A NEW CHUB (ACTINOPTERYGII, CYPRINIFORMES, CYPRINIDAE) FROM THE MIDDLE MIOCENE (EARLY CLARENDONIAN) ALDRICH STATION FORMATION, LYON COUNTY, NEVADA

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ABSTRACT

A new chub, *Lavinia lugaskii*, is described from the middle Miocene (early Clarendonian) Aldrich Station Formation of Lyon County, Nevada. *Lavinia lugaskii* represents a basal member of the *Lavinia-Hesperoleucus* lineage, indicating that this lineage diverged from a common ancestor with *Mylopharodon* before 12.5 – 12.0 million years before present. This is the oldest recognized species of *Lavinia* and the first new chub species to be documented from the Miocene of Nevada in over 30 years.

INTRODUCTION

A sample of fish fossils is now known from localities that occur in an outlier of the Aldrich Station Formation, exposed just west of Mickey Canyon on the northwest flank of the Pine Groove Hills, Lyon County, Nevada. All of the fish remains were recovered from a single stratigraphic level represented by a thin (~0.06 m) shale bed. This level can be traced laterally for about 0.5 km and yielded fossil fish remains at several points along its exposure. The fish producing shale bed is separated from a second slightly thicker, overlying shale bed by a thin sandstone bed. The two shale beds contain leaf impressions and yielded the Mickey Canyon Spring Flora from the Museum of Paleontology, University of California, Berkeley (UCMP), plant locality PA624 (Schorn and Shelton, 1991; Schorn et al., 1994). Previously, only one partial fish skeleton was recorded from PA624, which was collected by Howard Schorn and identified by Howard Hutchison as Cyprinidae (unpublished locality data, UCMP). An additional 70 specimens in the vertebrate paleontology collection of the Natural History Museum of Los Angeles County (LACM) from the lower fish producing shale bed, including three complete skeletons and 65 partial skeletons, allow a detailed analysis of this cyprinid fish and indicate it represents a new species. The purpose of this report is to describe this new cyprinid and compare it with other known fossil and extant chubs from the Great Basin and adjacent areas.

METHODS

Measurements of the skeletons and individual bones were made to the nearest 0.1 mm with a vernier caliper. Measurements of the pharyngeal teeth were made with an optical micrometer to the nearest 0.01 mm. Estimated standard lengths for partial skeletons were extrapolated using the mean ratios of the standard length to landmark measurements (e.g., ratios of the SL to head length, pectoral fin origin to pelvic fin origin length, the posterior anal and dorsal fin bases to caudal base lengths) for the three complete skeletons. Detailed locality data are on file at the Vertebrate Paleontology Section of the Natural History Museum of Los Angeles County. All taxa identifications were determined by the author using published accounts and comparative material in the vertebrate paleontology collections of the Natural History Museum of Los Angeles, the Museum of Paleontology, University of California, Berkeley, and the W. M. Keck Earth Science and Mineral Engineering Museum, University of Nevada, Reno. Additional comparative specimens of *Lavinia* (*L. hibbardi, L. condonianus*, and *L. exilicauda*) and *Hesperoleucus* were provided by Gerald R. Smith and Douglas W. Nelson of the University of Michigan. Older published Potassium-Argon radioisotopic ages presented herein were recalibrated using the IUGS constants following the method of Dalrymple (1979). Older published $^{40}Ar/^{39}Ar$ ages were recalibrated relative to the Fish Canyon Tuff sanidine interlaboratory standard at 28.02 Ma. Divisions and

boundaries of the North American Land Mammal ages follow Tedford et al. (2004).

Abbreviations are as follows: ap, greatest anteroposterior length; trgs, greatest oblique transverse width of pharyngeal tooth grinding surface; HL, head length; ht, greatest height of pharyngeal tooth above pharyngeal bone; Ma, millions of years before present; N, number of specimens; OR, observed range; SL, standard length; TL, total length; tr, greatest transverse width.

GEOLOGIC SETTING

The Wassuk Group is comprised of, from oldest to youngest, the Aldrich Station Formation, the Coal Valley Formation, and the Morgan Ranch Formation (Axelrod, 1956; Goliad and Stewart, 1984). The group has been studied extensively because it has yielded superposed faunas and floras of middle to late Miocene age (Axelrod, 1956; Evernden and James, 1964; Evernden et al., 1964; Gilbert and Reynolds, 1973; Golia and Stewart, 1984; Stewart and Reynolds, 1987; Schorn and Shelton, 1991; Wolfe et al., 1997; Kelly, 1998; Perkins et al., 1998; Kelly and Secord, 2009). Axelrod (1956) first described the group and Gilbert and Reynolds (1973) mapped the group and further defined the formational boundaries. The group was deposited in a large, northwest-trending basin that extended from about 5 km south of Coal Valley northwestward to the Mount Wilson area in the southern Singatze Range, or about 55 km north of Coal Valley (Gilbert and Reynolds, 1973; Golia and Stewart, 1984). During the deposition of the Aldrich Station Formation, the basin contained a large circumneutral, eutrophic lake with paludal conditions at the margin (Golia and Stewart, 1984). Wolf et al. (1997) provided evidence that the paleoaltitude during the deposition of the Aldrich Station Formation was at about its present altitude, or about 1.5 – 2 km above sea level.

Gilbert and Reynolds (1973) reassigned the uppermost portion of the Aldrich Station Formation of Axelrod (1956) to the base of the Coal Valley Formation. The Aldrich Station Formation is comprised of carbonaceous mudstone and siltstone, diatomaceous shale, sandstone, and pebble conglomerate (Axelrod, 1956; Gilbert and Reynolds, 1973). The type section of the Aldrich Station Formation occurs in Coal Valley, about 45 km southeast of the Mickey Canyon section, where it is about 755 m thick (Gilbert and Reynolds, 1973). In the Mickey Canyon section, the Aldrich Station Formation thins to about 370 m, mainly at the expense of the diatomaceous claystones and mudstones of middle portion of the formation (Gilbert and Reynolds, 1973). The age of the Aldrich Station Formation has been determined by biostratigraphic correlation of the flora

and a series of K-Ar dates on tuffs above and within the formation (Evernden and James, 1964; Evernden et al., 1964; Gilbert and Reynolds, 1973). Radiometric dates of tuffs within the Aldrich Station Formation range from about 11.5 to 12.8 Ma and tuffs within the overlying Coal Valley Formation range from about 11.5 to 6.98 Ma (Gilbert and Reynolds, 1973; Tedford et al., 2004; Kelly and Secord, 2009). In the vicinity of Mickey Canyon, a K-Ar radiometric date of 11.45 ± .25 Ma (corrected) was recorded by Gilbert and Reynolds (1973) from a tuff within the upper portion of the Aldrich Station Formation section. Based on the tephrochronologic correlation of silicic fallout tuffs, Perkins et al. (1998) provided ages for the Aldrich Hill 1 ash and Aldrich Hill 2 ash within the Aldrich Station Formation in the type section at Coal Valley of 12.07 ± 0.10 and 12.01 ± 0.10 Ma, respectively. The fish level in the Mickey Canyon section occurs near the base of the formation, well below the dated tuff. The shale of the fish level in the Mickey Canyon section contains large amounts of charcoal, similar to that found in the shales of the lower levels of the type section of the Aldrich Station Formation in Coal Valley. Also, the lower levels in the Mickey Canyon section contain coarse sandstone beds, similar to those in the lower levels of the type section in Coal Valley. Schorn and Shelton (1991) regard the Mickey Canyon Spring Flora as a correlative of the early Clarendonian Aldrich Station Flora because they contain many of the same species. Considering that the middle portion of the Aldrich Station Formation in the Mickey Canyon section is much reduced and similar lithologies are observed in the lower levels of the Mickey Canyon section and the type section in Coal Valley (Axelrod, 1956; Gilbert and Reynolds, 1973) along with the floristic correlations, it is probable that the lower half of the Mickey Canyon section is a correlative of the lower levels in the type section. Thus, the fish level in the Mickey Canyon section is most likely about 12.5 to 12.0 Ma in age, equivalent to the early Clarendonian North American Land Mammal age (Cl1 of Tedford et al., 2004).

The stratigraphy of the beds at the fish localities include the following, from highest to lowest: 1) a conspicuous ledge forming, yellowish-buff medium-grained sandstone (0.3 – 0.5 m thick); 2) a thin, light gray shale containing leaf impressions (0.1 – 0.2 m thick); 3) a thin, dark brown mudstone (0.05 m thick); 4) a greenish-buff, fine to pebbly sandstone (0.04 – 0.06 m thick); 5) a thin, light gray to greenish-brown laminated shale containing several bedding planes with numerous articulated fish and occasional leaf impressions (0.05 – 0.07 m thick); 6) a thin, dark brown, mudstone (0.05 m thick); 7) a resistant, dark reddish-brown, pebbly conglomerate (0.03 – 0.05 m thick); and 8) a thick sequence of yellowish-buff to

greenish-brown sandstones with minor shale beds (43 – 45 m thick). The fish producing shale bed may represent mass-mortality episodes of monospecific schools over a short geologic time scale because it is very thin, extends laterally for some distance with the fish fossils abundantly represented only on a few individual bedding planes within the shale bed, has only yielded a single species of fish with the majority of the individuals having a similar SL, and most of the fish fossils are articulated skeletons. The taphonomy of the fish producing shale bed of the Aldrich Station Formation appears to be very similar to that described by Bell et al. (1989) for the mass-mortality layers of fossil Stickleback fish of the Miocene Truckee Formation. However, further investigation is required to confidently determine whether this hypothesis is correct. The second overlying shale bed yielded the majority of the plant specimens comprising the Mickey Canyon Spring Flora with fish remains generally absent or rarely represented by disassociated bone fragments.

SYSTEMATIC PALEONTOLOGY

Class Actinopterygii
Order Cypriniformes
Family Cyprinidae
Lavinia Baird and Girard, 1854
Lavinia lugaskii new species
Figures 1-6, Tables 1-2

Holotype—LACM 154390, complete skeleton (part and counterpart) on shale matrix.

