91 (3.61-7.21) in SL; in males, middle or outer ray longest, usually reaching anus in small (under 6cm.) males, in larger males may extend past anal origin, length 3.67 (2.75-4.72) times in SL. Pectoral broad based, base 5.86 (4.58-6.68) in SL; base about 30-40° off vertical; pectoral outer margin strongly convex, most exteriorly extending pectoral ray 4th to 6th, usually 5th, length 2.55 (1.98-3.36) times in SL; in males, inner face of pectoral rays with serrated edge from a quarter of the pectoral length from its base to a quarter of the pectoral length from its tip; in very large females, a few tubercles may be present. Caudal truncate. Anus on moderate, generally rugose papilla slightly in advance of anal fin; male with conical, moderate penis, length 18.45 (5.72-29.29) times in SL.

Meristic formulae

Spinous dorsal 11 (10-12) (10.89); soft dorsal 15 (14-17) (15.34); pectoral 18 (16-20) (18.31); anal 17 (15-18) (17.08); pelvics I, 3; vertebrae 38 (36-40) (38.3); lateral line pores 38-45[1]; branchiostegals 6.

Colour in alcohol

Body ground colour light brown to tan on dorsum to just below hypaxial-epaxial body division; ahead of anal fin, dark colouration dips below that line; ground colour intensifies over suborbital stay, second suborbital, lachrymal, also on nape between postorbital tubercles, and supratemporal and lateral canals (except for lighter pineal region) bones in opercle often overlaid by dark streaks; usually no vermiculations, punculations on body; in western collections, very faint large blotches

1. After Knipowitsch, 1907; Andriashev, 1954.

on dorsum, the first under the spinous dorsal center, the second under the anterior third of soft dorsal, the third under the posterior third of soft dorsal, but very faint, the last on the peduncle; in eastern collections, these blotches, including third much darker, larger; usually many dark blotches along midlateral body aspect, these blotches coalescing with the larger dorsal blotches, with each other, and extending in fingers down below dark ground colour limit; these blotches darker, larger anteriorly, especially under pectoral; again, blotches darker in eastern than western collections; in males, colour of spinous dorsal dominated by grey of black, with 2-3 lighter bands, scattered light spots; in females, spinous dorsal primarily clear to lgiht yellow, with 2-3 oblique bands; soft dorsal with 3-5 oblique (rarely vertical) bands; pectoral with 4-6 transverse, narrow (narrow than pupil) bands; pectoral base with broad diffuse band; caudal with 4-5 transverse relatively wide bands, the band width often exceeding the interband width; pelvics in male with white spots; ventrum, lower border of premaxillary, maxillary, all of dentary, branchiostegals, ground colour of fins (except spinous dorsal), wedge on peduncle extending to upper margin of caudal, margin around lower three preopercular spines yellowish to white; male with white spots in pectoral axil; buccal cavity is pale; peritoneum pale; colour in juveniles essentially that of adults, except sexual dimorphism not evident.

Colour in Life

McAllister (1964) describes a male specimen, NMC 63-211 from Hudson Bay as follows: "...bright white spots on the abdomen, on the inside of the pectoral fins and on both sides of the pelvic fins; these spots turn yellowish on the posterior of the body. The vertical fins are striped black and yellowish; the chin is yellowish; the head and most of the body are dark brown; the pineal region is white; the eyes are bronze coloured; the buccal cavity is white." Examination of a specimen from Frobisher Bay (NMC 70-285) reveals similar colouration; in addition, pectoral with orange spots, ventrally with orange bands extending ventrally from dorsal pectoral bands. Preserved material tends to bleach somewhat, and entirely loses the orange colouration.

Maximum size

Increases towards the eastern Canadian, Greenland waters; largest western specimen seen by me was 14 cm. SL, Canadian Archipelago 19 cm. SL, Hudson Bay 20 cm. SL, Gulf of St. Lawrence 17 cm. SL. Backus (1957) records a pecimen of 23 cm. SL off the Labrador Coast. Andriashev (1954) records females to 21 cm.[1] in Soviet northern seas. Vladykov (1933) records a 23 cm.[2] female from Hudson Bay. Jensen (1952) reports females to 26 cm.[3] off western Greenland, 22 cm.[4] off eastern Greenland. Ehrenbaum (1901) found females to 14 cm.[5] in Spitzbergen.

Etymology

The species name, tricuspis from the Greek "τρι" (three), and the

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1,2,5. It is not certain whether these are total or standard lengths. If total length, they convert to about 18, 19 and 12cm. SL respectively.

3,4. Total length given. Standard length about 23 and 19 cm. respectively.

Latin "cuspis", (cusp), in reference to the usually three cusps on the upper preopercular spine.

Range

Gymnocanthus tricuspis ranges from the northern Bering Sea into the Arctic, in the Canadian Archipelago, Hudson Bay, Labrador, Gulf of St. Lawrence, Newfoundland, straying south to Newport, Maine; on both sides of Greenland, northern face of Spitzbergen, northern Norway, Murmansk, Novaya Zemlya, Barents, Kara, Laptev Sea, East Siberian Sea. Lutken (1876) reported two specimens from Iceland, but this species has not been recorded there since; if the record was genuine, *Gymnocanthus tricuspis* probably occurs off the cooler north coast.

Systematic notes

The synonymy records 27 names which have been applied to this species, doubtless a consequence of its very wide distribution in the water of many nations, its long taxonomic history, and its great variability. Various authors (Schmidt, 1927; Vladykov, 1933; Rendahl, 1931) have desiganted subspecies to allow for this variation. Mayr (1969:348) states that "the better the geographic variation of a species is known, the more difficult it becomes to delimit subspecies and the more obvious it becomes that many such delimitations are quite arbitrary." The variation of *Gymnocanthus tricuspis* from St. Lawrence Island to the Gulf of St. Lawrence was closely examined. There proved to be a very gradual increase in tubercle development and size, and intensification of colour pattern from west to east, the region of change being practically the entire distance. Schmidt's "subspecies"apparently represent trends in certain regions in the range of Gymnocanthus tricuspis, rather than discrete populations. Backus (1957) finds that in Labrador specimens there is a complete range of specimens from fully granulated to ungranulated. Secondly, relative anal papilla lengths are found to be variable. On these bases, he synonymizes Vladykov's G. t. hudsonius with the nominal species. In agreement with Backus and Mayr, in the absence of demonstrably discrete populations, I am inclined to synonymize all subspecies with the nominal species.

G. tricuspis has also been identified with at least four other distinct species (G. galeatus, G. detrisus, G. pistilliger, and G. ventralis (G. intermedius)) through a misture of nomenclatorial confusion and the inability to distinguish these species from the Arctic form. Indeed, in parts of its range, some specimens of G. tricuspis look remarkably similar to G. galeatus or G. pistilliger. If enough characters are examined, however, these unusual specimens may still be identified with G. tricuspis. For example, Vladykov (1933) lists G. galeatus from Hudson Bay. Its total fin count falls into the overlapping region between G. tricuspis and G. galeatus, as does its body depth. However, G. tricuspis shows greater sexual dimorphism than does G. galeatus, and in fact the spinous dorsal height of Vladykov's "G. galeatus" is outside the range encountered by this author for that species. Secondly, its tubercle development is unlike that of G. galeatus.

Similarly, many eastern G. tricuspis resemble G. pistilliger in their tubercle development, and may overlap that species meristically. However, in no males of the former species have the characteristic pistillae of the true *G. pistilliger* been found. Kumlien's (1879:128) contention (after Lutken, 1876) that Pallas'(1829) "pistils" were actually "only the half cruciform, spiny scales which distinguish a certain part of the side of the body in *G. tricuspis*" added to the confusion. He obviously never saw any true *G. pistilliger*, nor realized that the pistils on that form do indeed exist!

"*G. ventralis*" is almost certainly not identifiable with *G. tricuspis* since the latter's southernmost extent is still considerably north of the type-locality of the former. With all the variability of *G. tricuspis*, significantly, in the north Bering Sea where *G. tricuspis* is sympatric with *G. pistilliger*, *G. tricuspis* is most unlike *G. pistilliger*, possibly through competition and its resultant character displacement.

Material Examined

	Reference	Locality	No.	Coordinates	Depth in metres
1.	BC61-64	Chukchi Sea, Alaska	1	166 35'§, 67 31'N	
2.	BC61-65	"	1	165 23'W, 67 44'N	
3.	BC61-79	"	2	167 30'W, 67 13'N	
4.	BC61-82	"	2	165 34'W, 67 52'N	
5.	BC61-83	"	2	166 55'W, 67 50'N	
6.	BC61-86	"	3	168 12'W, 67 52'N	
7.	BC61-88	"	4	167 12'W, 68 25'N	
8.	BC61-99	"	20	166 54'W, 68 47'N	
9.	BC61-100	"	74	167 33'W, 68 34'N	
10.	BC61-102	"	17	168 52'W, 68 03'N	
11.	BC61-103	"	7	168 52'W, 68 32'N	
12.	BC61-105	"	30	164 22'W, 69 16'N	
13.	BC61-106	"	30	167 55'E, 68 25'N	
14.	BC61-107	"	25	167 55'W, 68 10'N	
15.	BC61-208	Baffin Is., NWT.	2	68 28'W, 63 44'N	5
16.	BC61-210	"	1	68 28'W, 63 44'N	5
17.	BC61-219	Davis Strait, Canada	1	62 45'W, 67 03'N	5
18.	BC61-220	Cumberland Sound, NWT	1	66 00'W, 62 30'N	5
19.	BC61-221	Admiralty Inlet, NWT	1	86 00'W, 73 00'N	7
20.	BC61-405	Chukchi Sea, Alaska	9	166 35'W, 67 44'N	
21.	BC61-407	"	4	167 12'W, 67 43'N	
22.	BC61-409	"	1	167 55'W, 67 43'N	

	Reference	Locality	No.	Coordinates	Depths in metres
23.	BC61-411	Chukchi Sea, Alaska	12	168 34'W, 68 10'N	
24.	BC61-414	"	20	168 34'W, 67 57'N	
25.	BC61-416	"	8	168 02'W, 67 57'N	
26.	BC61-417	"	4	167 22'W, 67 55'N	
27.	BC61-419	"	13	167 30'W, 69 03'N	
28.	BC61-420	"	36	166 12'W, 69 04'N	
29.	BC61-428	"	3	166 53'W, 69 17'N	
30.	BC61-431	"	30	165 35'W, 69 16'N	
31.	BC61-437	"	2	165 52'W, 69 03'N	
32.	BC61-440	"	40	166 22'W, 66 43'N	
33.	BC61-441	"	3	168 38'W, 65 44'N	
34.	BC61-442	"	2	167 12'W, 68 11'N	
35.	BC61-444	"	2	165 56'W, 67 44'N	
36.	BC63-559	Point Barrow, Alaska	9	156 53'W, 71 29'N	25
37.	BC63-710	"	1	156 29'W, 71 24'N	46.7
38.	BC63-711	"	1	156 19'W, 71 24'N	50.3
39.	BC63-713	"	5	156 19'W, 71 22'N	5.5
40.	BC63-717	"	2	156 47'W, 71 19'N	
41.	BC63-758	"	1	156 02'W, 71 21'N	6.1
42.	BC63-767	"	3	156 19'W, 71 24'N	6.1
43.	BC63-789	"	3	156 19'W, 71 22'N	
44.	BC63-790	"	10	156 19'W, 71 22'N	7.6
45.	BC63-791	"	12	156 46'W, 71 20'N	5.5

	Reference	Locality	No.	Coordinates	Depth in metres
46.	BC63-793	Point Barrow, Alaska	8	156 19'W, 71 22'N	6.1
47.	BC63-796	"	4	156 19'W, 71 22'N	6.1
48.	BC63-805	"	4	156 28'W, 71 23'N	
49.	BC63-818	"	12	156 19'W, 71 22'N	7.6
50.	BC63-823	"	149	156 19'W, 71 22'N	6.1
51.	BC63-836	"	3	156 19'W, 71 22'N	9.2
52.	BC63-842	Camden Bay, Alaska	2	145 10'W, 70 01'N	7.3
53.	BC63-862	Point Barrow, Alaska	2	156 21'W, 71 21'N	12.2
54.	BC63-1115	Wainwright, Alaska	2	160 07'W, 70 36'N	1.8-6.1
55.	BC63-1118	"	3	160 04'W, 70 40'N	19.2
56.	BC63-1121	"	3	160 06'W, 70 40'N	19.2
57.	BC63-1123	"	6	160 02'W, 70 42'N	19.2
58.	BC63-1127	"	200	160 07'W, 70 37'N	12.8-14.6
59.	BC63-1130	"	439	159 53'W, 70 44'N	18.3
60.	BC63-1131	Point Franklin, Alaska	58	159 33'W, 70 50'N	25.9
61.	BC63-1132	NWT	220	141 47'W, 70 54'N	12.8
62.	BC63-1133	Point Franklin, Alaska	7	158 48'W, 70 53'N	
63.	BC63-1135	Point Barrow, Alaska	1	156 32'W, 71 38'N	156.5
64.	BC63-1137	"	1	156 22'W, 71 34'N	161.0
65.	BC63-1141	"	1	156 19'W, 71 27'N	
66.	BC63-1147	"	1	156 23'W, 71 31'N	159.2
67.	BC63-1173	"	1	156 29'W, 71 24'N	24.4
68.	BC63-1201	St. Lawrence Is.,Alaska		171 42'W, 63 06'N	9.2
69.	BC63-1224	Point Barrow, Alaska	1	156 44'W, 71 19'N	

	Reference	Locality	No.	Coordinates	Depth in metres
70.	BC63-1470	Mackenzie Bay, NWT	1	134 22'W, 67 44'N	15
71.	BC72-1	St. Lawrence Is., Alaska	1	169 00'W, 65 47'N	
72.	BC72-119	Pond Inlet, Baffin Is.,NWT	1	77 59'W, 72 40'N	22.9
73.	NMC 58-64	Bernard Harbour, NWT	2	114 42'W, 68 48'N	
74.	NMC 58-258	Amadjuak Bay, Franklin	1	72 45'W, 64 00'N	
75.	NMC 59-340	St. Lawrence estuary, Rimovsky, P.Q.	1	68 34'W, 48 27'N	
76.	NMC 59-444	Ungava Bay, Quebec	6	67 30'W, 58 N	
77.	NMC 60-62	Term Point, NW Hudson Bay, NWT	2	83 59'W, 69 10'N	
78.	NMC 60-111	Frustration Bay, Rowley Is., Franklin, NWT	1	79 W, 69 N	
79.	NMC 60-466	Simpson Pt., Herschel Is., Yukon	36	139 00'W, 69 34'N	
80.	NMC 62-248	S.E.Ungava Bay, P.Q.	1	62 W, 58 N	
81.	NMC 62-296	Foxe Channel, NWT	1	80 W, 65 N	
82.	NMC 62-336	Liverpool Bay, NWT	2	129 W, 70 N	
83.	NMC 62-342	Chesterfield Inlet, NWT		91 W, 63 N	
84.	NMC 62-385	Cornwallis Is., NWT	2	75 W, 95 N	
85.	NMC 62-385	"	1	75 W, 95 N	
86.	NMC 62-402	Eureka, Slidre Fiord, Ellesmere Is., NWT	1	85 40'W, 80 N	
87.	NMC 62-404	Prince of Wales Strait, Banks Is., NWT	9	119 W, 72 30'N	
88.	NMC 62-413	Creswell Bay, Somerset Is., NWT	1	94 W, 72 20'N	
89.	NMC 62-428	Franklin Bay, NWT	4	126 W, 69 N	
90.	NMC 62-535	Belcher Is., Keewatin,NWT	1	78 W, 56 30'N	

Reference	Locality	No.	Coordinates	Depth in metres
91. NMC 62-555	SW Belcher Is., Keewatin, NWT	1	78 W, 56 30'N	16
92. NMC 63-233	Gulf Hazzard, Richmond Gulf, east central Hudson Bay, PQ	1	76 17'W, 56 15'N	7
93. NMC 64-474	Winton Bay Lagoon, Beckman Peninsula, SE Baffin Is., NWT	1	64 35'W, 63 24'N	
94. NMC 65-358	Cornwallis Is., NWT	1	95 W, 75 N	
95. NMC 65-367	Langton Bay in Franklin Bay, NWT	200	126 W, 69 N	
96. NMC 65-369	Darnley Bay, NWT		124 27'W, 70 10'N	
97. NMC 67-757	Saguenay Fjord, Chicoutimi, PQ	1	70 06'W, 48 16'N	34
98. NMC 70-41	Saguenay Fjord, near Ste. Rose-du-Nord, PQ	1	70 35'W, 48 23 N	
99. NMC 70-47	Saguenay Fjord, near Anse St. Jean, PQ	1	70 39'W, 48 18'N	
100. SU 7921	"Coal Bay" (Kvalvagen), Spitzbergen	1	18 E, 77 28'N	
101. SU 8090	Off E. Greenland	1	17 56'W, 72 25'N	
102. SU 48811	East of Peard Bay, Alaska	16	159 W, 71 N	
103. UW 7297	St. Lawrence Is., Alaska	11	171 35'W, 63 06'N	55.8
104. UW 7298	"	2	169 05'W, 63 58'N	39.3
105. UW 7299	"	1	162 04'W, 64 09'N	22.0
106. UW 7300	"	12	171 33'W, 63 06'N	55.8
107. UW 7301	"	2	166 52'W, 64 06'N	33.8
108. UW 7302	"	7	169 05'W, 63 58'N	39.3
109. UW 7303	"	18	167 23'W, 63 22'N	33.9
110. UW 7314	"	2	168 06'W, 62 16'N	32.9

	Reference	Locality	No.	Coordinates	Depth in metres
111.	UW 7355	St. Lawrence Is.,Alaska	10	167 28'W, 63 14'N	32.0
112.	UW 14258	"	5	167 48'W, 64 18'N	37.5
113.	UW 14298	"	10	165 56'W, 64 00'N	31.7
114.	UW 14338	"	3	168 11'W, 62 47'N	33.9
115.	UW 14345	"	2	171 33'W, 63 06'N	55.8
116.	UW 14745	"	1	167 20'W, 63 30'N	27.5
117.	UW 14746	"	3	171 18'W, 62 51'N	47.6
118.	UW 15747	"	7	167 58'W, 63 46'N	34.8
			1984		

Literature Records

No.	Location	Coordinates	Depth in metres	Reference
119.	"Spitzbergen"	77 00'N, 20 00'W		Kroger, 1844
120.	Hunde Island, Greenland	68 50'N, 53 10'W		Reinhardt, 1838
121.	Port Leopold, NWT	73 50'N, 90 17'W		"
122.	Henley Harbour	51 59'N, 55 51'W		Weiz and Packard
123.	Magdalene Bay, Spitzbergen	79 35'N, 10 58'E		Eaton, 1874
124.	? Iceland	No precise locality		Lutken, 1876
126.	Godthaab, Greenland	64 ;0'N, 51 40'W		Kumlien, 1879
127.	Niatilic Harbour, Greenland (? Niante Harbour, Canada)	?64 55'N, 66 15'W		"
132.	Holsteinburg, Greenland	66 55'N, 53 30'W		Dresel, 1884
133.	Godhavn, Greenland	69 20'N, 53 30'W		"
134.	Mossel Bay, Spitzbergen	79 54'N, 16 00'W		Smitt, 1893
137.	Point Barrow, Alaska	71 23'N, 156 29'W		Scofield, 1898
138.	Inglefield Gulf (Inglefield Bredning)	77 30'N, 67 30'W		Holmqvist, 1899
139.	Beeren Island (Bjornoya)	74 25'N, 19 00'E		Lonnberg, 1899
140.	Recherche Bay (Recherchefjorden)	77 34'N, 14 40'E		"
141.	Advent Bay (Adventfjorden)	78 16'N, 15 30'E		"
142.	Harbour of "Virgo" (? Virgohamna)	79 58'N, 9 30'E		"
143.	Goesbay (Gashamna), Spitzbergen	76 15'N, 15 53'E		Knipovich, 1901
144.	Storfjorden, Spitzbergen	77 30'N, 20 00'E		"

No.	Location	Coordinates	Depth in metres	Reference
145.	Isfjorden, Spitzbergen	78 15'N, 15 00'E		Knipovich, 1901
146.	Isfjorden, Spitzbergen	78 15'N, 15 00'E		Collett, 1905
147.	Bell Sound (Bellsund)	77 39'N, 14 15'E		"
148.	Murmansk	68 59'N, 33 08'E		Gratsjianov, 1907
	Egedesminde, Stordalen, Greenland	68 40'N, 52 40'W		Jensen, 1910
149.	Havnefjord, Norway	70 34'N, 23 03'E		Jensen, 1910
	Nain, Labrador	56 32'N, 61 41'E		Kendall, 1910
150.	Danmarks Havn, Greenland	77 00'N, 18 00'W		Johansen, 1912
151.	Hvalrosodden, Greenland	77 00'N, 18 00'W		"
153.	Godhavn, Greenland	69 20'N, 53 30'W		Fowler, 1914
154.	Upernavik, Greenland	72 50'N, 56 00'W		"
158.	Robertson Bay, NWT	79 35'N, 56 00'W		"
160.	Eisfjord (Isfjorden), Spitzbergen	78 15'N, 15 00'E		Holsten, 1919
161.	Eastport, Maine	44 55'N, 67 01'W		Bigelow and Welsh, 1925
162.	Chukchi Sea	68 55'N, 180 00'W		Rendahl, 1931a
164.	Bering Sea	64 52'N, 170 03'W		"
165.	Raleigh, Nfld.	51 34'N, 55 44'W		Jeffers, 1932
166.	St. Lawrence Estuary, Trois Pistoles, Que.	49 21'N, 68 10'W		Prefonfaine, 1933
167.	St. Lawrence Estuary, Cape Columbier, Que.	48 52'N, 68 51'W		"
168.	Nottingham Island, NWT	63 06'N, 78 00'W		Vladykov, 1933
169.	Port Burwell, NWT	60 25'N, 64 50'W		"

No.	Location	Coordinates	Depth in metres	Reference
171.	Temple Bay, Labrador	51 59'N, 55 55'W		Huntsman et al, 1935
172.	Bonne Esperance, Que.	51 24'N, 57 40'W		"
173.	Red Bay	67 55'N, 97 12'W		"
	Whales Point, NWT	64 12'N, 88 00'W		Pfaff, 1937
174.	Laptev Sea	75 00'N, 125 00'E	9-28	Andriashev, 1937
175.	Saunders Is., Wolstenholm Fjord, Greenland	77 00'N, 69 00'W		Hildebrand, 1939
176.	Marchison Sd., Greenland	77 30'N, 70 00'W		"
178.	Saglek Bay, Labrador	58 30'N, 63 00'W		"
179.	Lake Harbour, NWT	67 51'N, 69 53'W		Dunbar, 1947
182.	Danmarks Havn, Greenland	77 00'N, 18 00'W		Jensen, 1952
183.	Nanortalik, Greenland	60 10'N, 45 05'W		"
184.	Upernavik, Greenland	72 50'N, 56 00'W		"
186.	Wolstenholm Fjord, Greenland	77 00'N, 69 00'W		"
187.	Angsmagssalik, Greenland	65 40'N, 38 00'W		"
189.	Kangerdlugssiaq, Greenland	67 00'N, 36 00'W		"
190.	Scoresby Sound, Greenland	70 30'N, 23 00'W		"
192.	Kaiser Franz Josef Fjord, Greenland	73 00'N, 23 00'W		"
195.	Bentekoe Island, Greenland	73 10'N, 21 15'W		"
197.	Sabine Is., Greenland	74 35'N, 19 00'W		"
198.	Hammerfest, Norway	70 40'N, 23 44'W		Smitt, 1893
199.	Labrador Coast, several locations	55 30'N, 60 00'W		Backus, 1957

No.	Location	Coordinates	Depth in metres	Reference
200	Hebron Fjord, Lab.	58 06'N, 62 59'W	110-125	Gordon and Backus
201	Miramichi at Bushville, N.B.	?47 02'N, 65 20'W		McKenzie, 1959
202	Arctic Bay, NWT	73 02'N, 85 11'W	7	Ellis, 1962
203	Isfjord, Spitzbergen	78 15'N, 15 00'W	25	Hognestad, 1961
204	St. Mary's Bay, Nfld.	46 50'N, 53 47'W	109	Ellis, 1968
205	Random Sd., Nfld.	48 03'N, 53 40'W		"
206	Cape Broyle	47 05'N, 52 54'W	10	"
208	Mowat Is., NWT	56 58'N, 76 40'W		McAllister, 1964
209	St. Lawrence River, several locations	47 43'N, 69 50'W		Bergeron and Legendre, 1970
210	Saguenay River	48 10'N, 70 00'W		Drainville, 1970
211	Murmansk Sea	69 37'N, 56 43'E		Knipovich, 1903a
212	Nordenskjold	75 42'N, 124 41'E		"
213	Laguna Nerpalakh	75 20'N, 137 20'E		"
	Storfjord, Norway	62 28'N, 6 30'E		Knipovich, 1903b
215	Novaya Zemlya	70 00'N, 55 00'E		Schmidt, 1927
216	White Sea	66 00'N, 36 00'E		"
217	Kara Sea	69 25'N, 67 15'E		"
218	East Siberian Sea	76 06'N, 153 01'E		"
	Barents Sea	69 38'N, 57 21'E		Briskina, 1939
		69 35'N, 55 53'E		"
		69 07'N, 44 48'E		"

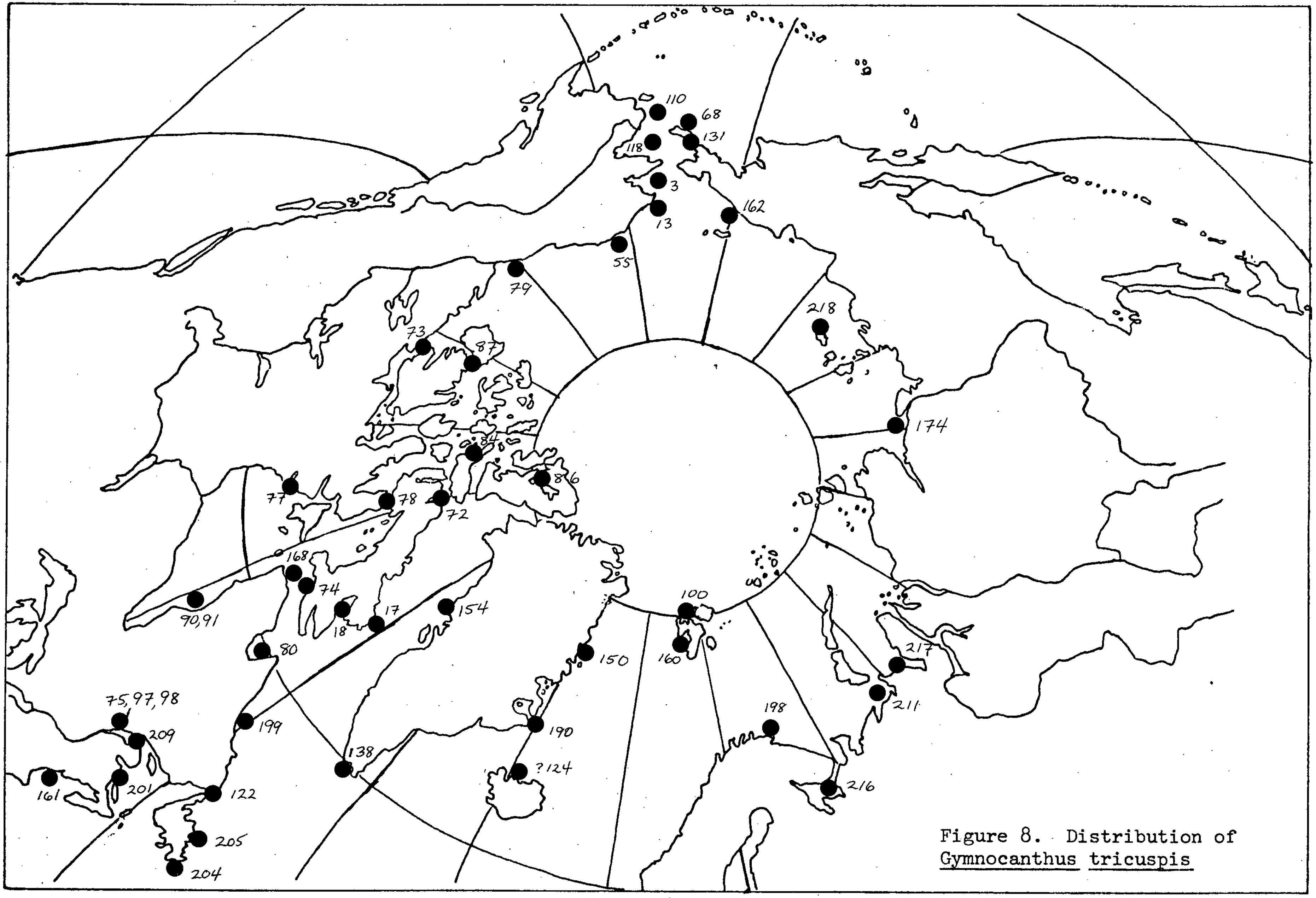

Figure 8. Distribution of Gymnocanthus tricuspis

Key to the ~~Specimens~~ Species of Gymnocanthus

In Gymnocanthus, there is overlap (with one exception) in all characters used to distinguish species. As a consequence, it is preferable to employ a mosaic of characters when identifying species.[1] Many characters will be ambiguous for any particular specimen, but in no specimen examined have all the characters studied proved ambiguous. For qualitative characters, refer to the diagrams supplied. All specimens should be forced into a natural pose with the opercles flat against the head, mouth closed, and body straight. This key is adequate for specimens 6cm. and larger. For smaller specimens, the morphometric characters are inadequate, and one must rely on meristic and qualitative characters, and distribution. See also "diagnostic characters".

1a. 1st, 2nd dorsal spines ahead of vertical through first pectoral ray origin (figure 13); dorsum pointed rather than rounded (figure 16); cleithral spines weak (figure 13); total fin count[2] 82 or over; range Sea of Japan, Hokkaido.

. . . G. herzensteini

1b. 1st or 2nd dorsal ray on vertical through first pectoral ray origin (figure 12); dorsum rounded or pointed (figures 16, 17); cleithral spines weak through strong (figures 11, 12, 14, 15); total fin count may be above or below 82.

. . . 2

2a. In fish 6 to 12cm., interorbital in head 12.0 times or fewer times; in fish over 12 cm., interorbital in head 9.0 or fewer times; range northern Hokkaido, to Southern Kamchatka.

. . . G. detrisus

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1. This is especially true of G. tricuspis which, over its total range may be quite variable.

2. The last anal ray, if appearing split, is counted as two rays. The total fin count includes both dorsals, both pectorals, and the anal fin.

2b. In fish 6 to 12cm., interorbital in head over 12.0 times; in fish over 12.0cm., interorbital in head more than 9.0 times.

. . . 3

3a. Total fin count 81 (see Footnote 2, p.124) or fewer; males with serrations on inner surface of pectoral rays; 37 or fewer vertebrae.

. . . 4

3b. Total fin count 82 (see Footnote 2, p.124) or greater; males lacking serrations on inner surface of pectoral rays; 36 or more vertebrae.

. . . 6

4a. Opercular membrane reaches or passes vertical through leading edge of first dorsal spine, rarely falling short of this line; cleithral spine moderate to strong, often emergent (figures 9, 10, 11); most juveniles (under 5cm.), some adults with supraorbital cirri (figure 9, 10); males with pistillae in pectoral axil; trunk with many subpupil sized punctulations; not entering Arctic or Atlantic waters.

. . . 5

5a. Cleithral spine long, sharp (figure 10); all specimens with supraorbital cirrus; ridges on nape low, not developed; tubercle behind suprapostorbital notch small or wanting (figure 10); seldom any development of bony granulations on opercular of upper preopercular shaft; in frontal profile, head usually as deep as or deeper than width; males with long, narrow pistillae (figure 15) in pectoral axillae, terminal width of pistillae twice that at base; range Korea, Japan, possibly Kamchatka.

. . . G. intermedius

5b. Cleithral spine shorter, blunter (figure 9); usually only juveniles (under 6cm.) with supraorbital cirri; ridges on nape developed; tubercles on nape well developed (figure 9); granulations often present of opercular bone, preopercular ascending shafts; in frontal profile, head as wide as or wider than deep; males with wide pistillae in pectoral axillae, terminal width three or more times that at base; (figure 14) range Japan to Seward, Alaska; Bering Sea to Pribilof Islands, north to St. Lawrence.

. . . G. pistilliger

4b. Opercular membrane short of vertical through leading edge of spinous dorsal in western[1] Arctic specimens, but may reach or pass this line in some eastern specimens; cleithral spine weak in western specimens, moderate in eastern forms; no specimens with cirri or pistillae; trunk without small punctulations; *G. tricuspis* entering Atlantic, Arctic waters.

. . . 6

6a. Total fin count 82-89; upper opercular margin straight; nasal spines usually longer than tubular anterior nares; lateral ethmoid-nasal spine distance large (figure 12); body slender, depth at pelvic girdle 4.8-6.4 times in SL; range Aleutian Islands, southeast Alaska, Pribilof Islands, possibly northeastern Kamchatka.

. . . *G. galeatus*

6b. Total fin count 76-85; upper opercular margin convex; tubular anterior nares usually longer than nasal spines; lateral ethmoid-nasal spine short (figure 11); body plump, depth at pelvic girdle 3.7-5.5 times in SL; range in Bering Sea north of 60 N. latitude; circumpolar, North Atlantic.

. . . *G. tricuspis*

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1. "Western" denotes the Bering Sea and from the Kara Sea through the Chukchi Sea to Point Barrow, Alaska; "eastern" denotes the rest of the Arctic and North Atlantic Ocean.

Figure 9. G. pistilliger lateral view. Note tubercular nape.

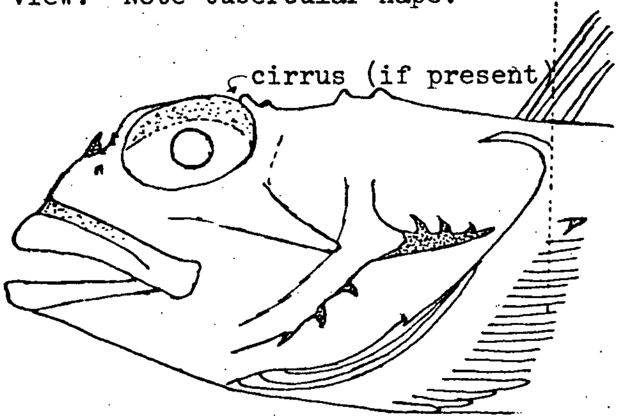
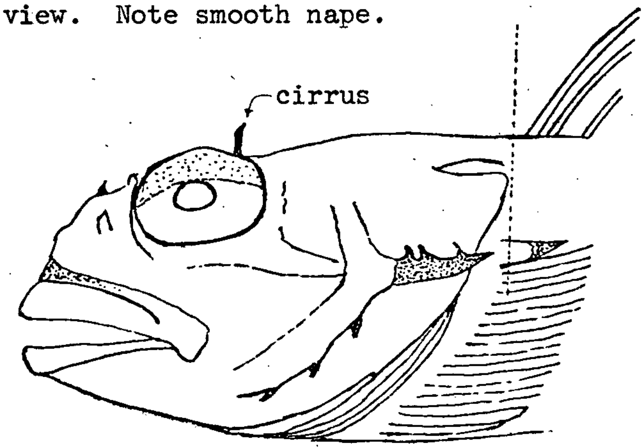


Figure 10. G. intermedius lateral view. Note smooth nape.



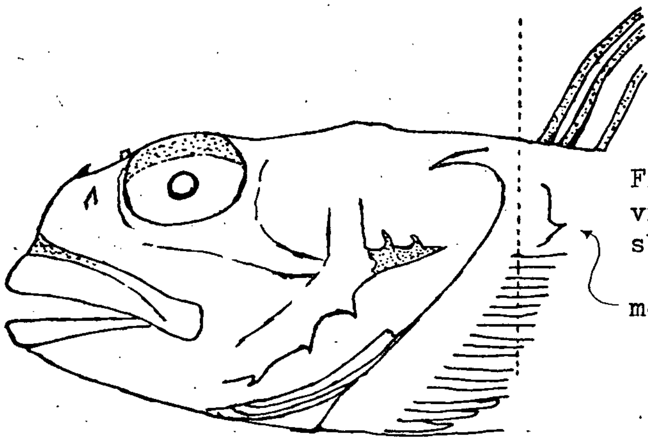


Figure 11. G. tricuspis lateral view. Nape variable; Note opercular shape.

