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ABSTRACT

The ichthyofauna of the high Andes is assumed to be of low taxonomic diversity. Only three fish genera, the killifish *Orestias* and the catfishes *Astroblepus* and *Trichomycterus* include species endemic to the Altiplano, the high-altitude plateau between the eastern and western slopes of the central Andes. The atherinid *Basilichthys* is known doubtfully from the Altiplano.

In the last revision of the genus *Orestias*, Tchernavin (1944a) recognized 20 species and five subspecies. This small number was taken as evidence of the low diversity of fish of the Titicaca Basin. However, in the past two years, five new *Orestias* species have been described, three from Lago Titicaca (Lauzanne, 1981) and two from the Altiplano of northern Chile (Arratia, 1982). With the benefit of large recent collections, 43 species of *Orestias* are recognized in the present revision, 14 being described as new (*O. gracilis, O. rotundipinnis, O. farfani, O. gymnotus, O. hardini, O. ctenolepis, O. ascotanensis, O. richersoni, O. multiporis, O. mundus, O. ututo, O. imarpe, O. tomcooni,* and *O. robustus*).

Seven synapomorphies described here define *Orestias* as a monophyletic group: (1) pelvic fins and fin girdle are absent; (2) vomer is absent; (3) middle anal and middle dorsal fin radials are cartilaginous, rather than ossified; (4) bony anterior and posterior ceratohyal are separated ventrally by a large gap filled with cartilage; (5) first postcleithrum is absent; (6) anguloarticular lacks a ventral extension parallel to the retroarticular; and (7) there is a unique squamation and head pore pattern characterized by a prominent lyre-shaped arrangement of minute neuromasts and a prominent median dorsal ridge of scales running from the top of the head to the dorsal fin origin.

Primary characters used to distinguish *Orestias* species are overall body shape and squamation pattern. Diversity of form is marked. There are large, troutlike midwater predators, such as *O. cuvieri,* diminutive inshore species such as *O. minutus* and *O. minimus,* and very wide-headed and wide-bodied species, with large, thick granulated scales, such as *O. luteus* and *O. albus.*

The diversity among *Orestias* species in Lago Titicaca, the large, high-altitude lake of the Altiplano of Peru and Bolivia, has led to the application of the term "species flock" to this group of lacustrine killifish. However, the *Orestias* of Titicaca do not form a monophyletic group, and it is recommended that the term "species flock" not be used for the killifishes limited to the lake.

The known range of *Orestias* extends from northern Peru to northern Chile. It is expected that the number will rise with additional collecting, because collections are lacking from many of the small, isolated lakes of the Altiplano; also, single specimens of apparently new species are known, yet remain undescribed.

The hypothesis of a close relationship between *Orestias* and the Anatolian cyprinodonts is reviewed.

INTRODUCTION

The killifish genus *Orestias* (Cyprinodontiformes, Cyprinodontidae) is endemic to the high-altitude lakes and tributary streams of the Peruvian, Bolivian, and Chilean Andes. In the present revision the genus is considered to comprise 43 species. The range of *Orestias* (fig. 1) extends from Ancash Province, northern Peru to Antofagasta Province, northern Chile. The distribution is coincident only in part with the catfish genera *Astroblepus* and *Trichomycterus* (see Arratia, 1982 and Arratia et al., 1978) and the silverside genus *Basilichthys,*[1] the only other fish genera with some species endemic to the Altiplano of the central Andes.

More than half of the 43 species of *Orestias* are endemic to the closed Titicaca Basin, and of those, 23 are known only from Lago Titicaca, the large (8100 km^2 surface area), high-altitude (3803 m) lake of the Altiplano, situated between lat. 15°S and 17°S and between long. 68°W and 71°W (with the midpoint of the lake at approximately 15°45′S and 69°25′W) in Peru and Bolivia (Richerson, Widmer, and Kittel, 1977).

In the last revision of *Orestias,* Tchernavin (1944a) formally recognized 20 species and five subspecies. Recently, three more species have been described from Lago Titicaca (Lauzanne, 1981), and two from the Altiplano of northern Chile (Arratia, 1982). In the present paper, 14 species are described as

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[1] The genus *Basilichthys* is known as an Altiplano endemic from just one specimen, 17.5 mm SL, FMNH 94184, collected by W. R. Allen, 1918–1919, from a pool below Acora, Peru, a village near Chucuito, near Bahia de Puno (fig. 22).

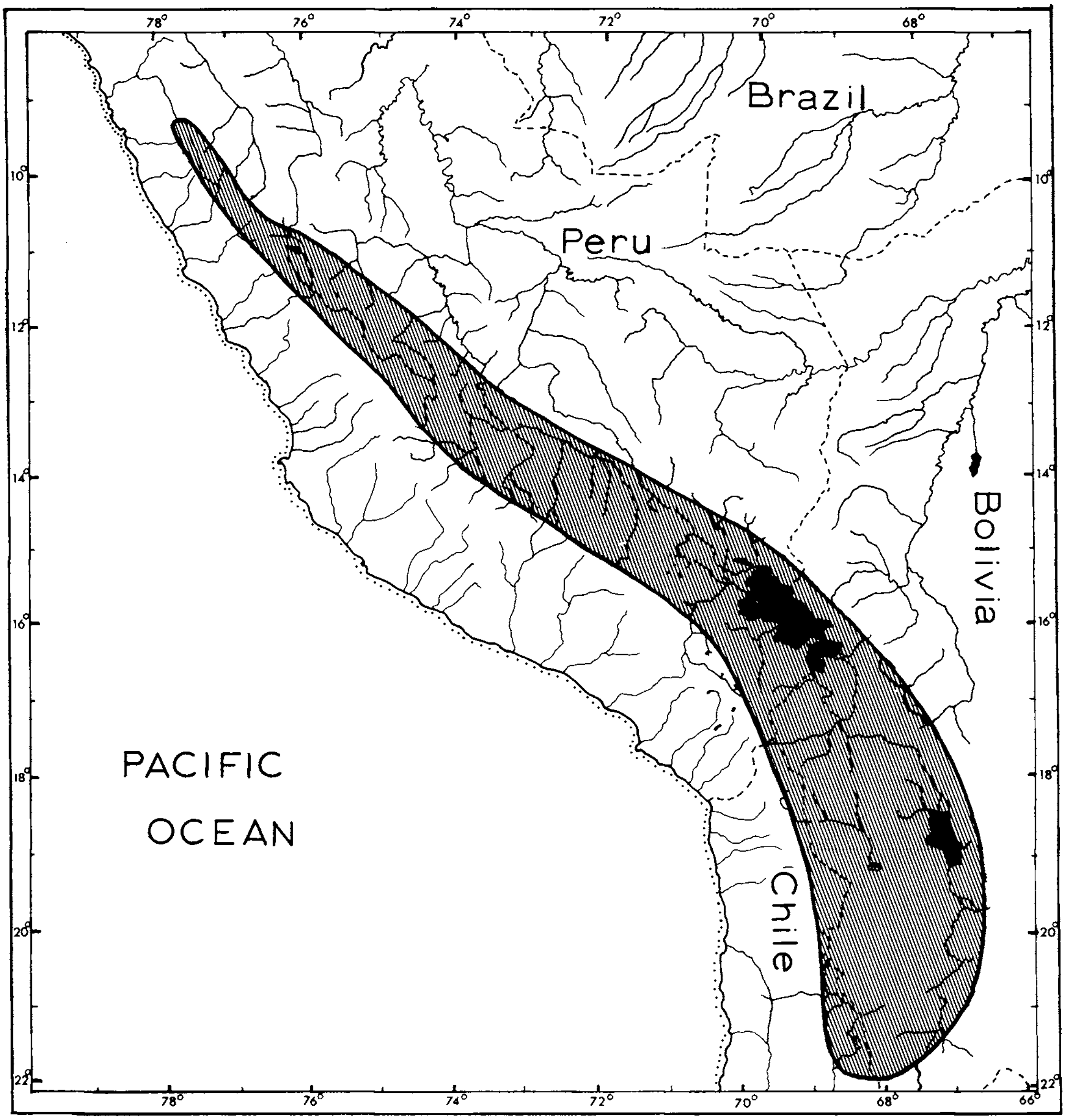

FIG. 1. Limits of the known range of the genus *Orestias*, cross-hatched and outlined by a solid line.

new. The majority of material used in the present revision was collected in five expeditions. The genus *Orestias* was first diagnosed by Valenciennes (1839) in his report on the collection by Pentland of a unique group of species from Lago Titicaca.

The second major expedition was by Alexander Agassiz and Samuel W. Garman of the Museum of Comparative Zoology, Harvard University. Revisions of *Orestias* by Garman (1876, 1895) greatly increased our knowledge of the Lago Titicaca ichthyofauna.

The third major expedition which established the abundance of species throughout most of the wide-ranging distributional limits of *Orestias*, including the Titicaca, Urubama, and Huallaga basins, was that by C. H. and A. Eigenmann and W. R. Allen of Indiana University. In 1918 and 1919 their expedition collected *Orestias* from Lago Junin (Lago

Chinchaycocha) in northern Peru, to Lago Ascotán in northern Chile. In part, this material formed the basis of a revision of *Orestias* by Allen, in Eigenmann and Allen (1942). However, Allen did not use most of the more than 10,000 specimens of *Orestias* collected on this expedition in his revision. They were distributed, many unsorted and uncatalogued, to the collections of the California Academy of Sciences and the Field Museum of Natural History. Representatives of several species were also deposited in the National Museum of Natural History and the University of Michigan, Museum of Zoology.

The Percy Sladen Expedition of 1937 added greatly to our knowledge of the Lago Titicaca ichthyofauna (see Transactions of the Linnean Society, 1939–1955, for a comprehensive report on the Percy Sladen Expedition). This material at the British Museum (Natural History) formed nearly the entire basis of Tchernavin's (1944a) revision of *Orestias,* as well as his revision of *Trichomycterus* (Tchernavin, 1944b).

Large collections of *Orestias,* primarily from Lago Titicaca, made in 1979 by Tom Coon, then with the University of California at Davis, are reviewed in the present study. The material has been deposited in the American Museum of Natural History, National Museum of Natural History, Smithsonian Institution, and the British Museum (Natural History).

Various geological hypotheses have been proposed concerning the age of Lago Titicaca (Moon, 1939; Newell, 1949; James, 1971, 1973). The isolation of the Altiplano from ocean drainage systems is estimated to have occurred in the Miocene, and the formation of Titicaca by Plio-Pleistocene times (James, 1973). Today, Titicaca is composed of three major sections (fig. 22): Lago Grande, a large steep-sided, deep (to 281 m) basin, and Lago Pequeño and Bahia de Puno, two smaller, shallower (to 40 m) basins. Most species are known only from the two smaller basins, but whether that represents the true distribution of *Orestias* or merely the ease of collection, is unknown.

In an effort to increase the productivity of Lago Titicaca, introductions of brown trout (*Salmo trutta fario*) in 1939, and rainbow trout (*Salmo gairdneri*) in 1941 were begun and continue to the present day in an effort to create a commercial trout fishery. The introductions were successful and the fishery existed on the lake until 1969 (Laba, 1979). Reasons for the collapse of the commercial fishery, economical, sociological, and biological are varied (see Everett, 1971, 1973; Laba, 1979). However, the presence of exotic species has had a negative biological effect on the native *Orestias.* The largest *Orestias* species, *O. cuvieri,* has not been obtained in recent decades and is presumed extinct. The threats to *Orestias* come from the trout, and the silverside *Basilichthys bonairensis* introduced in the 1950s (Laba, 1979).

Reports that the genus *Orestias* is nearly extinct in Titicaca (e.g., Géry, 1969; Villwock, 1972) are exaggerated, however. Large collections from Titicaca made by Coon and a French team from the Office de la Recherche Scientifique et Technique Outre Mer (O.R.S.T.O.M.) reveal that many species are still abundant, and that new species are present (Lauzanne, 1981; present revision). Perhaps more important, from a biogeographical perspective, recent collecting has greatly expanded the known distributional limits of the genus. Tim Hardin, an ecologist working through Colorado State University, in 1979 discovered *Orestias* in three small lakes situated northeast of Lima. This discovery not only revealed two new species, but also the possibility that *Orestias* species may be found in the numerous small lakes that characterize the Andes south of Ecuador. This revision of *Orestias* should, therefore, be considered preliminary, in that it attempts to summarize the known diversity of *Orestias,* with the knowledge that searches for a limit to its range, and assessment of abundance throughout the range, have still to be made. Emphasis is placed on morphology; for example, a description of the variety of squamation patterns exhibited by various species groups, and their usefulness in formulating a hypothesis of the phylogenetic history of the genus.

Unfortunately most collections prior to the Percy Sladen Expedition have incomplete or vague locality data. Thus, the majority of material known from outside the Titicaca Basin cannot be used to describe precise ranges.

Since the diagnosis of *Orestias* by Valenciennes (1839), its monophyly has never been challenged. The genus was defined by Parenti (1981) on the following three synapomorphic characters: pelvic fins and girdles absent; moderately lowset pectoral girdle lacks a first postcleithrum; and, vomer absent. Four additional, newly discovered or described defining characters are: cartilaginous middle dorsal and middle anal fin radials; ventral separation of the posterior and anterior ceratohyals by a large gap filled with cartilage; a unique squamation and head pore pattern; and, the absence of a ventral extension on the anguloarticular. A single median ovary or testis was mentioned by Valenciennes (1839) and subsequent workers as possibly diagnostic of *Orestias*. A comparison of the gonad morphology among *Orestias* and the genera of Anatolian cyprinodonts, some of which also share this character, is made in the present study.

In a recent revision of the killifishes, the order Cyprinodontiformes (Parenti, 1981), I suggested that *Orestias* has no close South American relatives, but is rather closely related to the Anatolian cyprinodonts, and most closely to *Kosswigichthys* (including *Anatolichthys*). Apart from Eigenmann's suggestion (1920) that *Orestias* might be closely related to the North American *Empetrichthys* (placed in the family Goodeidae by Parenti, 1981), and that of Foster (1967) that *Orestias* could be closely related to the South American aplocheiloid *Cynolebias*, this represented the only detailed statement concerning the relationship of *Orestias* to other killifishes.[2] In the present paper, I review briefly the relationship of *Orestias* to the Anatolian cyprinodonts, and the relationship of this larger group to the North, Middle, and South American cyprinodontines, which together with the Cuban and Jamaican *Cubanichthys*, comprise the family Cyprinodontidae (*sensu* Parenti, 1981, see table 2).

Using the methods of phylogenetic analysis (Hennig, 1966) I formulate a hypothesis for the phylogeny of the 43 currently recognized species (figs. 26–31). Since the revision of *Orestias* by Tchernavin (1944a), the Titicaca assemblage has been referred to or treated as a so-called species flock (e.g., Villwock, 1962; Kosswig and Villwock, 1964; Richerson, Widmer, and Kittel, 1977). The *Orestias* species in Lago Titicaca or the Titicaca Basin do not form a monophyletic group, however. Hence, the concept of Titicaca supporting a flock comprising all *Orestias* is refuted if monophyly is considered an essential part of the definition of a flock. Only a few recent discussions have questioned the application of the species flock concept to any group of related organisms in a lake (e.g., Reid, 1980, on Lake Lanao cyprinids) or treated the concept of a flock as a useful way of referring to a group of species in a lake prior to the acceptance or rejection of monophyly (e.g., Greenwood, 1979, and Stiassny, 1981, on African Rift Lake cichlids).

Orestias species in Lago Titicaca might be considered a flock if the definition of the term species flock includes a great diversity of form and habitat. I defer a discussion of the species flock concept and its relationship to the phylogeny and biogeography of *Orestias* species to another paper (Parenti, in press).

Thus, the aims of the present paper are to review the evidence for the relationship of *Orestias* to the Anatolian cyprinodonts and the rest of the subfamily Cyprinodontinae; describe in detail characters (such as those of squamation and osteology) that are useful to hypothesize phylogenetic relationships among the species, but have not been used extensively in previous studies on the genus; diagnose the recognizable species in addition to describing the new species; and present a detailed phylogenetic analysis of the species, as well as a key to their identification.

ACKNOWLEDGMENTS

The impetus for thus study was provided by Dr. Peter J. Richerson and Mr. Tom Coon, of the University of California, Davis, who sent a small sample of *Orestias* collected from Lago Titicaca in the mid-1970s to the Department of Ichthyology, American Museum of Natural History with the promise of collecting additional specimens while carrying

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[2] Eigenmann (1927, p. 52), without comment, described the range of *Orestias* as "Death Valley of Nevada and of the high plateau of Peru, Bolivia and Chile," and therefore, without presenting a formal synonymy, considered *Empetrichthys* of Nevada to be a junior synonym of *Orestias*. Most workers, however, followed Myers's 1931 suggestion that the two genera are not closely related.

out a limnological study of the lake. In 1979, Mr. Coon expertly accumulated nearly 4000 specimens of *Orestias, Trichomycterus* and the introduced *Basilichthys,* from the Titicaca Basin. I am grateful for the support of Dr. Richerson and Mr. Coon, and also that of Sr. L. Edgar Farfan Vizcardo, director of the Laboratorio de Puno, Instituto del Mar del Peru. They have all helped to inspire a cooperative study of the Titicaca Basin.

I am equally grateful to Mr. Tim Hardin, of Colorado State University, for collecting and donating *Orestias* specimens from northern Peru.

The taxonomic revision was initiated during the tenure of a Smithsonian Postdoctoral Fellowship at the National Museum of Natural History, Smithsonian Institution, and completed during the tenure of a NATO Postdoctoral Fellowship at the British Museum (Natural History). I thank my scientific advisers, Drs. Stanley H. Weitzman and Richard P. Vari (USNM) and Dr. P. Humphry Greenwood (BMNH) for their encouragement, advice, support, and discussions. This project has also benefited from the expert technical assistance and advice given unstintingly by colleagues at several institutions, including Ms. Janet Gomon and Ms. Susan Jewett (USNM), Ms. Bernice Brewster, Mr. James Chambers, Mr. Phil Crabbe, and Mr. Gordon Howes (BMNH), Ms. J. Abel (MNHN), and Mr. Michael Hearne and Ms. Pearl M. Sonoda (CAS).

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For information and the loan of specimens, and in certain cases accommodation during visits, I thank Dr. Donn E. Rosen, Ms. M. Norma Feinberg, and Ms. Carol Schleifer of the American Museum of Natural History, Dr. William Smith-Vaniz and Mr. William Saul of the Academy of Natural Sciences, Drs. Keith Banister, P. Humphry Greenwood, Ms. Bernice Brewster, Mr. James Chambers and Mr. Gordon Howes, of the British Museum (Natural History), Dr. William N. Eschmeyer, Mr. Michael Hearne and Ms. Pearl Sonoda, of the California Academy of Sciences, Drs. Robert K. Johnson, Donald J. Stewart and Mr. Christopher Spurrier, of the Field Museum of Natural History, Dr. William L. Fink and Mr. Karsten Hartel, of the Museum of Comparative Zoology, Dr. Marie-Louise Bauchot and Ms. Martine Desoutter, of the Muséum National d'Histoire Naturelle, Dr. Martien van Oijen, of the Rijksmuseum van Natuurlijke Historie, Dr. Robert R. Miller and Ms. Alexandra Snyder-Creighton of the Museum of Zoology, University of Michigan, and Drs. Stanley H. Weitzman, Richard P. Vari, and Ms. Susan Jewett of the National Museum of Natural History, Smithsonian Institution.

Mr. Richard Mayden and Mr. John Simmons of the University of Kansas, Museum of Natural History, prepared figures 52 and 53. These were supplied through the courtesy and cooperation of Drs. Arratia-Schultze and E. O. Wiley of the University of Kansas.

Much of the manuscript was patiently and professionally typed by Ms. Noreen Brewster.

The manuscript benefited greatly from the comments of several reviewers.

ABBREVIATIONS

INSTITUTIONAL

AMNH, American Museum of Natural History, New York

ANSP, Academy of Natural Sciences, Philadelphia

BMNH, British Museum (Natural History), London

CAS, California Academy of Sciences, San Francisco

FMNH, Field Museum of Natural History, Chicago

IU, Indiana University (now at CAS, FMNH, UMMZ, and USNM)

KU, University of Kansas, Museum of Natural History, Lawrence

MCZ, Museum of Comparative Zoology, Cambridge
MNHN, Muséum National d'Histoire Naturelle, Paris
RMNH, Rijksmuseum van Natuurlijke Historie, Leiden
SU, Stanford University (now at CAS)
UMMZ, University of Michigan, Museum of Zoology, Ann Arbor
USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

ANATOMICAL

Aa, anguloarticular
Ac, anterior ceratohyal
Afr, anal fin rays
Apal, autopalatine
B 1, 2, basibranchial 1, 2
Boc, basioccipital
Br, branchiostegal rays
Cb 1–5, ceratobranchial 1–5
Cl, cleithrum
Cor, coracoid
Den, dentary
E 1–4, epibranchial 1–4
End, endopterygoid
Exo, exoccipital
Fro, frontal
Hb 1–3, hypobranchial 1–3
Hs, hemal spines
Iac, interarcual cartilage
Ih, interhyal
Le, lateral ethmoid
Max, maxilla
Mes, mesethmoid
Mr 2, middle anal radial 2
Pas, parasphenoid
Pb 1–3, pharyngobranchial 1–3
Pc, posterior ceratohyal
Pcl, postcleithrum
Pmax, premaxilla
Pr 1, proximal anal radial 1
Pro, prootic
Pte, pterotic
Ptt, posttemporal
Qua, quadrate
Rad, radials
Ret, retroarticular
Sca, scapula
Scl, supracleithrum
Sph, sphenotic
Tpb 3, 4, toothplates of third and fourth pharyngobranchials
Vhh, ventral hypohyal
Open circles: cartilage
Stippling: bone

NOTE ON MATERIALS AND METHODS

To carry out the aims of this study, it was necessary to adopt a method of phylogeny reconstruction with the goal of creating a genealogy of *Orestias* species that best represents the one underlying, natural hierarchy. Such a method is necessary to test hypotheses concerning species flocks and patterns of distribution, as well as hypotheses of character evolution among cyprinodontid fishes. The method of phylogeny reconstruction adopted here is that of phylogenetic systematics or cladistics (formally presented by Hennig, 1966 and modified by many subsequent workers). The cladistic methodology is considered the best currently available for postulating such genealogical relationships (see Wiley, 1981 for a summary of the rationale and methods of phylogenetic systematics).

Outgroup comparisons for determining character polarity in *Orestias* are made by referring to related killifish genera, as well as to characters described in Parenti (1981) for cyprinodontiform fishes, and in Rosen and Parenti (1981) for atherinomorph fishes in general. Ontogenetic series were also examined when available, for determination of character state polarity.

Methods of counts and measurements are those proposed by Miller (1948) and Parenti (1981). All measurements are of straight-line distances recorded with metric dial calipers. I acknowledge the cautions of many workers on the use of ratios as they have been presented traditionally in systematic studies (see Humphries et al., 1981 for a brief review). Tchernavin (1944a) presented a series of ratios based on several measurements, taken from a lateral view, as characters to distinguish among taxa. I do not use many of the descriptive characters of Tchernavin, not only because they represent ratios, but because they were not useful for discriminating among the species. This is not to say that measurements cannot be used to discriminate among taxa. Measurements are important when no other data, or only ambiguous data, exist.

Measurements were used primarily to aid in identification of species in conjunction with descriptions of what I defined as consistent differences, such as, for example, wide head (as in *Orestias luteus*, fig. 7) versus a narrow head.

Description of osteological states follows Parenti (1981) except as noted.

Counterstained preparations of representatives of many species were prepared according to the alcian blue-alizarin Red S method outlined by Dingerkus and Uhler (1977). All descriptions of cartilaginous structures are based on the examination of such preparations with comparisons made with the collections of solely alizarin Red S-stained preparations of cyprinodontiforms in the BMNH and USNM.

RELATIONSHIPS OF KILLIFISHES OF THE TRIBE ORESTIINI

The genus *Orestias*, along with the Anatolian cyprinodonts distributed in fresh and brackish waters throughout the Mediterranean and Anatolia (see Parenti, 1981, p. 458, fig. 86, for distribution map), comprise the tribe Orestiini. Together with the North, Middle, and northern South American cyprinodonts of the tribe Cyprinodontini, they comprise the subfamily Cyprinodontinae, which, with its sister group, the subfamily Cubanichthyinae, containing the genus *Cubanichthys* of Cuba and Jamaica, comprise the family Cyprinodontidae *sensu stricto* (table 1).

Relationships among the genera of the Orestiini, and their relationship to other cyprinodontids are presented in figure 2; the character numbers in that figure correspond with those of the following discussion.

Fishes of the subfamily Cyrpinodontinae form a monophyletic group defined by the following five synapomorphic characters (Parenti, 1981, p. 521): (1) the second pharyngobranchial is offset relative to the third; (2) Meckel's cartilage is expanded posteriorly; (3) the transverse processes of the vertebrae are reduced and cup-shaped; (4) parietals are absent; and (5) outer jaw teeth generally are found in a single row and primitively are tricuspid.

Character number 3, reduced and cup-shaped transverse processes of the vertebrae, occurs in many but not all species of *Orestias* (e.g., they are small in *Orestias hardini*). The somewhat elongate transverse processes in some *Orestias* are therefore considered to be secondarily derived.

The inferred most primitive state of the fifth character, tricuspid uniserial outer teeth, is found among all Cyprinodontini and within the Orestiini, except for one species of *Kosswigichthys* (*K. asquamatus*) and *Orestias*. In *Orestias*, the outer teeth have been described as unicuspid or bicuspid and are in an irregular row, which has been interpreted as two or more rows in particular species.

Franz and Villwock (1972) studied tooth development in Anatolian cyprinodonts, and recognized three developmental stages: a single row of unicuspid teeth followed in development by an anterior, single row of tricuspid teeth, and finally by the addition of a labial row of tricuspid teeth. Typically in *Aphanius*, the most interior of the unicuspid teeth are lost, the middle row of tricuspid teeth persists as the prominent adult dentition, and the outer row is what is generally referred to as the replacement dentition. In *Kosswigichthys asquamatus*, the two rows forming anterior to the first in ontogeny consist of unicuspid rather than tricuspid teeth, and the interior, as well as the two anterior rows, persists in adults. Villwock (1976) describes the irregular placement of teeth in the upper and lower jaws of *Kosswigichthys* as a "slot-link" formation.

No ontogenetic studies are known to have been published on outer tooth formation within the Cyprinodontini. Adult members of this tribe typically have a single row of tricuspid outer jaw teeth, with several tricuspid labial replacement teeth. A juvenile *Cyprinodon variegatus* (BMNH 1948.8.6:1634–

TABLE 1
The Family Cyprinodontidae
(*sensu* Parenti, 1981)

Family Cyprinodontidae
  Subfamily Cubanichthyinae
    Genus *Cubanichthys*
  Subfamily Cyprinodontinae
   Tribe Orestiini
    Genus *Aphanius*
    Genus "*Aphanius*"
    Genus *Kosswigichthys*
    Genus *Orestias*
   Tribe Cyprinodontini
    Genus *Cyprinodon*
    Genus *Jordanella*
    Genus *Cualac*
    Genus *Floridichthys*
    Genus *Megupsilon*

1665, 18.8 mm SL) examined has a similar dental arrangement; there is no row of interior jaw teeth.

On the basis of ontogenetic patterns alone, one could describe the transition of cyprinodontine outer jaw dentition as from the presence of two rows and an outer replacement row to a loss of the most interior row. However, on the basis of the defined monophyly of the subfamily Cyprinodontinae, and on the distribution of all other known derived characters within the subfamily, I interpret the state of a single row of tricuspid teeth with an outer replacement row to be derived at the subfamily level, and the unicuspid, multirow adult teeth of *Kosswigichthys* and *Orestias* to be a secondarily derived state. Usually, such a character would be termed a "reversal" to a more primitive state. However, because of what is known about the ontogeny of tooth formation in Anatolian cyprinodonts, and the pattern of dentition in the tribe Cyprinodontini, it is most parsimonious to describe the derived state in *Kosswigichthys* and *Orestias* as the absence of the suppression of the most interior row.

Reduction or loss of characters is a common phenomenon among killifishes in general, and among the Orestiini in particular in which there are often reductions in squamation, tooth cusp number and pelvic fin development (e.g., Ermin, 1946; Villwock, 1976; Grimm, 1979).

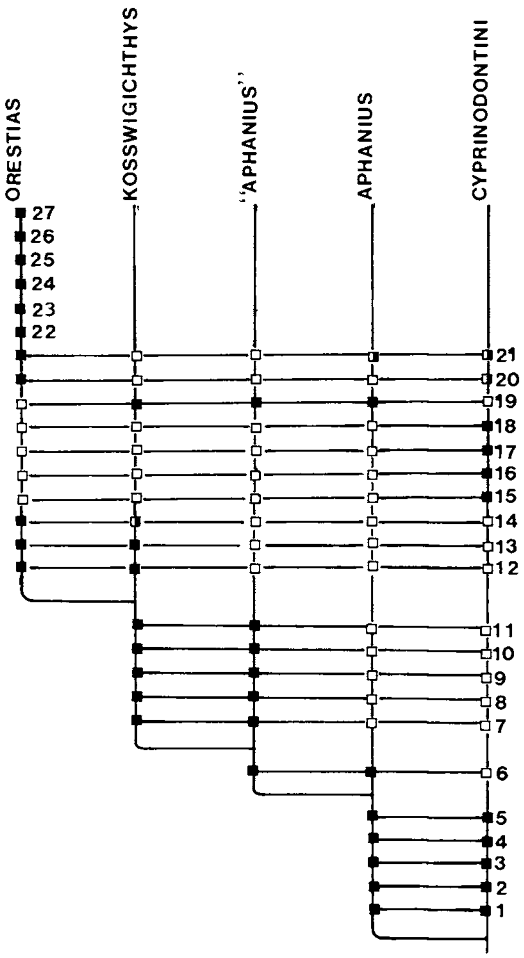

FIG. 2. Synapomorphy diagram of groups within the subfamily Cyprinodontinae (*sensu* Parenti, 1981). Characters are numbered as those in the text. Black square represents synapomorphy, open square symplesiomorphy, and a half-square synapomorphy found in just some members of the terminal taxon (see text for discussion).

Villwock (1976, p. 23) summarized the phenomenon of reductions in Anatolian cyprinodonts: "Populations living under more or less normal fresh-water conditions look like any *Aphanius* from other Anatolian freshwater systems. They show normal scaliness, normally shaped tricuspid teeth and no fin reductions. However, those *Aphanius* which live in the lake waters containing sulfate, show a high degree of scale-reduction, alterations in fin rays, or even total absence of pelvic fins and partial reduction in the lateral tips of their tricuspid teeth."

Characters such as reduction in squamation, or absence of pelvic fins are assessed as derived at those levels where they are invariant. For example, no species of *Orestias* has pelvic fins or fin girdles at any developmental stage. I use it as a derived character because it is invariant within the genus and also because pelvic fins are found in the hypothesized closest relative, *Kosswigichthys.*

The tribe Orestiini is defined as monophyletic by one synapomorphic character: (6) a broadly expanded medial process of the dentary (Parenti, 1981, p. 413, fig. 43) which gives the orestiines a characteristically robust lower jaw.

Anatolian cyprinodonts have often all been placed in the genus *Aphanius* (e.g., Villwock, 1976); there are over 30 nominal species, of which nine are recognized as valid by Villwock. I was unable to define the Anatolian cyprinodonts as a monophyletic group, and pointed out four derived characters that some species of *Aphanius* and the genus *Kosswigichthys* (including *Anatolichthys*) share with *Orestias* (Parenti, 1981, p. 457): (7) a cartilaginous interhyal; (8) a unique head sensory pore pattern represented by neuromasts; (9) a reduced or absent dermosphenotic; and (10) an upturned lower jaw associated with the embedding of the protractor hyoidei between the jaw suspensoria. An additional synapomorphic character that I discuss is: (11) ovaries and testes single in adults.

The species of *Aphanius* that were assessed as being more closely related to *Kosswigichthys* and *Orestias* than to the rest of the *Aphanius* species could not be defined as monophyletic. However, in order to emphasize their close relationship to the *Kosswigichthys-Orestias* sister group pair, they were referred to as "*Aphanius*" (Parenti, 1981, p. 522). I considered *Aphanius mento* to be representative of this group; other species of *Aphanius* that are more closely related to *Kosswigichthys* and *Orestias* include *chantrei* and *sophiae.* Although a cartilaginous interhyal was not given as diagnostic of "*Aphanius*" (Parenti, 1981, p. 523), its presence has been confirmed in additional material of "*A.*" *mento* (BMNH 1920.3.3:203–222).

In primitive species of the genus *Aphanius* and in the species of the Cyprinodontini the head pore and squamation pattern, considered here to be the primitive pattern of the Cyprinodontinae, is characterized by a series of pores and scales arranged in a particular pattern that varies somewhat among species (fig. 3A, B, C). The patterns of preopercular and mandibular pores, are also relatively invariant. In the derived pattern, seen in its most primitive state in "*A.*" *mento* (fig. 3D, E, F), there are no distinct pores; instead, there are minute neuromasts dorsally which also continue along the preopercle and lower jaw.

Kosswigichthys asquamatus is unscaled; the other species in the genus exhibit the derived state of the pore and squamation pattern as in "*A.*" *mento.*

The head pore pattern exhibits little variation among *Orestias* species. General characteristics of the pattern include a series of minute neuromasts arranged in a "lyre-shape" because it suggests the outline of a lyre. The dorsal cephalic neuromasts (fig. 3G) are in one or two rows across the snout and continue posteriorly, medial to the posterior nares, along the dorsal surface of the head lateral to the dorsal head scales. The neuromast series continues medially, then laterally along the preopercle and mandible. There are no preorbital pores; a series of neuromasts encircles the eye (fig. 3H). A similar neuromast pattern occurs in the South American aplocheiloid *Cynolebias* (Parenti, 1981, p. 371, fig. 13G, H, I) that has been assessed as convergent because *Cynolebias* clearly has the derived characters of the suborder Aplocheiloidei, family Rivulidae; whereas, *Orestias* has the derived characters of the suborder Cyprinodontoidei, family Cyprinodontidae.

In *Aphanius fasciatus* as well as in the species of the Cyprinodontini, the dermosphenotic is a long bone with a deep trough for the sensory canal. In genera that exhibit the derived neuromast pattern, the dermosphenotic is very reduced (e.g., as in "*Aphanius*" and some *Orestias*) or absent (e.g., as in

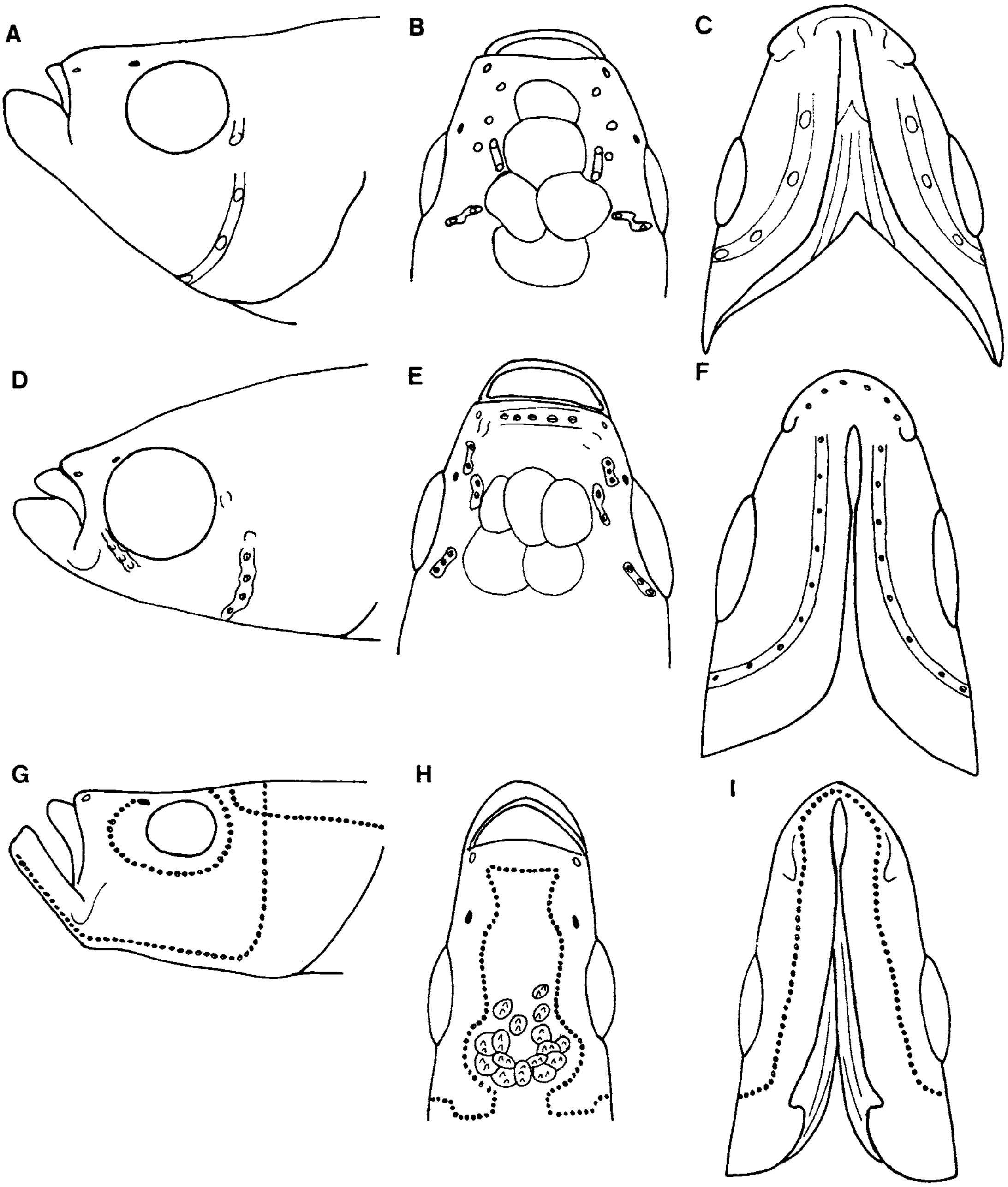

FIG. 3. *Aphanius fasciatus* (BMNH 1951.2.6:1–37): A. lateral view of preopercular and preorbital pores, B. dorsal view of supraorbital pores and squamation, C. ventral view of mandibular and preopercular pores; "*Aphanius*" *mento* (BMNH 1968.12.13:431–435): D. lateral view of neuromast pattern, E. dorsal view of neuromast pattern and squamation, F. ventral view of neuromast pattern; *Orestias cuvieri* (BMNH 1944.6.6:1–6): G. lateral view of neuromast pattern, H. dorsal view of neuromast pattern and squamation, I. ventral view of neuromast pattern. Diagrammatic representations of cephalic sensory pore and squamation patterns.

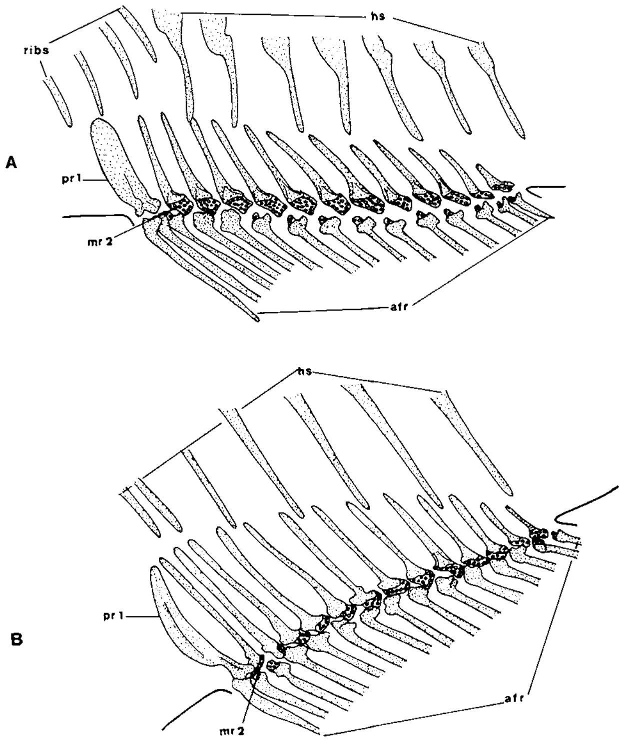

FIG. 4. A. *Orestias agassii* (AMNH 52147); B. *Orestias tomcooni* (AMNH 52189). Diagrammatic representation of internal anal fin supports, anterior is to the left.

some *Kosswigichthys* and other *Orestias*). When present in these genera, it has no trough and therefore carries no sensory canal.

Species of "*Aphanius*," *Kosswigichthys*, and *Orestias* have an upturned lower jaw that, in lateral view, in some cases is perpendicular to the body axis. A character correlated with this upturned lower jaw is the protractor hyoidei embedded between the jaw suspensoria. This character was described by Parenti (1981, p. 457) as an embedded urohyal, but is considered here to be more properly described as a muscle, rather than a bone, character.

Valenciennes (1839) mentioned the united ovaries and united testes as a character of *Orestias*. Tchernavin (1944a, p. 149) included in a series of characters for *Orestias* "ovary and testis single." An examination has confirmed the presence of this character in *Orestias*.

Konuralp (1955) studied the development and morphology of the gonads of Anatolian cyprinodonts. Concerning the development of the gonads in *Aphanius fasciatus*, he stated (pp. 180–181): "The ovary consists of two components, the right and left gonad. Even the gonad of almost mature females retains its original paired form very clearly . . . . The development of the testes proceeds much slower than that of the ovaries and they are usually of smaller size. Although the right and left testes of the male gonad are juxtaposed, they are normally not close to each other as the testes of *Aphanius sophiae*." Concerning the development of the gonads of *Aphanius cypris* (=*mento*), Konuralp stated (p. 179): "The left and right ovaries are united in the female . . . . The primary ovarian cavities of the right and left side join each other in order to form a common secondary ovarian cavity . . . . In the male, too, there are two gonads, one on the right and one on the left. These gonads can be distinguished from one another

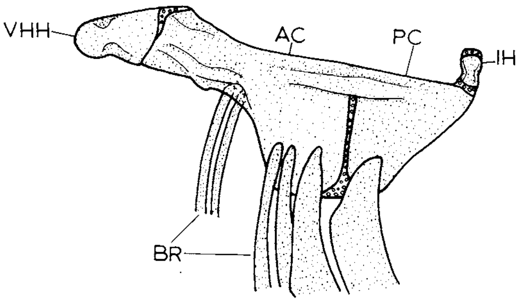

FIG. 5. *Cyprinodon variegatus* (BMNH 1948.8.6:1634–1665). Diagrammatic representation of hyoid bar.

but they are united." Konuralp also surveyed gonad morphology and development in *Kosswigichthys* and *Anatolichthys* and concluded that the gonads were united as in "*A.*" *mento.* [*Anatolichthys,* however, has some unique characteristics of gonad morphology.]

United gonads occur in other cyprinodontiform fishes, e.g., in viviparous goodeids (Hubbs and Turner, 1939). However, Konuralp (1955) considered the formation of the gonads of Anatolian cyprinodonts to be unique among cyprinodontids (equals oviparous cyprinodontiforms). Because goodeids are distantly related to orestiines, the early union of the gonads in *Orestias,* "*Aphanius,*" and *Kosswigichthys* is treated most parsimoniously as a synapomorphy of the three genera.

Kosswigichthys shares two derived characters with *Orestias*: (12) the posttemporal bone is straight, that is, the ventral limb is represented by a ligament; and (13) there is a reduction or absence of scales.

A third character, an increase in the number of vertebrae to 28 or more as opposed to a range of 24 to 27 among other members of the Cyprinodontinae, was used by Parenti (1981, p. 458) to unite *Kosswigichthys* and *Orestias* into a monophyletic group. Further investigation has shown that the level at which an increase in the number of vertebrae can be used as a derived character is ambiguous. Representatives of outgroups have lower vertebral counts (e.g., "*Aphanius*" *mento,* BMNH 1920. 3.3:203–222, has 25 vertebrae; *Aphanius dispar,* BMNH 1977.12.13:1–490, has 27 vertebrae). However, a specimen of *Aphanius fasciatus,* BMNH 1951.2.6:1–37, has 28. Also vertebral counts among the Cyprinodontini range from 24 to 29 (personal observ., Miller, 1956; Miller and Walters, 1972). The consistently high number of vertebrae in *Orestias* (30 or more) may be an additional defining character of the genus; however, our present poor knowledge of the relationships of species of Anatolian cyprinodonts makes the determination of polarity of vertebral counts problematic.

As I said before, a character such as 13 above, "reduction or absence of scales" is used only when it is consistent among members of the considered taxa. Particular patterns of scale distribution are used in the Phylogenetic Analysis section to define groups of *Orestias* species.

Three characters (19–21) are in conflict with the scheme of relationships as depicted in figure 2. In all Anatolian cyprinodonts

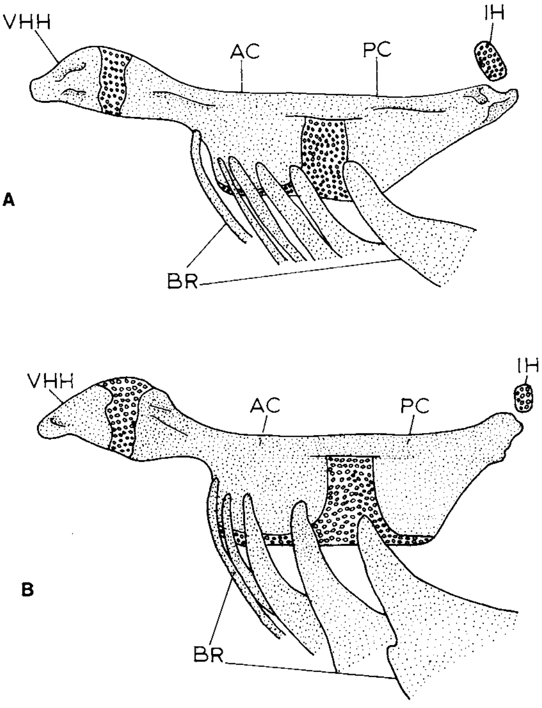

FIG. 6. A. *Orestias pentlandii* (SU 9306); B. *Orestias luteus* (AMNH 52130). Diagrammatic representation of hyoid bar.

(*Aphanius*, "*Aphanius*," and *Kosswigichthys*), the mesethmoid is cartilaginous (character 19) and never ossified as it is in most other cyprinodontiforms, including *Orestias* and the Cyprinodontini. Eight characters (seven through 14) oppose the formation of a group based on this single character.

In all *Orestias* species and in some species of the Cyprinodontini, the third and fourth pharyngobranchial toothplates are fused to form one large tooth-bearing element of the dorsal gill arches (character 20). The distribution of this character, and also the fact that it is found among other groups of cyprinodontiforms, makes it of questionable value in determining relationships. At this stage in our knowledge of cyprinodontiform systematics, it certainly should not be used to hypothesize that some species of the Cyprinodontini are more closely related to *Orestias*. Also, the tribe Cyprinodontini is a well-defined monophyletic group. Its defining characters are: (15) the supraoccipital forms the dorsal wall of the foramen magnum; (16) the neurapophyses of the first vertebra are angled anteriorly and firmly applied to the skull; (17) the exoccipital condyles are absent; and (18) the pharyngobranchial teeth are distributed in discrete rows.

Therefore, the genus *Orestias* may be defined by seven synapomorphies: (21) pelvic fins and fin girdles are absent; (22) the pectoral girdle lacks a first postcleithrum; (23) the vomer is absent; (24) the middle dorsal and middle anal radials are cartilaginous (fig. 4); (25) the anterior and posterior ceratohyal are separated ventrally by a large gap of cartilage (fig. 6) as opposed to the usual cyprinodontiform condition in which they are close together (fig. 5); (26) there is a unique squamation and head pore pattern, described in the Phylogenetic Analysis, and (27) the angularticular lacks a ventral extension parallel to the retroarticular (see Parenti, 1981, p. 413; fig. 43).

Pelvic fins and fin girdles are absent in some members of the Cyprinodontini and *Aphanius* species, as well as in all *Orestias* (character 21). The absence is used nevertheless as a defining character of *Orestias* because its presumed closest relative, *Kosswigichthys*, has pelvic fins and fin girdles under normal circumstances. Also, the character is corroborated by the existence of six additional derived characters (22 through 27).

PHYLOGENETIC ANALYSIS

In the last and most comprehensive treatment of *Orestias* by Tchernavin (1944a), there was no formal statement of relationships among all species. Tchernavin divided the species into four groups, referred to as Groups I to IV, each distinguished by overall body shape or squamation pattern. Group I of Tchernavin comprised *O. cuvieri* and *pentlandii*, the large, elongate midwater species of Lago Titicaca. Group II included species such as *O. agassii* and *luteus* which were characterized by relatively deep caudal peduncles and by the anterior ribs becoming large and swollen with age (i.e., increase in Standard Length) to form very wide-bodied adults in some species (see fig. 7). Group III included *O. gilsoni* and *tutini*, relatively small, inshore species of Lago Titicaca characterized by large eyes that project dorsally above the primary dorsal profile. Group IV included *O. mulleri* and *crawfordi*, the fully scaled, relatively deepwater species of Lago Titicaca.

