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MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 115

The Spiny-rayed Cyprinid Fishes (Plagopterini) of the Colorado River System

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JULY 5, 1960

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THE SPINY-RAYED CYPRINID FISHES (PLAGOPTERINI) OF THE COLORADO RIVER SYSTEM*

INTRODUCTION

THE freshwater fish faunas of Western North America, though limited, include a number of distinctive types (Miller, 1946; 1959). One of the endemic groups, the Plagopterini, comprising the cyprinid genera *Lepidomeda, Meda,* and *Plagopterus,* is herein revised. Despite the fact that the three genera have been known for 75 to 100 years, surprisingly little has been written concerning their classification, distribution, or biology.

Research grants from the Horace H. Rackham School of Graduate Studies of the University of Michigan supported much of the field work that made possible the conclusions regarding populations, ecology, and distribution as well as the systematic analyses herein reported. During our field operations of 1934, 1938, 1939, 1942, 1950, and 1959 we enjoyed the hospitality and profited from the assistance of officials and ranchmen too numerous to mention. Permission to study type specimens at the U. S. National Museum was given by Leonard P. Schultz; William Ralph Taylor kindly provided radiographs of the USNM syntypes of *L. jarrovii.* James E. Böhlke, Mrs. M. M. Dick, and Margaret H. Storey sent lists of pertinent material in their respective institutions (the Academy of Natural Sciences of Philadelphia, the Museum of Comparative Zoology of Harvard College, and the Natural History Museum of Stanford University). Ted Frantz of the Nevada Fish and Game Commission forwarded reports on Nevada waters, indicating changes since our 1938 field work, and also furnished a record of *L. mollispinis* from the Nevada portion of Beaver Dam Creek. Vasco M. Tanner of Brigham Young University made his collection available to us. W. L. Brudon took the photographs (Plates I–II), printed the radiograph (Plate III), and drew the pharyngeals (Fig. 2). Betty Anthony drafted the map (Fig. 1).

METHODS

Measurements were made and rays counted according to the criteria outlined by Hubbs and Lagler (1958:19–26).

Some of the diagnostic characters are best portrayed by radiographs (Pl. III). These show well the degree of spinous modification of the rays and the differential enlargement of the last two unbranched dorsal rays. They also yield the distinctive vertebral counts (Table 1). These counts include the hypural complex as one vertebra and the Weberian apparatus as four vertebrae.

* Contributions from the Museum of Zoology, University of Michigan, and from the Scripps Institution of Oceanography, New Series.

CHARACTERS AND RELATIONSHIPS OF THE PLAGOPTERINI AND CONSTITUENT GENERA

The three genera herein treated are unique among New World cyprinids in the ossification and other spinelike modifications of two anterior dorsal rays and of the pelvic rays. Cope (1874: 130–33) was so impressed with these specializations that he erected a subfamily, Plagopterinae, for these genera. His decision was widely followed, as by Jordan and Gilbert (1883: 148) and Jordan and Evermann (1896*a*: 204). Jordan, Evermann, and Clark (1930: 147), however, went to the extreme of elevating the group to family rank, under the name Medidae. Only Tanner (1936: 157, 171) has accepted this nominal family. Adopting the name Plagopterini, Hubbs (1955: fig. 2) reduced the group to tribal rank, under the subfamily Leuciscinae. We follow this classification.

The characters of the three genera seem to justify their retention in a common group, even though we treat it as of only tribal rank. The distinctiveness of the group receives some confirmation from the circumstance that the constituent genera are among the few North American cyprinids that are not known to hybridize with other genera (Hubbs, 1955).

The specializations of the more extreme members of this group (*Meda* and *Plagopterus*) are striking indeed, but since the less modified forms (comprising the genus *Lepidomeda*) closely resemble other American leuciscines, all three genera, pending the long deferred and much needed critical revision of American cyprinids, are most appropriately classed in the Leuciscinae. There seem to be no valid reasons for separating them from that subfamily. Resemblance is particularly close between *Lepidomeda* and several species referred to the genus *Gila,* and, even more strikingly, with a species of the Bonneville system, *copei,* that has been referred to a monotypic genus, *Snyderichthys* (Miller, 1945).[1] It is not now apparent whether such resemblance, extending even to details of coloration, is indicative of intimate relationship. In all of the obvious distinctive characters of the Plagopterini, *Lepidomeda* is the least modified.

The spinelike modification of the dorsal rays, rather well shown in the radiographs (Pl. III), is least marked in *Lepidomeda* and is variable within this genus, the only one of the three that is polytypic. The modification is strongest in the last unbranched ray, which in the different species is varyingly thickened, vitreous, and expanded on the lateral oblique wings, with the sagittal septum hardly evident by external examination and with

[1] Study of the comparative osteology of *Gila* and its relatives, by Teruya Uyeno, convinces us that *Snyderichthys* merits subgeneric recognition only (Osteology and phylogeny of the American cyprinid fishes allied to the genus *Gila.* Ph.D. thesis, Univ. Mich., 1960).

the transverse sutures largely obliterated in the thickened portion. The terminal two-fifths to one-fourth of the ray, however, remains typical of soft-rays in structure in that this portion is slender, flexible, and strongly articulated. The preceding unbranched ray is also modified toward a spine-like structure, but remains only about three-fifths as long as the main spine, is less thickened, and is little expanded on the oblique wings basally. Distally it is expanded transversely, and its soft, articulated tip is more or less vestigial. It is not, however, very pungent. The several rays following the main dorsal spine are only slightly dilated and spinelike on the lateral wings basally.

In *Meda* and *Plagopterus* the next to last unbranched dorsal ray is greatly enlarged and extends to a strong, pungent tip just short of the much reduced soft, slender, articulated tip of the last unbranched ray. The outer part of the anterior spine is vitreous and is devoid of evident articulations, but where the ray is thicker, nearer the middle of its length, articulations can be discerned. This ray is more massive than the last unbranched one, which its strong wings largely cover. The last unbranched ray is also very spinelike, except at the extreme tip. Several of the following rays are considerably but decreasingly dilated and spinelike in appearance on the basal half, but distally remain slender, branched, and articulated. The last rays are scarcely modified. The dorsal spines are strongest in *Plagopterus*, but even in this genus no new structures are involved.

In all three genera the branched pelvic rays are thickened, consolidated, vitreous, and otherwise spinelike on the basal half to three-fourths of their lengths, where the articulations are scarcely or not evident. The modification, however, is almost wholly confined to the ventral demitrich; that is, to the left demitrich in the right fin and to the right demitrich on the left pelvic. The two strikingly asymmetrical halves of the anterior branched rays are distinct basally, but posteriorly become fused in the spinous modification. In *Lepidomeda* the spinose demitrich is continued to the fin margin as a slender articulated appendage, and the spinous modification is less extreme than in the other genera. In this character, as in others, the species of *Lepidomeda* are modified to different degrees. In *Meda* and *Plagopterus* the ventral demitrichs are strong spines ending in pungent points on the ventral side of the fin about three-fourths of the way out. The extreme bases of the nearly normal (upper) demitrichs of the first few branched rays are slightly dilated and spinelike (scarcely so in *Lepidomeda*).

Several pectoral rays, behind the first unbranched ray, are somewhat spinelike near their bases in *Meda* and *Plagopterus*, but are only slightly so specialized in *Lepidomeda*. A further distinctive specialization of the pectoral rays is confined to the mature males. In *Lepidomeda* the rays at

this stage are only slightly dilated and retain a smooth front edge. In the mature males of *Meda* and *Plagopterus,* in contrast, the anterior several branched pectoral rays are greatly thickened and dilated, with the segments much broadened, and those along the front edge of the anteriormost branch are finely and irregularly denticulate.

The Plagopterini are characterized by having the more or less spinose pelvic fins attached to the belly by a membrane along the osseous part of the innermost ray. In *Lepidomeda* the membrane extends along about half the inner border of the fin; in *Meda* and *Plagopterus,* about two-thirds the length of the border. In all three genera the number of pelvic rays is reduced to seven, occasionally even fewer, very rarely to eight, which is the usual number in American cyprinids.

The primitiveness of *Lepidomeda* is further shown by its retention of scales, which, however, are somewhat degenerate. The entire body is scaly, except, in some species, where covered by the depressed paired fins. The scales of *Lepidomeda* (Cockerell, 1911: 213) are deeply embedded and transversely oval. Unlike those of most American cyprinids with small and not strongly imbricate scales, the scales of this genus lack basal radii (occasionally a few radii extend onto the lateral fields). *Plagopterus* and *Meda* are devoid of scales, unless they are vestigially represented by unsculptured platelets along the lateral line close to the head and, in *Plagopterus,* at the base of the dermal (sensory?) ridgelets on the anterodorsal part of the body (these dermal structures were definitely indicated as vestigial scales by Gilbert and Scofield, 1898: 497, and by Snyder, 1915: 584). If these platelets are remains of scales, *Meda* is the most extreme genus of the Plagopterini in the loss of squamation, which is one trend characteristic of the group.

Another feature of the Plagopterini that *Lepidomeda* exhibits to a less extreme degree than the other genera is the bright silvery coloration. In fact, as already noted, *Lepidomeda* is closely approached in this respect by *Gila* (*Snyderichthys*) *copei,* which is almost as silvery and also has dusky lateral mottlings. *Meda* and *Plagopterus* shine like burnished silver. *Meda* retains dark speckles on the back and on the lateral band. *Plagopterus* is almost uniformly silvery.

The general form of the head and body is also least modified in *Lepidomeda* (Pls. I–III). In that genus the premaxillaries are approximately terminal (varying from slightly prominent to slightly overhung) and the gape is variably oblique. In *Meda* the upper lip is weakly included and the mouth remains oblique. In *Plagopterus* the upper lip is definitely overhung by the snout and the mouth is nearly horizontal. The top of the head and the belly are rounded in *Lepidomeda,* though the contours are

variably turgid. In *Meda,* and more notably in *Plagopterus,* the top of the head is flattened transversely and longitudinally, the belly is also flattened, and the pectoral fins are lower and more transverse.

Lepidomeda is virtually devoid of conspicuous dermal sense organs. *Meda* has these organs slightly developed on the head, but not noticeably on the body. *Plagopterus,* most extreme in this character also, has the intermandibular region spongy with large, thick-set papillae, and has conspicuous, though short, raised longitudinal dermal ridges on the anterodorsal part of the body.

In conclusion, the Plagopterini are regarded as modified members of the Leuciscinae. Among the three constituent genera, *Lepidomeda* definitely seems to be the most generalized, and *Plagopterus* seems to be the most highly modified, except, perhaps, in squamation. The body form, high development of sense organs, and plain coloration of *Plagopterus* seem to be related to its life in swift, silty waters.

It is obvious that in the evolution of spinelike rays the Plagopterini have taken a course quite independent of that followed by the Old World spiny-rayed cyprinids, such as *Cyprinus* and *Barbus.*

DISTRIBUTIONAL RELATIONS

The singular group Plagopterini constitutes one of the main elements in the highly endemic fauna of the Colorado River system (Miller, 1946; 1959). It is confined, so far as known (Fig. 1), to the lower and middle parts of this drainage, including the remnants of a Pleistocene tributary system, comprising the Pluvial White and Carpenter rivers of southeastern Nevada (Hubbs and Miller, 1948: 96–100). Within this section of the Colorado River system the members of the group exhibit a rather astonishing degree of endemism.

Meda is confined to the clear and more permanently flowing creeks of the Gila River system in Arizona and New Mexico. For this reason, and because of the deterioration of stream flow in Arizona, the range of the species is becoming further reduced.

Plagopterus is seemingly now restricted to the Virgin River system in Utah, Arizona, and Nevada (Miller, 1952: 36), where it lives in the rather swift currents of generally silty streams. Until shortly before the turn of the century, prior to the time when the streams became disastrously reduced as the result of drought, erosion, water storage, and stream diversion, it also inhabited the lower Gila River system, from Tempe, where it lived with *Meda,* to the mouth of the Gila at Yuma (Gilbert and Scofield, 1898: 496; Snyder, 1915: 584).