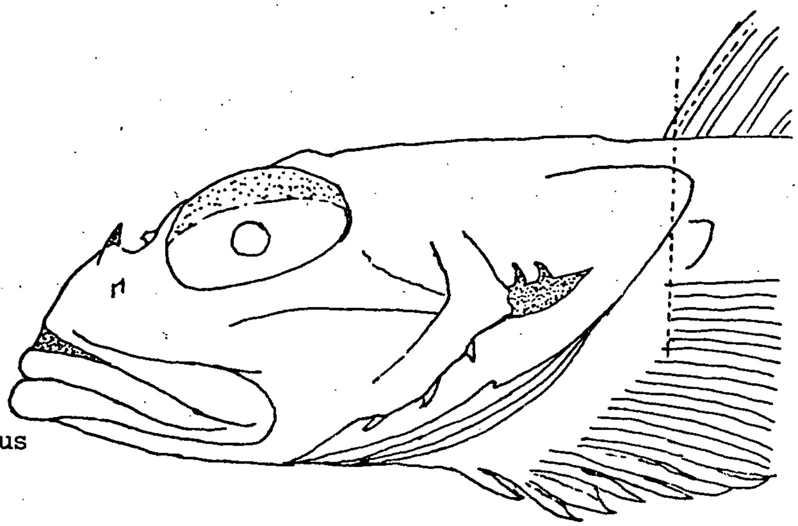


Figure 12.

G. galeatus lateral view. Note opercular shape, obsolete cleithral spine, spinous dorsal origin.

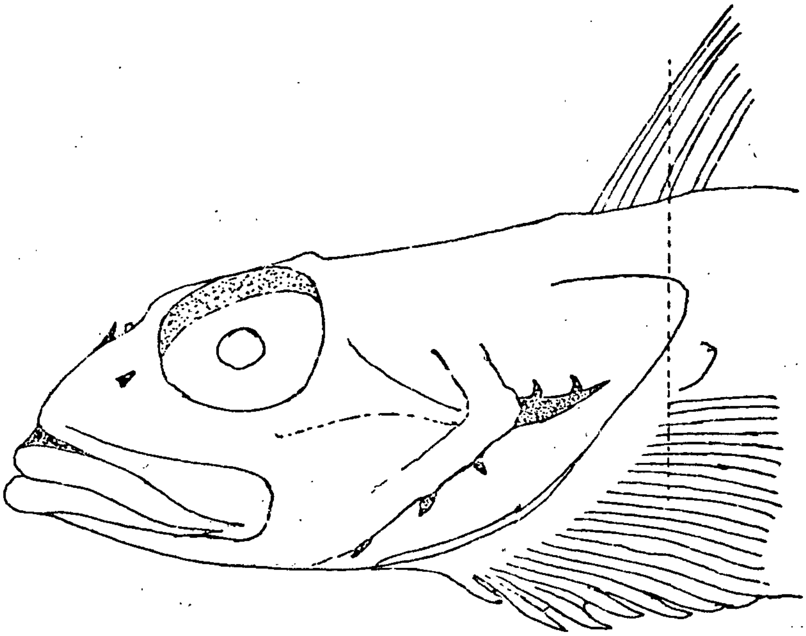
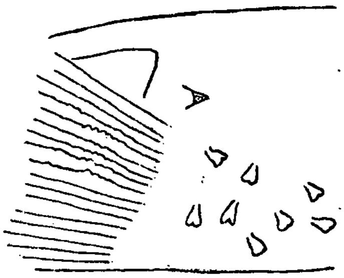


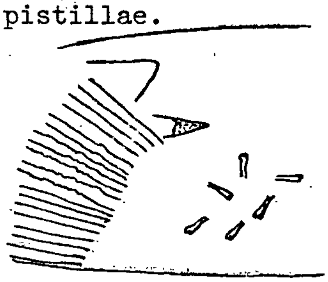
Figure 13. G. herzensteini lateral view. Note obsolete cleithral spine, spinous origin, high nape.

Figure 14. G. pistilliger pistillae



Note broad pistillae, pectoral serrations.

Figure 15. G. intermedius pistillae.



Note narrow pistillae, pectoral serrations.

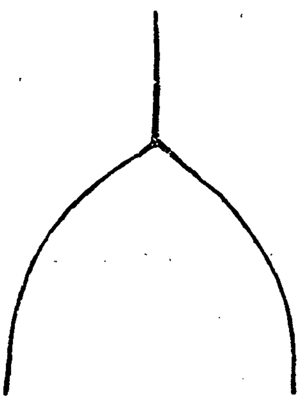


Figure 16. G. herzensteini cross section. Note pointed dorsum.

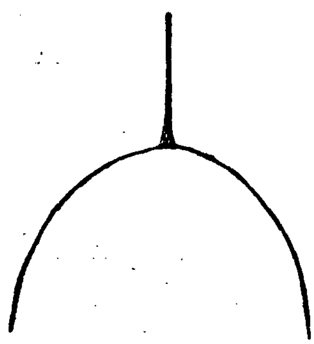


Figure 17. G. galeatus cross section. Note rounded dorsum.

Diagnostic Characters

Considering the enormous variability of the species of Gymnocanthus, the difficulty in identifying specimens, and the consequent profusion of invalid distribution records and range extensions, I choose to discuss all species under the same heading to reduce the confusion and repetition resulting from fragmentation of the topic.

G. galeatus's distribution, so far as is known from collection data and specimens available overlaps only with G. pistilliger from which it may be distinguished by the much greater size, the higher meristic counts, the more poorly developed sexual dimorphism (i.e., the fins are little longer in the male than the female, males lack pistillae, colour pattern differences between the sexes are slight), the greater development granulation, the comparatively tiny cleithral spine, the longer snout, the lesser developed nape tubercles. Although the key is adequate for fish to 6cm., G. galeatus and G. pistilliger may be distinguished as 2-3cm. fish in that even at this size, the nape tubercle and cleithral spine development is similar to that of adults; in addition, G. pistilliger possesses supraorbital cirri at this size. Lastly, meristic characters, though difficult to count are fully developed and may be utilized. Unlike the adults, both G. pistilliger and G.galeatus possess G. galeatus colouration as young.

G. galeatus approaches and may geographically overlap G. detrisus in the west, and G. tricuspis in the north though no verifiable collection data or specimens are available to prove overlap. G. galeatus is separable from G. detrisus in the subtle differences in tubercle development and foremost, the interorbital width. The interorbital grows allometrically, the proportional width of small G. detrisus approaching that of large G. galeatus. In equivalent sized individuals of 8cm. (smallest available specimen of G. detrisus) and larger, the interorbital difference is strikingly distinct. It is unknown whether larval or juvenile fish may be distinguished on the basis of interorbital width (figures 28-33, Table 1).

G. galeatus is certainly distinguishable from the north Bering G. tricuspis where their respective distributions might overlap. G. galeatus tends to have higher meristic characters; its snout is longer and less blunt; generally, the suprasuborbital stay canal in G. galeatus is very porous (4-6 pores, plus terminal pore) while in Bering Sea G. tricuspis there are few pores (1-2 pores plus terminal pore). Some eastern Arctic G. tricuspis may approach G. galeatus in pore number. Bering Sea G. tricuspis almost totally lack nape tubercles, and often have reduced granulation development.

It is unlikely that G. galeatus ever overlaps G. herzensteini or G. intermedius. G. galeatus may be easily distinguished from G. herzensteini by its lower scale density, shallower head, more posterior spinous dorsal origin, and colour pattern. The grossly different head shape, cleithral spine development, low meristic characters, and supraorbital cirrus of G. intermedius are always adequate to distinguish it from G. galeatus.

G. pistilliger is a very wide-ranging species, at least marginally overlapping the ranges of all the other species. It is very close to

G. tricuspis and may closely resemble specimens of that species from the Arctic. G. tricuspis appears to undergo character displacement in the northern Bering such that there, that species is quite distinct from those species with which it may be sympatric. In this region, G. pistilliger may be distinguished from G. tricuspis by the greater development of tubercles and granulations, the tendency toward lower meristic characters, the presence of pistillae (in the males), the lesser body depth, and the greater cleithral spine development in the former.

Its lower meristic characters, cleithral spine development, sexual dimorphism, and interorbital width are always adequate to distinguish G. pistilliger from either G. herzensteini or G. detrisus.

G. pistilliger may be distinguished from its closest relative, G. intermedius by the former's shallower head, greater tubercle development, smaller cleithral spine, different pistillae shape and usually, the absence of the supraorbital cirrus in adults.

G. tricuspis, being Arctic never overlaps the range of the temperate species, G. herzensteini, G. detrisus, and G. intermedius. However, since that species has been identified with G. detrisus once in the literature (Vladykov, 1933) it is perhaps expedient to distinguish them.

G. tricuspis has a shorter, more broad head than either G. herzensteini or G. intermedius. Interorbital widths are often poor criteria to use for identifying G. tricuspis since eastern Canadian specimens may possess wide interorbitals; these eastern samples also possess grossly developed nape tubercles unlike either G. detrisus or G. herzensteini, the other forms with wide interorbitals. In the north Bering, G. tricuspis possesses a relatively narrow interorbital; here, it also lacks postorbital tubercles, characteristic of G. herzensteini, detrisus, or intermedius. G. tricuspis may always be distinguished from G. intermedius in that the former possesses pistillae (males) and supraorbital cirri.

G. detrisus and G. herzensteini are similar, though the former tends to have a wider interorbital, a more sparse scale patch, and a wider, shallower head. G. herzensteini's spinous dorsal originates more anteriorly than in either G. detrisus or G. intermedius.

Finally, G. intermedius over 8cm. may be distinguished from most other species (the exception, G. pistilliger previously noted) by the presence of supraorbital cirri.

Meristic Variation

Meristically, there is much overlap in the six species of Gymnocanthus (figures 24-29) although the means and modes may differ significantly between species (figures 18-23). Species tend to have either high counts or low counts in all fins, rather than exhibiting a range of counts. Within a single fish there is little relation between unusually high or low counts in any particular fin and the counts for other fins. Therefore, adding fin counts tends to minimize the effect of one high or low count, and increases the separation of counts (Schultz and Welander, 1934). By using total fin ray and spine counts (see footnote 2, p.) G. pistilliger and G. intermedius can be distinguished from G. galeatus and G. herzensteini however neither G. tricuspis nor G. detrisus can be distinguished from any of the other four species using this criterion. Also, *G. pistilliger* and *G. intermedius* frequently may be distinguished from the other species by vertebral counts. These counts are included in the key as criteria of secondary importance since they can only be easily counted on x-ray plates.

Data are available (Soldatov and Lindberg, 1930; Thielemann, 1921; Knipovich, 1907; Backus, 1957) to compare geographically different populations of both *G. pistilliger* and *G. tricuspis*. Figure 30 shows data for specimens of *G. pistilliger* examined by me and comprised almost wholly of eastern Pacific collections, and for Lindberg and Soldatov's collections which are probably all from the western Pacific. While the ranges of counts remain about the same, western collections tend to have lower spinous dorsal (mean 9.53 versus 9.73) and pectoral ray (mean 17.99 versus 18.53) counts, but higher soft dorsal (mean 14.78 versus 14.40) and anal ray (mean 16.51 versus 16.09) counts. Although the literature records do not permit compilation of total counts, it appears that in western *G. pistilliger* the lower counts of the pectoral and spinous fin may compensate for the higher counts of the soft dorsal and anal fin. If so, the total count distribution closely resembles that of the eastern collections from which the total counts in the key were obtained.

Comparative data for *G. tricuspis* collections, consisting primarily of Arctic American specimens (examined by me), Labrador collections (Backus 1957) and Arctic Russian collections (Knipovich, 1907; Thieleman, 1921) show that except for the pectoral fin (which in Russian material has counts equivalent to those of American material), the Labrador and Russian collections tend to have higher fin counts. Total fin counts for

Russian collections also ranged higher than those of American G. tricuspis, but their means are very close (80.14 and 79.96 respectively) (Figure 19-23, 33, 34).

Cusp numbers show great variation and overlap, consequently they are not useful for species separation (Figure 33).

Figure 18. Range and variability of vertebral counts.

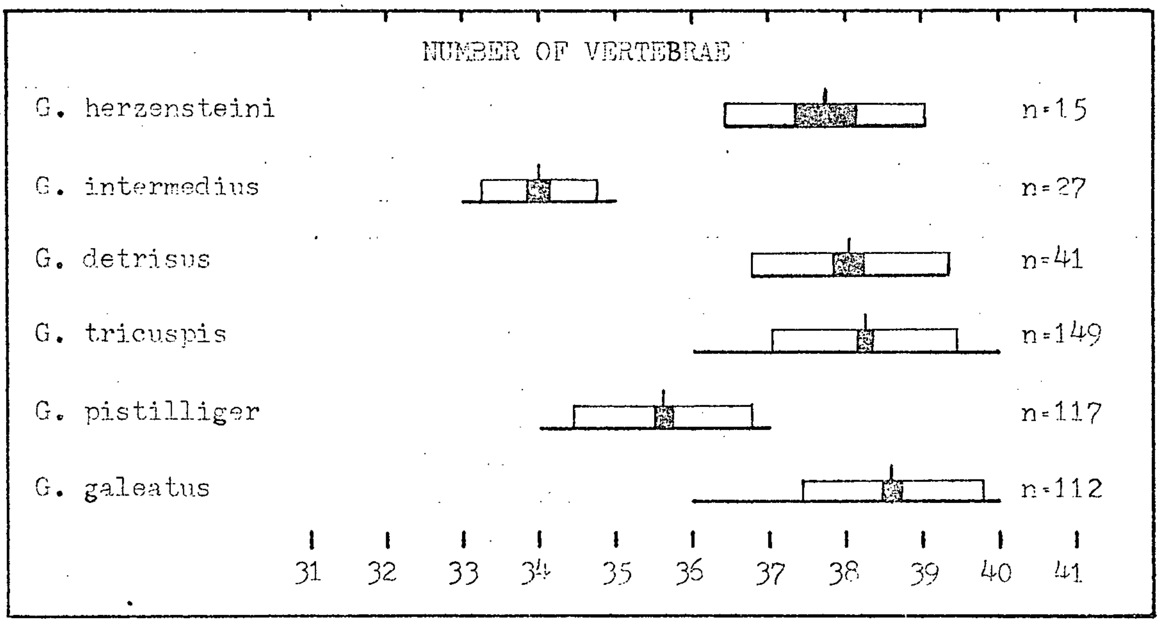


Figure 19. Range and variability of combined fin counts.

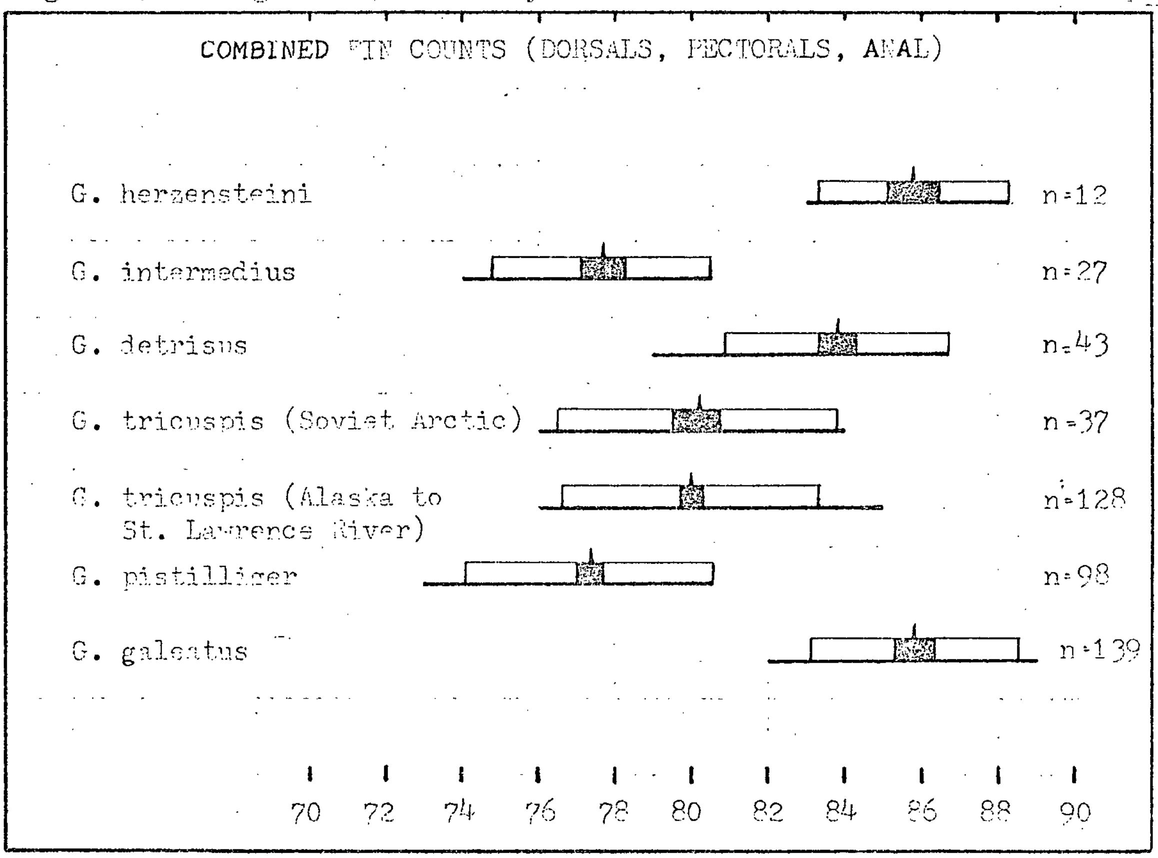


Figure 20

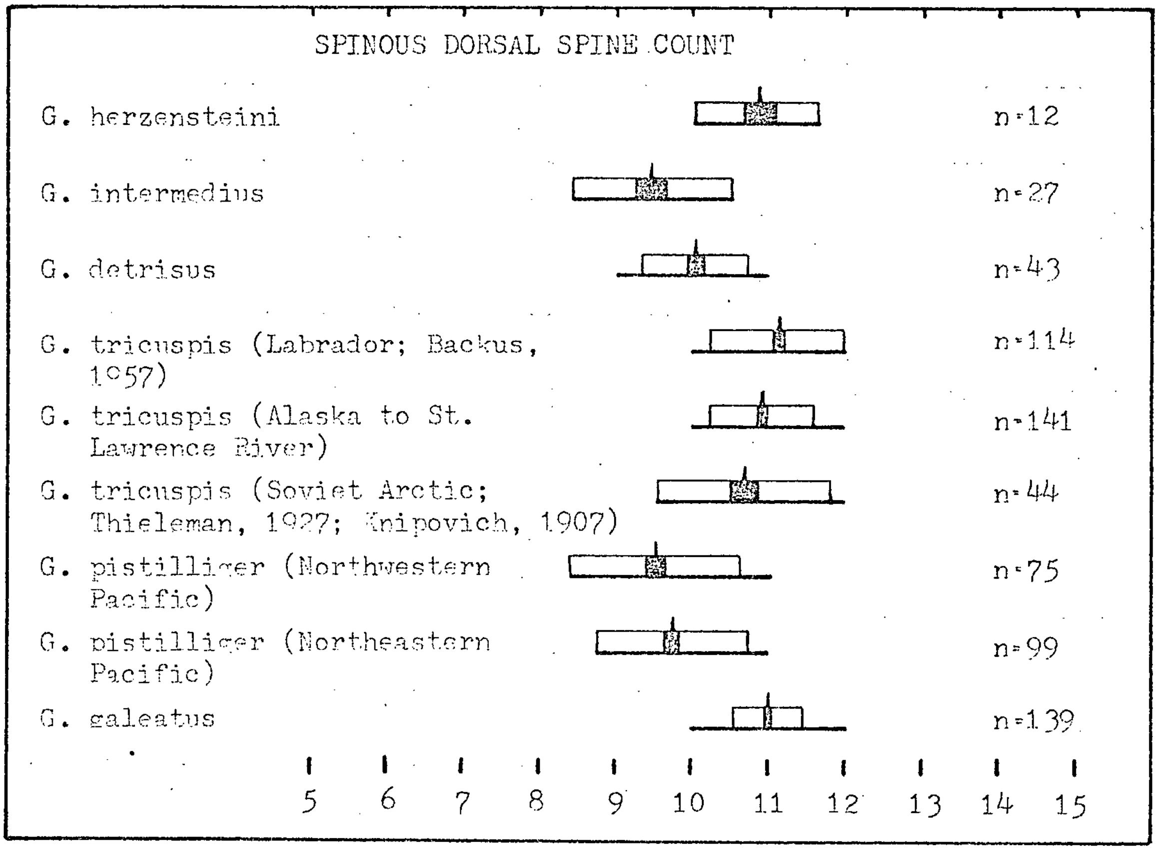


Figure 21

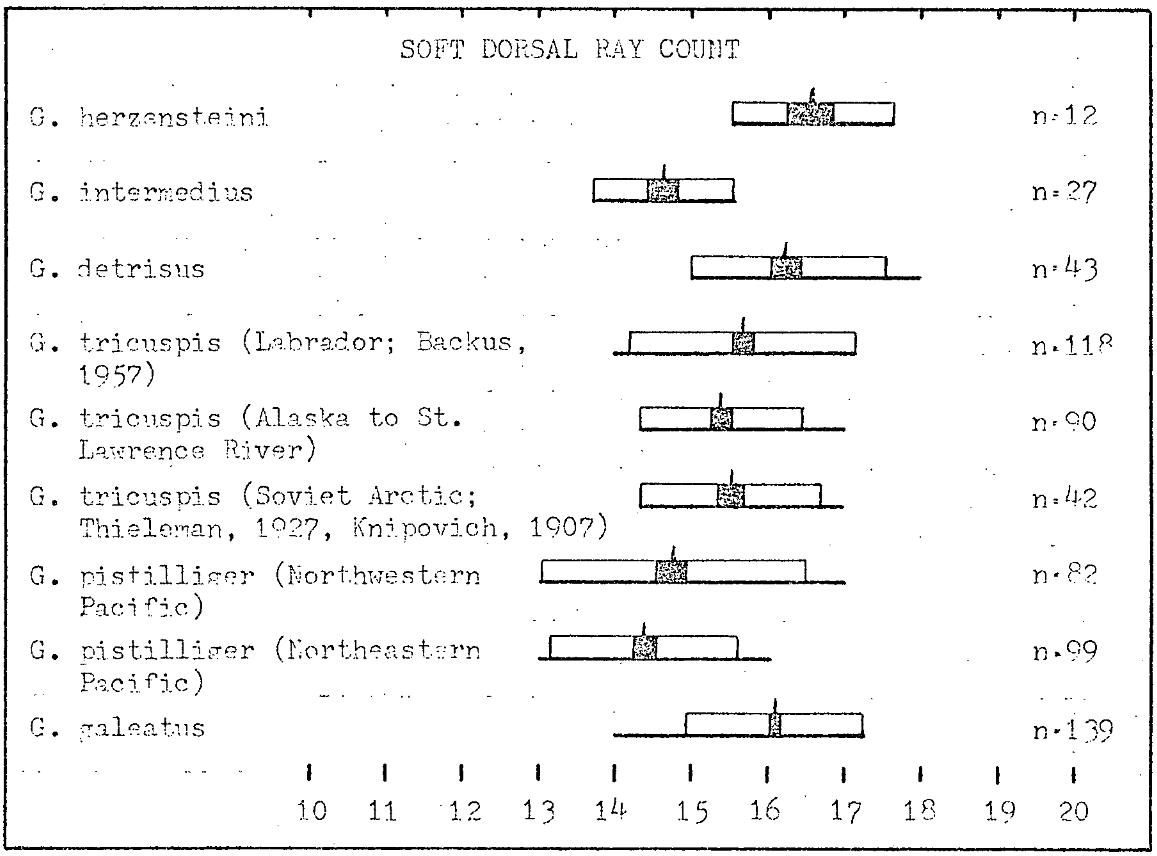


Figure 22

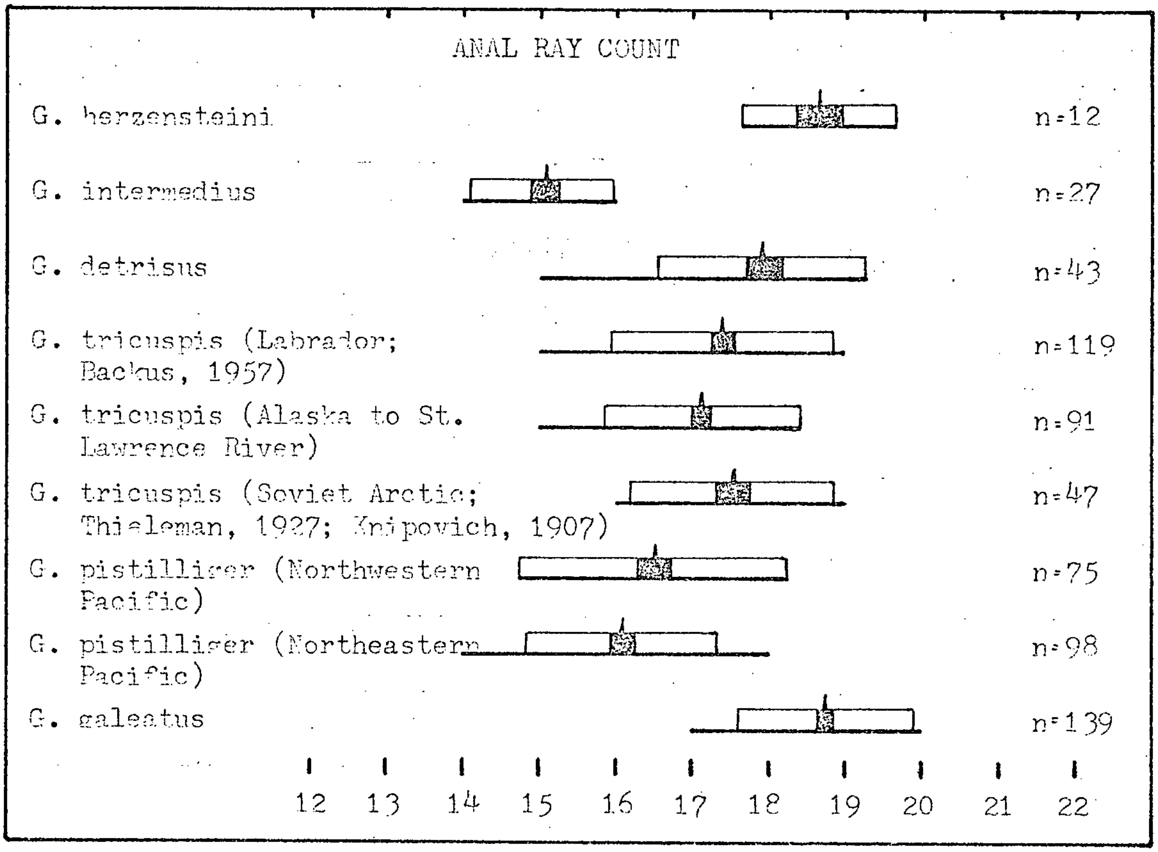


Figure 23

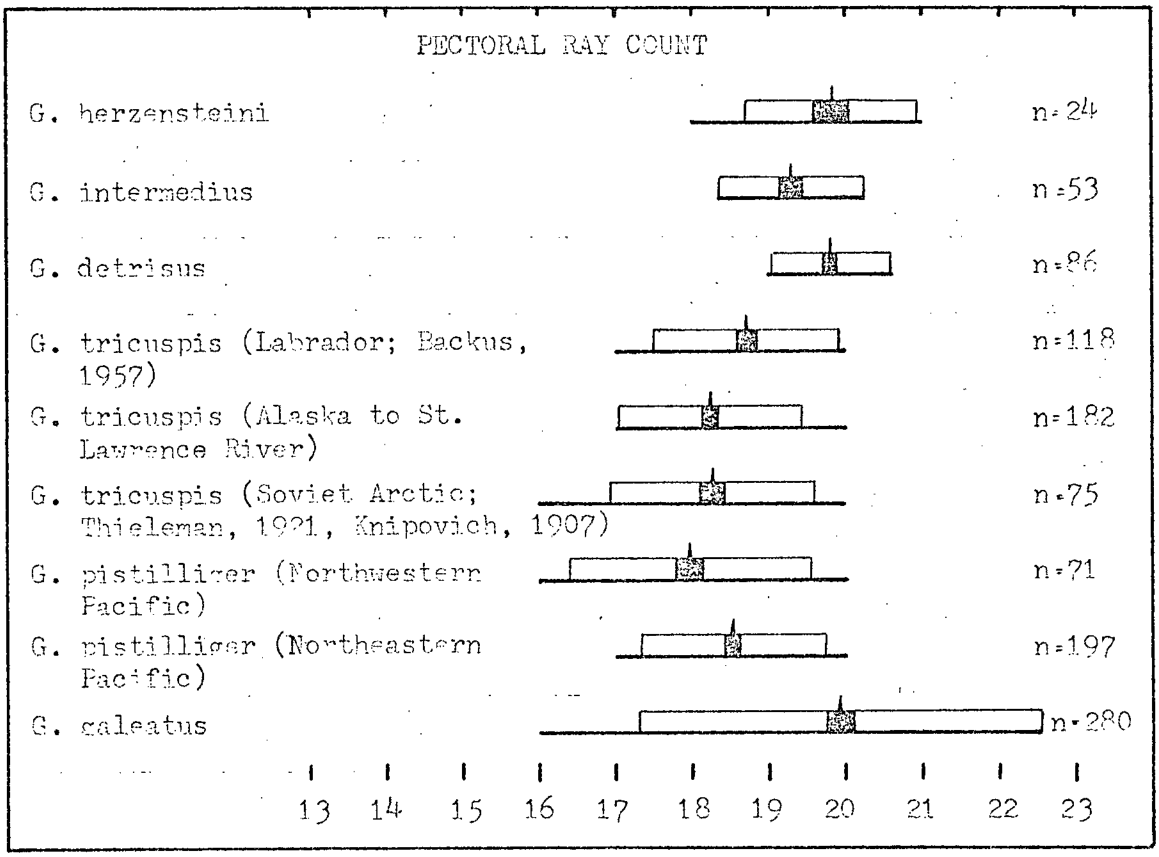


Figure 24. Distribution of total fin counts.

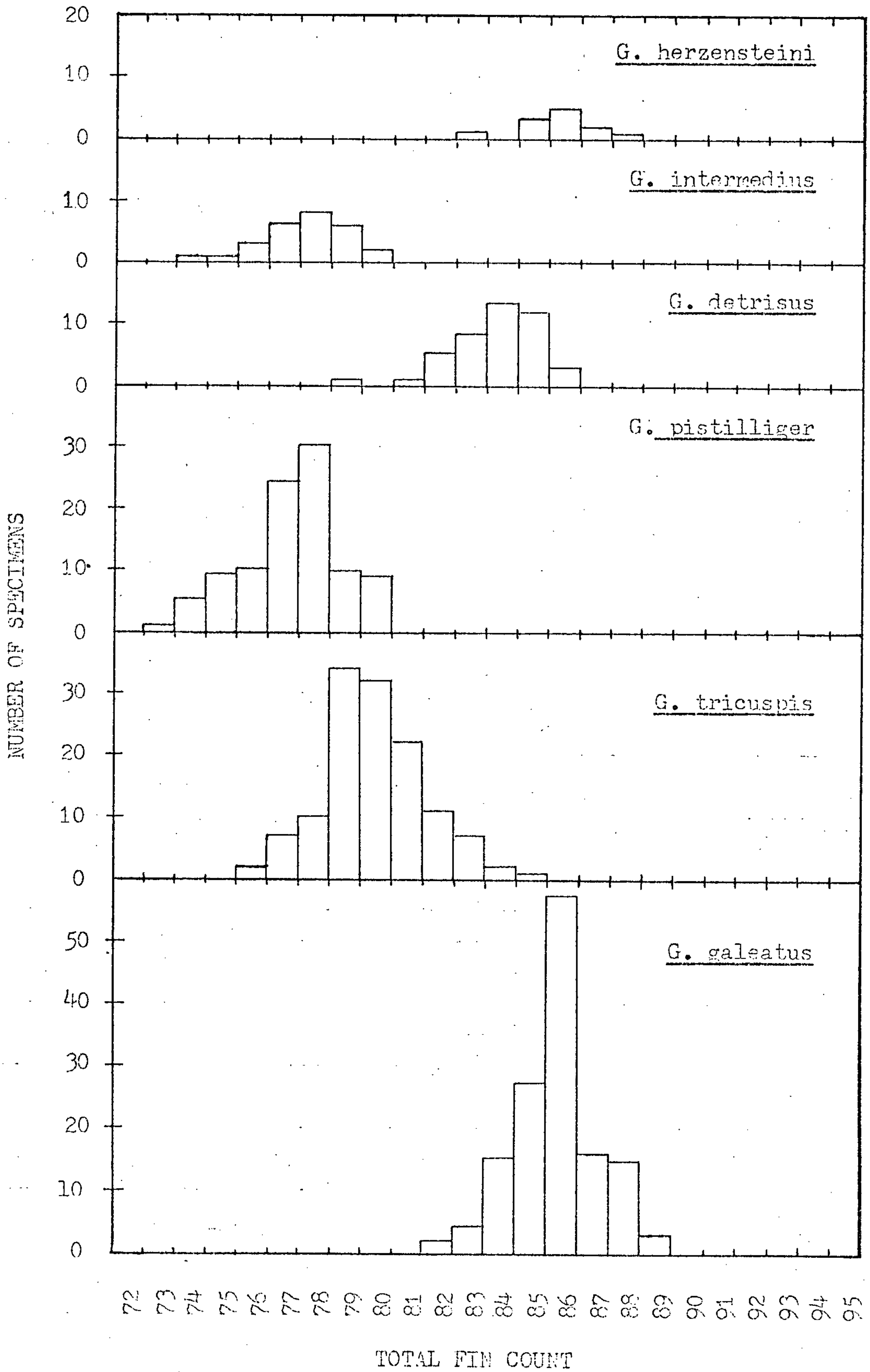


Figure 25. Distribution of vertebral counts.

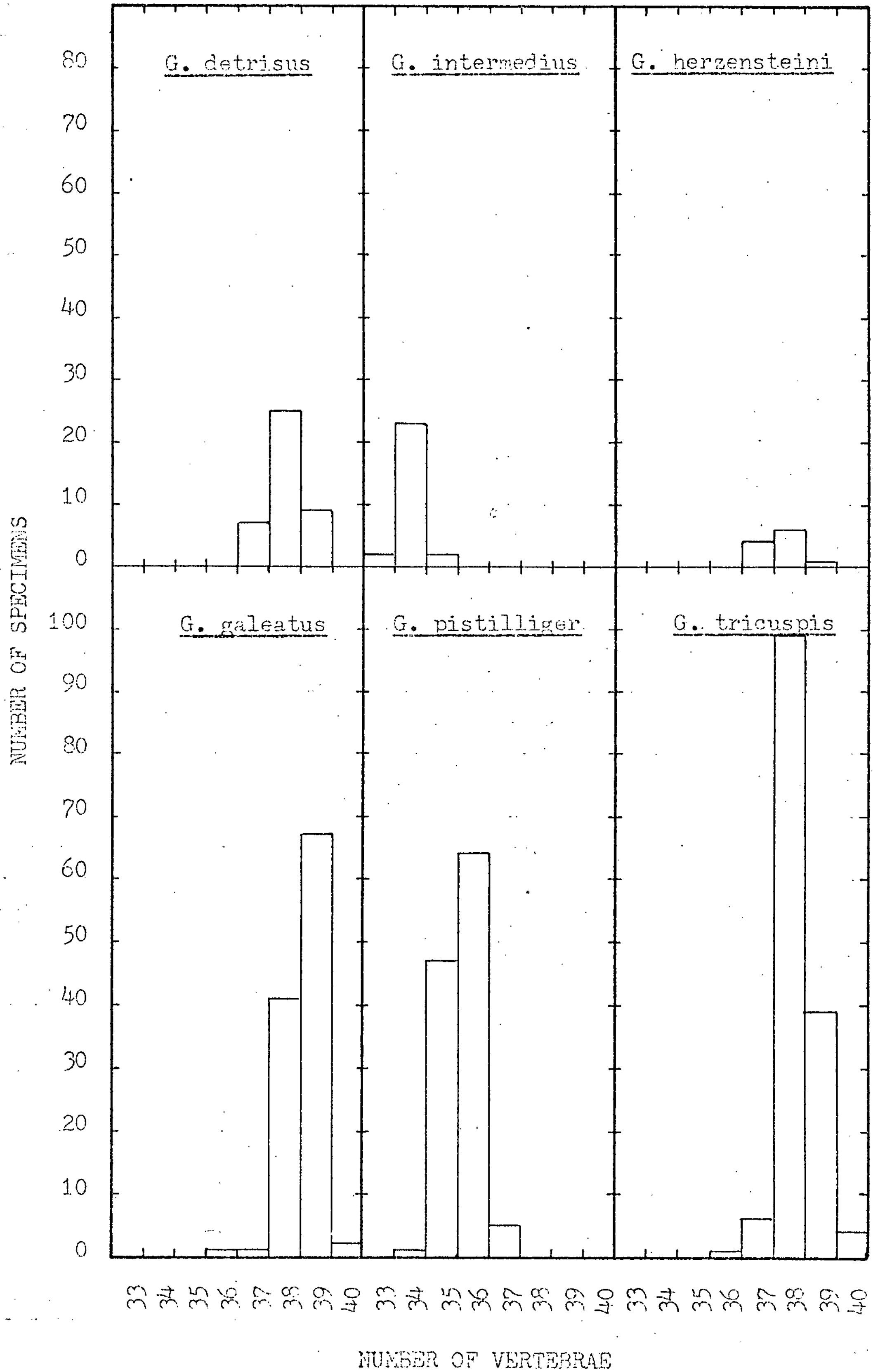


Figure 26. Distribution of spinous dorsal counts.

