

BREEDING TUBERCLES AND
CONTACT ORGANS IN FISHES:
THEIR OCCURRENCE,
STRUCTURE, AND
SIGNIFICANCE

MARTIN L. WILEY AND BRUCE B. COLLETTE

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MARTIN L. WILEY
Research Assistant Professor
Chesapeake Biological Laboratory

BRUCE B. COLLETTE
Assistant Laboratory Director
Bureau of Commercial Fisheries National Center for Systematics

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INTRODUCTION

BREEDING TUBERCLES are epidermal structures that function primarily in facilitating contact between individuals during spawning. They are used by some species for defense of nests and territories and perhaps for stimulation of females in breeding. Tubercles are present on some species in at least 15 families of fishes in four orders (see Summary of Families, page 151): Salmoniformes, suborder Salmonoidei (Salmonidae, Plecoglossidae, and Osmeridae) and suborder Galaxioidei (Retropinnidae); Gonorynchiformes, suborder Chanoidei (Kneriidae, Phractolaemidae); Cypriniformes, suborder Characoidei (Lebiasinidae and Parodontidae), and suborder Cyprinoidei (Cyprinidae, Gyrinocheilidae, Psilorhynchidae, Catostomidae, Homalopteridae, Cobitidae); and Perciformes, suborder Percoidei (Percidae). Superficially similar structures that are not sexually dimorphic have been reported in an African family of freshwater catfishes (Siluriformes, Mochokidae). Analogous dermal structures, known as contact organs, are present on the scales or fin rays of nine families in three orders: Atheriniformes, suborders Exocoetoidei (Belonidae) and Cyprinodontoidae (Oryziatidae, Cyprinodontidae, Anablepidae, and Poeciliidae); Cypriniformes, suborder Characoidei (Characidae and Gasteropelecidae); and Scorpaeniformes (Cottidae and Cottocomephoridae). In most species, breeding tubercles or contact organs are present only on the male or are more developed on the male than on the female.

Breeding tubercles and contact organs have long been known in the ichthyological literature under a bewildering variety of terms. Bloch

(1782) noted that tubercles have been described in an Italian minnow by Salviani (1557), and Kimura and Tao (1937) reported that pearl organs are mentioned in ancient Chinese literature. Most reports have been buried in taxonomic papers as part of the description of new species. Even the massive summary of the literature on reproduction of fishes by Breder and Rosen (1966) failed to find many of these scattered references. The purpose of the present paper is to summarize information on the occurrence, structure, and function of breeding tubercles and contact organs, to make generalizations about their importance to fishes, and to hypothesize about the origin of these structures. We believe that our paper will make more workers aware of breeding tubercles and contact organs and that systematists, ethologists, and other zoologists will look for these structures and use them in understanding the behavior and evolution of fishes. Wiley¹ (1969) compared the morphology and histology of the tubercles and contact organs of representative fishes in an attempt to devise a meaningful nomenclature for these nuptial structures. The literature review of the occurrence of breeding tubercles and contact organs was begun several years ago by Collette (1965). We have not tried to include all of the references on tubercles and contact organs; we have tried to include those we judged to be most important biologically and historically. We have collaborated on the biological and evolutionary significance of these structures.

¹ Adapted from a dissertation prepared in partial fulfillment of the requirements for the Ph.D. degree at The George Washington University.

SIGNIFICANCE OF KERATINIZATION

The ability to produce keratinized epidermal structures has been of great importance to tetrapods in their adaptation to a terrestrial existence. Among the various classes of tetrapods, a great variety of keratinized structures has evolved: desiccation resistant scales in reptiles; avian feathers for flight and insulation; mammalian hair; and warts, tubercles, claws, nails, and horns that serve many functions. Comparatively few fishes, however, have developed keratinized structures. Some authors (e.g. Burgess, 1956)

have even stated that it is unlikely that a keratinized layer is ever found in fish epidermis. The secondary sexual structures known as breeding tubercles, or pearl organs, are composed of substantial amounts of keratin. They are common in several families of cypriniform fishes and they are also known in a few gonorynchiform and salmonoid fishes. Similar epidermal tubercles occur on the scales of many colubrid snakes (Blanchard, 1931). Other examples of keratinized structures are the horny teeth of cyclo-

stomes (Jacoby, 1894; Warren, 1902; Sognaes and Lustig, 1955), the sharp jaws in many species of herbivorous minnows (for example, *Parabramis* [= *Megalobrama*] *terminalis*, Wu and Wang, 1932), and the horny teeth on the lips of the young in others (Kaiser, 1962); the frictional surface of the adhesive apparatus in various homalopterids, cyprinids, and silurids (Hora, 1922a; Saxena, 1959, 1961); and the occipital organ in the gonorynchiform genus *Kneria* (Peters, 1967).

FUNCTION

Breeding tubercles are present in regions that come in contact with the female or other males. They have three inferred primary functions: maintenance of body contact between the sexes during spawning; defense of nests and territories; stimulation of the females in breeding (see Reighard, 1903, 1904, 1910a, 1910b, 1943; Raney, 1940c). They may also function in sex and species recognition in some species. Males of species with well-developed tubercles are more likely to fight and hold territories (Hubbs and Cooper, 1936; Raney, 1947a). There is little evidence to support the suggestion made by Reighard that tubercles protect body and fin surfaces in nest building; that made by Branson (1962a) that tubercles also function in "holding to the substrate during oviposition" or "in tending the nest and eggs"; or that made by Branson (1962b) that anterior head tubercles are used "for scooping out the redd."

Contact organs are also present on those parts of the body and fins of the male which come in direct contact with the female during pre-spawning behavior or during the spawning act. The correlation between contact organ location and behavior suggests that they may be tactile, enabling the male to determine his exact position relative to the female (Foster, 1967). There is some morphological evidence that contact organs are tactile receptors. Vital staining of the anal fin rays of *Oryzias latipes* with methylene blue showed better innervation of the contact organ-bearing fin rays of the male than those of the female which lack contact organs (Egami and Nambu, 1961). By special staining, W. M. Kaill has shown that the anal fin contact organs of males of the African cyprinodont *Nothobranchius guentheri* each appear to receive a lateral branch from a nerve fiber which runs the length of the fin ray (see Foster, 1967, p. 556).

MORPHOLOGY AND HISTOLOGY

Most of the morphological and histological studies on nuptial tubercles have been done on various species of the Cyprinidae—for example: Solger (1879), Leydig (1892, 1895), Maurer (1895), Tozawa (1923, 1929), Graupner and Fischer (1933), Sato (1935), and Kimura and Tao (1937). Similar studies were made on the tubercles of a species of the Cobitidae by Jakubowski and Oliva (1967), on the contact organs of a species of the Oryziatidae by Oka (1931), on the tubercles of *Plecoglossus altivelis* by Ebina (1929), and on the tubercles of *Osmerus* by Richardson (1942).

Comparisons of nuptial tubercle morphology and histology reveal a number of highly significant differences among and within ordinal categories. Because of the extent and nature of these differences it is obvious that "nuptial tubercles" and their functional analogs, contact organs, have evolved independently in a variety of fish groups.

KINDS OF NUPTIAL TUBERCLES

Nuptial tubercles may be grouped into three general categories on the basis of their structure: (1) Tubercles consisting of aggregations of non-keratinized epidermal cells (if keratinization is present, it is confined to the most superficial layers of cells and may form a light cuticle). (2) Tubercles containing substantial numbers of fully keratinized cells that are organized to form a discrete, usually conical cap, a major component of the tubercle. (3) Contact organs (a term proposed by Newman, 1907) composed of dermal bony outgrowths or spicules projecting from a fin ray or scale margin and surrounded by the epidermis, through which the bony outgrowths may protrude.

KERATINIZATION PROCESS

The process of keratinization appears to be essentially the same in most of the fishes examined in the present study. Epidermal cells are produced by mitoses in a columnar to cuboidal stratum germinativum next to the basement membrane. The cells in more superficial layers hypertrophy and become polygonal. They are characterized by large vesicular nuclei with one or more prominent nucleoli and abundant, often granular, acidophilic cytoplasm. Well-developed intercellular spaces and many intercellular

bridges usually lie between the hypertrophied cells. The transition between hypertrophied cells and the keratinized layer is so abrupt that the transitional stage is rarely observed. During keratinization, the nuclei disappear or persist as pyknotic remnants in the flattened, irregular cells of the keratinized layer. The keratin becomes light orange to red, in Mallory's triple stain. In a typical preparation, undifferentiated epidermal cells of the germinal layer have light blue cytoplasm that becomes darker blue as cells hypertrophy and accumulate prekeratin granules, and violet in the largest cells before keratinization. The nuclei of hypertrophied cells contain prominent, darkly stained nucleoli. Figure 1 is a diagrammatic drawing of a *Phractolaemus ansorgei* tubercle (fig. 3D). In morphology it is typical also of many of the larger cyprinid tubercles that develop vascularized dermal papillae which extend into the hypertrophied epithelium of the tubercle core.

EXPERIMENTAL STUDIES

In most fishes, breeding tubercles and contact organs begin to develop before the spawning season, reach their maximum extent just before or during the spawning season, and then break off, slough off, become eroded, or gradually regress. The gonads and the pituitary seem to be the main organs that affect development of these nuptial structures. Many authors have studied

the effects of hormones on breeding colors, gonads, and ovipositor lengths in fishes (see summaries in Bretschneider and Duyvené de Wit, 1947; Hoar, 1951; Dodd, 1955; and Pickford and Atz, 1957) but most have ignored the effects on breeding tubercles or contact organs. What is known about the control of nuptial structure development comes mainly from Japanese research on breeding tubercles in the Cyprinidae and contact organs in the Japanese medaka, *Oryzias latipes*. Some information is also available for the Cobitidae and Plecoglossidae.

Gonadectomy prevents the development of nuptial structures or causes those already present to regress or to be shed more quickly than in normal males, as shown for goldfish (*Carassius auratus*) by Tozawa (1927, 1928); Japanese bitterling (*Acheilognathus intermedius*) by Tozawa (1929); Japanese medaka by Okada and Yamashita (1944); and a loach (*Misgurnus anguillicaudatus*) by Kobayashi (1951). Female *Oryzias* develop contact organs after testis transplantation (Nagata, 1936; Okada and Yamashita, 1944). Tubercles appeared on males of the bluntnose minnow (*Pimephales notatus*) after intraperitoneal injection of pituitary extract from unsexed carp and from frogs, sheep, and humans (Ramaswami and Hasler, 1955). Estrogen (estradiol) also caused tubercles to form on males of *P. notatus*. Ramaswami and Hasler

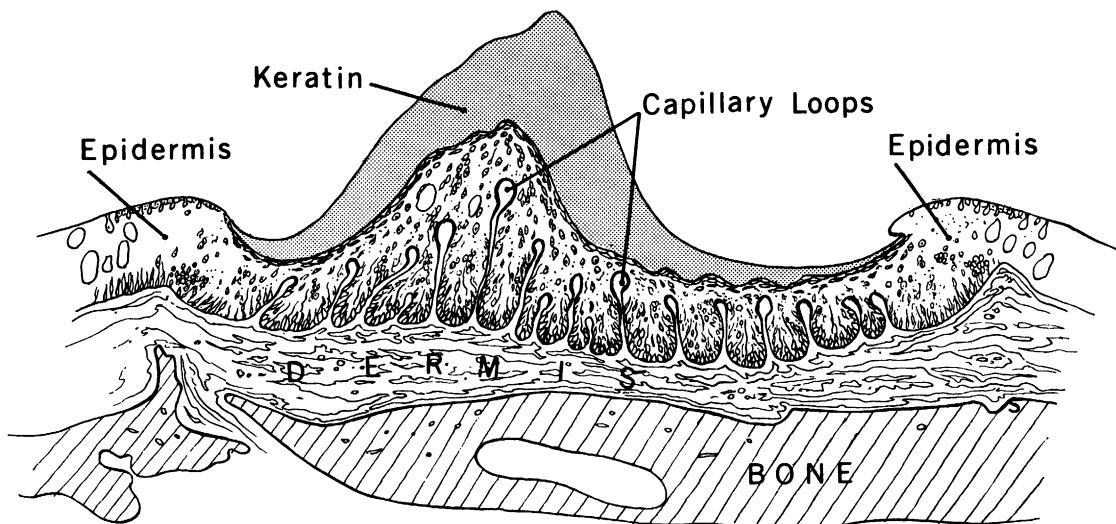


FIG. 1. Diagrammatic drawing of a section through a postorbital tubercle of *Phractolaemus ansorgei*. The hypertrophied epithelium supporting the keratinized cap is vascularized by blood vessels from the dermis. Compare with figure 3D.

determined further that testosterone propionate caused tubercles to develop in both sexes of *P. notatus*. Several hormones caused the development of nuptial structures in females whether or not they normally develop them: methyl-dihydro-testosterone in *Misgurnus* (Kobayashi, 1951); methyl-dihydro-testosterone (Okada and Yamashita, 1944; Egami, 1954c), testosterone propionate (Egami, 1954a), methylandrosterone diol and dehydroisoandrosterone (Arai and Egami, 1961), and 11-ketotestosterone (Arai, 1967) in *Oryzias*; and testosterone propionate in the minnow *Nocomis biguttatus* (Ramaswami and Hasler, 1955). Esterone slightly inhibits the development of contact organs of female *Oryzias* kept in solutions of testosterone propionate (Egami, 1954a). Thiourea also inhibits contact organ development of females kept in this solution and thyroxine counteracts this inhibitory effect (Egami, 1957).

Temperature and light also play a role in the development of nuptial structures. Contact organs develop faster at higher temperatures in androgen-treated females of *Oryzias* (Egami, 1954d). Their development becomes arrested if the fish are exposed to low temperatures, and development ceases at temperatures below 10° C. Pickford and Atz (1957, p. 469), who reported on unpublished observations of W. Chavin, noted that breeding tubercles appeared on males of the goldfish (*Carassius auratus*) within two weeks after increase in light duration from eight to 12 hours a day. The tubercles disappeared three to four weeks after a decrease in light from 12 to eight hours a day. Shiraishi and Takeda (1961) found that tubercles developed most quickly at a certain optimum of light duration in the ayu, *Plecoglossus altivelis*. All males held at eight hours daylight developed tubercles after one month. Males held at four and nine hours developed tubercles slightly later, as did the controls held in natural light. Males held at 12 hours of light needed four months for all individuals to develop tubercles, and males held at 16 hours of light never developed tubercles. Results for females were similar but less conclusive as females are much less apt to develop tubercles.

SYSTEMATIC VALUE

In addition to their functional significance, patterns of breeding tubercle and contact-organ distribution offer an aid to the understanding of species relationships. Similar distributions of contact organs or tubercles suggest similar reproductive behavior patterns, and behavioral similarities in turn suggest relationships. However, different distribution patterns may arise in closely related species through reinforcement of behavioral isolating mechanisms where the species are sympatric. Thus it does not follow that different distributions of nuptial structures mean that the species in question are unrelated. The reproductive patterns themselves are valuable characters, but they are far more difficult to use because live specimens are required for their study. Awareness of breeding tubercles aids the ethologist and the systematist because the study of tubercle development and distribution in preserved material may allow prediction of spawning behavior. Studies that utilized tuberculation as a systematic character are numerous in the Cyprinidae (Hubbs, 1930; Hubbs and Black, 1947; Gibbs, 1957a). In revisionary work now being done by Ernest A. Lachner on the genus *Nocomis*, nuptial tuberculation is one of the primary characters used to differentiate species-groups, species, and subspecies. Vladykov (1935) found that differences in sexual dimorphism were correlated with generic differences in the Chinese Cobitidae. Collette (1965) used breeding tubercles as an important character in darter (Percidae) classification.

Contact organs have also been used as systematic characters. In the Cyprinodontidae, Newman (1907, 1909) related contact organ function and structure to breeding biology, and Stenholt Clausen (1967) considered the phylogenetic implications of contact organ distribution in several African genera. Neal R. Foster has found contact organs to be valuable characters in his long-term studies on the evolution of reproductive behavior in cyprinodontoids (Foster, 1963, 1967, personal commun.). Géry used the distribution of contact organs as a systematic character in a series of papers on the Characidae (especially 1963a, 1964a, 1966b).

SUMMARY OF FAMILIES OF FISHES WITH EPIDERMAL BREEDING TUBERCLES
AND DERMAL CONTACT ORGANS¹

- Superorder Protacanthopterygii
 Order Salmoniformes
 Suborder Salmonoidei
 Salmonidae: trouts and whitefishes; Holarctic; fresh water; tubercles
 Plecoglossidae: East Asia; anadromous; tubercles
 Osmeridae: smelts, Holarctic; marine and fresh water; tubercles
 Suborder Galaxioidei
 Retropinnidae: whitebait; Australia and New Zealand; marine and fresh water; tubercles
 Order Gonorhynchiformes
 Suborder Chanoidei
 Phractolaemidae: Africa; fresh water; tubercles
 Kneriidae: Africa; fresh water; tubercles
 Superorder Ostariophysii
 Order Cypriniformes
 Suborder Characoidei
 Characidae: characins; Africa and South America; fresh water; contact organs
 Gasteropelecidae: hatchet fishes; South America; fresh water; contact organs
 Lebiasinidae: South America; fresh water; tubercles
 Parodontidae: South America; fresh water; tubercles
 Suborder Cyprinoidei
 Cyprinidae: carps and minnows; North America, Africa, Eurasia; fresh water; tubercles
 Gyrinocheilidae: Southeast Asia; fresh water; tubercles
 Psilorhynchidae: Southeast Asia; fresh water; tubercles
 Catostomidae: suckers; North America and Asia; fresh water; tubercles
 Homalopteridae: Southeast Asia; fresh water; tubercles
 Cobitidae: loaches; Eurasia; fresh water; tubercles
 Order Siluriformes
 Mochokidae: catfishes; Africa; fresh water; neither
 Superorder Atherinomorpha
 Order Atheriniformes
 Suborder Exocoetoidei
 Belonidae: needlefishes; world wide; fresh water and marine; contact organs(?)
 Suborder Cyprinodontoidei
 Oryziatidae: medakas; Asia; fresh water; contact organs
 Cyprinodontidae: killifishes; North and South America, Eurasia, Africa; fresh water and marine; contact organs
 Anablepidae: four-eyed fishes; Central and South America; fresh water; contact organs
 Poeciliidae: North and South America; fresh water; contact organs
 Superorder Acanthopterygii
 Order Scorpaeniformes
 Suborder Cottoidei
 Cottidae: sculpins; Holarctic; marine and fresh water; contact organs
 Cottocomphoridae: Lake Baikal, Siberia; fresh water; contact organs
 Order Perciformes
 Suborder Percoidei
 Percidae: perches and darters; North America and Europe; fresh water; tubercles

¹ Classification based on Greenwood, Rosen, Weitzman, and Myers, 1966.

MATERIALS AND METHODS

Most tuberculate specimens were obtained from museum collections. A few species of locally abundant North American fishes were collected expressly for the present study. Because gross morphology of tubercles and contact organs is of primary importance to the study, alcohol-fixed specimens (sometimes as old as 50 to 75 years) were used if formalin-fixed specimens were not available.

Because of the hardness and fragility of many of the tubercles, especially in old alcohol-fixed specimens, some experimentation was necessary to find the best method for sectioning. Tissuemat of 60° to 62° C. melting point proved to be most convenient for embedding and sectioning small or lightly keratinized tubercles. Large, highly keratinized tubercles were best processed by embedding in celloiden (Parlodion). Sections were cut on a rotary microtome at 10 μ for Tissuemat embedments, and at 7–10 μ for celloiden embedments after the block was impregnated with cedar oil (Humason, 1962). At first, sections were stained with hematoxylin and eosin, Mallory's triple stain, or hematoxylin for demonstrating nuclei and then Mallory's triple stain to differentiate tissues. For triple staining, however, the rapid one-step method with the Mallory-Heidenhain stain (Humason, 1962, after Cason, 1950) was found to be most convenient and reliable for differentiating tissues. Sections were cleared in xylene and mounted under glass with Permount.

ABBREVIATIONS

Specimens used for the present study are from the collections of the institutions that are listed below:

- A.N.S.P., Academy of Natural Sciences of Philadelphia
- B.M.N.H., British Museum (Natural History), London
- D.M., Dominion Museum, Wellington, New Zealand
- F.M.N.H., Field Museum of Natural History, Chicago
- K.U., University of Kansas Natural History Museum, Lawrence
- M.C.Z., Museum of Comparative Zoology, Harvard University, Cambridge
- M.N.H.N., Museum National d'Histoire Naturelle, Paris
- M.S.N.G., Museo Civico di Storia Naturale di Genova

- S.I.O., Scripps Institute of Oceanography, University of California, San Diego
- U.B.C., University of British Columbia, Vancouver
- U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor
- U.S.N.M., United States National Museum, Smithsonian Institution, Washington, D.C.
- Z.M.A., Zoologisch Museum, Universiteit van Amsterdam

Data included with each collection studied (when available) are the museum number, sex, and standard length (S.L.) in millimeters, abbreviated locality, and date of collection.

The order of presentation follows the classification of Greenwood et al., 1966 (see footnote on p. 151). Museum and literature names were generally accepted except when they were obviously incorrect.

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(Percidae); Dr. Ernest A. Lachner (Cyprinidae); and Dr. Stanley H. Weitzman (Characoidae). Mr. Samuel P. Atsides surveyed material of Cyprinodontoidae for contact organs and Lebiasinidae for breeding tubercles.

TUBERCLE DESCRIPTIONS

ORDER SALMONIFORMES

FAMILY SALMONIDAE

THE SALMONIDAE include three subfamilies (Norden, 1961): the Salmoninae (trouts and salmon); the Thymallinae (graylings); and the Coregoninae (whitefishes). Tubercles have been reported for two species of the Salmoninae, no Thymallinae, and numerous species of the Coregoninae.

SUBFAMILY SALMONINAE

Five genera in the Salmoninae are recognized (Norden, 1961): *Brachymystax* Günther (one species); *Hucho* Günther (four); *Salvelinus* Nilsson (about 13); *Salmo* Linnaeus (about nine); and *Oncorhynchus* Suckley (six). Other authors (Vladykov, 1954; Rounsefell, 1962) separate the monotypic *Cristivomer* Gill and Jordan from *Salvelinus*. Pappenheim (1909) reported tubercles on males of *Hucho hucho* (Linnaeus) at spawning time. Vladykov (1954) found that both sexes of *Cristivomer namaycush* (Walbaum) are tuberculate, and he illustrated tubercles on the scales anterior to the anal fin of a breeding male. *Cristivomer* is primarily lacustrine; other genera of Salmoninae are either anadromous, or at least more fluviatile (Berg, 1948, 1949; Rounsefell, 1958). Apparently, *C. namaycush* is the only species of the Salmoninae that spawns almost exclusively in lakes without constructing a redd (Royce, 1951; Rounsefell, 1958). It also lacks almost completely the specialized jaws or kype common to mature males of other species (Royce, 1951). In possession of breeding tubercles, lack of a kype, lack of sexual dimorphism, and almost exclusive lacustrine spawning, always without redd-building, *Cristivomer namaycush* shows surprising similarity to the Coregoninae. Males of the Atlantic salmon, *Salmo salar* Linnaeus, and the sea-trout, *Salmo trutta trutta* Linnaeus, were described by Menzies (1931) and Stokłosowa (1966) respectively, as developing rough and thickened skin during the breeding season. As Stokłosowa indicated, the thickened skin may be an adaptation that is functionally analogous to tuberculation in other fishes.

SUBFAMILY THYMALLINAE

The grayling subfamily consists of four species

in the genus *Thymallus* Cuvier (Berg, 1948, 1949; Norden, 1961). There are no reports of tubercles for this subfamily and we were unable to find tubercles on breeding males of *T. arcticus* (Pallas). While spawning, the male and female press tightly against each other and the greatly enlarged dorsal fin of the male is partly folded over the female (Fabricius and Gustafson, 1955).

SUBFAMILY COREGONINAE

Three genera are presently recognized (Norden, 1961): *Prosopium* (six species), *Coregonus* (about 20, including *Leucichthys*), and *Stenodus* (one). Tubercles have been reported on males of species in each genus and on females of some species.

Koelz (1929) is one of the few authors to use the distribution of breeding tubercles in the taxonomy of the Coregoninae. He attempted to separate the Great Lakes whitefishes into three groups on the basis of patterns of breeding tubercles: *Leucichthys*, tubercles of uniform thickness on the head and sides of male; *Coregonus*, tubercles distributed similarly but thickened medially and present on both sexes; *Prosopium*, tubercles present laterally but not on head. Unfortunately, we have found that these differences break down when adequate material is examined.

GENUS PROSOPIUM MILNER

Tubercles have been reported for at least three of the six species of round whitefishes: *Prosopium coulteri* (Eigenmann and Eigenmann), *P. williamsoni* (Girard), and *P. cylindraceum* (Pallas). We have examined tuberculate material of *P. coulteri* and *P. williamsoni*.

Both sexes of *Prosopium coulteri* are tuberculate. Males taken on May 23 (U.B.C. uncat., British Columbia, Outlet Bay, Cluculz Lake) have small white tubercles in the center of most of the lateral body scales but not on the lateral line scales. The tubercles extend onto four to six rows below and four rows above the lateral line. All the fins, except the adipose, are tuberculate: the rays of the lower half of the caudal fin; all of the anal rays; the dorsal rays, concentrated on the anterior three rays and the distal part of the posterior rays; the upper and lower surface of

the pelvic rays, but better developed on the upper surface; the upper surface of the pectoral rays, on the distal portion of the anterior five to six rays. Tubercles are present on the head: maxillary, dentary, branchiostegals, lower margins of the opercular bones, anterior to and below the eyes, and a scattered few on top of the head. Weisel and Dillon (1954) reported that tubercles are better developed on males than on females in *P. coulteri*. Eschmeyer and Bailey (1955) noted that males have larger rayed fins, which are probably involved in spawning.

The lateral distribution of tubercles on *P. williamsoni* is similar to that on *P. coulteri*, but tubercles appear to be absent from the head and fins. Tubercles begin to develop on males by early September (U.B.C. No. 56-577, British Columbia, Flathead River). They are present on eight to 10 rows of lateral scales on males by late October and early November (U.B.C. No. 62-33, and U.B.C. No. 63-2, British Columbia, Kokanee Creek). Occasionally a few are present on the dorsum from the posterior part of the head to the dorsal fin origin. None was found on the head or fins of these specimens but they may develop later as in *P. coulteri*. Females in these collections have tubercles on about six rows of lateral scales. Ellis (1914) reported tubercles on the sides of breeding males of *P. williamsoni*. Brown (1952) reported that spawning occurs in November in Montana with groups of two to five fish pressed against each other over gravel and rubble in riffle areas of streams.

Bensley (1915) and Koelz (1929) reported tubercles on about eight rows of lateral scales in males of *P. cylindraceum* from Georgian Bay, Ontario and Lake Huron in October and November. Normandeau (1969) used the stronger development of tubercles in males to sex fishes in his ecological study of this species in New Hampshire.

***Prosopium williamsoni* (Girard)**

Figure 2A

Male, 231 mm., S.L. U.S.N.M. No. 199462. Canada, British Columbia, November, 1962. A tubercle is formed by hyperplasia, a local thickening of the epidermis over the scale due to increase in the number of cells. Cell boundaries in the tubercle are indistinct and irregular but the cells are 10-15 μ in diameter, the same size as the ordinary epidermal cells outside the tubercle. With Mallory's triple stain, the cyto-

plasm is bright blue in the unkeratinized part and appears fibrous. It resembles collagen in appearance and staining reaction. The height of the tubercle section is 434 μ from the outer bony surface of the scale to tip. All the cells above a plane parallel to the scale surface are keratinized and they form a hemispheroid layer 184 μ thick and 556 μ wide. With H and E stain, the remnants of nuclei are prominent in the keratinized cells. Cellular detail, especially nuclear structure, is in general poor in this specimen.

In the ordinary epidermis and under the central part of the tubercle, cells of the germinal layer next to the basement membrane are cuboidal. In the area under the periphery of the tubercle, however, where the epidermis is thicker due to hyperplasia, the germinal layer and many of the cells in the layers above are columnar. Proceeding mesially, the longitudinal axes of the columnar cells tilt toward the center of the tubercle. In the deepest layers below the keratinized portion, the germinal layer is again cuboidal whereas the eight to 10 layers immediately above are oriented with their longitudinal axes parallel to the scale surface. Above them the cells are irregular in shape and organization.

The tilting of the cell axes noted above is peculiar to this species and may be due to centripetal forces exerted on the structure by shrinkage of the keratinized mass of cells at the surface. Another significant feature is that cell hypertrophy plays little or no part in development of the tubercle, a situation that is in contrast to all other keratinized tubercles studied.

GENUS COREGONUS LINNAEUS

There are numerous hard-to-identify species in northern and central Europe, northern Asia, and North America. We use the names given by the authors who have described tubercles. Typically, tubercles are present on the lateral scales in both sexes and they extend onto the head and fins in some species.