Relationships among the four groups were not specified, although Tchernavin's key and formal text implied that the incompletely scaled species of Groups I to III were a group distinct from the fully scaled species of Group IV. Also, a precise definition using characters that today we would recognize as synapomophies for each group was not presented. In spite of this, Tchernavin's groupings represent a reasonable first approximation of monophyletic groups within the genus, the definition and composition of which are specified more rigorously in the present revision.

The major monophyletic groups recognized are referred to as species complexes, the composition of which are listed in table 2. Group I of Tchernavin has been found to be monophyletic and is referred to as the *cuvieri* complex. Two species described recently by Lauzanne (1981), *O. ispi* and *O. forgeti,* are included.

Groups III and IV together form a well-defined monophyletic group, although neither of Tchernavin's groups is definable as monophyletic. Two monophyletic groups of species are recognized here, and referred to as the *gilsoni* and *mulleri* complexes.

Group II is referred to as the *agassii* complex. One of the group's subgroups comprises five species that share a derived squamation pattern. Because in the following discussion the pattern is compared with that of other species in the *agassii* complex as well as other species complexes, the five species together (*luteus, rotundipinnis, farfani, albus,* and *olivaceus*) are referred to as the *luteus* group.

Allen (Eigenmann and Allen, 1942) presented a dendrogram of *Orestias* species along with his succinct revision of the genus. Because the relationships were based primarily on overall phenetic similarity, and because there are several obvious misidentifications of species resulting in an unsupportable scheme of relationships, the information contained in the dendrogram is unusable for phylogenetic inference. Therefore, it is not analyzed or further commented on here.

Selected characters or character complexes used to define species or groups of species are explained below; additional characters used to formulate a hypothesis of the relationships of *Orestias* species are discussed in the synapomorphy scheme (pp. 150–160), and in the diagnosis of each species. When a character is invariant within a complex, it is described in the following discussion as being present in the complex rather than being described for each species. Similarly, when a character is primitive for a complex, it is described for the complex with remarks about its distribution within *Orestias.*

TABLE 2
Orestias species Recognized in the Present Study, Grouped into Species Complexes

cuvieri complex
- *cuvieri*
- *pentlandii*
- *ispi*
- *forgeti*

mulleri complex
- *gracilis*
- *mulleri*
- *crawfordi*
- *tutini*
- *incae*

gilsoni complex
- *gilsoni*
- *taquiri*
- *mooni*
- *uruni*
- *minimus*
- *minutus*
- *tchernavini*
- *tomcooni*
- *imarpe*
- *robustus*

agassii complex
- *agassii*
- *empyraeus*
- *frontosus*
- *polonorum*
- *elegans*
- *jussiei*
- *puni*
- *parinacotensis*
- *laucaensis*
- *tschudii*
- *gymnotus*
- *hardini*
- *ctenolepis*
- *ascotanensis*
- *richersoni*
- *multiporis*
- *mundus*
- *ututo*
- *silustani*
- *luteus*
- *rotundipinnis*
- *farfani*
- *albus*
- *olivaceus*

SQUAMATION[3] AND NEUROMAST PATTERN: As briefly discussed in the section on relationships within the tribe Orestiini, one of the defining characters of *Orestias* is its unique squamation and head pore pattern. A prominent feature of the pattern is a distinct median dorsal ridge of scales that covers the middorsal surface of the body from approximately the posterior limit of the head to the anterior base of the dorsal fin (see fig. 7). These scales are generally larger and thicker than surrounding scales, and are almost always arranged in a straight, median line. Correspondingly, scales on either side of the dorsal ridge are relatively thin, or may be absent altogether. The latter condition results in naked areas between the ridge and the lateral body scales in adults of distantly related species in the *cuvieri* and *agassii* complexes, although individual variation within species is marked. Variations on the general pattern of a well-formed dorsal ridge occur in several groups of species, as detailed below and in the synapomorphy scheme.

The dorsal surface of the head is incompletely covered with irregularly distributed thickened scales that have been referred to

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[3] In the present paper, the term squamation refers to types and patterns of distribution of scales on the body. The term scalation is considered to be a synonym of squamation and therefore is not used here.

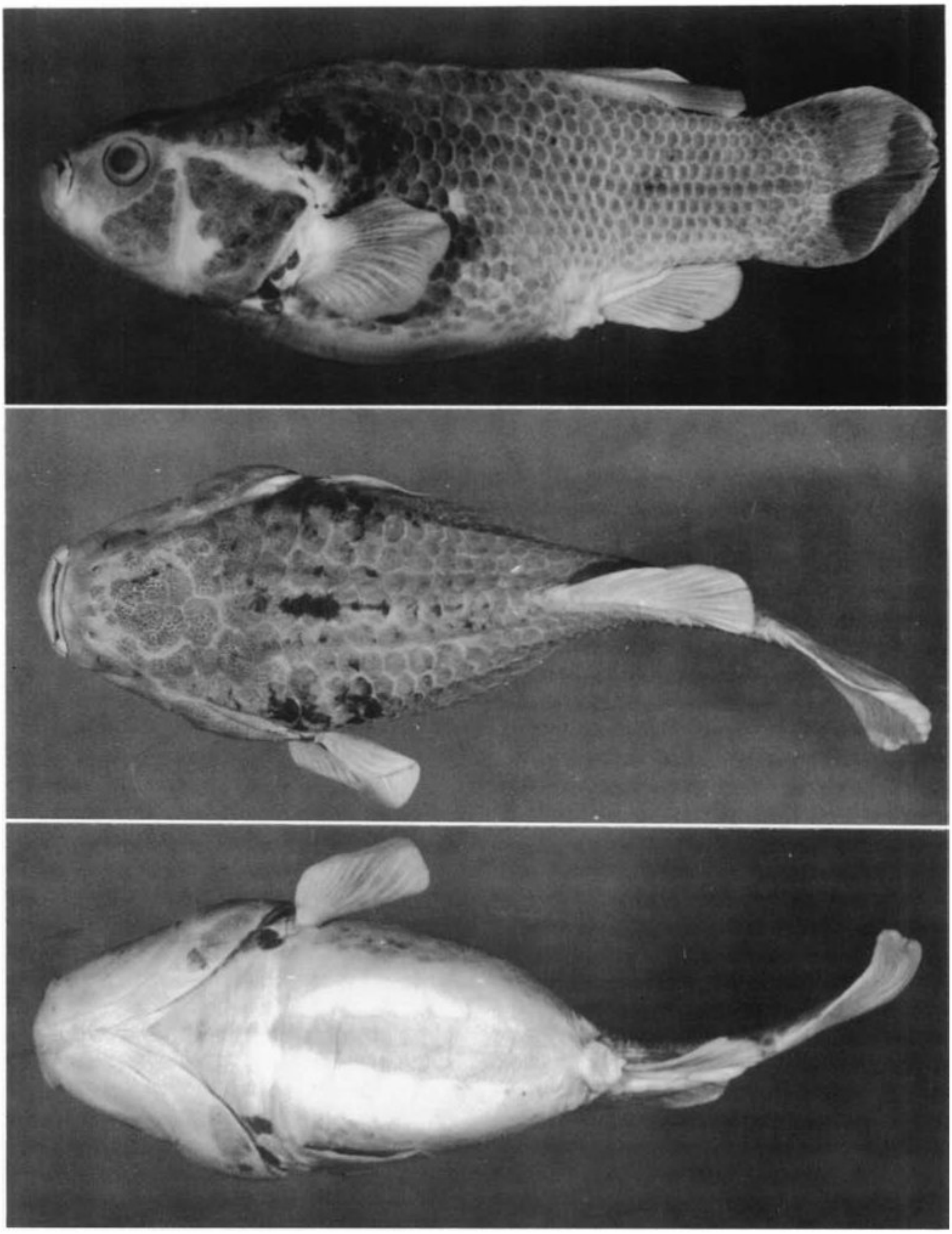

FIG. 7. *Orestias luteus* (AMNH 52134), 110.0 mm SL. Lateral, dorsal, and ventral views, from top to bottom, of an adult female.

as scutes in *Orestias* (Tchernavin, 1944a, 1946) although the term scutes is considered inappropriate here. These head scales may be granulated, as they often are in adult *cuvieri* and *pentlandii* of the *cuvieri* complex. Such granulations are always present in subadults and adults of the *luteus* group of the *agassii* complex, that is, in *luteus, rotundipinnis, farfani, albus,* and *olivaceus.*

The presence of thickened and granulated scales might be considered a synapomorphic character of the entire genus that has been lost or modified in the *gilsoni* and *mulleri* complexes, *ispi* and *forgeti* of the *cuvieri* complex, and the *agassii* complex minus the species of the *luteus* group. However, it is most parsimoniously treated as independently derived within the *luteus* group and in *cuvieri* and *pentlandii.* Along with *ispi,* these last two species form a monophyletic subgroup of the *cuvieri* complex with a defining character of very numerous, small lateral scales (see discussion of meristic characters, below).

Another modification of head scales occurs in a group of species within the *agassii* complex. Ten species (*jussiei, puni, tschudii, frontosus, ctenolepis, richersoni, multiporis, polonorum, empyraeus,* and *agassii*) are distinguished readily by having all scales on the head and the dorsal and lateral surfaces of the body anterior to the dorsal fin extremely smooth and barely overlapping. The dorsal scales are the thickest, are smooth, and have few or no discernible concentric striae. The five species of the *luteus* group are further distinguished from the rest of the *agassii* complex species by having granulated scales.

The derived neuromast pattern of *Orestias* species (fig. 3G, H, I) described in the section on relationships within the tribe Orestiini is very nearly obscured in large adults of these species by the abutting edges of the irregularly shaped scales.

In all species of the *agassii* complex, the body scales immediately posterior to the pectoral fin base are relatively large and form what will be referred to as a lateral shield. In the species of the *luteus* group that have a very wide head, these scales form thickened, granulated shoulders (see figs. 7, 8).

In most species of *Orestias,* the ventral surface from the tip of the lower jaw to the base of the anal fin, as well as the basal portion of the pectoral, dorsal, and anal fins are devoid of scales. A number of species of the *mulleri* complex, two species of the *cuvieri* complex (*ispi* and *forgeti*), and *O. mooni* of the *gilsoni* complex, are fully scaled. A fully scaled condition would initially be assessed as primitive for *Orestias* because that is the primitive condition for cyprinodontiform fishes. Problems with interpretations of degree of squamation have already been discussed with reference to the fact that the totally unscaled *Kosswigichthys asquamatus* is a member of the sister genus of *Orestias.* However, fully scaled species are not scaled in the same manner as other fully scaled cyprinodontines which have regular scale rows on the ventrum. Fully scaled *Orestias* have very small, thin, and irregularly distributed scales on the ventrum and on the basal portion of the pectoral, dorsal and anal fins; this I interpret as a derived condition. Juveniles of fully scaled species are fully or incompletely scaled, whereas juveniles of incompletely scaled species are incompletely and irregularly scaled. Thus, the fully scaled condition is not primitive for the genus.

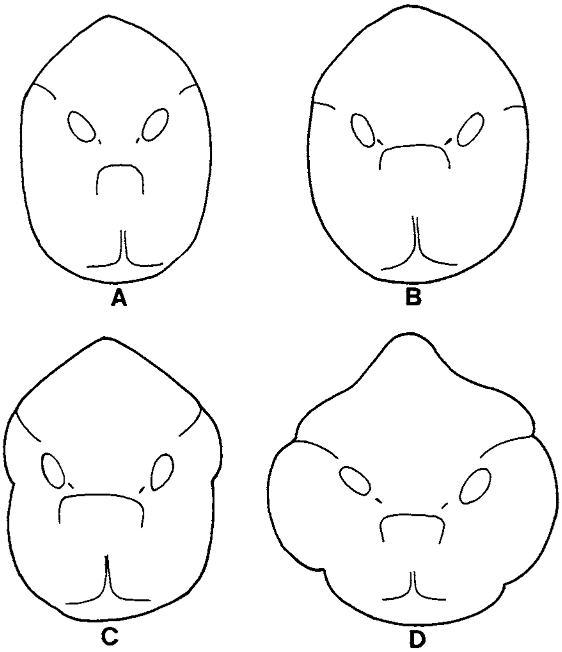

FIG. 8. Outline of anterior view of head A. *Orestias agassii,* B. *Orestias puni,* C. *Orestias albus,* and D. *Orestias luteus,* to illustrate differences in shape of head in wide-headed species.

Fully scaled species may be closely related to incompletely scaled species, as is the case with *forgeti* and *ispi,* which, along with *pentlandii* and *cuvieri* comprise the *cuvieri* complex. Together the last three species have a synapomorphy of an increase in the number of scales in a lateral series as well as a number of other characters (see table 7 and discussion on meristic characters, below). The numerous lateral body scales are thin and small.

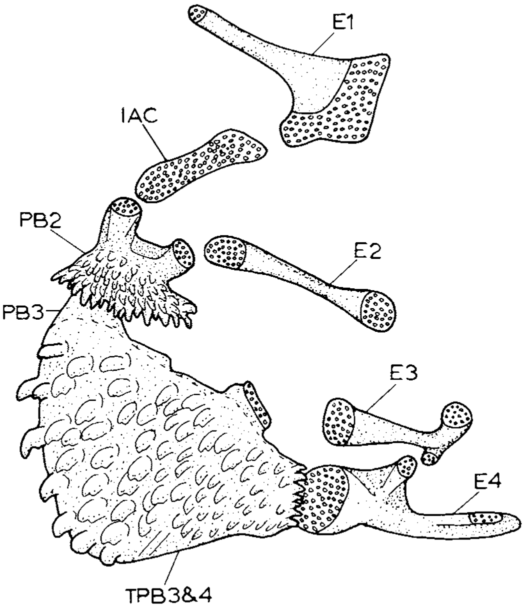

FIG. 9. *Orestias agassii* (AMNH 52147). Diagrammatic representation of dorsal gill arches, ventral view.

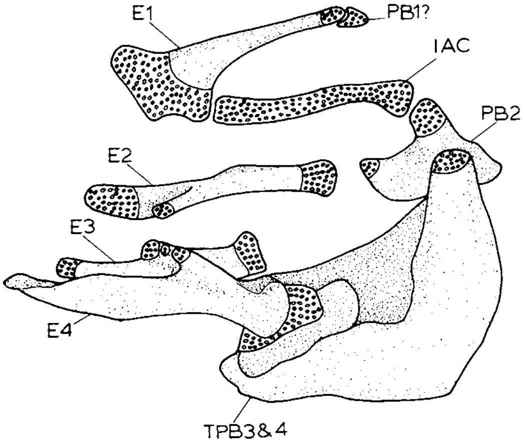

FIG. 10. *Orestias pentlandii* (SU 9306). Diagrammatic representation of dorsal gill arches, ventral view.

In general, larger species tend to be irregularly scaled, whereas smaller species tend to be fully scaled. Like all generalizations, however, this is not always true, and therefore the phylogenetic significance of incomplete squamation of *Orestias* remains problematic. Unique patterns which include incomplete squamation can be described, however.

Five species within the *agassii* complex (*gymnotus, ascotanensis, elegans, parinacotensis,* and *laucaensis*) share a reduced squamation pattern which has several unique characteristics. Aspects of the pattern may be seen best in the photograph of the holotype of *O. gymnotus* (fig. 55). The dorsal surface of the head is irregularly scaled; the median dorsal ridge is either fully present or represented by just a few, randomly placed scales. The ventral surface and basal portion of the pectoral, dorsal, and anal fins are unscaled. The lateral body scales are present in a unique pattern: beginning at the posttemporal, there are one or two uneven rows of lateral scales. The number of scale rows increases posteriorly so that there are four to five scale rows at the base of the caudal fin. (It should be noted that specimens of *parinacotensis* and *laucaensis* were not examined in this study; information is from Arratia, 1982, and the photographs of figs. 52 and 53).

Among *Orestias* species, ctenii are often present on scales of males, but are usually irregularly distributed and weakly formed. One species of the *agassii* complex from the Titicaca Basin (*O. ctenolepis*) is defined by having numerous ctenii on all head scales and all lateral body scales in males (fig. 59), excluding those of the lateral shield. As many as 10 ctenii per scale have been observed on lateral body scales.

HYOBRANCHIAL APPARATUS: Gill arch structure varies widely among *Orestias* species. General patterns of gill arches as well as of the hyoid bar are described in this section, with characteristics specific to species or species groups detailed in the synapomorphy scheme and systematic accounts.

In all *Orestias* species, the third and fourth pharyngobranchial toothplates are fused (figs. 9–12). These toothplates are found fused in other cyprinodontids (fig. 2, character 20), and will not be used as a defining character of *Orestias* for reasons discussed above.

The *cuvieri* complex comprises four species that are pelagic fishes in Lago Titicaca. They are plankton feeders (*ispi, pentlandii,* and *for-*

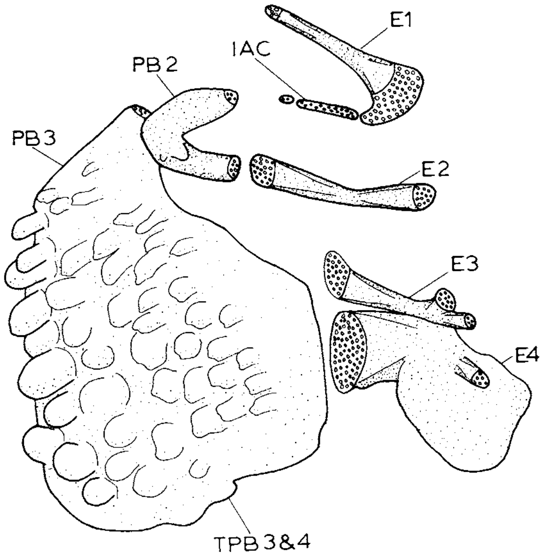

FIG. 11. *Orestias crawfordi* (AMNH 52126). Diagrammatic representation of dorsal gill arches, ventral view.

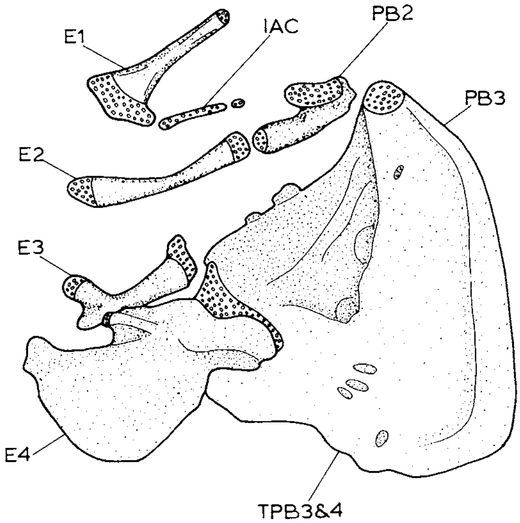

FIG. 12. *Orestias crawfordi* (AMNH 52126). Diagrammatic representation of dorsal gill arches, dorsal view.

geti) or omnivores (*cuvieri*). In all four species, the ventral branchial apparatus is elongate (fig. 15). The basihyal bone is long and narrow, rather than short and triangular (fig. 13) or rectangular (fig. 14) as it is in the Anatolian and certain other cyprinodontiforms. The fifth ceratobranchials (lower pharyngeals) are small and narrow, possess numerous simple teeth, and are very close together or fused in adults.

The dorsal gill arches are reduced in length relative to those of other species complexes and other cyprinodontids. The gill rakers are usually branched rather than simple, although this character varies among individuals.

A synapomorphic character of cyprinodontoids described by Parenti (1981) is a reduction of the interarcual cartilage to approximately one-half the length of the first epibranchial. This is the case for *Kosswigichthys asquamatus* (BMNH 1948.3.15:40–43) and most species of *Orestias* (fig. 9); however, in the *cuvieri* complex, the interarcual cartilage is increased in size to as long as, or longer than, the first epibranchial bone (fig. 10).

In the primitive state, the second pharyngobranchial bears a toothplate which has a series of simple teeth in one or several rows (fig. 9). In the *mulleri* and *gilsoni* complexes (fig. 11) the second pharyngobranchial is reduced to a U-shaped bone with a reduced toothplate that bears few or no teeth. Reduction in the number of teeth in the anterior section of the dorsal gill arches is correlated with the formation of rather larger molariform teeth on the third and fourth pharyngobranchial toothplates in two species of the *mulleri* complex (*O. crawfordi*, fig. 11, and *O. incae*). In these species, the fifth ceratobranchials (lower pharyngeals) have molariform teeth as well (fig. 16), larger and blunter in *crawfordi* than in *incae*.

Both *O. crawfordi* and *incae* are relatively deepwater killifish (taken at depths to 38 m) that feed on molluscs. Several species in the *luteus* group (e.g., *luteus, rotundipinnis,* and possibly *farfani*) also have molariform teeth on the fifth ceratobranchials and the third and fourth pharyngobranchial toothplates. The second pharyngobranchial toothplate in these three species has a primitive dentition; that is, one or more rows of conical teeth are present.

The correlation of molariform pharyngeal teeth and fused fifth ceratobranchials with a particular diet is not apparent among *Orestias* species. Within the *luteus* group, *O. lu-*

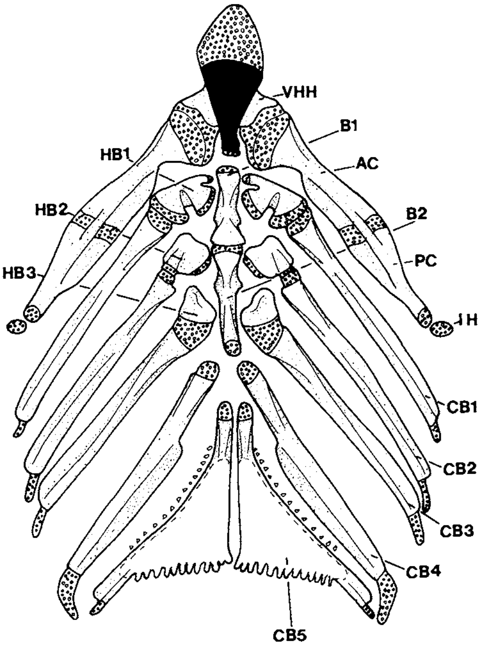

FIG. 13. *Orestias jussiei* (CAS 46175). Diagrammatic representation of ventral gill arches, dorsal view. Ossified portion of basihyal blackened. Dotted line represents outline of fifth ceratobranchial toothplates.

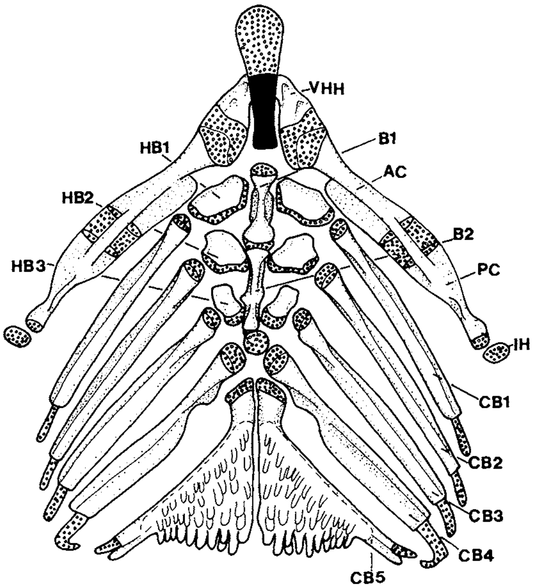

FIG. 14. *Orestias mulleri* (AMNH 52118). Diagrammatic representation of ventral gill arches, dorsal view. Ossified portion of basihyal blackened. Dotted line represents outline of fifth ceratobranchial toothplates.

teus has large pharyngeal teeth, many of which have rounded cusps, whereas the closely related *O. albus* has blunt-tipped, unicuspid pharyngeal teeth which could not properly be referred to as molariform. Both species have been reported to be molluscivores (Pellegrin, 1904a), and *O. albus* also to be a piscivore (Tchernavin, 1944a).

Blunt pharyngeal teeth are apparently correlated with the crushing of prey; however, fused fifth ceratobranchials (lower pharyngeals) are not. Pellegrin (1904a) reported fused lower pharyngeals in *O. luteus, albus, tschudii,* and *pentlandii.* However, the lower pharyngeals are close together in the first three species, but fused only in the last, *pentlandii,* and other species of the *cuvieri* complex. As previously discussed, members of the *cuvieri* complex are either strictly planktivorous or are omnivorous, indicating no correlation of fusion of lower pharyngeals with diet.

An autapomorphy of *O. crawfordi* is a large lateral flange on the fourth epibranchial bone (fig. 12). Associated with this flange is a large adductor IV muscle that fills the cupped surface of the bone. It is inferred that the condition allows for more efficient crushing of prey, although no functional analyses have been carried out to test this hypothesis.

The second epibranchial bone in some species of the *cuvieri, mulleri, gilsoni,* and *agassii* complexes bears a distinct dorsally directed process that is capped by a ball of cartilage (fig. 10). This process is different from the slight expansion of the second pharyngobranchial bone that is considered to be primitive for acanthopterygian fishes (see Rosen and Parenti, 1981, fig. 1) because it is a distinct process that bears a cap of cartilage. The process does not articulate with that of any other gill arch element, nor are the adductor II or levator externus II muscles modified in any species examined that have the process. The distribution of this character (it is not present in all species of any complex) makes it problematic for use in a phylogenetic analysis; I do not use it here to define any group of species.

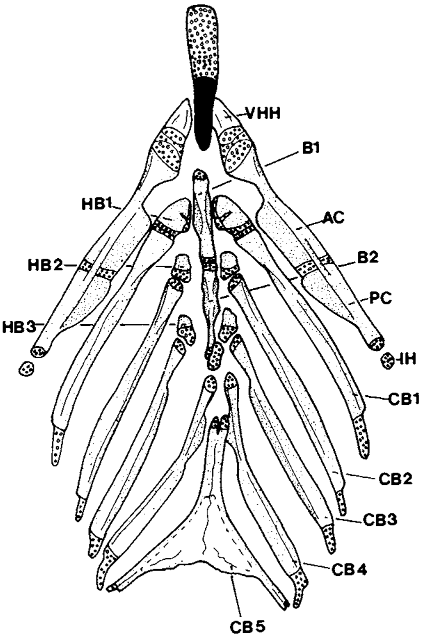

FIG. 15. *Orestias ispi* (AMNH 52111). Diagrammatic representation of ventral gill arches, dorsal view. Ossified portion of basihyal blackened. Dotted line represents outline of fifth ceratobranchial toothplates.

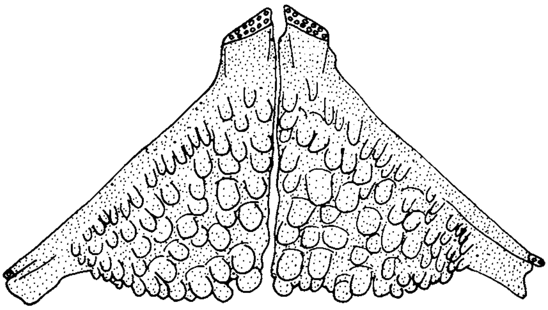

FIG. 16. *Orestias crawfordi* (AMNH 52126). Diagrammatic representation of fifth ceratobranchials (lower pharnygeals), dorsal view.

In all but five species of the *agassii* complex examined (*mundus, hardini, ututo, luteus,* and *albus*), the first hypobranchial bone is divided where it meets the first basibranchial (fig. 13). Both the anterior and posterior sections of the hypobranchial that meet the basibranchial have distinct cartilages. This condition is interpreted as derived because in other cyprinodontids, including *Kosswigichthys,* the first hypobranchial is simple, as it is in *Orestias mulleri* (fig. 14). However, a divided hypobranchial bone is found among some other cyprinodontoids as well. Thus, the character of the divided first hypobranchial may be an additional derived character of the *agassii* complex that has secondarily attained a condition in the five species named above similar to the primitive condition.

Both these gill arch characters (a process on the second epibranchial bone and a divided first hypobranchial bone) are recognized as derived characters. However, the distribution of the characters within the genus *Orestias* and among other killifishes makes their use in the phylogeny reconstruction questionable. I point them out here so that the distribution of such gill arch structures will become better known.

Two species of the *cuvieri* complex (*ispi* and *pentlandii*) are defined as sister species by an increase in the number and arrangement of branchiostegal rays, among other characters. In other *Orestias,* the Anatolian cyprinodonts and many other cyprinodontoids there are five branchiostegal rays. The primitive number of branchiostegal rays for cyprinodontiforms is six, with two hairlike rays present on the anterior arm of the anterior ceratohyal, separate from the four bladelike rays on the posterior section of the hyoid bar, as in *Cyprinodon variegatus* (fig. 5). When the branchiostegal number is reduced to five among cyprinodontoids, it is due to a reduction in the number of anterior hairlike rays (fig. 6B). In *ispi* and *pentlandii* there is just one anterior ray; the number of branchiostegal rays is increased to six by the addition of a fifth ray on the section of the hyoid bar posterior to the notch (fig. 6A).

FINS: Three synapomorphic character complexes of the fins have already been described as defining *Orestias.* These are the absence of pelvic fins and fin girdles; the presence of cartilaginous rather than ossified middle dorsal and anal fin radials (fig. 4); and the absence of the first postcleithral bone (fig. 17).

A unique form of the structure and position of the anal fin serves as a synapomorphic character of the *mulleri* and *gilsoni* complexes. Typically among oviparous cyprino-

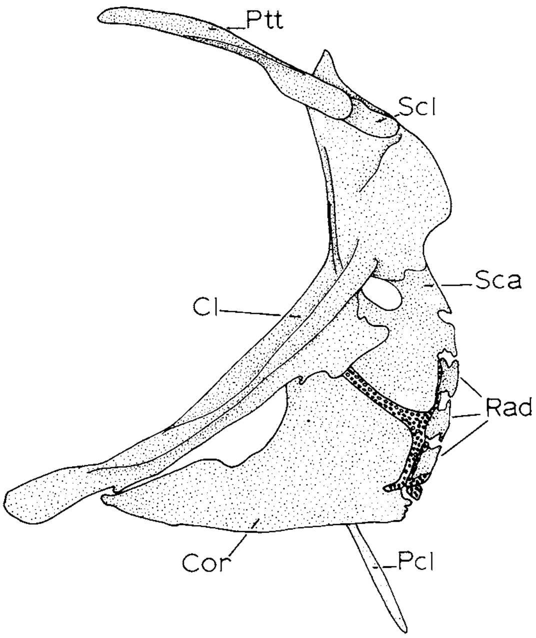

FIG. 17. *Orestias crawfordi* (AMNH 52126). Diagrammatic representation of left pectoral girdle. Anterior is to the left.

dontiform fishes, the longitudinal axis of the anal fin base is roughly parallel to the vertebral column. The proximal anal radials are therefore parallel to, and their tips extend between, the hemal spines (fig. 4A). The proximal radials are all of approximately the same length, becoming slightly shorter in the posterior section of the fin.

In the *mulleri* and *gilsoni* complexes, the anal fin is modified such that the longitudinal axis of the base of the fin lies at an angle away from the vertebral column (fig. 4B). The proximal anal radials do not lie between the hemal spines; they become relatively smaller anteroposteriorly.

A derived character for cyprinodontoids (*sensu* Parenti, 1981) is large inclinators of the anal fin that extend dorsally nearly to the division between the hypaxial and epaxial musculature. This is the generalized condition for *Orestias* species. In the *mulleri* and *gilsoni* complexes the anal inclinators are large; however, because the entire anal fin lies farther away from the vertebral column, the dorsal extent of the inclinators is the base of the hypaxial musculature.

In the *mulleri* complex, the dorsal and anal fin base extend beyond the primary body profile, as in *O. crawfordi* (fig. 38). In fishes of this complex, the dorsal and anal inclinators are greatly enlarged.

The *gilsoni* complex has one defining character, the caudal fin. Typically for killifishes, the caudal fin is rounded or truncate, and the procurrent caudal fin rays extend around the hypural plate in a nearly perfect semicircle (fig. 18B). In the *gilsoni* complex, the procurrent caudal fin rays lie closer to the vertebral column giving the caudal fin what can be described as a tapered external outline (fig. 18A).

Females of three species complexes (*gilsoni, mulleri,* and *agassii*) have a large anal pouch that extends over the base of the first several anal fin rays (e.g., figs. 7 and 69). There is also a large, unpigmented anal papilla. The pouch and papilla are notably absent in *O. uruni* of the *gilsoni* complex.

In three species of the *cuvieri* complex (*cuvieri, pentlandii,* and *ispi*) the caudal fin is distinctly lunate, whereas in all other species of *Orestias* it is rounded or truncate. Killifishes generally have rounded or truncate caudal fins, although a lunate caudal fin is found in, for example, the pelagic cyprinodontoid of Lake Tanganyika, *Lamprichthys tanganicanus* (Boulenger). The lunate caudal fin is interpreted as a derived character further indicating the closeness of relationship of the three *cuvieri* complex species named above.

CHROMOSOMES: Chromosome numbers have been reported in four species of *Orestias.* The primitive haploid number for cyprinodontiforms is 24, and that is the number reported for *O. luteus* and *O. agassii* (Lueken, 1962) and *O. parinacotensis* (Arratia, 1982). The fourth species, *O. laucaensis,* reportedly has a diploid chromosome number of 52 in males and 50 or 51 in females (Arratia, 1982). Both the increase in, and the sexually dimorphic nature of, chromosome number are defining characters of this species.

Sexual dimorphism of chromosome number has been reported in other cyprinodontiforms, in the goodeids (Uyeno and Miller, 1972) and in New World cyprinodontines (Uyeno and Miller, 1971; Miller and Walters, 1972; Levin and Foster, 1972). In both, males have fewer chromosomes than females (for goodeids, male 2n = 41, female 2n = 42; for cyprinodontines, male 2n = 47, female 2n = 48), a condition believed caused by centric fusion of an acrocentric autosome with a similar sex chromosome (Uyeno and Miller, 1972). Heterochromy is apparently present in *O. laucaensis*; however, the mechanism for the production of an increase in chromosome number is unknown (Arratia, 1982).

SEXUAL DIMORPHISM AND DICHROMATISM: Killifishes are characterized by being highly sexually dimorphic and dichromatic. Although certain aspects of the different patterns are difficult to analyze, Parenti (1981) concluded that females larger than males is the plesiomorphic condition for killifishes. This is true for *Orestias* in which adult females can dwarf adult males (e.g., *O. parinacotensis*, fig. 52). Also, in most species of *Orestias* where sample sizes are large enough for generalizations, males are far less numerous than females. One species in the *gilsoni* complex, *O. tchernavini*, was described from a holotype and 36 paratypes, all of which are female (Lauzanne, 1981); no males of this species have ever been reported. Collections of large females in high proportions are characteristic of other cyprinodontiform groups, such as viviparous poeciliids where all female gynogenetic species are known. No experimental work has been published reporting a mode of reproduction in all-female *Orestias* species. Collections are far too sparse and in the case of older material, lacking in precise locality data, to assess the reproductive biology of *Orestias* species with high proportions of females.

Sexual dichromatism among *Orestias* species of the *agassii* complex follows an ontogenetic pattern comparable to that found in other killifishes; that is, juvenile pigmentation patterns persist with little modification in subadult females, whereas the pattern changes in adult males and females.

Pellegrin (1904b) described four varieties of *O. agassii*, all based on differences in color pattern and size. The four varieties have all been determined as different life stages in *O. agassii*. Each of the four life stages has been identified in one collection from Lago Titicaca (fig. 19). *Orestias agassii* var. *inornata* was the name applied by Pellegrin to specimens that are uniformly dark brown or greenish brown on the dorsal and lateral surfaces, with the ventrum uniformly pale yellow and the fins clear. The variety was described from specimens 60 to 110 mm in total length from Lago Titicaca.

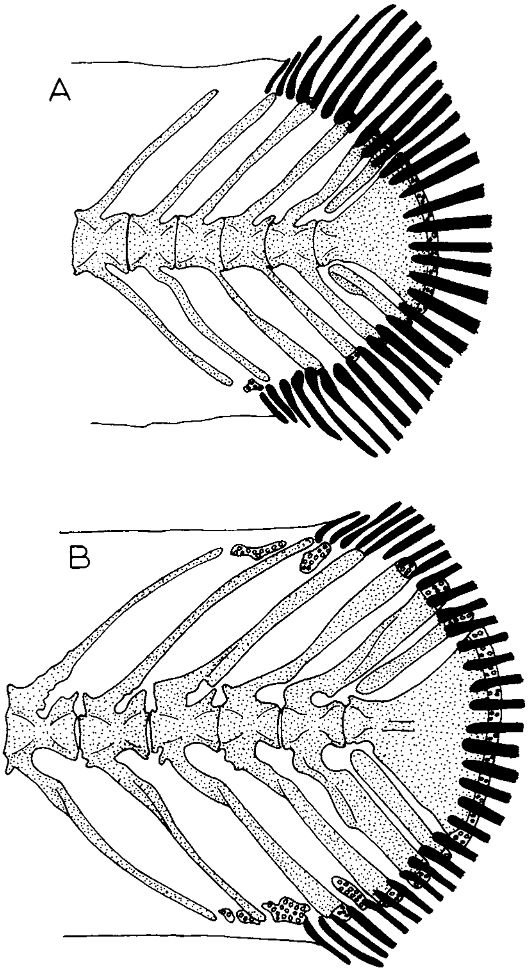

FIG. 18. A. *Orestias tomcooni* (AMNH 52189); B. *Orestias elegans* (CAS 46179). Diagrammatic representation of internal caudal fin supports and vertebral column. Basal portions of caudal fin rays blackened.

Orestias agassii var. *typica*, so named because Pellegrin believed that it most closely resembled the types of *O. agassii*, was used for specimens 70 to 110 mm in total length that are dark brown or greenish brown on the dorsal surface, but with a faint mottled pat-

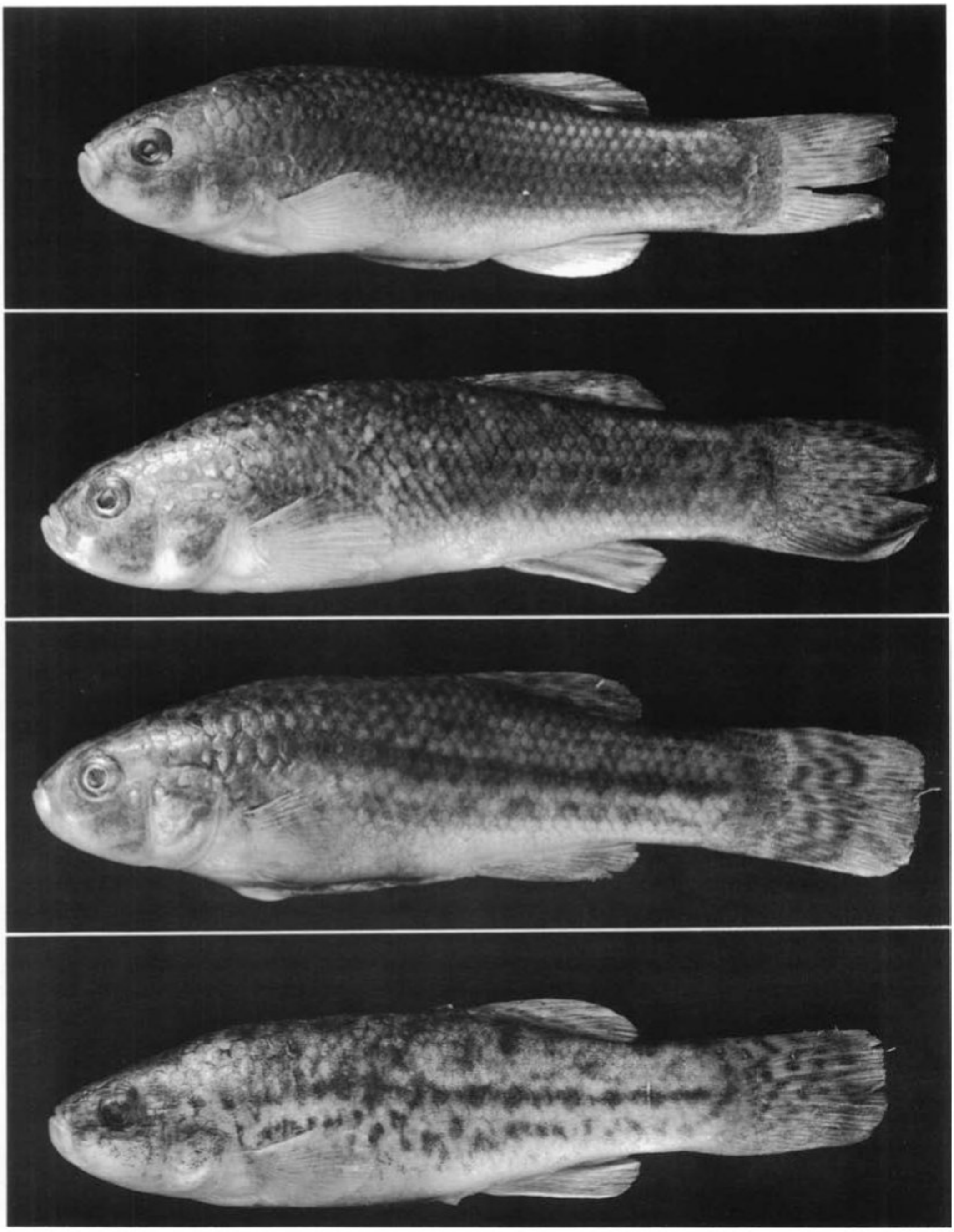

FIG. 19. *Orestias agassii* (AMNH 52148), from Bahia de Puno, Lago Titicaca. Ontogenetic changes in pigmentation pattern represented by, from top to bottom: adult male, 71.2 mm SL, adult female, 69.9 mm SL, adult female, 57.7 mm SL, subadult male, 41.3 mm SL.

tern elsewhere, and an indistinct dark lateral body band (fig. 19). Fins are slightly mottled rather than clear as in the *inornata* variety.

The third variety, *O. agassii* var. *senechali*, was distinguished from the *typica* variety by having a darker and therefore more distinct lateral body band and several indistinct dark blotches ventral to the band. It was described from specimens 50 to 70 mm in total length.

The fourth variety, *O. agassii* var. *crequii* (fig. 19) was described from specimens 55 to 70 mm in total length with mottled dorsal and lateral surfaces, including an interrupted lateral body band. Fins are mottled, rather than clear.

Species of the *agassii* complex pass through ontogenetic changes in color pattern similar to that described above for *O. agassii*; that is, juveniles have a relatively mottled, irregular pigmentation pattern that is retained with some modification, in the form of darkening, in subadult females. Adult males are nearly uniformly dark brown or greenish brown with pale yellow ventral surfaces. Very large adult females of the complex tend to be more uniformly darkened and therefore resemble males.

Species of the *cuvieri*, *gilsoni*, and *mulleri* complexes exhibit little or no ontogenetic change in color pattern; adults retain the pattern of juveniles. In the *gilsoni* and *mulleri* complexes, adults generally retain the typical mottled patterns of juveniles; in the *cuvieri* complex, both young and adults are uniformly colored with little mottling, and the dorsal surface slightly darker than the ventral.

A variety of color patterns characterize species or groups of species; these are dealt with in detail in the following sections. One species group of the *agassii* complex is defined by a particular pattern of fin pigmentation. In these species (*frontosus*, *empyraeus*, *tschudii*, *richersoni*, *ctenolepis*, and *polonorum*) there is a prominent band along the base of the pectoral fin rays (fig. 46) accompanied by a faint to dark band at the base of the dorsal and the anal fin rays. These pigments are not stable, and are barely discernible in specimens that have been preserved for a long period of time. In recently collected material, the pigments are much stronger. The pattern is seen best in large individuals of the species listed above; however, no single lot of any of the species contained specimens that all exhibited the pattern. Whether this is due to individual variation or simply vagaries in preservation and permanence of the pigments is unknown.

JAW AND JAW SUSPENSORIUM: *Orestias* species have relatively small mouths and upturned lower jaws. A defining character of the genus (fig. 2, character 27) is the absence of a ventral medial process in the anguloarticular bone of the lower jaw. Even with this reduction, the large medial process on the dentary gives *Orestias* a very robust lower jaw.

Two distantly related species of *Orestias* (*ispi*, fig. 34 and *jussiei*, fig. 50) have lower jaws that are perpendicular to the body axis. Other species (e.g., *O. tomcooni* fig. 71, and *O. pentlandii*, fig. 33) have lower jaws that approximate the vertical, but in no two species other than *ispi* and *jussiei* is the lower jaw so nearly perpendicular to the main body axis. However, a vertical jaw is attained in these two species in different ways. *Orestias jussiei* (fig. 20A) has characteristics of the jaw and jaw suspensorium that are considered primitive for the genus; *O. ispi* (fig. 20B) on the other hand, has characteristics of the system that uniquely define a group of species in the *cuvieri* complex (*ispi*, *pentlandii*, and *cuvieri*) as monophyletic. The relatively primitive jaw and jaw suspensorium characters of *O. jussiei* are described first and then contrasted with the states of these characters in *O. ispi*.

In *O. jussiei* (fig. 20A) the premaxilla has the S shape characteristic of all cyprinodontoid fishes (Parenti, 1981, fig. 3b). The ascending process of the premaxilla is narrow and comes to a slender point posteriorly. The rostral cartilage is absent in all *Orestias*. The dentary is a robust bone that carries a sensory canal. There is an irregular row of unicuspid teeth on both the premaxilla and the dentary. The maxilla has a large dorsal process which has an irregularly grooved surface.

In *O. ispi* (fig. 20B), the premaxilla is much wider in a lateral view than in *jussiei*, and the S shape is much less pronounced. The ascending process of the premaxilla is reduced slightly and blunt at the posterior tip. The dentary is a relatively large bone, except at

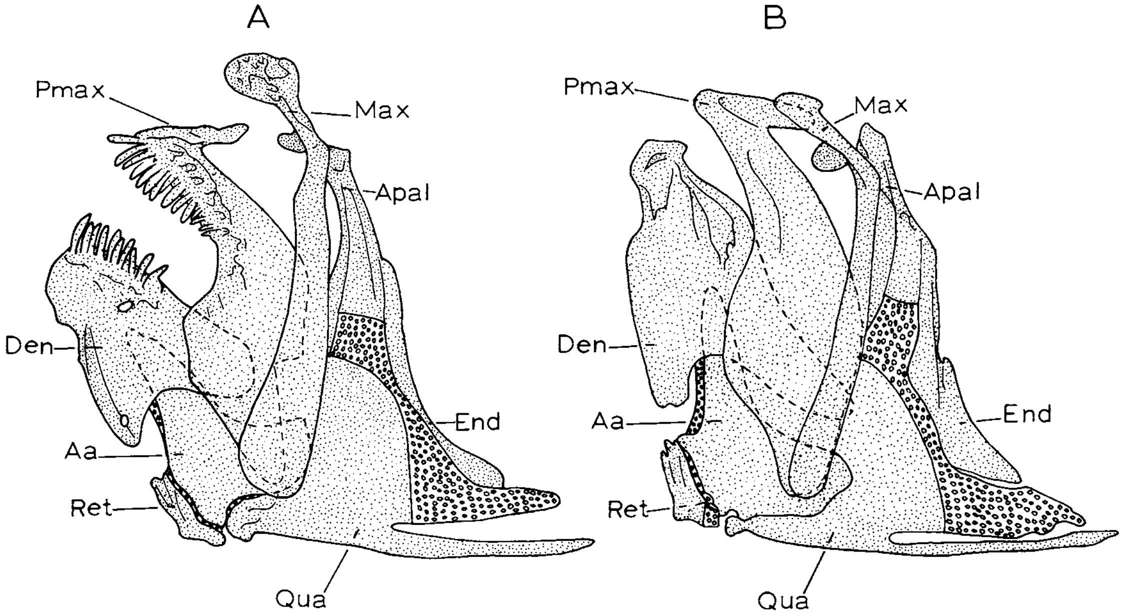

FIG. 20. A. *Orestias jussiei* (CAS 46175); B. *Orestias ispi* (AMNH 52111). Diagrammatic representation of left lateral view of jaws and jaw suspensoria.

the medial extent where it is constricted. There are no discernible troughs for sensory canals in the dentary. The maxilla is a much more slender bone with a small dorsal process that has an unsculptured dorsal surface.

The shapes and relative sizes of the premaxilla, dentary, and maxilla are essentially the same in *ispi, pentlandii, cuvieri.* The most striking difference is that the first two species have few or no teeth in the jaws (fig. 20B), whereas, quite in contrast, *cuvieri* (fig. 32) has a large mouth with one row of large, recurved, unicuspid teeth and an irregular row of smaller, unicuspid teeth interior to the large row. As discussed previously in the section on hyobranchial apparatus, *ispi* and *pentlandii* are planktivores, whereas *cuvieri* is an omnivore. Gill arch structure varies little among these three species, however.