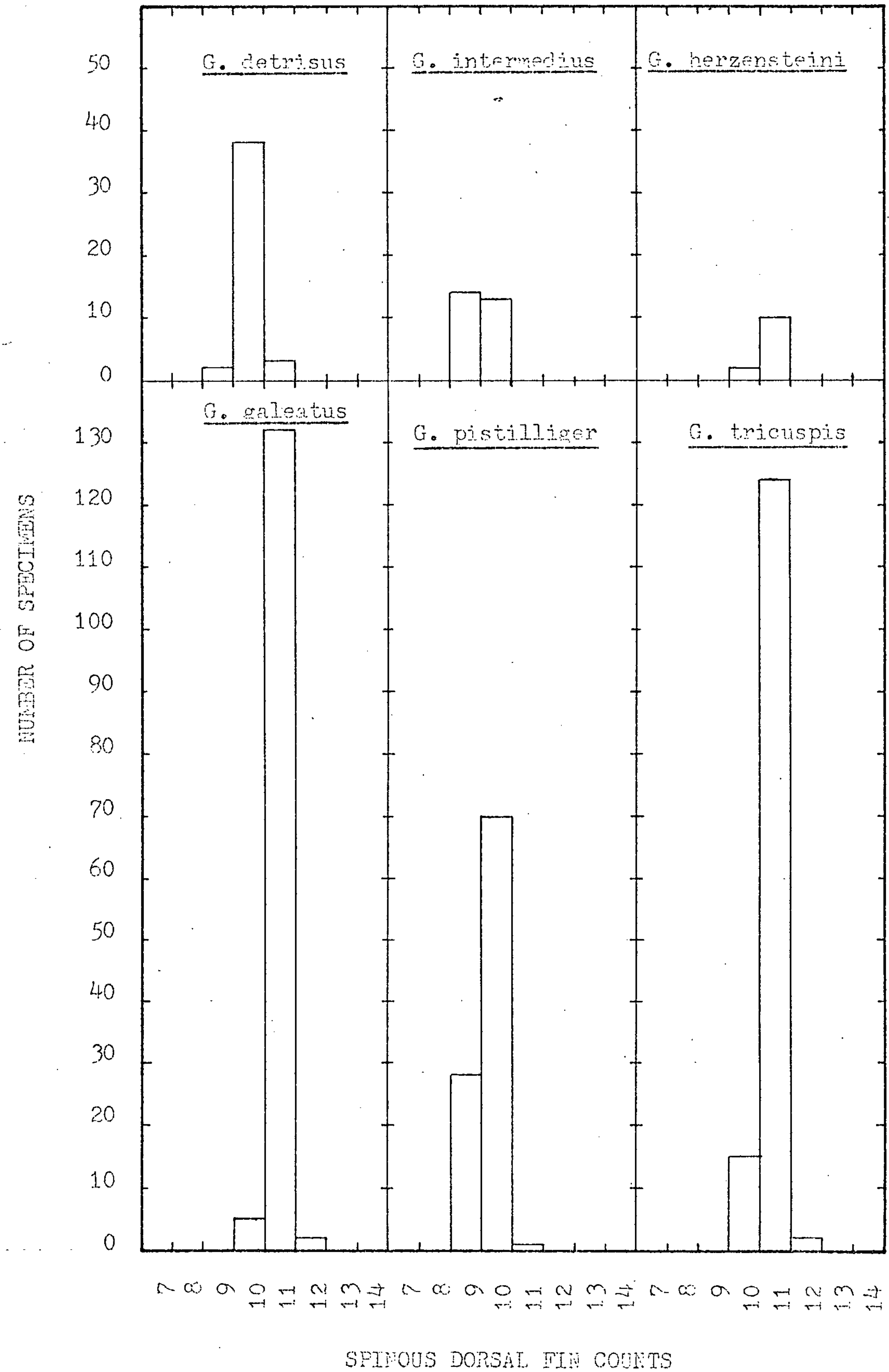


Figure 27. Distribution of soft dorsal fin counts.

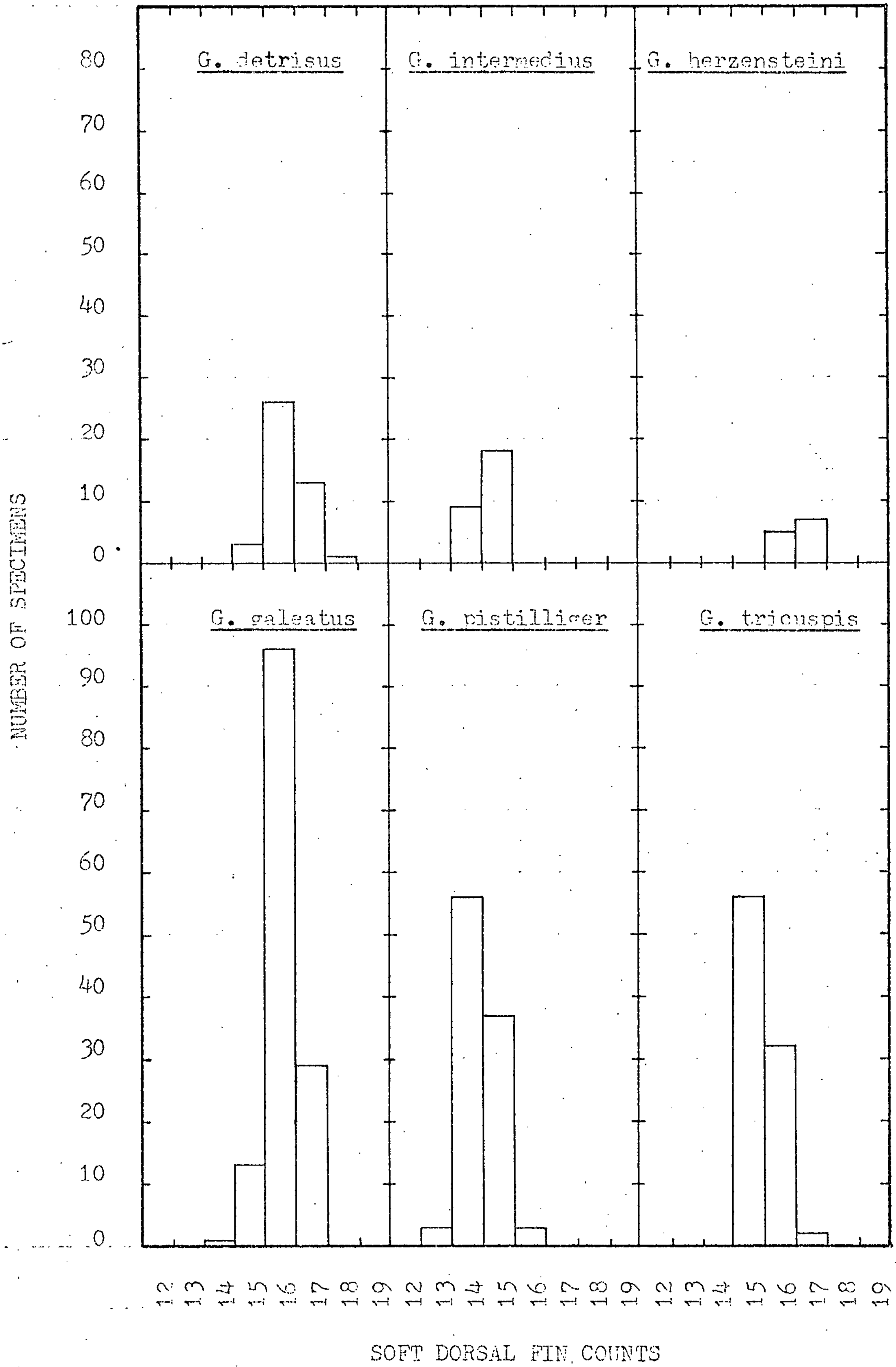


Figure 28. Distribution of anal ray counts.

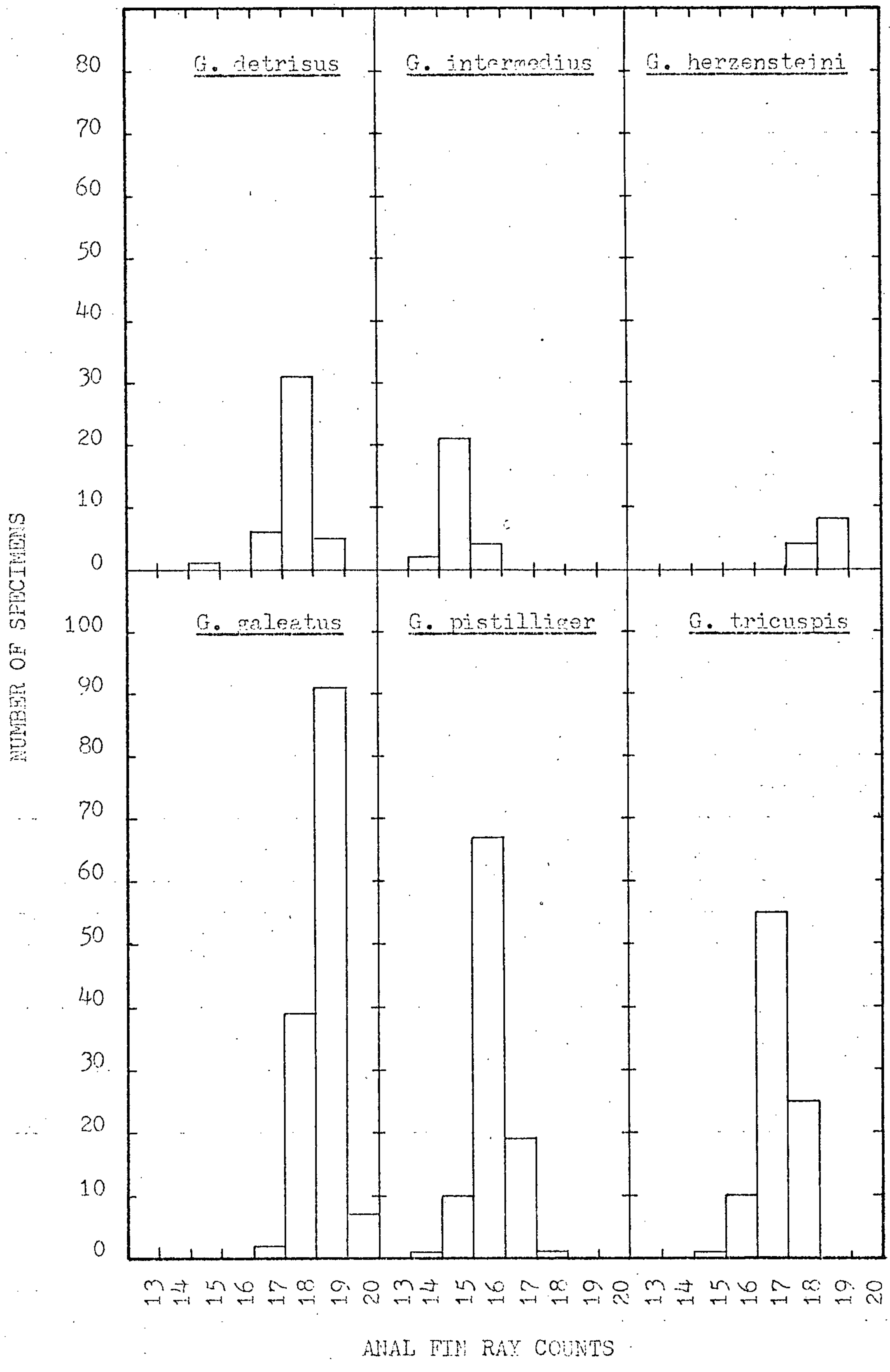


Figure 29. Distribution of pectoral fin ray counts.

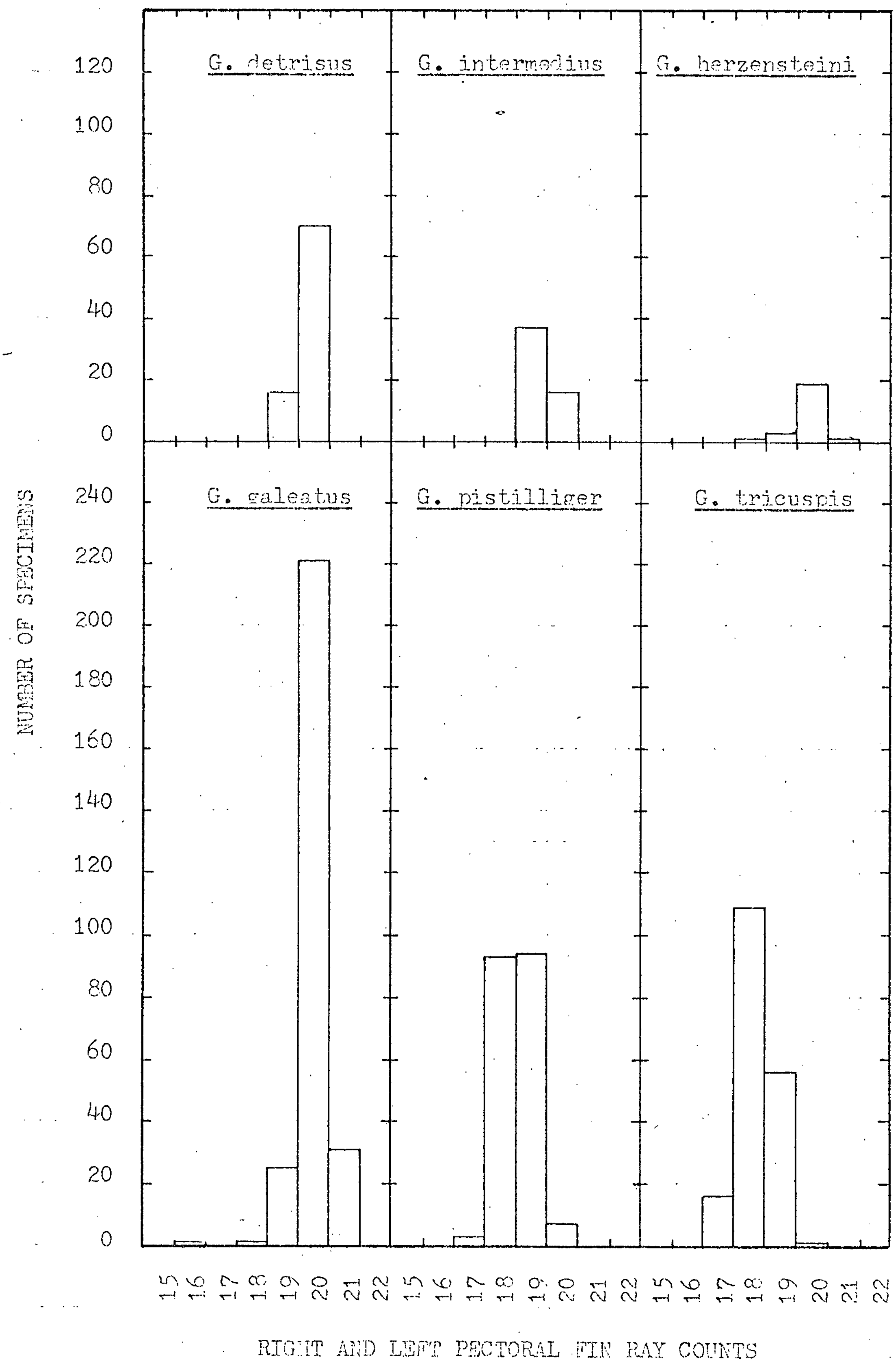


Figure 30. Gymnocanthus pistilliger fin counts.

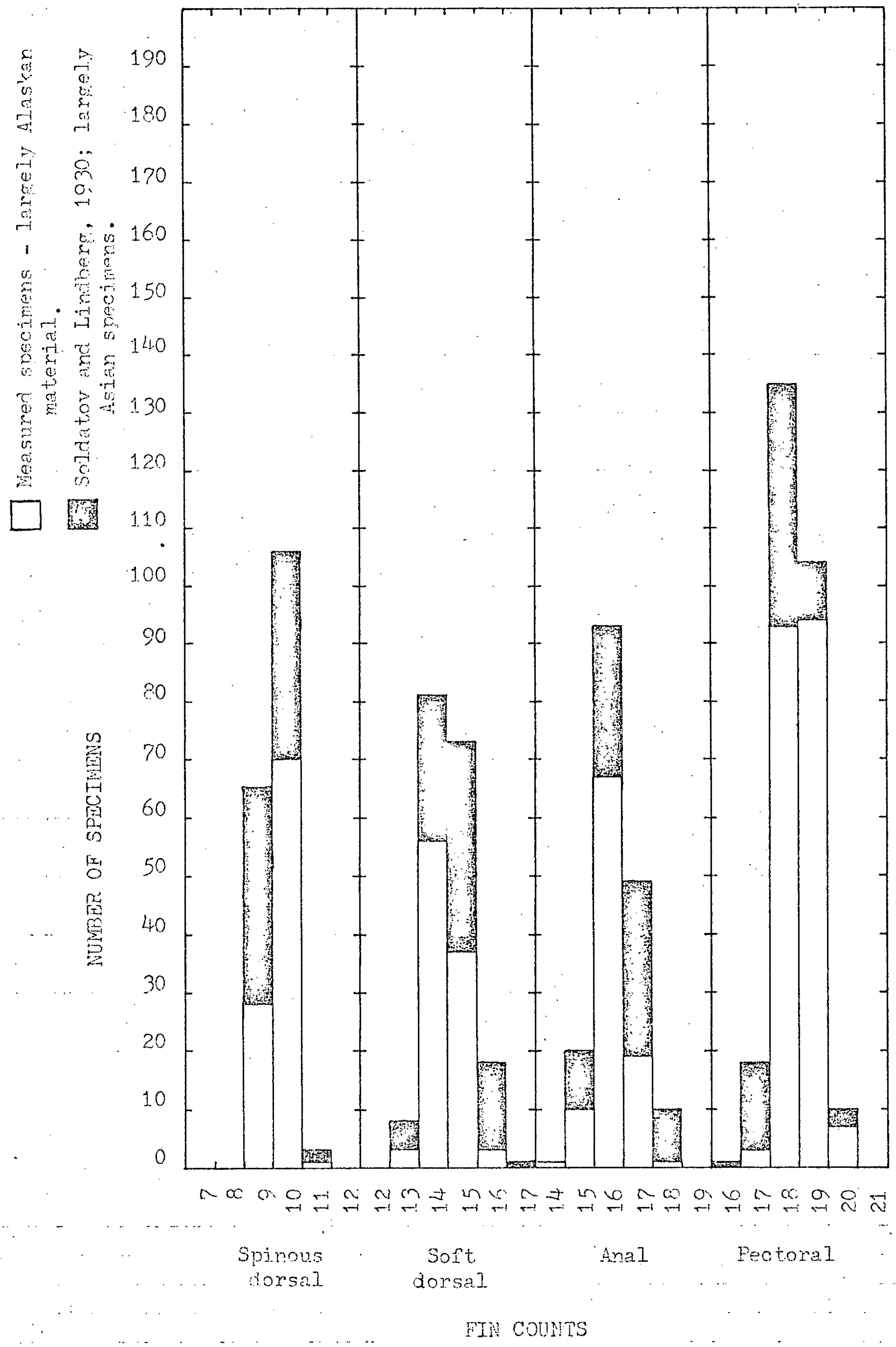


Figure 31. Gymnocanthus tricuspis fin counts.

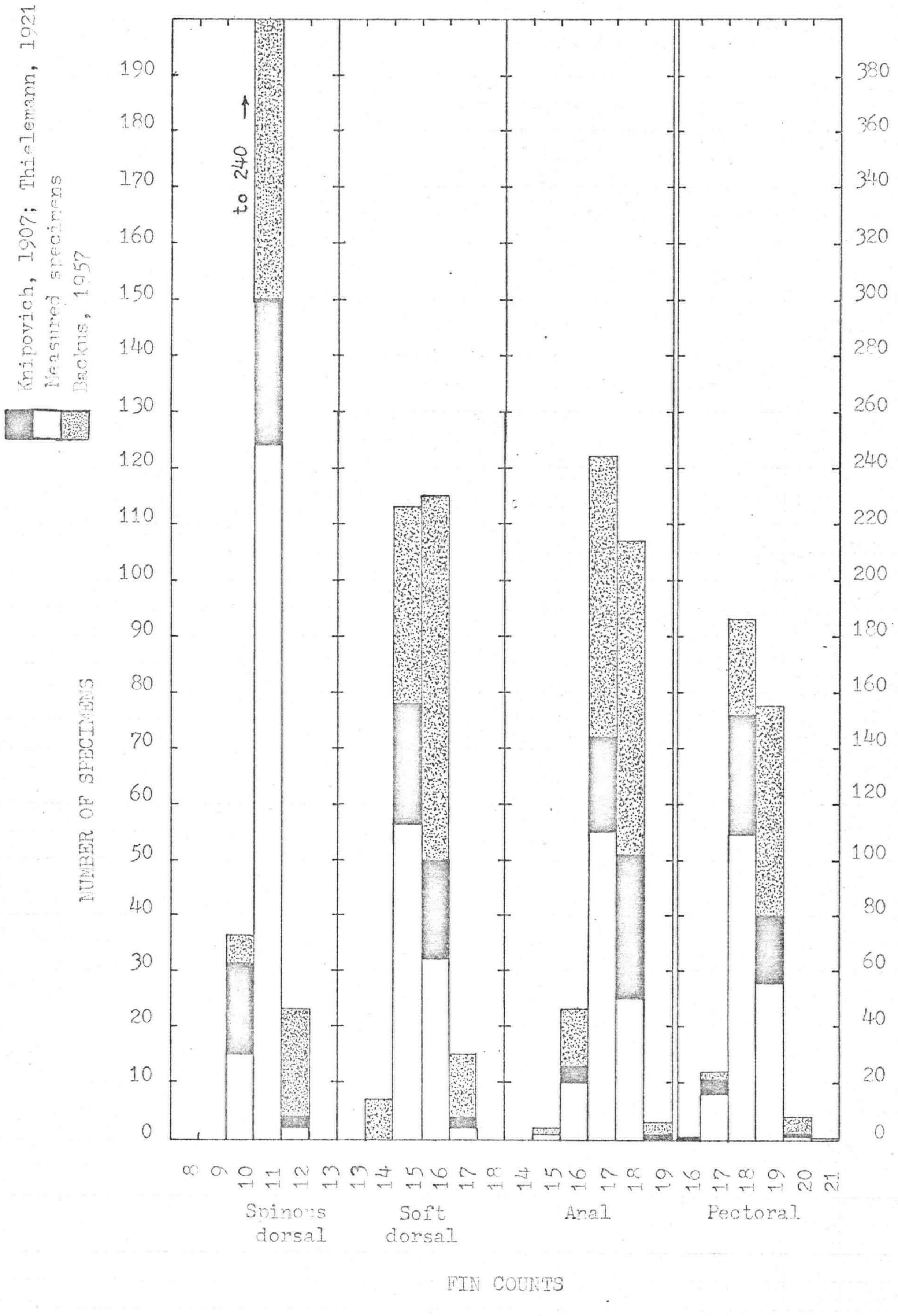


Figure 32. Gymnocanthus tricuspis. Total fin counts for different collection regions.

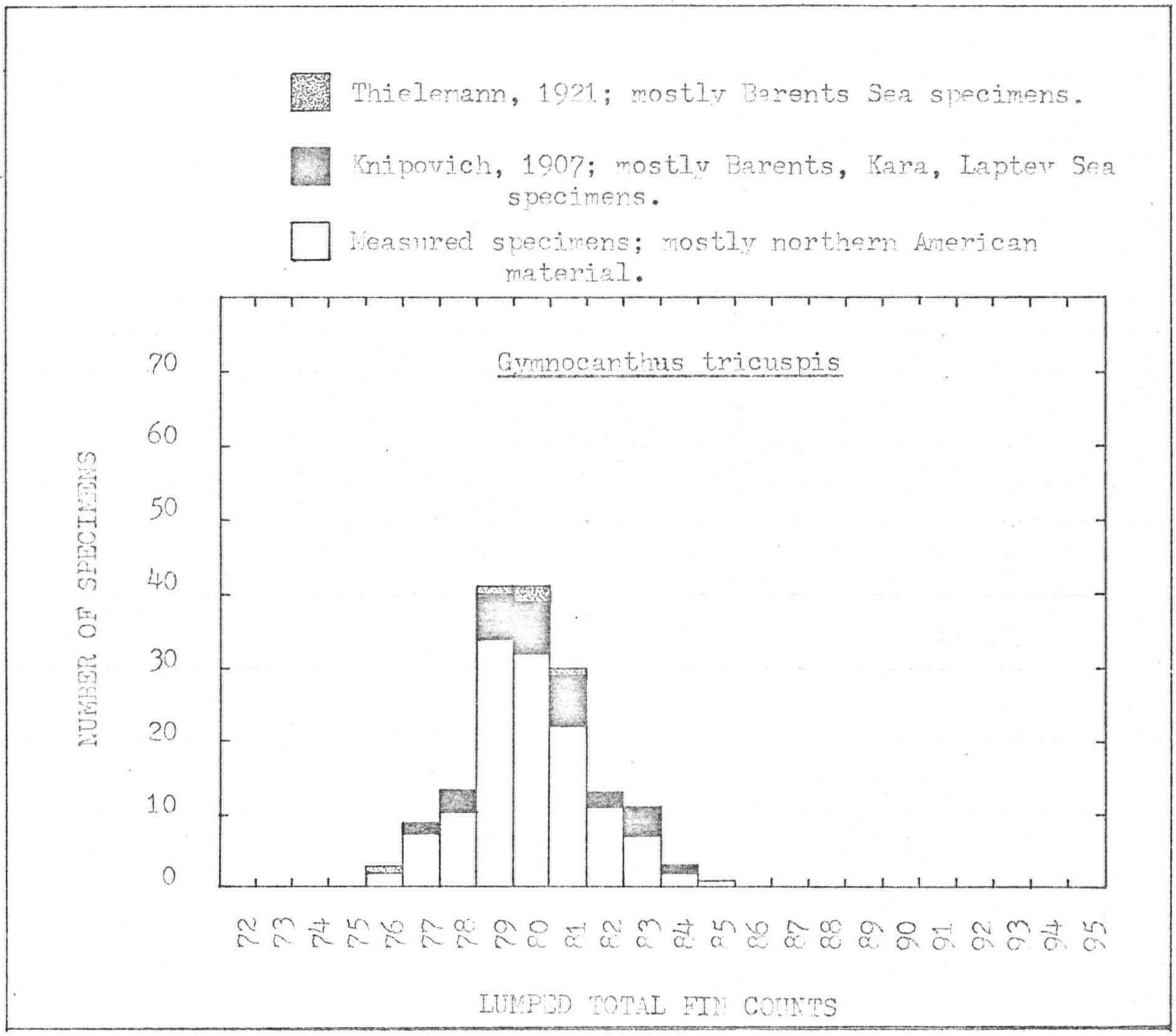
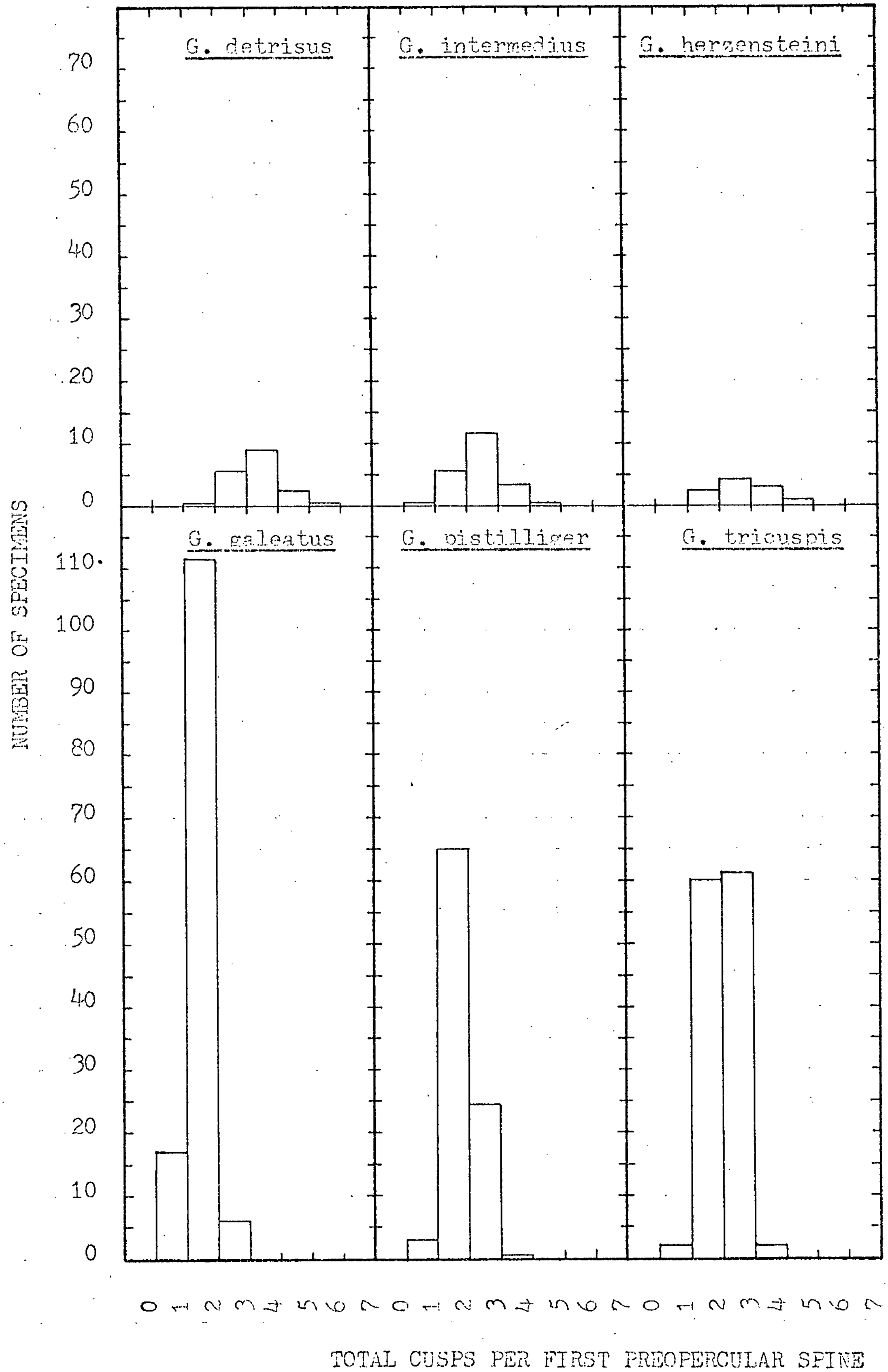


Figure 33. Distribution of cusp counts.



Morphometric Variation

In the genus *Gymnocanthus* morphometric differences while evident are usually slight. These characters are often variable within a species and may grow allometrically, making their taxonomic utilization unwise without allowing for the variation or allometry. Figures for interorbital versus head length, first predorsal versus SL, and head length versus SL are presented (figures 28-41). Slopes for the graphs are available from the regression equation given above. A covariance chart (table 1) giving probability of equivalent slopes between each of all six species is given. When values fall below .05, the slopes are considered significantly different.

G. herzensteini and *G. detrisus* have much more broad interorbitals than the other four species, while the interorbital of the latter is still significantly wider than that of the former. Reduced reliance should be placed on the slope for *G. tricuspis*. Eastern Canadian specimens of which I was able to examine relatively few tend to have broader interorbitals than the Arctic or northern Bering Sea specimens which formed the bulk of the points. One feature which is apparent in all six regression lines is that all cross the x-axis at a positive x value, suggesting that the interorbital characteristically grows allometrically in young fish. The data points suggest linear growth in older fish, but are not adequate to show any inflection point.

G. herzensteini, *G. detrisus*, and *G. intermedius* all tend to have elongate heads (table 2, figures 40-45) which in at least *G. herzensteini* is due to the elongate snout (table 4). *G. tricuspis* possesses a much shortened head.

The spinous predorsal length is a function of relative spinous dorsal origin, snout, and head length. Table 3 shows that the measurement is often significantly different between species. Though it was shown that the spinous dorsal originates further forward relative to the pectoral base in *G. pistilliger* and *G. herzensteini* than in other species, the predorsal distance is least for *G. tricuspis*, probably due to its abbreviated head. For neither head nor predorsal length does the regression line give any clear, consistant indication of allometric growth.

Sexually dimorphic characters examined (spinous dorsal, soft dorsal, pectoral, pelvic fin length) are plotted against SL. Both axes are logarithmically transformed to reduce the effect of allometry. Regression equations (for log transformed data) are given separately for males and females. X's are used for female data points, O's for male data points.

Covariance tables 5 - 8 indicate that few statistically significant differences exist between males of the various species with respect to their sexually dimorphic characters. Significance is reduced by the large variability in fin lengths and by the low numbers of males available, especially of *G. herzensteini*, *G. intermedius*, and *G. detrisus*. Proportional ranges and means of fin lengths are presented in figures 58, 59, and 60. These show clearly that the range of values is broad and overlapping.

Figures 61-79 show sexual dimorphism within each species. One trend apparent for the pelvic fin length is that for *G. intermedius*, *G. tricuspis*, and *G. pistilliger* the regression lines cross at very small SL, suggesting that dimorphism tends to develop at a smaller size in these species.

Although in no species is the pectoral length significantly sexually dimorphic the data for G. intermedius (figure 64) suggest that for this species a slight difference exists which might be significant if more data were available.

One interesting feature is that while G. tricuspis and G. pistilliger may show greater dimorphism between sexes than G. galeatus, these differences in the later species are more statistically significant because of their lower variability.

Table 1.

COVARIANCE MATRIX FOR INTERORBITAL WIDTH VERSUS HEAD LENGTH (Males and Females)

	G	P	T	D	I	H
G	XXX	XXX	XXX	XXX	XXX	XXX
P	0.7478	XXX	XXX	XXX	XXX	XXX
T	0.5863	0.8952	XXX	XXX	XXX	XXX
D	0.0000	0.0000	0.0000	XXX	XXX	XXX
I	0.1248	0.1303	0.0436	0.0000	XXX	XXX
H	0.0000	0.0000	0.0000	0.0000	0.0009	XXX

A 1. INDICATES INSUFFICIENT DATA. TRIPLE X REFERS TO IRRELEVANT VALUES SUCH AS A VALUE TO BE FOUND ELSEWHERE IN THE TABLE OR COVARIANCES OF A SPECIES VERSUS ITSELF. FRACTIONS OF LESS THAN 1. INDICATE LEVELS OF CONFIDENCE. .05 IS USUALLY TAKEN TO BE SIGNIFICANT. ABBREVIATIONS ARE G = G. GALEATUS, P = G. PISTILLIGER, T = G. TRICUSPIS, D = G. DETRISUS, I = G. INTERMEDIUS, H = G. HERZENSTEINI.

Figure 34. Interorbital versus head length.

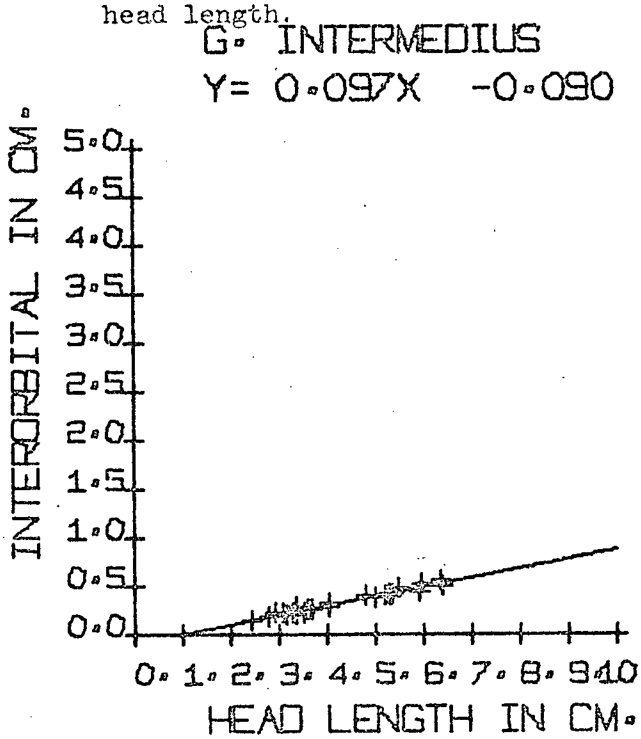


Figure 35. Interorbital versus head length.