Referred Specimens—From locality LACM 7743: complete skeleton, LACM 154333; partial skeletons, LACM 154334, 154335, 154336, 154337, 154338, 154339, 154340, 154341, 154342, 154343, 154344, 154345, 154346, 154347, 154348, 154349, 154350, 154351, 154352, 154353, 154354, 154355, 154356, 154357, 154358, 154359, 154360, 154361, 154362, 154363, 154364, 154365, 154366, 154367, 154368, 154369, 154370, 154371, 154372, 154373, 154374, 154375, 154376, 154377, 154378, 154379, 154380, 154381, 154382, 154383, 154384, 154385, 154397, 154459, 154461, 154462; partial skull, LACM 154460. From locality LACM 7744: partial skeletons, LACM 154386, 154387. From locality LACM 7745: complete skeleton, LACM 154389; partial skeletons, LACM 154388, 154391, 154392, 154393, 154394, 154395, 154396; opercle, LACM 154463. From locality UCMP PA624: partial skeleton, UCMP 141400.

Diagnosis—*Lavinia lugaskii* differs from *Lavinia hibbardi* (Smith, 1975) by having the following: 1) most anterior pharyngeal tooth of major row better developed (relatively larger) and always with well-

developed rugose grinding surface; 2) pharyngeal teeth of major row relatively more expanded transversely (deeper) and terminal tips more rounded (not sharply pointed) and more hooked (especially posterior two teeth); 3) pharyngeal tooth of minor row larger, longer, and with better developed, slightly striated grinding surface; 4) maxilla with much less developed mid-dorsal process (relatively much shorter) and ventral margin slightly convex (not nearly straight); and 5) lateral process of frontal positioned more posteriorly. It differs from *Lavinia condonianus* (Smith, 1975) by having the following: 1) most anterior pharyngeal tooth of major row much better developed (not peg-like); 2) all pharyngeal teeth of the major row notably compressed anteroposteriorly, moderately hooked at their tips, and have well-developed rugose grinding surfaces; 3) pharyngeal tooth of minor row relatively much larger and better developed (not rudimentary) with a slightly striated grinding surface; and 4) length of anterior arm of pharyngeal arch (portion anterior to first tooth of major row) significantly longer than length of major tooth row. It differs from extant *Lavinia exilicauda* Baird and Girard, 1854, by having the following: 1) pharyngeal tooth formula 1/5-5/1; 2) grinding surfaces of pharyngeal teeth relatively wider with much better developed, wavy linear, rugose ridges; 3) terminal tips of pharyngeal teeth of major row more rounded (not as sharply pointed) and less acutely hooked; 4) length of anterior arm of pharyngeal arch (portion anterior to first tooth of major row) significantly longer than major tooth row; 5) anterolateral foramen positioned more anteriorly on gnathal ramus; 6) mid-dorsal process of dentary relatively wider; 7) lateral process of frontal positioned more posteriorly; 8) relative head length larger (HL divisible into TL about 4.3-4.5 times); 9) dorsal fin origin not positioned as far posteriorly of pelvic fin origin; 10) anal fin origin positioned posterior to posterior margin of dorsal fin base; and 11) lower dorsal and anal fin ray counts. It differs from *Hesperoleucus* (= ?*Lavinia*) *symmetricus* (Baird and Girard, 1854) by having the following: 1) pharyngeal tooth formula 1/5-5/1; 2) pharyngeal teeth with much better developed rugose grinding surfaces and less sharply pointed terminal tips (more rounded); 3) length of anterior arm of pharyngeal arch (portion anterior to first tooth of major row) significantly longer than major tooth row; 4) relative head length slightly larger (HL divisible into TL about 4.3-4.5 times); 5) dorsal fin origin positioned slightly less posterior of pelvic fin origin; 6) anal fin origin positioned posterior to posterior edge of dorsal fin base; 7) pectoral fin ray count lower; and 8) much larger body size.

Type Locality—LACM 7745, Aldrich Station Formation, Mickey Canyon area, northwest flank of the Pine Groove Hills, Lyon County, Nevada.

Age—Middle Miocene (early Clarendonian North American Land Mammal age), about 12.5 – 12.0 Ma.

Etymology—Named in honor of the late Thomas P. Lugaski of the W. M. Keck Earth Science and Mineral Engineering Museum, University of Nevada, Reno, in recognition of his contributions to our knowledge of the Miocene chubs of Nevada.

Description—All of the specimens are preserved on the shale matrix bedding planes, resulting in most being compressed laterally and a few being compressed dorsoventrally. Most of the specimens are partial skeletons, but three specimens (holotype, LACM 154390, and referred specimens, LACM 154333 and 154389) are represented by nearly complete skeletons (Figures 1A-C, 2A-B). The holotype is particularly well preserved, even showing the scale impressions along the dorsal and ventral aspects of the body outline.

The general morphology of the head, body and fins is typically chub-like (Figures 1-2). The head length is divisible into the TL about 4.3 to 4.5 times. As compared with other middle Miocene chubs from Nevada, the body depth is moderately deep (maximum body depth divisible into TL about 4.2 – 4.3 times). The largest specimen (LACM 154341) is incomplete, missing the anterior part of the head, posterior end of the caudal peduncle, and most of the caudal fin, but is estimated to have had a TL of about 290 mm. Based on comparative ratios of the three complete skeletons, the size range of the TLs of the sample appears to be from about 140 to 290 mm, with the majority being between about 155 - 180 mm. The caudal peduncle is moderately robust with the least depth divisible into the TL about 13.7 - 14.2 times. The vertebrae count, not including the weberian apparatus, is 36. Morphometric and meristic data for the holotype and referred skeletons are presented in Table 1.

Pharyngeal teeth are present in 29 specimens, including the three most complete skeletons. The most complete pharyngeal in the sample is present on the partial, disarticulated skeleton of LACM 154397 (estimated SL undeterminable). In this specimen, the tooth bearing portion of the left pharyngeal was split away from the rest of the pharyngeal arch, but after preparation was precisely placed back into position. There are five teeth in the major row and one tooth in the minor row (Figure 3A-B). The first (most anterior) tooth of the major row exhibits the following characters: the smallest and shortest tooth of the major row; the tooth is moderately compressed anteroposteriorly; the grinding surface is elongated and contains rugose, wavy linear ridges; and the terminal tip is moderately pointed and slightly hooked. It is basically a slightly smaller version of the second tooth of the major row. The second tooth of the major row exhibits the following characters: the tooth base is

ovoid and moderately short; the grinding surface is moderately compressed anteroposteriorly and elongated transversely with rugose ridges and two small cuspules along each margin near the tip; and the tip is rounded and only slightly hooked. The third tooth of the major row differs from the second tooth by having the following: taller and larger; the terminal tip is slightly more rounded; and the grinding surface is slightly more elongated transversely and wider anteroposteriorly with extensive rugose ridges, but lacks the two small cuspules along the anterior margins. The fourth tooth of the major row differs from the third tooth by having the following: slightly greater in height; the grinding surface is slightly more elongated and slightly more compressed anteroposteriorly; and the terminal tip is slightly less rounded and more hooked. The fifth tooth of the major row is very similar to the forth tooth, but is slightly smaller and shorter, and is on an elevated platform of the pharyngeal. The single tooth of the minor row is tall and slightly compressed anteroposteriorly with a weakly developed grinding surface exhibiting slight striations and a slightly hooked tip. The measurements (in mm) for the teeth of the major row are (from anterior to posterior): first tooth, ap = 0.49, tr = 0.75, trgs = 0.70, ht = 1.51; second tooth, ap = 0.54, tr = 0.87, trgs = 1.08, ht = 1.90; third tooth, ap = 0.59, tr = 1.00, trgs = 1.20 , ht = 2.25; forth tooth, ap = 0.49, tr = 0.90, trgs = 1.13, ht = 2.54; and fifth tooth, ap = 0.44, tr = 0.59, trgs = 0.87, ht = 2.28. The measurements (in mm) for the minor row tooth are; ap = 0.21, tr = 0.26, trgs = 0.24, ht = 1.02. The length of the major tooth row is 4.4 mm. The anterior limb of the pharyngeal arch is elongated with a greatest length of 10.7 mm along the axis of the major tooth row and a length anterior to the first tooth of the major row of 7.0 mm. The dorsal limb is recurved posterolaterally with a total length of about 7.5 mm. The length from the tip of the dorsal limb to the tip of the anterior limb is 9.5 mm. The tooth formula for the right pharyngeal is 5/1.