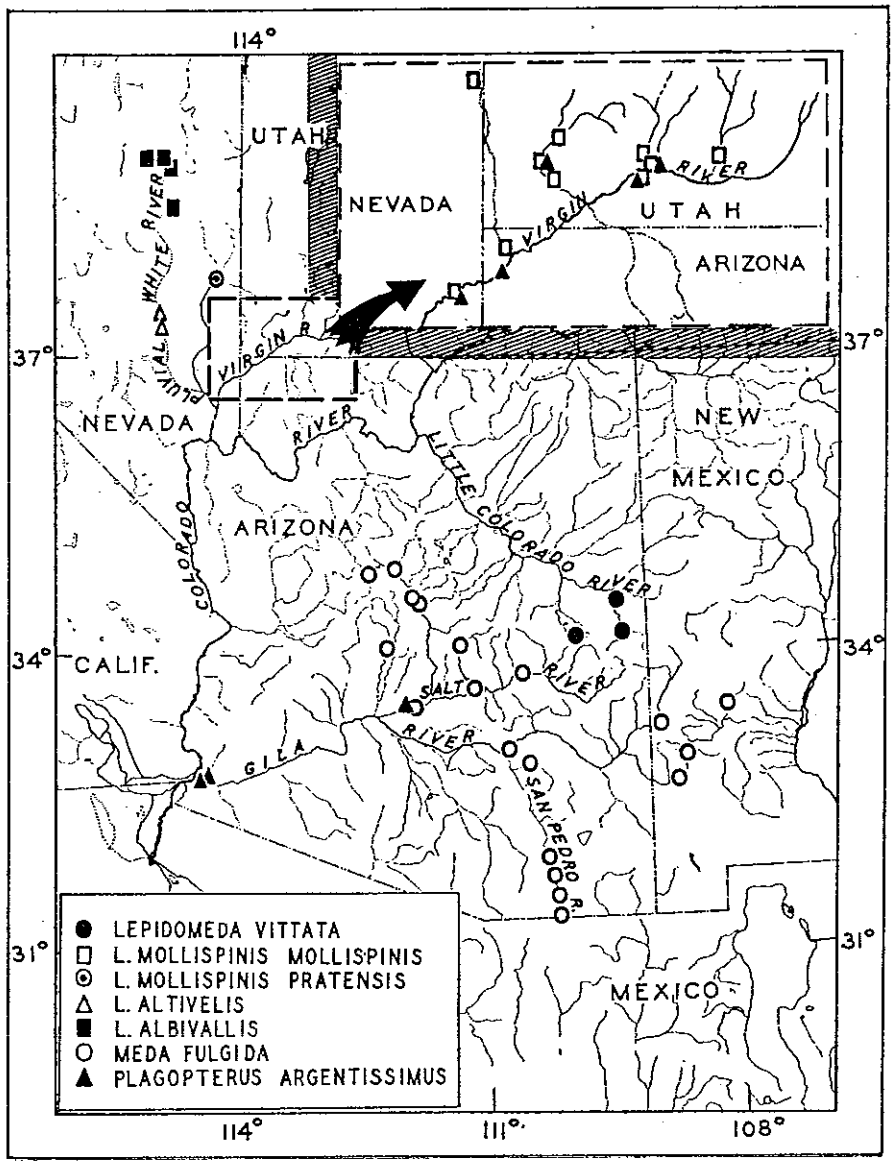

FIG. 1. Record stations showing the distribution of the plagopterin fishes.

(356)

Lepidomeda is largely confined to the more or less isolated remnants of the once abundant Pluvial drainage of the middle section of the Colorado River. It is known (1) from the isolated spring waters of the Pluvial White River system, Nevada, where, except for its preference for cool instead of warm waters, its distribution parallels that of *Crenichthys baileyi* (Hubbs and Miller, 1948: 96); (2) from a single spring marsh adjacent to Meadow Valley Wash (Pluvial Carpenter River), Nevada; (3) from the Virgin River and its tributary creeks, in the adjoining parts of Utah, Nevada, and Arizona; and (4) from the upper parts of the Little Colorado River system in east-central Arizona.

Presumably erroneous records for *Plagopterus* and *Lepidomeda* are discussed on pages 34–35 and 30, respectively.

The ranges of the seven forms of the Plagopterini are so limited, and the stream deterioration of the West has been so great, as to put the forms into the category of threatened species. We have just determined, through collecting in 1959 designed to test the point, that the two forms of most restricted range, namely *Lepidomeda mollispinis pratensis* of Big Spring near Panaca, and *Lepidomeda altivelis* of Ash Spring in Pahranagat Valley, both in Nevada, have already been exterminated.

SPECIATION

In line with the facts already presented, we postulate that the Plagopterini were derived in what now constitutes the Colorado River system from a species of *Gila* or from a similar, relatively unspecialized cyprinid genus; that *Lepidomeda* represents the ancestral type of the tribe; and that the more specialized genera, *Meda* and *Plagopterus*, arose from *Lepidomeda* in the same river system.

The origin of the group may have been fairly old, almost certainly as early as the Pliocene period. It is now believed by geologists that the Colorado system dates from a period that old, though the precise stream courses have changed (Repenning and Lance, paper in preparation). We have identified, from the Pliocene Bidahochi formation of northern Arizona, three species that seem referable to genera currently living in the Colorado River system (two to *Gila* and one to *Ptychocheilus*), and these extinct species appear to have been similar to the species of these genera now inhabiting this river system. The high specialization of *Meda* and *Plagopterus* strongly indicates a Tertiary origin for these genera, or for their common ancestor.

The distributional relationships suggest that *Meda* may have been isolated in the Gila River when, and if, the fauna of that stream was geographically separated from that of the main Colorado (Hubbs and Miller, 1948: 94–95). *Meda* has apparently found the big, swift, turbid Colorado River a barrier. In recent years the desiccation of the lower reaches of the Gila and the abundance of introduced predatory fishes in the Colorado have no doubt combined to restrict *Meda* to the Gila system, and to eliminate *Plagopterus* from this basin (Miller, in press).

The highly localized ranges of the five recognizable forms of *Lepidomeda* also indicate limited ecological tolerance, as well as a much more extensive distribution at some past time, presumably Pluvial. The occurrence of perhaps the most distinct species of the genus above the falls of the Little Colorado River suggests considerable antiquity for the period of more extensive and more continuous distribution.

The restriction of the four other forms of the genus to the Virgin River branch of the Colorado River and to the Pluvial tributaries of the Virgin River (Fig. 1) is rather difficult to explain, since the Virgin River has maintained its connection with the Colorado River. Lake Mead, which now floods the lower reaches of the Virgin River, presumably presents a distributional block, and the main river in previous years may have been an equally effective barrier. But at some earlier time the river did not present an insuperable barrier, because the genus occurs on both sides of this river in the region of Grand Canyon.

Within the remnants of the Pluvial Virgin River system, *Lepidomeda* has managed to persist widely in favorable situations. This illustrates two of the zoogeographical and speciational phenomena that are so beautifully exemplified through the arid American West (Hubbs and Miller, 1948), namely, (1) the indications of former, presumably Pluvial, periods of much greater and more continuous distribution—indications provided by chains of now isolated remnant populations of one form or of one series of closely related forms, and (2) the high incidence of differentiation among these isolated forms.

The two main populations of *Lepidomeda* in the Pluvial Virgin River are now well separated by the excessively arid lower parts of the Pluvial White River, and these two populations are now well differentiated. Each, however, is of rather general occurrence in a still more or less integrated stream complex—*L. albivallis* in the rather well-watered present White River Valley in southeastern Nevada, and *L. m. mollispinis* in the presently still largely intact Virgin River system. Within each area the several spring and creek populations remain reasonably consistent in characters, presum-

ably as a result of some interflow of genes and because the habitats in each area are rather similar.

The two other populations which we encountered in our rather extensive field work throughout the area, but which we have just found to have become extinct, were confined to single spring areas. They were differentiated from one another and from the distinctive forms of the White River and the Virgin River. The more strikingly differentiated of the two isolated spring forms was *L. altivelis,* which appears to have been almost wholly confined to the cooled outflow stream fed by the warm waters of Ash Spring, in Pahranagat Valley, Nevada, along the course of Pluvial White River. A few yearlings were also taken in the dirty olive-green, alkaline water of Upper Pahranagat Lake, but the lake population was presumably derived by flood transport from Ash Spring above. Oddly, *Lepidomeda* has not occurred during the period of our explorations in the two other major springs of Pahranagat Valley (Crystal and Hiko) nor in the other springs or lakes that were examined in this valley.

The other isolated form of *Lepidomeda* that we found (on July 10, 1938), namely *L. mollispinis pratensis,* was represented by an extremely meager population in a tiny stream flow in the marsh of Big Spring, along Meadow Valley Wash, near Panaca, Nevada. Assiduous collecting in the most favorable habitats yielded only the seven type specimens. How a local form persisted on such a slender thread until a few years ago is a mystery. This spring is in the drainage of Pluvial Carpenter River (Hubbs and Miller, 1948: 98–100), which joined Pluvial White River along the course of the present Moapa River, about 20 miles above its confluence with the Virgin River. None of the other springs or stream flows in the Meadow Valley Wash or its tributary Clover Valley (both in the basin of Pluvial Carpenter River), nor in Moapa Valley, have yielded *Lepidomeda.*

It is tempting to attribute the differentiation of the four forms of *Lepidomeda* other than *L. vittata* to the interval of about 11,000 years since the end of the Pluvial period. This seems to be a probable, but by no means necessary, conclusion. The present distributional pattern may have resulted from the differential survival in the several localities of forms that had already become differentiated, probably with ecological segregation, within Pluvially integrated waters. We have repeatedly found such ecotypic segregates in western waters. One example, within the general area under discussion, is furnished by two forms of the mountain suckers (*Pantosteus*), of which one, of pool-and-riffle creek type, occurs in the small tributaries of the Virgin River and the other occupies the very swift water of this river where it rushes through the defile in the Beaver Dam Mountains.