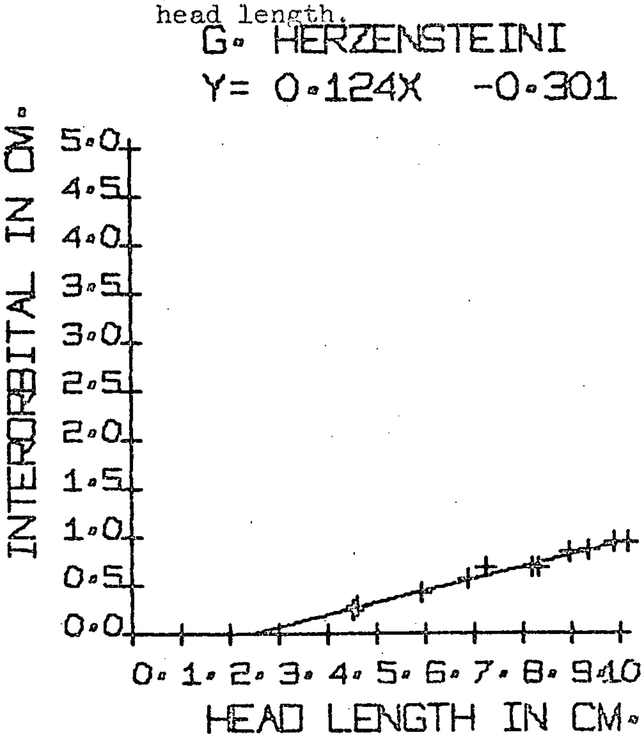


Figure 36. Interorbital versus head length.

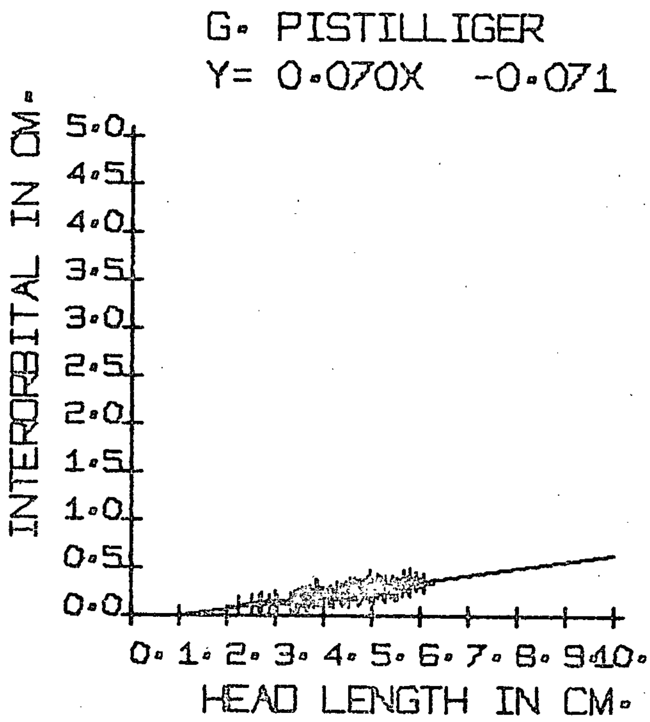


Figure 37. Interorbital versus head length.

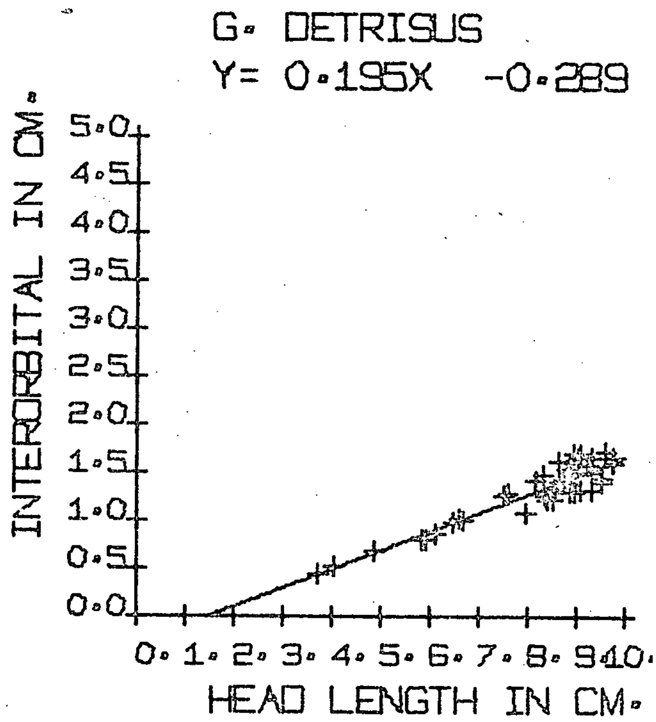


Figure 38. Interorbital versus head length.

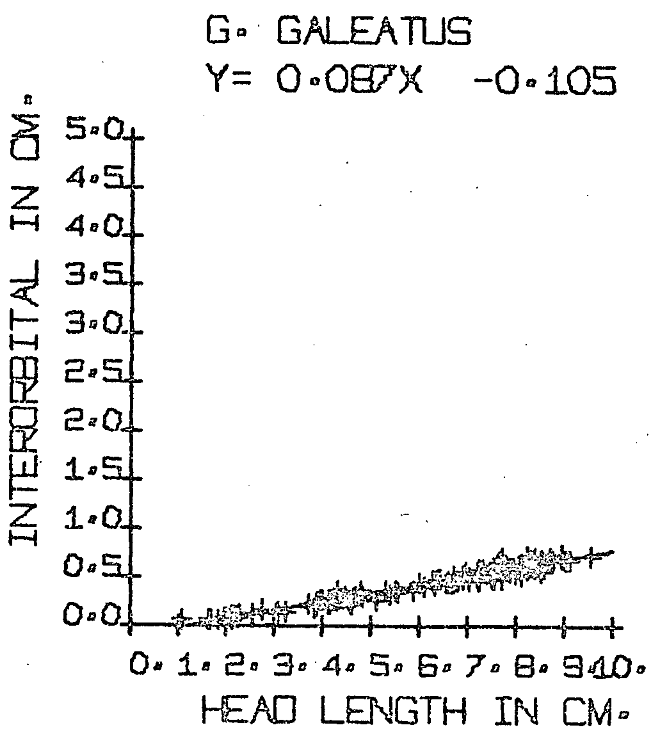


Figure 39. Interorbital versus head length.

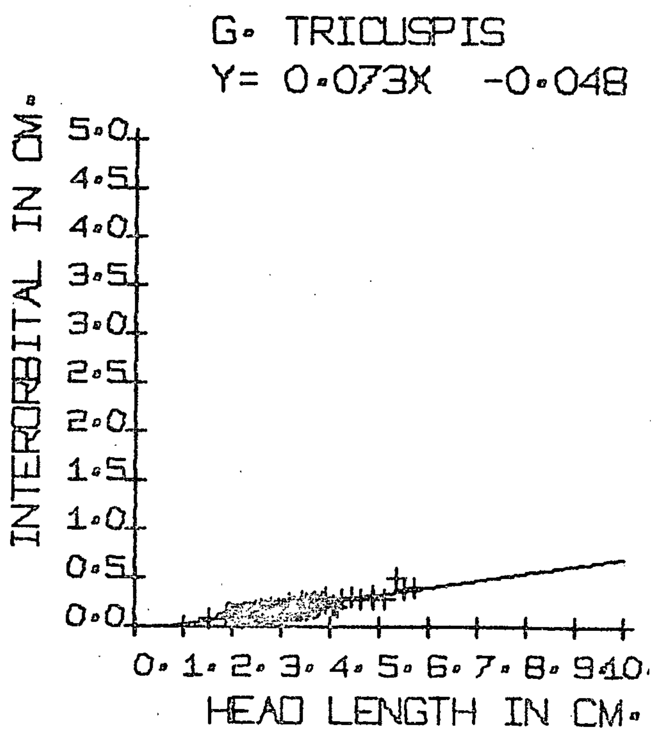


Table 2, 3.

COVARIANCE MATRIX FOR HEAD VERSUS STANDARD LENGTH
(Males and Females)

	G	P	T	D	I	H
G	XXX	XXX	XXX	XXX	XXX	XXX
P	0.1992	XXX	XXX	XXX	XXX	XXX
T	0.0004	0.0000	XXX	XXX	XXX	XXX
D	0.0000	0.0003	0.0000	XXX	XXX	XXX
I	0.0003	0.0008	0.0000	0.8066	XXX	XXX
H	0.0000	0.0000	0.0000	0.6058	0.7945	XXX

COVARIANCE MATRIX FOR FIRST PREDORSAL VERSUS STANDARD LENGTH
(Males and Females)

	G	P	T	D	I	H
G	XXX	XXX	XXX	XXX	XXX	XXX
P	0.0100	XXX	XXX	XXX	XXX	XXX
T	0.2506	0.0007	XXX	XXX	XXX	XXX
D	0.0000	0.0004	0.0000	XXX	XXX	XXX
I	0.0000	0.0009	0.0000	0.6637	XXX	XXX
H	0.0034	0.1295	0.0000	0.3366	0.1512	XXX

A 1. INDICATES INSUFFICIENT DATA. TRIPLE X REFERS TO IRRELEVANT VALUES SUCH AS A VALUE TO BE FOUND ELSEWHERE IN THE TABLE OR COVARIANCES OF A SPECIES VERSUS ITSELF. FRACTIONS OF LESS THAN 1. INDICATE LEVELS OF CONFIDENCE. .05 IS USUALLY TAKEN TO BE SIGNIFICANT. ABBREVIATIONS ARE G = G. GALEATUS, P = G. PISTILLIGER, T = G. TRICUSPIS, D = G. DETRISUS, I = G. INTERMEDIUS, H = G. HERZENSTEINI.

Figure 40.

Head length versus standard length.

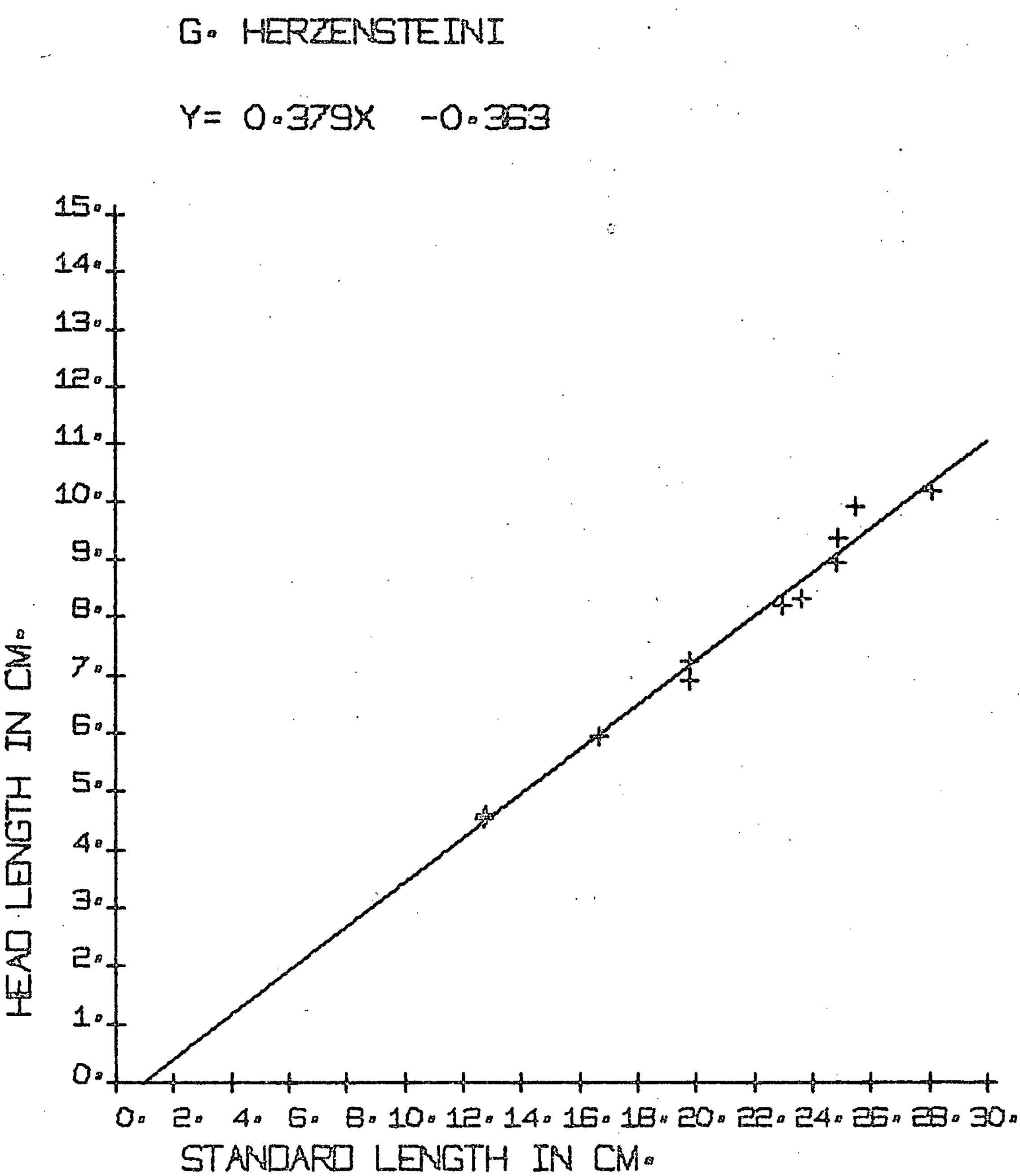


Figure 41.
Head length versus standard length.

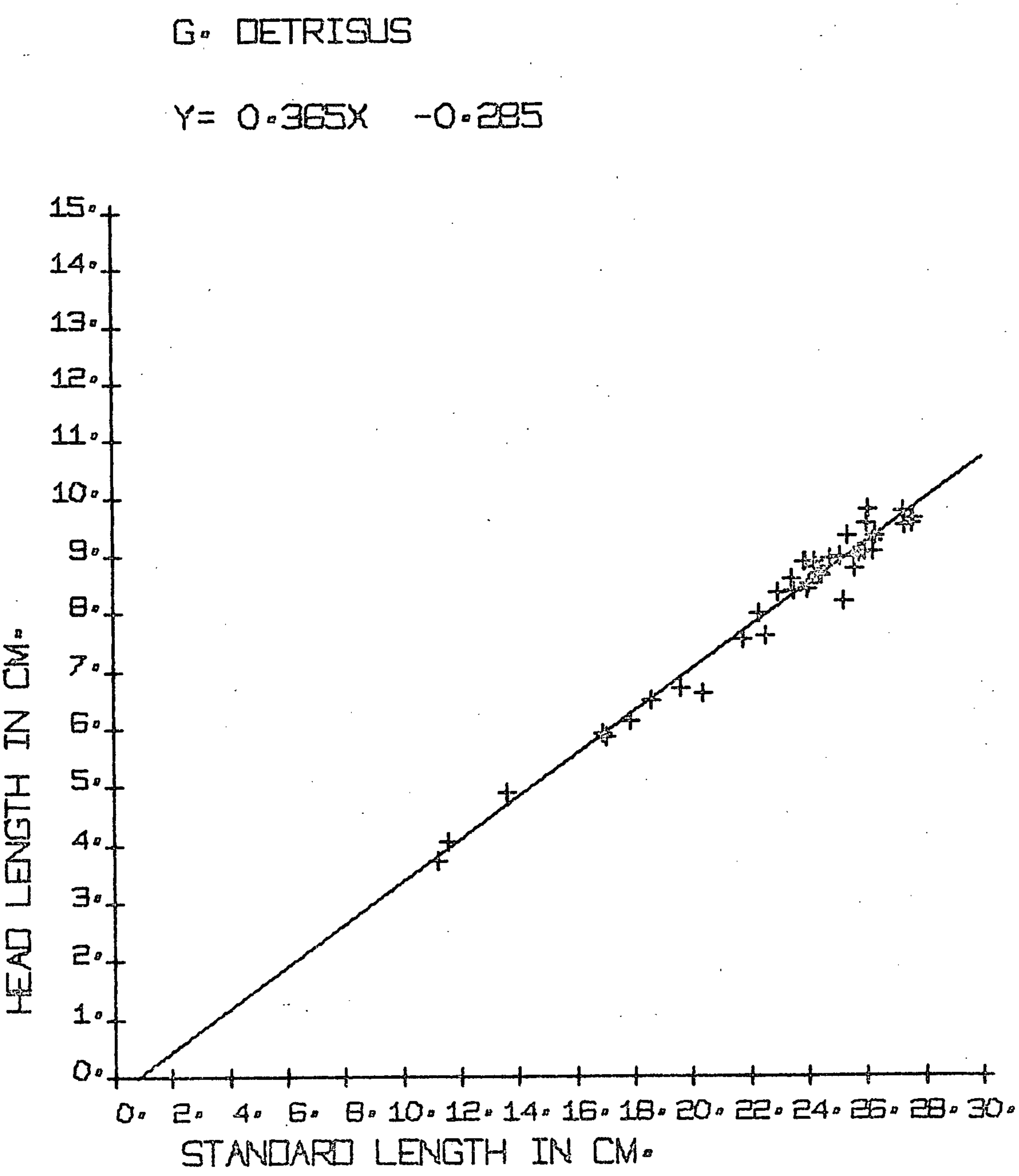


Figure 42.

Head length versus standard length.

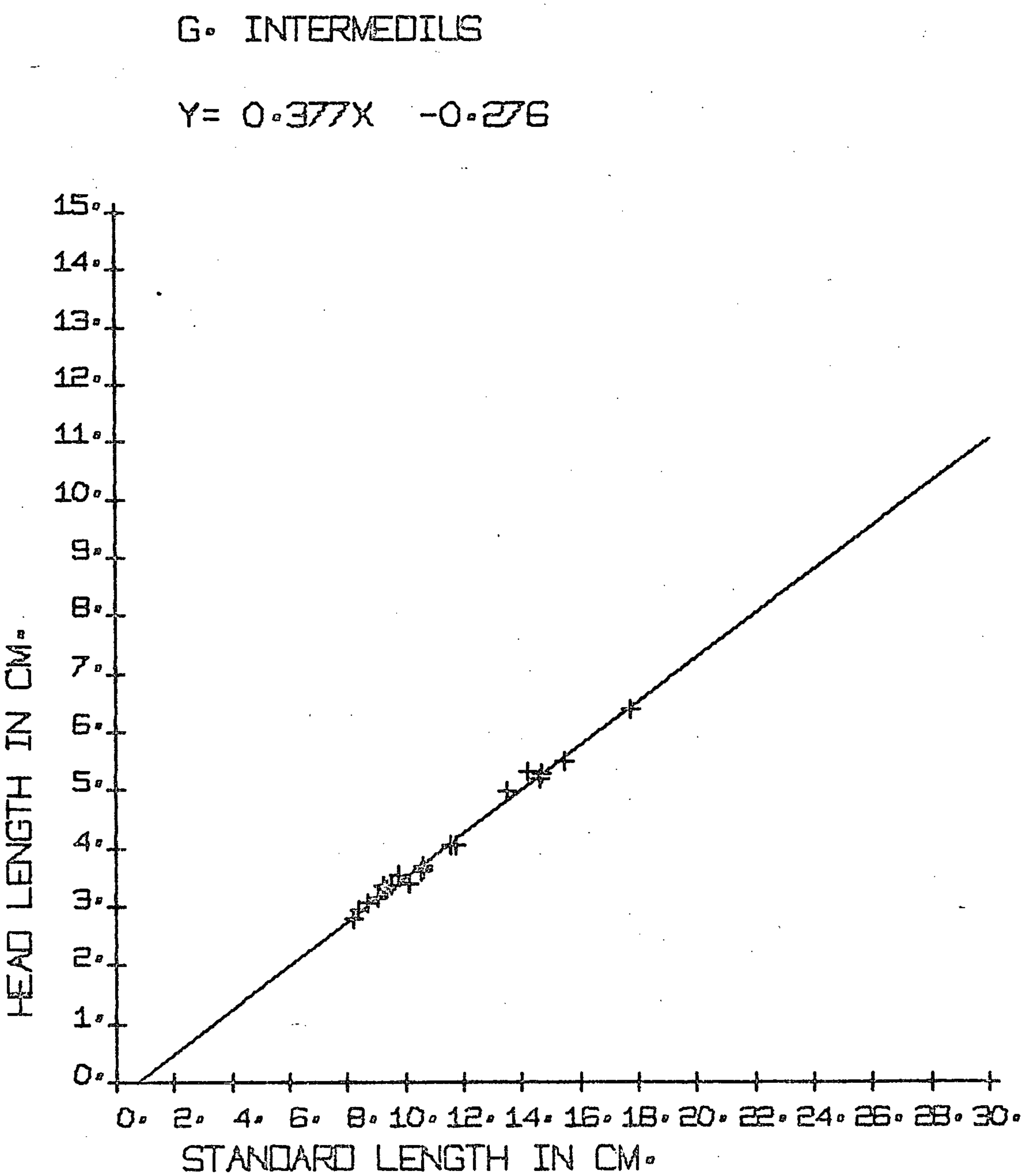


Figure 43.

Head length versus standard length.

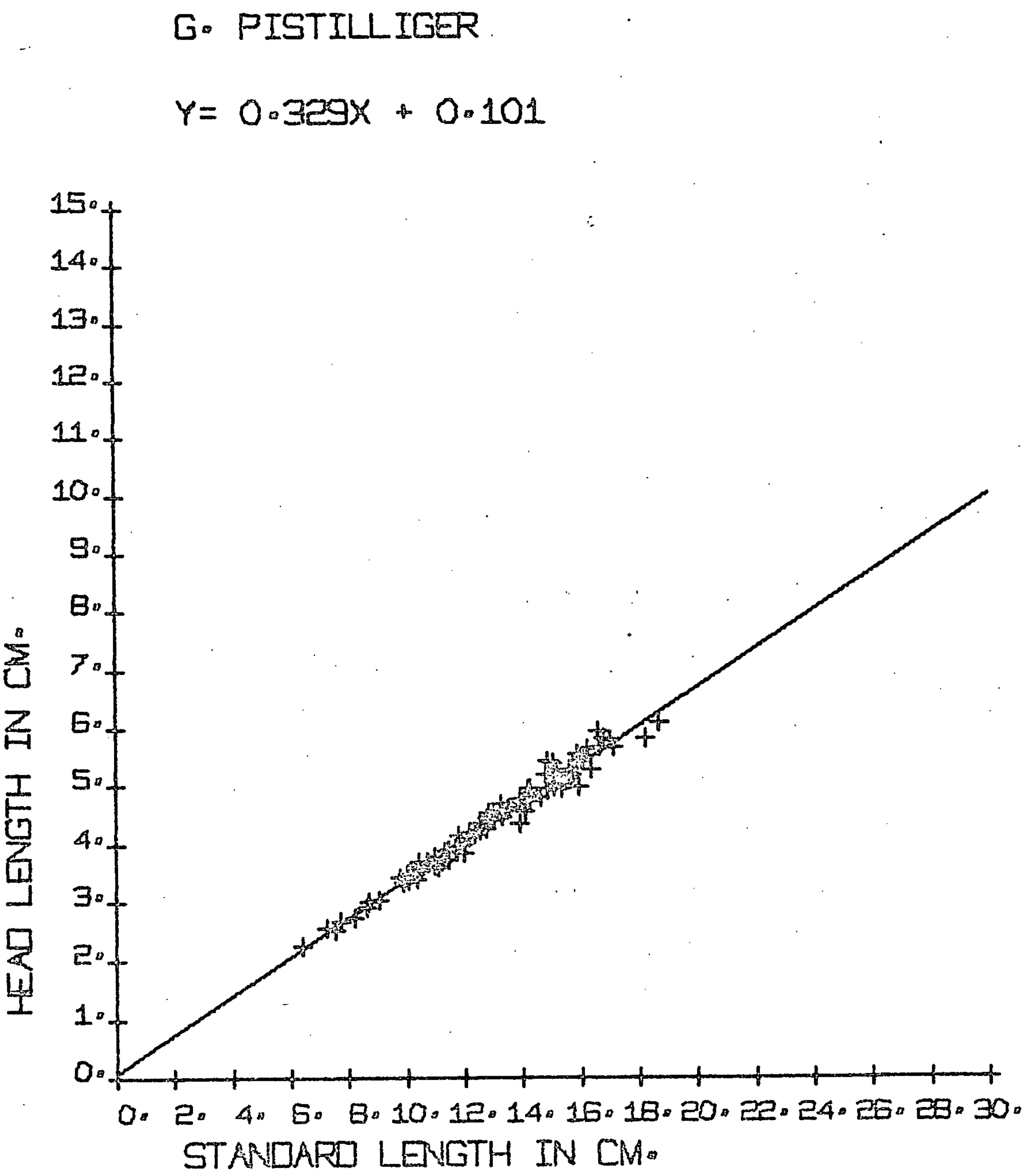


Figure 44.

Head length versus standard length.

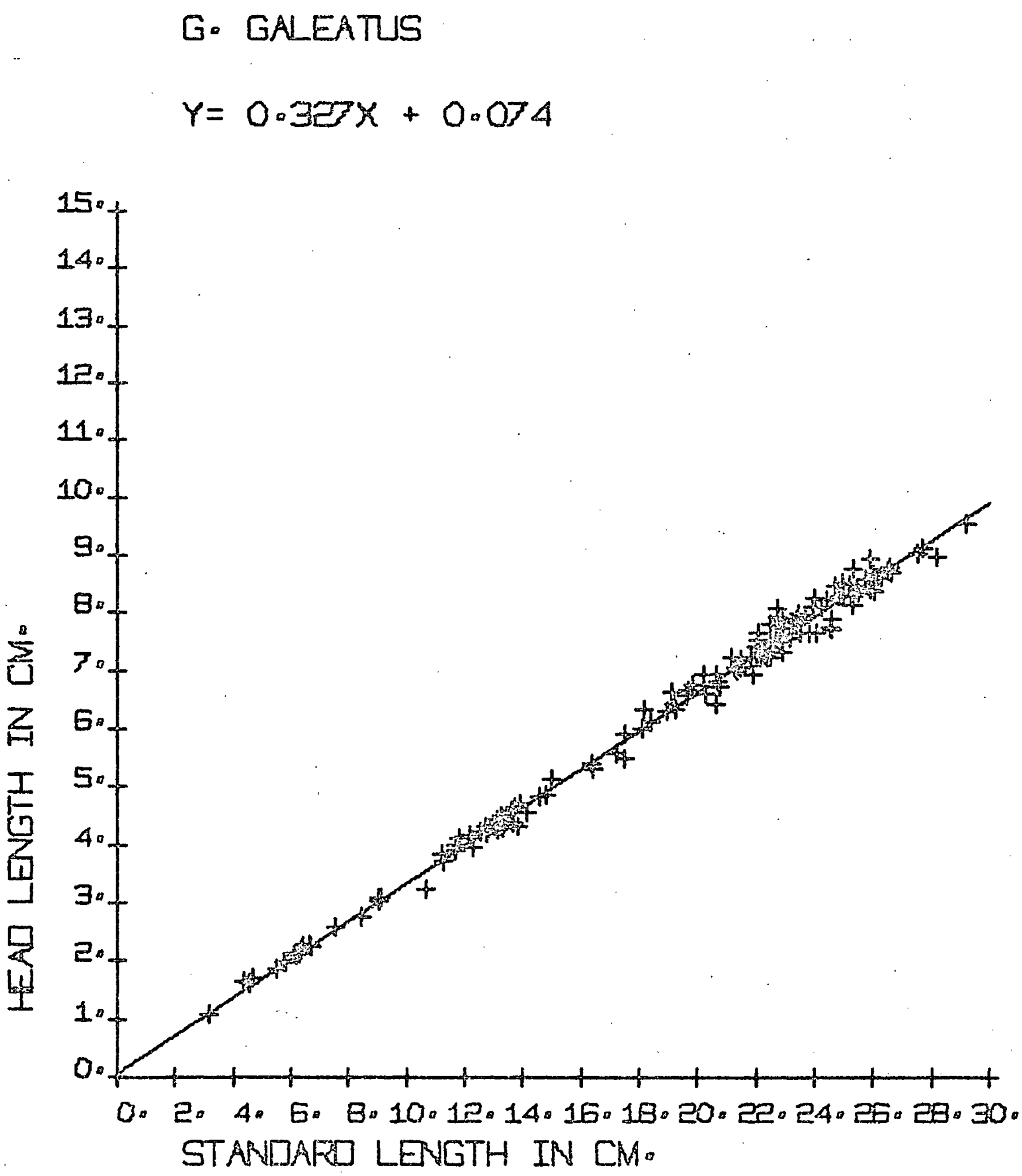


Figure 45.

Head length versus standard length.

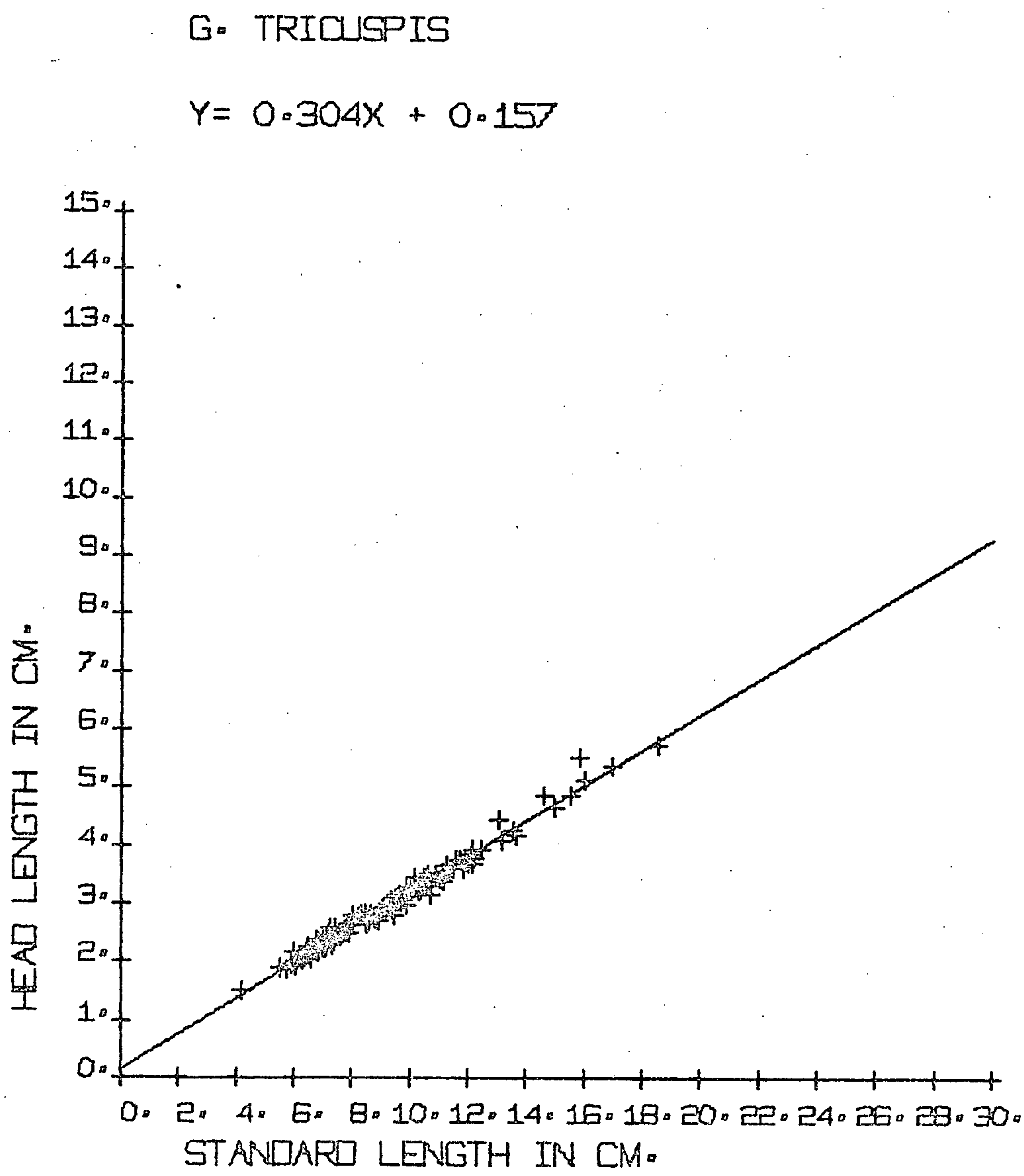


Figure 46.

Predorsal length versus standard length.

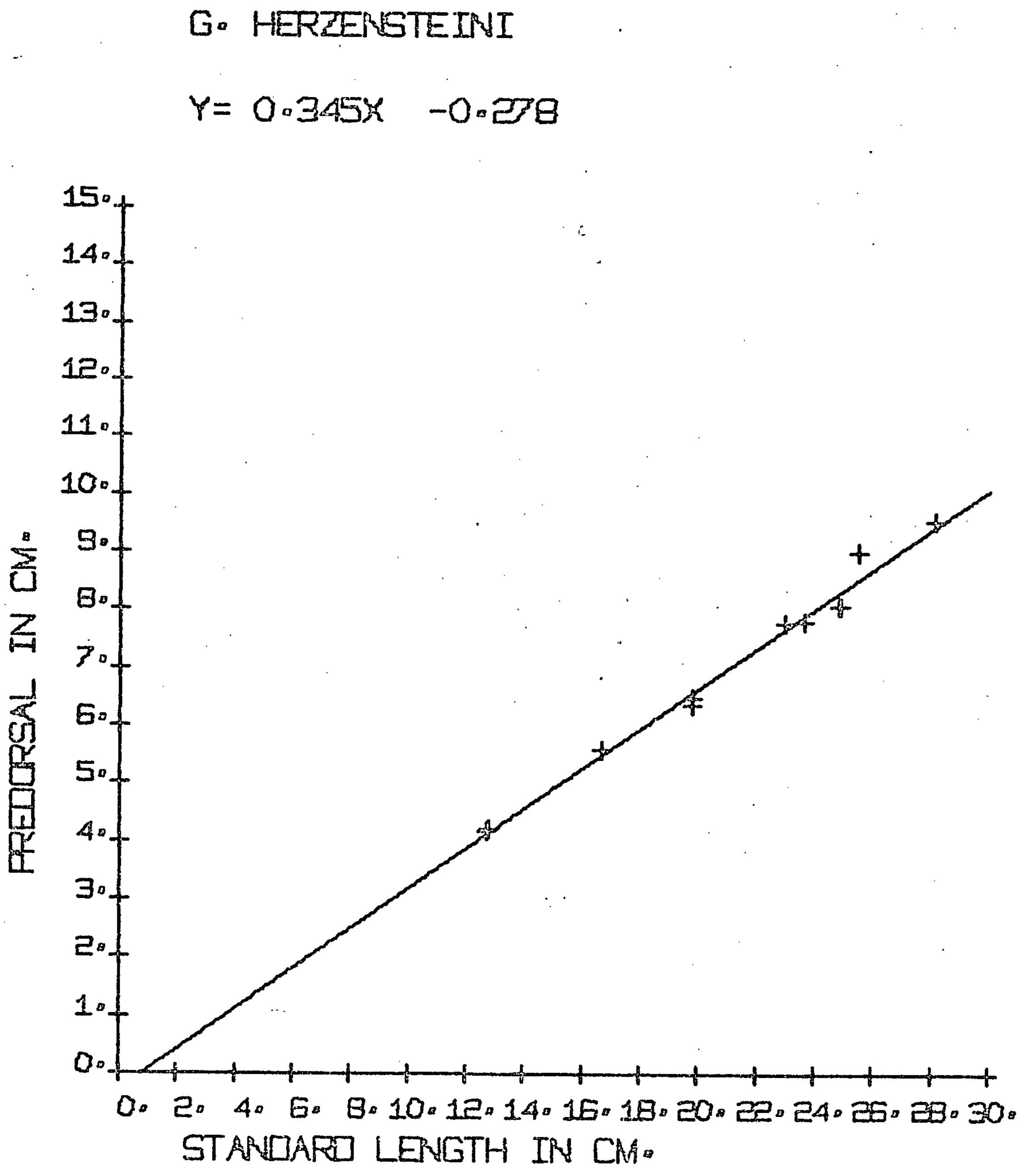


Figure 47.

Predorsal length versus standard length.