Tubercles are very well developed on males of *Coregonus clupeaformis* (Mitchill) from Squanga Lake, Yukon Territory, Canada (U.B.C. No. 60-665, November 28). The tubercles are large and white, elongated longitudinally and flattened dorsoventrally, and are concentrated on three rows of scales above and four rows below the lateral line. They extend from the center of the exposed field of a scale to its posterior margin. The tubercles on the scales above and below

these rows are smaller, rounder, and do not extend to the posterior border of the scale. Medium to small tubercles are scattered over the head including the branchiostegal rays. Tiny round tubercles are present on the dorsum and venter. Occasionally, tiny tubercles lie in a row on the leading pectoral and pelvic rays, also on the other rays, but on the latter they are still smaller. In a few specimens, they are present at the edges of the caudal fin rays. Females also have tubercles, but these are not as well developed as those of the male.

Many publications carry records of tubercles in European species of *Coregonus*. Early reports include: Siebold (1863) on both sexes of *Coregonus wartmanni* (Bloch); Nüsslin (1882) on *C. macrophthalmus* Nüsslin; Seeley (1886) on European species of *Coregonus*; Fatio (1890) on both sexes of *C. exiguus bondella* Fatio (with a color plate); Smitt (1892, 1895) on both sexes of *C. lavaretus* (Linnaeus); and Pappenheim (1909) on males of *C. oxyrhynchus* Linnaeus. In four species of *Coregonus*—*C. wartmanni*, *C. macrophthalmus*, *C. fera* Jurine, and *C. acronius* Rapp—Wagler (1937, pp. 438–439) found that both sexes were tuberculate, tubercles were better developed in males than in females, and the amount of tuberculation increased with the age of the fish. Berg (1948, 1949) reported tubercles on: *C. subautumnalis* Kaganowsky, scales above lateral line of males and sometimes in females; *C. nasus* (Pallas), head, fins, and part of the body of males and females but more numerous on males; *C. lavaretus lavaretoides* Berg, sides of head of males; *C. lavaretus muraenoides* Polyakov, elongate tubercles in rows on scales of both sexes; *C. lavaretus baicalensis* Dybowski, sides of body; and *C. lavaretus pidschian* Ruzskii, sides of body and head of males.

The first and most complete descriptions of breeding tubercles in North American *Coregonus* were by Koelz (1929) who described their distribution for each population of each species of Great Lakes *Coregonus* (including *Leucichthys*) where breeding material was available. He found that tubercles were concentrated on the lateral scales for several rows above and below the lateral line. In some species, tubercles extended onto virtually all the scales. He used breeding tubercle development and gonad development to determine the time and location of spawning. Both sexes are usually tuberculate but the tubercles are better developed in the male.

Coregonus clupeaformis (Mitchill) had the greatest extent of tuberculation, with tubercles covering the body, most of the head, the branchiostegal rays, the longest rays of the pectoral, pelvic, and caudal fins, and the first rays of the dorsal fin.

Other reports of tubercles on North American *Coregonus* are less complete. Pritchard (1928, 1930) reported tubercles on several rows of lateral scales on males of *C. artedi* LeSueur from Lake Ontario. They were more abundant on larger males than females and different from the horny pearl organs of the Cyprinidae and Cato-stomidae. McAllister (1962) reported tubercles on the head and body of *C. nasus* (Pallas) and *C. clupeaformis*. Lindsey (1963) discussed the Squanga Lake *C. clupeaformis* described above and presented a photograph of a highly tuberculate male. Specimens of *C. clupeaformis* taken in June (Squanga Lake, Lindsey, 1963), July (U.B.C. No. 58–267, Alaska), and September (U.B.C. No. 60–311, Northwest Territories) have poorly developed tubercles. Bensley (1915) and Hart (1930) also described the tubercles of *C. clupeaformis* (Georgian Bay and Bay of Quinte, Ontario) and Hart reported that spawning occurs at the end of October and the beginning of November.

The primary function of breeding tubercles in *Coregonus* is to maintain contact between the male and female during spawning. Fabricius and Lindroth (1954) reported that spawning pairs swim side by side pushing against each other. The conspicuous white color may enable the tubercles to function also as visual signals, and their hardness may provide tactile stimulation (Fabricius and Lindroth, 1954). Nüsslin (1907) believed the tubercles to be involved in stimulation, but Wagler (1941) pointed out that they lack sense organs.

***Coregonus clupeaformis stanleyi* (Kendall)**

Figure 2B

Male, 194 mm., S.L. U.S.N.M. No. 126878. Maine, Aroostook County, October 22, 1901. Tubercles present on all the scales of the body, those along the midline elongate, forming longitudinal keels. Tubercles are scattered sparsely and irregularly over the head.

A tubercle from below the dorsal fin near the lateral line is 295 μ high from basement membrane to tip and approximately 880 μ wide. The tubercle has no well-defined keratinized layer as in *Prosopium williamsoni*, possibly because the

tubercle is not completely developed. Some of the cells near the apex stain dark red but others are very dark blue. Cytologically the unkeratinized cells appear identical to those in *P. williamsoni* with fibrous-appearing basophilic cytoplasm.

PLECOGLOSSIDAE, OSMERIDAE, AND RETROPINNIDAE

The tubercles of *Plecoglossus*, the various smelts, and the retropinnids all have similar morphology, the chief differences being in shape and size. All are characterized by slight to moderate amounts of cellular hypertrophy and none to slight amounts of keratinization in the surface layers. *Mallotus catervarius* is unusual in that the largest hypertrophied cells are those nearest the stratum germinativum, and the cells nearer the surface are smaller. This situation is the reverse of the usual one. The bony, longitudinal thickening of the pectoral fin rays of *Spirinchus thaleichthys*, upon which tubercles are borne, appears to be similar to that described by Tang (1954) for the cyprinid, *Aristichthys nobilis*.

FAMILY PLECOGLOSSIDAE

The ayu, *Plecoglossus altivelis* Temminck and Schlegel, of rivers in Japan, China, and Korea, is the only species in this family. Jordan and McGregor (in Jordan and Hubbs, 1925, pp. 147-149) first reported that breeding male *Plecoglossus* have three cone-shaped wartlike pearl organs on the exposed surface of each scale and tubercles on the fin rays, particularly the anal fin. Ebina (1929) gave a more detailed description of the "nuptial organs" in adult males, writing that in October and November they cover almost the entire body surface, the head, gill covers, scales, adipose fin, and rays of all the other fins. These tubercles differ from those of cyprinids because they lack an outer cornified layer. Ebina also found large unicellular glands in the tubercles of *Plecoglossus*. Ebina (1930) and Matsui (1950, p. 23) reported that females also develop tubercles but they are not as widely distributed on the body, nor are they so well developed. Shiraishi and Takeda (1961) reported on the effect of photoperiodicity on the development of tubercles in this species.

Plecoglossus altivelis Temminck and Schlegel
Figure 2C, D

Male, 147 mm., S.L. U.S.N.M. No. 203421.

GENUS STENODUS RICHARDSON

Berg (1948, p. 310) noted the presence of breeding tubercles on the head and sides of males of *Stenodus leucichthys* (Güldenstädt) during the spawning season.

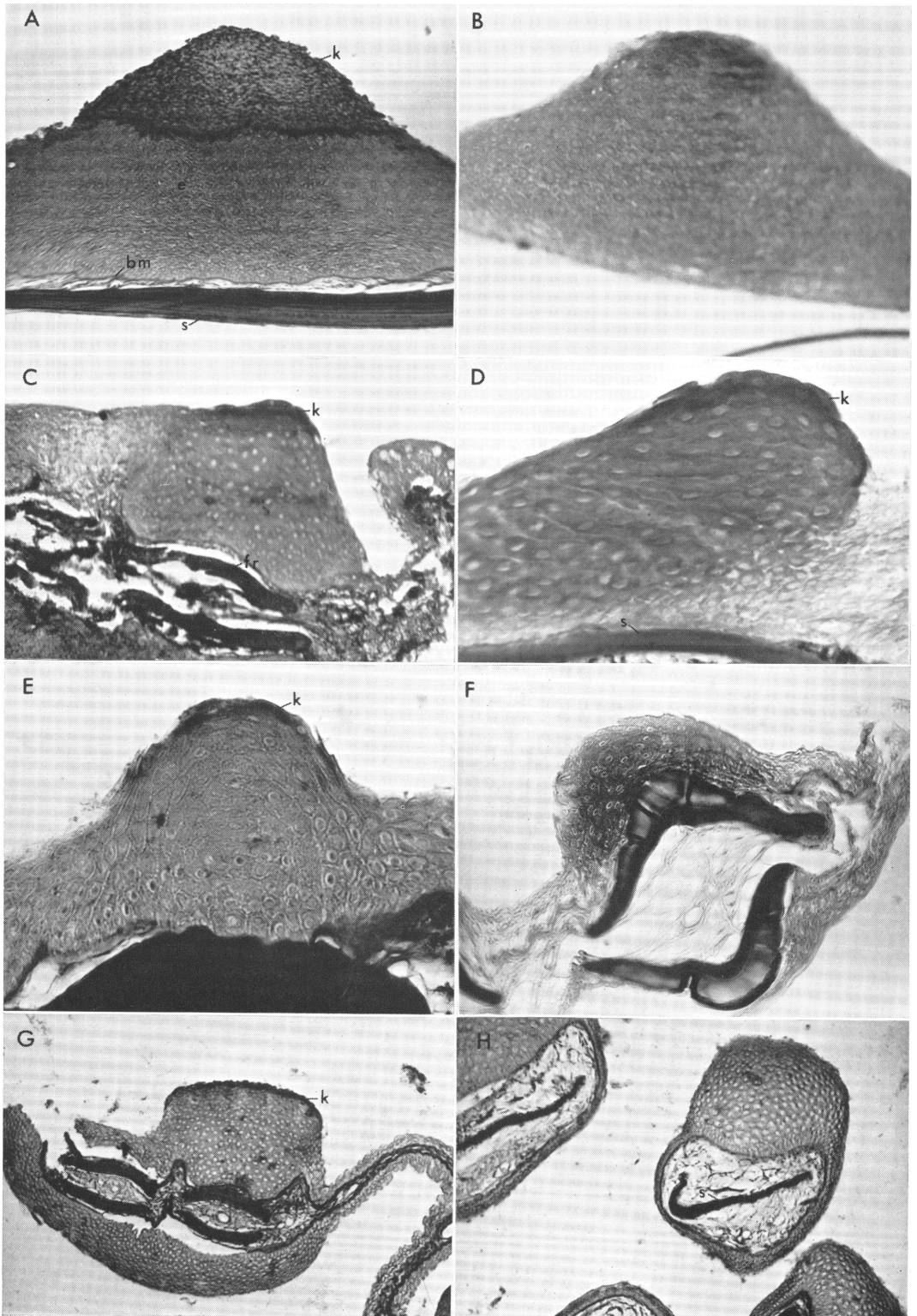
Japan. The specimen does not appear to have maximum development of the tubercles. Fine tubercles are on all the fins and on the dorsal and lateral surfaces of the head and body of nuptial males. The following description generally agrees with that of Ebina (1929) except that we found no unicellular glands in the tubercle.

A section of an anal fin ray tubercle is 213 μ high from the basement membrane to the tubercle tip and is about 360 μ wide. The tubercle is formed by hypertrophy of epidermal cells above the cuboidal germinal layer. Nuclei are large and vesicular and intercellular bridges are numerous and prominent. Most of the hypertrophied cells are somewhat flattened so that in section they are spindle shaped with the longitudinal axes oriented parallel to the basement membrane. The cells on the surface are squamous but much thicker than in ordinary epithelium (8-13 μ vs. 2 μ). Keratinization is slight; those cells having a red stain with Mallory's triple stain are irregularly distributed at the tubercle apex and the other squamous cells have a violet color. Even in the red-stained cells, nuclei are present. No "cuticle" as described by Ebina (1929) is apparent but, assuming that the tubercles of this specimen were not completely mature, a cuticle formed by complete keratinization of the outer cell layer might have developed later.

On anal rays 2 to 5 the tubercles are larger (400-500 μ diameter) than those sectioned. They are so crowded that in outline they form irregular polygons rather than circular ones, as do the smaller, less crowded tubercles. On some of the scales, particularly those of the area just above the anal fin, the thickened epidermis forms low pads that cover much of the posterior scale surface rather than forming discrete conical tubercles.

FAMILY OSMERIDAE

The smelt family includes six genera and 10 species (McAllister, 1963). Smelts are found in



boreal and subarctic waters of the Northern Hemisphere and are marine, anadromous, or fresh-water dwellers. Smelts spawn over sandy areas in fresh or salt water. Males do not grow as large as females, frequently have longer paired fins than females, and may develop enlarged scales along the lateral line. Breeding tubercles develop during the spawning season on the head, scales, and fins of males of all six genera.

GENUS *SPIRINCHUS* JORDAN AND EVERMANN

There are three species in *Spirinchus* (McAllister, 1963): *S. lanceolatus* (Hikita), *S. thaleichthys* (Ayres), and *S. starksi* (Fisk).

Breeding males of *Spirinchus lanceolatus* have the entire head and body, and both sides of all fins except the caudal and adipose, thickly covered with small warty tubercles (Jordan and Hubbs, 1925, p. 151). Our notes on a breeding male of this species (U.S.N.M. No. 48199) agree with Jordan and Hubbs's description except that tubercles are equally well developed on the caudal fin and are present on the adipose fin and on the branchiostegal rays as well. Hubbs (1925, p. 54) mentioned a tuberculate male from Hokkaido; Schultz and Chapman (1934, p. 73) contrasted the tubercles on *S. lanceolatus* with those on *S. dilatus* (= *S. thaleichthys*); and McAllister (1963, p. 10) reported tubercles on the upper and lower surfaces of the paired fins.

Spirinchus thaleichthys has fine tubercles on the upper surface of the paired fins and has less coarsely tuberculate scales on the body than does *S. lanceolatus* (Schultz and Chapman, 1934, p. 73). Hart and McHugh (1944, p. 26) and McAllister (1963, p. 12) also noted tubercles on the fin rays and scales of this species.

McAllister (1963, p. 14) reported that males of *S. starksi* have longer pectoral fins than do females and have tubercles on the head, scales, and lower fins. He cited Schultz and Chapman (1934) for the tubercle description of *S. starksi*,

but we find no mention of tubercles for *S. starksi* in their paper.

Spirinchus thaleichthys (Ayres)

Figure 2E

Male, 121 mm., S.L. U.S.N.M. No. 104689. Washington, Nooksack River, November 19, 1932. The lateral line region is dilated by the swelling of the underlying muscles, and the epidermis of the overlying scales is expanded to form a prominent longitudinal ridge. Tubercles on the pectoral fin rays are approximately 100 μ high and 110 μ wide. They are hemispherical, and are formed mainly by hypertrophy of the epidermal cells; those in the germinativum are cuboidal and about 8 μ in diameter, and the largest, hypertrophied cells are about 13 μ in diameter. One or two surface cell layers are of squamous epithelial cells which have keratinized to some extent, as they stain red with Mallory's triple stain. The lepidotrichia are also modified by the deposition of additional bone on the outer surface. This new bone can be distinguished by a different staining reaction; the older, underlying bone stains red, the new bone stains blue. Numerous strands of connective tissue extend into the new bone from the basement membrane and give support to the epidermal structures. Tubercles on the body have essentially the same structure as those on the fins.

GENUS *OSMERUS* LINNAEUS

This genus has one species with two subspecies (McAllister, 1963): *O. eperlanus eperlanus* (Linnaeus) and *O. e. mordax* (Mitchill). Males (U.B.C. No. 60-38, St. Lawrence Is., June 29) are covered with tubercles on the mouth, opercle, preopercle, branchiostegals, and the rest of the head; smaller tubercles on all the anal rays; tubercles on the entire ventral surface of the pelvic fin and all of the dorsal surface of the anterior 4-5 rays; tubercles on both anterior and posterior surfaces of all of the pectoral rays; and

FIG. 2. A. *Prosopium williamsoni* tubercle from lateral body scale. Male. Mallory's triple stain. $\times 92$. B. *Coregonus clupeaformis stanleyi* tubercle from lateral body scale. Note lack of keratin. Male. Mallory's triple stain. $\times 135$. C. *Plecoglossus altivelis* tubercle from anal fin. Male. Mallory's triple stain. $\times 118$. D. *Plecoglossus altivelis* tubercle from scale. Male. Mallory's triple stain. $\times 335$. E. *Spirinchus thaleichthys* tubercle from pectoral fin. Male. Mallory's triple stain. $\times 372$. F. *Thaleichthys pacificus* tubercle from pectoral fin. Note thickening of bone in lepidotrichia to form longitudinal ridges. Male. Mallory's triple stain. $\times 212$. G. *Mallotus villosus* tubercle from pectoral fin. Male. Mallory's triple stain. $\times 112$. H. *Mallotus villosus* lateral villous scale with hypertrophied epidermis. Male. Mallory's triple stain. $\times 112$.

Abbreviations: bm, basement membrane; fr, fin ray; k, keratinized epidermis; s, scale.

faint tubercles on the caudal fin rays. Virtually the only place lacking tubercles on these males is the adipose fin. Females from this collection have a few very small tubercles on the caudal fin, a few on both sides of the pectoral fin, and small ones on most of the body scales.

The literature contains several reports of tubercles on *Osmerus*. One of the earliest is by Smitt (1895, p. 871), who noted a "granular dermal eruption" on the scales of both sexes during the breeding season in Scandinavia. Kendall and Goldsborough (1908) found a spent male in Massabesic Lake, New Hampshire, which was covered with white tubercles. Creaser (1925) noted tubercles on males and showed them in a photograph (pl. 24). Langlois (1935) pointed out that both sexes have tubercles but those of the male have a longitudinal ridge. This difference was illustrated by Hoover (1936, fig. 1) who showed that they function in *Osmerus*, as in other fishes, primarily to maintain contact during spawning. He also discovered that when two tubercle-covered males came in contact with each other they quickly separated, but when a tuberculate male came in contact with a relatively nontuberculate female, he immediately drove her to the bottom or shoreward for spawning. Warfel, Frost, and Jones (1943) confirmed the sexually dimorphic features reported by Langlois, Hoover, and Richardson. Berg (1948, fig. 269) illustrated the body, head, and fins of a male covered with tubercles. McAllister (1963) reported that males have slightly larger paired fins than do females, large tubercles on the scales, small ones on the head and leading rays of all fins except the adipose. He noted that females had reduced tubercles.

Richardson (1942) described the structure of the tubercles on males as follows: "The individual tubercles result from the hypertrophy of the cells throughout the depth of the epidermis. This involves not only the intermediate and superficial layers, but also the columnar layer at this point. There is no indication of hyperplasia, and the thickness of the epidermis at the tubercle is due to the extensive increase in size of the individual cells of the several layers. The cells of the center of the tubercle characteristically show the greatest enlargement . . . The limits of the tubercle are sharply defined and there is no gradation or transition between the cells of the tubercle and the adjacent epidermal cells."

GENUS *THALEICHTHYS* GIRARD

Both sexes of *Thaleichthys pacificus* (Richardson), the only species in the genus, develop tubercles in the breeding season. There are small round tubercles all over the head, elongated ridgelike tubercles on the body scales, round tubercles on the anal fin rays, and small round tubercles on the dorsal fin rays (U.B.C. No. 57-60, Vancouver). Hart and McHugh (1944, fig. 5A) and McAllister (1963, fig. 7) showed the tubercles on an individual scale. McAllister (1963, p. 23) reported tubercles on the upper sides of the paired fins of males. He also noted that females have much reduced tuberculation. The paired fins of males are definitely longer than those of females (Hart and McHugh, 1944, p. 4).

Thaleichthys pacificus (Richardson)

Figure 2F

Male, 164 mm., S.L. U.S.N.M. No. 188123. Off Oregon coast. February 28, 1962. In a section of a branched pectoral fin ray, the lepidotrichia are thickened medially by deposition of additional bone to produce a longitudinal ridge along each fin ray. This new bone is differentiated in the sections by its blue staining and by a crenulated appearance, an artifact probably caused by differential shrinkage during preparation. Ridges are present on both the upper tuberculate side of the fin ray as well as on the lower nontuberculate side.

The tubercle is formed by hyperplasia and hypertrophy of epidermal cells to form a structure 53 μ and eight to ten cell layers thick. Laterally the cells are squamous in appearance and about 2.5 μ thick; the central cells are approximately 10 μ in diameter and polygonal. Some sections appear to give indications of some degree of keratinization of the surface cells since occasionally these cells may stain red in Mallory's triple stain. This reaction may be an artifact, however.

GENUS *ALLOSMERUS* HUBBS

Males of *Allosmerus elongatus* (Ayres), the only species in this genus, have coarse tubercles on the head, scales, median fin rays, and upper surface of rays of paired fins (McAllister, 1963, p. 26).

GENUS *HYPOMESUS* GILL

McAllister (1963) recognized three species, two with two subspecies, in *Hypomesus*: *H. pretiosus*

pretiosus (Girard), *H. p. japonicus* (Brevoort), *H. olidus* (Pallas), *H. transpacificus transpacificus* McAllister, and *H. t. nipponensis* McAllister. Jordan and Hubbs (1925, p. 152) reported that *H. olidus* and *H. pretiosus* agree with each other and the species of *Osmerus* and *Plecoglossus* in having the head, body, and fins of breeding males almost completely covered with minute warty tubercles. Males of *H. p. pretiosus* have small tubercles on the head, scales, and fin rays (Schaefer, 1936, p. 9; Hart and McHugh, 1944, p. 15; McAllister, 1963, p. 28). While spawning, one female is accompanied by one to four males who swim parallel to and slightly behind the female. The males swim pressed against the sides of the females. Spawning occurs in rapidly moving water over sandy beaches (Thompson and Associates, 1936).

Breeding males of *H. olidus* have tubercles on the head, scales, and rays of all fins (Hamada, 1961, p. 8–9; McAllister, 1963, p. 32). Tubercles are absent or reduced in females. Pectoral and pelvic fins are larger in males than in females (McAllister, 1963, p. 32). Berg (1948, p. 449) reported that males have tubercles on the scales, females only on the head. Males of *H. transpacificus nipponensis* have tubercles on the head, scales, and fin rays and have longer pectoral and pelvic fins than do females (McAllister, 1963, p. 37).

GENUS MALLOTUS CUVIER

Mallotus contains only *M. villosus* (Müller) according to McAllister (1963). In addition to the remarkable elongated scales along the prominent midlateral ridge of males, tubercles are also present. Small white breeding tubercles are on the upper surface of the pectoral and pelvic fins; the caudal and dorsal rays; the head, including the jaws, opercles, preopercles, and branchiostegals; and even on the modified lateral scales (U.B.C. No. 63–659, Alaska, August 15). Hart and McHugh (1944, p. 21) noted tubercles on the posterior surface of the pectoral rays and on the head region. McAllister (1963, p. 40) found a similar tubercle distribution in males and also reported that tubercles were absent in females. The males develop an upper and a lower spawning ridge along their bodies. These ridges, together with the enlarged fanlike tuberculate pectoral and pelvic fins, help a pair of males to grip a female while spawning in very shallow water over sandy beaches

(Perley, 1852; Lanman, 1874; Sleggs, 1933; Templeman, 1948; Pitt, 1958).

Mallotus villosus (Müller)

Figure 2G, H

Male, approximately 125 mm., S.L. U.S.N.M. No. 32949. Alaska, Golovin Bay. June, 1880. In this specimen, the largest tubercles are on the pectoral fins. Many, instead of being conical as those on the pelvic fins, are flattened and two to three times longer than wide. The effect is one of rows of minute pillows lining the fin rays, with usually one tubercle on each joint.

In cross section, one of the larger fin-ray tubercles is 210 μ wide and 130 μ high. The shape is roughly rectangular with the external corners rounded. The cells of the germinal layer are cuboidal but the overlying cells are irregular polygons. The entire structure is about 20 cell layers thick. The largest hypertrophied cells, approximately 10 μ diameter, are in the layers adjacent to the germinal layer and have nuclei about 7.5 μ diameter. Toward the surface successive layers become progressively smaller—to about 7 μ diameter. The surface two to three cell layers stain red in Mallory's triple stain but in general retain their polygonal shape and do not fuse into a rigid keratinized layer. These cells have a diameter of 5–6 μ .

Sections of the villous scales of the lateral ridge show a wide space with loose connective tissue fibers surrounding the scale. The outer epidermal layer is greatly thickened by hyperplasia and hypertrophy of the cells above the germinal layer. The appearance of the thickened epidermis is similar to that of the fin-ray tubercle except that no keratinization of the surface cells is evident.

FAMILY RETROPINNIDAE

This family contains the monotypic New Zealand genus *Stokellia* Whitley and nine nominal species of *Retropinna* Gill, five in New Zealand, three in Australia, and one on Chatham Island (Woods, 1968). Some species are confined to fresh water, others are estuarine, and still others marine, but all apparently spawn in fresh water (Stokell, 1949, 1955). There are literature reports of tubercles for *Stokellia anisodon* (Stokell) and *R. retropinna* (Richardson). Tubercles were described as "numerous small nodules" on the pectoral, pelvic, and anal fins and on the lower part of the body in the original description of

S. anisodon (Stokell, 1941). McMillan (1961) showed that tubercles develop on the scales and fins of mature breeding males but not on females. As in the Osmeridae, males have larger dorsal, anal, pectoral, and pelvic fins than do females. McMillan (1961, fig. 2) also illustrated mature adults showing the tubercles and larger fins of the male. In his original description of *R. abbreviata* (= *R. retropinna* according to Woods, 1968), McDowall (1965) reported that a 47 mm. male had nuptial tubercles on the lateroventral abdomen, and the pectoral, pelvic, anal, and caudal fins. Woods (1968) noted tubercles on the fin rays and scales of *R. retropinna*.

Retropinna retropinna (Richardson)

Figure 3A

Nuptial male, 115 mm., S.L. B.M.N.H. No.

1930.2.5.1, New Zealand, Waimakariri River. Very fine tubercles are distributed over the entire body and are sparsely scattered on the rays of all the fins. A tubercle from a lateral body scale is 65 μ high from the basement membrane to the tip and about 80 μ wide. It has a hemispherical shape and is formed by an aggregation of slightly hypertrophied cells that are about 5 μ in diameter. There is no evidence of keratinization.

Sections of the tubercles of *Retropinna chathamensis* Stokell (= *R. retropinna* according to Woods, 1968), Chatham Island, New Zealand, D.M. No. 3793, and *Stokellia anisodon*, Canterbury, New Zealand, D.M. No. 4009, figure 3B, are similar to those of *R. retropinna*.

ORDER GONORHYNCHIFORMES

Several species in two families (Kneriidae and Phractolaemidae) of the suborder Chanoidei, develop keratinized nuptial structures. In the genus *Kneria*, males of several species develop small breeding tubercles and an "occipital organ" that functions during breeding and is keratinized on the surface. In individuals of *Phractolaemus*, tubercles consist of a heavy conical cap of keratinized epithelium supported by a core of hypertrophied epithelial cells.

FAMILY KNERIIDAE

The Kneriidae are a family of small African fresh-water fishes of two genera (*Kneria* and *Parakneria*) and of about a dozen species of fast-moving streams (Poll, 1965; Peters, 1967). Poll (1933) first recognized that the opercular apparatus of *Xenopomatichthys* was a character of mature males. On the basis of this conclusion, Trewavas (1936) placed *Xenopomatichthys* in the synonymy of *Kneria*. Both Poll and Trewavas illustrated the structure. Peters (1967) made a comprehensive study of this structure including its morphology and histology. The occipital organ is divided into two parts, the anterior part on the operculum and the posterior on the post-opercular region. The part on the opercle is a circular disk with a wide, radially ridged rim and the postopercular portion is an elongate oval with a series of ridges transversing the surface. Peters concluded that the occipital organ acts as a clasper to hold the male and female in close

contact during breeding. In addition, the dorsum of the head and body has many fine tubercles that decrease in abundance posteriorly. The female also has small tubercles. In section, a small tubercle (fig. 3C) looks like a transverse section of the ridges in the occipital organ; Peters stated that the latter structure is formed by fusion of small tubercles. Note also the similarity of figure 3C to figure 9F, a tubercle of the homalopterid *Progastromyzon griswoldi*.