On LACM 154388 (estimated SL ~136 mm), a partial left pharyngeal is present with six teeth, but the dorsal and anterior limbs are missing (Figure 4A-C). One smaller tooth is positioned near and posterior to the base of the second tooth of the major row and probably represents a replacement tooth for the major row. A single tooth is also present slightly ventral to and between the teeth of the major row, but the position of its base and its morphology clearly indicate that it belongs to a minor row. Apparently, there were five teeth in the major row and one tooth in the minor row. The grinding surfaces of all of the teeth of the major row exhibit well-developed, rugose, linear ridges, whereas the grinding surface of the minor tooth is less developed with slight striations. The measurements (in mm) for the teeth of the major row
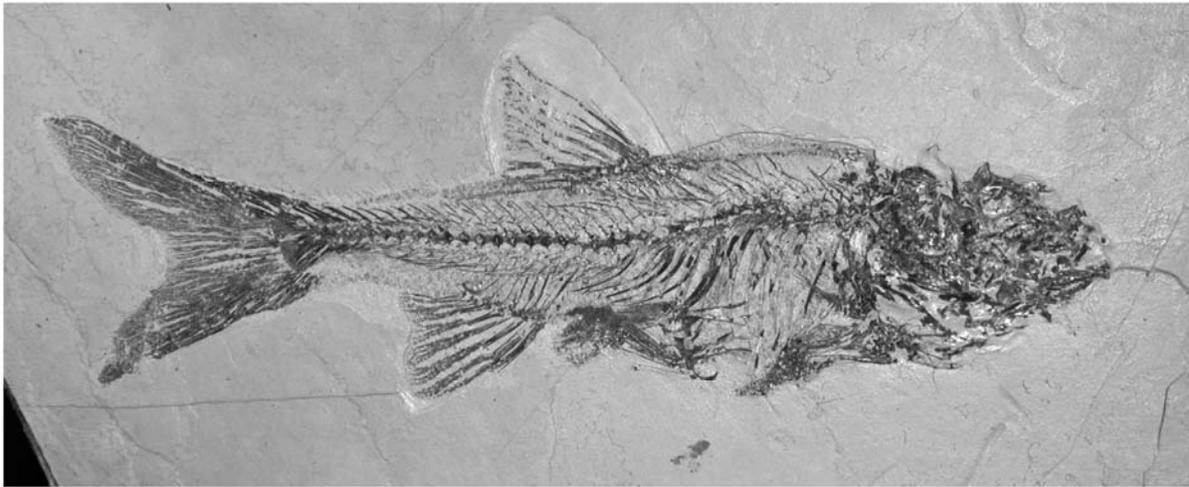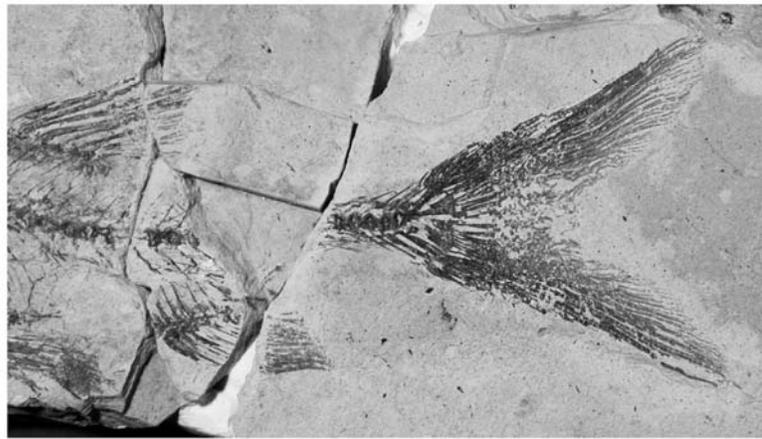
FIGURE 1. *Lavinia lugaskii*. A-B, skeleton of holotype (LACM 154390) showing part and counter part. C, skeleton of referred specimen (LACM 154389). All lateral views. Scale = 10 mm.

FIGURE 2. *Lavinia lugaskii*. A-B, skeleton showing part and counterpart, LACM 154333. C, partial skeleton showing detail of well forked tail, LACM 154363. All lateral views. Scales = 10 mm.

are (from anterior to posterior): first tooth, ap = 0.55, tr = 0.75, trgs = 1.05, ht = 1.80; second tooth, ap = 0.59, tr = 1.02, trgs = 1.18 , ht = 2.20; third tooth (?replacement tooth), ap = 0.50, tr = 0.74, trgs = 1.03, ht = 1.59; forth tooth, ap = 0.50, tr = 0.89, trgs = 1.09, ht = 2.49; and fifth tooth, ap = 0.44, tr = 0.55, trgs = 0.80, ht = 0.99. The measurements (in mm) of the minor row tooth are; ap = 0.19, tr = 0.25, trgs = 0.11, ht = 1.00. Little can be said of the morphology of the pharyngeal bone of LACM 154388 because it is compressed and damaged, with the anterior and dorsal limbs, and ventral-lateral portions missing.

On LACM 154393 (estimated SL ~132 mm), some of the bones of the head are disarticulated from the skeleton and imbedded in the surrounding matrix, including the pharyngeal arches (Figure 4D-E). The partial right pharyngeal of LACM 154393 has the mesial-ventral aspect exposed (Figure 4D). It possesses the two most anterior teeth of the major row, the bases and impressions in the matrix of the crowns of the third and forth teeth of the major row, the base of the fifth tooth of the major row, and the minor row tooth. These teeth exhibit the same morphology of those of LACM 154388 and 154397, and confirm that the right pharyngeal tooth formula is 5/1. The posterior teeth of the major row are on a moderately elevated platform. The anterior limb tapers anteriorly, is slightly downturned ventrally, and exhibits a marked narrowing below the anterior base of the most anterior tooth of the major row. The length of the anterior arm (8.0 mm, portion anterior to first tooth of major row) is significantly longer than the major tooth row base length (4.5 mm). The dorsal limb of the right pharyngeal is not visible because it extends into the matrix. No further attempt to remove the matrix from this specimen was done because the matrix is much harder than the bone and it would result in destruction of the bone. The alar margin is smoothly rounded except for a noticeable indentation anteriorly due to the narrowing at the base of the anterior limb. The greatest length of the right pharyngeal in the axis of the tooth row is 12.5 mm. The partial left pharyngeal of LACM 154393 has the mesial aspect exposed (Figure 4E). It possesses the bases of the five pharyngeal teeth of the major row and impressions in the matrix of the two most anterior teeth of the major row. The minor row tooth is not visible on the left pharyngeal due to the matrix and no attempt to remove the matrix was made because of the fragile condition of the bone. However, it is assumed that it was present since one occurs on the corresponding right pharyngeal and a single minor tooth is present on both left pharyngeals of LACM 154388 and 154397. The major tooth row length measured at the base of the teeth is 4.5 mm. The tip of the anterior limb of the left pharyngeal is missing with

a broken length of 4.6 mm. The dorsal limb is missing a portion of the bone in the center, but the outline of the missing portion is clearly visible because of the impression left in the matrix. The dorsal limb is recurved posterolaterally with a total length of 6.5 mm and a length from the middle of the major tooth row to the tip of 5.3 mm. The length from the tip of the dorsal limb to the broken tip of the anterior limb is 10.1 mm.

On LACM 154395 (estimated SL ~121 mm), a partial right pharyngeal and an isolated tooth are present. The right pharyngeal is split in half exhibiting the hollow bases of the teeth in the part and counter part. There are five teeth in the major row and one tooth in the minor row (Figure 5D). The length of the major tooth row is 3.8 mm. On LACM 154385 (estimated SL ~136 mm), a partial right pharyngeal is present with five teeth present in the major row. On LACM 154396 (estimated SL ~125 mm), partial left and right pharyngeal arches are visible. The left pharyngeal is missing the anterior end of the anterior limb and has the following present; the first (most anterior) tooth of the major row, the base and impression of the second tooth of the major row, the third tooth of the major row, and the base and impression of the fourth tooth of the major row, the base of the fifth tooth of the major row, and the base and impression of a single minor row tooth. The right pharyngeal is also missing most of the anterior limb and exhibits the most anterior tooth of the major row, the base and impression of the second tooth of the major row, and the bases of the third through fifth teeth of major row. LACM 154395, 154385, and 154396 confirm the pharyngeal tooth formula at 1/5-5/1. The teeth of these specimens exhibit the same proportions and morphology as the corresponding teeth in those of LACM 154388, 154393 and 154397, including the rugose, wavy linear ridges on the grinding surfaces.

On LACM 154379 (estimated SL ~114 mm), a partial left pharyngeal is present (Figure 5E). The left pharyngeal is damaged and missing a portion of the alar margin and the dorsal limb. This specimen exhibits the elongated anterior limb and the five teeth of the major row. The first two teeth of the major row are slightly broken away from their bases. The length of the major tooth row is about 4.0 mm, the greatest length of the anterior limb in the axis of the tooth row is 10.8 mm, and the length of the anterior limb anterior to the first tooth of the major row is 6.8 mm.

In addition to those described above, pharyngeal teeth are also present on the compressed bones of the head or in the matrix near the head on 22 other specimens (LACM 154333, 154335, 154340, 154343, 154344, 154350, 154355, 154358, 154361, 154373, 154374, 154375, 154376, 154378, 154380, 154381, 154382, 154383, 154384, 154389, 154390, 154394)

TABLE 1. Morphometric and meristic data for the holotype (LACM 154390) and referred specimens (LACM 154333, 154389) of *Lavinia lugaskii*. Thousandths of SL are included in parentheses.