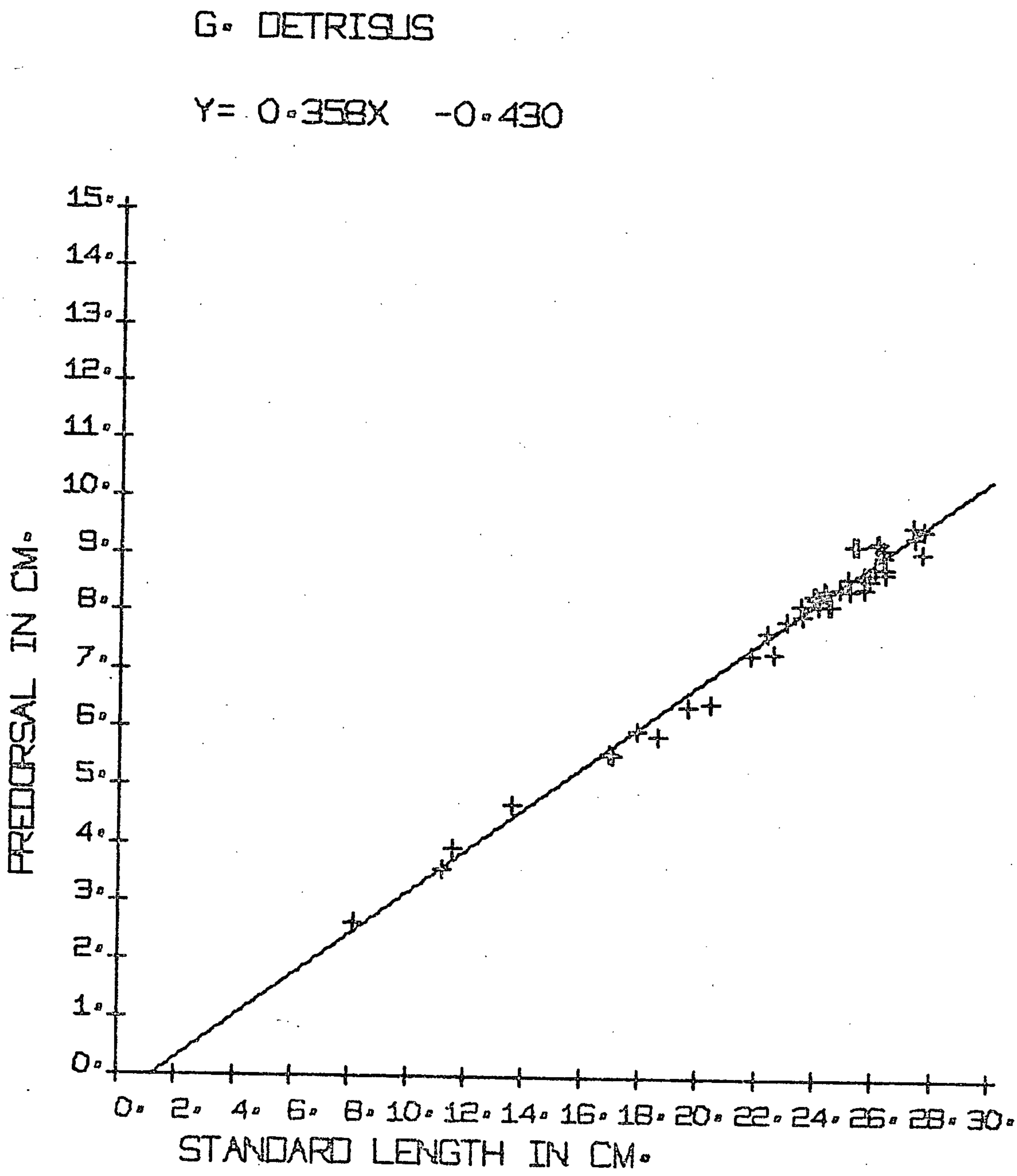


Figure 48

Predorsal length versus standard length.

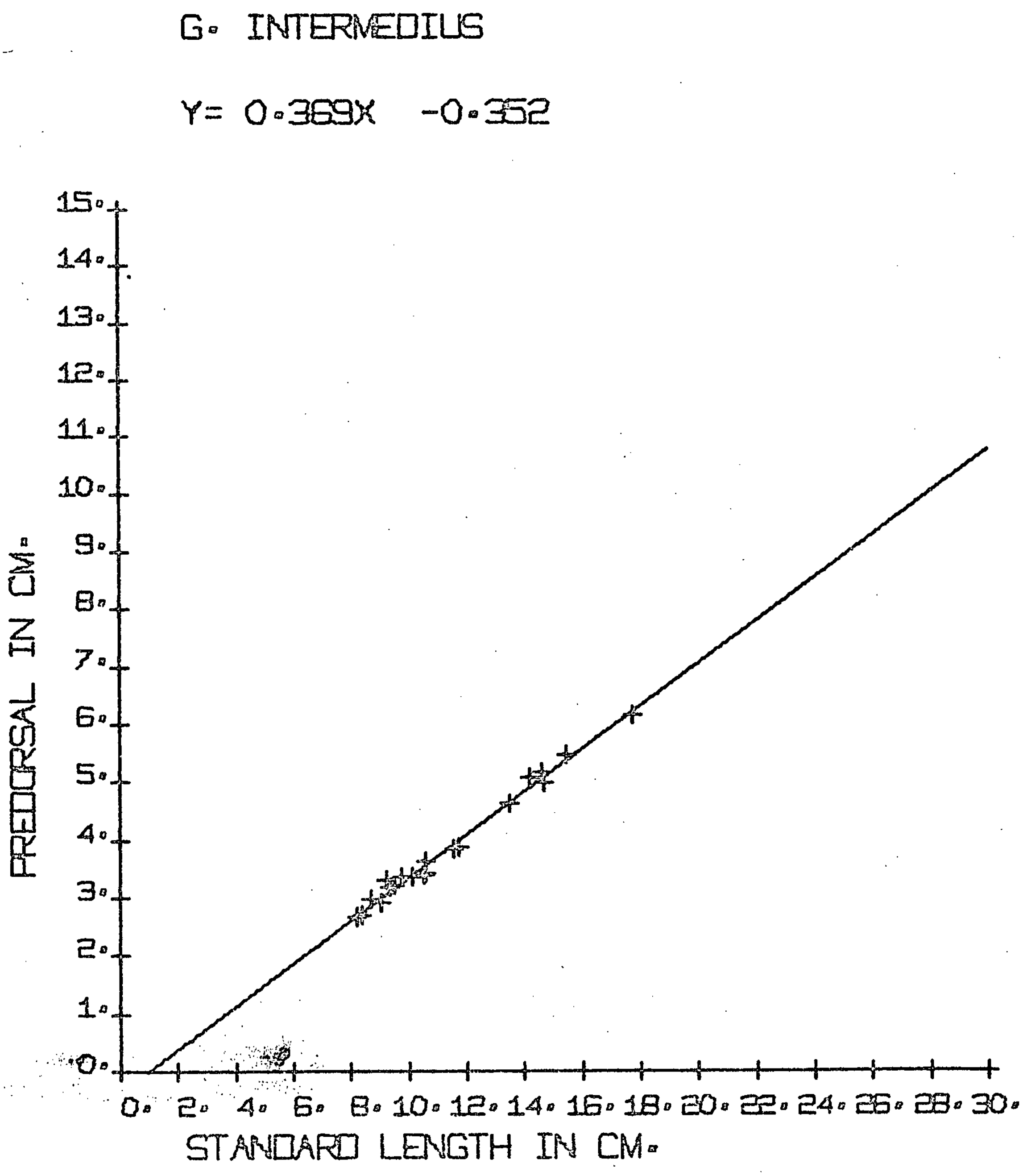


Figure 49.

Predorsal length versus standard length.

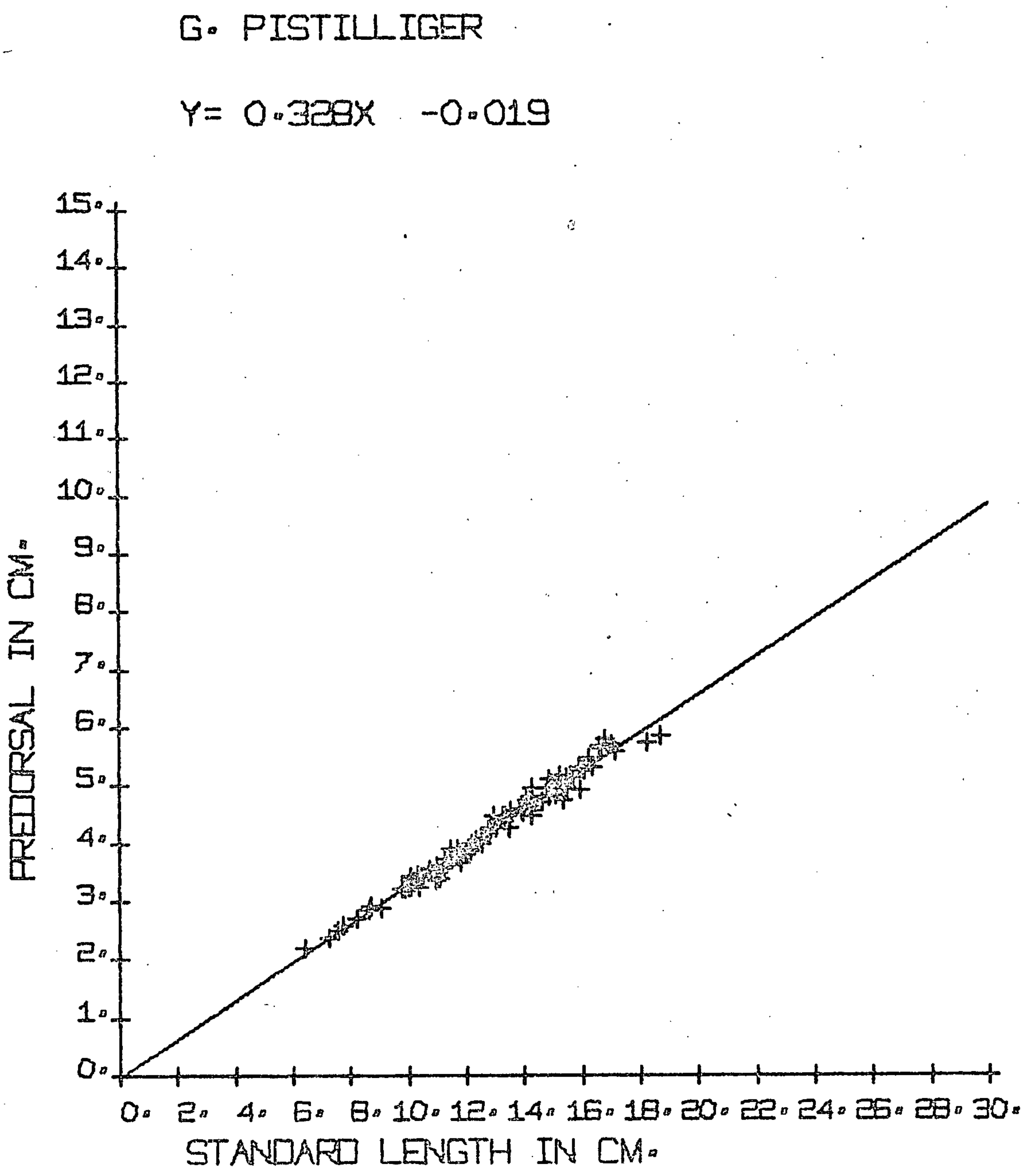


Figure 50.

Predorsal length versus standard length.

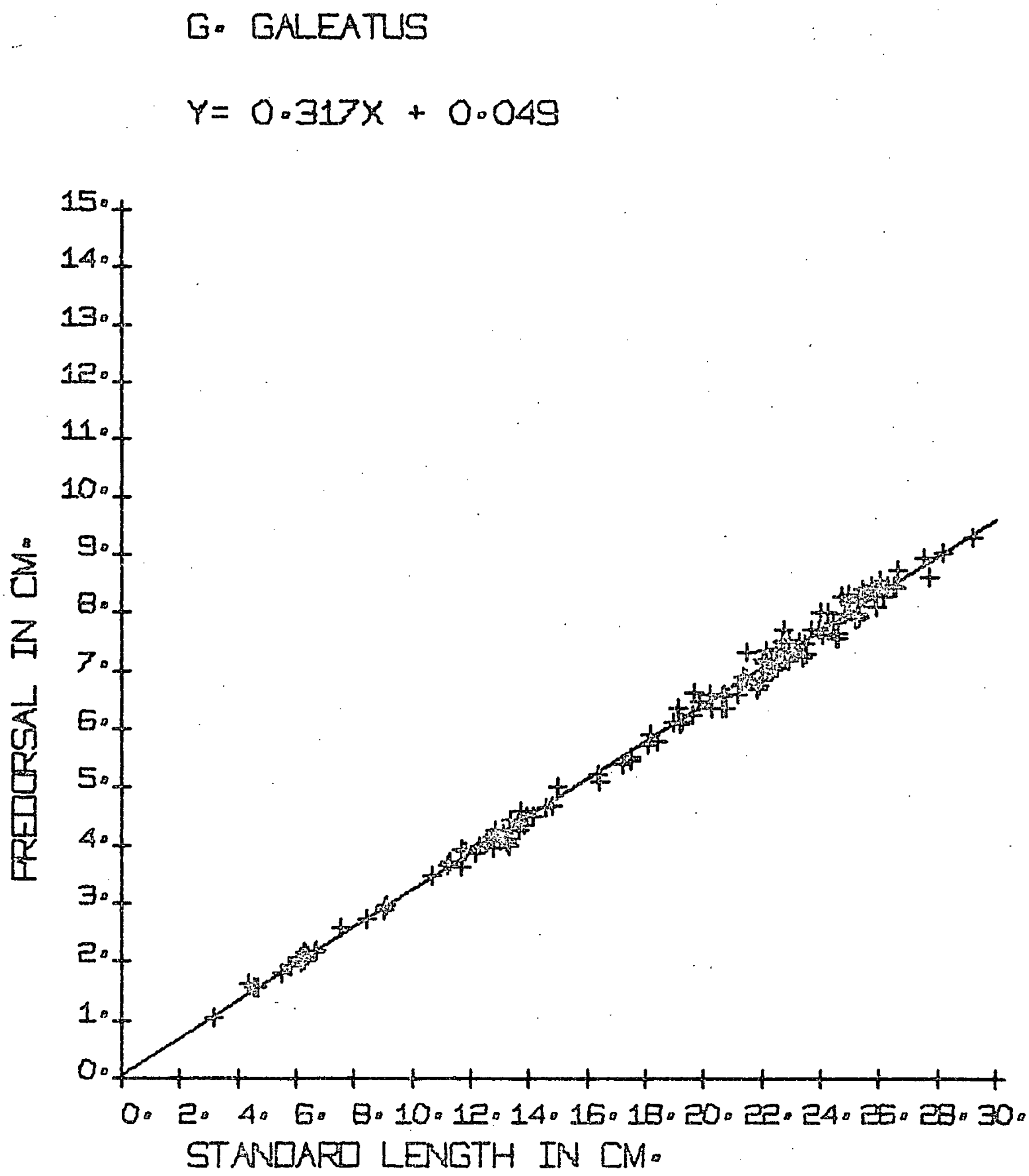


Figure 51.
Predorsal length verus standard length.

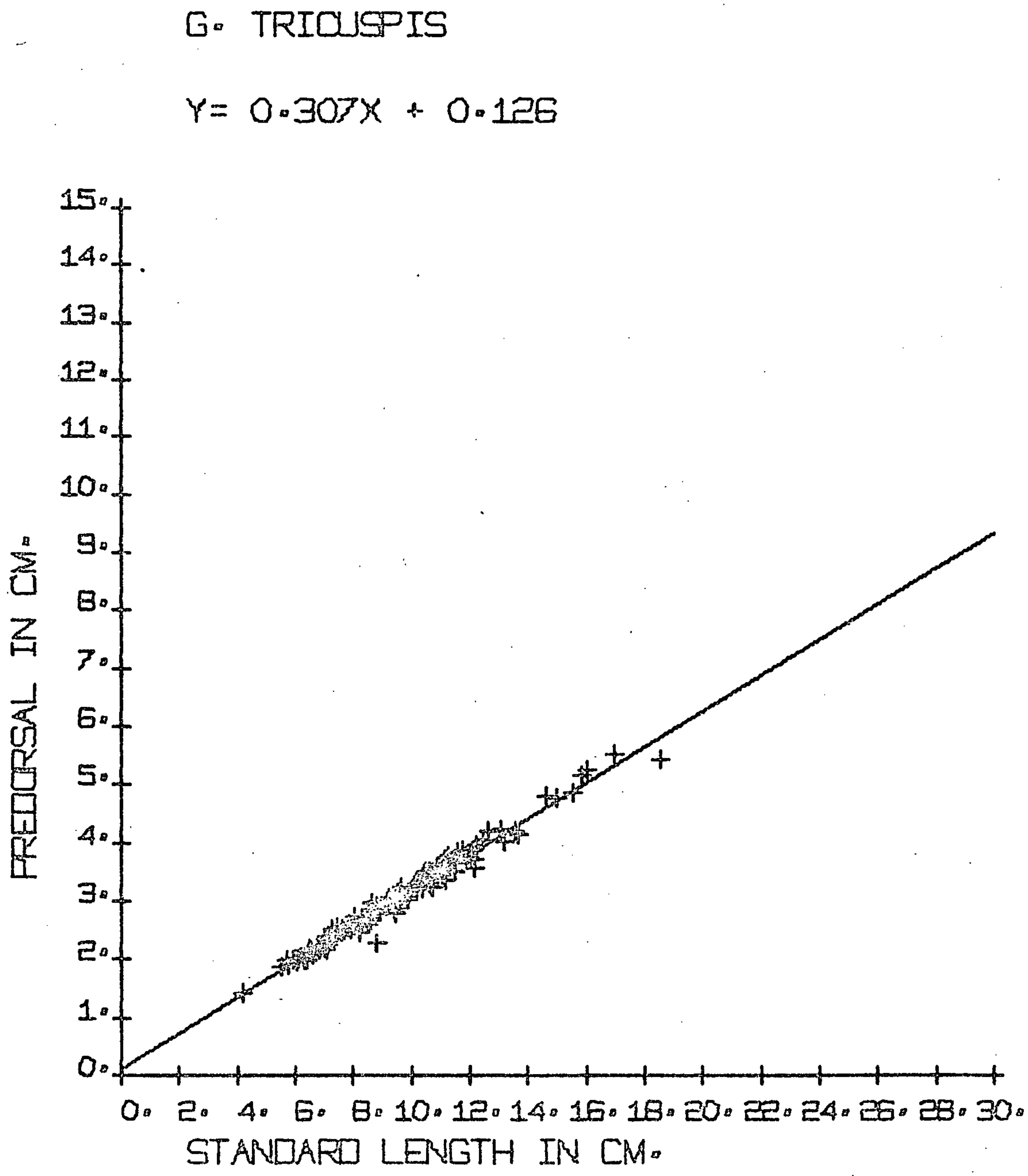


Table 4.

COVARIANCE MATRIX FOR SNOUT VERSUS HEAD LENGTH

	G	P	T	D	I	H
G	XXX	XXX	XXX	XXX	XXX	XXX
P	0.4603	XXX	XXX	XXX	XXX	XXX
T	0.4912	0.8725	XXX	XXX	XXX	XXX
D	0.1905	0.6190	0.4491	XXX	XXX	XXX
I	0.7887	0.7533	0.8087	0.5215	XXX	XXX
H	0.0377	0.0052	0.0006	0.0149	0.0197	XXX

A 1. INDICATES INSUFFICIENT DATA. TRIPLE X REFERS TO IRRELEVANT VALUES SUCH AS A VALUE TO BE FOUND ELSEWHERE IN THE TABLE OR COVARIANCES OF A SPECIES VERSUS ITSELF. FRACTIONS OF LESS THAN 1. INDICATE LEVELS OF CONFIDENCE. .05 IS USUALLY TAKEN TO BE SIGNIFICANT. ABBREVIATIONS ARE G = G. GALEATUS, P = G. PISTILLIGER, T = G. TRICUSPIS, D = G. DETRISUS, I = G. INTERMEDIUS, H = G. HERZENSTEINI.

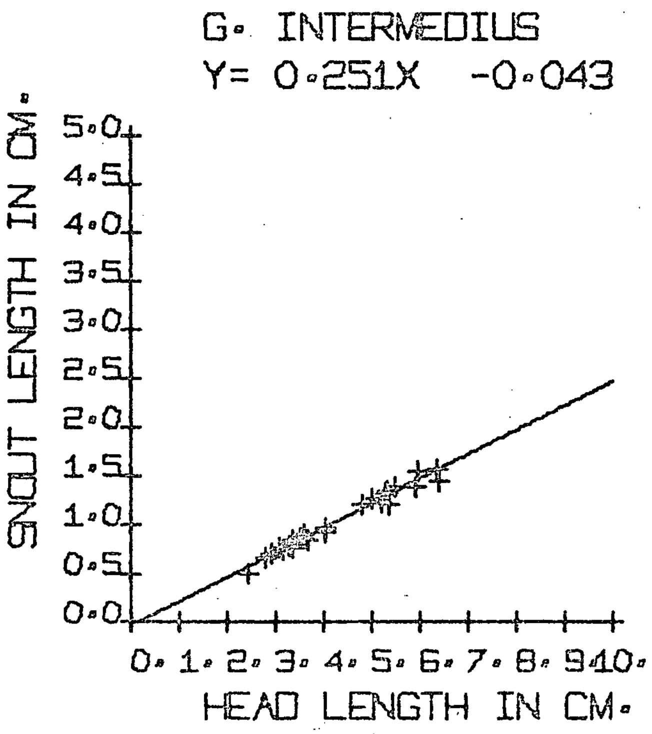


Figure 52. Snout length versus head length.

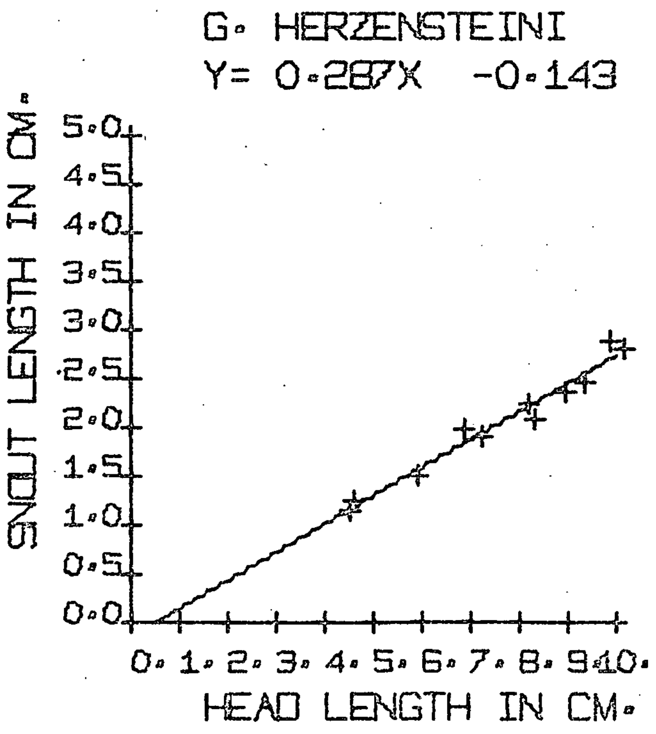


Figure 53. Snout length versus head length.

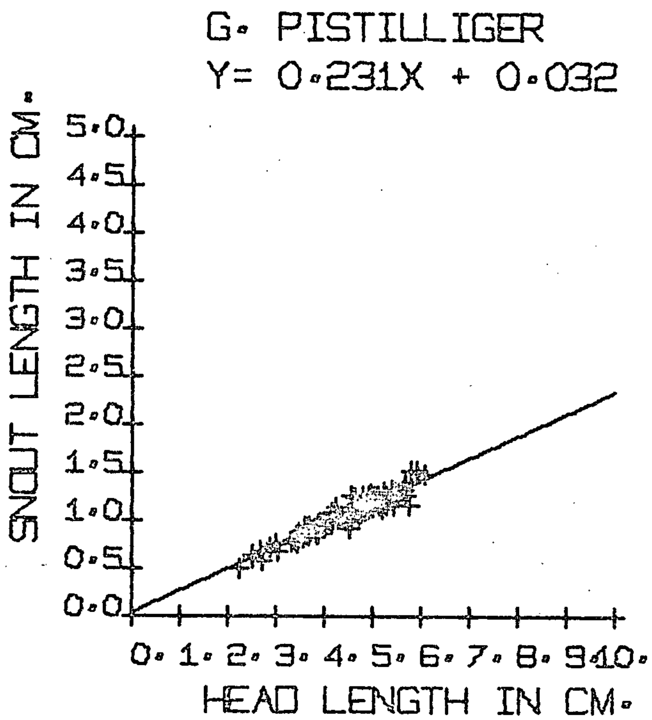


Figure 54. Snout length versus head length.

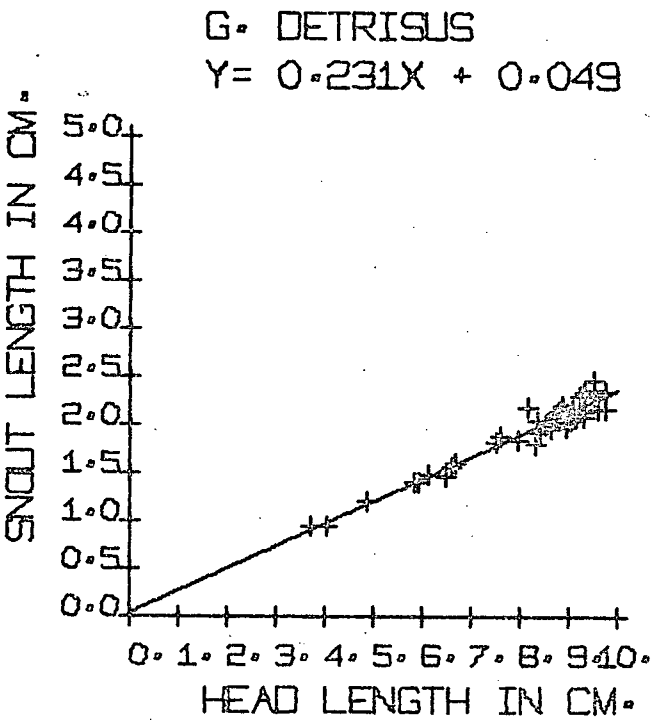


Figure 55. Snout length versus head length.

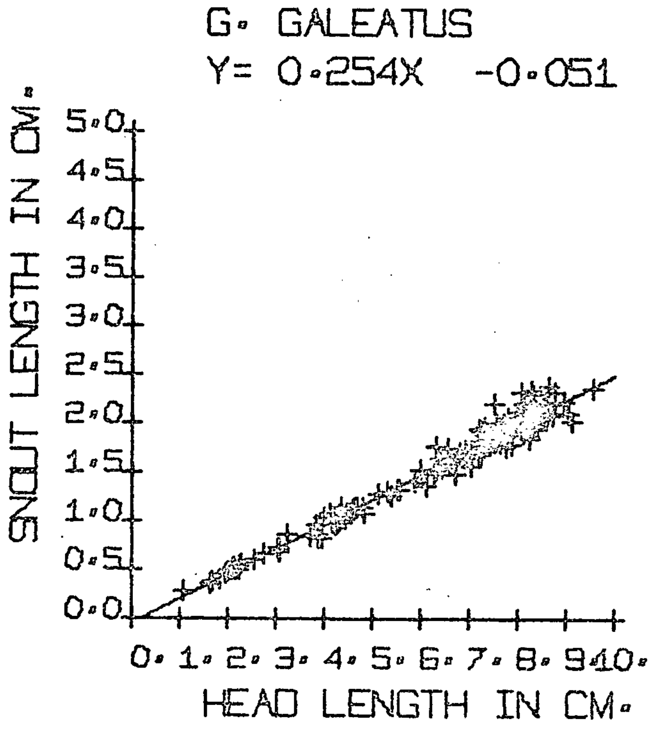


Figure 56. Snout length versus head length.

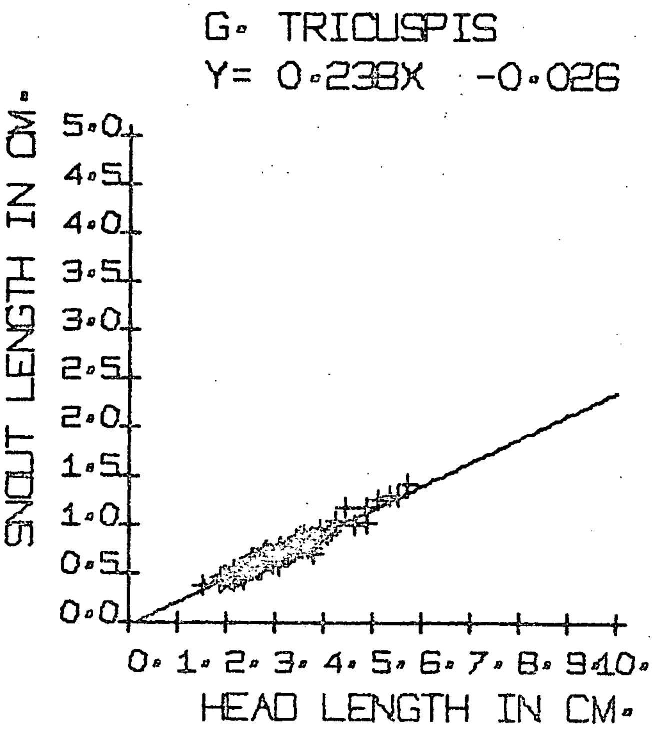


Figure 57. Snout length versus head length.

Tables 5, 6, 7.

PECTORAL FIN LENGTH VERSUS STANDARD LENGTH (Males only; double log transformed.)

	G	P	T	D	I	H
G	XXX	XXX	XXX	XXX	XXX	XXX
P	0.0397	XXX	XXX	XXX	XXX	XXX
T	0.0190	0.9274	XXX	XXX	XXX	XXX
D	0.0523	0.7048	0.5973	XXX	XXX	XXX
I	0.0071	0.2552	0.1402	0.3934	XXX	XXX
H	0.0011	0.0832	0.0258	0.1200	0.3264	XXX

PELVIC FIN LENGTH VERSUS STANDARD LENGTH (Males only; double log transformed.)

	G	P	T	D	I	H
G	XXX	XXX	XXX	XXX	XXX	XXX
P	0.3049	XXX	XXX	XXX	XXX	XXX
T	0.1928	0.1647	XXX	XXX	XXX	XXX
D	0.9265	0.5691	0.5776	XXX	XXX	XXX
I	0.7072	0.8376	0.4527	0.7397	XXX	XXX
H	0.1360	0.6328	0.1686	0.2695	0.2977	XXX

SPINOUS DORSAL HEIGHT VERSUS STANDARD LENGTH (Males only; double log transformed.)

	G	P	T	D	I	H
G	XXX	XXX	XXX	XXX	XXX	XXX
P	0.8984	XXX	XXX	XXX	XXX	XXX
T	0.0290	0.1450	XXX	XXX	XXX	XXX
D	0.0391	0.1369	0.0127	XXX	XXX	XXX
I	0.4878	0.6890	0.4523	0.0135	XXX	XXX
H	0.6761	0.7440	0.2193	0.1771	0.2844	XXX

Table 8.

SOFT DORSAL HEIGHT VERSUS STANDARD LENGTH (Males only; double log transformed)

	G	P	T	D	I	H
G	XXX	XXX	XXX	XXX	XXX	XXX
P	0.0190	XXX	XXX	XXX	XXX	XXX
T	0.0004	0.6256	XXX	XXX	XXX	XXX
D	0.5916	0.3520	0.1519	XXX	XXX	XXX
I	0.0596	0.9036	0.6260	0.3577	XXX	XXX
H	0.4122	0.5756	0.3452	0.8300	0.3621	XXX

Table 9.

COVARIANCE MATRIX BETWEEN MALES AND FEMALES FOR FIVE LOG TRANSFORMED MORPHOMETRIC CHARACTERS IN SIX SPECIES OF GYMNOCANTHUS.

ABBREVIATIONS ARE AS FOLLOWS, 1 = DEPTH AT PECTORAL GIRDLE, 2 = HEIGHT OF SPINOUS DORSAL, 3 = HEIGHT OF SOFT DORSAL, 4 = LENGTH OF PECTORAL FIN, 5 = LENGTH OF PELVIC FIN. A 1. IN THE MATRIX INDICATES INSUFFICIENT DATA.

	G	P	T	D	I	H
1	0.1338	0.6724	0.4211	0.7540	0.6877	0.2675
2	0.0000	0.0006	0.0025	0.3764	0.5945	0.0665
3	0.0000	0.0180	0.0002	0.1801	0.2274	0.0810
4	0.1419	0.5187	0.8778	0.2693	0.4741	0.1848
5	0.0000	0.0002	0.0001	0.0040	0.0109	0.6131

FRACTIONS OF LESS THAN 1. INDICATE LEVELS OF CONFIDENCE. .05 IS USUALLY TAKEN TO BE SIGNIFICANT. ABBREVIATIONS ARE G = G. GALEATUS, P = G. PISTILLIGER, T = G. TRICUSPIS, D = G. DETRISUS, I = G. INTERMEDIUS, H = G. HERZENSTEINI.

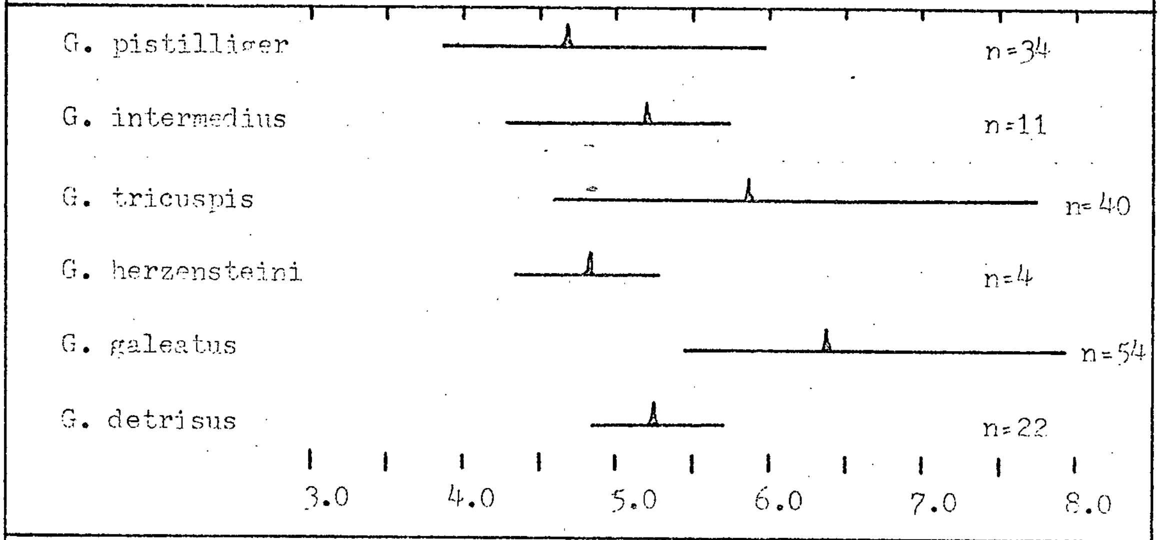


Figure 58. Spinous Dorsal Length / SL. Males only.

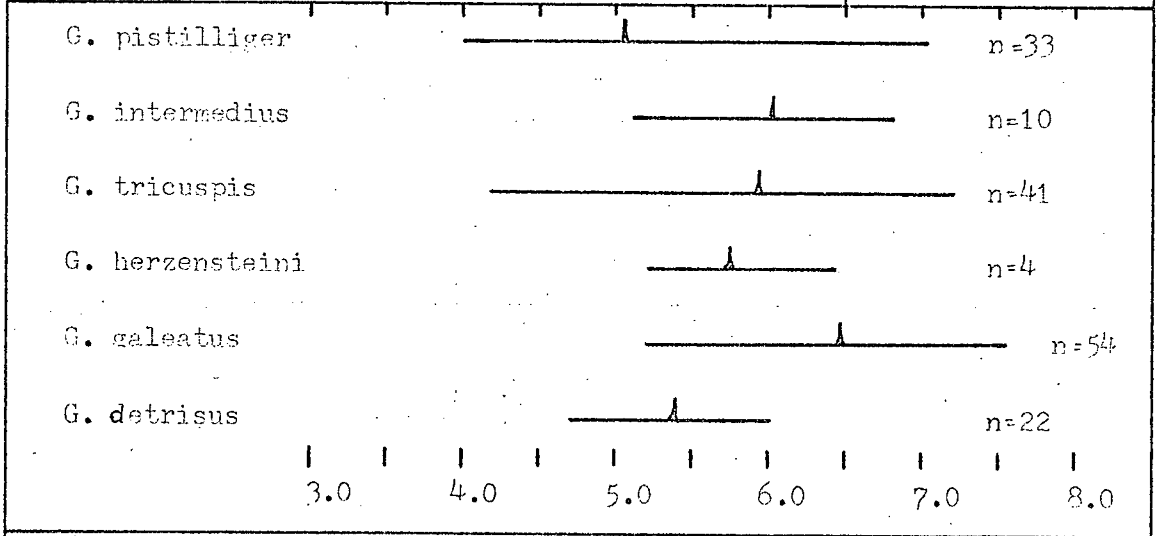


Figure 59. Soft Dorsal Length / SL. Males only.