There is little difference between the jaw suspensoria of *jussiei* and *ispi.* In both, as in all *Orestias,* the autopalatine has a blunt head that is not capped by cartilage.

SKULL: The vomer is absent in all *Orestias* species (fig. 2, character 23); this is the sole synapomorphic skull character of the genus. Other major features of the skull that are plesiomorphic for all *Orestias* and present in the *agassii* complex, are described for *O. agassii* (fig. 21A) and will serve as a basis of comparison for more derived skull types within the genus.

The mesethmoid is present as two large ossified discs that meet anteriorly to form a wedge located at the anterior extent of the anterior ramus of the parasphenoid (Rosen, 1964). The medial extensions of the lateral ethmoids meet or pass dorsal to this ramus.

The nasals are large, flat bones that lie dorsal to the ethmoid region. They are expanded in *Orestias* to nearly meet in the midline. The frontals are relatively flat bones that are curved ventrolaterally to form the dorsal rim of the orbit.

The dermosphenotic is absent. (It is present as a small ossified element in some specimens of *ascotanensis* and *mundus* of the *agassii* complex.) The dermosphenotic is either absent or present as a minute ossified element in *Kosswigichthys,* contrary to Parenti (1981) in which it was stated that the dermosphenotic is absent in that genus.

The first vertebra articulates with the skull via a well-developed basioccipital condyle,

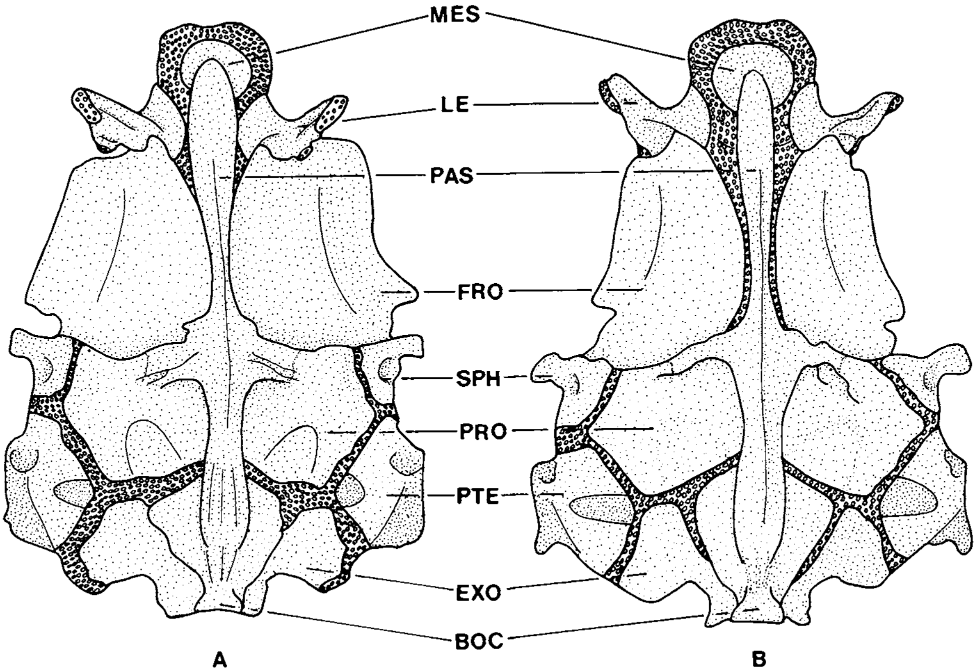

FIG. 21. A. *Orestias agassii* (BMNH 1862.11.15:34); B. *Orestias mulleri* (AMNH 52118). Diagrammatic representation of ventral view of skull.

and the two exoccipital condyles which have weakly formed articulation facets.

These characteristics of the skull are modified (i.e., found in a relatively more derived state) in the other species complexes. In the *mulleri, gilsoni,* and *cuvieri* complexes, the medial extensions of the lateral ethmoids do not meet, therefore do not pass dorsal to the anterior ramus of the parasphenoid (fig. 21B). The lateral ethmoids are both relatively smaller and their medial margins are farther apart.

The orbits project dorsally above the primary dorsal profile of the head in the *mulleri* and *gilsoni* complexes (see especially figs. 36, 63, and 69). The orbits are expanded to different degrees among the 15 species of the two complexes, but in all the frontal bones are convex along the dorsal rim of the orbit to accommodate the relatively large eyes.

MERISTIC CHARACTERS: Five meristic characters were found to be useful in discriminating among species or groups of species: (1) vertebrae; (2) dorsal fin rays; (3) anal fin rays; (4) pectoral fin rays; and (5) scales in a lateral series. The data accumulated for these characters are summarized in tables 3 through 7, respectively.

The modal number of vertebrae is 32, with an observed range of 30 to 38 (table 3). In three species, the mode is increased: in *cuvieri* and *tschudii* to 34, and in *pentlandii* to 37. These increases are most parsimoniously assessed as autapomorphies of each of the three species because they represent stages of separate transition series from a relatively low number of vertebrae in the outgroup *Kosswigichthys* which has 28. Two species, *taquiri* and *minimus,* have a mode of 30 vertebrae. This state may be a stage in a transition series from a low to a high number of vertebrae. Therefore, although useful in distinguishing *taquiri* and *minimus* from other *Orestias* species, it is not considered a synapomorphy for the two species.

Dorsal fin ray number ranges from 10 to 18, with a mode of 14 (table 4). In the sister species *crawfordi* and *incae* there is an increase in the modal number of dorsal fin rays to 16 and 17, respectively. *Kosswigichthys*

TABLE 3
Distribution of the Number of Vertebrae in *Orestias*

Species	Number of Vertebrae 30	31	32	33	34	35	36	37	38
cuvieri	—	—	—	2	4	4	—	—	—
pentlandii	—	—	—	—	—	—	1	5	1
ispi	—	5	19	9	—	—	—	—	—
forgeti	—	1	4	13	5	—	—	—	—
mulleri	—	4	3	—	—	—	—	—	—
gracilis	—	—	—	1	—	—	—	—	—
crawfordi	—	10	2	—	—	—	—	—	—
tutini	1	2	—	—	—	—	—	—	—
incae	—	10	—	—	—	—	—	—	—
luteus	—	2	4	1	—	—	—	—	—
rotundipinnis	—	1	2	—	—	—	—	—	—
farfani	—	—	—	1	—	—	—	—	—
albus	—	2	2	1	1	—	—	—	—
olivaceus	—	1	4	—	—	—	—	—	—
silustani	—	1	2	2	—	—	—	—	—
agassii	—	5	5	7	1	3	—	—	—
empyraeus	-	5	1	—	—	—	—	—	—
frontosus	—	1	2	—	1	—	—	—	—
polonorum	—	1	1	—	—	—	—	—	—
elegans	—	—	3	5	—	—	—	—	—
jussiei	—	1	5	2	—	—	—	—	—
puni	—	1	1	—	—	—	—	—	—
parinacotensis[a]	—	—	—	—	—	—	—	—	—
laucaensis[a]	—	—	—	—	—	—	—	—	—
tschudii	—	—	—	1	3	2	—	—	—
gymnotus	—	1	1	1	1	—	—	—	—
hardini	—	—	4	3	—	—	—	—	—
ctenolepis	—	—	1	—	—	—	—	—	—
ascotanensis	—	2	4	—	—	—	—	—	—
richersoni	—	—	1	—	—	—	—	—	—
multiporis	—	—	—	1	—	—	—	—	—
mundus	—	—	1	—	—	—	—	—	—
ututo	—	—	5	—	—	—	—	—	—
gilsoni	—	1	2	—	—	—	—	—	—
taquiri	4	1	—	—	—	—	—	—	—
mooni	—	—	3	3	1	—	—	—	—
uruni	—	2	1	1	—	—	—	—	—
minimus	2	—	—	—	—	—	—	—	—
minutus	—	1	—	—	—	—	—	—	—
tchernavini	2	13	10	—	—	—	—	—	—
imarpe	—	1	—	—	—	—	—	—	—
tomcooni	—	2	—	—	—	—	—	—	—
robustus	1	—	—	—	—	—	—	—	—

[a] *parinacotensis* and *laucaensis* have not been examined, and no vertebral counts recorded.

asquamatus (BMNH 1948.3.15:40–43) has 12 dorsal fin rays. Therefore, based on outgroup comparison, the increase in the former two species is considered to be one of their synapomorphies. The increase in the modal number of dorsal fin rays to 16 in *richersoni* is considered to be an autapomorphy of that species because on the basis of all other characters, it is assessed as a distant relative of *crawfordi* and *incae*.

TABLE 4
Distribution of the Number of Dorsal Fin Rays in *Orestias*

Species	Number of Dorsal Fin Rays								
	10	11	12	13	14	15	16	17	18
cuvieri	—	1	1	1	6	3	1	—	—
pentlandii	—	1	1	3	3	3	—	—	—
ispi	—	3	22	13	3	—	—	—	—
forgeti	—	—	—	2	16	15	6	—	—
mulleri	—	2	7	4	—	—	—	—	—
gracilis	—	—	1	2	1	—	—	—	—
crawfordi	—	—	—	—	—	1	8	2	1
tutini	—	—	2	2	—	—	—	—	—
incae	—	—	—	—	2	2	1	4	1
luteus	—	—	1	1	4	2	1	—	—
rotundipinnis	—	—	1	—	3	1	—	—	—
farfani	—	—	—	—	—	1	—	—	1
albus	—	—	—	1	3	5	—	—	—
olivaceus	—	—	—	—	1	4	—	—	—
silustani	—	—	—	1	5	2	1	—	—
agassii	—	2	7	7	11	7	2	—	—
empyraeus	—	3	1	4	1	2	—	—	—
frontosus	—	—	—	—	2	3	2	1	—
polonorum	—	—	—	1	4	—	—	—	—
elegans	—	—	—	1	4	6	—	—	—
jussiei	—	—	—	1	7	2	—	—	—
puni	—	—	—	1	2	2	—	—	—
parinacotensis	—	—	—	x……	……	……	x[a]	—	—
laucaensis	—	—	—	—	x……	x[a]	—	—	—
tschudii	—	—	—	—	1	4	2	—	—
gymnotus	—	4	2	1	4	—	—	—	—
hardini	1	5	3	—	—	—	—	—	—
ctenolepis	—	—	1	2	5	1	—	—	—
ascotanensis	—	—	1	2	3	1	—	—	—
richersoni	—	—	—	—	1	1	3	—	—
multiporis	—	—	—	2	5	3	2	—	—
mundus	—	—	2	5	4	—	—	—	—
ututo	3	2	1	—	—	—	—	—	—
gilsoni	—	—	2	3	4	1	—	—	—
taquiri	—	2	4	1	1	—	—	—	—
mooni	—	—	1	1	1	1	1	—	—
uruni	—	—	2	2	3	—	—	—	—
minimus	—	—	—	2	—	—	—	—	—
minutus	—	—	—	1	—	1	—	—	—
tchernavini	—	4	15	13	5	—	—	—	—
imarpe	1	4	1	—	1	—	—	—	—
tomcooni	—	—	1	5	—	—	—	—	—
robustus	—	1	2	3	3	1	—	—	—

[a] These data are taken from Arratia (1982) in which dorsal fin ray numbers were presented as a range, rather than frequency distribution.

A reduction in the modal number of dorsal fin rays to 10 in *ututo* and 11 in *hardini* is considered to be a synapomorphy of these two sister species.

Anal fin rays number from 10 to 19 with a mode of 15 (table 5). Because a specimen of *Kosswigichthys asquamatus* (BMNH 1948.3.15:40–43) has 12 anal fin rays, an in-

TABLE 5
Distribution of the Number of Anal Fin Rays in *Orestias*

Species	Number of Anal Fin Rays									
	10	11	12	13	14	15	16	17	18	19
cuvieri	—	—	—	—	1	2	3	2	2	1
pentlandii	—	—	—	—	—	2	4	3	1	—
ispi	—	—	—	—	—	—	15	20	4	2
forgeti	—	—	—	—	2	5	19	11	1	1
mulleri	—	—	3	6	2	1	—	—	—	—
gracilis	—	—	—	—	1	3	1	—	—	—
crawfordi	—	—	—	—	1	7	1	2	—	—
tutini	—	—	—	1	2	1	—	—	—	—
incae	—	—	—	—	2	1	2	4	1	—
luteus	—	—	—	—	2	5	2	—	—	—
rotundipinnis	—	—	—	1	2	3	—	—	—	—
farfani	—	—	—	—	—	1	1	—	—	—
albus	—	—	—	—	3	3	3	—	—	—
olivaceus	—	—	—	—	1	1	3	—	—	—
silustani	—	—	—	—	1	4	4	1	—	—
agassii	—	2	5	7	12	6	5	—	—	—
empyraeus	—	—	—	—	3	5	2	—	—	—
frontosus	—	—	—	—	—	6	1	2	—	—
polonorum	—	—	—	—	3	1	1	—	—	—
elegans	—	—	—	—	1	5	4	1	—	—
jussiei	—	—	—	2	6	2	—	—	—	—
puni	—	—	—	—	1	1	2	—	1	—
parinacotensis	—	—	—	—	x…………	………………	x[a]	—	—	—
laucaensis	—	—	—	—	x…………	x[a]	—	—	—	—
tschudii	—	—	—	—	—	2	5	4	—	—
gymnotus	—	2	1	4	2	1	—	—	—	—
hardini	1	2	5	—	—	—	—	—	—	—
ctenolepis	—	—	—	—	5	4	—	—	—	—
ascotanensis	—	—	1	4	4	—	—	—	—	—
richersoni	—	—	—	—	—	1	3	1	—	—
multiporis	—	—	—	—	2	6	2	2	—	—
mundus	—	—	—	3	6	2	—	—	—	—
ututo	2	3	1	—	—	—	—	—	—	—
gilsoni	—	—	—	2	2	2	—	—	—	—
taquiri	—	—	1	2	2	1	—	—	—	—
mooni	—	—	—	—	1	2	1	—	—	—
uruni	—	—	—	1	6	—	—	—	—	—
minimus	—	—	—	—	1	1	—	—	—	—
minutus	—	—	—	—	—	—	1	1	—	—
tchernavini	—	—	—	6	12	16	3	1	—	—
imarpe	—	—	2	2	1	1	—	—	—	—
tomcooni	—	—	—	1	1	4	—	—	—	—
robustus	—	—	—	3	2	2	—	—	—	—

[a] These data are taken from Arratia (1982) in which anal fin ray numbers were presented as a range, rather than a frequency distribution.

crease in the modal number of anal fin rays might be considered a synapomorphy of *Orestias* species. However, 12 anal fin rays is not an uncommon number in *agassii*, one of the more variable species. Also, a rather low modal number of 11 anal fin rays occurs in *ututo*; the range is from 10 to 12. The decrease is considered an autapomorphy of the species. Similarly, there is a distinct increase in the mode to 16 or 17 in the *cuvieri* com-

TABLE 6
Distribution of the Number of Pectoral Fin Rays in *Orestias*

Species	Number of Pectoral Fin Rays								
	14	15	16	17	18	19	20	21	22
cuvieri	—	—	2	2	2	—	—	—	—
pentlandii	—	—	—	1	6	4	1	—	—
ispi	—	1	7	23	10	—	—	—	—
forgeti	—	—	—	—	7	18	14	—	—
mulleri	—	—	—	5	3	5	—	—	—
gracilis	2	6	—	—	—	—	—	—	—
crawfordi	—	—	—	1	1	6	1	—	—
tutini	—	1	1	1	—	—	—	—	—
incae	—	—	1	2	4	2	1	—	—
luteus	—	—	—	—	—	2	4	3	1
rotundipinnis	—	—	—	—	—	2	3	—	—
farfani	—	—	—	—	—	—	2	—	—
albus	—	—	—	—	2	1	2	2	—
olivaceus	—	—	—	—	—	—	—	4	1
silustani	—	—	—	—	1	1	7	1	—
agassii	1	3	11	9	8	3	1	—	—
empyraeus	—	—	4	4	1	—	—	—	—
frontosus	—	—	1	4	1	1	—	—	—
polonorum	—	—	3	2	—	—	—	—	—
elegans	—	3	5	2	1	1	—	—	—
jussiei	—	1	4	4	1	—	—	—	—
puni	—	—	—	—	3	1	—	1	—
parinacotensis	—	—	x ⋯	⋯	⋯	⋯	x[a]	—	—
laucaensis	—	—	x ⋯	x[a]	—	—	—	—	—
tschudii	—	—	—	1	2	4	3	—	—
gymnotus	1	3	4	2	1	—	—	—	—
hardini	—	4	2	—	—	—	—	—	—
ctenolepis	—	1	2	5	1	—	—	—	—
ascotanensis	—	—	—	3	4	1	—	—	—
richersoni	—	—	1	—	3	1	—	—	—
multiporis	—	1	5	4	3	—	—	—	—
mundus	—	1	4	4	3	—	—	—	—
ututo	—	—	—	3	2	—	—	—	—
gilsoni	—	—	—	2	2	1	—	—	—
taquiri	—	—	1	2	2	—	—	—	—
mooni	1	3	5	1	—	—	—	—	—
uruni	—	1	2	1	—	—	—	—	—
minimus	—	1	1	—	—	—	—	—	—
minutus	—	1	—	1	—	—	—	—	—
tchernavini	1	5	6	23	1	1	—	—	—
imarpe	—	—	1	4	1	—	—	—	—
tomcooni	—	3	2	1	—	—	—	—	—
robustus	—	—	1	1	4	1	—	—	—

[a] These data are taken from Arratia (1982) in which pectoral fin ray numbers were presented as a range, rather than frequency distribution.

plex, considered to be an additional synapomorphic character of the included four species.

Pectoral fin rays number from 14 to 22, with a mode of 17 (table 6). An increase in the modal number to 20 or 21 is a synapomorphy of a group of *agassii* complex species. Similarly, an increase in the modal number to 19 is considered an independently acquired autapomorphy of *O. forgeti* of the *cu-*

TABLE 7

Distribution of the Number of Scales in a Lateral Series in *Orestias*

Species	Scales in a Lateral Series																														
	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
cuvieri	—	—	—	—	—	—	—	—	—	—	—	2	4	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
pentlandii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	2	—	5	—	6	—	1	1
ispi	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	3	8	7	4	9	4	1	2	—	1	—	—	—	—	—	—	—
forgeti	1	5	4	12	13	2	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
mulleri	—	—	—	—	2	1	1	3	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
gracilis	—	—	2	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
crawfordi	—	—	1	7	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
tutini	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
incae	—	—	1	5	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
luteus	—	3	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
rotundipinnis	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
farfani	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
albus	—	—	2	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
olivaceus	—	—	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
silustani	—	—	1	3	3	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
agassii	—	1	1	5	4	5	2	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
empyraeus	—	—	1	2	1	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
frontosus	—	—	—	—	1	4	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
polonorum	—	—	—	—	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
elegans	—	—	—	—	—	1	4	4	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
jussiei	—	—	—	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
puni	—	—	—	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
parinacotensis	—	x	………	………	………	………	………	………	x^a	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
laucaensis	—	—	x	………	………	………	………	………	………	………	x^a	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
tschudii	—	—	—	—	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
gymnotus	—	—	1	1	3	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
hardini	—	—	—	—	—	—	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ctenolepis	—	—	1	—	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ascotanensis	1	—	1	2	4	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
richersoni	—	—	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
multiporis	—	—	—	2	6	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
mundus	—	3	4	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ututo	—	—	—	1	3	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
gilsoni	—	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
taquiri	1	1	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 7—(*Continued*)

Species	Scales in a Lateral Series																															
	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
mooni	—	—	1	4	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
uruni	—	—	—	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
minimus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
minutus	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
tchernavini	—	1	—	—	3	9	6	6	8	1	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
imarpe	—	—	—	—	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
tomcooni	—	—	—	—	—	—	—	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
robustus	—	—	—	—	2	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[a] These data are from Arratia (1982) in which scales in a lateral series were given as a range, rather than a frequency distribution.

vieri complex. Pectoral fin rays number 13 or 14 in *Kosswigichthys,* indicating as for anal fin ray number, that an increase in the modal number may be a synapomorphy of *Orestias* species. However, surveys of pectoral fin ray number as well as anal fin ray number among all Anatolian cyprinodontids would be necessary to judge at what level the increase in fin ray number should be used as a synapomorphy. In the meantime, the low number of pectoral fin rays in *gracilis* (range 14 to 15, mode of 15) may be another character to distinguish this species from the rest of the *mulleri* complex (range 15 to 20, mode of 19).

The number of scales in a lateral series from the posterior margin of the supracleithrum to the hypural joint varies widely among *Orestias* species as well as among individuals (table 7). The range, when scales are present, is from 29 to 60. Juveniles and adults of some species (e.g., *minimus*) are totally unscaled. The modal number of scales in a lateral series is 32, yet many species have a wide range (e.g., *forgeti,* 29 to 39, with a mode of 33), and, *tchernavini,* 30 to 41, with a mode of 34).

A synapomorphic increase in lateral scale number occurs in three species of the *cuvieri* complex (*cuvieri, ispi,* and *pentlandii*) in which there is a modal number of 41, 48, and 57, respectively. The extremely high number in *ispi* and *pentlandii* is an additional synapomorphic character of these sister species.

Other differences in modal number of scales in a lateral series occur between pairs or larger groups of species and will be used in the synapomorphy scheme and key. For example, all members of the *mulleri* complex have a modal number of 31 or 32, except for *mulleri* which has a modal number of 36. Also, *tomcooni* of the *gilsoni* complex has a modal number of 37. The extremely high scale number in the *cuvieri* complex is assessed as synapomorphic; however, to judge whether the high modal numbers of *mulleri* and *tomcooni* are primitive or derived is confounded by the fact that in *Kosswigichthys* there are either no scales (as in *asquamatus*) or, for example, 37 scales (as in a representative of *K. splendens,* BMNH 1948.3.15:37–39).

A general statement that can be made about meristic variation within *Orestias* is that it is useful in distinguishing among species or

TABLE 8
Frequency Distribution of Length of the Head in *Orestias* (expressed in thousandths of Standard Length)

	Class Intervals of Head Length									
Species	150–174	175–199	200–224	225–249	250–274	275–299	300–324	325–349	350–374	375–399
cuvieri	—	—	—	—	—	—	2	4	1	1
pentlandii	—	—	1	2	2	—	—	—	—	—
ispi	—	—	5	25	23	3	—	—	—	—
forgeti	—	—	—	20	5	—	—	—	—	—
mulleri	—	—	—	—	1	4	5	—	—	—
gracilis	—	—	—	—	3	2	—	—	—	—
crawfordi	—	—	—	—	—	3	5	—	—	—
tutini	—	—	—	—	—	—	4	—	—	—
incae	—	—	—	—	—	3	4	—	—	—
luteus	—	—	—	—	—	1	2	3	2	2
rotundipinnis	—	—	—	—	—	—	3	2	—	—
farfani	—	—	—	—	—	—	1	1	—	—
albus	—	—	—	—	—	—	—	—	3	2
olivaceus	—	—	—	—	1	—	—	4	—	—
silustani	—	—	—	—	2	1	3	1	—	—
agassii	—	—	—	6	10	7	2	1	—	—
empyraeus	—	—	—	1	1	4	2	1	—	—
frontosus	—	—	—	1	3	—	—	—	—	—
polonorum	—	—	—	3	2	—	—	—	—	—
elegans	—	—	—	—	—	5	3	—	—	—
jussiei	—	—	—	—	—	2	6	—	—	—
puni	—	—	—	—	—	—	2	2	—	—
parinacotensis	—	—	x········	········	········	········	········x[a]	—	—	—
laucaensis	—	—	—	x········	········	········	········x[a]	—	—	—
tschudii	—	—	—	—	4	2	—	—	—	—
gymnotus	—	—	1	3	5	1	—	—	—	—
hardini	—	—	—	—	2	2	3	—	—	—
ctenolepis	—	—	—	3	6	—	—	—	—	—
ascotanensis	—	—	—	—	—	1	7	4	—	—
richersoni	—	—	—	—	5	—	—	—	—	—
multiporis	—	—	—	1	7	2	—	—	—	—
mundus	—	—	—	—	1	4	5	—	—	—
ututo	—	—	—	2	2	2	—	—	—	—
gilsoni	—	—	—	—	1	4	3	—	—	—
taquiri	—	—	—	—	1	1	3	—	—	—
mooni	—	—	—	—	5	2	2	—	—	—
uruni	—	—	—	—	1	2	2	—	—	—
minimus	—	—	—	—	—	—	1	—	—	—
minutus	—	—	—	—	1	1	—	—	—	—
tchernavini	—	—	—	7	27	3	—	—	—	—
imarpe	—	—	—	—	—	3	1	1	—	—
tomcooni	—	—	—	5	1	—	—	—	—	—
robustus	—	—	—	—	2	—	4	—	—	—

[a] These data are taken from Arratia (1982) in which head length was presented as a range, rather than a frequency distribution.

TABLE 9

Frequency Distribution of Width of the Head in *Orestias*
(expressed in thousandths of Standard Length)

	Class Intervals of Head Width										
Species	110–129	130–159	160–189	190–209	210–229	230–259	260–289	290–319	320–349	350–379	380–409
cuvieri	2	1	1	2	2	—	—	—	—	—	—
pentlandii	1	2	2	—	—	—	—	—	—	—	—
ispi	2	3	2	—	—	—	—	—	—	—	—
forgeti	1	3	3	—	—	—	—	—	—	—	—
mulleri	—	—	5	3	—	—	—	—	—	—	—
gracilis	1	3	—	—	—	—	—	—	—	—	—
crawfordi	—	—	—	—	7	2	—	—	—	—	—
tutini	—	—	2	1	1	—	—	—	—	—	—
incae	—	—	—	1	4	—	—	—	—	—	—
luteus	—	—	—	—	—	—	2	1	4	4	1
rotundipinnis	—	—	—	—	—	—	—	1	3	1	—
farfani	—	—	—	—	—	—	1	—	1	—	—
albus	—	—	—	—	—	2	3	—	—	—	—
olivaceus	—	—	1	—	—	2	2	—	—	—	—
silustani	—	—	2	5	1	—	—	—	—	—	—
agassii	—	9	15	4	—	—	—	—	—	—	—
empyraeus	—	2	3	3	—	—	—	—	—	—	—
frontosus	—	—	4	2	1	—	—	—	—	—	—
polonorum	—	2	3	—	—	—	—	—	—	—	—
elegans	—	5	2	—	—	—	—	—	—	—	—
jussiei	—	—	—	3	3	4	—	—	—	—	—
puni	—	—	—	—	—	—	2	—	—	—	—
parinacotensis	—	x	························	x[a]	—	—	—	—	—	—	—
laucaensis	—	x	························	x[a]	—	—	—	—	—	—	—
tschudii	—	—	4	1	1	—	—	—	—	—	—
gymnotus	3	4	2	—	—	—	—	—	—	—	—
hardini	—	—	7	—	—	—	—	—	—	—	—
ctenolepis	—	5	3	1	—	—	—	—	—	—	—
ascotanensis	—	1	2	4	3	—	—	—	—	—	—
richersoni	—	3	2	—	—	—	—	—	—	—	—
multiporis	—	1	9	—	—	—	—	—	—	—	—
mundus	—	1	5	5	—	—	—	—	—	—	—
ututo	—	—	5	1	—	—	—	—	—	—	—
gilsoni	—	—	—	7	1	—	—	—	—	—	—
taquiri	—	—	3	2	—	—	—	—	—	—	—
mooni	—	1	6	1	—	—	—	—	—	—	—
uruni	—	—	3	2	—	—	—	—	—	—	—
minimus	—	—	1	—	—	—	—	—	—	—	—
minutus	—	—	2	—	—	—	—	—	—	—	—
tchernavini	—	4	2	1	—	—	—	—	—	—	—
imarpe	—	—	1	4	—	—	—	—	—	—	—
tomcooni	2	2	—	—	—	—	—	—	—	—	—
robustus	—	—	1	3	2	—	—	—	—	—	—

[a] These data are taken from Arratia (1982) in which head width was presented as a range, rather than a frequency distribution.

TABLE 10
Frequency Distribution of Depth of the Body at Posterior Extent of the Head (expressed in thousandths of Standard Length)

	Class Intervals of Depth of Head								
Species	140–169	170–199	200–229	230–259	260–289	290–319	320–349	350–379	380–409
cuvieri	1	2	2	—	2	—	—	—	—
pentlandii	1	2	2	—	—	—	—	—	—
ispi	—	3	4	1	—	—	—	—	—
forgeti	—	1	4	3	—	—	—	—	—
mulleri	—	—	1	4	2	2	—	—	—
gracilis	—	1	3	—	—	—	—	—	—
crawfordi	—	—	—	—	2	2	5	—	—
tutini	—	—	—	—	3	1	—	—	—
incae	—	—	—	—	—	2	4	—	—
luteus	—	—	—	—	—	2	—	3	4
rotundipinnis	—	—	—	—	—	1	3	1	—
farfani	—	—	—	—	1	—	1	—	—
albus	—	—	—	—	—	3	4	—	—
olivaceus	—	—	—	1	—	3	1	—	—
silustani	—	—	—	—	4	2	1	—	—
agassii	—	1	6	9	10	2	1	—	—
empyraeus	—	—	—	4	2	1	—	—	—
frontosus	—	—	—	3	3	—	—	—	—
polonorum	—	—	1	2	2	—	—	—	—
elegans	—	—	5	2	1	—	—	—	—
jussiei	—	—	—	1	3	3	2	—	—
puni	—	—	—	—	—	—	1	2	1
parinacotensis	—	x……	…………	…………	…………	……x[a]	—	—	—
laucaensis	—	—	x……	…………	……x[a]	—	—	—	—
tschudii	—	—	—	3	4	1	—	—	—
gymnotus	—	—	4	5	—	—	—	—	—
hardini	—	—	5	2	—	—	—	—	—
ctenolepis	—	—	2	6	1	—	—	—	—
ascotanensis	—	—	1	3	3	4	—	—	—
richersoni	—	—	—	2	3	—	—	—	—
multiporis	—	—	3	7	—	—	—	—	—
mundus	—	—	1	4	5	—	—	—	—
ututo	—	—	2	3	1	—	—	—	—
gilsoni	—	—	2	5	2	—	—	—	—
taquiri	—	—	1	3	1	—	—	—	—
mooni	—	—	5	2	—	—	—	—	—
uruni	—	—	1	2	2	—	—	—	—
minimus	—	—	—	1	—	—	—	—	—
minutus	—	—	1	1	—	—	—	—	—
tchernavini	—	—	5	4	—	—	—	—	—
imarpe	—	—	—	4	1	—	—	—	—
tomcooni	—	1	2	1	—	—	—	—	—
robustus	—	—	1	1	4	—	—	—	—

[a] These data are taken from Arratia (1982) in which head depth was presented as a range, rather than a frequency distribution.

TABLE 11
Frequency Distribution of Depth of the Caudal Peduncle (expressed in thousandths of Standard Length)

Species	Class Intervals of Depth of Caudal Peduncle						
	050–074	075–099	100–124	125–149	150–174	175–199	200–224
cuvieri	—	1	3	2	—	—	—
pentlandii	—	3	2	—	—	—	—
ispi	—	26	21	2	—	—	—
forgeti	—	—	15	31	—	—	—
mulleri	—	—	1	6	1	—	—
gracilis	—	—	3	1	—	—	—
crawfordi	—	—	—	3	5	2	—
tutini	—	—	1	3	—	—	—
incae	—	—	1	1	1	4	—
luteus	—	—	—	—	3	3	2
rotundipinnis	—	—	—	—	1	3	—
farfani	—	—	—	—	1	1	—
albus	—	—	—	—	3	2	—
olivaceus	—	—	—	1	—	4	—
silustani	—	—	—	1	5	2	—
agassii	—	—	1	10	15	2	—
empyraeus	—	—	—	2	3	3	—
frontosus	—	—	1	1	5	—	—
polonorum	—	—	—	1	4	—	—
elegans	—	—	2	3	2	—	—
jussiei	—	—	—	1	4	1	—
puni	—	—	—	—	—	1	3
parinacotensis	—	—	x···········	···········	···········x[a]	—	—
laucaensis	—	—	—	x···········	···········x[a]	—	—
tschudii	—	—	1	2	2	—	—
gymnotus	—	2	3	4	—	—	—
hardini	—	—	1	6	—	—	—
ctenolepis	—	—	—	7	2	—	—
ascotanensis	—	—	—	3	5	2	—
richersoni	—	—	—	—	5	—	—
multiporis	—	—	—	4	6	—	—
mundus	—	—	—	2	5	1	—
ututo	—	—	1	2	2	1	—
gilsoni	—	7	2	—	—	—	—
taquiri	—	—	—	5	—	—	—
mooni	1	2	5	—	—	—	—
uruni	—	—	3	2	—	—	—
minimus	—	—	1	—	—	—	—
minutus	—	1	1	—	—	—	—
tchernavini	—	2	35	—	—	—	—
imarpe	—	—	1	4	—	—	—
tomcooni	—	1	2	1	—	—	—
robustus	—	—	2	4	—	—	—

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[a] These data are taken from Arratia (1982) in which depth of the caudal peduncle was given as a range, rather than a frequency distribution.

TABLE 12
Frequency Distribution of Preorbital Distance
(expressed in thousandths of Standard Length)

Species	Class Intervals of Preorbital Distance					
	020–039	040–059	060–079	080–099	100–119	120–139
cuvieri	—	—	—	2	3	3
pentlandii	—	2	4	—	—	—
ispi	—	—	3	4	1	—
forgeti	—	—	4	1	—	—
mulleri	—	—	5	4	—	—
gracilis	—	—	4	—	—	—
crawfordi	—	2	4	3	—	—
tutini	—	—	3	1	—	—
incae	—	—	—	4	2	—
luteus	—	2	4	4	—	—
rotundipinnis	—	—	2	1	—	—
farfani	—	—	2	—	—	—
albus	—	—	—	2	5	—
olivaceus	—	—	2	3	—	—
silustani	—	2	4	3	—	—
agassii	—	1	20	6	—	—
empyraeus	—	—	1	5	4	—
frontosus	—	—	4	2	—	—
polonorum	—	—	5	—	—	—
elegans	—	—	3	2	—	—
jussiei	—	—	4	5	—	—
puni	—	—	—	3	—	—
parinacotensis[a]	—	—	—	—	—	—
laucaensis[a]	—	—	—	—	—	—
tschudii	—	—	2	2	—	—
gymnotus	—	—	3	5	1	—
hardini	—	—	3	4	—	—
ctenolepis	—	—	9	—	—	—
ascotanensis	—	—	3	6	—	—
richersoni	—	1	4	—	—	—
multiporis	—	—	8	2	—	—
mundus	—	1	6	3	—	—
ututo	—	—	5	1	—	—
gilsoni	—	—	8	1	—	—
taquiri	—	—	2	2	1	—
mooni	—	—	5	2	—	—
uruni	—	—	4	1	—	—
minimus	—	—	—	1	—	—
minutus	—	1	—	1	—	—
tchernavini	3	2	—	—	—	—
imarpe	—	—	4	1	—	—
tomcooni	—	2	2	—	—	—
robustus	—	1	4	1	—	—

[a] No data available for these species.

species groups, and that obvious synapomorphies can be used to define groups of species; but, determination of polarity of increasing or decreasing modes is problematic.

MORPHOMETRIC CHARACTERS: Five additional characters that are useful for distinguishing among *Orestias* species and that are best described as morphometrics are:

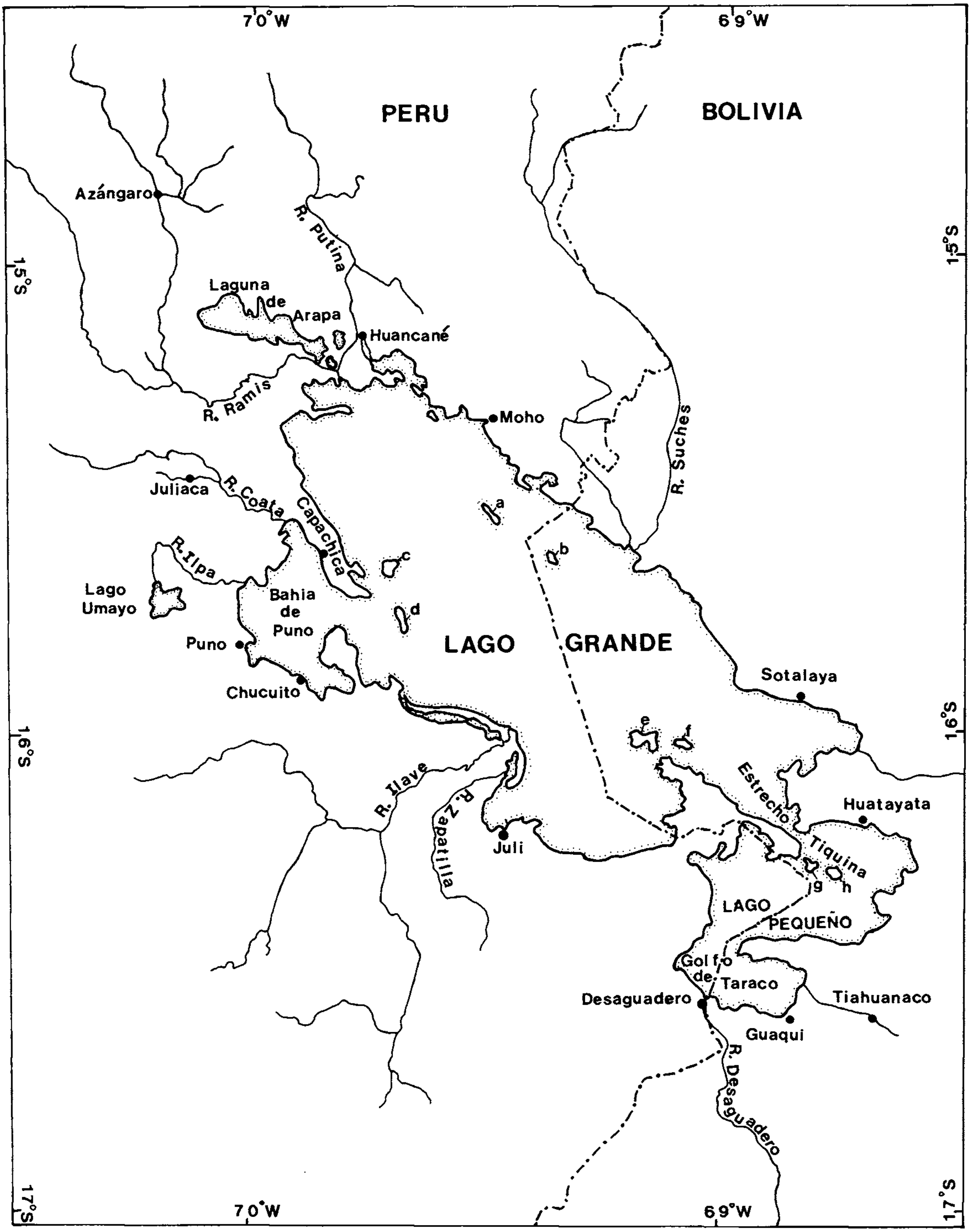

FIG. 22. Major divisions of Lago Titicaca, surrounding towns and tributaries. Labeled islands are: A. Soto, B. Chiquipa, C. Amantaní, D. Taquile, E. Titicaca, F. Coati, G. Taquiri, H. Paco.

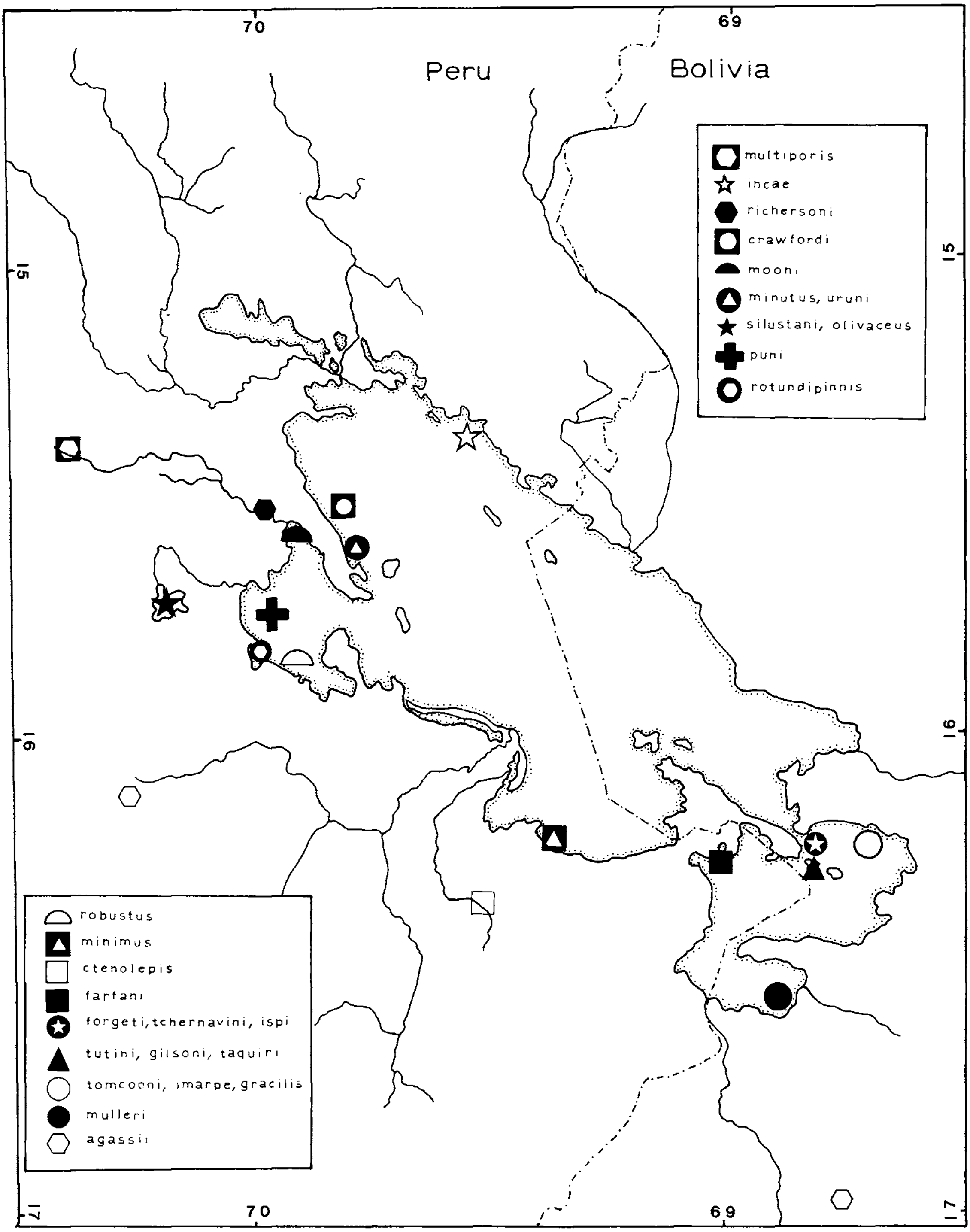

FIG. 23. Type localities within the Titicaca Basin. For names of sections of Lago Titicaca, towns, tributaries and islands, see figure 22. Not represented by a symbol because type locality is no more specific than "Lago Titicaca": *cuvieri, pentlandii, luteus, albus, tschudii,* and *frontosus.*

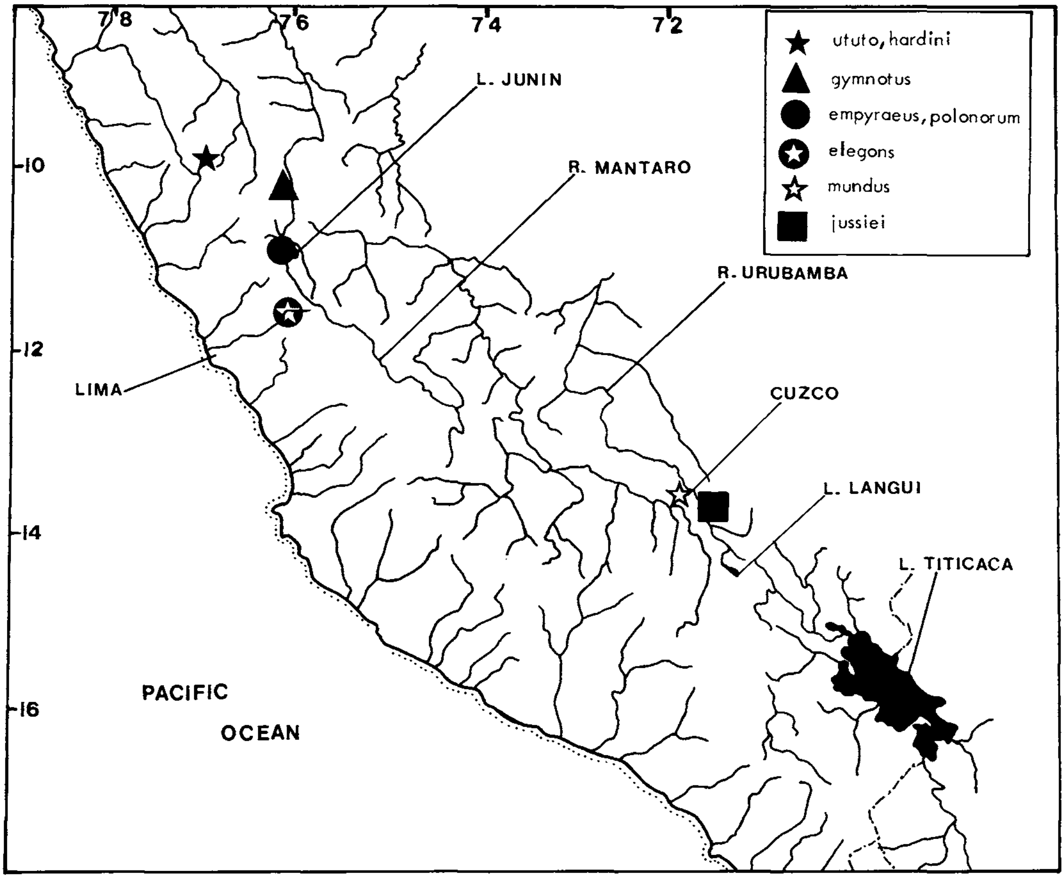

FIG. 24. Type localities north of the Titicaca Basin.

(1) length of the head, from tip of the lower jaw to the posterior extent of the operculum; (2) width of the head taken across the middle of the opercula; (3) depth of the body taken at the posterior margin of the operculum; (4) depth of the caudal peduncle; and (5) preorbital distance. The variation of these characters, expressed in terms of a sixth variable, SL, is summarized in tables 8 to 12, respectively. All are straight line measurements recorded with metric dial calipers.

Tchernavin (1944a, p. 147) pointed out that with an increase in size (i.e., SL) in *Orestias* species, there is an increase in the depth of the caudal peduncle, length of the head, width of the head, length of the snout and correlated changes in a variety of other morphometric characters. This is true as a general statement; however, morphometric characters are used as synapomorphies of species groups because, as will be discussed, all of these characters are not correlated.

The head is very large reaching nearly 40 percent of SL in four species: *cuvieri* of the *cuvier* complex and *luteus, rotundipinnis* and *albus* of the *agassii* complex (table 8). This character is autapomorphous for *cuvieri* and for *albus,* and an additional synapomorphic character of the two sister species, *luteus* and *rotundipinnis.*

The head (table 9) of the three species, *luteus, rotundipinnis,* and *farfani,* attains a width of over 34 percent of SL. In some individuals of *luteus,* the head is wider than it is long. Two other species of the *luteus* group (*olivaceus* and *albus*) have heads that are wider on the average than other *Orestias* but not so wide as in the three aforementioned species.

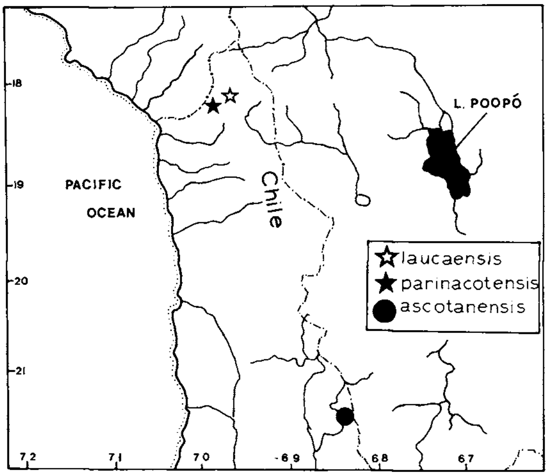

FIG. 25. Type localities in Chile.

A comparison of tables 8 and 9, shows that length of the head is not correlated with width of the head, as *cuvieri* has a head of average width.