| Character/measurement	Holotype LACM 154390	LACM 154333	LACM 154389
Fin ray count			
Dorsal	8	8	8
Pectoral	9	10	9
Pelvic	9	10	9
Anal	8	8	8
Caudal	19	19	19
Vertebrae count	36	36	36
SL	132.0 mm	115.5 mm	138.0 mm
TL	177.2 mm	153.0 mm	~181 mm
Head length	41.1 mm (311)	33.8 mm (285)	42.0 mm (302)
Head depth	33.6 mm (255)	25.7 mm (225)	~30 mm (~217)
Maximum body depth	41.5 mm (314)	36.0 mm (311)	42.0 mm (304)
Fins			
Dorsal fin length	30.0 mm (227)	~26 mm (~225)	30.5 mm (221)
Dorsal fin base length	15.3 mm (116)	-	16.3 mm (118)
Pectoral fin length	~29 mm (~220)	23.0 mm (199)	~25 mm (~181)
Pectoral fin base length	8.0 mm (60)	5.0 mm (43)	~5.6 mm (~41)
Pelvic fin length	~25 mm (~189)	21.7mm (188)	~23.5 mm (~170)
Pelvic fin base length	5.8 mm (44)	4.0 mm (35)	~5.5 mm (~40)
Anal fin length	26.6 mm (202)	22.5 mm (195)	~26 mm (~188)
Anal fin base length	15.3 mm (116)	12.6 mm (109)	16.9 mm (122)
Caudal fin length	45.2 mm (342)	37.5 mm (325)	~43 mm (~316)
Minimum caudal fin depth	~21.2 mm (~161)	~19.8 mm (~142)	~24 mm (~174)
Widest caudal fin depth	44.2 mm (335)	40.6 mm (356)	-
Snout to dorsal origin length	76.0 mm (576)	60.6 mm (525)	75.6 mm (548)
Snout to occupit length	40.5 mm (307)	30.2 mm (261)	36.6 mm (265)
Snout to pectoral origin length	41.0 mm (311)	31.5 mm (273)	39.7 mm (288)
Snout to pelvic origin length	72.0 mm (545)	63.6 mm (551)	73.5 mm (533)
Snout to anal origin length	95.0 mm (720)	85.2 mm (738)	101.6 mm (736)
Pectoral origin to pelvic origin length	34.0 mm (258)	32.5 mm (281)	35.5 mm (257)
Pectoral origin to anal origin length	58.0 mm (439)	58.5 mm (506)	63.1 mm (457)
Pectoral origin to dorsal origin length	45.7 mm (346)	33.1 mm (287)	41.6 mm (301)
Pectoral origin to caudal base length	98.0 mm (742)	91.5 mm (792)	102.1 mm (740)
Dorsal origin to occupit length	39.2 mm (297)	33.8 mm (292)	43.0 mm (312)
Dorsal origin to anal origin length	23.5 mm (178)	~26 mm (~225)	24.3 mm (176)
Pelvic origin to dorsal posterior base length	21.2 mm (161)	18.8 mm (142)	20.5 mm (148)
Pelvic origin to anal origin length	28.0 mm (212)	~31.3 mm (~271)	30.0 mm (217)
Pelvic origin to caudal base length	62.0 mm (470)	66.0 mm (571)	65.5 mm (475)
Pelvic origin to greatest caudal length	105.0 mm (795)	104.0 mm (900)	111.0 mm (804)
Anal origin to caudal base length	39.5 mm (299)	37.0 mm (320)	40.5 mm (293)
Length of caudal pedicle			
Dorsal fin posterior base to caudal base	43.0 mm (326)	42.0 mm (364)	42.9 mm (311)
Anal posterior base to caudal base	24.0 mm (182)	21.8 mm (189)	24.9 mm (180)
Caudal peduncle least depth	12.5 mm (71)	~11 mm (~95)	13.2 mm (96)
Relative positions			
Dorsal fin origin to pelvic fin origin	8 mm posterior (60)	5.5 mm posterior (50)	6.0 mm posterior (43)
Anal fin origin to posterior dorsal fin base	3 mm posterior (20)	2 mm posterior (20)	3.7 mm posterior (27)
TL/ head length	4.31	4.53	4.31
TL/caudal peduncle least depth	14.2	~13.9	~13.7
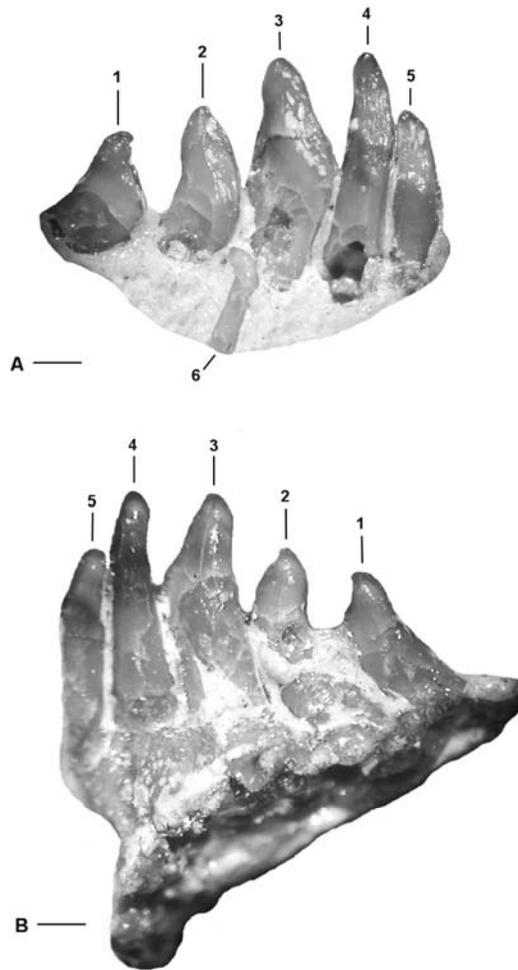
FIGURE 3. *Lavinia lugaskii*. Left pharyngeal teeth of LACM 154397. A, anterodorsal view: 1, first (most anterior) tooth of the major row; 2, second tooth of major row; 3, third tooth of major row; 4, fourth tooth of major row; 5, fifth tooth of major row; 6, minor row tooth. B, mesial view, tooth numbers correspond to positions of those in 3A. Scales = 0.5 mm.

including the holotype (Figure 5A-C). The teeth of these specimens agree in morphology with the corresponding teeth of those described above, including the rugose grinding surfaces.

Due to compression and some probable postmortem deterioration, the cranial and jaw bones are often broken apart, overlapping or fused together in the specimens, making it difficult to distinguish the morphology of individual bones. In addition, because the shale matrix was often split along the bedding plane to expose the fossil, many of the specimens have the bones split apart with portions on each half of the resulting part and counterpart. However in some cases, certain bones are disarticulated from the skeleton or complete enough to allow a description of their morphology.

The premaxillae are best preserved in LACM 154350 (estimated SL ~123mm) and LACM 154344 (estimated SL ~ 96 mm), wherein only their lateral aspects are exposed. The premaxilla extends anteriorly from the anteroventral margin of the maxilla to the tip of the snout and then turns posterodorsally at an acute angle as a smaller dorsal projection, giving the tip of the snout a somewhat pointed appearance. Measurements of the premaxillae of LACM 154350 and 154344 are, respectively: lengths from the anterior tip to the border of the maxilla = 8.4 and 5.8 mm; lengths of the dorsal posterior projection = 3.8 and 2.5 mm; and the greatest depths along the portion bordering the orifice = 2.4 and 2.1 mm.

The maxillae are best preserved in LACM 154462 (estimated SL = 137 mm), 154459 (estimated SL = 134 mm), and 154350. The maxilla of LACM 154462 is

almost complete with its lateral aspect exposed, only missing very small portions along the posterior edges of the posterior process. It is elongated anteroposteriorly (9.7 mm), with the greatest depth occurring across the body and dorsal process (4.2 mm), and gradually tapers anteriorly to a narrow (~ 1 mm) neck. The ventral margin is slightly convex. The dorsal process has a relatively wide base with a moderate height of about 2.5 mm. A relatively well-developed ridge for the insertion of the palatine ligament is present. The posterior process is moderately well developed and flairs out from a relatively narrow pedicel. The head of the maxilla is not visible because it extends mesiodorsally into the matrix. The partial maxilla of LACM 154350 has its lateral aspect exposed and exhibits the same morphology as that of LACM 154462. The measurements of LACM 154350 are total length ~8-9 mm, greatest depth across the body and dorsal process = 3.2 mm, the width of anterior neck between the dorsal process and head = 0.07 mm, and height of the base of the dorsal process = 2.5 mm. The partial maxilla of LACM 154459 has its mesial aspect exposed, including the head of the maxilla and part of the anteromesial (premaxillary) process, but the dorsal process and part of the posterior process are broken away. The head has a rounded outline with the anteromesial process extending ventrally from the head. The neck connecting the head to the anterior body of the maxilla is very short, so that the head is positioned close to the anterodorsal aspect of the maxilla. Composite lateral and mesial views of the maxilla outline based on LACM 154462, 154459, and 154350 are presented in Figure 6A-B.

The dentaries are best preserved in LACM 154390 (holotype), 154350, 154391 (estimated SL ~145 mm), and LACM 154462. The coronoid process of the dentary is centrally positioned and well developed with a rounded dorsal arch. The gnathal ridge is flaired laterally and the anterior end is mesially curved. The ventral edge is relatively flat with only a slight ventral deviation near the anterior tip. The anterolateral foramen is positioned well anterior to the midpoint of the gnathal ramus. Seven lateral pores are present along the lateroventral aspect of the dentary. The mechelian groove terminates anteriorly on the gnathal ramus at a level that is just posterior to the caudal end of the gnathal ridge. The measurements (in mm) of the dentaries of LACM 154390, 154350, 154391, and LACM 154462 are, respectively: lengths from the anterior tip to posterior tip, 12.7, ~12.9, 13.3, and 13.0; lengths from the anterior tip to the top of the coronoid process, 9.3, 8.0, 9.9, and 8.8; lengths from the anterior tip to the anterior base of coronoid process, 6.3, 6.0, 6.9, and 6.7; lengths from the top of the coronoid process to the posterior tip, ~7.4, 7.6, ~8.3, and 8.1; depths at the anterior tips (symphyses), 1.5,

1.4, 1.6, and 1.4; depths just anterior to the anterior base of coronoid process, 2.5, 2.3, 3.1, and 2.6; widths of the base of the coronoid process, 2.7, 2.8, 3.2, and 3.5; and depths from the highest point on the coronoid process to the ventral edge of dentary, 5.9, 6.0, 6.0, and 5.7. When the mouth is closed it forms an oblique angle of about 27 degrees relative to the horizontal axis of the head and the maxilla extends posteriorly to the level of the anterior edge of the orbit. A composite lateral view of the dentary outline based on LACM 154390, 154350, 154391, and 154462 is presented in Figure 6C.

The preopercle is complete and fairly well preserved in one specimen, LACM 154355 (estimated SL ~94 mm), wherein its mesial surface is exposed. It is shaped in a wide concave arc formed with an angle of 108 degrees and has the following measurements: width from the dorsal tip to the anteroventral tip, 13.0 mm; dorsal limb length from the apex, 7.6 mm; anteroventral limb length from the apex, 7.3 mm; and greatest depth at the apex of the angle between the dorsal and ventral limbs, 13.0 mm.

Although many specimens exhibit a partial opercle or partial outline of it in the matrix, the best preserved opercle is a disarticulated specimen (LACM 154463), which consists of almost the entire bone laterally exposed with only a few small areas along the ventral and posterior borders missing. However, the entire outline of the bone can be discerned because there are impressions left in the matrix where the bone is missing. The lateral aspect of the opercle outline is triangular in shape with the anterior articular process extending anterodorsally from the body as a narrow, elongated projection (Figure 6D). Overall, it is very similar in shape to those of other species of Pliocene *Lavinia* (see Smith, 1975). Measurements (in mm) for LACM 154463 are as follows (opercle measurements and terminology follow Miranda and Escala, 2005); distance from the tip of the articular process to the articular facet = 4.0, distance from the tip of the articular process to the inferior angle = 12.2, distance from the tip of the articular process to the superior angle = 8.7, distance from superior angle to inferior angle = 18.0, greatest distance between posterior angle and anterior edge = 11.8, and posterior angle height = 7.3.