FAMILY PHRACTOLAEMIDAE

This African fresh-water family contains one species with two subspecies, *Phractolaemus ansorgei ansorgei* Boulenger and *P. a. spinosus* Pellegrin, according to Thys van den Audenaerde (1961a). Males have four tusklike circumorbital tubercles and prominent spinelike tubercles on three rows of nine scales each above the lateral line. Smaller, less conspicuous tubercles are on the anal and caudal fin rays and posteriorly on several rows of scales above and below the lateral line. The female also has small tubercles on many lateral body scales, the caudal fin rays and head, but none is as well developed as on the male. Thys van den Audenaerde (1961a, 1961b) provided a summary of information on *Phractolaemus* tubercles as well as excellent drawings (1961a, figs. 2-5). The circumorbital tubercles of the male are probably used in fighting, whereas the lateral tubercles of both sexes probably aid in maintaining contact during spawn-

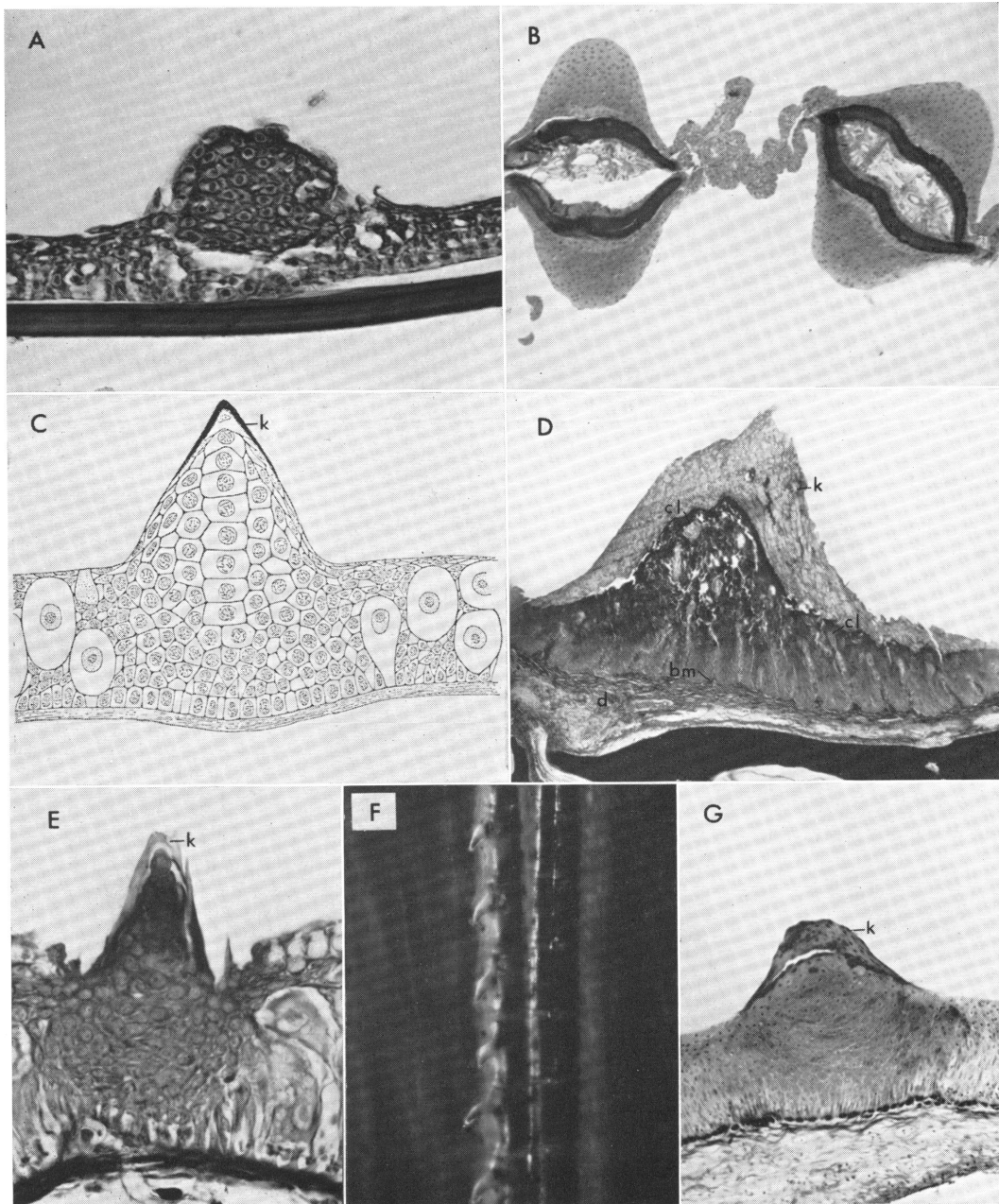


FIG. 3. A. *Retropinna retropinna* tubercle from lateral body scale. Male. Mallory's triple stain. $\times 394$. B. *Stokellia anisodon* tubercles from anal fin. Note lack of keratin. Male. H and E stain. $\times 128$. C. Drawing of a section through a small tubercle from the dorsal head surface of a male of *Kneria* sp. Sections through ridges of the occipital organ have similar appearance. Compare with figure 9F. $\times 480$. (After Peters, 1967.) D. *Phractolaemus ansorgei* postorbital tubercle. Note numerous capillary loops. Male. Mallory's triple stain. $\times 46$. E. *Phractolaemus ansorgei* tubercle from operculum. Female. Mallory's triple stain. $\times 366$. F. *Astyanax fasciatus aeneus* anal fin ray with hook on each segment. Male. $\times 26$. G. *Parodon hilarii* tubercle from lower surface of snout. Male. H and E stain. $\times 156$.

Abbreviations: bm, basement membrane; cl, capillary loop; d, dermis; k, keratin.

ing. The sharp spinelike tubercles above the lateral line of the male, however, may also be employed in agonistic behavior.

Tubercles were first noted by Boulenger (1901) in the original description of *Phractolaemus ansorgei*. He was unaware, however, that they were breeding tubercles that show sexual and seasonal variations. Jürgens (1910) described the tubercles on the head and caudal peduncle, illustrated them on the caudal peduncle and clearly indicated that they are secondary sex characters of the male analogous to the pearl organs of minnows. Brüning (1912) noted the presence of a double row of tubercles on the caudal peduncle of males. Pellegrin (1925) described *P. spinosus* as a new species on the basis of the well-developed tubercles around the eye and on the caudal peduncle scales. Poll (1932) pointed out that *P. spinosus* was based mainly on the sexually dimorphic nuptial tubercles of the male. Fowler (1949) described and illustrated tubercles in his original description of *P. spinosus carpenteri*.

***Phractolaemus ansorgei* Boulenger**

Figures 1, 3D, E

Male, 97 mm., S.L.; female, 92 mm., S.L. U.S.N.M. No. 203419. Belgian Congo, 1956. Fixed in Bouin's solution. A section of a male postorbital tubercle (figs. 1, 3D) is 900 μ high from the basement membrane to the keratinized

tip and 1690 μ wide at the keratinized base. Measured through the apex, the keratinized cap has a maximum thickness of 337 μ and tapers to the thickness of a few cells at the edges. A well-developed vascular system of capillary loops extends from the corium into the hypertrophied layer to just below the keratin layer, approaching to within 26 μ . This section contains 19 such loops which are spaced so that the farthest cells from a loop are only 70–80 μ distant. The longest loop is 262 μ long. Each is composed of what appears to be a capillary glomerulus of approximately 25 μ diameter, supplied by straight efferent and afferent vessels that are supported in common by collagen fibers extending from the corium.

A section of a tubercle from the caudal peduncle of the male is 570 μ high from tip to the bony outer surface of the scale and 550 μ in greatest width. It has a keratinized cap 77 μ thick at the tip tapering to 15–20 μ thick laterally midway between tip and the base where it is reduced to about 8–10 μ and three cell layers thick. Parts of three or four capillary loops are present in each medial section of this tubercle.

A microscopic opercular tubercle from the female (fig. 3E) projects 58 μ above the surface and is 52 μ wide at the base. The keratinized cap is 5 μ thick and consists of only one or two cell layers. No capillaries are present as in the large tubercles. The total distance from basement membrane to tip is 125 μ .

ORDER CYPRINIFORMES

SUBORDER CHARACOIDEI

Of the 16 families of characins, contact organs are present in many species of the Characidae and at least one species of the Gasteropelecidae, and breeding tubercles are probably present in all species of the Paradontidae and at least five species of the Lebiasinidae.

CHARACIDAE

The males of many species of characins develop specialized bony fin-ray contact organs, or hooks, that serve to hold the sexes in close contact during the active and sometimes violent movements of the spawning act. Some of the glandulocaudine characins, in which fertilization is internal (Nelson, 1964), have these structures well developed on the anal, caudal, and

pelvic fins. Schoenfeld (1935) stated that all the characins in which the male has an "anal hook" live in swift-running streams and that the male attaches itself to the female with this "hook" during spawning. This statement is an oversimplification of the function of this structure because a number of species with hooks live in relatively slow-moving streams. Structurally, the characid contact organs are similar to those developed in the Cyprinodontidae and Cottidae.

The earliest references to contact organs in the Characidae are in the aquarium literature: Myers (1922, 1923), Stroop (1932), Coates (1933) and Schoenfeld (1935) noted that males of *Ctenobrycon spilurus* (Cuvier and Valenciennes) and *Aphyocharax rubropinnis* Pappenheim have small "invisible" hooks on the anterior part of

the anal fin that often catch in a fine net when a fish is transferred. Characin hooks were then reported for *Hyphessobrycon flammeus* Myers and *H. heterorhabdus* (Ulrey) by Innes (1935) and for *H. scholzei* Ahl by Innes (1948). In describing South American characins, Fowler mentioned hooks on the anal rays of several of his new species: *Acrobrycon tarijae* and *Acestorhampbus bolivianus* (1940); *Odontostilbe iheringi* (1941); *Bryconamericus baudoensis* (1944); and *Creagrutus londoni* (1945). Schultz (1944) noted hooks or spinules on the anal fins of males of three new characins: *Saccoderma melanostigma*, *Hyphessobrycon sovichthys*, and *Hemibrycon dentatus jobonero*. Böhlke (1954a, p. 102) reported hooks on branched anal rays of *Piabucus dentatus* (Koelreuter) and (1954b, pp. 270–271) described the “hooks and spines” on the pelvic and anal fin rays of the holotype of *Planaltina myersi* Böhlke. In 1958, he described hooks on the fins of *Hysteronotus megalostomus* Eigenmann, *H. hesperus* Böhlke, *Bryconamericus peruanus* (Müller and Troschel), *Moenkhausia naponis* Böhlke, *Hemibrycon orcesi* Böhlke, and *Brachyhalcinus nummus* Böhlke and also illustrated the pelvic fin hooks of *H. megalostomus*. Adult males of *B. peruanus* had hooks on all the fins supported by rays, including the dorsal and pectoral fins, a situation unusual among characins.

Most recently, Géry has described and figured the hooks and hooklets in a series of papers on South American characins. Examples are given in the following list (Géry is the author of a species unless otherwise noted; abbreviations are used for the fins that have contact organs—A for anal, P₂ for pelvic, and C for caudal; fig. means the contact organs were illustrated): *Megal-amphodon roseus*, A (1960); *Hyphessobrycon georgettae*, A (1961a); *Hemigrammus pulcher haraldi* and *H. pulcher pulcher* Ladiges, A, fig. (1961b); *Tytocharax madeirae* Fowler, fig., *T. rhinodus* Böhlke, *T. atopodus* Böhlke, and *Xenrobrycon macropus* Myers and Miranda-Ribeiro, A and P₂ (1963a); *Hemigrammus vorderwinkleri*, *H. pronecki*, and *Hyphessobrycon tropis*, A (1963b); *Moenkhausia eigenmanni* and *Bryconamericus loisae*, A and P₂ (1964a); *Glandulocauda terofali*, A, P₂, and fig. (1964b); *Brittanichthys axelrodi*, A, C, fig., and *B. myersi*, A (1965a); *Moenkhausia l. lepidura* (Kner), A, *Bario steindachneri* (Eigenmann), A and P₂, *Hemigrammus ocellifer* (Steindachner), A, *H. schmardae* (Steindachner), A, *Hyphessobrycon tukunai*, A, and *Bryconamericus haraldi*, A (1965b);

Tytocharax boehlkei, A and P₂ (1965c); *Moenkhausia georgiae*, A (1965d); *Astyanax microlepis* (Eigenmann), A, and *Gephyrocharax caucanus* Eigenmann, A (1966a); *Boehlkea fredcochui*, A and P₂, *Coelurichthys microlepis* (Steindachner), A and C, *C. tenuis* Nichols, A (1966b); *Petitella georgiae* Géry and Boutière, A and fig., and *Hemigrammus rhodostomus* Ahl, A (Géry and Boutière, 1964); *Bryconops inpai* Knöppel, Junk, and Géry, A (Knöppel, Junk, and Géry, 1968). In addition to describing the hooks, hooklets, and “crochets” on the fins of characins, Géry has used them in distinguishing species—*Hemigrammus ocellifer* from *H. schmardae* (1965b) and *H. rhodostomus* from *Petitella georgiae* (Géry and Boutière, 1964) on the number of hooks per anal ray—and in discussing generic relationships among the glandulocaudine characins *Xenrobrycon*, *Tytocharax*, *Glandulocauda*, *Mimagoniates*, and *Coelurichthys* (1963a, 1964a, and 1966b).

Astyanax fasciatus aeneus (Günther)

Figure 3F

Male, 72 mm., S.L. U.S.N.M. No. 197467. Honduras, Rio Bonito drainage, June–July, 1962. Contact organs (hooks) are present on the ventral surface of the pelvic fin rays and on anal fin rays 4 to 14. The contact organs are formed by proximally directed, sharp bony processes growing from the fin rays. They are arranged in rows along the fin rays and have an epidermal investment through which the points may penetrate under pressure.

FAMILY GASTEROPELECIDAE

Several species of hatchet fishes probably have contact organs but we have found only one reference in the literature. Weitzman (1954, p. 225) stated that small *bony* [*italics ours*] hooks were present on anal fin rays 6–16 in males of *Carnegiella vesca* Fraser-Brunner.

FAMILY PARODONTIDAE

Of the 16 families of characoid fishes, only the Parodontidae and Lebiasinidae are known to develop true nuptial tubercles. Myers (1930a) first reported tubercles from the side, front, and inferior surface of the snout and internasal regions in his new *Parodon apolinari*. In *Parodon hilarii*, small tubercles on the snout and head are formed by keratinization of several layers of cells into a simple cap supported by hypertrophied

cells beneath; they resemble the simple tubercles of other cypriniform fishes, especially some in the family Cyprinidae. Species of the Parodontidae apparently do not develop contact organs as do many species of the Characidae.

We found tubercles on 10 species of the Parodontidae in the United States National Museum collection. *Apareiodon affinis* (Steindachner), U.S.N.M. No. 149942, has tiny white tubercles on the top of the head from the snout posterior to the first three or four rows of dorsal scales lateral to the orbits. A number of specimens of both sexes of *Parodon apolinari* Myers (U.S.N.M. Nos. 123756, 121296; A.N.S.P. Nos. 73150, 73151) are tuberculate. Tubercles cover the head, especially the interorbital region, and extend down and around the snout posteriorly to the lower lip. Tubercles are also on eight to 10 rows of scales from the occiput toward the dorsal fin origin. In some specimens, they extend onto the cheek and branchiostegal rays and most of the dorsolateral scales. Similar tubercle patterns were found in *Parodon buckleyi* Boulenger, U.S.N.M. Nos. 164041, 164054; *P. caquetae* (Fowler), U.S.N.M. Nos. 164024, 164053; *P. hilarii* Reinhardt, U.S.N.M. No. 120189; *P. suborbitale* Valenciennes, U.S.N.M. Nos. 121294, 121293, 121295; *P. tortuosus* Eigenmann and Norris, U.S.N.M. No. 149943; *P. ecuadoriensis* Eigenmann and Henn, U.S.N.M. No. 8535; *Saccodon cauae* Schultz and Miles, U.S.N.M. Nos. 121285, 120166, 123799; and *S. wagneri* Kner and Steindachner, U.S.N.M. No. 164026.

***Parodon hilarii* Reinhardt**

Figure 3G

Adult male, 79 mm., S.L. U.S.N.M. No. 120189. Bolivia, Tumupasa. December, 1921. Very fine conical tubercles are on the dorsal and lateral surfaces of the head of both sexes. Only adult males develop larger tubercles on the under side of the snout between the ventrally placed mouth and the tip of the snout.

A section of a snout tubercle is 182 μ high from basement membrane to tip and about 170 μ wide. The keratinized cap, in which pyknotic nuclei are visible with H and E stain, is 32 μ thick, and becomes thinner peripherally. The keratinized portion is supported by a mound of hypertrophied epithelial cells that are up to 8 μ in diameter. One or two cell layers above the columnar stratum germinativum, the cells are polygonal, becoming lenticular in the center,

and then polygonal again in the layers adjacent to the keratinized cap.

FAMILY LEBIASINIDAE

This small family of small to moderate-sized predacious South American characins has two subfamilies, the Lebiasininae and the Pyrrhulinae. Stanley H. Weitzman has kindly brought to our attention five tuberculate species representing two tribes of the latter subfamily, the Pyrrhulinini and the Nannostomini.

TRIBE PYRRHULININI

Small tubercles are arranged in a row along the posterior margins of some of the lateral scales of males in this tribe. A male of one unidentified species of *Pyrrhulina* (U.S.N.M. uncat., Surinam, Para District, June, 1969, 43 mm. S.L.), has two to four medium-sized tubercles on about 20 lateral scales. They resemble retropinnid tubercles, being formed by hyperplasia and lacking a keratinized layer. They are hemispheroid in shape and a section of one is 79 μ high and 182 μ wide with 10–12 cell layers. A male of another species of *Pyrrhulina* (Z.M.A. 106.130, French Guiana, Stodman's Island, April 19, 1967, 80 mm. S.L.) has two or three larger tubercles like the first species, but the tubercles are present on only eight posterior lateral scales on one side; a 61 mm. female lacks tubercles. Tubercles are more numerous (eight to 11) and smaller on two or three lateral rows of scales in a male of an unidentified species of *Copeina* (A.N.S.P. uncat., Venezuela, tributary of Lake Mozambique, May 25, 1969, 37 mm. S.L.). A section of one of these tubercles is almost identical with the *Pyrrhulina* tubercle except that it is smaller (52 μ high, 91 μ wide, with about 10 cell layers). The breeding habits of these three species are not known but they probably spawn with their bodies pressed together laterally as does *Copeina arnoldi* Regan as shown by Nieuwenhuizen (1964, 1967).

TRIBE NANNOSTOMINI

The tubercle pattern in the Nannostomini is strikingly different from that in the Pyrrhulinini. Tubercles appear to be restricted to the ventral parts of the head of males in this tribe. The tribe Nannostomini, contains nine small species which are not known to exceed 44.5 mm. S.L. (Weitzman, 1966). The males of some species have the

anal fin modified so that it can be cupped over the vent of the female during spawning. Tubercles are present on 33 males of *Nannostomus bifasciatus* Hoedeman, 27–43 mm. S.L., from Surinam and on no females. At maximum development (Z.M.A. No. 106.147), the tubercles cover the ventral surface of the head with the largest ones on the lower jaw. Rows of tubercles were found on the ventral margins of the infraorbital bones and the ventral margins of the hyoid arch of a large male *Poecilobrycon unifasciatus* (Steindachner) from British Guiana. Detailed information on the breeding habits of these two species is lacking, but it is plain from the photographs and description given by Nieuwenhuizen (1964) that the tubercles of male *N. bifasciatus* are in contact with the head and dorsum of the female during courtship.

***Nannostomus bifasciatus* Hoedeman**

Male, 37 mm., S.L. Z.M.A. No. 106.163. Surinam, Surinam River, March 20, 1967. Minute tubercles are distributed on the ventral surface of the head, on the lower jaw, and in several rows back to the isthmus. They can be seen only with magnification.

Sections of these tubercles reveal them to be formed by hypertrophy of epithelial cells to form low mounds that are about 160–180 μ in diameter and 65–80 μ high from basement membrane to tip. The hypertrophied cells reach about 13 μ in diameter and have large, vesicular nuclei. A few of the cells at the tip of some of the tubercles stained red with Mallory's triple stain, indicating some keratinization. No distinct keratinized cap is formed, however, as in tubercles of the Parodontidae.

SUBORDER CYPRINOIDEI

Members of all six families in the suborder Cyprinoidei develop breeding tubercles: the Cyprinidae, Gyrinocheilidae, Psilorhynchidae, Catostomidae, Homalopteridae (including Gastromyzonidae), and Cobitidae.

FAMILY CYPRINIDAE

The Cyprinidae are very numerous (about 2000 species), contain about 10 subfamilies (Bănărescu, 1968a) with many different and divergent adaptations, and are widely distributed over the North American, Eurasian, and African continents. Breeding tubercles have been much more widely studied in the minnows than in any other

family. Early European ichthyologists figured and described tubercles on cyprinids: Heckel (1838) *Schizothorax* (pl. 1), *Varicorhinus* (pl. 2); Heckel (1843) *Discognathus* [=Garra] (pl. 7), *Labeo* (pl. 20); and Heckel and Kner (1858) *Rhodeus* (fig. 52), *Leuciscus* [probably=*Rutilus*] (figs. 94 and 98). Siebold (1863, pp. 117–118) described and figured (pl. 1, fig. 1) tubercles on the males of the bitterling *Rhodeus sericeus* (Pallas) and described the tubercles on several other cyprinids. Seeley (1886), Smitt (1892), Leydig (1892, 1895), Pappenheim (1909), and Vladykov (1931) are among other Europeans to report breeding tubercles on cyprinids. Oliva (1953b) presented a comprehensive treatment of breeding tubercles in 11 species in his revision of the Czechoslovakian Cyprinidae. In addition, he included a historical review of sexual dimorphism in fishes.

Okada (1934, 1935) reported the presence of breeding tubercles on the following genera of Japanese cyprinid fishes: *Cyprinus*, *Carassius*, *Tribolodon*, *Acheilognathus*, *Ischikauia*, *Zacco*, *Opsariichthys*, and *Sarcocheilichthys*. He also divided the genera into groups, on the basis of the distribution of the tubercles. Kobayasi (1937) reported tubercles in the above nine genera of Japanese cyprinids and added *Pseudorasbora*, *Pseudoperilampus*, *Tanakia*, *Rhodeus*, *Abbottina*, *Gnathopogon*, and *Biwia* to the list of tuberculate genera. Okada (1960) recently summarized the tubercle distributions in most of the Japanese Cyprinidae.

In an extensive review of tubercles in Chinese minnows, Kimura and Tao (1937) reported tubercles on the snouts of males of *Discognathus*, *Amplolabrus*, *Epalzeorhynchus*, *Semilabeo*, *Labeobarbus*, *Cyclocheilichthys*, *Hemibarbus*, *Varicorhinus*, *Spinibarbus*, *Labeo*, *Cirrhina*, *Osteochilus*, *Discogobio*, *Ptychidio*, *Rhodeus*, *Pseudoperilampus*, *Acheilognathus*, *Paracheilognathus*, and *Acanthorhodeus*; on the snout and operculum of *Lissochilus* and *Opsarichthys*; on the snout and pectoral fin of *Carassius*, *Cyprinus*, *Pseudogobio* and *Abbottina*; on the snout and cheek of *Pseudorasbora*, *Sarcocheilichthys*, *Chilogobio*, *Gobio*, and *Leucogobio*; on the head of *Paraleucogobio*, *Rhinogobio*, *Saurogobio*, *Hypophthalmichthys*, *Aristichthys*, *Hemiculter*, *Ishikauia*, *Ctenopharyngodon*, *Elopichthys*, *Barilius*, *Suariobarbus*, *Ochetobius*, and *Phoxinus*; on the head and back of *Coreius*, *Xenocypris*, *Hemiculturella*, *Chanodichthys*, *Parabramis*, *Culter*, *Parapelecus*, *Nicholsiculter*, *Luciobrama*, *Culticula*, *Toxabramis*, and *Gobiobotia*; on

the interorbital of *Mylopharyngodon*; and on the head, back and anal fin of *Zacco*.

Bănărescu (personal commun.) reported that in the Chinese fish *Matsya* (*Spinibarbus*) *hollandi caldwelli* the tubercle distribution is asymmetric in all the tuberculate specimens that he has seen. The tubercles occur in a patch extending from the lateral surface of the snout to below the eye on either the right or left side. Whether other subspecies of *M. hollandi* have this pattern of tubercle distribution is not known.

Many reports have been published of tubercles in Indian and southeast Asian minnows. Sykes (1841) was one of the first workers to describe and figure tubercles on Indian minnows in five new species that he placed in *Cyprinus*, *Variacorhinus*, and *Barbus*. Hora and his co-workers have discussed breeding tubercles on many Indian cyprinids (see Raj, 1958 for summary). Fowler described or illustrated tubercles in three papers on Thai fishes: 1934, *Garra*, *Osteochilus*, *Scaphiodontopsis*, *Lissochilus*, and *Barbus*; 1935, *Osteochilus* and *Tylognathus*; and 1939, *Dangila*, *Acrossocheilus*, *Tylognathus*, and *Garra*. Smith (1945) described tubercles on breeding males of the following genera of Thai Cyprinidae: *Rasbora*, *Hampala*, *Cyclocheilichthys*, *Acrossocheilus*, *Scaphiodonichthys*, *Osteochilus*, *Labiobarbus*, *Tylognathus*, *Lobocheilus*, *Morulus*, *Garra*, and *Epalzeorhynchus*. Inger and Chin (1962) figured and described breeding tubercles on several species of North Borneo Cyprinidae.

In Africa, Fowler (1936) reported tubercles in *Labeo* and *Barilius* and Barnard (1943) reported them in *Labeo* and *Barbus*.

In North America, many workers have reported on breeding tubercles on minnows. Large numbers of tuberculate species were reported by Forbes and Richardson (1909), 10 genera, 21 species; Fowler (1912), eight genera, 14 species; and Trautman (1957), 10 genera, 37 species.

A number of workers have described breeding tubercles on females of species of the Cyprinidae: Smith (1908) on *Chrosomus erythrogaster* Rafinesque; Forbes and Richardson (1909) on *Notropis lutrensis* (Baird and Girard) and *N. rubrifrons* (Cope); Vladykov (1927), Tack (1940), and Frost (1943) on *Phoxinus phoxinus* (Linnaeus); Otterström (1931) on *Rutilus rutilus* (Linnaeus); Sato (1935) and Ikeda (1936a) on *Tribolodon hakonensis* (Günther); Hora and Misra (1936) on *Labeo dero* (Hamilton); Boku (1937) on *Carassius*

auratus; Raney (1939) on *Hybognathus regius* Girard; Hubbs and Walker (1942) on *Notropis longirostris* (Hay); Smith (1945) on *Acrossocheilus bantamensis* (Rendahl), *Scaphiodonichthys acanthopterus* (Fowler), *Garra taeniata* Smith, and *Epalzeorhynchus coatesi* (Fowler); Marshall (1947) on *Notropis chalybaeus* (Cope); Raney (1947a) on *Notropis procne* (Cope); Raney (1947b) on *Notropis cerasinus* (Cope) and *Chrosomus oreas* Cope; Oliva (1953b) on *Leuciscus cephalus* (Linnaeus); Suttkus and Raney (1955a) on *Notropis baileyi* Suttkus and Raney, *N. lutipinnis* (Jordan and Brayton), and *N. chrosomus* (Jordan); Pfeiffer (1955) and Miller (1962b, 1963) on *Notropis rubellus* (Agassiz); Trautman (1957) on *Hybopsis aestivalis hyostoma* (Gilbert) and *Notropis umbratilis cyanocephalus* (Copeland); Outten (1958) on *Notropis rubricroceus* (Cope); Okada (1960) on *Hemibarbus longirostris* (Regan) and *Moroco steindachneri* (Sauvage); Inger and Chin (1962) on *Nematabramis everetti* Boulenger, *Rasbora rutteri* Weber and de Beaufort, *R. hubbsi* Brittan, and *Paracrossocheilus acerus* Inger and Chin; Branson (1962b) on *Notropis pilsbryi* Fowler, *Dionda nubila* (Forbes), and *Hybopsis x-punctata* Hubbs and Crowe; etc. All agree that in species in which tubercles are present on both sexes the tubercles are more numerous and better developed on the male. Otterström (1931, p. 178) stated that tuberculate females of *Rutilus rutilus* were older (and larger) than non-tuberculate females.

Breeding tubercles have been reported on natural male hybrids of the following combinations in the Cyprinidae: *Notropis cornutus* (Mitchill) \times *N. rubellus* (Agassiz) by Raney (1940d) and Miller (1962b, 1963); and *Nocomis leptcephalus* (Girard) \times *Campostoma anomalum* (Rafinesque) by Raney (1947b). Raney (1940d) also reported tubercles on female hybrids of *Notropis cornutus* \times *N. rubellus* but Miller (1963) did not find any. Tubercles developed on experimental male hybrids of the following combinations in the Acheilognathinae: *Rhodeus ocellatus* (Kner) \times *R. sericeus amarus* (Bloch) by Duyvené de Wit (1960); *R. ocellatus* \times *Acheilognathus lanceolatus* (Temminck and Schlegel) by Duyvené de Wit (1961) and Holčík and Duyvené de Wit (1962a); *R. sericeus amarus* \times *A. himantegus* (Günther) by Duyvené de Wit (1962a); *A. lanceolatus* \times *A. limbatus* (Temminck and Schlegel) by Duyvené de Wit (1962b); *R. sericeus amarus* \times *R. o. ocellatus* by Holčík and Duyvené de Wit

(1962b); *R. sericeus amarus* × *A. lanceolatus* by Holčík and Duyvené de Wit (1964).