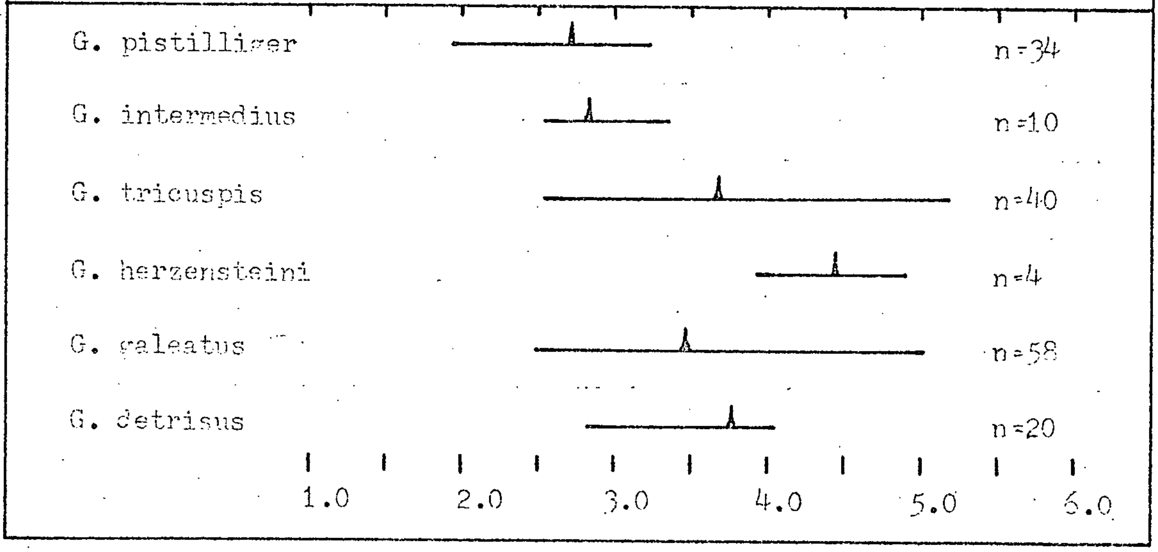


Figure 60. Pelvic Fin Length / SL. Males only.

Figure 61.

Spinous dorsal height versus standard length, males and females.

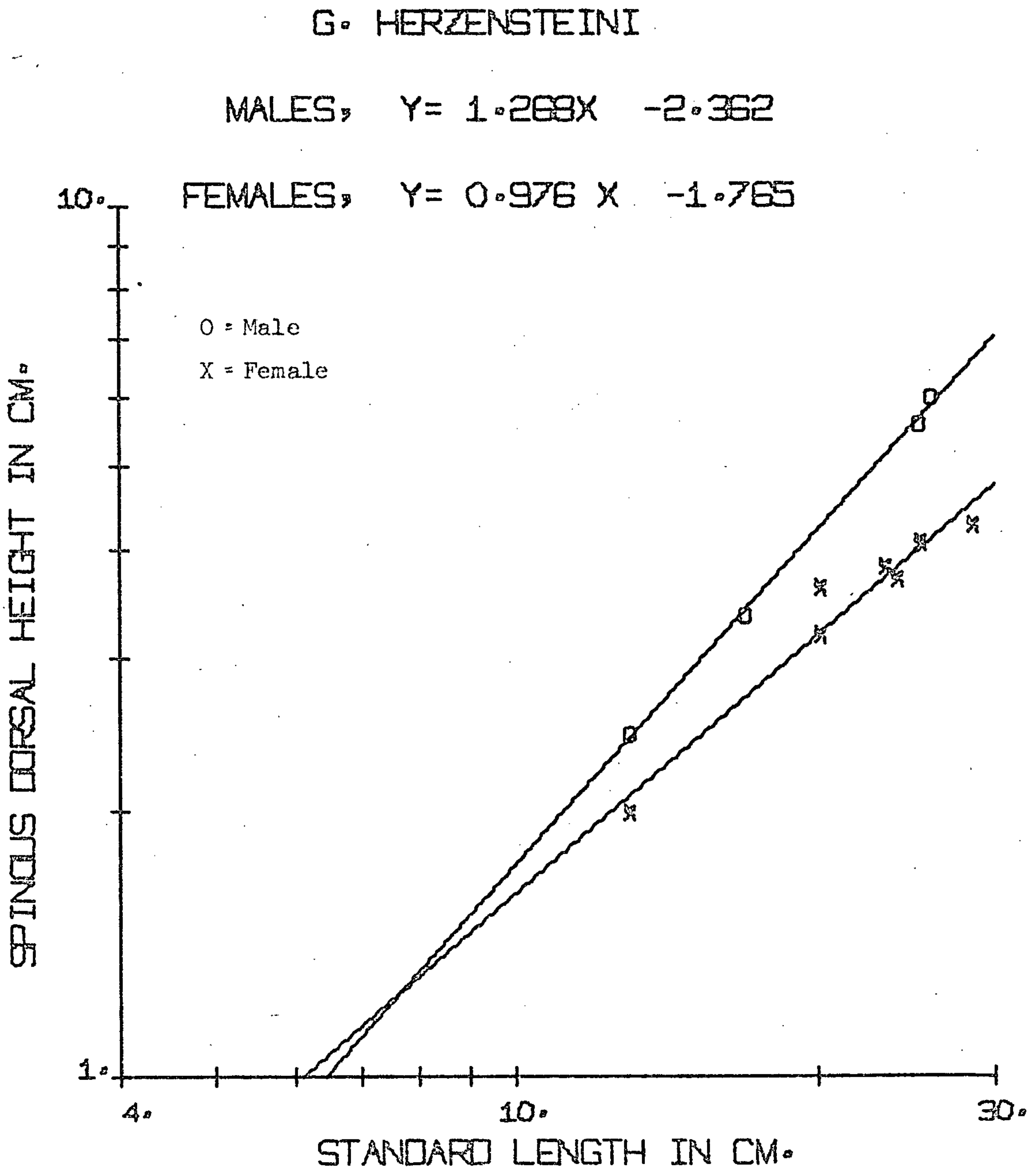


Figure 62.

Spinous dorsal height versus standard length, males and females.

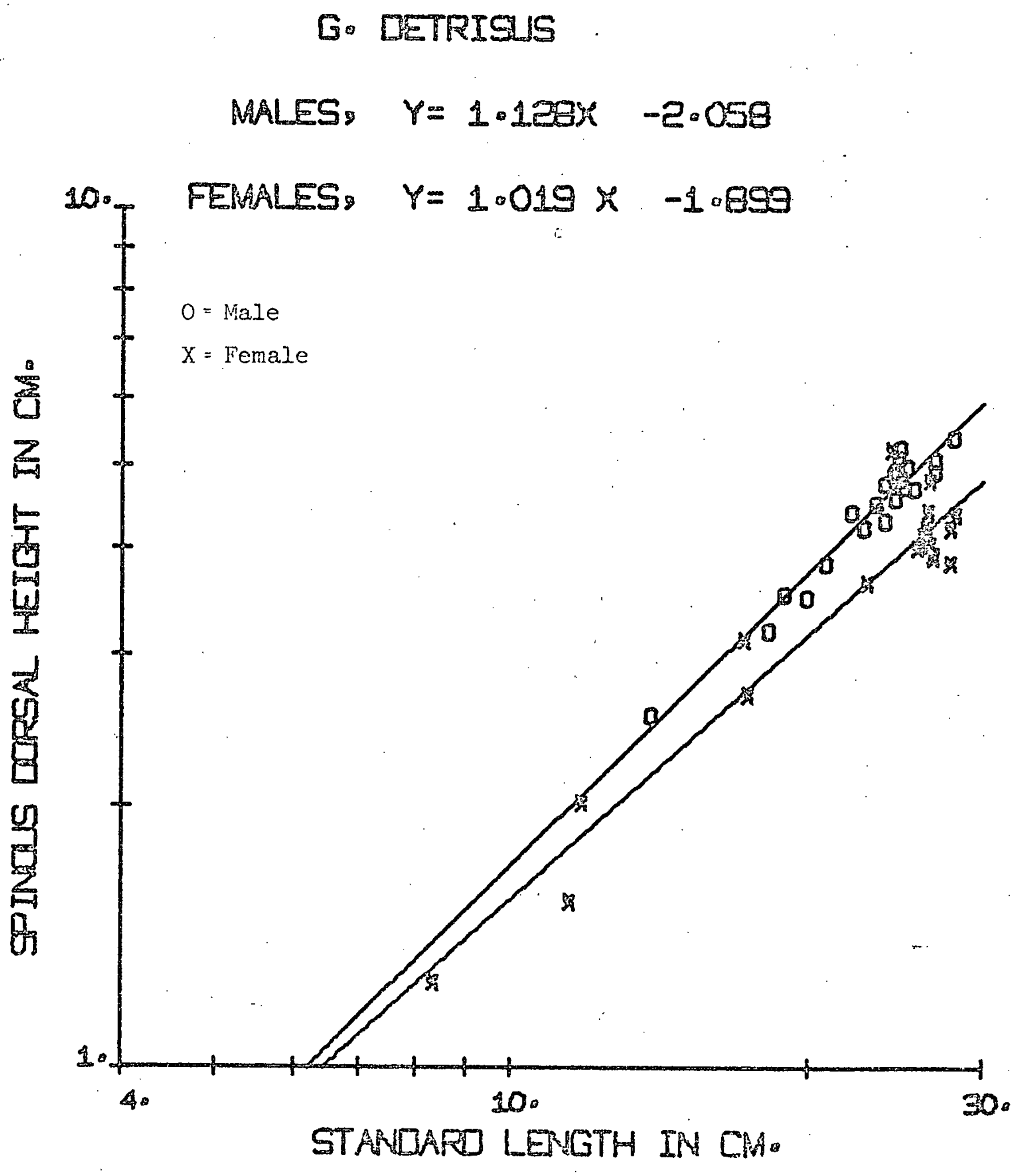


Figure 63.

Spinous dorsal height versus standard length, males and females.

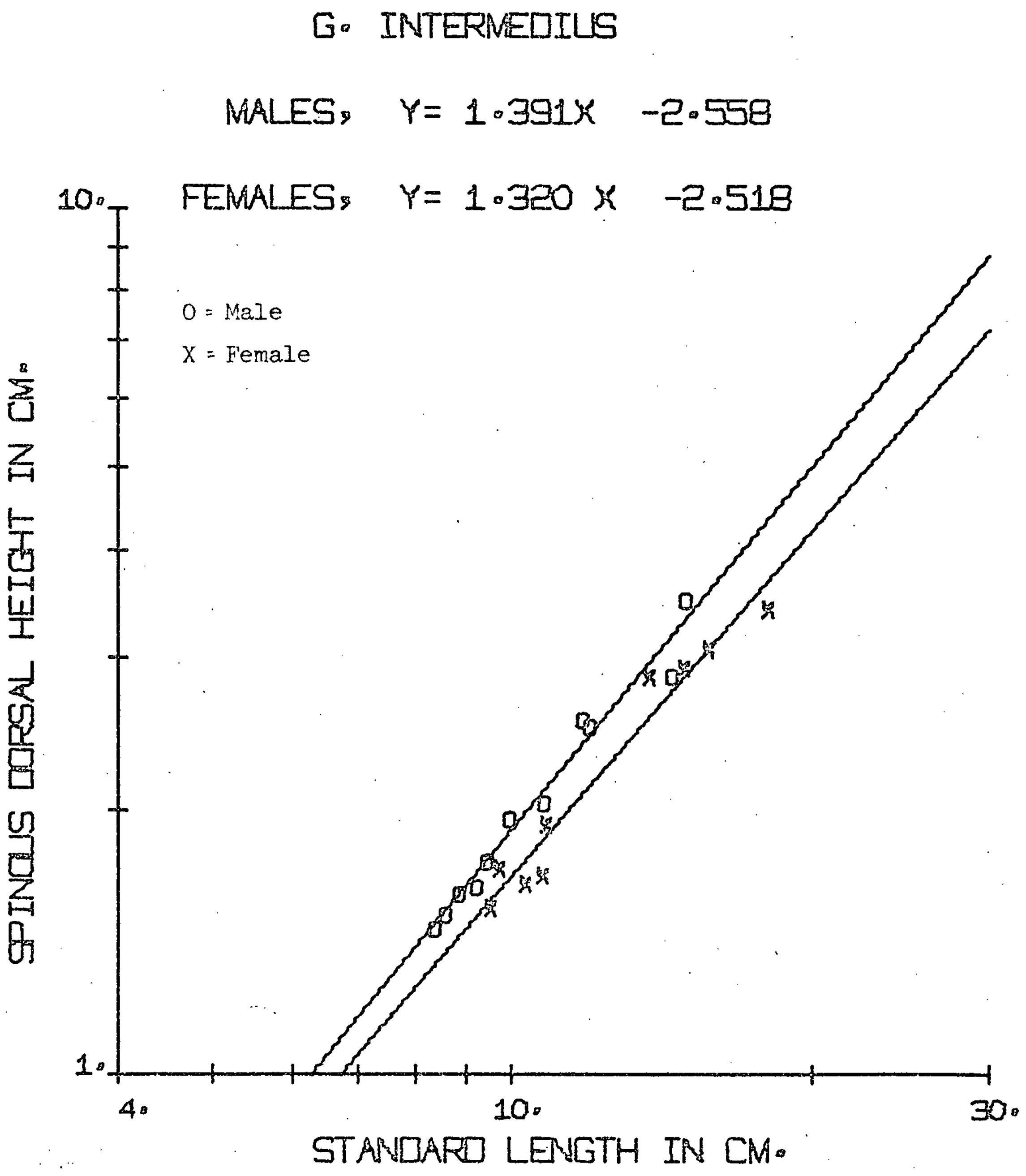


Figure 64.

Spinous dorsal height versus standard length, males and females.

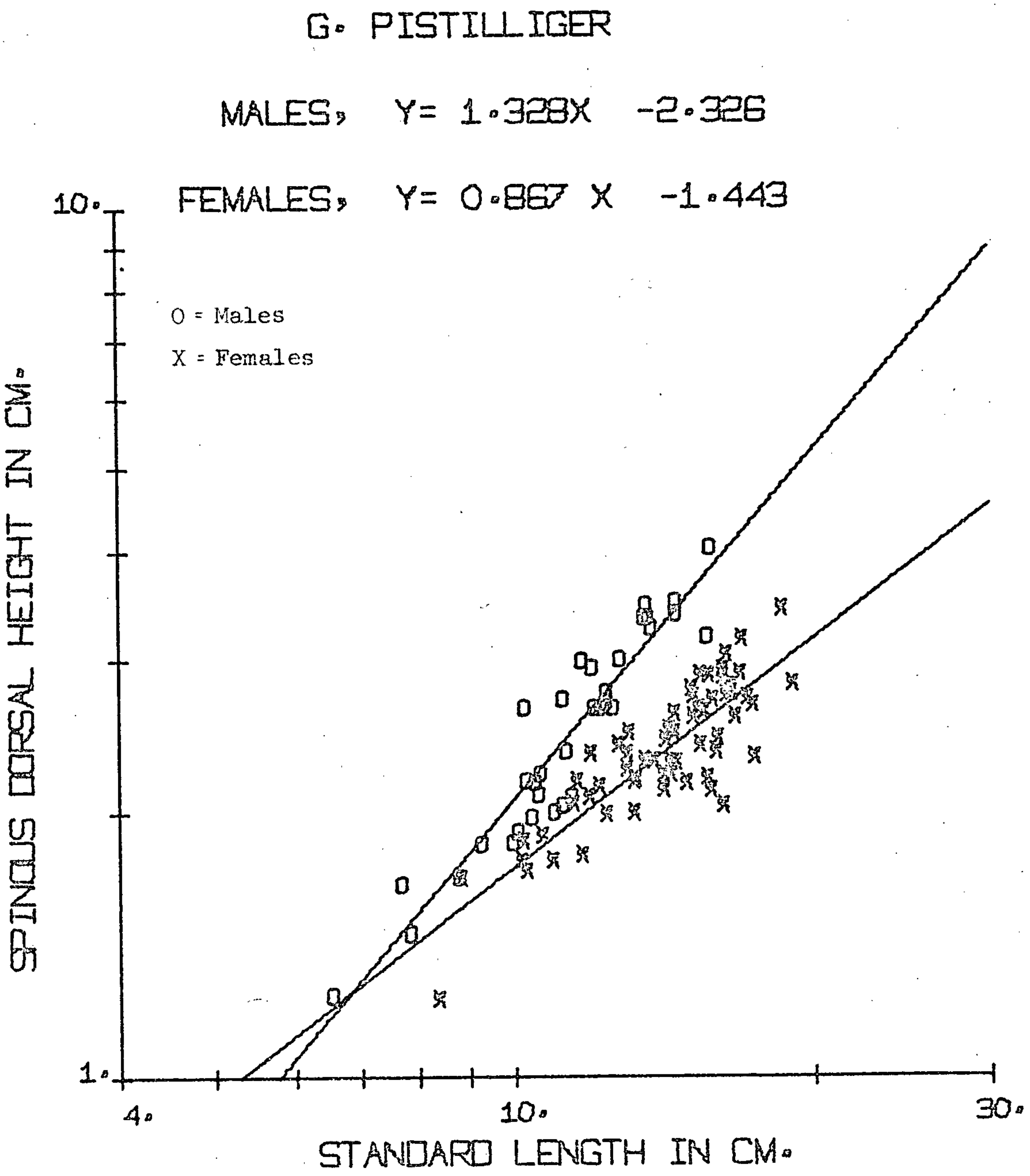


Figure 65.

Spinous dorsal height versus standard length, males and females.

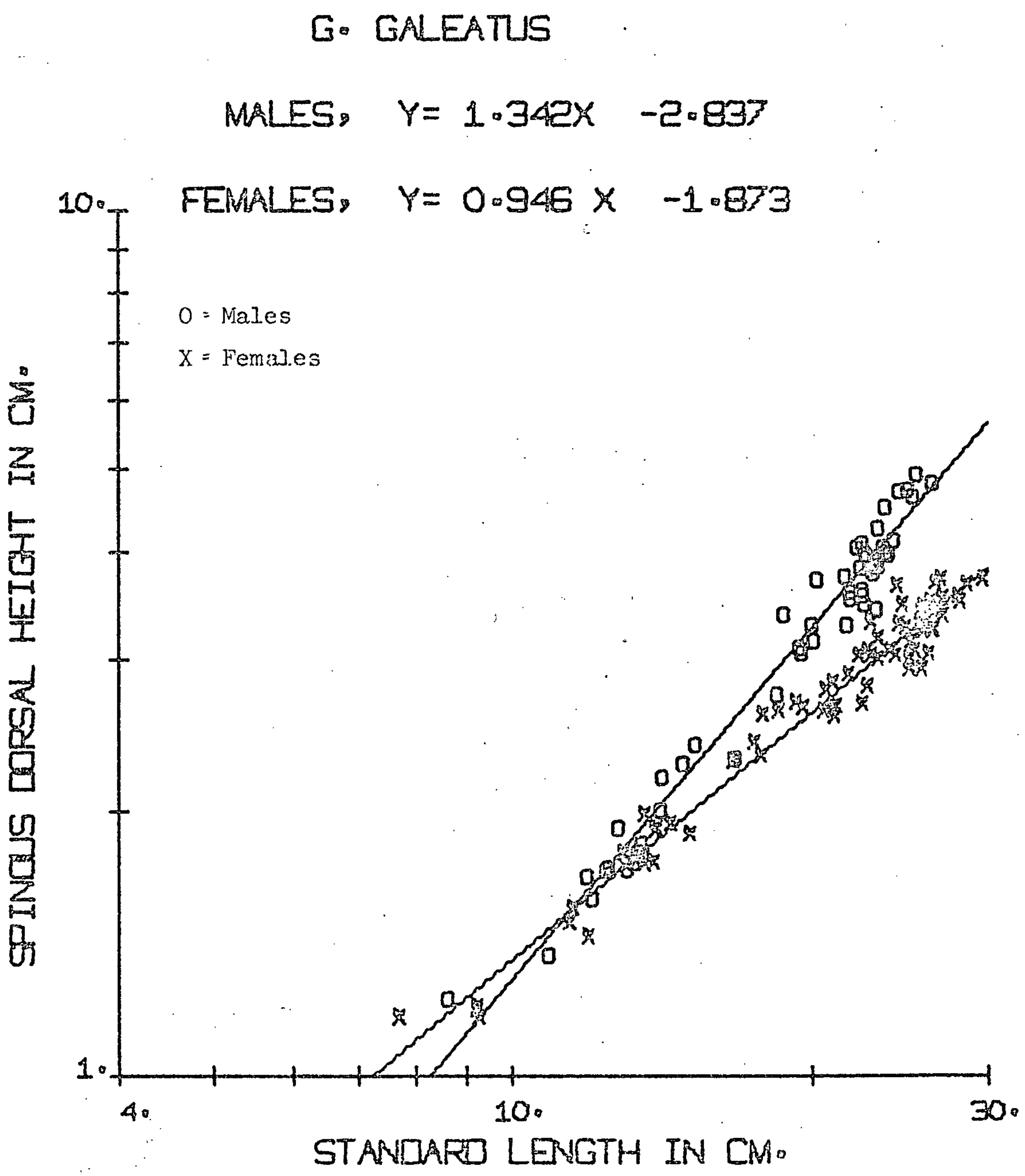


Figure 66.

Spinous dorsal height versus standard length, males and females.

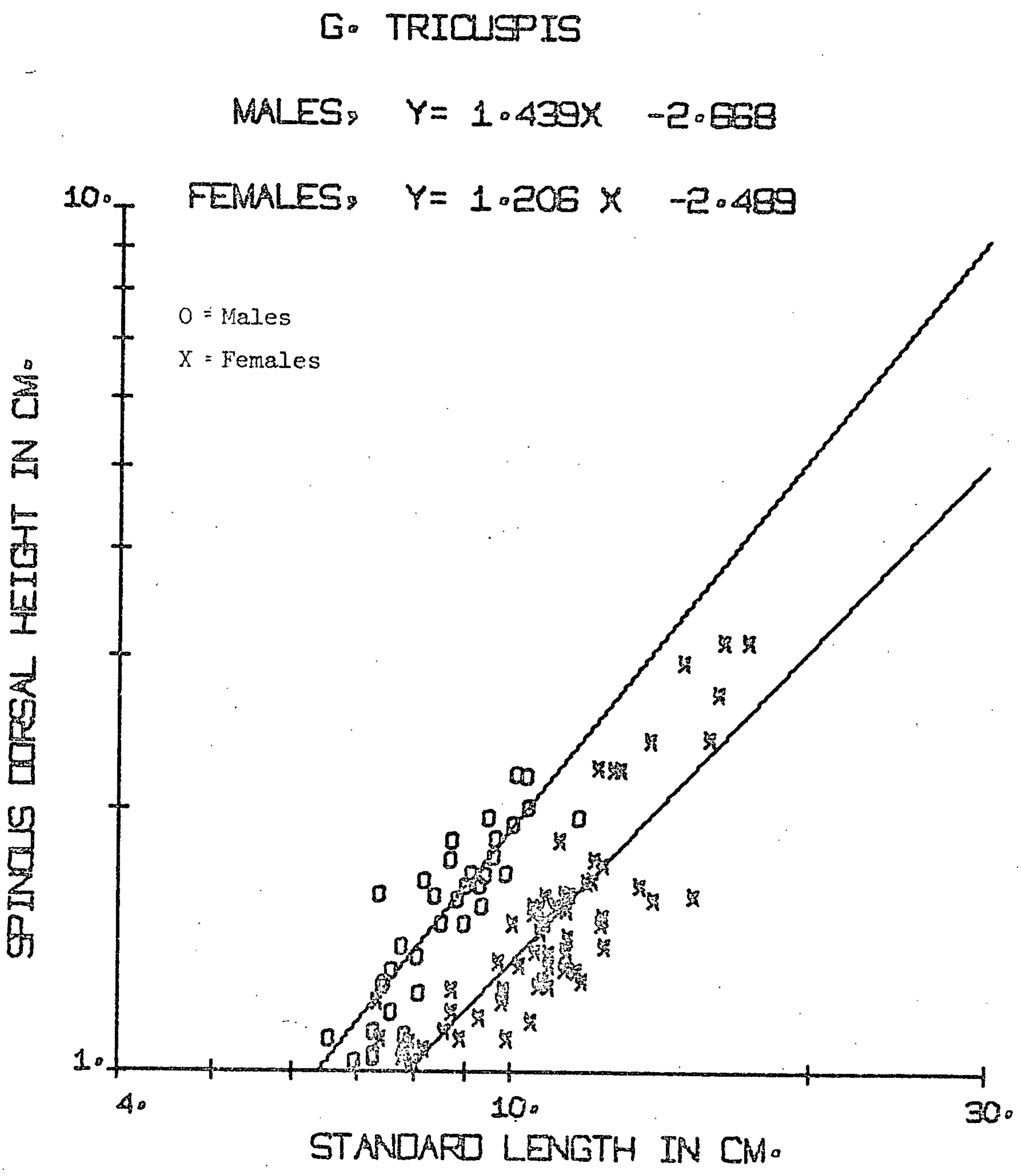


Figure 67.
Soft dorsal height versus standard length, males and females.

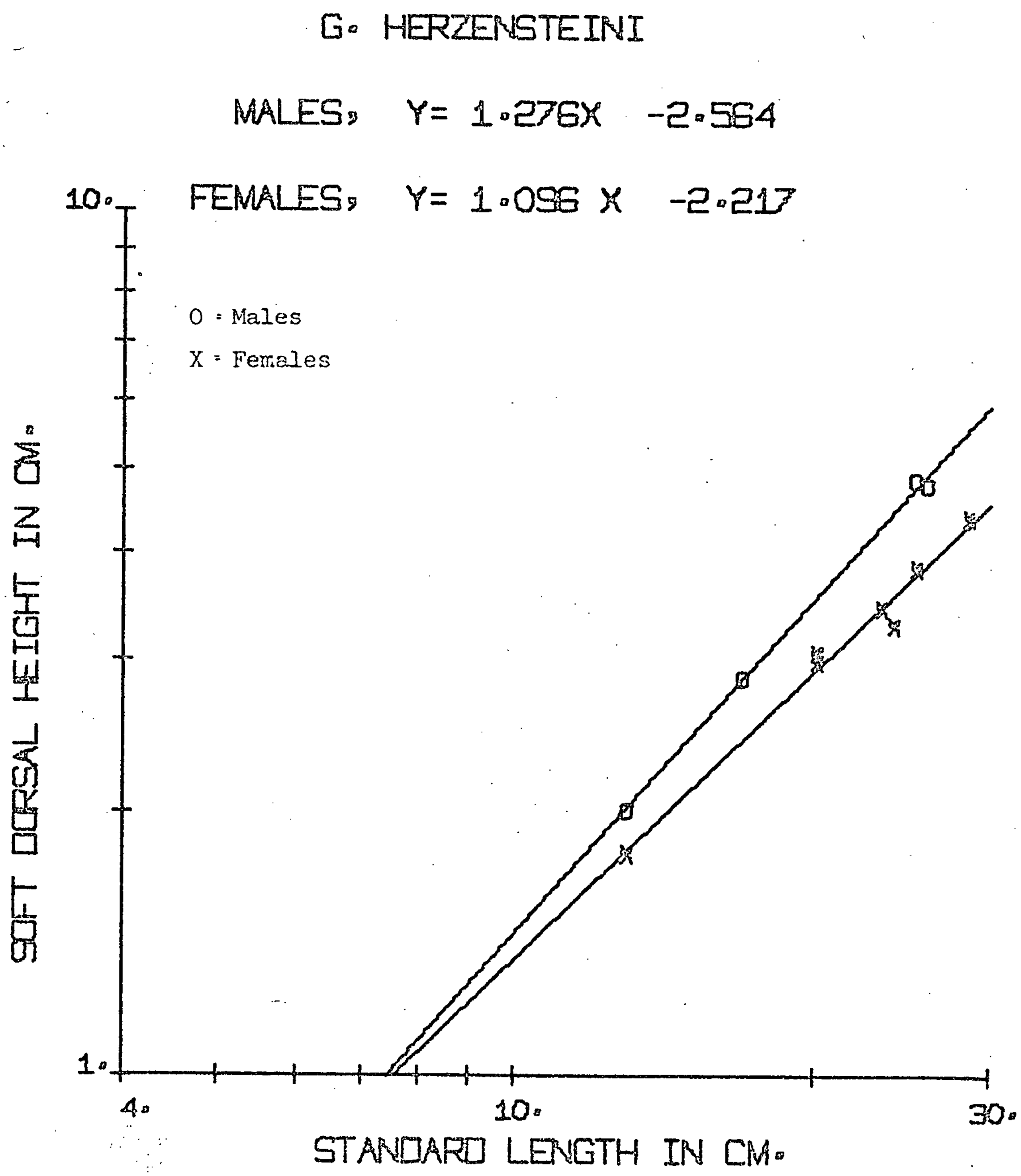


Figure 68.
Soft dorsal height versus standard length, males and females.

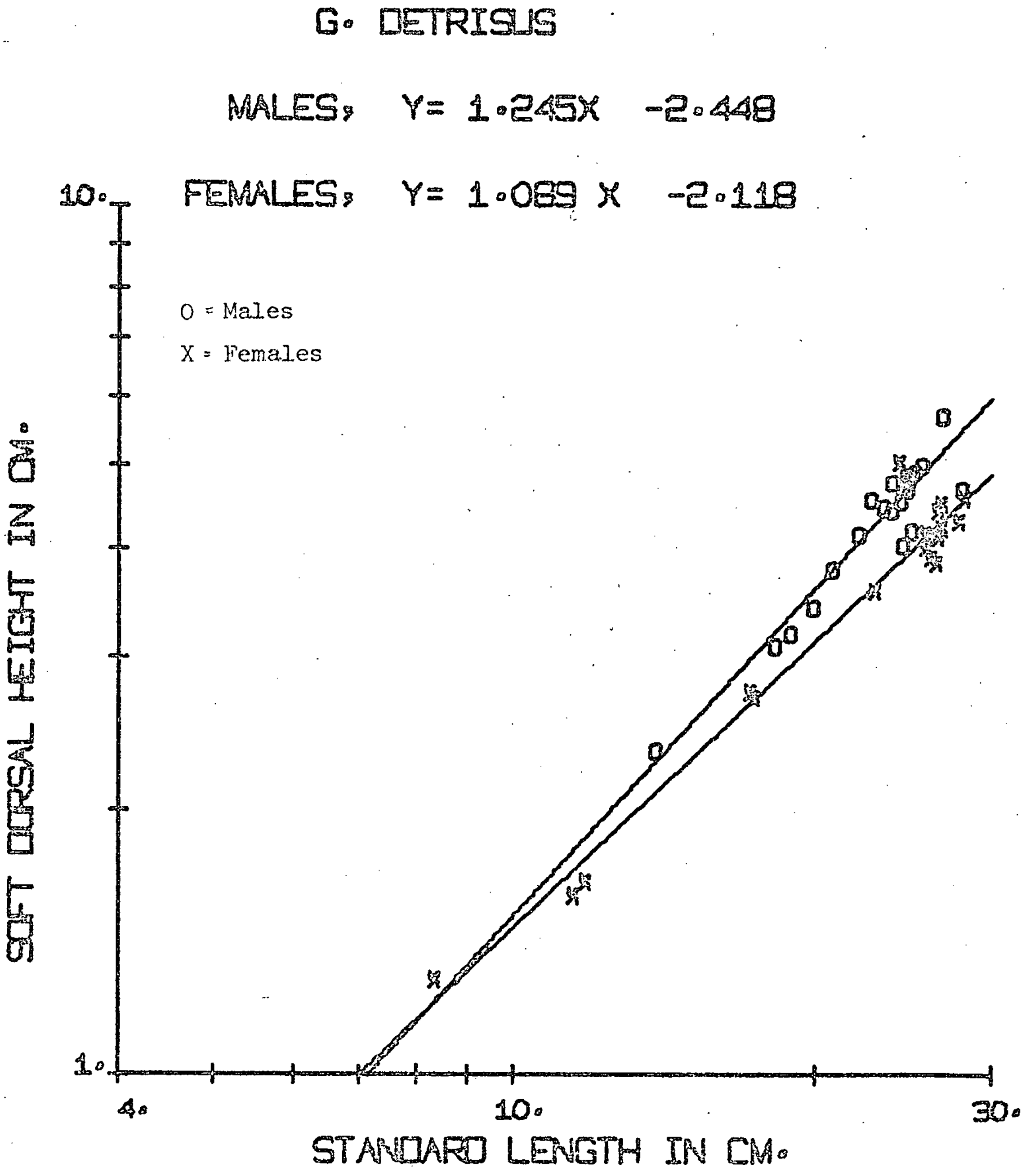


Figure 69.

Soft dorsal height versus standard length, males and females.

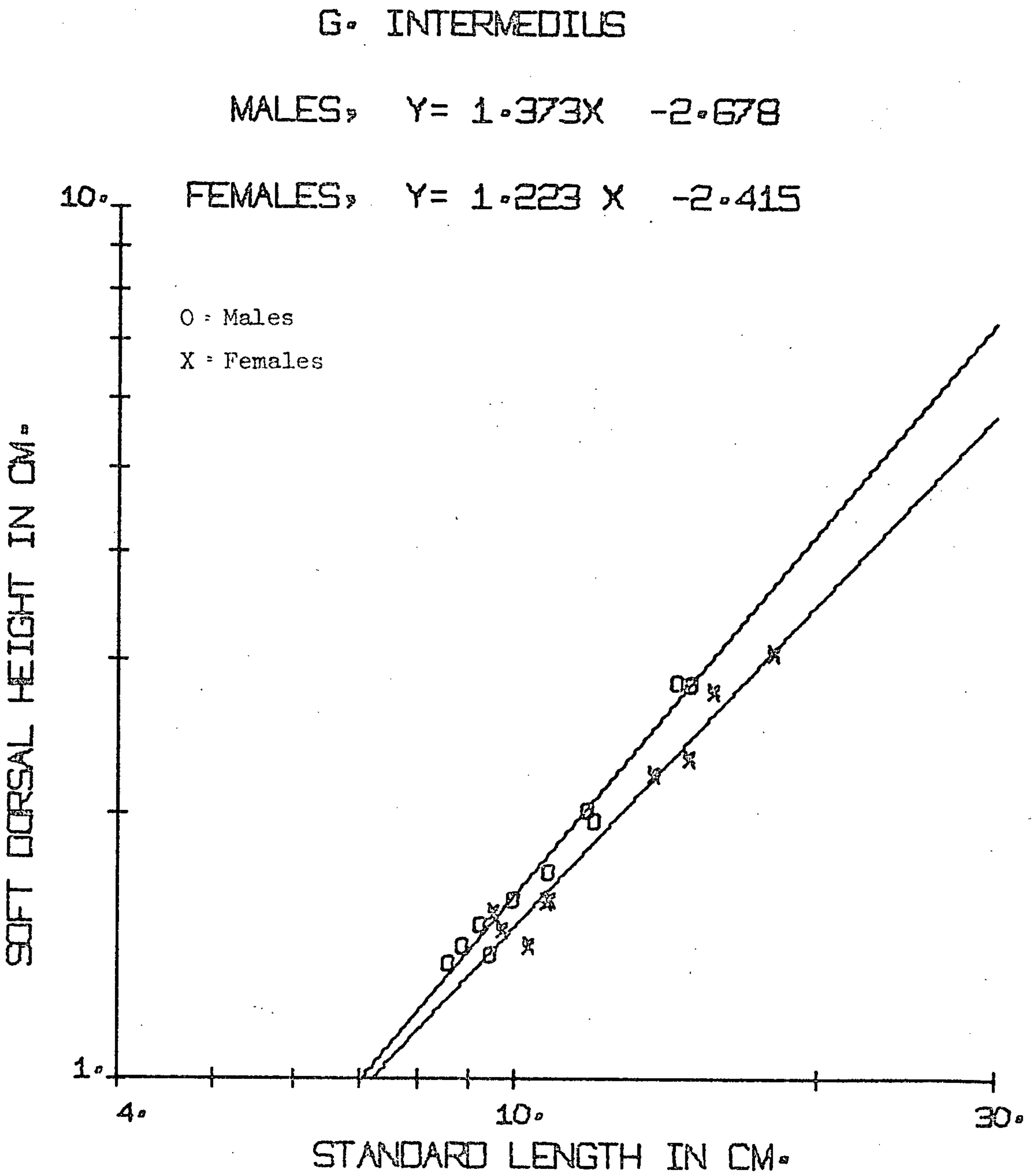


Figure 70.
Soft dorsal height versus standard length, males and females.