Partial frontals are common on many of the specimens, but they are usually incomplete or badly crushed. The best preserved frontals are on LACM 154459 and 154460 (a dorsoventrally preserved partial cranium, estimated SL undeterminable). On LACM 154459, the dorsal aspects of the frontals are exposed, whereas on LACM 154460 the ventral aspects are exposed. The dorsal and ventral outlines of the left frontals are presented in Figure 6E-F. The frontal of *L. lugaskii* is morphologically similar to those of *L.*
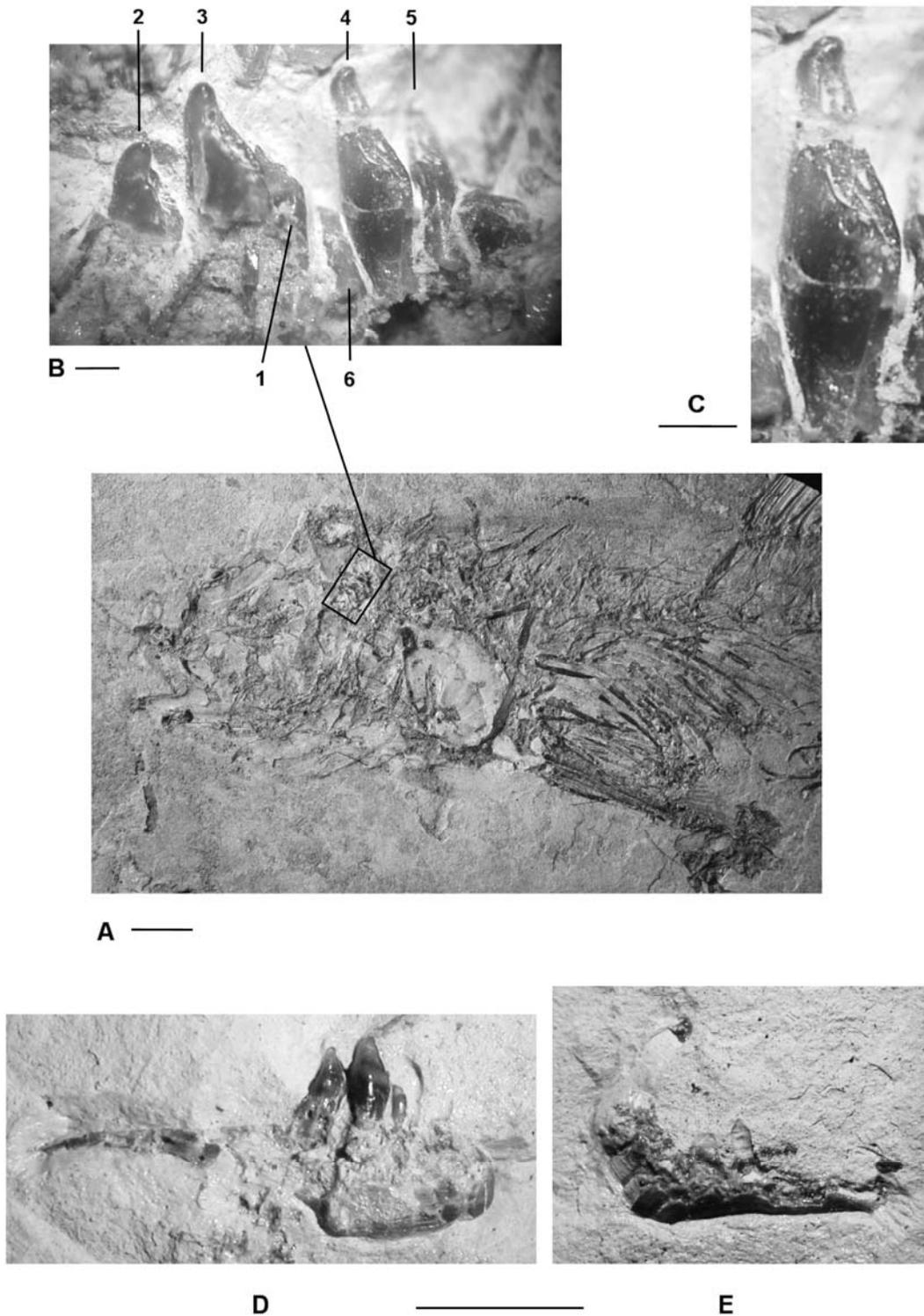
FIGURE 4. *Lavinia lugaskii*. A, partial skeleton showing location of partial pharyngeal arch, lateral view, LACM 154388, scale = 5 mm. B, enlarged area of A showing partial pharyngeal arch and teeth, anterodorsal view, scale = 0.5mm: 1, replacement tooth of major row; 2-5, major row teeth; 6, minor row tooth. C, close up of rugrose linear grinding surface of fourth tooth of major row, scale = 0.5 mm. D, partial right pharyngeal with first and second teeth of major row, bases and impressions in matrix of third and forth teeth of major row, base of fifth tooth of major row, and minor row tooth, mesial-ventral view, LACM 154393. E, partial left pharyngeal with impressions in matrix of two most anterior teeth of major row and bases of all five teeth of major row, mesial view, LACM 154393. Scales for D and E = 5 mm.

hibbardi (see Smith, 1975) and extant *Lavinia*, but the lateral process is positioned more posteriorly. For example, in *L. hibbardi* and extant *Lavinia* the tip of the lateral process is positioned posteriorly from the anterior edge of the frontal at about 55-58% of the total length, whereas in *L. lugaskii* it is positioned posteriorly at about 68% of the total length. Measurements (in mm) of LACM 154459 and 154460, respectively, are as follows; ap = 15.4 and 16.2, tr = 6.9 and 7.0, and distance between the anterior edge to tip of the lateral process = 10.4 and 11.0.

In one specimen (LACM 154361, estimated SL ~133 mm), the right cleithrum is disarticulated from the body and positioned on the matrix near the pelvic fin, exposing its mesial aspect. A distinct ridge is present that extends down from the dorsal tip of the vertical wing to the base of the horizontal wing. The measurements of LACM 154361 are follows (using those defined by Miranda and Escala, 2005): the vertical wing length = 11.5 mm; the horizontal wing length = 11.7 mm; the chord length (the widest length between the dorsal tip and the mesocoracoid articulation crest of the horizontal wing) = 19.1 mm; the external margin length (chord length minus the mesocoracoid articulation crest of the horizontal wing) = 18.0 mm; and the posterior angle within the wings = 97 degrees.

The pectoral and pelvic fins are of moderate size, while the dorsal, anal and caudal fins are relatively large (Table 2). The fin ray counts are as follows: dorsal, 8 (N = 30); pectoral, usually 9, with one at 10 (N = 18); pelvic, usually 9, with one at 10 (N = 27); anal 8 (N = 27); and caudal, usually 19, with one at 20 (N = 19). The dorsal fin is positioned posteriorly on the body with its origin posterior to the pelvic fin origin. The angle formed from the origin of the pelvic fin to the origin of the dorsal fin is 83 - 85 degrees posterior. The posterior portion of the dorsal fin extends beyond the origin of the anal fin (Figure 1). However, the anal fin origin is posterior to the dorsal fin posterior base. The caudal fin is rather deeply forked (Figure 2C). There are eight dorsal and eight ventral procurrent rays in the caudal fin. Coburn and Cavender (1992) regarded an equal number of dorsal and ventral procurrent caudal fin rays to be a derived condition, often seen in members of the Western North American chub group.

Discussion—The Aldrich Station chub exhibits the following suite of characters: 1) moderate size (TL ~140 – 290 mm); 2) the HL is divisible into the TL about 4.31 – 4.53 times; 3) the body is relatively deep (body depth 304 - 314 thousandths of SL); 4) the pharyngeal tooth formula 1/5 - 5/1; 5) all of the pharyngeal teeth of the major row are compressed anteroposteriorly and exhibit moderately rounded and hooked tips, and transversely elongated grinding surfaces with distinctive rugose, wavy linear ridges; 6) the minor row tooth is moderately tall and anteroposteriorly compressed, the grinding surface is slightly developed with faint striations, and the tip is slightly hooked; 7) the anterior arm of the pharyngeal arch (portion anterior to first tooth of major row) is significantly longer than the major tooth row length; 8) the dorsal process of the maxilla is moderately developed and centrally positioned; 9) the dentary has a mesially curved anterior tip, centrally positioned dorsal process, anteriorly positioned anterolateral foramen, laterally flaired gnathal ridge, and eight lateral pores; 10) the lateral process of the frontal is positioned posteriorly from the anterior margin at about 68% of the total length of the frontal; 11) the fin ray counts are dorsal 8, pectoral usually 9 (rarely 10), pelvic usually 9 (rarely 10), anal 8, and caudal usually 19 (rarely 20); 12) the dorsal, anal and caudal fins are relatively large; 13) the caudal fin is deeply forked; 14) the dorsal fin origin is positioned posterior to the pelvic fin origin; 15) the anal fin origin is positioned posterior to the dorsal fin posterior base; and 16) the caudal peduncle is moderate in depth (TL/caudal peduncle least depth = 13.7 - 14.2). The Aldrich Station chub is morphologically most similar to Pliocene *Lavinia hibbardi*, including the synapomorphic shared character state of well-developed rugose grinding surfaces on the pharyngeal teeth (see Smith et al., 1982, 2000, 2002) along with its dentary morphology that includes a mesially curved anterior tip of the gnathal ramus, a centrally positioned dorsal process, laterally flaired gnathal ridge, and eight lateral pores. These shared characters indicate that the Aldrich Station chub is referable of *Lavinia* and it is herein assigned to a new species, *L. lugaskii*.