ANALYTICAL KEY TO THE PLAGOPTERINI
(Constituting differential diagnoses)

1a.—*Lepidomeda* { 2a. { 3a. { 4a.—*L. mollispinis* { 5a.—*L. m. mollispinis* (1a) / 5b.—*L. m. pratensis* (1b) / 4b.—*L. albivallis* (2) / 3b.—*L. altivelis* (3) / 2b.—*L. vittata* (4)

1b. { 6a.—*Meda fulgida* (5) / 6b.—*Plagopterus argentissimus* (6)

1.
a. *Body* completely covered with scales (except in some species, where covered by the depressed paired fins). Second *dorsal spine* much stronger and longer than first, varying from weak to strong; neither spine pungent (Pl. III). Spiny (lower) demitrichs of branched *pelvic rays* without pungent tips, ending in slender, soft, articulated continuations, extending to margin of fin. Segments of *pectoral rays* in mature males little dilated; those on front margin of ventral demitrichs smooth-edged. *Head and belly* rounded; head about, or more than, two-thirds as deep as long. *Vertebrae* usually 41 to 43—(*Lepidomeda.*) 2

b. *Body* scaleless (except, perhaps, for unsculptured platelets along lateral line near head and, in *Plagopterus*, at base of dermal ridgelets on anterodorsal part of body). First *dorsal spine* much stronger than second and almost as long, always much enlarged, solidified, and strongly pungent (Pl. III). Spiny (lower) demitrichs of branched *pelvic rays* without soft continuations, the pungent tips definitely short of fin margin. Segments of *pectoral rays* in mature males greatly dilated; those on front margin of ventral demitrichs finely denticulate. *Head and belly* flattened; head much less than two-thirds as deep as long. *Vertebrae* usually 40.—(*Meda* and *Plagopterus.*) 6

2. (1a).
a. *Anal rays* 9 (not infrequently 8 in *L. albivallis*). Teeth in main row 5–4 (rarely 4–4). *Scales* fewer than 90 (except in *L. altivelis*). *Vertebrae* 42 to 44 3

b. *Anal rays* 8 (rarely 9). *Teeth* in main row 4–4. *Scales* usually more than 90. *Vertebrae* typically 41 or 42 (rarely 43). ADDITIONAL CHARACTERS.—*Mouth* moderately oblique, about as in *L. albivallis*. Second

dorsal spine about as strong as in *L. altivelis*. *Dorsal fin* moderately high (depressed length 2.05 to 2.3 in predorsal length) and moderately sharp. *Head* broad (its width 1.45 to 1.65 in its length). *Pigment* on opercles, shoulder girdle, and chin variable. Headwaters of Little Colorado River system, Arizona ..... (4) *L. vittata*

3. (2a).
   a. *Mouth* less oblique (a line from uppermost tip of premaxillary to middle of caudal peduncle passes below middle of pupil). *Snout* more rounded. *Dorsal spines* variably weaker. *Dorsal fin* low to moderate (depressed length 2.2 to 2.4 in predorsal length, except in *L. m. pratensis*), and varyingly less pointed. *Head* broader (width 1.5 to 1.85 in its length). *Pigment* on shoulder girdle extending variably forward beyond scapular bar.—(*L. mollispinis* and *L. albivallis*.).....4
   b. *Mouth* more oblique (a line from uppermost tip of premaxillary to middle of caudal peduncle passes above middle of pupil). *Snout* sharper. *Dorsal spines* stronger. *Dorsal fin* higher (depressed length 1.8 to 2.1 in predorsal length), and more sharply pointed than in any other form. *Head* more compressed (width 1.9 to 2.0 in its length). Almost no *pigment* on shoulder girdle in advance of scapular bar. ADDITIONAL CHARACTERS.—*Pigment* on opercles about as in *L. mollispinis*; a band of coarse pigment crossing chin behind upper lip. *Pelvic-fin length* 1.4 to 1.5 in head. *Upper-jaw length* 1.15 to 1.3 in postorbital. (Formerly) cooled, swift outflow from Ash Spring and Upper Pahranagat Lake, Pahranagat Valley, Nevada (in course of Pluvial White River) ..... (3) *L. altivelis*

4. (3a).
   a. *Melanophores* confined to upper half of opercle and to upper part of upper limb of preopercle; lower half of outer face of shoulder girdle in adults lacking pigment in front of vertical from pectoral insertion. *Size* smaller (only rarely more than 80 mm. in standard length) and *colors* less bright. *Dorsal spines* weaker. *Pharyngeal arch and teeth* (Fig. 2) much smaller and more delicate (in an average adult about 0.10 per cent weight of fish); the whole arch flatter (more compressed dorsoventrally); anterior angle usually sharp and conspicuous; edge of dorsal surface medially and on anterior limb usually rather sharply ridged (the pharyngeal arch and tooth distinctions are not sharp in the localized form *L. m. pratensis*, of which no large adults are known). Virgin River system in Utah, Nevada, and Arizona, and (formerly) Big Spring in Meadow Valley, Nevada.—(*L. mollispinis*) 5
   b. *Melanophores* typically extending across opercle and subopercle, and to angle of preopercle; lower half of outer face of shoulder girdle in

adults with considerable pigment in front of vertical from pectoral insertion. *Size* larger (commonly 80–90 mm., largest 103 mm. in standard length) and *colors* particularly bright. *Dorsal spines* stronger. *Pharyngeal arch and teeth* (Fig. 2) much more massive (in an average adult about 0.25 per cent weight of fish); the whole arch thicker (less flattened dorsoventrally); anterior angle usually less conspicuous, more evenly rounded; edge of dorsal surface usually broadly rounded. ADDITIONAL CHARACTERS.—*Pelvic-fin length* 1.4 to 1.8 in head length. *Upper-jaw length* 1.1 to 1.5 in postorbital. Springs and spring-fed creeks in Recent White River Valley (upper headwaters of Pluvial White River system), Nevada ..... (2) *L. albivallis*

5. (4a).

a. *Dorsal fin* lower and more rounded (its depressed length 1.45 to 1.65 in distance from dorsal origin to occiput); when the fin is erected at about 45° the outer edge in the adult usually slopes downward and backward. *Pelvic fin* shorter (length 1.5 to 1.85, usually 1.65 to 1.8, in head length). *Mouth* smaller (upper-jaw length 1.4 to 1.8, usually 1.45 to 1.6, in postorbital), and less oblique (a line from uppermost tip of premaxillary to middle of caudal peduncle passes below pupil). Virgin River system in Utah, Nevada, and Arizona..... ..... (1a) *L. m. mollispinis*

b. *Dorsal fin* higher and more pointed (its depressed length 1.2 to 1.45 in distance from dorsal origin to occiput); when the fin is erected at about 45° the outer edge in the adult is usually about vertical. *Pelvic fin* longer (length 1.35 to 1.6, usually about 1.5, in head length). *Mouth* larger (upper-jaw length 1.25 to 1.4 in postorbital), and more oblique (a line from uppermost tip of premaxillary to middle of caudal peduncle passes through lower part of pupil). (Formerly) outflow of Big Spring, in meadow adjacent to Meadow Valley Wash, in course of Pluvial Carpenter River, Nevada .. (1b) *L. m. pratensis*

6. (1b).

a. No developed *barbel* (there may be a slight dermal swelling at end of upper lip or at lower posterior corner of maxillary). *Intermandibular region* scarcely papillose. No *dermal ridgelets* on body. Principal *dorsal rays* 7 (rarely 8); *anal rays* usually 9. *Teeth* in main row 4–4 (rarely 5–4). *Mouth* moderately oblique. *Breast region* less flattened. Gila River system, Arizona and New Mexico.—(Genus *Meda*) .... (5) *Meda fulgida*

b. A well-developed *barbel* pendant from end of upper lip. *Intermandibular region* spongy with coarse, close-set papillae. *Dermal* longitudinal *ridgelets* (overlying minute platelets) on anterodorsal part of

body. Principal *dorsal rays* 8 or 9; *anal rays* usually 10. *Teeth* in main row usually 5–4 (rarely 4–4). *Mouth* nearly horizontal. *Breast region,* including pectoral fins, more flattened. Virgin River system, Utah, Nevada, and Arizona, and (formerly) lower Gila River system, Arizona.– (Genus *Plagopterus.*) ..... (6) *Plagopterus argentissimus*

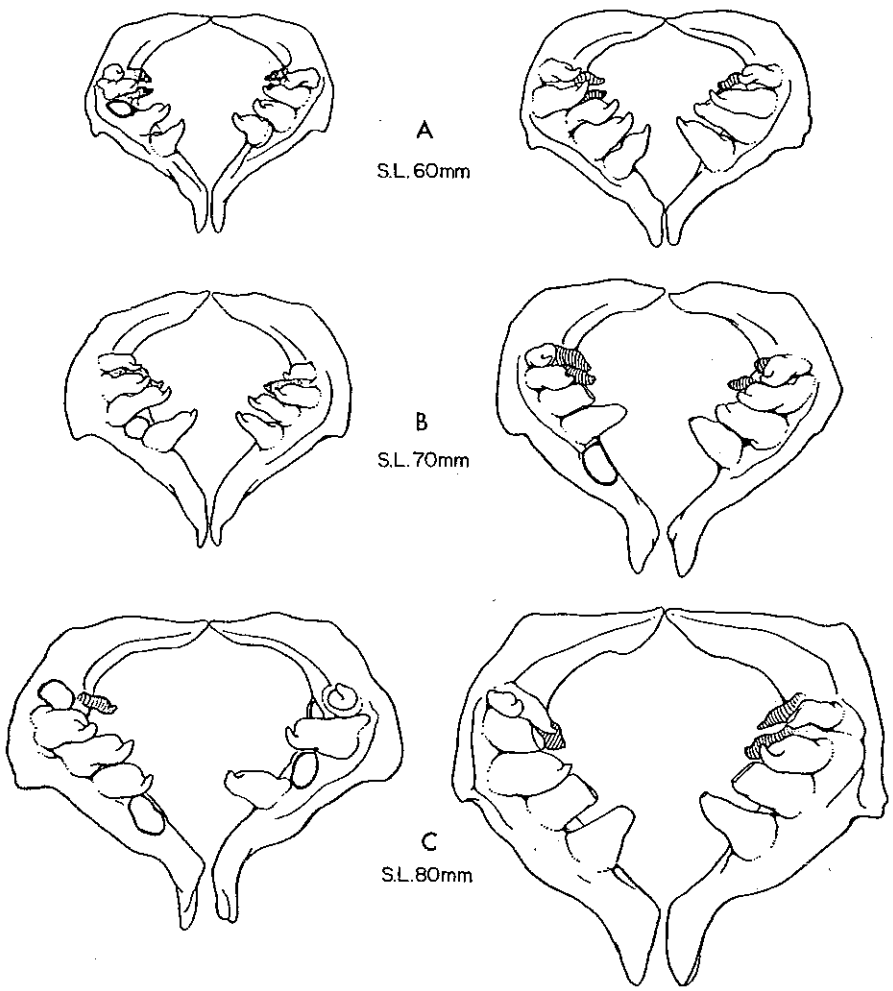

FIG. 2. Pharyngeal arches and teeth of *Lepidomeda m. mollispinis* (left column) and *Lepidomeda albivallis* (right column) at comparable sizes. A, *L. m. mollispinis,* UMMZ 162849; *L. albivallis,* UMMZ 132180. B, *L. m. mollispinis,* UMMZ 162849; *L. albivallis,* UMMZ 124980. C, *L. m. mollispinis,* UMMZ 141674; *L. albivallis,* UMMZ 124980.

GENUS *Lepidomeda* Cope

Lepidomeda.—Cope, 1874: 131 (original description; classification). Cope and Yarrow, 1875: 642 (diagnosis repeated). Jordan and Gilbert, 1883: 148, 251 (comparisons; description). Jordan and Evermann, 1896a: 204, 328 (comparisons; description; key to species). Eddy, 1957: 104 (comparison). Moore, 1957: 94, 138 (characters and comparisons).

TYPE SPECIES.—*Lepidomeda vittata* Cope (designated by Jordan and Gilbert, 1883: 251).

Rubric 1a of the analytical key is the differential diagnosis of this plagopterin genus. Additional characters are the biserial pharyngeal teeth, silvery peritoneum (overlain by sparse to numerous brown puncticulations), moderate intestine with one large S-loop, and no barbel. The four species (five forms) are distinguished in the same key. The range of the genus is outlined on page 11.

Lepidomeda mollispinis, new species
Middle Colorado Spinedace

DIAGNOSIS.—A species of *Lepidomeda* distinguished by having 5–4 teeth in the main row, a relatively weak and soft-tipped (second) dorsal spine, 9 anal rays, typically fewer than 90 lateral-line scales, the depressed length of the dorsal fin less than the head length, the sides of the body mostly silvery, and with melanophores confined to upper half of opercle and to upper part of ascending limb of preopercle (see rubrics 1a, 2a, 3a, and 4a of the analytical key, pp. 14–15). The synonymy and type designation are given below under the heading of the nominate subspecies. An additional subspecies of restricted range, *L. m. pratensis*, is recognized.

Lepidomeda mollispinis mollispinis, new subspecies
(Pl. I, A; Pl. III, B)
Virgin River Spinedace

Lepidomeda vittata (misidentification; not of Cope, 1874).—Tanner, 1932: 135 (Santa Clara Creek, at Veyo, Washington Co., and other localities in the Virgin River drainage, Utah); 1936: 171 (in part; record for Santa Clara Creek only). Wallis, 1951: 87 (from bait tank, Boulder Beach dock, Lake Mead, Nevada; stock originally obtained in Santa Clara Creek, near St. George, Utah). Eddy, 1957: 104, fig. 261 (in part; "Utah" and, in part, "Nevada").