Orestias luteus and *rotundipinnis* are extremely deep-bodied (table 10) as are three other species of the *luteus* group (*farfani, olivaceus,* and *albus*). Also, there is an increase in the depth of the body within the *mulleri* complex, with *crawfordi, tutini,* and *incae* reaching a depth of over 34 percent of SL. Being deep-bodied is also a synapomorphy of a group within the *agassii* complex; that is, species of the *luteus* group and *O. puni* and *jussiei.*

Depth of the body (table 10) is correlated in a number of species with depth of the caudal peduncle (table 11). On the average, all members of the *agassii* complex have a relatively deep caudal peduncle. A deep caudal peduncle occurs also in *crawfordi* and *incae,* two relatively deep-bodied species of the *mulleri* complex.

By comparison with *Kosswigichthys,* an elongate, narrow-bodied genus, the increase in depth of the body and of the caudal peduncle is most parsimoniously assessed as independently derived in the *mulleri* and in the *agassii* complexes.

The preorbital distance (from the tip of the lower jaw to the anterior rim of the orbit) reaches nearly 14 percent of SL in *cuvieri* (table 12). This derived character can also be described as an increase in the length of the lower jaw (fig. 32) which is the longest in the genus in *cuvieri.*

EXPLANATION OF SYNAPOMORPHY DIAGRAMS

A single diagram depicting the relationships and distribution of synapomorphic characters among the 43 species of *Orestias* would be a confusing and cumbersome figure. Therefore, six synapomorphy diagrams are presented: (1) a diagram of relationships among the four species complexes and the defining characters of each monophyletic complex (fig. 26); individual diagrams of relationship among, and the defining characters of species within, the (2) *cuvieri* complex (fig. 27), (3) *mulleri* complex (fig. 28), (4) *gilsoni* complex (fig. 29), (5) *agassii* complex, excluding species of the *luteus* group (fig. 30), and (6) *luteus* group (fig. 31).

The numbering of synapomorphic characters continues in sequence from figure 2, in which the 20 characters used in discussing relationships of cyprinodontids are numbered 1 through 20, and the seven defining characters of *Orestias* are numbered 21 through 27.

The following synapomorphies are those described in detail in the previous section, or are additional, newly described data, supplemented by data from Allen, in Eigenmann and Allen (1942), Tchernavin (1944a, 1946), Lauzanne (1981), and Arratia (1982).

RELATIONSHIPS AMONG THE FOUR SPECIES COMPLEXES (fig. 26): The *cuvieri, mulleri,* and *gilsoni* complexes together form a monophyletic group defined by three synapomorphies.

(28) Epipleural ribs are strongly bifid in adults, as opposed to being simple in the *agassii* complex. In just one species of these three complexes, *forgeti,* the ribs are only weakly bifid.

(29) Lateral ethmoids are relatively far apart (fig. 21B), rather than being close to the parasphenoid (fig. 21A), and their medial extensions do not meet or pass dorsal to the anterior ramus of the parasphenoid. Some species of the *agassii* complex (e.g., *hardini*)

approach the latter condition; their phylogenetic position will be discussed along with the relationships within that complex.

(30) There is no marked ontogenetic change in color pattern, with adults showing little or no sexual dichromatism. (*Orestias mundus* of the *agassii* complex is defined by its uniform, light brown color with a dark median line in all specimens examined. However, because of the inferred relationships of *mundus* to other *agassii* complex species, the pattern is considered to be independently derived in *mundus*.)

The *mulleri* and *gilsoni* complexes together share three synapomorphies.

(31) Orbits project dorsally above the primary dorsal profile of the head, and the eyes are much larger than in other complexes. To a certain degree, the eyes project more dorsally in the *gilsoni* complex, although the extent is difficult to quantify. Therefore, this possibly further derived state is not used as an additional defining character of the *gilsoni* complex.

(32) Longitudinal axis of base of anal fin not parallel to the vertebral column, but rather is angled anteriorly away from the body axis (fig. 4B), fin base projecting slightly beyond primary ventral profile, creating a distinct transition between abdomen and caudal peduncle.

(33) The second pharyngobranchial is reduced to a U-shaped bone, and bears a toothplate with few or no teeth (fig. 11).

Synapomorphies of Four Species Complexes

cuvieri complex

(34) The ventral branchial apparatus is elongate, including the basihyal which is narrow (fig. 15) rather than being triangular (fig. 13) or more rectangular (fig. 14), as in the three other complexes.

(35) Fifth ceratobranchials (lower pharyngeals) are narrow and very close together or fused along the midline in adults (fig. 15).

(36) Dorsal gill arches are reduced relative to the size of the ventral gill arches.

(37) Interarcual cartilage a long, thick rod, equal to or longer than the first epibranchial bone (fig. 10).

(38) There is an increase in the modal number of anal fin rays to 16 or 17, with an observed range of from 14 to 19. The modal number for the genus is 15 (table 5). The outgroup genus *Kosswigichthys* has 12 anal fin rays; therefore, the increase is considered to be derived within the *cuvieri* complex.

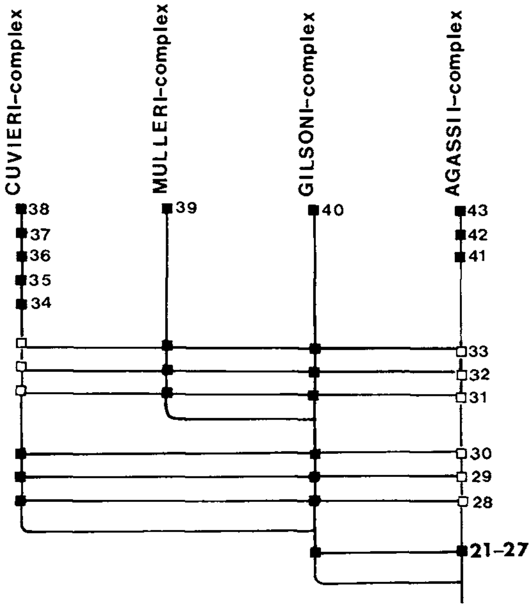

FIG. 26. Synapomorphy diagram of *cuvieri, mulleri, gilsoni* and *agassii* complexes. Characters are numbered as those in the text. Black squares represent synapomorphies, open squares symplesiomorphies.

mulleri complex

(39) Base of the dorsal as well as that of the anal fin projects beyond the primary body profile (figs. 36 to 40), and usually covered with small, thin scales.

gilsoni complex

(40) The procurrent caudal fin rays lie mostly interior to the body profile and therefore closer to the vertebral column (fig. 18A), giving the caudal fin a tapered external appearance.

agassii complex

(41) Lateral scales, from the operculum to a point at about the posterior extent of the pectoral fin, are enlarged with concentric striae absent or present to a limited degree. This so-called lateral shield is present in a modified form in *gymnotus, elegans, ascotanensis, parinacotensis,* and *laucaensis* as well as *uturo, hardini,* and *mundus*. These modifica-

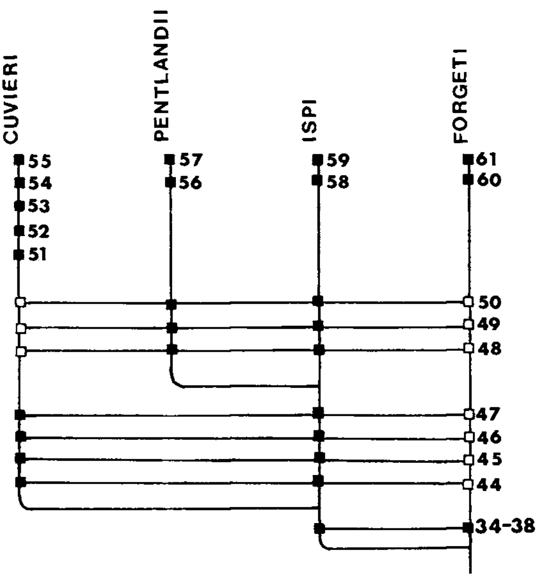

FIG. 27. Synapomorphy diagram of species of *cuvieri* complex. Characters are numbered as those in the text. Black squares represent synapomorphies, open squares symplesiomorphies.

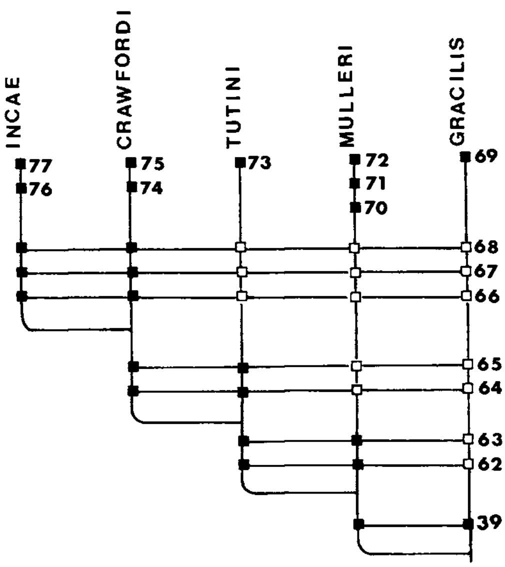

FIG. 28. Synapomorphy diagram of species of the *mulleri* complex. Characters are numbered as those in the text. Black squares represent synapomorphies, open squares symplesiomorphies.

tions are discussed in the explanation of the *agassii* complex synapomorphy diagram (fig. 30).

(42) Caudal peduncle is relatively deep in adults, reaching over 22 percent of SL. (There is an increase in the depth of the caudal peduncle in two sister species of the *mulleri* complex, *incae* and *crawfordi,* which is assessed as an independently derived character because of those species' close relationship to the other species of the *mulleri* and *gilsoni* complexes.)

(43) Scales on dorsal portion of head, particularly those of the median ridge, enlarged, and usually with no or few discernible concentric striae. A similar condition is found in some large adults of *cuvieri* and *pentlandii,* although rarely in the latter species. Also, in these two large species of the *cuvieri* complex the dorsal scales are never as large relative to those lateral to the median dorsal ridge as in the *agassii* complex. In *ispi* and *forgeti* and species of the *mulleri* and *gilsoni* complexes, a median dorsal ridge is distinguishable, yet these scales are not thickened, nor smooth or granulated. Therefore, the large, smooth scales of the *agassii* complex is considered as another of its synapomorphic features.

Relationships among species of the *cuvieri* complex (fig. 27): The four species of the *cuvieri* complex (*cuvieri, pentlandii, ispi,* and *forgeti*) are defined as a monophyletic group by the five synapomorhies (characters 34 through 38) discussed above for figure 26.

Orestias cuvieri, pentlandii, and *ispi* form a monophyletic group defined by four synapomorphies.

(44) There is an increased modal number of scales in a lateral series to 41 in *cuvieri,* 48 in *ispi,* and 57 in *pentlandii,* with an observed range of from 40 to 60 (table 7).

(45) Caudal fin is lunate, rather than rounded or truncate, and the caudal peduncle is constricted at the base of the caudal fin (figs. 32 to 34).

(46) Premaxilla with a blunt ascending process, and much wider in a lateral view and the S shape less pronounced (fig. 20B) than in other *Orestias* species (fig. 20A).

(47) Dentary is a robust bone that is constricted near its medial end (fig. 20B).

Orestias pentlandii and *ispi* are defined as sister species by three synapomorphies.

(48) There are few or no teeth in the outer jaw in adults (fig. 20B); juveniles almost always have a few simple teeth.

(49) There are six branchiostegal rays, with just one ray anterior to or in the notch on the anterior ceratohyal (fig. 6A).

(50) There is a further increase in the modal number of scales in a lateral series to 48 in *ispi* and 57 in *pentlandii,* with an observed range of from 41 to 60 (table 7).

Autapomorphies of the four species:

O. cuvieri

(51) Mouth is extremely large, and there are large, recurved unicuspid outer jaw teeth (fig. 32).

(52) There is an increase in the modal number of vertebrae to 34 with an observed range of from 33 to 35 (table 3).

(53) The head is relatively long, its length reaching nearly 40 percent of SL (table 8).

(54) Preorbital distance is greater than in all other *Orestias,* reaching nearly 14 percent of SL (table 12).

(55) This is the largest species in the genus, attaining an observed maximum SL of 220 mm.

O. pentlandii

(56) There is an increased modal number of vertebrae to 37, with an observed range of from 36 to 38 (table 3).

(57) There is a further increase in the number of scales in a lateral series, with a modal number of 57 and an observed range of from 51 to 60 (table 7).

O. ispi

(58) The main axis of the lower jaw is at a 90-degree angle to the body axis.

(59) The body is fully scaled, with very small, thin, irregularly distributed scales.

O. forgeti

(60) There is an increase in the modal number of pectoral fin rays to 19, with an observed range of from 18 to 20 (table 6).

(61) The body is fully scaled with relatively small, thin scales, but not as small as those of *ispi.*

Relationships among species of the *mulleri* complex (fig. 28): The five species of the *mulleri* complex (*gracilis, mulleri, tutini, crawfordi,* and *incae*) are defined as a monophyletic group by character 39, base of the dorsal as well as that of the anal fin extends beyond the primary dorsal and ventral profiles, respectively.

Orestias mulleri, tutini, crawfordi, and *incae* form a monophyletic group defined by two synapomorphies.

(62) There is an increase in the depth of the body to 23 percent or more of SL (table 10).

(63) Body is fully scaled with thin, small scales, except in *tutini* which, although possessing small, thin scales, is not fully scaled. It is impossible to determine whether the state in *tutini* represents the primitive condition, or if *tutini* has secondarily lost scales.

Orestias tutini, crawfordi, and *incae* form a monophyletic group defined by two synapomorphies.

(64) There is a further increase in the depth of the body to over 26 percent of SL (table 10).

(65) The body is laterally compressed, rather than being relatively fusiform.

Orestias crawfordi and *incae* are defined as sister species by three synapomorphies.

(66) There is an increase in the modal number of dorsal fin rays to 16 in *crawfordi,* with an observed range of from 15 to 18, and to 17 in *incae,* with an observed range of from 14 to 18 (table 4).

(67) The depth of the caudal peduncle is increased to 15 percent or more of SL (table 11).

(68) Pharyngeal teeth are molariform (fig. 11), although they are consistently broader and more blunt in the lower pharyngeals of *crawfordi* (fig. 16).

Autapomorphies of the five species:

O. gracilis

(69) The modal number of pectoral fin rays is reduced to 15, with an observed range of from 14 to 15, as opposed to a modal number of 17 for the genus (table 6).

O. mulleri

(70) The modal number of scales in a lateral series is increased to 36, with an observed range of from 33 to 38 (table 7).

(71) Maximum SL obtained (92 mm) is the

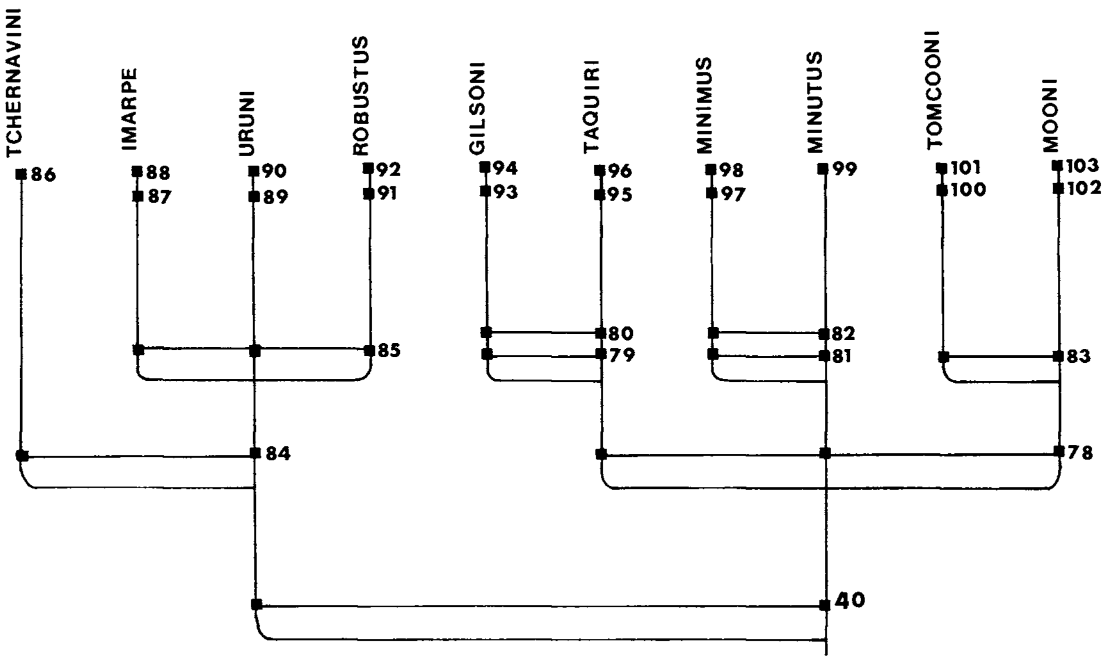

FIG. 29. Synapomorphy diagram of species of *gilsoni* complex. Characters are numbered as those in the text. Black squares represent synapomorphies.

greatest within the *mulleri* and *gilsoni* complexes.

(72) The modal number of anal fin rays is reduced to 13, with an observed range of from 12 to 15 (table 5).

O. tutini

(73) Dorsal surface of the head, and operculum of males with fleshy, tubercle-like projections, covering the ctenii of underlying scales. Basal portion of dorsal, anal, and pectoral fins, and either side of median dorsal ridge unscaled; all scales of males apparently ctenoid (all specimens partially descaled).

O. crawfordi

(74) Fourth epibranchial bone with a huge lateral flange (figs. 11 and 12), and associated large adductor IV that fills the cupped surface of the bone.

(75) Pharyngeal teeth (fig. 16) are consistently broader and therefore may be described as more molariform than in *incae.*

O. incae

(76) The most laterally compressed fishes in the genus *Orestias,* with the ventral surface of largest adults nearly keeled.

(77) Males with four to five irregular medium to dark brown bars on a lighter brown background; females with fainter bars (all specimens faded in preservation).

Relationships among species of the *gilsoni* complex (fig. 29): the 10 species of the *gilsoni* complex are defined as monophyletic by the unique structure of the caudal fin described as character 40 (fig. 26).

Before presenting the synapomorphies which describe the relationships among species of the *gilsoni* complex, a comment on several of the species is required. Two, *minutus* (fig. 68) and *minimus* (fig. 67) were described by Tchernavin (1944a) from two specimens each. The trivial names of both species are in reference to the small size of mature adults: *minimus* was described from two gravid females, 23.0 and 28.0 mm in SL; *minutus* was described from two gravid females, 24.0 and 28.0 mm. Tchernavin (1944a) assumed that adult males, if found, would be markedly smaller, following the trend exhibited by other *Orestias* species.

One problem with determining the uniqueness of maturity at a small size (i.e., SL) is that collections of other, apparently closely related species, also from the Percy Sladen Titicaca Expedition, were eviscerated for parasite study and their gender or state of sexual maturity cannot be determined. It is generally assumed that fishes decline in rate of increase of SL at maturity. However, this phenomenon should be further investigated with laboratory populations to determine its generality, especially in killifishes. Therefore, it is only tentatively that I accept the uniqueness of maturity at a small size in *minimus* and *minutus*.

Orestias gilsoni, taquiri, minimus, minutus, tomcooni, and *mooni* form a monophyletic group defined by one synapomorphy.

(78) Small fishes with an overall body shape characterized by a robust head and relatively narrow caudal peduncle (see tables 10 and 11) creating an abrupt transition between abdomen and caudal peduncle.

Orestias gilsoni and *taquiri* are defined as sister species by two synapomorphies.

(70) There is an increase in the modal number of pectoral fin rays to 17 or 18, with an observed range of from 16 to 19 (table 6).

(80) Pigmentation pattern characterized by a silvery background with from six to nine irregular bars (see figs. 63 and 64).

Orestias minimus and *minutus* are defined as sister species by two synapomorphies.

(81) Maturity of adults (only females known) is reached at a small size (23.0 mm SL in *minimus* and 24.0 mm SL in *minutus*).

(82) There is a reduction in the number of scales in a lateral series to 30 or less (*minimus* is unscaled; table 7).

Orestias tomcooni and *mooni* are defined as sister species by one synapomorphy.

(83) Main axis of lower jaw is at an abrupt (nearly 90-degree) angle to the body axis.

Orestias tchernavini, imarpe, uruni, and *robustus* form a monophyletic group defined by one synapomorphy.

(84) Pigmentation pattern is characterized by a light cream to yellow background covered with dark melanophores arranged in a distinctive marbled pattern (figs. 66, 69, 70, and 72).

Orestrias imarpe, uruni, and *robustus* form a monophyletic group defined by one synapomorphy.

(85) Robust body, with the depth of the caudal peduncle reaching nearly 15 percent of SL (table 11).

Autapomorphies of the 10 species:

Orestias tchernavini

(86) The head is relatively laterally compressed, with a width as low as 13 percent of SL (table 9).

O. imarpe

(87) Lips thick and fleshy (fig. 70).

(88) There is a reduction to 11, in the modal number of dorsal fin rays, with an observed range of from 10 to 14 (table 4).

O. uruni

(89) Basal portion of the pectoral fin is at the posterior margin of the operculum which obscures the pectoral fin base, rather than being farther posterior, hence separated from the operculum and exposing the pectoral fin base.

(90) Anal pouch and papilla are much reduced or absent.

O. robustus

(91) Body very robust overall; width of the head reaches nearly 23 percent of SL (table 9).

(92) There is a gentle rise in the dorsal profile from the tip of the snout to the base of the dorsal fin, and a gentle downward slope in the ventral profile from the tip of the lower jaw to the base of the anal fin (fig. 72).

O. gilsoni

(93) The head is relatively wide and greatly flattened dorsally, its width reaching nearly 23 percent of SL (table 9).

(94) Caudal peduncle is relatively narrow; its depth is less than 10 percent of SL in most specimens (table 11).

O. taquiri

(95) There is a reduction to 12 in the modal number of dorsal fin rays, with an observed range of from 11 to 14 (table 4).

(96) There is a reduction in the modal number of vertebrae to 30, as opposed to a mode of 32 for the genus as a whole, and a modal number of 31 for the *gilsoni* complex with an observed range of from 30 to 31 (table 3).

O. minimus

(97) The body is totally unscaled.

(98) There is a reduction in the modal number of vertebrae to 30 (see character 96 above for *O. taquiri*).

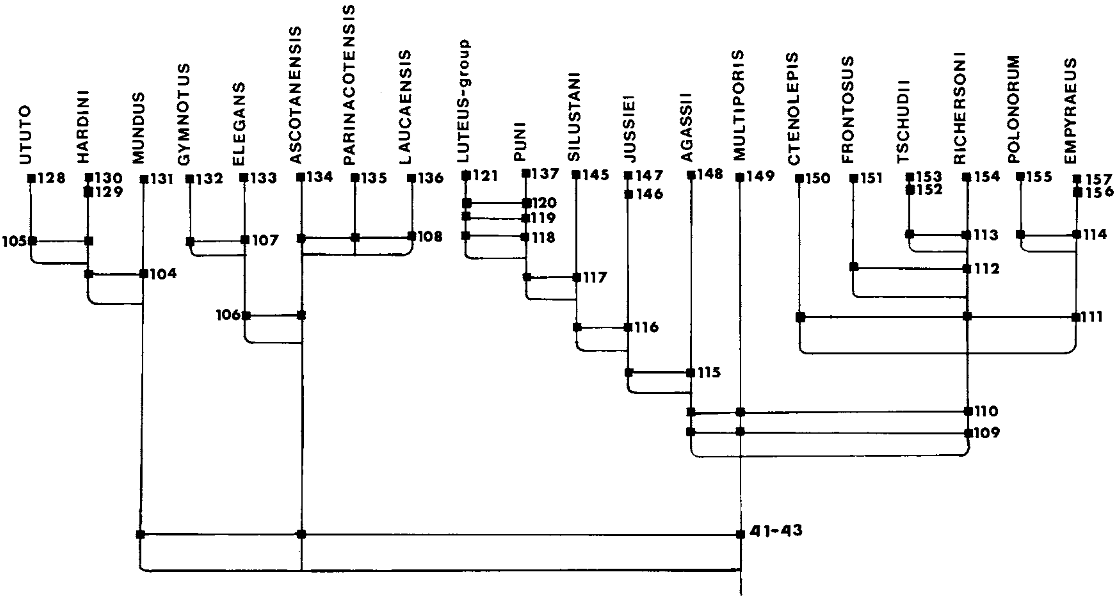

FIG. 30. Synapomorphy diagram of species of *agassii* complex. For relationships within the *luteus* group, see figure 31. Characters are numbered as those in the text. Black squares represent synapomorphies.

O. minutus

(99) There is an increase in the number of anal fin rays to 16 or 17, as opposed to a mode of 15 (table 5).

O. tomcooni

(100) The modal number of scales in a lateral series is increased to 37, with an observed range of from 36 to 38 (table 7).

(101) Distinctive body shape characterized by a relatively narrow (table 9) and deep head (table 10), with an even more abrupt transition between the anterior part of the body and the caudal peduncle (fig. 71) than is diagnostic of the group comprising *gilsoni, taquiri, minimus, minutus, tomcooni,* and *mooni.*

O. mooni

(102) A fully scaled species, with very small, thin irregularly distributed scales covering the ventrum and the basal portion of the pectoral, dorsal, and anal fins.

(103) There is an increase in the modal number of vertebrae to 32 or 33, with an observed range of from 32 to 34 (table 3).

Relationships among species of the *agassii* complex (figs. 30 and 31); the fishes of the *agassii* complex are defined as a monophyletic group by the three synapomorphies discussed for figure 26 (characters 41 through 43).

Species of the *agassii* complex are divided into three groups on the basis of squamation patterns described below. Each pattern is assessed as a uniquely derived condition, and therefore as a defining character for one of the three groups. The patterns do not appear to be part of a recognizable transition series, although further data on ontogeny of squamation patterns might lead to a resolution of the trichotomy at the base of the cladogram of figure 30, by supporting a transition series hypothesis for these characters.

Orestias ututo, hardini, and *mundus* form a monophyletic group defined by one synapomorphy.

(104) Lateral scales, those of the so-called lateral shield, are larger than surrounding scales more so than in other *agassii* complex species. Lateral shield scales overlap to a great degree, such that only the posterior margins of scales are visible.

Orestias ututo and *hardini* are defined as sister species by one synapomorphy.

(105) There is a decrease in the modal number of dorsal fin rays to 10 in *ututo* and 11 in *hardini,* with an observed range in both of from 10 to 12 (table 4).

Orestias gymnotus, elegans, ascotanensis, parinacotensis, and *laucaensis* form a monophyletic group defined by one synapomorphy.

(106) Body irregularly scaled, and in a particular pattern. Unique characteristics of the pattern concern the configuration of the lateral scales: from the posttemporal, scales run posteriorly in one or two uneven rows. The number of scale rows increases posteriorly to become a series of approximately four to five rows at the base of the caudal fin. Dorsal scales may be irregularly and sparsely distributed. Typically, there are no scales beneath the pectoral fin (fig. 55). (Specimens of *parinacotensis* and *laucaensis* have not been examined; a description of these species' irregular squamation pattern [Arratia, 1982] agrees in many respects with that given above, although is not complete enough to determine if the pattern is identical with that of *gymnotus, elegans* or *ascotanensis.* See Systematic Accounts for further remarks.)

Orestias gymnotus and *elegans* are defined as sister species by one synapomorphy.

(107) Body relatively elongate, with a correspondingly relatively slender body, the depth of which is as low as 20 percent of SL (table 10).

Orestias ascotanensis, parinacotensis, and *laucaensis* are defined as a monophyletic group by one synapomorphy.

(108) Extent of squamation sexually dimorphic, with females tending to be more fully scaled than males; *O. ascotanensis* females, for example, have several complete lateral scale rows, whereas males have one row anteriorly, and several posteriorly.

Orestias jussiei, puni, agassii, silustani, multiporis, luteus, farfani, rotundipinnis, albus, olivaceus, ctenolepis, frontosus, tschudii, richersoni, polonorum, and *empyraeus* form a monophyletic group defined by two synapomorphies.

(109) Anterior ribs become enlarged and swollen with age (i.e., with increased SL) to create rather wide-bodied individuals (see figs. 7 and 8).

(110) Scales on dorsal surface of head, as well as lateral body scales, enlarged and thickened, especially in larger individuals, with few or no concentric striae, not overlapping in larger individuals and usually interdigitating along their perimeters. Lateral scales may have scattered flecks of dark pigment (e.g., fig. 48). These head and lateral scales cannot be removed easily, and give these fishes an armored appearance.

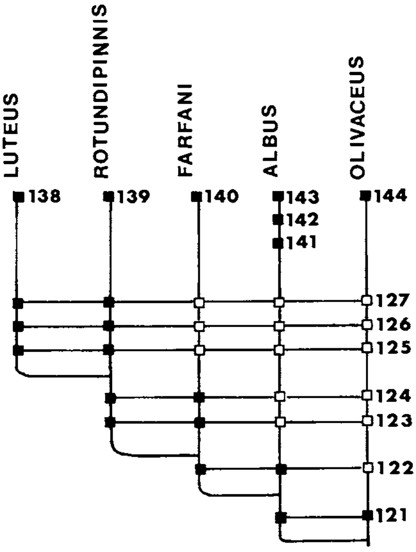

FIG. 31. Synapomorphy diagram of species of *luteus* group of the *agassii* complex. Characters are numbered as those in the text. Black squares represent synapomorphies.

Orestias ctenolepis, frontosus, tschudii, richersoni, polonorum, and *empyraeus* form a monophyletic group defined by one synapomorphy.

(111) Pigmentation pattern characterized by a dark band at the base of the dorsal, anal and particularly the pectoral fin rays (see, e.g., fig. 46). Pigments are not stable and are barely discernible in specimens that have been preserved for a long period of time.

Orestias frontosus, tschudii, and *richersoni* form a monophyletic group defined by one synapomorphy.

(112) The modal number of dorsal fin rays is increased to 15 or 16, with an observed range of from 14 to 17 (table 4).

Orestias tschudii and *richersoni* are defined as sister species by one synapomorphy.

(113) Body laterally compressed, especially posterior to the origin of the dorsal fin.

Orestias polonorum and *empyraeus* are defined as sister species by one synapomorphy.

(114) Median dorsal ridge extremely irregular and incomplete, formed by small, smooth scales.

Orestias agassii, jussiei, silustani, puni, olivaceus, albus, rotundipinnis, farfani, and *luteus* (the last five species forming the *luteus* group) form a monophyletic group defined by one synapomorphy.

(115) In the largest adults, depth of the body reaches nearly 35 percent of SL (table 10), and is typically more than 29 percent. (However, *agassii* is a variable species, and large adults are not represented in all collections. See Systematic Accounts for further remarks.)

Orestias jussiei, silustani, puni, olivaceus, albus, farfani, rotundipinnis, and *luteus* form a less inclusive monophyletic group defined by one synapomorphy.

(116) Width of the head is on the average 19 percent or more of SL (table 9). (*Orestias puni, jussiei, silustani,* and *olivaceus* do not have the pronounced shoulders of *albus, farfani, rotundipinnis,* and *luteus*; this character easily separates the wide-bodied species. See character 122, below.)

Orestias silustani, puni, olivaceus, albus, farfani, rotundipinnis, and *luteus* form a less inclusive monophyletic group defined by one synapomorphy.

(117) Pectoral fins are relatively large, the modal number of fin rays is increased to 20, with an observed range of from 18 to 22 (table 6).

Orestias puni, olivaceus, albus, farfani, rotundipinnis, and *luteus* form a less inclusive monophyletic group defined by three synapomorphies.

(118) Dorsal profile is arched just posterior to the head (figs. 7, 41 through 44) creating an abrupt transition, in the dorsal profile, between the head and body.

(119) Body is relatively deep, reaching a depth of just over 40 percent of SL (table 10).

(120) Head is relatively wide, reaching a width of over 28 percent of SL in *puni, albus,* and *olivaceus,* and more than 34 percent of SL in *farfani, rotundipinnis,* and *luteus* (table 9).

Orestias olivaceus, albus, farfani, rotundipinnis, and *luteus* (the *luteus* group; fig. 31) form a less inclusive monophyletic group defined by one synapomorphy.

(121) Scales from the snout to the base of the dorsal fin, the preopercular and opercular regions, and dorsal to the pectoral fin are thick, and covered with dense granulations (fig. 7).

Orestias albus, farfani, rotundipinnis, and *luteus* form a less inclusive monophyletic group defined by one synapomorphy.

(122) Head at a point just dorsal to the operculum is swollen; that is, the scales are extremely large and thick, and give the body a rather angular appearance (fig. 8). This swelling is slightly less pronounced in young individuals, particularly those of *albus.*

Orestias farfani, rotundipinnis, and *luteus* form a monophyletic group defined by two synapomorphies.

(123) Head is very wide, reaching a width of more than 34 percent of SL (table 9).

(124) Scales on the operculum are thick and granulated, such that the operculum appears to be swollen, and arched slightly away from the head (fig. 8).

Orestias rotundipinnis and *luteus* are defined as sister species by three synapomorphies.

(125) Head is wider than in any other two *Orestias* species, reaching nearly 38 percent of SL in *rotundipinnis,* and 41 percent of SL in *luteus* (table 9).

(126) Pharyngeal teeth are molariform, with large, rounded cusps. (The state of this character is questionable in *farfani.*)

(127) Fifth ceratobranchials (lower pharyngeals) are closely apposed, although not fused.

Autapomorphies of each of the 24 species:

O. ututo

(128) There is a decrease in the modal number of anal fin rays to 11, with an observed range of from 10 to 12 (table 5).

O. hardini

(129) When a complete series of scales in a lateral series is present, there is an increase in the number to a range of from 36 to 38 (table 7).

(130) Squamation incomplete, with dorsal surface of some specimens, and ventral sur-

face of all specimens, devoid of scales. Lateral series often incomplete.

O. mundus

(131) Juveniles through adults all uniformly light brown, with a thin, median dark line through scales of the lateral series.

O. gymnotus

(132) Body narrow and elongate, nearly fusiform in largest adults (fig. 55) as exemplified by a relatively narrow head, width nearly as low as 10 percent of SL (table 9), as well as a low depth of the body (table 10).

O. elegans

(133) There is an increase to 35 or 36 in the modal number of scales in a lateral series, with an observed range of from 34 to 38 (table 7).

O. ascotanensis

(134) A robust species, with a relatively long head, reaching nearly 35 percent of SL (table 8).

O. parinacotensis

(135) Straight dorsal head profile and head greatly flattened in both males and females (fig. 52).

O. laucaensis

(136) Diploid number of chromosomes is increased to 52 in males and 50 or 51 in females, as opposed to a plesiomorphic diploid number of 48 in males and females (Arratia, 1982).

O. puni

(137) Caudal peduncle is very deep, reaching a depth of more than 22 percent of SL (table 11; see also fig. 51).

O. luteus

(138) Wide-headed (width of head reaching more than 40 percent of SL; table 9), with a relatively long head, reaching nearly 40 percent of SL (table 8). Some individuals are known which have heads wider than long.

O. rotundipinnis

(139) Pectoral fins nearly perfectly rounded, rather than with elongate middle rays (fig. 41).

O. farfani

(140) An elongate species of the *luteus* group with a relatively straight ventral profile, and correspondingly, a body that is not so deep as in *albus, rotundipinnis,* and *luteus* (table 10).

O. albus

(141) Lower jaw very robust, creating a prominent "chin" (fig. 43).

(142) Head relatively long, more than 35 percent of SL in adults (table 8).

(143) Dorsal body profile slopes very gently posteriorly, with no abrupt transition, from the anterior base of the dorsal fin to the base of the caudal fin, the rays of which flare out slightly at its base (fig. 43).

O. olivaceus

(144) Orbits are oriented dorsolaterally (fig. 44), such that in dorsal view, both orbits are nearly completely visible.

O. silustani

(145) Dorsal head and body profile very nearly straight from the tip of the snout to the anterior base of the dorsal fin (fig. 45).

O. jussiei

(146) Lower jaw is at a 90-degree angle to the body axis (fig. 50).

(147) Dorsal profile convex, rising very sharply from tip of snout to middle of median dorsal ridge (fig. 50).

O. agassii

(148) Head squamation irregular, usually with no head scales anterior to the orbit, and scales absent from either side of the median dorsal ridge in young individuals. (See Systematic Accounts for further remarks on the definition of this variable species.)

O. multiporis

(149) Neuromasts, often found in groupings of two or three, extend along the median dorsal ridge from top of the head to base of the dorsal fin. Scales in, and above and below, the lateral series with multiple neuromasts.

O. ctenolepis

(150) All but the scales of the lateral shield are ctenoid in males, with up to 10 ctenii per scale.

O. frontosus

(151) Snout blunt and head rounded (fig. 47) throughout all observed life stages.

O. tschudii

(152) There is an increased modal number of pectoral fin rays to 19, with an observed range of from 17 to 19 (table 6).

(153) There is an increased modal number of vertebrae to 34, with an observed range of from 33 to 35 (table 3).

O. richersoni

(154) Unique pigmentation pattern characterized by a black lower jaw margin, faint to jet black spot at dorsal margin of the operculum, and a faint to dark black band at base of the pectoral fin rays. Body a deep olive green dorsally with an iridescent background fading to light yellow-green ventrally.

O. polonorum

(155) Head rectangular in lateral view, with a straight dorsal profile and angular "chin" (fig. 48).

O. empyraeus

(156) Head, especially in larger adults, tapers toward mouth (fig. 46), with associated large preorbital distance (ranging between 8 and 12 percent of SL, table 12).

(157) Lips thick and fleshy in largest adults (fig. 46).

KEY TO *ORESTIAS* SPECIES

This key provides an aid to identification of species. It corresponds with the synapomorphy diagrams of figures 26 through 31. Synapomorphic and autapomorphic characters in the key bear the same number as those in the diagrams.

1A. (28) Epipleural ribs weakly to strongly bifid in adults; (29) lateral ethmoids relatively far apart (fig. 21B), and with medial extensions that do not meet or pass dorsal to anterior ramus of the parasphenoid; (30) no marked ontogenetic change in color pattern, with adults showing little or no sexual dichromatism; lateral scales not enlarged, not smooth, with or without granulations; dorsal head scales not enlarged, with or without granulations. 2A

2A. (34) Ventral branchial apparatus elongate, basihyal narrow (fig. 15); (35) fifth ceratobranchials narrow, very close together or fused along midline in adults, toothplates with numerous simple teeth; (36) dorsal gill arches reduced in size relative to ventral gill arches; (37) interarcual cartilage a long, thick rod, equal to or greater in length than first epibranchial bone (fig. 10); (38) modal number of anal fin rays 16 or 17 (table 5); orbits do not project dorsally above surface of head, eyes small to moderate; anal fin roughly parallel to vertebral column, fin base not extending beyond primary ventral profile; second pharyngobranchial bone robust, and with large toothplate bearing numerous simple teeth .... *cuvieri* complex. 3A

3A. (60) Modal number of pectoral fin rays 19; modal number of scales in lateral series 33, less than 40 scales; caudal fin truncate, caudal peduncle not constricted; premaxilla a narrow bone with pointed ascending process; dentary narrow, not constricted near medial end. Estrecho Tiquina, Lago Pequeño and Bahia de Puno .... *Orestias forgeti* Lauzanne

3B. Modal number of pectoral fin rays less than 19; (44) scales in lateral series 40 or more (table 7); (45) caudal fin lunate, caudal peduncle constricted at base of caudal fin; (46) premaxilla with blunt ascending process, bone wide in lateral view, S shape not pronounced; (47) dentary robust, constricted near its medial end (fig. 20B). 4A

4A. (48) Few or no teeth in outer jaws in adults, juveniles with a few, simple teeth; (49) 6 (rarely 5) branchiostegal rays, with just one ray anterior to or in notch on anterior ceratohyal; (50) modal number of pored scales in lateral series 48 or more (table 7); modal number of vertebrae 32 or 37, not with intermediate number of 34 or 35 (table 3); head not large, length less than 30 percent of SL (table 8); preorbital distance not reaching 12 percent of SL (table 12); moderate to large individuals, not more than 200 mm SL. 5A.

5A. (56) Modal number of vertebrae 37 (table 3); (57) scales in lateral series modally 57 (table 7); lower jaw not at 90-degree angle to body axis; ventrum and sometimes either side of median dorsal ridge unscaled. Lago Titicaca and the Cuzco Valley .... *Orestias pentlandii* Valenciennes

5B. Modal number of vertebrae 32 (table 3); scales in lateral series modally 48 (table 7); (58) lower jaw at 90-degree angle to body axis; (59) body fully scaled with very small, thin irregularly distributed scales. Estrecho Tiquina in Lago Pequeño, Isla Taquile in Bahia de Puno and the Capachica Peninsula .... *Orestias ispi* Lauzanne

4B. (51) Mouth large, enlarged, recurved unicuspid outer jaw teeth (fig. 32); five branchiostegal rays with just one ray anterior to or in notch on anterior ceratohyal; modal number of pored scales in lateral series 41 (table 7); (52) modal number of vertebrae 34 (table 3); (53) head large, reaching nearly 40 percent of SL (table 8); (54) preorbital distance reaching nearly 14 percent of SL (table 12); (55) largest fishes in genus *Orestias*, adults reaching 220 mm SL. Lago Titicaca .... *Orestias cuvieri* Valenciennes

2B. Ventral branchial apparatus not elongate, basihyal usually rectangular (fig. 14); fifth ceratobranchials moderate, close together but not fused in midline, dorsal gill arches not reduced; interarcual cartilage approximately one-half length of epibranchial bone (figs. 11 and 12); modal number of anal fin rays 14 or 15, rarely 16 or 17 (table 5); (31) orbits project dorsally above surface of head, eyes large; (32) anal fin angled anteriorly away from the body axis, fin base projecting slightly beyond primary ventral profile, creating a distinct transition between abdomen and caudal peduncle; (33) second pharyngobranchial reduced to a U-shaped bone, bears small toothplate with few or no teeth (fig. 11). 6A

6A. (39) Base of the dorsal as well as the anal fin projects beyond primary dorsal and ventral profile (figs. 36 to 40), usually covered with small, thin scales; procurrent caudal fin rays do not lie mostly interior to the body profile, and therefore not relatively close to the vertebral column (fig. 18B) .... *mulleri* complex

7A. (69) Modal number of pectoral fin rays 15 (table 5); narrow bodied, with depth less than 23 percent of SL (table 10); ventral surface and basal portion of dorsal, anal and pectoral fins unscaled. Huatayata, Lago Pequeño and Bahia de Puno .... *Orestias gracilis*, new species

7B. Modal number of pectoral fin rays more than 15 (table 5); (62) relatively deep bodied, depth of body 23 percent or more of SL (table 10); (63) body fully scaled, except in species with granulated dorsal scales. 8A

8A. (70) Modal number of scales in lateral series 36 (table 7); (71) largest fishes in *mulleri* and *gilsoni* complexes, reaching an SL of 92 mm; (72) modal number of anal fin rays 13 (table 5); depth of body usually less than 26 percent of SL (table 10); body relatively fusiform, not laterally compressed. Bahia de Moho, Lago Pequeño, Capachica Peninsula, and ?Bahia de Puno .... *Orestias mulleri* Valenciennes

8B. Modal number of scales in lateral series less than 36 (table 7); relatively small to medium-sized fishes, 79 mm greatest SL attained; modal number of anal fin rays greater than 13 (table 5); (64) depth of body reaching over 26 percent of SL (table 10); (65) body laterally compressed. 9A

9A. (73) Dorsal surface of the head and operculum of males with fleshy, tubercle-like projections covering ctenii of underlying scales, basal portion of dorsal, anal and pectoral fins, and either side of dorsal ridge unscaled, all scales of males apparently with ctenii; modal number of dorsal fin rays 12 or 13 (table 4); depth of caudal peduncle less than 15 percent of SL (table 11); pharyngeal teeth pointed. Isla Taquiri, Lago Pequeño .... *Orestias tutini* Tchernavin

9B. Fully scaled; (66) modal number of dorsal fin rays 16 or 17 (table 4); (67) depth of caudal peduncle 15 percent or more of SL (table 11); (68) pharyngeal teeth molariform (figs. 11 and 16). 10A

10A. (74) Fourth epibranchial bone with huge lateral flange (figs. 11 and 12), and associated large adductor IV that fills the cupped surface of the bone; (75) pharyngeal teeth consistently broad (fig. 16); no ventral keel; males and females with faintly mottled color pattern. Bahia de Puno and Bahia de Taman, on the Capachica Peninsula .... *Orestias crawfordi* Tchernavin

10B. Fourth epibranchial bone without huge flange, adductor IV not expanded; pharyngeal teeth molariform, but not as broad as in *crawfordi* (fig. 16); (76) most laterally compressed fishes in genus *Orestias*, ventral surface of adults nearly keeled; (77) males with four to five medium to dark brown bars on a lighter brown background, females with fainter bars (although all known specimens faded). Bahia de Moho and ?Bolivia .... *Orestias incae* Garman

6B. Base of dorsal fin does not extend beyond primary dorsal profile; (40) procurrent caudal fin rays lie mostly interior to the body profile, closer to vertebral column (fig. 18A) giving caudal fin a tapered external appearance .... *gilsoni* complex

11A. (78) Small fishes with overall body shape characterized by a robust head and relatively narrow caudal peduncle (tables 10 and 11) creating an abrupt transition between abdomen and caudal peduncle; pigmentation pattern either uniform overall or with barred pattern, but never with marbled pattern. 12A

12A. (79) Modal number of pectoral fin rays 17 or 18 (table 6); (90) pigmentation pattern characterized by silvery background with from six to nine irregular bars (figs. 63 and 64); sexual maturity reached at over 25.0 mm SL; scales in lateral series more than 30 (table 7); lower jaw not at right angle to body axis. 13A

13A. (93) Head relatively wide and greatly flattened dorsally, its width reaching nearly 23 percent of SL (table 9); (94) caudal peduncle relatively narrow, depth usually less than 10 percent of SL (table 11); modal number of dorsal fin rays 14 (table 4); modal number of vertebrae 32 (table 3). Isla Taquiri and off Tiahuanaco, Lago Pequeño.................. .... *Orestias gilsoni* Tchernavin

13B. Head not relatively wide or greatly flattened dorsally, width less than 21 percent of SL (table 9); caudal peduncle not extremely narrow, depth not less than 12.5 percent of SL (table 11); (95) modal number of dorsal fin rays 12 (table 4); (96) modal number of vertebrae 30 (table 3). Isla Taquiri, Lago Pequeño .... *Orestias taquiri* Tchernavin

12B. Modal number of pectoral fin rays less than 17 (table 6); pigmentation pattern uniformly pale overall; (81) sexual maturity reached at less than 25.0 mm SL; (82) scales in lateral series 30 or less (table 7); lower jaw not at right angle to body axis. 14A

14A. (97) Body unscaled; (98) modal number of vertebrae 30 (table 3); anal fin rays less than 16. Molinopampa and Sucuné, Lago Grande .... *Orestias minimus* Tchernavin

14B. Body incompletely scaled; modal number of vertebrae greater than 30; (99) number of anal fin rays 16 or 17 (table 5). Bahia de Uruni, Lago Grande .... *Orestias minutus* Tchernavin

12C. Modal number of pectoral fin rays less than 17 (table 6); pigmentation pattern with pale yellow background and dark melanophores overall; sexual maturity reached at over 25.0 mm SL; scales in a lateral series more than 30 (table 7); (83) lower jaw at abrupt (nearly 90-degree) angle to body axis. 15A

15A. (100) Modal number of scales in lateral series 37 (table 7); (101) distinctive body shape characterized by relatively narrow (table 9) and deep (table 10) head, with an even more abrupt transition between abdomen and caudal peduncle than diagnostic of group comprising *gilsoni, taquiri, minimus, minutus, tomcooni,* and *mooni*; ventrum and basal portion of pectoral, dorsal and anal fin unscaled; modal number of vertebrae less than 32 (table 3). Near villages of Huatayata and Vilurcuni, Lago Pequeño....... *Orestias tomcooni,* new species

15B. Modal number of scales in lateral series 32 (table 7); transition between abdomen and caudal peduncle not as great as in *tomcooni*; (102) body fully scaled; (103) modal number of vertebrae 32 or 33 (table 3). Bahia de Coata and Bahia de Taman, Lago Titicaca .... *Orestias mooni* Tchernavin

11B. Small to moderately sized fishes, with overall a relatively robust body and no abrupt transition between abdomen and caudal peduncle; (84) pigmentation pattern characterized by light cream to yellow background covered with dark melanophores arranged in a distinctive marbled pattern (figs. 66, 69, 70 and 72). 16A

16A. (86) Head relatively compressed laterally, width as low as 13 percent of SL (table 9); depth of caudal peduncle less than 12.5 percent of SL (table 11). Estrecho Tiquina, Lago Pequeño .... *Orestias tchernavini* Lauzanne

16B. Head not laterally compressed, its width 16 percent or more of SL (table 9); (85) robust body, depth of caudal peduncle reaching nearly 15 percent of SL (table 11). 17A

17A. (87) Lips thick and fleshy (fig. 70); (88) modal number of dorsal fin rays 11 (table 4); basal portion of pectoral fin exposed, not obscured by operculum; anal pouch and papilla cover base of first several anal fin rays; width of head less than 21 percent of SL (table 9); dorsal and ventral profile relatively straight, not arched gently. Bahia de Puno and Lago Pequeño .... *Orestias imarpe,* new species

17B. Lips thin, not thick and fleshy; modal number of dorsal fin rays 14 (table 4); (89) basal portion of pectoral fin meets posterior extent of operculum which obscures pectoral fin base; (90) anal pouch and papilla reduced or absent; width of head less than 21 percent of SL (table 9); dorsal and ventral profile relatively straight, not arched gently. Bahia de Uruni, Lago Grande .... *Orestias uruni* Tchernavin

17C. Lips thin, not thick and fleshy; modal number of dorsal fin rays 13 or 14 (table 4); basal portion of pectoral fin exposed, not obscured by operculum; anal pouch and papilla cover base of first several anal fin rays; (91) body very robust overall, width of head reaches nearly 23 percent of SL (table 9); (92) gentle rise in dorsal profile from tip of snout to base of dorsal fin, and gentle downward slope in ventral profile from tip of lower jaw to base of anal fin (fig. 72). Bahia de Puno, and the Capachica Peninsula ..... *Orestias robustus,* new species

1B. Epipleural ribs simple, not bifid; lateral ethmoids relatively close together (fig. 21A), and with medial extensions that usually meet or pass dorsal to the anterior ramus of the parasphenoid; except in one case (*mundus*), there is a marked ontogenetic change in color pattern, with juveniles and subadult females exhibiting a mottled pattern with a blotched median line and blotched dorsal and lateral surfaces and fins; adult females and subadult to adult males with near uniformly dark dorsal and lateral surfaces, light ventrum and relatively clear fins; (41) lateral scales, from operculum to a point at about the posterior extent of pectoral fin, large and smooth or granulated, forming a so-called lateral shield; (43) dorsal head scales; especially those of median dorsal ridge, enlarged and smooth or granulated, scales of median dorsal ridge large relative to those lateral to the ridge .... *agassii* complex

18A. (104) Lateral scales of the lateral shield larger than surrounding scales, overlapping to a great degree, such that only posterior margins of scales are visible; ventrum and basal portion of pectoral, dorsal and anal fins unscaled, otherwise scaled; anterior ribs not large and swollen, body not wide; scales of median dorsal ridge not smooth or granulated. 19A

19A. (131) Juveniles through adults all uniformly straw-colored to light brown overall, with a thin, median dark line on lateral surface; modal number of dorsal fin rays 13 (table 4). Cuzco, Peru ... . *Orestias mundus,* new species

19B. Individuals undergo ontogenetic change in pigmentation pattern such that juveniles have mottled pattern and adults are more uniformly colored; (105) modal number of dorsal fin rays 10 or 11. 20A

20A. (128) Modal number of anal fin rays 11 (table 5); modal number of scales in lateral series 33 (table 7); ventral surface and basal portion of pectoral, dorsal and anal fins unscaled. Lago Ututo, Peru .... *Orestias ututo,* new species

20B. Modal number of anal fin rays 12 (table 4); (129) when lateral series of scales complete, range 36 to 38 (table 7); (130) squamation often incomplete with dorsal surface sometimes, and ventral surface always, unscaled. Lagos Yanacocha and Llacsha, Peru .... *Orestias hardini,* new species

18B. (106) Body incompletely scaled in particular pattern: scales run posteriorly from the posttemporal in one or two uneven rows, number of rows increasing posteriorly to become a series of four to five rows at base of caudal fin; dorsal scales may be irregularly and sparsely distributed; anterior ribs not large and swollen, body not wide; scales of median dorsal ridge with few distinct concentric striae, no granulations. 21A

21A. (107) Body relatively slender and elongate, depth of body as low as 20 percent of SL (table 10); no sexual dimorphism in scale pattern or number. 22A

22A. (132) Body extremely narrow and elongate, nearly fusiform in largest adults, with narrow head, width nearly as low as 10 percent of SL (table 9); modal number of scales in lateral series 34 (table 7). Pasco Province, Peru .... *Orestias gymnotus,* new species

22B. Body narrow and elongate, but not nearly as fusiform as in *gymnotus,* width of head not less than 13 percent of SL (table 9); (133) modal number of scales in lateral series 35 or 36. Río Santa Eulalia, Peru .... *Orestias elegans* Garman

21B. Body not slender and elongate, not fusiform; (108) sexually dimorphic in that females tend to be more fully scaled than males. 23A

23A. (134) Robust species, with relatively long head, reaching nearly 35 percent of SL (table 8); males and females with convex dorsal profile; diploid number of chromosomes not known. Lago Ascotán, Chile .... *Orestias ascotanensis,* new species

23B. Head not relatively long, not reaching 32.5 percent of SL (table 8); (135) males and females have a straight dorsal profile, head greatly flattened; diploid number of chromosomes 48 in males and females. Bofedales de Parinacota, Chile .... *Orestias parinacotensis* Arratia

23C. Head not relatively long, not reaching 32.5 percent of SL; males and females with convex dorsal profile; (136) sexually dimorphic chromosome number, males with diploid chromosome number of 52, females with diploid chromosome number of 50 or 51. Río Lauca, Parinacota, Chile .... *Orestias laucaensis* Arratia

18C. (110) Dorsal head scales as well as lateral scales enlarged and thickened, with few or no concentric striae, not overlapping in larger individuals and usually interdigitating along their perimeters, scales cannot be removed easily, giving these fishes an armored appearance, lateral scales with scattered flecks of dark pigment; (109) anterior ribs enlarged and swollen in wide-bodied, large adults. 24A

24A. (111) Pigmentation pattern characterized by dark band at base of dorsal, anal and pectoral fin rays, in which band is most prominent; neuromasts in and above and below lateral series single, not in groupings of two or more; body not relatively deep, depth typically less than 29 percent of SL (table 10). 25A

25A. (150) All but scales of lateral shield ctenoid in males, with up to 10 ctenii per scale; modal number of dorsal fin rays 14 (table 4); median dorsal ridge and scales on either side of ridge present and ctenoid in males. Río Zapatilla, Peru .... *Orestias ctenolepis,* new species

25B. Scales of males not extremely ctenoid, if ctenii present, with just a few ctenii per scale only on lateral and posterior scales; (112) modal number of dorsal fin rays 15 or 16 (table 4); median dorsal ridge and scales on either side of ridge present, not ctenoid. 26A.