Smith (1975) described the genus *Idadon* from the Glenns Ferry Formation, Idaho, and assigned two species to it, the type species *I. condonianus* (Cope, 1883) and *I. hibbardi*. Subsequent investigators (e.g., Smith et al., 1982; Smith and Miller, 1985) noted that *Idadon* exhibited similarities, especially the rugose or striated grinding surfaces of the pharyngeal teeth, to extant *Lavinia* and other Pliocene representatives of *Lavinia*. Smith et al. (2000) provided evidence that *Idadon* should be regarded as a junior synonym of *Lavinia* and referred *I. hibbardi* to *Lavinia (Idadon) hibbardi*, and Smith et al. (2002) provided further evidence in support of this synonymy. Smith et al. (2002) regard *Mylopharodon* Ayres, 1855, as the closest sister taxon to *Lavinia* and *Hesperoleucus* Snyder, 1913. *Lavinia lugaskii* is easily distinguished from all species of *Mylopharodon* by the morphology of its pharyngeal teeth (not molariform). Undetermined species of *Lavinia* have also been recorded from

earliest Pliocene (latest Hemphillian) sediments in the Madeline Plains, California, earliest Pliocene (latest Hemphillian) sediments in Cache Valley, Utah, the early to late Pliocene (early to late Blancan) Sunrise Pass Formation, Nevada, the late Pliocene (late Blancan) Magazine Road Local Fauna, Honey Lake, California, and late Pliocene (late Blancan) sediments in the south end of Secret Valley, California (McClellan, 1977; Kelly, 1994; Wagner et al., 1997; Smith et al., 2002; K. Gobalet, per. communication, 2009).

Lavinia hibbardi and L. condonianus from the Glenns Ferry Formation are known from large samples of isolated pharyngeal arches and other bones (Smith, 1975). Lavinia hibbardi is characterized by having the following (Smith, 1975; Smith et al., 2000): 1) five pharyngeal teeth in major row and one or two rudimentary teeth in the minor row; 2) all or nearly all of the pharyngeal teeth of the major row exhibit rugose grinding surfaces; 3) the length of the anterior arm of the pharyngeal (portion anterior to the first tooth of the major row) is longer than the major tooth row; 4) the maxilla has a high mid-dorsal process whose depth is more than one-half of the maxilla length, a relatively straight ventral margin, and a posterior (dentary) process that is large and flairs out from a slender pedicel; and 5) the dentary has a gnathal ramus with flaired lateral edges and a large coronoid process that is positioned near the midpoint, and is mesially curved anteriorly. Lavinia condonianus differs from L. hibbardi by having the following (Smith, 1975): 1) the anterior most tooth of the major row of the pharyngeal teeth is peg-like, the second tooth is conic-molariform, and the subsequent teeth are less compressed anteroposteriorly (more round in cross section) and less sharply pointed; 2) the rugose grinding surfaces are less developed and usually restricted to the posterior teeth of the major row; and 3) the length of the anterior arm of the pharyngeal (portion anterior to the first tooth of the major row) is relatively shorter and subequal to the length of the major tooth row.

Other samples of fossil Lavinia sp. from the Pliocene have not been formally described or assigned specific status, but Smith et al. (2002) provided a list of the following shared characters that support their assignment to the genus: 1) the pharyngeal teeth have slightly to moderately corrugated grinding surfaces; 2) the dentary has a laterally flaired gnathal ramus, medially positioned coronoid process, mesially curved anterior end, and eight lateral pores; and 3) in the Cache Valley sample, high fin ray counts, like extant Lavinia exilicauda. Extant Lavinia has been well described in the literature (e.g., Baird and Girard, 1854; Snyder, 1913; Fowler, 1924; Murphy, 1945, 1948; Coburn and Cavender, 1992; Smith et al., 1982, 2000, 2002; Moyle, et al., 1995; Moyle, 2002). It is characterized by having the following: 1) pharyngeal teeth usually 0/5-5/0 (sometimes 0/4-4/0) with the grinding surfaces striated; 2) the anterolateral foramen of the dentary is positioned on the caudal portion of the gnathal ridge (at least halfway back or more) and eight lateral pores are usually present; 3) the dentary has a gnathal ramus with flaired lateral edges and a large coronoid process that is positioned near the midpoint, and is mesially curved anteriorly; 4) the head is relatively small (HL is divisible into TL about 5.3 times); 5) the dorsal fin is positioned posteriorly on the body with its origin well posterior to the pelvic fin origin; 6) the anal fin is long with its origin anterior to or even with the posterior edge of the dorsal fin base; 7) high fin ray counts (dorsal usually 10-13, pectoral 17, pelvic 19, anal usually 11 – 14); 8) a large forked caudal fin; 9) a narrow caudal peduncle; and 10) moderate to large size (maximum SL >350 mm).

Hesperoleucus, regarded by some investigators as a junior synonym of Lavinia (e.g., Moyle, 2002; Aguilar and Jones, 2009) and represented by extant H. symmetricus, has been well described in the literature (e.g., Barid and Girard, 1854; Snyder, 1913; Murphy, 1945, 1948; Hopkirk, 1973; Brown et al., 1992; Moyle, et al., 1995; Moyle, 2002; Smith et al., 2002). It is characterized by having the following: 1) pharyngeal teeth 0/5 - 4/0 with striated grinding surfaces; 2) the anterolateral foramen is positioned anteriorly on the gnathal ramus; 3) the dentary has a gnathal ramus with flaired lateral edges and a large coronoid process that is positioned near the midpoint, and is mesially curved anteriorly; 4) the relative size of the head is moderate (HL divisible into TL about 4.8 times); 5) the dorsal fin origin is positioned well posterior to the pelvic fin origin; 6) the dorsal and anal fins are relatively large; 7) the anal fin origin is slightly anterior to the posterior dorsal fin base; 8) the fin ray counts are dorsal usually 7-9, pectoral usually 12-13, pelvic usually 8-9, and anal usually 6-8; 9) a moderately forked caudal fin; 10) a narrow caudal peduncle; and 11) small size (SL = 60.4 mm, OR = 33.1 – 85.5 mm, TL usually <100mm).

Lavinia lugaskii can be easily distinguished from L. hibbardi and all other recognized species of Lavinia by the differences listed in the diagnosis above. Lavinia lugaskii can also be easily distinguished from Hesperoleucus symmetricus, the putative closest sister taxon to Lavinia (Smith et al., 2002), by the differences listed in the diagnosis above. Although the samples of Lavinia sp. from the Pliocene have not yet been formally described, L. lugaskii differs from the Cache Valley Lavinia sample from Utah by having lower fin ray counts and better developed rugose grinding surfaces on the pharyngeal teeth.

Three other species belonging to the western chub group have been previously described from the
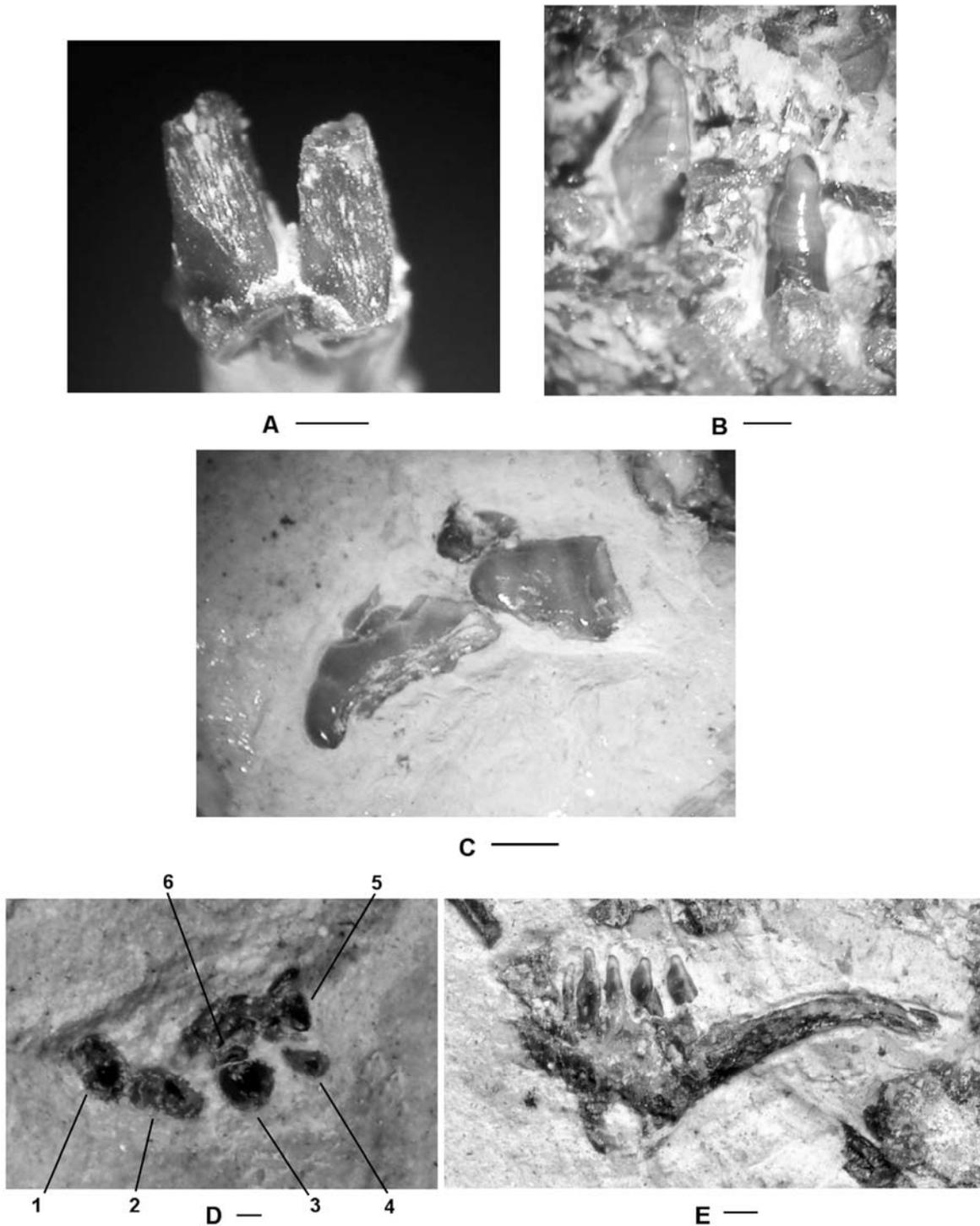
FIGURE 5. *Lavinia lugaskii*. A-C, pharyngeal teeth of holotype, LACM 154390, showing morphology and rugose grinding surfaces: A, partial left forth and fifth teeth of major row (removed from matrix along side of B to expose grinding surfaces, tips are missing), dorsal view; B, left second and third teeth of major row, mesial view; and C, three partial teeth of right pharyngeal, posterior dorsal view. D, cross section of pharyngeal teeth, LACM 154395, showing five teeth of major row (numbers 1 – 5) and minor row tooth (number 6). E, partial right pharyngeal, LACM 154379, showing elongated anterior limb and five teeth of major row, mesial view. Numbered tooth positions correspond to those in Figure 3B. Scales for A-D = 0.5 mm, scale for E = 1 mm.