Lepidomeda species.—Miller, 1952: 18, 35, fig. 21 (distribution; habitat; characters in key; use as bait fish). Moore, 1957: 138 (in part; mention of evidently undescribed species in Nevada and Utah related to *L. vittata*).

DIAGNOSIS.—This subspecies is most closely related to *L. m. pratensis*,

from which it differs in having the dorsal fin less elevated and more rounded, the pelvic fins shorter, and the mouth smaller and less oblique (see rubric 5a of key).

TYPES.—The holotype, UMMZ 141673, an adult 88 mm. long, was seined by C. L., L. C., and E. L. Hubbs from Santa Clara River, 3 mi. SE of Shivwitz and 4.5 mi. NW of Santa Clara, Washington Co., Utah, on July 29, 1942. Secured with the holotype were 103 paratopotypes, 23–80 mm. long, UMMZ 141674. An additional 604 specimens were examined from localities in Arizona, Nevada, and Utah as follows: Arizona: UMMZ 141662 (381, 22–77 mm.), Beaver Dam Cr. at U. S. 91 crossing near Littlefield, Coconino Co., July 28, 1942. Nevada: UMMZ 105496 (68, 36–78 mm.), Virgin R., Clark Co. (near Utah border), Sept., 1938; UMMZ 125013 (12, 39–65 mm.), Virgin R. W of Bunkerville, Clark Co., Aug. 31, 1938. Utah (Washington Co.): UMMZ 85955 (2, 48–54 mm.), Santa Clara R., June, 1928; UMMZ 124764 (17, 20–62 mm.), trib. Virgin R. near La Verkin, July 3, 1938; UMMZ 124772 (38, 22–71 mm.), Virgin R. at mouth of La Verkin and Ash creeks, July 3, 1938; UMMZ 162849 (86, 22–74 mm.), Santa Clara R., 2.5 mi. below Gunlock, June 17, 1950. See inset, Fig. 1.

CHARACTERS.—Body form and coloration are indicated on Plate I, A. Principal dorsal rays 8 (in 46 specimens); anal rays, 8 (4), 9 (41), 10 (1); pelvics 7–7 (36), 6–7 (1). The dental formula is typically 2, 5–4, 2, varying as follows: 2, 5–4, 2 (19), 2, 4–5, 2 (1), 2, 4–4, 2 (3), and 3, 5–4, 2 (1). Lateral-line scales about 77 to 91, varying as follows: 77 (1), 81 (1), 82 (2), 83 (4), 84 (1), 85 (4), 86 (2), 87 (2), 88 (3), 91 (1). Vertebrae 42 to 44 (Table 1).

TABLE 1
VERTEBRAL VARIATION IN THE PLAGOPTERINI

Species	Number of vertebrae						No.	Ave.
	39	40	41	42	43	44		
Lepidomeda m. mollispinis	..	..	..	15	12	6	33	42.73
Lepidomeda m. pratensis	..	..	..	1	3	..	4	42.75
Lepidomeda albivallis	..	..	..	1	25	5	31	43.13
Lepidomeda altivelis	..	..	..	3	10	3	16	43.00
Lepidomeda vittata	..	..	10	9	1	..	20	41.55
Meda fulgida	2	20	8	1	..	..	31	40.26
Plagopterus argentissimus	4	19	9	..	..	..	32	40.16

Life colors were noted in the field as follows: body silvery, with a more or less brassy sheen and with sooty specklings on sides; axils of paired fins

and basal band on anal fin orange-red to translucent orange-pink; a little spot of golden red at upper end of gill-slit. Younger fish look whitish in the water and some adults have the sides blackish, especially conspicuous in the water.

The nuptial tubercles, best developed on males in a collection of June 17, but evident also in July specimens, are distinctive. Those on the head are almost wholly confined to the dorsal surface, extending onto the sides only in a definite patch across the upper part of the opercle. They are irregularly scattered over the dorsal surface, from near the occipital edge forward to the upper part of the snout and outward to the orbital margins. They are of moderate size, and their spiny tips are weakly curved forward. Tubercles occur on the scales over the entire body, but become obsolescent on the midsides and belly. Those near the margin of the head, between the lateral lines, are considerably strengthened. Here the partly fused tubercles form a single straightish transverse (or vertical) series, with the points essentially erect. On the caudal peduncle the points are smaller and form a more curved series on each scale. On the breast the tubercles are somewhat strengthened, and usually single on each scale. The scales in a band just behind the shoulder girdle, above the pectoral fin, have the soft tissue considerably swollen, and are weakly tuberculate. On the first pectoral ray there is a single file of tubercles, and on the outer part of several succeeding rays a file branched once near the base. Each tubercle has one to several weakly antrorse spiny points. Weak tubercles line pelvic and anal rays. Despite our large collections none of the other species seems to be represented by nuptial males.

This subspecies often attains a total length of nearly four inches. The largest specimen we have seen is the holotype, about 4.25 inches long (88 mm. in standard length). It is the only specimen among 718 that is longer than 80 mm.

HABITAT.—This subspecies is common in the Virgin River and its tributaries in Utah, Arizona, and Nevada (Fig. 1), in moderate to swift current, chiefly in pools. Where the collections were made the bottom was usually sand and gravel, often with stones and occasionally with boulders and some mud. Green algae and sparse pondweed were often associated, and depth of capture varied from 1 to 3 feet. The water was either clear or, as in the Virgin River, very milky; with bottom visibility from about 3 inches to 3 feet.

ASSOCIATES.—Fish species taken with *L. m. mollispinis* include *Pantosteus delphinus utahensis* (Tanner), *Catostomus latipinnis* Baird and Girard, *Rhinichthys osculus* (Girard), and *Plagopterus argentissimus* Cope. *Micropterus salmoides* (Lacépède) was caught at the type locality.

ETYMOLOGY.—The name *mollispinis* is derived from the Latin *mollis,* soft, and *spina,* spine, in reference to the relatively weak and soft-tipped main (second) dorsal spine.

Lepidomeda mollispinis pratensis, new subspecies
(Pl. I, B; Pl. III, C)
Big Spring Spinedace

DIAGNOSIS.—Like *L. m. mollispinis,* but differing in the higher and more pointed dorsal fin, the longer pelvic fins, and the smaller and more oblique mouth (see rubric 5b of key).

TYPES.—The holotype, UMMZ 124799, an adult 55 mm. long, was seined by C. L. Hubbs and family, R. R. Miller, and A. J. Calhoun from Big Spring, about 1 mile NE of Panaca, Lincoln County, Nevada, on July 10, 1938. Taken with this specimen were six paratopotypes, 48 to 56 mm. long, UMMZ 136097.

CHARACTERS.—Plate I, B, shows the general appearance of this localized and now extinct subspecies. Principal dorsal rays 8, anal rays 9, pelvics 7–7 (6), 6–7 (1). The teeth number 2, 5–4, 2 in 3, and the lateral-line scales vary from 82 to 90 (about 89 in the holotype). Vertebrae number 42 or 43 (only 4 specimens countable; Table 1).

In life *L. m pratensis* was bright silvery. Some specimens were lemon to orange in the axils of the paired fins, on the basal part of the anal fin, near the upper edge of the shoulder girdle, on the vertical arm of the preopercle, and above the mouth.

DISTRIBUTION, LOCALIZATION, AND EXTINCTION.—Our field explorations have indicated that this fish has very recently become extinct in the one spring-fed marsh in which the last few individuals persisted until 1938, or a few years later. This marsh is fed chiefly from a single source, Big Spring, which issues from the base of low hills about 1 mile northeast of Panaca, Lincoln County, Nevada. The meadow occupies a basin off the east side of Meadow Valley Wash, which here dissects the remnants of a lacustrine fill. Meadow Valley Wash follows the ancient course of Pluvial Carpenter River, which was the main, eastern affluent of Pluvial White River (Hubbs and Miller, 1948: 96–100) (Fig. 1).

Prior to recent agricultural modifications Big Spring discharged onto and spread over the large wet meadow, and doubtless provided a more favorable fish habitat than presently exists. The natural overflow course can

still be followed for about a mile across the meadow. Between 1938, when the seven types of *Lepidomeda mollispinis pratensis* were collected, and 1959, when the subspecies was found to have become extinct, the source was dammed and a contoured ditch was constructed to divert the spring effluent to the upper part of the meadow. In 1938 the outflow followed the natural channel until it spread out. The channel was generally 1 to 3 feet wide and as deep as 2 feet. It contained watercress (*Nasturtium*) above, pondweeds of the *Potamogeton pectinatus* and floating types, and rushes, below. The bottom was of firm to soft clay, with some gravel. The current was slight over most of the course, but occasionally swift. The water was clear, but easily roiled. On July 10, with the air at 94°F., the water temperature was 84°. Here, in 1938, in the stream within the meadow area, we seined, by prolonged effort, along with the seven types of *Lepidomeda mollispinis pratensis,* 31 half-grown mountain suckers, *Pantosteus* sp., and 312 young to adult speckled dace, *Rhinichthys osculus* (Girard), both representing local forms characteristic of the remnants of Pluvial Carpenter River.

By 1959 the generally abandoned natural channel had become very largely clogged with silt and a variety of submerged and emergent plants, chiefly chara, *Nasturtium, Decodon,* a broad-leafed *Potamogeton,* green and blue-green algae, and *Scirpus.* Except for about a half-dozen stretches of 10 to 20 feet the stream was almost completely choked and partially dammed, with silt and weeds filling the stream bed from the original more or less gravelly bottom to the surface. The water was rather clear but very readily roiled. The flow, of seepage origin, was slight; in most places, barely perceptible. On July 4, 1959, when the air was 84.5°F., the water temperature varied from 75° to 81°. In the open-water stretches, where the width averaged 3 to 4 feet, intensive and thorough seining, following removal by hand of the excess of water weeds and muck, yielded only one of the three native species that held out here 21 years previously. This was the *Rhinichthys,* which had not only survived but had even become concentrated—to confirm the ubiquity and adaptability of this dace. In addition we found, in considerable density, a large population of the western mosquitofish, *Gambusia affinis affinis* (Baird and Girard), a scourge of native fishes. Another introduction, the bullfrog, *Rana catesbeiana* Shaw, now also abounded, greatly outnumbering the native *Rana pipiens* Schreber.

The diversion of water, with, no doubt, the occasional stoppage of flow in the ditch (which, furthermore, originates above the former habitat of the native fishes), presumably led to the rapid and catastrophic deterioriation of the original habitat and to the decline in the population of the two

more susceptible native fishes, the *Pantosteus* and the *Lepidomeda*. The introduced species almost certainly contributed to the extirpation of the *Pantosteus* and to the extermination of the *Lepidomeda*.

The flow of the Spring is almost surely less than it was formerly. According to Angel (1881: 491), writing of Panaca: "The water supply is abundant, being taken from Warm Spring, which is about one and one-half miles east of the town. A large stream of water, about three feet deep and six feet wide, is thrown out from the spring, and the quantity is not affected by the seasons. This is the principal source of water supply for the whole valley."

Our field studies in 1938 and 1959 indicated, with an approach to certainty, that no populations of *Lepidomeda* have persisted in any other remnants of Pluvial Carpenter River. In July, 1938, about two miles below Panaca, the flow of Meadow Valley Wash was found to contain only a fishless trickle of slightly alkaline seepage from the irrigated fields above. Just above the box canyon, above the section of Meadow Valley in which Caliente lies (about 14 miles southwest of Panaca), enough water issued from springs to restore a stream that averaged eight feet wide, continuing as a surface flow through Rainbow Canyon below Caliente. We fished in this canyon on the same day as at Big Spring, but caught no specimens of *Lepidomeda*; in the lowermost, permanent section of Meadow Valley Wash (13 miles by road above Moapa) we took only *Pantosteus* and *Rhinichthys* in a thorough collection on July 13, 1938. On March 1, 1938, the wash had been subjected to a very severe flood, which may have had a marked effect on the fish fauna.