26A. (151) Snout blunt and head rounded; body fusiform, not laterally compressed. Lago Pequeño, Bahia de Puno, Capachica Peninsula and Sotalaya....... *Orestias frontosus* Cope

26B. Snout slightly tapered, not blunt; (113) body laterally compressed, especially posterior to dorsal fin origin. 27A.

27A. (152) Modal number of pectoral fin rays 19 (table 6); (153) modal number of vertebrae 34 (table 3); body dark brown to black dorsally, pale yellow ventrally, no spot at dorsal margin of operculum. Bahia de Puno, Capachica Peninsula, Guaqui and Taraco, Lago Pequeño .... *Orestias tschudii* Castelnau

27B. Modal number of pectoral fin rays 18 (table 6); modal number of vertebrae 32 (table 3); (154) pigmentation pattern characterized by black lower jaw margin, faint to jet black spot at dorsal margin of operculum, and faint to dark black band at base of pectoral fin rays, body deep olive green dorsally with iridescent background, and light yellow-green ventrally. Río Coata, Peru .... *Orestias richersoni,* new species

25C. Scales of males not extremely ctenoid, if ctenii present, there are just a few ctenii per scale only on lateral and posterior scales; modal number of dorsal fin rays less than 15 (table 4); (114) median dorsal ridge extremely irregular and incomplete, formed by small, smooth scales. 28A.

28A. (155) Head rectangular in lateral and dorsal view, with straight dorsal profile and angular "chin"; lips relatively thin, not thick and fleshy. Lago Junin, Peru .... *Orestias polonorum* Tchernavin

28B. (156) Head in lateral profile, especially in larger adults, tapers toward mouth, with associated large preorbital distance ranging between 8 and 12 percent of SL (table 12); (157) lips thick and fleshy in largest adults. Lago Junin and its tributary streams, Río Mantaro and Río Huallaga .... *Orestias empyraeus* Allen

24B. Pigmentation pattern without dark band at base of dorsal, anal and pectoral fin rays, body in largest adults dark brown dorsally and laterally, light yellow ventrally, juveniles with mottled pattern; (149) neuromasts, often found in groupings of two or three, extend along median dorsal ridge from top of head to base of dorsal fin, scales in and above and below lateral series with multiple neuromasts. Río de Lampa, northwestern arm of Río Coata, Peru .... *Orestias multiporis,* new species

24C. Pigmentation pattern without dark band at base of dorsal, anal and pectoral fin rays, body in largest adults dark brown dorsally and laterally, light yellow ventrally, juveniles with mottled pattern; neuromasts in and above and below lateral series single, not in groups of two or more; (115) in largest adults, depth of body reaches nearly 35 percent of SL, and is typically more than 29 percent (table 10). 29A

29A. (148) Head squamation irregular, usually with no head scales anterior to the orbit, or on either side of dorsal ridge in young individuals; width of head on average less than 19 percent of SL (table 9). Throughout Urubamba and Titicaca Basins, Salar de Uyuni and northern Chile .... *Orestias agassii* Valenciennes

29B. Head fully scaled with large, thickened scales, either smooth or granulated; (116) width of head on average 19 percent or more of SL (Table 9). 30A

30A. (146) Lower jaw at 90-degree angle to body axis; (147) dorsal profile convex, rising very sharply from tip of snout to middle of median dorsal ridge; modal number of pectoral fin rays less than 19 (table 6). Río Guasacona, Lago Urcos and Lago Chinchero, Urubamba Basin .... *Orestias jussiei* Valenciennes

30B. Lower jaw not at abrupt angle to body axis; dorsal profile not convex; (117) pectoral fins large, modal number of fin rays 20 (table 6). 31A

31A. (145) Dorsal profile nearly straight from tip of snout to anterior base of dorsal fin; body not relatively deep, reaching a depth just under 35 percent of SL (table 10); head not relatively wide, less than 23 percent of SL (table 9). Lago Umayo .... *Orestias silustani* Allen

31B. (118) Dorsal profile arched abruptly just posterior to head; (119) body relatively deep, reaching a depth just over 40 percent of SL; (120) head relatively wide, over 28 percent SL (table 9). 32A

32A. (137) Caudal peduncle deep, reaching depth of over 22 percent of SL (table 11); all scales smooth, no granulations. Bahia de Puno, Capachica Peninsula, Lago Umayo .... *Orestias puni* Tchernavin

32B. Depth of caudal peduncle not so great as in *puni*, on the average less than 20 percent of SL (table 11); (121) scales from snout to base of dorsal fin, preopercular and opercular regions, and dorsal to pectoral fin thick and covered with dense granulations. 33A

33A. (144) Orbits oriented dorsolaterally, such that in dorsal view, both orbits nearly completely visible; head and scales around and on operculum not swollen. Lago Umayo, Bahia de Puno, and ?Bolivia .... *Orestias olivaceus* Garman

33B. Orbits not oriented dorsolaterally; (122) head swollen at a point just dorsal to operculum, scales extremely large and thick, giving body a very angular appearance. 34A

34A. (141) Lower jaw robust, creating prominent "chin"; (142) head relatively long, over 35 percent of SL (table 8); (143) dorsal profile slopes very gently, with no abrupt transition from anterior base of dorsal fin to base of caudal fin, the rays of which flare out slightly at its base; head width less than 29 percent of SL (table 9); scales on operculum not swollen, operculum not arched away from head. Bahia de Puno, Capachica Peninsula, Moho and Huancané .... *Orestias albus* Valenciennes

34B. Lower jaw not robust, no prominent "chin," head length usually under 35 percent of SL, although longer in large adults of *luteus* (table 8); dorsal profile with abrupt transition between anterior base of dorsal fin and caudal peduncle; (123) head wide, reaching width of over 34 percent of SL (table 9); (124) scales on operculum thick and granulated such that operculum appears swollen and arched slightly away from head. 35A

35A. (140) Elongate species of *luteus* group with relatively straight ventral profile, and correspondingly a body depth less than 35 percent of SL (table 10); head width less than 35 percent of SL (table 9); fifth ceratobranchials not as close together as in *rotundipinnis* and *luteus*, teeth not molariform. Lago Pequeño and Chililaya, Bolivia .... *Orestias farfani*, new species

35B. Robust and rotund species of the *luteus* group; (125) head wide reaching over 37 percent of SL (table 9); (126) pharyngeal teeth molariform with large, rounded cusps; (127) fifth ceratobranchials very close together. 36A

36A. (138) The most wide-headed species in *Orestias*, width of head reaching over 40 percent of SL, head also relatively long, reaching nearly 40 percent of SL (tables 8 and 9); pectoral fins with elongate middle rays. Localities throughout Lago Titicaca, Lago Umayo, Laguna de Arapa, and Huancané................ .... *Orestias luteus* Valenciennes

36B. Head not as wide, on the average as in *luteus*, reaching just under 38 percent of SL (table 9); (139) pectoral fins nearly perfectly rounded, without elongate middle rays. Bahia de Puno, Capachica Peninsula, Lago Pequeño .... *Orestias rotundipinnis*, new species

SYSTEMATIC ACCOUNTS

GENUS *ORESTIAS*[4] VALENCIENNES

Orestias Valenciennes, 1839, p. 118 (type species *Orestias cuvieri* Valenciennes, in Cuvier and Valenciennes, 1846, by subsequent designation of Eigenmann, 1910, p. 461).

DIAGNOSIS: Defined as a monophyletic group by the following seven synapomorphies: no pelvic fins or fin girdles; no vomer; no first postcleithrum; cartilaginous middle anal and middle dorsal radials; anterior and posterior bony ceratohyals separated ventrally by a large gap filled with cartilage; a

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[4] Allen, in Eigenmann and Allen (1942) used the name *Protorestias* (p. 353) to refer to a hypothetical ancestor of the genus *Orestias*; no type species was designated. The name is still available, and is therefore not listed in formal synonymy of *Orestias*.

unique squamation and head pore pattern characterized by a dorsal median ridge of scales from the head to the dorsal fin and a lyre-shaped arrangement of neuromasts on the dorsal surface of the head; and, anguloarticular lacks a ventral extension parallel to the retroarticular.

DESCRIPTION: First pleural rib on parapophysis of second vertebra; hypurals fused into a hypural fan; epipleural ribs bifid or not; transverse processes of vertebrae elongate or reduced and cup-shaped.

Anal fin inclinators large, nearly meeting or ventral to the division between hypaxial and epaxial musculature; first proximal radial present; middle dorsal and middle anal radials cartilaginous.

One dorsal fin ray articulates with first two dorsal radials; dorsal fin origin opposite or slightly in advance of or behind anal fin origin.

Autopterotic fossa of moderate size; lateral ethmoid enlarged medially or not, when enlarged reaching anterior ramus of parasphenoid; parasphenoid not broad anteriorly; supraoccipital and epiotic processes present or absent; nasals flat and broad, nearly meeting in midline.

Neural arches of the first vertebra open, not forming a spine, or just meeting to form a blunt spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; exoccipital condyles reduced; supraoccipital excluded from formation of foramen magnum; parietals absent.

Mesethmoid ossified; pelvic fins and girdles absent; interarcual cartilage approximately one half of, or equal or greater in length to, first epibranchial, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow or long and broad anteriorly; no tooth patches on hypobranchials; no teeth on fourth ceratobranchials; dorsal hypohyal absent; no anterior extension of anterior ceratohyal ventral to the ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow or wide at its base; interhyal not ossified; two ossified basibranchials.

Preorbital bone flat and broad, sensory canal reduced; dermosphenotic reduced or absent; preopercle with reduced sensory canal; pectoral girdle lowset, first postcleithrum absent; posttemporal with ligamentous ventral limb; posttemporal and supracleithrum separate.

Vomer absent; medial ramus of maxilla straight with pronounced dorsal process with or without a groove, dorsal processes nearly meet in the midline, ventral processes narrow; rostral cartilage absent; outer ramus of maxilla robust.

Premaxillary ascending processes narrow and blunt or pointed, not meeting in the midline; outer ramus of premaxilla with alveolar process, indented posteriorly to form an S shaped ramus. No ethmomaxillary ligament. Uni- or slightly bicuspid outer teeth in one or two irregular rows or outer teeth absent.

Dentary with a robust medial extension; coronoid process on dentary not overlapping that of anguloarticular; retroarticular not elongate; autopalatine with head angled anteriorly, ventral process elongate, reaching quadrate; metapterygoid absent; anguloarticular lacks a ventral extension parallel to the retroarticular.

Orbital rim free; anterior naris not tubular; cephalic sensory pore system represented by a lyre-shape pattern of minute neuromasts. Ventral surface scaled or not; basal portion of dorsal and anal fins scaled or not; scales often absent from either side of median dorsal ridge; scales often large and granulate or smooth.

Females larger than males, or sexes of approximately the same size; dorsal and anal fins rounded, never with fin extensions; caudal fin rounded, truncate or lunate; pectoral fin rounded or with extended central rays.

REMARKS: The diagnosis and description of the genus *Orestias* are presented in a format similar to that of Parenti (1981) for other cyprinodontiform genera. Diagnoses of species contain primarily the derived characters whereas descriptions of new species include additional characters that are considered to be useful in identification.

SPECIES COMPOSITION AND RANGE: Forty-three species in the high-altitude lakes and tributary streams of the Peruvian, Chilean, and Bolivian Andes from Ancash Province, northern Peru to Antofagasta Province, northern Chile (fig. 1).

NOTE ON SYNONYMIES: Compilations of,

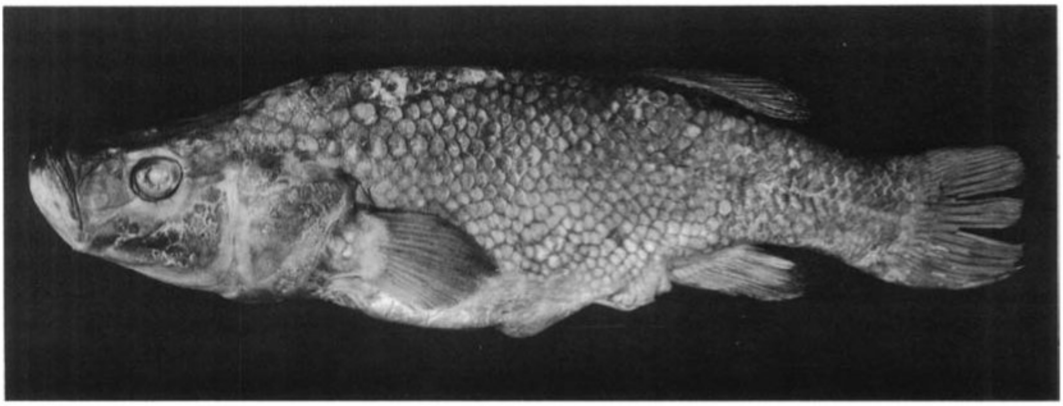

FIG. 32. *Orestias cuvieri* Valenciennes, BMNH 1944.6.6:15–18, female, 180 mm SL.

and references to, *Orestias* species have appeared in Günther (1866), Garman (1876, 1895), Eigenmann and Eigenmann (1892), Eigenmann (1894a, 1894b, 1910), Cope (1876, 1878), Pellegrin (1904a, 1904b, 1906), Allen, in Eigenmann and Allen (1942), Fowler (1916), Evermann and Radcliffe (1909, 1917), Rendahl (1937) and Zuñiga (1941). These and other references were included in the comprehensive synonymies of Tchernavin (1944a), and for that reason are not repeated here in exhaustive species synonymies. The abbreviated synonymies of previously described *Orestias* species summarize information on synonyms of recognized species and orthography of trivial names, and include, for species described before 1944, Tchernavin's (1944a) reference to the species. Also, anatomical references and distribution records published since 1944 are included.

To the extent that it was possible to determine on what material earlier records were based, identifications were reconfirmed. Records for Bolivian species by Terrazas (1970) are believed to be based on literature reports and are all unconfirmed.

Orestias cuvieri Valenciennes

Figures 3G, H, I, 32

Orestias Cuvieri. Valenciennes, 1839, p. 118 (*nomen nudum*); Valenciennes, in Cuvier and Valenciennes, 1846, pp. 225–230 (original description, Lago Titicaca).

Orestias Humboldtii. Valenciennes, 1839, p. 118 (*nomen nudum*).

Orestias Humboldti. Valenciennes, in Cuvier and Valenciennes, 1846, pl. 534, pp. 233–235 (original description, Lago Titicaca); Terrazas, 1970, p. 33 (Bolivia, unconfirmed record).

Orestias Cuvierii. Valenciennes, in Cuvier and Valenciennes, 1846, pl. 532.

Orestias cuvieri. Tchernavin, 1944a, pp. 153–158 (characters, synonymy, distribution); Villwock, 1962, p. 615 (distribution, ecology); Kosswig and Villwock, 1964, p. 98 (distribution); Villwock, 1964, pp. 285–291 (discussion of hybridization with *Orestias pentlandii* in Lago Titicaca); Terrazas, 1970, p. 33 (Bolivia, unconfirmed record).

DIAGNOSIS: An incompletely scaled member of the *cuvieri* complex most closely related to the sister species, *ispi* and *pentlandii,* distinguished by five derived characters: species with the largest individuals in *Orestias,* reaching 220 mm SL; mouth extremely large, lower jaw robust, outer teeth large, unicuspid, recurved and in one large outer row, and a smaller, irregular inner row; head long, its length reaching nearly 40 percent of SL (table 12); increased modal number of vertebrae to 34 with an observed range of from 33 to 35 (table 3); and, preorbital distance greater than in all other *Orestias,* reaching nearly 14 percent of SL (table 12).

REMARKS: Meristic and morphometric data for *cuvieri* are summarized in tables 3 through 12.

Orestias cuvieri Valenciennes has not been collected from Lago Titicaca in recent years, and is presumed to be extinct (see Villwock, 1964). The validity of the report of *O. hum-*

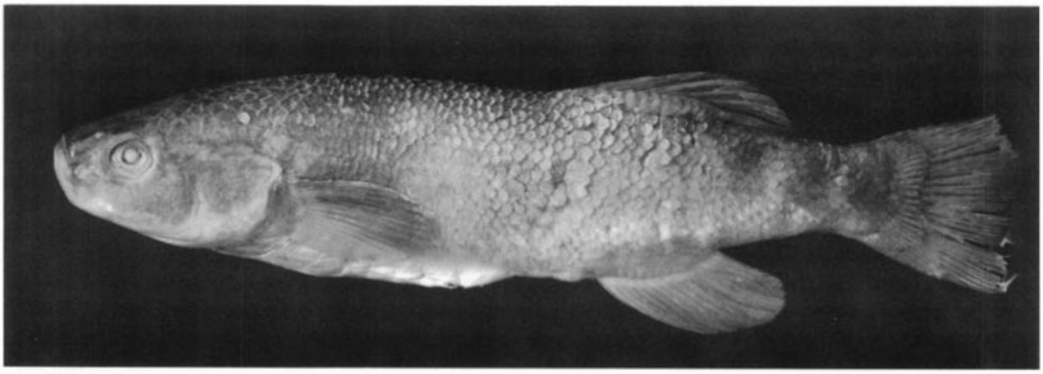

FIG. 33. *Orestias pentlandii* Valenciennes, BMNH 1944.6.6:22–25, female, 156 mm SL.

boldti Valenciennes, a synonym of *cuvieri*, from Bolivia (Terrazas, 1970) is in doubt. Allen, in Eigenmann and Allen (1942) used the name *humboldti* for one lot determined as *Orestias mulleri* Valenciennes (CAS 46174 and USNM 167731, both formerly IU 16078), whereas Tchernavin (1944a) treated *O. humboldti* as a synonym of *O. cuvieri*.

MATERIAL: Holotype (MNHN A.9593), an adult female, 175 mm SL, collected by M. Pentland, *ca.* 1839, from Lago Titicaca.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: BMNH 1862.11.15:46–48 (three subadults, 73–87 mm); BMNH 1862.11.15:78 (one subadult, 54 mm); BMNH 1858.11.5:13–15 (three subadults, 60–83 mm, one cleared and counterstained for bone and cartilage); BMNH 1890.2.25:56 (one adult female, 180 mm); BMNH 1862.11.15:31 (one adult female, 180 mm); BMNH 1875.6.7:1–2 (two adults, 180–190 mm); BMNH 1936.5.6:46 (one adult male, 180 mm); USNM 53480 (one adult); MNHN A.4415; MCZ 3931 (four adults); MCZ 3928 (27 juveniles, 17.6–33.1 mm, one cleared and counterstained for bone and cartilage); MCZ 3926 (six adults); MCZ 31112 (one adult); MCZ 6461 (one adult); RMNH 2740 (1); RMNH 2733 (3); RMNH 16211 (2); SU 9331 (two adults, 185–220 mm); UMMZ 56895 (1); syntypes of *Orestias humboldti* Valenciennes: MNHN 2670 (two subadults, 66–86.5 mm); MNHN 5829 (11 juveniles, 25–42 mm); MNHN A.9595 (three subadults, 58–74 mm); MNHN A.9596 (two subadults, 70–76 mm); MNHN A.9597 (four subadults, 67.4–90 mm).

Bahia de Chucuito: FMNH 41121 (1); Capachica Peninsula: USNM 133148 (two adults, gill arches of one cleared and counterstained for bone and cartilage); BMNH 1944.6.6:12–14 (three adults, 170–180 mm); BMNH 1944.6.6:15–18 (five adults, 185–200 mm); Puno: MCZ 3927 (four adult specimens to 220 mm).

RANGE: A midwater species known from several localities throughout Lago Titicaca, recorded from Puno, Bahia de Moho, and the Capachica Peninsula (see Tchernavin, 1944a, p. 158, and fig. 22 for localities), and from Bolivia, presumably from Lago Titicaca, although, as stated above, the identity of the specimens reported by Terrazas (1970) has not been confirmed.

Orestias pentlandii Valenciennes

Figures 6A, 10, 33

Orestias Pentlandii. Valenciennes, 1839, p. 118 (*nomen nudum*); Valenciennes, in Cuvier and Valenciennes, 1846, pp. 230–232 (original description, Lago Titicaca).

Orestias Pentlandi. Valenciennes, in Cuvier and Valenciennes, 1846, pl. 533.

Orestias bairdii. Cope, 1876, p. 185 (original description, Lago Titicaca).

Orestias bairdi. Eigenmann, 1894a, p. 54 (compiled).

Orestias Petlandi. Zuñiga, 1941, pp. 81–86 (misprint).

Orestias pentlandii. Tchernavin, 1944a, pp. 158–160 (characters, synonymy, distribution); Villwock, 1962, p. 615 (distribution, ecology); Kosswig and Villwock, 1964, p. 98 (distribution); Villwock, 1964, pp. 285–291 (discussion

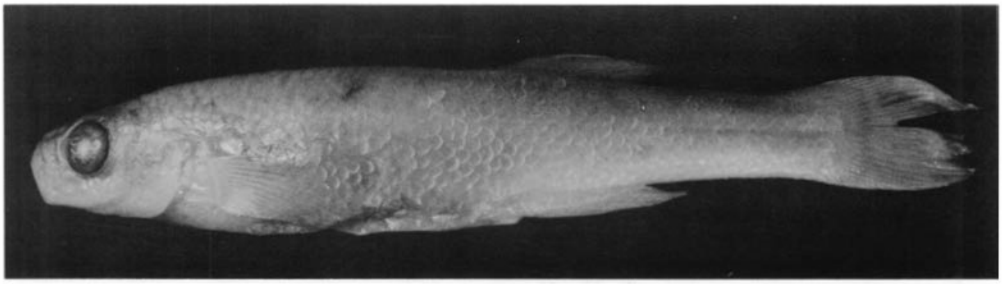

FIG. 34. *Orestias ispi* Lauzanne, Holotype, MNHN 1981:605, female, 62 mm SL.

of hybridization with *Orestias cuvieri* in Lago Titicaca).

DIAGNOSIS: An incompletely scaled member of the *cuvieri* complex, most closely related to *ispi* and like it with small conical or no outer jaw teeth in adults. One of the larger *Orestias,* individuals reaching 200 mm SL; with the highest number of vertebrae in the genus, the modal number increased to 37, with an observed range of from 36 to 38 (table 3); highest number of scales in a lateral series, the modal number increased to 57, with an observed range of from 51 to 60 (table 7).

REMARKS: Meristic and morphometric data for *pentlandii* are summarized in tables 3 through 12.

MATERIAL: Syntypes (MNHN A.9594), two adults, 163–168 mm SL, collected by M. Pentland, *ca.* 1839, from Lago Titicaca.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: MNHN A.9598 (one subadult); SU 9306 (two adults, gill arches of one cleared and counterstained for bone and cartilage); RMNH 8848 (1); RMNH 15481 (1); RMNH 16210 (1); USNM 53478 (8); USNM 163837 (1); USNM 23246 (2); MCZ 31110 (1); MCZ 35059 (2); MCZ 3938 (4); MCZ 6460 (1); MCZ 3939 (3); MCZ 6459 (1); AMNH 1117 (1); BMNH 1965.10.6:12 (one adult, 160 mm); BMNH 1890.2.25:55 (one adult, 200 mm); BMNH 1852.11.15:28–29 (two adults, 155–170 mm); BMNH 1944.6.6: 21 (one subadult, 75 mm); BMNH 1944.6.6: 26–29 (seven adults, 150–170 mm); Lago Titicaca: Bahia de Puno: USNM 133146 (ex. BMNH 1944.6.6:40) (one adult); USNM 77613 (3); MCZ 3940 (2); FMNH 81629 (5); FMNH 41109–41110 (2); FMNH 80323 (1); IU 16084 (at CAS) (two adults, 150 mm); AMNH 52110 (one adult, 130 mm); BMNH 1944.6.6:22–25 (five adults, 150–160 mm); BMNH 1944.6.6:36–40 (eight adults, 135–160 mm); BMNH 1944.6.6:41–48 (11 adults, 160–170 mm); Isla Taquile: AMNH 52198 (1).

Urubamba Basin: Cuzco Valley: MCZ 3941 (3).

RANGE: Recorded from Bahia de Puno (fig. 22), Lago Titicaca in the Titicaca Basin, and from the Cuzco Valley, in the Urubamba Basin.

Orestias ispi Lauzanne

Figures 15, 20B, 34

Orestias ispi. Lauzanne, 1981, pp. 73–79 (original description, Estrecho Tiquina, Lago Pequeño, Lago Titicaca, Bolivia).

DIAGNOSIS AND REMARKS: One of the two smaller, fully scaled species of the *cuvieri* complex most closely related to the large, incompletely scaled *pentlandii,* distinguished from the other species in the complex by very thin, small, irregularly distributed scales that are more weakly formed than in the other fully scaled *cuvieri* complex species, *forgeti,* and by a lower jaw that is at a 90-degree angle to the main body axis.

Young as well as adults of *ispi* may be confused with young of its sister species, *pentlandii,* but may easily be distinguished by its lower number of vertebrae (modal number 32, range 31 to 33 as opposed to a modal number of 37 and a range of from 36 to 38 for *pentlandii*) and its lower number of scales in a lateral series (modal number 48, range 41 to 53 as opposed to a modal number of 57 and a range of from 51 to 60 for *pentlandii*).

Lauzanne (1981) compared *ispi* to *forgeti* and to *mooni* of the *gilsoni* complex because

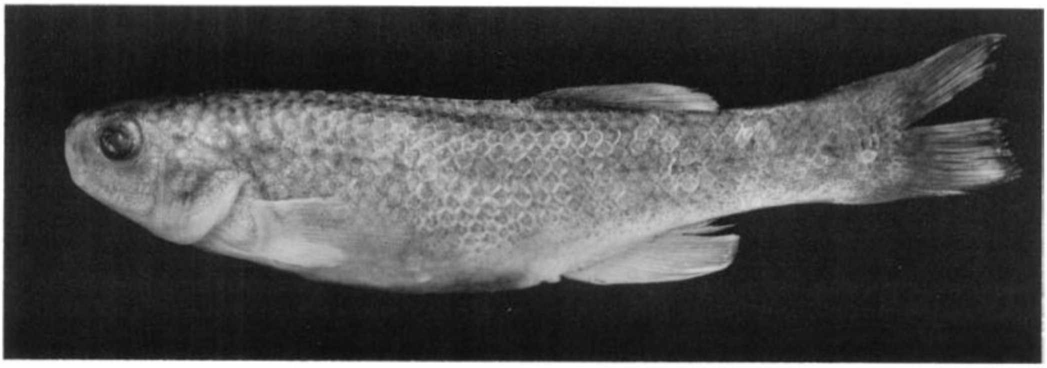

FIG. 35. *Orestias forgeti* Lauzanne, Holotype, MNHN 1981:603, female, 73 mm SL.

these species are relatively small, elongate and are fully scaled; however, he also concluded that *ispi* was more closely related to *pentlandii* than to *mooni*.

Additional meristic and morphometric data are summarized in tables 3 through 12. Also, additional characters not compared among all *Orestias* in this paper are discussed in Lauzanne (1981).

MATERIAL: Holotype (MNHN 1981:605), an adult female, 62 mm SL, collected October 15, 1979, from Estrecho Tiquina, Lago Pequeño, Lago Titicaca. Paratypes (MNHN 1981:606) 40 adult males and females, 46.5 to 76.5 mm, taken along with the holotype.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: AMNH 38400 (four adults, 43–62.5 mm); AMNH 38422 (one subadult, 28.5 mm). Bahia de Puno: Isla Taquile: AMNH 48641 (232 adults and subadults); BMNH 1982.12.6:51–120 (70 adults and subadults, 46–54 mm, two cleared and counterstained for bone and cartilage); AMNH 48643 (73 adults and subadults); USNM 228147 (200 adults and subadults); USNM 228148 (238 adults and subadults); BMNH 1982.12.6:37–50 (14 subadults, 39–56 mm); AMNH 52111 (99 adults, 47–60 mm, three cleared and counterstained for bone and cartilage). Capachica Peninsula: AMNH 48640 (610 adults and subadults); AMNH 48462 (269 adults and subadults); AMNH 52112 (102 adults and subadults, 47–59 mm, two cleared and counterstained for bone and cartilage).

RANGE: Known from the type locality, Estrecho Tiquina in Lago Pequeño (figs. 22 and 23), Isla Taquile in Bahia de Puno, and the Capachica Peninsula (fig. 22), all Lago Titicaca.

Orestias forgeti Lauzanne
Figure 35

Orestias forgeti. Lauzanne, 1981, pp. 79–84 (original description, Estrecho Tiquina, Lago Pequeño, Lago Titicaca, Bolivia).

DIAGNOSIS: One of the two small, fully scaled species of the *cuvieri* complex, with irregularly distributed scales on ventrum thinner than dorsal and lateral scales, although not so thin and as irregularly distributed as in the other fully scaled species, *ispi*; the plesiomorphic species of the *cuvieri* complex, distinguished from *cuvieri, pentlandii,* and *ispi* by a relatively large pectoral fin with an increase in the modal number of pectoral fin rays to 19, range 18 to 20, as opposed to a modal number of 17 with a range of 15 to 20 (table 6) in the three other species.

REMARKS: Additional meristic and morphometric data for this species are summarized in tables 3 through 12. Also, additional characters not compared here for all *Orestias* are discussed in Lauzanne (1981). Lauzanne compared *forgeti* with *ispi* because both are fully scaled and planktivorous, and with *mulleri* and *agassii* because of the similarity in overall body proportions, however, he made no firm statement concerning the relationship of *forgeti* to any other *Orestias* species.

MATERIAL: Holotype (MNHN 1981:603), an adult female, 73 mm SL, collected October 15, 1979, from Estrecho Tiquina, Lago Pe-

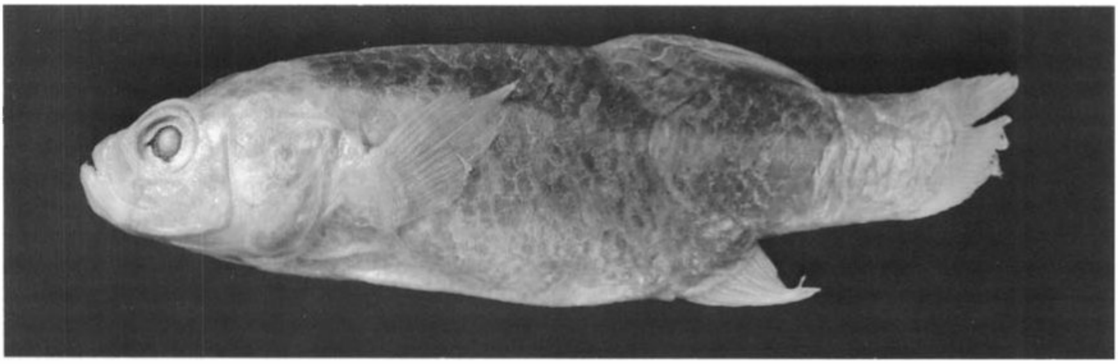

FIG. 36. *Orestias mulleri* Valenciennes, Syntype, MNHN A.9605, female, 71 mm SL.

queño, Lago Titicaca. Paratypes (MNHN 1981:604), 40 adult males and females, 56 to 84 mm, taken along with the holotype.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: Bahia de Puno, between Puno and Chucuito, near village of Ojjerani: AMNH 52113 (four adults, 63–74.5 mm, one cleared and counterstained for bone and cartilage); AMNH 48645 (one adult, 66.5 mm); AMNH 48647 (one adult, 74 mm); AMNH 52114 (two adults, 57.5–59 mm).

RANGE: Known from the type locality, Estrecho Tiquina in Lago Pequeño (figs. 22 and 23), and near the village of Ojjerani, between Puno and Chucuito, Bahia de Puno (fig. 22).

Orestias mulleri Valenciennes

Figures 14, 21B, 36

Orestias Mulleri. Valenciennes, in Cuvier and Valenciennes, 1846, pp. 240–241 (original description, Guaqui [Guaichu], Lago Pequeño, Lago Titicaca).

Orestias humboldti (not *Orestias humboldti* Valenciennes). Allen, in Eigenmann and Allen, 1942, pp. 355–357, pl. xvii, fig. 2 (misidentification).

Orestias müllerí. Tchernavin, 1944a, pp. 222–225 (characters, synonymy, distribution); Terrazas, 1970, p. 34 (Bolivia, unconfirmed record).

DIAGNOSIS: The largest fishes of the *mulleri* complex, reaching 92 mm SL; fully scaled, with irregularly distributed scales covering the ventrum; most closely related to a group comprising *tutini, crawfordi,* and *incae* but distinguished from these more laterally compressed, deeper bodied species by an increase in the modal number of scales in a lateral series to 36, with a range of from 33 to 38 (table 7), as opposed to a modal number of 31 or 32, with a range of from 30 to 36 in other species of the *mulleri* complex; and, a decrease in the modal number of anal fin rays to 13, with a range of from 12 to 15 (table 5), as opposed to a modal number of 15, with a range of from 13 to 18 for the other *mulleri* complex species. Additional morphometric and meristic data for this species are summarized in tables 3 through 12.

MATERIAL: Syntypes (MNHN A.9605), two adult females, 67 to 71 mm SL, collected by M. Pentland, *ca.* 1839, from Guaqui [Guaichu], Lago Pequeño, Lago Titicaca.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: BMNH 1862.11.15:32, 33, 59, 73 (4); BMNH 1862.11.15:71 (1); BMNH 1858.11.5:10 (1); AMHN 38423 (two adults, 62.5–68 mm); Bahia de Moho: CAS 46174 (ex. IU 16078) (20 subadult to adult males and females, 43–75 mm, one cleared and counterstained for bone and cartilage); USNM 167731 (ex. IU 16078) (11); Bahia de Puno: village of Ojjerani, about 10 km S of Puno: AMNH 52211 (one adult, 58 mm); AMNH 52115 (two adults, 56–60 mm); AMNH 52116 (two adults, 71–76 mm); AMNH 52117 (two adults, 58–59 mm) Capachica Peninsula: AMNH 52118 (45 adult males and females, 64–92 mm, two cleared and counterstained for bone and cartilage).

RANGE AND REMARKS: Allen, in Eigenmann and Allen (1942), diagnosed and illustrated large specimens of *O. agassii* Valenciennes (IU 17098) as *O. mulleri*

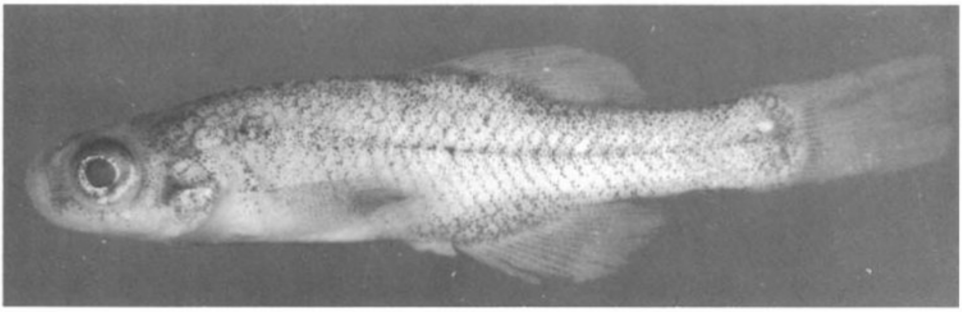

FIG. 37. *Orestias gracilis,* new species, Paratype, AMNH 52121, male, 30 mm SL.

Valenciennes, and *O. mulleri* (IU 16078) as *O. humboldti* Valenciennes, a synonym of *O. cuvieri* Valenciennes. *Orestias mulleri,* therefore, is not as abundant and widespread as indicated by Allen. It is known with certainty from several localities in Lago Titicaca, including Bahia de Moho, Lago Pequeño, and the Capachica Peninsula. One specimen (AMNH 52119) from northeast of Isla Esteves in Bahia de Puno is tentatively referred to *mulleri*; although, it is most likely an undescribed species.

A lectotype was not designated from the two syntypes because it is not known whether they comprise Valenciennes' entire type series.

Orestias gracilis, new species

Figure 37

DIAGNOSIS: A relatively small, slender-bodied species of the *mulleri* complex, with a dorsal and anal fin base that project just slightly beyond the primary body profile; body overall relatively light straw-colored, with scattered, small melanophores that are dense on the dorsal surface; fins relatively clear to slightly mottled; pectoral fin small at its base, rays elongate, reaching more than halfway between base and vertical through origin of anal fin; modal number of 15 pectoral fin rays (range of from 14 to 15) as opposed to a modal number of 17 pectoral fin rays for the genus, and a modal number of 19 (range of from 15 to 20) for other species of the *mulleri* complex (table 6).

DESCRIPTION AND REMARKS: Additional morphometric and meristic data for *gracilis* are summarized in tables 3 through 12. Although no one morphometric trait separates *gracilis* from other *Orestias* species, it can be seen that *gracilis* (fig. 37) is a relatively slender-bodied (tables 9 through 11) species of the *mulleri* complex. It differs in just one meristic character, number of pectoral fin rays, modally 15 (range of from 14 to 15), which is below the modal number of 17 for the genus and 19 for the *mulleri* complex (table 6). As noted in Phylogenetic Analysis, the closest relative of *Orestias,* the genus *Kosswigichthys,* has a low number of pectoral fin rays also. However, *gracilis* is clearly a member of a relatively derived, well-defined subgroup of *Orestias* (comprising the *mulleri* and *gilsoni* complexes); therefore, the low number of pectoral fin rays in *gracilis* is considered to be secondarily derived, and hence, autapomorphic.

Adults to 40 mm SL. Males and females overall straw-colored, with scattered, small melanophores that increase in number (hence density) dorsal to the midlateral scales; fins clear to slightly mottled.

Orbits project slightly above dorsal surface of head; dorsal surface slightly to abruptly convex posterior to the head. Ventral surface and basal portion of dorsal, anal and pectoral fins unscaled. Scales thin and delicate. Males with breeding tubercles on dorsal and anal fins. Caudal fin truncate. Pectoral fin narrow and elongate, reaching just over halfway between pectoral fin base and anal fin. Anal papilla large (see fig. 37), extending beyond basal portion of anal fin and fin rays. Basal portion of dorsal and anal fins project slightly beyond primary body profile.

Outer jaw teeth small, unicuspid, with

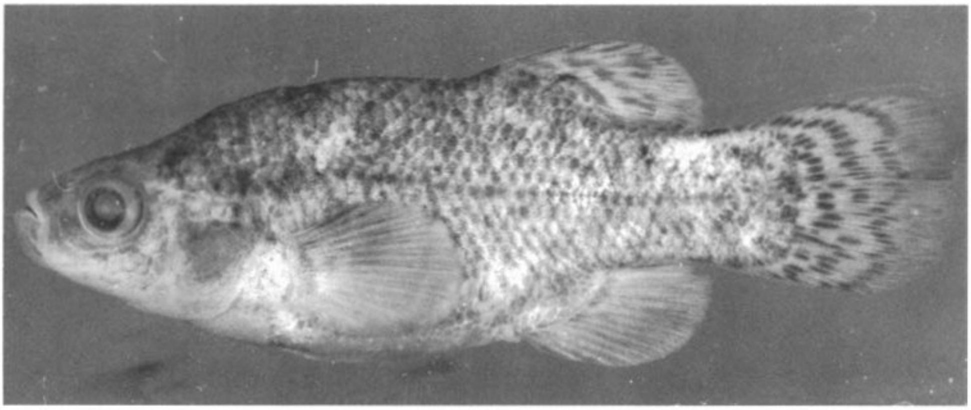

FIG. 38. *Orestias crawfordi* Tchernavin, AMNH 52125, male, 56 mm SL.

pointed tips that barely protrude through the epithelium covering upper and lower jaws, arranged in one irregular row.

There is one specimen among the six not considered as part of the type material, but nonetheless tentatively referred to *gracilis.* This specimen (AMNH 52123), an adult male, 35 mm SL, is slightly deeper bodied than the type and other specimens, and has eight (or possibly nine) discrete dark blotches dorsally, rather than scattered, small melanophores. Pectoral fin rays number 15. The color pattern and structure of the caudal fin (the procurrent rays appear to be slightly nearer the vertebral column, as they are in the *gilsoni* complex) suggest that this specimen may be a member of an undescribed species within the *gilsoni* complex,

MATERIAL: Holotype (AMNH 52120), an adult male, 40 mm SL, collected October 2, 1979 by Tom Coon and M. Reed, near the village of Huatayata, from 0 to 30 m from the shore at a depth of from 0 to 1 m, on the northeastern side of Lago Pequeño, Lago Titicaca. Paratypes (AMNH 52121), three specimens, 26 to 31 mm, taken along with the holotype (one cleared and counterstained for bone and cartilage).

ADDITIONAL MATERIAL (not part of the type series): Bahia de Puno, village of Ojjerani: AMNH 52123 (one adult male, 35 mm); Lago Pequeño: AMNH 52122 (five adults, 33.3–37.7 mm).

RANGE: Known from the type locality (figs. 22 and 23) in Lago Pequeño, and tentatively by one specimen (AMNH 52123) from Bahia de Puno on the western side of Lago Titicaca.

ETYMOLOGY: The trivial name *gracilis,* a Latin adjective meaning slender, thin, or simple, referring to the overall elongate and delicate appearance of this species.

Orestias crawfordi Tchernavin

Figures 11; 12; 16; 17; 38

Orèstias crawfordi. Tchernavin, 1944a, pp. 226–227 (original description, Bahia de Taman, northeastern side of the Capachica Peninsula, Lago Grande, Lago Titicaca).

DIAGNOSIS: A deep-bodied, laterally compressed, fully scaled species of the *mulleri* complex, most closely related to *incae,* and like it with an increased number of dorsal fin rays (table 4), an increased depth of the caudal peduncle (table 11), and molariform pharyngeal teeth; distinguished from *incae* by two derived characters: larger, molariform pharyngeal teeth that have rounded (fig. 16), rather than slightly pointed cusps; and a fourth epibranchial bone with a huge posterior flange (figs. 11 and 12) and an associated large adductor IV.