TABLE 2. Comparative morphometric and meristic data for *Lavinia lugaskii* and three other Miocene chub species from Nevada. All measurements in parentheses are in thousandths of standard length.

	Lavinia lugaskii	*Gila? esmeralda* [3,4,5]	*Gila turneri* [1,2,3,4,5]	*Siphateles traini* [5]
Total length	140 - ~290 mm	126 mm	142 mm	65.2-89.5 mm
Vertebrae count	36	36	39	39
Fin ray count				
Dorsal	8	8	9	7-8
Pectoral	9-10	14	11	13
Pelvic	9-10	8	9	8
Anal	8	8	10	8
Caudal	19 -20	19-21	23	18-20
Head length	(285-311)	(240)	(291)	(255-316)
Head depth	(217-255)	(253)	(180)	(174-221)
Maximum body depth	(304-314)	(290)	(189)	(166-246)
Fins				
Dorsal fin length	(221 -227)	(161)	(157)	(134-178)
Dorsal fin base length	(116-118))	(103)	(111)	(106)
Pectoral fin length	(181- ~220)	-	(122)	(88-157)
Pelvic fin length	(170 – 189)	-	(144)	(91-145)
Anal fin length	(188 – 202)	(142)	(163)	(93-163)
Caudal fin length	(304 – 352)	(337)	(283)	(216-330)
Min. caudal depth	(142 - 174)	(84)	(72)	(110)
Snout to dorsal origin length	(525-576)	(547)	(577)	(573-592)
Snout to occupit length	(261-307)	-	(254)	(286-338)
Snout to pelvic origin length	(533-551)	(640)	(567)	(501-571)
Snout to anal origin length	(720-738)	(753)	(747)	(734-823)
Pectoral origin to anal origin length	(439-506)	-	(433)	(413)
Pelvic origin to dorsal origin length	(287 - 346)	(258)	(236)	(191-226)
Pelvic origin to anal origin length	(186-271)	(128)	(193)	(151-288)
Pelvic origin to caudal base length	(470-571)	(452)	(444)	(463-537)
Anal origin to caudal base length	(293-320)	(316)	(272)	(288)
Position of dorsal origin to pelvic origin	moderately posterior	well anterior	slightly posterior	even
Position of anal fin origin to dorsal posterior fin base	slightly posterior	moderately posterior	well posterior	even
Forked caudal fin	deeply	moderately	moderately	moderately
TL/head length	4.31-4.53	5.25	3.50	3.99-4.76
TL/caudal peduncle least depth	13.7 - 14.2	-	16.1	-

1, Lucas (1900). 2, La Rivers (1962). 3, La Rivers (1966). 4, Lugaski (1977). 5, Lugaski (1979).

middle to late Miocene of Nevada. These include two species of *Gila* Baird and Girard, 1853, and one species of *Siphateles* Cope, 1883 (*Gila turneri* [Lucas, 1900], *Gila? esmeralda* [La Rivers, 1966], and *Siphateles traini* [Lugaski, 1979]). However, the generic assignments of some of these species have varied or been questioned since they were first described (e.g., La Rivers, 1962, 1966; Lugaski, 1977; Smith et al., 2002). For completeness, comparison of *L. lugaskii* to these species is warranted (Table 2).

The holotype of *Gila turneri* is from the valley of the Silver Peak Range at the southwest end of the Big Smokey Valley, Silver Peak Quadrangle, Esmeralda County, Nevada, but the exact locality has never been relocated (Lugaski, 1977). The age of the type locality is undetermined, but likely to be middle Miocene (late Barstovian to middle Clarendonian) based on the age of the "Esmeralda Formation" in the Silver Peak Quadrangle (Robinson, 1966; Abers and Stewart, 1972; Diamond and Ingersoll, 2002). *Gila turneri* has also been recorded from the middle part of the "Esmeralda Formation" of Stewart Valley, Mineral County, Nevada (Smith et al. 2002). The middle part of the formation in Stewart Valley has been radioisometrically dated (Ar^{40}-Ar^{39}) at 11.74 ± 0.03 and 11.58 ± 0.05, indicating a middle Miocene (Clarendonian) age (Swisher, 1992). Lucas (1900) originally referred this species to *Leuciscus* Cuvier, 1817. La Rivers (1962) referred this species to *Richardsonius* Girard, 1856, which was followed by Uyeno and Miller (1963) who questionably referred this species to *Gila*.

Lavinia lugaskii differs from *G. turneri* by having the following (Table 2): 1) larger body size; 2) the maximum head and body depths are relatively larger; 3) the relative head length is less (HL is divisible into TL about 4.3 - 4.6 times); 4) the total vertebrae count is lower; 5) the dorsal, pectoral, anal, and caudal fin ray counts are lower; 6) the dorsal, pectoral, pelvic, anal, and caudal fins are relatively larger; 7) the dorsal fin origin is positioned slightly more posterior to the pelvic fin origin; 8) the caudal peduncle is more robust; and 9) the caudal fin is more deeply forked. The morphology of the pharyngeal arches and teeth of *G. turneri* have not been reported.

Gila? esmeralda is from sedimentary unit 2 of the Esmeralda Formation (Albers and Stewart, 1972) exposed seven miles southeast of Coaldale Junction, Esmeralda County, Nevada (Lugaski, 1977). Evernden and James (1964) dated this unit by K-Ar at 13.0 Ma (corrected), indicating a probable late Barstovian age for the fish fauna. Lugaski (1977) noted that the lacustrine deposits that yielded *G.? esmeralda* represent a different depositional basin from the lacustrine deposits that yielded *G. turneri*. Smith (1975) regarded *G.? esmeralda* as a probable junior

synonym of *G. turneri*, but Lugaski (1977) provided convincing evidence that *G.? esmeralda* is distinct from *G. turneri*. Dowling et al. (2002) and Smith et al. (2002) only questionably regarded *G. esmeralda* as belonging to *Gila* because it exhibits certain similarities to *Siphateles*.

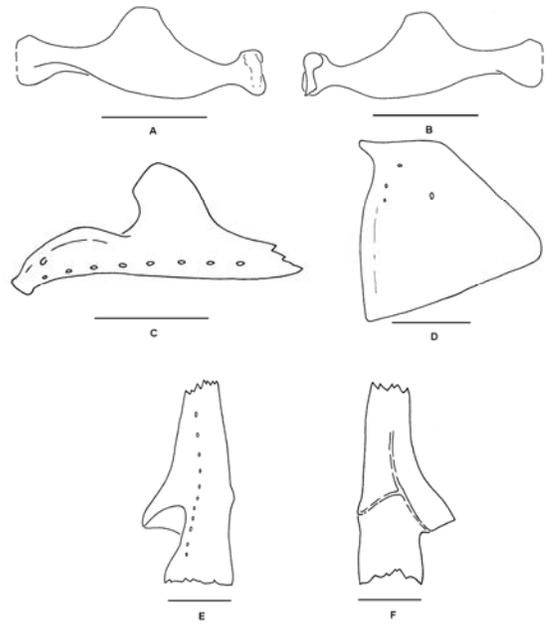*Lavinia lugaskii* differs from *G.? esmeralda* by having the following (Table 2): 1) larger body size; 2)

FIGURE 6. *Lavinia lugaskii*. A-B, composite right maxilla outline based on LACM 154462, 154459, and154350, A, lateral view, anterior right, B, mesial view, anterior left. C, composite left dentary outline based on LACM 154390, 154350, 154391, and 154462, lateral view, anterior left. D, left opercle, LACM 154463, lateral view. E, left frontal, LACM 154459, dorsal view, anterior up. F. left frontal, LACM 154460, ventral view, anterior up. Scales = 5 mm.

the relative head length is greater (HL is divisible into TL about 4.3 – 4.6 times); 3) the pectoral fin ray count is lower and pelvic fin ray count is higher; 4) the dorsal and anal fins are relatively larger; 5) the snout to pelvic fin origin length is relatively shorter; 6) the dorsal fin origin is positioned posterior to the pelvic fin origin, whereas in *G.? esmeralda* it is positioned well anterior to the pelvic fin; 7) the anal fin origin is positioned slightly less posterior to the dorsal fin posterior base; and 8) the caudal fin is more deeply forked. The morphology of the pharyngeal arches and teeth of *G.? esmeralda* have not been reported.

Siphateles traini is from the zeolite beds exposed on the west side of Jersey Valley, Pershing County,

Nevada (Lugaski, 1979). Deffeyes (1959) and Papke (1972) divide the lacustrine deposits into three units in the Jersey Valley area as follows; basal unit at least 427 m (1700 ft) thick, a middle unit 314 m (1,030 ft) thick, and an upper unit of unknown thickness. The uppermost portion of the upper unit contains the zeolite beds that yielded *S. traini* (Deffeyes, 1959; Johnson, 1977). Mammalian fossils of middle Miocene (Clarendonian) age occur 213 m (700 ft) below the fish locality level (Deffeyes, 1959; Johnson, 1977), indicating a possible late Clarendonian or early Hemphillian age for *S. traini*. However, Dowling et al. (2002) regard the type locality to be earliest Pliocene (latest Hemphillian) in age, or about 6 Ma.