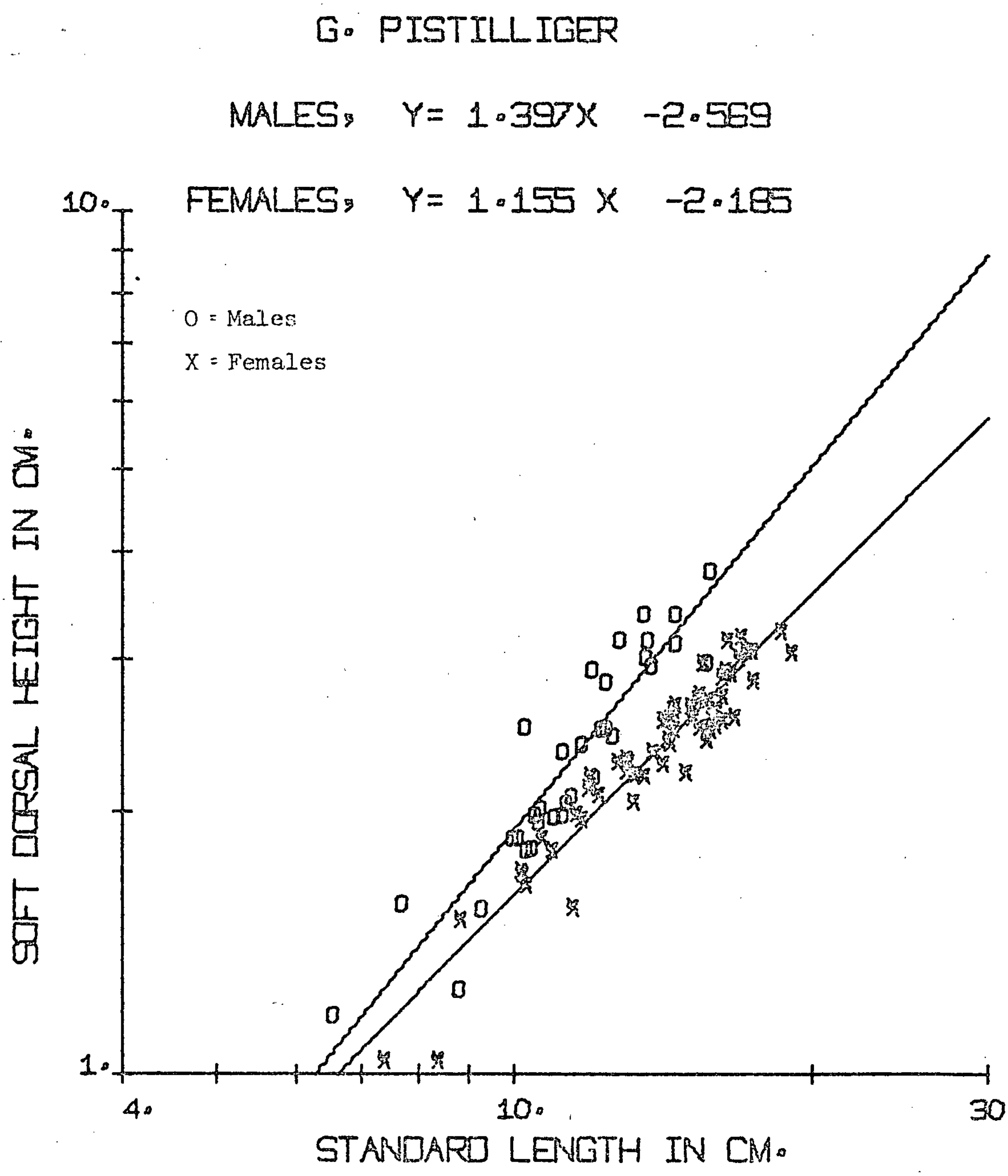


Figure 71.
Soft dorsal height versus standard length, males and females.

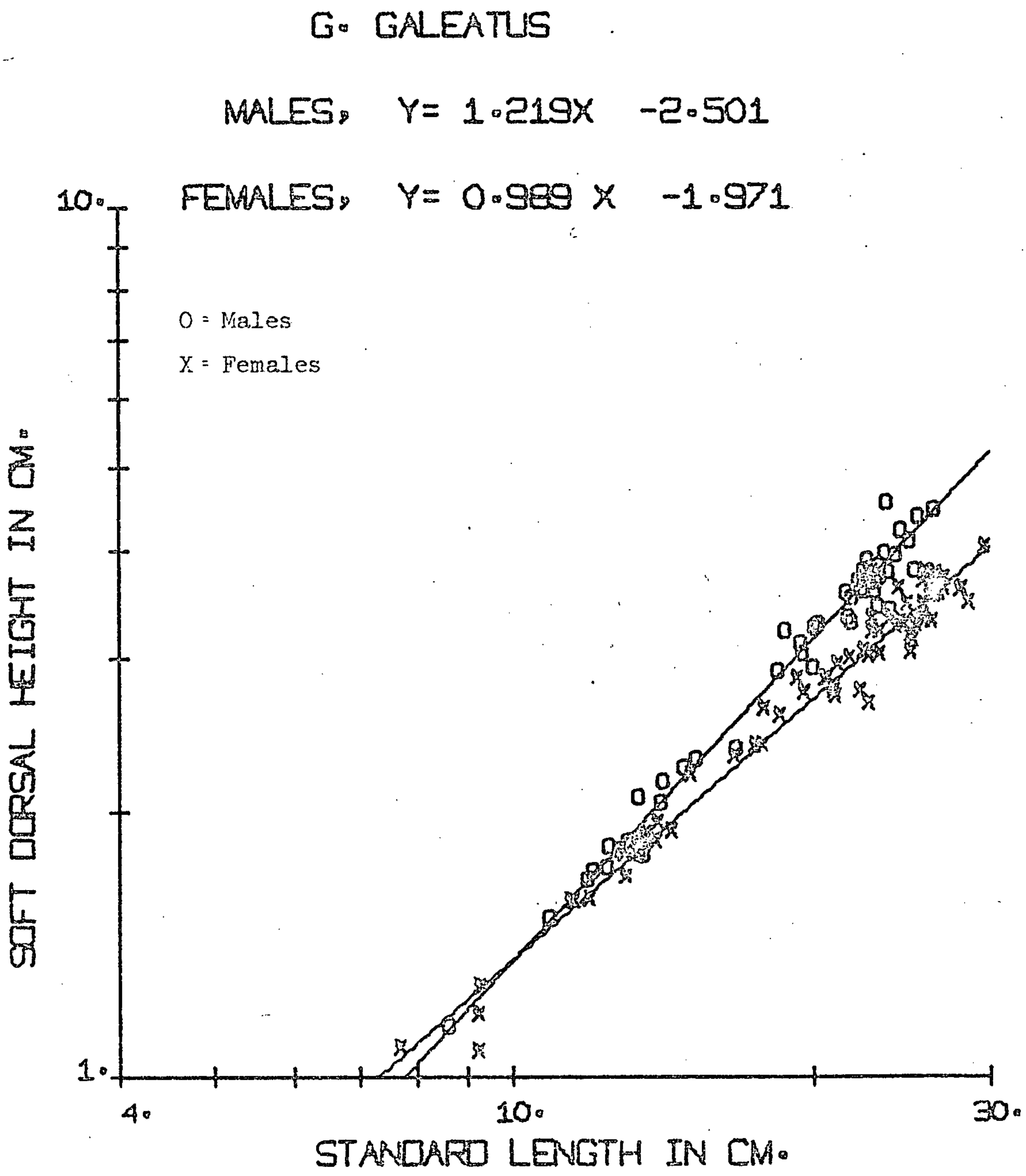


Figure 72.

Soft dorsal height versus standard length, males and females.

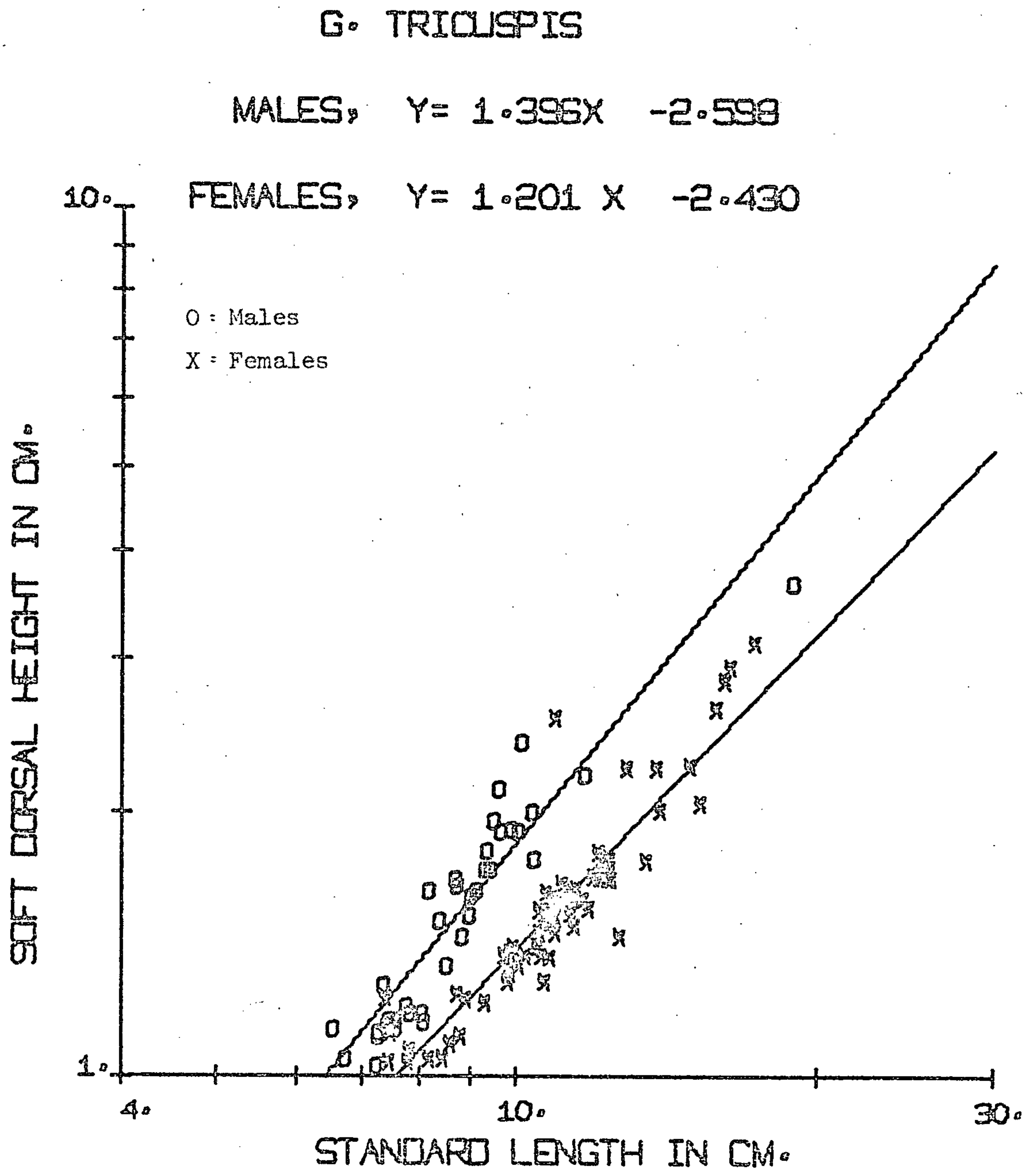


Figure 73.
Pelvic fin length versus standard length, males and females.

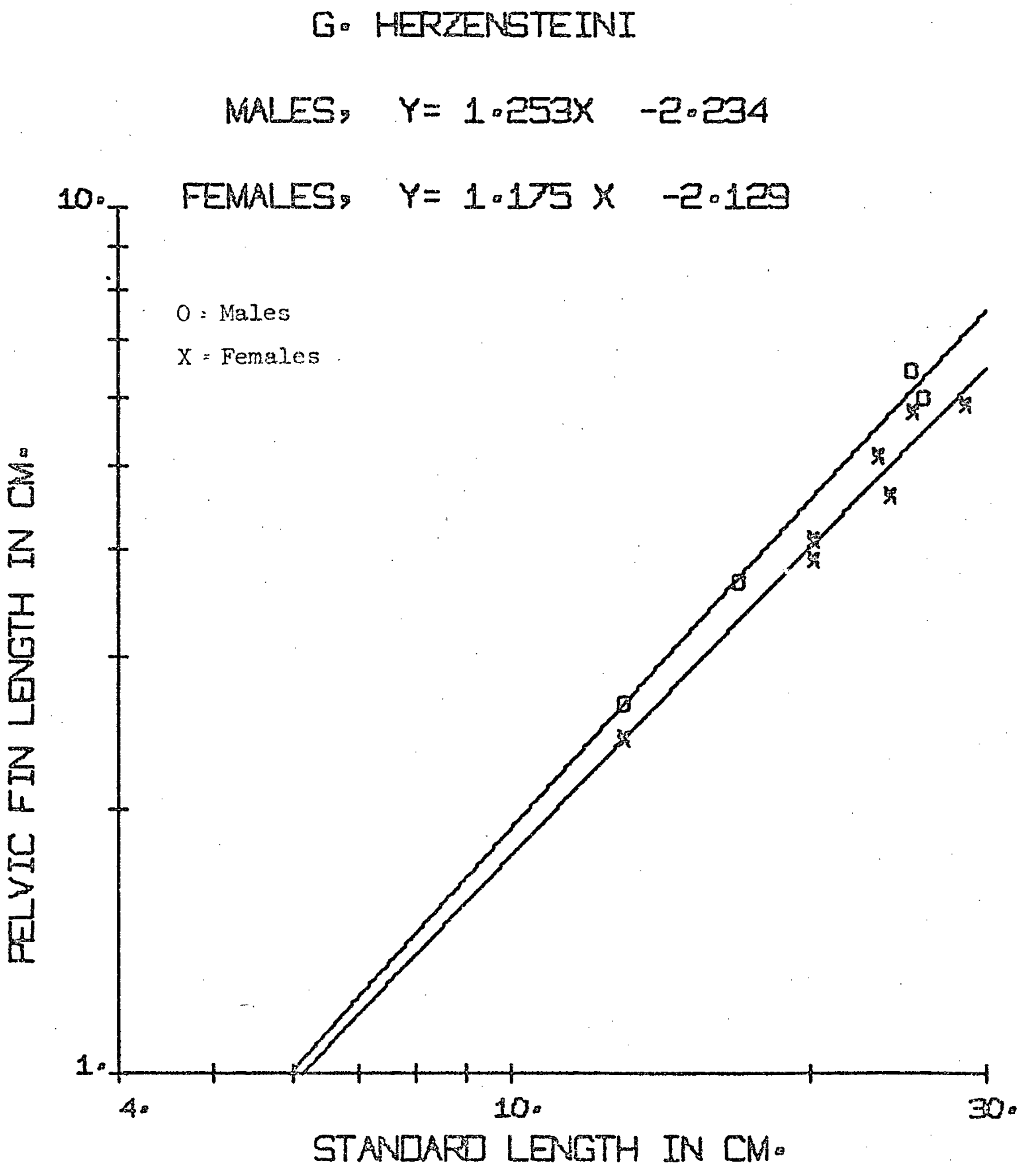


Figure 74.

Pelvic fin length versus standard length, males and females.

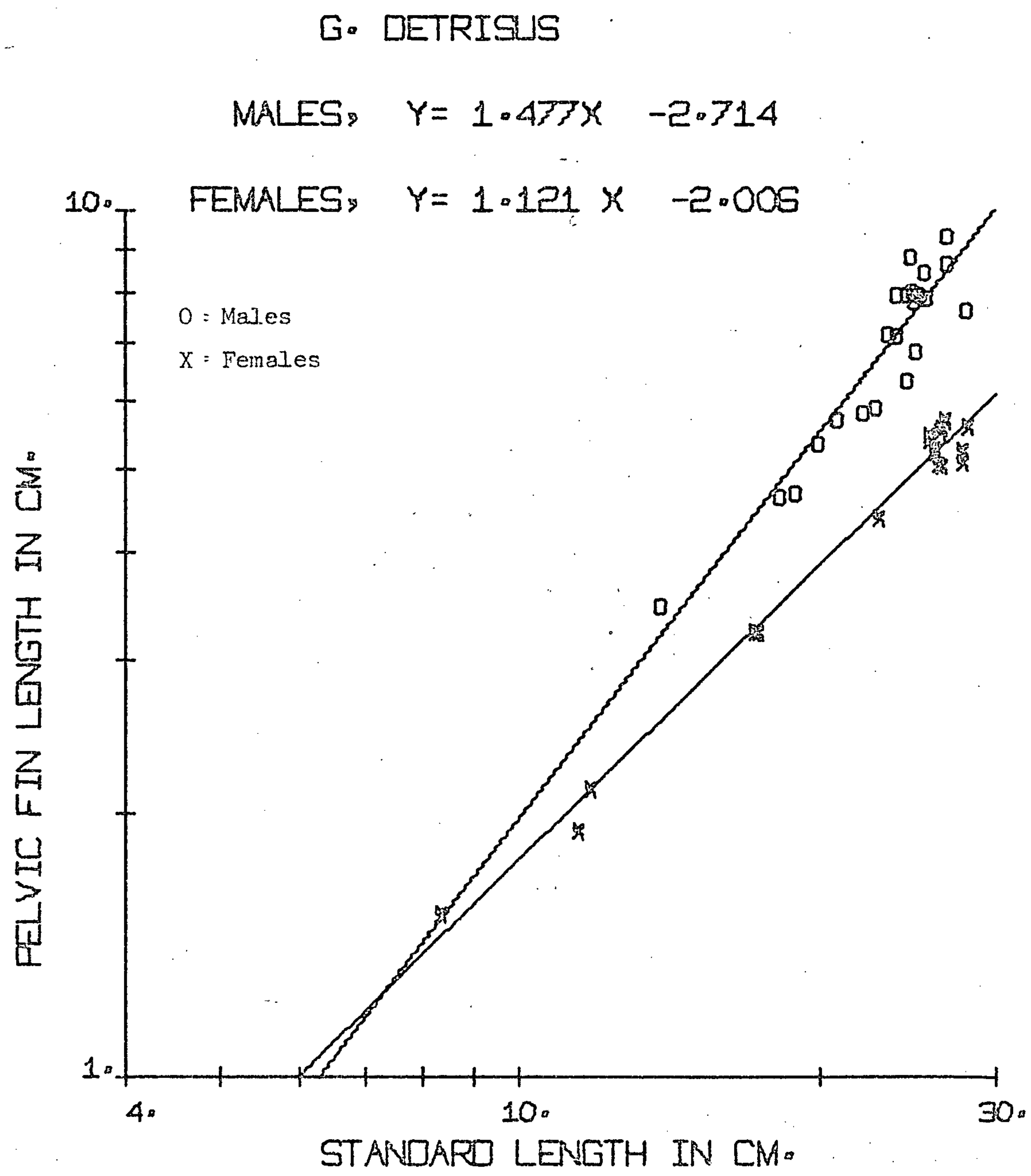


Figure 75.

Pelvic fin length versus standard length, males and females.

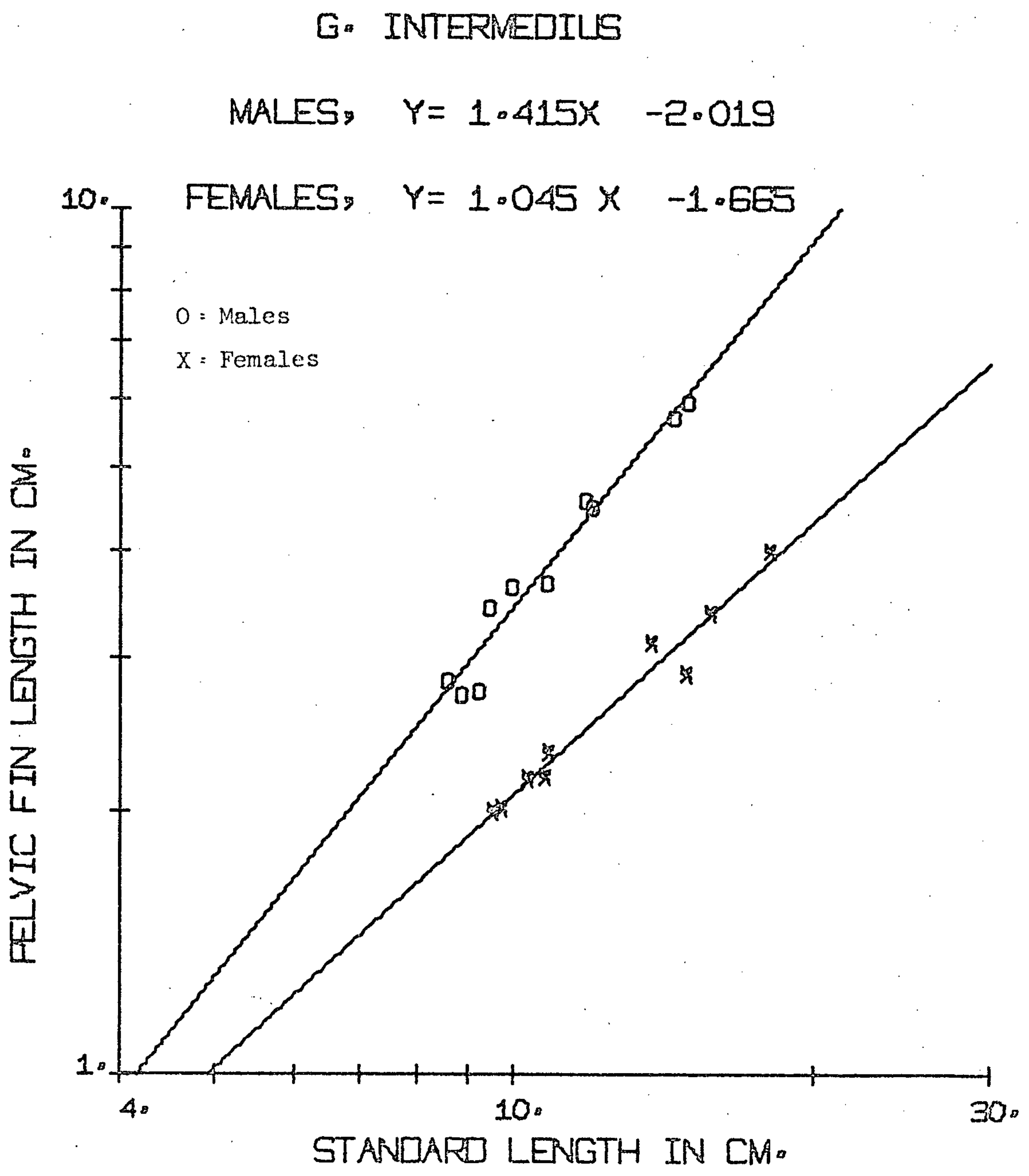


Figure 76.

Pelvic fin length versus standard length, males and females.

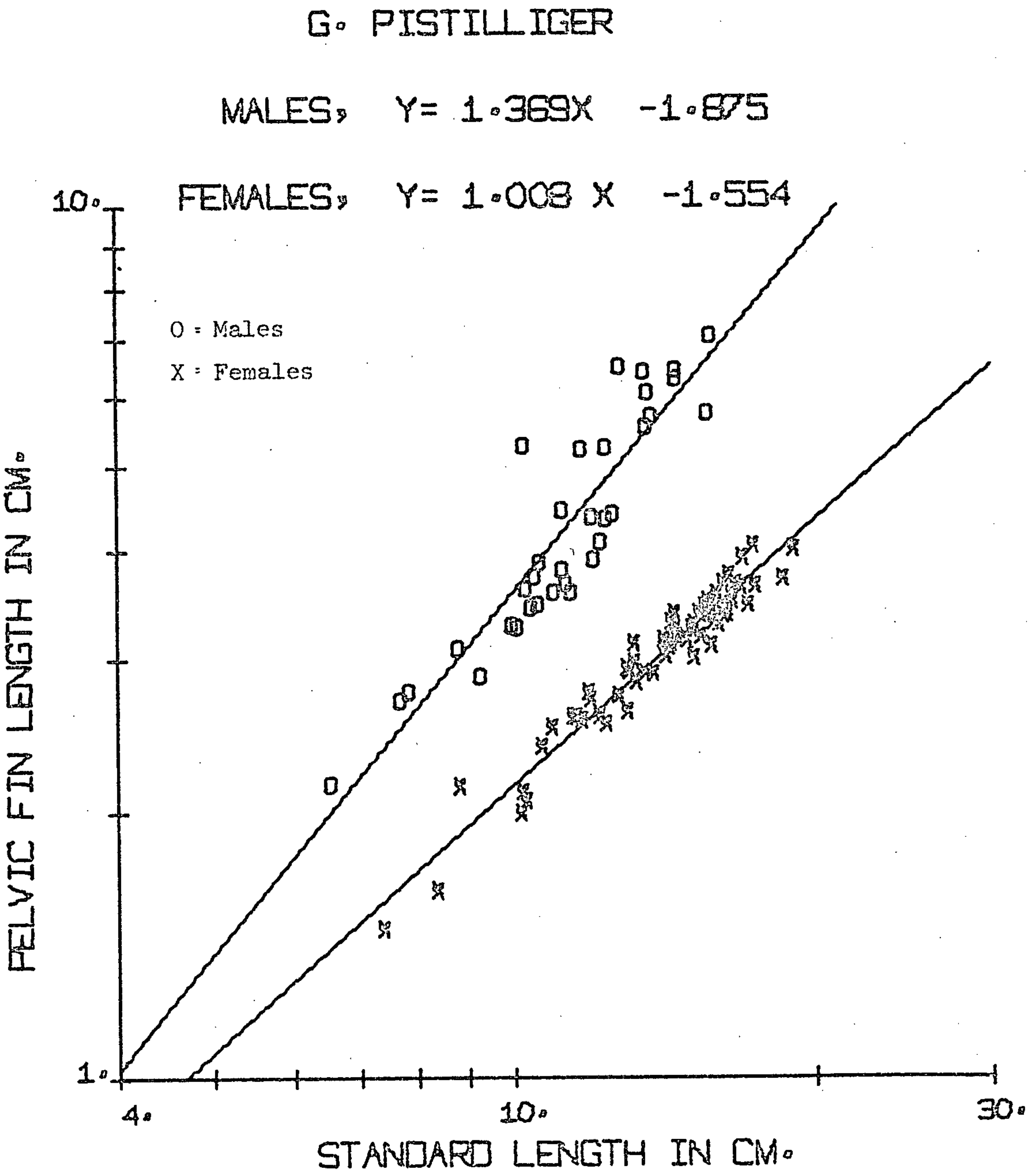


Figure 77.

Pelvic fin length versus standard length, males and females.

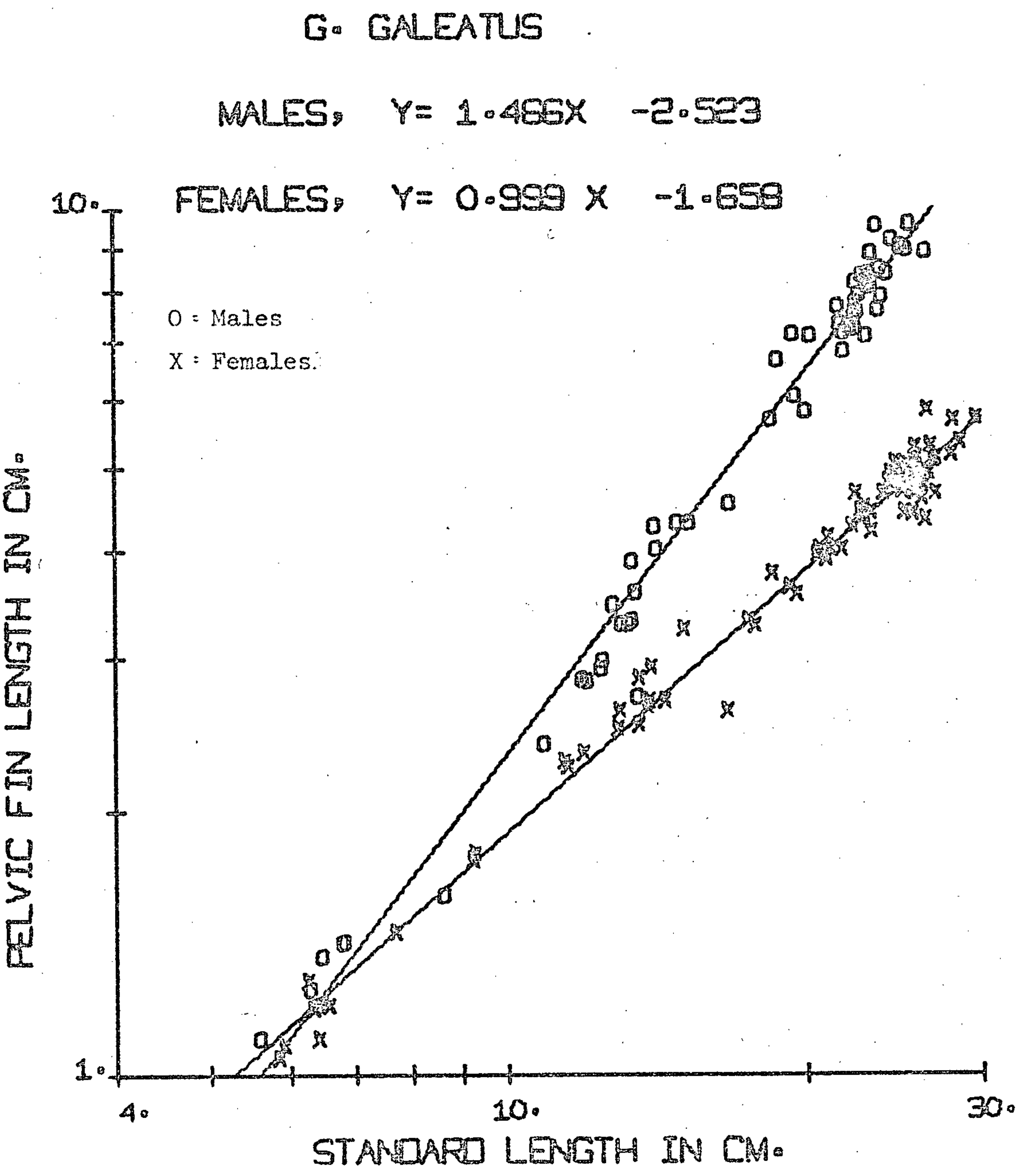


Figure 78.

Pelvic fin length versus standard length, males and females.

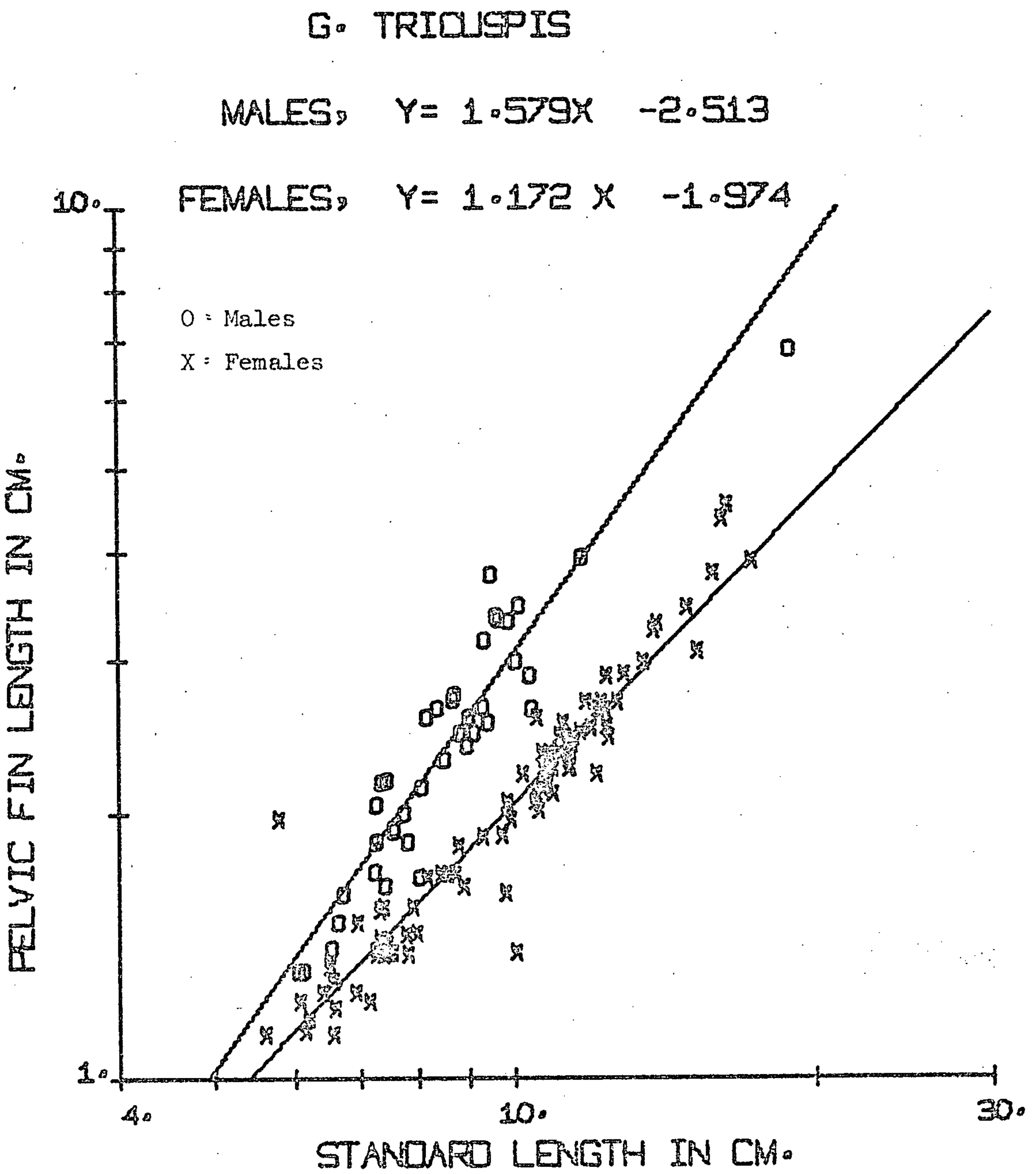
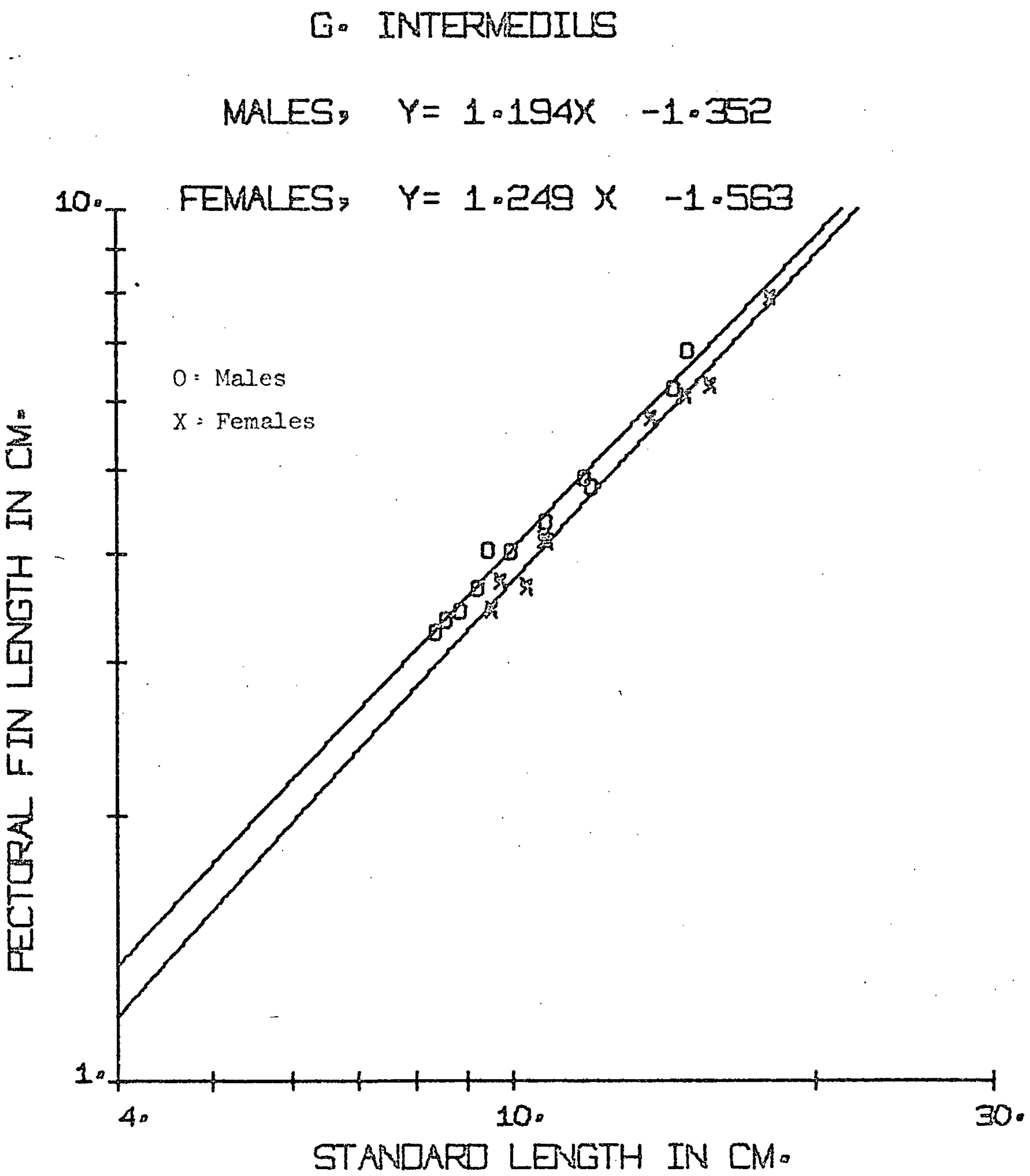


Figure 79.