In the genus *Nocomis*, ontogenetic studies of tubercle development with body growth provided useful comparative data in the recognition of natural cyprinid hybrids (Lachner, Jenkins, and Wiley, MS.). Five intrageneric *Nocomis* hybrids are recognized among the seven species known in the genus. Among them, the most commonly collected is *N. leptocephalus* × *N. micropogon*. This hybrid and other, less frequent, interspecific *Nocomis* hybrids, are usually intermediate between the parental species in regard to distribution and number of head tubercles. Tubercle distribution also proved useful in the recognition of the following natural intergeneric cyprinid hybrids involving *Nocomis*:

- N. biguttatus* × *Notropis cornutus*
- N. leptocephalus* × *Campostoma anomalum*
- N. leptocephalus* × *Notropis coccogenis*
- N. leptocephalus* × *Clinostomus funduloides*
- N. micropogon* × *Notropis cornutus*
- N. micropogon* × *Rhinichthys cataractae*

Probably more is known about the breeding behavior of minnows than about any other family with tuberculate species. This statement holds particularly for North American minnows in which many observers have been aware of the importance of tubercles in reproductive behavior (Reighard, 1903, 1904, 1910b, 1943; Smith, 1908; Raney, 1939, 1940a, 1940b, 1940c, 1940d, 1947a, 1947b; Hubbs and Walker, 1942; Marshall, 1947; Lachner, 1952; and Miller, 1962a).

Three studies have been concerned with the change of number of tubercles with age. Kimura and Tao (1937) studied in detail the breeding tubercles and nuptial coloration of three species of Chinese minnows: *Pseudorasbora parva* (Temminck and Schlegel), *Abbottina rivularis* (Basilewsky), and *Sarcocheilichthys nigripinnis* (Günther). They reported on the development of breeding tubercles through the year; variations with size, age, and season; distribution of tubercles on the body; and the shape, size, and structure of the tubercles. Koehn (1965), who studied the course of development of the nuptial tuberculation of *Notropis lutrensis* (Baird and Girard) through the reproductive period, found that the head tuberculation develops from a linear to a profuse or scattered pattern as the number of tubercles increases and that tubercle distribution on the body is nearly constant and appears to be functionally associated with the breeding activities.

Lachner and Jenkins (MS.) observed that in two undescribed species of *Nocomis* the number of tubercles on the heads of males increases with age in successive breeding seasons until a maximum number, characteristic of each species, is attained. As the number increases, the posterior limit of development is extended until most of the dorsum of the head is tuberculate in large, mature males of the same two species.

Suzuki (1941) compared the pattern of development, distribution on the body, and size and number of tubercles in *Pseudorasbora parva* (Temminck and Schlegel) and *P. pumila* Miyaji.

In the Cyprinidae, more than for any other family, workers have used the patterns of breeding tubercles in taxonomy. Siebold (1863, p. 83) was among the first to point out that the breeding tubercles of cyprinids vary in shape, number, and distribution among the different genera and species. Okada (1934) placed many of the genera of Japanese minnows into groups on the basis of the distribution of the breeding tubercles. In the United States, breeding tubercle distribution was used by Hubbs and Black (1947) in *Pimephales*; Lachner (1952) and Lachner and Jenkins (1967) in *Nocomis*; and Gibbs (1957a, 1957b, 1961) in *Notropis*. Lachner's several studies (unpublished) of the North American nest-building chubs, *Nocomis*, employed the presence of large nuptial tubercles as a primary systematic character, and he thus elevated *Nocomis* from the ranks of *Hybopsis* synonyms. He further demonstrated that tubercle numbers and distributions are the most useful characters in the recognition of three species-groups within *Nocomis*, as well as differentiating among the species of *Nocomis* and the subspecies of *N. leptocephalus*. Bănărescu and Nalbant (1965) found that one of the most distinctive differences between *Abbottina* and *Pseudogobio* was the presence of well-developed breeding tubercles on the head and first pectoral ray in *Abbottina* and the absence of tubercles in *Pseudogobio*. Many workers have used tubercle patterns as characters in differentiating between closely related species, particularly in the North American genus *Notropis* (e.g., Hubbs, 1941; Raney, 1947b; Hubbs and Raney, 1947; Bailey and Suttkus, 1952; Bailey, Winn, and Smith, 1954; Suttkus and Raney, 1955a and 1955b) and also in Old World genera, such as *Labeo* (Hora, 1936a) and *Zacco* (Bănărescu, 1968b).

Most of the morphological and histological work on nuptial tubercles has been done on

species of the Cyprinidae. Solger (1879) stained the skin of preserved *Gobio fluviatilis* [= *G. gobio*] and *Chondrostoma nasus* to demonstrate that tubercle anlage are present outside the breeding season. Leydig (1892) however, stated that Solger mistakenly identified "die Becherorgane" (pit organ) and not germinal tubercles. Leydig reviewed the early references to tubercles and described their morphology in *Cyprinus carpio*, *Rhodeus amarus*, *Phoxinus laevis* [= *P. phoxinus*], *Discognathus lamta* [= *Garra* sp.], and *Leuciscus virgo* [= *Rutilus pigus*]. By comparing the structure of *Rhodeus* and *Discognathus* [= *Garra*] tubercles, which have "sackchenartige Eintiefungen" (saclike depressions), with the peculiar "poren" of Indian cyprinids, he concluded that the structures, about which other authors had speculated as having a sensory function, are really sites of undeveloped tubercles. In a later paper, Leydig (1895) figured the tubercles of *Cyprinus carpio*, *Rhodeus amarus* (without a keratinized cap), and *Discognathus lamta* [= *Garra* sp.]. He remarked on the similarities in morphology and development of tubercles, mammalian hair, saurian femoral pores, and skin sense organs.

Maurer (1895) figured and described a section through an *Idus melanotus* [= *Leuciscus idus*] tubercle and wrote that *Barbus fluviatilis* [= *B. barbus*] and *Phoxinus laevis* [= *P. phoxinus*] have similar tubercles. His work is faulted, however, by a lengthy discussion (supported by illustrations) in which he attempted to show that "Hautsinnesknospen" (epidermal sensory buds) on the head of *B. barbus* represent developmental stages of a tubercle.

Other studies that give histological and morphological descriptions of breeding tubercles include those on the goldfish, *Carassius auratus* (Linnaeus). Goldfish tubercles are epidermal and consist of two types of cells according to Tozawa (1923). In the formation of breeding tubercles, the number of cell layers increases from the normal 15–20 to 25–30. The layers of hypertrophied cells bulge exteriorly to form the tubercle and internally to form a pocket in the dermis. The hypertrophied cells are covered with a cornified cap, 90–150 μ thick, composed of scaly cornified cells with pyknotic nuclei or without nuclei. Similar structure has been reported for the breeding tubercles of other cyprinids: *Acheilognathus intermedius* (Temminck and Schlegel) by Tozawa (1929); *Tribolodon hakonensis* (Günther) by Sato (1935); *Pseudo-*

rasbora parva (Temminck and Schlegel), *Abbottina rivularis* (Basilewsky), and *Sarcocheilichthys nigripinnis* (Günther) by Kimura and Tao (1937) and *Rutilus rubilius* and *R. rubilio* by Aisa (1958, 1959). Rauther (1927) reviewed and discussed tubercle morphology and histology including work on other keratinized structures in fishes.

In reviewing the tubercle morphology of the various species presented in this study it is obvious that nuptial tubercle structure in cyprinids is extremely variable between species. The tubercles with the simplest structure are the minute ones, as in *Phenacobius mirabilis*, and the small ones which are found on the pectoral fin surfaces of many other species. These tubercles show hypertrophy and hyperplasia of the epithelial cells, those on the surface keratinizing to form a cap of compacted cells supported internally by a core of hypertrophied epithelial cells. The largest tubercles with a similar degree of simplicity are found in *Leuciscus*, *Barbus*, and *Pseudorasbora*. In these genera, the tubercles do not exceed 1.0 mm. in height and consist simply of a conical keratinized cap supported by an internal core of hypertrophied epithelium. Larger tubercles such as those in the North American genera *Pimephales*, *Nocomis*, *Campostoma*, and *Semotilus* are more complex due to the presence of vascularized dermal papillae which extend into the epithelial core and by the presence in some, such as *Campostoma*, of a keratinized cap composed of several distinct layers. In these tubercles, the dermal papillae are accompanied by a layer of the stratum germinativum and probably serve the dual function of providing nutrition to the rapidly growing epidermal cells of the tubercle and increasing the number of germinative cells required for the rapid growth that is characteristic of developing tubercles.

In some Eurasian and African cyprinids, such as species of *Labeo* and *Garra*, tubercles form as keratinized caps supported by the hypertrophied and hyperplastic epithelium of underlying pit or saclike epithelial invaginations. Throughout the hypertrophied cells of the tubercle pit are numerous vascularized dermal papillae which, in this type, are devoid of any accompanying germinal epithelium. The significance of the vascularized saclike structure cannot be determined with certainty; however, it appears to function in the maintenance of a relatively large epithelial structure over an extended reproduc-

tive period. Many of the species having this type of tubercle are tropical or subtropical and probably have reproductive periods that extend over weeks or even months. Individuals that are reproductively active during this period can thus maintain their nuptial tuberculation.

The epithelial-pit tubercles appear to be distinct from those in cyprinids that do not develop a pit. Intermediate forms exist, however, and the series represented successively by *Pseudorasbora parva*, *Nocomis leptcephalus*, *Onychostoma leptura*, *Garra taeniata*, *Garra gotyla*, and *Labeo annectens* may demonstrate an evolutionary sequence of epithelial-pit tubercles. In *Pseudorasbora*, the keratinized cap is supported by a simple core of hypertrophied epithelium. In *Nocomis*, the core is supplied by vascularized dermal papillae that are accompanied by stratum germinativum whereas in *Onychostoma* and succeeding examples, the dermal papillae lack accompanying germinativum. In *Garra taeniata*, a rather open epithelial pit is developed, becoming deeper and more flask-shaped in *G. gotyla* and, comparatively, deep and narrow in *Labeo*.

Leuciscus souffia muticellus Bonaparte

Figure 4A

Male, 107 mm., S.L. M.S.N.G. No. 39008. Italy, Fiume Gerivia (Ponte de Laccio). June 1, 1963. A tubercle from the top of the head between the eye and the snout, about 390 μ high from basement membrane to tip, and 550 μ wide, is formed by simple hyperplasia and hypertrophy of the epidermal cells which keratinize in the surface layers. The germinativum in the adjacent epidermis is columnar, but becomes cuboidal or irregular beneath the tubercle. The epidermal cells in the core of the tubercle are progressively larger toward the keratinized surface, those adjacent to it being 12 to 15 μ in diameter. The keratinized portion forms a cone approximately 660 μ wide and is composed of three laminae of flattened cells, each six to eight cell layers thick, forming a structure approximately 105 μ thick. The presence of mitotic figures in the layers near the stratum germinativum and the presence of numbers of partially keratinized cells adjacent to the keratinized layer indicate that this is a growing tubercle which is not yet mature.

Barbus longiceps Cuvier and Valenciennes

Figure 4B

Male, 227 mm., S.L. F.M.N.H. No. 62123.

Israel, Lake Tiberias. March 20, 1950. A tubercle from below the eye is 640 μ high from basement membrane to keratinized tip and 500 μ wide. The keratinized cap is a conical structure that has a uniform thickness from base to apex. It is approximately 200 μ thick and is composed of compacted, keratinized cells which stain a bright orange in Mallory's triple stain. Keratinizing cells extend into the epidermis laterally about 150 μ on each side. Under the lateral, lightly keratinized area, the cells are hypertrophied like the epidermis of the tubercle core. The stratum germinativum is composed of columnar epithelium and the cells in the layers above are irregularly polygonal and become larger toward the keratinized layer where they reach a maximum diameter of approximately 16 μ . The cytoplasm of the hypertrophied cells stains violet but the cytoplasm of the undifferentiated peripheral epidermis stains light blue. The only evidence of vascularization of the epidermal core is a single short dermal capillary loop, approximately 60 μ long. The appearance of the partially keratinized cells adjacent to those fully keratinized suggests that growth was still taking place at the time of preservation and that this tubercle might have grown larger.

Pseudorasbora parva (Temminck and Schlegel)

Figure 4C

Male, 70 mm., S.L. U.S.N.M. No. 203429. Taiwan. Tubercles are present just below the eye, between the eye and the mouth, and on the chin. A suborbital tubercle section is 530 μ high from basement membrane to tip and 790 μ wide. The keratinized cap is about 170 μ thick at the apex and contains about 20 cell layers laterally, tapering to a few cell layers at the edges. The stratum germinativum is columnar; above it, the violet-staining hypertrophied cells of the epidermal core reach 50 μ diameter in the layers adjacent to the keratin layer.

Phenacobius mirabilis (Girard)

Figure 4D

Nuptial male, 62 mm., S.L. U.S.N.M. No. 203428. Kansas, Chase County, Neosho River drainage. March 30, 1963. Very small tubercles are scattered over the entire dorsal surface of the head and laterally on the opercles, the upper surface of the pectoral fins, and the posterior edges of the scales of the dorsum ventrally to the lateral line and posteriorly to the dorsal fin.

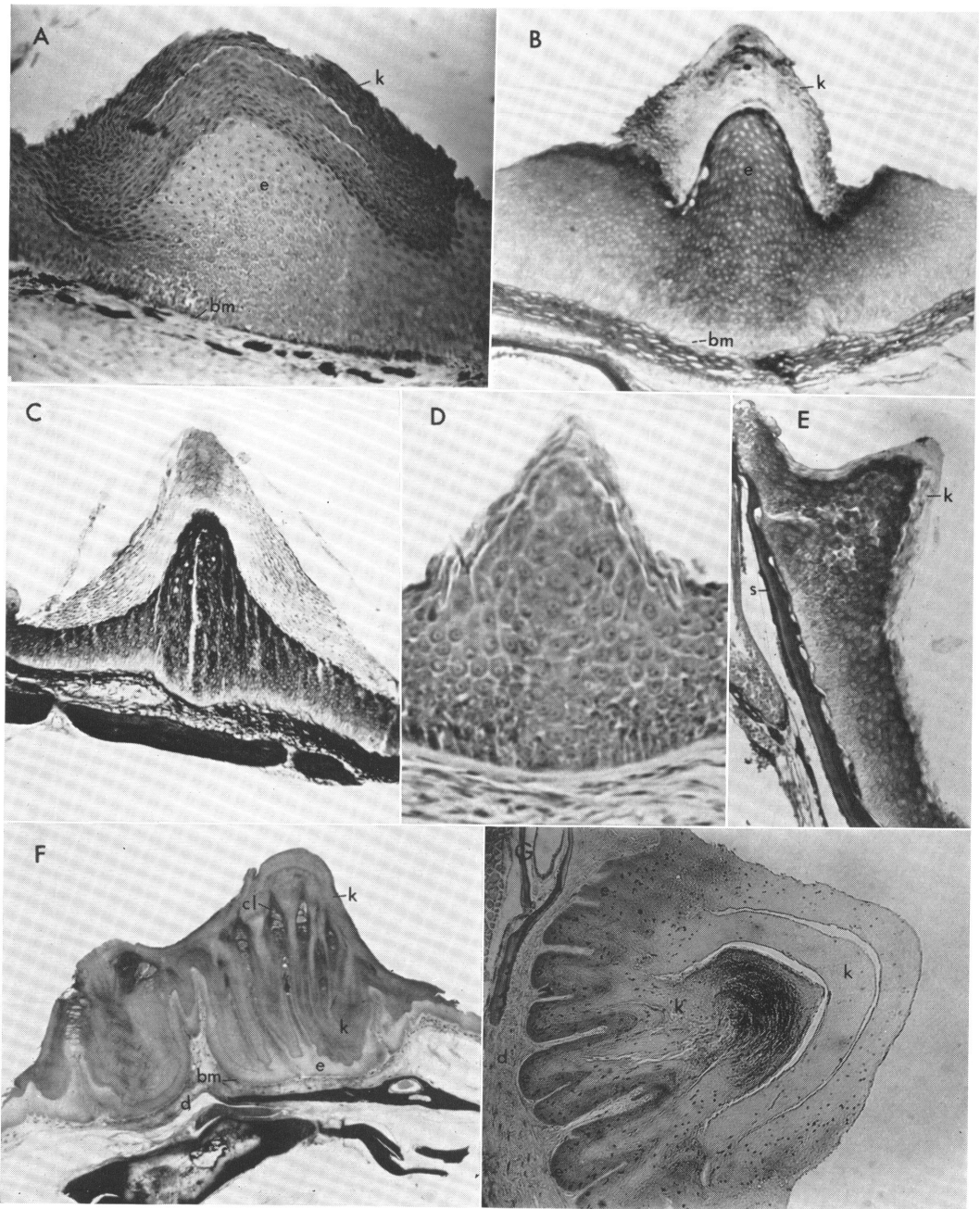


Fig. 4. A. *Leuciscus souffia muticellus* tubercle from dorsum of head. Male. H and E stain. $\times 106$. B. *Barbus longiceps* tubercle from below eye. Male. Mallory's triple stain. $\times 75$. C. *Pseudorasbora parva* tubercle from below eye. Male. Mallory's triple stain. $\times 75$. D. *Phenacobius mirabilis* tubercle from operculum. Male. H and E stain. $\times 315$. E. *Clinostomus funduloides* tubercle from dorsolateral scale. Male. Mallory's triple stain. $\times 161$. F. *Semotilus atromaculatus* tubercle from snout. Structure formed by fusion of two adjacent tubercles. Male. Mallory's triple stain. $\times 12$. G. *Campostoma anomalum* postocular tubercle. Lighter colored tissue extending into the epidermal interdigitations is keratinized. Male. H and E stain. $\times 26$.

Abbreviations: bm, basement membrane; cl, capillary loop; d, dermis; e, epidermis; k, keratin; s, scale.

A median section of a tubercle from the opercle is 165 μ high from basement membrane to tip and approximately 130 μ in width. The keratinized cap is about 10 μ thick and is composed of only two or three cell layers. The germinativum is columnar, the cells above become progressively larger toward the tip of the tubercle, reaching a maximum diameter of 10–12 μ . The tubercles on the pectoral fin have approximately the same size and morphology.

***Clinostomus funduloides* Girard**

Figure 4E

Nuptial male, 60.5 mm., S.L. U.S.N.M. No. 203433. Virginia, Craig County, James River drainage. May 29, 1964. The entire body is tuberculate. The dorsal and lateral scales have one tubercle each and form rows on the body. Tubercles are present on the head laterally and dorsally, on the breast, on the upper surface of the pectoral and pelvic fins, and on the anal and dorsal fins. The tubercles are largest on the top of the head.

A median section through a scale tubercle from an area just anterior and lateral to the dorsal fin is about 194 μ high from basement membrane to keratinized tip, and about 210 μ in diameter across the base. It is situated near the posterior margin of the scale and is inclined posteriorly, its vertical axis forming an angle of approximately 60 degrees with the underlying scale. A keratinized layer of epidermal cells that is continuous with the keratinized cap of the tubercle, extends anteriorly for about 200 μ and forms an obtuse angle with the anterior surface of the cap. The unkeratinized cells underlying this extensive region of keratinized surface cells are hypertrophied in the same manner as the cells in the core of the tubercle. It appears that the tubercle is surrounded by a keratinized layer that forms a collar covering almost one-half the surface of the exposed portion of each scale. This feature is not readily apparent in the whole preserved specimen. The thickness of the keratinized cap varies from about 25 μ on the anterior surface to about 10 μ on the posterior surface. The stratum germinativum is cuboidal underneath the tubercle becoming low columnar to columnar anteriorly. The largest polygonal, hypertrophied cells are approximately 39 μ in diameter. The basement membrane is closely adherent to a 2–5 μ thick layer of dense con-

nective tissue and closely follows the surface contour of the scale.

A section through a head tubercle that is 550 μ high and 650 μ wide has the same essential features except that it is more massive and lacks any suggestion of a keratinized collar. No vascularized dermal papillae extend into the hypertrophied epidermis of these tubercles, but the dermis underlying the head tubercle is vascularized to an extent that is not apparent in the adjacent dermis.

***Semotilus atromaculatus* (Mitchill)**

Figure 4F

Nuptial male, 184 mm., S.L. U.S.N.M. No. 203424. West Virginia, Tucker County, Red Creek. June 13, 1956. Tubercles are very large on the snout and above the eye and small on the pectoral fins, the posterior edges of the scales from a point below the center of the dorsal fin to the caudal fin including all the scales on the caudal peduncle, and on the upper edge of the caudal fin.

The snout tubercle sectioned was formed by fusion of two closely adjacent tubercles to form an elongate keratinized ridge that is 2.7 mm. high from basement membrane to tip and 6.4 mm. long. The entire structure is composed of an almost solid mass of keratinized epithelium that is penetrated at intervals by vascularized dermal papillae that are spaced approximately 400 to 650 μ apart. Each papilla contains a vascularized dermal core, a layer of low columnar or cuboidal epithelium (germinativum), and layers of hypertrophied epithelial cells that grade into the keratinized layer. The largest unkeratinized cells are polygonal and may be up to 25 μ in diameter.

The tubercle occupies a depression that may be 500 μ below the level of the surrounding epidermis with keratinized tissue extending well into it. The dermal layer adjacent to the epidermis is composed of dense collagenous fibers forming a layer ranging from 100 to 200 μ thick and containing numerous melanocytes. Along much of its length the tubercle is closely appressed to underlying dermal bone from which it is separated by a connective tissue layer which in some places is only 100 μ thick. In areas adjacent to the tubercle the dense connective tissue layer immediately below the epidermis is thinner and is underlain by a thick layer of less dense collagenous tissue.

Campostoma anomalum (Rafinesque)

Figure 4G

Nuptial male, 123 mm., S.L. U.S.N.M. No. 203435. Missouri, Laclede County, Gasconade River. April 7, 1963. Large tubercles border the upper half of the orbit, are on the top of the head, and cover the dorsal and lateral body surface down to two scale rows below the lateral line. About half the scales in the tuberculate areas of the body bear tubercles, one in the center of the exposed portion of each scale.

A section through a large postocular tubercle is 2.4 mm. high from the deepest portion of the epidermis to the keratinized tip and 2 mm. wide. It occupies a depression 1.3 mm. deep with the keratinized portion extending 1.1 mm. above the surrounding epidermis. The keratinized portion, which makes up the bulk of the tubercle, is a laminated structure composed of two concentric keratinized cones that are 180 to 220 μ thick and fit over a solid keratinized core. Several vascularized dermal papillae extend into the tubercle as far as 650 μ . The low columnar to cuboidal germinativum and adjacent hypertrophied epithelial cells closely follow the contours of the dermis to form an interdigitating structure with the keratinized tissue. The thickness of the unkeratinized epithelium ranges from approximately 50 to 250 μ ; thickness is greatest at the periphery of the tubercle and least laterally along some of the median dermal papillae. The largest polygonal unkeratinized cells are up to 30 μ in diameter. Scattered throughout both the keratinized and unkeratinized portions of the tubercle are numerous melanocytes; these cells are less abundant in the adjacent undifferentiated epidermis.

Notropis chrysocephalus (Rafinesque)

Figure 5A

Nuptial male, 148 mm., S.L. K.U. No. 7876. Missouri, Greene County, White River drainage. May 11, 1963. Tubercles are large on top of the head, on the snout in front of the eye, and on the lower jaw; tubercles are smaller on the nape and the upper surface of the pectoral fins.

A section of a snout tubercle is approximately 1.0 mm. high from basement membrane to tip and 1.54 mm. wide. The keratinized cap is composed of two lamellae and is about 250 μ thick. The epithelial core is penetrated by several vascularized dermal papillae, the largest approximately 200 μ long. The columnar germinativum follows the contours of the dermal papillae. The largest hypertrophied cells near the tip of the unkeratinized core are approximately 25 μ in diameter.

Nocomis biguttatus (Kirtland)

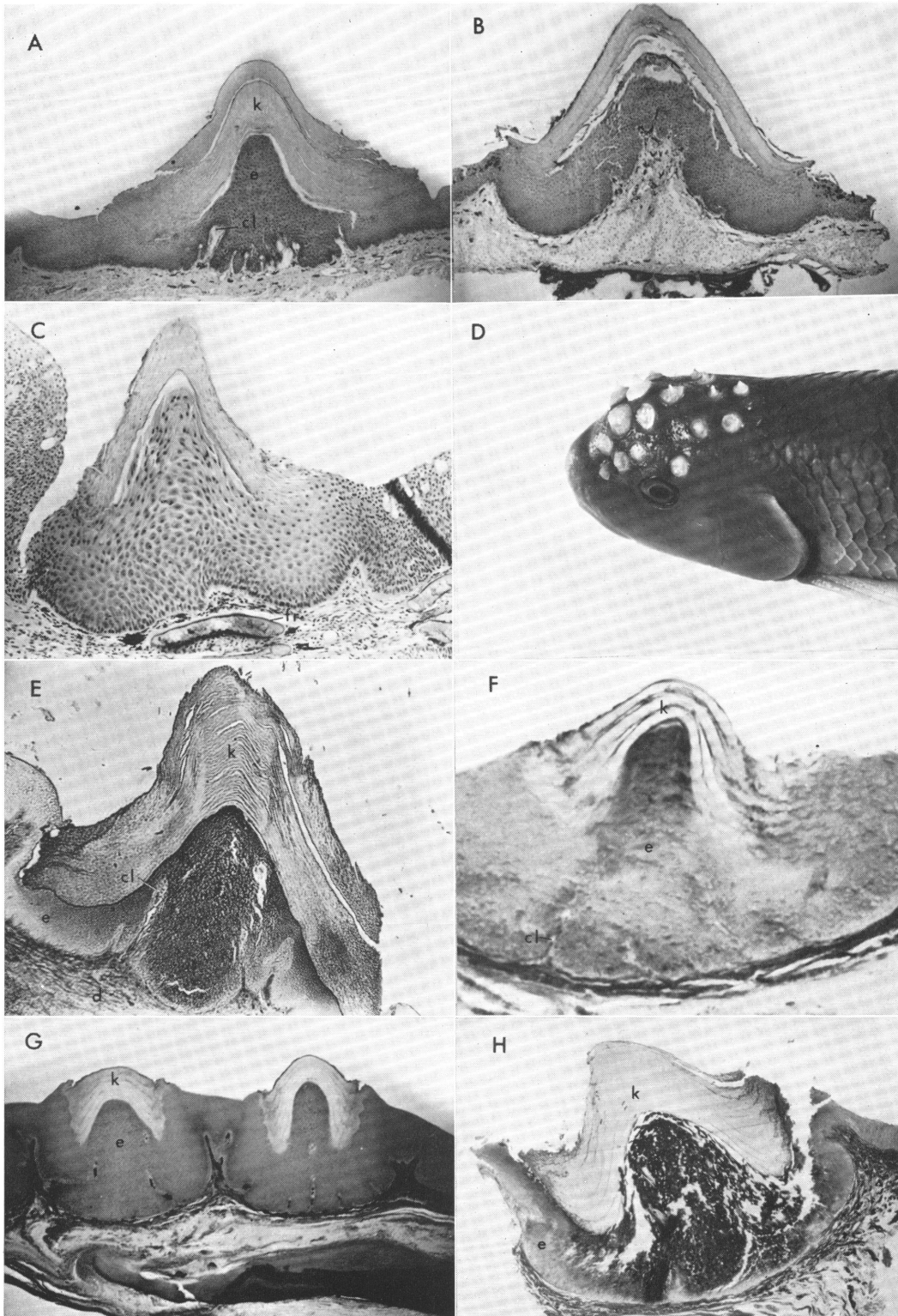
Figure 5B, C

Mature nuptial male, 122 mm., S.L. K.U. No. 7295. Wisconsin, Iowa County, Pecatonica River. June 14, 1962. Tubercles are large on top of the head; smaller tubercles are on the upper pectoral fin surface.