Absence of *Lepidomeda* was also indicated by our 1938 collections along the former upper course of Pluvial Carpenter River and in Lake or Duck Valley, which may have discharged into this Pluvial stream. Collections from the old stream course were made (1) between Camp Valley and Eagle Valley in the headwaters of the creek of Camp Valley Wash, about 25 miles due northeast of Pioche, (2) in adjacent springs, and (3) in the canyon between Spring Valley and Eagle Valley, about 21 miles northeast of Pioche. Furthermore, thorough collections made in 1950 and 1959 in Clover Creek, the main eastern tributary of Meadow Valley Wash, at two points in Nevada, contained no *Lepidomeda*, and no fish of any kind were visible in the deeply entrenched stream in the northern outskirts of Caliente.

ETYMOLOGY.—The name *pratensis* is derived from the Latin, meaning pertaining to or growing in a meadow, in reference to the extensive meadowland about Big Spring.

NOTE ON SUBSPECIFIC STATUS.—This localized form is accorded sub-

specific status on the assumption that it was not completely differentiated from the form here named *Lepidomeda mollispinis mollispinis*.

Lepidomeda albivallis, new species
(Pl. I, C; Pl. III, E)
White River Spinedace

Lepidomeda species.—Sumner and Lanham, 1942: 319 (Preston Spring). Miller, 1952: 19, 35, fig. 22 (distribution, habitat, characters in key; use as bait fish). Moore, 1957: 138 (in part; mention of undescribed species in Nevada related to *L. vittata*).
Lepidomeda vittata (misidentification, not of Cope).—La Rivers and Trelease, 1952: 118 (in part; White River). La Rivers, 1952: 97 (in part; White River). Eddy, 1957: 104 ("White River" in vernacular name only).

DIAGNOSIS.—A species of *Lepidomeda* distinguished from others in having 5–4 teeth in the main row, lateral-line scales typically fewer than 90, mouth moderately oblique, dorsal fin of moderate height, melanophores extending well below level of lateral line, and in other details of pigmentation (see key, rubrics 1a, 2a, 3a, and 4b).

TYPES.—The holotype, UMMZ 173781, an adult 69.5 mm. long, was collected by C. L. Hubbs and family from White River, just below the mouth of Ellison Creek, about 5 miles NW of Preston, along the Tonopah–Ely highway (T. 13 N, R. 61 E), White Pine County, Nevada, on September 10, 1934. The 428 paratopotypes, UMMZ 132180 (16–98 mm.), were taken with the holotype. An additional 579 specimens were secured as follows: White Pine Co.: UMMZ 124980 (61, 37–103 mm.), from Preston Big Spring, 2 mi. NW of. Preston, Aug. 26, 1938; UMMZ 124984 (17, 17–88 mm.), from Lund Spring at Lund, Sept. 15, 1938; UMMZ 124973 (14, 39–90 mm.), from Nicholas Spring in Preston, Aug. 26, 1938; UMMZ 124977 (371, 24–83 mm.), outflow of Preston Big Spring and Nicholas Spring, Preston, Aug. 26, 1938; UMMZ 138331 (5, 73–93 mm.), from spring near Preston, Sept. 28, 1941 (U. N. Lanham, coll.). Nye Co.: UMMZ 124990 (111, 12–96 mm.), from springs at Hendrix Ranch (southern ranch of Sunnyside group), Aug. 27, 1938.

CHARACTERS.—Pigmentation and general body form are portrayed in Plate I, C. Principal dorsal rays 7 (4), 8 (97); anal rays 8 (24); 9 (75), 10 (2); pelvic rays 7–7 (82), 7–6 (1), 6–7 (5), 7–4 (1). The dental formula is typically 2, 5–4, 2, varying as follows: 2, 5–4, 2 (20), 2, 5–5, 2 (1). Lateral-line scales number about 79 to 92: 79 (1), 80 (1), 82 (5), 83 (3), 84 (2), 85 (5), 86 (3), 87 (2), 88 (1), 89 (2), 90 (3), 92 (2). The vertebrae range from 42 to 44 (Table 1).

This appears to be the most brightly colored of the four species of *Lepidomeda*. Life colors of postnuptial males were noted at the time of collection as follows: The body is bright brassy green to olive above, brassy over bright silvery on sides, and silvery white below, splashed with sooty on the sides. Dorsal and caudal fins pale olive-brown to pinkish brown, with the rays often deep-olive and with the rather clear interradial membranes faintly flushed with rosy color; pectorals yellowish with orange-red axils; anal and pelvic fins bright orange-red, in the young only toward the base anteriorly, but in adults over most of these fins, which otherwise are whitish. Lower edge of caudal peduncle with a speckled diffusion of orange-red in adults. Some coppery-red to red on side of face, at upper end of gill opening, on preorbital just behind mouth, and along upper arm of preopercle. Cheeks and opercles with rather strong gilt reflections; the gular membranes watery yellow. Lateral line more strongly gilt than adjacent parts of body. In females the coloration is similar but less intense.

Remnants of tubercles on postnuptial males collected on August 27 indicate that this pattern in the species is similar to that of *L. m. mollispinis*.

This is the largest species of *Lepidomeda*, commonly attaining a total length over 4 inches; the largest specimen (UMMZ 124980) is nearly 5 inches long (103 mm. S. L.).

HABITAT.—This species occurs in cool springs (65–71°F.), their outflows, and in White River, in the upper part of the ancient White River system of eastern Nevada (Fig. 1). In all the spring habitats the water was clear in the source pools, which varied from about 15 by 25 feet to 60 by 80 feet in major dimensions. The bottom was mostly gravel and sand, with some mud; the fish were generally captured in water not over 2 feet deep (up to 5 feet in Lund Spring); watercress, a fine-leafed *Potamogeton*, and rushes were the common aquatic plants, often dense. The current in the spring-fed ditches and in White River was swift to moderate.

ASSOCIATES.—The following species were associated with *Lepidomeda albivallis*: *Pantosteus intermedius* (Tanner), *Rhinichthys osculus* (Girard), and *Crenichthys baileyi* (Gilbert). *Salmo gairdneri* (Richardson), *S. trutta* Linnaeus, *Salvelinus fontinalis* (Mitchill), and *Archoplites interruptus* (Girard) have been planted in the same waters, and centrarchids, likely bluegill, *Lepomis macrochirus* Rafinesque, and largemouth bass, *Micropterus salmoides*, have been stocked in a reservoir in White River Valley at Sunnyside, according to information received from Ted Frantz.

ETYMOLOGY.—The name *albivallis* is from the Latin *albus*, white, and *vallis*, valley, in reference to the restriction of the new species to the White River Valley, in White Pine and Nye counties, Nevada.

Lepidomeda altivelis, new species
(Pl. I, D; Pl. III, D)
Pahranagat Spinedace

Lepidomeda vittata (misidentification, not of Cope).—Gilbert, 1893: 231 (3 from Pahranagat Valley, Nev., regarded as probably *L. vittata*; former connection with Colorado River). Jordan and Evermann, 1896*a*: 328 and 1896*b*: 265 ("Pahrangat Valley" only). Jordan, Evermann, and Clark, 1930: 147 ("Pahranagat Valley, Nev.," only). Tanner, 1936: 171 (reference to Pahranagat Valley material, evidently that recorded by Gilbert). La Rivers and Trelease, 1952: 118 (in part; Pahranagat Valley). La Rivers, 1952: 97 (in part).

Lepidomeda jarrovii.—Jordan and Evermann, 1896*a*: 328, 1896*b*: 265 (record from springs in desert of southern Nevada only). Jordan, Evermann, and Clark, 1930: 147 (Nevada record only).

Lepidomeda jarrovi.—Eddy, 1957: 104 ("Nevada" only).

Lepidomeda species.—Moore, 1957: 138 (in part, mention of undescribed species in Nevada related to *L. vittata*).

We have examined two juveniles in poor condition (USNM 46118) representing two of the three specimens that Gilbert thought probably referable to *L. vittata* (the other is in the Natural History Museum of Stanford University); they agree with our concept of *L. altivelis*.

DIAGNOSIS.—A species of *Lepidomeda* distinguished by the combination of 5–4 teeth in the main row, 9 anal rays, an oblique mouth, high and sharp dorsal fin, and a compressed head (see rubrics 1a, 2a, and 3b in key). *L. altivelis* has the longer mandible of *L. albivallis*, the silvery coloration of *L. mollispinis*, and is distinctive in its very oblique mouth, high and expansive dorsal fin, more compressed head, and generally finer scales.

TYPES.—The holotype, UMMZ 125004, an adult 56 mm. in standard length, was collected by Carl L. Hubbs and family from the outflow of Ash Spring, from .25 to 2.5 miles (in straight line) below the spring source, in Pahranagat Valley, Lincoln Co., Nevada, on August 29, 1938. Sixteen paratopotypes, UMMZ 125005 (33–66 mm.), were taken with the holotype. Seven other specimens, UMMZ 124813 (33–41 mm.), were seined in Upper Pahranagat Lake, Lincoln Co., Nevada, by Hubbs and party on July 12, 1938.

CHARACTERS.—The form and coloration are portrayed in Plate I, D. Principal dorsal rays 8 (24); anal rays 8 (1), 9 (21), 10 (2); pelvics 7–7 (21), 5–7 (1), 8–7 (1). The pharyngeal teeth number 2, 5–4, 2 in ten specimens, and the lateral-line scales are 84 to 95 in ten (90 or more in six), approximately 92 in the holotype. Vertebrae 42 to 44 (Table 1). This species attains a miximum length of about 3.75 inches (66 mm. S. L.).

DISTRIBUTION, HABITAT, AND ASSOCIATES.—This species was secured by

us in 1938 at only two localities in Pahranagat Valley, Nevada: (1) the outflow of Ash Spring, about 6 miles north of Alamo, and (2) Upper Pahranagat Lake, on U. S. Highway 93, 6 miles south of Alamo. Thorough collecting in Ash Spring proper and in Crystal and Hiko springs in the same valley failed to reveal the species, and indicated that it shunned constantly warm water (temperatures were 79° to 90°F. at the sources of these springs).

Although the two habitats from which this species is known are strikingly different, the samples from each locality agree well in all diagnostic features. This circumstance strengthens the hypothesis that the observed differences between the recognized forms in this genus are not environmentally induced.

In the outflow of Ash Spring, from .25 to 2.5 miles in a straight line below its head, the water was very clear (bottom clearly visible at 6 feet), the greatly meandering channel 5 to 20 feet wide, and the current generally swift (rarely quiet; in places very swift). The bottom comprised sand, gravel, mud, and boulders; the depth of water was up to 6 feet. Vegetation consisted in general of abundant bulrushes and submerged weeds, but the stream was partly clear of weeds; the banks (about 5 feet high) were wooded, and beyond were grass and farm land. The collection was made between noon and evening on August 29, 1938, using a seine in the upper part, and derris root below (where *Lepidomeda* was taken). In the upper part the water was 88°F., but below was much cooler.

Species taken with *Lepidomeda altivelis* in the outflow from Ash Spring were: *Cyprinus carpio* Linnaeus, *Gila robusta jordani* Tanner, *Rhinichthys osculus velifer* Gilbert, *Pantosteus intermedius* (Tanner), and *Crenichthys baileyi* Gilbert. The native fishes are all endemic as species or subspecies to the immediate region or to the whole Pluvial White River system.