Lavinia lugaskii differs from *S. traini* by having the following (Table 2): 1) larger body size; 2) the maximum head and body depths are relatively larger; 3) the total vertebrae count is lower; 4) the pectoral fin ray count is lower and the pelvic fin ray count is higher; 5) the dorsal, pectoral, pelvic, and anal fins are relatively larger; 6) the dorsal fin origin is positioned posterior to the pelvic fin origin, whereas in *S. traini* they are even; 7) the anal fin origin is positioned posterior to the dorsal posterior fin base, whereas in *S. traini* they are even; 8) the pectoral fin origin to anal fin origin length is relatively longer; and 9) the caudal fin is more deeply forked. The morphology of the pharyngeal arches and teeth of *S. traini* have not been reported.

An additional Miocene record of *Gila* from Nevada is *Gila* sp. from the late Miocene (Hemphillian) Truckee Formation exposed near the communities of Fernley and Hazen, Nevada, about 90 km northeast of the Mickey Canyon section (Smith, 1981; Baumgartner, 1982; Smith et al., 2002). *Lavinia lugaskii* is easily distinguished from *G.* sp. by having pharyngeal teeth with rugose, wavy ridged grinding surfaces and a relatively shorter dentary. *Lavinia lugaskii* can also be distinguished from all other species of *Gila* and *Siphateles* by having rugose grinding surfaces on the pharyngeal teeth.

The distinguishing characters of *L. lugaskii* clearly indicate that it is distinct from the three previously named Miocene chub species and *G.* sp. from Nevada. In addition, *L. lugaskii* was recovered from lacustrine sediments that were deposited in a large depositional basin that was separated from those that yielded *G. turneri*, *G.*? *esmeralda*, *S. traini*, and *G.* sp. Whether this separate depositional basin was connected by any drainage system to the other basins is currently unknown (Gilbert and Reynolds, 1973; Golia and Stewart, 1984).

As noted above, Smith et al. (2000, 2002) provided convincing evidence that *Idadon* is junior synonym of *Lavinia* based on their shared dentary morphology and the presence of striated, rugose grinding surfaces on the pharyngeal teeth. However, the degree of the development of the rugose grinding surfaces is not equal in the four species of *Lavinia* and *Hesperoleucus*. It is well-developed in *L. lugaskii* and *L. hibbardi*, moderately to well-developed on some of the pharyngeal teeth of *L. condonianus*, and weakly developed in extant *Lavinia* and *Hesperoleucus* (Smith, 1975; Smith et al., 2000). Similarly, the minor row of pharyngeal teeth varies with the *L. lugaskii* having one moderately well-developed tooth, *L. hibbardi* and *L. condonianus* having one or two rudimentary teeth, and extant *Lavinia* and *Hesperoleucus* having none. The number of teeth in the major row also differs with species of *Lavinia* usually having five (sometimes four in *L. exilicauda*) and *Hesperoleucus* usually having five on the left pharyngeal and four on the right pharyngeal. The fin ray counts also vary between these taxa, with *L. lugaskii* having relatively low counts (e.g., dorsal and anal = 8), extant *Lavinia* having high counts (e.g., dorsal = 10-13, anal = 11-14), and *Hesperoleucus* having low counts (e.g., dorsal = 7-9, anal = 6-8). The fin ray counts for *L. condonianus* and *I. hibbardi* are unknown (Smith, 1975; Smith et al., 2000). *Lavinia hibbardi* and *L. condonianus* further differ from extant *Lavinia* by having pharyngeal teeth that are more rounded in cross-section (relatively wider) and less hooked terminally (Smith et al., 2000). The earliest Pliocene (latest Hemphillian or ~6 Ma) sample of *Lavinia* sp. from Cache Valley, Utah, has not been formally described or compared with other members of the *Lavinia-Hesperoleucus* lineage, but Smith et al. (2002) note that it exhibits slightly corrugated grinding surfaces on the pharyngeal teeth, flaired dentaries, and high fin ray counts. These character states, especially the high fin ray counts and weakly corrugated grinding surfaces of the teeth, are most similar to those of extant *Lavinia*. Thus, middle Miocene *Lavinia lugaskii*, certain Pliocene representatives of *Lavinia*, extant *Lavinia*, and *Hesperoleucus* seem to form a morphocline with each taxon exhibiting morphologically different character states for the fin ray counts (unknown for *L. hibbardi* and *L. condonianus*), rows and numbers of pharyngeal teeth, and development of rugose grinding surfaces on the teeth. However, it is difficult to determine with certainty the polarities of these character states based on an incomplete fossil record with significant chronological gaps. Moreover, the polarities of some of the character states of the dentary have not been adequately determined and some of them (mesially curved anterior end and flaired lateral edges of the gnathal ramus) are also shared in some degree with *Orthodon* Girard, 1856, or *Mylopharodon* (Smith, 1975; Smith et al., 2000), which would indicate that these character states may be sympleisomorphic for *Lavinia* and *Hesperoleucus*. Although, it appears that

the weakly corrugated grinding surfaces on the pharyngeal teeth and high fin ray counts seen in extant *Lavinia* and *L.* sp. from Cache Valley are probably derived character states because, in much older *L. lugaskii*, the rugose grinding surfaces are much better developed and the fin ray counts are lower.

CONCLUSIONS

In series of papers analyzing morphological and molecular data, a general consensus is emerging in support a monophyletic Western North American chub group consisting of three ancient lineages (Coburn and Cavender, 1992; Simons and Mayden, 1998, 1999; Dowling et al., 2002; Smith et al., 2002). One of these lineages is the western chub group that is further divided in four clades: the *Mylopharodon-Lavinia-Hesperoleucus* and *Siphateles* clade; the *Gila-Acrocheilus-Klamathella* clade; the *Relictus-Eremichthys* clade; and the *Ptychocheilus* clade (Smith et al., 2002). The *Mylopharodon-Lavinia-Hesperoleucus* and *Siphateles* clade is further divided into two subgroups, the *Mylopharodon-Lavinia-Hesperoleucus* subgroup and the *Siphateles* subgroup.

The occurrence of *Lavinia lugaskii* in the middle Miocene indicates that the *Lavinia-Hesperoleucus* lineage is older than previously thought. The *Mylopharodon-Lavinia-Hesperoleucus* subgroup is regarded as the closest sister group to the *Siphateles* subgroup with *Mylopharodon* and *Lavinia* diverging from a common ancestor after the divergence of *Mylopharodon* and *Siphateles* from their common ancestor (Dowling et al, 2002; Smith et al., 2002). Moyle (2002) regards *Hesperoleucus* as a junior synonym of *Lavinia* based on protein and molecular similarities and the fact they are interfertile (e.g., Miller, 1945; Hopkirk, 1973; Avise et al., 1975; Avise and Ayala, 1976; Moyle and Massingill, 1981), whereas Smith et al. (2002) regard *Hesperoleucus* as generically distinct from *Lavinia* based on the fossil record and morphological differences. Smith et al. (2002) considered the molecular similarity of these two taxa as probably a result of introgression (see also Smith, 1992). Based on nuclear and mitochondrial DNA similarities, Aguilar and Jones (2009) recently provided additional evidence of a close relationship between these two taxa.

The oldest record of *Mylopharodon* is *M. doliolus* Smith and Kimmel, 1982 (in Smith et al., 1982) from the middle Miocene (early Clarendonian, about 12 Ma) Esmeralda Formation of Nevada (Smith et al., 1982, 2002; Smith and Cossel, 2002). *Lavinia* was previously known from the earliest Pliocene (latest Hemphillian) to Recent (Smith, 1975; McClellan, 1977; Wagner et al., 1997; Smith et al., 2002) and *L. lugaskii* extends this lineage at least six million years to the middle

Miocene (early Clarendonian), or about 12.5 – 12.0 Ma. Based on molecular sequences, Dowling et al. (2002) estimated the time of divergence of *Lavinia* and *Mylopharodon* from a common ancestor to be about 6 Ma and that of *Siphateles* and *Mylopharodon* to be about 12 Ma. Also based on molecular sequences, Smith et al. (2002) regarded the divergence of *Siphateles* and *Mylopharodon* from a common ancestor, estimated at more than 8 Ma, to have occurred before that of *Lavinia* and *Mylopharodon* from their common ancestor. If one accepts the previous hypothesis that *Mylopharodon* is the closest sister taxon to the *Lavinia-Hesperoleucus* lineage (Dowling et al., 2002; Smith et al., 2002), then the occurrence of *L. lugaskii* at 12.5-12.0 Ma would indicate that this lineage diverged from a common ancestor with *Mylopharodon* earlier than the early Clarendonian.

Although resolving the generic status of *Hesperoleucus* is beyond the scope of this paper, certain implications arise with the occurrence of *L. lugaskii* in the middle Miocene. The fossil record of *Hesperoleucus* is limited, wherein it has only been recorded from the late Pleistocene to Holocene. If *Hesperoleucus* diverged from a common ancestor with an earliest Pliocene or later representative of *Lavinia*, which appears to be supported by the protein and molecular evidence and the putative shared derived character state of weakly corrugated grinding surfaces on the pharyngeal teeth, then *Lavinia* becomes paraphyletic unless *Hesperoleucus* is regarded as a synonym of *Lavinia*. Conversely, if *Hesperoleucus* diverged from a common ancestor with *L. lugaskii* prior to the middle Miocene (before 12.5-12.0 Ma), the shared character state of weakly corrugated grinding surfaces observed in *L. exilicauda* and *H. symmetricus* is due to convergence, and the protein and molecular similarities are due to introgression, then *Hesperoleucus* could be retained at generic rank and *Lavinia* would not be a paraphyletic taxon, but this would necessitate a long ghost lineage for *Hesperoleucus*. However, determining which of these phylogenetic scenarios is most likely correct must await more complete fossil records for both taxa.

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