MATERIAL AND REMARKS: Syntypes (BMNH 1944.6.6:157–158), one adult male, 65.7 mm SL, and one adult female, 65 mm, collected September 17, 1937 by the Percy Sladen Titicaca Expedition, at a depth of from 36 to 38 m, from Bahia de Taman on the northeastern side of the Capachica Peninsula. No lectotype is designated because Tcher-

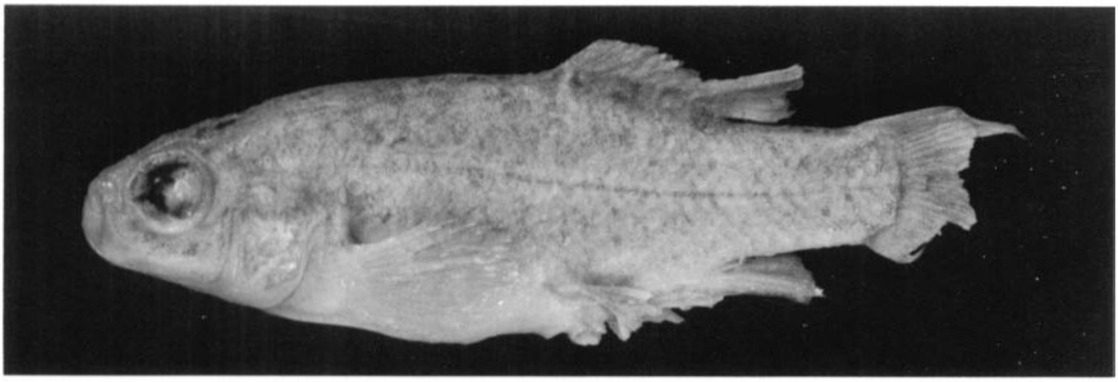

FIG. 39. *Orestias tutini* Tchernavin, Holotype, BMNH 1944.6.6:544, male, 34 mm SL.

navin (1944a, p. 226) listed three specimens, the two listed here, and a third from Pentland's collection, obtained by the BMNH from the MNHN, in his description of *crawfordi,* and only the first two specimens were found in the BMNH. Therefore, the complete syntype series has not been examined.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: Bahia de Puno, village of Ojjerani, about 10 km S of Puno: BMNH 1982.12.6:25–34 (10 adult males and females, 54–74 mm); AMNH 52124 (three adults, 43–63 mm); AMNH 52125 (20 adult males and females, 54–64 mm); AMNH 52126 (21 adult males and females, 59–69 mm, two cleared and counterstained for bone and cartilage); AMNH 52127 (nine adult males and females, 59–79 mm); AMNH 52128 (four adult males and females, 59–68 mm); Escallami: AMNH 52129 (one subadult, 36 mm).

RANGE: Known from Bahia de Puno and Bahia de Taman, the northeastern side of the Capachica Peninsula, Lago Titicaca (figs. 22 and 23).

Orestias tutini Tchernavin
Figure 39

Orestias tutini. Tchernavin, 1944a, pp. 219–220 (original description, Isla Taquiri, Lago Pequeño, Lago Titicaca).

DIAGNOSIS AND REMARKS: The smallest fishes of the *mulleri* complex, reaching 35 mm SL, most closely related to the two other laterally compressed species of the complex (*crawfordi* and *incae*), distinguished by the dorsal surface of the head and the operculum of males covered with fleshy, tubercle-like projections covering the ctenii of underlying scales; and the basal portion of the dorsal, anal and pectoral fins and along each side of the median dorsal ridge unscaled. All scales of males apparently ctenoid, however, all specimens have been partially descaled. The species is known only from the type series of four specimens which are faded and poorly preserved. Because the species is incompletely scaled, Tchernavin (1944a) placed it in his Group III along with other incompletely scaled species such as *gilsoni.* However, I place the species in the *mulleri* complex along with some fully scaled *Orestias* species because it has the defining character of the complex, that is, the bases of the dorsal as well as the anal fin project beyond the primary body profile.

MATERIAL: Holotype (BMNH 1944.6.6:544), an adult male, 34 mm SL, collected July 30, 1937 by the Percy Sladen Titicaca Expedition, at a depth of from 2.7 to 2.8 m, Isla Taquiri in Lago Pequeño. Paratypes (BMNH 1944.6.6:545–547) three adults, 32 to 35 mm, taken along with the holotype.

RANGE: Known only from the type locality, Isla Taquiri, an island in the northeastern section of Lago Pequeño (figs. 22 and 23).

Orestias incae Garman
Figure 40

Orestias Incae. Garman, 1895, pp. 155–156 (original description, Bahia de Moho, Lago Titicaca).

FIG. 40. *Orestias incae* Garman, Syntype, MCZ 3948, female, 57 mm SL.

Orestias incae. Tchernavin, 1944a, pp. 225–226 (characters, distribution, synonymy); Terrazas, 1970, p. 33 (Bolivia, unconfirmed record).

DIAGNOSIS AND REMARKS: A member of the *mulleri* complex most closely related to *crawfordi* from which it is distinguished by two derived characters: the most laterally compressed fishes in the genus *Orestias*, with ventral surface nearly keeled in larger adults; and, males with four to five irregular, medium to dark brown vertical bars on a light brown background, females with fainter bars.

Orestias incae is known with certainty only from the syntype series, 17 subadult to adult males and females collected in 1875 by S. W. Garman from Bahia de Moho on the northeastern side of Lago Grande, Lago Titicaca (fig. 22). Tchernavin (1944a, p. 226) stated that eight specimens described by Garman (1895) were the only ones known. However, Garman (1895, p. 156) stated that dorsal and anal fin rays were counted on only eight specimens, without giving an indication of the total number of specimens used in his description. I have located syntypes of *incae* in three collections (MCZ, USNM, BMNH), and do not choose one as a lectotype here because I do not know whether all syntypes have been located.

This is one of the more distinctive species within *Orestias*, and may show more sexual dichromatism than is commonly found within species of the *gilsoni* and *mulleri* complexes. However, all specimens are faded in alcohol and do not offer the opportunity to describe completely this variation. Meristic and morphometric data are summarized in tables 3 through 12.

MATERIAL: Syntypes (MCZ 3948), 12 subadults to adults, 40 to 57 mm SL, (USNM 120281, ex. MCZ 3948) four adults, 49 to 52 mm, (BMNH 1939.7.17:2, ex. MCZ 3948) one adult female, 52 mm, collected January 1875, by S. W. Garman, from Bahia de Moho, Lago Titicaca.

RANGE: Known only from the type locality, Bahia de Moho (figs. 22 and 23). Terrazas (1970) lists *incae* from Bolivia, presumably also from Lago Titicaca, although this is an unconfirmed record.

Orestias luteus Valenciennes

Figures 6B, 7, 8D

Orestias luteus. Valenciennes, 1839, p. 118 (*nomen nudum*); Valenciennes, in Cuvier and Valenciennes, 1846, pp. 243–244 (original description, Lago Titicaca); Tchernavin, 1944a, pp. 204–209 (characters, synonymy, distribution); Lueken, 1962, pp. 195–198 (karyology); Villwock, 1962, p. 615 (distribution, ecology); Kosswig and Villwock, 1964, p. 96 (distribution); Terrazas, 1970, p. 34 (Bolivia, unconfirmed record).

Orestias cypho. Fowler, 1916, pp. 427–429 (original description, said to have been taken from snake collected near La Paz, Bolivia).

DIAGNOSIS AND REMARKS: A member of the *luteus* group of the *agassii* complex, most closely related to *rotundipinnis*, differing from it by having elongate middle rays of the pectoral fin, and defined by being wide-headed (width of head reaching over 40 percent of SL; table 9), with a relatively long head, reaching nearly 40 percent of SL in the largest adults (table 8).

There is a great deal of variation among individuals of *luteus* in the shape of the head, particularly in the degree of arching of the dorsal surface. Also, the head may be distorted to a great degree upon preservation and during storage. Fowler (1916) based his description of *Orestias cypho* on one specimen, claiming that its convex dorsal profile was arched more abruptly than in *luteus*. This specimen was reportedly taken from inside a snake. Because of the great variety of head shapes, I do not support the division of *luteus* into several species or subspecies on the basis of differences in head shape, nor do I recognize *O. cypho*. However, additional large samples of well-preserved specimens may present the opportunity to recognize more than one taxon.

Additional morphometric and meristic data for *luteus* are summarized in tables 3 through 12.

MATERIAL: Holotype (MNHN A.9608), an adult female, 126 mm SL, collected by M. Pentland, *ca.* 1839, from Lago Titicaca.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: AMNH 38424 (one adult, 105 mm); AMNH 38428 (one adult, 150 mm); BMNH 1909.6.15:13 (one adult female, 127 mm); USNM 53487 (1); Capachica Peninsula: BMNH 1944.6.6:425–429 (nine adult males and females, 91–125 mm); BMNH 1944.6.6:430–433 (four adults, 112–128 mm); BMNH 1944.6.6:435–436 (two adults, 72–125 mm); BMNH 1944.6.6:437–439 (five adults, 116–121 mm); BMNH 1944.6.6:440–442 (six adults, 75–115 mm); USNM 133147 (ex. BMNH 1944.6.6:444) (1); BMNH 1944.6.6:445–447 (three adults, 106–116 mm); AMNH 52130 (seven adult males and females, 82–104 mm, gill arches of two cleared and counterstained for bone and cartilage); Bahia de Puno: AMNH 52131 (15 adults, 83.5–98 mm); AMNH 52132 (two adults, 73–78 mm); AMNH 52134 (one female, 110 mm); Chucuito: FMNH 41112–41114 (three adults); Isla Taquile: AMNH 52133 (one adult, 98 mm); Lago Pequeño: Bahia by Vilurcuni: AMNH 52135 (one adult, 87 mm); AMNH 52136 (one adult, 97 mm); Sucuné: BMNH 1944.6.6:450–451 (two, juvenile and subadult); Yungayo: CAS 46178 (ex. IU 16104) (10 juveniles to subadults); Bahia de Moho: CAS 46176 (ex. IU 16079) (42 juveniles to adults, 30.5–100 mm); Sotalaya: AMNH 52137 (four adults, 79–85 mm); Bolivia: ANSP 21920, holotype of *Orestias cypho* Fowler (one adult, 125 mm), said to have been taken from a snake collected near La Paz; Lago Umayo: BMNH 1944.6.6:452 (one juvenile); FMNH 88762 (193 juveniles to adults); FMNH 77386 (120 juveniles); CAS 48259 (13 juveniles to adults); Huancané: USNM 167733 (6), USNM 167732 (19 juveniles to subadults), CAS 45794 (ex. IU 16086) (40 juveniles to subadults), CAS 46177 (ex. IU 16090) (10 juveniles to subadults); Laguna de Arapa: FMNH 77553 (12), IU 16109 (at CAS) (three subadults to adults, 42.9–77.5 mm).

RANGE: Known from several localities throughout Lago Titicaca, including Bahia de Puno, the Capachica Peninsula, Isla Taquile, Bahia de Moho, Lago Pequeño, Sotalaya, Huancané, and outside the main body of the lake in Lago Umayo and Laguna de Arapa (figs. 22 and 23).

Orestias rotundipinnis, new species

Figure 41

DIAGNOSIS: A wide-headed (width ranging between 29 and 38 percent of SL, table 9), deep-bodied (depth at posterior extent of head ranging between 29 and 38 percent of SL, table 10) species of the *luteus* group of the *agassii* complex, most closely related to *O. luteus* Valenciennes, but differing from that species by having rounded pectoral fins, rather than having elongate middle rays of the pectoral fins.

DESCRIPTION: Morphometric and meristic data for this species are summarized in tables 3 through 12. These data demonstrate that *rotundipinnis* does not differ from *luteus*, its sister species, in most of these characters, although *luteus* tends to be a relatively wider- and longer-headed species than *rotundipinnis*. Its most striking difference, and the character by which *rotundipinnis* is defined, is the nearly perfectly rounded pectoral fin in both males and females (fig. 41). In all specimens determined as *O. luteus*, the pectoral fin is

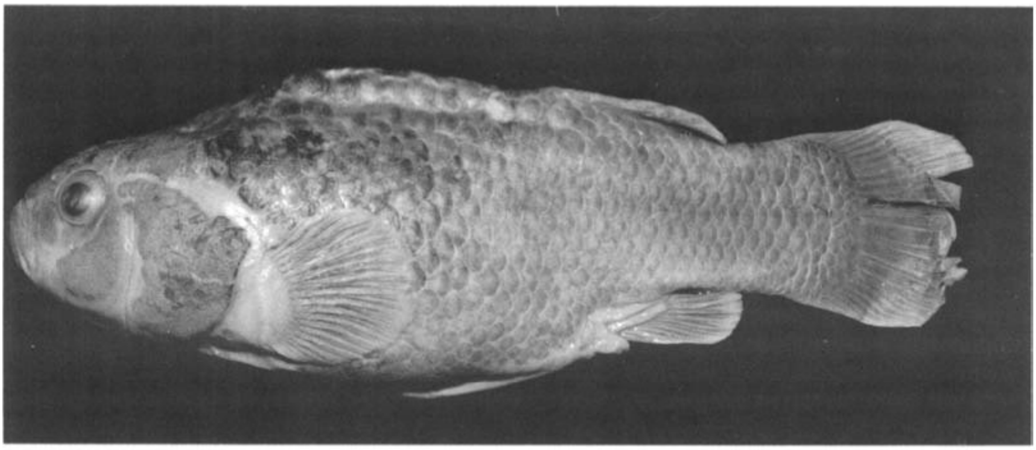

FIG. 41. *Orestias rotundipinnis,* new species, Holotype, AMNH 52138, female, 109 mm SL.

distinctly pointed posteriorly, owing to its elongate middle rays.

Dorsal profile of body arched abruptly posterior to the head; head scales thick and granulated; scales of and above operculum thickened causing these areas to appear swollen. Preorbital region, ventrum, and basal portion of the dorsal and anal fins unscaled; basal portion of pectoral fin may be fully scaled (as on right side of holotype) or unscaled (as on left side of holotype), or irregularly scaled. Males with ctenii on posterior lateral scales.

Adults to 115 mm SL. Body grayish brown laterally, darker gray dorsally, ventrum a grayish cream color. All fins with dark margins of rays. Males with breeding tubercles on dorsal, anal and pectoral fins.

Outer jaw teeth unicuspid, slightly pointed, brown tips just protruding beyond epithelium covering upper and lower jaws; teeth in a single regular or irregular row.

REMARKS: Just two specimens, which are similar in overall shape, coloration and squamation, are given type status. The rest of the material referred to *rotundipinnis* differs from these two specimens primarily in two characters, either in (1) pigmentation (i.e., they are significantly darker), or (2) shape of the head (i.e., they do not have such a steep rise in the dorsal profile posterior to the head). It appears, therefore, that the rounded pectoral fin, a distinctly derived character, may eventually be used to define a larger group of *luteus* group species, now known as separate collections of *rotundipinnis.* These may be recognized as individual taxa when additional material is at hand.

MATERIAL: Holotype (AMNH 52138), an adult female, 109 mm SL, collected September 2, 1979 by Tom Coon at a depth of from 1 to 2 m, from just NE of Isla Esteves, Bahia de Puno, Lago Titicaca. Paratype (AMNH 52139), an adult female, 95 mm, taken along with the holotype.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: AMNH 38426 (one adult male, 115 mm); Lago Pequeño, near Vilurcuni: AMNH 52140 (one adult male, 85 mm), near Huatayata: AMNH 52199 (one subadult, 67.5 mm); Bahia de Puno: AMNH 52141 (one adult male, 85 mm); Capachica Peninsula: AMNH 52142 (one adult female, 104 mm), BMNH 1944.6.6:434 (two adults, 108–115 mm), BMNH 1944.6.6:443 (four adults, 95–115 mm).

RANGE: Known from several localities in Bahia de Puno, the Capachica Peninsula, and Lago Pequeño, Lago Titicaca (figs. 22 and 23).

ETYMOLOGY: The trivial name *rotundipinnis,* a noun in apposition, from the Latin roots *rotundus,* an adjective meaning round, and *pinnis,* the ablative plural of *pinna,* a feminine noun meaning wing or feather, in reference to the rounded margin of the pectoral fins.

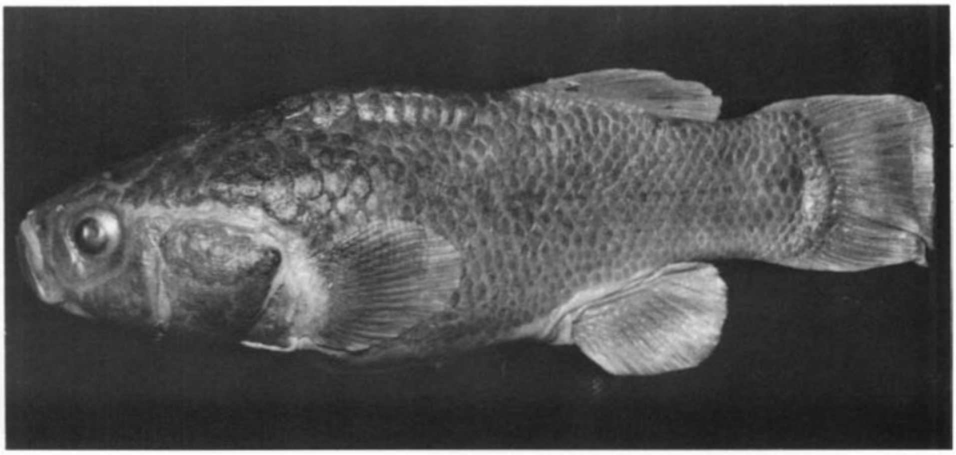

FIG. 42. *Orestias farfani,* new species, Holotype, AMNH 52143, female, 106 mm SL.

Orestias farfani, new species
Figure 42

DIAGNOSIS: A species of the *luteus* group of the *agassii* complex that in many characteristics, particularly those pertaining to recorded morphometric (tables 8 through 12) and qualitative characters of body shape, is intermediate between the robust yet relatively slender-headed *albus* and *olivaceus* and the extremely wide-headed *luteus* and *rotundipinnis,* more closely related to the last two species, in sharing with them a head width that reaches nearly 35 percent or more of SL (table 9), and having the operculum as well as the head swollen owing to the presence of greatly thickened and granulated scales. Distinguished from all other species of the *luteus* group by having a relatively straight ventral profile, and therefore, also a body that is not as deep as that of *albus, luteus,* and *rotundipinnis* (table 10).

DESCRIPTION AND REMARKS: Morphometric and meristic data for this species are summarized in tables 3 through 12. An elongate species within the *luteus* group, distinguished by its straight ventral profile; intermediate in many characters between *albus* and *olivaceus,* the relatively slender-headed species, and *luteus* and *rotundipinnis,* the relatively wide-headed species of the group.

Orestias farfani is known from only two specimens, the holotype (106.0 mm SL), collected near the village of Vilurcuni, Lago Pequeño, Peru, and a second (115.0 mm SL) from Chililaya, Lago Titicaca, Bolivia. Nonetheless, it is recognized as a distinct species because the large, well-preserved holotype is distinguished readily from all other species in the genus.

Head scales, and those of the median dorsal ridge and lateral shield large, thick, and covered with dense granulations; scales dorsal to operculum thickened, creating an angular shoulder; opercular scales thickened, operculum stands away from head (as in fig. 8D); scales present on either side of median dorsal ridge; ventrum and basal portion of dorsal and anal fins unscaled. Caudal fin truncate.

Head and body medium brown dorsally, fading to light cream ventrally; minute light brown melanophores scattered overall (color pattern for the holotype; second specimen faded in alcohol).

Outer jaw teeth unicuspid, in one irregular row, tips light brown, barely protruding through epithelium covering upper and lower jaws.

MATERIAL: Holotype (AMNH 52143), an adult female, 106.0 mm SL, collected August 28, 1979 by Tom Coon and Sr. Acho, at a depth of from 1 to 2 m, at a distance of from 30 to 50 m from the shore, near the village of Vilurcuni, Lago Pequeño, Lago Titicaca.

ADDITIONAL MATERIAL (no type status): SU 9283, an adult female 115.0 mm, collected

FIG. 43. *Orestias albus* Valenciennes, MNHN 05.189, male, 125 mm SL.

by P. O. Simons (no date recorded), from Chililaya, Lago Titicaca, Bolivia.

RANGE: Known from the type locality as described above in Lago Pequeño, and Chililaya, both Lago Titicaca, in the Titicaca Basin (figs. 22 and 23).

ETYMOLOGY: The trivial name *farfani,* a genitive, in honor of Sr. L. Edgar Farfan Vizcardo, director of the Laboratorio de Puno, Instituto del Mar del Peru (IMARPE), to commemorate my appreciation for his generosity and support given to research on Lago Titicaca.

Orestias albus Valenciennes

Figures 8C, 43

Orestias albus. Valenciennes, 1839, p. 118 (*nomen nudum*); Valenciennes, in Cuvier and Valenciennes, 1846, pp. 242–243 (original description, Lago Titicaca); Tchernavin, 1944a, pp. 209–212 (in part, characters, synonymy, distribution); Terrazas, 1970, p. 34 (Bolivia, unconfirmed record).

Orestias Neveui. Pellegrin, 1904b, pp. 95–96 (original description, Lago Titicaca).

Orestias neveni. Eigenmann, 1910, p. 461 (misprint).

Orestias Neveu. Zuñiga, 1941, pp. 81–86 (misprint).

DIAGNOSIS AND REMARKS: One of the larger species of the *luteus* group of the *agassii* complex, distinguished by three autapomorphies: a robust lower jaw forming a prominent "chin" (fig. 43); a relatively long head, reaching nearly 40 percent of SL (table 8); and, a unique body shape characterized by a dorsal profile of the body that slopes very gently posteriorly, with no abrupt transition from the anterior of the base of the dorsal fin to the base of the caudal fin, the rays of which flare out slightly at its base (fig. 43).

Orestias neveui Pellegrin was described from one specimen fully scaled on the dorsal surface of the body rather than having scales absent from either side of the median dorsal ridge, as is the case for the syntypes of *O. albus* Valenciennes. However, the presence or absence of scales from either side of the median dorsal ridge is variable within numerous *Orestias* species (including, for example, *cuvieri* and *pentlandii* of the *cuvieri* complex) and is not considered a character useful for specific differentiation.

Tchernavin (1944a, p. 212) included Pellegrin's (1906) record of *O. albus* from Lago Ascotán, Chile in his description. The specimens on which this record was based (MNHN 05.186–188) have been examined and determined as *O. ascotanensis,* a new species (pp. 196–197).

Additional meristic and morphometric data for *O. albus* are summarized in tables 3 through 12.

MATERIAL: Syntypes (MNHN A.9607), 2 adults, one male 132 mm SL, one female 142.4 mm SL, collected by M. Pentland, *ca.* 1839.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: BMNH 1862.11.15:30 (one adult female, 121 mm); MNHN 05.189 (one

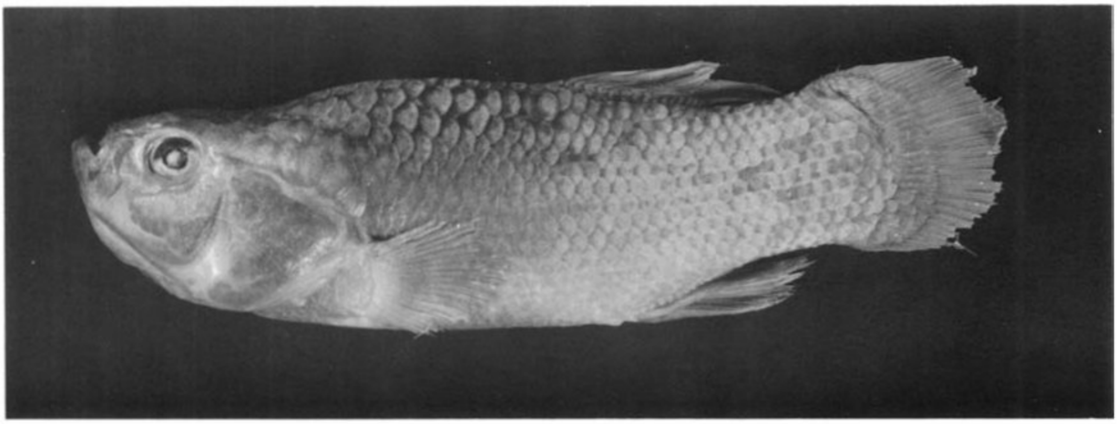

FIG. 44. *Orestias olivaceus* Garman, Syntype, MCZ 3946, male, 85.5 mm SL.

adult male, 125 mm, holotype of *O. neveui* Pellegrin); USNM 53522 (two adults); MCZ 27697 (one adult); Bahia de Uruni: BMNH 1944.6.6:49 (one adult male 97.8 mm, gill arches cleared and counterstained for bone and cartilage); Capachica: BMNH 1944.6.6: 50 (one adult female, 125 mm); Lago Pequeño, off Río Tiahuanaco: BMNH 1944.6.6: 51 (one adult male, 110 mm); Bahia de Taman: BMNH 1944.6.6:52 (one juvenile, 44 mm); Moho: MCZ 3948 (one adult); Bahia de Puno: FMNH 77410 (two adults); MCZ 3949 (one adult); CAS 40772 (two adults, 112–125 mm); AMNH 52197 (one adult female, 100 mm); Chucuito, FMNH 41120 (one adult); village of Ojjerani, S of Puno: AMNH 52144 (four subadults to adults, 60.0–90.5 mm); AMNH 52145 (one adult, 115 mm); AMNH 52146 (three adults, 95–108 mm); BMNH 1982.12.6:1 (one adult, 122 mm); Huancané: CAS 46180 (ex. IU 16091) (38 juveniles, 32–55 mm).

RANGE: Known from several localities in Lago Titicaca, including Bahia de Puno, the Capachica Peninsula and two of its northeastern bays (Taman and Uruni), Moho, and Huancané (figs. 22 and 23).

Orestias olivaceus Garman
Figure 44

Orestias olivaceus. Garman, 1895, pp. 152–159 (original description, Lago Umayo); Tchernavin, 1944a, pp. 199–204 (in part, characters, synonymy, distribution); Terrazas, 1970, p. 34 (Bolivia, unconfirmed record).

DIAGNOSIS AND REMARKS: A member of the *luteus* group of the *agassii* complex, distinguished from all other *Orestias* by orbits that are oriented dorsolaterally (see fig. 44), such that in dorsal view, both orbits are nearly completely visible.

Tchernavin (1944a) considered *O. silustani* Allen to be, in part, a synonym of *olivaceus* and, in part, a synonym of *agassii*; however, see comments for that species below for justification of its specific recognition. In addition, Tchernavin considered *O. affinis* Garman to be, in part, a synonym of *olivaceus,* and in part, a synonym of *agassii.* In fact, Tchernavin (1944a, pp. 199–204) regarded *affinis* as representing a hybrid between *olivaceus* and *agassii* in Lago Umayo. *Orestias affinis* Garman is considered herein (pp. 182–185) to be a synonym of *O. agassii* Valenciennes, although, the possibility that it represents a hybrid has not, of course, been refuted.

Orestias olivaceus, like all other species in the *luteus* group, has thick granulated scales on the dorsal surface of the head and body. Specimens examined are uniformly medium brown, although Garman (1895, p. 153) states that the species is olive dorsally, and silvery ventrally, and that individuals "of two inches" are olivaceous.

Morphometric and meristic data are summarized in tables 3 through 12.

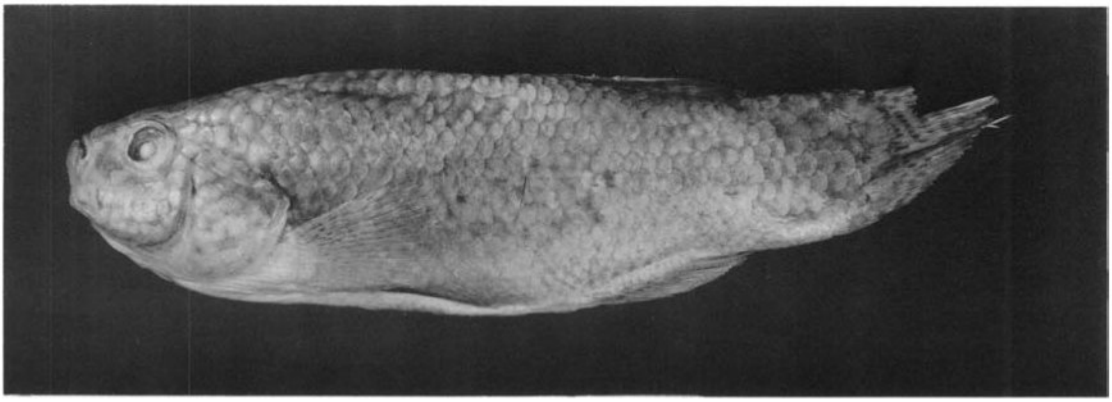

FIG. 45. *Orestias silustani* Allen, Holotype, CAS 44205, female, 84 mm SL.

Orestias olivaceus is known only from the syntype series of six specimens from Lago Umayo, and one recently collected specimen from Bahia de Puno, Lago Titicaca. Syntypes of *olivaceus* are present in two collections (MCZ and BMNH). I do not choose one as a lectotype here because Garman did not state the number of specimens on which he based his description of *olivaceus* and I do not know whether all syntypes have been located.

MATERIAL: Syntypes (MCZ 3946), five juvenile to adult males and females, 35 to 85.5 mm SL, (BMNH 1939.7.17:1, ex. MCZ 3946) one adult?, 60 mm, all collected 1875 by S. W. Garman from Lago Umayo.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: Bahia de Puno: AMNH 52163 (one adult, 93 mm).

RANGE: Known from Lago Umayo and Bahia de Puno, Lago Titicaca (figs. 22 and 23), and reported from Bolivia by Terrazas (1970), an unconfirmed record.

Orestias silustani Allen
Figure 45

Orestias silustani. Allen, in Eigenmann and Allen, 1942, pp. 366–367 (original description, Lago Umayo); Terrazas, 1970, p. 34 (Bolivia, unconfirmed record).

Orestias agassii. Tchernavin, 1944a, p. 162 (in part, possibly error in compilation of synonymy).

Orestias olivaceus. Tchernavin, 1944a, pp. 199–204 (in part, characters, synonymy, distribution).

DIAGNOSIS AND REMARKS: A relatively robust species of the *agassii* complex, distinguished by its nearly straight dorsal profile of the head and body in the largest adult (holotype). The smallest specimens of *silustani* are not readily distinguishable from the smallest juveniles within the *luteus* group of the *agassii* complex. Although all the scales of the adult holotype are smooth, those of a juvenile (60 mm SL) are granulated. The juvenile paratypes are presumed to be conspecific with the holotype solely because of their being collected together. Adult members of the *luteus* group have densely granulated scales. Whether the granulated scales of the juveniles catalogued as *silustani* represent the primitive condition of granulation, or are actually young of another species (e.g., *O. olivaceus*, a *luteus* group species also found in Lago Umayo), awaits the examination of additional comparative material with more precise collecting data. At present, *silustani* is recognized as a distinct species because the largest adult (fig. 45) is readily distinguished from all other *Orestias*. This specimen (CAS 44205, ex. IU 16097) was indicated as the type (equals holotype) by Allen, in Eigenmann and Allen (1942, pl. xix, fig. 1). All remaining 17 specimens of IU 16097 (now CAS 44206) are listed herein as possible paratypes, although it is not clear which of them Allen wished to be considered part of the type series. Allen indicated that the description (p. 366) was to be based on five specimens, 55 to 86 mm in total length, catalogued as IU 16097. After removal of the holotype from IU 16097, it is impossible to tell on which four remaining specimens Allen based his description.

Tchernavin (1944a) listed *silustani* in the synonymies of both *agassii* (p. 162) and *olivaceus* (p. 199). However, in his table I, p. 144, Tchernavin lists *silustani* as a synonym only of *olivaceus.* Therefore, I believe that the listing of *silustani* in the synonymy of *agassii* should be considered a compilation error.

Meristic and morphometric data for this species are summarized in tables 3 through 12.

MATERIAL: Holotype (CAS 44205, ex. IU 16097), an adult female, 86 mm SL, collected January 1919, by W. R. Allen, from Lago Umayo. ?Paratypes (CAS 44206, ex. IU 16097), 17 juvenile to subadult males and females, 39 to 66 mm, taken along with the holotype.

RANGE: Known only from Lago Umayo (figs. 22 and 23).

Orestias agassii Valenciennes

Figures 4A, 8A, 9, 19, 21A

Orestias Agassii. Valenciennes, in Cuvier and Valenciennes, 1846, pp. 238–239 (original description, Río de Corocoro and San Antonio de Esquilaches, Peru).

Orestias Agassizii. Valenciennes, in Cuvier and Valenciennes, 1846, p. xv.

Orestias Agassisii. Valenciennes, in Cuvier and Valenciennes, 1846, pl. 536.

Orestias ortonii. Cope, 1876, p. 186 (original description, Lago Titicaca).

Orestias ortoni. Eigenmann, 1894a, p. 54 (compiled).

Orestias affinis. Garman, 1895, p. 152 (original description, Lago Umayo).

Orestias tirapatae. Boulenger, 1902, pp. 153–154 (original description, Tirapata, Peru).

Orestias Agassizi. Pellegrin, 1904b, p. 93 (characters).

Orestias Agassizi Var. *inornata.* Pellegrin, 1904b, p. 93 (original description, as a variety, Lago Titicaca and Lago Poopó).

Orestias Agassizi Var. *typica.* Pellegrin, 1904b, p. 93 (original description, as a variety, Lago Titicaca).

Orestias Agassizi Var. *Senechali.* Pellegrin, 1904b, p. 94 (original description, as a variety, Lago Titicaca).

Orestias Agassizi Var. *Crequii.* Pellegrin, 1904b, p. 94 (original description, as a variety, Lago Titicaca).

Orestias uyunius. Fowler, 1940, pp. 63–64 (original description, Salar de Uyuni, Bolivia).

Orestias agassii owenii. not *O. owenii* Valenciennes, Tchernavin, 1944a, pp. 177–182 (characters, distribution, synonymy).

Orestias agassii. Tchernavin, 1944a, pp. 162–177 (in part, characters, synonymy, distribution); Lueken, 1962, pp. 195–198 (karyology); Villwock, 1964, p. 285 (discussion of hybridization with *Orestias olivaceus* Garman).

Orestias langui. Tchernavin, 1944a, pp. 197–199 (original description, headwaters of the Río Urubamba, Langui, Peru).

Orestias agassi. Parenti, 1981, p. 526 (listed material).

DIAGNOSIS AND REMARKS: The most widespread, abundant and variable species with *Orestias*; a member of the *agassii* complex most closely related to a group including *O. jussiei, silustani, puni,* and the *luteus* group (see fig. 30), and like them, relatively deep bodied, particularly in the largest adults (table 10). *Orestias agassii* is generally distinguished from other species in this group by a very irregular head squamation pattern, usually with no head scales anterior to the orbit, and scales absent from either side of the median dorsal ridge, especially in younger individuals.

As recognized by Tchernavin (1944a, pp. 162–177), *O. agassii* included *O. empyraeus* Allen, *elegans* Garman, *tschudii* Castelnau, and possibly *silustani* (however, see diagnosis and remarks for that species, above), all recognized as distinct species in the current revision. *Orestias uyunius* Fowler and *O. langui* Tchernavin are placed in the synonymy of *agassii.* Furthermore, several populations of *agassii* of Tchernavin are recognized as distinct species, such as specimens from Lago Ascotán, Chile, described herein as *O. ascotanensis,* below. One important result of these taxonomic changes is that *agassii* is no longer recognized as a species ranging throughout the distributional limits of *Orestias.* It is now defined as a species found throughout the Urubamba and Titicaca basins and in northern Chile (Arratia, 1982).

Most species within the *agassii* complex vary little in number of dorsal and anal fin rays (tables 4 and 5). Recognition of individual species in the past has been based primarily on differences in overall body shape. This criterion is used in the present study to recognize several species (e.g., *frontosus*); however, specimens such as those referred to *uyunius* Fowler and *langui* Tchernavin fall within the typical range of variation for one or several populations referred to *agassii*. Some of the characters used previously to define species or subspecies now placed in the synonymy of *agassii* may be found in the future to represent consistent differences among populations which might be considered additional species within the *agassii* complex. This problem is outside of the present revision, however. Morphometric and meristic data for *agassii* are summarized in tables 3 through 12.

Several different spellings of the specific modifier of *Orestias agassii* Valenciennes appear in Valenciennes, in Cuvier and Valenciennes (1846), as listed in the synonymy, above. It is not obvious from the work how Valenciennes wished to form a patronym honoring Agassiz. Therefore, the spelling of *Orestias agassii* Valenciennes used here is the one that appears above the original description. It is also the one used by the majority of modern workers on *Orestias* (e.g., Tchernavin, 1944a, Villwock, 1964, and Lauzanne, 1981).

MATERIAL: Syntypes (MNHN A.9601), two adults, 77 to 79 mm SL, from Río de Corocoro; (MNHN A.9602), six subadults to adults, 49.5 to 59.7 mm, from San Antonio de Esquilaches, both Titicaca Basin.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: Syntypes of Pellegrin's (1904b) varieties of *agassii*: *crequii* (MNHN 05.181–183), three males, 45 to 58 mm SL; *senechali* (MNHN 05.179–180), two females, 39.7 to 69 mm, and (MNHN 05.174–178), five males, 52.4 to 57 mm; *typica* (MNHN 05.171–173), three adults, 74.6 to 79 mm; *inornata* (MNHN 05.166–168) three adults, 69.5 to 80 mm; holotype of *Orestias ortonii* Cope: (ANSP 21577) one adult male, 126 mm.

MCZ 3935 (45 juvenile to adult males and females, 22.0–62.0 mm); BMNH 1862.11.15: 34 (10 adult males and females, 50–63 mm, one cleared and counterstained for bone and cartilage); BMNH 1858.11.3:347 (24); AMNH 20353 (eight juveniles) (two cleared and counterstained for bone and cartilage); MCZ 31111; MCZ 6462; MCZ 3937; MCZ 3932; USNM 53516; USNM 23259 (1); ANSP 6983 (1); USNM 127095 (1); San Pablo: USNM 167743 (5); CAS 48256 (12); Chucuito: CAS 48251 (1); USNM 167740 (2); Bahia de Moho: FMNH 77373 (24); FMNH 77364 (31); CAS 40771 (ex. IU 16087) (100 juveniles); CAS 46165 (ex. IU 16088) (100 juveniles); UMMZ 179282 (ex. IU 16076) (2); Capachica Peninsula: BMNH 1944.6.6:309–320 (102); BMNH 1944.6.6:308 (1); BMNH 1944.6.6:301–305 (11); BMNH 1944.6.6:245–249 (six males); BMNH 1944.6.6:306 (4); BMNH 1944.6.6:331 (3); BMNH 1944.6.6:326–330 (10); BMNH 1944.6.6:291 (nine juveniles); BMNH 1944.6.6:322–325 (5); USNM 133143 (1); AMNH 52147 (39 juveniles to adult males and females, 25–77.8 mm, four cleared and counterstained for bone and cartilage); USNM 228142; Bahia de Puno: CAS 46172 (24); FMNH 80321 (31); USNM 228145 (20); USNM 228140 (30); AMNH 52148 (76 juvenile to adult males and females, 36.7–133 mm); AMNH 52149 (13 adult males and females, 61–116 mm); BMNH 1982.12.6:2–24 (23, 70–106 mm); AMNH 52153 (six adults, 75–110 mm); AMNH 52152 (seven adults, 60–94 mm); AMNH 52151 (four adults, 60–85 mm); AMNH 52154 (one adult, 85 mm); AMNH 52155 (37 juveniles, 13.5–23.1 mm); AMNH 52156 (two adults, 67.7–70 mm); Isla Taquile: AMNH 52157 (two adults, 52–62 mm); Lago Pequeño: Huatayata: AMNH 52158 (14 juveniles to adults, 31.9–88 mm); Vilurcuni: AMNH 52150 (two adults, 86.5–112 mm); AMNH 52159 (six adults, 71–74 mm); AMNH 52160 (63 juveniles to adults, 8.3–69.0 mm); Guaqui: FMNH 77374 (202); CAS 46353 (ex. IU 16099) (17).

Lago Umayo: Syntypes of *Orestias affinis* Garman (MCZ 27698) 14 subadults to adults, 41.5–62.6 mm.

USNM 120280 (ex. MCZ 27698) (four subadults to adults, 45–54 mm); Río Ilave: UMMZ 179277 (ex. IU 16119) (3); CAS 48250 (ex. IU 16119) (five subadults, 41–78 mm); Ilave: CAS 46167 (ex. IU 16116) (12): Río Caminaque below Ilave: UMMZ

179276 (ex. IU 16118) (15); CAS 42534 (ex. IU 16118) (20).

Lago Poopó: Additional syntypes of *inornata* Pellegrin: (MNHN 05.169–170) two females, 46–54.3 mm.

CAS 46352 (ex. IU 16098) (50); USNM 167734 (ex. IU 16098) (14).

Río de Lampa: UMMZ 179278 (ex. IU 16124) (20); CAS 46164 (ex. IU 16124) (46).

Lago Saracocha: FMNH 77379 (147); USNM 167737 (15); Río Saracocha: USNM 133150 (2); BMNH 1944.6.6:63–68 (6).

Laguna de Arapa: CAS 46354 (ex. IU 16110) (4); BMNH 1944.6.6:225–234 (42 juveniles).

Río de Azángaro: UMMZ 179287 (ex. IU 16128) (23).

Río de Molino, near Juli: CAS 48260 (ex. IU 16127) (71); UMMZ 179286 (ex. IU 16127) (18); Río de Juli: CAS 46152 (ex. IU 16106) (76).

Huancané: CAS 46351 (ex. IU 16115) (70); CAS 46350 (ex. IU 16089) (5).

Río de Tiahuanaco: UMMZ 179280 (ex. IU 16126) (11); CAS 46161 (ex. IU 16126) (29).

Río Mauri at Calacota: UMMZ 179269 (ex. IU 15239?) (23); CAS 46162 (ex. IU 15239?) (38); Río Mulato: UMMZ 179270 (ex. IU 15250) (15); FMNH 77388 (106); Río Desaguadero at Calacota: UMMZ 179272 (ex. IU 16093) (21); CAS 40774 (ex. IU 16093) (86); CAS 46168 (ex. IU 16093) (66).

Pampa de Acora: UMMZ 179274 (ex. IU 16112) (13); CAS 48246 (ex. IU 16112) (80); FMNH 77385 (514).

Crucero Alto: CAS 46173 (ex. IU 14660?) (1); CAS 46171 (ex. IU 15243) (3); USNM 167739 (ex. IU 15243) (2).

Río de Santa Rosa: CAS 48249 (ex. IU 17867) (28).

Río de Eucalyptus at Eucalyptus: FMNH 77378 (66); UMMZ 179275 (ex. IU 16114) (20).

Río Colorado at Viacha: FMNH 88670 (165); CAS 48253 (ex. IU 16108) (31); UMMZ 179273 (ex. IU 16108) (11).

Río Grande de Lipez: CAS 46170 (ex. IU 16125) (73).

Río de Chupa: UMMZ 179284 (ex. IU 16111) (6); FMMH 88763 (26); FMNH 77391 (349).

Lago Huaypo: UMMZ 179271 (ex. IU 16067) (20); CAS 46157 (ex. IU 16067) (49).

Río Ilpa: AMNH 52161 (25 subadults to adults, 31–57 mm).

Río Ayaviri: AMNH 52162 (28 subadults to adults, 20–55 mm).

Lagunillas: UMMZ 179268 (ex. IU 16122) (18); CAS 46159 (ex. IU 16122) (72); BMNH 1944.6.6:342–349 (nine males, one cleared and counterstained for bone and cartilage); BMNH 1944.6.6:350–354 (seven females, one cleared and counterstained for bone and cartilage); BMNH 1944.6.6:332–341 (20 males and females, one cleared and counterstained for bone and cartilage).

Urubamba Basin: Lago Urcos: FMNH 89062 (189); CAS 46348 (ex. IU 16063) (19); USNM 167729 (ex. IU 16063) (5); Cuzco: Hacienda Urco: FMNH 70368 (48).

Pueblo Urubamba: FMNH 94185 (74); swamps at upper edge of Urubamba: CAS 48247 (ex. IU 16068) (48).

Río Huatanay: Isenchaca: UMMZ 179281 (ex. IU 16071) (6).

Río Layo: BMNH 1944.6.6:364 (four juveniles); BMNH 1944.6.6:361–362 (two juveniles); BMNH 1944.6.6:363 (one juvenile); BMNH 1944.6.6:53–62 (17 juveniles to subadults).

Cailloma: FMNH 70366 (105 juveniles to adults); FMNH 70369 (49 juveniles to adults).

Tirapata: Syntypes of *Orestias tirapatae* Boulenger (BMNH 1902.7.29:129–133) four adult females, one juvenile; Ríos de Pucara y Porque: UMMZ 179283 (ex. IU 16092) (11); CAS 46158 (ex. IU 16092) (31).

Río de Langui: FMNH 77372 (62); CAS 46349 (ex. IU 16073) (16); CAS 46153 (ex. IU 16074) (18); Laguna Langui: CAS 46154 (ex. IU 16072) (31); BMNH 1944.6.6:365–369 (20); BMNH 1944.6.6:370 (1); Langui Village, Upper Urubamba: Holotype of *Orestias langui* Tchernavin (BMNH 1944.6.6:152) one adult female, 62 mm; Paratypes (BMNH 1944.6.6:153–156) four adult males.

Salar de Uyuni: department of Potosí at Llica: holotype of *Orestias uyunius* Fowler (ANSP 68866) one adult female, 81 mm, Paratypes (ANSP 68867–68891) 25 juveniles to adults; ANSP 83977 (non-type material) (73 juveniles to adults, 23–63 mm).

RANGE: The most wide-ranging species of

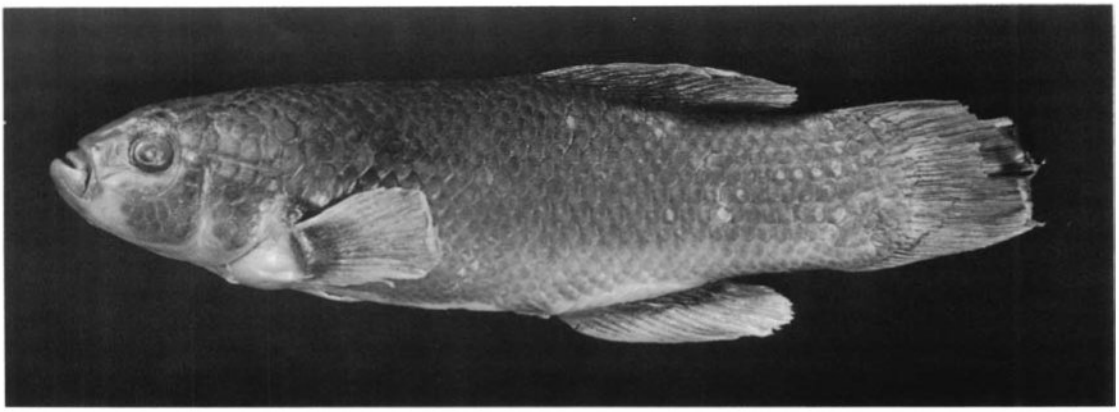

FIG. 46. *Orestias empyraeus* Allen, Paratype, CAS 44196, male, 101 mm SL.

the genus *Orestias,* found throughout localities in the Urubamba and Titicaca basins, as well as the Salar de Uyuni, in southern Bolivia, and in northern Chile (see Arratia, 1982 for Chilean localities).

Orestias empyraeus Allen
Figure 46

Orestias empyraeus. Allen, in Eigenmann and Allen, 1942, pp. 367–370 (original description, Lago Junin, Peru).

Orestias elegans. (Not *Orestias elegans* Garman). Allen, in Eigenmann and Allen, 1942, p. 371 (in part).

Orestias agassii. Tchernavin, 1944a, pp. 162–177 (characters, distribution, synonymy).

DIAGNOSIS: A species of the *agassii* complex most closely rclated to *polonorum,* distinguished from it and other species of the complex by a head that in dorsal profile tapers toward the snout, and an associated large preorbital distance, ranging between 8 and 12 percent of SL (table 12); and, lips thick and fleshy in largest adults. Additional morphometric and meristic data are summarized in tables 3 through 12.

MATERIAL AND REMARKS: In the description of *empyraeus,* Allen, in Eigenmann and Allen (1942, pp. 367–368) listed 13 IU catalogue numbers for referred material. He mentioned (p. 369) "the type, 120 mm. long, Lake Chinchaycocha (15238)." This specimen, 124 mm SL, and figured in plate xx of Allen, has been identified as the holotype, now CAS 44195, an adult male, collected by W. R. Allen on September 6, 1918 from Lago Chinchaycocha (=L. Junin, fig. 24). Additional specimens from this IU lot are paratypes: CAS 44196 (10 juveniles to adults); CAS 44197 (6). Additional paratype material at CAS: Peru: Pachaca: CAS 44200 (ex. IU 15234) (8); Lago Yanamaté: CAS 44198 (ex. IU 15241) (66); Río Mantaro at Zigzag: CAS 44201 (ex. IU 15236) (originally 53 spec., 48 *empyraeus,* 5 cf. *Trichomycterus* sp.); Tilarnioc: CAS 44202 (ex. IU 15237) (23); Jauja: CAS 44199 (ex. IU 15233) (83); Huancayo: CAS 48248 (ex. IU 15232) (50 juveniles to adults, 18–94 mm); Lago Junin: CAS 46163 (ex. IU 15239) (35 juveniles to adults, 14–65 mm); Cerro de Pasco, at railway to Goyllarisquisga: CAS 46356 (ex. IU 15248) (54 juveniles to adults, 15–52 mm); Lago Pocobamba, near Cerro de Pasco: CAS 46155 (ex. IU 15246) (17 juveniles to adults, 15–40 mm).