At Upper Pahranagat Lake on July 12, 1938, the water was dirty olive-green and was alkaline to the taste, with bottom visibility about 2 feet. Vegetation comprised a heavy growth of flooded cockleburs. The shore was an alkali flat. The bottom was firm to soft clay soil and we seined to 100 feet from shore, where the water depth did not exceed 3 feet. Associated with *L. altivelis* here were *Pantosteus intermedius* and many carp; the lake was worked between 8:30 and 9:00 A.M., when the water was 74°F., the air 89°F.

The three specimens recorded by Gilbert (1893: 231) from "Pahranagat Valley, Nevada" could have come either from the outflow of Ash Spring or from Pahranagat Lake, since collections were made at both localities by members of the Death Valley Expedition.

EXTERMINATION OF THE SPECIES.—Field study on July 2–3, 1959, undertaken to test the point, indicated that this highly localized species, like

Lepidomeda mollispinis pratensis of Big Spring, near Panaca, had become exterminated during the previous 21 years. The thorough collecting in 1959 failed to reveal a single specimen of *Lepidomeda* in the outlet of Ash Spring or in or about the Pahranagat Lakes, where the species was collected in 1891 and in 1938. A spring-fed ditch in the bed of Maynard Lake, southernmost of the Pahranagat chain, yielded on July 2, 1959, only the local form of *Rhinichthys osculus*. Upper Pahranagat Lake and its outlet on the same day yielded only *Cyprinus carpio*. In the pools of Ash Spring proper, where the water temperature is 89°F., the local (typical) form of *Crenichthys baileyi* still occurred commonly, though for some reason in less abundance than in 1938. In an examination of the outlet stream this cyprinodont occurred down to and into the diversion ditches 5 to 7 miles north of Alamo. Seining at several points in the outlet, supplemented by a visual examination along nearly the whole length of the natural flow and by a thorough application of rotenone in the lower half-mile of the natural creek and the upper mile of the diversion ditch then in operation, on July 3, 1959, indicated the fish population of the outlet, at water temperatures of 86 to 88°F. (air temperature 88.5°F.), to consist of moderate numbers of the *Crenichthys* and of the *Gila*, hordes of carp, and a considerable number of another introduced pest, *Gambusia affinis affinis*. Not a single sucker (*Pantosteus intermedius*) or a single *Lepidomeda* was secured. Since for about 2.5 miles the stream has retained essentially its original bed and condition, with only limited diversions, and since the water source has remained uniform, the probable local extirpation of the *Pantosteus* and the almost certain complete extermination of the *Lepidomeda* is most plausibly attributable largely to the increased abundance of carp and to the establishment of the mosquitofish (*Gambusia*). Both of these introduced species have had a deleterious effect on native fish life in many western waters (Sigler, 1958; Miller, in press). The establishment of bullfrogs, *Rana catesbeiana*, may also have played a role in the modification of the habitat.

ETYMOLOGY.—The name *altivelis* is from the Latin *altus*, meaning high, and *velum*, a sail, in reference to the high, expanded dorsal fin.

Lepidomeda vittata Cope
(Pl. II, A; Pl. III, A)
Little Colorado Spinedace

Lepidomeda vittata.—Cope, 1874: 131 (original description, Colorado Chiquito River, Arizona). Cope and Yarrow, 1875: 642–43, pl. 26, figs. 2–2a (redescription of types). Jordan and Copeland, 1876: 155 (listed; "Colorado, Arizona"). Jordan and Gilbert, 1883: 252 (description, after Cope). Jordan, 1885*b*: 821 (listed). Jordan and Ever-

mann, 1896*a*: 328 (description; range, in part); 1896*b*: 265 (range, in part). Fowler, 1925: 415 (description of syntype). Jordan, Evermann, and Clark, 1930: 147 (reference; range, in part). Eddy, 1957: 104 (characters [from Jordan and Evermann] only). Moore, 1957: 138 (range).

Lepidomeda jarrovii.—Cope, 1874: 132 (original description, Colorado Chiquito River, Arizona). Cope and Yarrow, 1875: 643–44, pl. 26, figs. 1–1a (redescription of types). Jordan and Copeland, 1876: 155 ("Colorado"). Jordan and Gilbert, 1883: 252 (description, after Cope). Jordan, 1885*b*: 821 (listed). Jordan and Evermann, 1896*a*: 328 (description; range, in part); 1896*b*: 265 (range, in part). Jordan, Evermann, and Clark, 1930: 147 (reference; Rio Colorado Chiquito, Arizona, only).

Lepidomeda jarrovi.—Eddy, 1957: 104 (characters [from Jordan and Evermann] and "Arizona" only).

DIAGNOSIS.—A species of *Lepidomeda* differing from its relatives in having 4–4 teeth in the main row, 8 anal rays, usually more than 90 lateral-line scales, and typically 41 or 42 vertebrae (see rubric 2b of key).

SYNONYMY.—An examination of the extant types of *Lepidomeda vittata* and *L. jarrovii*, and of our topotypes (the first specimens of the species taken since these nominal species were described about 65 years previously), yields no indication that more than the one species occupies the Little Colorado River system. We therefore synonymize the species and adopt the name *L. vittata*.

The four syntypes (USNM 15785) of *L. vittata* are in poor condition and one is represented by the head only (a fifth fish, now segregated in a vial, is *Rhinichthys osculus*). All three have 8 anal rays and probably 8 dorsal rays; the teeth number 4, 2 on the right side of one specimen.

The two syntypes (USNM 15786) of *L. jarrovii*, about 53 and 67 mm. in standard length, are in poor condition, but appear conspecific with *L. vittata*. Each has 8 dorsal and 8 anal rays, 7 pelvic rays on each side, 2, 4–4, 2 teeth (with 1 or 2 teeth in each specimen represented by alveoli only), about 90 and 95 lateral-line scales, and 42 vertebrae in the larger specimen (vertebrae abnormal, 41 or 42 in smaller syntype). These counts agree well with those diagnostic of *L. vittata*. The "greater elongation of form, weakness of squamation and peculiarity of coloration" advanced by Cope as distinguishing features of *L. jarrovii* we interpret as phenotypic variations.

There is a syntype of *Lepidomeda vittata* in the Academy of Natural Sciences of Philadelphia (19853), and there are three in the Museum of Comparative Zoology (18816).

A second lot (original number 5X, USNM 15779) referred to *L. jarrovii* by Cope and Yarrow (1875: 644), and also attributed to "Colorado Chiquito River, Ariz.," proves on re-examination to be referable to *Gila robusta* Baird and Girard.

CHARACTERS.—The form of the body, head, and fins is shown in Plate II, A. The principal dorsal rays number 8 (in all 30 specimens counted); anal rays 8 (68), 9 (2); pelvics 7–7 (29), 6–8 (1). The pharyngeal teeth are consistently 4–4 in the main row, but are about as often 1 as 2 in the lesser row. The following formulas were observed: 1, 4–4, 1 (7), 1, 4–4, 2 (2), 2, 4–4, 1 (3), 2, 4–4, 2 (8). The teeth are missing in unusual frequency; many of those listed were represented by alveoli. In three specimens there were no teeth on either arch. Cope recorded the formula as 2, 4–4, 2, as did Fowler for a syntype. The scales in the lateral line number 89 to 105 in twelve specimens, including the syntypes of *L. jarrovii*, but they are embedded and difficult to count and usually appear to be lacking on the body where covered by the depressed paired fins. Vetebrae number 41 to 43 (Table 1).

The life colors were thus described: the axils of the paired fins are bright orange to reddish orange; a trace of these colors shows on the distal part of the anal fin; otherwise the fins are watery white, with the rays white to yellowish-orange. The sides are brilliantly silvery. The scales show light bluish to greenish-brass reflections.

L. vittata attains a total length of about four inches. The largest specimen we have (in UMMZ 131099) is 84 mm. in standard length.

ERRONEOUS RECORDS.—*L. vittata* has been attributed to several other localities, all, we believe, in error. These are entered in the synonymies of the other species. Tanner (1932: 135) reported *L. vittata* from Fremont River, Utah, but in his general report on Utah fishes (Tanner, 1936: 161, 171) he did not repeat the record, and no one else has recorded any plagopterin from above Grand Canyon; nor have we taken any there. We now feel that the Fremont River report should be disregarded, especially since no specimens to support the record have been found in Dr. Tanner's collections by him or by us.

DISTRIBUTION AND HABITAT.—This species seems to be restricted to the upper parts of the Little Colorado River system, eastern Arizona, well above Grand Falls, on and near the northern slopes of the White Mountains (Fig. 1). The types of the two nominal species were recorded only as from the "Colorado Chiquito River." The actual type locality or localities of *Lepidomeda vittata* and *L. jarrovii* has not been specified, but the itinerary of the Wheeler Survey (Wheeler, 1889: 58–77) indicates that the specimens were collected in the headwaters of the Little Colorado somewhere between the mouth of the Zuni River and Sierra Blanca (White Mountain). Our three series bear the following data: UMMZ 124754 (73, 39–69 mm.), Little Colorado R., Apache Co., 7,000 feet, T. 12 N, R. 28 E, July 1, 1938; UMMZ

137082 (130, 21–76 mm.), Little Colorado R., 5 to 6 mi. S of St. Johns, Apache Co., July 16, 1939; and UMMZ 131099 (6, 75–84 mm.), Showlow Cr. below dam at Lakeside, Navajo Co., T. 22 E, R. 9 N, June 13, 1939. At the three stations the water was described as yellow, brownish-white, and murky; current, slight to swift; bottom, thick mud, sand, clay, gravel, and rock; depth of capture, 1 to 3 feet; and vegetation, white water buttercup (rather thick in patches), chara, some rushes, and algae.

Associates.—The following were taken with *L. vittata*: four native fishes, *Catostomus latipinnis* Baird and Girard, *Pantosteus delphinus* (Cope), *Rhinichthys osculus* (Girard), and *Gila r. robusta* Baird and Girard, and three introduced species, *Cyprinus carpio, Ictalurus melas* (Rafinesque), and *Lepomis cyanellus* Rafinesque. Hemphill (1954: 41) reported *Gila robusta elegans* Baird and Girard from Lyman Reservoir (near St. Johns), but no specimens are available for checking the identification; however, this subspecies was described from the Zuni River, New Mexico, a flood-tributary to the Little Colorado River. Hemphill also listed five other introduced species: largemouth bass, *Micropterus salmoides* (Lacépède); bluegill, *Lepomis macrochirus* Rafinesque; brown trout, *Salmo trutta* Linnaeus; "several hundred bullhead catfish"; and channel catfish, *Ictalurus punctatus* (Rafinesque). Becker's Lake (near Springerville) contained two additional exotic fishes, the golden shiner, *Notemigonus crysoleucas* (Mitchill) and yellow perch, *Perca flavescens* (Mitchill), which were presumably eliminated by treatment with toxaphene, after which rainbow trout, *Salmo gairdneri* Richardson, were stocked (Hemphill, 1954: 42). Whether the *Lepidomeda* will persist (or has persisted) in competition with such introduced predators and competitors is an open question.

Genus *Meda* Girard

Meda.—Girard, 1856: 191–92 (original description); 1859: 50 (description and comparisons). Günther, 1868: 263–64 (description quoted; remark on dorsal spine; placed in Leuciscina, not Xenocypridina). Cope 1874: 131, and Cope and Yarrow, 1875: 641 (characters and comparisons). Jordan and Gilbert, 1883: 148, 252 (comparisons; description). Jordan, 1885*a*: 122, and 1885*b*: 821 (*Plagopterus* treated as synonym; species). Jordan and Evermann, 1896*a*: 204, 328 (comparisons; description). Eddy, 1957: 105 (characters). Moore, 1957: 94, 138 (characters and comparisons).

Type Species.—*Meda fulgida* Girard (by monotypy).

Meda is one of the two endemic genera of the Gila River basin in Arizona and New Mexico (the other is *Tiaroga*). *Meda* is easily distinguished from the other plagopterin genera by the characters in the analytical key (rubrics 1b and 6a).