Pectoral fin length versus standard length, males and females.



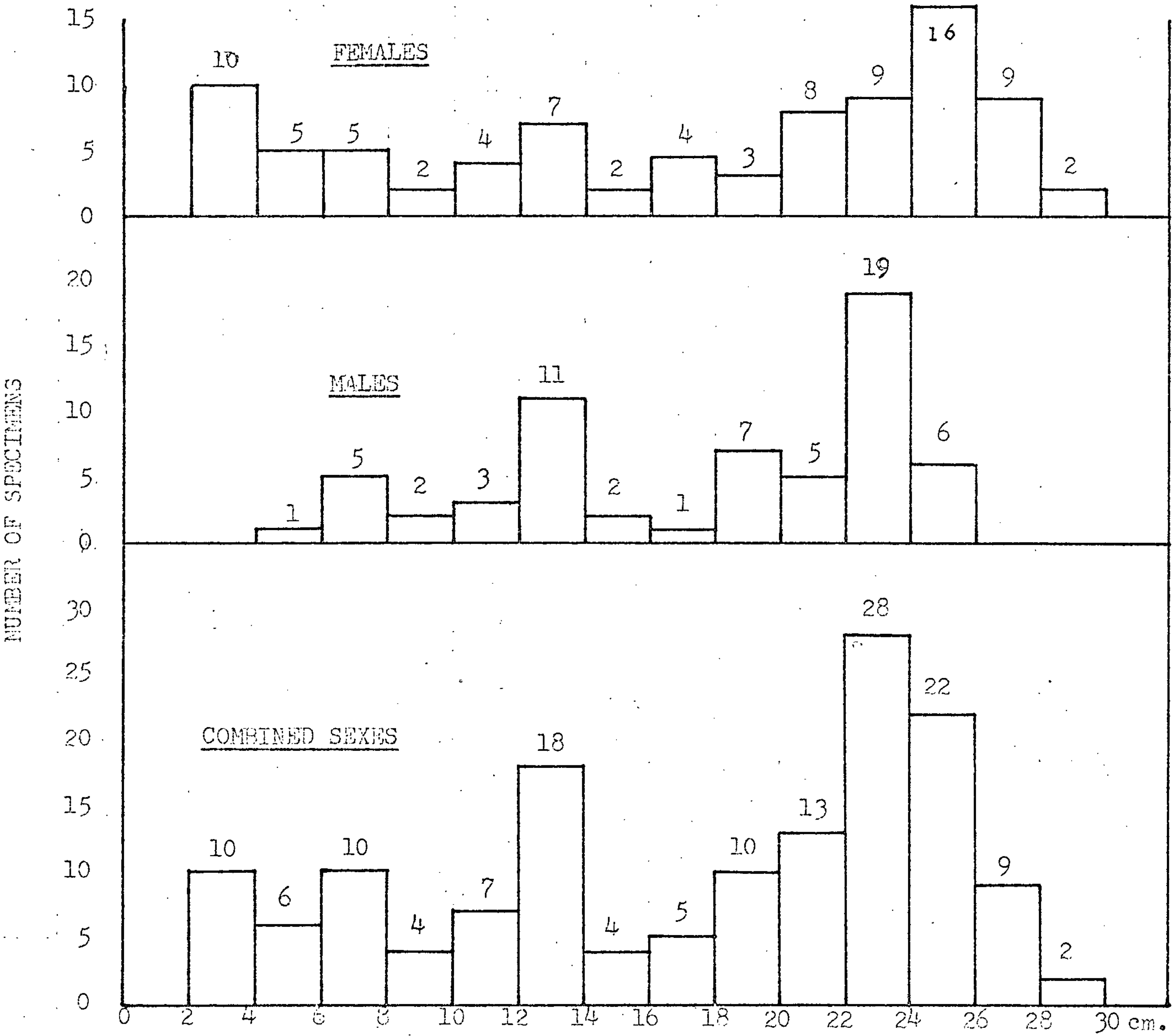


Figure 80. Histogram of Length-Frequency Data for *Gymnocanthus galeatus*. See text for discussion.

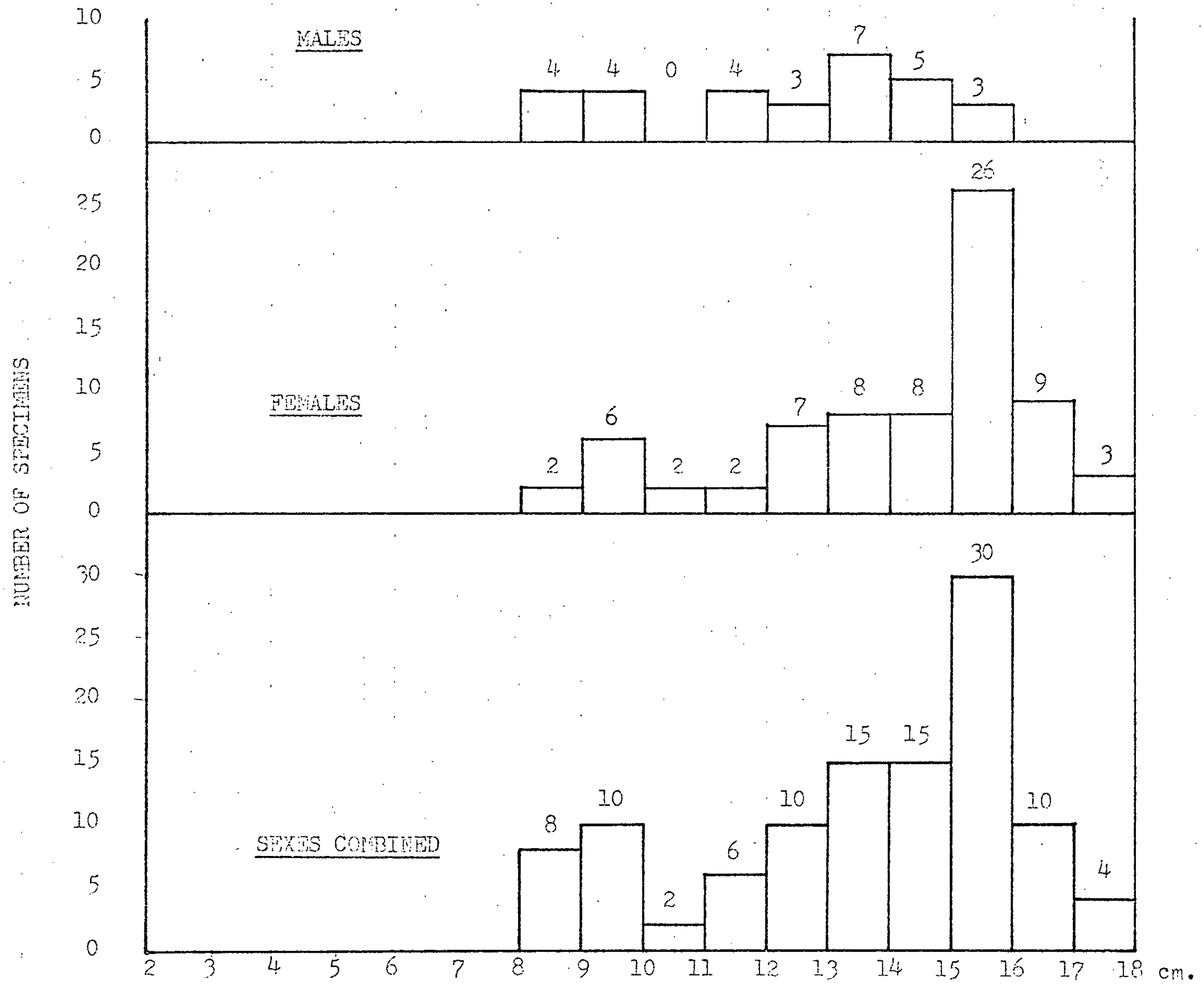


Figure 81. Length - Frequency histogram for <u>Gymnocanthus pistilliger</u>. See text for discussion.

Breeding

In the absence of direct observational data, breeding times only may be inferred from gonadal maturity, and the presence of young in various stages of development. Using these techniques, it is possible to estimate the breeding times for four species.

A gravid female _G. herzensteini_ (BC72-118) was releasing eggs when caught in mid-February. Two other females from this collection were recently spent, suggesting a breeding period of midwinter. Gravid female _G. tricuspis_ have been taken from the Chukchi Sea (eg. BC61-102, BC61-106) in mid-August while young (20-35cm.) may be taken in July-August. Andriashev (1954) reports gravid females and spawning males in late September in the Kara and White Seas. He also reports young of 18-30 mm. being taken in July-September. Breeding in _G. tricuspis_ probably takes place in the late summer to early autumn, while the young mentioned are the young of the previous year. Recently spent _G. galeatus_ females (BC62-444) have been taken in May, while females with immature eggs (UW-1644) have been collected in December. Juveniles (15-20mm.) are collected in mid to late July (BC65-17, BC65-21). Similarly, spent female _G. pistilliger_ may be taken in mid-April to mid-May (BC61-515, BC62-719) and juveniles (22-26mm.) may be collected in early August (BC63-1438). Breeding in these latter two species seems to be in mid-spring, while the young noted are young of the year. (O+)

A length-frequency analysis of 110 _G. pistilliger_ caught by the author in July off Kodiak, Alaska show peaks at 9-10, 13-14, and 15-16 cm. (figure 81). Some collections (BC63-1026) show the presence of a fourth, prerecruitment size-class (1+) of 4-6cm. _G. pistilliger_ otolith examination reveal only three annuli reliably. It would appear that the 1+ annulus is obscure and has been consistently missed by the author. 2+ fish average 9.3 cm., and 3+ fish average about 13.5 cm., males being slightly smaller than females. By 4+ years, the females reach 15.6 cm., while the males grow only very slightly, averaging 13.5 cm.

Andriashev (1954) summarizes some of the known growth data for _G. tricuspis_. In the Laptev Sea in September, the sizes are about 20 mm. at 0+, 40-50 mm. at 1+, and 70-80 mm. at 2+. Again, males grow more slowly, reaching 90-100 mm. at 3+ and 110-120 mm. at 4+, while females reach 110-120 mm. at 3+, and 140 mm. at 4+. Similar data were obtained by that author for Chukchi Sea fishes.

Both otoliths and bones (ie. cleithra) of the 17 specimens of _G. galeatus_ obtained in Kodiak proved difficult to read and results were inconclusive. A rough length-frequency diagram (figure 80) lumping collections primarily from Kodiak to the Aleutian Islands taken between May and July in 1961 and 1962 show distinct peaks at 4-6 cm. (1+) and 12-14 cm. (2+). For larger fish peaks are obscure. Separating the data for the sexes reveal peaks at 22-24 cm. for males and 24-26 cm. for females. The scatter about these peaks suggests that they may be concealing at least two (3+, 4+) and perhaps more peaks. Judging from earlier growth, _G. galeatus_ grows more quickly than either _G. tricuspis_ or _G. pistilliger_, reaching a greater final size than either of these species. Furthermore, that the largest fish are always females suggests that again, females grow faster than males.

Sexual Dimorphism

Sexual dimorphism in the genus *Gymnocanthus* is pronounced. Foremost is the possession of a penis by males of all species. As pointed out in the morphometric discussion, the fins in males tend to be much longer and larger than in females. The pelvic fin length, perhaps the most startling sexually dimorphic character varies between species. In the short pelvic fin species (*G. detrisus*, *G. herzensteini*) the male's pelvic fins reach or just pass the anus, while in *G. intermedius*, *G. pistilliger*, *G. galeatus*, and *G. tricuspis* the male's pelvics usually reach the anal origin and frequently far surpass it. In females of all species the pelvics seldom, if ever, reach the anus. Similarly, males tend to have longer dorsal fins, expecially the spinous dorsal. The spinous dorsal margin tends to be strongly convex in males, and weakly convex in females. *G. pistilliger*, *G. intermedius*, and *G. tricuspis* show marked colour dimorphism. The males of these species possess large white blotches in the pectoral axillae, on the pelvics, and on the spinous dorsal fin. In addition, the spinous dorsal ground colour is dusky in the males of these species, but tends to be clear in the females. Males of these three species possess serrations on the pectoral ray medial surfaces. Only males of *G. intermedius* and *G. pistilliger* possess pectoral axillary processes or pistillae. Males of all other species and females of all species lack such distinctive colouration, pistillae, and serrations. Lastly, males of *G. tricuspis*, *G. pistilliger*, and *G. galeatus* have been shown to grow more slowly than females, and the male maximum size is smaller. From examination of collections of *G. herzensteini*, *G. intermedius*, and *G. detrisus* it appears that in these, also, the largest specimens are always female. Probably females of these latter species also grow more quickly than males.

Distribution

Of the six species of *Gymnocanthus*, four species (*G. intermedius*, *herzensteini*, *detrisus*, and *pistilliger*) occur in the northwest Pacific, and with the exception of *G. pistilliger* are endemic to this area. *G. pistilliger* also occurs on the Aleutians and as far east as Seward, Alaska. Northward, they have been collected in Bristol Bay, off the Pribilof Islands, and possibly as far north as the Bering Strait. *G. galeatus* is known from the Near Islands in the Aleutians to southeast Alaska, and north to the Pribilof Islands and Bristol Bay. *G. tricuspis* occurs as far south as Norton Sound in the Bering Sea and throughout the American and Soviet Arctic (Schmidt, 1927; Andriashev, 1964). In the Atlantic, it ranges as far south as Maine in the west (Leim and Scott, 1966) and Spitzbergen (Schmidt, 1927) and northern Norway (Andriashev, 1964) in the east.

Although Gymnocanthus is a cold-loving group, its depth distribution is not well enough known to correlate species distributions with temperature regimes. In the North Pacific, southern collections of *Gymnocanthus* (ie. around Hokkaido, Sea of Japan) invariably occur where there are southern currents of cold arctic or subarctic water such as the Liman, North Korean, or Oyashio Currents. Apparently, nowhere in the distribution of species other than *G. tricuspis* do water temperatures drop below 1°C. In Bristol Bay and along the western Alaska coast to the Bering Straits, the waters are warmed by a branch of the Alaskan Stream which feeds between the east Aleutians and flows along the coast resulting in G. pistilliger's range being extended along the eastern Bering Sea shore. The temperature distribution of G. tricuspis is significantly different from that for other species. Around St. Lawrence Island, the bottom temperature may vary from 2° below 0°C (Ellson et al, 1950). In the western Canadian Arctic there exists a thin surface layer 0-20m. thick, from -1.0 to 2.2°C. In the Canadian Arctic Archipelago, this surface layer is maintained. In Baffin Bay, the temperature may reach 5°C, but plunges to -1.0° within 30 meters (Bailey, 1954). Similarly, in Hudson Bay, Ungava Bay, and by virtue of the icy Labrador Current, Labrador, and the Gulf of St. Lawrence, temperatures tend to be below 2°C at depths greater than 25-35 meters. G. tricuspis is clearly characteristic of variable, but usually very cold water. Andriashev (1954) reports this species to be found at 3°-4°C off Spitzbergen and in the Barents Sea, and at 1.4° to 12.5°C in the White Sea, "but over most of the range is mostly encountered at temperatures below or close to 0°C." Leim and Scott (1966) state that it is confined to cold water between -1.7° to 5°C. Andriashev also points out that G. tricuspis is subjected to a wide variation of salinity, usually from 32-35°/oo, but from 16 to 30°/oo in the Laptev Sea, and 23.7 to 27.0°/oo in the White Sea. Similar salinity conditions apparently occur in the Canadian Arctic (Bailey, 1957). There is no indication that the other species are subjected to salinity variation of this nature. It is perhaps significant that the maximum depth of capture in the Beaufort and Chukchi Sea, about 25 metres, corresponds approximately with the depth of the slightly warmed, less saline surface layer in this region below which the temperature may drop to below -1.0°C. Collections of G. galeatus and G. pistilliger off South Alaska show that while the former is seldom taken at less than 50 meters (except for juveniles), the latter is seldom taken at over 50 meters.

Neither the species distribution nor the oceanographic data are adequate for speculation on the parameters affecting distribution beyond what is presented herein.

Phylogeny

Several authors (Jordan, 1901; Svetovidov, 1948, 1952; Ekman, 1967) have argued that, in Jordan's words, "any species... has had its origin in or near that region in which it is most abundant and characteristic." On this basis it would appear that the Northwestern Pacific with its four species, three of them endemic, served as the rejion of origin of the genus Gymnocanthus.

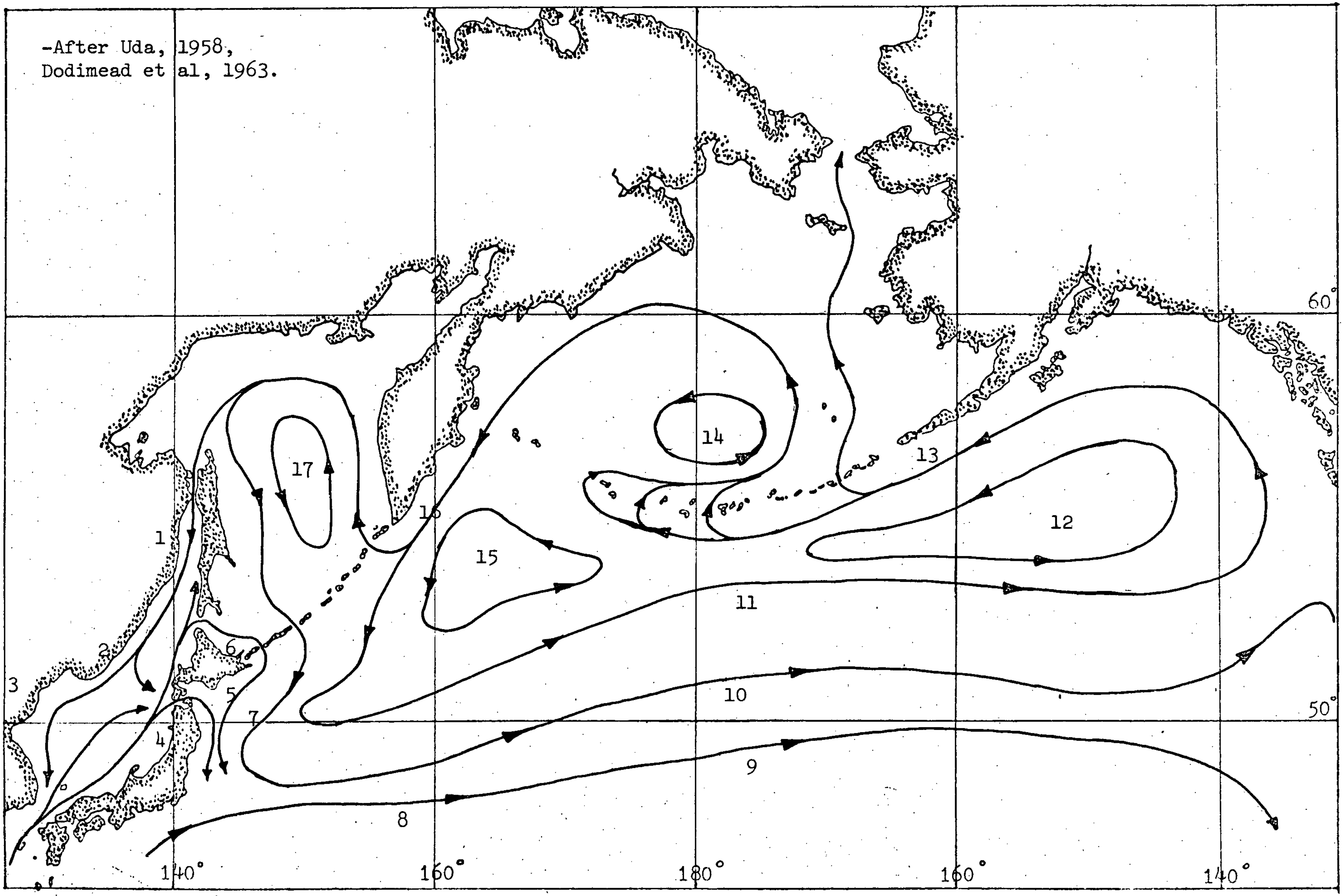
There exist several arguments against this thesis. For example, Darlington (1957) states that acceptance of Jordan's premise necessitates acceptance of the supposition that the rate of speciation versus extinction is close throughout the species' range. Secondly, since extant current systems and concomitant water character regimes in the Northwest Pacific are complex (Jordan, 1901; Uda, 1958ab) it is probably unwise to lump species occuring there as species from a single region. Finally, Wilimovsky (1963) and Dodimead et al (1963) note that the Alaskan Stream, Western Subarctic, and Oyashio currents run westward along the Aleutians, Kamchatka, and the Kurile Islands, while the eastward flowing Kuroshio, Aleutian, and North Pacific currents pass far to the south of the Aleutian

Figure 82.

North Pacific Oceanic Surface circulation pattern.

Currents

1. Liman Cold Current
2. Japanese Sea Central Cold Current
3. North Korean Current
4. Tusima Warm Current
5. Tugaru Warm Current
6. Soya Warm Current
7. Oyashio Current
8. Kuroshio
9. North Pacific Current
10. West Wind Drift
11. Subarctic Current
12. Alaskan Cyre
13. Alaskan Stream
14. Bering Sea Gyre
15. Western Subarctic Gyre
16. East Kamchatka Current
17. Okhotsk Sea Gyre



-After Uda, 1958,
Dodimead et al, 1963.
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8
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10
11
12
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14
15
16
17
60°
50°
140°
160°
180°
160°
140°

chain. This, Wilimovsky maintains, would permit forms evolving in the Aleutians to drift west, but would prevent Japanese forms from moving east (Figure 82). Presumably, the Aleutian species might migrate as adults throughout the shallow Aleutian shelf but would be prevented from migrating to Asia by the deep, broad passes between the Rat, Near and Komandorski Islands. The pelagic larvae (Taranetz, 1941) could, however, drift across unidirectionally. Indeed, while both G. pistilliger and G. galeatus occur on both sides of these passes as one might expect if pelagic larvae were carried west no Japanese forms have conclusively been shown to exist in the Aleutians, again a predictable result if both adult and larvae are prevented from migrating east. Summarizing, it is impossible to say just where Gymnocanthus evolved. Assuming oceanographic conditions have remained more or less constant since the evolution of the genus, the author favours its origin as being in the Alaskan Aleutian chain.

Bolin (1947) postulated a primitive cottid to be a slightly compressed, heavy-bodied, large-headed form with four preopercular spines, teeth on the vomer (= prevomer), palatines, premaxillaries, and dentaries; four complete gills with the slit behind the fourth extensive; gill membranes joined, but free from isthmus; shortbased soft dorsal and anal fins; dorsals joined by membrane; split fin rays; ctenoid scales; anus only slightly in advance of anal fin; few cirri and no special intromittent organ. In several respects, Gymnocanthus is considerably evolved from the primitive cottid precursor in that it totally lacks palatine and prevomerine teeth; its dorsals are entirely separate, even to the extent that intermediate pterygiophores do not support rays or spines; all fins except caudal with simple rays; pelvics have been reduced to I, 3; the slit behind the last gill arch is small or wanting; scales are reduced and restricted in distribution, and a well developed, conical penis is present in males.

Gymnocanthus forms a very tightly knit group which is easily distinguished from all other extant cottid genera, and is clearly monophyletic in origin. So distinct is Gymnocanthus that it is impossible at this time to do any more than idly speculate on its intergeneric affinities. The intrageneric variation is slight enough, however, that most specific differences are probably due to divergent evolution, and that similarities are due to conservation of generic characters rather than convergence.

Gymnocanthus is thought to have evolved in several directions from the ancestral prototype which is postulated to be similar to G. herzensteini. This species possesses a deeper, more compressed head than other species (except G. intermedius), and has the most numerous and widely distributed scales. If G. herzensteini is primitive, then perhaps the low nape lacking ridges and tubercules characteristic of both this species and G. intermedius, and high fin count characteristic of G. herzensteini are also primitive. G. tricuspis, G. pistilliger, and G. intermedius possess subpectoral pistillae, and at least juveniles of both sexes have supraorbital cirri. Characters such as persistantly different cephalic ridge development, shape of pistillae, shape of head, and foremost, overlaping distributions exclude the possibility of these being subspecies or local morphs.

As already noted. G. intermedius shares with G. herzensteini the the narrow head and smooth nape, and may be derived from a G. herzensteini the narrow head and smooth nape, and may be derived from a G. herzensteini like ancestor.

G. tricuspis is a variable, widespread species and, in view of its very reduced armature, tubercle, and cephalic sensory canal pore development is probably a highly modified form. Schmidt (1928) lists his "Gymnocanthus tricuspis orientalis" as ranging from the Bering Sea to the Kara Sea. This form is apparently identical with the Bering and Chuckchi Sea specimens examined by me. Examinations of Arctic specimens reveals that there is a gradual shift from the smooth naped Chukchi Sea forms to the almost G. pistilliger-like forms in the Gulf of St. Lawrence. In the absence of any absolute break or even short-distance shift in morphometric or meristic characters, I suggest that G. tricuspis is a single, widely ranging species, and that Vladykov's (1933) and Schmidt's (1927) subspecies merely represent extremes of this variation. Pickard (1963) shows the prevailing Arctic currents to be clockwise. Dispersal is probably a consequence of both adult migration and passive larval transport, and the Arctic current cited may account for the greater range of "G. tricuspis orientalis" in the Asian Arctic than the American Arctic. Although meristically, G. tricuspis is intermediate between G. galeatus and the intermedius-pistilliger line, it is probably closer to the latter for reasons outlined previously.

G. galeatus, herzensteini, and detrisus all share an obsolete cleithral spine and high meristic characteristics, suggesting close relationship. G. detrisus has a strongly depressed head and a very broad interorbital and concomitantly narrow lachrymal, while G. herzensteini has a compressed head and a moderate interorbital. G. galeatus is variable, some specimens with slightly compressed heads reminiscent of the latter, but most specimens with weakly depressed heads like the former. I disagree with Soldatov and Lindberg (1930) and Vladykov (1933) who suggest that they are all subspecies. These species distributions are quite distinct, and they are always distinguishable on the basis of any of armature, width and shape of interorbital, head shape, or colour patterns. I suggest that the heavy scale development, unusual head shape, dorsal origin, and tubercle development tend to set G. herzensteini evolutionarily somewhat away from the other two species. Probably, G. detrisus and G. galeatus are very closely related in that only interorbital width and colour separate them.

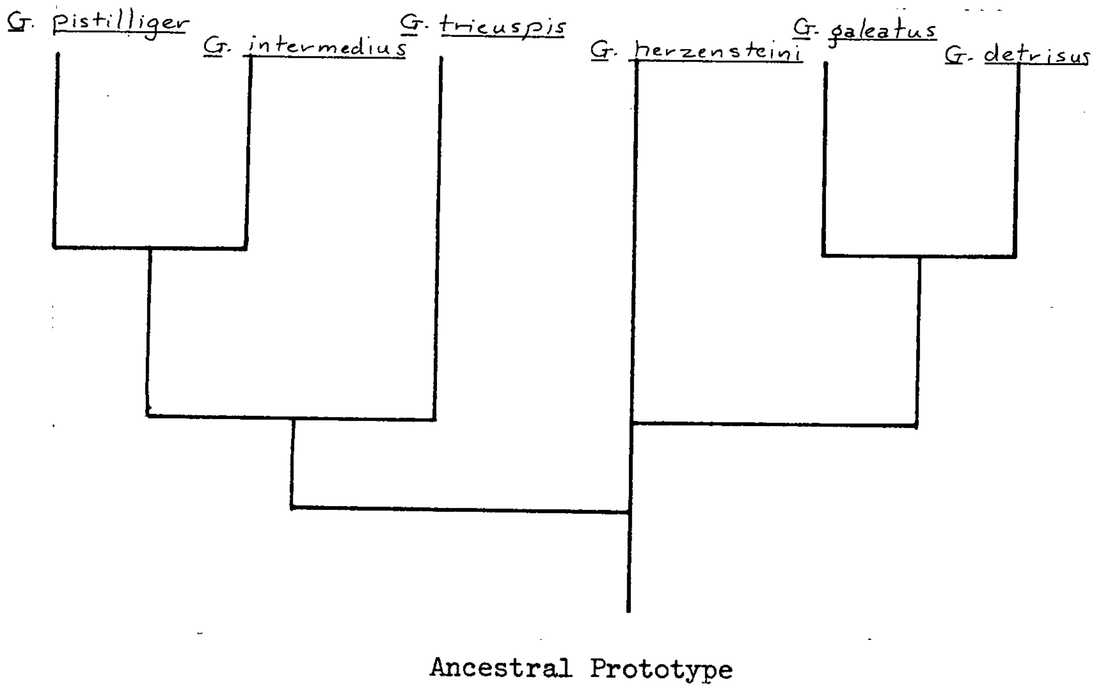

Figure 83. Hypothetical evolution of the species of Gymnocanthus.

Sandercock and Wilimovsky (1968) suggested that possibly as a result of Pleistocene sea level changes, several cottid forms have evolved in species pairs. _G. galeatus_ and _G. pistilliger_ are species pairs in that they occur sympatrically, look very similar, but are separated by depth. Though the data are weaker, _G. herzensteini_ and _G. intermedius_ also appear to occur sympatrically but are separated by depth. In contradiction to Sandercock and Wilimovsky, as pointed out earlier, I feel that these species pairs arose by parallel evolution of two lines rather than local divergent evolution.

Summary

1. The scorpaeniform fishes are one of the dominant piscine groups in the North Pacific.
2. One cottid genus, Gymnocanthus, contains six species all of which possess edentulous prevomer and palatines, bony granulations on the nape, pelvic formula I,3, gill membranes free from isthmus and other characters.
3. Cephalic sensory systems were demonstrated by injecting the canals of bleached specimens with Indian ink. A broad range of pore and dentritic development was evident, but differences between species were not constant enough to be taxonomically useful. Gymnocanthus galeatus generally had the most dentritic and porous system; G. tricuspis had the least dentritic and porous system.
4. A long taxonomic history, great variation, and wide range have resulted in the erection of seven genera and eleven nominal species. This paper recognizes one genus (Gymnocanthus) and six species (G. detrisus, tricuspis, galeatus, intermedius, herzensteini, pistilliger).
5. Species differences include meristic characters, form and development of sexual dimorphism, body and head depth, shape of back, interorbital width, preopercular spine lèngth, and colour. These differences are often slight but taken as a group are adequate to distinguish all six species.
6. Meristic characters, though often significantly different between species usually overlap greatly. Overlap may be reduced by lumping fin counts.

7. Some sexually dimorphic morphometric characters (pelvic fin, soft dorsal, spinous dorsal fin lengths) are log transformed and plotted against log transformed SL. The regression lines, though statistically significantly different between males and females within a species are seldom significantly different between males between species, due partly to the great variability of these characters, and partly to the frequently small samples. In _G. intermedius_, _pistilliger_, and _tricuspis_ sexual dimorphism appears at a smaller size than in the other three species.
8. Time of maturity and appearance of young suggest that _G. tricuspis_ spawns in late summer to autumn, while _G. pistilliger_, _galeatus_, and _herzensteini_ breed in late winter to early spring.
9. In all species, the largest specimens are females, suggesting that females grow more quickly than males.
10. Length-frequency histograms and otolith annuli counts suggest that in _G. galeatus_, _tricuspis_, and _pistilliger_ the sexual growth rate difference is greatest after the second year. _G. pistilliger_ and _tricuspis_ appear to be four year fish, while _G. galeatus_ may live longer.
11. All species except _G. tricuspis_ are from the North Pacific. Four (_G. detrisus_, _herzensteini_, _intermedius_, _pistilliger_) are found in the Northwest Pacific. Northeast Pacific representatives are _G. galeatus_ and _G. pistilliger_. _G. tricuspis_ is circumpolar, extending south only where there are very cold currents or water bodies.

12. The North Pacific species seem to prefer very low temperatures but avoid subzero (°C) temperatures. G. tricuspis is restricted to areas where subzero temperatures are sometimes encountered. This species may also be adapted to withstand greater salinity variation than the other five species can tolerate.

13. G. galeatus is a deeper ranging species than G. pistilliger. G. tricuspis tends to stay in the shallow water, possibly within the range of the warmed, less saline surface layer.

14. Gymnocanthus forms a very distinct, closely related group of species that are considerably evolved from the primitive form postulated by Bolin (1947).

15. The genus probably evolved in the Aleutian Islands and was carried west as planktonic larvae by currents. Migration as adults was possible throughout the shallow Aleutian shelf and Alaska peninsula, but not across the deep channel between the Near and Komandorski Islands.

16. Gymnocanthus has split into two lines of evolution, one containing G. tricuspis, intermedius, and pistilliger and characterized by the smaller maximum size, greater developed sexual dimorphism, and moderate to heavy cleithral spine, the other containing G. galeatus, detrisus, and herzensteini and characterized by the larger size, reduced dimorphism, and obsolete cleithral spine.

17. Though G. galeatus and G. pistilliger, and G. herzensteini and G. intermedius superficially fulfil the criteria of sibling species, they are postulated to have arisen by parallel rather than divergent evolution.

Conclusions

1. The genus *Gymnocanthus* is a well defined group of sculpins. Six species, *Gymnocanthus herzensteini*, *detrisus*, *intermedius*, *pistilliger*, *galeatus*, and *tricuspis* are recognized herein. No subspecies have been recognized.
2. No profound osteological differences between species exist.
3. All six species share a common basic cephalic sensory canal system. Though differences in degree of dendritic development occur between species, these systems are too variable to be of any value in distinguishing species.
4. The species are shown to have both distinct and overlapping distributions. Where distributions overlap, no hybridization is evident.
5. Most species can be distinguished by a combination of meristic characters, head length, interorbital width, predorsal length, cleithral spine development, and presence and shape of pistillae in males.
6. Meristic variation within a species may be minimized by totalling fin counts; total counts are often statistically significantly different (if not entirely different) between species.
7. In widely ranging species (e.g. *G. pistilliger*, *G. tricuspis*), total fin counts of specimens from widely separated parts of the range are not significantly different from each other.
8. The bony interorbital grows allometrically in young fish, isometrically in older fish. Head and predorsal length grow isometrically.

9. The spinous dorsal, soft dorsal, and pelvic fin length are sexually dimorphic in all species. These fins are proportionately longer in males, and these differences appear earlier in G. intermedius, G. tricuspis, and G. pistilliger than in G. herzensteini, G. galeatus, and G. detrisus.
10. Sexual dimorphism, present in all species is most pronounced in G. intermedius, G. tricuspis, and G. pistilliger.
11. Gymnocanthus is a cold loving group, being found only where arctic or subarctic water masses exist.
12. All species except G. tricuspis avoid below 0.°C. temperatures.
13. Gymnocanthus probably arose in the Aleutian Islands and was carried as planktonic larvae to Asian, migrating as adults through the rest of the range.
14. The genus is moderately modified from the presumed primitive form, and has divided into two lines of evolution, one containing G. pistilliger, G. intermedius, and G. tricuspis, the other containing G. galeatus, G. detrisus, and G. herzensteini.

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