A submedial section through a head tubercle is approximately 1.1 mm. high and 1.7 mm. wide. The keratinized cap is composed of two distinct lamellae that total about 110 μ thick laterally. The cap is expanded basally to form a buttress at right angles to the plane of the keratinized laminae, and is about 250 μ wide. A large dermal papilla with contours that approximate the surface contours of the tubercle

FIG. 5. A. *Notropis chrysocephalus* tubercle from snout. Short vascularized dermal papillae extend into epidermal core. Male. H and E stain. $\times 34$. B. *Nocomis biguttatus* tubercle from dorsum of head. Dermis extends well above level of base of tubercle. Male. H and E stain. $\times 34$. C. *Nocomis biguttatus* tubercle from pectoral fin. Male. H and E stain. $\times 114$. D. Head of nuptial male *Nocomis leptocephalus*. Large tubercles are borne on nuptial crest. Approx. $\times .65$. E. *Nocomis leptocephalus* tubercle from nuptial crest on dorsum of head. Vascularized dermal papillae extend into epidermal core. Male. Mallory's triple stain. $\times 28$. F. *Varicorhinus* sp. tubercle from snout. Keratinized cap is composed of three lamellae. Male. Mallory's triple stain. $\times 94$. G. *Acrossocheilus formosanus* tubercle from snout. Keratinized cap has six lamellae. Male. Mallory's triple stain. $\times 32$. H. *Onychostoma leptura* tubercle from snout. Tubercle occupies a moderate depression in the dermis and the keratinized cap has seven lamellae. Male. Mallory's triple stain. $\times 35$.

Abbreviations: cl, capillary loop; d, dermis; e, epidermis, fr, fin ray; k, keratin.



extends well above the level of the base of the keratinized cap. From this main papilla, several smaller vascularized papillae extend into the epidermis of the tubercle. The hypertrophied epithelium of the tubercle follows the contours of the surface of the tubercle and forms a layer approximately $300\ \mu$ thick. The largest hypertrophied cells are about $18\ \mu$ in diameter. The underlying dermis, especially in the main papilla, is well vascularized adjacent to the tubercle epithelium. Numerous stellate melanocytes are also prominent.

A section of a pectoral fin tubercle is $410\ \mu$ high from the basement membrane to tip and approximately $300\ \mu$ wide. The lateral walls of the keratinized cap are $36\ \mu$ thick and the largest hypertrophied cells in the core of the tubercle are about $21\ \mu$ in diameter. Except for a small dermal papilla extending about $25\ \mu$ toward the center of the tubercle, the tubercle is not noticeably vascularized.

Nocomis leptocephalus (Girard)

Figure 5D, E

Male, 147 mm., S.L. U.S.N.M. No. 194715. Virginia, Montgomery County, South Fork Roanoke River. May, 1964. Tubercles are on a nuptial crest of fibrous connective tissue on the dorsum of the head and on the upper surface of the pectoral fin rays.

The section of a nuptial crest tubercle is 2.0 mm. high from basement membrane to tip and 2.3 mm. wide. The conical keratinized cap is composed of flattened cells which form laminae that tend to pull apart, causing preparation artifacts. Laterally the cap is approximately $400\ \mu$ thick. The epidermal core is composed of violet-staining polygonal epithelial cells and is penetrated by a series of vascularized dermal papillae which may extend to within $50\ \mu$ of the keratinized layer. The larger papillae may be $750\ \mu$ long and are composed of a series of whorled, spiraling capillaries that are supported by prominent amounts of collagenous tissue and accompanied by small undifferentiated germinal epithelial cells. Various parts of at least 12 of these loops are visible in one section. Except for prominent concentrations immediately below each tubercle, the loose connective tissue of the nuptial crest has few blood vessels.

Varicorhinus sp.

Figure 5F

Tuberculate male, 129 mm., S.L. U.S.N.M.

No. 85922. China, Fukien Province, Min River drainage. November–December, 1921. Tubercles are on the snout just above the lip and extend laterally to below the nares.

A snout tubercle is $510\ \mu$ high from basement membrane to tip and approximately $510\ \mu$ in width. The keratinized cap is made up of three distinct lamellae that are each about $210\ \mu$ thick. Cellular details in this preparation are very indistinct, but a number of vascularized dermal papillae, accompanied by the germinativum, extend well into the hypertrophied epithelium of the tubercle core.

Acrossocheilus formosanus (Regan)

Figure 5G

Nuptial male, 117 mm., S.L. U.S.N.M. No. 161708. Formosa, Taiko River. April 12, 1952. Snout tubercles extend to below the nares; some large tubercles are on the anal fin, and fine tubercles on the scales begin at about the level of the middle of the dorsal fin and extend posteriorly to the tail.

The snout tubercle sectioned is approximately $800\ \mu$ high from basement membrane to tip and $740\ \mu$ wide. The keratinized cap is made up of six distinct lamellae and extends approximately $330\ \mu$ below the level of the surrounding epidermis. Each lamella is approximately $20\text{--}25\ \mu$ thick and the whole structure is about $120\ \mu$ thick laterally, flaring out basally to form a widened buttress. The hypertrophied epithelial core is penetrated by vascularized dermal papillae which are accompanied, at least basally, by columnar germinal epithelium. The largest polygonal cells near the tip of the epithelial core are approximately $25\ \mu$ in diameter. Each tubercle occupies a slight depression in the dermis and is bounded peripherally by a ridge of dermis which extends to within $150\ \mu$ of the epidermal surface. Distally, the vascularized epidermal papillae are devoid of germinal epithelium and in some sections are separated from the keratinized layer by only two or three cell layers.

Onychostoma leptura (Boulenger)

Figure 5H

Tuberculate specimen, 121 mm., S.L. F.M.N.H. No. 14759. China, Hainan, Nodea. Four tubercles lie in a row on the tip of the snout.

A section of a snout tubercle is 1.32 mm. high

from basement membrane to tip and approximately 1.65 mm. wide. The lateral walls of the keratinized cap are approximately 250 μ thick and six or seven indistinct lamellae recurve basally to form an expanded, buttress-like structure that is the site of attachment to the adjacent epithelium. Several vascularized dermal papillae, accompanied by little, if any, discernible germinal epithelium, penetrate the hypertrophied epithelium to near the tip of the tubercle. The hypertrophied polygonal cells of the tubercle core are about 18 μ in diameter and are very loosely attached to each other in this preparation, tending to fall out of the sections. The tubercle occupies a depression in the dermis that is approximately 670 μ deep and 1650 μ wide.

***Garra taeniata* Smith**

Figure 6A

Female, 71 mm., S.L. U.S.N.M. No. 108003. Thailand, waterfall stream near Trang. September 10, 1933. The snout is tuberculate.

A section of a snout tubercle is 1060 μ high from basement membrane to tip and 770 μ wide. The vertical height of the keratinized cap is approximately 600 μ and the cap is about 75 μ thick laterally near the apex, tapering gradually to about 50 μ near the base. The hypertrophied epithelium of the tubercle core occupies a depression in the dermis that extends approximately 450 μ below the surrounding epidermal surface; it is made up of polygonal hypertrophied cells that are of almost uniform size, averaging about 13 μ in diameter, and is penetrated by numerous vascularized dermal papillae that extend almost to the keratinized layer. The vascularized papillae lack any accompanying stratum germinativum and they have little collagenous connective tissue; they contain occasional melanocytes. Underlying the epidermis is a layer of dense collagenous connective tissue that is about 25 μ thick, increasing to approximately 60 μ beneath the tubercle.

***Garra gotyla* (Gray)**

Figure 6B

Immature tuberculate female, 65 mm., S.L. U.S.N.M. No. 165121. India, Uttar Pradesh. February 16, 1949. The snout has a well-developed median proboscis and a transverse lobe at the tip. The end of the proboscis, trans-

verse lobe, and sides of the head in front of the nares are covered with several large tubercles.

A section through a tubercle from the transverse process of the snout is 800 μ high from basement membrane to tip and about 440 μ wide. The keratinized cap extends about 300 μ above the level of the adjacent epidermal surface. The epidermal core of the tubercle occupies a depression in the dermis that is almost circular and has a maximum width of 460 μ . Several vascularized dermal papillae extend into the hypertrophied epithelium, one reaching to within four cell layers (41 μ) of the keratinized cap. These papillae lack germinal epithelium and contain little connective tissue. The germinativum, which is continuous with the germinativum of the surrounding epidermis, is cuboidal to low columnar; the overlying cell layers are polygonal and quickly become hypertrophied to form a solid core of cells which reach approximately 13 μ diameter in the layers adjacent to the keratinized layer. Between the stratum germinativum and the dense connective tissue that encloses the epithelial core is a complex network of anastomosing capillaries and small blood vessels from which arise the capillary loops that extend into the epithelial core of the tubercle. The lateral wall of the keratinized cap is approximately 30 μ thick, gradually tapering to a thin edge at the base. The tuberculate transverse process is a fibrous pad of collagenous connective tissue.

***Labeo annectens* Boulenger**

Figure 6C

Tuberculate specimen, 149 mm., S.L. U.S.N.M. No. 119178. Africa, Cameroons, Sakbayeme. 1922. Specimen eviscerated. Tubercles on snout.

A section through a snout tubercle is approximately 1000 μ high from basement membrane to keratinized tip and 400 μ wide at the surface. The keratinized cap is approximately 56 μ thick laterally and is abruptly truncated at the base where it contacts the relatively undifferentiated cells of the epidermal rim surrounding the tubercle. The outer edge at the base flares laterally to form a thin projecting collar that is continuous with the main keratinized cap. The core of hypertrophied polygonal cells occupies a depression approximately 750 μ deep and 460 μ wide, forming a flask-shaped structure sur-

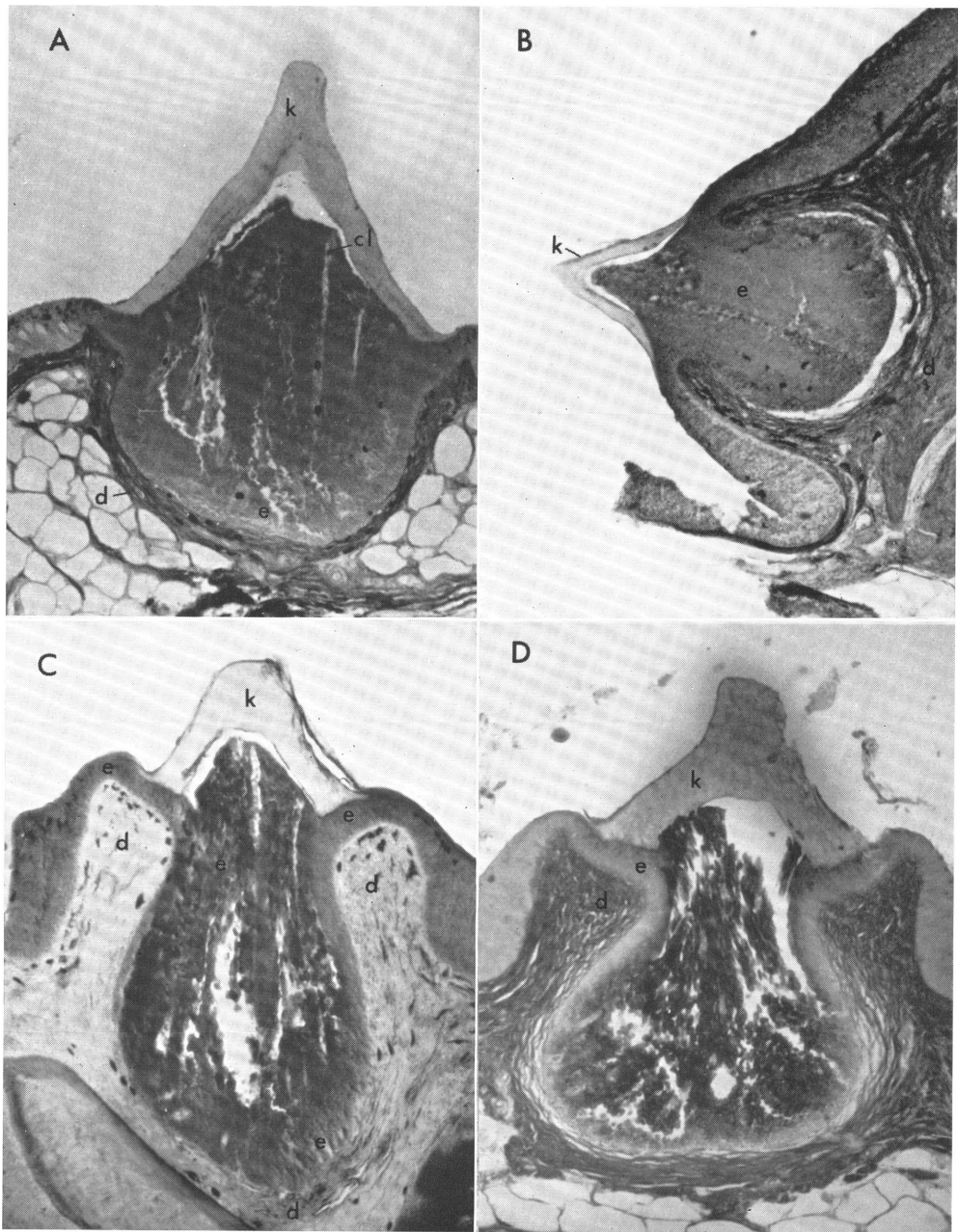


FIG. 6. A. *Garra taeniata* tubercle from snout. Tubercle pit is relatively shallow and open. Female. Mallory's triple stain. $\times 58$. B. *Garra gotyla* tubercle from snout. Tubercle pit is relatively deep and enclosed by dermis. Female. Mallory's triple stain. $\times 58$. C. *Labeo annectens* tubercle from snout. Tubercle pit is deep and well developed. Mallory's triple stain. $\times 69$. D. *Labeo parvus* tubercle from snout. Mallory's triple stain. $\times 66$.

Abbreviations : cl, capillary loop; d, dermis; e, epidermis; k, keratin.

rounded by dense connective tissue. The cells in the central portion of the hypertrophied core are fusiform, approximately $39\ \mu$ long, and $8\ \mu$ wide whereas those deeper and more lateral in the expanded portion of the flask-shaped core are polygonal and about $15\ \mu$ in diameter. The same feature is also present in tubercles of *Labeo parvus* (fig. 6D) in which the flask-shaped core is wider, and flattened at the bottom.

In this type of tubercle the vascular papillae originate from the base or bottom of the hypertrophied core. The longest papillae extend the entire distance from the base to the tip of the hypertrophied epithelium just below the keratinized tip. In *Labeo* and *Garra* they can clearly be seen to consist of simple ascending and descending vessels that lie in close apposition and follow the same course.

OTHER SPECIES EXAMINED

Sections of the large snout tubercles of *Pimephales notatus* (Rafinesque), K.U. No. 5750, and *Zacco platypus* (Temminck and Schlegel), U.S.N.M. No. 203431, each have several capillary loops in their hypertrophied epithelial cores and are similar to the large tubercles of *Nocomis leptcephalus*. The *Z. platypus* tubercles differ significantly from those of *N. leptcephalus* only by the presence of a keratinized epithelial layer that is continuous with the keratinized caps of the opercular tubercles. Sections of the tubercles of *Labeo diplostomus* (Heckel), F.M.N.H. No. 2293, *Labeo parvus* Boulenger, F.M.N.H. No. 55333, and *Lobocheilus bo* (Popta), F.M.N.H. No. 68528, are all similar to those of *Labeo annectens*.

FAMILY GYRINOCHEILIDAE

The Gyриноcheilidae are one of the most peculiar cyprinoid families in mouth structure, absence of pharyngeal teeth, and presence of both exhalant and inhalant gill openings (Hora, 1923; Smith, 1945). It is a southeast Asian family consisting of the genus *Gyrinocheilus* with two species: *G. aymonieri* (Tirant) and *G. pennocki* (Fowler) according to Smith (1945). In raising the group to family level, Hora (1923) noted the tubercles that stud the proboscis of *G. aymonieri* (as *G. kaznakovi* Berg). Fowler (1937, pp. 159–161) described and illustrated the tubercles on the snout of the holotype of *G. pennocki*. Smith (1945, p. 284) reported that rostral tubercles begin to appear on *Gyrinocheilus*

aymonieri about 100 mm. long. He found tubercles in both sexes but those of males much better developed. In our material of *G. aymonieri*, tubercles begin in juveniles. Prominent rostral tubercles are present in both sexes and become largest in females.

Sections of a large rostral tubercle (figs. 7, 8B) reveal a number of unique structural features. The tubercle consists of an invagination of epithelium into a thickened pad of collagenous connective tissue, forming a sac or pitlike structure similar to that in some of the cyprinid fishes. There the similarity ends. The functional tubercle at the surface is made up of a solid cone of keratinized epithelial cells. It is not a hollow keratinized cone filled with and supported by a core of hypertrophied epithelium. Below the functional tubercle is a second, fully formed replacement that apparently moves to the surface and replaces the functional one when it is lost. Below the replacement may be one or two aggregations of hypertrophied epithelial cells that are in the process of keratinizing to form additional replacements. The development of replacement tubercles is much like that described for cyclostome teeth by Jacoby (1894), Warren (1902), and Sognnaes and Lustig (1955). In cyclostomes, the functional teeth are replaced from below by teeth also formed by keratinization of hypertrophied cells. The *Gyrinocheilus* tubercle pit is highly vascularized by a series of parallel, vertically oriented blood vessels (fig. 8D) that give off numerous capillaries which anastomose to form a complex network of blood vessels that completely encloses and penetrates throughout the peripheral layers of the tubercle epidermis. An additional unique feature is that all of the epithelial cells in the pit and contributing to tubercle formation are binucleate. The very fine, minute tubercles that are common in the male do not develop from a pit and are not vascularized but have a morphology similar to that of cobitid and homalopterid tubercles. Binucleate cells are not as apparent in these small tubercles as they are in the large ones but can be seen in some sections.

Gyrinocheilus aymonieri (Tirant)

Figures 7, 8A–E

Female, 157 mm., S.L. U.S.N.M. No. 117721. Thailand. Tubercles are present on several elevated fleshy pads from the tip of the snout back

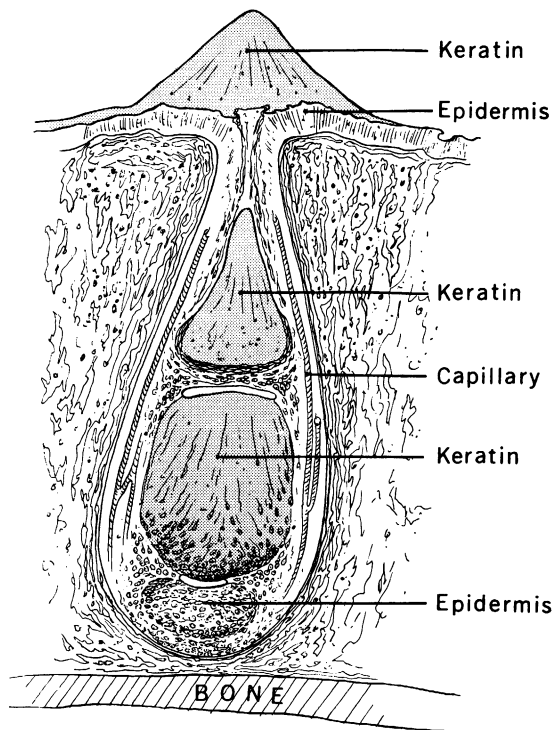


FIG. 7. Diagrammatic drawing of a section through a *Gyrinocheilus ayonieri* snout tubercle showing developing replacement tubercles. Compare with figure 8B.

to a line between the anterior edges of the orbits. Male, 125 mm., S.L. The rostral tubercles are not so well developed as in the female. Numerous minute tubercles are scattered over the entire dorsal and lateral surfaces of the head and are concentrated in a patch anterior to each eye and on a thick fleshy pad that occupies the space between the lateral corner of the mouth and the insertion of the pectoral fin. The upper surfaces of the branched pectoral fin rays are tuberculate.

A section was made of a rostral pad of the female including several tubercles and the underlying bone to which the pad is attached (figs. 7, 8B). The bulk of the pad is a dense network of collagenous connective tissue fibers. The tubercles are an invagination of the epidermis into this collagenous pad. On the surface is a solid keratinized cone about $400\ \mu$ high and $640\ \mu$ wide; below it, extending to a depth of $2000\ \mu$, is an elongate flask-shaped epidermal pit approximately $600\ \mu$ wide. Immediately below the surface tubercle is a second tubercle

that is fully keratinized and is apparently a replacement for the tubercle at the surface. The portion of the replacement tubercle in the section is $440\ \mu$ wide and $550\ \mu$ long. Below it, and separated by an aggregation of cells about $90\ \mu$ thick, is a mass of large, orange-staining epidermal cells that appears to be the precursor of a third tubercle. This mass is $420\ \mu$ wide and about $640\ \mu$ long. In its upper layers, cell borders and nuclei are indistinguishable and the cytoplasm appears fibrous. Basally the cells are distinct and spindle-shaped—about $50\ \mu$ long and $10\ \mu$ wide—and have prominent nuclei. Immediately below is yet another mass of cells which occupies a space that is approximately $330\ \mu$ high and $500\ \mu$ wide and forms the base of the epithelial core.

The dorsal surface of the tuberculate pad is covered by a keratinized layer that is continuous with the keratinized surface tubercles and forms a layer 15 to $18\ \mu$ thick. The stratum germinativum of the undifferentiated epithelium adjacent to the tubercles is high columnar becoming lower under the keratinized surface, then cuboidal at the level where the descending epithelial invagination becomes vertical, and finally loses its identity as a distinct layer at about the level of the apex of the replacement tubercle. Below the level of the first replacement tubercle, the epithelial cells surrounding the two incipient replacement tubercles are loosely associated and all appear to be binucleate (fig. 8E). These cells have an irregular shape but tend to be flattened with their longest axis parallel to the surface of the enclosing collagenous connective tissue capsule. Many of the irregular polygonal cells in the basal layers at the bottom of the invaginated epithelial core contain mitotic figures (fig. 8E), indicating that this is the site of cellular reproduction. The entire epidermal structure is supplied by a basket-like network of blood vessels and capillaries that penetrates throughout the loose and peripherally situated cells of the stratum germinativum (fig. 8D). The vascular system is composed of a series of blood vessels that are about $12\ \mu$ in diameter and, spaced about $80\ \mu$ apart, run parallel to each other from the base of the epithelial core to near the surface below the functional tubercle. These small parallel blood vessels give off numerous capillaries which anastomose to form a complex network that completely encloses the epithelial core.

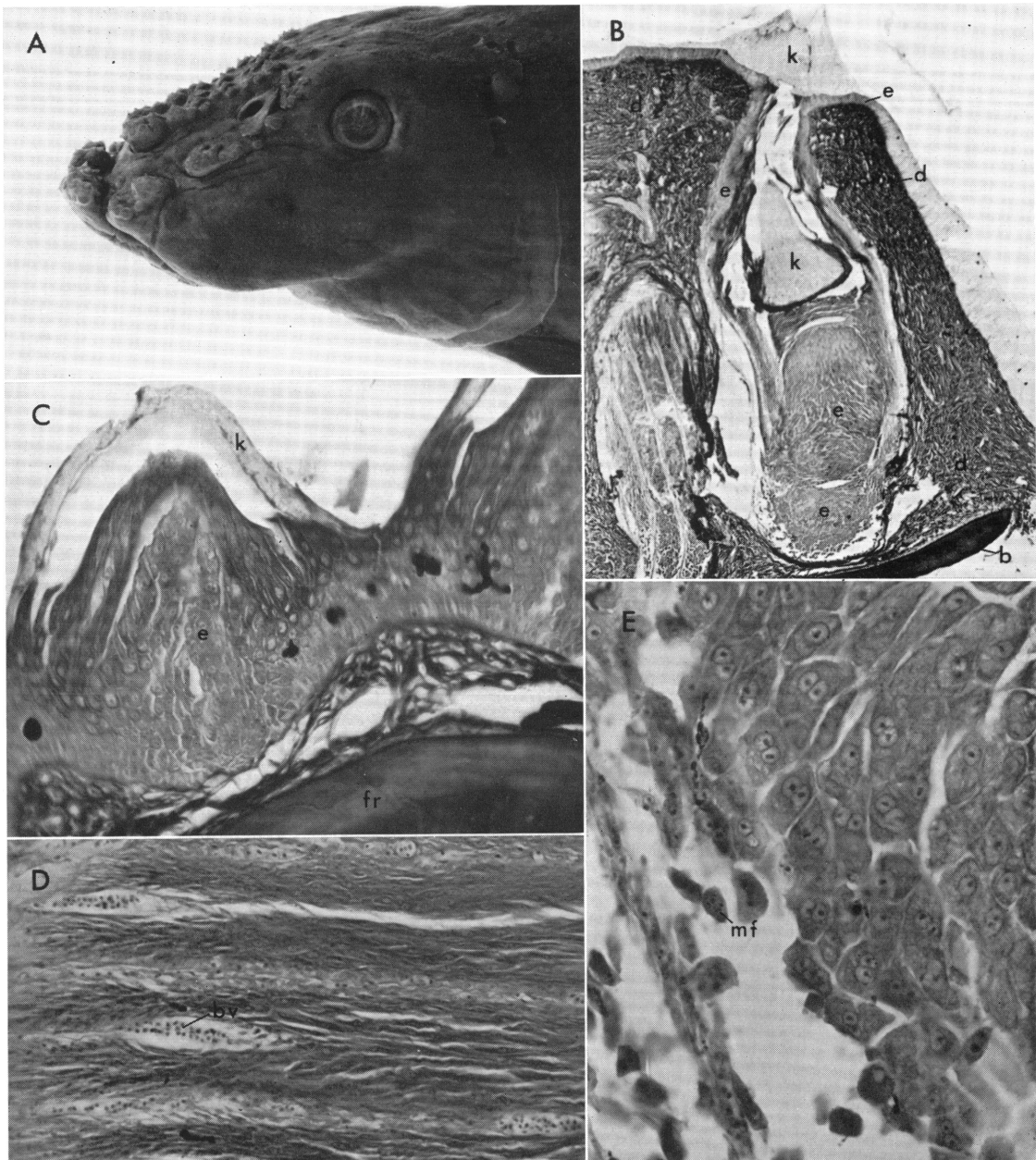


FIG. 8. A. Head of adult female *Gyri-nocheilus aymonieri*. Large tubercles are borne on raised, fleshy rostral pads. Approx. $\times 1.7$. B. *Gyri-nocheilus aymonieri* tubercle from snout with replacement tubercle in pit. Below are two aggregations of unkeratinized cells, presumed tubercles forming. To left is section through vascularized periphery of adjacent tubercle pit. Female. Mallory's triple stain. $\times 35$. C. *Gyri-nocheilus aymonieri* tubercle from pectoral fin. Male. Mallory's triple stain. $\times 330$. D. Section through epidermis of periphery of tubercle pit in *Gyri-nocheilus aymonieri* showing parallel blood vessels of the tubercle vascular system. H and E stain. $\times 266$. E. Binucleate epithelium in *Gyri-nocheilus aymonieri* tubercle pit. Several cells on left show presumed mitotic figures. H and E stain. $\times 333$.

Abbreviations: b, bone; bv, blood vessel; d, dermis; e, epidermis; fr, fin ray; k, keratin; mf, mitotic figure.

In a section passing through three adjacent tubercles, each has replacement tubercles in the same relative position and stage of development. It thus appears that the surface tubercles are lost simultaneously and that they are replaced by the synchronous upward movement of the pre-formed tubercles from below.

A section through one of the male rostral tubercles is similar to that of the female but it is considerably smaller; the flask-shaped epidermal core is approximately $900\ \mu$ deep and $550\ \mu$ wide. One fully formed replacement tubercle is in place below the functional tubercle but only one other replacement tubercle is being formed below that instead of two as in the female. This difference may be due, however, to a difference in maturity as some males are much larger than this specimen.

In a submedial section through two closely adjacent pectoral fin tubercles (fig. 8C), each is about $170\ \mu$ high from basement membrane to tip and $180\ \mu$ wide. They each have outer keratinized caps that are approximately $12\text{--}13\ \mu$ thick and that are joined where they meet. The stratum germinativum of the adjacent epidermis is columnar but becomes cuboidal then low and almost squamous beneath the center; the core of each is made up of polygonal hypertrophied epithelium with cell diameters of about $8\ \mu$. The two cell layers adjacent to the keratinized cap are in the process of keratinizing in both and have abundant fibrous, orange-staining cytoplasm. They are columnar, their longitudinal axes are parallel to the vertical axis of the tubercle, and they are arranged in a uniformly ordered layer. A space $5\ \mu$ wide separates this layer from the keratinized cap and is probably a preparation artifact. Sections through other small tubercles have the subsurface layer completely keratinized, forming a second distinct layer of keratin. In some sections stained with H and E, binucleate hypertrophied cells can be distinctly seen as in the much larger rostral tubercles. Although the connective tissue just below the basement membrane contains blood vessels, there is no evidence of vascularization extending into the epidermal core. The details of structure described for the small pectoral fin tubercles apply equally to those of similar size on the head.