Meda fulgida Girard
(Pl. II, B; Pl. III, F)
Spikedace

Meda fulgida.—Girard, 1856: 192 (original description; Río San Pedro, Arizona); 1859: 50, pl. 28, figs. 9–10 (redescription, with figures; list of specimens). Günther, 1868: 264 (after Girard). Cope, 1874: 131, and Cope and Yarrow, 1875: 641–42 (listed). Jordan and Copeland, 1876: 155 (Arizona). Jordan and Gilbert, 1883: 252 (after Girard). Jordan, 1885*a*: 122, and 1885*b*: 821 (characters). Jordan and Evermann, 1896*a*: 329 (description; Río Gila). Jordan and Evermann, 1896*b*: 265 (reference; Río Gila). Gilbert and Scofield, 1898: 497–98 (description of specimens from Chino and Tempe, Arizona). Fowler, 1925: 415 (notes on 2 syntypes and 15 others from San Francisco River, New Mexico). Jordan, Evermann, and Clark, 1930: 147 (listed; reference; range). Winn and Miller, 1954: 282, 284, pls. 1–2 (development of larval characters; photo of postlarva; comparison with associated postlarvae). Illick, 1956: 215–18 (cephalic lateral-line system). Eddy, 1957: 105, fig. 263 (characters and range; compiled). Koster, 1957: 72 (description; habitat). Moore, 1957: 138 (range).

CHARACTERS.—Principal dorsal rays 7 (54), 8 (2); anal rays 8 (5), 9 (48), 10 (3); pelvics 7–7 (17), 7–6 (1), 6–7 (2). The pharyngeal teeth typically number 1, 4–4, 1; the following formulas were noted in 24 specimens (12 counts original, remainder from Gilbert and Scofield, 1898, and Fowler, 1925): 1, 4–4, 1 (19), 1, 4–4, 2 (2), 2, 4–4, 1 (1), 2, 4–4, 2 (1), and 1, 5–4, 1 (1). Vertebrae vary from 39 to 42 (Table 1).

In life the sides shine like burnished silver, with bluish reflections; the back is olive to olive-gray, with silvery-white speckles between the sides and dorsum. There are bright cream to yellow-orange spots at either end of the dorsal-fin base, at the upper edge of the procurrent caudal rays, in the axil of the pectoral fin, and on either side of the small spot at the caudal base. There is rather prominent dark mottling on the upper sides and sometimes a bit of rose is mixed with the silvery color of the sides; the abdomen may be tinged yellowish (Koster, 1957: 72). Gilbert and Scofield (1898: 498) described their material as "bright silvery, with reddish brown mottlings along back"; and the "body pale yellowish below."

This is a small species, not attaining a total length of 3 inches; the largest specimen we have seen is 60 mm. in standard length. It spawns in late spring and early summer; individuals as small as 4.0 mm. standard length were caught at night on May 6, 1950.

DISTRIBUTION.—For nearly 50 years this fish was known only from the San Pedro River, the major southern tributary of the Gila River in southern Arizona. When the stream had a more ample flow, in the nineteenth century, this species presumably occurred also in the headwaters of the San Pedro in México (Miller and Winn, 1951: 84). *Meda* has been reported

from numerous places in the Gila River system of New Mexico and Arizona as far downstream as Tempe (Fig. 1).

Syntypes are in the collections of the United States National Museum (No. 154), in the Academy of Natural Sciences of Philadelphia, two (53, 60–61), and in the Museum of Comparative Zoology, one (No. 1959).

HABITAT.—*Meda fulgida* seeks moving water 2 to 4 feet deep, typically inhabiting the swift, deep pools, or the deeper upper parts of long pools, near riffle mouths, over sandy or gravelly bottom. On the Gila River about 6 miles northeast of Redrock, Grant County, New Mexico (May 6–7, 1950), some adults were observed on shallow riffles where the rocks were covered with long streamers of green algae. At Verde River just above Camp Verde, Arizona, on September 2, 1938, adults were common on a very swift riffle over bedrock bottom. Young occur in backwater areas, over silt and sand bottoms, adjacent to swift pools.

GENUS *Plagopterus* Cope

Plagopterus.—Cope, 1874: 130 (original description; classification). Cope and Yarrow, 1875: 640 (description; comparison). Jordan and Gilbert, 1883: 148, 252 (comparisons; diagnosis). Jordan and Evermann, 1896*a*: 204, 329 (comparisons; description). Eddy, 1957: 105 (characters). Moore, 1957: 138 (characters and comparisons).

TYPE SPECIES.—*Plagopterus argentissimus* Cope (by monotypy).

Plagopterus, in most features the most specialized genus of the Plagopterini, is readily distinguished from the other genera by characters given in the key (rubrics 1b and 6b). At the present time its known distribution is limited to the Virgin River system (Fig. 1, insert) and its predilection for a swift-water habitat further restricts it ecologically. Formerly it also occurred in the Gila River (p. 9).

Plagopterus argentissimus Cope
(Pl. II, C; Pl. III, G)
Woundfin

Plagopterus argentissimus.—Cope, 1874: 130 (original description; "San Luis Valley, Western Colorado"; repeated in Cope and Yarrow, 1875: 640–41). Jordan and Copeland, 1876: 155 (locality repeated). Jordan and Gilbert, 1883: 253 (description and record, after Cope). Jordan and Evermann, 1896*a*: 329 (description; Colorado Basin in western Colorado; Fort Yuma); 1896*b*: 266 (reference; same localities). Gilbert and Scofield, 1898: 496–97 (Gila R. at Yuma and Salt R. at Tempe, Ariz., spring of 1890; description of new material). Ellis, 1914: 70 (occurrence in Colorado doubted). Snyder, 1915: 584 (Gila R. near Gila City, Ariz., between 1892 and 1894; brief des-

cription). Fowler, 1925: 415 (notes on 2 syntypes). Jordan, Evermann, and Clark, 1930: 147 (listed; reference; range repeated). Shapovalov and Dill, 1950: 386 (listed from California; woundfin proposed as common name). Miller, 1952: 18, 36, fig. 20 (characters in key; distribution; use as baitfish). Böhlke, 1953: 36 (syntype listed from Colorado Chiquito R., Ariz.). Illick, 1956: 215–18, figs. 31–33 (cephalic lateral-canal system). Eddy, 1957: 105, fig. 262 (characters; range). Moore, 1957: 138 (range).

Meda argentissima.—Jordan, 1885*a*: 122, and 1889*b*: 821 (characters; generic reference).

CHARACTERS.—The number of principal dorsal rays varies from 8 to 10, and the anal rays from 9 to 11, as follows: D. 8 (67), 9 (23), 10 (3); A. 9 (9), 10 (73), 11 (11). The pelvic rays number 7 in each fin (in 55 specimens, one had 6–7 and one 7–6). The dental formula is typically 1, 5–4, 1, but varies as follows: 1, 5–4, 1 (14), 1, 5–5, 1 (1), 2, 5–4, 1 (2), 2, 5–4, 2 (2), and 1, 4–4, 1 (2). Fowler (1925: 415) recorded 1, 4–4, 1 or 1, 5–4, 1 for two syntypes; Cope (1874: 130) gave the formula as 2, 5–4, 2. Vertebrae vary from 39 to 41 (Table 1).

This, the most silvery of American cyprinids, was well named by Cope. When taken from the water the body shines like burnished silver, showing blue reflections from the sides. The axil of the pectoral fin was watery yellow on individuals caught on July 3, 1938.

This species attains a somewhat larger size than does *Meda fulgida*, frequently 3 inches; the largest is about 3.5 inches long (71 mm. standard length). It probably spawns in late spring and summer, for specimens 19 mm. in standard length were obtained on July 29 and on September 15 in Arizona and Utah (UMMZ 141669, 124766).

DISTRIBUTION.—The stated type locality of this species is obviously erroneous. The only fishes known from the isolated waters of San Luis Valley, Colorado (tributary in Pluvial times to the Rio Grande), are *Salmo clarki*, *Gila nigrescens*, and *Pimephales promelas* (Ellis, 1914: 47; Hubbs and Miller, 1948: 117–18; local testimony). Ellis doubted that *Plagopterus* occurs in Colorado. No type specimen was designated by Cope, who based the species on "numerous specimens"; there are two syntypes in the Academy of Natural Sciences of Philadelphia (19851–52), two in the Museum of Comparative Zoology (18817), three in the United States National Museum (15576), and one in the Stanford Natural History Museum (2003). The syntypes in the National and Stanford collections bear the locality "Colorado Chiquito River," in Arizona, but this is probably also incorrect since the species is not otherwise known from the Little Colorado. Other species collected by naturalists of the Wheeler Survey (1871–1874) also bear erroneous locality data, as, for example, *Ceratichthys biguttatus*, a species native to eastern United States, attributed to "Harmony, Utah" (in the Bonneville basin).

We think it probable that the types were obtained in the Virgin River in Washington County, southwestern Utah, an area from which fishes (e.g., *Gila seminuda* Cope and Yarrow) were collected by Wheeler Survey naturalists. The expedition in 1872 maintained a base at Toquerville, which is on La Verkin Creek, worked the Virgin River valley and canyon, and visited St. George (Wheeler, 1889: 46–57). The species is known today only from the Virgin River system. Our largest collection (192 young to adult, UMMZ 124770) came from the Virgin River at the mouth of La Verkin and Ash creeks (T. 41 N, R. 13 W).

Although Jordan and Evermann (1896*a*: 329) designated USNM 15776 as "type," this does not constitute a lectotype designation since the jar contains three specimens and there are others from the same lot in other museums, as specified above.

HABITAT.—This species frequents swift shallows over stone, sand, or mud bottom, but some adults live in deeper holes, though generally not over 1.5 feet deep. In the Virgin River near Bunkerville, Nevada, it was the only fish found in water described as dirty-orange liquid mud, with swift current, and perhaps it was the only fish capable of tolerating such a "swift mud" environment. In the preserving jar filled with this water nearly one inch of sediment precipitated.

SUMMARY AND GENERAL CONCLUSIONS

The American spiny-rayed cyprinid fishes, revised in this paper, constitute a compact and distinctive group, which was named Plagopterinae by Cope (1874) and Medidae by some recent authors, but which we treat as a tribe, Plagopterini, within the Leuciscinae. It is one of the characteristic elements in the freshwater fish fauna of Western North America. The Plagopterini embrace the monotypic genera *Meda* and *Plagopterus* and the polytypic genus *Lepidomeda*. Of the two previously recognized species of *Lepidomeda*, one (*jarrovii*) is synonymized, and three additional species, one with two subspecies, are now described. The plagopterins are among the few groups of American cyprinids that do not engage in interspecific hybridization.

Lepidomeda appears to be the most generalized as well as the most diverse of the plagopterin genera. It seems to have arisen from *Gila* or some similar genus. *Meda* and *Plagopterus* are strikingly specialized, particularly in the spinelike modification of the dorsal and pelvic rays. The spinose development of the anterior dorsal rays has been independent in the Plagopterini and in such Old World genera as *Cyprinus* and *Barbus*.

Spinosity of the pelvic rays is a unique feature of the plagopterins, and involves only the lower half of each ray—the left demitrich in the right fin and the right demitrich in the left fin (other examples of bilaterally asymmetric modification of fin rays were presented by Hubbs and Hubbs, 1945: 295–96, fig. 2).

Other features of specialization accentuated in *Meda* and *Plagopterus* are loss of scales, intense silvery color, sexual dimorphism in pectoral-ray structure, and, in *Plagopterus,* development of dermal ridges with basal platelets.