Additional paratypes of catalogued IU material have been identified as follows from the collections of the USNM and UMMZ: Lago Junin: USNM 167741 (ex. IU 15239) (nine subadults to adults, 47–99 mm); Tilarnioc: USNM 167742 (ex. IU 15237) (five juveniles to adults, 33–65 mm); Huancayo: UMMZ 179288 (ex. IU 15232) (four subadults to adults, 43–73.5 mm); Río Mantaro at Zigzag: UMMZ 179289 (ex. IU 15236) (originally 25 specimens, 24 juveniles to adult *empyraeus,* 21–50 mm, one juvenile cf. *Trichomycterus* sp.).

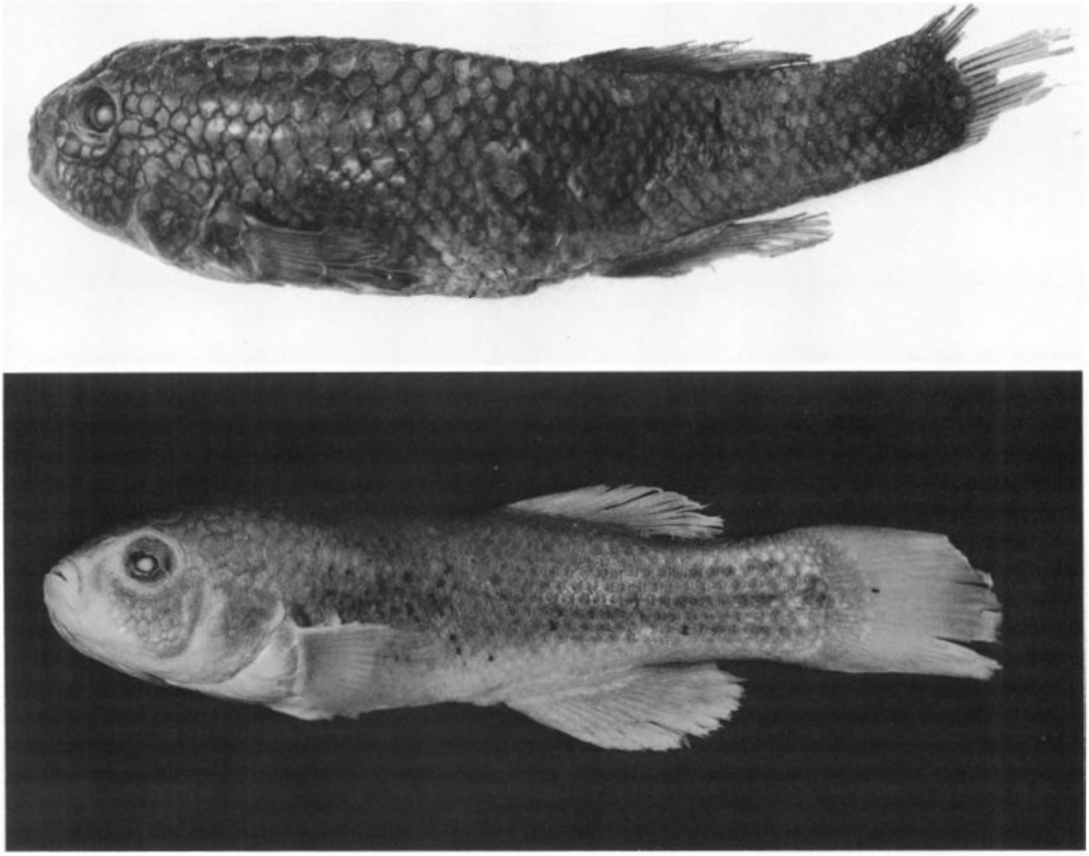

FIG. 47. *Orestias frontosus* Cope, above, Syntype, ANSP 21555, male, 152 mm SL; below, BMNH 1944.6.6:79–83, male, 91 mm SL (Syntype of *Orestias pequeni* Tchernavin).

The identification of additional type material in institutions that received IU material is a possibility when these specimens are again reviewed; however, the identification as type material requires caution. Much of the type material listed by Allen may not be identified positively, lots may contain primarily catfish and may be catalogued as such, or the same IU catalogue number may have been given to two or more lots and must be checked with the IU catalogues now at CAS.

Two specimens were removed from IU 15238, not recatalogued, but referred by Allen to *O. elegans*. These specimens, two adults from Lago Junin, are bleached and have lost many of their scales; however, I tentatively refer them to *empyraeus* (CAS 48258).

ADDITIONAL MATERIAL: Lago Junin: CAS 44203 (18 juveniles to adults, 17–93 mm, two adults, 50–54 mm cleared and counterstained for bone and cartilage); FMNH 77545 (53), BMNH 1875.10.5:8 (one adult, 108 mm).

RANGE: Known primarily from Lago Junin in northern Peru (fig. 24) and its tributary streams, as well as Río Huallaga and the Río Mantaro.

Orestias frontosus Cope

Figure 47

Orestias frontosus. Cope, 1876, p. 187 (original description, Lago Titicaca).

Orestias agassii tschudii. Tchernavin, 1944a, pp. 182–185 (in part, characters, synonymy, distribution).

Orestias agassii pequeni. Tchernavin, 1944a, pp.

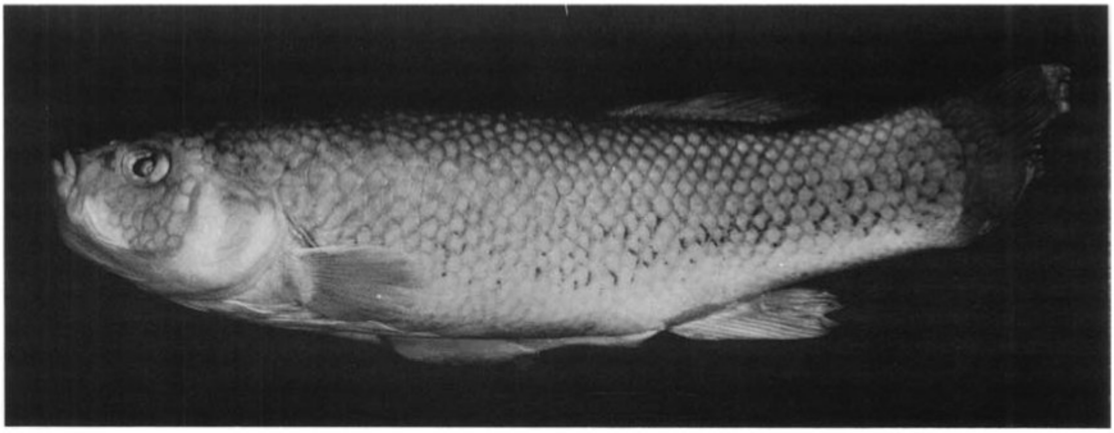

FIG. 48. *Orestias polonorum* Tchernavin, Lectotype, BMNH 1944.6.6:223, female, 120 mm SL.

185–186 (original description as an infraspecies, Lago Pequeño, Lago Titicaca).

DIAGNOSIS AND REMARKS: A member of the *agassii* complex, closely related to *tschudii* and *richersoni*, but differing from them in having a very blunt snout and rounded head throughout life (see fig. 47). The large individuals of *frontosus* also have a very pronounced band along the base of the pectoral fin rays, characteristic of a larger group of *agassii* complex species to which *frontosus* belongs.

Tchernavin (1944a) did not consider *O. frontosus* Cope to be distinct from *O. agassii tschudii* Castelnau, and yet he recognized *O. agassii pequeni* as distinct, naming it as new. Both *tschudii* and *pequeni* were recognized as infraspecies of *agassii*, a rank Tchernavin considered to be (p. 144) "of lesser taxonomic significance . . ." than the categories of species or subspecies.

Within the species *frontosus* as recognized here, several degrees of pigmentation of the fins are represented, ranging from clear and having almost no melanophores in the syntype series of *pequeni* (BMNH 1944.6.6:79–83), dusky in the syntypes of *frontosus* (ANSP 21555–6), to pectoral fins with a very pronounced dark band along the basal portion of the rays in specimens collected recently from Lago Titicaca. The basal portions of the dorsal and anal fin rays have a weak to very strong dark band also. It is unknown to what degree these pigments fade in preservation, although they are always most prominent in recently collected specimens.

Morphometric and meristic data for *frontosus* are summarized in tables 3 through 12.

MATERIAL: Syntypes (ANSP 21555–6), one adult male, 155 mm SL, one adult female, 141 mm SL, collected by J. Orton, 1873, from Lago Titicaca.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: USNM 127096 (two adults, 82.9–105 mm); BMNH 1890.2.7:57–58 (two adults); Capachica Peninsula: AMNH 52172 (five adults, 109–140 mm); AMNH 52173 (26 adults, 91–135 mm); AMNH 52170 (one adult, 105 mm); BMNH 1944.6.6:183 (1); Bahia de Puno: AMNH 52171 (one adult, 111 mm); village of Ojjerani: AMNH 52169 (eight subadults to adults, 52–127 mm); Sotalaya: AMNH 52166 (27 adults, 80–108 mm); Lago Pequeño: off Isla Taquiri: Syntypes of *O. agassii pequeni* Tchernavin (BMNH 1944.6.6:79–83) six adult males and females, 86 to 105 mm, collected July 30, 1937, at a depth of from 2.7 to 2.8 m, Percy Sladen Titicaca Expedition. Lago Pequeño: village of Vilurcuni: AMNH 52164 (one adult, 114 mm); AMNH 52165 (two adults, 117–125 mm); Huatayata: AMNH 52167 (one adult, 87 mm); AMNH 52168 (three subadults, 75–77 mm).

RANGE: Known from several localities throughout Lago Titicaca, including Lago Pequeño, Bahia de Puno, the Capachica Peninsula, and Sotalaya, on the eastern shore (figs. 22 and 23).

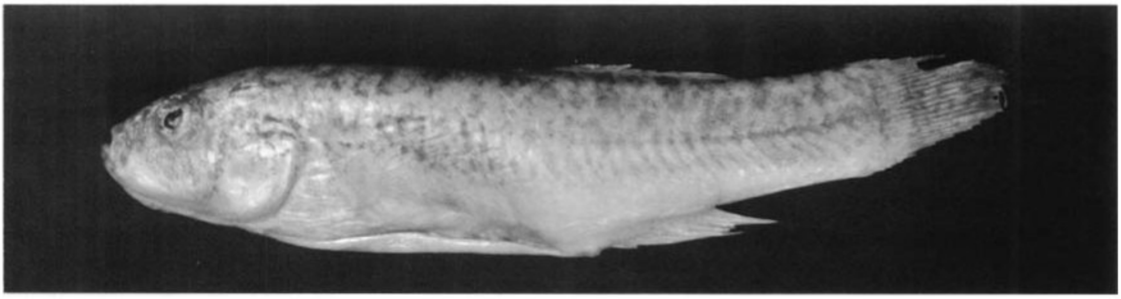

FIG. 49. *Orestias elegans* Garman, Syntype, MCZ 27694, female, 44 mm SL.

Orestias polonorum Tchernavin

Figure 48

Orestias polonorum. Tchernavin, 1944a, pp. 195–197 (original description, Lago Junin, Peru).

DIAGNOSIS AND REMARKS: A species of the *agassii* complex, most closely related to *empyraeus* with which it shares an extremely irregular and incomplete median dorsal ridge formed by small, smooth scales; distinguished from all other species of the complex by a head that is rectangular in lateral view, with a straight dorsal profile and angular "chin" (fig. 48).

The five syntypes, the only known specimens, are faded in alcohol except for the presence of scattered, discrete dark spots distributed randomly over the dorsal and lateral surfaces. The largest specimen (BMNH 1944.6.6:223) is figured by Tchernavin (1944a, p. 195) and is therefore chosen as the lectotype. Morphometric and meristic data for these five specimens are summarized in tables 3 through 12.

MATERIAL: Lectotype (BMNH 1944.6.6: 223), an adult female, 120 mm SL, collected 1937 by H. Morrison from Lago Junin, designated herein. Paralectotypes (BMNH 1875.10.5:4–7) four adults, 105 to 117 mm, collected by Jelski, member of the Count K. Branicki Expedition to South America in 1866–1867, from Lago Junin.

RANGE: Known only from the type series, Lago Junin, Peru (fig. 24).

Orestias elegans Garman

Figures 18B, 49

Orestias elegans. Garman, 1895, p. 149 (original description, headwaters of the Río Santa Eulalia where it meets the Río Rimac, Peru).

Orestias agassii elegans. Tchernavin, 1944a, pp. 186–189 (characters, synonymy, distribution).

DIAGNOSIS AND REMARKS: A slender and elongate species of the *agassii* complex, most closely related to *gymnotus*, another elongate species, both members of a larger group of *agassii* complex species that are defined as a

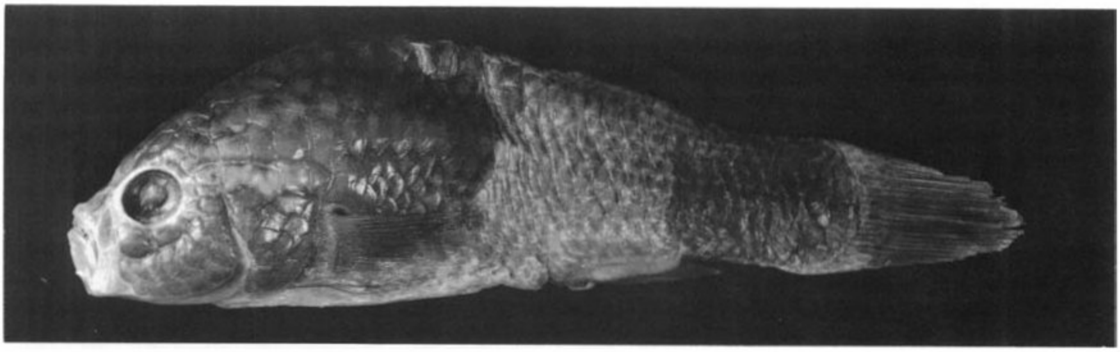

FIG. 50. *Orestias jussiei* Valenciennes, Syntype, MNHN A.9599, female, 80.5 mm SL.

monophyletic group by a reduced squamation pattern characterized by a unique distribution of lateral scales (pp. 123–126); *elegans* is distinguished by an increase in the modal number of scales in a lateral series to 35 or 36, with an observed range of from 34 to 38 (table 7). Its closest relative, *gymnotus*, has a modal number of 34 scales in a lateral series, with an observed range of from 31 to 35 scales (table 7). Additional morphometric and meristic data for *elegans* are summarized in tables 3 through 12.

Most specimens examined are bleached; however, some do have a silvery ventral and lateral surface of the body, as noted by Garman (1895, p. 149) in his original description. Syntypes have been located in the collections of the MCZ and BMNH. However, it is not known whether all syntypes have been examined, and therefore, no lectotype is designated.

MATERIAL: Syntypes (MCZ 27694) 10 juvenile to subadult males and females, 32 to 49 mm SL (BMNH 1939.7.17:3, ex. MCZ 27694) one subadult, 48 mm, collected by S. W. Garman, in small lakes among the headwaters of the Rio Santa Eulalia where it meets the Río Rimac.

ADDITIONAL MATERIAL: Peru: Río Santa Eulalia: CAS 46179 (ex. IU 15242) (46 juvenile to adult males and females, 24–87 mm, four of the juveniles to adults, 37–64 mm cleared and counterstained for bone and cartilage).

RANGE: Known only from the Río Santa Eulalia in northern Peru (fig. 24), on the Pacific slope of the Andes.

Orestias jussiei Valenciennes

Figures 13, 20A, 50

Orestias Jussiei. Valenciennes, in Cuvier and Valenciennes, 1846, pp. 235–238 (original description, Río Guasacona, Peru).

Orestias Jussieui. Castelnau, 1855, pl. 27, fig. 1.

Orestias Owenii. Valenciennes, in Cuvier and Valenciennes, 1846, pp. 241–242 (original description, Lago Urcos, Peru).

?*Orestias Oweni.* Rowntree, 1903, p. 69 (report of ductus pneumaticus located to the right of middorsal line).

Orestias jussiei. Tchernavin, 1944a, pp. 189–191 (in part, characters, distribution, synonymy).

DIAGNOSIS AND REMARKS: A relatively robust species of the *agassii* complex with large, thick, smooth head and body scales, distinguished from other members of the complex by: a lower jaw at a 90-degree angle to the body axis (figs. 20A and 50); and, a convex dorsal profile, rising very sharply from the tip of the snout to the middle of the median dorsal ridge. The latter character, a convex dorsal profile, is evident in juveniles as well as large adults (fig. 50).

Morphometric and meristic data for *jussiei* are summarized in tables 3 through 12.

Tchernavin (1944a, p. 177) stated that the types of *Orestias owenii* Valenciennes, of the collection of the Muséum National d'Histoire Naturelle, were lost. He based his diagnosis of *Orestias agassii owenii* (pp. 177–182) on specimens of *Orestias agassii* from Lago Urcos, in the Urubamba Basin, the type locality of *O. owenii* Valenciennes. The types of Valenciennes' *owenii,* however, are still in existence in the MNHN. I examined these and determined them to be the young of *O. jussiei,* known also from the Urubamba Basin.

Orestias jussiei puni Tchernavin is treated as a valid species in the present revision (pp. 189–190).

MATERIAL: Syntypes (MNHN A.9599), three adults, 68 to 80 mm SL, collected from the Río Guasacona in the Urubamba Basin.

ADDITIONAL MATERIAL: Urubamba Basin: Lago Urcos: Syntypes of *Orestias owenii* Valenciennes (MNHN A.9606), five juveniles, 33 to 55 mm; Lago Chinchero: CAS 46175 (ex. IU 16066) (37 juvenile to adult males and females, 30–84 mm, four cleared and counterstained for bone and cartilage); USNM 167730 (ex. IU 16066) (7).

RANGE: Known from several localities in the Urubamba basin (Río Guasacona, Lago Urcos, and Lago Chinchero) (fig. 24).

Orestias puni Tchernavin

Figures 8B, 51

Orestias jussiei puni. Tchernavin, 1944a, pp. 194–195 (original description, as a subspecies, Bahia de Puno, Lago Titicaca).

DIAGNOSIS AND REMARKS: A robust member of the *agassii* complex, distinguished from all other species in the complex (minus *O. luteus*) by: a very deep caudal peduncle,

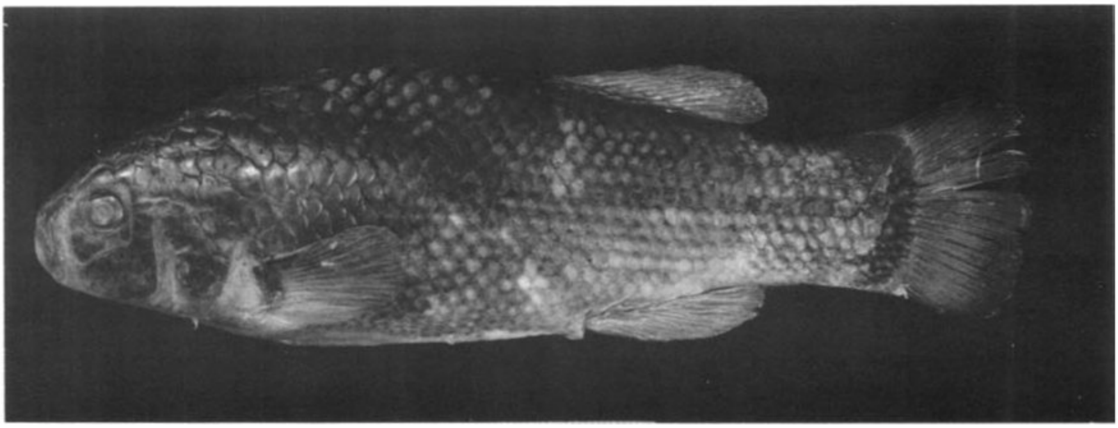

FIG. 51. *Orestias puni* Tchernavin, AMNH 52175, female, 111 mm SL.

reaching a depth of over 22 percent of SL (table 11). *Orestias luteus* is the only other species in the genus in which individuals have such a deep caudal peduncle. However, *puni* is readily distinguished from all species of the *luteus* group by large, thick smooth scales on the head and body, rather than granulated scales which is diagnostic of the *luteus* group. Morphometric and meristic data are summarized in tables 3 through 12.

MATERIAL: Syntypes (BMNH 1944.6.6: 179–180), two adults, one male 124 mm SL, one female 122 mm, collected August 1, 1937 (BMNH 1944.6.6:181), one adult, 117 mm, collected August 5, 1937 (BMNH 1944.6.6: 182) one adult, 120 mm, collected July 22, 1937, all collected by the Percy Sladen Titicaca Expedition, from Bahia de Puno, Lago Titicaca.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: AMNH 52174 (one adult, 80 mm); Capachica Peninsula: AMNH 52175 (two adults, 111–120 mm); Lago Umayo: CAS 46355 (ex. IU 16095) (8).

RANGE: Known from Bahia de Puno and the Capachica Peninsula in Lago Titicaca, and Lago Umayo (figs. 22 and 23).

Orestias parinacotensis Arratia
Figure 52

Orestias parinacotensis. Arratia, 1982, pp. 100–103 (original description, Bofedales de Parinacota, Chile).

DIAGNOSIS: One of the four species of *Orestias* (the others are *agassii, ascotanensis,* and *laucaensis* of the *agassii* complex) with members in Chile, most closely related to the latter two species. *Orestias parinacotensis* is distinguished by a straight dorsal head profile and a head that is greatly flattened in both males and females (see fig. 52).

REMARKS: *Orestias parinacotensis* Arratia has not been examined, as notice of deposition of specimens was received just prior to publication of this revision. The holotype of this species, as well as that of *O. laucaensis,* is deposited in the Colección de Ictiología, Laboratorio de Biología, Universidad de Chile, Santiago-Sur. Additional specimens (including paratypes) have been deposited in the collection of the University of Kansas, Museum of Natural History. Morphometric and meristic data presented in the current paper (tables 4 through 11) are from a prepublication copy of Arratia (1982).

RANGE: Known from the Chilean Altiplano, in Parinacota, Chile (fig. 25). See also Arratia (1982) for remarks on the locality.

Orestias laucaensis Arratia
Figure 53

Orestias laucaensis. Arratia, 1982, pp. 103–104 (original description, Río Lauca, Parinacota, Chile).

DIAGNOSIS: One of the four species (*agassii, parinacotensis, ascotanensis,* in addition to *laucaensis*) of *Orestias* with members in Chile,

FIG. 52. *Orestias parinacotensis* Arratia, above, Paratype, KU 19213, female, 62.3 mm SL; below, Paratype, KU 19213, male, 44.5 mm SL.

most closely related to the last two species, all of the *agassii* complex. *Orestias laucaensis* is the only species of *Orestias* known to have sexually dimorphic chromosome numbers. The diploid number of chromosomes is increased to 52 in males, and 50 or 51 in females, as opposed to a plesiomorphic diploid number for teleosts of 48 in both males and females (see discussion, above).

REMARKS: *Orestias laucaensis* Arratia has not been examined (see remarks under *O. parinacotensis* Arratia, above). The holotype of this species is deposited in the Colección de Ictiología, Laboratorio de Biología, Universidad de Chile, Santiago-Sur. Additional specimens (including paratypes) have been deposited in the collection of the University of Kansas, Museum of Natural History. Morphometric and meristic data for this species (tables 4 through 11) are from a pre-publication copy of Arratia (1982).

RANGE: Known from Río Lauca, Parinacota, Chile, on the Chilean Altiplano (fig. 25). See also Arratia (1982) for remarks on the locality.

Orestias tschudii Castelnau
Figure 54

Orestias Tschudii. Castelnau, 1855, pp. 51–52 (original description, Lago Titicaca).

Orestias Tschudi. Bleeker, 1860, p. 487 (compiled).

Orestias agassii tschudii. Tchernavin, 1944a, pp. 182–185 (in part, characters, synonymy, distribution).

DIAGNOSIS: A member of the *agassii* complex, with large, thick, smooth head and body scales, closely related to *richersoni*, diagnosable by: an increased modal number of 19 pectoral fin rays, with an observed range of from 17 to 20 (table 6), and an increased modal number of 34 vertebrae, with an observed range of from 33 to 35 (table 3).

REMARKS: See remarks under *O. frontosus* (p. 187) for pertinent comments on this species.

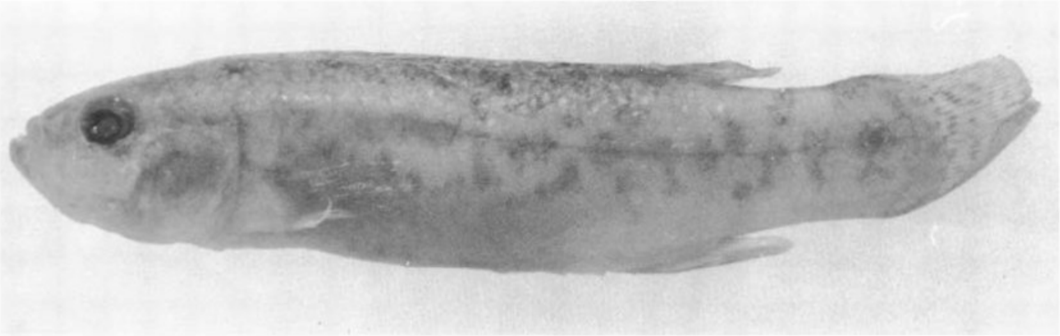

FIG. 53. *Orestias laucaensis* Arratia, Paratype, KU 19124, female, 67.4 mm SL.

MATERIAL: Syntypes (MNHN A.9604) three adults, 118 to 129 mm SL, collected from Lago Titicaca.

ADDITIONAL MATERIAL: Titicaca Basin: Lago Titicaca: AMNH 38425 (one adult, 125 mm); AMNH 38427 (one adult, 145 mm); Bahia de Puno: BMNH 1944.6.6:162–167; BMNH 1944.6.6:168–172; BMNH 1944.6.6: 204–211 (12); BMNH 1944.6.6:212–217; AMNH 52177 (19 adult males and females, 79–102 mm); FMNH 88806 (9); Capachica Peninsula: BMNH 1982.12.6:124–131 (eight adults, 99–112 mm); AMNH 52176 (47 adults, 88–132 mm); BMNH 1944.6.6:190–197; BMNH 1944.6.6:218–221 (4); BMNH 1944.6.6:198–203 (7); BMNH 1944.6.6:184–187 (8); CAS 48252 (16 subadults to adult, 40–131 mm); Huancané: BMNH 1944.6.6: 222 (1); Lago Pequeño: Taraco: BMNH 1944.6.6:94–101 (one cleared and counterstained for bone and cartilage); BMNH 1944.6.6:84–93 (20); Guaqui: BMNH 1944.6.6:142–151; BMNH 1944.6.6:122–131; BMNH 1944.6.6:132–141 (one cleared and counterstained for bone and cartilage); BMNH 1944.6.6:112–121 (juveniles).

RANGE: Known from several localities in Lago Titicaca, including Bahia de Puno, the Capachica Peninsula, Guaqui and Taraco, Lago Pequeño (fig. 22).

Orestias gymnotus, new species
Figure 55

DIAGNOSIS: A very slender and elongate species of the *agassii* complex, nearly fusiform in overall body shape as exemplified by its relatively narrow head (table 9) and low depth of the body (table 10), and as the trivial name implies, one of the nearly unscaled species in the *agassii* complex, with few or no head scales, an incompletely formed median dorsal ridge, and no lateral scales dorsal or ventral to the lateral, median rows of scales (fig. 55).

DESCRIPTION AND REMARKS: Morphometric data summarized in tables 8 through 12 serve to show that *gymnotus* is a very slender and elongate species within the *agassii* complex; meristic data summarized in tables 3 through 7 for the species fall within the average range of values for the *agassii* complex.

The squamation pattern of *gymnotus* (found to a certain degree among related species, including *ascotanensis* and *elegans*) is relatively invariant within the species. The pattern can be seen in the photograph of the holotype (fig. 55), an adult female. Scales run posteriorly from the posttemporal in one or two rows. The number of scale rows increases posteriorly to become a series of four to five rows at the base of the caudal fin. Scales are absent from the ventrum, and basal portions of the pectoral, dorsal, and anal fins. Despite the sparse squamation, it can still be seen (fig. 55) that *gymnotus* has enlarged, smooth scales just posterior to the operculum, diagnostic of the *agassii* complex.

Adults to over 60 mm SL. Color patterns of juvenile through adult males and females typical of those described for Pellegrin's (1904b) varieties of *O. agassii*, above. Large adults are medium to light brown overall, with a pale yellow ventrum; usually, there are minute dark brown melanophores overall. Juveniles have an incomplete to complete dark brown midlateral line of pigment, and

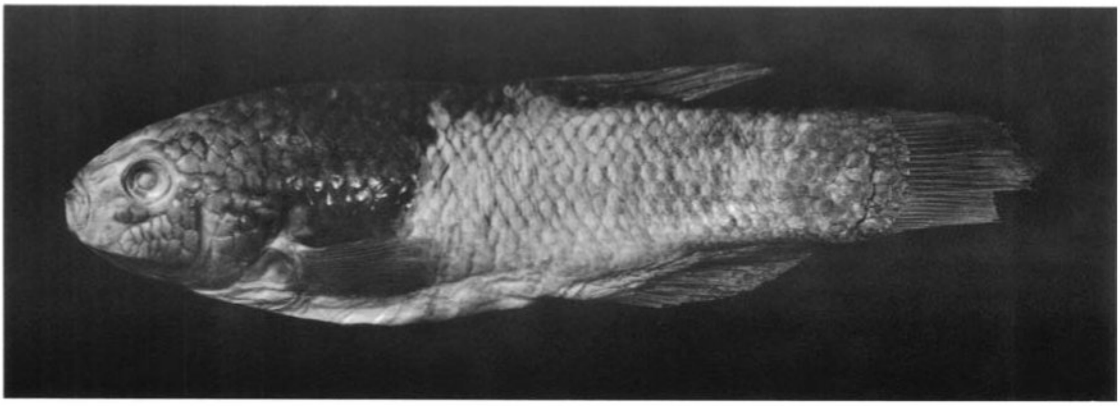

FIG. 54. *Orestias tschudii* Castelnau, Syntype, MNHN A.9604, male, 129 mm SL (posterior section of body partially descaled).

large, dark blotches dorsally, and often several blotches ventral to the midlateral line. Fins with small brown spots, or clear. Caudal fin truncate.

Outer jaw teeth unicuspid, in one irregular row. Tips of teeth slightly pigmented, barely protruding beyond thick epithelium covering upper and lower jaws.

MATERIAL: Holotype (CAS 40700, ex. IU 16102), an adult female, 62.0 mm SL, collected 1918 by C. H. Eigenmann, from Challhaucocha, near Quishuarcancha, northwest of Cerro de Pasco, Pasco Province, northern Peru, at an elevation of approximately 4062 m. Paratypes (CAS 51309) 38 juvenile to adult males and females, 15.0 to 52.0 mm, three cleared and counterstained for cartilage and bone, taken along with the holotype.

ADDITIONAL MATERIAL: From the type locality as described above (no type status): CAS 51310 (3); Pasco Province: Arroyo Tusi at Pocobamba (4154 m): FMNH 77905 (122), CAS 48257 (ex. IU 16061) (73); Arroyo Cuchis: CAS 40768 (37).

RANGE: Known from several localities in Pasco Province, northern Peru, just north of Lago Junin (fig. 24).

ETYMOLOGY: The trivial name *gymnotus,* an adjective, from the Latinized Greek root *gymnos,* meaning naked or lightly clad, and the Latin adjectival suffix *-tus* denoting possession, in reference to the sparse squamation pattern.

Orestias hardini, new species
Figure 56

DIAGNOSIS: A species of the *agassii* complex, most closely related to *O. ututo,* another

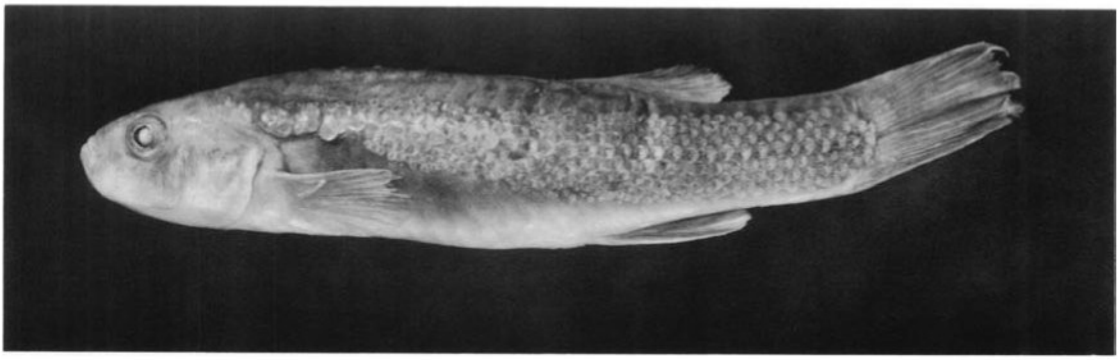

FIG. 55. *Orestias gymnotus,* new species, Holotype, CAS 40700, female, 62 mm SL.

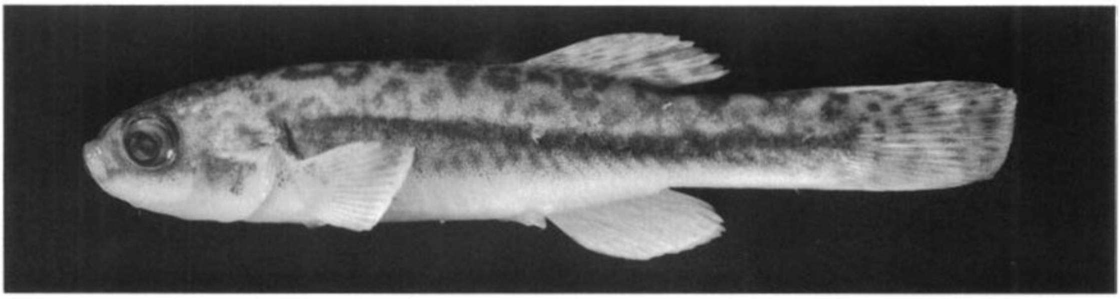

FIG. 56. *Orestias hardini*, new species, Holotype, AMNH 52178, male, 29 mm SL.

new species (p. 200) with which it shares a low number of dorsal fin rays (modally 10 in *ututo*; 11 in *hardini*, observed range in both of from 10 to 12; table 4). Distinguished by a high number of scales in a lateral series; when the series is complete, scale number observed to range from 36 to 38 (table 7). Squamation incomplete, with dorsal surface of some specimens and ventral of all, devoid of scales. Lateral scale series often incomplete or absent.

DESCRIPTION AND REMARKS: Morphometric and meristic data for this species are summarized in tables 3 through 12. *Orestias hardini* is most closely related to *O. ututo* with which it shares a low number of dorsal fin rays (see comments above and table 4). It is most easily distinguished from *ututo* by a high number of scales in a lateral series, ranging from 36 to 38 in *hardini*, as opposed to a range of 32 to 37, with a mode of 33 in *ututo* (table 7). The squamation of *hardini* is also often irregular, with the lateral series of scales often incomplete or absent. Ventral surface and basal portions of pectoral, dorsal, and anal fins unscaled.

In other meristic and morphometric characters, *hardini* differs little from the average values of these data for the *agassii* complex. Color pattern is typical of that described for Pellegrin's (1904b) varieties of *O. agassii* (pp. 131–133); that is, background is cream to yellow, with a distinct dark midlateral line, and brown blotches dorsally. Dorsal, pectoral, and caudal fins with small brown melanophores; anal fin clear. Blotches in dorsal fin may be arranged in two regular rows.

Outer jaw teeth unicuspid, in a single, irregular row. Tips brown, protrude slightly beyond epithelium covering upper and lower jaws.

Orestias hardini is a small species; a gravid female 38.5 mm SL is the largest known specimen. However, as noted in Phylogenetic Analysis, the nature and distribution of diminutive body size in *Orestias* is unknown. Killifishes apparently may continue to grow at sexual maturity. Large, mature adults otherwise referable to *hardini* should not be placed in another new species until the possibility that *hardini* continues to grow at sexual maturity is investigated further.

MATERIAL: Holotype (AMNH 52178, ex. AMNH 38415), an adult male, 29.0 mm SL, collected June 5, 1979 by Tim Hardin, from Lago Yanacocha, Peru (approx. 10°S, 77°15′W). Paratypes (AMNH 38415), four juvenile to adult males and females, 19.0 to 38.5 mm, one cleared and counterstained for bone and cartilage, taken along with the holotype; (AMNH 38411), four juveniles, 13.5 to 20.0 mm, collected June 13, 1979, by Tim Hardin, from Lago Llacsha, Peru (approx. 9°45′S, 77°33′W).

RANGE: Known from lagos Yanacocha and Llacsha (fig. 24) two small isolated lakes in northern Peru, outside the Titicaca and Urubamba basins. The Lago Llacsha locality represents the northernmost limit of the genus.

ETYMOLOGY: The trivial name *hardini*, in honor of Tim Hardin, in appreciation of his collecting *Orestias* in northern Peru.

Orestias ctenolepis, new species

Figures 57A, B

DIAGNOSIS: A slender species of the *agassii* complex, in which males possess extremely ctenoid scales (with up to 10 ctenii per scale)

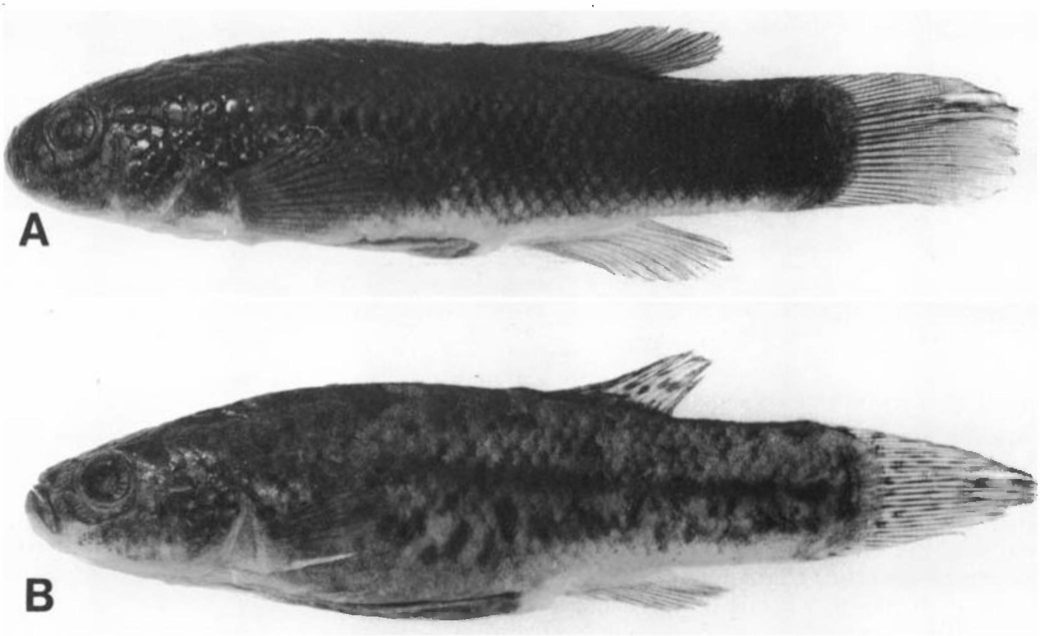

FIG. 57. *Orestias ctenolepis,* new species, A. Holotype, AMNH 52179, male, 68 mm SL; B. Paratype, AMNH 52180, female, 56.8 mm SL.

over most of the body, including the dorsal surface of the head and median dorsal ridge; only those scales immediately posterior to the base of, and medial to, the pectoral fin (i.e., those of the lateral shield) are strictly cycloid and have not been observed to possess ctenii. All fins of both males and females delicate and not covered with a thick membrane; upper and lower jaw margins "frilled," that is covered with small, delicate papillae.

DESCRIPTION AND REMARKS: Morphometric and meristic data for *ctenolepis* are summarized in tables 3 through 12. It is a relatively slender-bodied species of the *agassii* complex, but not so slender as *gymnotus,* and not differing significantly in meristic and morphometric data from the average values for these characters in other species of the complex. Distinguished from all other *Orestias* by the males having nearly all scales (except those of the lateral shield) with up to 10 ctenii per scale. The maximum number of ctenii occurs on the scales posterior to the lateral shield. Males also have breeding tubercles on the anal, dorsal and pectoral fins. Adults to 68 mm SL.

Individuals of *ctenolepis* apparently go through the same ontogenetic changes in color pattern described for Pellegrin's varieties of *O. agassii* (pp. 131–133); that is, juveniles and subadult to adult females (fig. 57B) have a mottled midlateral line that becomes more pronounced with increased size (i.e., SL), and they are mottled over the dorsal surface of the head and body immediately ventral to the midlateral line. In adults males and some adult females, both the dorsal surface and the midlateral line become darker with increased size, the midlateral line expanding with the result that the largest adults are nearly uniformly deep chocolate brown dorsally and laterally (fig. 57A). Both males and females are light cream ventrally. There is a faint bar at the base of the pectoral fin rays.

Basal portions of the dorsal, anal and pectoral fins, and ventrum unscaled. The holotype and several paratypes (one as small as 40 mm SL) have the area on either side of

FIG. 58. *Orestias ascotanensis,* new species, Holotype, USNM 236790, female, 54 mm SL (caudal fin broken).

the median dorsal ridge unscaled. In some of the smaller specimens, scales have been lost, making an accurate count of scales in a lateral series impossible (see table 7).

The "frilled" upper and lower jaw margins help to identify the species, but this state does not represent a unique characteristic of *ctenolepis,* as such papillae occur in some populations of *O. agassii* not recognized as distinct taxonomically in this study.

Outer jaw teeth unicuspid, with clear, unpigmented tips, arranged in a single, irregular row, which could be interpreted as two rows in some specimens.

MATERIAL: Holotype (AMNH 52179), an adult male, 68.0 mm SL, collected September 7, 1979 by Tom Coon, from the headwaters of the Río Zapatilla, in Río Camellaque, near Km 24 on the Ilave-Mazo Cruz Road, near Tiutiri, Chucuito Province, Peru, Río Zapatilla drainage. Paratypes (AMNH 52180), eight juvenile to adult males and females, 37.0 to 63.0 mm, taken with the holotype.

RANGE: Known only from the type locality, Río Zapatilla, just south of Lago Grande and west of Lago Pequeño, in the Titicaca Basin (figs. 22 and 23).

ETYMOLOGY: The trivial name *ctenolepis,* a noun in apposition, from the Latinized Greek root *ctenos,* meaning comb, and *lepis,* meaning scale, in reference to the presence of ctenoid scales over most of the body of adult males.

Orestias ascotanensis, new species

Figure 58

DIAGNOSIS: A robust species of the *agassii* complex, closely related to *parinacotensis* and *laucaensis,* the two other *Orestias* species endemic to Chile, sharing with them a sexual dimorphism in which females tend to be more fully scaled than males; females have several complete lateral scale rows, whereas, males usually have one anteriorly, gradually increasing to several posteriorly. Head relatively long for a species of the *agassii* complex not a member of the *luteus* group, and the one character by which *ascotanensis* is readily distinguished; the length of the head reaches nearly 35 percent of SL (table 8).

DESCRIPTION AND REMARKS: Morphometric and meristic data for *ascotanensis* are summarized in tables 3 through 12, showing that whereas *ascotanensis* differs little in meristic characters from the other species in the *agassii* complex, the morphometric characters indicate that it is a robust species, most easily distinguished by its relatively long head (table 8).

Sexual dimorphism and dichromatism among killifishes is well-documented (e.g., see Parenti, 1981, and references therein). *Orestias ascotanensis* shares with other species of the *agassii* complex a sexual dichromatism described for *O. agassii,* above; that is, subadult females and juveniles have a relatively mottled pattern, whereas males (and often larger females) have a more uniform light to dark brown pigmentation pattern. In males and females, the ventrum is pale yellow to cream, and otherwise unpigmented. Adults to over 60 mm SL.

Orestias ascotanensis also shares with *O. parinacotensis* Arratia and *O. laucaensis* Arratia sexual dimorphism with regard to degree of squamation. Females of all three species tend to be more fully scaled than

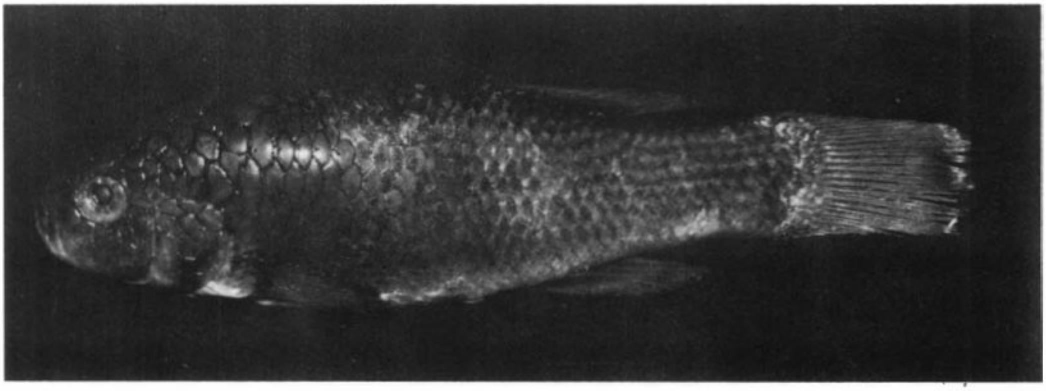

FIG. 59. *Orestias richersoni,* new species, Holotype, AMNH 52181, male, 85 mm SL.

males; although, the extent of the variation among large samples of all three species has not been documented.

Ventrum and basal portion of the pectoral, dorsal, and anal fins unscaled. Caudal fin truncate.

Lower jaw upturned slightly more than in other species of the *agassii* complex, except for *jussiei* and *albus,* the species with which specimens now referred to *ascotanensis* have been confused (Pellegrin, 1906; Tchernavin, 1944a).

Outer jaw teeth unicuspid, tips unpigmented and protruding beyond epithelium covering upper and lower jaws.

MATERIAL: Holotype (USNM 236790, ex. USNM 167744), an adult female, 54.0 mm SL, collected March, 1919 by W. R. Allen from Lago Ascotán, Chile. Paratypes (USNM 167744, ex. IU 16060), 15 juvenile to adult males and females, 36.5 to 53.0 mm, taken along with the holotype; (CAS 46160, ex. IU 16060), 48 juvenile to adult males and females, 22.5 to 62.0 mm, two cleared and counterstained for bone and cartilage, taken along with the holotype.

ADDITIONAL MATERIAL (not part of the type series): Lago Ascotán: FMNH 77384 (160 juvenile to adult males and females); MNHN 05.186–188 (three subadults to adults, 33.4–49.3 mm); MCZ 58680 (eight juveniles to adults).

RANGE: Known only from Lago Ascotán (Salar de Ascotán), Chile, a salt basin in the northwestern section of Chile (fig. 25).

ETYMOLOGY: The trivial name *ascotanensis* to denote the occurrence of this species in Lago Ascotán, Chile.

Orestias richersoni, new species

Figure 59

DIAGNOSIS: A species of the *agassii* complex distinguished by a unique pigmentation pattern characterized by a faint to jet black spot at the dorsal margin of the operculum, a black margin of the lower jaw, and a faint to dark band at the base of the pectoral fin rays that extends dorsally onto the lateral shield of scales. Body a deep olive green to dark brown dorsally, with an iridescent background and a faint grayish yellow ventrum.

DESCRIPTION AND REMARKS: Meristic and morphometric data for this species are summarized in tables 3 through 12. A species of the *agassii* complex most closely related to *tschudii,* and like it with a somewhat laterally compressed body, especially posterior to the origin of the dorsal fin. Differing from *tschudii* meristically by a lower number of vertebrae (32), the higher number (mode of 34, range 33 to 35) autapomorphic for *tschudii* (table 3).

Distinguished by its color pattern, the unique component of which is a faint to jet black spot at the dorsal margin of the operculum. The black margin of the lower jaw and faint to dark band at the base of the pectoral fin rays are present in other species of *Orestias*; however, in no other species (including recently collected material) is the pigmentation such a deep black, being nearly jet black in most specimens.