FAMILY PSILORHYNCHIDAE

This is a small family of peculiar fishes known

from the Himalayas and the Assam Hills of India, Burma, and Nepal. They have been assigned by various authors to the Cyprinidae, Cobitidae, and Homalopteridae but are now considered as an independent family (Hora and Mukerji, 1935; Hora, 1952). Four species, all in the genus *Psilorhynchus*, are recognized (Menon and Datta, 1964). Sections were made of tubercles from the operculum, pectoral fin, and scales of 67 mm. S.L. male *Psilorhynchus homaloptera* Hora and Mukerji (obtained through the courtesy of Dr. A. G. K. Menon, Zoological Survey of India, Calcutta, Reg. No. F4246/2). In essential features and size they resemble cobitid or homalopterid tubercles and look much like figure 10B.

FAMILY CATOSTOMIDAE

The suckers are a predominantly North American family of 14 genera and about 80 species of medium size to large size fresh-water fishes. The males of many species develop breeding tubercles on the head, body, and fins, and a number of authors have reported on them. Forbes and Richardson (1909) described breeding tubercles on *Ictiobus*, *Carpiodes*, *Erimyzon*, *Minytrema*, *Catostomus* and *Moxostoma*. Fowler (1912) illustrated them on species of *Cycleptus*, *Carpiodes*, *Catostomus*, *Erimyzon* and *Moxostoma*. Ellis (1914) reported tubercles on the top of the head of breeding male *Carpiodes velifer* (Rafinesque), and on the anal rays of breeding male *Catostomus griseus* (Girard). Reighard (1920) described tubercles and their functions in great detail for three species of suckers: *Catostomus catostomus* (Forster), *Moxostoma aureolum* [= *M. erythrurum* (Rafinesque) according to Hubbs, 1930], and *Hypentelium nigricans* (LeSueur). Hubbs (1930) used the distribution of breeding tubercles as a character in his key to the species of *Erimyzon* and to the Mississippi and Great Lakes species of *Moxostoma*. Raney and Lachner (1946c) described tubercles on the type of their *Thoburnia hamiltoni*. Raney and Lachner reported tubercles on both sexes of *Hypentelium nigricans* (1946a), *Thoburnia rhothoeca* (Thoburn) (1946b), and *Hypentelium roanokense* Raney and Lachner (1947) and in all species the tubercles were better developed on the male than those on the female. Dence (1948, pp. 100–102) gave a detailed description of breeding tubercles on the dwarf sucker, *Catostomus commersonii utawana* Mather. Tubercles are present

on the scales and fins of both sexes but are generally weaker and less conspicuous in the female. Robins and Raney (1956) gave complete descriptions of the nuptial tubercles on five species of the subgenus *Scartomyzon* of *Moxostoma*: *lachneri* Robins and Raney, *rupiscartes* Jordan and Jenkins, *cervinum* (Cope), *robustum* (Cope), and *ariommmum* Robins and Raney. Later Robins and Raney (1957), described the tubercles on two more species of this subgenus: *austrinum* (Bean) and *mascoetae* Regan. Both sexes usually had tubercles but they were better developed on males. Trautman (1957) figured and described tubercles on males of *Moxostoma erythrurum*, *M. a. aureolum* (LeSueur) [= *M. macrolepidotum* (LeSueur)], *M. valenciennesi* Jordan, *M. carinatum* (Cope), *Hypentelium nigricans*, *Minytrema melanops* (Rafinesque), *Erimyzon sucetta kenerlyi* (Girard), and *E. oblongus claviformes* (Girard). He also found that breeding females of *Hypentelium nigricans* often have small tubercles on the fins. Meyer (1962) reported well-developed tubercles on the anal fin and the ventral portion of the caudal fin in males of *M. erythrurum*, *M. macrolepidotum* (LeSueur), and *M. anisurum* (Rafinesque). He also found that females of these species had tubercles that were barely visible macroscopically. Branson (1962a) described the tubercle patterns in *Cycleptus elongatus* (LeSueur), *Ictiobus bubalus* (Rafinesque), *Moxostoma poecilurum* (Jordan), *M. carinatum*, *M. duquesnei* (LeSueur), *Hypentelium nigricans*, *Minytrema melanops*, *Erimyzon oblongus* (Mitchill), *Chasmistes brevirostris* Cope, *Catostomus macrocheilus* Girard, and *C. luxatus* (Cope). Unfortunately, he failed to integrate his observations with those of Fowler (1912), Reighard (1920), Hubbs (1930), and other such important works describing tubercles in suckers. Branson's attempt to interpret the evolution of the Catostomidae from the patterns of tubercle distribution that Gibbs (1957a) found in the minnows of the subgenus *Cyprinella* (lines of tubercles changing to scattered tubercles) is an invalid use of this character. Tubercle patterns of each group of fishes must be studied and interpreted separately. Branson and McCoy (1966) concluded that *Xyrauchen texanus* (Abbott) was probably more closely related to individuals of *Catostomus* than to individuals of *Chasmistes* on the basis of similarities in breeding tubercle distribution. Smith (1966) reported breeding tubercles on four species of the subgenus *Pantosteus* of the genus *Catostomus*. Huntsman

(1967) showed that tubercle distribution in the three species of carpsuckers (*Carpoides*) was species specific.

Two species, *Moxostoma erythrurum* and *Erimyzon sucetta*, are represented in the present study; they are distinctly different from each other in tubercle morphology. The tubercles of *M. erythrurum* are simply mounds of cells formed by epithelial hypertrophy and hyperplasia with keratinization of the tissue above a plane parallel to the surface. In contrast, the snout tubercle of *E. sucetta* is a solid keratinized cone supported by vascularized hypertrophied epithelium and closely resembles some of the larger cyprinid tubercles.

***Moxostoma erythrurum* (Rafinesque)**

Figure 9A

Male, 238 mm., S.L. K.U. uncatalogued. Kansas, Neosho River drainage. March 30, 1963. Tubercles on snout and on anal and caudal fins.

A section of an anal fin tubercle is about 600 μ high from basement membrane to tip. The tubercle is formed by hyperplasia and hypertrophy of the epidermal cells; keratinization takes place in all the cells lying above a plane parallel to the basement membrane. The dome-shaped keratin structure thus formed is 186 μ thick and 396 μ wide. The stratum germinativum is columnar beneath the central part of the tubercle and the cells above are hypertrophied, reaching an average diameter of approximately 18 μ before keratinizing. An intercellular space approximately 2 μ wide and containing numerous intercellular bridges surrounds each of the hypertrophied cells. Two weakly developed dermal papillae about 50 μ long extend into the base of the tubercle. In other tubercles on this specimen these papillae are better developed, but seem not to be significantly vascularized as they are in many other cypriniform fishes. The appearance of mitotic figures in the stratum germinativum and the early collecting date suggest that this specimen is not fully mature and that the tubercles might have become significantly larger.

***Erimyzon sucetta* (Lacépède)**

Figure 9B

Male, 180 mm., S.L. U.S.N.M. No. 203418. South Carolina, Congaree River. April 13, 1954.

The side of the snout has four large tubercles below the nares and anterior to the eye, and numerous small tubercles lie along the anal fin rays.

A section through a snout tubercle is 1.74 mm. high from basement membrane to tip and about 2.65 mm. wide. The keratinized cap consists of a solid cone that contains a relatively shallow core of nonkeratinized epithelium. The maximum thickness is 1160 μ for the keratinized cap and 580 μ for the unkeratinized epithelial core. Portions of at least 20 vascularized dermal papillae penetrate the hypertrophied epithelium; the longest is about 285 μ long and extends to within about 160 μ of the keratinized layer. Each papilla is accompanied by a layer of columnar stratum germinativum, contains abundant amounts of collagenous fibers, and has ascending and descending vessels that are tightly coiled distally to form a glomerulus-like structure. The hypertrophied cells reach a maximum size of approximately 25 μ and have numerous intercellular bridges crossing the prominent intercellular space surrounding each cell.

FAMILY HOMALOPTERIDAE

This family of small loachlike fishes inhabits torrential streams of southeastern Asia. Silas (1953) recognized two families, the Homalopteridae with 12 genera and 53 species, and the Gastromyzonidae with 16 genera and 31 species. Greenwood et al. (1966) considered them all one family. Several new Bornean species were described subsequently by Inger and Chin (1961, 1962).

Homalopterids often have breeding tubercles scattered over the entire body of both sexes. Although superficially like those of cyprinids, homalopterid tubercles differ in the way that the hypertrophied cells are organized and develop into the keratinized cap. The keratinized cap is composed of a single layer of cells but the layer of hypertrophied cells beneath are all en-

larged to about the same size, are in the same stage of keratinization, and form a well-defined, uniform layer that is destined to become another keratin cap. Tubercles apparently persist for long periods of time, so that this type of growth represents a means whereby the keratinized cap may be replaced as it is worn off or otherwise lost.

SUBFAMILY HOMALOPTERINAE

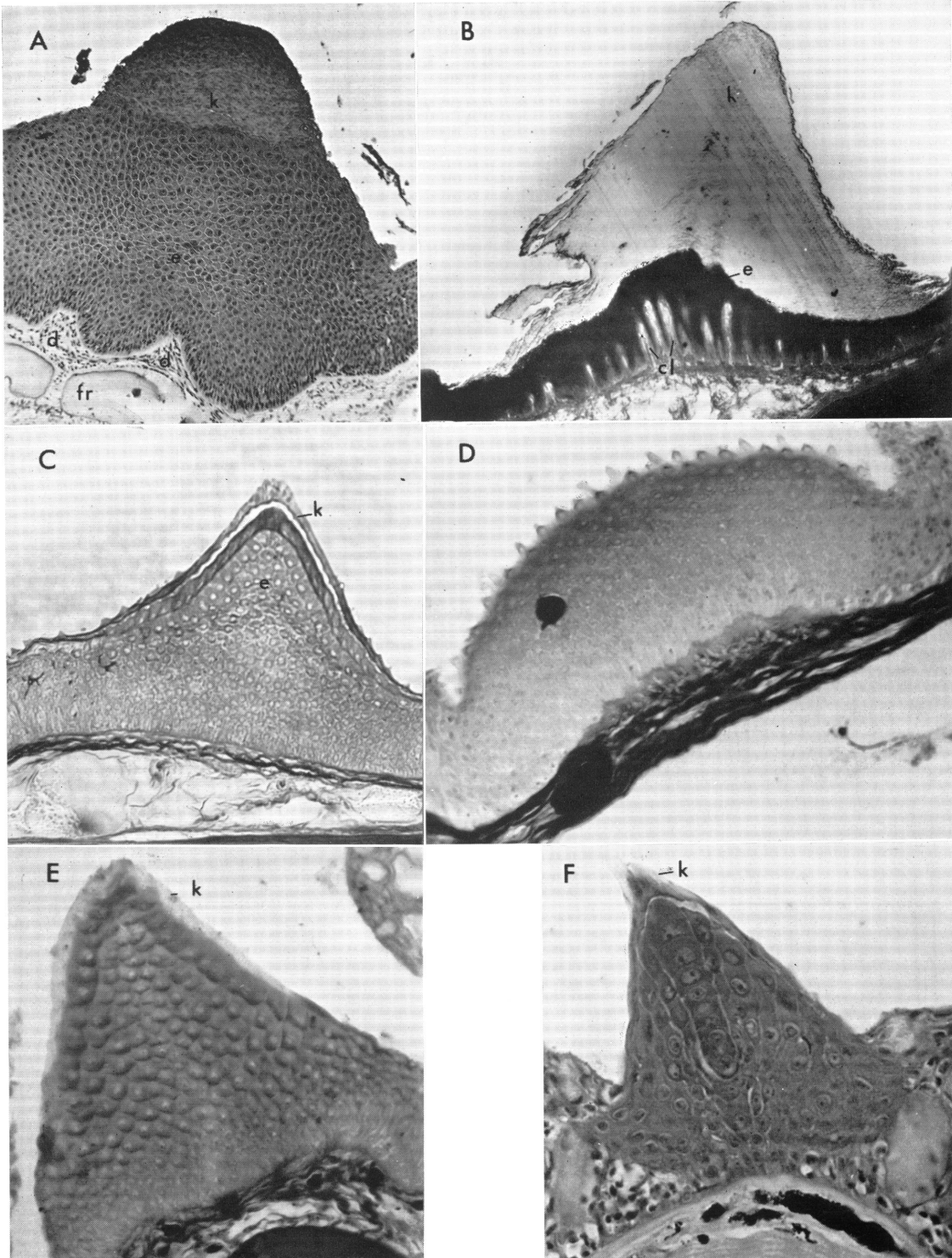
Several workers have noted or figured tubercles without clearly pointing out that they were breeding tubercles. Hora (1932, p. 286) reported short, wartlike spinous projections on the head of *Homaloptera smithi* Hora; Fowler (1939) noted that many specimens had the whole upper surface of the head and anterior part of the back studded with numerous small tubercles. Smith (1945, p. 280) figured tubercles in his original description of *Balitoropsis bartschi* and described them as "dermal papillae" in his holotype (a ripe female, U.S.N.M. No. 107963). In a brief survey of the homalopterines in the U.S. National Museum, we found tubercles on males of *Bhavana australis* (Jerdon) (U.S.N.M. No. 165107), *Sinogastromyzon wui* Fang (U.S.N.M. No. 87615), *Hemimyzon formosanum* (Boulenger) (U.S.N.M. No. 161711), and on both males and females of *Homaloptera smithi* (U.S.N.M. No. 109821). Most of these species have tubercles on the snout or dorsal surface of the head; tubercles frequently extend farther posteriorly, especially in males.

Hemimyzon formosanum (Boulenger) Figure 9C

Female, 61.5 mm., S.L. U.S.N.M. No. 203430. Taiwan. Body, head, and fins are tuberculate, except for the flattened ventral surface and the caudal fin. The head and caudal peduncle tubercles are large and obvious but those elsewhere on the body and fins are almost microscopic.

FIG. 9. A. *Moxostoma erythrurum* tubercle from anal fin. Male. H and E stain. $\times 89$. B. *Erimyzon sucetta* tubercle from snout. Tubercle core is well vascularized. Mallory's triple stain. $\times 35$. C. *Hemimyzon formosanum* tubercle from the operculum. Note keratinizing layer beneath keratin cap. Female. Mallory's triple stain. $\times 148$. D. *Balitoropsis bartschi* tubercle from below eye. Small, unicellular, conical projections cover the surface. Female. Mallory's triple stain. $\times 286$. E. *Gastromyzon borneensis* tubercle from pectoral fin. Mallory's triple stain. $\times 310$. F. *Progastromyzon griswoldi* tubercle from below naris. Center of epithelial core is filled by column of hypertrophied cells. Compare with figure 3C. Male. H and E stain. $\times 528$.

Abbreviations: cl, capillary loop; d, dermis; e, epidermis; fr, fin ray; k, keratin.



A section of a tubercle on the operculum is approximately $220\ \mu$ high from basement membrane to tip and $410\ \mu$ wide. The cells above the columnar stratum germinativum are hypertrophied, the largest cells lying near the surface. The keratinized cap, approximately $8\ \mu$ thick laterally, gradually tapers to a very thin layer only 1 to $2\ \mu$ thick basally, and is made up of a single layer of cells. It is formed by the cells becoming vertically flattened or squamous, the more basal cells overlapping those nearer the apex. The first layer of hypertrophied cells below the keratinized cap is in the process of keratinizing; these cells are somewhat flattened and parallelogram-shaped with their longitudinal axes oriented parallel to the vertical axis of the tubercle. Immediately below the keratinizing layer is another layer of cuboidal cells approximately $10\ \mu$ wide. Tubercles on the pectoral fin and caudal peduncle are similar to the one just described.

***Balitoropsis bartschi* Smith**

Figure 9D

Female, 79 mm., S.L. U.S.N.M. No. 107963. Thailand, Trang Province, waterfall stream on Kao Chong. September 2, 1933. Low rounded tubercles cover the entire dorsal and lateral surface of the head; some of the larger ones on the head dorsum are elongate. Elongate epidermal thickenings on the center of each scale, especially those anteriorly, produce a keeled effect with ridges running the length of the fish.

A section through a tuberculate patch from below one eye shows structures that are markedly different from other tubercles examined. Each is a mound of epithelial tissue that consists of a solid mass of violet-staining, slightly hypertrophied cells that are largest in the surface layers. Covering the surface are small, unicellular, conical projections that are 10 to $13\ \mu$ high. The stratum germinativum is columnar and the overlying cells are only slightly hypertrophied, the largest reaching a diameter of about 12 to $15\ \mu$. One of these tubercles is about $105\ \mu$ high from basement membrane to surface and about $260\ \mu$ wide; the lateral borders are delimited from the adjacent epidermis by a shallow sulcus.

OTHER SPECIES EXAMINED

Other species of homalopterines examined have a tubercle morphology similar to that of

Hemimyzon formosanum. They are *Balitoria brucei* Gray, M.N.H.N. No. 28:216; *Sinogastromyzon sanhoensis* Fang, B.M.N.H. No. 1933.7.26.8; *Sinogastromyzon wui* Fang, U.S.N.M. No. 87615; and *Bhavana australis* (Jerdon), U.S.N.M. No. 165107.

SUBFAMILY GASTROMYZONINAE

Tuberculation in the Gastromyzoninae is very similar to that in the Homalopterinae. Tubercles have been figured for three species: *Pseudogastromyzon fasciatus* (Sauvage) by Hora (1932); *Progastromyzon griswoldi* in the original description by Hora and Jayaram (1951) and by Inger and Chin (1962); and *Liniparhomaloptera disparis* (Lin) by Fang (1935). Inger and Chin (1961) described the tubercles of five species of Bornean *Gastromyzon*. Both sexes of *G. borneensis* Günther, *G. punctulatus* Inger and Chin, and *G. fasciatus* Inger and Chin have small tubercles on the dorsal surfaces of the head and pectoral fins and larger ones on the tip of the snout. *Gastromyzon pauciradiatus* Inger and Chin is similar but females have tubercles only on the snout. *Gastromyzon nieuwenhuisi* (Poopa) lacks tubercles on the pectoral fins. In 1962, Inger and Chin described the tubercles of two more Bornean gastromyzonines: *Glaniopsis hanitschi* Boulenger (snout, sides of head, chin, and the dorsal surface of the pectoral rays in mature males) and *Progastromyzon griswoldi* (head and first four or five pectoral rays in mature males, indistinct tubercles on the snout and sides of the head in mature females). We have also found tubercles on males of *Beaufortia pingi* Fang (U.S.N.M. No. 89373) and on males and females of *G. borneensis* (U.S.N.M. No. 113324).

***Gastromyzon borneensis* Günther**

Figure 9E

Specimen, not sexed, 64 mm., S.L. B.M.N.H. No. 1894.6.30.196-7. North Borneo. Fine tubercles are scattered over the entire dorsal and lateral body surfaces including the fins. Larger tubercles are on the snout and caudal peduncle. In the other specimens examined both sexes have the tubercles equally developed.

A section of a pectoral fin tubercle is $170\ \mu$ high from basement membrane to tip and $182\ \mu$ wide. The stratum germinativum is columnar laterally becoming cuboidal below the center of the tubercle. The epithelial cells of the tubercle core are hypertrophied; the largest lie in a layer

just below the unicellular keratinized cap. The largest hypertrophied cells are approximately $10\ \mu$ wide and are cuboidal, forming a uniform layer beneath the keratinized cap which is about $10\ \mu$ thick laterally near the apex, gradually tapering to a thin layer basally.

Progastromyzon griswoldi (Hora and Jayaram)

Figure 9F

Male, 70 mm., S.L. F.M.N.H. No. 68133. North Borneo. July 27, 1959. The dorsal and lateral surfaces of the entire head and body are tuberculate as are all the fins, except for the caudal. The pectoral fin rays have many tubercles dorsally and tubercles are concentrated on the caudal peduncle and the lateral surface of the head below the nares.

A tubercle from the patch below a nostril is $100\ \mu$ high from basement membrane to tip and about $70\ \mu$ wide. The stratum germinativum is low columnar, and hypertrophied epithelial cells form the core of the tubercle. A prominent feature of this tubercle is a column of cells that extends from about the center of the core to the apex. It is made up of about 10 cells that are closely adherent one above the other, gradually increasing in width from about $24\ \mu$ at the base to about $32\ \mu$ at the apex. The keratinized cap is thin and made up of one layer of cells as it is in others of this group.

FAMILY COBITIDAE

The loaches are Eurasian fresh-water fishes presently placed in three subfamilies (Nalbant, 1963; Bănărescu, 1968a): the Botiinae (two genera, about 10 species); the Cobitinae (15 genera, about 25 species); and the Noemacheilinae (several genera, more than 100 species). We have found only one record in the literature of breeding tubercles for the Botiinae, and Nalbant (1963) reported "sexual dimorphism not evident" for *Botia* and *Leptobotia*. Sexual dimorphism has been known for a long time in the other two subfamilies but the earliest reports mention only the "lamina circularis," a fleshy pad on the upper surface of the pectoral fin in males. Smitt (1892, p. 705) was one of the first to report breeding tubercles, on the dorsal surface of the pectoral fin of males of *Cobitis taenia* (Linnaeus).

Many species of loaches develop tubercles on the head and the upper surface of the pectoral

fin. Cobitid tubercles are most similar to homalopterid tubercles in that in the layer of hypertrophied cells beneath the keratinized cap all are enlarged to about the same size, are in the same stage of keratinization, and form a well-defined, uniform layer that is destined to become another keratin cap. Homalopterid tubercles persist for a long time and the pectoral fin tubercles of loaches such as *Noemacheilus* also seem permanent (P. Bănărescu, personal commun.).

Hora noted breeding tubercles in a number of species of Indian loaches, and reported (1922b) on sexual dimorphism in two species of *Diplophysa*—*papillosolabiata* Kessler and *stewarti* Hora—and in five species of *Noemacheilus*—*yasinensis* Alcock, *lhasae* Regan, *microps* (Steindachner), *tibetanus* Regan, and *tenuis* Day. He described two tuberculate areas in the males of these species: one in the suborbital region, sometimes extending back onto the opercle; the second on the fleshy patch of skin in the middle of the upper surface of the pectoral fin. Some specimens also had a few tubercles on the ventral surface of the pectoral fin. In 1927, Hora added *N. montanus* (McClelland) to this list and in 1934, *N. choprai* Hora. Hora (1936b) stated that *N. stoliczkae* (Steindachner) and three new species (*deterrai*, *hutchinsoni*, and *panguri*) were sexually dimorphic like *N. tibetanus* (in his 1922b paper). His figure of a male *N. stoliczkae* (1936b, pl. 12, fig. 7) showed two tuberculate patches on the snout.

Vladykov (1935), who reported on the sexual dimorphism in several species of loaches, noted tubercles on the pectoral fins of *Cobitis taenia*, *Misgurnus fossilis* (Linnaeus), *Leptobotia fasciata* (Dabry de Thiersant), *Barbatula barbatula* (Linnaeus), *B. toni posteroventralis* Nichols, and *B. stoliczkai* (Steindachner). Tubercles were also present beneath the eye and on the opercle in *Barbatula*. He felt that differences in sexual dimorphism were correlated with generic differences in Chinese cobitids.

In a series of papers, Ikeda reported on sexual dimorphism in Japanese loaches and breeding tubercles on: *Misgurnus anguillicaudatus* (Cantor), *Cobitis biwae* Jordan and Snyder, and *C. taenia striata* Ikeda (1936b); *C. taenia japonica* Temminck and Schlegel (1937a), and *Barbatula toni oreas* (Jordan and Fowler) (1937b). Okada (1960) summarized these papers and also described minute tubercles on the head, anterior abdomen, back, pectoral and dorsal fins of

breeding males of *Lefua nikkonis* (Jordan and Fowler). Kobayashi (1951) performed experimental studies on sexual characters in *Misgurnus anguillicaudatus* as noted previously.

Several studies of loach tubercles are recent. Oliva (1953a) figured tubercles on the upper surface of the pectoral fin of male *Noemacheilus barbatulus*; Jakubowski and Oliva (1967) discussed and figured the histological structure of the tubercles of this species. Inger and Chin (1962) described tubercles on three species of Bornean loaches: *Acanthopthalmus sandakanensis* Inger and Chin, *Noemacheilus selangoricus* Duncker, and *N. olivaceus* Boulenger. Bănărescu and Nalbant (1964) reported tubercles on the pectoral fin rays of two species of the Turkish *Noemacheilinae*: *Noemacheilus angorae* Steindachner and *N. lendli* Hanko; and later (1966) on two species from Afghanistan and Iran, *N. persa* (Heckel) and *N. griffithi afghana* Hora. Băcescu-Meşter (1967) figured and discussed tubercles on the pectoral fin of a new subspecies of *N. barbatulus*.

Noemacheilus (Orthrias) barbatulus (Linnaeus)

Figure 10A

Male, 104 mm., S.L. B.M.N.H. No. 1874.7. 4.8–12. Transylvania. Tubercles are scattered over the head and on the branched rays of the upper surface of the pectoral fins.

The dorsal surfaces of the branched pectoral fin rays are covered by numerous small tubercles that coalesce basally to form a continuous thickened pad of epithelial tissue that is keratinized on the surface. An individual tubercle is 255 μ high from basement membrane to tip. The keratinized cap, which is continuous with that of the adjacent tubercle, is about 9 μ thick and

made up of a single layer of keratinized epithelial cells. The hypertrophied cells immediately below the keratinized layer are about 13 μ wide, are regularly arranged in a well-defined layer, and appear to be undergoing keratinization. The cells become progressively smaller toward the columnar stratum germinativum.

Noemacheilus sp.

Figure 10B

Male, 92 mm., S.L. U.S.N.M. No. 130130. China. August, 1935. Tubercles are present on the dorsal surfaces of the branched pectoral fin rays and in a triangular patch extending from the lateral corner of the mouth to below the eye.

The tubercles on the head and the pectoral fins are arranged in dense patches and are fused together basally so that the keratinized layer forms a continuous sheet. In this specimen the entire fused sheet can be removed intact, revealing underneath another layer that has the same aspect as the surface layer. A section of a pectoral fin tubercle is 130 μ high from basement membrane to tip and approximately 95 μ wide. The morphology of this tubercle is like that described for *Noemacheilus barbatulus* except that in this specimen the individual cells making up the keratinized cap can be distinguished. They are flattened laterally, and overlap like shingles on a roof but in reverse, that is, those at the apex are overlapped by those farther down on the side of the tubercle. The cells immediately below the keratinized cap, the largest of the hypertrophied cells, are about 13 μ long and arranged in a well-defined layer.

Misgurnus anguillicaudatus (Cantor), U.S.N.M. No. 130354, has a tubercle morphology like the other cobitids described.

ORDER SILURIFORMES

Many of the 31 families of catfishes recognized by Greenwood et al. (1966) contain species that have various types of plates and projections on their bodies and fins. Only one family, however, the Mochokidae, have been reported to have structures that might be breeding tubercles or contact organs.

FAMILY MOCHOKIDAE

Several species of mochokid catfishes are known to have tubercle-like structures distribut-

ed over their dorsal surfaces. Whitehead (1958) mentioned their presence in *Chiloglanis brevibarbis* Boulenger and described a Mallory's stained section of a *C. somereni* Whitehead tubercle, and we have sectioned tubercles from *C. brevibarbis* and *Synodontis acanthomias* Boulenger. Although Whitehead (1958) thought that *Chiloglanis* tubercles might be homologous to cyprinid tubercles, our study indicates that they are not. Instead, the tubercles consist of mounds of hypertrophied epithelium, with the surface

cells keratinized to form a thin cuticle, and possess small conical unicellular projections that give the surface of the tubercle a rugose appearance. This type of tubercle was also found in *Balitoropsis bartschi* (Homalopteridae). *Balitoropsis* and *Chiloglanis* are adapted for existence in torrential streams. Macroscopically similar tuberculation occurs on similarly adapted species in the catfish families Sisoridae and Astroblepidae. Since these structures occur in juveniles as well as in adults (in *Chiloglanis* at least) and have a general distribution over the body, they probably do not have a nuptial function but may have some hydrodynamic significance correlated with adaptation to torrential currents. The significance of this type of structure was suggested by Hora (1930) in a discussion on evolution and adaptations of the torrential steam fauna in India.

***Chiloglanis brevibarbis* Boulenger**

Figure 10C, D

Specimen, not sexed, 47 mm., S.L. B.M.N.H. No. 1937.6.4.44-54. Africa, Kenya. Minute tubercles are distributed over the entire dorsal and lateral surface of the body.

A tubercle section from the right operculum (fig. 10C) is 144 μ high from basement membrane to tip and approximately 260 μ wide. The stratum germinativum below the tubercle is columnar, the tubercle being formed by hypertrophy of the overlying cells. The largest of the hypertrophied cells are 12 to 13 μ in diameter. The two outer layers are flattened to varying degrees and appear to contain at least some keratin as they stain orange in Mallory's triple stain. The nuclei remain visible in most of them

and some form small, conical, unicellular projections that are about 5 μ high. The section of the tubercle is asymmetrical, one side rising to the rounded apex at a slope of about 20 degrees, then breaking sharply to form a slight overhang above the undifferentiated epidermis adjacent to it. A section through a different tubercle (fig. 10D) which is only about 100 μ high shows the same essential internal features but the entire surface of the low, conical structure is thickly covered by small projecting cone-shaped cells. This is very similar to the tubercle described in the homolopterid fish *Balitoropsis bartschi*.