The entire group is confined to the Colorado River system, in which it probably arose in Pliocene time. Major differentiation probably continued through Pleistocene time, with isolation and minor speciation during the Postglacial disruptions of the drainage. The highly localized distribution of the species has been accentuated by stream deterioration due to human activities, as well as to the recent drought. The introduction of exotic fishes, particularly *Gambusia* and *Cyprinus,* along with agricultural operations, may have further restricted their distributions. Two forms of *Lepidomeda* (*L. mollispinis pratensis* and *L. altivelis*), which even in 1938 were confined, in reduced populations, to the outlet waters of single isolated springs, were found in 1959 to have become extinct.

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Accepted for publication March 7, 1960

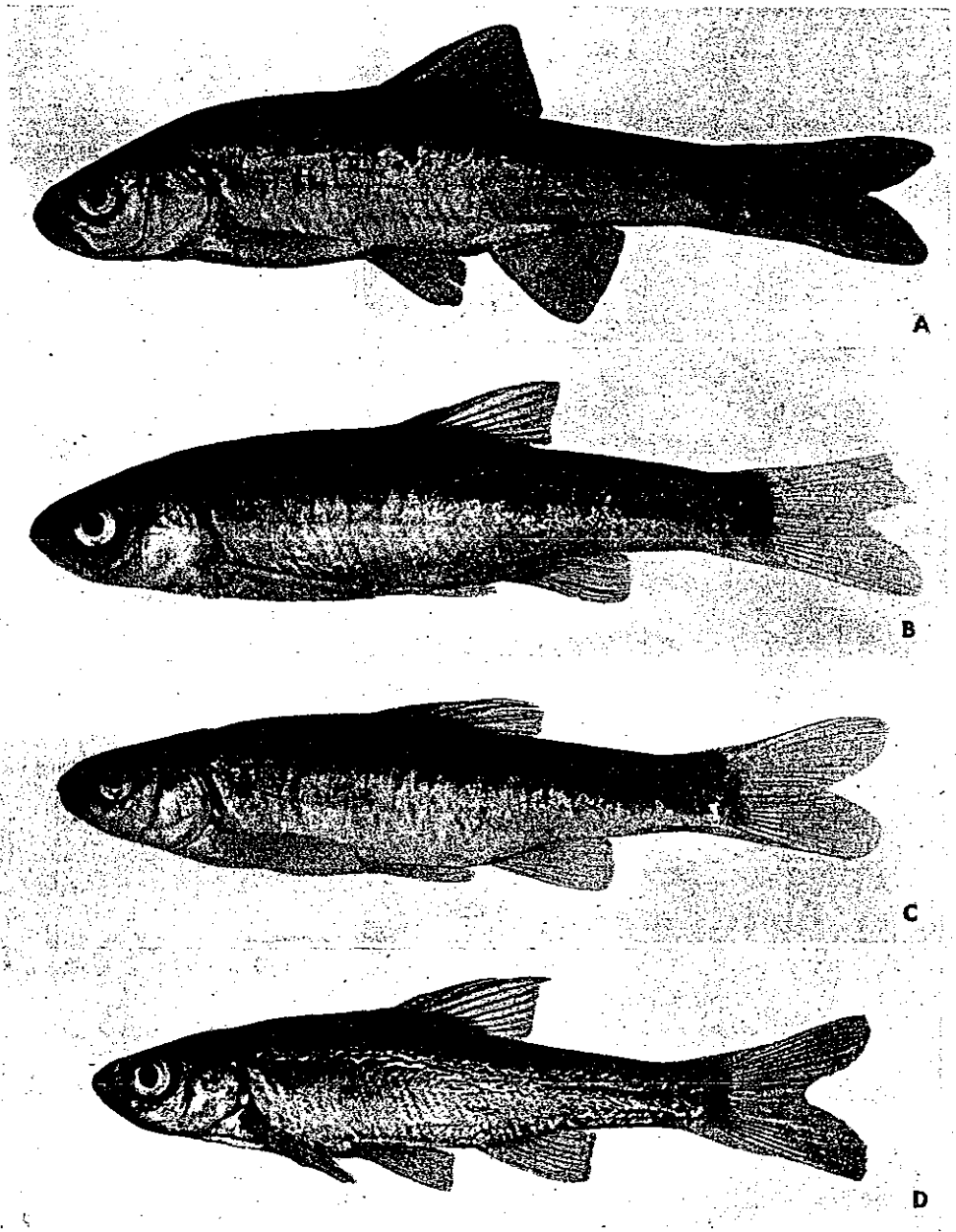

PLATE I

Three new species of *Lepidomeda*

A, Holotype of *L. m. mollispinis,* UMMZ 141673, 88 mm. S.L.
B, Holotype of *L. m. pratensis,* UMMZ 124799, 55 mm. S.L.
C, Holotype of *L. albivallis,* UMMZ 173781, 69.5 mm. S.L.
D, Holotype of *L. altivelis,* UMMZ 125004, 56 mm. S.L.

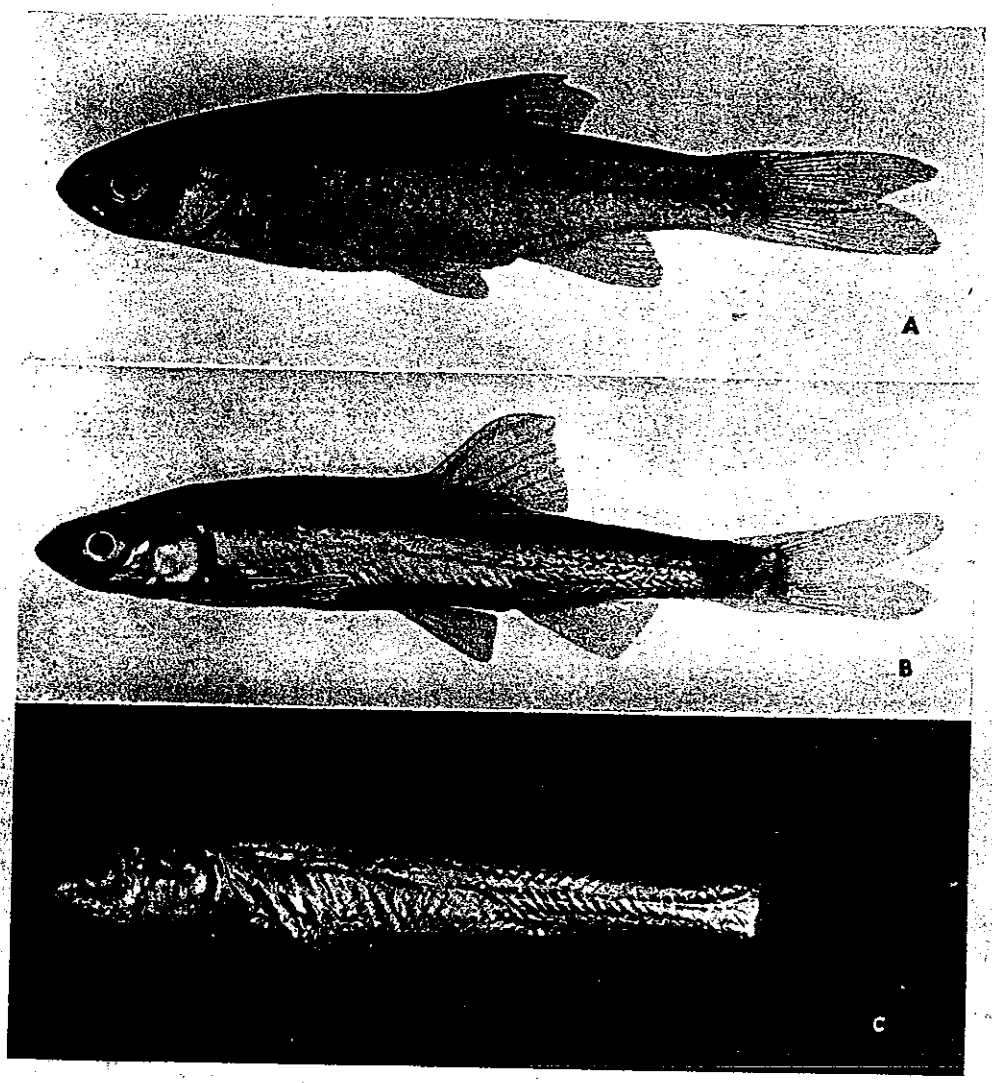

PLATE II

Three species of plagopterin fishes

A, *Lepidomeda vittata*, UMMZ 124754, 62 mm. S.L.
B, *Meda fulgida*, UMMZ 125030, 51 mm. S.L.
C, *Plagopterus argentissimus*, UMMZ 141669, 58 mm. S.L.

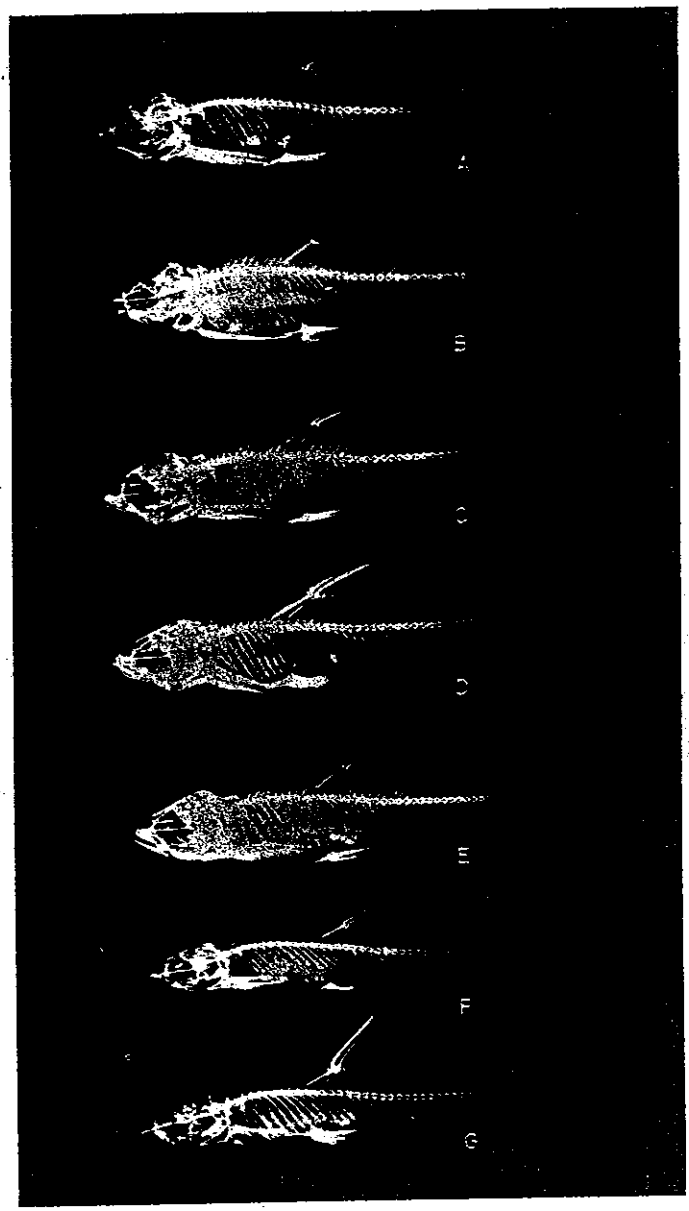

PLATE III

Radiographs of the seven forms of the Plagopterini

A, *Lepidomeda vittata*, UMMZ 137082, 55 mm. S.L.
B, *Lepidomeda m. mollispinis*, UMMZ 162849, 56 mm. S.L.
C, *Lepidomeda m. pratensis*, UMMZ 136097, 56 mm. S.L.
D, *Lepidomeda altivelis*, UMMZ 125004 (holotype), 56 mm. S.L.
E, *Lepidomeda albivallis*, UMMZ 132180, 54 mm. S.L.
F, *Meda fulgida*, UMMZ 162738, 49 mm. S.L.
G, *Plagopterus argentissimus*, UMMZ 141669, 53 mm. S.L.