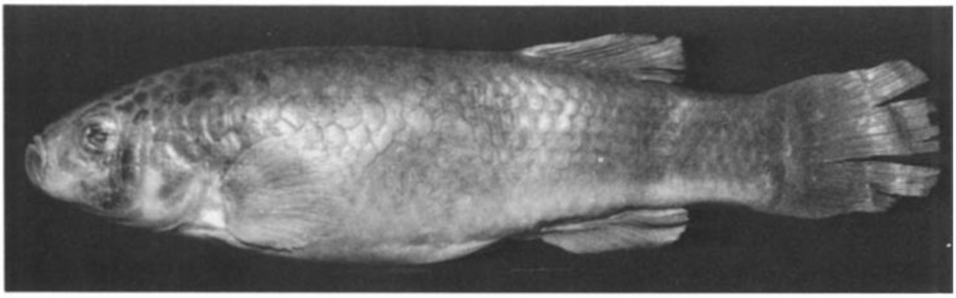

FIG. 60. *Orestias multiporis,* new species, Holotype, CAS 46166, female, 85 mm SL.

Adults to 85 mm SL. Males with ctenii on scales posterior to the large and smooth scales of the lateral shield. Ventral surface of body from a vertical through the posterior extent of pectoral fin to the anal fin bare to fully scaled in some larger adults. Males with breeding tubercles on anal, dorsal and pectoral fin rays. Basal portion of pectoral, anal and dorsal fin unscaled. Caudal fin truncate.

Outer jaw teeth unicuspid, in two regular or irregular rows, tips pointed and unpigmented, projecting beyond epithelium covering upper and lower jaws.

MATERIAL: Holotype (AMNH 52181), an adult male, 85.0 mm SL, collected on September 4, 1979 by Tom Coon and Pedro Quispe, from the Río Coata, at a bridge just upstream from Coata, Lago Titicaca drainage, Peru. Paratypes (AMNH 52182), four subadults to adults, 60.0 to 81.0 mm, taken along with the holotype.

RANGE: Known only from the type locality, the Río Coata near Coata, draining into Lago Titicaca, just south of the Capachica Peninsula (figs. 22 and 23).

ETYMOLOGY: The trivial name, *richersoni,* in honor of Peter J. Richerson who with coworkers is carrying out a limnological study of Lago Titicaca; to commemorate my appreciation for his encouraging a multidisciplinary and international study of Lago Titicaca.

Orestias multiporis, new species
Figure 60

DIAGNOSIS: A robust species of the *agassii* complex, with relatively thick, fleshy lips, orbits near the dorsal surface of the head, and a dorsal profile that slopes gently dorsally from the tip of the snout to the anterior base of the dorsal fin. Distinguished from all other *Orestias* species by having the median dorsal ridge and lateral series scales, without granulations, and with multiple neuromasts, occurring in groups of two or more.

DESCRIPTION: Distinguished from all other *Orestias* species by a unique neuromast pattern, characterized by a series of two or more neuromasts grouped together on each of the scales of the lateral series and the median dorsal ridge. A member of the *agassii* complex, indistinguishable from most other species in the complex in any morphometric or meristic characters (data for this species are summarized in tables 3 through 12).

Adults to 85.0 mm SL. All pigmentation patterns characteristic of Pellegrin's varieties of *O. agassii* present in the type series: juvenile males and females and subadult females with mottled pattern, subadult and adult males and adult females dark overall, except for ventral surface which is light cream to yellow in all individuals. Ventrum and basal portion of pectoral and anal fins unscaled, basal portion of dorsal fin nearly fully scaled. Fully scaled on either side of median dorsal ridge. All scales smooth, never any granulations, concentric striae present just to a limited degree. Males often with breeding tubercles on anal and dorsal fins; all fins clear to slightly mottled. Caudal fin truncate. Anal pouch small.

Outer jaw teeth unicuspid, with pointed cusps, slightly pigmented, arranged in one scattered row, embedded in epithelium covering upper and lower jaw margins, tips not visible in most specimens.

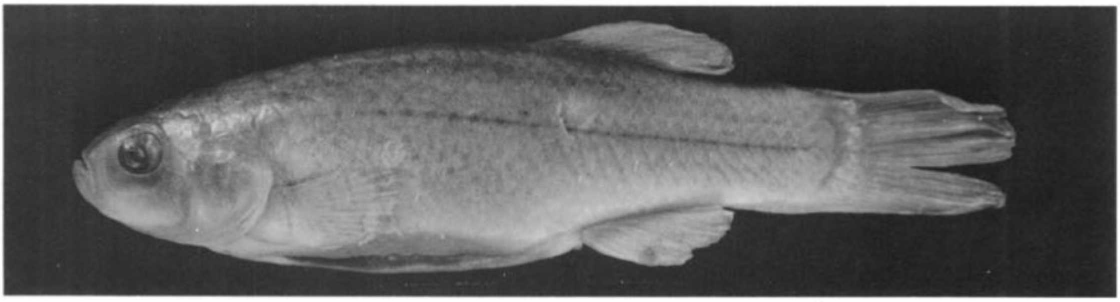

FIG. 61. *Orestias mundus,* new species, Holotype, FMNH 41135, female, 45 mm SL.

REMARKS: In the hypothesis of relationships within the *agassii* complex (fig. 30), *multiporis* is considered to be in an unresolved trichotomy with two larger groups of *agassii* complex species; *multiporis* lacks the defining characters of both groups. Nonetheless, it is possible that some populations now referred to *agassii* will be found to be more closely related to *multiporis* than to any other *Orestias* species. This presumption is based on the fact that many collections of *agassii* are represented only by juveniles which have the generally juvenile characteristic of an incomplete dorsal squamation, but about which adult squamation characters are unknown.

MATERIAL: Holotype (CAS 46166), an adult female, 85 mm SL, collected November 1918 by W. R. Allen at Maravillas, then a station on the southern railway, near Río de Lampa (figs. 22 and 23), Peru. Paratypes (CAS 51311), 37 juvenile to adult males and females, 43–80 mm, taken along with the holotype.

RANGE: Known only from the type locality (fig. 23), on the Río de Lampa, northwestern arm of the Río Coata (fig. 22), a tributary of Lago Titicaca, Titicaca Basin.

ETYMOLOGY: The trivial name *multiporis,* a noun in apposition, from the Latin prefix *multi-*, meaning many or much, and *poris,* plural of the noun *porus,* meaning a pore or passage, in reference to the multiple series of neuromasts along the median dorsal ridge and the lateral series.

Orestias mundus, new species
Figure 61

DIAGNOSIS: A member of the *agassii* complex distinguished from all other species in the complex by being uniformly colored throughout life, body with a pale yellow ventral surface becoming light brown dorsally, all fins clear or dorsal fin faintly dusky, and a dark thin, midlateral line.

DESCRIPTION AND REMARKS: Meristic and morphometric data for this species, summarized in tables 3 through 12, fail to distinguish *Orestias mundus* from other species of the *agassii* complex. Nonetheless, it is one of the most distinct and easily identifiable species in the complex, differing from the other species by its relatively plain color pattern exhibited with little variation in all known life stages of both males and females. The absence of marked ontogenetic change in pigmentation pattern is characteristic of species of the *gilsoni, mulleri,* and *cuvieri* complexes; however, *mundus* possesses the defining characters of the *agassii* complex. Therefore, this pigmentation pattern is most parsimoniously considered to be autapomorphic for *mundus.*

Adults to 45.0 mm SL. Ventral surface, basal portions of pectoral, dorsal and anal fins unscaled, scales present or absent from either side of median dorsal ridge. Breeding tubercles present on anal fin of males. Caudal fin truncate.

Outer jaw teeth unicuspid, with pointed slightly pigmented tips protruding just beyond thick epithelium covering upper and lower jaws.

MATERIAL: Holotype (FMNH 41135, ex. FMNH 41130–41140), an adult female, 45.0 mm SL, collected December 9 to 12, 1941, by C. C. Sanborn, from Cuzco, Peru. Paratypes (FMNH 41130–41134, 41136–41140), 110 juvenile to adult males and females, 10.0

FIG. 62. *Orestias ututo,* new species, Holotype, AMNH 52183, male, 48 mm SL.

to 41.0 mm, one adult cleared and counterstained for bone and cartilage, taken along with the holotype.

RANGE: Known only from the type locality, Cuzco, Peru in the Urubamba Basin (fig. 24).

ETYMOLOGY: The trivial name *mundus,* a Latin adjective meaning neat or trim, in reference to the unadorned, nearly uniform color pattern from juvenile through adult males and females.

Orestias ututo, new species
Figure 62

DIAGNOSIS: A species of the *agassii* complex most closely related to *hardini,* sharing with it a low number of dorsal fin rays, the modal number reduced to 11 in *hardini* and 10 in *ututo,* with an observed range in both species of from 10 to 12 (table 4). Distinguished from *hardini* and all other *Orestias* by a decrease in the modal number of anal fin rays to 11, with an observed range of from 10 to 12 (table 5).

DESCRIPTION AND REMARKS: Morphometric and meristic data for *ututo* are summarized in tables 3 through 12. *Orestias ututo* is distinguished from all other *Orestias* by its low number of anal fin rays (modally 11; observed range 10 to 12).

Other characters in tables 3 through 12 do not serve to distinguish *ututo* from the average values for *agassii* complex species; however, they do show that it is a relatively robust species, deep bodied (table 10) and with a deep caudal peduncle (table 11).

Adults to over 40 mm SL. Juveniles with the typical color pattern of the *agassii* complex, above; that is, a rather mottled pattern, often with a more or less distinct midlateral line of blotches. Adult females with a distinct midlateral line, and darkly pigmented dorsally. Adult male holotype (fig. 62) is rather uniformly pigmented, with a pale yellow background and scattered minute dark melanophores. The color pattern of this adult male is most similar to the unique pattern diagnostic of *Orestias mundus,* but differs by being darker overall. The holotype of *ututo* is the only large male of the species known; a larger sample size is therefore necessary to determine if there is more variation within adult pigmentation.

Ventrum and basal portion of pectoral, dorsal, and anal fin unscaled; scales on either side of the median dorsal ridge present or absent. Caudal fin truncate.

Outer jaw teeth unicuspid, in one or two irregular rows; tips black, protruding through epithelium on upper and lower jaws.

MATERIAL: Holotype (AMNH 52183, ex. AMNH 38416), an adult male, 48.0 mm SL, collected May 26, 1979 by Tim Hardin, from Lago Ututo, Peru (approx. 9°50′S, 77°30′W). Paratypes (AMNH 38416), five juvenile to adult males and females, 16.4 to 31.0 mm, taken along with the holotype.

ADDITIONAL MATERIAL (not part of type series): cf. *ututo*: Huayre, Peru (FMNH 70367), 11 juveniles to adults.

RANGE: Known from Lago Ututo, Peru (fig. 24), north of both the Urubamba and Titicaca basins, and possibly Huayre, Peru.

ETYMOLOGY: The trivial name, *ututo,* to denote the occurrence of this species in Lago Ututo, Peru.

FIG. 63. *Orestias gilsoni* Tchernavin, Lectotype, BMNH 1944.6.6:524, female, 43 mm SL.

Orestias gilsoni Tchernavin
Figure 63

Orestias gilsoni. Tchernavin, 1944a, pp. 217–219 (original description, Isla Taquiri, Lago Pequeño, Lago Titicaca).

DIAGNOSIS: A species of the *gilsoni* complex most closely related to *taquiri* with which it shares an increase in the modal number of pectoral fin rays to 17 or 18, with an observed range of 17 to 19 (table 6), and a color pattern characterized by a silver background with six to nine irregular bars. *Orestias gilsoni* is distinguished from other members of the *gilsoni* complex by a head that is relatively wide (width reaching nearly 23 percent of SL; table 9) and flattened dorsally; and, by a relatively narrow caudal peduncle, its depth usually less than 10 percent of SL (table 11). The combination of these two characters (a wide and flat head and a narrow caudal peduncle) gives *gilsoni* a distinctive overall body shape. Additional morphometric and meristic data for *gilsoni* are summarized in tables 3 through 12.

MATERIAL: Lectotype (BMNH 1944.6.6: 524), a female, 43 mm SL, collected July 30, 1937 by the Percy Sladen Titicaca Expedition at a depth of from 2.7 to 2.8 m from Isla Taquiri, Lago Pequeño, Lago Titicaca, designated herein. Paralectotypes: (BMNH 1944.6.6:525), a ?male, 28 mm collected with the lectotype; (BMNH 1944.6.6:526–530), eight juvenile to adult males and females, 18 to 34 mm; (USNM 133140, ex. BMNH 1944.6.6:526–530), one adult female, 33 mm, collected with the lectotype; (BMNH 1944.6.6:531) one adult female, 25 mm collected July 28, 1937 by the Percy Sladen Titicaca Expedition, at a depth of from 2.5 to 2.9 m, off Tiahuanaco.

RANGE: Known from Isla Taquiri and off Tiahuanaco, Lago Pequeño, Lago Titicaca (figs. 22 and 23).

Orestias taquiri Tchernavin
Figure 64

Orestias taquiri. Tchernavin, 1944a, pp. 221–222 (original description, Isla Taquiri, Lago Pequeño, Lago Titicaca).

DIAGNOSIS AND REMARKS: A species of the *gilsoni* complex most closely related to *gilsoni,* sharing with it an increase in the modal number of pectoral fin rays to 17 or 18, with an observed range of from 16 to 18 (table 6), and a color pattern characterized by a silvery background with from six to nine irregular bars. Distinguished from *gilsoni* by a reduction in the modal number of dorsal fin rays to 12, with an observed range of from 11 to 14 (table 4) as opposed to a modal number of 14, with an observed range of from 12 to 15 in *gilsoni*; and, a reduction in the modal number of vertebrae to 30, with an observed range of from 30 to 31 (table 3), as opposed to a modal number of 32 vertebrae, with an observed range of from 31 to 32 in *gilsoni.* Additional meristic and morphometric data for *taquiri* are summarized in tables 3 through 12.

MATERIAL: Holotype (BMNH 1944.6.6: 534), an adult female, 26 mm SL, collected July 30, 1937 by the Percy Sladen Titicaca Expedition, at a depth of from 2.7 to 2.8 m, from Isla Taquiri, Lago Pequeño, Lago Titicaca. Paratypes: (BMNH 1944.6.6:535, an adult male, 23 mm; (BMNH 1944.6.6:536–

FIG. 64. *Orestias taquiri* Tchernavin, Holotype, BMNH 1944.6.6:534, female, 26 mm SL.

542) nine juvenile to adult males and females, one male and one female cleared and counterstained for bone and cartilage); (USNM 133141), an adult male, 26 mm, all taken with the holotype.

RANGE: Known only from Isla Taquiri, one of the two larger islands in Lago Pequeño, Lago Titicaca (figs. 22 and 23).

Orestias mooni Tchernavin
Figure 65

Orestias mooni. Tchernavin, 1944a, pp. 228–230 (original description, Bahia de Coata in Bahia de Puno, Lago Titicaca).

DIAGNOSIS AND REMARKS: A fully scaled species of the *gilsoni* complex closely related to *tomcooni,* and like it, with a lower jaw that is at a nearly 90-degree angle to the body axis (fig. 65). In addition to being fully scaled with irregularly distributed small, thin scales, *mooni* is distinguished by an increase in the modal number of vertebrae to 32 or 33, with an observed range of from 32 to 34 (table 3), as opposed to 31 vertebrae in *tomcooni.* Additional morphometric and meristic data are summarized in tables 3 through 12.

Tchernavin (1944a) placed this species in Group IV, along with *mulleri, incae,* and *crawfordi* because all four species are fully scaled. However, as discussed in the Phylogenetic Analysis, the division of *Orestias* species into fully scaled and unscaled forms is artificial, and therefore, not the basis on which species complexes are defined in the present study. Lauzanne (1981) describing *ispi,* another fully scaled species, comparing it with *mooni* concluded that the two were not closely related, a viewpoint that is upheld here.

MATERIAL: Holotype (BMNH 1944.6.6: 503), an adult female, 35 mm SL, collected June 1, 1937, by the Percy Sladen Titicaca Expedition, from Bahia de Coata in Bahia de Puno, Lago Titicaca. Paratypes: (BMNH 1944.6.6:504–520), 35 juvenile to adult males and females, 16 to 32 mm; (USNM 133139), an adult female, 28 mm, all taken with the

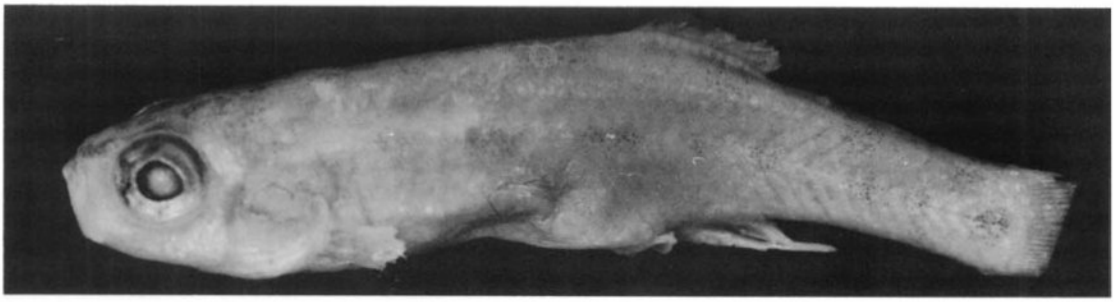

FIG. 65. *Orestias mooni* Tchernavin, Holotype, BMNH 1944.6.6:503, female, 35 mm SL.

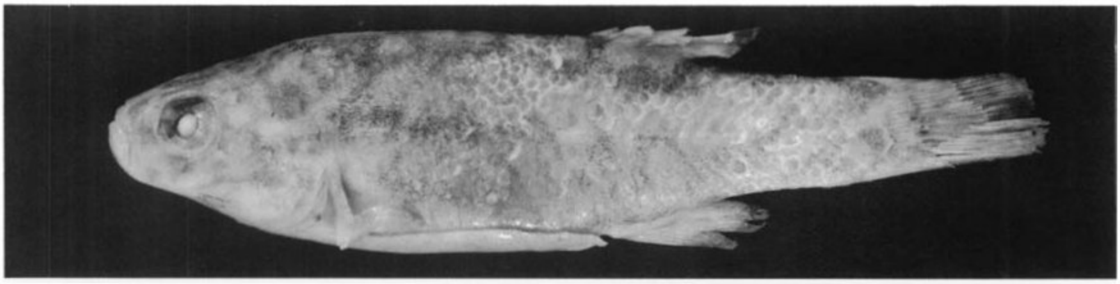

FIG. 66. *Orestias uruni* Tchernavin, Lectotype, BMNH 1944.6.6:173, female, 43 mm SL.

holotype; (BMNH 1944.6.6:522), two adults eviscerated, 24 to 31 mm, collected by the Percy Sladen Titicaca Expedition from Bahia de Taman, Lago Titicaca.

RANGE: Known from Bahia de Coata and Bahia de Taman, Lago Titicaca (figs. 22 and 23).

Orestias uruni Tchernavin
Figure 66

Orestias uruni. Tchernavin, 1944a, pp. 213–214 (original description, Bahia de Uruni on the north side of the Capachica Peninsula, Lago Grande, Lago Titicaca).

DIAGNOSIS AND REMARKS: One of the relatively robust species of the *gilsoni* complex, most closely related to *tchernavini, robustus* and *imarpe,* sharing with them a marbled color pattern. Distinguished from these species by the base of the pectoral fin nearly meeting the posterior margin of the operculum, nearly obscuring the basal portion of the pectoral fin; and, by a reduced or absent anal pouch and papilla. The polarity of the last character is ambiguous because the anal pouch and papilla are present to varying degrees among most species of the *mulleri, gilsoni,* and some species of the *agassii* complexes. However, the absence of these structures in *uruni* serves to distinguish it from closest relatives, and, therefore, at one level, is considered to be autapomorphic. Meristic and morphometric characters for *uruni* are summarized in tables 3 through 12.

MATERIAL: Lectotype (BMNH 1944.6.6:173), an adult female, 43 mm SL, collected August 9, 1937, by the Percy Sladen Titicaca Expedition, at a depth of 0.9 m from the Bahia de Uruni on the north side of the Capachica Peninsula, Lago Grande, Lago Titicaca, designated herein. Paralectotypes (BMNH 1944.6.6:174–177), four adults, 40 to 50 mm, collected with the lectotype.

RANGE: Known only from the type locality, Bahia de Uruni on the north side of the Capachica Peninsula, Lago Grande, Lago Titicaca (figs. 22 and 23).

Orestias minimus Tchernavin
Figure 67

Orestias minimus. Tchernavin, 1944a, pp. 216–217 (original description, Molinopampa, on the southeastern shore of Lago Grande, Lago Titicaca).

DIAGNOSIS AND REMARKS: One of the diminutive species of the *gilsoni* complex, known only from two adult females, 23 to 28 mm SL, most closely related to the other diminutive species of the complex, *minutus,* but distinguished by being totally unscaled, and by having 30, rather than 31, vertebrae (table 3). Additional meristic and morphometric data for *minimus* are summarized in tables 3 through 12. See also remarks under *minutus,* below.

MATERIAL: Holotype (BMNH 1944.6.6:532), an adult female, 23 mm SL, collected July 16, 1937, by the Percy Sladen Titicaca Expedition, at a depth of from 10 to 11 m, from Molinopampa, on the southeastern shore of Lago Grande, Lago Titicaca. Paratype (BMNH 1944.6.6:533), an adult female, 28 mm, collected July 13, 1937, by the Percy Sladen Titicaca Expedition, at a depth of from 14 to 16 m, from Sucuné, southeast of Bahia de Moho, Lago Grande, Lago Titicaca.

RANGE: Known from just two localities in Lago Grande, Lago Titicaca: Molinopampa,

FIG. 67. *Orestias minimus* Tchernavin, Paratype, BMNH 1944.6.6:533, female, 28 mm SL.

on the southeastern shore (figs. 22 and 23), and Sucuné, southeast of Bahia de Moho (fig. 22).

Orestias minutus Tchernavin
Figure 68

Orestias minutus. Tchernavin, 1944a, pp. 215–216 (original description, Bahia de Uruni on the northeastern side of the Capachica Peninsula, Lago Grande, Lago Titicaca).

DIAGNOSIS AND REMARKS: A diminutive species of the *gilsoni* complex, known from two adult females, 24 to 28 mm SL, most closely related to *minimus*, the other diminutive species in the complex. Defined by an increase in the number of anal fin rays to 16 or 17, as opposed to 14 or 15 for *minimus*. Additional meristic and morphometric data for *minutus* are summarized in tables 3 through 12.

As noted in the explanation of the synapomorphy diagrams, both *Orestias minutus* and *minimus* are known only from diminutive adult females. Although there are some undetermined specimens in the collection of the AMNH which could be referred to *minutus*, both species are known with certainty from only two specimens each. These specimens, which constitute the type series of each species, are bleached and have fins broken. Nonetheless, each species is distinct and recognized in this study. Because of the poor state of preservation, neither of the two syntypes of *minutus* is chosen as lectotype.

MATERIAL: Syntypes (BMNH 1944.6.6: 159–160), two adult females, 24 to 28 mm SL, collected July 9, 1937 by the Percy Sladen Titicaca Expedition, at a depth of 1.3 m, from Bahia de Uruni on the northeastern side of the Capachica Peninsula, Lago Grande, Lago Titicaca (figs. 22 and 23).

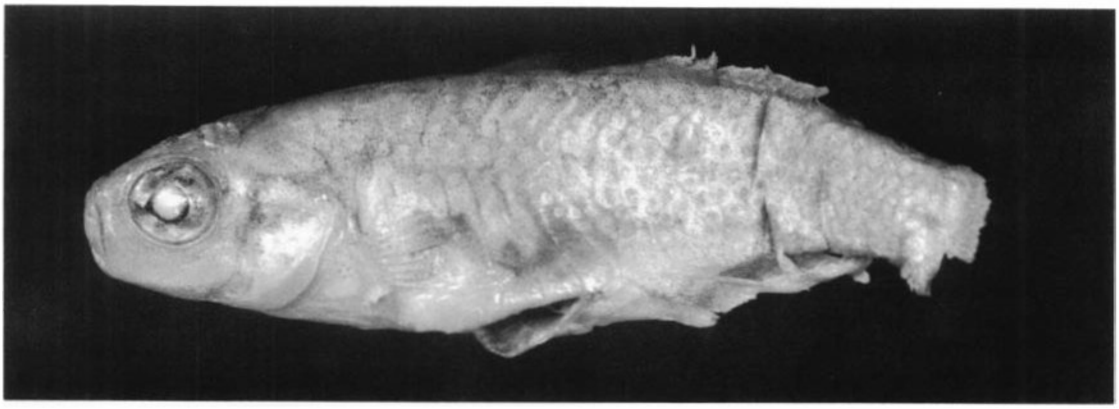

FIG. 68. *Orestias minutus* Tchernavin, Syntype, BMNH 1944.6.6:159–160, female, 28 mm SL.

FIG. 69. *Orestias tchernavini* Lauzanne, Holotype, MNHN 1981:770, female, 46.5 mm SL.

Orestias tchernavini Lauzanne
Figure 69

Orestias tchernavini. Lauzanne, 1981, pp. 84–89 (original description, Estrecho Tiquina, Lago Pequeño, Lago Titicaca).

DIAGNOSIS AND REMARKS: A species of the *gilsoni* complex most closely related to *imarpe, uruni,* and *robustus* which together form a group distinguished by their overall marbled pigmentation pattern. *Orestias tchernavini* is distinguished by a relatively laterally compressed head, the width of which is as low as 13 percent of SL (table 9). Additional morphometric and meristic data for *tchernavini* are summarized in tables 3 through 12, and characters not compared among all *Orestias* as part of this study are discussed in Lauzanne (1981).

Tchernavin (1944a, pp. 230–231) gave characters for, but did not formally name, a species that he referred to as "*Orestias* sp. no. 1." He considered it to be closely related to species in his Group III, which includes species now considered to be part of the *gilsoni* complex. Lauzanne (1981, pp. 88–89) stated that his new species, *tchernavini,* was conspecific with the specimen referred to by Tchernavin as sp. no. 1. The specimen (BMNH 1944.6.6:161) is poorly preserved and I cannot confirm this identification. However, I agree with Lauzanne (1981, p. 89) that *tchernavini* is rather closely related to *minimus, gilsoni,* and *mooni.*

The holotype and 36 paratypes by which *tchernavini* is known are all females. As stated in Phylogenetic Analysis, female *Orestias* are found in much higher proportions than males. Whether or not this has any relation to a particular mode of reproduction is unknown.

MATERIAL: Holotype (MNHN 1981:770), an adult female, 46.5 mm SL, collected October 15, 1979 from Estrecho Tiquina, Lago Pequeño, Lago Titicaca. Paratypes (MNHN 1981:771), 36 adult females, 41 to 54.5 mm, taken along with the holotype.

RANGE: Known only from the type locality, Estrecho Tiquina, Lago Pequeño, Lago Titicaca.

Orestias imarpe, new species
Figure 70

DIAGNOSIS: One of the more robust species of the *gilsoni* complex, distinguished primarily by thick and fleshy lips; a relatively small dorsal fin with a modal number of 11 rays (observed range of from 10 to 14, table 4); and large eyes that project above the primary dorsal profile of the head to a greater extent than in *robustus, tchernavini,* and *uruni,* the other robust species within the complex (fig. 70).

DESCRIPTION: Meristic and morphometric data for this species are summarized in tables 3 through 12.

A robust (most closely-related to *tchernavini, uruni,* and *robustus*) and one of the larger, species of the *gilsoni* complex attaining an SL of 57 mm. *Orestias imarpe* is readily distinguished from these other robust species by its relatively small dorsal fin (rays modally 11, range 10 to 14), and thick and fleshy lips. Also, the eyes project above the primary dorsal profile of the head to a greater extent than in other robust *Orestias* species; however, whereas this character helps to separate *imarpe* from the other species, it is not considered to be a uniquely derived character of *imarpe,* since the extent of the projection of the orbits above the primary dorsal profile

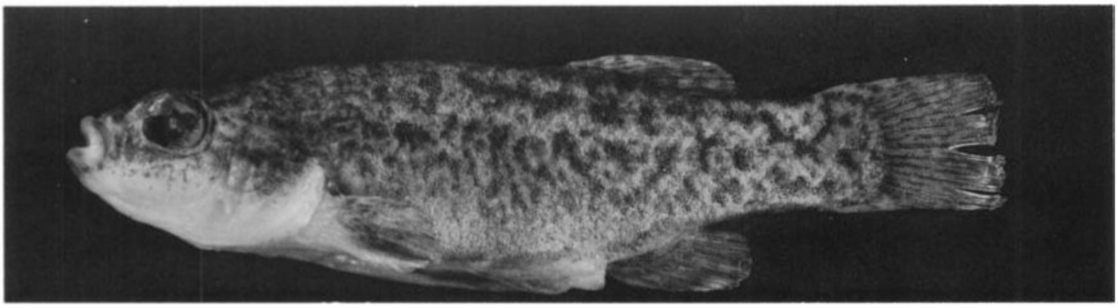

FIG. 70. *Orestias imarpe*, new species, Holotype, AMNH 52184, female, 51 mm SL.

of the head varies within species of the *mulleri* and *gilsoni* complexes.

Body with cream-colored background, marbled with medium brown reticulations, fins dusky or with discrete blotches. Ventral surface light yellow. Lower jaw with brown blotches or incomplete band of pigment. Marbled pattern characteristic of the group including *tchernavini, uruni,* and *robustus* as well as *imarpe,* faded extensively in alcohol in two paratypes that are preserved with mouths wide open. The fading is most likely due to stress of capture and preservation. Another effect of stress of capture on pigmentation pattern that can be seen in many of the specimens collected in 1979 by Tom Coon that has not been described elsewhere in this paper is the presence of a dark band circumventing the body at a point equal to the highest point of the dorsal arch. This can be seen in the figures of *luteus* (fig. 7). In many cases, the dark dorsal band is simply the result of the dorsal scale covering being scraped off; however, in a large number of lots, the ventral band appears to represent a change in pigmentation. This band is presumably caused by stress of capture in experimental gill nets used extensively by Coon.

Ventrum, basal portion of pectoral, anal, and dorsal fins unscaled; scales of median dorsal ridge small, ridge incomplete in some specimens.

Outer jaw teeth unicuspid, with pointed tips just protruding beyond epithelium covering upper and lower jaw margins.

MATERIAL: Holotype (AMNH 52184), an adult female, 51.0 mm SL, collected August 22, 1979, by Tom Coon and assistants near village of Ojjerani, between Puno and Chucuito, Bahia de Puno, Lago Titicaca, at a depth of from 1 to 2 m at a distance of from 70 to 100 m from the shore. Paratypes: (AMNH 52185), five adults, 53–57 mm, (one cleared and counterstained for bone and cartilage) taken with the holotype.

ADDITIONAL MATERIAL (not part of type series): Bahia de Puno: BMNH 1982.12.6: 35–36 (two adults, 53–56.1 mm), AMNH 52186 (four adults, 50–54 mm); Lago Pequeño, near village of Vilurcuni: AMNH 52187 (one adult, 56 mm).

RANGE: Known from the type locality in Bahia de Puno, and from near the village of Vilurcuni, Lago Pequeño (figs. 22 and 23).

ETYMOLOGY: The trivial name *imarpe,* the abbreviated title used by the Instituto del Mar del Peru.

Orestias tomcooni, new species

Figures 4B, 18A, 71

DIAGNOSIS: An elongate species of the *gilsoni* complex readily distinguished by its overall body shape characterized by a relatively narrow (table 9) and deep head (table 10), with an even more abrupt transition between the anterior part of the body and the caudal peduncle than is diagnostic of a subgroup of the complex comprising *gilsoni, taquiri, minimus, minutus, tomcooni,* and *mooni* (fig. 71). Modal number of scales in a lateral series increased to 37, with an observed range of from 36 to 38 (table 7).

DESCRIPTION AND REMARKS: Morphomet-

FIG. 71. *Orestias tomcooni,* new species, Holotype, AMNH 52188, female, 53 mm SL.

ric and meristic data for this species are summarized in tables 3 through 12. Only one such character (modal number of scales in a lateral series increased to 37) distinguishes it from other *gilsoni* complex species; nevertheless, it is readily distinguished from all other *Orestias* by its overall body shape, with an abrupt transition between the anterior part of the body and the caudal peduncle. Adults to over 50 mm SL. Caudal fin truncate.

Orestias tomcooni is most closely related to *O. mooni,* with which it shares the condition of having the lower jaw at a nearly 90-degree angle to the body axis (figs. 65 and 71). In addition to its diagnostic characters, *tomcooni* may be distinguished from *mooni* by its unscaled (rather than fully scaled) ventral surface and basal portion of the pectoral, dorsal and anal fins. Also, *mooni* tends to be uniformly straw-colored overall, whereas *tomcooni* has a yellow to cream background with mottled lateral and dorsal surfaces.

Outer jaw teeth unicuspid with darkly pigmented tips that protrude just beyond epithelium covering upper and lower jaws. Teeth arranged in one or two irregular rows.

MATERIAL: Holotype (AMNH 52188), an adult female, 53.0 mm SL, collected October 2, 1979 by Tom Coon and M. Reed, near the village of Huatayata, at a distance of from 0 to 30 m from the shore, at a depth of from 0 to 1 m, on the northern side of Lago Pequeño. Paratypes (AMNH 52189) five subadult to adult males and females, 37.0 to 41.0 mm, two cleared and counterstained for bone and cartilage, taken along with the holotype; (AMNH 52190) nine juvenile to adult males and females, 18.0 to 42.0 mm, collected August 28, 1979 by Tom Coon, near the village of Vilurcuni, on the western side of Lago Pequeño.

RANGE: Both Peruvian and Bolivian shores of Lago Pequeño (fig. 22).

ETYMOLOGY: The trivial name *tomcooni,* in honor of Tom Coon with gratitude and appreciation for his expert collection of more than 3000 specimens of *Orestias* from the Titicaca Basin in 1979, which formed the impetus for the present revision.

Orestias robustus, new species
Figure 72

DIAGNOSIS: As the trivial name suggests, one of the more robust species in the genus *Orestias,* the width of the head reaching nearly 23 percent of SL (table 9), and an overall body shape characterized by a gentle rise in the dorsal profile from the tip of the snout to the base of the dorsal fin, and a gentle downward slope in the ventral profile from the tip of the lower jaw to the base of the anal fin. Most closely related to a group of species in the *gilsoni* complex (*uruni, imarpe,* and *tchernavini*) with which it shares an overall marbled pigmentation pattern.

DESCRIPTION AND REMARKS: Additional morphometric and meristic data for this species are summarized in tables 3 through 12.

Adults to over 50 mm SL. A robust species of the *gilsoni* complex, distinguished by one morphometric character (a greater width of the head) from other species in the complex with which it shares an overall marbled pigmentation pattern.

Eyes project just slightly above primary dorsal profile; overall body shape robust with

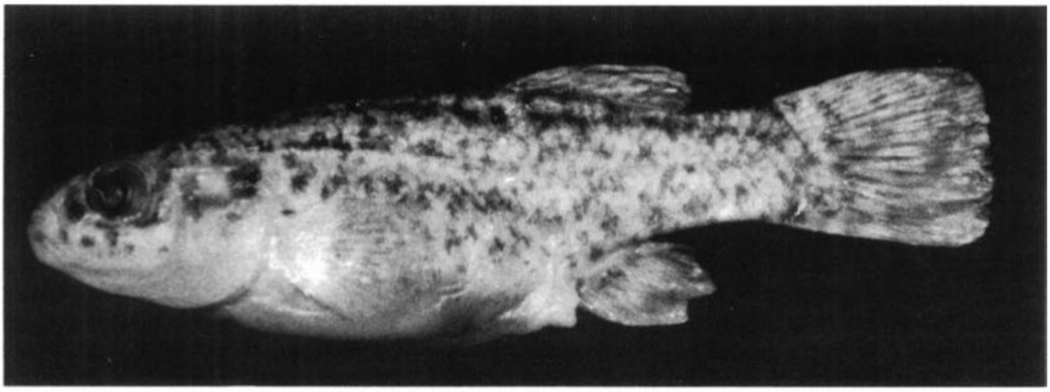

FIG. 72. *Orestias robustus,* new species, Holotype, AMNH 52191, female, 45 mm SL.

a convex dorsal and convex ventral profile, contributing to the species' rounded, robust appearance.

Ventral surface, and basal portion of pectoral, dorsal and anal fins unscaled (or basal portion of fins with several scales). Caudal fin truncate. Males with ctenoid scales on head as well as posteriorly; breeding tubercles on anal fin. Scales present or absent from either side of median dorsal ridge.

Outer jaw teeth unicuspid, in one irregular row; tips barely protrude beyond epithelium covering upper and lower jaws.

MATERIAL: Holotype (AMNH 52191), an adult female, 45.0 mm SL, collected August 24, 1979, by Tom Coon and assistants, at a depth of from 1 to 2 m, at a distance of from 70 to 100 m from shore near the village of Ojjerani, between Puno and Chucuito, Bahia de Puno, Lago Titicaca. Paratypes (AMNH 52192), three adults, 47.0 to 48.0 mm, taken with the holotype; (AMNH 52193) eight specimens, 32 to 48 mm, one cleared and counterstained for bone and cartilage, collected August 21, 1979; (AMNH 52194) two adult females, 48.0 to 57.0 mm, collected August 23, 1979; (BMNH 1982.12.6:122–123) two adult females, 51.0 mm, collected August 25, 1979, all from the type locality.

ADDITIONAL MATERIAL (not part of type series): From type locality: (AMNH 52195), one female, 46.0 mm; Escallami, Lago Grande north of Capachica Peninsula: (AMNH 52196), four juvenile to adult males and females, 25.0–37 mm.

RANGE: Known from the type locality near the village of Ojjerani in Bahia de Puno, Lago Titicaca (figs. 22 and 23) and from north of the Capachica Peninsula in Lago Grande (fig. 22).

ETYMOLOGY: The trivial name *robustus,* a Latin adjective, meaning strong or robust, in reference to the overall robust appearance of this species.

?*Orestias cuvieri* × *Orestias pentlandii*

REMARKS: The two species of *Orestias* that attain the greatest standard length, *O. cuvieri* (maximum of 220 mm SL recorded) and *O. pentlandii* (maximum of 200 mm SL recorded) are known from collections throughout Bahia de Puno, as well as other localities in Lago Titicaca. They were considered by Tchernavin (1944a) to be sister species. The two species are readily distinguished by the presence of large, recurved outer jaw teeth in *cuvieri,* as opposed to few or no teeth in the outer jaws of *pentlandii.* In addition, *cuvieri* has a larger head, fewer and larger scales in a lateral series, and fewer vertebrae than *pentlandii.* With the description of *O. ispi* by Lauzanne (1981), which is hypothesized to be most closely related to *O. pentlandii, cuvieri,* and *pentlandii* are no longer considered to be sister species (see Phylogenetic Analysis, Explanation of Synapomorphy Diagrams, and Systematic Accounts for these three species).

Tchernavin (1944a) discussed several specimens collected by the Percy Sladen Titicaca Expedition that he considered to be hybrids between *O. pentlandii* and *cuvieri.* These specimens (BMNH 1944.6.6:19–20), two mature males, are intermediate between *pentlandii* and *cuvieri* in several characters including squamation (scales are smaller and more numerous than in *cuvieri*) and head length (head shorter than in *cuvieri* but longer than in *pentlandii*). In both specimens, there is a distinct, large outer row of recurved, unicuspid teeth in the jaws, clearly a character of *cuvieri.* Body length (165 to 170 mm SL) is within the expected range for males of both *cuvieri* and *pentlandii.*

Tchernavin (1944a, p. 161) concluded that the specimens were most likely hybrids, stating: "Both specimens were taken from among a school of ripe *Orestias cuvieri* and probably are the result of interbreeding between this species and *Orestias pentlandii.*" Villwock (1964) concurred with this conclusion; however, he did not rule out the possibility that these specimens represented males of *O. cuvieri.*

These specimens cannot be assigned with certainty to either *cuvieri* or *pentlandii.* They may represent a third, undescribed species of *Orestias,* however current collections of these large species are not adequate for such a hypothesis to be evaluated.

Orestias rospigliosii Eigenmann and Allen

Orestias rospigliosii. Eigenmann and Allen, 1942, p. 381 (*nomen nudum*).

REMARKS: Allen, in Eigenmann and Allen (1942) published the name of a new species, *Orestias rospigliosii* in honor of Dr. Carlos Rospigliosi y Vigil, former director of the Zoological Museum of the University of San Marcos. The authorship of the species was attributed to both Eigenmann and Allen. There were to be five specimens, the largest (53 mm total length) the holotype, collected by C. H. Eigenmann, December 8, 1918 from Río Langui, Peru, above 12,000 feet elevation. A catalogue number of IU 12290 is given for the type series; however, this number pertains to a lot identified as the characiform *Curimatella alburnus.* The morphometric and other descriptive data are vague and do not serve to identify a distinct species of *Orestias.* Allen concluded the description by stating (p. 381): "Having been unable to find the types, the description is incomplete, and I do not know where the species belongs."

My own examination of former Indiana University material of CAS, FMNH, USNM, and UMMZ failed to locate the types. There were numerous collections in the area of Río Langui by Eigenmann and coworkers in December 1918. One lot at CAS, IU 16075, collected on December 8, 1918 from Río Langui by C. H. Eigenmann and M. Medina, contains five specimens that are distorted beyond identification and appear to have been dried out at one time. Therefore, *Orestias rospigliosii* Eigenmann and Allen must be considered a *nomen nudum.*

Orestias pentlandii var. *fuscus* Garman

Orestias pentlandii var. *fuscus.* Garman, 1895, p. 148 (*nomen nudum*).

REMARKS: Garman (1895) concluded his diagnosis of *Orestias pentlandii* by stating (p. 148): "Specimens from the Cuzco Valley are about two-thirds as large as those described; they are much darker on the back, above the lateral line, and apparently belong to a distinct variety, *fuscus.*"

No designated type material has been located for this variety; although, there are specimens identified as *O. pentlandii* from the Cuzco Valley in the MCZ collections (MCZ 3941). Garman's sentence does not serve to sufficiently distinguish *fuscus* from other forms of *Orestias.* Therefore, *Orestias pentlandii* var. *fuscus* Garman is treated as a *nomen nudum.*

SUMMARY

Forty-three species of *Orestias* (table 2) are recognized in the present revision. Fourteen are described as new (*gracilis, rotundipinnis, farfani, gymnotus, hardini, ctenolepis, ascotanenis, richersoni, multiporis, mundus,ututo, imarpe, tomcooni,* and *robustus*).

Of the 25 forms recognized by Tchernavin (1944a), two (*uyunius* and *langui*) are treated as synonyms of *agassii,* one (*O. agassii owenii*) is treated as a synonym of *jussiei,* and one (*O. agassii pequeni*) is treated as a synonym of *frontosus,* recognized here as a distinct species, although treated by Tchernavin as a synonym of *O. agassii.* The remaining forms (both species and subspecies) of Tchernavin are all recognized at the rank of species. The use of the subspecific rank is abandoned here. Tchernavin's subspecies of *O. agassii* are judged not closely related (i.e., they do not form a monophyletic group).

The genus *Orestias* is a well-defined monophyletic group. Seven synapomorphies serve, as a group of characters, to distinguish the genus from other cyprinodontoid fishes; these are: (1) the pelvic fins and fin girdle are absent in all ontogenetic stages examined, (2) the vomer is absent, (3) the middle anal and middle dorsal radials are cartilaginous, rather than being ossified, (4) the anterior and posterior ceratohyal are separated ventrally by a large gap filled with cartilage, as opposed to being nearly in contact, (5) the first postcleithrum is absent, (6) the anguloarticular lacks a ventral extension parallel to the retroarticular, and (7) there are unique squamation and head pore patterns, the latter characterized by a prominent lyre-shaped arrangement of minute neuromasts, the former by a prominent dorsal ridge of scales running from the top of the head to the anterior base of the dorsal fin.

The neuromast pattern is very similar to that found in the lowland, tropical South American killifish genus *Cynolebias* and has been suggested as evidence for the common ancestry of that genus and *Orestias.* However, it was shown in a revision of cyprinodontiform fishes (Parenti, 1981) that the two genera are clearly members of different suborders of killifishes, and that this similarity in head pore pattern should therefore be treated as a convergence.

In that cyprinodontiform revision it was hypothesized that *Orestias* has no close South American relatives, but is in a monophyletic group with the Anatolian cyprinodonts (*Aphanius* and its relatives), and most closely related to the genus *Kosswigichthys.* Evidence for this hypothesis is reviewed in the present paper, and is upheld. However, further osteological study of Anatolian cyprinodonts is needed to hypothesize the polarity of a number of characters.

Species of the genus *Orestias* are divided into four monophyletic groups, referred to as species complexes.

The *cuvieri* complex comprises four species (*cuvieri, pentlandii, ispi,* and *forgeti*) defined as monophyletic primarily by characters of the gill arches. The ventral gill arches are narrow and elongate, and the dorsal gill arches are reduced in size relative to the ventral gill arches. The fifth ceratobranchials are closely apposed, and are often fused along the midline. Inner teeth are simple and numerous.

Diversity among species of the *cuvieri* complex reflects the diversity found within the other three complexes and among the genus *Orestias* as a whole. Two of the species (*cuvieri* and *pentlandii*) are large, midwater forms of Lago Titicaca; *cuvieri* has large recurved outer teeth and is an omnivore. *Orestias pentlandii,* like its sister species *ispi,* has few or no outer teeth and is a planktivore.

The *gilsoni* complex comprises 10 species (*gilsoni, taquiri, mooni, uruni, minimus, minutus, tchernavini, tomcooni, imarpe,* and *robustus*) defined as a monophyletic group by a derived caudal fin structure. They are all relatively small, inshore forms found in Lago Titicaca. A number of species (e.g., *minimus, minutus,* and *tchernavini*) are known only from females. The relatively large sample size of *tchernavini* (it is known from 37 specimens) suggests that a high proportion of or all females within species of *Orestias* may indicate the existence of a particular reproductive pattern rather than sampling error. A high proportion of females is not an uncommon phenomenon within killifishes; the extent and nature of the phenomenon needs to be investigated further.

The *mulleri* complex comprises five species (*mulleri, gracilis, crawfordi, tutini,* and *incae*) defined as a monophyletic group by the character of having the dorsal as well as the anal fin base extending beyond the primary dorsal and ventral profile. The extension of the anal fin beyond the primary ventral profile is one character shared by the *mulleri* and *gilsoni* complexes, which are most closely related.

The *agassii* complex comprises 24 species (*agassii, empyraeus, frontosus, polonorum, elegans, jussiei, puni, parinacotensis, laucaensis, tschudii, gymnotus, hardini, ctenolepis, ascotanensis, richersoni, multiporis, mundus, ututo, silustani, luteus, rotundipinnis, farfani, albus,* and *olivaceus*). The last five comprise what is referred to as the *luteus* group.

All species of the *agassii* complex have a series of enlarged and thickened lateral scales known as the lateral shield. In a number of species, these scales, as well as the head scales are large and smooth, with few or no discernible concentric striae. In the *luteus* group, the head and lateral scales are large and thick, and covered with granulations. Species of the *luteus* group tend to be extremely wide-bodied and wide-headed.

Killifishes, as a group, are highly sexually dimorphic and dichromatic. Among *Orestias* species, females are generally much larger than males. All but one species of the *agassii* complex undergo an ontogenetic change in color pattern that is characteristic of most other killifish. Juveniles and subadult females exhibit a mottled pattern. With age, the pattern gets denser and adult males and females are dark on the dorsal and lateral surface, whereas the ventral surface is light. Species within the three other complexes, and *mundus* of the *agassii* complex, do not undergo such an ontogenetic change in color pattern, and there is little or no sexual dichromatism. Both juveniles and adults are nearly uniformly pigmented.

The genus *Orestias* extends throughout the Andean Altiplano and beyond, ranging from Ancash Province, northern Peru to Antofagasta Province, northern Chile. The greatest concentration of species is found within the Titicaca Basin, and specifically Lago Titicaca, the large, high-altitude lake of the Altiplano of Peru and Bolivia.

The diversity of *Orestias* in Titicaca has been used as justification for the application of the term "species flock" to these killifishes. However, the *Orestias* of Lago Titicaca do not form a monophyletic group. Therefore, insofar as the concept of a species flock may be implicit in its monophyly of included taxa, it is recommended that the term not be applied to all *Orestias* species in Lago Titicaca.

The introductions of rainbow and brown trout, as well as silversides, into Lago Titicaca has threatened the endemic *Orestias* fauna. *Orestias cuvieri,* the species with large adults believed to have been in direct competition with the introduced trout, is presumed extinct. However, reports that *Orestias* as a genus is extinct in Titicaca are wrong. Recent collecting has revealed that many species are abundant, and that new species remain to be described. Exploration of the many small, isolated lakes of the high Andes is expected to reveal additional new species of this diverse and species-rich genus of killifishes.

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