***Synodontis acanthomias* Boulenger**

Figure 10E

Specimen, unsexed, 150 mm., S.L. F.M.N.H. No. 55352. Africa, Belgian Congo. Small tubercles are closely spaced over the dorsal and lateral surfaces of the head and on the nape posterior to the dorsal fin.

A tubercle from near the corner of the mouth is 144 μ high and approximately 270 μ wide in section. It is an asymmetrical cone; one side slopes at an angle of about 20 degrees and forms an obtuse angle with the opposite side which slopes upward at an angle of about 85 degrees. The stratum germinativum is columnar, the overlying cells are lenticular then become polygonal at the apex and have a maximum size of about 13 μ .

The outer layer of cells is keratinized and has a number of unicellular, conical projections that extend about 5 μ above the surface. Laterally the tubercle is limited by a shallow sulcus and has a few mucous cells under its borders.

ORDER ATHERINIFORMES

SUBORDER EXOCOETOIDEI

FAMILY BELONIDAE

The 28 species of epipelagic fishes comprising the needlefish family Belonidae are found in fresh waters, estuaries, and marine habitats. Needlefishes range in size from 42 to 950 mm. body length (end of opercle to caudal base). Most needlefishes are marine. Four genera (*Belonion*, *Potamorrhaphis*, *Pseudotylorus*, and *Xenentodon*) are restricted to fresh water as are a few species of *Strongylura*. We include the Belonidae in this paper on the basis of the spine-

bearing scales of the South American fresh-water *Pseudotylorus angusticeps* (Günther) as noted by several previous authors (McDonagh, 1938; Fernández Yépez, 1948; Collette and Berry, 1965; Schollaert, 1965). The scales have more and larger teeth posteriorly. They are present in both sexes starting from 93 mm. in body length. Two males (98-194 mm.) and four females (139-251 mm.) of 31 specimens examined completely lacked spines. Not enough specimens have adequate collection dates so we cannot say whether these spines are seasonal. The most

reasonable explanation that we can offer is that they are contact organs which develop in breeding individuals of both sexes. Their presence in *Pseudotylosurus* is one of the distinguishing characters of the genus (Collette and Berry, 1965) and further links the Belonidae with other atheriniform fishes (Rosen, 1964; Greenwood et al., 1966).

***Pseudotylosurus angusticeps* (Günther)**

Figure 10F

Male, 170 mm. in body length. U.S.N.M. No. 163892. Ecuador, Rio Cotapino drainage. October, 1950. Scale from the midlateral region of the posterior one-third of the body. The scales in this area have two to four contact organs each, with three the most usual number.

The scale figured is about 700 μ in diameter with three contact organs projecting from the posterior border. The shortest contact organ in the center is 101 μ long and the longest is 202 μ long. In this specimen, most of the epidermis is gone so that the normal relationship of epidermis to scale is destroyed.

SUBORDER CYPRINODONTOIDEI

Contact organs develop as bony dermal outgrowths of the scale margin or fin ray and are found in at least four of the eight families presently recognized in the suborder Cyprinodontoidae: Oryziatidae, Cyprinodontidae, Anablepidae, and Poeciliidae. They were first reported by Garman (1895) as "small spines appearing on the fins of males in several genera" of cyprinodonts at breeding time. The term contact organ was first employed by Newman in his studies of the North American Cyprinodontidae (see Newman, 1907, 1909). Numerous subsequent papers have referred to contact organs in this family. Their development has been well studied experimentally in the Japanese medaka *Oryzias latipes* (Temminck and Schlegel) and

these data comprise most of what is known of the physiological control of contact organ (or breeding tubercle) development (see Experimental Studies, p. 149). No contact organs were found in a survey of the U.S.N.M. material of the Goodeidae (11 species in nine genera). Material of the Adrianichthyidae, Horaichthyidae, and Jenynsiidae was too limited for us to be at all confident of the absence of contact organs.

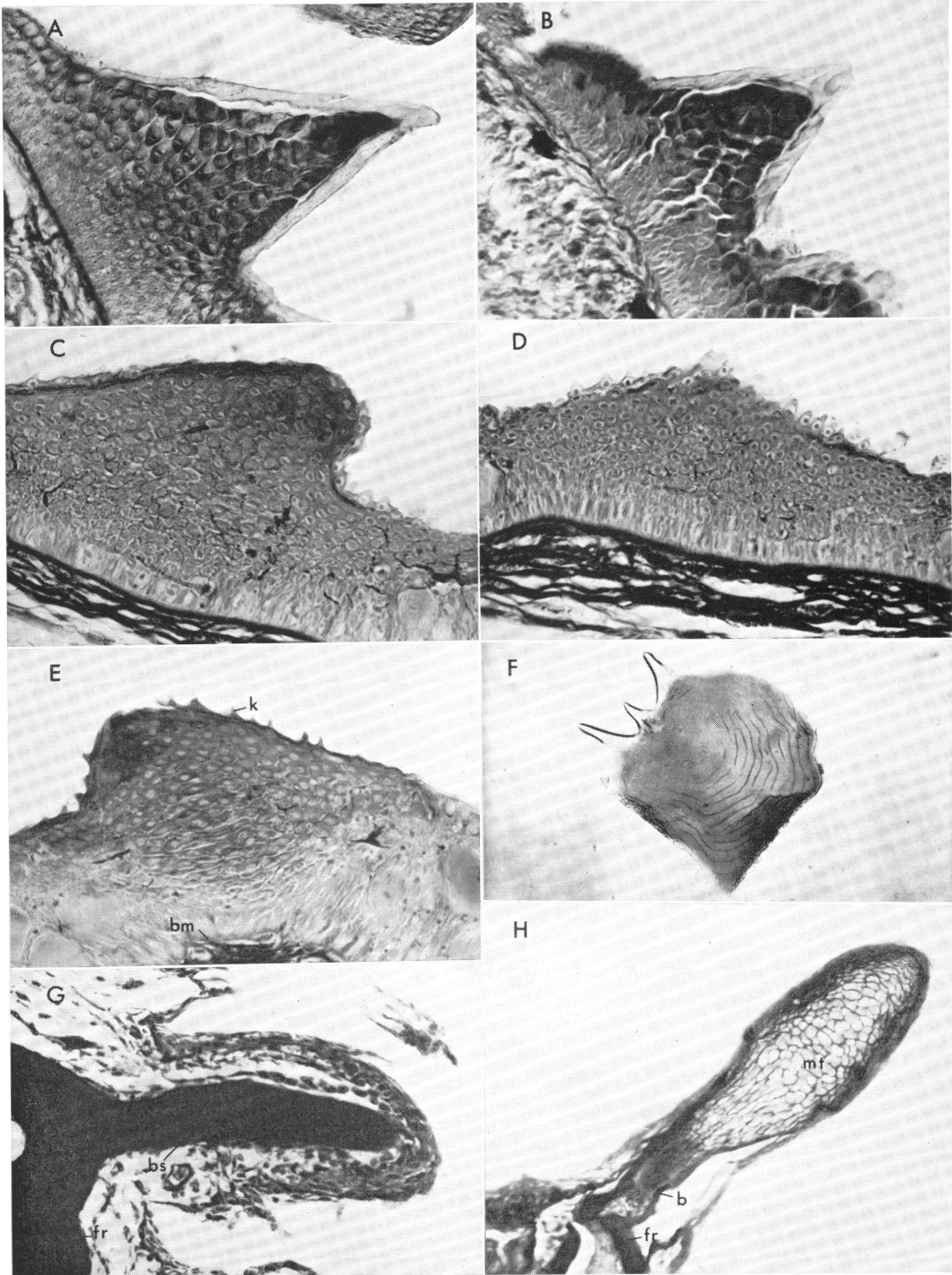
FAMILY ORYZIATIDAE

This recently recognized family consists of seven species of rice fishes or medakas of the genus *Oryzias* according to Rosen (1964): *O. latipes* (Temminck and Schlegel), *O. melastigma* (McClelland), *O. celebensis* (Weber), *O. timorensis* (Weber and de Beaufort), *O. javanicus* (Bleeker), *O. curvinotus* (Nichols and Pope), and *O. minutillus* Smith. They are found in fresh and brackish water from India to Japan. Contact organs are well known (as "papillary processes") in the Japanese medaka *Oryzias latipes*, and are apparently absent in the dwarf species *O. minutillus* according to Scheel (1969a).

In *Oryzias latipes* contact organs develop as males reach maturity and they remain throughout the year (Oka, 1931; Okada and Yamashita, 1944), although they become slightly reduced in the winter (Egami, 1954b, p. 7). Oka (1931) discussed their histological structure and development and found that their size continues to increase as the male grows. The contact organs develop as bony processes of the fin ray and have a mesenchyme-filled axial space that is continuous with the space in the center of the fin ray. With increasing age, the process is further ossified so that the axial space is gradually reduced in size. This structure is similar to that of the cyprinodontid *Cynolebias whitei*. The development of contact organs is under the control of the testes (Okada and Yamashita, 1944). Contact organs on males are less well

FIG. 10. A. *Noemacheilus barbatulus* tubercle from pectoral fin. Male. Mallory's triple stain. $\times 234$. B. *Noemacheilus* sp. tubercle from pectoral fin. Male. Mallory's triple stain. $\times 313$. C. *Chiloglanis brevibarbis* tubercle from operculum. Mallory's triple stain. $\times 308$. D. *Chiloglanis brevibarbis* tubercle from operculum. Note unicellular projections on surface. Mallory's triple stain. $\times 268$. E. *Synodontis acanthomias* tubercle from near corner of mouth. Note unicellular projections on surface. Mallory's triple stain. $\times 258$. F. *Pseudotylosurus angusticeps* scale from posterior one-third of body. Three contact organs project from posterior margin of scale. Male. $\times 60$. G. *Fundulus heteroclitus* contact organ from anal fin. Male. Mallory's triple stain. $\times 285$. H. *Cynolebias whitei* contact organ from pectoral fin. Male. Mallory's triple stain. $\times 288$.

Abbreviations: b, bone; bm, basement membrane; bs, bony spicule; fr, fin ray; k, keratin; mt, mesenchymal tissue.



developed in the northern parts of Honshu than in other parts of Japan (Egami, 1954b, p. 9). Ono and Uematsu (1957) and Egami and Nambu (1961) showed the importance of the contact organ-bearing dorsal and anal fins in the spawning behavior of *Oryzias latipes*.

FAMILY CYPRINODONTIDAE

The killifishes are a large family (about 45 genera and 300 to 400 species) of oviparous top minnows found in shallow fresh, estuarine, and marine waters of North and South America, Europe, Africa, and Asia (Foster, 1967). Myers (1955) recognized seven subfamilies, one of which (Oryziatinae) was subsequently raised to family level¹ by Rosen (1964). Sexually mature males of most cyprinodontids have contact organs on the fin rays and scales (Foster, 1963, 1967; Stenholt Clausen, 1967). We have examined material with contact organs and have found literature records for the Fundulinae, Cyprinodontinae, Orestiatinae, Rivulinae, and Procatopodinae (including Lamprichthyinae). We have not found any literature records of contact organs in the African Pantanodontinae and do not know if contact organs are present.

Foster (1967 and personal commun.) examined specimens of more than 100 species in 34 genera, and concluded that the widespread occurrence of contact organs suggested that they arose early in the evolution of killifishes. If that is so, an evolutionary trend exists in different phyletic lines toward loss of contact organs in those forms which depend heavily upon vision, hearing, and the cephalic lateral line system in their courtship behavior. Forms in which they have been lost include *Fundulus notatus* and species of the Indian genus *Aplocheilus*, the African genus *Epiplatys*, and the South American genera *Pterolebias*, *Rachovia*, and *Austrofundulus*.

Newman (1907, 1909) was the first to study contact organs in detail. He reported them on three species of Fundulinae—*Fundulus heteroclitus* (Linnaeus), *F. majalis* (Walbaum), *F. diaphanus* (LeSueur); and one species of the Cyprinodontinae—*Cyprinodon variegatus* Lacépède. Apparently overlooking Newman's papers, Fowler (1916) discussed and figured scale and fin ray

contact organs (as "spinules") in six species of *Fundulus* plus *Lucania parva* (Baird and Girard) and *Cyprinodon bovinus* Baird and Girard. Myers (1930b) figured and discussed (as "ctenii") the extremely well-developed contact organs on the scales of *Fundulus lima* (Vaillant). Raney et al. (1953) noted "breeding tubercles" on *Cyprinodon variegatus*. Miller (1956, p. 4) compared the distributions of contact organs on the scales of five genera of the Cyprinodontinae: *Cyprinodon*, *Floridichthys*, *Garmanella*, *Jordanella*, and *Cualac*. He also contrasted the distribution of "tubercles" on the fins of breeding males of these genera.

The Orestiatinae are a subfamily of 20 species, all in the genus *Orestias*, of Lake Titicaca and other High Andean lakes and rivers (Tchernavin, 1944). In his revision, Tchernavin reported sharp, curved spines on the dorsal, anal and pectoral fins of males of *O. cuvieri* Valenciennes, *O. pentlandii* Valenciennes, *O. agassii* Valenciennes, *O. jussiei* Valenciennes, *O. albus* Valenciennes, *O. tutini* Tchernavin, and *O. crawfordi* Tchernavin. Spines were also present on the scales of *O. agassii*. In the species in which females also had spines, they were less well developed and present in larger specimens. We have examined contact organs on the scales and dorsal and anal fin rays of male *Orestias agassii* (U.S.N.M. No. 167740) and find them similar to contact organs in other cyprinodontids.

The earliest descriptions of contact organs in the Rivulinae were by de Carvalho (1957) and Nieuwenhuizen (1961) in *Cynolebias whitei* Myers, a South American annual killifish. De Carvalho described them as "sensitive tactile papillae," Nieuwenhuizen as "small antennae." Stenholt Clausen (1967) has made the most comprehensive survey of contact organs in a geographic area in his paper on tropical Old World cyprinodonts. This is apparent from the title of chapter I, "Ctenoidy, a nearly universal character in cyprinodonts." He devoted most of his attention to contact organs in the subfamilies Rivulinae and Procatopodinae. He found contact organs in all procatopodine genera (*Aplocheilichthys*, 11 species; *Hypsopanchax*, three species; *Lamprichthys*, one species; *Poro-panchax*, two species; *Hylopanchax*, one species; and *Plataplochilus*, one species) except in *Procatopus*, and many African rivulines: (*Aphyosemion*, 10 species; *Nothobranchius*, five species; and *Roloffia*, two species). He included photographs of the "ctenoid" scales of *Lamprichthys*

¹ Although Rosen first raised the group to family rank, "Oryziatidae, new family," the first use of a family-group name was by Myers (1938), who erected the tribe Oryziatini. The name Oryziatidae is, therefore, attributable to Myers.

tanganicanus (Boulenger), *Poropanchax rancureli* (Daget), *P. macrophthalmus* (Meinken), *Aphyosemion sjostedti* (Lönnerberg), *A. spurrelli* (Boulenger), *A. gulare* (Boulenger), and *Roloffia occidentalis* (Stenholt Clausen) and of the contact organs on the anterior pelvic fin ray of *Poropanchax normani* (Ahl). Scheel (1968) has also reported contact organs on scales or fin rays of African species of *Aphyosemion*, *Nothobranchius*, *Roloffia*, and *Pachypanchax*. Scheel (1969b) used the absence of contact organs in males of the South American *Austrofundulus dolichopterus* Weitzman and Wourms as another indication of his belief that *Austrofundulus* and *Cynopoecilus* are not closely related.

Newman (1907, 1909) named these structures "contact organs" because males of the cyprinodontids which he studied had them well developed in the regions that come into contact with females during courtship or spawning and in areas that come into contact with other males in fighting. In addition to Newman's careful descriptions of spawning and his figures of the spawning positions, several other references correlate breeding behavior with the distribution of contact organs. Among them are: Raney et al. (1953) for *Cyprinodon variegatus* (Lacépède) and de Carvalho (1957) for the South American *Cynolebias whitei*. Nieuwenhuizen (1961) reported on the breeding behavior of *Pterolebias elegans* (= *Cynolebias whitei*) and stated that the "series of small antennae" (=contact organs) on the inside of the male's pectoral fin served a sensory function by informing the male when the female was in position to commence the spawning act. The possibility of a sensory function might be verified by the demonstration of innervation of the contact organs but this requires special fixation of specimens and different histological techniques than those employed in the present study. Barlow (1961) described the breeding behavior of *Cyprinodon macularius* Baird and Girard but did not mention contact organs although they are present on the head scales and some of the posterior body scales of breeding males (S.I.O. No. 58-73, April 11). Foster (1963) correlated the contact organ distribution with the breeding behavior of several American killifishes. Scheel (1968) noted that contact organs were used by male Rivulinae to maintain their position relative to the female in prespawning and spawning behavior.

Ermin (1946, pp. 250-258) described and

figured contact organs on the Anatolian cyprinodontine *Kosswigichthys asquamatus* Sözer. This monotypic genus has the body scales greatly reduced in number and size—15 to 20 scales, 85 to 190 μ in diameter—yet contact organs are present on most of the scales in males. Perhaps the only reason *Kosswigichthys* has not become completely naked is that the few remaining scales are needed to bear contact organs important in reproductive behavior.

Two authors have made extensive taxonomic use of contact organs in the Cyprinodontidae. Foster (1963, and personal commun.) studied contact organ distribution, breeding behavior, and systematic position of a number of North American killifishes. He concluded that contact organ distribution is very similar among closely related species. For example, *Lucania parva* and *L. goodei* Jordan are closely related, have similar breeding behavior, and have identical contact organ distributions. Stenholt Clausen (1967) examined many African cyprinodonts specifically for contact organs. He frequently found "ctenoidy and fin papillae" useful in distinguishing taxa. For example, the complete lack of contact organs is the best character for distinguishing *Procatopus* from *Hypsopanchax*. *Plataplochilus* differs from other genera except *Lamprichthys* in having two rows of particularly ctenoid scales on the lacrimal bone.

Fundulus heteroclitus (Linnaeus)

Figure 10G

Male, 57.5 mm., S.L. U.S.N.M. No. 203434. Maryland, Chesapeake Bay drainage. May 17, 1964. Contact organs are present on the anal fin rays.

A contact organ on the anal fin is formed by a bony spicule that grows from the outer surface of the lepidotrichium and is enclosed by a sheath of corium and epidermis. The height from the lepidotrichial origin to the epidermal tip is 170 μ and its total width is 86 μ . The contact organs of this species have previously been described by Newman (1907, 1909).

This same type of structure also occurs on the posterior margins of the scales in many species of cyprinodontids and has been described by Newman in *Fundulus majalis*, *F. diaphanus*, and *Cyprinodon variegatus*. In addition, sections were made of contact organs in *Fundulus stellifer* and *F. catenatus*, and all are essentially identical in

morphology, differing only in size. Abrasion may cause the bony spicule to penetrate and project through the epidermal surface.

***Cynolebias whitei* Myers**

Figure 10H

Male, 52 mm., S.L. U.S.N.M. No. 177530. Brazil. Large club-shaped contact organs are distributed along the rays of the posterior pectoral fin surface.

The contact organ originates as an outgrowth of the lepidotrichium and is a club-shaped structure 208 μ long from its origin, 39 μ wide at its narrow base, and 65 μ wide across the expanded tip. The bulk of the structure is made up of a core of mesenchymal cells that reach 12 μ in diameter and are supported by a flask-shaped collar or sheath of bone that grows outward from the lepidotrichium for about 100 μ . The mesenchyme-filled space enclosed by the bony sheath is continuous with the space in the center of the fin rays. The dermis, with a thin layer of epidermis, is continuous over the entire surface and is vascularized by capillaries that extend completely to the tip. This structure is similar to that described for *Oryzias latipes* (Oryziatidae).

FAMILY ANABLEPIDAE

Three species of viviparous four-eyed fishes (*Anableps*) occur in the fresh and brackish waters of Central America and northern South America. Garman (1895) noted that the scales of *Anableps microlepis* Müller and Troschel appeared rough due to the greater firmness of "the small spines around the free edges of the scales." Fowler (1916) reported contact organs (as "spinules") on the scales of both sexes of *Anableps anableps* Linnaeus. His figure of the distribution of the contact organs showed them more widespread in the male than in the female. Scheel (1968) also noted that he had found "ctenoid structures" in *Anableps*.

Examination of *Anableps* in the United States National Museum collections revealed contact organs on the posterior margins of the scales of all three species: *A. dowei* Gill (U.S.N.M. No. 121906, El Salvador), contact organs on the scales of males; *A. microlepis* (U.S.N.M. Nos. 167715 and 66112, British Guiana, two females), contact organs on virtually all the scales; *A. anableps* (U.S.N.M. No. 52579, Amazon River), contact organs on the lateral scales of male and

female, but extending farther dorsally and ventrally in the male.

FAMILY POECILIIDAE

The Poeciliidae are small viviparous top minnows found in fresh and brackish waters of the New World from north and central United States south to northern Argentina. They are one of the dominant groups of fishes in the West Indies and Middle America and include such well-known aquarium fishes as guppies, platies, swordtails, and mollies. In their recent review, Rosen and Bailey (1963) recognized three subfamilies (two monotypic), five tribes, 21 genera, and 138 species. A survey of the Poeciliidae in the United States National Museum collections revealed that males in three genera (as recognized by Rosen and Bailey) in two tribes had contact organs: *Poecilia* in the Poeciliini; *Poeciliopsis* and *Phallichthys* in the Heterandriini. In spite of extensive behavioral and genetic work on the family, contact organs had been briefly mentioned for only *Poeciliopsis* previously (Miller, 1960; Rosen and Bailey, 1963), although *Xenodexia ctenolepis* Hubbs of the Xenodexiinae has been known to have "ctenoid" scales all over the body of males, females, and juveniles (Hubbs, 1950).

The discovery of contact organs in these three genera of the Poeciliidae is of ethological and systematic importance. As reported by Rosen and Tucker (1961), in species of these three genera the male "contacts" the female before copulation. In the Poeciliidae, contact organs are concentrated on the snout of the male and apparently serve a stimulatory function during courtship of the female. Structurally, they are identical with the contact organs of cyprinodontids and may be considered homologous.

Contact organs are of systematic importance in the genus *Poecilia* (as recognized by Rosen and Bailey, 1963). Contact organs were found in United States National Museum material of seven of 11 species of the subgenus *Poecilia*: *caucana* (Steindachner), U.S.N.M. No. 121685; *montana* Rosen and Bailey, U.S.N.M. No. 87358; *vivipara* Bloch and Schneider, U.S.N.M. No. 101444; *sphenops* Valenciennes, U.S.N.M. No. 47424, 84361, 114394; *latipinna* (LeSueur), U.S.N.M. No. 166102; *petensis* (Günther), U.S.N.M. No. 32579; and *velifera* (Regan), U.S.N.M. Nos. 92938, 50515. Robert R. Miller kindly confirmed their presence in *latipunctata*

Meek and *sulphuraria* (Alvarez) and Luis R. Rivas did so for *elegans* (Trewavas). Males are not normally present in the gynogenetic Amazon molly *P. (P.) formosa* (Girard). No contact organs were found on available United States National Museum material of a number of the 21 species of the subgenera *Lebistes*, *Pamphorichthys*, or *Limia*. This difference between *Poecilia* on the one hand and *Lebistes*, *Pamphorichthys*, and *Limia* on the other, indicates the differences in breeding behavior and serves as further evidence of the distinctness of *Poecilia* at the subgeneric, or perhaps generic level. Liley (1966) has contrasted the breeding behavior of *P. (P.) vivipara* with three species of the subgenus *Lebistes*: *reticulata* Peters, *parae* Eigenmann, and *picta* Regan. Only *P. (P.) vivipara* shows the characteristic contacting or nuzzling of the female.

Our survey of United States National Museum material revealed contact organs on only one species each of *Poeciliopsis* and *Phallichthys*—*Poeciliopsis turrubarensis* (Meek) and *Phallichthys amates* (Miller). In addition, Miller (1960) reported "ctenii on scales of males" of his new

species *P. viriosa*. Presumably *Phallichthys fairweatheri* Rosen and Bailey and some other species of *Poeciliopsis* also will be found to have contact organs when adequate breeding material is examined.

***Poecilia sphenops* Valenciennes**

Figure 11A

Male, 62 mm., S.L. U.S.N.M. No. 114394. Guatemala. March 21, 1947. Contact organs are on the borders of the scales on the dorsal head surface and nape, opercles, and ventral head scales. They are concentrated on the snout just posterior to the upper lip.

The contact organs on the scale borders just posterior to the upper lip appear identical in structure to those of species of *Fundulus*. They are formed on the edges of the scales by slender ossified extensions which project at right angles to a height of approximately 50 to 100 μ above the adjacent epidermal surface and are covered by a thin layer of skin which is continuous with that covering the scale.

ORDER SCORPAENIFORMES

FAMILY COTTIDAE

Several species of marine sculpins develop contact organs. Smitt (1895) reported that the inside surfaces of the pectoral and pelvic rays of *Myoxocephalus scorpius* (Linnaeus) were armed with a row of sharp teeth. Vladykov (1933) reported "tubercles" on the surface of pectoral fin rays and sometimes on the pelvic fin rays of three Hudson Bay species: *Triglops pingeli beani* (Gilbert); *Gymnocanthus galeatus* Bean; and *Myoxocephalus groenlandicus* (Cuvier and Valenciennes). We have examined contact organs on two species. In males of *Myoxocephalus scorpius* they occur on the posterior surface of the pectoral fin rays as bifurcate structures supported internally by bony processes growing from the fin ray. They are inclined proximally and very heavily constructed, suggesting that they are used during mating to clasp the female. In *Melleles papilio* Bean, males develop long slender contact organs on the ventral surface of the pelvic fin rays. These structures appear too weak to have a clasping function and may therefore serve as sensory structures. Histological demonstration of the

presence of innervation would be useful in confirming this hypothesis.

***Myoxocephalus scorpius* (Linnaeus)**

Figure 11B, C

Male, approximately 202 mm., S.L. U.S.N.M. No. 64604. Labrador. August 20, 1908. Contact organs are present on the posterior, distal one-third to one-half of the first 10 pectoral fin rays. Distally the structures are low and conical, becoming larger proximally with expanded tips that develop into bifurcate structures in the largest contact organs, the most proximal ones again becoming simple. Their longitudinal axis is inclined toward the body of the fish.

A section through a contact organ shows a thick pedestal of bone growing from the surface of the fin ray, with two longer lateral projections and a shorter medial one. The bony pedestal is approximately 435 μ in diameter basally, and the whole structure is 880 μ high. The thickness of the skin covering the contact organ is variable; the epidermis is from about 34 to 80 μ thick and has numerous mucous cells in the surface layer. No obvious sensory structures are present.

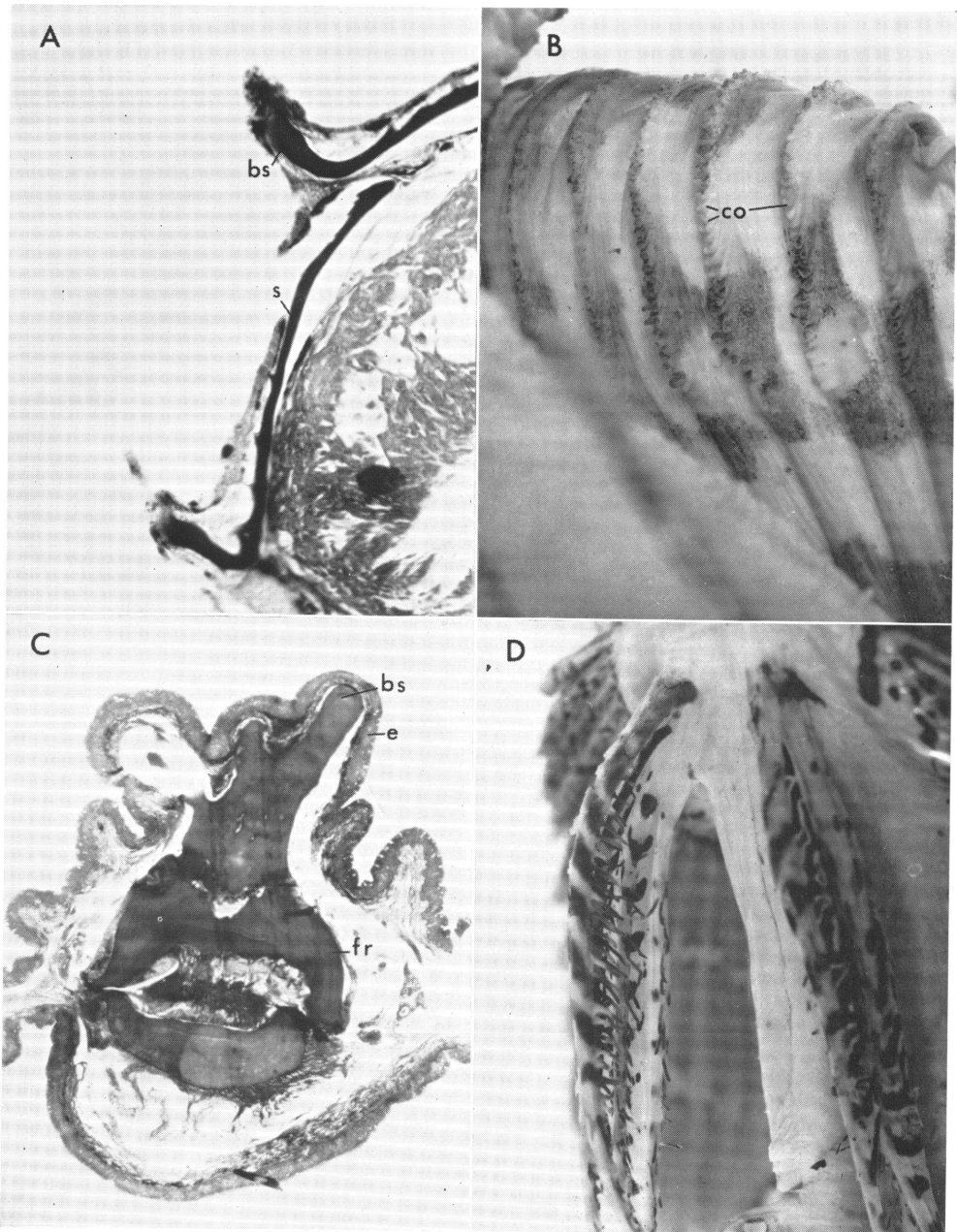


FIG. 11. A. *Poecilia sphenops* contact organs from snout. Male. Mallory's triple stain. $\times 173$. B. Posterior surface of male *Myoxocephalus scorpius* pectoral fin showing rows of contact organs along fin rays. $\times 1.7$. C. *Myoxocephalus scorpius* contact organ from pectoral fin. Male. Mallory's triple stain. $\times 30$. D. Pelvic fin of male *Melletes papilio* showing rows of long, flexible contact organs. $\times 1.3$.

Abbreviations: bs, bony spicule; co, contact organ; e, epidermis; fr, fin ray; s, scale.

Melletes papilio Bean

Figure 11D

Male, 175 mm., S.L. U.S.N.M. No. 86277. Bering Sea, off Robbin Island. A single row of long, flexible contact organs extends along the ventral surface of each of the four rays in the pelvic fins.

The contact organs are outgrowths of the fin ray and may be up to 4.0 mm. long, about 300 μ in diameter, and are supported by a bony core that is about 150 μ in diameter. Preservation of cellular detail is poor; however, the epidermis of the contact organ and fin ray is richly supplied with large flask-shaped secretory cells that may be up to 34 μ wide and 26 μ high and make up the bulk of the epidermal tissue.

FAMILY COTTOCOMEPHORIDAE

This fresh-water family of eight genera and 17 species is mostly confined to Lake Baikal in Siberia. It is an offshoot of the Cottidae and considered as only a subfamily of the Cottidae by some authors.

Berg (1907) illustrated and discussed the large round pearl-like tubercles of "epithelialen Ursprungen" that develop on the inner side of the pectoral fin rays of male *Cottocomephorus grewingki* (Dybowski) during the spawning period. Later (1949, p. 1174), he also reported epithelial tubercles on the pectoral fin rays of male *C. comephoroides* Berg. It seems more likely that these sexually dimorphic structures are dermal contact organs as in the Cottidae rather than epidermal breeding tubercles, but no specimens were available for us to examine.

ORDER PERCIFORMES**FAMILY PERCIDAE**

Of the approximately 120 species of perches and darters that make up this fresh-water family, breeding tubercles are present in 48 species in five genera in two tribes: the North American *Etheostomatini* and the similarly adapted European *Romanichthyini*. The relatively few (14) earlier reports of tubercles in this family were summarized in the recent survey by Collette (1965). Breeding tubercle patterns proved useful systematic characters at several taxonomic levels in the Percidae. The presence of tubercles in the *Etheostomatini*, but not in the other tribe of the Percinae (*Percini*) and their presence in the *Romanichthyini* but not in the other tribe of the *Luciopercinae* (*Luciopercini*) at first suggested a close relationship between the *Etheostomatini* and the *Romanichthyini*, both of which contain small bottom-dwelling fishes. However, the dorsal distribution of the tubercles in the *Romanichthyini* contrasted with the ventral distribution in the *Etheostomatini* coupled with osteological data indicate that tubercles have developed independently in the two tribes (Collette, 1963 and 1965). This view is further confirmed by the presence of structures similar to taste buds in the area below the first dorsal fin of both genera of *Romanichthyini* and their absence in the *Etheostomatini*.

Within the *Etheostomatini*, tubercle patterns are of little taxonomic value at the generic level,

if only three large inclusive genera (*Percina*, *Ammocrypta*, and *Etheostoma*) are recognized (Collette, 1965). Within *Percina* and *Etheostoma*, however, tubercle patterns are useful at the subgeneric and species-group levels. The subgenus *Etheostoma* consists of two closely related tuberculate species-groups and one non-tuberculate group. The subgenera *Hololepis* and *Microperca* have similar tubercle patterns and, on the basis of other characters, appear to be closely related (Collette, 1962 and 1965). The presence of chin tubercles in *Etheostoma* (*Hololepis*) *gracile* (Girard) and *E. (H.) zoniferum* (Hubbs and Cannon) confirms the close relationships of these two species. Groups of darters that include both tuberculate and nontuberculate species may be shown to represent different lines of evolution.

Several recent workers have studied breeding tubercles in darters as an additional taxonomic character. Miller (1968) found no geographic variation in tubercle patterns in *Etheostoma blennioides* Rafinesque. Distler (1968) did find geographic variation in tubercles in *E. spectabile* (Agassiz): different subspecies had different patterns and one subspecies (*E. s. fragi* Distler) lacked tubercles completely. In *E. fusiforme* (Girard), tubercles are present on more specimens for a longer period of time and are also better developed in southern populations than in northern populations (Collette, 1965). This north to south increase in tuberculation paral-

lets a clinal increase in the number of inter-orbital scales and in the number of ctenii on these scales (Collette, 1962).

Tubercles on the anal fin and body and perhaps those on the under sides of the pelvic fins probably function to keep the male in position over or alongside the female in spawning (Winn, 1958; Collette, 1962 and 1965). Chin tubercles, such as are present in *Etheostoma gracile*, and perhaps those on the pelvic fins, appear to stimulate the female as hypothesized by Collette and confirmed by Braasch and Smith (1967).

Histologically, percid tubercles are formed by hyperplasia accompanied by moderate hypertrophy of the epidermal cells to form conical mounds of tissue. In the mature structures the surface cells are somewhat keratinized to form a thin, rugose cuticle. Instead of tubercles, breeding males of some darters develop thickened ridges of epidermis along the rays of some of the fins. A section through one of these ridges in *Etheostoma swanannoa*, a darter with tubercles on the body only appears to be identical to a fin-ray tubercle of *Percina evides*. It is possible that tubercles in some darters may have been derived phylogenetically from ridges. The presence of a rugose cuticle on the surface of both tubercles and ridges suggests that they have good frictional properties that would make them effective in maintaining contact between spawning individuals.

SUBFAMILY LUCIOPERCINAE

TRIBE ROMANICHTHYINI

Romanichthys valsanicola Dumitrescu,

Bănărescu, and Stoica

Figure 12A, B

Male, 84.5 mm., S.L. M.C.Z. No. 40966. Rumania, Arges River. Tubercles are on scales over most of body but they are concentrated dorsally, and on all fins including the dorsal and caudal fins.

A tubercle from the body just below the second dorsal fin consists of a thickening of the epithelium on the posterior surface of the scale and is low and mound-shaped in cross section. It is formed primarily by hyperplasia, the cells being only slightly larger than those in the stratum germinativum, which are low columnar or cuboidal. The structure is about 130 μ high and 400 μ wide, whereas the adjacent undifferentiated epithelium is only about 65 μ thick.

The cells on the surface are of irregular shape with pyknotic nuclei and may be somewhat keratinized.

A pelvic fin tubercle, formed by hyperplasia and slight hypertrophy, is 86 μ high, about 156 μ wide, and has a hemispherical shape. The polygonal hypertrophied cells above the low columnar stratum germinativum are 12 to 13 μ in diameter, whereas the surface cells have a somewhat shriveled appearance (suggesting a degree of keratinization), giving the surface of the tubercle a rugose texture.

Numerous epidermal sensory structures are present in this species which were not noted in the darters examined. These structures are of two types: (1) Groups of elongate columnar cells resembling taste buds are attached basally to a dermal papilla and distally reach the free surface of the epidermis. In Mallory's triple stain they have red nuclei and dark blue cytoplasm. (2) Cells resembling those just described for the taste buds are also individually scattered throughout the epidermis. They reach the surface distally but apparently are not supported by a dermal papilla. Both types of structures are found in the epidermis below the dorsal fin and on the pelvic fin.

Zingel streber (Siebold)

Figure 12C

Tuberculate male, 140 mm., S.L. U.S.N.M. No. 204048. Czechoslovakia, Danube River near Radvan. June, 1968. Tubercles are present on the dorsal and much of the lateral surface of the head and body. Except on the head, where some of the larger scales have more than one tubercle, there is only one per scale. Tubercles are absent from the fins, the ventrum, and the lateral part of the body that is covered by the adpressed pectoral fins. Most of the tubercles, especially on the body, are elongate and form longitudinal ridges. The tubercles originate near the center of the exposed portion of each scale. On the body below and anterior to the first dorsal fin, many are expanded anteriorly to form T-shaped structures. In the area below the first dorsal and posterior to the pectoral, the tubercles are inclined so that the tail of the "T" points dorsally. In some tubercles, the inclination may form an angle of as much as about 45 degrees with the longitudinal axis of the fish. The tubercles on a 132 mm. S.L. female from

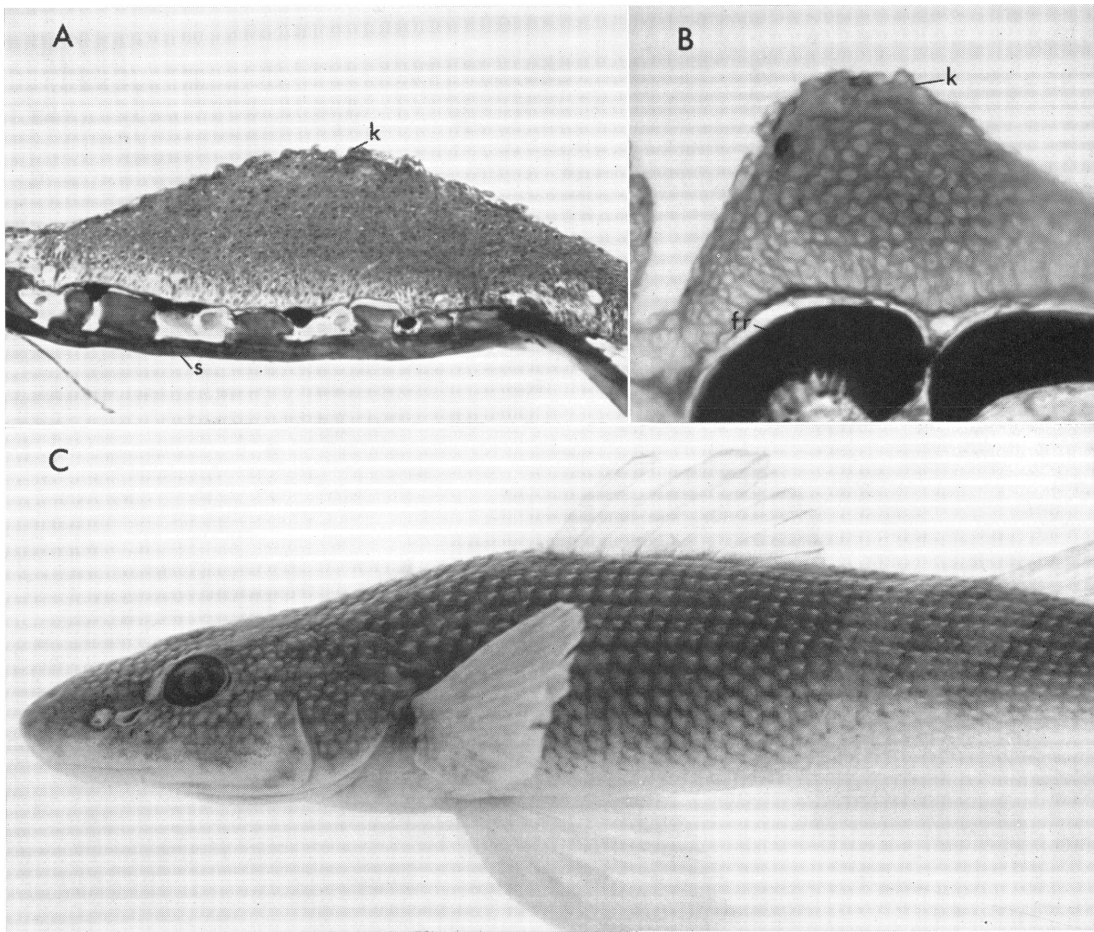


FIG. 12. A. *Romanichthys valsanicola* tubercle from body just below second dorsal fin. Male. Mallory's triple stain. $\times 160$. B. *Romanichthys valsanicola* tubercle from pelvic fin. Male. Mallory's triple stain. $\times 352$. C. Mature *Zingel streber* male. The tubercles are elongate and expanded anteriorly to form a "T" shape. Below the dorsal fin the axes of the tubercles are inclined at an angle to the longitudinal axis of the fish. $\times 1.9$.

Abbreviations: fr, fin ray; k, keratin; s, scale.

the same collection are similar in distribution and orientation although not so well developed.

A section through the "tail" of a tubercle from just below the first dorsal fin of the male is about 130μ wide. The tubercle is formed by hyperplasia; size of the tubercle cells seems to be the same as the cells in adjacent epithelium. There is no evidence of keratinization. The tubercles of the female have similar shape, orientation, and distribution as those of males, but are not so large. The structures that look like taste buds that were described in *Romanichthys* are also present in *Z. streber* in the area below the first dorsal fin.

In body shape and in having tubercles that form longitudinal ridges, *Z. streber* is remarkably similar to the homalopterid fish, *Balitoropsis bartschi*.

SUBFAMILY PERCINAE

TRIBE ETHEOSTOMATINI

Percina evides (Jordan and Copeland)

Figure 13A, B

Tuberculate male, 66 mm., S.L. U.S.N.M. No. 203425. North Carolina, Tennessee River drainage, May 29, 1964. Many small tubercles line the ventral surface of the branched pelvic

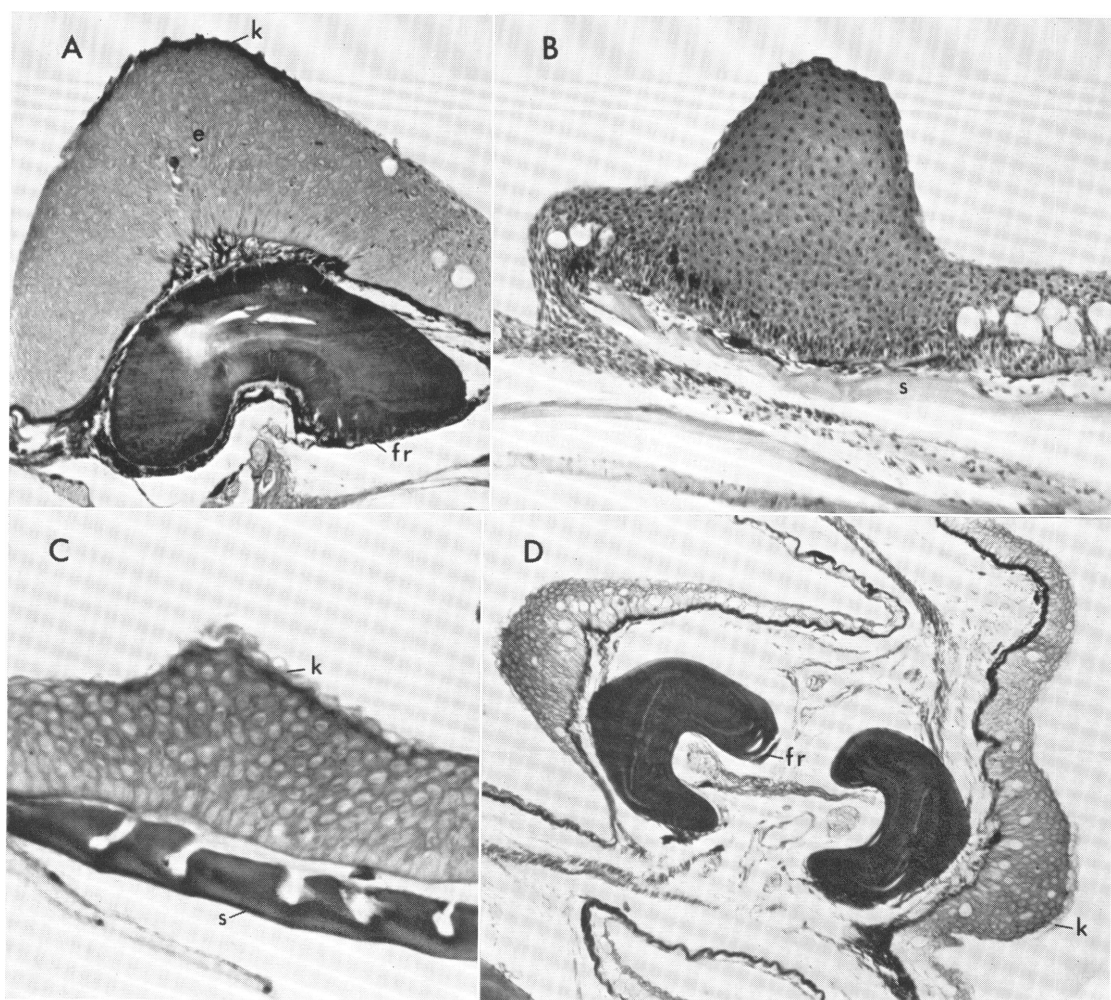


FIG. 13. A. *Percina evides* tubercle from anal fin. Male. Apex has thin keratinized layer. Mallory's triple stain. $\times 149$. B. *Percina evides* tubercle from scale adjacent to anal fin. Male. H and E stain. $\times 167$. C. *Etheostoma swanannoa* tubercle from scale just anterior to anus. Surface has thin keratinized layer. Male. Mallory's triple stain. $\times 292$. D. *Etheostoma swanannoa* epidermal ridges from anal fin. Male. Mallory's triple stain. $\times 138$. Abbreviations: e, epidermis; fr, fin ray; k, keratin; s, scale.

and anal fin rays and the lower part of the caudal fin. Tubercles are also present on the belly beginning at the pelvic fin origin and extending back onto the caudal peduncle, and on the caudal peduncle extending dorsad to the level of the lateral line.

A section of an anal fin tubercle (fig. 13A) is 174μ high from basement membrane to tip and about 460μ across the base. The width of the tubercle is greater than, and basally follows, the contour of the underlying fin ray. The tubercle is formed by hyperplasia and hypertrophy of the

epithelium over the columnar stratum germinativum, the maximum size of the polygonal cells is about 10μ . The surface cells, at and extending to just below the apex, stain dark red with Mallory's triple stain and present a rugose appearance that indicates a degree of keratinization.

A tubercle on a scale from the area adjacent to the anal fin (fig. 13B) is 223μ high from basement membrane to tip, 196μ wide, and has a bluntly rounded outline. In general aspect it is similar to the anal fin tubercle.

Etheostoma swanannoa Jordan and Evermann

Figure 13C, D

Male, 62.5 mm., S.L. U.S.N.M. No. 203427. North Carolina, Tennessee River drainage. May 30, 1964. Nuptial males have thickened epidermal pads on the scales of the belly just anterior to the anus and thickened epidermal ridges along the rays of the ventral side of the pelvic fins and on the anal fin.

A section through one of the pads from a scale just anterior to the anus (fig. 13C) is 86 μ high from basement membrane to tip and approximately 180 μ wide. It consists of slightly hypertrophied cells over a columnar stratum germinativum, the outer cells being keratinized and, in the process, shrinking to give the surface a rugose appearance. A cross section through

the thickened epidermal ridge of an anal fin ray (fig. 13D) is very similar to cross sections of tubercles in other species of darters. It is about 92 μ high and 160 μ wide, has the thin layer of keratinized surface cells, and is formed by moderate hypertrophy and hyperplasia of the epidermal cells.

OTHER SPECIES EXAMINED

Etheostoma spectabile (Agassiz) has tubercles on the body, anal, pelvic, caudal, and pectoral fins. Sections of those on the body and anal fin have the same features as does *Percina evides*. *Etheostoma blennioides newmanii* (Agassiz), U.S.N.M. No. 203426 has tubercles on the body that are low and padlike and in section have the same features as those on the body of *Etheostoma swanannoa*.

CONCLUSIONS

EVALUATION OF THE NUPTIAL TUBERCLE morphology of the species considered in the present study leads to two general conclusions: (1) The terminology formerly used is of little value in distinguishing between morphologically different types of tubercles. (2) Tubercle morphology has potential use as a character in studies of systematic and phylogenetic relationships of certain groups of fishes. After these two general conclusions are reviewed, an explanation is offered as to why some fishes have tubercles, or contact organs, and some do not.

TUBERCLE TERMINOLOGY

It is apparent that the terminology referring to the various kinds of nuptial structures is ambiguous and of little value in distinguishing between morphologically different types. In addition to breeding tubercle, the only valid and useful term is "contact organ" as defined by Newman (1907) for the dermal structures that develop in cyprinodontoids and which we have applied to the similarly constructed characoid "hooks" and to cottoid "spines."

The morphological diversity of epidermal nuptial tubercles, from nonkeratinized structures to those that contain an abundance of keratin, precludes any simple and concise terminology from being developed. The term "pearl organ," alluding to the color of tubercles in living fish of some species, although commonly used in the literature, has been applied so vaguely that its continued use should be discouraged. In some species, tubercles have a pearly color which makes the use of the term "pearl organ" appropriate, but many other fishes wherein the term has been applied, lack such coloration.

The terms breeding and nuptial tubercle are now widely used to refer to a broad class of structures that usually develop at maturity and usually coincide with the reproductive period. These terms can be used and qualified in specific situations by addition of appropriate descriptive adjectives. The description should include the presence or absence of a well-developed keratin cap, degree of development of an epithelial pit, and amount and nature of the vascularization of the epithelial core.

TUBERCLE MORPHOLOGY AS A SYSTEMATIC AND PHYLOGENETIC CHARACTER

Morphology and histology of nuptial tubercles have not been used as systematic characters. The present study, however, indicates that tubercle morphology might be so used in some fish groups if the structures were worked out for more species.

The morphological similarities of tubercles in the families Plecoglossidae, Osmeridae, and Retropinnidae have been discussed. From osteological studies, Chapman (1941) concluded that *Plecoglossus* was more closely allied to the Osmeridae than to the Salmonidae, where it had been placed by earlier workers. The similarity of tubercle morphology between the two groups supports Chapman's conclusion. It would be instructive, however, to know what the tubercles of *Cristivomer namaycush* are like before additional comments are made regarding similarities of the salmonid tubercles with those of the other Salmoniformes.

One important phylogenetic relationship suggested by the present study is that indicated for the gonorynchiform and cypriniform fishes. The tubercles of individuals of *Phractolaemus*, with a heavy, keratinized cap, hypertrophied epithelium, and dermal capillary loops extending into the tubercle core, are very much like those of some cyprinids. Cross sections of *Kneria* occipital organs and tubercles are similar to homalopterid or cobitid tubercles. The implication is that the Gonorynchiformes and the Cypriniformes have been derived from some common ancestor that likewise produced keratinized epidermal structures. Such a relationship, based on osteology, was proposed and discussed by Greenwood et al. (1966). Additional evidence was provided by Pfeiffer (1967), who demonstrated the presence, in certain of the Gonorynchiformes, of well-developed "Kolbenzellen" (club cells) and a "Schreckreaktion" (fright reaction). Club cells and a fright reaction are common in many of the Cypriniformes. Pfeiffer was able to elicit a fright reaction in some of the Gonorynchiformes by using cypriniform alarm substance, and vice versa. As both these groups possess this type of reaction and the peculiar epidermal cells associated with it, and have

similar nuptial tubercle morphology, the evidence of relationship discussed by Greenwood et al. (1966) is further strengthened.

Tubercle morphology may indicate relationships within the Cyprinoidei. The degree of similarity in tubercle morphology of cobitids, homalopterids (including gastromyzonids), and the smallest tubercles of individuals of *Gyrinocheilus* indicates the possibility that these groups, especially cobitids and homalopterids, are more closely related to each other than to cyprinids or catostomids.

The great variability in tubercle morphology in the Cyprinidae reflects the divergence that has occurred as the members of this speciose group have adapted to a wide variety of freshwater habitats. The cyprinids used in the present study represent a more or less random sample of tuberculate specimens that were available. Used in conjunction with other characters, comparison of tubercle morphology (i.e., determining the degrees of similarity or differences in regard to the various tubercle characters described) may be valuable in indicating relationships among certain groups, especially at the supergeneric and subfamily levels. Much more work is needed however, including study of samples from as many species and genera of the various subfamilies as possible, before this character can be of practical use in cyprinid systematics.

EVOLUTION OF BREEDING TUBERCLES AND CONTACT ORGANS

Breeding tubercles and contact organs are restricted to fishes belonging to the cohort Euteleostei Greenwood, Myers, Rosen, and Weitzman (equals Division III of Greenwood et al., 1966) and they are not known to occur in any elopomorph, clupeomorph, or osteoglossomorph fishes. Thus, the potential for the development of these structures was apparently present in ancestral euteleosteans and this potential has manifested itself in diverse groups of the Euteleostei. To explain their presence, we must consider what the fishes with them have in common. First, fishes that have breeding tubercles, or the species within a group that have them, are fresh-water or inshore marine inhabitants. The analogous dermal contact organs present in the Characidae, Cyprinodontoidei, and Cottidae are also developed in fresh-water and inshore marine species. No pelagic, or epipelagic marine fishes are known to develop

tubercles or contact organs. We believe that these structures originally evolved to enable the breeding individuals to maintain close contact in spawning to insure fertilization of the eggs. This function is particularly important in fishes that spawn in fast-moving water (e.g. stream riffles and wave-swept beaches).

Secondly, 21 of the 24 families with these nuptial structures belong to groups of fishes with cycloid scales. Only three families (Percidae, Cottidae, and Cottocomephoridae) belong to the great group of higher fishes—the Acanthopterygii—which usually have ctenoid scales. The structure of contact organs and ctenii is remarkably similar. As Newman (1907) long ago suggested, ctenoid scales may have evolved in higher fishes to replace permanently the temporary contact organs and breeding tubercles found during the breeding season in lower fishes.

In discussing the distinctive poeciliid *Xenodexia*, Hubbs (1950) stated that "it is hardly conceivable that the typically ctenoid scale of *Xenodexia* was independently evolved." The same might be said for the cyprinodontid *Lamprichthys* and the belonid *Pseudotyloturus*. However, we feel that the presence of "typical" ctenoid scales in a few members of these three atherinomorph families is further evidence that contact organs evolved independently and became genetically fixed in several lines of fishes as permanent (in *Xenodexia* and *Lamprichthys*) non-dimorphic contact organs. We believe that there is no fundamental difference among cycloid scales, ctenoid scales, and those scales having evolved ctenii to serve as contact organs—ctenoid scales may have had great enough adaptive values to have evolved widely among higher fishes.

If ctenoid scales evolved to replace contact organs and breeding tubercles, why are so many species of only the Percidae, of the three major fresh-water percoid families, tuberculate? Neither tubercles nor contact organs are present in the Centrarchidae and Cichlidae, moderate-sized fishes living in predominantly lentic habitats. The larger lentic species of Percinae (*Perca* and *Gymnocephalus*) and Luciopercinae (*Stizostedion*), also lack tubercles. It is the small species which comprise the Romanichthyini and Etheostomatini that develop tubercles and most of these spawn in stream riffles. Tubercles apparently evolved independently in each tribe in addition to ctenoid scales, in response to the

strong selective pressure to keep the spawning pairs together in fast-moving water. Some of the more specialized subgenera of *Etheostoma*, such

as *Hololepis* and *Microperca*, have secondarily returned to lentic situations but have retained their tubercles.

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